

**Patterns of variability in *Azorella selago* Hook. (Apiaceae) on  
sub-Antarctic Marion Island: climate change implications**

by

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Declaration:

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

Signature.....

Date.....

## Abstract

Understanding the responses of species to climate change is a scientific problem that requires urgent attention, especially under current conditions of global climate change. The large and rapid rates of climate change reported for sub-Antarctic Marion Island makes the island highly suitable for studying the biotic consequences of climate change. Furthermore, the extreme environments on the island result in a close coupling of the biotic (e.g. population dynamics) and abiotic (e.g. climate) factors. Therefore, examining the response of the dominant and keystone plant species on the island, *Azorella selago* Hook. (Apiaceae), to climate-associated environmental change (e.g. temperature) may provide insight into how *A. selago* and the associated species communities will be affected by climate change. This study described the variability in microclimate temperatures associated with *A. selago* across altitudinal gradient and between the eastern and western sides of Marion Island. Microclimate temperatures were also compared to the island's Meteorological data to determine variation between temperatures experienced by *A. selago* cushion-plants in the field and those recorded at the island's Meteorological Station. Temperature variation inside and outside *A. selago* cushions was also examined. *Azorella selago* cushions were found to have a buffering effect on temperature, such that species occurring epiphytically on *A. selago* experience more moderate temperatures than the surrounding environment. However, *A. selago* were found to experience more extreme temperatures than temperatures recorded at the Meteorological Station. Therefore, *A. selago* may possibly experience greater environmental warming than recorded by the Meteorological Station. While temperatures decline with altitude, temperature conditions on the western side of the island were more temperate than the eastern side. This presents the first record of temperature conditions on the western side of the island. This study also quantified fine-scale (e.g. within-site) and broad-scale (e.g. island-wide) variability patterns of *A. selago* (morphology, phenology, and epiphyte load) across Marion Island. Altitudinal gradient and climatic exposure at different sides of the island were used to understand the likely effects of climate associated environmental change on this dominant component of the fellfield

habitat. Site-specific processes were found to determine the spatial structure of *A. selago* characteristics at fine-scales. However, broad-scale observations established strong responses of *A. selago* characteristics to altitudinal gradients and different sides of the island. *Azorella selago* morphological features (e.g. plant size and leaf size) were found to be more responsive to differences between the eastern and western sides of the island than to altitudinal gradient. *Azorella selago* micro-morphological features (e.g. leaf trichomes and stomatal densities) were also found to be more responsive to climatic exposure at different sides of the island than to altitudinal gradient. However, differences in *A. selago* epiphyte density (e.g. *Agrostis magellanica*) and phenology resembled microclimate temperatures in that they were more responsive to altitudinal gradient than to side of the island differences. From these results it can therefore be predicted that the *A. selago* of Marion Island is likely to be morphologically fairly resilient to moderate climatic shifts, although at lower altitudes and on the eastern side of the island, it may be outcompeted by the epiphytic grass, *Agrostis magellanica*. The results also suggest that the warming climate of Marion Island may result in an early occurrence of phenological processes particularly at lower altitudes and the eastern side. *Azorella selago* at lower altitudes and on the eastern side of Marion Island are therefore expected to largely show more symptoms of climate change (e.g. warming) on this species. *Azorella selago* is also predicted to move up altitudinal gradients in response to warming.

## Opsomming

'n Begrip van hoe spesies reageer op klimaatsverandering is 'n wetenskaplike vraag wat onmiddellike aandag benodig, veral onder huidige globale klimaatsverandering. Die groot en snelle tempo waarteen klimaatsverandering waargeneem word op sub-Antarktiese Marion Eiland, maak die eiland hoogs geskik om die biotiese gevolge van klimaatsverandering te bestudeer. Verder veroorsaak die uiterste omgewing van die eiland tot 'n nabye koppeling tussen die biotiese (bv. populasie dinamika) en abiotiese (bv. klimaat) faktore. Dus, deur die reaksies van 'n dominante- en sleutel-spesie op die eiland, *Azorella selago* Hook. (Apiaceae), op klimaat-geassosieerde omgewingsverandering (bv. temperatuur) te bestudeer, mag insig verskaf hoe *A. selago* en geassosieerde spesie gemeenskappe geaffekteer sal word deur klimaatsverandering. Hierdie studie beskryf die wispelturigheid in mikroklimaat temperature geassosieer met *A. selago* oor 'n hoogte gradiënt asook tussen die oostelike en westelik dele van Marion Eiland. Mikroklimaat temperature was ook vergelyk met die eiland se Meteorologiese data met die doel om die mate van variasie tussen temperature verduur deur *A. selago* kussing-plantte in die natuurlike omgewing met die van die eiland se Meteorologiese stasie te vergelyk. Temperatuur variasie binne en buite *A. selago* kussing-plantte is ook vasgestel. Dit was gevind dat *Azorella selago* kussing-plantte die temperatuur buffer, met die gevolg dat spesies wat epifities op *A. selago* voorkom, meer gematigde temperature ondervind as die onmiddellike omgewing om die plant. Daar is egter gevind dat *A. selago* meer uiterste temperature ondervind as temperature gemeet by die Meteorologiese stasie. Dus mag *A. selago* groter omgewings verwarming ervaar as wat temperature gemeet by die Meteorologiese stasie dui. Terwyl temperatuur afneem met 'n toename in hoogte, was temperatuur aan die westekant van die eiland mere gematig as die oostekant. Dit verskaf die eerste rekord van temperatuur toestande aan die westekant van die eiland. Hierdie studie bepaal ook die fyn-skaal (e.g. binne-terrein) en groot-skaal (e.g. oor die eiland) variasie patrone van *A. selago* (morfologie, fenologie, en epifiet lading) oor Marion Eiland. Die hoogte gradiënt en klimaat blootstelling aan verskillende kante van die eiland is gebruik om die waarskynlike effekte van klimaats-geassosieerde omgewings

verandering op die dominante deel van die felfield habitat te verstaan. Daar is gevind dat terrein spesifieke prosesse die ruimtelike struktuur van *A. selago* se klein-skaal eienskappe bepaal. Groot-skaalse waarnemings dui egter 'n sterk antwoord van *A. selago* eienskappe op die hoogte gradiënt en aan verskillende kante van die eiland. *Azorella selago* morfologiese eienskappe (e.g. plant- en blaar grootte) is gevind om meer te reageer op verskille tussen oostelike en westelike kante van die eiland as op die hoogte gradiënt. *Azorella selago* mikromorfologiese eienskappe (e.g. blaar trigome en stomata digtheid) is ook gevind om meer te reageer op omgewings blootstelling tussen verskillende kante van die eiland as op die hoogte gradiënt. Verskille in *A. selago* epifiet digtheid (e.g. *Agrostis magellanica*) en fenologie het egter mikroklimaat temperature gevolg, in dat beide meer gereageer het op die hoogte gradiënt as eiland-kant verskille. Hierdie resultate voorspel dus dat dit waarskynlik is dat *A. selago* van Marion Eiland morfologies redelik terugspringend sal wees ten opsigte van matige klimaatsverandering, al mag dit uitgekompeteer word deur die epifitiese gras, *Agrostis magellanica* by lae hoogtes en aan die oostekant van die eiland. Hierdie resultate dui ook dat verwarming van Marion Eiland se klimaat 'n vervroeging van fenologiese prosesse mag hê, veral by lae hoogtes en aan die oostekant van die eiland. Dus word dit verwag dat *Azorella selago* by lae hoogtes en aan die oostekant van Marion Eiland om meer simptome van klimaatsverandering (e.g. verwarming) te dui. Dit word ook voorspel dat *Azorella selago* opwaarts teen die hoogte gradiënt sal beweeg in reaksie tot verwarming.

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... dedicated to my mother Nokhaya Winniefred Nyakatya and to my late  
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## General Introduction

### *Climate change*

Changes in global climate are predicted to have an effect on the composition, structure and function of many ecosystems throughout the world (Wookey et al. 1993). General patterns attributed to climate change include poleward shifts in species ranges in response to regional warming (Parmesan et al. 1999; Klanderud and Birks 2003; Wilson et al. 2005). These range shifts occur at population levels by means of changes in ratios of extinctions and colonizations at the northern and southern boundaries of the range (Parmesan et al. 1999; Wilson et al. 2005). Effects of climate change such as these are now apparent in many parts of the world, particularly in the polar and sub-polar regions where Global Circulation Models (GCMs) predict climate change effects to be most pronounced (Wookey et al. 1993). Polar ecosystems in regions are therefore expected to experience rapid rates of climate-associated environmental change.

Changes in climate occur as a result of both natural and anthropogenic factors (IPCC 2001). The natural factors that may induce climate change include natural variations in the incoming solar radiation and/or the injection of large quantities of aerosols in the atmosphere by volcanic eruptions (IPCC 2001). Anthropogenic activities (e.g. combustion of fossil fuels, agriculture and land use changes) also induce climate change by modifying the concentrations of atmospheric constituents or properties of the surface that absorb or scatter radiant energy. Records of past changes in atmospheric composition over the last millennium demonstrate a rapid rise in greenhouse gases. This rise is attributed to industrial growth since the 1750s (i.e. the beginning of the industrial revolution) (IPCC 2001). These records suggest that the 20<sup>th</sup> century is likely to have been the warmest century for the Northern Hemisphere. During the twentieth century the human population increased from 1.6 billion to over 6.0 billion (McCarty 2001). This rise in human population is likely to have increased the demand on the earth's resources and consequently affected many aspects of

the earth system. Changes in the composition of the atmosphere, the climate, the abundance of invasive species, and the area of managed landscapes have also been reported since the twentieth century (Shaw et al. 2002). Such changes are likely to be even greater this century as anthropogenic actions continue to impact on the environment. Last century the Earth's climate warmed by approximately 0.6 °C (IPCC 2001; Walther et al. 2002). Over the same period, sea level rose by 10 – 25 cm. There has also been an increase in the frequency of extreme weather events, such as droughts, floods, and heat waves, particularly in the Northern Hemisphere.

There is insufficient data available for the Southern Hemisphere prior to the year 1860 to compare recent warming with changes over the last century (IPCC 2001). However, it is expected that warming may be lower in the southern hemisphere compared to the northern hemisphere since there is smaller land surface available in the south to respond to changes in radiative energy (Kennedy 1995; IPCC 2001). Nonetheless, Global Circulation Models predict that climate change effects will be most pronounced in the polar regions including Antarctica, where surface air temperatures are expected to increase by up to 1 °C per decade (Lewis Smith 1994; Beniston et al. 1997). Although it is difficult to include precipitation in climate change models due to the fact that water exists in various forms (i.e. ice, snow, free water, and water vapour), it is predicted that variability in the distribution (temporal and spatial) patterns of precipitation will increase as a result of climate warming (Hodkinson et al. 1999). A number of stations in the Antarctic and on sub-Antarctic islands have in fact reported rapid environmental warming along with changes in precipitation patterns over the last 30 to 50 years (Smith 2002; Walther et al. 2002). One such station is on sub-Antarctic Marion Island.

### *Marion Island*

Marion Island (46° 55'S, 37° 45'E) is the larger of the two islands that form the Prince Edward Islands. The islands were annexed by the South African

government in 1947/48 and were declared nature reserves (Van Zinderen Bakker 1971). Immediately after the annexation, a Meteorological Station was established on the northeastern side of Marion Island. Since then, South Africa has maintained a permanent presence on the island, concerned with Meteorological observations at first and scientific work followed later (Hanel and Chown 1999). The first scientific expedition to the islands took place in the summer of 1965/66, and since then a scientific programme has been running consistently at the islands (Hanel and Chown 1999). Marion Island is positioned about halfway between Africa and Antarctica in the sub-Antarctic region of the South Indian Ocean (Fig. 1). The island lies 1800 km southeast of Africa, 2300 km north of Antarctica and 21 km southwest of its smaller neighbour, Prince Edwards Island (Smith and Steyn 1982). Marion Island is volcanic in origin and is estimated to be approximately 250 000 years old (Pakhomov and Froneman 1999). The Island is approximately 300 km<sup>2</sup> in area and is topographically very uneven and steep, rising from sea level to 1230 m a.s.l. in less than 5 km (Huntley 1972). The island experiences a typically sub-Antarctic oceanic climate, characterised by cloudy, cold, wet and windy conditions (Fig. 2). The dominant winds are northwesterly and they can reach gale-force in more than 100 days a year (Smith and Steenkamp 1990).

The biota of Marion Island is relatively species poor and this can be attributed to its moderately recent origin, extreme isolation and its past glaciations (Smith and Steenkamp 1990). There are no indigenous land mammals, although marine mammals such as elephant seals and various species of fur seals regularly visit the shores for breeding and/or moulting. There is only one indigenous land bird (e.g. sheathbill); penguins and various species of sea birds are constantly present on the island. There are 22 indigenous vascular plants, about 80 mosses, 36 liverworts and 50 lichens (Gremmen et al. 1998). Many of the vascular plant species on the island occur over a wide range of available habitats (Smith and Steenkamp 1990). The harsh environment on Marion Island results in a close coupling of plant community structure with abiotic variables such as moisture, exposure, temperature and wind-blown salt spray

(Smith 1978). Vascular plants can therefore potentially be used for the biological monitoring of climate associated environmental changes (e.g. temperature) on the island. Although vascular plants are possibly not the most sensitive or most responsive indicators of such change, their restricted powers of dispersal and often slow rates of reproduction places a severe restriction on the speed with which they disperse. Vascular plants characteristics are therefore expected to have evolved to track environmental gradients, especially in cold environments where rates of biological activity are slow (Hodkinson and Bird 1998; Körner 2003).

#### Azorella selago

*Azorella selago* Hook. (Apiaceae) is the most dominant and widely distributed vascular plant on Marion Island and in the entire sub-Antarctic region (Huntley 1972; le Roux and McGeoch 2004). On Marion Island *A. selago* occurs from sea level to the extreme limit of vascular plant growth at 765 m a.s.l (Huntley 1972). *Azorella selago* plants grow in the form of hard and compact cushions of about 15-30 cm in height and on average 20-40 cm in diameter (Huntley 1972; Fig. 3). These plants occur as individual cushions of various, most commonly circular, shapes or spread out to form continuous carpets. The plant's compact cushion growth form makes it resistant to damage or injury by frost or wind action (Huntley 1972). Temperature is considered the most important limiting factor to the altitudinal distribution of vascular plants on the island, preventing the occurrence of temperature-sensitive species (e.g. *Blechnum penna-marina*) at higher altitudes (Smith 1978). Wind chill also plays an important role at high altitudes and its effect is exaggerated by the acceleration of wind speeds about mountain peaks (Van Zinderen Bakker 1978). Some species of bryophytes (e.g. mosses) are limited by moisture availability and they flourish at high altitudes where humidity is high (Smith 1978).

The composition, structure and function of terrestrial ecosystems is determined by both biotic and abiotic factors. On Marion Island it is largely soil

moisture, temperature (e.g. wind chill) and exposure to wind that determine variation between plant communities (Smith and Steenkamp 2001). The main source of soil nutrients on the island is salt spray, although guano deposits are also important to some extent (Huntley 1971). Soil nutrients are thought to be lower at high altitudes since there is very little animal activity higher up and the great distance from the main source of nutrients (the ocean) also plays a role. The substrate at high altitudes is loose owing to the accumulation of windblown ash from adjacent cones (Schulze 1971). Gremmen classified the island's vegetation into 41 plant communities. These communities are further subdivided into six habitat types: the coastal saltspray; fellfield; slope; biotic grassland; biotic herbfield; mire; and the polar desert (Smith and Steenkamp 2001). One use of this classification is to serve as a framework to evaluate the biological and ecological responses to the observed climate and human-induced changes (largely via invasive species) that are currently occurring on the island (Smith and Steenkamp 2001).

#### *The fellfield habitat*

The fellfield habitat (also known as wind desert or fjaeldjmark) is a windswept terrestrial habitat, which forms on exposed rocky areas of mainly grey, but also black lava. The fellfield habitat is widespread throughout the sub-Antarctic region and is considered the oldest terrestrial habitat in this region (Barendse and Chown 2001). On Marion Island fellfield occurs at low altitude sites of about 150 m a.s.l. extending up to approximately 750 m a.s.l. (Smith 1978). This habitat is characterised by low temperatures, strong winds, intense frost at night, low plant cover and high bare rock cover (Van Zinderen Bakker 1978). The hard cushions of *Azorella selago* appear scattered, separated by a typical wind-desert pavement of volcanic rocks (Fig. 4). Mosses, lichens, liverworts and a variety of small invertebrates live within this surface of volcanic rocks protected from wind, low temperatures and desiccation (Van Zinderen Bakker 1978). These bryophytes, micro-invertebrates together with other vascular plants (e.g. *Agrostis*

*magellanica* (Lam.) Vahl. (Poaceae) are thought to avoid the harshest conditions of fellfields by occurring epiphytically on *A. selago* cushion-plants (Smith 1978). Changes in temperature, wind and/or precipitation will strongly influence fellfield plant communities since these are some of the important drivers of vegetation community structure in fellfield habitats (Smith and Steenkamp 1990). Fellfield communities are hence considered to be amongst the most vulnerable of Marion Island's habitats to climate change (Barendse and Chown 2001). The occurrence of these fellfield communities over a broad altitudinal range together with changes in mean temperatures with altitude provides a unique opportunity to study population change in relation to environmental variables, including climate change.

#### *Climate change research*

Predictions of global climate warming have become widely recognized and accepted over the last 10 years (Rustad et al. 2001), and there has been a growing need for more information on the response of ecosystems to climate change. For example, a number of temperature-manipulation experiments have been conducted around the world to predict the effects of temperature change on species (Rustad et al. 2001). However, recent experimental studies have shown that temperature-manipulation experiments (field and laboratory) alone are not enough and can be misleading in predicting the effect of climate change, since there are many complex factors in the field that can be altered by temperature manipulations (Bergstrom and Chown 1999). It has therefore been argued that altitudinal transects provide a useful, complimentary tool for the development of models that enable the prediction of climate change effects on populations (Whittaker and Tribe 1996).

Marion Island has a mean temperature of 5.5 °C and an annual precipitation that exceeds 2500 mm (Huntley 1972). The climate is thermally stable with a mean temperature difference of 3.6 °C between the coldest and warmest months and a mean diurnal temperature difference of 1.9 °C (Smith

2002). With regard to the fact that dominant winds are northwesterly, it is therefore thought that precipitation and cloudiness on the western side of the island will be greater than on the east and that these will be greater at high altitudes due to orographic effects (Schulze 1971; Fig. 2). The western side of Marion Island is also expected to be colder than the eastern side (Schulze 1971), although this has never been quantified on the island before. However, records from data collected on the eastern side of the island near the meteorological station indicate that the climate in the region is changing rapidly. In the past three decades the annual mean temperature of the island increased by 0.04 °C per year to a total increase of 1.2 °C between 1969 and 1999; mean annual precipitation (in the form of rain) decreased by 25 mm per year to a total decrease of 850 mm/yr between 1965 and 1999; and the total annual radiation increased on average by 3.3 hours per year to a total increase of 158.4 hours/yr between 1951 and 1999 (Smith 2002). The ability of *A. selago* to spread throughout Marion Island is a result of adaptations to both the biotic and abiotic components of the island. Such adaptations can either be physiological, morphological, as well as phenological. It is thought therefore that trends of climate associated environmental change may be apparent on *A. selago* characteristics.

The aims of this thesis therefore were (i) to investigate microclimate temperature variability associated with *A. selago* across Marion Island and inside *A. selago* cushions. *Azorella selago* microclimate temperatures were also compared to the island's Meteorological Station temperature data to determine how similar or different temperatures experienced by *A. selago* in the field are to the island's Meteorological Station temperature data. (ii) Also examined in this thesis are the fine-scale (e.g. within-site) and broad-scale (e.g. island-wide) variability patterns in the morphology, phenology and epiphyte load of *A. selago* across Marion Island. The range and direction of such variability was also measured. Altitudinal gradient and side of the island were used as analogues for understanding the likely effects of climate associated environmental change on this dominant component of the fellfield habitat. Each chapter in this thesis is

written in a publication format and therefore there is some overlap in the methods sections and in the introduction of the study system.

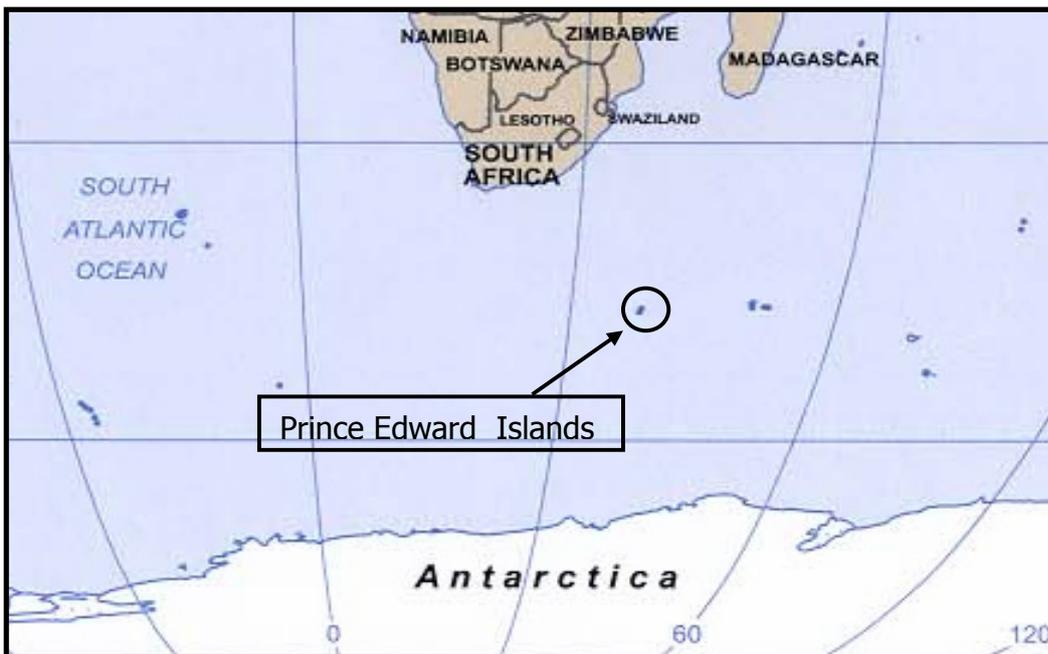
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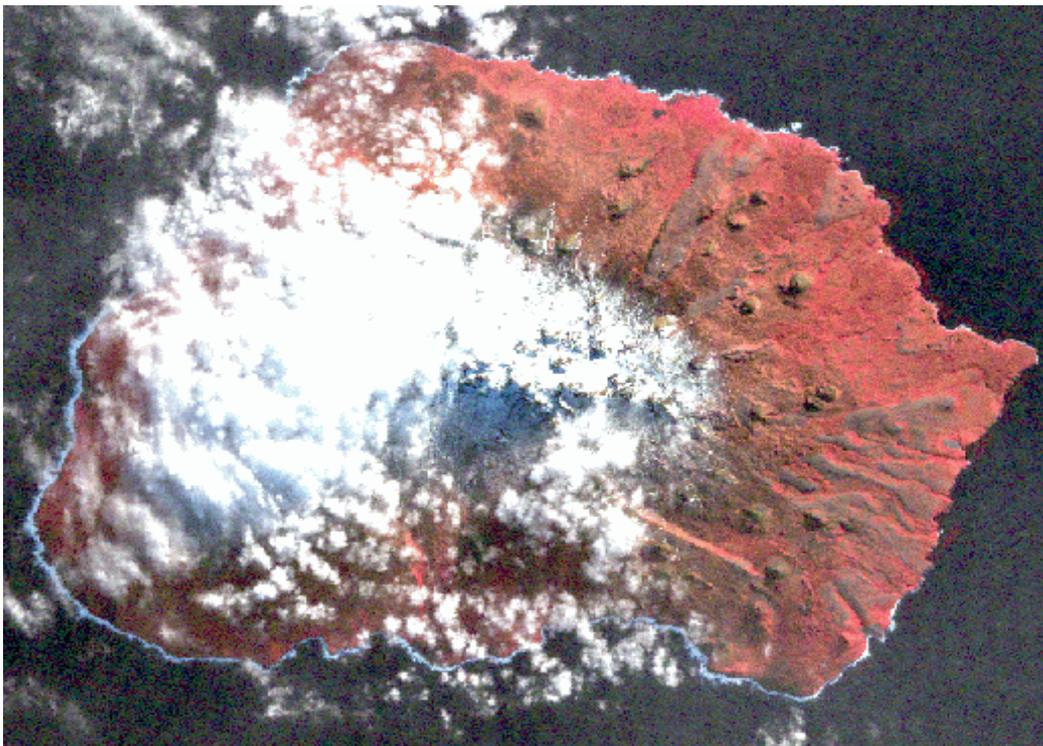
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development to simulated environmental change in sub-antarctic and high arctic plants. *Oikos* 67: 490 - 502

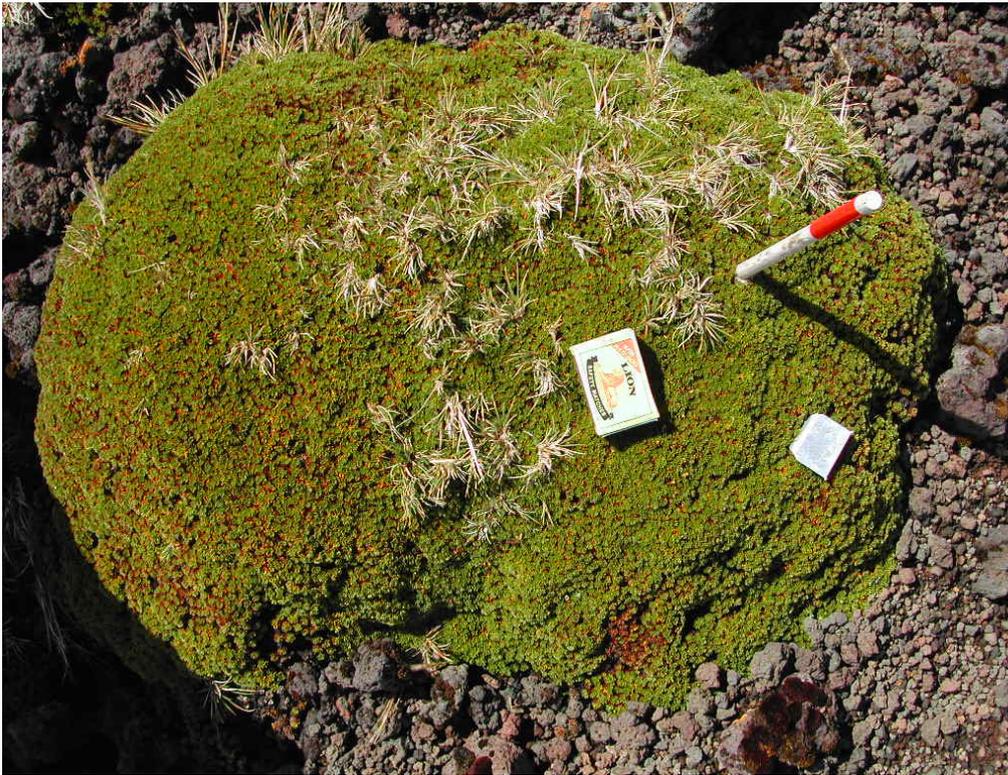


**Fig. 1** The location of the Prince Edward Islands (Marion and Prince Edward) in the Southern Indian Ocean

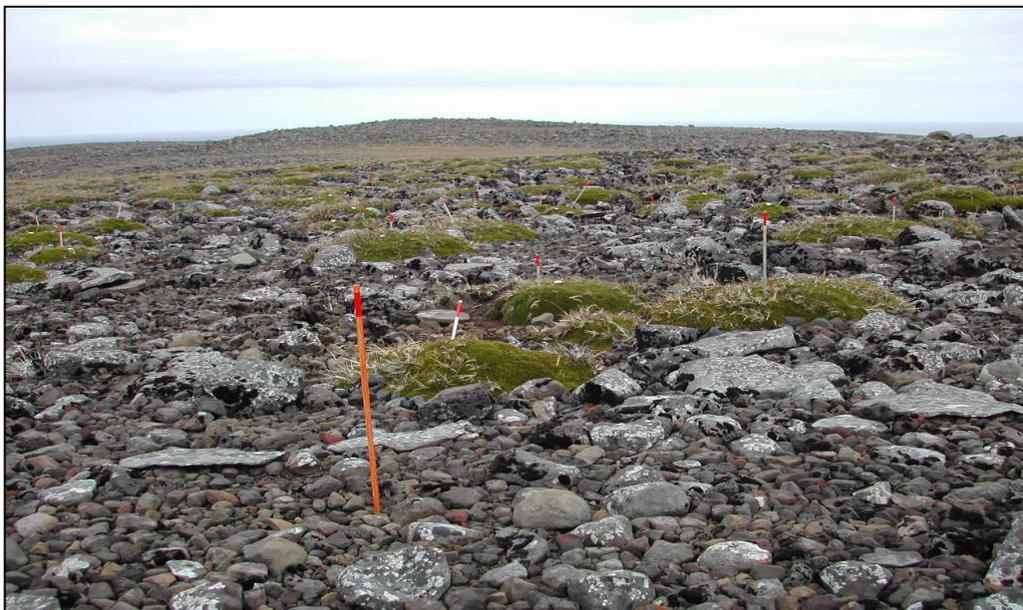


**Fig. 2** A satellite picture of Marion Island. The vegetated part of the island is shown in red and the white indicates cloud distribution.

<http://denali.gsfc.nasa.gov/islands/marion>



**Fig. 3** The cushion-plant, *Azorella selago* with the grass, *Agrostis magellanica* growing epiphytically on the plant. Inserted on the cushion is a growth measuring stick and a metal tag showing cushion number. A matchbox (52 x 41 mm) is used as a reference scale



**Fig. 4** A fellfield habitat with *Azorella selago* plants scattered in a matrix of volcanic grey lava

## **Chapter 1: The microclimate associated with a keystone plant species (*Azorella selago* Hook., Apiaceae) on Marion Island**

### **Introduction**

The need for information on the response of species and ecosystems to climate change has increased over the last two decades (Tweedie and Bergstrom 2000; Rustad et al. 2001). Consequently, a growing number of studies from a wide range of regions are being conducted to examine for example, changes in the behaviour, ranges and interactions of species, which are thought to be associated with climate change (Erasmus et al. 2002; Walther 2003; Peñuelas et al. 2004). Although much still remains to be learnt about species and community responses to climate change (McGeoch et al. 2006), changes in climate, especially temperature, are well known to affect species at several levels (Callaghan and Carlsson 1997).

For example, temperature affects the phenology and physiology of species (Walther et al. 2002), their range and distribution (Parmesan et al. 1999), the composition of, and interactions within communities (Heegaard and Vandvik 2004), and the structure and dynamics of ecosystems (Smith and Steenkamp 1990; McCarty 2001). Although temperature is not the only environmental variable (or element of climate) affecting species, it is one of the most important (Jones 1992, Chown and Crafford 1992; Root et al. 2003). The direct effects of temperature on species and ecosystems are well documented (Convey 1997, 2001). For example, low temperatures are generally known to cause a delay in certain plant phenological activities (e.g. flowering) pending the onset of suitable temperatures; low temperatures may also cause slower growth rates that result in smaller cells and leaf sizes (Esau 1965; Pyšek and Liška 1991; McCarty 2001). The observed northward movement of species' range boundaries have also been attributed to regional warming (Parmesan et al. 1999; Thomas and Lennon 1999). These examples demonstrate the essential role that temperature

plays in explaining the phenology, morphology, and distribution of species in a particular region (Walther et al. 2002; Walther 2003).

The most important factor in the relationship between climate and species characteristics is essentially the climate immediately surrounding the individual, i.e. the microclimate (Unwin 1980; Körner 2003). Microclimate is the climate near the ground and to which an individual is directly exposed. It is determined by fine scale topography, landform, vegetation, substrate, and aspect (Bale et al. 1998). In some instances species create or manipulate the microclimate to which they are exposed, to enable them to survive and function in that position (Unwin 1980; Körner 2003). In other instances, species rely on phenotypic plasticity to develop and reproduce under a range of microclimatic conditions (Schoettle and Rochelle 2000; Hummel et al. 2004; Terblanche et al. 2005). Microclimate is therefore climate that is most significant for the comfort, behaviour and viability of a species (Griffiths 1976; Körner 2003). Importantly, microclimate may differ significantly from meteorological temperatures and other climate readings, primarily in the rate at which changes occur in space and time (Rosenberg et al. 1983). Therefore, it is essential to study the microclimate experienced by species in order to understand their likely response to climate change (Griffiths 1976; Wookey et al. 1993). It is also important to know how these microclimates differ from standard meteorological records to be able to predict probable changes in the microclimate under changing meso- and macroclimatic condition in a region (Chown and Crafford 1992).

The effects of climate change on species are expected to be more apparent in high latitude regions, such as in the sub-Antarctic (Tweedie and Bergstrom 2000). Records of data from many stations on sub-Antarctic Islands have shown rapid environmental warming, along with changes in precipitation patterns (Walther et al. 2002). For example, on sub-Antarctic Marion Island (46° 54'S, 37° 45'E) (one of the two islands forming the Prince Edward Islands), records of data collected at the Meteorological Station on the eastern side of Marion Island shows that annual mean temperature on the island has increased by 1.2 °C since 1969, annual mean precipitation (in the form of rain) decreased

by 850 mm (~ 25 % decrease) since 1965, and total annual radiation increased by 158.4 hours (~ 3.3 hrs/yr) since 1951 (Smith 2002).

All the Meteorological data available for Marion Island has to date been recorded on the eastern side of the island. This includes largely the Meteorological Station data (collected since 1952 by the South African Weather Bureau), which is recorded at 25 m a.s.l., close to the Island's Meteorological Station (46° 53' S, 37° 52' E). The island is topographically uneven and steep (particularly on the western side) with dominant northwesterly winds (Smith and Steenkamp 1990). It is therefore expected that the climate on the western side of the island would be different and possibly colder than on the eastern side (Schulze 1971). It is also thought that the high mountain peaks at the central part of the island may possibly obstruct the clouds flowing with the dominant northwesterly wind. The central high mountain peaks may then result in a high degree of cloudiness and precipitation on the western side (Schulze 1971). However this has never been quantified on the island. In terms of microclimates, Chown and Crafford (1992) recorded temperatures of three microhabitats (i.e. inside a *Poa cookie* (Poaceae) tiller, 0.5 cm below the surface of an *Azorella selago* cushion, and 2 cm below the soil surface adjacent to the *A. selago* cushion) over a period of five months on the eastern side of the island, also close to the island's Meteorological Station. Blake (1996) recorded temperatures along a transect gradient from Junior's to First Red Hill on the eastern side of the island. Temperatures were recorded at three sites of different altitudes at 120, 10, and 1 cm above the ground and at 1, 5, 10, and 20 cm below. Finally, le Roux et al. (2005) measured temperatures 15 mm below *A. selago* cushion surfaces at Skua Ridge (approximately 1 km from the Meteorological Station) also on the eastern side of the island. Temperature has thus never previously been recorded and reported for the western side of Marion Island.

Marion Island is relatively species poor (Smith and Steenkamp 1990), and one important species on the island is the cushion forming vascular plant *Azorella selago* Hook. (Apiaceae) (Huntley 1972; le Roux et al. 2005). It occurs in a variety of habitats, from sea level to the extreme limit of vascular plant growth

at 765 m a.s.l (Huntley 1972; le Roux and McGeoch 2004). *Azorella selago* is the most abundant and widely distributed vascular plant on the island, particularly in fellfield habitats, where *A. selago* cushion-plants appear scattered, in a typical epilithic biotope of volcanic rocks (Van Zinderen Bakker 1978). Fellfield habitats are widespread on Marion Island and throughout the sub-Antarctic region (Barendse and Chown 2001). On Marion Island fellfield habitats occur at low altitude sites of about 150 m a.s.l., extending up to approximately 750 m a.s.l. (Smith 1978). This habitat is characterised by low temperatures, strong winds, intense frost at night, low plant cover and high bare rock cover (Van Zinderen Bakker 1978). Many vascular plants, bryophytes and a variety of micro-invertebrates occur epiphytically on *A. selago*, thereby receiving not only protection from the harsh conditions of the fellfield substrate but also foothold since the soils are poorly developed (Schulze 1971; Smith 1978; Hugo et al. 2004). The strong interaction of *A. selago* with other species (vascular plants, bryophytes, micro-invertebrates) and its contribution towards the structure and function of fellfield habitats makes it a keystone species on Marion Island (Batabyal 2002; le Roux and McGeoch 2004; le Roux et al. 2005; McGeoch et al. 2006). Changes in temperature, wind and/or precipitation will strongly influence fellfield plant communities since these are some of the important drivers of vegetation community structure in fellfield habitats (Smith and Steenkamp 1990). Chown and Crawford (1992) found that the actual temperatures experienced by *A. selago* in the field were 1 – 4 °C higher than temperatures recorded at the Meteorological Station. The *A. selago* dominated fellfield communities are hence considered to be among the most vulnerable habitats to the changing climate of Marion Island (Barendse and Chown 2001; le Roux et al. 2005).

Thus, this study aims to (i) determine how microclimate temperatures associated with *A. selago* change across Marion Island, both along the altitudinal gradient inhabited by this species, and between the east and the western sides of the island; (ii) determine the degree to which temperature is buffered inside *A. selago* cushions; (iii) also examine the differences between microclimate

temperatures associated with *A. selago* and temperatures measured at the island's Meteorological Station.

## **Materials and methods**

### *Altitudinal temperature readings*

Microclimate temperature was recorded along four transects established across altitudinal gradients on Marion Island. One transect was located between Junior's Kop and First Red Hill on the eastern side of the island (hereafter referred to as Tafelberg Transect) (Fig. 1.1). Also on the eastern side of the island, another transect sloped between Stony Ridge and Halfway Kop (hereafter referred to as Stony Ridge Transect) (Fig. 1.1). On the western side of the island, one transect was positioned inland of the Mixed Pickle Cove from Neville towards Saalrug (hereafter referred to as Mixed Pickle Transect) (Fig. 1.1). Another transect on the western side lay inland of Swartkop Point, along Stevie and Bakkerkop (hereafter referred to as Swartkop Transect) (Fig. 1.1). Within each transect, plant microclimate temperature was recorded in fellfield habitat sites located at low (~150 – 250 m a.s.l.), middle (~350 – 450 m a.s.l.) and high (> 550 m a.s.l.) altitudes (Table 1.1). At each altitude, a site consisting of 50 *A. selago* cushion-plants (used as part of a broader study) was demarcated. Microclimate temperature was recorded hourly for two months during winter (June and July 2002) and summer (November and December 2002) by inserting a DS 1921K Thermocron I-Button (a temperature recording data-logger with  $\pm 0.5^{\circ}\text{C}$  accuracy) 3 cm into three randomly selected cushion-plants in each site. The selected cushions were of variable size and vitality (measured as percentage surface area covered by dead plant tissue and epiphytes). Although of variable vitality, all cushion-plants used for microclimate temperature recordings had low epiphyte cover and little dead plant material (Appendix 1A). I-Buttons were always inserted away from epiphytes and any damaged or dead parts of the cushion surface. Nonetheless, cushion height (vertical distance between the

highest point of the cushion surface and the ground beneath it); surface area (measured using a 1 m<sup>2</sup> flexible sampling grid, with each cell totalling 4 cm<sup>2</sup> in area); percentage of dead cushion surface (measured by counting the number of grid cells containing predominantly dead plant stems) and the density of the dominant epiphyte, *Agrostis magellanica* (Lam.) Vahl. (Poaceae)) (determined by counting the number of *Agrostis magellanica* individuals rooted in each cushion) were measured.

#### *Within cushion temperature readings*

Temperature was also recorded on Skua Ridge (46°52'02"S, 37°50'17"E), a low altitude (106 m above sea level) fellfield habitat on the northeastern side of the island, about 1 km from the Meteorological Station (Fig. 1.1). Four *Azorella selago* cushion-plants of similar size (about 15 - 30 cm in height and about 30 - 40 cm in diameter) and vitality were randomly selected on Skua Ridge, approximately 3 m apart from each other. Three I-Buttons were inserted to different depths (10 cm, 5 cm and just below the surface) within each cushion, and another was placed on the ground surface next to each cushion. Temperature was recorded hourly for 10 days in each season (winter: 11 - 21 July 2002; spring: 19 - 29 September 2002; summer: 02 - 12 January 2003; and autumn: 19 - 29 February 2003).

#### *Meteorological temperature readings*

The Meteorological temperature data (recorded from the Stevenson Screen) was obtained from the Meteorological Station (46°53'S, 37°52'E), run by the South African Weather Bureau, located on the northeastern side of Marion Island at about 25 m above sea level. The component of the continuous Stevenson Screen (1.5 m above the ground) temperature data selected was that matching each I-Button sampling period, i.e. two months in winter (2002), two months in summer (2002), and for the 10 days in each season as listed above.

### Data Analysis

General linear models (here abbreviated throughout as GLM) (Stat Soft, Inc. 1984 - 2003) were used to test for differences in the means of temperature characteristics (e.g. means, minima, and maxima) between: (i) the Stevenson Screen and *A. selago* microclimate temperatures, (ii) microclimate temperatures at different altitudes and between the eastern and western sides of the island, and at (iii) different positions inside and outside *A. selago* cushions. A linear regression analysis was also conducted to determine whether *A. selago* microclimate temperatures were related to cushion-plant characteristics such as cushion height; cushion surface area; percentage of dead cushion surface; and the density of the epiphyte, *Agrostis magellanica*.

### Results

Temperatures recorded across Marion Island were on average 3.27 °C higher in summer than in winter (Figs 1.2, 1.3). Temperatures declined with altitude at a lapse rate of 0.0046 °C.m<sup>-1</sup> in winter and 0.0058 °C.m<sup>-1</sup> in summer (Fig. 1.2).

$$\text{Lapse rate } (\Gamma) = - \frac{T2 - T1}{dz} \dots\dots\dots(1)$$

Where *T1* is the temperature at the base location, *T2* is the temperature at the second location, and *dz* is the difference in elevation between the two locations (Harlow et al. 2004). As temperature decreased with altitude, temperature range also decreased (Appendix 1B). Temperature range was 2.92 °C higher in summer than in winter (Appendix 1B). In winter, microclimate temperatures were cooler on the eastern side of the island than on the west (winter:  $F_{(3, 708)} = 4.67$ ;  $p < 0.05$ ) (Fig. 1.3). However, in summer microclimate temperatures were warmer on the eastern side of the island than on the west (summer:  $F_{(3, 720)} = 25.5$ ;  $p < 0.05$ ) (Fig. 1.3). This result means that the eastern side of the island experienced more extreme temperatures than the western side.

The regression models of microclimate temperature on altitude, side of the island, and plant characteristics (e.g. height; surface area; percentage of dead

surface; and density of *A. magellanica*) were significant for only maximum winter microclimate temperatures ( $R^2 = 0.57$ ,  $F_{(9, 26)} = 6.26$ ,  $P < 0.001$ ); mean summer microclimate temperatures ( $R^2 = 0.89$ ,  $F_{(9, 26)} = 32.69$ ,  $P < 0.001$ ); and maximum summer microclimate temperatures ( $R^2 = 0.44$ ,  $F_{(9, 26)} = 4.07$ ,  $P = 0.002$ ) (Table 1.2; Fig. 1.4). However, plant characteristics did not contribute significantly to microclimate temperature variation, except for cushion surface area that was negatively related to mean summer microclimate temperatures (Table 1.2). Maximum winter microclimate temperatures were significantly higher on the eastern side of the island than on the western side with no significant differences between altitudes (Table 1.2; Fig. 1.4a). Mean summer microclimate temperatures were higher on small cushions than on large cushions; higher on the eastern side of the island than on the western side; and higher at middle and low altitudes than at high altitude sites (Table 1.2; Fig. 1.4b). Side of the island had no effect on maximum summer microclimate temperatures at low altitudes (Fig. 1.4c). However, at middle and high altitudes maximum summer microclimate temperatures were higher on the eastern side of the island than on the western side (Table 1.2; Fig. 1.4c).

There were significant differences between the Stevenson Screen temperatures and the microclimate temperatures both in winter and summer (Winter:  $F_{12, 767} = 31.15$ ;  $p < 0.05$ ) (Summer:  $F_{12, 780} = 19.19$ ;  $p < 0.05$ ) (Figs 1.5, 1.6; Appendix 1B). In winter, the Stevenson Screen temperatures were consistently 2.95 °C higher than the microclimate temperatures (Fig. 1.5; Appendix 1B). In contrast, in summer the microclimate temperatures fluctuated around the Stevenson Screen temperatures (Fig. 1.6). In winter the lowest microclimate temperatures were reached at around 8:00 in the morning and the highest at around 14:00 in the afternoon, whereas in summer the lowest microclimate temperatures were reached at around 5:00 in the morning and the highest at around 15:00 in the afternoon (Figs 1.5, 1.6).

Temperature fluctuations (range) were clearly higher in summer than in winter and the Stevenson Screen temperatures were generally much more stable than the microclimate temperatures (Figs 1.5, 1.6). In winter, the Stevenson

Screen temperatures always peaked and dropped before the microclimate temperatures (Fig. 1.5). In summer, microclimate temperatures on the eastern side of the island reached maximums higher than the Stevenson Screen's and on the west only the low altitude microclimate temperatures peaked higher than the Stevenson Screen 's (Fig. 1.6).

There were no significant differences in mean temperatures between the Stevenson Screen temperature and temperatures recorded at different positions inside and outside *A. selago* cushions on Skua Ridge in all the seasons (Fig 1.7; Appendix 1C). However, temperature range was significantly different throughout the seasons and was always declining with depth inside *A. selago* cushions (Appendix 1C) to lowest temperature ranges at 10 cm inside the cushions (Table 1.3; Fig. 1.7; Appendix 1C). Temperature extremes (minima and maxima) were reached outside the cushions first, followed by the cushion surface and the deeper part of the cushion reached the extremes last (Fig. 1.7).

## Discussion

This study is the first to quantify temperature differences between the eastern and western sides of Marion Island. Our findings challenge the speculation by Schulze (1971), and the long held view that the western side of the island is colder than the eastern side. By contrast, in winter the western side of the island was 0.45 °C warmer than the eastern side, whereas in summer the western side was indeed 1.42 °C cooler than the eastern side. The western side of the island experiences more moderate temperatures than the eastern side, and therefore populations of *A. selago* on the western side of the island are exposed to a more temperate climate.

The observed decline in mean temperature and temperature range with altitude suggest that at higher altitudes *A. selago* experience lower microclimate temperatures that are also less variable than at lower altitudes. The reduced microclimate temperature variation at higher altitudes and on the western side of the island may be attributed to greater *A. selago* cushion compactness due to stronger winds at these sites (van Zinderen Bakker 1971, Huntley 1972). The mixing effect of the wind may also play a role in reducing microclimate temperature variation, particularly on the western side of the island and at high altitudes where the prevalence of strong winds is high (Schulze 1971; Smith and Steenkamp 1990; Chown and Crafford 1992; Rouault et al. 2005). However the incidence of cloudiness and strong winds is perceived to have decreased under the current climate warming on Marion Island (Smith and Steenkamp 1990; le Roux and McGeoch, submitted), therefore the buffered temperature at high altitudes and on the western side of the island is likely to change.

The low mean microclimate temperature recorded at high altitudes is amongst the key environmental factors thought to limit vascular plant distribution on Marion Island (Huntley 1970; Smith 1978). Most vascular plants are often limited to the warmer low altitude sites, sheltered from cold winds and exposed to high radiation (Huntley 1970; Smith 1978). *Azorella selago* is the vascular plant species with the most extensive altitudinal distribution on the island (Huntley

1972; Smith 1978). The current warming climate on Marion Island may provide favourable growth conditions and areas of colonisation at high altitude sites (Robinson et al. 2003; Becker et al. 2005), such that plant populations that are currently restricted to the warmer lower altitude sites may expand and colonise sites at higher altitudes that were previously thermally adverse to them (Gremmen 1997; Gremmen et al. 1998; Gabriel et al. 2001). The warmer climate may therefore induce increased plant biomass at high altitudes, however other factors such as soil stability, soil moisture and nutrients availability may also limit vascular plant distribution.

In winter, the difference between the Stevenson Screen recorded temperatures and the *A. selago* microclimates was greater on the eastern side of the island (3.18 °C) than on the western side (2.73 °C). The difference was also greater at higher altitudes than at lower altitudes. These results suggest that the Stevenson Screen winter temperatures are not only higher than the microclimate temperatures, but they are more indicative of the conditions on the western side of the island and at lower altitudes. In summer the *A. selago* microclimate temperatures fluctuated about the relatively buffered Stevenson Screen temperatures. These results are in contrast with the findings by Chown and Crafford (1992) that the *A. selago* summer microclimate temperatures were consistently 1 - 4 °C higher than the Stevenson screen temperatures. Altitude may be a contributing factor to the contrasting results, since the Chown and Crafford (1992) study was conducted closer to the Meteorological Station than the recordings conducted for this study. Altitude may also be used to explain the buffered trend in the Stevenson Screen temperatures, since the Stevenson Screen temperatures were recorded at much lower altitudes and at 1 m above the ground compared to the microclimate temperatures. The Stevenson Screen temperatures are also likely to be dampened, compared to more inland sites, by the close proximity of the Meteorological Station to the isothermal waters of the surrounding Southern Ocean (Smith and Steenkamp 1990). *Azorella selago* therefore experience more extreme summer temperatures than recorded by the Stevenson Screen, particularly on the eastern side of the island and at lower

altitudes. In general these results suggest that the winter climate recorded by the Stevenson Screen (Smith 2002) is relatively similar to the conditions on the western side and at lower altitudes, and the summer climate recorded by the Stevenson Screen is similar to the conditions on the eastern side and at lower altitudes.

Although there were no significant differences in microclimate temperatures recorded outside and at different depths inside *A. selago* cushions, the cushion-plants however presented thermally buffered microclimate temperatures. This was demonstrated by the decline in temperature fluctuation with depth inside *A. selago* cushions. The moderate temperature and temperature fluctuation inside *A. selago* cushions may provide optimum thermal environments for a variety of epiphytes occurring on *A. selago*. The high microarthropods species richness on *A. selago* relative to the ground matrix attest to the possible buffering effect of *A. selago* against the harsh abiotic conditions of the fellfield habitat (Barendse and Chown 2001; Hugo et al. 2004). A preliminary study of the vertical distribution of the *A. selago* microarthropod community on Marion Island found differences in species richness at different depth inside *A. selago* cushions (HP Leinaas, unpublished), suggesting that also for microarthropods favourable microclimate conditions vary with depth inside *A. selago* cushions.

Since the highest microclimate temperatures were recorded at low altitudes and on the eastern side of Marion Island, continued warming of the island is therefore like to result to even warmer conditions at these sites (i.e. low altitudes and the eastern side) compared to high altitudes and the western side. Plant species across Marion Island can therefore be expected to reflect these climate differences in their characteristics (e.g. morphology, phenology, distribution and interactions), especially since temperature is considered amongst the most important climate variables affecting plant species (Jones 1992, Chown and Crafford 1992; Root et al. 2003). It can therefore be predicted that the impacts of future climate change on Marion Island will be proportionally greater at low altitudes and on the eastern side if the island.

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**Table 1.1** Description of 12 sampling sites located in fellfield habitats along four altitudinal transects on Marion Island

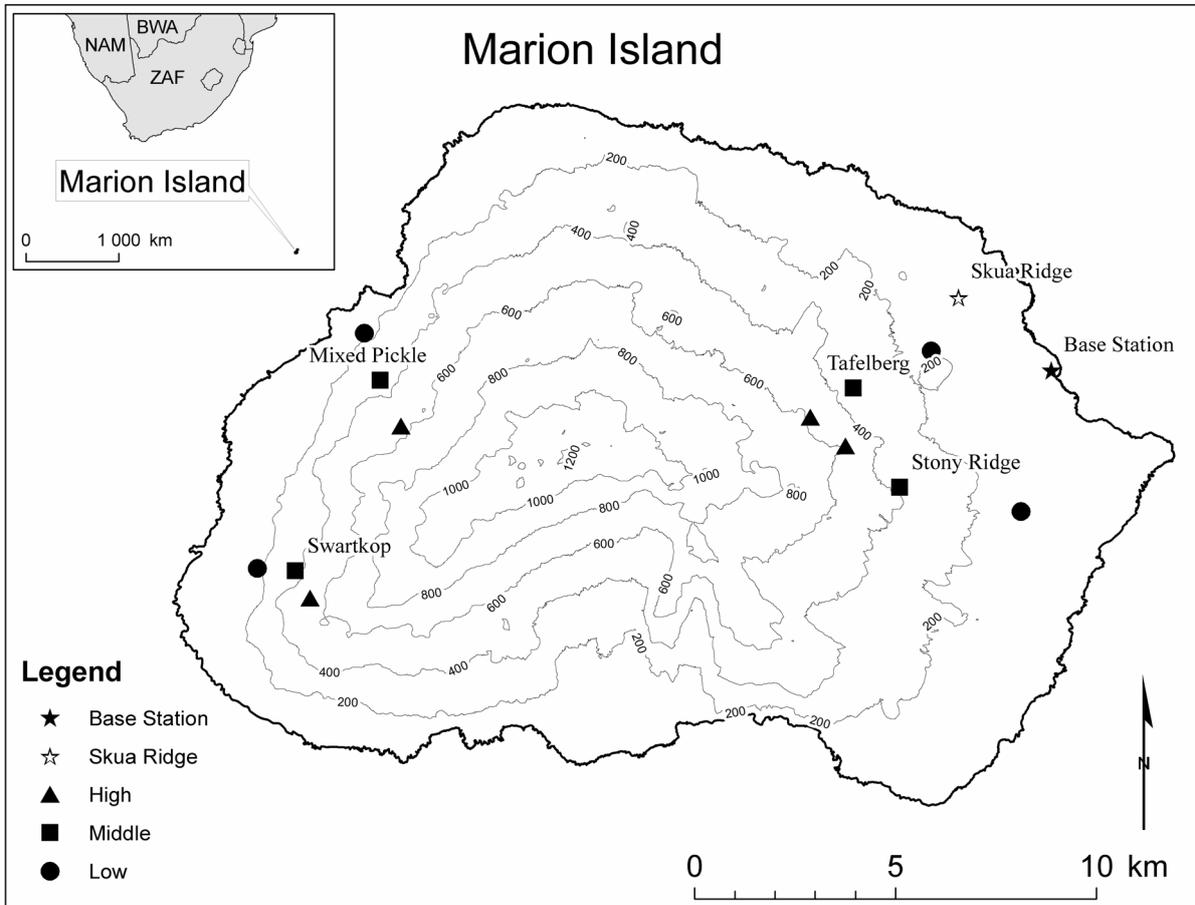
Site	Side of the island	Position 46°South	Position 37°East	Altitude (m asl)	Plant density (100 m <sup>-2</sup> )	Aspect	Lava type
<b>Tafelberg</b>							
Low	East	52' 749"	49' 651"	176	1.100	Flat	Black
Middle	East	53' 276"	48' 125"	375	0.137	Flat	Grey
High	East	53' 670"	47' 293"	588	0.260	South	Black
<b>Stony Ridge</b>							
Low	East	54' 917"	51' 435"	176	0.901	Flat	Grey
Middle	East	54' 608"	49' 062"	380	0.299	Flat	Grey
High	East	54' 059"	47' 978"	620	0.146	South	Black
<b>Mixed Pickle</b>							
Low	West	52' 574"	38' 539"	222	1.551	North East	Black
Middle	West	53' 224"	38' 858"	375	1.124	Flat	Black
High	West	53' 839"	39' 268"	600	0.368	Flat	Black
<b>Swartkop</b>							
Low	West	55' 789"	36' 481"	216	1.081	North East	Black
Middle	West	55' 818"	37' 225"	415	1.188	Flat	Black
High	West	56' 195"	37' 520"	575	0.493	Flat	Black

**Table 1.2** Significant General Linear Models (GLM) of *Azorella selago* microclimate characteristics (side refers to side of the island)

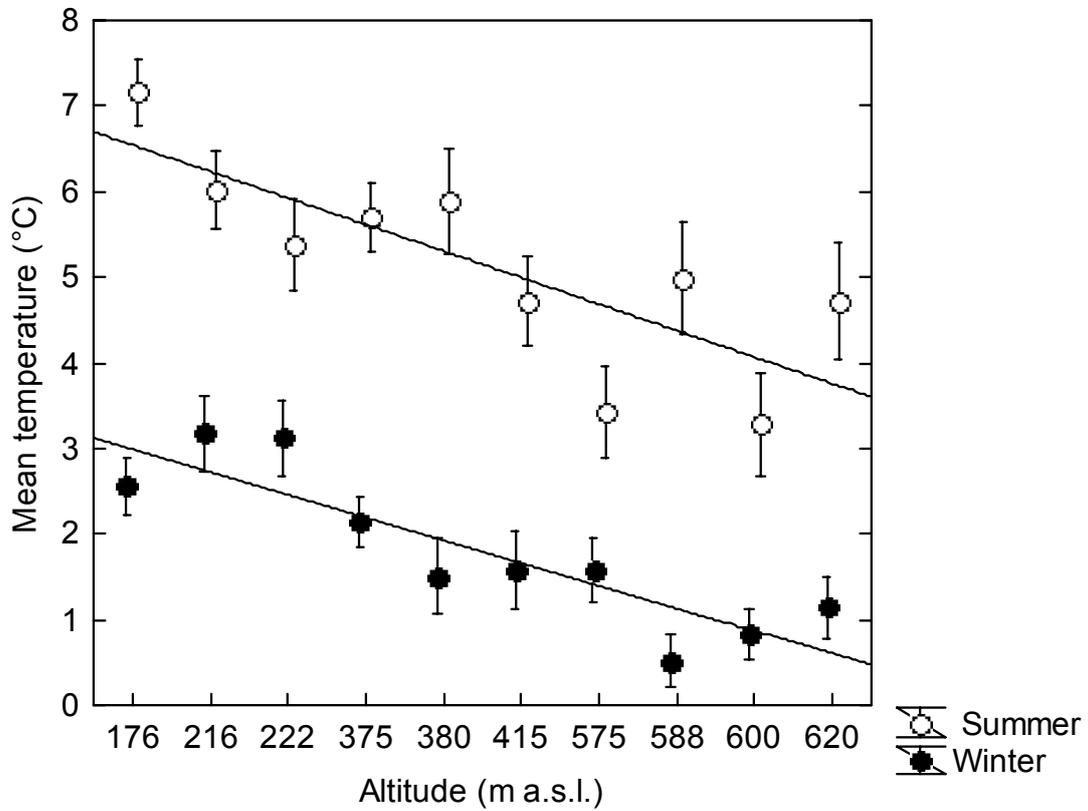
Temperature	F <sub>(9, 26)</sub>	P	Adjusted R <sup>2</sup>	Variable	d.f	F	p-value
<i>Winter</i>							
Maximum	6.26	< 0.001	0.57	Height	1	0.35	0.55
				Surface area	1	< 0.01	0.95
				% Dead surface	1	0.04	0.83
				<i>Agrostis</i> density	1	0.65	0.42
				<b>Island side</b>	<b>1</b>	<b>22.80</b>	<b>&lt; 0.001</b>
				Altitude	2	0.06	0.94
				Island side * Alt.	2	0.99	0.38
				<i>Summer</i>			
Mean	32.69	< 0.001	0.89	Height	1	0.98	0.33
				<b>Surface area (-)</b>	<b>1</b>	<b>6.13</b>	<b>0.02</b>
				% Dead surface	1	1.65	0.21
				<i>Agrostis</i> density	1	0.33	0.56
				<b>Island side</b>	<b>1</b>	<b>52.59</b>	<b>&lt; 0.001</b>
				<b>Altitude</b>	<b>2</b>	<b>53.22</b>	<b>&lt; 0.001</b>
				Island side * Alt.	2	0.18	0.83
				Maximum	4.07	0.002	0.44
Surface area	1	1.92	0.17				
% Dead surface	1	0.18	0.67				
<i>Agrostis</i> density	1	0.02	0.88				
<b>Island side</b>	<b>1</b>	<b>16.07</b>	<b>&lt; 0.001</b>				
Altitude	2	0.60	0.55				
<b>Island side * Alt.</b>	<b>2</b>	<b>5.68</b>	<b>0.008</b>				

**Table 1.3** Mean seasonal temperature ( $^{\circ}\text{C}$ ) differences ( $\pm$  s.d.) between the Stevenson Screen (Met. Data) and positions inside (5 cm & 10 cm deep) and outside (cushion surface and ground adjacent to the cushion) *Azorella selago* cushion-plants (n = 10)

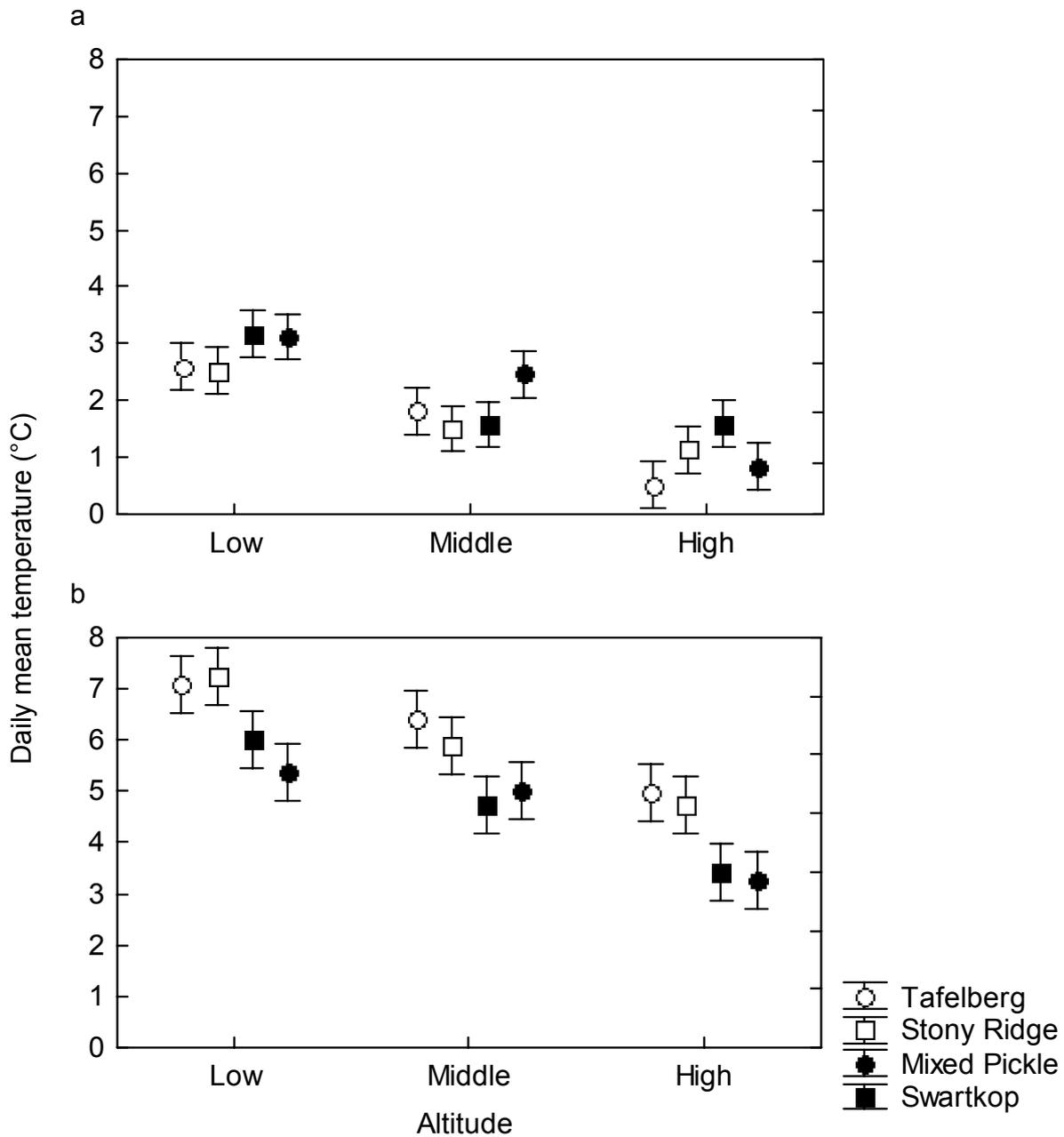
Position differences	Winter	Spring	Summer	Autumn
Met. Data - Ground	2.05 $\pm$ 0.40	0.64 $\pm$ 1.14	-0.18 $\pm$ 0.97	-1.80 $\pm$ 2.45
Ground - Surface	0.24 $\pm$ 0.64	-0.31 $\pm$ 0.71	-0.57 $\pm$ 0.59	-0.08 $\pm$ 0.82
Ground - 5 cm	0.34 $\pm$ 10.6	0.09 $\pm$ 1.98	-0.85 $\pm$ 0.73	0.28 $\pm$ 0.84
Ground - 10 cm	-4.05 $\pm$ 4.00	-0.09 $\pm$ 2.30	-0.84 $\pm$ 0.70	0.29 $\pm$ 1.10
Surface - 5 cm	0.10 $\pm$ 0.52	0.40 $\pm$ 1.48	-0.29 $\pm$ 0.22	0.36 $\pm$ 0.47
Surface - 10 cm	0.54 $\pm$ 1.00	0.22 $\pm$ 1.83	-0.27 $\pm$ 0.29	0.38 $\pm$ 0.83



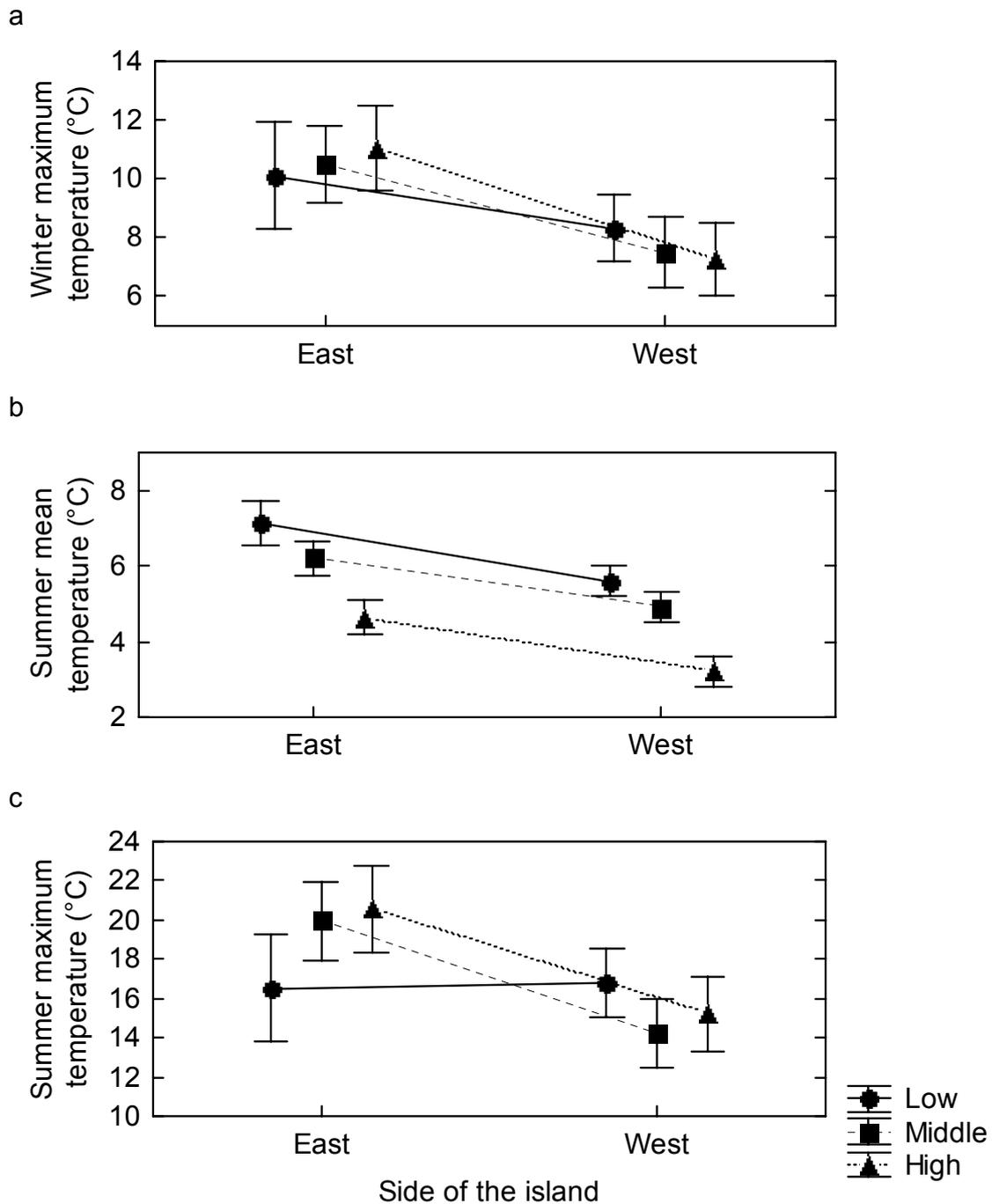
**Fig. 1.1** A Map of Marion Island illustrating positions of the four altitudinal gradients and the sampling sites within each gradient. Positions of the Skua Ridge site and the Meteorological Station (Base Station) are also depicted (Map by Dr JM Kalwij)



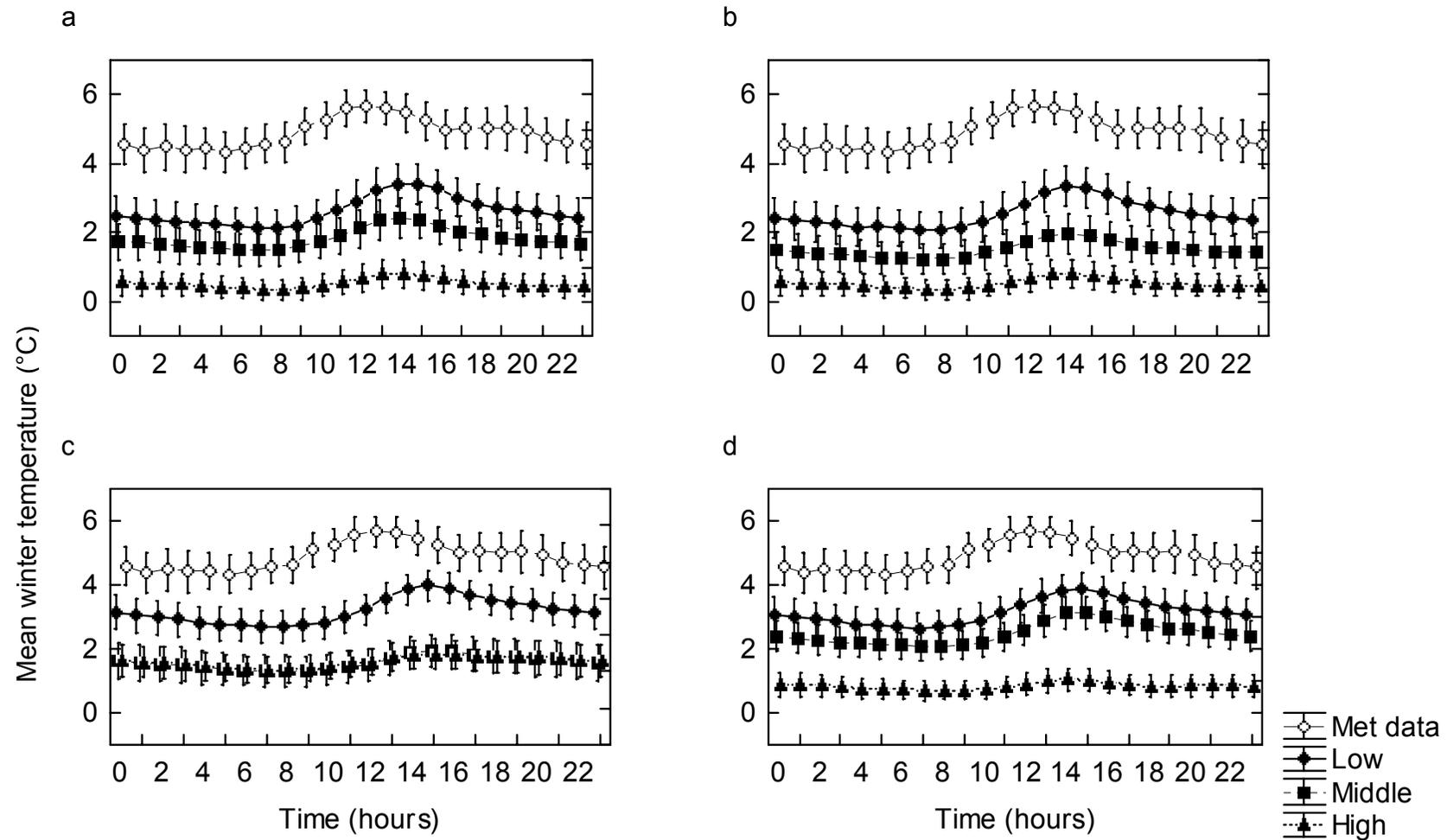
**Fig. 1.2** Mean ( $\pm$  s.e.) summer (N = 60) and winter (N = 60) temperatures across all sampled altitudes on Marion Island



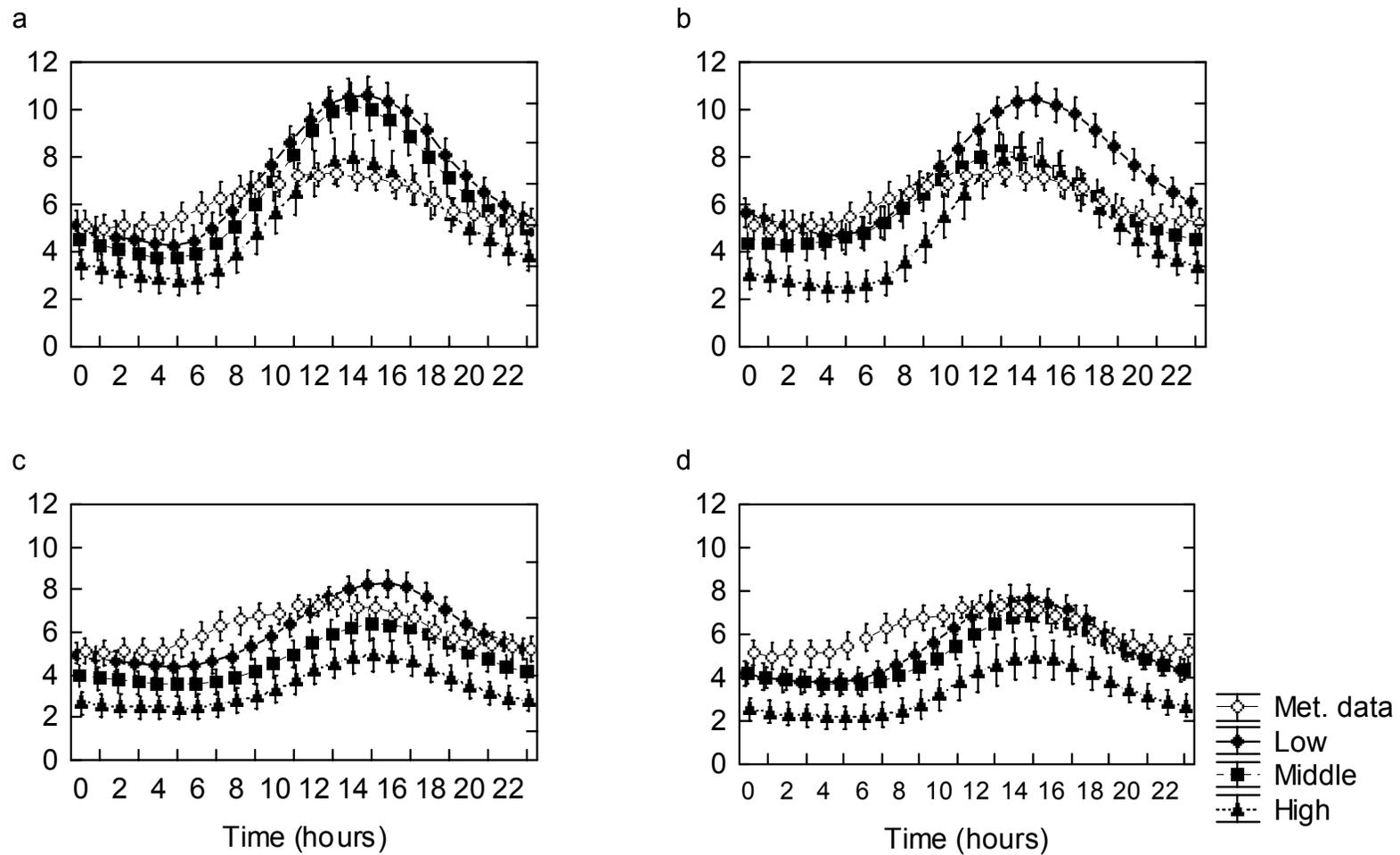
**Fig. 1.3** Daily mean ( $\pm$  s.e.) temperatures across four altitudinal gradients (Tafelberg, Stony Ridge, Mixed Pickle, and Swartkop) in **a.** winter (N = 60 days) and in **b.** summer (N = 60 days) on Marion Island. Open symbols are sites on the eastern side of the island and closed symbols are sites on the western side



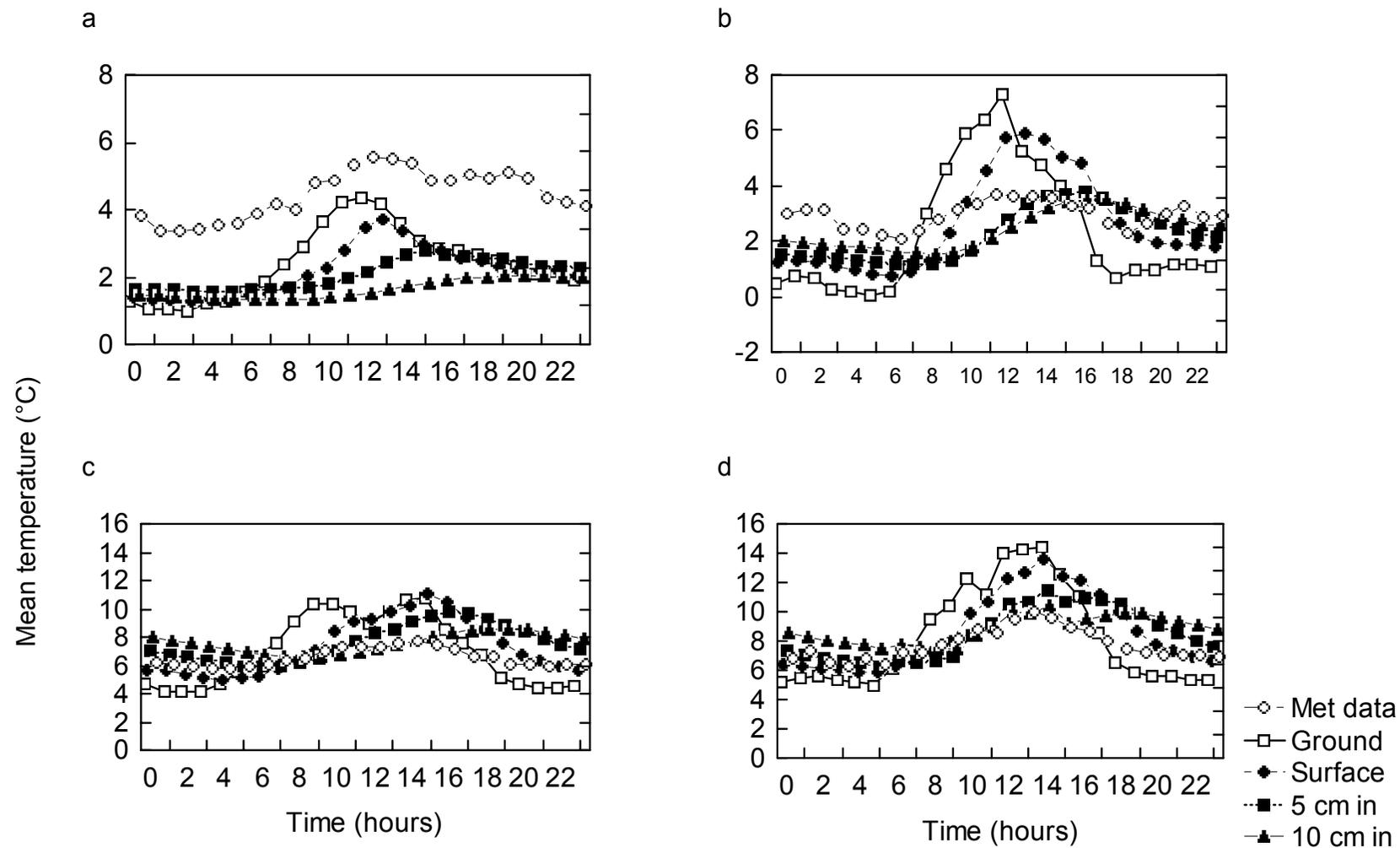
**Fig. 1.4** GLM interaction plots of mean ( $\pm$  s.e.) microclimate temperature characteristics (**a.** winter maximum temperature; **b.** summer mean temperature; and **c.** summer maximum temperature) of *Azorella selago* corrected for the effects of cushion height; cushion surface area; % dead cushion surface; and epiphyte (*Agrostis magellanica*) density across altitudes on the eastern and western sides of the island



**Fig. 1.5** Mean ( $\pm$  s.e.) winter hourly temperatures (N = 60 days) of the Stevenson Screen (Met. data) and across altitudinal gradients (low, middle and high altitude sites) in: **a.** Tafelberg; **b.** Stony Ridge; **c.** Swartkop; **d.** Mixed Pickle



**Fig. 1.6** Mean summer hourly temperatures ( $\pm$  s.e.) (N = 60 days) of the Stevenson Screen (Met. data) and across altitudinal gradients (low, middle and high altitude sites) in: **a.** Tafelberg; **b.** Stony Ridge; **c.** Swartkop; and **d.** Mixed Pickle



**Fig. 1.7** Mean ( $\pm$  s.e.) hourly temperatures of the Stevenson Screen (Met. Data) and different positions inside and outside *Azorella selago* cushions in **a.** winter; **b.** spring; **c.** summer; and in **d.** autumn ( $n = 10$  days). Note difference in scaling of temperature axes for clarity

**Appendix 1A** Characteristics of *Azorella selago* cushion plants in which I-Buttons were inserted in the 12 sampling sites across the island

<b>Site</b>	<b>Plant number</b>	<b>Plant Height (cm)</b>	<b>Plant Surface Area (m<sup>2</sup>)</b>	<b>% Dead Plant surface</b>	<b><i>Agrostis</i> Density (m<sup>-2</sup>)</b>
Tafelberg Low	09	16.0	22.41	12.25	5.93
	33	6.5	3.06	8.82	21.24
	48	15.0	18.77	11.03	8.26
Tafelberg Mid	52	19.0	45.90	2.75	1.07
	73	17.5	51.30	5.53	0.19
	89	25.0	137.48	0.26	1.78
Tafelberg High	108	39.0	23.04	4.69	0.00
	130	58.5	90.23	2.64	0.00
	149	49.5	72.00	5.31	0.00
Stony Ridge Low	18	21.0	21.15	7.45	11.82
	30	18.0	25.97	9.71	9.05
	38	18.0	22.77	1.58	4.74
Stony Ridge Mid	60	20.0	159.95	2.60	0.88
	75	14.0	75.20	5.33	1.64
	94	16.0	35.55	6.33	4.50
Stony Ridge High	108	17.5	10.22	2.64	0.00
	111	32.0	125.51	7.71	0.00
	134	28.0	40.37	3.79	0.00
Mixed Pickle Low	07	19.0	11.70	8.85	1.37
	28	12.5	6.03	8.21	1.33
	41	12.5	4.68	9.62	0.21
Mixed Pickle Mid	60	13.0	13.01	10.73	0.00
	79	10.5	37.13	7.27	0.00
	94	11.0	48.38	4.19	0.00
Mixed Pickle High	125	11.5	14.63	3.38	0.00
	145	24.0	35.55	6.71	0.00
	150	21.0	54.23	0.91	0.00
Swartkop Low	05	17.0	32.49	6.51	1.29
	29	28.0	11.93	9.81	0.75
	35	29.0	33.08	4.08	2.12
Swartkop Mid	52	13.0	39.74	12.34	0.00
	84	23.0	25.07	4.85	0.00
	96	22.0	54.00	3.75	0.00
Swartkop High	115	13.0	44.91	1.30	0.00
	129	13.0	27.63	4.89	0.00
	149	17.0	15.57	3.18	0.00

**Appendix 1B** Daily mean temperature (°C) characteristics ( $\pm$  SD) for 12 sampling sites across the Island and for the Stevenson Screen (Met. data). Winter: N = 60 days and summer: N = 60 days. Also included are the P and F statistics of the GLMs results (L, M, H stand for Low, Middle, High)

Site	Mean	Minimum	Maximum	Range	% CV
<b>Winter:</b>	$F_{12, 767} = 31.15;$ $P < 0.05$	$F_{12, 767} = 18.28;$ $P < 0.05$	$F_{12, 767} = 29.80;$ $P < 0.05$	$F_{12, 767} = 15.09;$ $P < 0.05$	$F_{12, 767} = 1.24;$ $P > 0.05$
Met. Data	4.86 $\pm$ 1.78 <sup>a</sup>	2.52 $\pm$ 2.17 <sup>a</sup>	7.00 $\pm$ 2.20 <sup>a</sup>	4.48 $\pm$ 2.03 <sup>a</sup>	37.96 $\pm$ 61.21 <sup>a</sup>
Tafelberg-L	2.60 $\pm$ 1.88 <sup>bc</sup>	1.18 $\pm$ 1.49 <sup>bcd</sup>	4.26 $\pm$ 2.28 <sup>bc</sup>	3.08 $\pm$ 1.68 <sup>b</sup>	51.83 $\pm$ 73.19 <sup>a</sup>
Tafelberg-M	1.82 $\pm$ 1.68 <sup>cdef</sup>	0.75 $\pm$ 1.20 <sup>cde</sup>	3.19 $\pm$ 2.27 <sup>cde</sup>	2.44 $\pm$ 1.72 <sup>bc</sup>	53.64 $\pm$ 74.80 <sup>a</sup>
Tafelberg-H	0.52 $\pm$ 1.19 <sup>g</sup>	0.02 $\pm$ 0.57 <sup>e</sup>	1.26 $\pm$ 1.90 <sup>g</sup>	1.24 $\pm$ 1.47 <sup>d</sup>	54.21 $\pm$ 169.97 <sup>a</sup>
Stony Ridge-L	2.52 $\pm$ 1.89 <sup>bcd</sup>	1.18 $\pm$ 1.44 <sup>bcd</sup>	4.14 $\pm$ 2.41 <sup>bcd</sup>	2.96 $\pm$ 1.70 <sup>b</sup>	47.21 $\pm$ 46.35 <sup>a</sup>
Stony Ridge-M	1.50 $\pm$ 1.72 <sup>efg</sup>	0.55 $\pm$ 1.19 <sup>de</sup>	2.89 $\pm$ 2.43 <sup>def</sup>	2.35 $\pm$ 1.78 <sup>bc</sup>	13.21 $\pm$ 196.99 <sup>a</sup>
Stony Ridge-H	1.14 $\pm$ 1.39 <sup>fg</sup>	0.45 $\pm$ 0.83 <sup>de</sup>	2.21 $\pm$ 2.24 <sup>efg</sup>	1.76 $\pm$ 1.80 <sup>cd</sup>	35.55 $\pm$ 48.74 <sup>a</sup>
Mixed Pickle-L	3.13 $\pm$ 1.73 <sup>b</sup>	1.75 $\pm$ 1.50 <sup>ab</sup>	4.76 $\pm$ 2.07 <sup>b</sup>	3.01 $\pm$ 1.63 <sup>b</sup>	39.39 $\pm$ 21.20 <sup>a</sup>
Mixed Pickle-M	2.46 $\pm$ 1.54 <sup>bcde</sup>	1.38 $\pm$ 1.15 <sup>bc</sup>	3.77 $\pm$ 1.98 <sup>bcd</sup>	2.39 $\pm$ 1.57 <sup>bc</sup>	34.73 $\pm$ 20.46 <sup>a</sup>
Mixed Pickle-H	0.84 $\pm$ 1.13 <sup>fg</sup>	0.28 $\pm$ 0.65 <sup>e</sup>	1.57 $\pm$ 1.75 <sup>fg</sup>	1.29 $\pm$ 1.39 <sup>d</sup>	31.33 $\pm$ 50.78 <sup>a</sup>
Swartkop-L	3.17 $\pm$ 1.67 <sup>b</sup>	1.88 $\pm$ 1.48 <sup>bc</sup>	4.72 $\pm$ 1.88 <sup>b</sup>	2.84 $\pm$ 1.45 <sup>b</sup>	36.68 $\pm$ 22.48 <sup>a</sup>
Swartkop-M	1.58 $\pm$ 1.76 <sup>def</sup>	0.50 $\pm$ 1.41 <sup>de</sup>	2.91 $\pm$ 2.31 <sup>cdef</sup>	2.41 $\pm$ 1.72 <sup>bc</sup>	22.10 $\pm$ 174.09 <sup>a</sup>
Swartkop-H	1.59 $\pm$ 1.47 <sup>cdef</sup>	0.72 $\pm$ 1.03 <sup>cde</sup>	2.85 $\pm$ 2.34 <sup>def</sup>	2.13 $\pm$ 1.95 <sup>bcd</sup>	73.40 $\pm$ 168.95 <sup>a</sup>
<b>Summer:</b>	$F_{12, 780} = 19.19;$ $P < 0.05$	$F_{12, 780} = 15.39;$ $P < 0.05$	$F_{12, 780} = 21.31;$ $P < 0.05$	$F_{12, 780} = 18.11;$ $P < 0.05$	$F_{12, 780} = 9.20;$ $P < 0.05$
Met. Data	6.10 $\pm$ 1.83 <sup>abcd</sup>	3.64 $\pm$ 1.74 <sup>ab</sup>	8.57 $\pm$ 2.61 <sup>bc</sup>	4.93 $\pm$ 2.19 <sup>cde</sup>	25.63 $\pm$ 10.93 <sup>a</sup>
Tafelberg-L	7.07 $\pm$ 2.17 <sup>ab</sup>	3.71 $\pm$ 1.97 <sup>ab</sup>	11.19 $\pm$ 2.90 <sup>a</sup>	7.48 $\pm$ 2.49 <sup>a</sup>	39.38 $\pm$ 17.11 <sup>abcd</sup>
Tafelberg-M	6.41 $\pm$ 2.40 <sup>abc</sup>	3.12 $\pm$ 1.87 <sup>abc</sup>	10.75 $\pm$ 3.42 <sup>a</sup>	7.63 $\pm$ 2.82 <sup>a</sup>	44.84 $\pm$ 20.29 <sup>bcde</sup>
Tafelberg-H	4.98 $\pm$ 2.56 <sup>de</sup>	2.29 $\pm$ 1.73 <sup>cde</sup>	8.39 $\pm$ 3.63 <sup>bc</sup>	6.10 $\pm$ 2.80 <sup>abc</sup>	48.86 $\pm$ 22.35 <sup>cde</sup>
Stony Ridge-L	7.25 $\pm$ 2.15 <sup>a</sup>	4.17 $\pm$ 1.86 <sup>a</sup>	10.80 $\pm$ 2.73 <sup>a</sup>	6.63 $\pm$ 1.95 <sup>ab</sup>	33.94 $\pm$ 12.96 <sup>abc</sup>
Stony Ridge-M	5.90 $\pm$ 2.42 <sup>bcde</sup>	3.34 $\pm$ 1.86 <sup>abc</sup>	8.62 $\pm$ 3.02 <sup>bc</sup>	5.28 $\pm$ 2.11 <sup>bcd</sup>	33.10 $\pm$ 15.55 <sup>abc</sup>
Stony Ridge-H	4.72 $\pm$ 2.62 <sup>ef</sup>	1.89 $\pm$ 1.62 <sup>de</sup>	8.58 $\pm$ 3.98 <sup>bc</sup>	6.69 $\pm$ 3.18 <sup>ab</sup>	61.62 $\pm$ 60.30 <sup>e</sup>
Mixed Pickle-L	5.37 $\pm$ 2.06 <sup>cde</sup>	2.92 $\pm$ 1.76 <sup>bcd</sup>	8.10 $\pm$ 2.89 <sup>bc</sup>	5.18 $\pm$ 2.56 <sup>bcde</sup>	36.45 $\pm$ 20.67 <sup>abc</sup>
Mixed Pickle-M	5.00 $\pm$ 1.81 <sup>de</sup>	3.19 $\pm$ 1.53 <sup>abc</sup>	7.15 $\pm$ 2.57 <sup>bcd</sup>	3.96 $\pm$ 2.23 <sup>de</sup>	28.74 $\pm$ 16.36 <sup>ab</sup>
Mixed Pickle-H	3.28 $\pm$ 2.35 <sup>g</sup>	1.48 $\pm$ 1.47 <sup>e</sup>	5.54 $\pm$ 3.79 <sup>d</sup>	4.05 $\pm$ 3.21 <sup>de</sup>	53.86 $\pm$ 51.33 <sup>de</sup>
Swartkop-L	6.02 $\pm$ 1.76 <sup>abcde</sup>	3.83 $\pm$ 1.61 <sup>ab</sup>	8.75 $\pm$ 2.63 <sup>b</sup>	4.92 $\pm$ 2.44 <sup>cde</sup>	29.11 $\pm$ 15.61 <sup>ab</sup>
Swartkop-M	4.72 $\pm$ 2.00 <sup>ef</sup>	2.93 $\pm$ 1.58 <sup>bcd</sup>	6.76 $\pm$ 2.73 <sup>cd</sup>	3.83 $\pm$ 2.13 <sup>de</sup>	29.87 $\pm$ 16.74 <sup>ab</sup>
Swartkop-H	3.42 $\pm$ 2.08 <sup>fg</sup>	1.73 $\pm$ 1.40 <sup>e</sup>	5.44 $\pm$ 3.04 <sup>d</sup>	3.70 $\pm$ 2.34 <sup>e</sup>	34.86 $\pm$ 30.06 <sup>abc</sup>

**Appendix 1C** Daily mean temperature (°C) characteristics ( $\pm$  s.d.) at different positions inside and outside *Azorella selago* cushion-plants and for the Stevenson Screen (Met. Data) measured over four seasons (N = 10 days). Also included are the P and F statistics of the GLMs results

Position	Mean	Minimum	Maximum	Range	% CV
<b>Winter:</b>	$F_{4, 45} = 2.51;$ $P > 0.05$	$F_{4, 45} = 1.13;$ $P > 0.05$	$F_{4, 45} = 3.99;$ $P < 0.05$	$F_{4, 45} = 13.57;$ $P < 0.05$	$F_{4, 45} = 1.02;$ $P > 0.05$
Met. Data	4.46 $\pm$ 2.41 <sup>a</sup>	1.71 $\pm$ 2.49 <sup>a</sup>	6.71 $\pm$ 3.21 <sup>a</sup>	5.00 $\pm$ 1.57 <sup>a</sup>	36.10 $\pm$ 17.18 <sup>a</sup>
Above Ground	2.42 $\pm$ 2.47 <sup>a</sup>	2.42 $\pm$ 2.47 <sup>a</sup>	5.29 $\pm$ 2.72 <sup>ab</sup>	2.87 $\pm$ 0.82 <sup>a</sup>	100.48 $\pm$ 129.88 <sup>a</sup>
Below Surface	2.17 $\pm$ 2.32 <sup>a</sup>	2.17 $\pm$ 2.32 <sup>a</sup>	4.48 $\pm$ 2.79 <sup>ab</sup>	2.3 $\pm$ 0.98 <sup>ab</sup>	72.65 $\pm$ 133.95 <sup>a</sup>
5 cm	2.08 $\pm$ 2.04 <sup>a</sup>	2.08 $\pm$ 2.04 <sup>a</sup>	3.18 $\pm$ 2.39 <sup>b</sup>	1.1 $\pm$ 0.69 <sup>bc</sup>	46.15 $\pm$ 25.18 <sup>a</sup>
10 cm	1.63 $\pm$ 1.71 <sup>a</sup>	1.63 $\pm$ 1.71 <sup>a</sup>	2.5 $\pm$ 2.01 <sup>b</sup>	0.87 $\pm$ 0.62 <sup>c</sup>	39.4 $\pm$ 31.24 <sup>a</sup>
<b>Spring:</b>	$F_{4, 45} = 0.14;$ $P > 0.05$	$F_{4, 45} = 1.43;$ $P > 0.05$	$F_{4, 45} = 1.91;$ $P > 0.05$	$F_{4, 45} = 5.50;$ $P < 0.05$	$F_{4, 45} = 1.41;$ $P > 0.05$
Met. Data	2.96 $\pm$ 2.71 <sup>a</sup>	0.84 $\pm$ 2.69 <sup>a</sup>	4.99 $\pm$ 3.17 <sup>a</sup>	4.15 $\pm$ 1.37 <sup>ab</sup>	14.28 $\pm$ 50.03 <sup>a</sup>
Above Ground	2.32 $\pm$ 3.09 <sup>a</sup>	2.32 $\pm$ 3.09 <sup>a</sup>	8.13 $\pm$ 5.71 <sup>a</sup>	5.81 $\pm$ 3.45 <sup>a</sup>	87.92 $\pm$ 106.96 <sup>a</sup>
Below Surface	2.63 $\pm$ 2.78 <sup>a</sup>	2.63 $\pm$ 2.78 <sup>a</sup>	6.85 $\pm$ 6 <sup>a</sup>	4.22 $\pm$ 3.64 <sup>ab</sup>	97.45 $\pm$ 180.05 <sup>a</sup>
5 cm	2.23 $\pm$ 1.73 <sup>a</sup>	2.23 $\pm$ 1.73 <sup>a</sup>	4.09 $\pm$ 2.86 <sup>a</sup>	1.86 $\pm$ 1.55 <sup>b</sup>	26.2 $\pm$ 58.34 <sup>a</sup>
10 cm	2.41 $\pm$ 1.55 <sup>a</sup>	2.41 $\pm$ 1.55 <sup>a</sup>	3.76 $\pm$ 2.17 <sup>a</sup>	1.35 $\pm$ 1 <sup>b</sup>	37.07 $\pm$ 21.52 <sup>a</sup>
<b>Summer:</b>	$F_{4, 45} = 1.12;$ $P > 0.05$	$F_{4, 45} = 12.73;$ $P < 0.05$	$F_{4, 45} = 7.40;$ $P < 0.05$	$F_{4, 45} = 30.33;$ $P < 0.05$	$F_{4, 45} = 19.31;$ $P < 0.05$
Met. Data	6.56 $\pm$ 1.76 <sup>a</sup>	4.38 $\pm$ 1.52 <sup>b</sup>	8.92 $\pm$ 1.78 <sup>b</sup>	4.54 $\pm$ 1.18 <sup>bc</sup>	21.69 $\pm$ 6.45 <sup>bc</sup>
Above Ground	6.74 $\pm$ 1.52 <sup>a</sup>	6.74 $\pm$ 1.52 <sup>a</sup>	12.09 $\pm$ 2.47 <sup>a</sup>	5.35 $\pm$ 2.14 <sup>a</sup>	47.72 $\pm$ 17.29 <sup>a</sup>
Below Surface	7.3 $\pm$ 1.22 <sup>a</sup>	7.3 $\pm$ 1.22 <sup>ab</sup>	11.88 $\pm$ 1.97 <sup>a</sup>	4.57 $\pm$ 1.75 <sup>a</sup>	34.09 $\pm$ 10.32 <sup>b</sup>
5 cm	7.59 $\pm$ 1.28 <sup>a</sup>	7.59 $\pm$ 1.28 <sup>bc</sup>	10 $\pm$ 1.48 <sup>ab</sup>	2.41 $\pm$ 0.9 <sup>b</sup>	21.08 $\pm$ 6.79 <sup>bc</sup>
10 cm	7.58 $\pm$ 1.28 <sup>a</sup>	7.58 $\pm$ 1.28 <sup>c</sup>	8.71 $\pm$ 1.36 <sup>b</sup>	1.14 $\pm$ 0.47 <sup>c</sup>	11.31 $\pm$ 4.17 <sup>c</sup>
<b>Autumn:</b>	$F_{4, 45} = 0.67;$ $P > 0.05$	$F_{4, 45} = 1.06;$ $P > 0.05$	$F_{4, 45} = 2.63;$ $P = 0.05$	$F_{4, 45} = 4.65;$ $P < 0.05$	$F_{4, 45} = 4.99;$ $P < 0.05$
Met. Data	7.87 $\pm$ 2.53 <sup>a</sup>	5.58 $\pm$ 2.24 <sup>a</sup>	10.82 $\pm$ 3.27 <sup>a</sup>	5.24 $\pm$ 2.18 <sup>b</sup>	20.51 $\pm$ 9.29 <sup>b</sup>
Above Ground	8.57 $\pm$ 2.8 <sup>a</sup>	8.57 $\pm$ 2.8 <sup>a</sup>	17.15 $\pm$ 4.87 <sup>a</sup>	8.58 $\pm$ 4.17 <sup>a</sup>	51.4 $\pm$ 27.72 <sup>a</sup>
Below Surface	8.86 $\pm$ 2.55 <sup>a</sup>	8.86 $\pm$ 2.55 <sup>a</sup>	14.73 $\pm$ 4.76 <sup>a</sup>	5.87 $\pm$ 3.65 <sup>ab</sup>	36.11 $\pm$ 20.82 <sup>ab</sup>
5 cm	8.74 $\pm$ 2.69 <sup>a</sup>	8.74 $\pm$ 2.69 <sup>a</sup>	12.86 $\pm$ 5.72 <sup>a</sup>	4.12 $\pm$ 4.01 <sup>ab</sup>	26.54 $\pm$ 16.64 <sup>ab</sup>
10 cm	9.02 $\pm$ 2.64 <sup>a</sup>	9.02 $\pm$ 2.64 <sup>a</sup>	11.67 $\pm$ 5.73 <sup>a</sup>	2.65 $\pm$ 3.84 <sup>b</sup>	16.44 $\pm$ 13.58 <sup>b</sup>

## **Chapter 2: Fine-scale variability patterns in *Azorella selago* Hook. (Apiaceae) on sub-Antarctic Marion Island**

### **Introduction**

Spatial patterns are generally observed in all ecological systems (Legendre 1993; Nash et al. 1999). Most species occur in patchy, random or gradient patterns across landscapes (Kielt et al. 2002; Tirado and Pugnaire 2005). These patterns may be generated by ecological processes such as species interactions (e.g. territoriality), microsite requirements, and distance-limited dispersal (Kielt et al. 2002; Turner 2005). The identification and understanding of interactions between ecological processes and spatial patterns in ecological data forms the primary concern of most ecological studies (Turner 2005; Wagner and Fortin 2005).

The analysis of spatial patterns in species characteristics may be used to generate hypotheses about processes responsible for the observed patterns (Legendre and Legendre 1998; Liebhold and Gurevitch 2002; Perry et al. 2002). Although different processes may generate the same or different patterns, analyses of such patterns may provide clues about the identity of the underlying processes (Liebhold and Gurevitch 2002). The existence of certain spatial patterns may rule out specific ecological processes (Liebhold and Gurevitch 2002). For example, a random pattern in species distribution may suggest the absence of competition amongst species in a community (Bolker and Pacala 1999). Studies of spatial patterns in species characteristics are necessary particularly since mechanisms responsible for such patterns change across scale. Also, there is an increasing need to predict species response to environmental change, particularly under the current conditions of climate change (Wessman 1992; Mancera et al. 2005).

One tool for predicting processes generating spatial patterns in species data is the quantification of spatial autocorrelation in species characteristics (Liebhold and Gurevitch 2002; Perry et al. 2002). Spatial autocorrelation is the pattern in which observations from nearby locations or individuals are likely to be more similar (positive autocorrelation) or dissimilar (negative autocorrelation) than expected by chance alone (Legendre 1993; Dale et al.

2002; Fortin et al. 2002). Presence of spatial autocorrelation in data indicates lack of independence between pairs of observations and this can generate false results in the analyses, since standard statistical approaches are based on assumptions of independence between observations (Legendre 1993; Fortin 1999; Diniz-Filho et al. 2003). Quantification of spatial autocorrelation may however also determine the existence of spatial patterns in species data and the scale of influence of the causal processes (Chung and Noguchi 1998; Fortin 1999; Selmi and Boulinier 2001).

Most studies of species responses to environmental change tend to focus on broad-scale species patterns in relation to major climatic gradients (Blois et al. 2002). However, plants do not only respond to averages across landscapes, but also to mechanisms operating at fine scales (Purves and Law 2002). In the last two decades studies have shown that the scale of observation influences the recognition and interpretation of patterns in species characteristics (Legendre 1993; Cushman and McGarigal 2004; Morzaria-Luna et al. 2004). Together with the occurrence of spatial autocorrelation in species data, the scale of observation may also influence the interpretation of spatial analysis (Legendre 1993; Fortin 1999). It is therefore important to define and quantify spatial autocorrelation at the finest possible scale of observation (e.g. within site) in order not to violate statistical assumptions of independence between observations (Legendre 1993; Diniz-Filho et al. 2003) and to examine fine-scale patterns and the extent of spatial variation in species data (McGeoch and Price 2004). Understanding the fine-scale ecological patterns of a species may provide basis for understanding the broad-scale ecological patterns of a species (McGeoch and Price 2004).

On Marion Island (46°55'S, 37°45'E), plant characteristics (e.g. morphology, phenology, and epiphyte load) are strongly related to biotic and abiotic environmental factors (Gremmen 1997; Smith and Steenkamp 2001; le Roux and McGeoch 2004). Differences in climate between the eastern and western sides of the island have been shown to play a major role in determining the spatial structure of the morphological characteristics of *Azorella selago* Hook. (Apiaceae) (le Roux and McGeoch 2004; Nyakatya, Chapter 3). The altitudinal gradient was shown to be significant in the spatial distribution of the dominant epiphyte on *A. selago*, *Agrostis magellanica*

(Lam.) Vahl. (Poaceae) (le Roux 2004; Nyakatya, Chapter 3). However, spatial autocorrelation in *A. selago* characteristics have never been extensively quantified on the island. Fine scale variability patterns of *A. selago* characteristics are also poorly understood. Thus, this study investigates spatial patterns of *A. selago* growth rate, size (cushion diameter; cushion height; and cushion surface area), density of reproductive structures (flower buds; flowers; and fruits), percentage of dead cushion surface and the density of the dominant epiphyte (e.g. *Agrostis magellanica*). This study also quantifies the spatial autocorrelation in *A. selago* characteristics within fellfield stands of *A. selago* on Marion Island. The results obtained from this study will therefore provide an improved understanding of the spatial structure of *A. selago* characteristics and the scale of influence of the underlying processes.

## **Materials and Methods**

### *Study Area*

The study was conducted on Marion Island, the larger of the two islands that form Prince Edward Islands in the sub-Antarctic region of the Southern Indian Ocean. Sampling sites were situated in fellfield habitats of mainly grey lava and also on black lava at altitudes of between 150 and 650 m a.s.l. *Azorella selago* (Apiaceae), the cushion-forming dicotyledonous plant forms a dominant aerial structure of these fellfield habitats (Huntley 1972; Gremmen 1981; le Roux and McGeoch 2004). In fellfield habitats *A. selago* appears scattered in a background of volcanic rocks. Many plants such as *Agrostis magellanica* as well as other non-grass species and microarthropods occur epiphytically on *A. selago* plants (Barendse and Chown 2001; Hugo et al. 2004; le Roux 2004).

### *Sampling Design*

*Azorella selago* cushion-plants were surveyed between April 2002 and April 2003. Four altitudinal transects were established across the island. One transect was orientated between Junior's Hill and First Red Hill on the eastern side of the island (hereafter referred to as Tafelberg Transect). Another

transect sloped from Stony Ridge to Halfway Kop also on the eastern side of the island (hereafter referred to as Stony Ridge Transect). On the western side of the island, one transect was positioned inland of the Mixed Pickle Cove, from Neville towards Saalrug (hereafter referred to as Mixed Pickle Transect). Another transect lay inland of Swartkop Point, along Stevie and Bakkerkop (hereafter referred to as Swartkop Transect). Each transect was divided into three altitudinal bands (150 - 250, 350 - 450, > 550 m a.s.l.) with one sampling site in each band per transect. In each sampling site 50 cushion-plants (> 0.15 m in diameter) were used to measure various characteristics of *A. selago*. The sites also consisted of cushion-plants that were less than 0.15 m in diameter. The sites were clearly marked with corner markers. A Nikon Total Station DTM350 Theodolite was used to measure the exact relative position of each plant within a site as well as all corners of the sampling sites to establish the relative position of individual plants within a site.

#### *Plant Growth Rate, Size and Density*

Plant growth rate was measured by inserting wooden sticks ( $\pm 10$  -15 mm in diameter, 40 - 60 mm long) vertically into each cushion (> 15 cm in diameter to minimise the damage) of every site until these growth rate markers were embedded in the ground underneath the cushion (to minimize the effect of frost heave). The sticks were then marked with a line flush with the surface of the cushion after insertion. After a year the growth rate markers were re-marked with a line flush with the new surface and the distance between the two lines was measured and converted to growth rate (see also le Roux and McGeoch 2004). Two measures of plant size were taken; plant height was determined by measuring the vertical distance between the highest point of the cushion surface and the ground beneath it. Surface area of the cushion was measured using a 1 m<sup>2</sup> flexible sampling grid, with each cell totalling 4 cm<sup>2</sup> in area. A scaled photograph of each plant was also taken to estimate cushion size using image analyser software (SigmaScan Pro 5.0, Illinois, USA). The theodolite was used to measure the area of each sampling site and all *A. selago* plants in a site were counted to estimate plant density. These

methods and measurements were similar to those used by Huntley (1971) and also by le Roux and McGeoch (2004).

#### *Plant Vitality and Epiphyte Load*

Plant vitality was determined in two ways: First by measuring the epiphyte load of all cushion-plants in all sites, and secondly by measuring the percentage of the cushion surface that was dead. Epiphyte load was used as a measure of vitality because the growth of epiphytes may have negative impact on the plant occupied and other cushion-plant species have been reported to collapse due to colonization by epiphytes (Pyšek and Liška 1991). Epiphyte load was determined by counting the number of *Agrostis magellanica* (the dominant epiphyte) rooted in each plant and the presence or absence of other plant species growing on *A. selago*. The percentage of cushion surface that was dead was measured by counting the number of grid cells containing predominantly dead plant stems (calculated as a proportion of total number of grid cells covering the plant, and converted to area).

#### *Plant Reproduction Phenology*

Phenological measurements were taken twice for every cushion-plant in every site using the 1 m<sup>2</sup> flexible sampling grid. These measurements were conducted over the summer season (October 2002 to March 2003) and were temporally far apart between transects due to long walking distances between sites and bad weather conditions encountered during the periods of measurements. The measurements taken using the sampling grid were: presence, and numbers of flower buds, flowers and fruit. These numbers was used with cushion size (surface area) to calculate flower bud density, flower density, and fruit density of each plant.

#### *Data Analysis*

Spatial analysis by distance indices (SADIE software, available from <http://www.rothamsted.bbsrc.ac.uk/pie/sadie/>) was used to quantify the spatial

structure of *A. selago* plant distribution within sampling sites across the island. An index of aggregation ( $I$ ), measured by calculating the minimum distance that the sampled individuals would need to move in order to achieve absolute aggregation, was used as a measure of spatial structure (Perry 1995). Values of  $I > 1$  indicate aggregation,  $I < 1$  indicates regularity, and  $I \sim 1$  suggests randomness (Perry et al. 1996). Indices of aggregation: (a) ( $I_A$ ) for all plants within a site and (b) ( $I_B$ ) for only plants that were greater than 0.15 m in diameter were calculated for each site and tested for statistical significance across all sites. A Mann-Whitney U test statistic was used to test for significant differences in mean Aggregation Indices between the eastern and western sides of Marion Island.

Spatial pattern in *A. selago* morphology, epiphyte load and reproduction variables were also quantified for each sampling site using version 4.3 of the Spatial Autocorrelation Analysis Programme (SAAP 4.3) (Wartenberg 1989). The *A. selago* variables measured were all not normally distributed, and so all data were log-transformed and the transformed values were used to calculate Moran's  $I$  (Nash et al. 1999). Correlograms based on 11 distance classes were used (following Sturge's rule: Number of distance classes =  $1 + 3.3 \cdot \log_n(m)$ ) to graphically present changes in the autocorrelation coefficients with physical distance between pairs of plant units (Legendre and Legendre 1998). Following Dutilleul & Legendre (1993) recommendation of the use of equal-frequency distance classes for even precision and power in estimation and testing, distance classes with equal number of point pairs were used in the analyses. The Bonferroni approximation was then used to evaluate the overall significance of each correlogram. The shape of the correlograms was used to indicate the type and extent of spatial structure present within stands of plants (Legendre 1993).

## Results

Spatial analysis by distance indices (SADIE) showed aggregation indices ranging from 0.7 to 1.7 for all the 12 sites sampled on the island (Table 2.1). Sites on the western side of the island had higher numbers of juvenile cushion-plants (using size as an estimator of age structure) than sites on the

eastern side (Figure 2.1). *Azorella selago* were however more aggregated on sites on the eastern side of the island than those on the western side (Table 2.1). When all (juvenile and mature) *A. selago* in a site were included in the analysis, cushion-plants were significantly aggregated in six sites and five of these were on the eastern side of the island (Table 2.1). However there was no significant difference in mean Aggregation Index ( $I_A$ ) between the eastern and western sides of the island when all (juvenile and mature) cushion-plants were included in the analysis. Whereas, when only the mature cushion-plants (> 0.15 m in diameter) were included in the analysis, *A. selago* were significantly aggregated in only two sites, also on the eastern side of the island (Table 2.1). There was also a significant difference ( $p < 0.05$ ) in mean Aggregation Index ( $I_B$ ) between the eastern and western sides of the island ( $U = 5.500$ ;  $p = 0.045$ ;  $n = 6$ ).

Tables 2.2 - 2.4 indicate that there were extremely high variations in growth rate, epiphyte density, and in the density of reproductive structures between individuals within stands of *A. selago*. The percentage coefficient of variation for growth rate ranged from 73.05 to 171.75 between sites. Cushion growth rate showed no significant spatial structure at any site at this scale (Table 2.5). For cushion height, the only significant spatial structure was at Swartkop middle site (Fig. 2.2). The plant height correlogram showed positive autocorrelation only after 4.5 m to 5 m (Fig. 2.2). *Azorella selago* cushion diameter was significantly spatially autocorrelated in five sites out of the 12 sampled on the island (Fig. 2.3a - e; Table 2.5) and the shapes of these diameter correlograms were dissimilar among the five sites (Fig. 2.3a - e). At Tafelberg middle site, the diameter correlogram showed a clear spatial gradient of positive autocorrelation at short distances (5 m) coupled with negative autocorrelation at larger distances (15 m) (Fig. 2.3a). The Stony Ridge middle site cushion diameter showed a more patchy spatial structure, with positive autocorrelation after 2.4 m to 3.5 m (Fig. 2.3b). Cushion diameter was positively autocorrelated up to 1.8 m at Mixed Pickle middle site (Fig. 2.3c); between 2.6 m and 3.1 m at Swartkop low site (Fig. 2.3d); and at 1.2 m at Swartkop middle site (Fig. 2.3e).

A significant spatial structure of cushion surface area was observed in five sites out of the 12 sampled on the island (Fig. 2.4a - e; Table 2.5). Fig. 2.4

indicates that the spatial correlograms of cushion surface area were dissimilar in shape between the five sites. No significant positive autocorrelation of Moran's  $I$  coefficient was observed at Tafelberg low site (Fig. 2.4a), however, the Tafelberg middle site correlogram showed a clear spatial gradient with positive autocorrelation at short distances (up to 6.5 m) and negative autocorrelation from 15 m and beyond (Fig. 2.4b). The other 3 sites had patchy patterns of cushion surface area (Fig. 2.4c - e). At Stony Ridge high site, surface area was positively autocorrelated up to 6.6 m and at Swartkop low site surface area was positively autocorrelated only after 2.6 m to 3.1 m (Fig. 2.4c - d). Cushion surface area was positively autocorrelated up to 1.2 m at Swartkop middle site (Fig. 2.4e).

Only three sites of the 12 sampled on Marion Island presented significant spatial correlograms for percentage of dead surface area on *A. selago* (Fig. 2.5a - c; Table 2.5; Appendix 2A and 2B). All three significant correlograms portrayed patchy patterns of percent dead surface area, with Tafelberg high site having positive autocorrelation after 10.9 to 12.9 m (Fig. 2.5a). At Stony Ridge low site, percentage of dead surface area was positively autocorrelated to 2.2 m, and up to 2.4 m at Stony Ridge middle site (Fig. 2.5b - c). Correlograms of *Agrostis magellanica* density were significantly structured at five of the eight sites recorded on the island (Fig. 2.6a - e; Table 2.5; Appendix 2A and 2B). *Agrostis magellanica* density was positively autocorrelated after 6.5 m to 8 m at Tafelberg middle site (Fig. 2.6a). At Stony Ridge low site, *A. magellanica* density was positively autocorrelated up to 3.1 m and up to 1.3 m at Mixed Pickle middle site (Fig. 2.6b - c). At Swartkop low site, *A. magellanica* density was positively autocorrelated from 6.1 to 7m and it was positively autocorrelated from 4 m to 4.5 m at Swartkop middle site (Fig. 2.6d - e).

Flower bud density also showed no significant spatial structure at any site within stands of *A. selago* plants (Table 2.5). Flower density was significantly spatial autocorrelated at Stony Ridge high and Mixed Pickle low sites (Fig. 2.7a - b). The correlograms showed patchy patterns of flower densities with positive autocorrelation after 6.6 to 8.2 m for Stony Ridge high site and after 2 m to 2.4 m for Mixed Pickle low site (Fig. 2.7a - b). The spatial correlograms for fruit densities indicated that fruit densities were significantly

autocorrelated at 5 of the 12 sites on Marion Island (Fig. 2.8a - e; Table 2.5; Appendix 2A and 2B). Four of these sites showed patchy patterns of fruit densities. At Tafelberg middle site, fruit density was positively autocorrelated to 3.6 m and at Stony Ridge low fruit density was positively autocorrelated only after 5 m to 6.3 m (Fig. 2.8a - b). Fruit density was also positively autocorrelated up to 4.7 m at Stony Ridge high and up to 1.3 m at Mixed Pickle middle sites (Fig. 2.8c - d). Swartkop middle plot fruit density showed a pattern of spatial gradient with positive autocorrelation at short distances (1.7 m) and negative autocorrelation at larger distances (Fig. 2.8e).

## Discussion

This study revealed that *A. selago* cushion-plants (particularly the mature plants) generally occur in a random spatial pattern in fellfield habitats on Marion Island, a trait that is comparatively rare in nature (Brown et al. 1995; Perry et al. 2002). In addition, the prevalence and form of a spatial structure was highly inconsistent across both *A. selago* characteristics and sites. *Azorella selago* became more randomly distributed when juvenile plants were excluded from the analysis, a trait that suggests self-thinning of the *A. selago* population, as the plants grow older (Westoby 1984; Begon et al. 1996). This self-thinning process occurs when an increase in average body size is accompanied by a decrease in population density (Dunham and Vinyard 1997; Guiñez and Castilla 2000), and this is not uncommon particularly in resource (e.g. nutrients) constricted populations such as the fellfield population of *A. selago* on Marion Island (Smith and Steenkamp 2001).

Different substrate types between the eastern and western sides of the island may be the basis for the observed differences in the aggregation of *A. selago* plants between the two sides. The relatively nutrient-poor grey lava, with high incidence of volcanic rocks (e.g. bare ground), dominates the eastern side of the island (Verwoerd 1971; Kent and Gribnitz 1983; McDougall et al. 2001). The additional physical challenges presented by the grey lava (compared to black lava) may be the result of a slightly more aggregated distribution of *A. selago* on the eastern side, if suitable soils or better

environmental conditions are more restricted or patchily distributed on grey lava landscapes (Callaway 1997; Tirado and Pugnaire 2005).

There were significant spatial patterns found in the morphology, epiphyte density (e.g. *Agrostis magellanica*), and density of the reproductive structures of *A. selago* at the site level. However, these patterns were not consistent across the sites sampled on the island. There was also a low prevalence of positive spatial autocorrelation for all variables at all sites. These results suggest that at fine scales (e.g. within site), *A. selago* characteristics are determined by processes that are site-specific (Liebhold and Gurevitch 2002; McGeoch and Price 2004). Site-specific processes may originate from the occurrence of fine scale micro-gradients or microsite differences in environmental variables (Mancera et al. 2005). Possible environmental variables that may differ across relatively small distances include, soil type; soil moisture; available sunlight; nutrient availability; aspect and microtopography (Bullock and Burkhart 2005). Such variation may not be too surprising in this particular system given the unevenness of the island's topography and the strong effect that the physical environment has on fellfield plant populations (Smith and Steenkamp 1990; Bergstrom and Chown 1999). This result is also supported by a related study by le Roux and McGeoch (2004) at three sites on the island that found very high between-site variability in *A. selago*'s growth rate.

Other studies conducted on the same system yet at a larger scale of observation (e.g. across the island), established a strong response of *A. selago* characteristics to altitudinal gradients and to different sides of the island (le Roux and McGeoch 2004; le Roux 2004; Nyakatya, Chapter 3). These findings suggest that whereas *A. selago* and its characteristics are not strongly and consistently spatially structured at a fine-scale (e.g. a patch or a stand of plants), the species does respond predictably to processes operating at larger island-wide scales. Furthermore, the inconsistency and low prevalence (from 0 to a maximum of 50% prevalence) of spatial autocorrelation in *A. selago* characteristics (e.g. plant growth rate; plant size; dead plant surface; epiphytes density and density of reproductive structures) within fellfield stands across the island, particularly in the first distance class, suggests that *A. selago* individuals within a site can generally be used as

independent replicates in standard statistical analysis of broad-scale variability patterns (Legendre 1993; Nash et al. 1999).

Quantification of the fine-scale patterns in *A. selago* characteristics has shown that, individuals of *A. selago* are randomly distributed in fellfield vegetation stands on the island and that there are no strong or consistent patterns of spatial autocorrelation within *A. selago* characteristics. Consequently no precise conclusions can be made about processes underlying patterns of *A. selago* variability at this spatial scale (e.g. within site). Best predictors of *A. selago* variability at present thus appear to be those possibly operating at broad scales (e.g. landscape and/or island wide) (see Chapter 3).

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**Table 2.1** Spatial analyses by distance indices (SADIE) results for the distribution of *Azorella selago* plants within 12 sampling sites across Marion Island. Also included are plant density and a list of acronyms used to indicate site names in the subsequent tables.  $I_A$  is the index of aggregation for all *Azorella selago* plants in a site.  $I_B$  is the index of aggregation for only *Azorella selago* plants greater than 15 cm in diameter. (\* indicate significant aggregation at  $P < 0.05$ )

Site	Acronym	Plant Density (100 m <sup>2</sup> )	Index of aggregation ( $I_A$ )	Index of aggregation ( $I_B$ )
<b>Tafelberg</b>				
Low	TBL	110	1.237*	1.098
Middle	TBM	14	1.665*	1.467*
High	TBH	26	1.680*	1.087
<b>Stony Ridge</b>				
Low	SRL	90	1.094	0.974
Middle	SRM	30	1.272*	1.077
High	SRH	15	1.261*	1.258*
<b>Mixed Pickle</b>				
Low	MPL	155	1.072	0.741
Middle	MPM	112	1.065	0.867
High	MPH	37	1.196	0.943
<b>Swartkop</b>				
Low	SKL	108	1.173	1.063
Middle	SKM	119	1.217	1.098
High	SKH	49	1.372*	0.991
<b>Eastern side</b>	Mean ± s.d.	47.50 ± 41.62	1.368 ± 0.244	1.160 ± 0.176
<b>Western side</b>	Mean ± s.d.	96.67 ± 44.94	1.183 ± 0.113	0.951 ± 0.132

**Table 2.2** Mean ( $\pm$  sd) and coefficient of variation (% CV) of growth rate and size characteristics (height and diameter) of *Azorella selago* plants recorded on 12 sites across Marion Island

Site	Growth Rate (mm/yr)		Plant Height (m)		Plant Diameter (m)	
	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV
<b>Tafelberg</b>						
Low	1.28 $\pm$ 1.52	119.28	0.13 $\pm$ 0.03	27.18	0.66 $\pm$ 0.39	58.37
Middle	1.91 $\pm$ 2.27	116.34	0.18 $\pm$ 0.05	30.32	1.16 $\pm$ 0.70	60.17
High	3.48 $\pm$ 2.59	95.91	0.37 $\pm$ 0.17	46.79	1.14 $\pm$ 0.76	66.98
<b>Stony Ridge</b>						
Low	0.26 $\pm$ 0.20	79.23	0.19 $\pm$ 0.04	19.24	0.77 $\pm$ 0.24	30.71
Middle	0.11 $\pm$ 0.15	140.67	0.14 $\pm$ 0.03	24.53	0.91 $\pm$ 0.37	40.26
High	0.35 $\pm$ 0.27	77.56	0.32 $\pm$ 0.15	46.04	0.84 $\pm$ 0.35	41.35
<b>Mixed Pickle</b>						
Low	1.78 $\pm$ 1.85	99.59	0.17 $\pm$ 0.03	18.92	0.59 $\pm$ 0.26	44.05
Middle	2.28 $\pm$ 2.01	87.90	0.14 $\pm$ 0.04	28.41	0.71 $\pm$ 0.25	35.33
High	3.83 $\pm$ 3.93	100.95	0.14 $\pm$ 0.04	26.80	0.72 $\pm$ 0.23	31.23
<b>Swartkop</b>						
Low	0.30 $\pm$ 0.22	73.05	0.19 $\pm$ 0.05	27.13	0.65 $\pm$ 0.31	48.23
Middle	0.16 $\pm$ 0.18	107.75	0.19 $\pm$ 0.05	26.05	0.70 $\pm$ 0.25	35.97
High	0.30 $\pm$ 0.52	171.75	0.15 $\pm$ 0.07	48.00	0.80 $\pm$ 163	202.6

**Table 2.3** Mean ( $\pm$  sd) and coefficient of variation (% CV) of *Azorella selago*'s surface area, dead surface area and density of the epiphyte, *Agrostis magellanica*

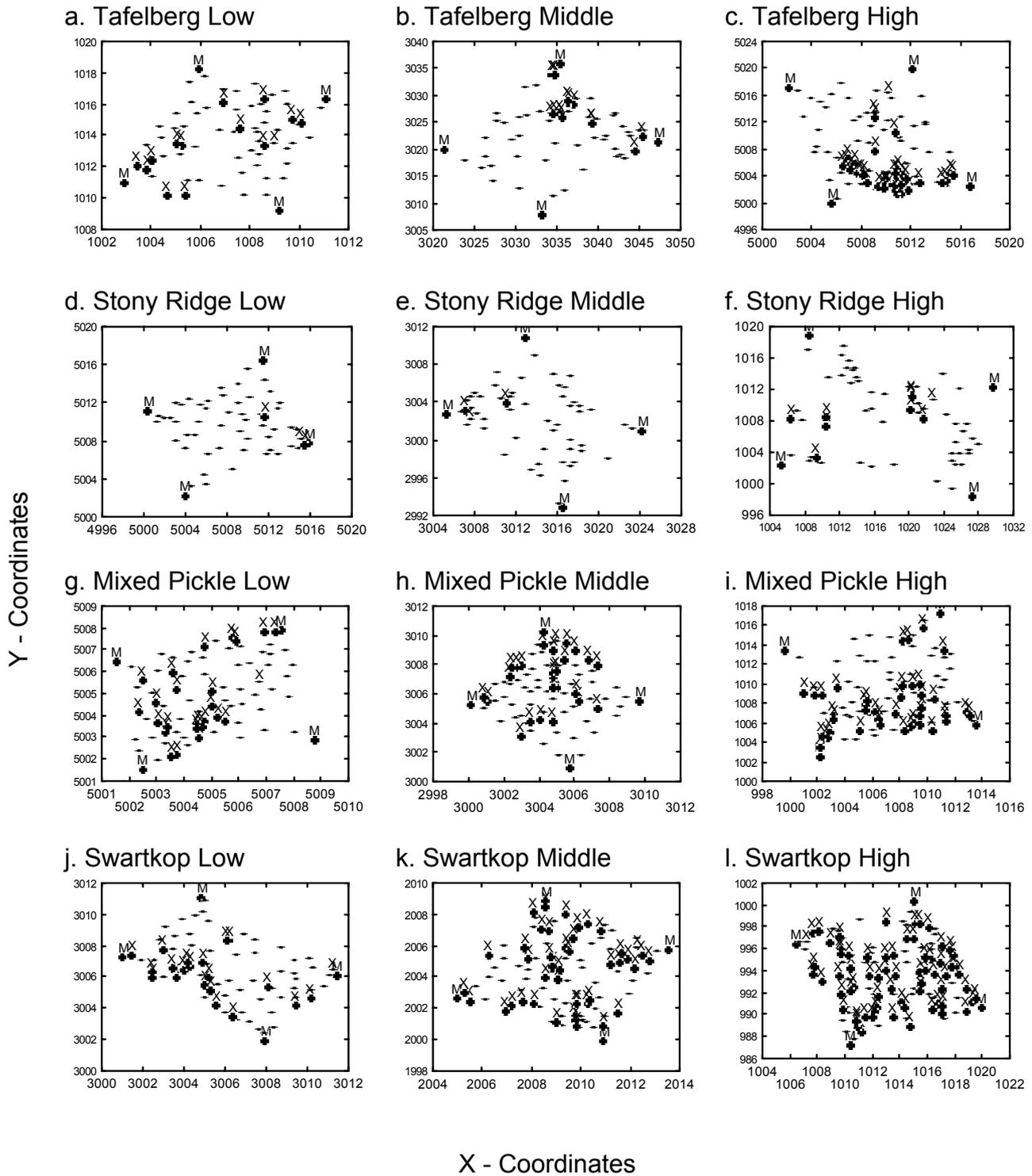
Site	Plant Surface Area (m <sup>2</sup> )		Dead Plant Surface (%)		Density (m <sup>-2</sup> ) of <i>A. magellanica</i>	
	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV
<b>Tafelberg</b>						
Low	0.19 $\pm$ 0.14	74.14	11.66 $\pm$ 5.11	43.88	1008.91 $\pm$ 417.18	41.35
Middle	0.51 $\pm$ 0.44	86.15	5.30 $\pm$ 4.09	77.18	316.95 $\pm$ 406.63	128.29
High	0.52 $\pm$ 0.53	102.35	4.09 $\pm$ 2.60	63.65	0	-
<b>Stony Ridge</b>						
Low	0.34 $\pm$ 0.18	52.12	6.34 $\pm$ 4.30	67.88	805.59 $\pm$ 316.59	39.30
Middle	0.40 $\pm$ 0.29	73.31	7.07 $\pm$ 6.00	84.82	517.80 $\pm$ 1454.73	280.94
High	0.46 $\pm$ 0.31	67.92	4.54 $\pm$ 3.85	84.70	0.06 $\pm$ 0.40	707.11
<b>Mixed Pickle</b>						
Low	0.18 $\pm$ 0.11	61.07	9.45 $\pm$ 4.02	42.53	3094.91 $\pm$ 4277.45	138.21
Middle	0.25 $\pm$ 0.14	54.40	8.32 $\pm$ 3.33	40.06	166.04 $\pm$ 283.39	170.68
High	0.25 $\pm$ 0.16	59.45	8.28 $\pm$ 5.54	66.86	0	-
<b>Swartkop</b>						
Low	0.28 $\pm$ 0.45	163.47	7.02 $\pm$ 4.37	62.24	152.07 $\pm$ 164.11	107.92
Middle	0.26 $\pm$ 0.16	61.38	6.72 $\pm$ 2.82	41.99	5.12 $\pm$ 11.23	219.51
High	0.17 $\pm$ 0.12	70.69	4.57 $\pm$ 5.58	121.98	0	-

**Table 2.4** Mean ( $\pm$  sd) and coefficient of variation (% CV) of the density of *Azorella selago*'s reproductive structures (flower buds, flowers and fruits)

Site	Flower Bud Density ( $\text{mm}^{-2}$ )		Flower Density ( $\text{mm}^{-2}$ )		Fruit Density ( $\text{mm}^{-2}$ )	
	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV	Mean $\pm$ SD	% CV
<b>Tafelberg</b>						
Low	0.00011 $\pm$ 0.00028	254.55			0.00086 $\pm$ 0.0014	170.93
Middle	0.00099 $\pm$ 0.00324	327.27			0.00141 $\pm$ 0.00138	97.87
High	0.00182 $\pm$ 0.00483	265.38			0.00201 $\pm$ 0.00302	150.25
<b>Stony Ridge</b>						
Low			0.00007 $\pm$ 0.00027	385.71	0.00356 $\pm$ 0.00281	78.93
Middle					0.00252 $\pm$ 0.00227	90.08
High	0.00114 $\pm$ 0.00326	285.96	0.00469 $\pm$ 0.00752	160.34	0.00422 $\pm$ 0.00707	167.57
<b>Mixed Pickle</b>						
Low	0.00928 $\pm$ 0.01352	145.69	0.00299 $\pm$ 0.00492	164.55	0.00648 $\pm$ 0.01021	157.56
Middle	0.03103 $\pm$ 0.03822	123.17	0.00258 $\pm$ 0.00864	327.91	0.01839 $\pm$ 0.01974	107.34
High	0.12287 $\pm$ 0.12780	104.01			0.07566 $\pm$ 0.07360	97.28
<b>Swartkop</b>						
Low					0.00077 $\pm$ 0.00086	111.69
Middle			0.00023 $\pm$ 0.00036	156.52	0.00119 $\pm$ 0.00101	84.87
High	0.00045 $\pm$ 0.00112	248.89	0.00059 $\pm$ 0.00081	137.29	0.00194 $\pm$ 0.00208	107.22

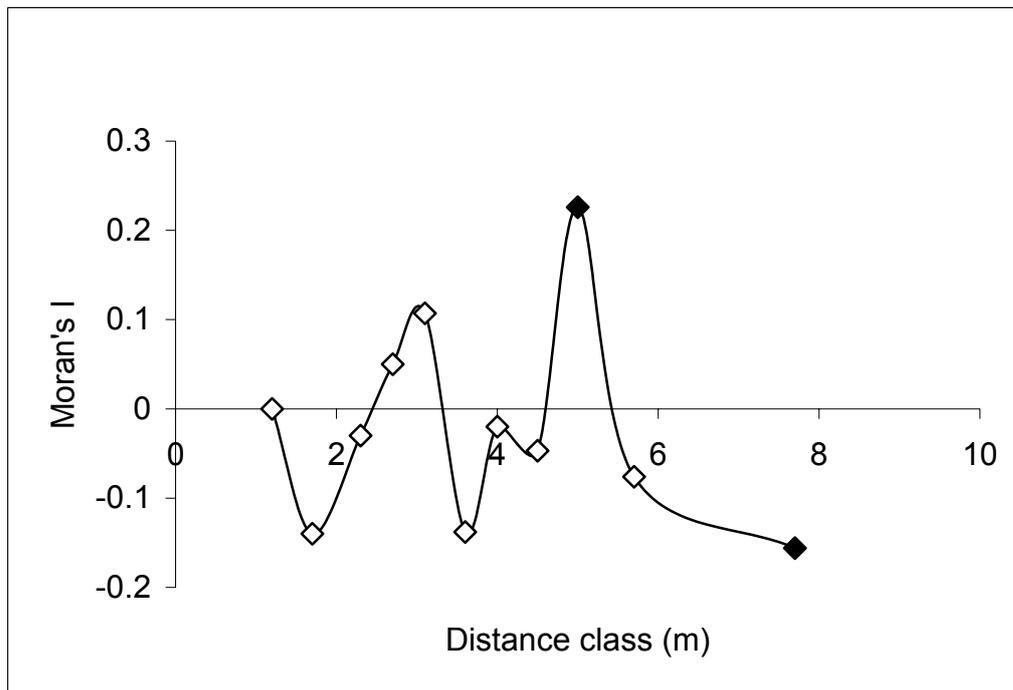
**Table 2.5** Prevalence of significant spatial autocorrelation of *Azorella selago*'s variables at different sites across Marion Island (see Table 2.1 for acronyms)

Variables	Prevalence of significant correlograms	Sites and distance over which significant positive autocorrelation occurred (m)
Growth rate (mm/yr)	0/12	0
Height (m)	1/12	SKM (4.5 - 5.0)
Diameter (m)	5/12	TBM (5.0); SRM (2.4 - 3.5); MPM (1.8); SKL (2.6 - 3.1); SKM (1.2)
Surface area (m <sup>2</sup> )	5/12	TBM (6.5); SRH (6.6); SKL (2.6 - 3.1); SKM (1.2)
Dead surface area (%)	3/12	TBH (10.9 - 12.9); SRL (2.2); SRM (2.4)
<i>Agrostis</i> density (m <sup>-2</sup> )	5/8	TBM (6.5 - 8); SRL (3.1); MPM (1.3); SKL (6.1 - 7); SKM (4.0 - 4.5)
Flower bud density (m <sup>-2</sup> )	0/8	0
Flower density (m <sup>-2</sup> )	2/4	SRH (6.6 - 8.2); MPL (2.0 - 2.4)
Fruit density (m <sup>-2</sup> )	5/12	TBM (3.6); SRL (5.0 - 6.3); SRH (4.7); MPM (1.3); SKM (1.7)



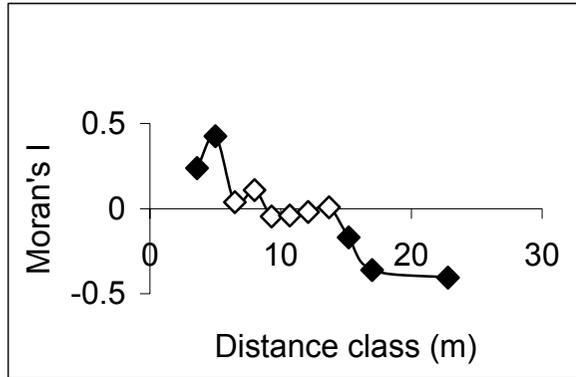
**Fig. 2.1** The distribution of *Azorella selago* individuals in 12 sampling sites across Marion Island. Filled circles represent *A. selago* (diameter > 0.15 m) from which various measurements were taken, X 's represent small cushion-plants (diameter < 0.15 m) from which no measurements were taken and M 's are the corner markers of the sampling sites. Cushion numbers were removed for clarity

## Swartkop Middle

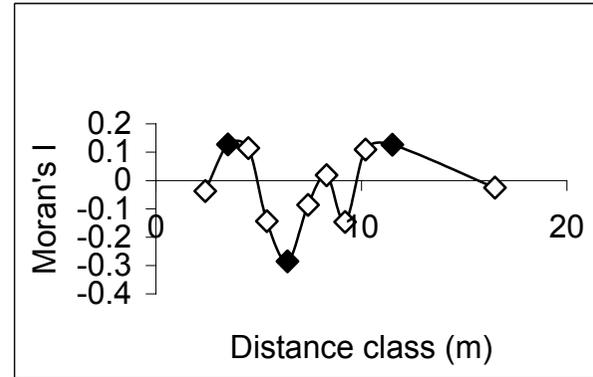


**Fig. 2.2** Correlogram of *Azorella selago* height at SKM, the only site that had a significant correlogram for plant height after Bonferroni correction ( $P < 0.05$ ). Distance classes with equal number of point pairs (111 pairs) were used in the analysis. Filled symbols represent significant Moran's I values ( $P < 0.05$ ). Empty symbols represent non-significant Moran's I values

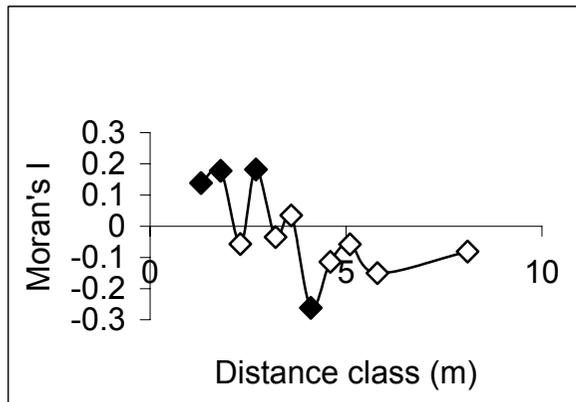
a. Tafelberg Middle



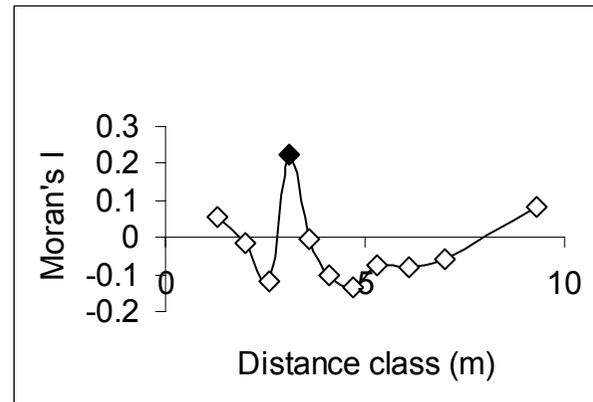
b. Stony Ridge Middle



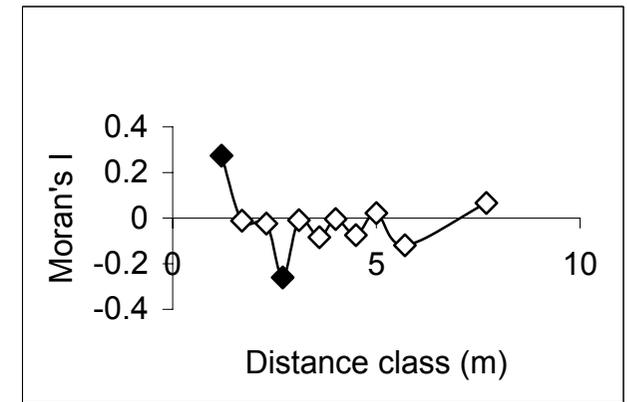
c. Mixed Pickle Middle



d. Swartkop Low

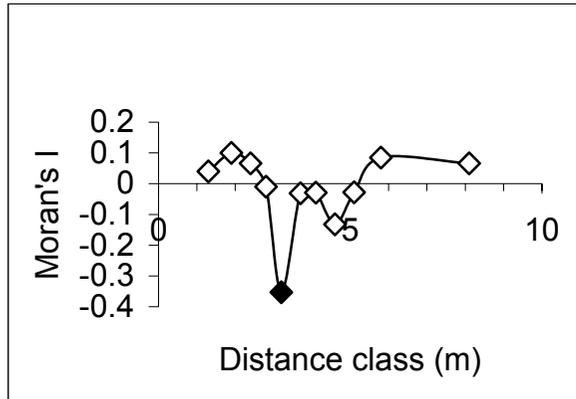


e. Swartkop Middle

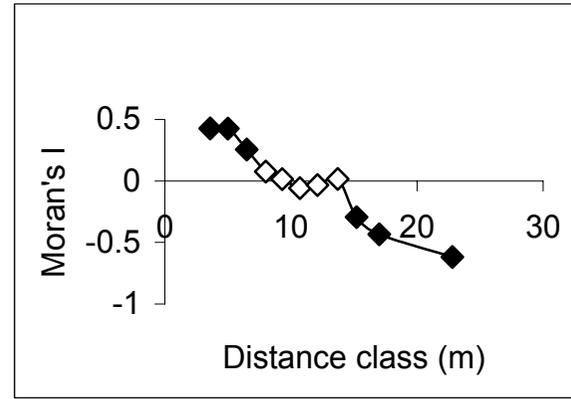


**Fig. 2.3** Correlograms showing the spatial structure of *Azorella selago* diameter for sites that showed an overall significant autocorrelation after progressive Bonferroni correction (**a.** TBM; **b.** SRM; **c.** MPM; **d.** SKL; and **e.** SKM). Distance classes with equal number of point pairs (111 pairs) were used. Filled symbols correspond to Moran's I values significant at  $P < 0.05$ . Empty symbols represent non-significant Moran's I values

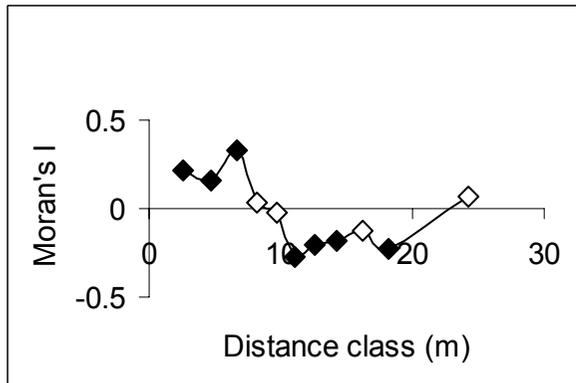
a. Tafelberg Low



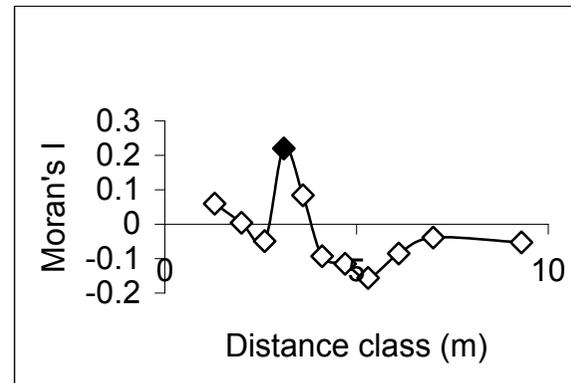
b. Tafelberg Middle



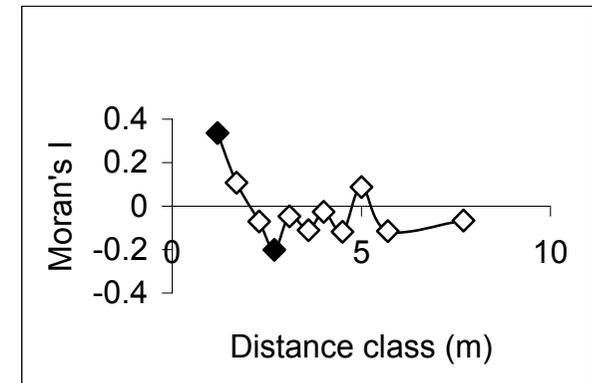
c. Stony Ridge High



d. Swartkop Low

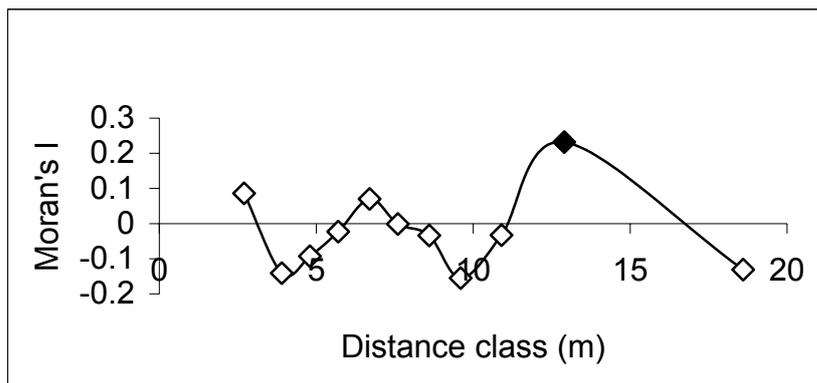


e. Swartkop Middle

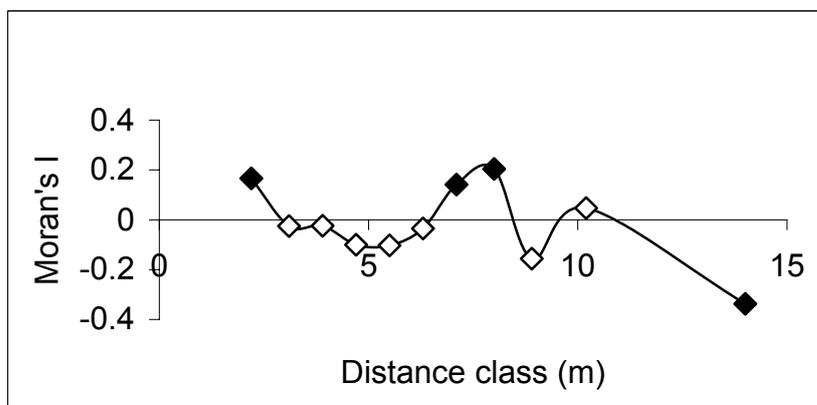


**Fig. 2.4** Spatial patterns of *Azorella selago*'s surface area at sites with overall significance ( $P < 0.05$ ) after Bonferroni correction (**a.** TBL; **b.** TBM; **c.** SRH; **d.** SKL; and **e.** SKM). Distance classes with equal number of point pairs (111 pairs; 107 in **c.**) were used in the analysis. Filled symbols represent significant I values at  $P < 0.05$  and empty symbols represent non-significant Moran's I values

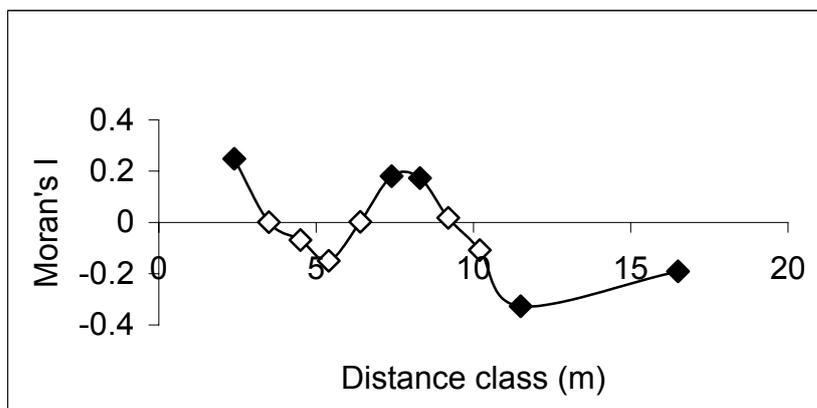
## a. Tafelberg High



## b. Stony Ridge Low

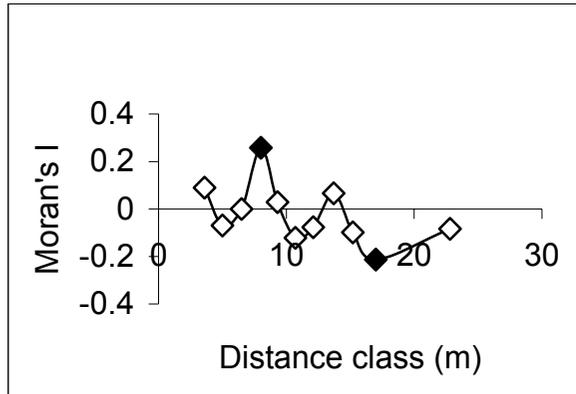


## c. Stony Ridge Middle

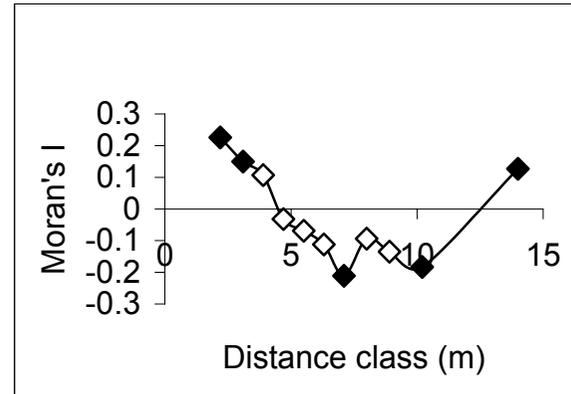


**Fig. 2.5** Correlograms showing the spatial structure of *Azorella selago*'s percentage of dead surface area at sites with an overall significance ( $p < 0.05$ ) after Bonferroni correction (**a.** TBH; **b.** SRL; and **c.** SRM). Distance classes with equal number of point pairs were used in the analysis (111 pairs). Filled symbols correspond to significant Moran's I values ( $P < 0.05$ ) and empty symbols represent non-significant Moran's I values

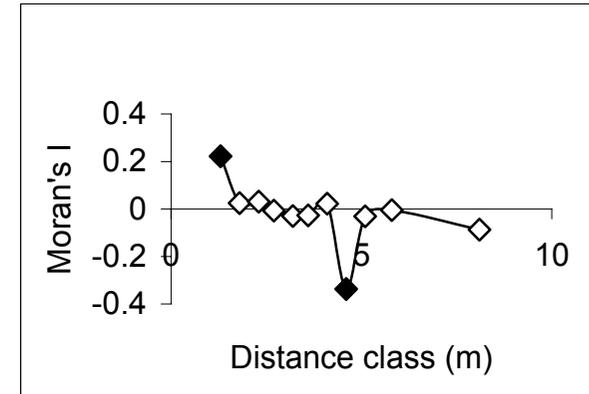
a. Tafelberg Middle



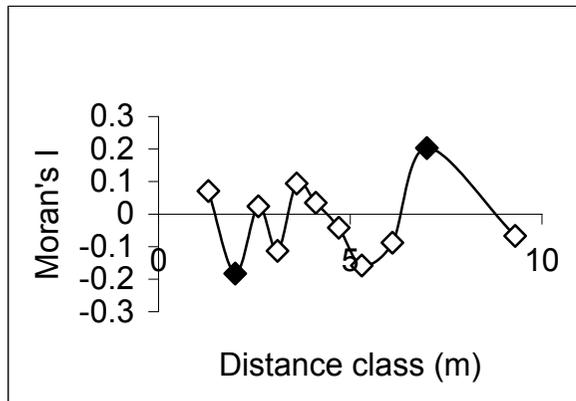
b. Stony Ridge Low



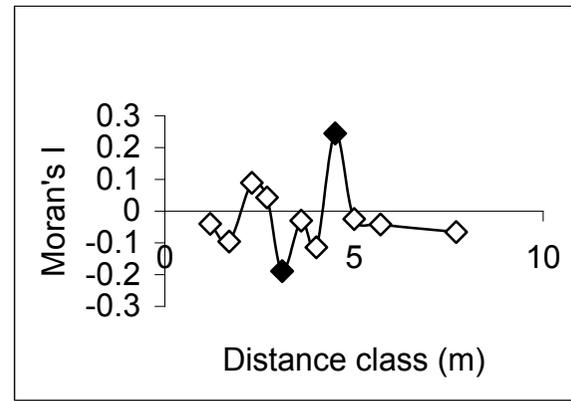
c. Mixed Pickle Middle



d. Swartkop Low

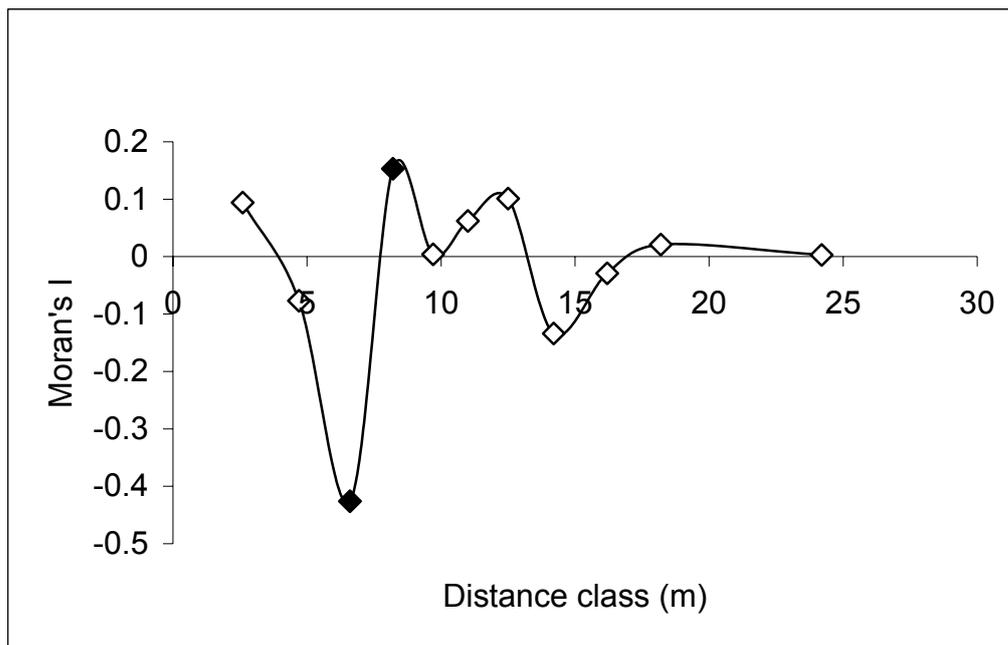


e. Swartkop Middle

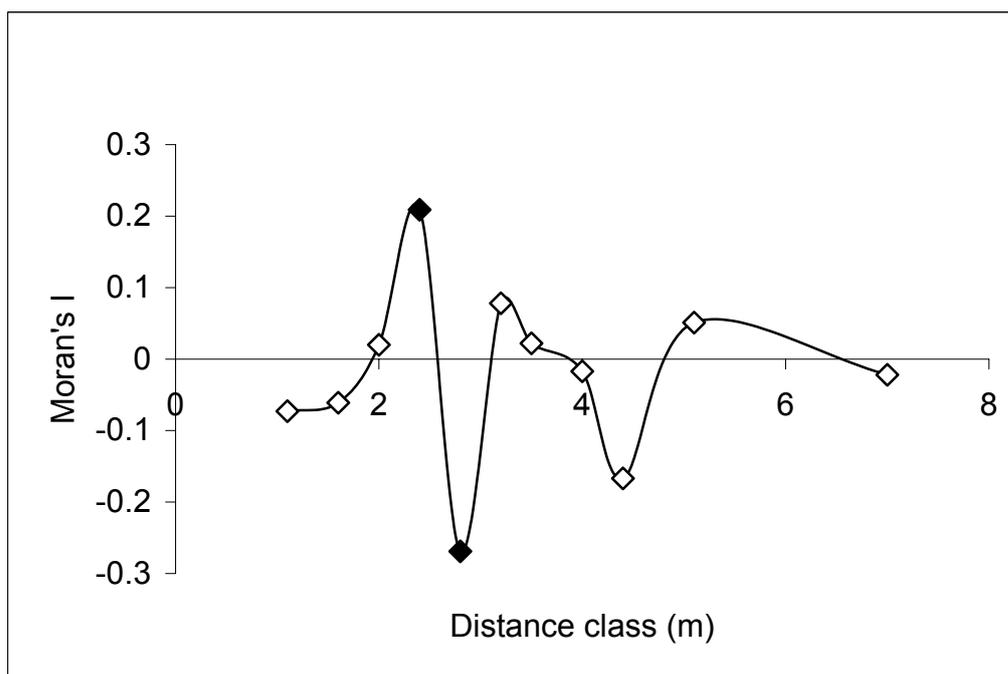


**Fig. 2.6** Correlograms of the spatial structure of *Azorella selago*'s *Agrostis* density at sites with overall significance ( $p < 0.05$ ) after Bonferroni correction (a. TBM; b. SRL; c. MPM; d. SKL; and e. SKM). Distance classes with equal number of point pairs (111 pairs) were used. Filled symbols correspond to Moran's I significant at  $P < 0.05$ . Empty symbols represent non-significant Moran's I values

## a. Stony Ridge High

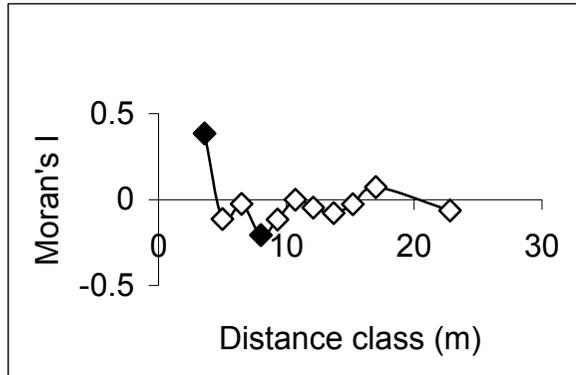


## b. Mixed Pickle Low

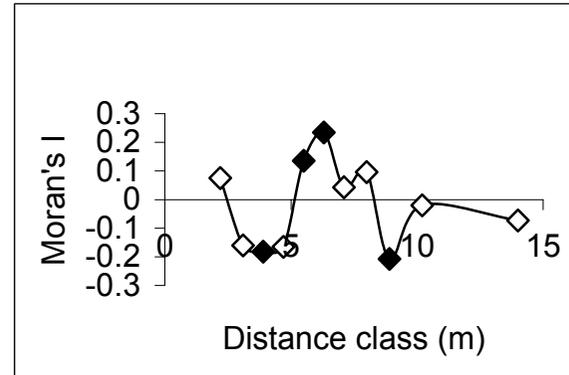


**Fig. 2.7** Correlograms of *Azorella selago*'s flower density. Distance classes with equal number of point pairs (107 pairs) were used in the analysis and both correlograms were significant at  $P < 0.05$  after Bonferroni corrections (**a.** SRH and **b.** MPL site). Filled symbols represent significant Moran's I values ( $P < 0.05$ ) and empty symbols represent non-significant Moran's I values

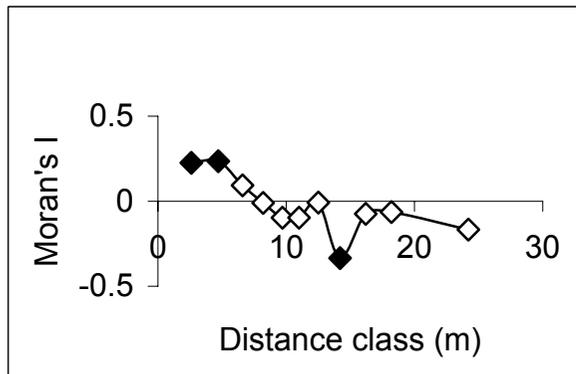
a. Tafelberg Middle



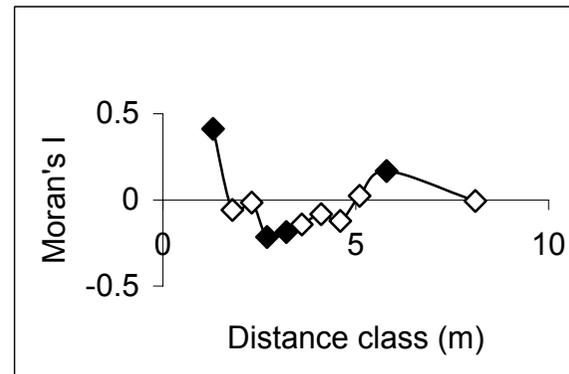
b. Stony Ridge Low



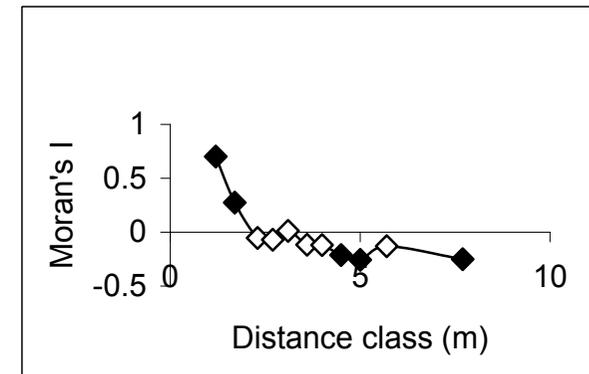
c. Stony Ridge High



d. Mixed Pickle Middle



e. Swartkop Middle



**Fig. 2.8** Spatial correlograms of *Azorella selago*'s fruit density based on distance classes with equal number of point pairs (111 pairs; 107 in **c.**). All correlograms showed an overall significance at  $P < 0.05$  after Bonferroni correction (**a.** TBM; **b.** SRL; **c.** SRH; **d.** MPM; and **e.** SKM site). Filled symbols represent significant Moran's I values at  $P < 0.05$ . Empty symbols represent non-significant Moran's I values

**Appendix 2A** Spatially autocorrelated variables of *Azorella selago* at all 12 sites across the island

Site	Prevalence of significantly autocorrelated variables	Positively autocorrelated variables
<b>Tafelberg</b>		
Low	1/8	Surface area
Middle	4/8	Diameter; Surface area; <i>Agrostis</i> and Fruit density
High	1/7	Dead surface
<b>Stony Ridge</b>		
Low	3/7	Dead surface; <i>Agrostis</i> and Fruit density
Middle	2/7	Diameter; Dead surface
High	3/8	Surface area; Flower and Fruit density
<b>Mixed Pickle</b>		
Low	1/9	Flower density
Middle	4/8	Diameter; <i>Agrostis</i> ; Flower buds and Fruit density
High	0	None
<b>Swartkop</b>		
Low	3/6	Diameter; Surface area; <i>Agrostis</i> density
Middle	5/7	Diameter; Height; Surface area; <i>Agrostis</i> and Fruit density
High	0	None

**Appendix 2B** Summary of autocorrelated variables of *Azorella selago* at different altitudes and on the eastern and western sides of the island

Sites	Autocorrelated variables (and prevalence of significance)
Low	Diameter (1/4); Surface area (2/4); Dead surface (1/4); <i>Agrostis</i> (2/4); Flowers (1/4); Fruits (1/4).
Middle	Diameter (4/4); Height (1/4); Surface area (2/4); Dead surface (1/4); <i>Agrostis</i> (3/4); Buds (1/4); Fruits (3/4).
High	Surface area (1/4); Dead surface (1/4); Flowers (1/4); Fruits (1/4).
East	Diameter (2/6); Surface area (3/6); Dead surface (3/6); <i>Agrostis</i> (2/4); Flowers (1/1); Fruits (3/6).
West	Diameter (3/6); Height (1/6); Surface area (2/6); <i>Agrostis</i> (3/4); Buds (1/4); Flowers (1/3); Fruits (2/6).

### **Chapter 3: Spatial variability in *Azorella selago* Hook. (Apiaceae) across sub-Antarctic Marion Island**

#### **Introduction**

Since the 1970's, there has been an increase in the recognition of the spatial context within which ecological processes take place (Levin 1992; Murdoch and Aronson 1999; Ettema and Wardle 2002). For example, at large scales global climate patterns are important drivers of macroecological patterns, and at finer scales, site-specific factors and biotic interactions become more important (Fuhlendorf and Smeins 1996). Multiscale approaches are therefore important in studies examining ecological variability (Levin 1992; Liebhold and Kamata 2000; Vieira and Gonzalez 2003), since there is no single correct scale to view entire population, community or ecosystem variability patterns (Avois-Jacquet and Legendre, submitted). Quantitative and interpretational errors may also occur if scale differences in patterns and processes are not taken into consideration (Legendre 1993; Fortin 1999). Therefore, understanding patterns of spatial variability provides important information on the underlying mechanisms driving such variability (Schenk et al. 2003; Fashing and Gathua 2004).

The South Indian Ocean islands are particularly suitable for examining spatial variability patterns in terrestrial systems, especially under the rapid climate-induced changes that these comparatively simple ecosystems are experiencing (Smith and Steenkamp 1990; Bergstrom and Chown 1999). Not only do these islands occur in a region of noticeable changes in climate (Marshall and Chown 2002), they also represent some of the only terrestrial habitats in the sub-Antarctic region (Gremmen et al. 1998; Bergstrom and Chown 1999). The thermally stable climate experienced by the sub-Antarctic islands is oceanic in nature and is characterized by cold, cloudy, wet and windy conditions (Gremmen 1997; Tweedie and Bergstrom 2000). At a regional scale, the structure and function of the terrestrial biotic systems is relatively similar across sub-Antarctic islands, and this is due to the relatively similar conditions produced by their cold oceanic climates, geographic isolation and means of nutrient inputs (Smith and French 1988). However, at

the island-scale the climate is modified by topographical changes over short distances (Gottfried et al. 1999), and the terrestrial biota is therefore expected to vary with changes in topography, geomorphology and nutrient availability (Blake 1996; Smith and Steenkamp 2001). The fact that these islands are generally small, species poor, with minimal levels of disturbance by humans provides further motivation for their suitability for monitoring species changes over space and time, within a relatively natural system (Wookey et al. 1993; Bergstrom and Chown 1999).

Sub-Antarctic Marion Island (46°54'S, 37°45'E) provides a typical example of a South Indian Ocean island (Boelhouwers 2003). The vegetation of Marion Island is relatively species poor (Smith and Steenkamp 1990; Gremmen 1997). The island supports a wide range of habitats ranging from high altitude polar deserts to low altitude coastal grasslands (Gremmen et al. 1998; Gabriel et al. 2001). In addition, vascular plants occur over a wide range of the available habitats on the island (Smith and Steenkamp 1990). However, vegetation in general is mostly concentrated in the relatively wetter lowlands, below 300 m a.s.l. (Huntley 1970; Scott 1985). Temperature, moisture and nutrient availability are considered the most important factors that limit the altitudinal distribution of vascular plants on the island (Smith 1978).

*Azorella selago* Hook. (Apiaceae) is the most abundant and widely distributed vascular plant on Marion Island (Huntley 1972). It occurs from sea level to the extreme limit of vascular plant growth at 765 m a.s.l (Huntley 1972). *Azorella selago* plants grow in the form of hard and compact cushions of approximately 15-30 cm in height and 20-40 cm in diameter (Huntley 1972). *Azorella selago* is particularly dominant in fellfield habitats (a windswept terrestrial habitat, which forms on exposed rocky areas of mainly grey, or black lava) where it appears scattered, separated by a typical wind-desert pavement of volcanic rocks (Huntley 1972). Populations of bryophytes and a variety of small invertebrates live within the ground cover of volcanic rocks protected from wind, low temperatures and desiccation (Van Zinderen Bakker 1978). These populations together with other vascular plants (e.g. *Agrostis magellanica* (Lam.) Vahl. (Poaceae) avoid the harshest conditions of fellfields by occurring epiphytically on *A. selago* (Smith 1978). Changes in temperature, wind and/or precipitation will strongly influence fellfield plant communities

since these are some of the important abiotic drivers of vegetation community structure in fellfield habitats (Smith and Steenkamp 1990). Fellfield communities are hence considered to be amongst the most vulnerable of Marion Island's habitats to climate change (Barendse and Chown 2001). The occurrence of these fellfield communities over a broad altitudinal range together with changes in mean temperatures with altitude provides a unique opportunity to study variability in this species in relation to environmental variables, including climate change.

The main aim of this study was thus to quantify spatial variability in the morphology, phenology, reproductive effort and epiphyte load of *Azorella selago* plants across Marion Island, and to determine the range and direction of this variability. Combined with knowledge of microclimatic variation across the island, predictions are then made about the likely effects of climate change on *A. selago*.

## **Materials and Methods**

*Azorella selago* plants were surveyed between April 2002 and April 2003. Four altitudinal transects were established across the island. One transect was spanning Junior's Kop and First Red Hill on the eastern side of the island (hereafter referred to as Tafelberg Transect) (Fig. 1.1). Another transect sloped from Stony Ridge to Halfway Kop also on the eastern side of the island (hereafter referred to as Stony Ridge Transect) (Fig. 1.1). On the western side of the island, one transect was positioned inland of the Mixed Pickle Cove, from Neville towards Saalrug (hereafter referred to as Mixed Pickle Transect) (Fig. 1.1). Another transect was placed upslope from Swartkop Point, along Stevie and Bakkerkop (hereafter referred to as Swartkop Transect) (Fig. 1.1). Each transect was divided into three altitudinal bands (~150 - 250, 350 - 450, > 550 m a.s.l.) with one site in each band. Each set of three sites (low, middle and high altitude sites) is referred to as a 'transect' for convenience. In each site 50 *A. selago* cushion-plants that were greater than 15 cm in diameter were used for taking various kinds of measurements. Only non-destructive measurements were taken from cushions that were less than 15 cm in diameter, and this was done to avoid damaging young plants, since

recruitment in this species appears to be very low or at least very patchy (Le Roux and McGeoch 2004). The sites were clearly marked with corner markers and cushion tags for long-term monitoring purposes. The exact and relative position of each plant within a site, its nearest neighbours, and the corners of each sampling site were determined using a Nikon Total Station DTM350 Theodolite, with an accuracy of 10 mm (Anonymous 2001). Since there are no fixed reference points on the island, a Garmin 12MAP GPS (global positioning systems) was used to obtain the approximate geographic co-ordinates of each site. Within these sites, a variety of quantitative measurements of *A. selago* were taken.

During summer (January 2003), 10 cushion-plants were randomly selected in each site. From these plants, five stems were collected from the centre of each plant, dried at  $\pm 60$  °C for 48 hours. Approximately 250 g of soil were collected from each site (five samples from across the site, combined and mixed) and also dried at  $\pm 60$  °C for 48 hours. The dried leaves and soil were all packed in watertight containers and returned to South Africa for nutrient content analysis, conducted by Bemlab (Pty) Ltd (AECI Building W2, De Beers Road, Somerset West, 7613).

Leaf samples were ashed and taken up in HCl acid. They were then analysed on an ICP (Inductively Coupled Plasma) emission spectrometer against certified standards. The soil pH was determined by adding 25 ml of 1M KCl to 10 g of soil, and this was read after an hour. Electrical resistance was analysed by preparing a soil paste with deionized water, then resistance was measured in a standard USDA soil cup. Extractable cations were analysed by adding 5 g of soil to a 50 ml ammonium acetate solution, the mixture was shaken for 30 minutes and filtered. The filtrate was then analysed for Na, K, Ca, and Mg with the ICP. Extractable phosphorus was analysed with the use of  $\text{NH}_4\text{F}$ -solution (186 g  $\text{NH}_4\text{F}$  in 5 litre deionized water) and a Bray 2 extracting solution (600 ml  $\text{NH}_4\text{F}$  solution in a 20 litre aspirator, 10 litres deionized water and 200 ml conc. HCl (AR) added, diluted to 20 litres and well-mixed). Soil (6.6 g) was placed in an extraction bottle and 50 ml of Bray 2 solution was added. The mixture was shaken for 40 seconds by hand before it was filtered. The filtrate was then analysed for P with the ICP. The

organic carbon was measured by the Walkley-Black method (standard BemLab Pty (Ltd) procedures).

#### *Growth Rate, Size and Density*

Plant growth rate was measured by inserting wooden sticks ( $\pm 10$  mm in diameter, 40 - 60 mm long) vertically into each cushion (> 15 cm in diameter to minimise the damage) of every site until these growth rate markers were embedded in the ground underneath the cushion (to minimize the effect of frost heave). The sticks were then marked with a line flush with the surface of the cushion after insertion. After a year the growth rate markers were re-marked with a line flush with the new surface and the distance between the two lines was measured and converted to growth rate (see also le Roux and McGeoch 2004). Three measures of plant size were taken; plant height was determined by measuring the vertical distance between the highest point of the cushion surface and the ground beneath it. Plant circumference was measured using a flexible tape and the surface area of the plant was measured using a 1 m<sup>2</sup> flexible sampling grid, with each cell totalling 4 cm<sup>2</sup> in area. A scaled photograph of each plant was also taken to estimate cushion size using image analyser software (SigmaScan Pro 5.0, Illinois, USA). The theodolite was used to measure the area of each sampling site and all *A. selago* plants in a site were counted to estimate plant density. These methods and measurements were similar to those used by Huntley (1971) and also by le Roux and McGeoch (2004).

#### *Leaf Morphology*

From the 10 randomly selected cushion-plants (same plants used for nutrient samples) in each site, 20 green leaves were collected randomly across each cushion. Ten leaves were weighed and their trichomes were counted under the dissecting microscope. The leaves were then pressed onto a hardcover sheet and used for size determination (i.e. Whole Leaf Area and Green Leaf Area) with the image analyser software. The Green Leaf Area was used to calculate trichome density. From the remaining leaves, five leaves from three

cushion-plants in each site were coated with nail varnish on both sides and the coating was peeled off when dry. Stomatal imprints on the peels were counted under a compound microscope at 400X magnification and converted to number of stomata per 0.175 mm<sup>2</sup>.

#### *Plant Vitality and Epiphyte Load*

Plant vitality was determined in two ways: First by measuring the epiphyte load of all cushion-plants in all sites, and secondly by measuring the percentage of the cushion surface that was dead. Epiphyte load was used as a measure of vitality because the growth of epiphytes may have negative impact on the plant occupied and other cushion-plant species have been reported to collapse due to colonization by epiphytes (Pyšek and Liška 1991). Epiphyte load was determined by counting the number of *Agrostis magellanica* (the dominant epiphyte) rooted in each plant and the presence or absence of other plant species growing on *A. selago*. The percentage of cushion surface that was dead was measured by counting the number of grid cells containing predominantly dead plant stems (calculated as a proportion of total number of grid cells covering the plant, and converted to area).

#### *Plant Phenology and Reproduction*

Phenological measurements were taken twice for every cushion-plant in every site using the 1 m<sup>2</sup> flexible sampling grid. These recordings were temporally far apart between transects due to long walking distances between sites and bad weather conditions encountered during the periods of recording. However, phenological changes within transects (i.e. altitudinal comparisons) can be compared because the time between recordings for each transect was within 2 to 20 days (Table 3.1). All recordings were conducted over the summer season from October 2002 to March 2003 (Table 3.1). The measurements taken using the sampling grid were: percentage of the cushion surface that was green, yellow, and/or brown; presence, distribution and number of flower buds, flowers and fruit. The percentage measurements were conducted by estimating, in a single grid cell, the fraction of the grid cell

covered the green, brown or yellow surface. An average of ten grid cells randomly scattered across the surface of the cushion-plant was then used to estimate the percentage of the cushion surface that was covered by green, yellow or brown leaves. Plants were also photographed after each phenological measurement to compare the manually collected phenological data with data from image analysis.

As listed above, the sampling grid was also used to determine the number of flower buds, flowers, and fruits on each plant. This number was used with cushion size (surface area) to calculate flowering and fruit density of each plant. In addition, ten plants were selected randomly in each site. Ten fruits were collected from each of these plants and weighed individually.

### *Data Analysis*

General Linear Models (GLM) (Stat Soft) were used to determine the relationship between *A. selago* characteristics and the environmental predictors (altitude and side of the island). The models were constructed separately for each dependent variable (plant growth rate, plant height, plant circumference, plant surface area, *Agrostis* density, leaf area, trichome density, and stomatal density) to test for the effects of the environmental predictor (the factors side of the island and altitude were included in a multifactor model) and the interaction between predictors and plant characteristics. The results are presented in the text and the differences between levels of the factors and their interactions are presented as interaction plots.

Multivariate analysis (CANOCO v4.5; Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003) was used to determine variability patterns in soil and leaf nutrients between sampling sites across Marion Island. Principal Components Analysis (PCA) was chosen after examining the gradient lengths of nutrients (longest gradient was shorter than 3.0) in the environmental space following Detrended Correspondence Analysis (DCA) (Lepš and Šmilauer 2003), and performed on soil and leaf nutrient data that were centered and standardized by samples. PCA results are presented as ordination biplots (Lepš and Šmilauer 2003).

Redundancy Analysis (RDA) was conducted to examine differences in leaf nutrient composition between different altitudes, sides of the island, the four transect gradients, and the combination of these (CANOCO v4.5; Ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). RDA was chosen after examining the gradient lengths of nutrients (longest gradient was shorter than 3.0) in the environmental space following Detrended Correspondence Analysis (DCA) (Lepš and Šmilauer 2003). RDA was performed on leaf nutrient data that were centered and standardized by nutrients and the results are displayed in ordination biplots. Monte Carlo permutation tests (499 permutations) were used to test the significance of the relation with environmental variables (e.g. altitude, side of the island, transect gradient, and the combination of these) (Lepš and Šmilauer 2003). The eigenvalues for the first two axes were used to indicate how much of the total variance in the nutrient data was explained by the environmental variables (Lepš and Šmilauer 2003).

## Results

There were significant differences in plant growth rates between sampling sites across Marion Island (Full model  $R^2 = 0.04$ ;  $F_{(5, 296)} = 4.01$ ;  $p < 0.05$ . Altitude:  $p < 0.0001$ ; Side:  $p > 0.05$ ; Altitude X Side:  $p > 0.05$ ) (Fig. 3.1a). Plant growth rates were more strongly related to altitude, with small differences between sides of the island (Fig. 3.1a). Although significant differences between sites were not consistent with altitude, high altitude plants had the highest growth rates on both sides of the island (Fig. 3.1a). Significant differences in plant height between sites ( $R^2 = 0.43$ ;  $F_{(5, 590)} = 90.85$ ;  $p < 0.05$ . Altitude:  $p < 0.05$ ; Side:  $p < 0.05$ ; Altitude X Side:  $p < 0.05$ ) (Fig. 3.1b) were also not consistent with altitude. However, high altitude plants on the eastern side of the island displayed the greatest plant heights (Fig. 3.1b). Both plant circumference ( $R^2 = 0.17$ ;  $F_{(5, 590)} = 26.21$ ;  $p < 0.05$ . Altitude:  $p < 0.0001$ ; Side:  $p < 0.0001$ ; Altitude X Side:  $p < 0.0001$ ) (Fig. 3.1c) and surface area ( $R^2 = 0.11$ ;  $F_{(5, 590)} = 16.61$ ;  $p < 0.001$ . Altitude:  $p < 0.001$ ; Side:  $p < 0.0001$ ; Altitude X Side:  $p < 0.001$ ) (Fig. 3.1d) showed significant differences across the island, but these were also not consistent with altitude (Figs 3.1c, d). These variables

were greater on the eastern side of the island compared to the western side, particularly at mid and high altitudes (Figs 3.1c, d). Plant surface area thus showed a stronger response to side of the island than to altitude.

There were also significant differences in whole leaf area between sites ( $R^2 = 0.21$ ;  $F_{(5, 1178)} = 61.44$ ;  $p < 0.001$ . Altitude:  $p < 0.01$ ; Side:  $p < 0.001$ ; Altitude X Side:  $p > 0.05$ ) (Fig. 3.2a) with a tendency for whole leaf area to increase with altitude (Fig. 3.2a). Whole leaf area was generally larger on the eastern side of the island (Fig. 3.2a). Differences in whole leaf area were greater between sides of the island than altitude (Table 3.2). Trichome densities were also significantly different across the island ( $R^2 = 0.54$ ;  $F_{(5, 1178)} = 281.78$ ;  $p < 0.001$ . Altitude:  $p < 0.05$ ; Side:  $p < 0.0001$ ; Altitude X Side:  $p < 0.0001$ ) (Fig. 3.2b) with a clear tendency for trichome density to be greater on the western side of the island than on the eastern side (Fig. 3.2b). Significant differences in trichome densities were not consistent with altitudinal gradient, but differences were strongly related to side of the island (Fig. 3.2b). Stomatal density was high on the ventral leaf surface with very few scattered stomata on the dorsal surface (Table 3.2). Ventral leaf surface stomatal densities were significantly different between sites across the island ( $R^2 = 0.84$ ;  $F_{(5, 30)} = 38.44$ ;  $p < 0.001$ . Altitude:  $p < 0.01$ ; Side:  $p < 0.0001$ ; Altitude X Side:  $p < 0.05$ ) (Fig. 3.2c) and there were no significant differences in the dorsal leaf stomatal densities (Figs 3.2c, d). Ventral leaf stomatal densities were greater on the eastern side of the island than on the western side and these differences were also strongly related to side of the island than to altitude (Fig. 3.2c).

Significant differences in the dominant plant epiphyte (*A. magellanica*) densities ( $R^2 = 0.25$ ;  $F_{(3, 394)} = 47.11$ ;  $p < 0.05$ . Altitude:  $p < 0.0001$ ; Side:  $p < 0.001$ ; Altitude X Side:  $p < 0.01$ ) (Fig. 3.2) were more consistent with altitude (Fig. 3.2). Plants at low altitude sites had the highest *A. magellanica* densities followed by plants at middle altitude sites (Fig. 3.3). At high altitudes *A. magellanica* densities were zero (Table 3.2). The density of *A. magellanica* was also significantly greater on the eastern side of the island (Fig. 3.3).

During the period of phenological recordings (October 2002 to March 2003) temperatures on the island (Stevenson Screen) increased from October to reach peak summer temperatures in February, thereafter temperatures

declined through March and April (Fig. 3.4). From spring to summer (October/November - January/February), the fraction of green surfaces on plants increased by approximately 10 - 17 % for Tafelberg and 3 - 12 % for Mixed Pickle (Tables 3.3, 3.4; Figs 3.5a, c). During the same period, the brown fraction of plant surfaces decreased by approximately 14 - 19 % in Tafelberg and 7 - 15 % in Mixed Pickle (Tables 3.3, 3.4; Figs 3.5a, c; Appendix 3D). There was a slight increase of approximately 5 % in the yellow fraction of plant surfaces (Tables 3.3, 3.4; Figs 3.5a, c; Appendix 3F). From summer to autumn (December - February/March), there was a decrease in the fraction of green surface, which varied from 9 - 15 % in Stony Ridge and 1 - 5 % in Swartkop (Tables 3.3, 3.4; Figs 5b, d; Appendix 3D). The brown fraction of plant surfaces increased by approximately 5 % in Stony Ridge and 2 % in Swartkop (Tables 3.3, 3.4; Figs 5b, d; Appendix E). The yellow fraction of plant surfaces also increased by approximately 4 - 9 % in Stony Ridge and by approximately 5 % in Swartkop (Tables 3.3, 3.4; Figs 3.5b, d; Appendix 3F).

There was a decrease in flower bud density from spring to summer (Tafelberg and Mixed Pickle) and in autumn (Figs 3.6a - d; Appendix 3G). In spring (October, November and December), flower bud densities increased with altitudinal gradient and none were recorded in summer and autumn (January, February and March) (Table 3.5; Figs 3.6a - d; Appendix 3G). In October and November (Tafelberg and Mixed Pickle) flower buds were present across altitudes and in December (Stony Ridge and Swartkop) flower buds were only recorded at high altitude sites (Table 3.5; Appendix 3G). No flowers were recorded in October (e.g. Tafelberg) and only low densities of flowers were recorded in the low and middle altitude sites in November (e.g. Mixed Pickle) (Table 3.5; Appendix 3H). In December (e.g. Stony Ridge and Swartkop) there were still flowers recorded across altitudes at increasing densities with altitudinal gradients (Table 3.5; Appendix 3H). Fruit densities increased with altitudinal gradient from spring to summer (Figs 3.6a, c; Appendix 3I) followed by a decrease from summer to autumn (Figs 3.6b, d; Appendix 3I). In October (Tafelberg) there were no fruits recorded and in November (Mixed Pickle) only low densities of fruits were recorded in the low altitude sites (Table 3.5; Appendix 3I). In December (Stony Ridge and

Swartkop) fruits were present in high densities (Table 3.5; Appendix 3I). In February and March fruits were still present in all transects at lower densities and increasing with altitudinal gradients (Table 3.5; Appendix 3I).

The soil characteristics of sites on the eastern side of the island were quite variable compared to those on the western side of the island, which were quite similar with the exception of the Mixed Pickle high site (Fig. 3.7a). The first axis of the soil PCA ordination diagram explained 51.7 % of the variance and the second axis explained 22.0 %. Both these axes show a clear separation between plots on the eastern side of the island and plots on the western side (Fig. 3.7a). Leaf nutrient samples also showed separation along the first axis with low sites on the positive side and middle sites on the negative side of the first axis (Fig. 3.7b). The first axis of the leaf samples PCA ordination diagram explained 29.0 % of the variance and the second axis explained 23.2 % (Fig. 3.7b).

Redundancy Analysis (RDA) showed significant differences in the composition of leaf nutrients between altitudes (F-ratio = 3.86; p-value = 0.002). However, both axes of the RDA ordination diagram explained very low variation between altitudes. The first axis explained 4.6 % of the variance separating the middle from high altitude sites, and the second axis explained 2.1 % of the variance separating the low from middle and high altitude sites (Fig. 3.8a). Nutrients such as Ca and B were positively correlated with low altitudes, Mn and P with middle altitudes, and Zn, Cu, N and Fe with high altitudes (Fig. 3.8a). The composition of leaf nutrients was also significantly different between the east and the western sides of Marion Island (F-ratio = 3.12; p-value = 0.004). However, again both axes of the RDA ordination diagram explained very low variation between the eastern and western sides of the island. The first axis explained only 2.8 % of the variance separating the eastern and western sides of the island while the second axis explained only 2.03 % of the variance separating Mn from all the other nutrients (Fig. 3.8b). Mn was the only nutrient that was associated with island side and Mn concentrations were higher on the western side of the island (Fig. 3.8b).

There were also significant differences in the composition of leaf nutrients between the four altitudinal transects across the island (F-ratio = 5.14; p-value = 0.002). Both axes of the RDA ordination diagram explained

low variation between transects. The first axis explained 7.3 % of the variance separating Swartkop and Tafelberg from Mixed Pickle and Stony Ridge transects. The second axis explained only 3.2 % of the variance separating the Swartkop transect from Tafelberg, Mixed Pickle and Stony Ridge. The Mixed Pickle and Stony Ridge transects were more similar in their leaf nutrients composition (Fig. 3.8c). Mn showed a strong correlation with the Swartkop transect on the western side of the island. Zn, N, and Mg were respectively correlated with Tafelberg, Mixed Pickle, and Stony Ridge (Fig. 3.8c). Differences in the compositions of leaf nutrients across all site combinations (i.e. altitude; side of the island; and transect) were also significant (F-ratio = 4.93; p-value = 0.002). Again both axes of the RDA ordination diagram explained low variance between site combinations. The first axis of the ordination diagram explained 7.7 % of the variance separating middle sites from the low and high sites; the western sites from the eastern sites; and Tafelberg sites from Mixed Pickle and Stony Ridge sites (Fig. 3.8d). The second axis explained 5.9 % of the variance separating high sites from middle and low sites; eastern sites from western sites; and the Swartkop sites from Mixed Pickle and Stony Ridge sites. It was only Mn and N that showed strong correlations with Swartkop and Stony Ridge transects and no other nutrients showed strong correlations with any of the environmental predictors.

## Discussion

The most conspicuous spatial variation in *Azorella selago* across Marion Island was the differences in plant size between the eastern and western sides of the island. Although no differences in growth rate were found between the two sides, plants on the eastern side were generally larger than plants on the western side of the island. The older grey lava on the eastern side predominantly covers the island and the relatively younger black lava dominates the western side (McDougall et al. 2001). The observed differences in soil nutrients between the eastern and western sides of Marion Island may be a function of different substrates between the two sides. It is thought that these differences in substrate types and age maybe some of the reasons for the differences in plant size between the eastern and western sides of Marion

Island. le Roux and McGeoch (2004) also found a positive correlation between *A. selago* plant size and age of landscapes on Marion Island.

Pattern of variation in *A. selago* leaf size across Marion Island resembled that of plant size, suggesting that the same factors that determine plant size may also play a role in determining leaf size. *Azorella selago* leaves on the eastern side of the island were bigger than those on the western side. Like plant size, leaf size showed stronger response to side of the island than altitude. Differences in leaf nutrients between the low and middle altitude sites may be due to the close proximity of the low altitude sites to the surrounding ocean and animal activity (Smith and French 1988), however leaf nutrients were generally poorly explained by location on the island. Trichome and stomatal densities also showed stronger responses to side of the island than altitude. The observed patterns in *A. selago* size and leaf morphology rules out the possibility that temperature maybe accountable, since temperature showed a stronger response to altitude than side of the island (Nyakatia chapter 1). The supposed differences in moisture, light and wind intensities between the eastern and western sides of the island maybe responsible for the observed patterns in *A. selago*'s leaf morphology. Variations in leaf morphology across Marion Island may result from trade-offs in leaf adaptations for optimising resource acquisition and/or protection against environmental constraints (Gutschick 1999; Press 1999).

Most plants respond to wind stress (e.g. mechanical damage) by reducing their stem lengths and leaf sizes (Clemente and Marler 2001). The smaller leaf surfaces on the western side of the island might therefore be a response of *A. selago* plants to mechanical wind stress induced by the stronger and more dominant winds on the western side of Marion Island (Schulze 1971; Van Zinderen Bakker 1978). Higher trichome densities on *A. selago* plants on the western side may increase the boundary layer thickness of *A. selago* leaves and hence reducing the impact of the wind (Press 1999). Trichomes may also enhance light capturing for photosynthesis under the more cloudy (or limited light) conditions on the western side by increasing the reflection of radiation onto mesophyll cells (Gutschick 1999; Press 1999). Differences in moisture and light availability in the environment can select for differences in plant stomatal densities (Goodfellow 2001; Hetherington and

Woodward 2003). The stronger and dominant winds on the western side may increase transpiration and hence induce drought stress on plants at the microclimate level. The lower stomatal densities on the western side can therefore be explained by the negative correlation between stomatal density and drought stress (Brownlee 2001; Hetherington and Woodward 2003). Plants growing under high levels of light have increased stomatal densities (Brownlee 2001); this can also be used to explain the higher stomatal densities on *A. selago* plants on the less cloudy (more light) eastern side of Marion Island. The functional significance of patterns in trichome and stomatal densities on the island however require further experimental investigation.

Variation in the density of the dominant *A. selago* epiphyte on Marion Island (*Agrostis magellanica*) matched that of *A. selago* microclimate temperature, suggesting that the distribution of the epiphyte (*A. magellanica*) on the island may be limited by temperature. It can therefore be predicted that continued warming on the island might result in the expansion of the distribution range of *A. magellanica* (currently restricted up to 450 m a.s.l.) to higher altitudes. It is also apparent that the length, start and end of the observed phenological conditions of *A. selago* were also (like temperature) more responsive to altitudinal gradients. Although the phenological data collection was inappropriate to assess differences between sides of the island, however a limited response to side of the island was evident. Phenological stages were early and more rapid at the warmer low altitudes and eastern side of the island, however at high altitudes and on the west, phenological stages had longer durations. Warming can therefore be predicted to result in a shift (e.g. early and longer) in the start and duration of spring related phenological events across the island.

*Azorella selago* of Marion Island is likely to be morphologically fairly resilient to moderate climate warming, however the species maybe outcompeted by the epiphytic grass, *Agrostis magellanica*. Such effects of warming are expected to be relatively greater at low altitudes and on the eastern side of the island, since the warmest microclimates were recorded at these sites (Chapter 1). It is also predicted that *A. selago* may expand its distribution range to higher altitudes in response to warming, although other limiting factors may still be active.

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**Table 3.1** Periods of phenological recordings for the 12 sampling sites across Marion Island

Site	First recording	Second recording
<b><i>Tafelberg</i></b>		
Low	24 October 2002	20 January 2003
Middle	28 October 2002	24 January 2003
High	12 November 2002	01 February 2003
<b><i>Stony Ridge</i></b>		
Low	20 December 2002	23 March 2003
Middle	15 December 2002	19 March 2003
High	10 December 2002	17 March 2003
<b>Mixed Pickle</b>		
Low	30 November 2002	09 February 2003
Middle	28 November 2002	10 February 2003
High	24 November 2002	10 February 2003
<b>Swartkop</b>		
Low	23 December 2002	13 February 2003
Middle	24 December 2002	12 February 2003
High	25 December 2002	11 February 2003

**Table 3.2** Means ( $\pm$  s.d.) of *Azorella selago* size, epiphyte density, and leaf morphological measurements recorded at 12 sampling sites across Marion Island

Site	Growth rate (mm/yr) (n = 50)	Height (m) (n = 50)	Circumference (m) (n = 50)	Surface Area (m <sup>2</sup> ) (n = 50)	<i>Agrostis</i> Density (m <sup>-2</sup> ) (n = 50)	Whole Leaf Area (mm <sup>2</sup> ) (n = 50)	Trichome Density (mm <sup>-2</sup> ) (n = 10)	Ventral Stomatal Density (0.175 mm <sup>-2</sup> ) (n = 3)	Dorsal Stomatal Density (0.175 mm <sup>-2</sup> ) (n = 3)
<b>Tafelberg</b>					1008.91	$\pm$ 186.45			
Low	1.28 $\pm$ 1.52	0.13 $\pm$ 0.03	1.79 $\pm$ 0.84	0.19 $\pm$ 0.14	417.18	$\pm$ 31.29	0.73 $\pm$ 0.42	51.62 $\pm$ 3.94	1.60 $\pm$ 0.11
Middle	1.91 $\pm$ 2.27	0.18 $\pm$ 0.05	3.73 $\pm$ 2.05	0.51 $\pm$ 0.44	316.95	$\pm$ 221.39	0.87 $\pm$ 0.61	60.13 $\pm$ 2.15	2.51 $\pm$ .59
High	3.48 $\pm$ 2.59	0.37 $\pm$ 0.17	3.23 $\pm$ 1.81	0.52 $\pm$ 0.53	406.63	$\pm$ 38.94	1.07 $\pm$ 0.95	53.78 $\pm$ 0.54	1.70 $\pm$ 0.26
<b>Stony Ridge</b>					0	$\pm$ 33.35			
Low	0.26 $\pm$ 0.20	0.19 $\pm$ 0.04	2.16 $\pm$ 0.68	0.34 $\pm$ 0.18	805.59	$\pm$ 190.44	0.71 $\pm$ 0.55	55.57 $\pm$ 4.42	1.96 $\pm$ 0.65
Middle	0.11 $\pm$ 0.15	0.14 $\pm$ 0.03	2.73 $\pm$ 1.22	0.40 $\pm$ 0.29	316.59	$\pm$ 30.02	0.75 $\pm$ 0.39	55.87 $\pm$ 2.77	1.90 $\pm$ 0.21
High	0.35 $\pm$ 0.27	0.32 $\pm$ 0.15	3.17 $\pm$ 1.50	0.46 $\pm$ 0.31	517.80	$\pm$ 211.89	1.37 $\pm$ 0.95	43.11 $\pm$ 2.22	2.10 $\pm$ 0.56
<b>Mixed Pickle</b>					1454.73	$\pm$ 28.49			
Low	1.78 $\pm$ 1.85	0.17 $\pm$ 0.03	2.04 $\pm$ 0.94	0.18 $\pm$ 0.11	0.06 $\pm$ 0.40	$\pm$ 39.67	3.18 $\pm$ 1.35	40.88 $\pm$ 2.26	1.83 $\pm$ 0.28
Middle	2.28 $\pm$ 2.01	0.14 $\pm$ 0.04	2.28 $\pm$ 0.86	0.25 $\pm$ 0.14	3094.91	$\pm$ 157.59	3.65 $\pm$ 1.30	35.36 $\pm$ 1.53	2.07 $\pm$ 0.42
High	3.83 $\pm$ 3.93	0.14 $\pm$ 0.04	2.14 $\pm$ 0.67	0.25 $\pm$ 0.16	4277.45	$\pm$ 32.17	2.64 $\pm$ 1.05	37.20 $\pm$ 0.54	2.09 $\pm$ 0.17
<b>Swartkop</b>					166.04	$\pm$ 178.24			
Low	0.30 $\pm$ 0.22	0.19 $\pm$ 0.05	1.77 $\pm$ 0.81	0.28 $\pm$ 0.45	283.39	$\pm$ 28.99	3.89 $\pm$ 1.48	39.75 $\pm$ 2.48	1.89 $\pm$ 0.48
Middle	0.16 $\pm$ 0.18	0.19 $\pm$ 0.05	2.13 $\pm$ 1.44	0.26 $\pm$ 0.16	186.60	$\pm$ 30.11	2.59 $\pm$ 0.69	38.58 $\pm$ 0.98	1.47 $\pm$ 0.57
High	0.30 $\pm$ 0.52	0.15 $\pm$ 0.07	1.78 $\pm$ 0.62	0.17 $\pm$ 0.12	0	$\pm$ 180.58	3.02 $\pm$ 1.52	34.18 $\pm$ 2.42	2.27 $\pm$ 0.73

**Table 3.3** Mean change in phenological traits ( $\pm$  s.d.) recorded in 12 sampling sites across Marion Island between October 2002 and January 2003 for the Tafelberg sites; December 2002 and March 2003 for the Stony Ridge sites; December 2002 and February 2003 for the Swartkop sites; and November 2002 and February 2003 for the Mixed pickle sites. A plus (+) sign represents an increase and a minus (-) sign represents a decrease in the phenological trait

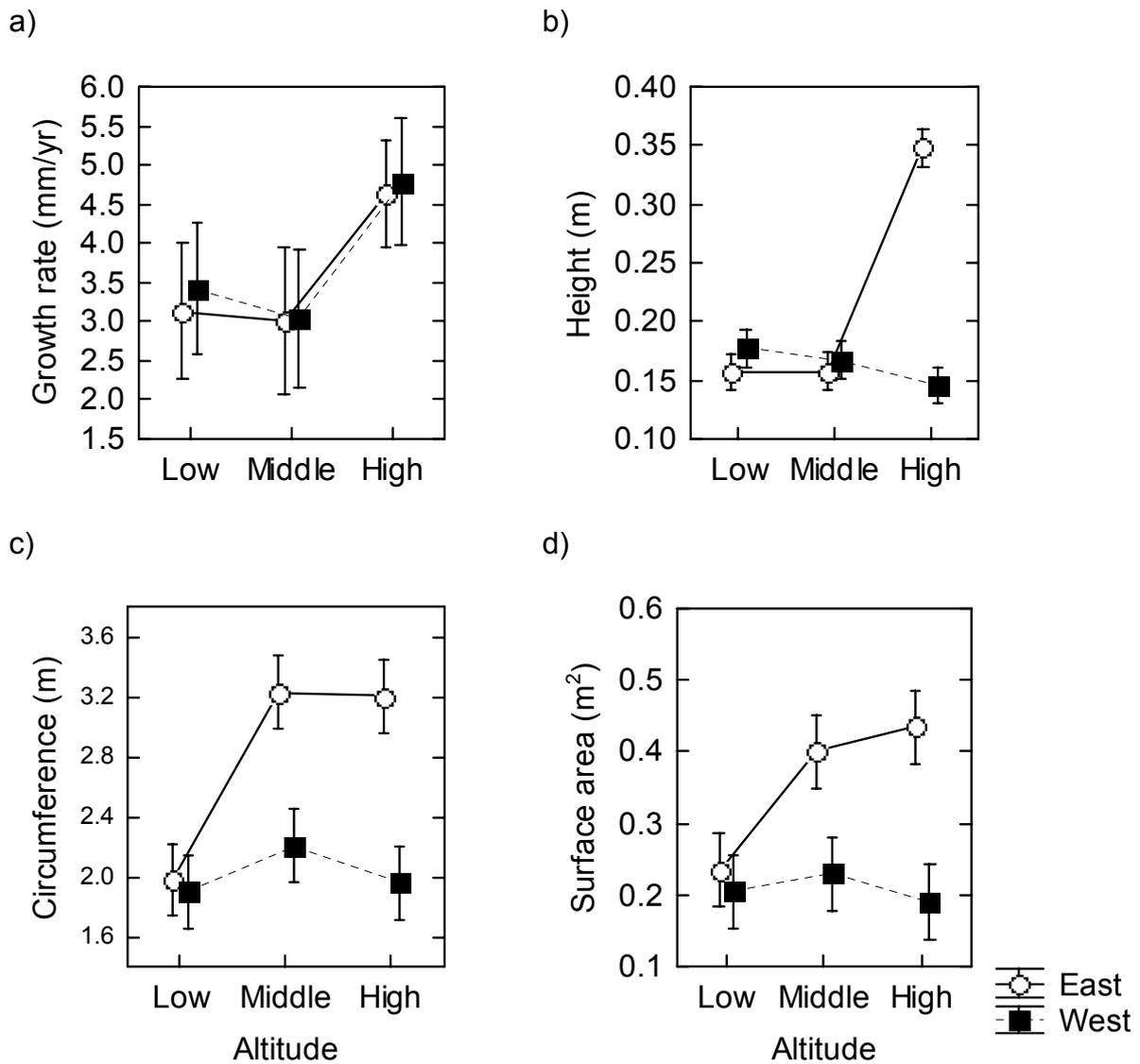
Site	% Green surface	% Brown surface	% Yellow surface	Flower bud density (m <sup>-2</sup> )	Flower density (m <sup>-2</sup> )	Fruit density (m <sup>-2</sup> )
<b>Tafelberg</b>						
Low	15.3 $\pm$ 7.7 <sup>ab</sup>	-19.6 $\pm$ 7.8 <sup>ab</sup>	4.3 $\pm$ 1.4 <sup>a</sup>	-19.4 $\pm$ 63.1 <sup>ab</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	152.5 $\pm$ 326.7 <sup>abc</sup>
Middle	17.0 $\pm$ 7.6 <sup>a</sup>	-21.0 $\pm$ 7.5 <sup>a</sup>	4.0 $\pm$ 1.4 <sup>a</sup>	-747.6 $\pm$ 3670.8 <sup>ab</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	734.2 $\pm$ 844.8 <sup>ab</sup>
High	10.7 $\pm$ 8.0 <sup>bc</sup>	-14.5 $\pm$ 7.5 <sup>c</sup>	3.7 $\pm$ 1.6 <sup>a</sup>	-2883.0 $\pm$ 13923.4 <sup>a</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	917.3 $\pm$ 1173.8 <sup>a</sup>
<b>Stony Ridge</b>						
Low	-10.8 $\pm$ 6.2 <sup>ij</sup>	4.9 $\pm$ 5.6 <sup>g</sup>	6.0 $\pm$ 2.0 <sup>b</sup>	0.0 $\pm$ 0.3 <sup>b</sup>	-22.6 $\pm$ 80.9 <sup>a</sup>	-1125.7 $\pm$ 1081.5 <sup>d</sup>
Middle	-15.3 $\pm$ 7.8 <sup>j</sup>	5.6 $\pm$ 7.4 <sup>g</sup>	9.7 $\pm$ 2.4 <sup>c</sup>	0.0 $\pm$ 0.0 <sup>b</sup>	-0.1 $\pm$ 0.3 <sup>a</sup>	-1051.2 $\pm$ 1299.5 <sup>d</sup>
High	-9.1 $\pm$ 7.8 <sup>hi</sup>	4.8 $\pm$ 7.6 <sup>g</sup>	4.3 $\pm$ 2.3 <sup>a</sup>	-483.5 $\pm$ 1231.9 <sup>ab</sup>	-1906.9 $\pm$ 3015.8 <sup>b</sup>	-1580.9 $\pm$ 3316.7 <sup>d</sup>
<b>Mixed Pickle</b>						
Low	3.5 $\pm$ 5.5 <sup>de</sup>	-7.7 $\pm$ 5.8 <sup>de</sup>	4.2 $\pm$ 2.0 <sup>a</sup>	-85.0 $\pm$ 140.4 <sup>ab</sup>	-35.1 $\pm$ 77.9 <sup>a</sup>	36.0 $\pm$ 88.6 <sup>bc</sup>
Middle	7.9 $\pm$ 6.6 <sup>cd</sup>	-12.0 $\pm$ 6.7 <sup>cd</sup>	4.1 $\pm$ 2.1 <sup>a</sup>	-367.7 $\pm$ 495.2 <sup>ab</sup>	-17.8 $\pm$ 60.5 <sup>a</sup>	207.9 $\pm$ 244.8 <sup>abc</sup>
High	12.3 $\pm$ 6.8 <sup>bc</sup>	-15.8 $\pm$ 7.0 <sup>bc</sup>	3.5 $\pm$ 1.6 <sup>a</sup>	-1984.3 $\pm$ 2701.7 <sup>ab</sup>	0.0 $\pm$ 0.0 <sup>a</sup>	948.0 $\pm$ 1106.7 <sup>a</sup>
<b>Swartkop</b>						
Low	-5.9 $\pm$ 5.4 <sup>gh</sup>	2.1 $\pm$ 5.6 <sup>g</sup>	3.8 $\pm$ 1.8 <sup>a</sup>	-0.1 $\pm$ 0.7 <sup>b</sup>	-3.0 $\pm$ 11.6 <sup>a</sup>	-89.4 $\pm$ 113.6 <sup>c</sup>
Middle	-1.3 $\pm$ 5.8 <sup>fg</sup>	-2.7 $\pm$ 5.7 <sup>f</sup>	4.0 $\pm$ 2.0 <sup>a</sup>	-1.0 $\pm$ 7.1 <sup>b</sup>	-57.7 $\pm$ 94.3 <sup>a</sup>	-118.8 $\pm$ 214.2 <sup>c</sup>
High	2.3 $\pm$ 6.1 <sup>ef</sup>	-5.7 $\pm$ 6.7 <sup>ef</sup>	3.4 $\pm$ 1.3 <sup>a</sup>	-92.0 $\pm$ 271.5 <sup>ab</sup>	-116.8 $\pm$ 272.4 <sup>a</sup>	-73.6 $\pm$ 307.2 <sup>bc</sup>

**Table 3.4** A diagrammatic representation of the density and distribution of *Azorella selago* reproductive structures recorded on 12 sampling sites across Marion Island. The recordings were conducted between October 2002 and February 2003 for Tafelberg; December 2002 and March 2003 for Stony Ridge; December 2002 and February 2003 for Swartkop; and November 2002 and February 2003 for Mixed Pickle. ● = Flower buds, ■ = Flowers, ▲ = Fruits, size of the symbols correspond to density (low, medium, and high) and empty symbols represent absence of reproduction structures

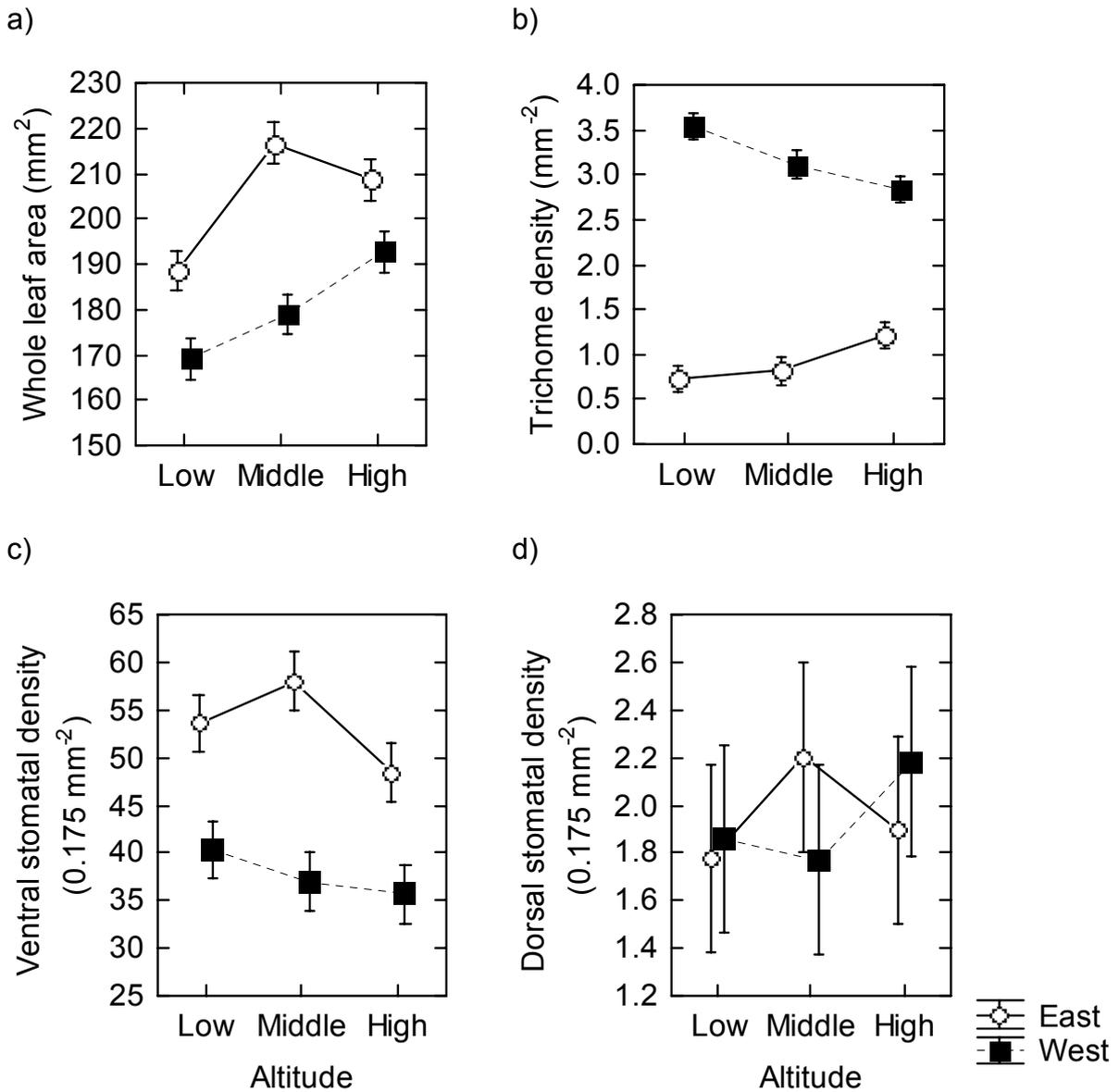
Site	October	November	December	January	February	March
<b>Tafelberg</b>	● □ △			○ □ ▲		
Low						
Middle			○ ■ ▲			○ □ ▲
High		● ■ ▲			○ □ ▲	
<b>Stony Ridge</b>			● ■ ▲		○ □ ▲	
Low						
Middle	● □ △			○ □ ▲		○ □ ▲
High			○ □ ▲			
<b>Mixed Pickle</b>		● ■ ▲			○ □ ▲	
Low						
Middle			● ■ ▲		○ □ ▲	
High	● □ △			○ □ ▲		○ □ ▲
Swartkop						
Low			● ■ ▲			○ □ ▲
Middle		● □ △			○ □ ▲	
High			● ■ ▲		○ □ ▲	

**Table 3.5** A diagrammatic representation of the density and distribution of *Azorella selago* reproductive structures averaged across altitudinal gradients on Marion Island. Recordings were conducted between October 2002 and February 2003 for Tafelberg; December 2002 and March 2003 for Stony Ridge; December 2002 and February 2003 for Swartkop; and November 2002 and February 2003 for Mixed Pickle. ● = Flower buds, ■ = Flowers, ▲ = Fruits, size of the symbols correspond to density (low, medium, and high) and empty symbols represent absence of reproduction structures

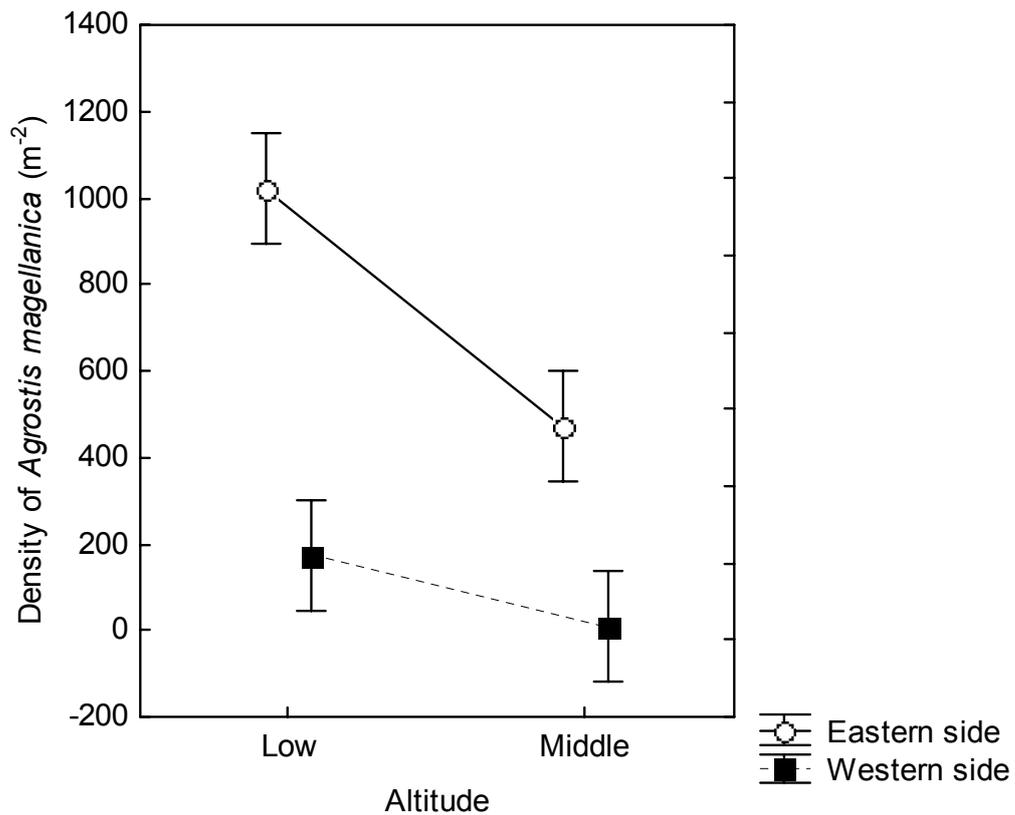
Altitude	October	November	December	January	February	March
Low	● □ Δ	● ■ ▲	● ■ ▲	○ □ ▲	○ □ ▲	○ □ ▲
Middle	● □ Δ	● ■ Δ	● ■ ▲	○ □ ▲	○ □ ▲	○ □ ▲
High	● □ Δ	● □ Δ	● ■ ▲	○ □ ▲	○ □ ▲	○ □ ▲



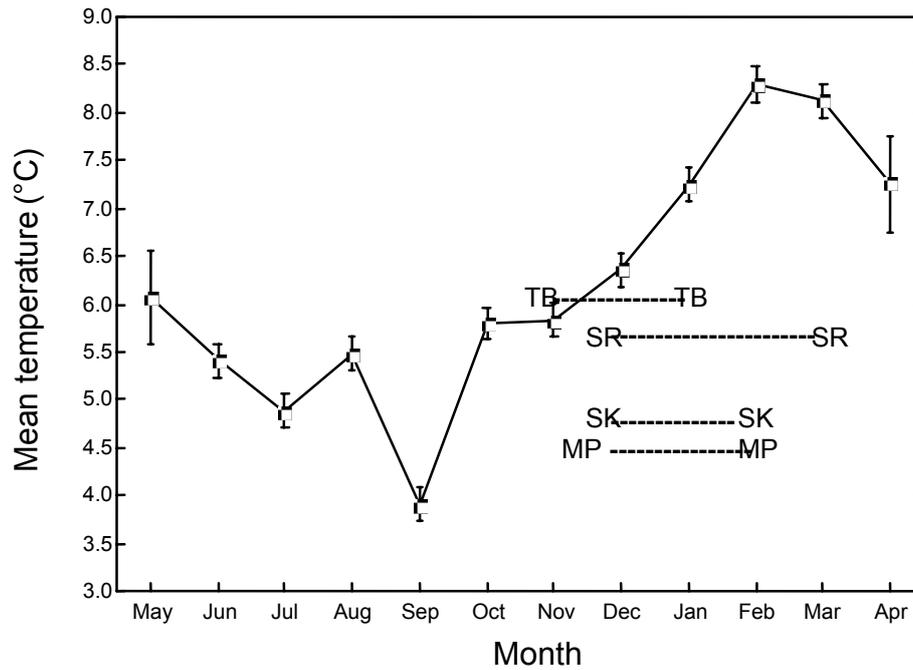
**Fig. 3.1** General Linear Models interaction plots showing **a.** mean growth rate, **b.** height, **c.** circumference, and **d.** surface area of *Azorella selago* cushion-plants recorded across altitudinal transects on the east and western side of Marion Island (vertical bars represent standard errors)



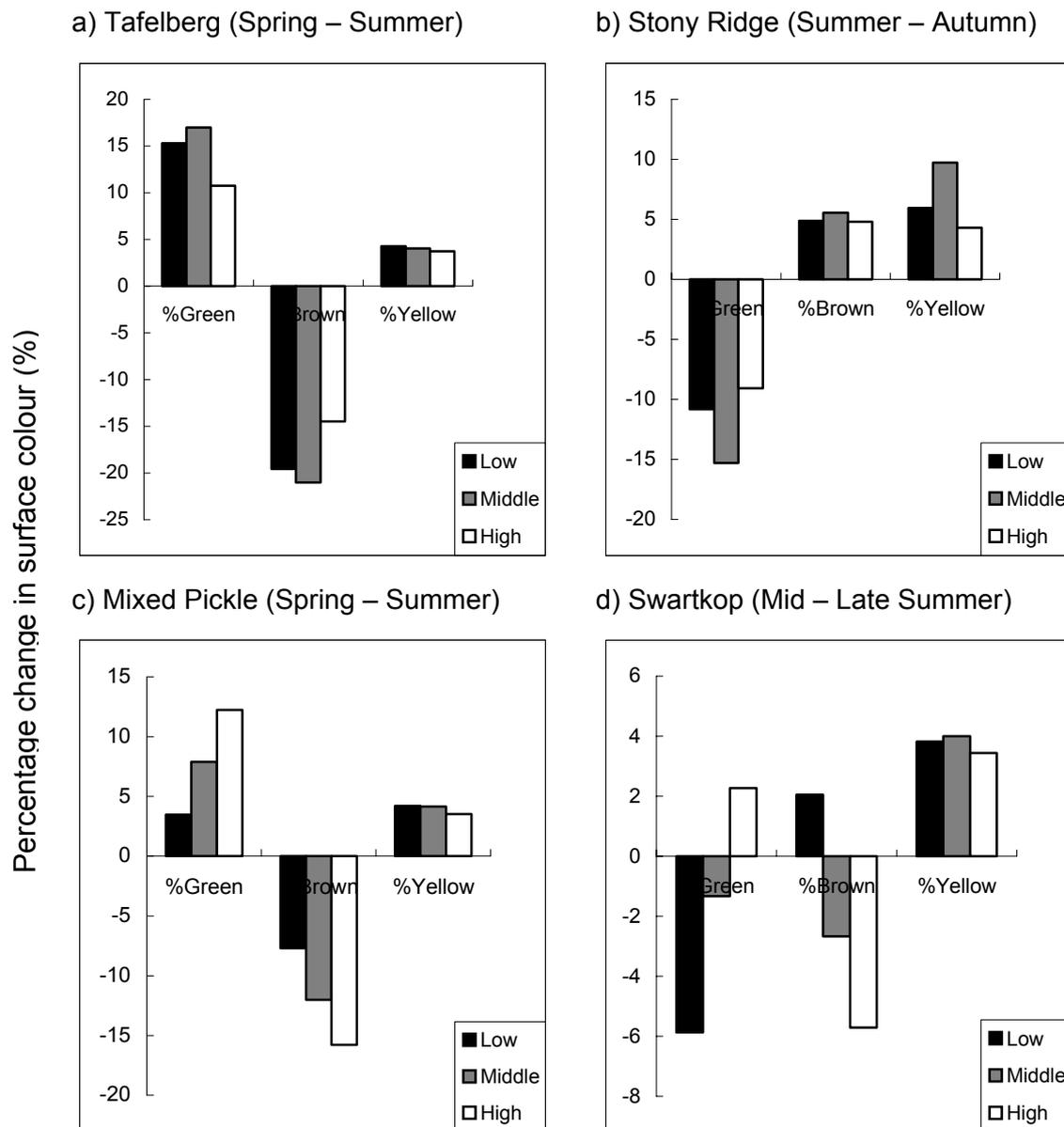
**Fig. 3.2** Mean leaf area **a.** trichome density **b.** and stomatal density (**c.** Ventral surface and **d.** dorsal surface) of *Azorella selago* leaves collected on sites along altitudinal transects on the eastern and western sides of the island (vertical bars represent standard errors)



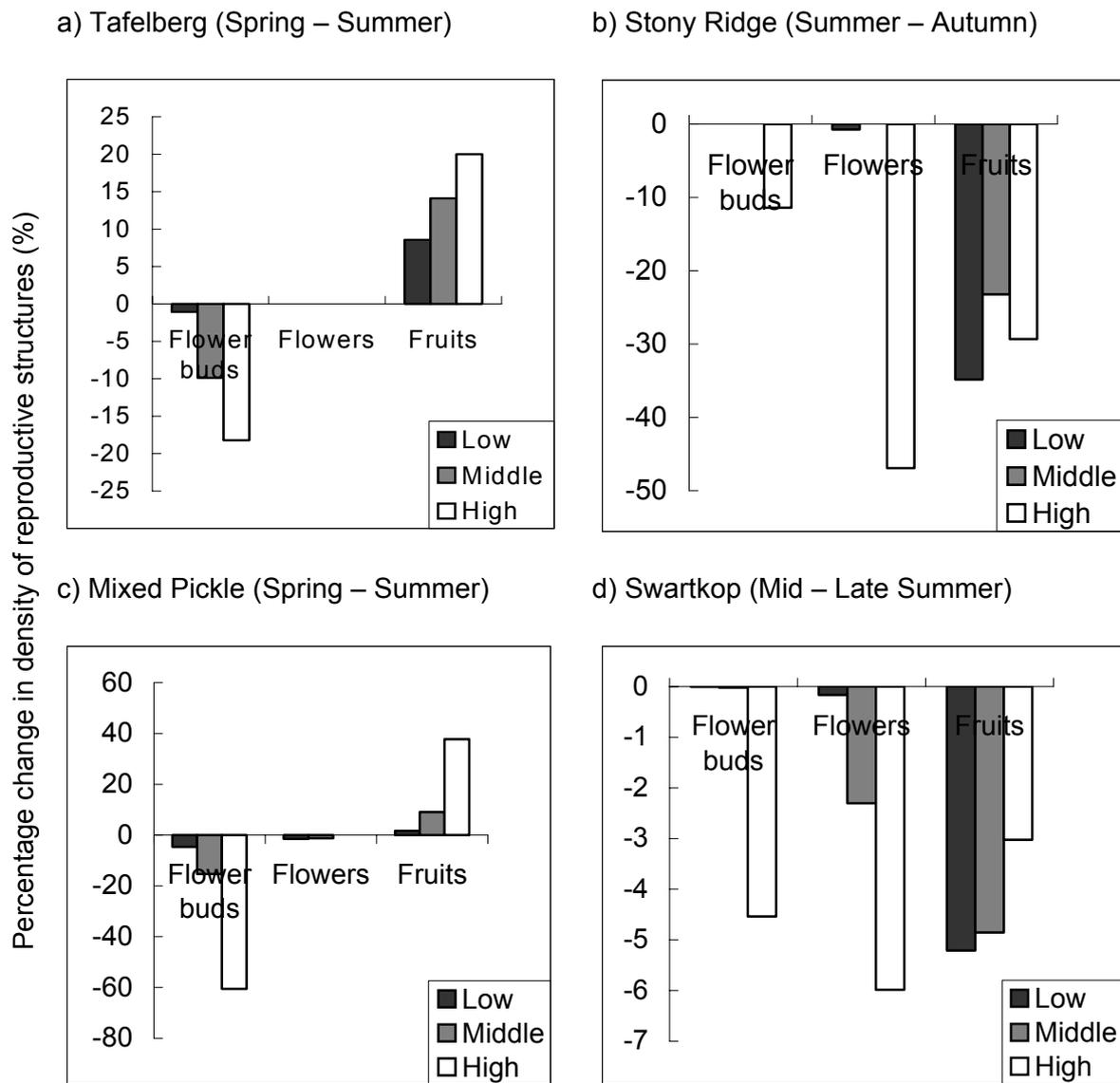
**Fig. 3.3** Mean epiphyte (*Agrostis magellanica*) density on *Azorella selago* plants across altitudinal transects on the east and western sides of the island (vertical bars represent standard errors). *Agrostis magellanica* was absent from high altitude



**Fig. 3.4** Mean monthly temperatures recorded by the Stevenson screen at Marion Island's meteorological station from May 2002 to April 2003. The horizontal dotted lines represent mean *Azorella selago* microclimate temperatures for the period over which phenological readings were taken in each transect (Vertical bars represent standard errors)

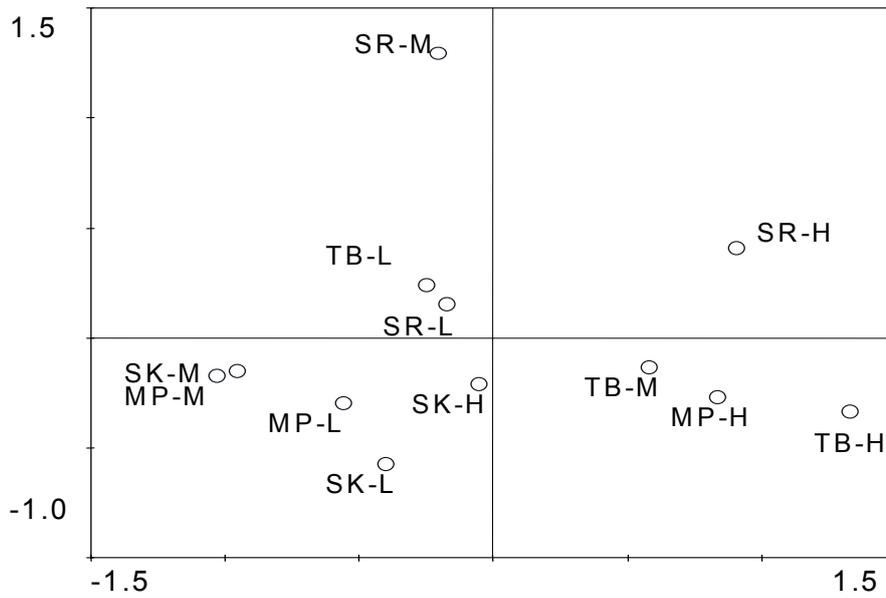


**Fig. 3.5** Mean percentage change in *Azorella selago* surface leaf colour recorded in two different periods (between October '02 and January '03 for Tafelberg; December '02 and March '03 for Stony Ridge; December '02 and February '03 for Swartkop; and November '02 and February '03 for Mixed Pickle) along four altitudinal transects (**a.** Tafelberg, **b.** Stony Ridge, **c.** Mixed Pickle, and **d.** Swartkop) on Marion Island (n = 50)

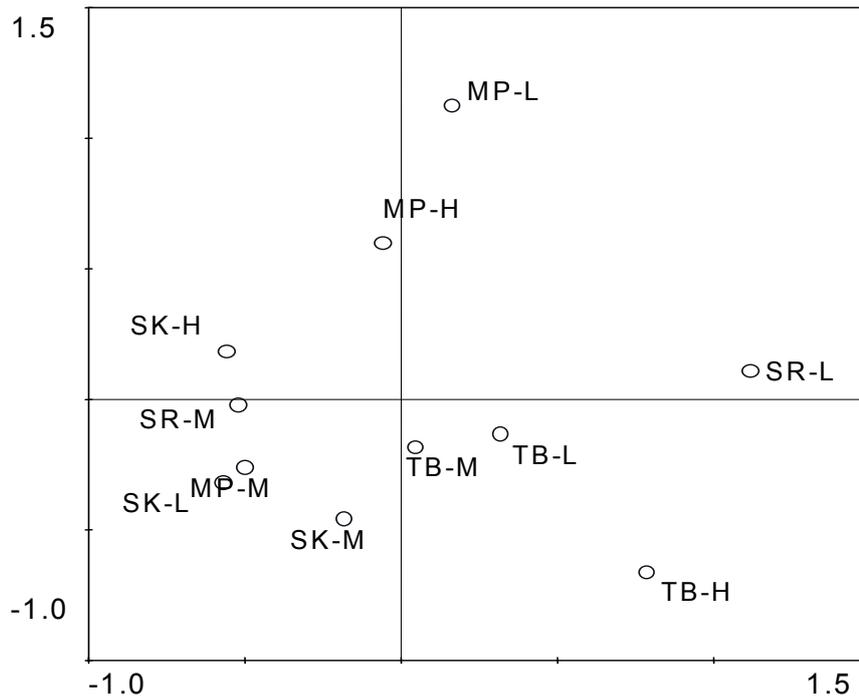


**Fig. 3.6** Mean change in the densities of *Azorella selago* reproductive structures recorded in two different periods (between October '02 and January '03 for Tafelberg; December '02 and March '03 for Stony Ridge; December '02 and February '03 for Swartkop; and November '02 and February '03 for Mixed Pickle) along four altitudinal transects (a. Tafelberg, b. Stony Ridge, c. Mixed Pickle, and d. Swartkop) on Marion Island (n = 50)

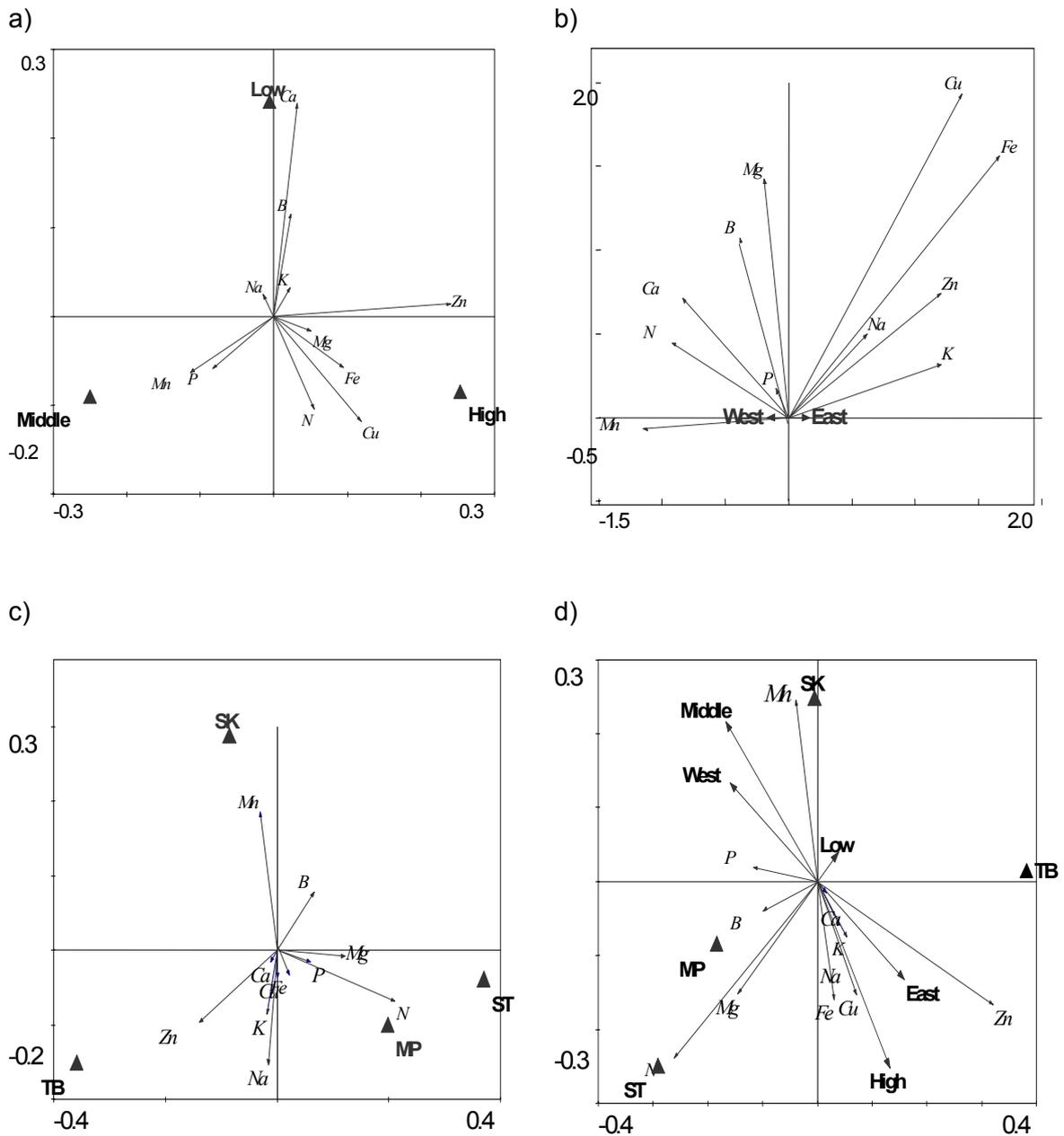
a)



b)



**Fig. 3.7** Principal Components Analysis (PCA) ordinations for **a.** soil and **b.** leaf nutrients from twelve sampling sites across Marion Island. (TB = Tafelberg; SR = Stony Ridge; MP = Mixed Pickle; SK = Swartkop and L, M, H represent low, middle and high altitudes respectively)



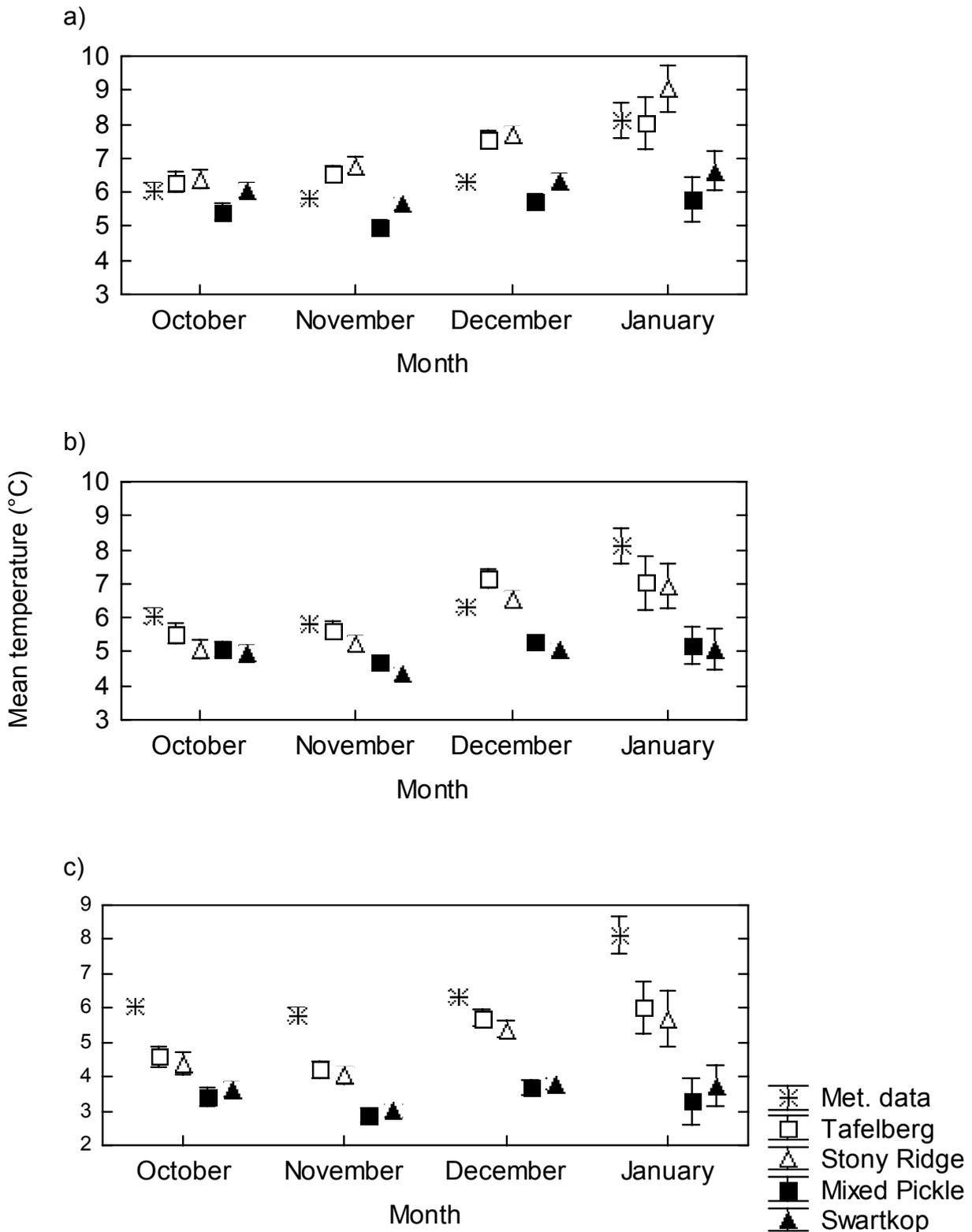
**Fig. 3.8** Redundancy Analysis (RDA) ordinations of leaf nutrients across **a.** altitudinal gradient (Low, Middle, and High); **b.** side of the island (east and west); **c.** the four sampled gradients on Marion Island (TB = Tafelberg; ST = Stony Ridge; MP = Mixed Pickle; SK = Swartkop); and **d.** all plot combinations shown in **a – c**, (i.e. altitude; side of the island; and transect).

**Appendix 3.A** Soil nutrients and selected attributes of fellfield habitat sites along four altitudinal transects on Marion Island

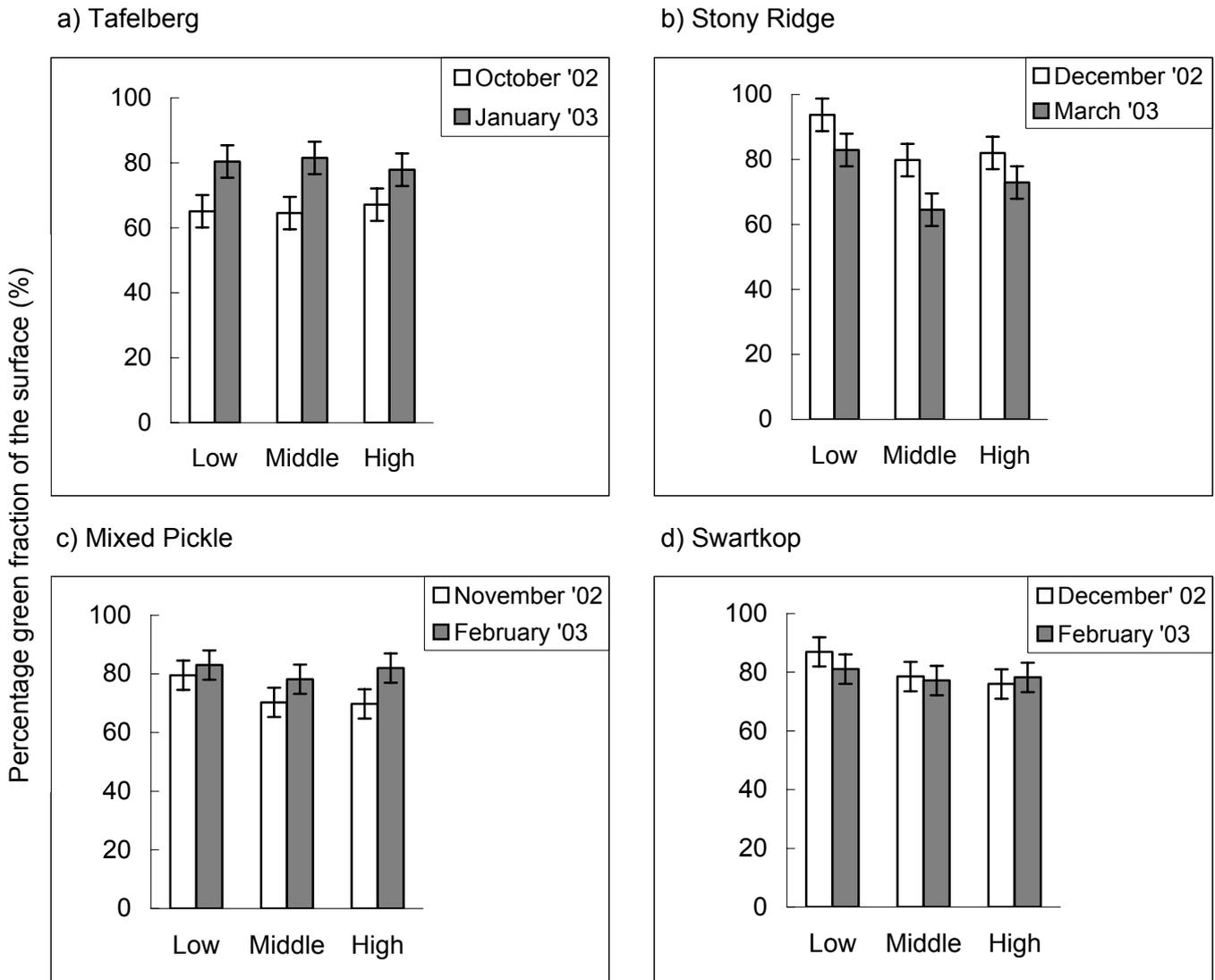
<i>Site</i>	PH (KCl)	Resist. (Ohm)	H (cmol/kg)	Stone (vol.%)	P Bray II (mg/kg)	K (mg/kg)	Na cmol (+)/kg	K cmol (+)/kg	Ca cmol (+)/kg	Mg cmol (+)/kg	% C	%Na	% K	% Ca	% Mg	T-value cmol (+)/kg
Tafelberg																
Low	4.7	2460	3.3	21	1	110	0.28	0.28	0.75	1.16	7.29	4.92	4.86	12.96	20.05	5.77
Middle	5.1	5150	1.59	13	0	17	0.09	0.04	0.17	0.25	2.23	4.01	2.02	7.9	11.73	2.14
High	5.3	6100	1.06	14	11	18	0.05	0.05	0.01	0.05	1.63	3.83	3.74	0.82	4.17	1.21
Stony Ridge Low	4.9	2360	2.6	15	1	44	0.3	0.11	1.08	1.09	5.37	5.86	2.19	20.85	21.02	5.19
Middle	4.8	2170	2.95	1	1	201	0.53	0.51	1.91	1.49	6.48	7.14	6.94	25.89	20.13	7.39
High	5.3	4600	1.36	10	1	25	0.12	0.06	0.06	0.15	2.34	6.7	3.58	3.52	8.57	1.75
Mixed Pickle Low	4.5		3.19	38	32	79	0.44	0.2	1.51	2	5.34	6	2.76	20.59	27.24	7.35
Middle	4.4		5.61	33	5	153	0.63	0.39	3.04	3.94	14.56	4.63	2.88	22.34	28.96	13.62
High	4.9		0.83	23	27	19	0.06	0.05	0.04	0.17	1	5.18	4.35	3.38	14.5	1.14
Swartkop Low	4.7	2170	2.83	40	18	43	0.29	0.11	1.42	1.52	4.6	4.7	1.77	23.03	24.63	6.17
Middle	4.3		5.84	13	8	127	0.48	0.33	2.12	3.07	13.38	4.02	2.75	17.93	25.93	11.83
High	5.1	2730	1.71	32	4	26	0.17	0.07	0.49	0.73	10.94	5.34	2.14	15.37	23.08	3.16

**Appendix 3.B** Mean ( $\pm$  s.d.) of nutrient concentrations in *Azorella selago* leaves from fellfield habitat sites across altitudinal gradients on Marion Island

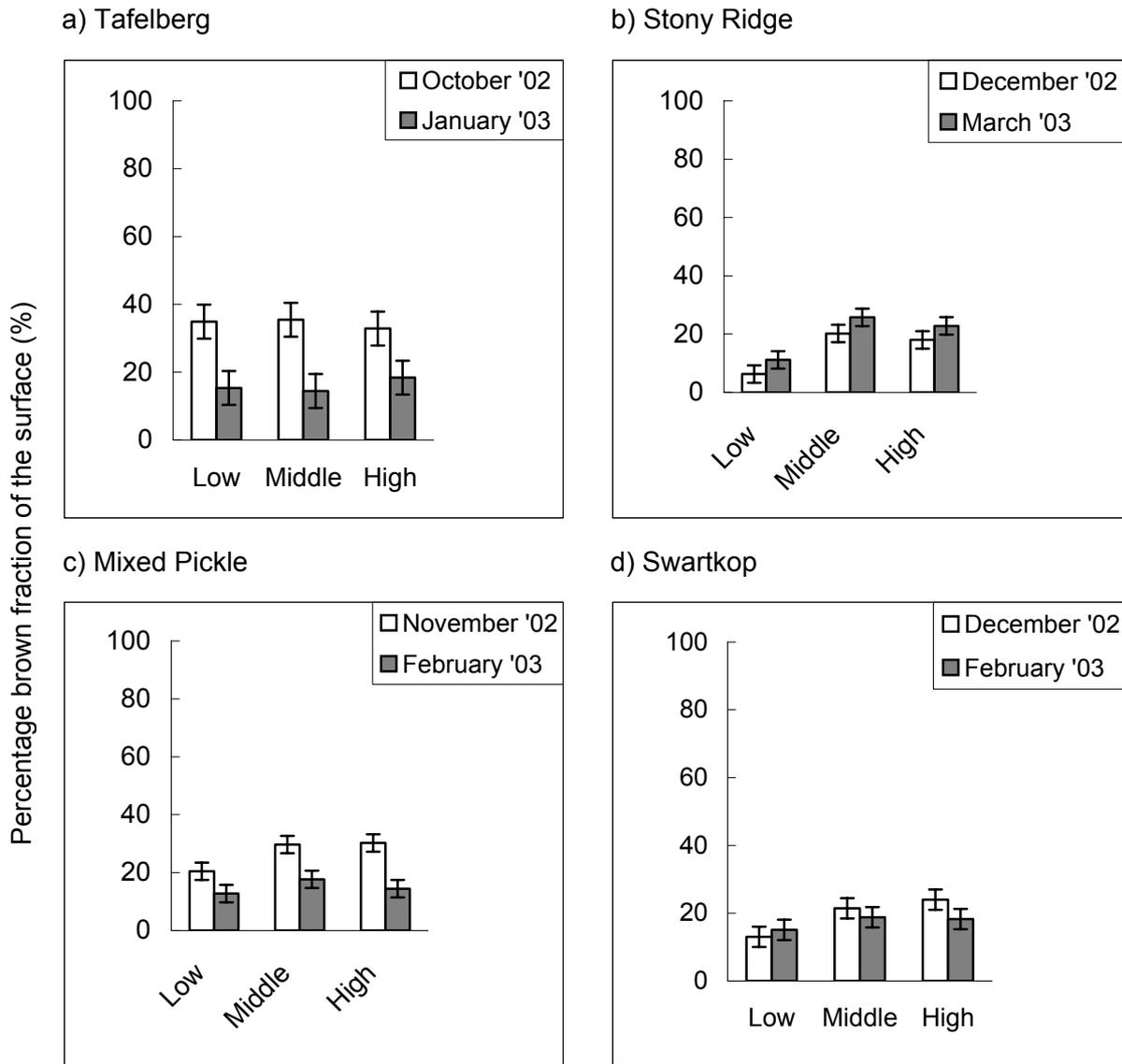
Site	% N	% P	% K	% Ca	% Mg	Na (mg/kg)	Mn (mg/kg)	Fe (mg/kg)	Cu (mg/kg)	Zn (mg/kg)	B (mg/kg)
Tafelberg	0.81	0.07	0.31	0.72	0.30	1566.7 $\pm$	195.7	6985.7	12.3	17.2	20.
Low	$\pm$ 0.05	$\pm$ 0.01	$\pm$ 0.09	$\pm$ 0.14	$\pm$ 0.04	405.47	$\pm$ 49.02	$\pm$ 056.01	$\pm$ 2.98	$\pm$ 4.39	$\pm$ 2.26
Middle	0.83	0.07	0.38	0.86	0.31	1231.5	372.2	3445.3	9.3	30.8	20
	$\pm$ 0.06	$\pm$ 0.01	$\pm$ 0.14	$\pm$ 0.15	$\pm$ 0.06	$\pm$ 174.67	$\pm$ 158.05	$\pm$ 2329.5	$\pm$ 2.16	$\pm$ 7.86	$\pm$ 1.05
High	0.81	0.08	0.24	0.9	0.31	2006.0	242.8	8832.2	18.7	72.4	17.6
	$\pm$ 0.14	$\pm$ 0.01	$\pm$ 0.05	$\pm$ 0.15	$\pm$ 0.05	$\pm$ 578.0	$\pm$ 43.59	$\pm$ 3434.4	$\pm$ 4.08	$\pm$ 20.91	$\pm$ 2.63
Stony Ridge	0.5	0.08	0.51	0.85	0.33	1905.0	152.2	2894.2	9.0	32.5	18.9
Middle	$\pm$ 0.19	$\pm$ 0.01	$\pm$ 0.09	$\pm$ 0.11	$\pm$ 0.05	$\pm$ 651.15	$\pm$ 31.4	$\pm$ 2543.9	$\pm$ 1.7	$\pm$ 5.7	$\pm$ 3.25
Mixed Pickle	0.79	0.1	0.41	0.71	0.24	1349.0	209.7	4234.6	8.6	26.3	18.8
Middle	$\pm$ 0.19	$\pm$ 0.01	$\pm$ 0.09	$\pm$ 0.08	$\pm$ 0.02	$\pm$ 288.25	$\pm$ 49.11	$\pm$ 1992.2	$\pm$ 1.96	$\pm$ 4.19	$\pm$ 2.15
Swartkop	0.76	0.08	0.4	0.61	0.29	1880.5	129.3	3412.7	9.4	28.2	16.3
Low	$\pm$ 0.16	$\pm$ 0.01	$\pm$ 0.12	$\pm$ 0.09	$\pm$ 0.05	$\pm$ 257.91	$\pm$ 35.14	$\pm$ 1736.1	$\pm$ 1.43	$\pm$ 6.53	$\pm$ 1.77
	0.76	0.07	0.35	0.7	0.26	1714.5	464.2	2398.3	8.1	26.9	17.6
Middle	$\pm$ 0.05	$\pm$ 0.01	$\pm$ 0.07	$\pm$ 0.09	$\pm$ 0.05	$\pm$ 339.32	$\pm$ 177.95	$\pm$ 2233.4	$\pm$ 2.64	$\pm$ 7.34	$\pm$ 2.46
	0.92	0.07	0.42	0.72	0.27	1656.6	140.8	2456.7	7.7	13.9	17.5
High	$\pm$ 0.06	$\pm$ 0.01	$\pm$ 0.13	$\pm$ 0.07	$\pm$ 0.03	$\pm$ 314.47	$\pm$ 16.35	$\pm$ 579.67	$\pm$ 1.42	$\pm$ 1.79	$\pm$ 1.58



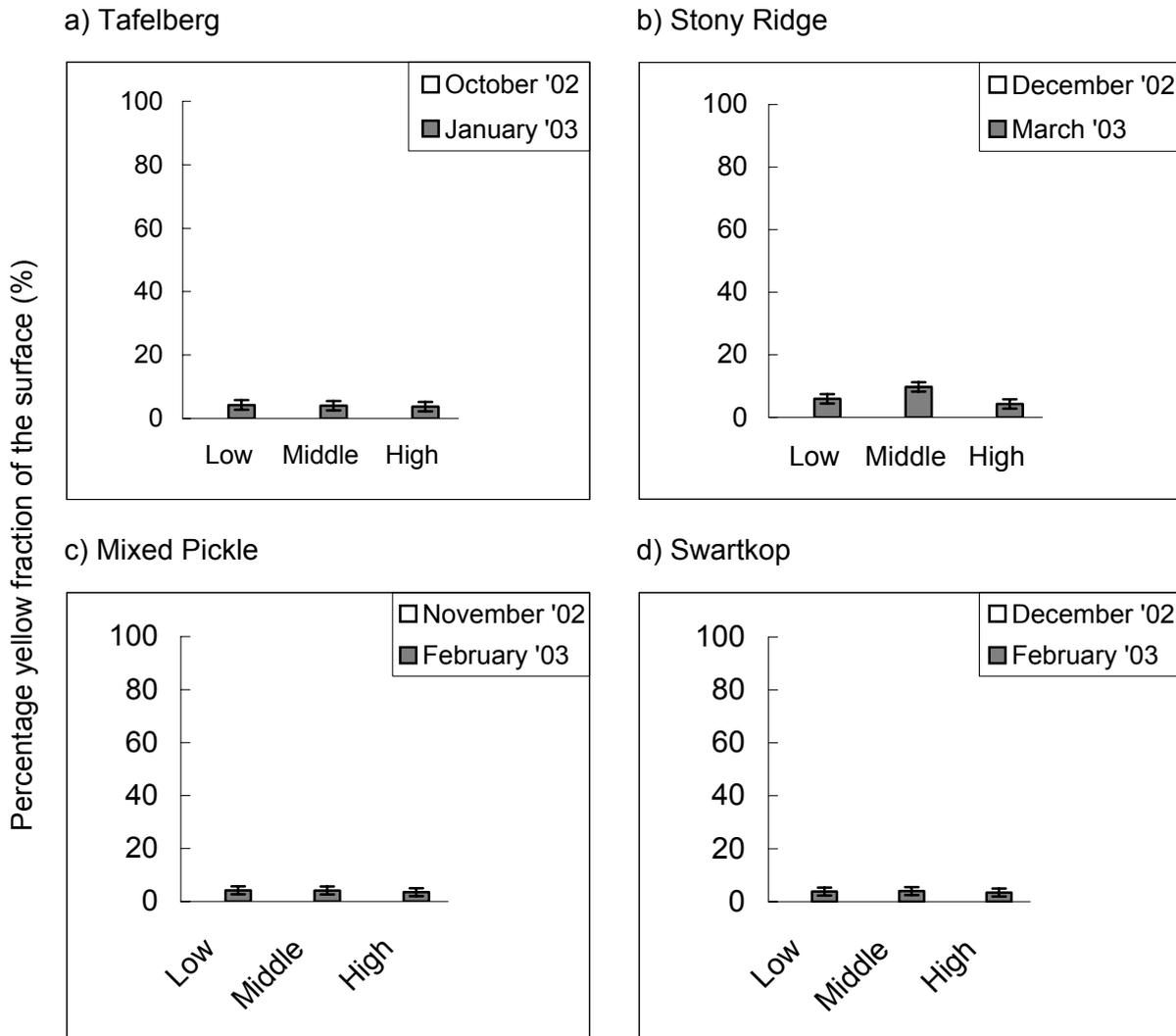
**Appendix 3.C** Mean monthly temperatures ( $\pm$  s.e.) for the Stevenson screen (Met. data) and different altitudinal plots (**a.** low, **b.** middle and **c.** high) across four transect gradients recorded from October 2002 to January 2003



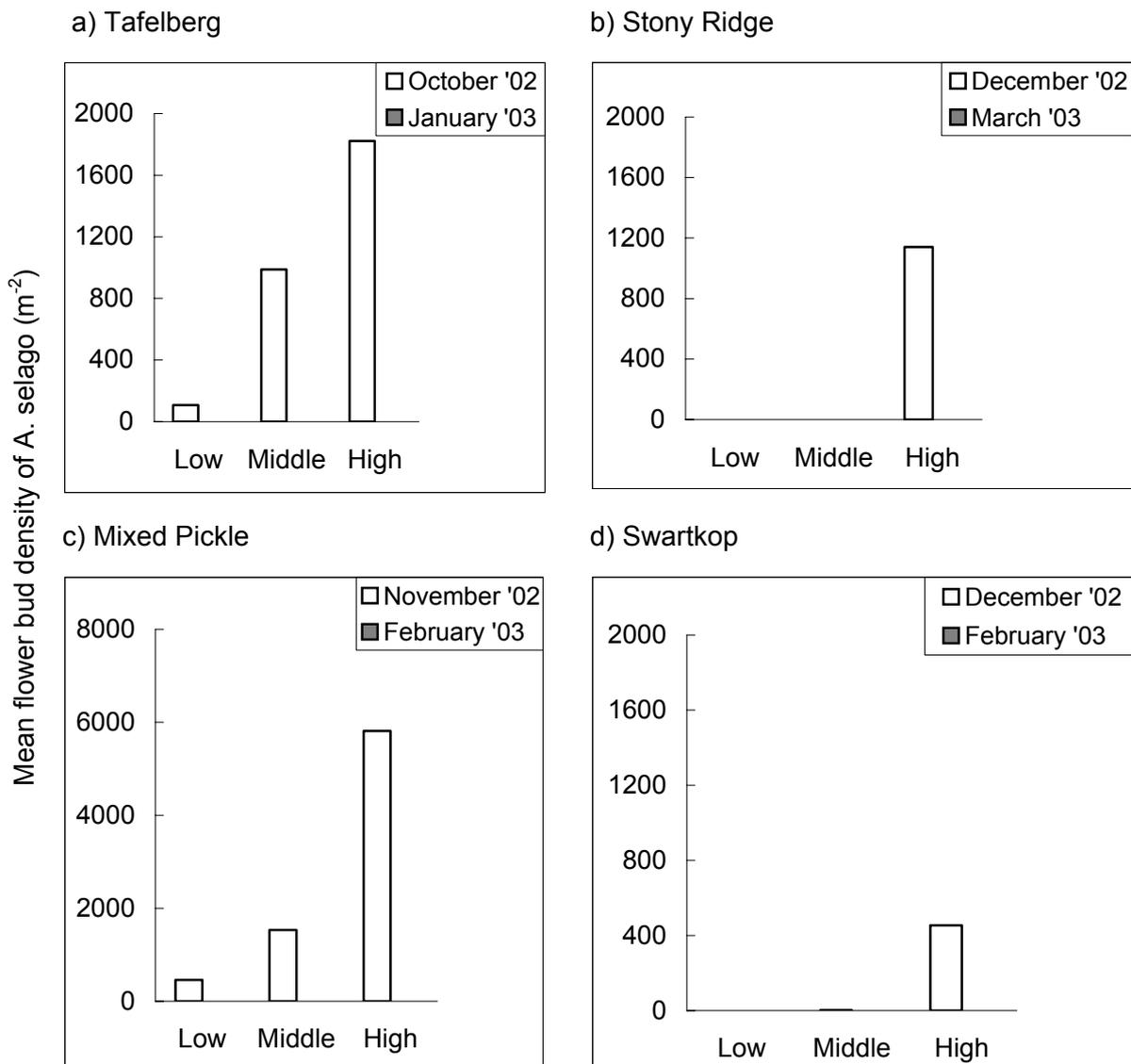
**Appendix 3.D** Mean ( $\pm$  se) percentage of green fraction of the surface of *Azorella selago* recorded at two different periods along four altitudinal gradients on Marion Island (n = 50)  
**a.** Tafelberg, **b.** Stony Ridge, **c.** Mixed Pickle, and **d.** Swartkop



**Appendix 3.E** Mean ( $\pm$ ) percentage of brown fraction of the surface of *Azorella selago* plants recorded at two different periods along four altitudinal gradients on Marion Island (n = 50) **a.** Tafelberg, **b.** Stony Ridge, **c.** Mixed Pickle, and **d.** Swartkop



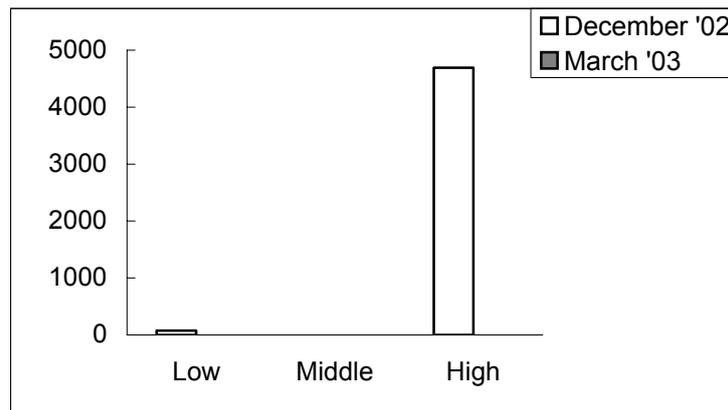
**Appendix 3.F** Mean ( $\pm$ ) percentage of yellow fraction of the surface of *Azorella selago* plants recorded at two different periods along four altitudinal gradients on Marion Island (n = 50) **a.** Tafelberg, **b.** Stony Ridge, **c.** Mixed Pickle, and **d.** Swartkop



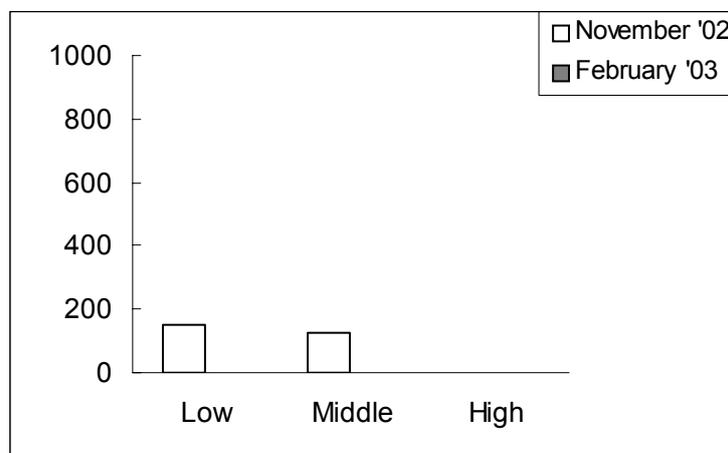
**Appendix 3.G** Mean density of *Azorella selago* flower buds recorded at two different periods along four altitudinal gradients on Marion Island (n = 50) **a.** Tafelberg, **b.** Stony Ridge, **c.** Mixed Pickle, and **d.** Swartkop

Mean flower bud density of *A. selago* (m<sup>-2</sup>)

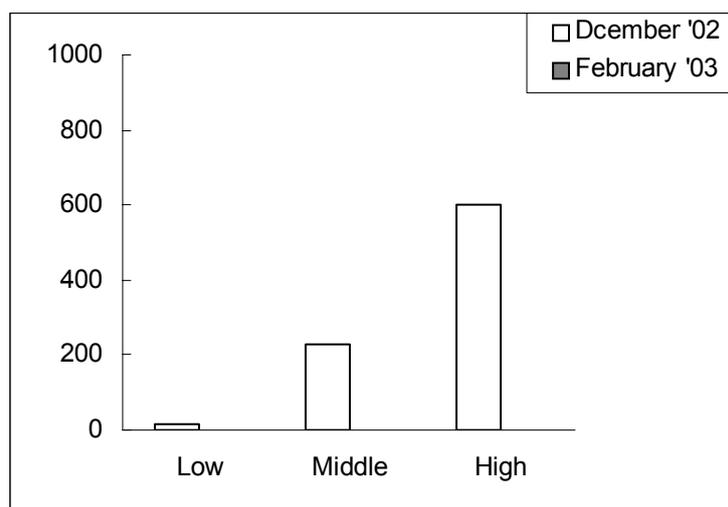
a) Stony Ridge



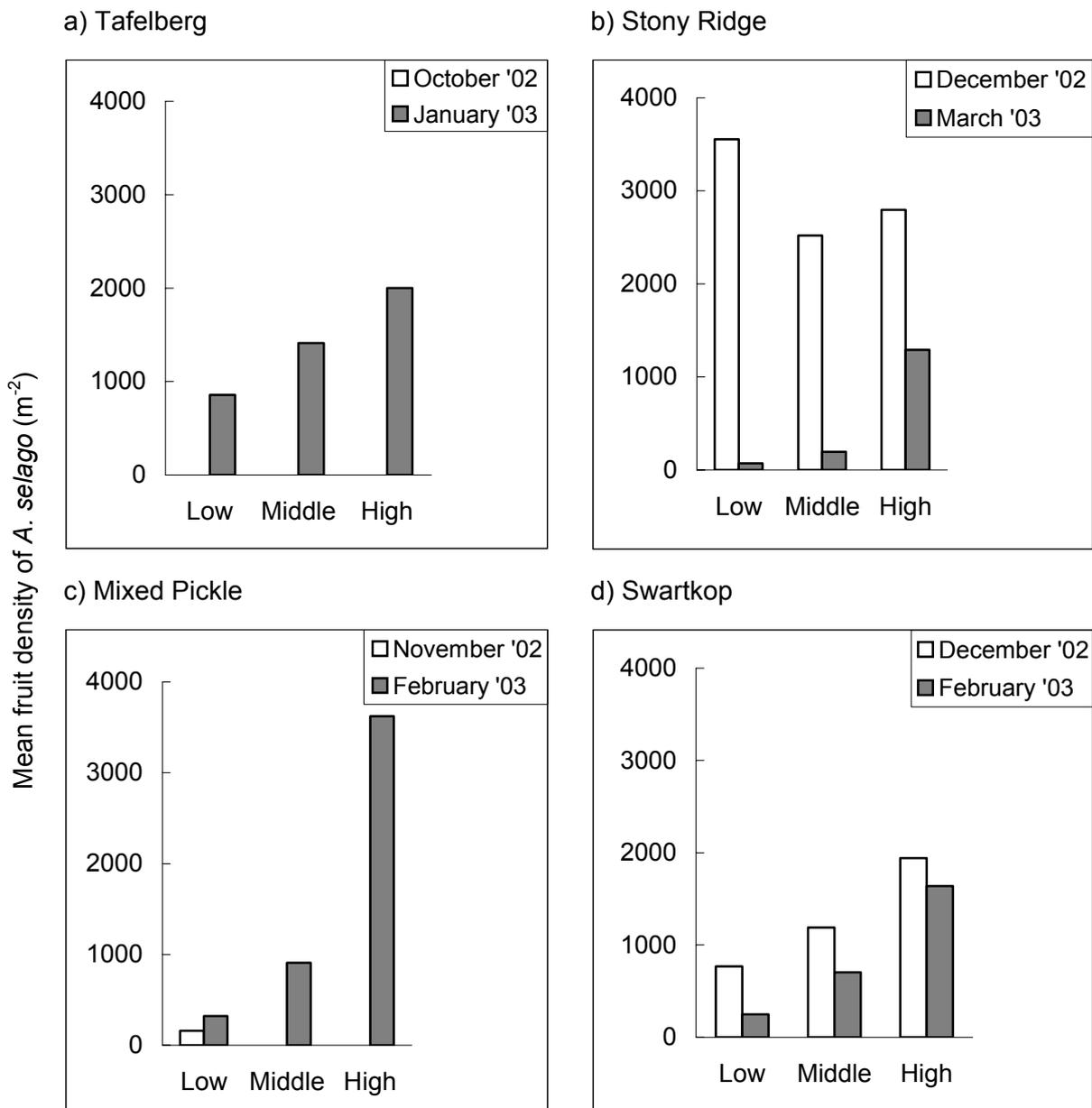
b) Mixed Pickle



c) Swartkop



**Appendix 3.H** Mean density of *Azorella selago* flowers recorded at two different periods along four altitudinal gradients (a. Stony Ridge, b. Mixed Pickle, and c. Swartkop) on Marion Island (n = 50). No flowers were recorded on Tafelberg during periods of recordings



**Appendix 3.1** Mean density of *Azorella selago* fruits recorded at two different periods along four altitudinal gradients on Marion Island (n = 50) a. Tafelberg, b. Stony Ridge, c. Mixed Pickle, and d. Swartkop

## General Conclusion

This thesis is a descriptive study of the spatial variability in *A. selago* characteristics across environmental gradients on Marion Island. It also presents the first quantification of temperature differences between the eastern and western sides of Marion Island. The eastern side of the island experienced more extreme temperatures (e.g. warm summers and cold winters) than the western side, which experienced relatively buffered temperatures (Chapter 1). This buffered temperature on the western side is thought to be the result of cloud cover, which predominates high altitudes and the western side of the island (Schulze 1971; Smith and Steenkamp 1990; Chown and Crafford 1992). *Azorella selago* cushion-plants were also found to have a buffering effect on temperature (Chapter 1), such that species occurring epiphytically and inside *A. selago* experience more moderate temperatures than the surrounding environment. The expected temperature decline with altitude was coupled with a decline in temperature fluctuation with altitude, a feature that was also observed with vertical depth inside *A. selago* cushion-plants. Warming of the island is therefore likely to change these temperature patterns and consequently affect *A. selago* characteristics and associated species communities. The effects of warming are also likely to be greater out in the field than the Meteorological Station suggests, because *A. selago* microclimate temperatures in the field were more extreme compared to the buffered Meteorological Station temperature data.

At a fine-scale (e.g. within fellfield stands of *A. selago*), adult plants of *A. selago* were most commonly randomly distributed in fellfield habitats (Chapter 2). Also at this scale, site-specific characteristics were found to determine the spatial structure of *A. selago* characteristics. Since there is no data available on abiotic variables at fine-scales, it was therefore difficult to predict climate change effects at fine-scales. However, broad-scale (e.g. across the island) observations of *A. selago* characteristics established strong responses of *A. selago* to altitudinal gradients and to different sides of the island (Chapter 3). The morphology of *A. selago* plants was more responsive to differences between the eastern and western sides of the island. *Azorella selago* plants and plant leaves were larger on the eastern side than the

western side of the island (Chapter 3). These plant size differences were consistent with different types and ages of the dominant substrates in the two sides of the island. The different substrates between the eastern and western sides of the island are possibly the basis for the observed differences in soil nutrients between the two sides. Larger plants occurred on the predominantly grey lava substrate in the eastern side (McDougall et al. 2001), and smaller plants on the predominantly young black lava substrate on the western side (McDougall et al. 2001). Trichome and stomatal densities were also more responsive to differences between the eastern and western sides of the island than to altitude (Chapter 3). The expected difference in moisture, light and wind between the eastern and western sides of the island is thought to be responsible for the observed patterns in *A. selago* leaf structures. Differences in the density of *Agrostis magellanica* were consistent with the microclimate temperatures, suggesting that temperature may be the factor limiting distribution of *A. magellanica* on the island. It can be predicted therefore that continued warming on the island may increase the biomass of epiphytic *A. magellanica* and shading the host plant *A. selago*. Expansion of *A. magellanica* distribution to higher altitudes can also be predicted. This study was also successful in evaluating patterns in the phenology of *A. selago* across altitudinal gradients on Marion Island. As expected, phenology was more responsive to temperature variation (Walther 2003). The phenology of *A. selago* plants was also more consistent with microclimate temperatures. Phenological events were early and more rapid at the warmer lower altitudes while at higher altitudes; phenological events were late and had longer durations. Continued warming on the island is therefore predicted to cause early and longer duration of phenological events across Marion Island.

This study provides data, which (their interpretation) might lead to predictions about the likely impact of climate change on *A. selago* plants and associated species in fellfield habitats. The study supports the possibility that ecosystem response to climate change can be predicted by understanding how climate change will affect the major species in a plant community. However, the only climate variable investigated in this study was the effects of temperature on two important species on Marion Island (e.g. *A. selago* and *A. magellanica*), but other climate variables are also likely to be important and

can therefore impinge on climate change predictions. More work on other microclimate variables (particularly precipitation) across Marion Island is necessary for the better understanding of climate change effects on Marion island ecosystems. Nonetheless, the research presented here provides a sound basis for understanding spatial variation in a keystone species on Marion Island, and it is also the most spatially comprehensive study of a vascular plant species on the island to date.

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