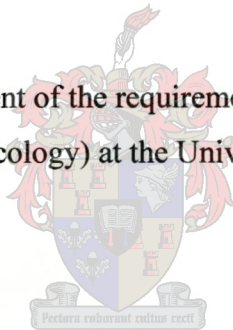


***Azorella selago* (Apiaceae) as a model for examining climate
change effects in the sub-Antarctic**

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Thesis presented in partial fulfilment of the requirements for the degree of Magister
Scientiae (Conservation Ecology) at the University of Stellenbosch



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December 2004

Declaration:

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

Signature.

Date

Abstract

There is increasing evidence that the rapid and anomalous changes in climate experienced in the last century have had widespread ecological impacts. Indeed, sub-Antarctic Marion Island has experienced particularly large increases in temperature and declines in rainfall. However, the effects of these changes on the island's extensive fellfield vegetation remain largely unexamined. The aim of this study was to examine the sensitivity of a dominant and keystone fellfield plant species, the cushion-forming *Azorella selago* Hook. (Apiaceae), to changes in climate. Three complementary approaches (two mensurate, one experimental) were used, and all showed that *A. selago* is likely to change in response to further changes in climate. First, the unimodal age class distribution of *A. selago* suggested that the species' establishment is episodic, and therefore reliant on specific (possibly climatic) conditions. *Azorella selago* growth rate was related to environmental factors, suggesting that both the establishment and growth rate of the species is likely to be sensitive to changes in climate. Second, altitudinal variation in *A. selago* plant attributes suggested that the species' morphology would be responsive to changes in climate (assuming that a spatial gradient in climate is a suitable analogue for similar changes in climate over time). Plant height, leaf size and trichome density differed most consistently over altitude across the island. The altitudinal range of some epiphyte species, as well as the cover and species richness of epiphytes growing on *A. selago*, also showed consistent patterns along the altitudinal gradient. These cushion plant and epiphyte attributes appeared to be related to climatic factors, and are therefore predicted to change in response to further shifts in climate. Finally, *A. selago* showed a rapid vegetative response to short-term experimental reductions in rainfall and increases in temperature and shading. Reduced rainfall accelerated autumnal senescence, shortening the species' growing season. Plants were relatively unaffected by the magnitude of warming imposed, although the foliar nutrient concentrations of some elements were higher in warmed plants than in control plants. Experimental shading of *A. selago* (simulating a predicted indirect effect of climate change: increased cover of the dominant epiphyte species, *Agrostis magellanica* (Lam.) Vahl (Poaceae)) caused greater stem elongation, and the production of larger, thinner leaves, with lower trichome densities and higher foliar nutrient concentrations of some elements. Given this sensitivity of *A. selago* to shading, it is possible that

changes in epiphyte load could overshadow the direct effects of changes in climate on this species. Ongoing changes in climate are predicted for the next century. Based on the results of this study the following scenarios are proposed. Continued warming and drying of the island will potentially favour the upslope expansion of *A. selago* (although also shortening its growing season) and decrease the abundance of its dominant epiphyte. Under such a scenario fellfield primary production may decline. In contrast, under warming alone, most epiphyte species could increase in abundance and expand their altitudinal ranges upslope. This would bring about much heavier shading of *A. selago* plants, leading to a short-term increase in stem growth and leaf nutrient concentrations. However, ultimately a decline in *A. selago* abundance and production would also be expected if cushion plants experience stem mortality under longer-term shading. Nonetheless, monitoring *A. selago* leaf size, trichome density and phenology, as well as the altitudinal range of dominant epiphyte species (attributes that this research suggests may be most sensitive to short-term changes in climate), will indicate the biological consequences of these changes in climate. This study, therefore, shows that further climate changes on Marion Island will affect *A. selago* and its epiphytes, with likely repercussions for fellfield communities.

Opsomming

Daar is toemende bewys dat die vinnige en onreëlmatige veranderinge in klimaat oor die laaste half-eeu wye ekologiese gevolge gehad het. Inderdaad, sub-Antarktiese Marion Eiland het 'n ook 'n besondere groot toename in temperature en daling in reënval ervaar. Nogtans is die gevolge van hierdie veranderinge op die eiland se uitgebreide dorveld (fellfield) plantegroei nog nie nagevors nie. Die doel van hierdie studie was om die sensitiwiteit van 'n dominante hoeksteen spesie, die kussingvormige *Azorella selago* Hook. (Apiaceae), aan veranderinge in klimaat te ondersoek. Drie aanvullende metodes (twee waarnemend, een eksperimenteel) was gebruik, en al drie het aangedui dat *A. selago* waarskynlik sal reageer op verdere veranderinge in klimaat. Eerstens, die enkelpiek-vormige ouderdomsverspreiding van *A. selago* dui daarop dat die spesie ongereeld vestig, en is daarom afhanklik van spesifieke (dalk klimatiese) toestande. Verder, was *A. selago* se groeitempo aan omgewingsfaktore verwant. As gevolg hiervan sal die spesie se vestiging en groeitempo vermoedelik sensitief vir klimaatsveranderinge wees. Tweedens, veranderinge in *A. selago* eienskappe met 'n toename in hoogte bo seespieël (hoogte) dui daarop dat die spesie se morfologie sal reageer op veranderinge in klimaatstoestand (op voorwaarde dat 'n ruimtelike verandering in klimaat goed ooreenstem met 'n soortgelyke verandering in klimaat oor tyd). Planthoogte, blaaroppervlakte en trigoomdigtheid het geleidelik met hoogte verander oor die eiland. Die verspreiding en bedekking van sommige epifitiese spesies, asook epifiet spesie rykheid, was ook aan hoogteverwant. Hierdie verwantskap tussen *A. selago* (en die epifiete) en hoogte is vermoedelik deur klimatiese faktore veroorsaak, en daarom word voorspel dat dit sal verander soos die klimaat verander. Laastens, het *A. selago* 'n vinnige vegetatiewe reaksie tot korttermyn eksperimentele vermindering in reënval en toename in temperatuur en beskaduwing gewys. 'n Afname in reënval het blaarveroudering versnel, en dus *A. selago* se groeiseisoen verkort. Plante het min verander as gevolg van hoër temperature, alhoewel die konsentrasie van sommige plantvoedingstowwe hoër was in blare van verwarnde plante as in die wat gewone temperature ervaar het. Eksperimentele beskaduwing van *A. selago* (wat 'n verwagde indirek effek van klimaatsverandering naboots, naamlik die toename in bedekking van *A. selago* deur die dominante epifiet spesie, *Agrostis magellanica* (Lam.) Vahl (Poaceae)) het stingel groei versnel, en veroorsaak dat groter en dunner blare met laer trigoomdigthede en

hoër konsentrasies van sommige plantvoedingstowwe op die plante groei. As gevolg van die sensitiwiteit van *A. selago* op beskaduwing, is dit moontlik dat die gevolge van veranderinge in die bedekking van epifiete belangriker sal wees as die direkte gevolge van klimaatsverandering. Verdere klimaatsveranderinge word vir die volgende eeu voorspel. Gebaseer op die resultate van hierdie navorsing, word twee moontlike toekomstige omstadighede voorgestel. Toenemende verwarming en verdroging van die eiland sal vermoedelik veroorsaak dat *A. selago* op hoër hoogtes voorkom (alhoewel die spesie se groeiseisoen ook sal verkort), en dat die volopheid van *A. magellanica* sal afneem. In so 'n geval sal dorveld se plantproduksie waarskynlik effens verminder. In teenstelling, as die eiland slegs verwarm (sonder 'n verandering in reënval) kan die volopheid en verspreiding van epifiet spesies waarskynlik toeneem. Dit sal vermoedelik tot 'n toename in the verskaduwing van *A. selago* lei, wat tot 'n kort-termyn verhoging van stingel groeitempo en plantvoedingstof konsentrasies sal lei. Alhoewel, uiteindelik, word 'n vermindering van *A. selago* volopheid en groei verwag as plantstingels van lang-termyn beskaduwing vrek. Nietemin, as die blaargroote, trigoomdigtheid en groeiseisoenlengte van *A. selago* en die hoogte verspreiding van die dominante epifiet spesie gemonitor word (eienskappe wat deur hierdie studie aangedui is as gevoelig aan kort-termyn veranderinge in klimaat), kan die biologiese gevolge van hierdie klimaatsveranderinge aangewys word. Hierdie navorsing bewys dus dat verdere veranderinge in klimaat op Marion Eiland 'n invloed sal hê op *A. selago* en geassosieerde epifiete, met moontlike gevolge vir die hele dorveld gemeenskap.

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the National Research Foundation.

Acknowledgements

First, I thank the Lord, my strength and refuge, without Whom this work would not have been possible.

I thank, and am forever in debt to, my supervisor, Prof. Melodie McGeoch, for her patience, enthusiasm and tireless support, both in the office and in the field.

This research was conducted as part of the Biocomplexity and Change project, and benefited from the input of S.L. Chown, V.R. Smith, N.J.M. Gremmen, A. Valentine, S. Holness, D. Marshall, C. Hänel, P. Convey, S. Milton, K.J. Gaston, D. Bergstrom and Y. Frenot. I also thank S.L. Chown for his advice and assistance on this particular research, as well as for his comments on various manuscripts. R. Veldtman, B.J. Sinclair, E.A. Hugo, R.D. Mercer, J.A. Deere, A. Botes, C. Krug, R. Krug and M. Greve also commented on various manuscripts and are thanked for their thoughtful comments. R. Krug is also thanked for programming the simulation model used in Chapter 2, and for critical discussion of the technique. I thank M. Nyakatya, E.A. Hugo, W. Wilkinson, M. Greve and many others for field assistance (often under difficult circumstances), M. Heynes and R.D. Mercer for help in administrative matters, and A. Valentine for helpful discussion of foliar nutrient concentration data.

I thank the Department of Environmental Affairs and Tourism, South Africa, for providing the financial and logistic support for this project, and to the National Research Foundation and the University of Stellenbosch for additional financial support.

Finally, I thank my family, friends (especially the residents of Paul Roos Street # 1 and 2) and colleagues (especially the members of the Spatial, Physiological and Conservation Ecology Group and the Department of Conservation Ecology), for their unfailing support, encouragement and love.

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Chapter 1: General introduction

There is increasing evidence that the rapid and anomalous changes in climate experienced in the last century have had widespread ecological impacts (Hughes, 2000; McCarthy, 2001; Walther et al., 2002; Parmesan and Yohe, 2003). Anthropogenic activities have changed the earth's atmospheric composition and land cover, altering the planetary energy budget by reducing the loss of long wave radiation to space (IPCC, 2001). As a consequence, mean global surface temperatures have risen by 0.6 °C over the last 100 years, changing at a rate unprecedented in the last millennium (Callaghan et al. 1992; IPCC, 2001). Warmer air masses have accelerated the global hydrological cycle, increasing precipitation in some areas, as well as altering cloud and wind patterns (IPCC, 2001).

These changes in climatic conditions have altered the abundance, distribution, physiological performance and phenology of species (e.g. Grabherr et al., 1994; Menzel and Fabian, 1999; Parmesan et al., 1999; Thomas and Lennon, 1999; Sturm et al., 2001; Fitter and Fitter, 2002; Peñuelas and Boada, 2003; Saavedra et al., 2003; Sanz-Elorza et al., 2003). Altered environmental conditions have also caused the spatial and/or temporal disassociation of communities (due to individualistic responses to changes in abiotic factors: Harrington et al., 1999; Stenseth and Mysterud, 2002), in addition to changing ecosystem-level processes (due to changes in community composition and species dominance: Kennedy, 1995b; Brown et al., 1997; Chapin et al., 1997). In the near future, however, even larger impacts can be expected, since the changes in climate already experienced are small relative to those predicted for the next century (IPCC, 2001). Further planetary warming of up to 5.8 °C is possible within the next 100 years, and even under a best-case scenario further warming of 1.4 °C is expected (IPCC, 2001).

Climate change in polar and sub-polar systems

High latitude ecosystems are ideally suited to studying the biological consequences of these changes in climate, because they have three main advantages over other systems for climate change research (Callaghan et al., 1992; Kennedy, 1995b; Bergstrom and Chown, 1999; Davies and Melbourne, 1999; Smith, 2002). First, high latitude ecosystems, in agreement with recent trends, will experience the largest and most

rapid changes in climate (Callaghan et al., 1992; IPCC, 2001). At high northern latitudes, warming greater than the global average (up to 8 °C over the next 100 years) and large increases in precipitation are likely (IPCC, 2001). Similar changes are predicted for the southern hemisphere (4 – 6 °C warming over Antarctica: IPCC, 2001), and are supported by recent climate trends. For example, the Antarctic Peninsula has warmed by 1 °C in summer and 4 – 5 °C in winter over the last 50 years (Robinson et al., 2003; although localized cooling has also occurred, see Doran et al., 2002). These changes represent considerable and rapid shifts in climatic conditions.

Second, the biological responses to changes in climate are expected to be most pronounced at high latitudes (Davies and Melbourne, 1999). Polar and sub-polar species are thought to be near their physiological limits and will therefore show disproportionately large responses to changes in climate (Davies and Melbourne, 1999). Further, these systems are becoming more susceptible to colonization by exotic species that are able to respond more rapidly to the ameliorating climatic conditions (Bergstrom and Chown, 1999; Davies and Melbourne, 1999). As a result, large changes in species' distributions and community function and composition are expected (Bergstrom and Chown, 1999).

Finally, the biological responses to climate change may be most discernable at high latitudes. As a result of generally low species richness, the influence of biotic factors are minimal relative to abiotic effects, and climate change impacts are thus more easily identified (Callaghan and Jonasson, 1995; Callaghan et al., 1997). High latitude areas are also among the least disturbed ecosystems globally and therefore allow the effects of climate change to be observed unconfounded by other anthropogenic effects (Callaghan et al., 1997). These characteristics make high latitude ecosystems potentially sensitive indicators of the biological effects of climate change.

Indeed, long-term monitoring programs at high latitudes yield evidence of these advantages. For example, Sturm et al. (2001) documented increased shrub abundance in the Alaskan Arctic during the past 50 years, which correlates with higher temperatures in the region over the same period. In addition, by examining seasonal cycles of atmospheric CO₂ concentration, Myneni et al. (1997) found a seven day increase in the length of the growing season at high northerly latitudes between 1981-1991, which is also thought to be due to rising temperatures. Finally, long-term-monitoring in the Antarctic has revealed increases in the abundance and distribution

of the continent's two native phanerogams, correlating with recent warming trends (Smith, 1994).

Undeniably, climate change research at high latitudes has revealed much about the biological consequences of changes in climate. For example, in Arctic and sub-Arctic ecosystems, community production consistently increases under nutrient addition (simulating enhanced atmospheric deposition and mineralization under warming), but is unaffected by changes in temperature and rainfall. Similarly, at the species-level, plant functional type is a good predictor of species' response to changes in temperature and nutrient levels. However, beyond these broad patterns, no other generalizations can yet be made other than the individualistic nature of species' responses (Arft et al., 1999; Dormann and Woodin, 2002). For example, plant species differ in their sensitivity to changes in temperature, water availability, light and nutrients (Chapin and Shaver, 1985; Chapin et al., 1997). In addition, species' responses are often spatially (high vs. low latitude: Havström et al., 1993; Wookey et al., 1993; Arft et al., 1999) and temporally (short- vs. long-term response: Chapin et al., 1995) variable, suggesting the need for further species-level studies (particularly of dominant species) if the effects of climate change are going to be predicted with an accuracy exceeding the coarse scale enabled by current generalizations. This is possibly particularly true for the high latitude southern hemisphere ecosystems that are ecologically distinct from northern hemisphere equivalents and relatively poorly researched (Smith and French, 1988; Callaghan et al., 1992).

Prince Edward Islands

The sub-Antarctic Prince Edward Islands (comprising Prince Edward Island and the larger Marion Island) are a high latitude southern hemisphere system suited to studying the effects of climate change. These islands have recently experienced large and rapid changes in climate, as evidenced by a continuous weather record on Marion Island, which shows a significant increase in temperature (1.2 °C) on the islands over the last 50 years (Smith, 2002). Considering the oceanic climate of the islands (mean annual temperature 5.1 °C, mean diurnal variation 1.9 °C: Schulze, 1971), this represents considerable warming. Similarly, a 25% reduction in rainfall (i.e. 700 mm less) since the 1960's also constitutes a substantial change in climate (Smith, 2002).

Finally, the number of sunshine hours on the island has increased significantly since the 1950's, indicating a reduction in cloudiness over the island (Smith, 2002).

The biological consequences of these changes in climate are already evident on the islands. For example, the cover of a temperature-sensitive sedge, *Uncinia compacta* R. Br. (Cyperaceae), increased significantly between 1973 and 1992 on Prince Edward Island, probably in response to the warmer, drier conditions over that period (Chown and Smith, 1993). Recent warming is also thought to be responsible for higher population densities of the introduced house mouse (*Mus musculus* L. Muridae) on Marion Island (Smith, 2002), and thereby indirectly affecting the indigenous species that the mice feed upon (e.g. the sedge *Uncinia compacta* and ectemnorhine weevil species; Chown and Smith, 1993) and compete with (e.g. Lesser Sheathbills *Chionis minor*; Huyser et al., 2000).

Various species-, community- and ecosystem-level predictions have been made for the effects of future changes in climate on Marion Island. For example, under rising temperatures, vascular plants are expected to spread to higher altitudes on the island (to the disadvantage of bryophyte communities: Smith and Steenkamp, 1990). Interestingly, the island's vegetation is predicted to be more sensitive to changes in rainfall and wind than to temperature, because these factors appear to more strongly determine the character of the vegetation growing at a site (Gremmen, 1981; Smith and Steenkamp, 1990). Indeed, this has already been shown for the lichen *Turgidosculum complicatulum* (Nyl.) Kohlm. et Kohlm. which has a coastal distribution on the island. This species' carbon acquisition will change little under 2 °C of warming, but could show large changes in response to altered moisture levels (Smith and Gremmen, 2001). At the ecosystem-level, the ameliorating climate conditions are expected to increase primary productivity. However, as outlined by Smith and Steenkamp (1990), mouse predation on soil invertebrates could depress decomposer populations to a level where nutrient demand by the vegetation exceeds nutrient mineralization by the invertebrates, leading to imbalances between production and decomposition. Further, warmer conditions are thought to be more favourable for the establishment of exotic species, as well as for the spread of established exotics (Bergstrom and Chown, 1999; Smith, 2002), with potentially serious consequences for community structure and functioning (see e.g. Gremmen et al., 1998).

However, as for most other research on Marion Island (Smith et al., 2001), these predictions and observations are biased towards the coastal vegetation. As a result, the effects of climate change on the higher altitude fellfield vegetation remain unexamined, despite the large area this vegetation type covers on Marion Island and the rest of the sub-Antarctic (Barendse and Chown, 2001). Thus studies of the dominant fellfield plant species are necessary to improve our understanding of the biological consequences of climate change on the Prince Edward Islands.

Azorella selago

Azorella selago Hook. (Apiaceae) is the dominant vascular fellfield species (Fig. 1; Huntley, 1972; Orchard, 1989; Frenot et al., 1993). It is a long-lived, pioneer species with a cushion growth form (Frenot et al., 1993), occurring across much of the sub-Antarctic (see Chapter 3, page 44 for more information about the distribution of the genus). The species is also common in a variety of other habitats. For example, the species occurs from sea-level to 765 m a.s.l. on Marion Island (Moore, 1968; Gremmen, 1981; Smith et al., 2001) and between 450 and 1150 m a.s.l. on Tierra del Fuego (Orchard, 1989; Mark et al., 2001). Generally, *A. selago* is most common in cold and exposed areas, where its growth form is thought to reduce wind stresses and the plant's rate of heat and moisture loss (Ashton and Gill, 1965; Huntley, 1971; Callaghan and Emanuelsson, 1985; Wickens, 1995).

Azorella selago cushions have a central taproot, from which stems arise radially and branch dichotomously (Frenot et al., 1993). Its leaves are small, tough and lobed, and its petioles form a sheath around the stem (Orchard, 1989). The surface of the plants is hard and compact because its leaves are tightly packed and its stems grow closely against each other (Orchard, 1989). Cushion growth stops in autumn, and by winter all leaves have senesced. However, cushions retain these old leaves, forming a rich, moist, humus-like collection of organic matter inside the plant (Huntley, 1971). The species can show marked morphological variability, apparently linked to its environmental conditions (Huntley, 1972). For example, cushions growing in sheltered environments tend to have a longer growing season, faster stem growth, larger leaves and a more hemispherical growth form than those from more exposed locations (Huntley, 1971, 1972).

Cushions can host dense and diverse epiphyte (Huntley, 1972) and invertebrate communities (Barendse and Chown, 2001; Hugo et al., submitted). At higher altitudes some plant species are limited to epiphytic growth on the cushions (Huntley, 1972) and invertebrate density in cushions greatly exceeds that on the surrounding soils (Barendse and Chown, 2001). The grass *Agrostis magellanica* (Lam.) Vahl (Poaceae) is the dominant epiphyte on the cushions (Fig. 1), although at least another 15 vascular plant species and numerous bryophyte and lichen species also grow epiphytically on the cushions (Huntley, 1971; pers. obs). As a result of varying epiphyte cover, autumnal senescence and environmental conditions, cushions can have diverse and complicated surface cover (Fig. 2).

Azorella selago is a keystone species on Marion Island (*sensu* Begon et al., 1996), in part because it hosts considerable densities of epiphytes and invertebrates, but also due to its contribution to biomass, succession and geomorphological processes on the island (Huntley, 1972; Smith, 1978; Scott, 1985; Frenot et al., 1998; Selkirk, 1998; Boelhouwers et al., 2000). Marion Island supports 38 vascular plant species (including 14 introduced species) and approximately 40 liverwort, 80 moss and 100 lichen species have been recorded on the island (Smith, 1978; Smith and Steenkamp, 1990). However, *A. selago* is one of only six species that contribute significantly to the islands' standing crop (Smith, 1978). *Azorella selago* also plays an important role in succession on Marion Island (Scott, 1985; see also Frenot et al., 1998), since it is able to colonize loose scoraceous slopes, recent lava flows and glacial forelands of retreating glaciers (Huntley, 1972; Frenot et al., 1998). The species may also influence geomorphological processes on the island (see e.g. Selkirk, 1998; Boelhouwers et al., 2000).

Because of *A. selago*'s slow growth and longevity and the harsh environment within which it grows (Huntley, 1972; Frenot et al., 1993), the species can be considered a stress-tolerator (*sensu* Grime, 1979, 2003), and is therefore expected to respond slowly (if at all) to changes in climate. Indeed, Frenot et al. (1993) found small climatic fluctuations to have no effect on cushion growth rate on Kerguelen Island, and Huntley (1972) suggested that the species' phenology is "temperature-insensitive". Nevertheless, this species' response to climate change requires investigation because this has not been tested explicitly, and because it is an important component of fellfield habitat.

Thesis aims and outline

The objective of this research was to investigate the sensitivity of *Azorella selago* to changes in climate. To achieve this, three complementary methods were employed to examine the responsiveness of the species to climate change (study sites shown in Fig. 3).

First, the assumptions and accuracy of a procedure for aging cushion plants (McCarthy, 1992; Frenot et al., 1993; Molau, 1997; McCarthy, 1999) were tested, and the age structure of *A. selago* populations examined (reported in Chapter 2). The age class distribution of a population enables population dynamics to be inferred and can reveal the influence of past events (Callaghan and Emanuelsson, 1985; Callaghan and Carlsson, 1997).

Second, the variation in *A. selago* morphology and its epiphytes was documented along three altitudinal transects (reported in Chapter 3). Examining *A. selago*'s response to gradual spatial changes in climate suggests how it might respond to similar changes in climate over time (Fielding et al., 1999; Tweedie, 2000; Rustad et al., 2001; Smith et al., 2002).

In the fourth chapter, the short-term vegetative response of *A. selago* to changes in rainfall, temperature and shading was experimentally determined. As highlighted by Havström et al. (1993) and Kennedy (1995a), experimental studies are difficult to conduct in a "controlled and realistic manner", but are an important complement to other methods since they enable the effect of specific factors to be examined within otherwise natural conditions (Wookey et al., 1993). By using a procedural control and measuring the changes in microclimate affected by the treatments, the effects of two abiotic (i.e. reduced rainfall and increased temperature) and one biotic (i.e. increased shading by epiphytes) change on *A. selago* were assessed.

Each of these chapters was written as an individual manuscript and there is thus some repetition in each. Finally, a general conclusion (Chapter 5) provides a brief summary of the findings from the preceding chapters, and discusses the potential of *A. selago* and its epiphytes for monitoring the biological consequences of climate change.

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FIGURE 1. The sub-Antarctic cushion plant Azorella selago, supporting a dense epiphyte load of Agrostis magellanica. The matchbox (52 x 41 mm) is provided for scale.



FIGURE 2. Portion of an Azorella selago cushion, supporting epiphytic bryophytes (Ditrichum sp.) and small Agrostis magellanica grasses (approximately one and a half times life-size).

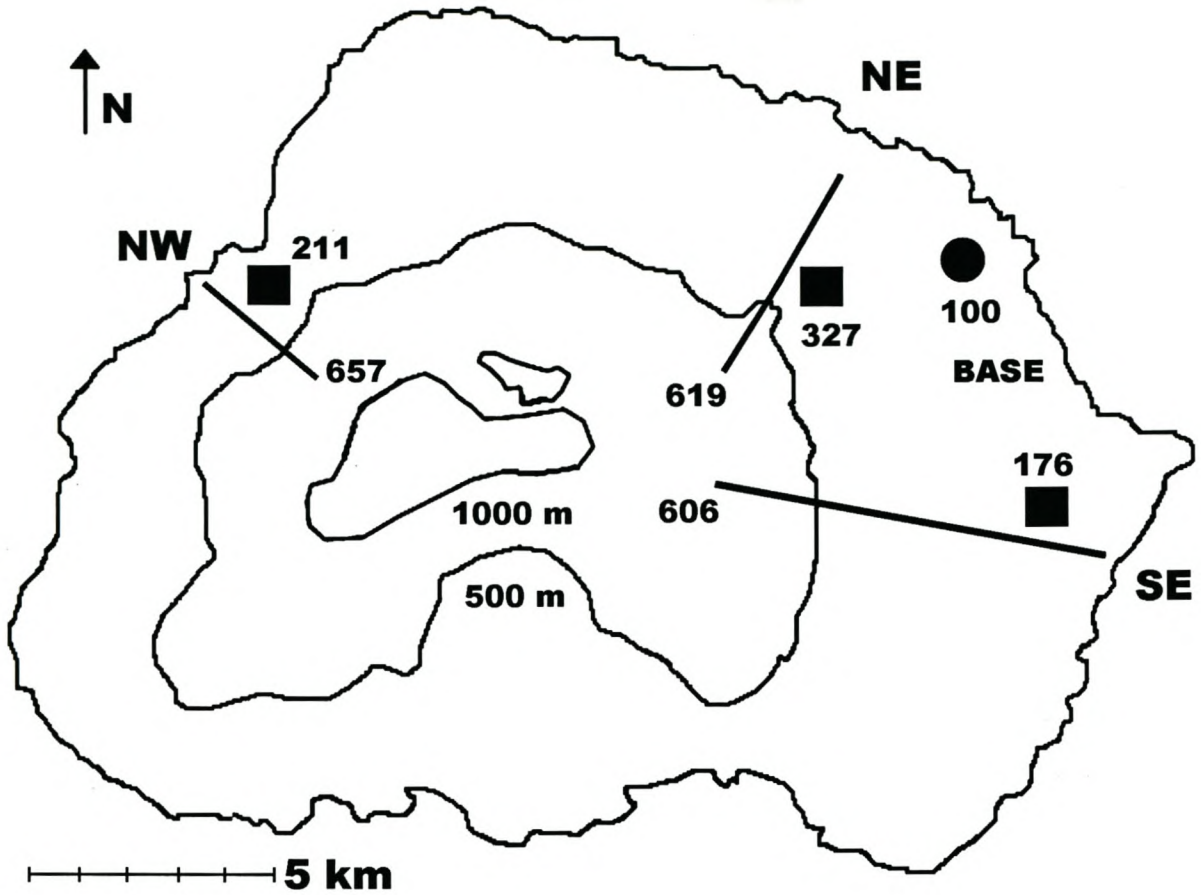


FIGURE 3. Schematic of Marion Island indicating the location of the study sites (transects - straight lines; quadrats - squares; site of experiment - circle) and the 500 and 1000 m a.s.l. contour lines. The maximum altitude (in m a.s.l.) of each transect, the mean altitude of each quadrat and the site of the experiment, and the location of the scientific base and meteorological station (Base) are also indicated.

Chapter 2: The use of size as an estimator of age in the sub-Antarctic cushion plant, *Azorella selago* (Apiaceae)

Introduction

Rising concern about the effects of current environmental change has led to increased interest in past environments (Bluemle et al., 1999; Trotter et al., 2002). However, the scarcity of historical records and information from long-term monitoring programs has necessitated the reconstruction of past environmental conditions from proxy records of climate and geomorphology (e.g. Bluemle et al., 1999; Mann, 2002). For example, dendrochronology, and in some cases lichenometry, has been used to reconstruct local temperature and precipitation levels (e.g. Vogel et al., 2001; Cook et al., 2002), glacial fluctuations, debris flow and snow-avalanche frequencies (McCarroll, 1993; Winchester and Harrison, 1994; Winchester and Chaujar, 2002) and to estimate the age of landforms and surface features (Winchester and Harrison, 2000; Bradwell, 2001). Compared to methods such as the analysis of isotope ratios or pollen records, phytometric techniques (i.e. the use of plant growth or performance as a surrogate for an unmeasured variable) can potentially provide information on comparatively more recent environments and at finer spatial and temporal scales (Callaghan et al., 1989; Trotter et al., 2002).

Although most widely applied, dendrochronology and lichenometry are not the only phytometric methods that have proved useful for estimating the age of individual plants and the minimum time since substrate disturbance. For example, Callaghan et al. (1989) estimated the age of *Cassiope tetragona* (Ericaceae, evergreen dwarf shrub) in the Arctic from seasonal patterns in the sizes of leaves produced. Methods such as this are particularly useful because they extend the application of phytometric methods to higher latitudes, where trees and known-age sites may be absent (often precluding the use of traditional dendrochronology and lichenometry respectively; although see e.g. Elvebakk and Spjelkavik, 1995; McCarthy, 2003). Indeed, it is in the polar and sub-polar regions where long-term environmental data is especially valuable, because the rate and magnitude of climate change is high in these areas, and is predicted to remain so (IPCC, 2001).

Previous studies have demonstrated the phytometric potential of cushion plants (dicotyledonous plants with a cushion-type growth form) (e.g. McCarthy, 1992;

Molau, 1997), which are a conspicuous component of high latitude vegetation (particularly in the southern hemisphere; Aleksandrova, 1980). In the sub-Antarctic (Kerguelen Island), Frenot et al. (1993) estimated the age of the cushion plant *Azorella selago* Hook. (Apiaceae) as the ratio of plant size to annual growth. *A. selago* is a long-lived species with a wide altitudinal range and broad geographic distribution in the sub-Antarctic. As a result, the species could potentially be used to estimate the age of landforms and contribute to the understanding of geomorphological processes across the region (see e.g. Winchester and Harrison, 2000; see Hall, 2002 for review of sub-Antarctic periglacial landforms and processes).

The results of any phytometric analysis must, however, be interpreted cautiously. In dendrochronology, for example, missing annual growth rings, false rings, irregular growth patterns and incorrect sampling height can lead to false age estimates (Vogel et al., 2001; Niklasson, 2002). Lichenometric analyses have similar problems and simplistic assumptions that disregard lichen biology, ignoring in particular the spatial and temporal variability of growth rates due to local differences in habitat, climate and competition (McCarthy, 1999; Winchester and Chaujar, 2002), reduce the method's reliability. Therefore, researchers in the field have highlighted the importance of testing the assumptions of phytometric methods and of recognizing their limitations (McCarthy, 1997, 1999; Winchester and Harrison, 2000; Trotter et al., 2002).

The phytometric model outlined earlier implicitly assumes plant growth rate to be independent of space and time, and to vary randomly around a mean growth rate for the extent of the area examined. If growth rate varies in a non-random fashion (e.g. in response to competition or variation in local habitat suitability), then mean site growth rate will not be representative of the annual size increase of all plants at a site. This may greatly reduce the reliability of plant age estimates. However, the validity of these assumptions, and the effect of their likely violation on age estimates, can currently not be assessed because there are few published studies documenting the growth of *A. selago* (Huntley, 1972; Frenot et al., 1993, 1998).

The objective of this study was thus to test if the phytometric model (outlined by Frenot et al., 1993) can potentially provide unbiased and accurate age estimates for *A. selago* on sub-Antarctic Marion Island (Prince Edward Islands: 46°55'S, 37°45'E). We quantify the spatial variability in *A. selago* and evaluate the effect of this variability on the accuracy of the phytometric model. The relationships between plant

growth rate, plant size and a suite of spatial (altitude and position on the island which are used as surrogates for abiotic environmental variation) and biotic (nearest neighbour characteristics and epiphyte load) variables were examined 1) to test the phytometric model's assumption that growth rate varies independently of plant size, and 2) to identify the relative influence of spatial location and selected biotic variables on plant size and growth rate. A simulation model is used to evaluate the sensitivity of the phytometric model's age estimates to the variability around mean site growth rate found. These results are then used to evaluate the efficiency of *A. selago* as a phytometer.

Methods

Azorella selago and the phytometric model

Azorella selago is a cushion-forming perennial that grows in a variety of habitats, and is able to colonize recently deglaciated and high-altitude areas (Huntley, 1972; Frenot et al., 1993). It often dominates the vegetation of these habitats (Huntley, 1972), and is widespread across the sub-Antarctic (Moore, 1968; Frenot et al., 1993).

Azorella selago cushions are commonly hemispherical on Marion Island, with short stems carrying simple leaves and growing radially from the center of each plant (Orchard, 1989). At the plant's surface both the leaves and the stems grow tightly against each other, creating a hard and compact surface. *A. selago* leaves turn brown at the start of the austral winter, and discontinuities in the colour of leaves retained on the stem allow up to the past five years' growth to be determined (a method requiring destructive sampling; used by Frenot et al., 1993). Alternatively, the growth rate of *A. selago* plants can be measured by quantifying annual increases in the size of each plant (a non-destructive method facilitated by the plants' compact surface; used by Huntley, 1972). In this study, Huntley's (1972) non-destructive method was considered more appropriate for use within a conservation area.

Frenot et al.'s (1993) model estimated plant age as:

$$\text{Age (years)} = \frac{\text{Size (mm)}}{\text{Growth rate (mm/year)}} \quad \dots \text{Eq. 1,}$$

where size was measured by plant diameter and growth rate as the annual increase in plant diameter. On Marion Island, growth rate was measured as the annual increase in

plant height, and accordingly plant size was measured as plant height. In this study we used vertical growth rather than radial growth (following Huntley, 1972), because vertical growth markers were considered to be less damaging to the plant and less susceptible to disturbance. The assumptions and rationale of Frenot et al.'s (1993) model are identical regardless of the measure of plant size (and its associated measure of growth rate) used.

Study sites

Marion Island (46°55'S, 37°45'E; the larger of the two Prince Edward Islands) experiences an oceanic climate, characterized by low (mean temperature in warmest month 7.3 °C, and in coldest month 3.2 °C) but stable temperatures (mean diurnal variation 1.9 °C), high relative humidity (on average 83 %), cloud cover and rainfall (approximately 2500 mm per annum, distributed evenly throughout the year), and strong winds (dominated by prevailing westerly winds; exceeding gale force on more than 100 days per year: Schulze, 1971). Marion Island is of volcanic origin and has a dome-like profile, rising to 1230 m a.s.l. (Verwoerd, 1971). Three transects and three quadrats of *A. selago* were sampled between April 2001 and April 2002 (see Fig. 3, Chapter 1, page 15). Transects were orientated along the altitudinal gradient on the island and each comprised 100 plants (although the length of transects differed due to topographical differences between the eastern and western sides of the island; see Fig. 3, Chapter 1, page 15). Transects began at the highest altitude plant in the area, and successive plants were sampled every 4 - 6 m decline in elevation thereafter. Plants were selected to be representative of surrounding plants, although only plants > 0.15 m in diameter were considered. The transects included both grey (older and undulating due to glacial erosion) and black (younger and more irregular) lava (Verwoerd, 1971). Although detailed mesoclimatic data are not available for the island, higher altitude sites are colder, windier and cloudier than lower altitudes, and rainfall is maximal at intermediate elevations (Blake, 1996). A quadrat of 200 plants (> 0.15 m diameter) was surveyed adjacent to each transect (see Fig. 3, Chapter 1, page 15). All plants within the demarcated 200-plant area, including those < 0.15 m diameter, were measured. Only the size, and not the growth rate and relative position, of small plants (i.e. < 0.15 m diameter) were determined, because of the risk of measurement-related damage resulting in their mortality.

Plant measurements

Each plant was marked with an aluminum tag. A thin (≤ 10 mm diameter) wooden rod (growth-rate marker) was carefully inserted vertically into each plant and into the underlying soil. Growth-rate markers were inserted approximately halfway between the center of a plant and its perimeter. By marking the height of the plant against the marker immediately after insertion and again before removal one year later, annual vertical growth (hereafter growth rate; $\text{mm}\cdot\text{year}^{-1}$) was determined for each individual (following Huntley, 1972). These growth-rate markers were inserted as deeply as possible into the soil underlying the plant to limit any potential movement by frost-heave. Depth of freeze-thaw on Marion Island is shallow, reaching a maximum depth of 0.2 m at high altitudes in open soils (Boelhouwers et al., 2003). Thus, because our growth-rate markers were inserted approximately 0.15 m into the soil underneath plants, and because cushion plants buffer the temperature of underlying soil (see e.g. Arroyo et al., 2003), frost-heave did not affect the plant vertical growth measurements taken in this study. Nonetheless, growth-rate markers that showed any signs of dislodging as a result of any disturbance (approximately 12 % of the 900 growth-rate markers) were excluded from analyses.

Three size measurements were taken for each plant, i.e. maximum diameter, diameter perpendicular to the maximum diameter (hereafter perpendicular diameter), and height of the plant. Height was determined by measuring the vertical distance between the highest point of the plant surface and the ground beneath it using a stadia rod. The relative position of each individual ($> 15\text{cm}$ diameter) within a quadrat or transect was determined using a Nikon Total Station DTM350 Theodolite, with an accuracy of 10 mm (Anonymous, 2001). The altitude of the highest plant in each transect was determined using a Garmin 12MAP GPS, because no suitable known-points were available on the island to determine the exact altitude and geographic position using the theodolite (readings were cross-checked against a topographical map of the island: Langenegger and Verwoerd, 1971).

The influence of biotic and abiotic environmental conditions on plant growth rate and size were considered by examining the relationship between plant characteristics and selected variables. Our intention was not to identify mechanistic explanations for variability observed in *A. selago*, but rather to quantify variability in

plant characteristics and evaluate the effect of this variability on the accuracy of the phytometric model. This study was designed to encompass plants from as broad a geographic and altitudinal range on the island as possible, and in addition to measure those biotic variables thought to have the greatest likely impact on plant growth rate. First, the spatial position of the plants (i.e. locality co-ordinates of each plant within the quadrats and altitude of plants along the transects) was used as a surrogate for abiotic environmental variation (on the rationale that plants on different parts of the island and at different altitudes are exposed to different abiotic environmental conditions; see also Koenig, 2002). Thus, hereafter, the net influence of abiotic factors on plant characteristics are considered in analyses by inclusion of these spatial variables. Second, nearest neighbour characteristics and epiphyte load were measured directly, because these were the two biotic factors thought most likely to affect plant growth rate. The number of *Agrostis magellanica* (Lam.) Vahl (Poaceae) individuals growing epiphytically on each plant was counted as a measure of epiphyte load. This grass is the dominant epiphyte on *A. selago* on Marion Island, and at mid altitudes may cover up to 61% of the surface of plants (le Roux and McGeoch, unpublished). Within quadrats, the distance between each plant and its ten nearest-neighbours was calculated. Preliminary analyses showed that data for the two nearest neighbours explained the most variation in plant size and growth rate (hereafter 2NN distance). Therefore, the mean maximum diameter, perpendicular diameter, height and growth rate of the two-closest plants were also calculated (hereafter 2NN maximum diameter, 2NN perpendicular diameter, etc.). To ensure that nearest-neighbour distances were not overestimated for plants at the edge of the sampled quadrat, progressively more outer plants were excluded from analyses until the nearest-neighbour distances of the outermost plants were approximately similar to those of the central plants. This required the exclusion of the outermost 35 – 40 % of plants.

Analyses

Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference tests for Unequal N were used to identify which sites differed from each other in terms of plant size and growth rate. Logarithmic or square-root transformations were used to achieve normal distributions for all variables where necessary (normality assessed using Shapiro-Wilk's W test). Data from each site were analysed separately, except where

calculating mean plant size and growth rate across the island. Analyses were repeated with and without the inclusion of those plants that showed no vertical growth during the study period (approximately 15% of all plants measured; the size and epiphyte load of these plants did not differ significantly from those for which growth was recorded).

To test if variability in plant growth rate increased with plant size, the coefficient of variation (CV) of growth rate was determined for different plant size classes. The number of size classes used for these analyses was determined using Sturge's rule (Legendre and Legendre, 1998). The relationship between plant size class and its CV of growth rate (arcsine transformed) was then examined using simple linear regression (Collet, 1991).

Partial regression analyses

Potential biases in the model, and resulting biases in age estimates (i.e. any systematic deviation of the ages estimated by the phytometric model from the real ages of the plants sampled), were examined by considering the influence of spatial and biotic factors on plant size and growth rate. To identify the proportion of variability in plant size and growth rate explained by spatial (i.e. using geographic co-ordinates and altitude as a surrogate for environmental variation, see above) and biotic (i.e. nearest-neighbour characteristics, epiphyte load) variables, trend surface analysis and partial regression approaches to the analysis of spatially explicit data were used (Legendre and Legendre, 1998). This is currently one of the approaches adopted to incorporate spatial position into explanatory models, i.e. modelling the spatial variation in plant size or growth rate as a linear combination of biotic variables and geographic coordinates of each plant (see e.g. Brewer and Gaston, 2002; Lobo et al., 2002). This method also accounts for biases that may occur as a result of the spatial non-independence of data points (Legendre and Legendre, 1998). Trend surface analysis was thus performed on growth rate and plant size measures to test for spatial structure in these variables across the quadrats (transect data were analysed differently; see below). A third-order polynomial combining the geographic co-ordinates, X and Y, for each plant was fitted to each dependent variable using general linear models. The least significant term in each model was identified and excluded, and the model refitted to the data. Following the method described by Legendre and Legendre

(1998), this process (backwards elimination) continued until all remaining spatial terms contributed significantly to the model. The final model thus describes the broad-scale spatial trends (if any) of the variable modelled across the quadrat (Legendre and Legendre, 1998).

Biotic variables that contributed significantly to explaining variation in plant size and growth rate were then determined for each quadrat. Models of plant size and growth rate were again constructed by backwards elimination, with all environmental variables initially included (Growth rate = Plant size + 2NN distance + 2NN size + 2NN growth rate + Epiphyte load; Plant size = Growth rate + 2NN distance + 2NN size + 2NN growth rate). Epiphyte load was not included in plant size models because there was a significant relationship between plant size and epiphyte load (data pooled over quadrats; maximum diameter: $R^2 = 0.40$, $F_{1,456} = 309.44$, $p < 0.01$; height: $R^2 = 0.09$, $F_{1,456} = 45.42$, $p < 0.01$), and plant size places a limit on epiphyte load (see Lyons et al., 2000). Thereafter, partial linear regression analyses were conducted in which independent variables included the best-fit trend surface model variables (abiotic variables; *sensu* "spatial component": Legendre and Legendre, 1998), nearest-neighbour characteristics and epiphyte load (biotic variables; *sensu* "environmental component": Legendre and Legendre, 1998). In these partial regression analyses the variation in plant size or growth rate was divided into fractions representing the proportion explained by the biotic variables (A), either biotic variables or spatial (abiotic) terms (B: spatially structured biotic effect), the spatial terms (C), and remaining unexplained variation (D: Legendre and Legendre, 1998). This method identifies the relative contribution of the biotic and abiotic variables to the variation explained by a model, although it does not specifically quantify the importance of individual variables (Legendre and Legendre, 1998; see also Brewer and Gaston, 2002; Lobo et al., 2002 for application of this approach). Full models were considered statistically significant if they exceeded the Bonferroni-corrected, table-wide significance level ($\alpha = 0.05/18 = 0.0028$) (Rice, 1989).

The same method was then modified and applied to the plant size and growth rate data for each transect. Because plants in the transects were distributed across an altitudinal gradient, altitude (rather than geographic co-ordinates) was used as a surrogate for abiotic variation (i.e. included as the spatial component during variance partitioning), enabling the proportion of explained variability attributable to altitude to be calculated. The environmental component included in variance partitioning for the

transects was then also calculated (i.e. Growth rate = Plant size + Epiphyte load; Plant size = Growth rate).

Simulation model

Simulation models of plant ages were constructed to investigate the influence of variability in growth rate and plant size on plant age estimates. In the absence of temporal data, the observed spatial (between-plant) variability in growth rate was used as a surrogate for temporal variation in the growth rate of individual *A. selago* plants. Although the validity of this surrogacy approach cannot currently be assessed, the objective here was merely to demonstrate how the accuracy of age estimates is affected by variability in growth rate and plant size. Nine idealized plant sizes (heights) were selected to represent a range of plant sizes documented on Marion Island, i.e. 75, 150, 225, ...and 675 mm (while the greatest plant height sampled was 600 mm, larger plants were also observed on the island). These heights were each successively reduced by subtracting randomly-selected (with replacement) growth rate values chosen from a 'set of observed values' (described below), until plant height was reduced to, or less than, zero. Thus,

$$H - \sum_{j=1}^x y_j = h_j \quad \text{until } h_j \leq 0 \quad \dots \text{Eq. 2,}$$

where H = plant height (mm), y_j = growth rate ($\text{mm}\cdot\text{year}^{-1}$) value randomly chosen from the set of observed values used for the simulation, h_j = plant height j years ago, and x = plant age (years).

The number of times height was required to be reduced was then recorded as one simulated age for a plant of that size. This process was repeated 10^4 times to generate distributions of simulated plant ages for each plant size. The mean and one standard deviation around the mean (i.e. ± 68 % of simulated ages closest to the mean) were calculated for each distribution (two standard deviations around the mean, i.e. ± 95 % of simulated ages closest to the mean, were also calculated and are reported). This standard deviation (1 S.D.) provided a measure of the accuracy of the phytometric model's (Eq. 1) age estimates, assuming that accuracy is inversely proportional to the range of plant ages simulated for a plant of a given size.

The 'set of observed values' from which growth rate values (y_j) were selected comprised either i) all the growth rate values measured at a site, or ii) three sets of randomly generated values with normal distributions. These randomly generated growth rate distributions had identical means ($4.26 \text{ mm}\cdot\text{year}^{-1}$ = mean plant growth rate measured across Marion Island), but different standard deviations (2.9 (=observed S.D. of growth rate across Marion Island), 0.29, 0.029). Randomly generated growth rate distributions (ii) were used in addition to measured site growth rates (i), because the range of variability in growth rate in the measured data was low, and a greater range of variability was necessary to determine if variability in growth rate influenced the S.D. of age estimates. The relationship between variability in growth rate (measured as CV) and the S.D. of the age estimates was examined for both the measured (i) and generated (ii) data sets using simple linear regression. Changes in the S.D. of age estimates with plant size were similarly examined. Annual growth increments were selected ignoring possible temporal autocorrelation in growth rates. However, in the presence of temporal autocorrelation standard deviations are likely to be reduced, and the approach taken here is the more conservative. Moreover, the results of the simulation model are likely to underestimate the phytometric model's accuracy, because the range of growth rate values used are wide relative to those expected for an individual plant over time (ranges of growth rate values used varied between 1.4 – 11.0 and 1.0 – 16.0 $\text{mm}\cdot\text{year}^{-1}$, which are ranges double that previously recorded for *A. selago*: Huntley, 1972; Frenot et al., 1993).

Results

Plant size, growth rate and age

The distribution of *A. selago* plant size and growth rate at each site were right-skewed, with the majority of plants ranging from 0.40 to 1.15 m in diameter (mean \pm S.E. (m): maximum diameter = 0.59 ± 0.01 , perpendicular diameter = 0.36 ± 0.01 , height = 0.13 ± 0.01 , $n = 1038$) (Fig. 1). The growth rate of plants ranged between 0.7 - 21.0 mm per year (mean \pm S.E. (mm) = 4.26 ± 0.11 , excluding plants not showing growth). The three plant size measurements were significantly positively related to each other (maximum diameter – height: $R^2 = 0.16$, $F_{1, 1036} = 202.24$, $p < 0.001$; perpendicular diameter – height: $R^2 = 0.21$, $F_{1, 1036} = 275.74$, $p < 0.001$), most strongly

so for maximum and perpendicular diameter ($R^2 = 0.58$, $F_{1, 1036} = 1432.92$, $p < 0.001$). As a result, only maximum diameter and height were used as plant size measures in subsequent analyses. Similar results were obtained when analyses were performed using growth rate data excluding or including plants showing zero growth and only results from analyses excluding zero growth plants are reported.

Growth rate was not related to plant height (all sites $p > 0.05$). In addition, there was no clear relationship between variability in growth rate and plant size (Table 1). The coefficient of variation in growth rate across plant size classes was high (between 50 and 65 %; Table 1). Plant size and growth rate differed significantly between sites on Marion Island (Fig. 2). Amongst the sites, the NE Transect had the largest plants, and plant growth rates were highest in the NE and NW Transects (Fig. 2).

Age estimates (from the phytometric model; Eq. 1), were found to be non-normally distributed ($p > 0.05$ for all sites) with right-skewed distributions (Fig. 1d). Mean plant age estimated for the six study sites ranged between 26 and 41 years (Table 1). The tallest plants in the NW and SE Transects were estimated to be the oldest sampled; 84 and 97 years old respectively (Table 1).

Partial Regression Analyses

Plant size and growth rate were weakly related to the explanatory variables measured in this study; less than 36 % of the variation observed in either size or growth rate was explained (Table 2). Variance partitioning, nonetheless, generally attributed most (3 - 16 %) of the explained variation to biotic factors ('A'; Table 2). Spatially-structured biotic factors ('B'; Table 2) accounted for an additional 0 to 19 % of the variability in plant characteristics (the small negative value in Table 2 merely indicates that the biotic and abiotic variables have effects of an opposite direction on plant growth rate in the NE Quadrat; Legendre and Legendre, 1998). Therefore, in the full regression models up to an additional 19 % of variability in plant size and growth rate could possibly be attributed to the biotic variables recorded in the study. However, this variability may equally be a result of some abiotic variable sharing a common spatial structure with the biotic variables (i.e. this proportion of explained variation cannot be confidently attributed to either category; Legendre and Legendre, 1998). Finally,

abiotic variables ('C', Table 2) accounted for between 0 to 27 % of observed variability in plant size and growth rate.

Biotic variables

Among the biotic variables, plant size (height and diameter) in the quadrats was consistently significantly related to the distance and size of nearest neighbours (Table 2). The mean maximum diameter of the two nearest neighbours (2NN) was always significantly positively related to plant maximum diameter (Table 2, Fig. 3). Similarly 2NN distance and 2NN height were significantly positively related to plant diameter and height respectively (Table 2). While the strength of these relationships varied, nearest-neighbour characteristics were the most consistent predictors of plant size in the quadrats.

Both epiphyte load and altitude contributed significantly to explaining plant size and growth rate, although these relationships were neither strong nor consistent. Epiphyte load was significantly negatively related to plant growth rate in two of the models and positively in one (Table 2). Altitude contributed significantly to explaining plant height or growth rate in three of the transect models (Table 2). Plant height declined significantly with increasing altitude in two cases, whereas plant growth rate increased with altitude in one of the models (Table 2). Therefore, in addition to nearest-neighbour characteristics, in some cases plant size and growth rate were related to altitude and epiphyte load.

Simulation model

Simulation model results showed that the magnitude of one S.D. around the mean plant age estimate is influenced by the size of the plant being aged, as well as the variability in site growth rate. Variability in growth rate and the standard deviation around mean age were significantly positively related in the three randomly generated data sets (generated with low, medium and high variability in growth rate; for all plant sizes: slope estimates > 0.65 , $R^2 > 0.9$, $F_{1, 1} > 100.0$, $p < 0.05$). However, no significant relationships were found between the accuracy of age estimates and the variability in growth rate for the measured data sets (for all plant sizes: $F_{1, 4} < 0.27$, $p > 0.5$). Using both measured and generated growth rate distributions (i and ii in

Methods), the standard deviation around the mean estimated age increased significantly with plant size (all data sets: slope estimates between 0.001 - 0.008, $R^2 > 0.9$, $F_{1,7} > 64.0$, $p < 0.01$, except for the generated data set with the least variation in growth rate, since S.D. of simulated ages was zero for some size classes; Table 3). Therefore, within any particular site, small plants (i.e. 75 mm tall) could be aged more accurately (S.D. = 1.8 – 2.6 years) than large plants (600 mm tall: S.D. = 4.9 – 6.0 years; using the observed growth rate data, Table 3). Averaged over all plant sizes, the mean accuracy of age estimates (i.e. averaged across the second row of all plant heights in Table 3) was approximately 4.5 years.

Discussion

The results of this study confirm the potential of *A. selago* as a phytometer for estimating minimum landscape age. The first assumption important for the use of Frenot et al.'s (1993) phytometric model to estimate the age of *A. selago* was supported, i.e. that plant growth rate is independent of plant size. However, the second assumption was not supported, because plant characteristics were related to biotic and abiotic factors, and differed across the island. As expected, plant characteristics were not independent of site-specific habitat or environmental characteristics and age estimates could, as a consequence, be biased. In addition, variability in growth rate was high across all plant size classes, and was shown to reduce the accuracy of plant age estimates. Although these findings highlight limitations for the application of *A. selago* as a phytometer, they also suggest possible avenues for improving the reliability of the phytometric model.

Azorella selago sizes and growth rates observed in this study were within the ranges reported from previous studies in the sub-Antarctic (Moore, 1968; Huntley, 1972; Frenot et al., 1993; Frenot and Gloaguen, 1994; Frenot et al., 1998). For example, the results of the phytometric model (albeit in the absence of support for one of its two assumptions) confirm that *A. selago* plants are long-lived. The age of the oldest individuals sampled in this study ranged from 55 - 96 years. This is comparable to plants on Kerguelen Island (Frenot et al., 1993). Some between-island and -study differences in plant characteristics were, however, apparent. For example, an extremely tight link between plant diameter and height was quantified for Kerguelen Island ($R^2 = 0.93$; Frenot et al., 1993), whereas the same was not true on Marion

Island ($R^2 = 0.16$, this study). Frenot et al.'s (1993) radial growth rate estimates were lower than the mean vertical growth rate observed here ($t = 5.63$, d.f. = 590, $p < 0.01$). Similarly, Huntley's (1972) estimates of vertical growth rate on Marion Island were also lower than those observed in this study. However, because *A. selago* has not been extensively surveyed on these islands, and because we show within-island variability to be high for Marion, between-island comparisons remain premature.

Plant size and growth rate have to date not been found to be related in *A. selago* (Frenot et al., 1993; this study). Therefore, despite the high spatial variability observed in growth rate, the use of a linear function to model the relationship between size and age for the species is justified. The phytometric model's second assumption was, however, violated by the demonstration that plant size and growth rate on Marion Island differed between sites, and that these variables were, at least partly, related to biotic and abiotic variables. Much stronger relationships were found between plant size, rather than growth rate, and environmental characteristics. Plant size is, nonetheless, a cumulative product of growth rate over time and thus also contributes to the violation of this assumption. Therefore, the dependence of plant characteristics on environmental variables will result in biased plant estimates.

These between-site differences versus within-site variability in plant characteristics have different implications for the application of the phytometric model. First, between-site differences in plant growth rate highlight the importance of site-specific growth rate estimates. It is therefore not possible to estimate plant ages at one site on the island using growth rate data from another. Furthermore, the assumption that larger plants are older than smaller individuals is not necessarily true, especially when comparing plants from different sites. Second, the implication of within-site relationships between plant characteristics and environmental variables is that age estimates will be biased. One or more unmeasured variables are clearly also important determinants of plant characteristics, because more than 65 % of the variation in these characteristics was not explained. To reduce environmental bias in age estimates, the determinants of *A. selago* growth rate need to be identified. Variability in soil moisture and nutrients, wind exposure and snow cover, due to topographical and micro-climatic variation, are known to be important determinants of plant performance in arctic and alpine communities (Callaghan et al., 1997; Jumpponen et al., 1999), and are likely to be equally important in the sub-Antarctic (both at fine scales and between areas on single islands) (Frenot et al., 1993). A more

complete understanding of the determinants of plant growth rate may enable the incorporation of these variables into the phytometric model, reducing the effect of environmental bias on age estimates.

The usefulness of the phytometric model clearly depends on both the biases in, and the accuracy of, its results. For example, very accurate age estimates are of little worth if the model's answers are strongly biased by the effect of unaccounted for environmental variation. Similarly, unbiased age estimates are of limited value if their accuracy is very poor. While it is theoretically possible to remove bias from the model (e.g. by including major variables that influence *A. selago* growth rate), the accuracy of age estimates is determined by temporal variability in growth rate. Despite the importance of such variation, it has not been explicitly quantified for *A. selago* (although Frenot et al., 1993 noted no significant difference in mean plant growth rate over five successive years). If growth rate varied non-randomly over time, this would contribute to bias in plant age estimates. For example, if soil quality or climate (i.e. factors showing long-term trends) strongly influence plant growth rate, current short-term measures of growth rate may not be representative of historical growth rates (Trotter et al., 2002). By contrast, the effect of random temporal variation is a reduction in the accuracy of age estimates. This was demonstrated by the simulation model that showed that 1) age estimates for young plants are likely to be more accurate than those of old plants (see also Molau, 1997; Campana, 2001), and 2) with increasing temporal variability in growth rate there is decline in accuracy of age estimates. Under a simulated scenario of high temporal variability in growth rate (incorporated using the extent of between-plant variability in growth rates as a surrogate), a plant of 300 mm could, for example, be estimated with 68% probability as being between 68 and 77 years old. Generally, under this high temporal variability scenario plants could be aged to within 2-7 years with 68 % probability, and to within 4 – 15 years with 95 % probability. Therefore, except where high-resolution age estimates are required, the usefulness of the phytometric model may not be limited by the level of accuracy it provides. This would be particularly true where temporal variation in growth rate lower than that used in the simulation model here.

Phytometry using *A. selago* in the sub-Antarctic, like other phytometric techniques, must therefore necessarily rely on fairly detailed information on the spatial and temporal variability in the species and its environment (McCarthy, 1997). Data on the temporal variation in growth rate is required to quantify the accuracy of

the model's age estimates, although even the wide range of growth rates used in the simulation model produced age estimates accurate to within 2-15 years. Bias in the model may be reduced by developing a more complete understanding of the ecology of the plant species, identifying determinants of its growth rate and using site-specific growth rate estimates. Explicit inclusion of such information into the phytometric model for *A. selago* will improve its reliability and value as a tool for reconstructing past environmental conditions in the sub-Antarctic.

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TABLE 1

Coefficient of variation of growth rate (% CV) (across all size classes), and the results of the regression of CV against plant height classes for each site. Age (years) estimates for plants at each site also provided. Minimum ages not estimated for plants within transects.

Site	Coefficient of variation					Estimated plant age			
	CV %	n ¹	R ²	d.f.	F	Mean (± S.E.)	n ¹	Min.	Max.
SE Quadrat	51.7	147	0	1, 6	0.21	26.7 ± 0.6	256	6.9	55.0
NE Quadrat	58.8	127	0.15	1, 6	2.25	26.3 ± 0.6	240	5.3	64.4
NW Quadrat	53.1	157	0	1, 6	0.01	33.4 ± 0.8	242	2.1	83.0
SE Transect	50.3	72	0.83	1, 5	26.11*	41.0 ± 1.3	100	-	96.6
NE Transect	64.7	82	0	1, 5	0.02	29.2 ± 1.4	100	-	71.4
NW Transect	53.7	75	0	1, 5	0.83	26.3 ± 1.3	100	-	83.5

¹ number of plants, * significant at $p < 0.05$

TABLE 2. Proportion of variation in plant diameter, height and growth rate attributable to biotic and spatial variables. Standardized coefficient estimates are provided for the biotic variables and altitude to indicate the direction and magnitude of effects.

Variable	Quadrat	Independent variables ¹		Proportion of variation explained (%)				P <	
		(coefficient estimate)	Spatial terms	Total	Biotic; A ²	Biotic x Spatial; B ³	Spatial; C ⁴		
Diameter	SE	2NN Diam. ⁵ (0.36)	y, xy ² , y ³	24.04	9.93	12.65	1.46	F _{4, 114} = 10.34	0.001
	NE	2NN Diam. (0.21), 2NN Dist. (0.28)	- ⁶	13.78	13.78	-	-	F _{2, 90} = 8.35	0.001
	NW	2NN Diam. (0.06), 2NN Dist. (0.38)	y, y ² , y ³ , x ² , x ³	35.62	11.96	19.35	4.31	F _{7, 110} = 10.25	0.001
Height	SE	2NN Height (0.43)	y, x ² , x ² y, x ³	25.82	16.26	6.62	2.94	F _{5, 113} = 9.21	0.001
	NE	2NN Height (0.25)	-	5.42	5.42	-	-	F _{1, 91} = 6.27	0.014 ⁷
	NW	2NN Height (0.28)	x ² , xy, x ² y	21.29	5.14	12.39	3.76	F _{4, 113} = 8.91	0.001
Growth rate	SE	-	-	-	-	-	-	-	-
	NE	Diam. (-0.25), Epiphyte load (0.28)	x ² y, xy ²	10.96	3.55	- 0.02	7.41	F _{4, 89} = 3.86	0.006 ⁷
	NW	-	y, y ² , y ³	4.99	-	-	4.99	F _{3, 114} = 3.05	0.032 ⁷
Diameter	Transect								
	SE	-	-	-	-	-	-	-	-
	NW	Growth rate (0.28)	-	6.63	6.63	-	-	F _{1, 73} = 6.25	0.015 ⁷
Height	SE	-	Altitude (-0.47)	21.14	-	-	21.14	F _{1, 70} = 20.04	0.001
	NE	-	-	-	-	-	-	-	-
	NW	-	Altitude (-0.53)	27.43	-	-	27.43	F _{1, 73} = 28.96	0.001
Growth rate	SE	Diam. (0.20), Epiphyte load (-0.22)	Altitude (0.29)	18.47	3.52	9.58	5.37	F _{3, 68} = 6.36	0.001
	NE	Epiphyte load (-0.38)	-	13.48	13.48	-	-	F _{1, 80} = 13.62	0.001
	NW	Diam. (0.25)	-	5.19	5.19	-	-	F _{1, 73} = 5.05	0.028 ⁷

¹ Independent variables contributing significantly in final model (p < 0.05). ² Variation in plant characteristics explained by biotic variables. ³ Variation in plant characteristics explained by biotic and spatial variables, but which cannot be split between the two components. ⁴ Variation in plant characteristics explained by spatial variables. ⁵ 2NN Diam. = mean maximum diameter of two nearest neighbours, 2NN Dist. = mean distance to two nearest neighbours, 2NN Height = mean height of two nearest neighbours, Diam. = maximum diameter. ⁶ No significant contribution by variables. ⁷ Models no longer significant after significance levels adjusted using the Bonferroni table-wide alpha = 0.003.

TABLE 3

Simulated ages (mean simulated age and three measures of variability around that mean age, i.e. estimate of accuracy) for three idealised plant heights using measured growth rate data from the six study sites.

Plant height	Variable (years)	Quadrat			Transect		
		SE	NE	NW	SE	NE	NW
75 mm	Mean age	18.6	19.9	16.7	11.2	12.1	18.6
	1 S.D. around mean ¹	2.2	2.6	2.1	2.1	2.2	1.8
	2 S.D. around mean ²	4.4	5.2	4.2	4.2	4.4	3.6
	Min. – Max.	10 - 27	11 - 30	9 - 24	4 - 18	6 - 23	11 - 27
300 mm	Mean age	72.6	77.6	64.9	42.7	45.6	72.3
	1 S.D. around mean	4.3	5.2	4.2	4.2	4.3	3.5
	2 S.D. around mean	8.6	10.4	8.4	8.4	8.6	7.0
	Min. – Max.	57 - 89	54 - 97	50 - 82	30 - 56	30 - 65	57 - 92
600 mm	Mean age	144.7	154.6	123.2	84.8	91.1	144.5
	1 S.D. around mean	6.2	7.3	6.0	6.0	6.0	4.9
	2 S.D. around mean	12.4	14.6	12.0	12.0	12.0	9.8
	Min. – Max.	121 - 172	129 - 182	106 - 150	65 - 104	70 - 116	124 - 168

¹ Approximately 68 % of simulated plant ages fall within the mean age \pm 1 S.D., ² Approximately 95 % of simulated plant ages fall within the mean age \pm 2 S.D.

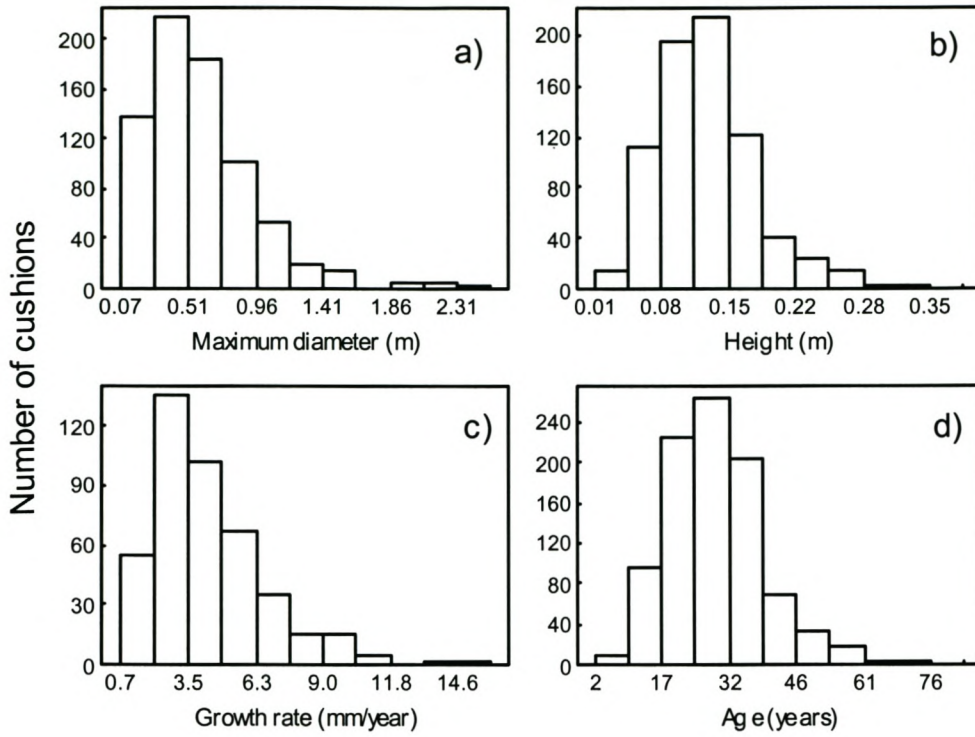


FIGURE 1. Frequency distributions for *Azorella selago* cushion plants across all quadrats of a) maximum diameter ($n = 738$), b) height ($n = 738$), c) growth rate ($n = 527$), d) estimated plant age ($n = 738$, using mean growth rate for each quadrat to estimate age).

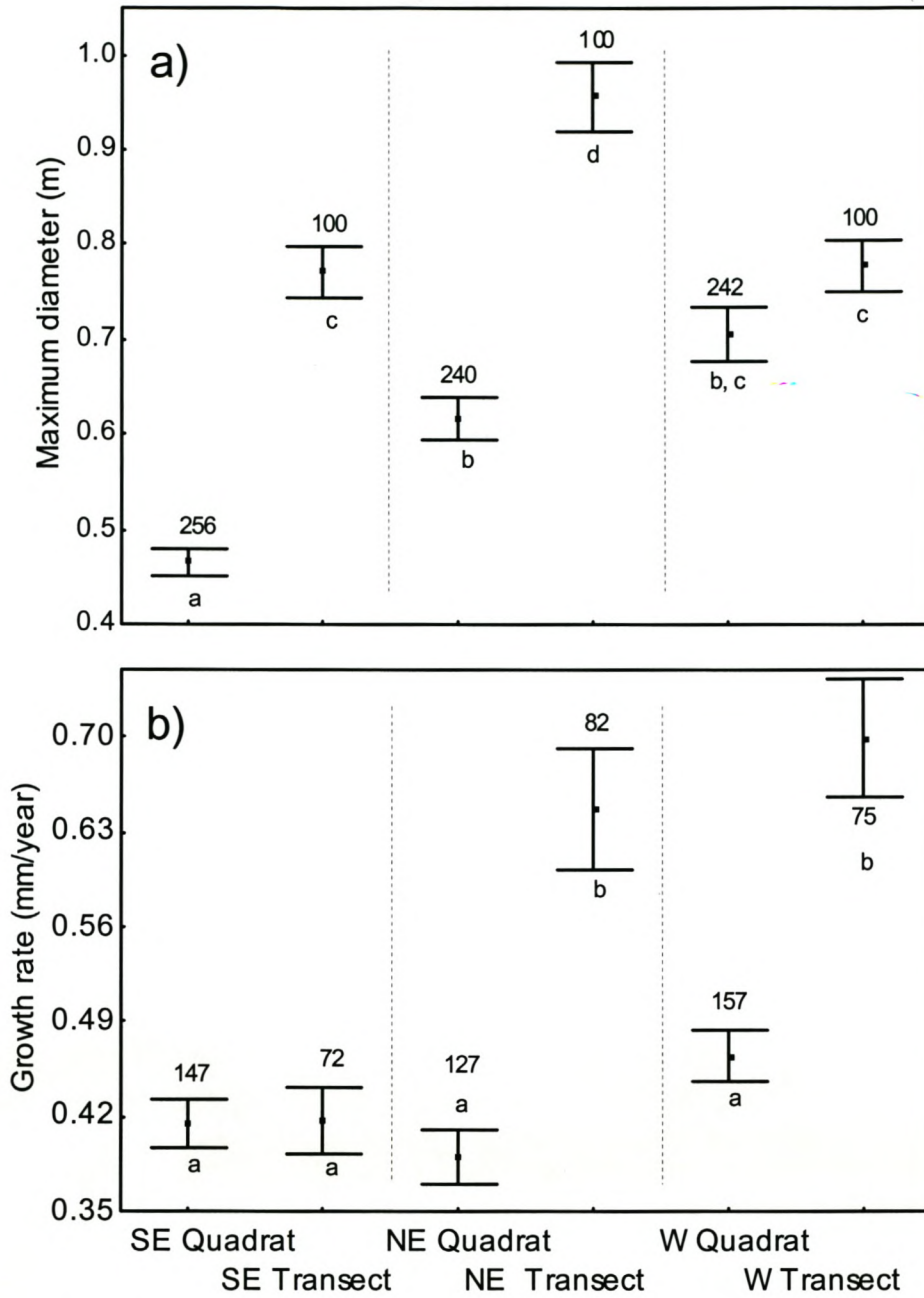


FIGURE 2. Mean (\pm S.E.) a) maximum diameter and b) growth rate of *Azorella selago* plants sampled at each site. Number above whiskers indicates sample size. Sites not sharing a letter (below whiskers) were significantly different at $p < 0.05$.

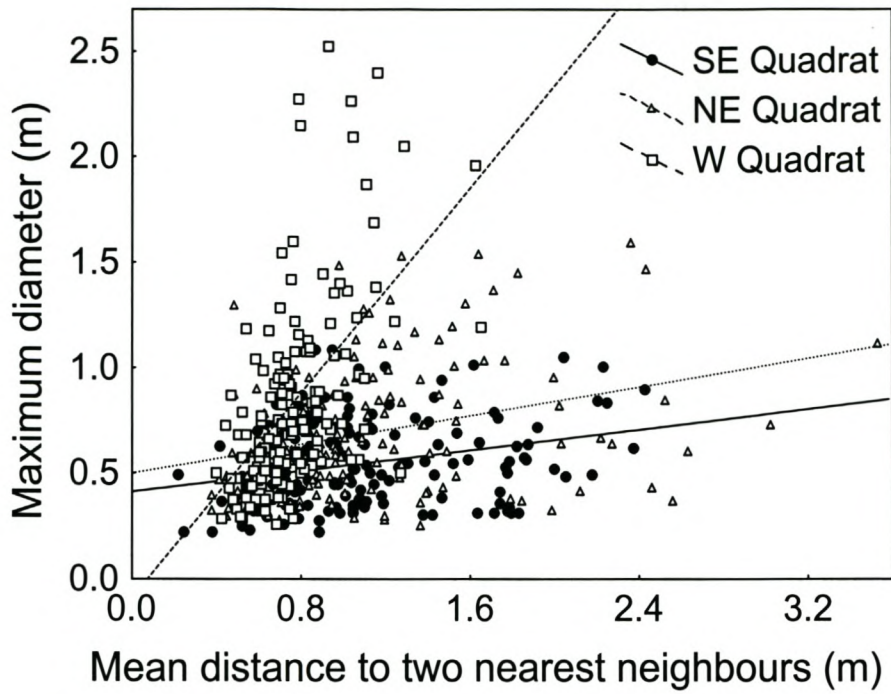


FIGURE 3. Relationships between Azorella selago plant maximum diameter and distance to its two nearest neighbours for each quadrat (simple linear regression lines fitted for illustration, see Table 2 for full model results).

Chapter 3: Altitudinal variation in the sub-Antarctic cushion plant *Azorella selago* and its epiphytes

Introduction

Altitudinal gradients are suited to studying the relationship between plants and their environment, because even a narrow altitudinal range can encompass a steep environmental gradient (Bowman et al., 1999; Körner, 2000; Md Nor, 2001). Indeed, the morphology and physiology of many plant and animal species vary markedly across altitude in direct response to climatic variation (e.g. Kudo, 1995; Schoettle and Rochelle, 2000; Chown and Klok, 2003). For example, the growth of *Pinus sylvestris* (Pinaceae) declines with increasing altitude due to lower temperatures at higher elevations (James et al., 1994). Similarly, mechanisms that protect plants from damage from UV-B radiation have been shown to increase over a 2000 m elevational range corresponding to a gradient of increasing radiation (Filella and Peñuelas, 1999). The aggregate effect of such within-species variation across altitudinal gradients is that community-level changes also occur across altitude (e.g. differences in vegetation structure, species richness and composition, production: Begon et al., 1996; Brown, 2001; Mark et al., 2001; Andrew et al., 2003). Therefore, both species and community characteristics commonly vary with altitude as a consequence of elevational differences in environmental factors.

Field-based gradient studies of plant-environment relationships (e.g. along an altitudinal gradient) offer several advantages over experimental studies with the same objectives (Hodkinson and Wookey, 1999). Gradient studies are able to identify the effects of one set of environmental variables, while controlling for the effects of others. For example, using an altitudinal transect, the influence of climatic variables (e.g. temperature, rainfall and wind) can be examined, while minimizing broad-scale differences in photoperiod, vegetation type, geology and ecological history (Fielding et al., 1999; Körner, 2000; Brown, 2001; Smith et al., 2002). Additionally, species distribution and abundance patterns along altitudinal gradients represent long-term responses to a gradual spatial change in natural conditions (Rustad et al., 2001). In contrast, experimental studies generally observe short-term responses to sudden changes in environmental conditions, often in artificial environments (e.g. laboratory studies).

With increasing interest in the biological consequences of climate change, biotic differences (i.e. within-species or between-community variation) along altitudinal gradients have been used to forecast the potential biological effects of changes in climate (Hodkinson and Bird, 1998; Fielding et al., 1999; Tweedie, 2000; Smith et al., 2002). For example, vegetation at warmer, low altitude sites is used as an analogue for the response of plants at colder high altitude sites to increased temperatures. Similarly, the vegetation structure of windier high elevation sites can be used to forecast the potential effects of increased winds on plants at lower sites. Using this approach, Tweedie (2000) predicted increased leaf production and reproductive output for six plant species on sub-Antarctic Macquarie Island under a scenario of climate warming.

However, predictions of species (and community) responses to climate change based on changes along an altitudinal gradient must be made cautiously, since altitude is only a “distal” predictor of vegetation patterns (Austin, 2002). In other words, altitude (an indirect gradient) does not directly determine the vegetation at a site, but is only correlated with the causal (“proximal”) mechanism (i.e. a direct gradient, like temperature or rainfall: Austin et al., 1984; Austin, 2002). Since multiple environmental variables change simultaneously across altitude, causality cannot confidently be attributed to a single environmental factor (Cavelier, 1996; Halloy and Mark, 1996; Pausas and Austin, 2001; Austin, 2002). Therefore, for example, the biological consequences of changes in temperature will be reflected in the differences in the species and communities along an altitudinal gradient, although these differences will also reflect their responses to other factors that vary along the same gradient.

Interpretation of altitudinal patterns are complicated by at least two other factors. First, fine-scale variation in micro-environmental conditions can veil larger-scale altitudinal patterns (Halloy and Mark, 1996; Andrew et al., 2003). For example, Smith et al. (2002) attributed their lack of significant altitudinal trends in microbial activity to high local-scale variability. Second, the upper and lower altitudinal boundaries of species (or communities) may be determined by different factors (analogous to species’ northern and southern distributional boundaries: Parmesan et al., 1999; Thomas and Lennon, 1999; Gaston, 2003). For example, the upper elevational limit to montane rainforest is determined by temperature and its lower boundary by competition (Cavelier, 1996). Thus, considering these limitations,

altitudinal patterns should be viewed as a heuristic tool for hypothesis generation and for understanding the sensitivity, and the potential responses, of vegetation to changes in climate, rather than as a basis for the prediction of vegetation patterns under altered climates.

A species that occurs across a wide range of altitudes is the cushion plant *Azorella selago* Hook. (Apiaceae). *Azorella selago* is widespread across the sub-Antarctic (even occurring in the southern portions of South America), and covers a wide altitudinal range within its geographic distribution (Moore, 1968; Huntley, 1972; Gremmen, 1981; Frenot et al., 1993). For example, the species occurs between 450 and 1150 m a.s.l. on Tierra del Fuego (Orchard, 1989; Mark et al., 2001; see also Gremmen, 1981). On sub-Antarctic Marion Island, *A. selago* has the widest altitudinal distribution of any vascular plant, occurring from sea-level to 765 m a.s.l., the altitudinal limit of vascular plants on the island (Huntley, 1970). Across this altitudinal extent the species experiences a wide range of environmental conditions. For example, higher altitudes on Marion Island are colder, drier and windier, with deeper soil freezing and less solar radiation, than lower altitudes (Schulze, 1971; Blake, 1996; Boelhouwers, 2003; Holness, 2003; J.A. Deere, unpublished; M. Nyakatya, unpublished; Fig. 1). In addition, it seems that rainfall and the frequency of freeze-thaw events both peak at mid-altitudes (Blake, 1996; Boelhouwers, 2003; Holness, 2003; Fig. 1).

Across its altitudinal range a diversity of vascular and non-vascular plants grow epiphytically on *A. selago* plants (Huntley 1972). Because these epiphytes alter the microclimate experienced by the cushion plants (e.g. reduce solar radiation and wind, and buffer temperature and moisture regimes; see e.g. Arroyo et al., 2003; Freiberg, 2001), they potentially affect the performance of the cushion plants, although the form of this relationship is still unclear (e.g. see Table 2, Chapter 2, page 36). Equally poorly known is the altitudinal distribution (i.e. extent) of individual epiphyte species as well as the altitudinal variation in epiphyte species richness on the island. The distribution of individual epiphyte species along the elevation gradient identifies the environmental factors potentially important for determining their upper and lower altitudinal limits, and therefore allows some (preliminary) predictions of the effects of changes in climate on these species. Similarly, matching the current altitudinal variation in epiphyte species richness to environmental gradients helps to

formulate likely scenario's of shifts in species richness with further changes in climate on Marion Island.

The objective of this study was thus to quantify altitudinal variation in *A. selago* cushion morphology, leaf morphology, surface cover and epiphyte species composition across three transects on Marion Island. Fine-scale variability in these attributes is also determined at a single site along each transect, and compared to transect-scale variability. These altitudinal patterns are then related to the environmental gradients on the island, and hypotheses generated on the influence of abiotic and biotic factors on the characteristics of *A. selago* cushions and their epiphyte communities.

Methods

Study species

Azorella selago is a long-lived, cushion-forming vascular plant species that is widely distributed across the sub-Antarctic (Huntley, 1972; Frenot et al., 1993). It is a pioneer species, colonizing loose scoriaceous slopes, recent lava flows and glacial forelands of retreating glaciers (Huntley, 1972; Frenot et al., 1998). The species is common in a variety of habitats, and on Marion Island is the dominant vascular plant species in the cold, wind-swept fellfield habitats (Moore, 1968; Huntley, 1972; Gremmen, 1981). Other *Azorella* species occur on the sub-Antarctic Macquarie Island (*A. macquariensis*: Orchard, 1989), the lower latitude Falkland Islands (4 spp.: Moore, 1968) and throughout the high latitude and altitude areas of South America (more than 70 species, including the widespread *A. compacta*: Wickens, 1995).

Azorella selago cushions have a central taproot, from which stems arise radially and branch dichotomously (Frenot et al., 1993). Its leaves are lobed (deeply incised, forming finger-like leaflets), with widened petioles forming a sheath around the stem (Orchard, 1989). Cushion growth stops in autumn, and by winter all leaves have turned brown (autumnal senescence). Old leaves are retained, forming a rich, moist, humus-like collection of organic matter inside the plant (Huntley, 1971; see also Ashton and Gill, 1965).

Azorella selago cushions have a hard and compact surface as leaves are tightly packed and stems grow closely against each other (Orchard, 1989). However, even in

summer (i.e. no autumnal senescence), few cushions have a completely green surface. Cushions can be covered by patches of dead stems (black or grey in colour), spaces between stems (“gaps”; but usually restricted to sheltered plants), and epiphytes.

Cushions can host dense and diverse epiphyte (Huntley, 1972) and invertebrate communities (Barendse and Chown, 2001). The most common epiphytes on *A. selago* on Marion Island include the grass *Agrostis magellanica* (Lam.) Vahl (Poaceae; see Fig. 1, Chapter 1, page 13), the low scrambling shrub *Aceana magellanica* Vahl (Rosaceae), and the fern *Blechnum penna-marina* (Poir) Kuhn (Polypodiaceae). Other epiphyte species include the mat dicot *Ranunculus biternatus* Sm. (Ranunculaceae), the rosette dicot *Cotula plumosa* Hook. f. (Asteraceae), the tussock grass *Poa cookii* Hook. (Poaceae), and a variety of mosses, lichens and liverworts (Huntley, 1972). These species can be regarded as facultative or casual epiphytes (following Benzing, 1989 and Kress, 1989) respectively), since a single population, at least at low altitudes, will contain some individuals growing on cushion plants (i.e. showing epiphytism) and others growing in the soil.

Study sites

Azorella selago was surveyed in three transects and three quadrats (six sites) on Marion Island (46°55'S, 37°45'E; the larger of the two Prince Edward islands) between April 2001 and April 2002 (same plants as used in Chapter 2). Two transects were on the eastern side of the island (running along Long Ridge and Stoney Ridge; the north-east and south-east transects respectively), while the third (ending at Mixed Pickle Cove; north-west transect; see Fig. 3, Chapter 1, page 15) was on western side. Transects were orientated along the altitudinal gradient on the island and each comprised 100 cushions. Transects began at the highest altitude cushion in the area, and successive cushions were sampled every 4 - 6 m decline in elevation thereafter. Cushions were selected to be representative of surrounding cushions, although only cushions > 0.15 m in diameter were considered (smaller cushions were not selected because of the risk of measurement-related damage resulting in their mortality). The transects mainly covered fellfield vegetation, although the lowest 15 – 30 cushions in each transect grew in fernbrake habitats (high *Aceana magellanica* and *Blechnum penna-marina* cover: Smith et al., 2001). The western transect was confined to black basalt lava flows. In contrast, the eastern transects were predominantly on older grey

lava (i.e. smoothed by glacial erosion), except for the highest 20 – 30 plants which were growing on black lava.

To determine fine-scale variation in cushion characteristics and epiphyte load, a quadrat was surveyed next to (approximately halfway along) each transect. Quadrat size was determined by the smallest area required to sample 200 cushions (> 0.15 m diameter). The quadrats were all located in fellfield habitat (Smith et al., 2001).

Altitudinal gradients on Marion Island

Altitudinal patterns in temperature, wind speed, radiation, rainfall and freeze-thaw events have been documented for Marion Island (Fig. 1). Mean air, soil and within-plant temperatures decline with increasing altitude (Blake, 1996; Boelhouwers, 2003; Holness, 2003; J.A. Deere, unpublished; M. Nyakatya, unpublished). In contrast, wind speed increases consistently with altitude (Blake, 1996), consistent with predictions (Schulze, 1971). Solar radiation declines with altitude, although photon flux density does not differ between elevations (Blake, 1996). Total rainfall was found to peak at a mid-altitude site (550 m a.s.l.), and was lowest and most erratic at the highest altitude measured (Blake, 1996). However, the relationship between rainfall and the amount of water actually available to plants (plant-available moisture) is less clear, because the warmer conditions at low altitudes and the stronger winds at high altitudes increase evaporation rates (Ashton and Gill, 1965; Gremmen, 1981). Furthermore, altitudinal variation in infiltration rates, soil depth and soil water holding capacity has not been documented for the island, and may vary greatly across elevations. However, since such data are not available, we assume that rainfall is a suitable surrogate for plant-available moisture. Marion Island also exhibits an altitudinal gradient in the duration and frequency of freeze-thaw events. Mid altitudes experience freeze-thaw events most often, with lower altitudes experiencing fewer of these cycles (Boelhouwers et al., 2003). Higher altitudes also experience fewer cycles than mid altitudes, but they are of longer durations and with deeper soil freezing than other altitudes (Boelhouwers et al., 2003).

Ground cover and vegetation also change over the altitudinal gradient on Marion Island. Rock cover increases with altitude (data in Smith et al., 2001), causing increasingly uneven surface cover at higher elevations, and creating a diversity of microhabitats (Gremmen, 1981). Total plant cover and the richness of vegetation

types is highest at low altitudes, declining with increasing elevation (data in Smith et al., 2001). Primary production is highest in the vegetation types that are most common at low altitudes (compared to those at higher altitudes: Smith, 1978), and therefore was assumed to decline with altitude.

These patterns are probably similar across all three transects, although some differences potentially exist. Most importantly, the western side of the island has recently been shown to be cooler than the east (within-plant temperatures; M. Nyakatya, unpublished), and probably experiences greater net precipitation and winds due to its exposure to the dominant westerly winds (Schulze, 1971; Gremmen, 1981).

Cushion plant measurements

Before the start of the 2001-2002 growing season, three size measurements were taken for each cushion, i.e. maximum diameter, diameter perpendicular to the maximum diameter (hereafter perpendicular diameter), and height of the plant. The number of *Agrostis magellanica* individuals growing epiphytically on each cushion was counted, and the presence of other epiphyte species (vascular plants and mosses) noted. Cushion growth rate (i.e. annual height increase) was determined by carefully inserting a thin (≤ 10 mm diameter) wooden stick through each cushion and into the underlying soil. Cushion height was marked against the stick immediately after insertion and again before removal after autumnal senescence (April 2002). Annual vertical growth was thus measured by the height difference between the two marks (hereafter growth rate; mm/year; see Chapter 2 for details). Cushions were examined for mouse-burrows (*Mus musculus* are alien on Marion Island: Avenant and Smith, 2003), and none were found in study cushions.

During middle to late growing season (October 2001 – February 2002), cushions were revisited. Each cushion was photographed from above (from a height of approximately 1.5 m). The relative position of each cushion (> 0.15 m diameter) within a transect was determined using a Nikon Total Station DTM350 Theodolite (Nikon Corporation, Tokyo, Japan) with an accuracy of 10 mm in three dimensions (Anonymous, 2001). The altitude of the highest cushion in each transect was determined using a Garmin 12MAP GPS (Garmin International, Kansas City, USA), because no suitable known-points were available on the Island to determine the exact altitude and geographic position using the theodolite (readings were cross-checked

against a topographical map of the island: Langenegger and Verwoerd, 1971). In addition, ten stems were randomly sampled from the top of each cushion. Twenty green leaves (two leaves per stem) were pressed, their trichomes and leaflets counted, and their images digitised using a flatbed scanner (HP Scanjet 5470c; Hewlett-Packard, Palo Alto, USA).

Later, cushion size and surface cover were determined using image analysis software (SigmaScan Pro version 5.0; SPSS, Illinois, USA). Cushion diameter (maximum and perpendicular), area, perimeter and shape factor were determined from the overhead photographs (following e.g. Belyea and Lancaster, 2002; for the three transects and the SE quadrat only). Shape factor was calculated as:

$$4 \cdot \pi \cdot \text{area} / \text{perimeter}^2 \quad \dots \text{Eq. 1,}$$

ranging from 0 (straight line) to 1 (perfect circle: Anonymous, 1999). Images were calibrated against an object of known size in each photograph. Measurements from photographs were validated against field measurements (following Belyea and Lancaster, 2002), and were similar (simple linear regression: maximum diameter: $R^2 = 0.86$, $p < 0.001$; perpendicular diameter: $R^2 = 0.73$, $p < 0.001$). Image analysis was then used to measure the fraction of each cushion's surface covered by epiphytes (grouped as *Agrostis magellanica*, other vascular plant species, or moss), dead stem areas (brown or black stem or leaf patches) and healthy tissue (green leaves; methods similar to Rousseaux et al., 2001). Small epiphytic plants (e.g. *Ranunculus biternatus*) were not always visible on the photographs, but due to their small size they were unlikely to have an effect on epiphyte cover estimates. Gaps between stems contributed very little to cushion surface cover (usually associated with sheltered cushion; see Chapter 4), and were not measured.

Leaf images were similarly analysed. Image analysis software (SigmaScan Pro version 5.0) was used to measure each leaf's surface area, length, width and perimeter (see Fig. 2, Chapter 4, page 127). Trichomes density was calculated per mm^2 leaf area, as leaflet area was not available for the leaves (trichomes do not grow on leaf stems and therefore these values are lower than those in Chapter 4 which are expressed as trichomes per mm^2 leaflet area). Mean values for each plant were calculated from all twenty leaves, with damaged leaves excluded from calculations.

Statistical analyses

Analysis of variance (ANOVA) and Tukey's Honest Significant Difference tests for Unequal sample sizes were used to test if variables differed between sites. Bootstrapped p-values were used where data did not meet ANOVA's assumption of normality (Bruce et al., 1999; Good, 1999). Bootstrapping was performed with 10^4 iterations, using Resampling Stat's Software (Bruce et al., 1999). The variability of each variable was quantified by calculating its coefficient of variation (CV: Zar, 1984), and these values were compared between sites.

The relationship between altitude and plant characteristics was initially examined using simple linear regression (for continuous variables) and generalized linear models (using a Poisson distribution for count data: Dobson, 2002; using a binomial distribution for proportion data: Collet, 1991). Next, the relationship between each variable and altitude was examined using polynomial regression (following e.g. Md Nor, 2001). To test if a second-order polynomial model provided a better fit to the data, the significance of the reduction in unexplained variance (for simple linear regression: F-test, d.f. = 1; Quinn and Keough, 2002) or unexplained deviance (for generalized linear models: χ^2 test, d.f. = 1; Dobson, 2002) in the polynomial model was calculated. A significant decrease in unexplained variance (or deviance) indicated that the polynomial model provided a better fit to the data than a linear model.

For graphical representation of epiphyte species richness and epiphyte prevalence, data were divided into eight altitudinal bands (following Sturge's rule; < 100, 100 – 175, 175 – 250, ..., 475 – 550, > 550 m a.s.l.: Legendre and Legendre, 1998), although all analyses were performed on continuous altitude data.

Results

The variables used to describe cushion and leaf morphology were strongly correlated (Table 1), and gave similar results in all analyses. Therefore, results are only reported for cushion area, leaf area and trichome density, and not for the other variables listed in Table 1.

Between-site comparisons

Cushion plant and leaf morphology differed between transects and between quadrats (Tables 2, 3). While the objective of this study was not to compare the sites with each other, these results provide useful baseline data and allow the relative influence of altitudinal vs. other spatial variability on the island to be evaluated, and are thus presented. Cushion surface area was highest in the NW and SE transects, while cushion shape did not differ between transects (Table 2). *Azorella selago* leaves were largest in the NW and NE transects and quadrats (Tables 2, 3). Similarly, leaves from the NW and NE quadrats had significantly more leaflets than those from the SE quadrat (Table 3). The NW transect and quadrat had the highest trichome densities; nearly three times the densities in the NE and SE sites (Tables 2, 3; Fig. 2a).

Cushion surface cover and epiphyte abundance and mean species richness also differed significantly between sites. Cushions in the SE transect had a significantly lower proportion of their surface area covered by green leaves (hereafter green fraction) than plants in the NE or NW transect (Table 2; Fig. 2b). The SE transect cushions also had the highest proportion of their surface covered by patches of dead stems (hereafter dead fraction; Table 2). Cushions in the SE transect also had the highest proportion of their surface covered by the epiphyte *Agrostis magellanica* (hereafter *Agrostis* cover), as well as the highest abundance of this epiphyte (Table 2; Fig. 2c). In contrast, *Agrostis* abundance was highest in the NW quadrat (Fig. 2c). Both the proportional cover of other vascular epiphyte species (i.e. excluding *Agrostis*) and epiphyte species richness was lowest in the SE and highest in the NW transect and quadrat (Table 2).

All plant characteristics, with the exception of the number of leaflets per leaf, were highly variable (mean CV > 15 %; Table 4). Within-quadrat variability in plant and epiphyte attributes was similar to variability across the transects, except for one attribute. Total leaf area was approximately 50 % less variable within quadrats than across transects (Table 4). Trichome density was the only cushion characteristic which was much more variable when data over the sites were pooled (CV = 61 %) than when considered separately (CV ranged from 25 to 49 %; Table 4). This is due to the large between-site (in both quadrats and transects) differences in this variable (see Tables 2, 3; Fig. 2a).

Altitudinal trends in cushion morphology and epiphyte cover

Cushion plant characteristics varied across altitude, although not always consistently between transects (Table 5). Patterns of epiphyte abundance and cover were strongest and most consistent, while relationships between cushion morphology and altitude tended to be weaker and less consistent. The abundance (Fig. 3) and proportional cover (Fig. 4) of *Agrostis* peaked at mid-altitudes in all three transects, although maximum abundance and cover (as well as the altitude at which this was attained) differed between transects. Cushion cover was dominated by *Agrostis* cover (e.g. Fig. 4), which on average covered 6.4 % of each cushion's surface (the species grew epiphytically on 169 cushions in the transects). The proportion of cushion surface covered by other vascular epiphyte species (i.e. excluding *Agrostis*) was strongly related to altitude, and in all three transects declined strongly with increasing elevation (e.g. Fig. 4). These epiphytes (chiefly *Blechnum penna-marina*, *Aceana magellanica* and *Cotula plumosa*) occurred on 57 cushions in the transects and covered on average 2.6 % of cushion surfaces (despite a maximum cover of nearly 50 % on some cushions). Similarly, moss cover was low (on average < 1 %) and restricted to a few cushions in each transect (20 – 39 cushions per transect). However, unlike vascular epiphyte cover, moss cover was weakly and inconsistently related to altitude (Table 5). Finally, cushion dead fraction was only weakly related to altitude and consistently occupied a small proportion of each cushion's surface (only 23 cushions did not have any dead stem areas and only 14 cushions had a dead fraction exceeding 10 % of their surface). Cushion green fraction increased significantly with altitude in all three transects, but was strongly negatively related to *Agrostis* cover (Spearman's correlation: $r = - 0.688$, $p < 0.001$). This was not surprising as cushion green fraction and *Agrostis* cover on average comprise 93.5 % of cushion surfaces, and therefore an increase in either is likely to be at the expense of the other.

Leaf area was significantly related to altitude in two transects (NW and NE, with the smallest leaves at mid altitudes), but not in a third (Table 5; Fig. 5). Cushion height and shape factor declined consistently (albeit weakly) with altitude, while trichome density was positively related to altitude (Table 5; Fig. 5). The cushion surface area and numbers of leaflets were weakly (or not at all) and inconsistently related to altitude (Table 5).

Altitudinal patterns in epiphyte species richness and distribution

Epiphyte species richness was strongly and consistently related to altitude, peaking at mid-altitudes (Table 5; Fig. 6a). This pattern was composed of two contrasting species richness patterns. First, non-vascular epiphyte species richness peaked at higher elevations and declined rapidly towards lower altitudes (Fig. 6b). Second, vascular epiphyte species richness was highest at sea-level and declined gradually with increasing altitude (Fig. 6c). Total epiphyte species richness differed between transects, with the most species (16) recorded on the NW transect, and only ten in the SE transect. The prevalence (i.e. number of cushions on which the epiphyte was recorded) and distribution of vascular epiphytes differed between species and transects (Fig. 7; Table 6). *Agrostis* and *Ranunculus biternatus* occurred on more cushions, and at higher altitudes, than other vascular epiphytes. *Blechnum* and *Aceana* were the only other vascular epiphytes that occurred on more than 10 % of the sampled cushions, and were generally restricted to altitudes below 200 m a.s.l. (a single individual of *Aceana* was observed at 397 m a.s.l. in the SE transect). Comparing transects, *Agrostis* had a narrower altitudinal range in the NW transect than in the NE or SE transects (despite lowest prevalence in the NE transect). Similarly, the distribution of the other vascular epiphytes differed between sites. As an extreme example, *Cotula*, which was absent from the NW and SE transects but grew epiphytically on approximately 10 % of cushions in the NE transect (Fig. 7).

Mosses grew epiphytically on *A. selago* across the length of all the altitudinal transects (from 50 m to 650 m a.s.l.), although no species occurred along the entire gradient. Species like *Breutelia integrifolia* and Unidentified Moss sp. 1 were common at mid and high altitudes, but were absent at the lowest altitudes (neither recorded below 100 m a.s.l.; Fig. 7). In contrast, *Sanionia uncinata* occurred mostly at low altitudes, never exceeding 370 m a.s.l. (Fig. 7). The prevalence (and presence) of epiphytically growing mosses also differed between transects. For example, *Ditrichum* sp. grew epiphytically on approximately 80 % fewer cushions in the NW transect than in the NE or SE transects. Similarly, *Racomitrium* sp., *Andreaea* sp. and Unidentified mosses spp. 2 and 3 were common on cushions in the NW transect, but not at the other sites.

Three broad patterns of elevational distributions were evident from these epiphyte species. First, “low altitude” species with the highest prevalence at low altitudes, declining towards higher altitudes (e.g. *Blechnum*, *Aceana*, *Cotula*, *Sanionia*). These species generally had a narrow altitudinal range (roughly from sea-level to 200 m a.s.l.). Second, “high altitude” species showing highest prevalence at high altitudes, declining towards sea-level (e.g. *Breutelia*, *Racomitrium*, *Ditrichum*). These species generally had the largest altitudinal ranges (usually from 150 m a.s.l. to over 550 m a.s.l.). No vascular plants showed this distribution. Finally, “mid altitude” species with peak prevalence at mid altitudes (e.g. *Agrostis*, *Ranunculus*, *Andreaea*, Unidentified Moss spp. 1 and 3). Species generally showed the same altitudinal distribution pattern in all three transects, although the exact form differed.

Discussion

Altitudinal trends in cushion and leaf morphology

Despite high fine-scale variability, altitudinal trends were observed in cushion and leaf morphology. Leaf morphology is a sensitive indicator of environmental conditions (Halloy and Mark, 1996), and was therefore expected to vary along the altitudinal transects. Surprisingly, *A. selago* leaf size showed a unimodal (concave) relationship with altitude, in contrast to most species where leaf size declines with increasing elevation (e.g. Kudo, 1995; Cavelier, 1996; Halloy and Mark, 1996; Cordell et al., 1998; Schoettle and Rochelle, 2000). In a comparable study, the leaf size of five sub-Antarctic plant species were negatively related to altitude on Macquarie Island (Tweedie, 2000). In the same study, however, the leaf size of a sixth species, *Aceana magellanica*, was non-linearly related to altitude, although its leaf size was maximal at mid-altitudes (Tweedie, 2000), while in this study *A. selago* leaves were smallest at mid-altitudes. Changes in leaf size over altitude have been attributed to a variety of environmental factors (e.g. temperature, rainfall and soil moisture, wind, frost frequency, nitrogen limitation, and shading: Cavelier, 1996; Halloy and Mark, 1996; Schoettle and Rochelle, 2000; Tweedie, 2000), and there is still uncertainty about how these factors affect leaf size (Cavelier, 1996). Altitudinal variation in rainfall and freeze-thaw frequency (since both peak at mid altitudes) matched that of *A. selago* leaf size on Marion Island. However, if moisture were a

limiting resource to *A. selago*, smaller leaves should be favoured when moisture availability is low, i.e. the opposite pattern of leaf size variation would be expected (Daubenmire, 1947). The hypothesis that leaf size is influenced by frost frequency (smaller leaves suffer less damage from frost than larger leaves: Parkhurst and Loucks, 1972) is, therefore, at present the most plausible explanation for the unusual altitudinal variation in leaf size on Marion Island.

In agreement with other species, the trichome density of *A. selago* leaves increased with altitude (e.g. Cordell et al., 1998). Due to the multiple possible functions of trichomes (Gutschick, 1999; Press, 1999), the functional significance of changes in trichome density is unclear (Cordell et al., 1998). High trichome density can improve the insulation of leaves, by increasing the leaf boundary layer thickness and thereby reducing heat loss (Press, 1999). Similarly, by maintaining the boundary layer around leaves, trichomes can reduce water loss and improve water use efficiency (Cordell et al., 1998; Press, 1999), particularly at the low atmospheric pressures associated with higher altitudes (Halloy and Mark, 1996). Interestingly, it has also been suggested that trichomes help leaves remain dry. Higher trichome densities reduce the “wettability” of leaf surfaces, keeping stomata unobstructed and reducing the risk of freeze-associated damage and fungal infections (Halloy and Mark, 1996; Cordell et al., 1998; Press, 1999). However, trichomes perform these functions simultaneously (Press, 1999), and at higher altitudes a greater trichome density is probably advantageous because it provides stronger buffering against changes in leaf temperature and moisture (by maintaining the leaf boundary layer) and protects against freezing (by reducing wettability). Comparing trichome density between transects provides support for some of these hypotheses, because trichome density was highest in the colder and windier NW transect (suggesting that it is advantageous at lower temperatures and/or strong winds).

Although not as clear as the altitudinal trends in leaf morphology, both cushion height and shape factor (i.e. roundness) tended to decrease with increasing altitude. Plant height generally decreases with increasing altitude (Grace and Norton, 1990; Davies and Melbourne, 1999), and cushion height was therefore expected to follow the same pattern. The low stature of the higher altitude cushion plants has implications for their water and energy balance. Growing closer to the ground keeps the plant’s leaves within the surface boundary layer, thereby reducing heat and water loss (lower convective heat loss and evaporative water loss: Grace, 1977). For

example, the tissue temperature of *krumholtz* (low-growing individuals surviving at or above the treeline) *Pinus sylvestris* trees exceeds that of conspecifics at lower altitudes, allowing them to achieve higher growth rates than individuals below the treeline (Grace and Norton, 1990). Similarly, the higher temperatures associated with the prostrate growth form of *Muhlenbergia richardsonis* (an alpine C4 grass) enables the species to occur at higher altitudes than other C4 species (Sage and Sage, 2002). The decline in cushion shape with altitude (i.e. cushion perimeter becoming less round and more irregular at higher altitudes) is probably due to this decline in plant height with altitude. Low-growing, high altitude cushions grow around obstructions, whereas taller low altitude cushions are able to grow over obstacles, maintaining their hemispherical shape. This altitudinal trend is probably exacerbated by the greater rock cover and higher proportional cover of black lava (unweathered and uneven) at high altitudes, compared to lower altitudes with a higher proportional cover of older grey lava (undulating topography due to glacial scouring; i.e. fewer obstructions to cushion growth: Verwoerd, 1971).

These altitudinal differences in cushion and leaf morphology, in addition to the species' growth form, might explain how *A. selago* achieves a similar growth rate across its > 750 m altitudinal range on Marion Island (Chapter 2). First, the plant's cushion-type growth form causes the plant to lose heat (Huntley, 1971) and moisture (the inside of cushions are usually wet: pers. obs; see also Callaghan and Emanuelsson 1985) more slowly than their surroundings. Then, because of their low stature and dense trichome cover, high altitude *A. selago* plants might have an even more favourable microclimate, enabling the species to maintain a similar growth rate on average across altitudes.

Elevational patterns in cushion cover

In contrast to expectations, cushion dead fraction was not consistently related to altitude. This suggests that stem mortality is not related to temperature, wind or other factors that change consistently over the altitudinal gradient. Similarly, the inconsistent relationship between the proportion of cushions covered by mosses and altitude suggests that moss epiphyte cover is also not determined by variables that co-vary with altitude. Indeed, the altitudinal distribution of mosses is suggested to be less strongly determined by climatic variables than that of vascular plants (Theurillat et al.,

2003). Nonetheless, cushion surface cover did change over altitude because of vascular epiphyte cover differences across elevation. This variation in epiphyte cover with altitude potentially has implications for *A. selago*, because it can alter the environmental conditions experienced by cushions. For example, dense epiphyte cover could extend the cushion's boundary layer further from its surface (buffering it against changes in temperature and moisture: see Freiberg, 2001), but would also reduce the surface area available for photosynthesis, and shade adjacent parts of the cushion (discussed in full in Chapter 4). Therefore, while changes in temperature or rainfall (within the range experienced across the altitudinal gradient) are unlikely to alter the epiphytic moss cover or dead fraction of cushions, a change in climate could alter vascular epiphyte cover. As a result, climate change may indirectly (through its effects on epiphytes) alter *A. selago*'s performance by changing cushions' photosynthetic area and altering their microclimate.

Altitudinal distribution of epiphyte species

Because cushion cover was found to be strongly influenced by the presence of epiphytically-growing plants, it is important to understand what determined the distribution of these species. Hypotheses about the factors limiting the distribution of these epiphyte species (and therefore mediating their influence on the cushion plants) can be generated by qualitatively examining their altitudinal ranges. The spatial distribution of a species is potentially limited by four factors: the species' abiotic tolerances, its ability to disperse, its interactions with other species (e.g. competitive and facilitative interactions), and "hard" boundaries (e.g. the sea for terrestrial organisms or host range limit for parasites: Whitehead, 1951; Krebs, 1978; Huston, 1994; Gaston, 2003). Of these potential limitations, dispersal is the least likely to restrict the altitudinal range of epiphytes on Marion, because these species produce small seeds (see Bergstrom et al., 1997) or spores that are probably easily transported across the island by strong winds. The only hard boundaries to species on Marion Island are the sea and absence of land above 1230 m a.s.l., although species that are restricted to growth on *A. selago* (e.g. vascular plants at high altitudes) are limited by the upper and lower altitudinal limits of the cushion plant.

Abiotic factors and biotic interactions must therefore explain the remaining altitudinal boundaries. Due to physiological and energetic constraints, species have a

limited ability to endure both these abiotic and biotic challenges (Smith and Huston, 1989), suggesting that species that are able to tolerate abiotic stresses (e.g. high altitude conditions) are generally poor competitors (analogous to Grime's (1979, 2003) "stress-tolerant" species). Further, species that are strong competitors in favourable environments are predicted to have poorer environmental tolerances (Grime's (1979, 2003) "competitive" species). As a result, the relative competitive ability of species change consistently along an environmental gradient (e.g. with increasing altitude: Smith and Huston, 1989), with stronger competitors continually being replaced by stronger tolerators, as environmental conditions shift beyond the tolerances of the competitors. Therefore, along an altitudinal gradient, the upper altitudinal boundary of a species may be expected to be set by abiotic constraints, and its lower by biotic interactions. Indeed, Ashton and Gill (1965) and Taylor (1955) suggested that the upper boundary of fellfield species on Macquarie Island may be set by wind exposure and their lower boundary by shading.

Upper altitudinal boundary

Of the abiotic constraints limiting the upper altitudinal boundary of plants, temperature is often suggested to be most important (e.g. Holten, 2003), although the mechanisms through which low temperatures limit plant growth are still unclear (Hoch et al., 2002). However, stronger winds at higher altitudes can also limit growth, via enhanced cooling, accelerated water loss or mechanical damage (Warren Wilson, 1959; Huntley, 1971; Grace, 1977; Ennos, 1997). Indeed, both temperature and wind potentially limit the upper altitudinal distribution of vascular plants (including *A. selago*) on Marion (Huntley, 1970, 1971) and Macquarie Islands (Taylor, 1955; Ashton and Gill, 1965). Rainfall peaks at mid-altitudes on Marion Island (near the upper altitudinal limit of *A. selago*), and is therefore probably not limiting to epiphytes at higher altitudes. Similarly, differences in freeze-thaw frequency and depth (important to northern European alpine plants: Holten, 2003), are unlikely to directly influence the epiphytes, since they are rooted inside the cushion plants. Finally, salt-spray determines the upper altitudinal limit for some coastal species (e.g. *Cotula plumosa* and *Crassula moschata*, which are susceptible to shading: Taylor, 1955), by suppressing their competitors (Huntley, 1971). Therefore, low temperatures

and strong winds probably limit the upper altitudinal boundary of most species on Marion Island.

The importance of these factors (temperature and wind) is apparent for the dominant epiphyte on the cushion plants, the grass *Agrostis magellanica*. The prevalence, cover, distribution and abundance of *A. magellanica*, were lowest on the cooler, wetter and windier NW transect than on the eastern transects. This pattern is probably not related to the higher rainfall on the western side of the island, since this species' peak abundance was at mid altitudes along the altitudinal transects (where rainfall is highest). The lower temperatures and stronger winds experienced on the NW transect therefore appear to constrain the epiphyte's performance. These transect-specific distribution and abundance patterns also explain the contrasting *Agrostis* abundances between the transects and quadrats, since altitudinal variation in *Agrostis* abundance can override transect effects. Therefore, low temperatures and/or strong winds may limit *Agrostis* at high altitudes, and variation in these environmental factors can explain the species' transect-specific abundance and distribution.

Therefore, the upper elevational limit of most epiphyte species (except the salt-spray-dependent species) is probably determined by increasing climatic severity with increasing altitude. As a result, if climatic conditions ameliorate, some epiphyte species may colonize upslope cushions (e.g. *Agrostis* may spread to higher altitudes under warmer temperature and milder winds: see also Grabherr et al., 1994; Peñuelas and Boada, 2003; Sanz-Elorza et al., 2003), possibly to the disadvantage of the cushions being colonized (see Chapter 4).

Lower altitudinal boundary

Abiotic factors are unlikely to determine lower elevational limits of epiphyte species on Marion Island. The higher temperatures at lower altitudes appear to be within the thermal tolerances of the sub-Antarctic plant species that have been studied (e.g. Tallis, 1959; Bate and Smith, 1983; Pammenter et al., 1986; Smith and Gremmen, 2001), and the lower wind speeds are unlikely to have a negative influence on any species. Salt spray does not limit species, since rain generally washes the salt away before it reaches toxic concentrations in the soil (Huntley, 1971). Less rainfall at lower elevations could explain the lower altitudinal boundary for some epiphyte

species (Holten, 2003), but altitudinal variation in plant-available moisture is probably a stronger determinant of species' ranges and is still undocumented for the island.

Biotic interactions therefore probably set the lower altitudinal boundary of most epiphyte species (e.g. competition for space and light, due to higher epiphyte and general plant cover: see Holten, 2003). The decline in prevalence of high altitude species (e.g. mosses like *Breutelia*, *Ditrichum*, *Racomitrium*) towards lower altitudes is probably due to shading from the taller *Agrostis magellanica* (at mid altitudes) and *Aceana magellanica* and *Blechnum penna-marina* (at lower altitudes). However, this explanation is not entirely satisfactory, since other low-growing species (e.g. *Ranunculus biternatus* and *Andreaea* spp.) co-exist with *Agrostis magellanica* on *A. selago* cushions at mid altitudes.

Equally paradoxical, at lower altitudes *Agrostis* appears to be excluded by the low-growing *Blechnum* and *Aceana*. However, while *Blechnum* and *Aceana* would not be able to shade a fully-grown *Agrostis* grass, they are potentially able to overgrow young *Agrostis* individuals. Therefore, for example, if viable *Agrostis* seeds are produced more irregularly or take a longer time to germinate (see e.g. Frenot and Gloaguen, 1994) than the propagules of *Aceana* or *Blechnum*, then priority effects (i.e. pre-empting space: Begon et al., 1996) could be important (i.e. *Agrostis* seedlings would have difficulty establishing on a cushion supporting high *Aceana* or *Blechnum* epiphyte load). Similarly, if these other epiphytes have greater longevity than *Agrostis*, they could slowly replace *Agrostis* by colonizing the gaps left when an *Agrostis* individual dies. Therefore, the lower altitudinal boundary of epiphyte species is most likely to be a consequence of biotic interactions, particularly competition (although historical factors, etc. could also be important).

Epiphyte species richness

Related to the factors limiting the altitudinal range of particular epiphyte species are the factors determining the variation in epiphyte species richness across altitudinal gradients. Epiphyte species richness peaked at mid-altitudes (200 – 350 m a.s.l.), in agreement with a previous study of epiphytes (Wolf, 1993; see also e.g. Brown, 2001; Md Nor, 2001 for examples of other plant and animal taxa). The different altitudinal patterns in species richness shown by the non-vascular (peaking at mid-altitudes; Fig. 6b) and vascular (declining with altitude; Fig. 6c) epiphytes on Marion Island also

agrees with some previous studies (e.g. Wolf, 1993; Freiberg and Freiberg, 2000; Theurillat et al., 2003), and suggests that different factors may drive species richness in each group (e.g. see Theurillat et al., 2003; Table 7).

A wide variety of hypotheses have been advanced to explain altitudinal variation in species richness (reviewed in Heaney, 2001; see Table 7). Some of these hypotheses can be evaluated using our data set, while data from Marion Island is lacking to test others (Table 7). The null hypothesis (H_0 ; Table 7) is rejected because species richness is significantly related to altitude. Similarly, the hypothesis that species richness declines with altitude is rejected because species richness increases with altitude at lower elevations.

The hypotheses that species richness increases with area or productivity are also rejected, since the island's area (Table 1 in Smith et al., 2001) and productivity (Smith, 1978) are greatest at low altitudes. If the frequency and intensity of competitive interactions are assumed to be positively related to the proportion of the cushion surface covered by epiphytes (i.e. epiphytes experience stronger competition on cushions with higher total epiphyte cover), then the hypothesis that species richness increases with declining competition can be rejected (since epiphyte cover, and therefore competition among epiphytes, is lowest at high altitudes; see e.g. Fig. 4). In addition, the hypothesis that species richness declines with increasing frequency of disturbances can also be rejected, since disturbance is probably highest at coastal sites (due to animal activity). Epiphytes are unaffected by soil freeze-thaw cycles (since they are rooted in cushion plants) which is the other potentially dominant form of disturbance on Marion Island. Rainfall peaks at mid altitudes on Marion Island (Blake, 1996), and therefore the hypothesis that species richness increases with rainfall cannot be rejected. Assuming that the abundance pattern of *Agrostis magellanica* is roughly representative of the combined abundance of all the epiphyte species, our data also provides some tentative support for the hypothesis that epiphyte species richness peaks where epiphyte abundance is maximal. However, comparing transects shows that epiphyte species richness is lowest in the SE transect where *Agrostis* abundance was highest, and highest in the NW transect where *Agrostis* was least abundant, suggesting that this hypothesis alone cannot explain epiphyte species richness patterns across Marion Island. Three hypotheses predicted species richness to peak at altitudes where the diversity of habitats, microhabitats and resources are maximal (H_5 , H_9 and H_{10} , respectively). Habitat diversity is highest at low altitudes

(there are more vegetation types present between sea-level and 100 m a.s.l. than in higher altitudinal bands: Smith et al., 2001), and therefore cannot explain the mid-altitude peak in epiphyte species richness. Resource and microhabitat diversity are also possibly highest at lower altitudes (especially if epiphyte resource and microhabitat diversity is positively related to habitat diversity), although are difficult to assess because both biotic and abiotic heterogeneity must be considered. Therefore, these hypotheses could not be rigorously assessed. Finally, the remaining hypotheses (Table 7) could also not be suitably evaluated using our data. Therefore, within the limits of our data set, epiphyte species richness appears to be best predicted by rainfall. This is supported by the observation that epiphyte species richness is also highest at the wetter NW transect, although the mechanism by which higher rainfall allows more species to co-exist is not clear.

These results must, however, be considered within the context of three caveats. Some vascular plants known to grow epiphytically on *A. selago* were not recorded during the survey (e.g. *Montia fontana*, *Uncinia dikei*, *Juncus scheuchzerioides*, *Crassula moschata*, *Hymenophyllum peltatum*, *Lycopodium magellanica*: Huntley, 1970, 1971, 1972; *Sagina procumbens*: pers. obs). Also, moss species richness may have been underestimated due to morphological similarity of congeneric species. Finally, liverwort and lichens were not recorded because of identification difficulties and their small size. However, the patterns described relate to mean species richness per cushion, and these problems only affect the estimates of total epiphyte species richness (i.e. comparing between sites). Therefore, despite the limitations of the altitudinal transects, this suggests that climate change could affect species richness patterns, particularly if factors influencing water availability change.

Conclusion

Azorella selago morphology and surface cover, and epiphyte composition and species richness varied across the altitudinal gradient on Marion Island. Assuming that a gradual spatial change in climate is a suitable analogue for a temporal change in climate, this suggests that *A. selago* cushion height, leaf size and trichome density will be responsive to changes in climate. Similarly, the altitudinal zonation of epiphyte species suggests that the altitudinal limits of some species could shift under further changes in climate, with potential implications for the performance of *A. selago* under

altered epiphyte loads. Therefore, altitudinal patterns in cushion characteristics and epiphyte abundance and distribution on Marion Island suggest that *A. selago* may be directly and indirectly affected by changes in climate.

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TABLE 1

Relationship between strongly related variables, calculated by pooling data across all sites. Calculations were repeated individually for each site's data, but yielded very similar results. Slope values are untransformed. ¹ log-transformed, ² square-root transformed.

Independent variable	Dependent variable	R ²	F	d.f.	p	slope ± SE
Cushion area	Maximum diameter ¹	0.82	2189.47	1, 487	< 0.001	0.43 ± 0.02
Cushion area	Perpendicular diameter ¹	0.66	951.52	1, 487	< 0.001	0.32 ± 0.02
Cushion area	Perimeter ¹	0.88	3559.99	1, 487	< 0.001	0.50 ± 0.01
Leaf area	Leaf length ²	0.94	13838.67	1, 887	< 0.001	1.64 ± 0.02
Leaf area	Leaf width ²	0.93	11755.38	1, 887	< 0.001	1.28 ± 0.02
Leaf area	Leaf perimeter ²	0.66	1740.93	1, 887	< 0.001	3.25 ± 0.07
Trichome density	Number of trichomes ²	0.87	6180.82	1, 887	< 0.001	4.48 ± 0.10

TABLE 2

Azorella selago characteristics in the transects (mean \pm SE). Differences between transects tested using ANOVA, with bootstrapped *p*-values where data violate assumption of normality. *A. magellanica* = *Agrostis magellanica*. ¹ log-transformed, ² square root transformed, ³ from Chapter 2, † bootstrapped *p*-value, * non-significant after sequential Bonferroni correction (Rice, 1989). Groups not sharing a letter differ at *p* < 0.05.

	F	d.f.	p	NW Transect	N	NE Transect	N	SE Transect	N	
Cushion growth rate and morphology										
Growth rate (mm/yr) ^{1,3}	13.43	2, 226	<	0.80 \pm 0.03	75	0.73 \pm 0.03	82	0.57 \pm 0.02	72	
Cushion surface area (m ²) ¹	8.78	2, 286	< 0.001	-0.50 \pm 0.03	95	-0.36 \pm 0.03	96	-0.51 \pm 0.03	98	
Height (m) ^{1,3}	0.66	2, 296	0.515	-0.76 \pm 0.02	99	-0.76 \pm 0.02	100	-0.79 \pm 0.01	100	
Cushion shape	1.01	2, 286	0.365	0.48 \pm 0.02	95	0.50 \pm 0.02	96	0.48 \pm 0.01	98	
Leaf morphology										
Leaf area (mm ²) ¹	8.89	2, 286	< 0.001	1.35 \pm 0.01	95	1.36 \pm 0.01	96	1.31 \pm 0.01	98	
Leaflets ¹	1.04	2, 286	0.356	0.71 \pm 0.01	95	0.70 \pm 0.01	96	0.70 \pm 0.01	98	
Trichome density (per mm ²) ²	342.05	2, 286	< 0.001	1.22 \pm 0.02	95	0.70 \pm 0.02	96	0.67 \pm 0.01	98	
Cushion surface cover										
Green fraction	15.15	2, 286	< 0.001	† 91.09 \pm 0.85	95	86.15 \pm 1.20	96	84.14 \pm 1.21	98	
Dead fraction	5.93	2, 286	0.010*	† 3.47 \pm 0.32	95	2.79 \pm 0.40	96	4.52 \pm 0.36	98	
<i>A. magellanica</i> cover	10.48	2, 286	< 0.001	† 2.70 \pm 0.57	95	6.23 \pm 1.15	96	10.20 \pm 1.07	98	
Moss cover	3.78	2, 286	0.093	† 0.28 \pm 0.06	95	0.49 \pm 0.16	96	0.10 \pm 0.03	98	
Other epiphyte spp. Cover	5.57	2, 292	0.015*	† 2.46 \pm 0.74	95	4.35 \pm 0.85	96	1.03 \pm 0.48	98	
Epiphyte abundance and species richness										
<i>A. magellanica</i> individuals	17.53	2, 297	< 0.001	† 12.44 \pm 2.36	100	22.32 \pm 4.07	100	42.14 \pm 4.12	100	
Epiphyte species richness	12.78	2, 297	< 0.001	† 2.79 \pm 0.12	100	2.15 \pm 0.11	100	2.07 \pm 0.10	100	

TABLE 3

Azorella selago characteristics in the quadrats (mean \pm SE). Differences between quadrats tested using ANOVA, with bootstrapped *p*-values where data violate assumption of normality. *A. magellanica* = *Agrostis magellanica*. ¹ log-transformed, ² from Chapter 2, † bootstrapped *p*-value. All values remain significant after sequential Bonferroni correction (Rice, 1989). Groups not sharing a letter differ at *p* < 0.05.

	F	d.f.	p	NW Quadrat	N	NE Quadrat	N	SE Quadrat	N			
Cushion growth rate and morphology												
Growth rate (mm/yr) ^{1,2}	5.71	2, 428	0.004	0.61 \pm 0.02	157	a	0.54 \pm 0.02	127	b	0.57 \pm 0.02	147	ab
Cushion surface area (m ²) ¹	-			-			-			5.06 \pm 0.02	200	
Height (m) ^{1,2}	61.96	2, 597	< 0.001	-0.82 \pm 0.01	200	a	-0.98 \pm 0.01	200	b	-0.95 \pm 0.01	200	b
Cushion shape	-			-			-			0.47 \pm 0.01	200	c
Leaf morphology												
Leaf area (mm ²) ¹	10.01	2, 597	< 0.001	1.23 \pm 0.01	200	a	1.23 \pm 0.01	200	a	1.21 \pm 0.01	200	b
Leaflets	25.08	2, 597	< 0.001	† 5.10 \pm 0.01	200	a	5.07 \pm 0.01	200	a	5.00 \pm 0.01	200	b
Trichome density (per mm ²)	805.61	2, 597	< 0.001	† 1.53 \pm 0.02	200	a	0.64 \pm 0.02	200	b	0.53 \pm 0.02	200	c
Cushion surface cover												
Green fraction	-			-			-			78.03 \pm 14.99	200	
Dead fraction	-			-			-			6.69 \pm 6.25	200	
<i>A. magellanica</i> cover	-			-			-			15.27 \pm 13.80	200	
Moss cover	-			-			-			0.01 \pm 0.08	200	
Other epiphyte spp. cover	-			-			-			0	200	
Epiphyte abundance and species richness												
<i>A. magellanica</i> individuals	37.21	2, 597	< 0.001	† 39.47 \pm 2.16	200	a	15.04 \pm 2.16	200	b	18.59 \pm 2.16	200	c
Epiphyte species richness	87.80	2, 478	< 0.001	† 3.07 \pm 0.06	200	a	2.30 \pm 0.06	200	b	1.69 \pm 0.09	81	c

TABLE 4

Variability in Azorella selago characteristics expressed as coefficient of variation (%). Data analysed separately for each site, and pooled for the "All sites" values. A. magellanica = Agrostis magellanica. ¹ from Chapter 2.

	NW		NE		SE		All sites
	Transect	Quadrat	Transect	Quadrat	Transect	Quadrat	
Cushion growth rate and morphology							
Growth rate ¹	53.7	53.6	64.7	60.5	50.3	51.5	62.0
Cushion surface area	78.5	-	70.6	-	82.0	80.5	97.1
Cushion maximum diameter ¹	36.0	53.1	37.8	45.9	34.5	39.9	47.3
Cushion height ¹	50.7	36.0	46.9	36.0	32.1	30.5	45.8
Cushion shape	31.2	-	33.4	-	24.9	27.1	29.1
Leaf morphology							
Total leaf area	31.1	14.0	29.5	14.8	25.6	13.2	27.0
Leaflets	3.8	3.7	3.9	2.7	4.1	2.2	3.3
Trichome density	24.6	25.8	48.7	31.7	44.2	31.5	61.2
Cushion surface cover							
Green fraction	9.1	-	13.7	-	14.2	19.2	16.3
Dead fraction	91.1	-	139.1	-	78.6	93.5	104.7
<i>A. magellanica</i> cover	204.9	-	180.3	-	103.7	90.4	124.0
Moss cover	216.8	-	321.0	-	304.5	693.0	443.7
Other epiphyte spp. cover	263.3	-	171.6	-	430.5	693.0	327.9
Epiphyte abundance and species richness							
<i>A. magellanica</i> individuals	189.4	110.7	182.5	158.4	97.9	98.2	138.7
Epiphyte species richness	41.79	-	52.2	-	49.2	46.4	50.5

TABLE 5. Relationship between altitude and various characteristics of *Azorella selago*. The form, shape and fit of the relationships that provide the best fit to the data are shown. Where neither monomial nor polynomial regression explained a significant proportion of the variation in a plant characteristic the slope of the best fitting curve is shown in brackets. Where a quadratic curve provided the best fit but the curve appeared approximately linear over the range of data examined, shape is indicated by just negative or positive (as for linear). *A. magellanica* = *Agrostis magellanica*. Minimum = quadratic curve with a minimum, maximum = quadratic curve with maximum. ¹ curve showing a lower plateau, ² curve showing an upper plateau. See appendices A, B, C, D and E for statistics.

Variable	NW Transect			NE Transect			SE Transect			Max. R ²
	Best fit	Shape	R ²	Best fit	Shape	R ²	Best fit	Shape	R ²	
Cushion growth rate and morphology										
Cushion growth rate		(positive)			(negative)		linear	positive	0.15	0.15
Cushion area	quadratic	minimum	0.07		(negative)			(positive)		0.07
Cushion height	quadratic	negative ¹	0.37		(negative)		linear	negative	0.19	0.37
Cushion shape factor	quadratic	negative ¹	0.25	quadratic	negative	0.50	linear	negative ¹	0.19	0.50
Leaf morphology										
Leaf area	quadratic	minimum	0.25	quadratic	minimum	0.32		(negative)		0.32
Leaflets	quadratic	minimum	0.18		(negative)		linear	negative	0.06	0.18
Trichome density	quadratic	positive ²	0.23	linear	positive	0.41	linear	positive	0.07	0.41
Cushion surface cover										
Green fraction	linear	positive ²	0.34	quadratic	minimum ¹	0.28	quadratic	minimum ¹	0.27	0.34
Dead fraction	quadratic	maximum	0.23	quadratic	positive	0.29		(negative)		0.29
<i>A. magellanica</i> cover	quadratic	negative	0.49	quadratic	maximum	0.57	quadratic	maximum	0.38	0.57
Moss cover	quadratic	maximum	0.11	quadratic	positive	0.29		(negative)		0.29
Other epiphyte spp. Cover	quadratic	minimum	0.65	quadratic	minimum	0.82	quadratic	negative ¹	0.45	0.82
Epiphyte abundance and species richness										
<i>A. magellanica</i> individuals	quadratic	negative	0.59	quadratic	maximum	0.79	quadratic	maximum	0.50	0.79
Epiphyte species richness	quadratic	maximum	0.25	quadratic	maximum	0.34	quadratic	maximum	0.34	0.34

TABLE 6

Altitudinal distribution of species growing epiphytically on Azorella selago. ¹ minimum and maximum altitude at which species was recorded on *A. selago* (calculated where more than four records available), ² from Huntley (1970), ³ moss, ⁴ liverwort, ⁵ exceeded by an observation in the NE transect. See appendix F for additional data.

Species	Family	Number of occurrences				Range (m a.s.l.) ¹				Upper record ²
		NW	NE	SE	All sites	NW	NE	SE	All	
<i>Agrostis magellanica</i>	Poaceae	50	36	77	163	80 - 387	60 - 437	65 - 477	60 - 477	585
<i>Breutelia integrifolia</i>	Bartramiaceae ³	55	23	45	123	148 - 649	165 - 597	109 - 583	109 - 649	
<i>Ditrichum</i> sp. (<i>D. conicum</i> ?)	Ditrichaceae ³	7	60	49	116	273 - 649	165 - 619	67 - 583	67 - 649	
<i>Ranunculus biternatus</i>	Ranunculaceae	24	20	18	62	69 - 556	190 - 606	202 - 431	69 - 606	582 ⁵
Unidentified moss sp. 1	Bryophyte	28	12	5	45	153 - 602	197 - 418	253 - 548	153 - 602	
<i>Blechnum penna-marina</i>	Polypodiaceae	6	25	5	36	55 - 144	60 - 158	58 - 218	55 - 218	275
<i>Sanionia uncinata</i>	Amblystegiaceae ³	22	10	2	34	55 - 367	60 - 144		55 - 367	
<i>Aceana magellanica</i>	Rosaceae	17	14	3	34	64 - 193	65 - 158		64 - 397	530
<i>Racomitrium</i> sp.	Grimmiaceae ³	25		2	27	244 - 583			208 - 583	
Unidentified moss sp. 2	Bryophyte	25			25	177 - 465			177 - 465	
<i>Andreaea</i> sp.	Andreaeaceae ³	8	1		9	270 - 485			270 - 498	
Unidentified moss sp. 3	Bryophyte	9			9	244 - 452			244 - 452	
<i>Cotula plumosa</i>	Asteraceae		9		9		65 - 69		65 - 69	65 ⁵
<i>Lycopodium saururus</i>	Lycopodiaceae		2	1	3					415
<i>Poa cookii</i>	Poaceae	1	2		3					590
<i>Callitriche antarctica</i>	Callitrichaceae	2			2					535
<i>Colobanthus kerguelensis</i>	Caryophyllaceae	2			2					320
<i>Jamesoniella</i> sp.	Jungermanniaceae ⁴	1			1					
	Species richness	16	12	10	18					

TABLE 7

Hypotheses concerning variation in species richness (S) along altitudinal gradients (modified from Heaney, 2001).

	Supported by this study?	
H ₀ : No altitudinal variation in SpRns	No	
H ₁ : S increases with decreasing altitude	No	Some support from vascular epiphytes
H ₂ : S increases with area	No	Some support from vascular epiphytes
H ₃ : S increases with productivity	No	Some support from vascular epiphytes
H ₄ : S increases with infrequency of disturbance	No	
H ₅ : S increases with habitat diversity	No	
H ₆ : S increases with rainfall	Possible	
H ₇ : S increases with epiphyte abundance and/or biomass	Possible	
H ₈ : S increases with decreasing competition	No, but difficult to evaluate	Some support from non-vascular epiphytes
H ₉ : S increases with habitat complexity	No, but difficult to evaluate	
H ₁₀ : S increases with resource diversity	No, but difficult to evaluate	
H ₁₁ : S peaks in areas of community interdigitation	Could not evaluate	
H ₁₂ : S peaks in areas that have had the highest rates of speciation	Not relevant at scale of Marion Island	

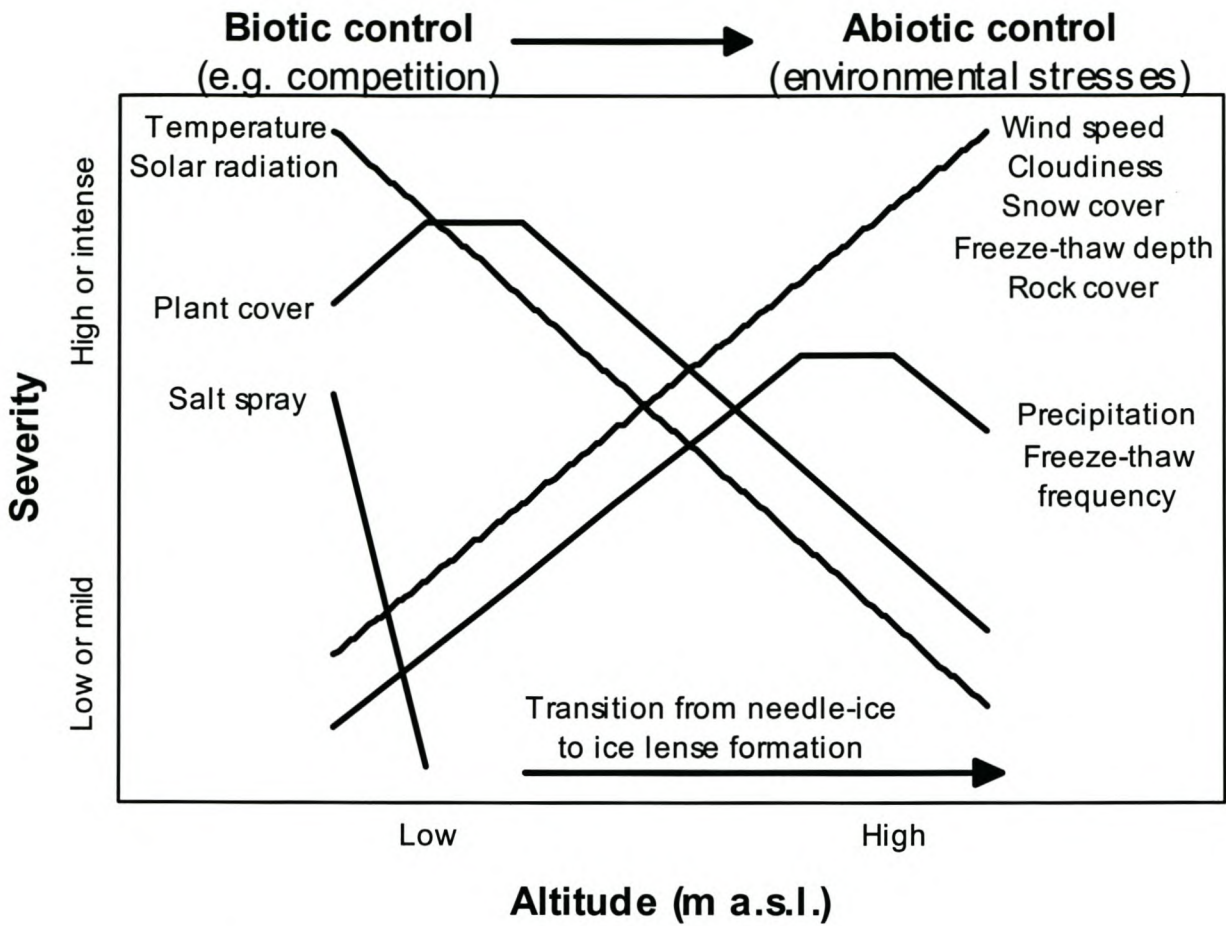


FIGURE 1. Idealized representation of altitudinal gradients in biotic and abiotic variables on Marion Island (based on Huntley, 1971; Schulze, 1971; Blake, 1996; Smith et al., 2001; Boelhouwers, 2003; Holness, 2003; J.A. Deere, unpublished data; M. Nyakatya, unpublished data). The altitudinal gradient probably represents a shift in the relative importance of biotic and abiotic variables in controlling community composition (see text).

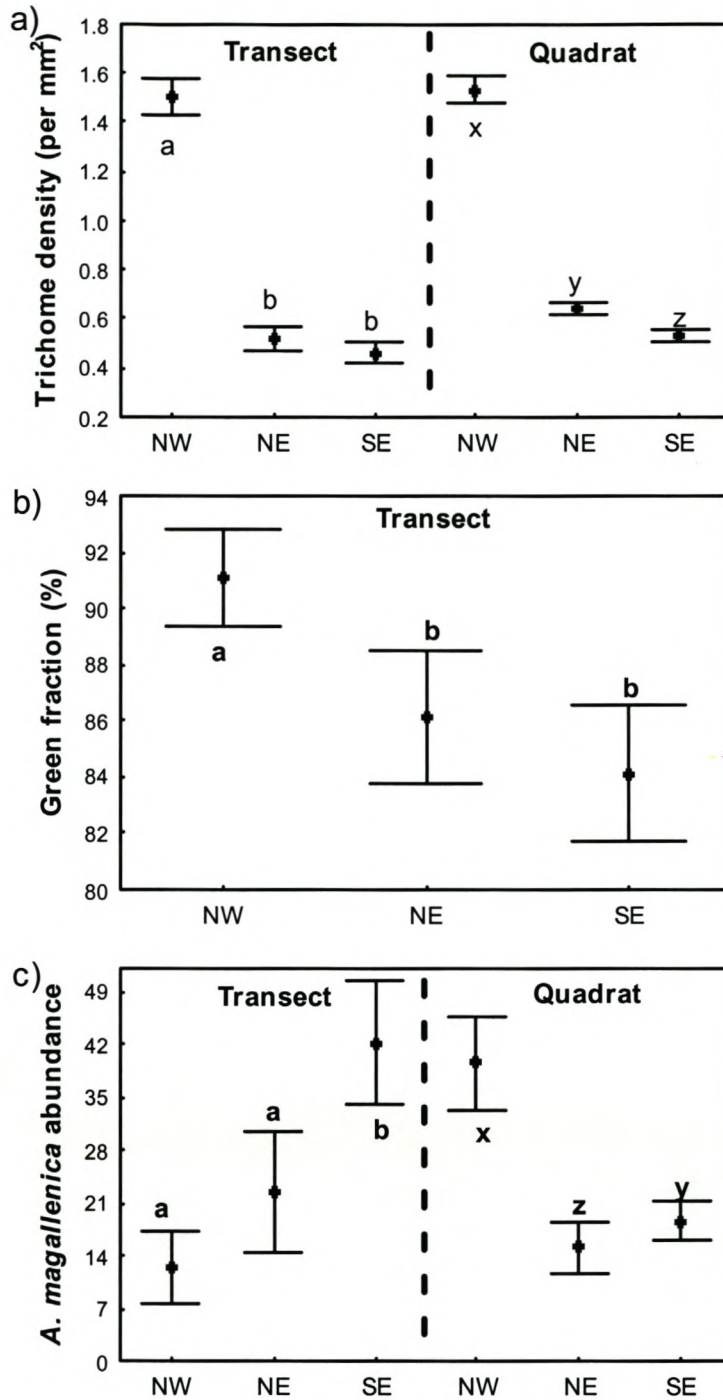


FIGURE 2. Differences in a) trichome density, b) proportion of cushion surface covered by green leaves (i.e. green fraction), and c) *Agrostis magellanica* abundance between sites. Data from transects and quadrats analysed separately. Groups not sharing a letter are significantly different at $p < 0.05$.

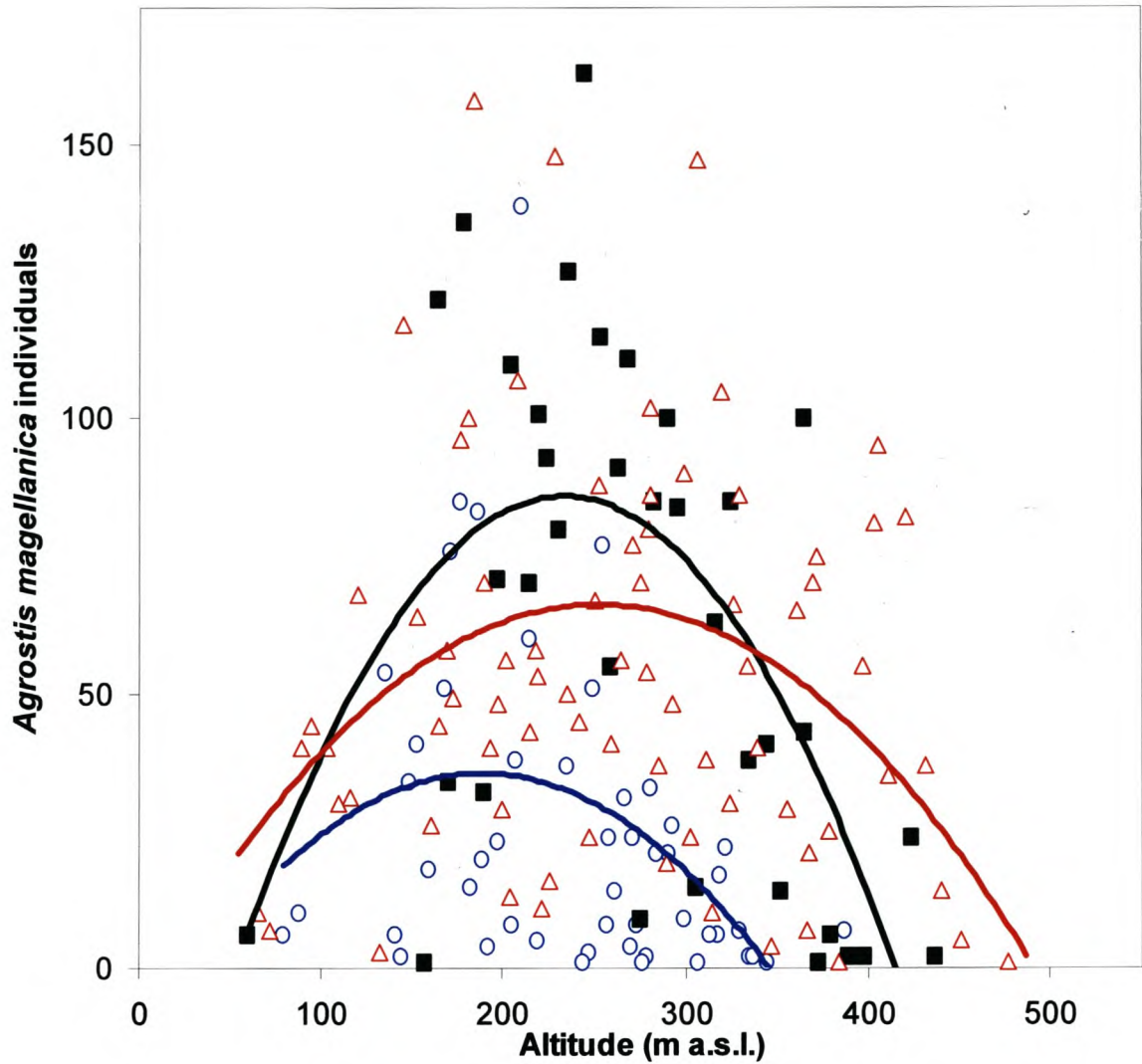


FIGURE 3. Altitudinal variation in epiphytic *Agrostis magellanica* abundance on *Azorella selago* (blue circles \circ - NW transect, black squares \blacksquare - NE transect, red triangles \triangle - SE transect). Zero values have been excluded for clarity in this graph (46 % of zero values are from altitudes exceeding 450 m a.s.l.). Curves indicate the best fit of a quadratic curve to data (for non-zero values; NW transect: $y = -16.96 + 0.57x - 0.01x^2$; NE transect: $y = -57.53 + 1.23x - 0.01x^2$; SE transect: $y = -7.30 + 0.58x - 0.01x^2$).

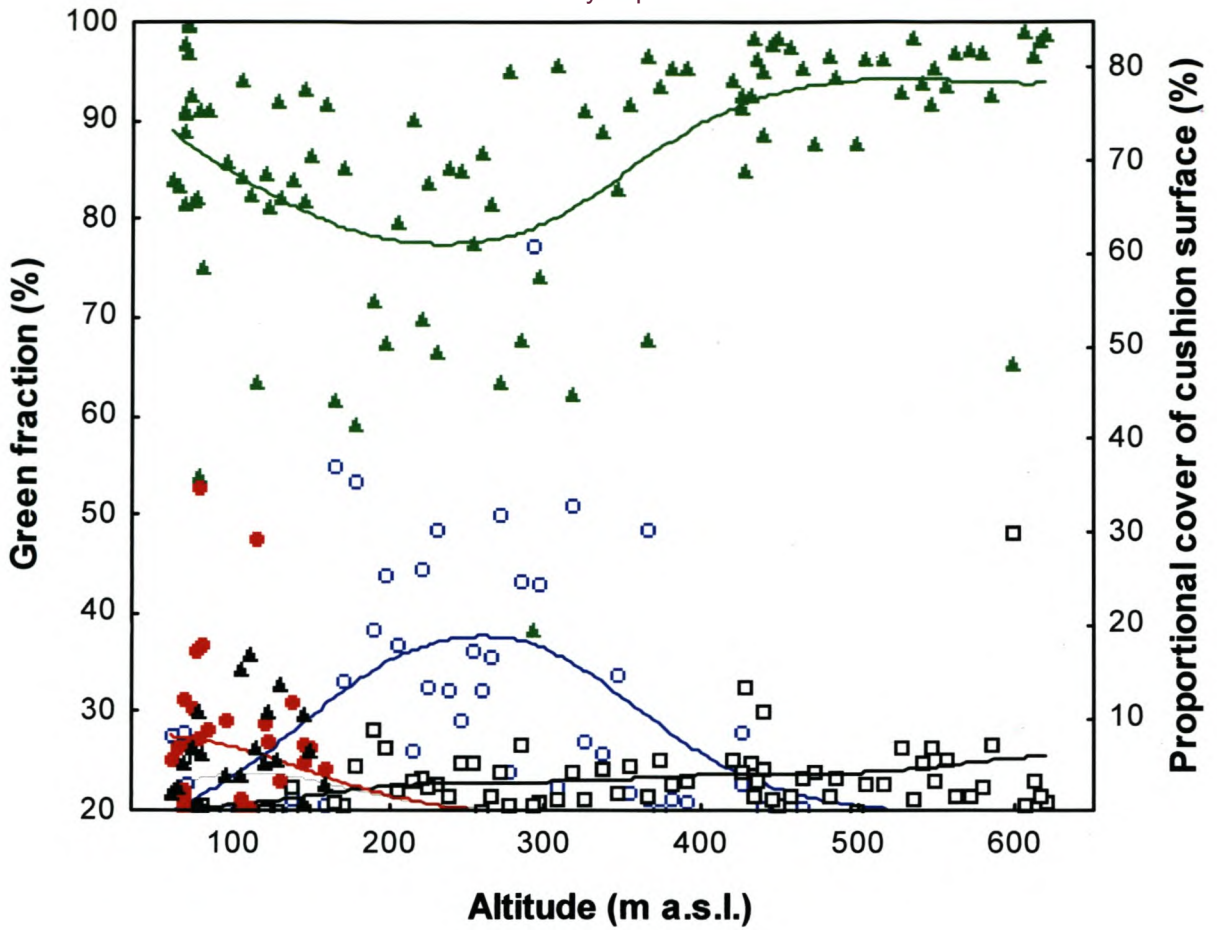


FIGURE 4. Altitudinal patterns in *Azorella selago* cover in the NE transect. Green triangles (▲) – cushion green fraction (left axis), black squares (□) – cushion dead fraction, blue circles (○) – *Agrostis magellanica* cover, black triangles (▲) – *Aceana magellanica* cover, red circles (●) – *Blechnum penna-marina* cover). Lines represent trends in data (fitted using distance weighted least squares).

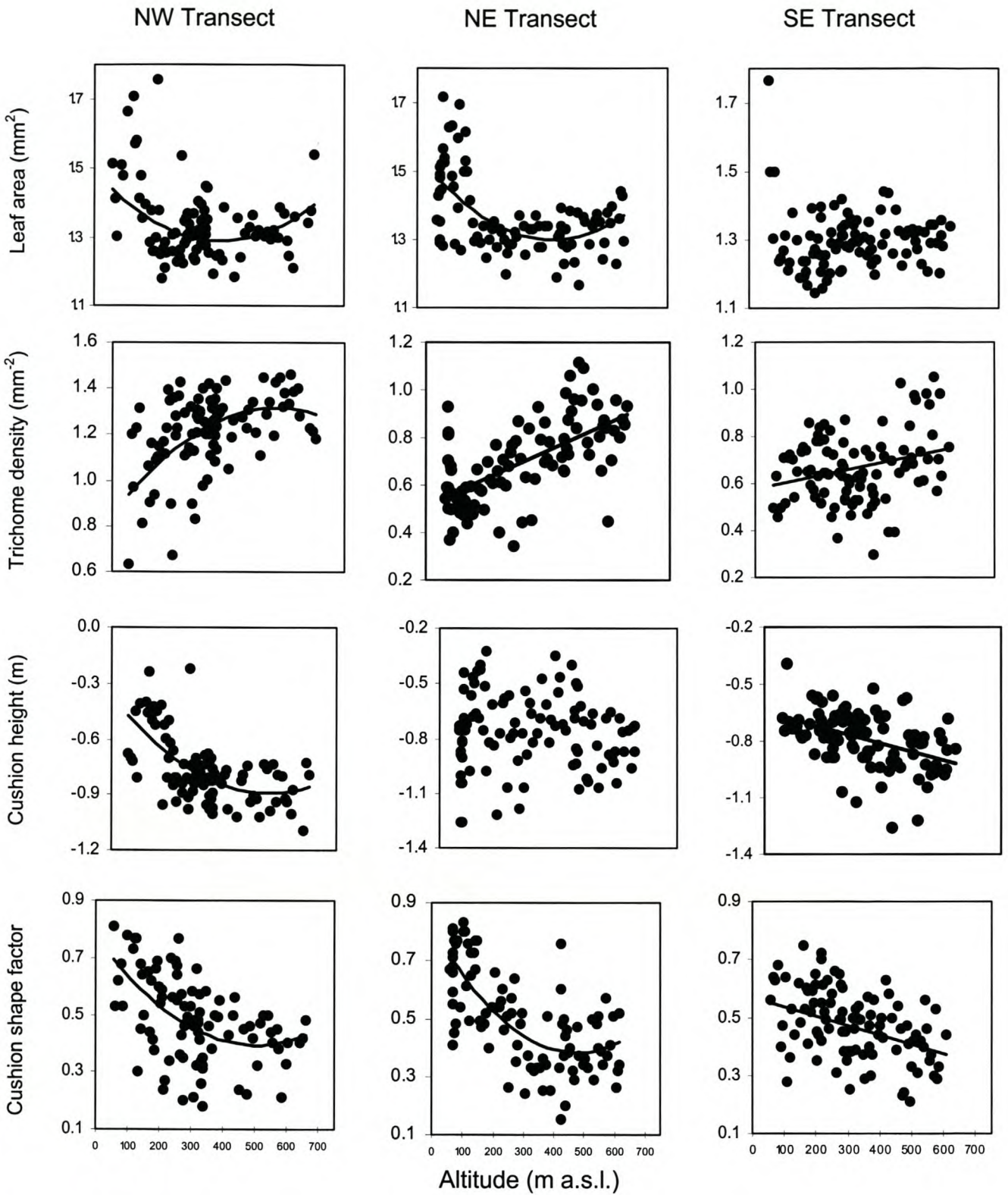


FIGURE 5. Altitudinal trends in *Azorella selago* leaf area (log-transformed), trichome density (square root-transformed), cushion height (log-transformed) and cushion shape in the transects.

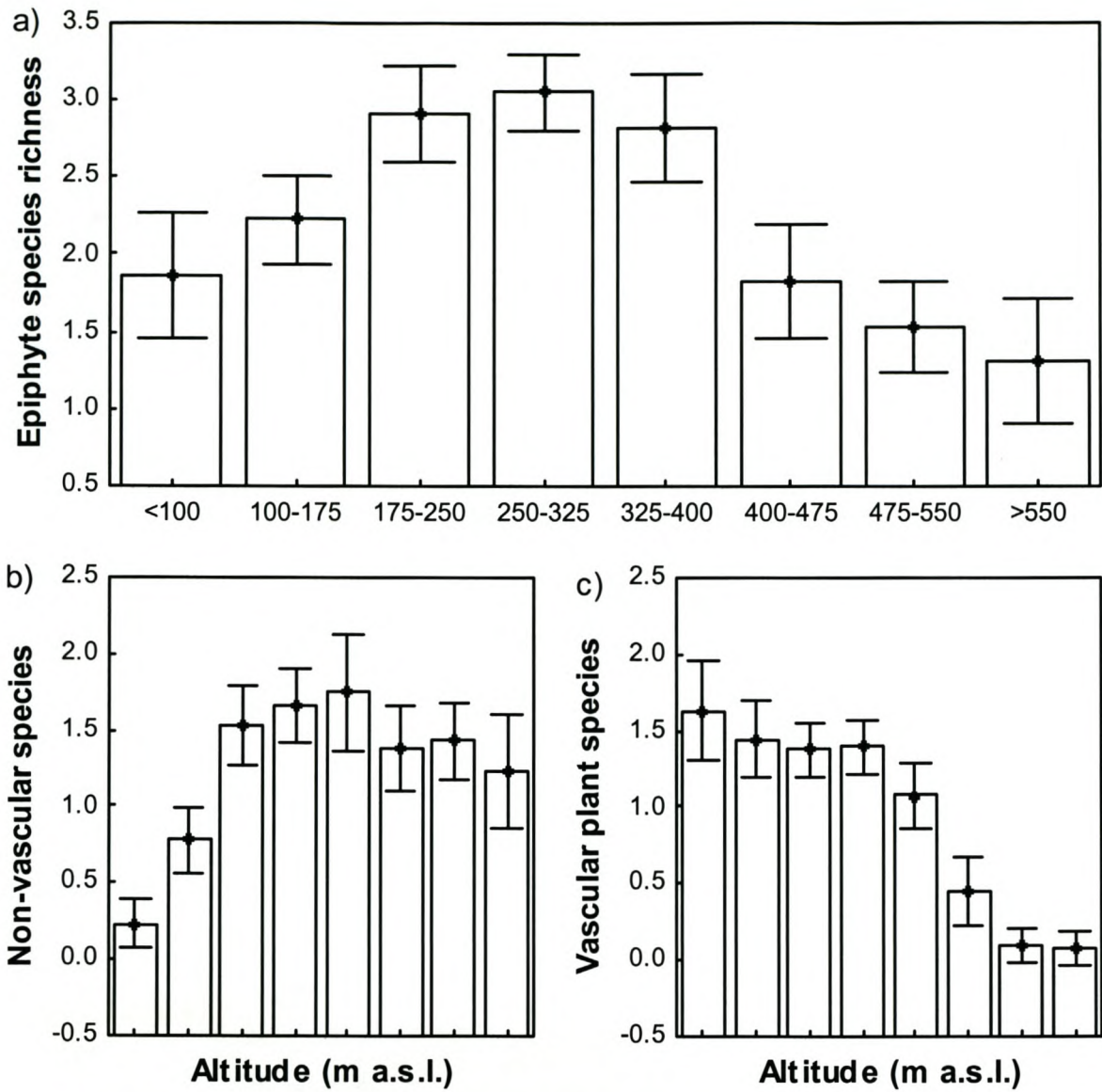


FIGURE 6. Altitudinal variation in the species richness of a) all epiphytes, b) non-vascular epiphytes (i.e. mosses), and c) vascular epiphytes on *Azorella selago*. Results were similar for all transects, so data pooled across all three transects for this figure. The same altitudinal classes are used in all three graphs. Sample size of nine to 19 cushion plants per altitudinal band.

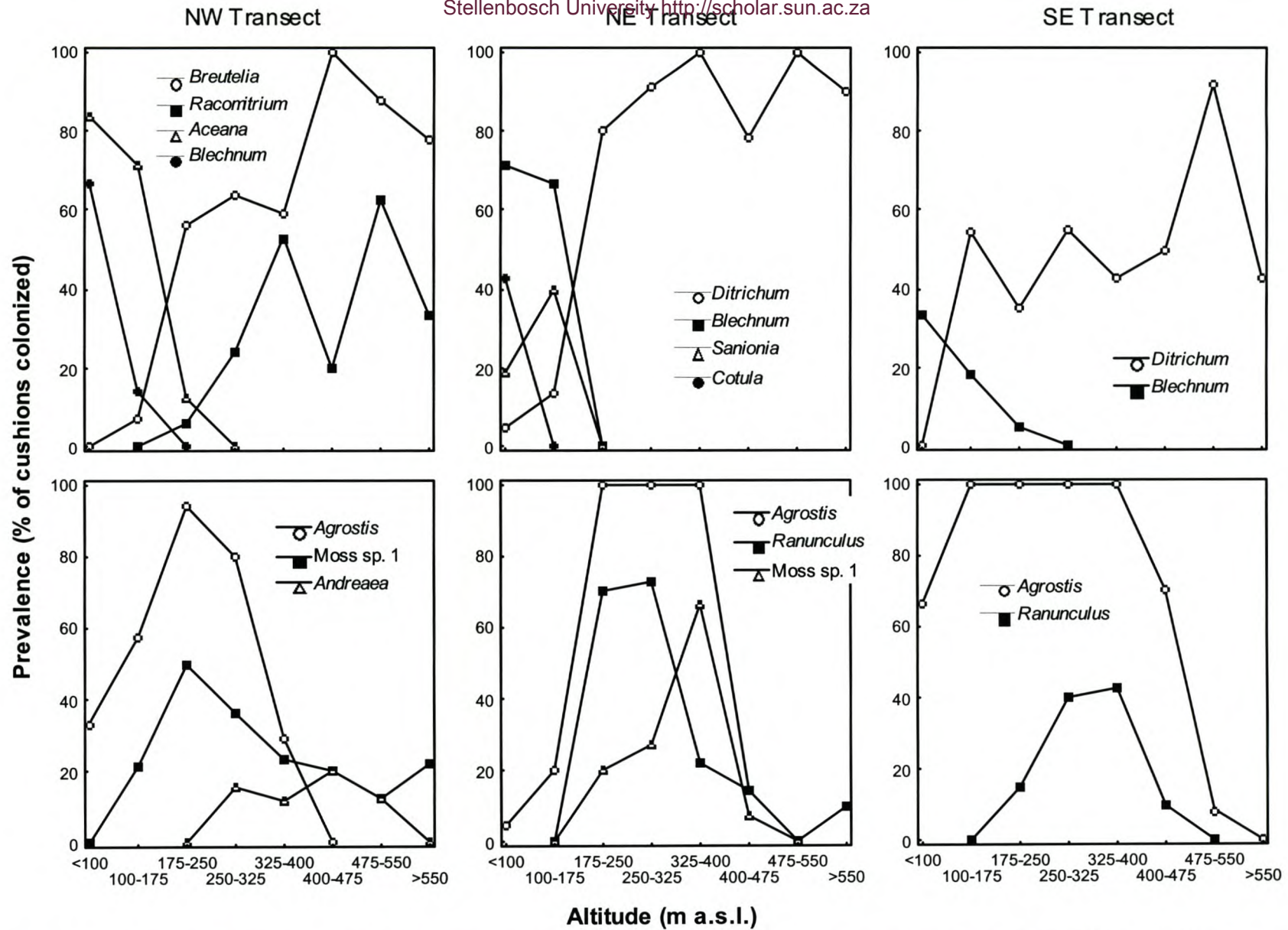


FIGURE 7. Altitudinal variation in the prevalence (the percentage of *Azorella selago* cushions colonized within altitudinal band) of epiphyte species. See Table 6 for full species names.

APPENDIX A

Simple linear regression of Azorella selago cushion growth rate, cushion morphology and leaf morphology against altitude. ¹ sign of the linear coefficient, ² log-transformed, ³ square-root transformed.

Dependent variable	NW Transect					NE Transect					SE Transect				
	R ²	F	df	p	Coeff. ¹	R ²	F	df	p	Coeff.	R ²	F	df	p	Coeff.
Cushion growth rate and morphology															
Cushion growth rate ²	< 0.01	0.15	1, 73	0.701	+	< 0.01	0.01	1, 80	0.976	-	0.15	13.6	1, 70	< 0.001	+
Cushion area ²	0.02	3.37	1, 93	0.070	-	0.01	2.12	1, 94	0.148	-	< 0.01	0.97	1, 96	0.327	+
Cushion height ²	0.30	41.47	1, 93	< 0.001	-	< 0.01	0.41	1, 95	0.522	-	0.19	24.55	1, 98	< 0.001	-
Cushion shape factor ²	0.20	24.05	1, 93	< 0.001	-	0.42	69.66	1, 94	< 0.001	-	0.20	25.13	1, 96	< 0.001	-
Leaf morphology															
Leaf area ²	0.06	7.19	1, 92	0.009	-	0.19	23.52	1, 94	< 0.001	-	< 0.01	0.25	1, 96	0.621	-
Leaflets ²	0.04	4.59	1, 92	0.035	-	0.03	3.90	1, 94	0.051	-	0.06	7.26	1, 96	0.008	+
Trichome density ³	0.19	23.35	1, 92	< 0.001	+	0.41	66.29	1, 94	< 0.001	+	0.07	8.00	1, 96	0.006	+

APPENDIX B

Polynomial (quadratic) regression of Azorella selago cushion growth rate, cushion morphology and leaf morphology against altitude. ¹ sign of the linear coefficient, ² sign of the quadratic coefficient, ³ log-transformed, ⁴ square-root transformed.

Dependent variable	R ²	F	d.f.	p	Coefficient	
					Linear ¹	Quadratic ²
NW Transect						
Cushion growth rate and morphology						
Cushion growth rate ³	0.02	1.92	2, 72	0.154	-	+
Cushion area ³	0.07	4.61	2, 92	0.012	-	+
Cushion height ³	0.37	28.82	2, 92	< 0.001	-	+
Cushion shape factor ³	0.25	17.02	2, 92	< 0.001	-	+
Leaf morphology						
Leaf area ³	0.25	16.23	2, 91	< 0.001	-	+
Leaflets ³	0.18	11.10	2, 91	< 0.001	-	+
Trichome density ⁴	0.23	14.84	2, 91	< 0.001	+	-
NE Transect						
Cushion growth rate and morphology						
Cushion growth rate ³	0.02	1.75	2, 79	0.180	-	+
Cushion area ³	0.01	1.24	2, 93	0.295	-	+
Cushion height ³	0.03	2.24	2, 94	0.112	+	-
Cushion shape factor ³	0.50	48.8	2, 93	< 0.001	-	+
Leaf morphology						
Leaf area ³	0.32	23.34	2, 93	< 0.001	-	+
Leaflets ³	0.02	1.99	2, 93	0.143	-	-
Trichome density ⁴	0.40	32.84	2, 93	< 0.001	+	+
SE Transect						
Cushion growth rate and morphology						
Cushion growth rate ³	0.33	18.34	2, 69	< 0.001	-	+
Cushion area ³	-0.01	0.49	2, 95	0.617	+	+
Cushion height ³	0.19	12.32	2, 97	< 0.001	-	+
Cushion shape factor ³	0.19	12.47	2, 95	< 0.001	-	-
Leaf morphology						
Leaf area ³	0.01	1.70	2, 95	0.187	-	+
Leaflets ³	0.05	3.67	2, 95	0.029	+	-
Trichome density ⁴	0.11	6.75	2, 95	0.002	-	+

APPENDIX C

Straight-line regression of Azorella selago cushion surface cover variables and epiphyte characteristics against altitude, using Generalized Linear Models. ¹ sign of the linear coefficient, ² binomial distribution, ³ Poisson distribution, ⁴ logit link-function, ⁵ log link-function, ⁶ log-log link function, A. magellanica = Agrostis magellanica.

Variable	d.f.	Scaled dev./d.f.	% Explained deviance	Log-likelihood ratio	p	Coeff. ¹
NW Transect						
Cushion surface cover (%)						
Green fraction ^{2,4}	93	0.92	34.13	-2736.75	< 0.001	+
Dead fraction ^{2,4}	93	1.00	6.32	-1422.78	< 0.001	+
<i>A. magellanica</i> fraction ^{2,4}	93	0.76	19.21	-1111.12	< 0.001	-
Moss fraction ^{2,4}	93	0.65	0.71	-182.91	0.453	-
Other epiphyte cover ^{2,4}	93	0.42	60.92	-787.10	< 0.001	-
Epiphyte abundance and species richness						
<i>A. magellanica</i> ^{3,5}	93	0.82	23.93	-1261.83	< 0.001	-
Epiphyte species richness ^{3,5}	93	0.53	13.59	-90.1095	0.042	-
NE Transect						
Cushion surface cover (%)						
Green fraction ^{2,4}	93	0.85	18.73	-3770.07	< 0.001	+
Dead fraction ^{2,4}	93	0.82	24.66	-1175.51	< 0.001	+
<i>A. magellanica</i> fraction ^{2,6}	93	0.79	4.92	-2199.95	< 0.001	-
Moss fraction ^{2,4}	93	0.46	26.25	-273.69	< 0.001	+
Other epiphyte cover ^{2,4}	93	0.98	66.08	-1314.4	< 0.001	-
Epiphyte abundance and species richness						
<i>A. magellanica</i> ^{3,5}	95	0.86	4.68	-2957.86	< 0.001	-
Epiphyte species richness ^{3,5}	95	0.59	6.40	-103.21	0.081	-
SE Transect						
Cushion surface cover (%)						
Green fraction ^{2,4}	96	0.91	15.24	-4206.96	< 0.001	+
Dead fraction ^{2,4}	96	0.91	0.04	-1805.79	0.757	+
<i>A. magellanica</i> fraction ^{2,4}	96	0.96	8.25	-3177.78	< 0.001	-
Moss fraction ^{2,4}	96	0.50	4.29	-76.71	0.180	-
Other epiphyte cover ^{2,4}	96	0.20	42.52	-433.48	< 0.001	-
Epiphyte abundance and species richness						
<i>A. magellanica</i> ^{3,5}	98	1.04	16.20	-2007.06	< 0.001	-
Epiphyte species richness ^{3,5}	98	0.55	6.66	-124.90	0.049	-

APPENDIX D

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Polynomial (quadratic) regression of *Azorella selago* cushion surface cover variables and epiphyte characteristics against altitude, using generalized linear models. ¹ sign of the linear coefficient, ² sign of the quadratic coefficient, ³ binomial distribution, ⁴ Poisson distribution, ⁵ logit link-function, ⁶ log link-function, ⁷ log-log link function, *A. magellanica* = *Agrostis magellanica*.

Variable	d.f.	Scaled dev./d.f.	%Explained deviance	Log-likelihood ratio	p	Co-efficient	
						Linear ¹	Quadratic ²
NW Transect							
Cushion surface cover (%)							
Green fraction ^{3,5}	92	0.92	34.51	-1004.71	< 0.001	+	+
Dead fraction ^{3,5}	92	0.92	23.03	-1398.32	< 0.001	+	+
<i>A. magellanica</i> fraction ^{3,5}	92	0.81	49.24	-2735.46	< 0.001	+	-
Moss fraction ^{3,5}	92	0.77	10.77	-178.91	0.014	+	+
Other epiphyte cover ^{3,5}	92	0.50	65.12	-765.81	< 0.001	+	-
Epiphyte abundance and species richness							
<i>A. magellanica</i> ^{4,6}	92	0.78	59.49	-721.38	< 0.001	+	-
Epiphyte species richness ^{4,6}	92	0.46	24.52	-87.02	0.006	+	+
NE Transect							
Cushion surface cover (%)							
Green fraction ^{3,5}	92	0.74	28.46	-1792.69	< 0.001	-	+
Dead fraction ^{3,5}	92	0.71	28.62	-1168.13	< 0.001	+	+
<i>A. magellanica</i> fraction ^{3,7}	92	0.83	57.36	-3722.46	< 0.001	+	+
Moss fraction ^{3,5}	92	1.34	29.43	-270.90	< 0.001	+	+
Other epiphyte cover ^{3,5}	92	1.00	81.90	-1218.15	< 0.001	+	-
Epiphyte abundance and species richness							
<i>A. magellanica</i> ^{4,6}	94	0.78	78.89	-720.67	< 0.001	+	-
Epiphyte species richness ^{4,6}	94	0.42	33.82	-94.96	< 0.001	+	+
SE Transect							
Cushion surface cover (%)							
Green fraction ^{3,5}	95	0.92	26.79	-2985.18	< 0.001	-	+
Dead fraction ^{3,5}	95	0.91	0.04	-1805.78	0.952	+	+
<i>A. magellanica</i> fraction ^{3,5}	95	0.90	38.94	-4147.58	< 0.001	+	+
Moss fraction ^{3,5}	95	0.42	4.30	-76.71	0.407	+	+
Other epiphyte cover ^{3,5}	95	0.29	45.09	-425.76	< 0.001	-	+
Epiphyte abundance and species richness							
<i>A. magellanica</i> ^{4,6}	97	0.97	50.08	-1281.17	< 0.001	+	+
Epiphyte species richness ^{4,6}	97	0.39	34.47	-116.81	< 0.001	+	+

APPENDIX E

Test of if the inclusion of a quadratic term (i.e. second order polynomial model) significantly improves the proportion of variance (F -test; simple linear regression) or proportion of deviance (Chi^2 test; GLZ) in *Azorella selago* characteristics explained by a linear model (i.e. first order polynomial model). *A. magellanica* = *Agrostis magellanica*.

	NW Transect		NE Transect		SE Transect		Mean R ²	
	F	p	F	p	F	p	monomial	polynomial
Cushion growth rate and morphology								
Cushion growth rate	3.68	0.059	3.50	0.065	19.48	< 0.001	0.06	0.12
Cushion area	5.68	0.019	0.37	0.545	0.01	0.913	0.01	0.02
Cushion height	11.49	0.001	4.05	0.047	0.27	0.604	0.17	0.19
Cushion shape	8.15	0.005	16.48	< 0.001	0.05	0.824	0.27	0.32
Leaf morphology								
Leaf area	23.50	< 0.001	18.72	< 0.001	3.16	0.079	0.08	0.19
Leaflets	16.81	< 0.001	0.11	0.745	0.13	0.718	0.04	0.08
Trichome density	5.25	0.024	0.05	0.815	5.15	0.025	0.22	0.25
	Chi ²	p	Chi ²	p	Chi ²	p		
Cushion surface cover (%)								
Green fraction	2.56	0.110	95.22	< 0.001	118.75	< 0.001	22.70	29.92
Dead fraction	48.90	< 0.001	14.77	< 0.001	0.00	0.958	10.34	17.23
<i>A. magellanica</i> fraction	212.82	< 0.001	814.51	< 0.001	385.20	< 0.001	10.79	48.52
Moss fraction	7.99	0.005	5.57	0.018	0.00	0.972	10.42	14.83
Other epiphyte cover	42.58	< 0.001	192.50	< 0.001	15.44	< 0.001	56.51	64.04
Epiphyte abundance and species richness								
<i>Agrostis magellanica</i>	1080.90	< 0.001	4474.38	< 0.001	1451.77	< 0.001	14.94	62.82
Epiphyte species richness	6.19	0.013	16.50	< 0.001	16.18	< 0.001	8.88	30.94

APPENDIX F

Altitudinal distribution of species growing epiphytically on Azorella selago. ¹ 1st quartile – 3rd quartile, ² log-transformed prior to ANOVA, ³ SE Transect excluded from analysis. All values in m a.s.l. Groups not sharing a letter differ at $p < 0.05$ (where letters are not indicated none of the groups differ significantly).

Epiphyte species	NW Transect		NE Transect		SE Transect		All transects Min - Max	ANOVA		
	q25 - q75 ¹	median	q25 - q75	median	q25 - q75	median		F	d.f.	p
<i>Agrostis magellanica</i>	188 - 292	256	217 - 349	273	194 - 335	264	60 - 477	1.876	2, 158	0.157
<i>Breutelia integrifolia</i> ²	270 - 475	331	a 245 - 498	373	ab 218 - 362	293	b 109 - 649	4.550	2, 119	0.012
<i>Ditrichum</i> sp.	307 - 568	509	276 - 514	424	235 - 487	327	67 - 649	2.850	2, 113	0.062
<i>Ranunculus biternatus</i> ²	197 - 383	299	222 - 326	267	264 - 335	291	69 - 606	0.191	2, 58	0.827
Unidentified moss sp. 1 ²	206 - 332	278	287 - 376	349	293 - 441	406	153 - 602	2.051	2, 42	0.141
<i>Blechnum penna-marina</i> ²	64 - 87	80	71 - 122	83	65 - 132	121	55 - 218	0.688	2, 30	0.510
<i>Sanionia uncinata</i>	142 - 334	215	a 69 - 130	112	b -	-	55 - 367	14.242	1, 28 ³	0.001
<i>Aceana magellanica</i> ²	87 - 153	122	69 - 127	110	-	-	64 - 397	1.442	1, 24 ³	0.242
<i>Racomitrium</i> sp.	310 - 495	337	-	-	-	-	208 - 583			
Unidentified moss sp. 2	250 - 329	284	-	-	-	-	177 - 465			
<i>Andreaea</i> sp.	309 - 395	327	498 - 498	498	-	-	270 - 498			
Unidentified moss sp. 3	283 - 362	321	-	-	-	-	244 - 452			
<i>Cotula plumosa</i>	-	-	67 - 69	69	-	-	65 - 69			

Chapter 4: Effects of simulated climate change on a dominant vascular plant species, *Azorella selago*, on sub-Antarctic Marion Island

Introduction

High latitudes are predicted to experience the greatest temperature increases at the greatest rates (IPCC, 2001). Indeed, in these regions large and rapid changes in climate have already been documented, the ecological consequences of which may be diverse and widespread (Kennedy, 1995b; Callaghan and Carlsson, 1997; Callaghan et al., 1997; Hughes, 2000; Walther et al., 2002). There is some evidence that changes in climate at high latitudes have already directly altered species' physiology, phenology and distribution, potentially leading to changes in species interactions and community structure (Kennedy, 1995b; Hughes, 2000; Walther et al., 2002). For example, higher temperatures can accelerate many physiological processes (including photosynthesis and growth: Callaghan et al., 1992), and are thought to be responsible for increased plant growth observed at high latitudes in the northern hemisphere (Myneni et al., 1997; Sturm et al., 2001). Warming can also alter phenological patterns, for example by extending the duration of species' growing seasons (Myneni et al., 1997; Sturm et al., 2001). Other plant responses to increased temperatures include changes in plant and leaf morphology, shifts to earlier spring events, altered nutrient relations and thermal stress damage (e.g. Michelsen et al., 1996; Robinson et al., 1998; Arft et al., 1999; Jonasson et al., 1999; Fitter and Fitter, 2002; Parmesan and Yohe, 2003). Warming can also alter species' reproductive performance and establishment success, and thereby species distributions. For example, the two vascular plant species native to the Antarctic, *Colobanthus quitensis* and *Deschampsia antarctica*, have increased their range and abundance dramatically over a 27-year period in response to increasing summer temperatures (Smith, 1994; see also Sturm et al., 2001). The biological effects of changes in rainfall are less well understood, particularly at high latitudes (Hodkinson et al., 1999). Changes in rainfall will alter the moisture stress experienced by plants, and consequently most plant physiological processes (including respiration and photosynthesis: Salisbury and Ross, 1992; Hughes, 2000). Altered rainfall patterns could therefore lead to changes in plant growth, production and nutrient relations, as well as biomass allocation and

phenological patterns (Callaghan et al., 1992; Kennedy, 1995b; Callaghan and Carlsson, 1997; Hodkinson et al., 1999).

The biological effects of changes in climate are, however, not limited to the direct effects on species physiology, phenology and distribution. Because responses to climate change are generally species-specific (species differ in the sign, magnitude and/or rate of their responses: Chapin et al., 1995), climate change will also alter species interactions (e.g. shift competitive balance, decouple mutualisms: Harrington et al., 1999; Stenseth and Mysterud, 2002; Saavedra et al., 2003). These indirect effects include increased shading of low-growing plants, a response that has already been observed in some experimental systems and which is predicted to be important in the Arctic (Callaghan et al., 1992; Callaghan and Jonasson, 1995; Callaghan and Carlsson, 1997). For example, Jonasson et al. (1999) reports how increased shading from shrubs reduces moss cover under warming and fertilization treatments in the Scandinavian Arctic. There is therefore significant evidence of climate change effects on high latitude plant communities, and under current climate change projections further biological changes are expected (Hughes, 2000).

In general, high latitude plant communities and their component species are well suited to experimental climate manipulation, partly due to their low height and low species diversity (Kennedy, 1995a, 1995b; Callaghan et al., 1997; Davies and Melbourne, 1999). In these communities, comparatively small treatments or samples can cover an area representative of an entire community, and therefore enable sufficient replication (Kennedy, 1995a). Additionally, in these challenging environments the influence of biotic factors are low relative to abiotic effects, and climate change impacts are thus more readily discernable (Callaghan and Jonasson, 1995; Callaghan et al., 1997). An important component of these high latitude plant communities are species with cushion growth-forms (e.g. Griggs, 1956; Mark et al., 2001). Due to their life history attributes (and characteristics of their environment), cushion plants are potentially good models for studying the biological effects of climate change. First, they have characteristics typical of species predicted to be unable to respond rapidly to change (slow growth, longevity of plant, stems and leaves), and are therefore potentially vulnerable (Molau, 1997). Second, the cushion growth-form simplifies and facilitates a number of measurement and monitoring techniques (e.g. growth rate: Huntley, 1972; Frenot et al., 1993; age estimation: McCarthy, 1992; Molau, 1997; Chapter 2). Finally, cushion plants often have

important and varied ecosystem functions, and could be considered keystone species in some systems. For example, they often host dense and diverse epiphyte and invertebrate communities (Griggs, 1956; Huntley, 1972; Barendse and Chown, 2001), and can influence geomorphological processes (see Selkirk, 1998; Boelhouwers et al., 2000).

In this paper we test the direct and indirect effects of continued warming and drying on the cushion plant species, *Azorella selago* Hook. (Apiaceae), on sub-Antarctic Marion Island. *Azorella selago* is a ubiquitous species on the island (Huntley, 1972; Smith et al., 2001), and host to a high diversity of epiphytes and invertebrates (Huntley, 1972; Barendse and Chown, 2001). Over the last half century the island has experienced large and rapid changes in climate, probably due to changes in atmospheric circulation patterns (Smith, 1994; Smith, 2002). Since the 1960's mean temperatures on the island have risen by 1.2 °C, and rainfall dropped by 25 % (Smith, 2002). These changes represent a considerable alteration in climate, and could greatly alter the island's vegetation (Smith, 1994; Smith, 2002). It has been predicted that changes in rainfall will have larger effects than temperature on plant communities on Marion Island, because vegetation patterns on the island are strongly influenced by hydrological factors (Gremmen, 1981; Smith and Steenkamp, 1990). Nonetheless, under a scenario of continued warming the abundance and distribution of vascular plant species are predicted to increase (Smith and Steenkamp, 1990). This may be particularly true for highly responsive species, such as *Agrostis magellanica* (Lam.) Vahl (Poaceae), the dominant epiphyte on *A. selago* (Huntley, 1971; Dormann and Woodin, 2002). Such an increase in epiphyte abundance may have considerable effects on *A. selago*, since the species is sensitive to shading (see Bergstrom et al., 1997). In this study we therefore simulate the direct effects of increased temperature and decreased rainfall, and examine the short-term vegetative response of *A. selago* to these changes. The possible indirect effect of climate change on *A. selago* by shading is also investigated.

Methods

Study species

Azorella selago Hook. (Apiaceae) is widely distributed across the sub-Antarctic islands and is a dominant species in some habitats (Moore, 1968; Huntley, 1972; Walton, 1976; Frenot et al., 1993). It is a long-lived pioneer species, colonizing loose scoraceous slopes, recent lava flows and glacial forelands of retreating glaciers (Huntley, 1972; Frenot et al., 1993). The species has a central taproot, from which stems arise radially and branch dichotomously (Frenot et al., 1993). The leaves of *A. selago* are small and lobed (deeply incised, forming finger-like leaflets) and their widened petioles form a sheath around the stem (Orchard, 1989). *Azorella selago* cushions have a hard and compact surface as leaves are tightly packed and stems grow closely against each other (Orchard, 1989). The species has a 7½ to 8½ month growing season on Marion Island (longer in sheltered environments; Huntley, 1972). In autumn growth ceases and by the onset of winter cushion leaves have turned brown (autumnal senescence; on Marion Island mid-April and mid-June respectively; Huntley, 1972). Old leaves are retained, forming a moist, humus-like collection of organic matter inside the plant (Huntley, 1971).

The cushion-growth form occurs in many plant families, and is thought to be advantageous in cold, dry and windy environments (Ashton and Gill, 1965; Huntley, 1972; Callaghan and Emanuelsson, 1985; Wickens, 1995). The hemispherical, prostrate and streamlined growth-form of cushion plants reduces their wind-resistance and decreases their surface to volume ratio, thereby minimizing water and heat loss (Huntley, 1971). Due to the presence of epiphytes, the surface of cushions can be quite heterogeneous, and few cushions have a completely green surface (i.e. capable of photosynthesis: Chapter 3). The surface of cushions can also comprise patches of dead stems, areas of senescent leaves (indicating the progress of autumnal senescence) and sometimes also spaces between stems (“gaps”; pers. obs).

Study site: Climate and location

Marion Island experiences an oceanic climate, characterized by low but stable temperatures (mean annual temperature 5.1 °C, mean diurnal variation 1.9 °C), high

relative humidity (on average 83 %) and rainfall (approximately 2500 mm per annum, distributed evenly throughout the year), and strong winds (exceeding gale force on more than 100 days per year; Marion Island's climate is discussed in full by Schulze, 1971; Smith, 2002).

The experiment was conducted on the eastern side of Marion Island over an area of approximately 100 x 150 m (western end of Skua Ridge: center 46° 52' 02"S 37° 50' 17"E, maximum altitude 106 m a.s.l.; see Fig. 3, Chapter 1, page 15). Skua Ridge is a basalt lava flow, with thin skeletal soil and a smoothed and rounded topography due to glacial erosion (Verwoerd, 1971). This site was chosen for logistic (fellfield area closest to scientific base), ecological (relatively flat and *A. selago* cushions support a relatively low density of epiphytes) and conservation reasons (it is located outside of wilderness and protected areas, albeit undisturbed; Anonymous, 1996). The vegetation is mesic fellfield (Smith and Steenkamp, 1990), dominated by *A. selago* cushions, *Agrostis magellanica* (mostly growing epiphytically on *A. selago*, but also as isolated independent plants at this altitude) and mosses (mostly *Andreaea* spp. and *Ditrichum* spp., with the latter also growing epiphytically on *A. selago*: Gremmen, 1981).

The extent of the area within which the experiment was conducted was determined by the minimum area within which enough suitable experimental cushions could be allocated. Sampling requirements for experimental cushions were that they fell within the median size range for the site (0.3 – 0.7 m maximum diameter determined in a pilot study; see also Chapter 2). In addition, experimental cushions could not be sheltered by large rocks, or be closer than 5 m from the nearest experimental cushion (to ensure treatments did not affect each other). Treatment cushions were also required to be relatively healthy (subjectively assessed, but partly determined by epiphyte load and proportion of surface covered by dead stem patches; see Huntley, 1972), free from mouse-burrows (House mice *Mus musculus* L. (Muridae) are alien on Marion Island and burrow into these plants: Avenant and Smith, 2003), and have a low *Sagina procumbens* L. (alien Caryophyllaceae species) epiphyte load. Treatments were then randomly applied to the selected experimental plants.

Treatments

Five treatments were imposed, with unmanipulated plants used as controls. Treatments were imposed for one year, starting in April 2002. They were applied subsequent to “before” measurements and removed in April 2003 (prior to “after” measurements). The treatments were designed to simulate further reductions in rainfall and increased shading by epiphytes.

Fixed-location rainout shelters constructed from clear polycarbonate sheets (Lexan Thermoclear LTC 6/2RS/1300, General Electric Structured Products, Massachusetts, USA; edges sealed to reduce condensation within the sheets) of 1.4 m x 1.9 m were used to minimize direct rainfall received by individual plants (“warm-dry” treatment; Fig. 1a). The polycarbonate sheets initially transmitted > 80 % of wavelengths > 380 nm, and < 10 % of wavelengths < 375 nm (the ultra-violet wavelengths: Anonymous, 2002; verified at the University of Stellenbosch, South Africa). The low transmission of ultraviolet-B radiation by the rainout shelters could complicate interpretation of results, as UV-B inhibits growth in some species (Rousseaux et al., 2001). However, *A. selago*'s responses to changes in UV-B are predicted to be limited, based on leaf morphology (high trichome density, thick leaves: Rousseaux et al., 2001) and chemistry (high concentration of diterpenoids, which are possibly UV-screening compounds: Ormrod and Hale, 1995). Results are, therefore, interpreted assuming a negligible effect of reduced UV-B radiation. Rainout shelters were secured > 0.1 m above the top of each plant and were angled such that runoff was displaced downslope of the plant (design similar to Yahdjian and Sala, 2002). This treatment was not designed to eliminate all water sources to the treatment cushions, and the plants still received moisture inputs from lateral soil water movement, surface flow and condensation.

Because a variety of unwanted microclimatic differences are often imposed by climate manipulation treatments (“chronic” microclimate modifications: Havström et al., 1993; Kennedy, 1995a; Fay et al., 2000), the shelters were designed to minimize these changes wherever possible. To minimize changes in temperature, wind conditions and CO₂ and water vapour concentrations, the sides of the rainout shelters were open, and a large space maintained between the top of the plants and the shelter. The low altitude of our experimental site minimized problems associated with treatments altering snow cover, as snow cover was present on the site for only a few

days during the experiment (< 15 , M. Nyakatya, pers. comm.) In addition, a procedural control (see below) was designed and deployed to separate the effects of a rainfall reduction from other shelter effects (following Kennedy, 1995a).

Perforated rainout shelters were used as procedural controls (Fig. 1b). Perforations were evenly-spaced and comprised three large slits (approximately 0.04 m long and 0.8 m wide, running perpendicular to the slope of the rainout shelter) and eight smaller holes (diameter 0.04 m) between the slits. The perforations allowed the treatment plants to receive approximately natural rainfall, but maintained the other effects of the shelter. The effects of drying were then inferred by comparing plant responses between the warm-dry treatment and procedural control, since they differed only in the amount of direct precipitation received. Similarly, the impact of secondary shelter effects (i.e. changes in temperature, light and relative humidity) can also be assessed by comparing plants from the procedural control with control plants.

Shading was effected by covering treatment cushions with green shade cloth (following e.g. Chapin and Shaver, 1985; Cavender-Bares et al., 2000), reducing light transmission by approximately 80 % (Alnet, Somerset West, South Africa; validated on site). Two types of increased shading were simulated; shade cloth was fixed over an entire plant (“shade” treatment; simulating heavy epiphyte cover observed on some low altitude cushions), or only a portion (randomly chosen side (half) of each cushion) of the treatment plants (“half-shade” treatment; simulating a more modest increase in epiphyte cover, Fig. 1c). The “half-shade-dry” treatment was imposed by covering a half-shade cushion with a rainout shelter. The lower temperatures and reduced wind under the shade cloth (due to reduced incident radiation and increased sheltering respectively) were considered to simulate the effects of increased shading by epiphytes. In other words, reductions in light intensity, temperature and wind speed are all expected simultaneously under increased epiphyte load. The half-shade and half-shade-dry treatments (“half-cushion” treatments) were analysed separately from the other treatments (“whole-cushion” treatments, i.e. where treatment applied evenly across entire plant), because the exposed half of the cushion was used as a within-plant control for the effect of shading.

Rainout shelters blown away during the experiment and not replaced within one week were excluded from all analyses (in total five replicates were lost). At the end of the experiment, unequal numbers of replicates thus remained (control = 28, warm = 12, warm-dry = 16, shade = 14, half-shade = 14, half-shade-dry = 9).

Cushion measurements

Before treatments were applied, a number of measurements were taken to ensure no *a priori* differences between experimental groups. The maximum diameter, diameter perpendicular to maximum diameter (hereafter perpendicular diameter), and height of each cushion was measured. The number of epiphytic *A. magellanica* individuals on each plant was counted. Distance to, and diameter of each plant's five nearest neighbours were measured (known to influence *A. selago* growth rate; Chapter 2). Soil depth was measured at four points around the base of each cushion (north-east (NE), south-east (SE), north-west (NW) and south-west (SW) sides), because Frenot et al. (1993) suggested that soil properties influence *A. selago* growth rate. Foliar nutrient concentrations were also tested for *a priori* differences between treatments. Leaf samples were taken from the center of ten randomly-selected cushions in each treatment. Green leaves from these samples were dried for 48 hours at 60°C, and returned to South Africa to be ashed, taken up in hydrochloric acid, and nutrient concentration (N, P, K, Ca, Mg, Na, Mn, Fe, Cu, Zn, B) determined with an inductively coupled plasma emission spectrometer against certified standards (performed by BemLab Analytical Laboratories, Somerset-West, South Africa).

Additionally, before treatments were imposed, cushion height was marked against thin (≤ 10 mm diameter) wooden sticks inserted diagonally through the cushions and deeply into the underlying soil (in both the shaded and exposed halves of the half-cushion treatments). The height of the cushion surface was again marked against the stick at the end of the experiment, with the difference between the marks equaling stem growth over the year. Growth rate therefore represents the change in cushion surface height over a year, but is not necessarily related to the increase in cushion biomass (i.e. production) due to differences in stem tissue density between cushions (Huntley, 1972; pers. obs). Diagonal positioning was used in preference to vertical positioning of the sticks (as used by Huntley, 1972; Chapter 2) because the latter would have obstructed experimental manipulations (growth rate measurements are therefore not comparable between this study and others).

At the end of the experiment, measures of leaf morphology, foliar nutrient concentration, surface cover and soil nutrient concentrations were made. Immediately after removing a treatment, an overhead photograph was taken of each cushion (from

1.5 m above cushion), *A. magellanica* individuals counted, and a sample of leaves collected. Two leaves were selected from each of ten randomly sampled sub-stems (avoiding the sides of the cushion, damaged leaves and dead stem patches) for determination of leaf morphology. The remainder of the sample was analysed for foliar nutrient concentration using the method outlined above. Leaf samples were taken from both the shaded and exposed sections of the half treatments. Simultaneously, four soil samples ($\pm 100 - 300$ grams dry mass) were collected adjacent to each cushion (from NE, NW, SE and SW sides), and a tissue core (70 mm diameter x 70 mm height) was taken from the center of each plant. Soil samples were taken to test if soil nutrient content had been influenced by the treatments (following e.g. Chapin and Shaver, 1985; Chapin et al., 1995; Jonasson et al., 1999), and tissue cores to test if the amount of moisture in the cushions differed between treatments. Plant tissue cores were dried at 60 °C for 24 hours and core moisture content calculated (% of dry mass). Soil samples were pooled, mixed, air-dried at approximately 25 °C for at least five days and returned to South Africa for analysis of soil nutrients (methods following Sparks et al., 1996). Phosphorus (Bray II extraction), potassium, calcium, magnesium and sodium (ammonium acetate extraction) concentrations were determined using an inductively coupled plasma emission spectrometer. Total carbon was determined by Walkley Black acid digestion. Soil samples were saturated with de-ionised water and electrical resistance measured in a standard USDA soil cup, and their pH read from a KCl-soil mixture (all soil analyses performed by BemLab Analytical Laboratories, Somerset-West, South Africa).

Leaves were weighed, and trichomes and leaflets counted. They were then pressed onto card and leaf images captured using a flatbed scanner (HP Scanjet 5470c). Image analysis software (SigmaScan Pro version 5.0; SPSS, Illinois, USA) was then used to measure each leaf's surface area, length, width, perimeter and shape factor (methods similar to Rousseaux et al., 2001; Belyea and Lancaster, 2002). The shape factor was calculated as:

$$4 \cdot \pi \cdot \text{area} / \text{perimeter}^2 \quad \dots \text{Eq. 1,}$$

ranging from 0 (straight line) to 1 (perfect circle) (Anonymous, 1999). These measurements were taken separately for the entire leaf, the leaf sheath (yellow on live leaves) and the green leaf area (i.e. the remaining green tissue, including the leaflets; Fig. 2). Damaged, old (i.e. > four days since collection) or senesced leaves were

excluded from calculations. Specific leaf area (SLA; unit leaf area per unit wet mass; dry mass could not be determined simultaneously with other leaf measurements), trichome density (per mm² leaflet area, as trichomes only grow on the leaflets and not on the leaf sheath) and the proportion leaf area comprising leaflets were calculated.

Cushion size and surface cover were determined by image analysis of the photographs taken (SigmaScan Pro version 5.0). Images were calibrated against an object of known size and orientation (north-pointing) in each photograph, and cushion diameter (maximum and perpendicular), area and circumference determined (following e.g. Belyea and Lancaster, 2002). Measurements from photographs were validated against field measurements (following Belyea and Lancaster, 2002), and were similar (simple linear regression: maximum diameter: $R^2 = 0.80$, $p < 0.001$; perpendicular diameter: $R^2 = 0.62$, $p < 0.001$). Image analysis was then used to measure the fraction of each cushion's surface covered by epiphytes (split into *A. magellanica* vs. other epiphytes for analyses), dead stem area (i.e. grey or black stems or leaves), senescent tissue (i.e. brown or yellow leaves) and healthy tissue (i.e. green leaves; methods similar to Cavender-Bares et al., 2000; Rousseaux et al., 2001). Two methods were used to measure the extent of senescent tissue (i.e. progression of autumnal senescence). For the "brown" method, all pixels falling within a range of brown colours were selected and tallied ("Colour Threshold" option of SigmaScan), while for "browning" measurements were taken only of contiguous areas of browned tissue (subjectively selected). This distinction was made because brown pixels were not necessarily clustered together, and therefore not always representative of the manner in which senescence has been observed (i.e. patchily distributed) on cushions. Both these measures of autumnal senescence gave similar results, and therefore only results from browning measurements are presented. For shaded plants, the gap area between stems (i.e. where stems did not grow tightly against each other and the inside of the cushion was visible) was also measured (gap area was small on exposed cushions, and therefore not measured in the control, procedural control and warm-dry plants).

Mean *A. magellanica* individual size (mm²/individual) was calculated for all treatments by dividing cushion area covered by *A. magellanica* epiphytes by the number of grass individuals on that cushion. Field observations suggested that *A. magellanica* epiphyte load was unevenly distributed across cushions. To test this, images were split into quarters (NE, SE, NW and SW quarters), and each quarter

analysed separately (procedure as above). As *Agrostis magellanica* cover differed between treatments, all analyses were repeated after excluding *A. magellanica* covered areas, i.e. using a reduced measure of total cushion surface. However, results generally did not differ whether analyses were adjusted for *A. magellanica* or not, and thus only results from analyses excluding *A. magellanica* cover are discussed. Half-cushion treatments were again analysed separately. The shaded and exposed halves of half cushions were analysed individually, with the transition area between the shaded and exposed areas excluded.

Micro-environment measurements

Over the course of the experiment, the effect of treatments on microclimatic conditions were quantified using iButton (Thermochron DS1921G, Dallas Semiconductor, Texas, USA) and Hobo (Hobo Pro RH/Temp, Onset Computing, Massachusetts, USA) dataloggers (following recommendations of Kennedy, 1995a). Temperature was measured throughout the year, and relative humidity, light intensity and soil moisture determined in April 2002 and April 2003. iButtons were used to measure temperature within cushions (15 mm below cushion surface; 0.5°C resolution, with hourly intervals) for four sampling periods (“Autumn” 73 days, commencing 28/4/2002; “Winter” 64 days, commencing 3/8/2002; “Spring” 48 days, commencing 7/12/2002; “Summer” 27 days, commencing 19/2/2003). At least eight replicates were present for each treatment within each sampling period. For all analyses mean treatment temperature (i.e. average of all replicates) was used. Hobo dataloggers (0.1 % resolution, hourly measurement intervals) were used to measure relative humidity around treatment cushions for shorter durations during the study (once in April 2002, three sampling periods in April 2003). Paired (i.e. treatment and control) dataloggers were placed under and next to treatments (0.3 m under and 0.3 m outside rainout shelters, and under the shade cloth and immediately adjacent to the shade cloth), with humidity sensors facing a standardized direction.

Soil moisture was determined gravimetrically on three occasions in April 2003 while the treatments were in place (following e.g. Chapin and Shaver, 1985; Michelsen et al., 1996). Paired soil samples were collected from 0.3 m under and 0.3 m outside the rainout shelters (i.e. warm-dry and half-shade-dry treatments, and procedural control). On the first sampling occasion soil samples were also collected

from immediately adjacent to other treatments. Samples were dried at 100°C for 48 hours, and percentage soil moisture (dry mass) determined.

The reduction in photosynthetically active radiation caused by the treatments was determined using a Li-Cor Quantum sensor (Li-Cor BioSciences, Nebraska, USA) during April 2003 before the treatments were removed. Paired measurements were made in ambient light and under the treatments (sensor held vertical), and repeated three times at each treatment replicate. Measurements were repeated on two consecutive but contrasting days (a clear day and a cloudy day).

Statistical analyses

Normality of all data were tested using a Shapiro-Wilks W test, and transformed to achieve approximate normality where possible. Differences between samples were tested using ANOVA, with a bootstrapped p-value where the data violated ANOVA assumptions (Good, 1999). Bootstrapping was calculated with 10^4 iterations, using Resampling Stat's Software (Bruce et al., 1999; for recent examples of use see García et al., 2002; Howes Keiffer and Ungar, 2002). Changes in temperature affected by treatments were analysed using an ANOVA on the temperature differences (control minus treatment; to remove daily and seasonal cycles in temperature). Paired data (i.e. paired measurements from the exposed and the shaded halves of the same cushions, or soil moisture data from under and next to the same rainout shelter) were analysed using a paired t-test (bootstrapped p-value used when data were non-normally distributed). The exposed portions of the half-cushion treatments were used as within-cushion controls for the effect of shading. Tukey's Honest Significant Difference tests (for normally-distributed variables) or their non-parametric equivalent (post-hoc comparison of mean ranks for all groups: Zar, 1984) were used to determine which sample means differed from each other.

Results

Treatment assignment

There were no *a priori* cushion size differences between treatments (maximum diameter: $F_{92,5} = 0.094$, $p = 0.993$; perpendicular diameter: $F_{92,5} = 0.398$, $p = 0.849$;

height: $F_{92, 5} = 1.052$, $p = 0.392$). In addition, there were no differences between mean nearest neighbour distances ($F_{92, 5} = 1.091$, $p = 0.371$) or neighbour diameters ($F_{92, 5} = 0.631$, $p = 0.677$). Soil depth (on each side of the plants and mean plant soil depth; all $p > 0.50$) and *a priori* epiphyte load (number of *A. magellanica* individuals: $F_{89, 5} = 0.489$, $p = 0.784$) also did not differ between treatments. Foliar nutrient concentrations (all nutrients: $F_{5, 54} < 1.325$, $p > 0.268$) did not differ between treatments, and were generally within the range of values reported from *A. selago* on Marion Island (leaf calcium concentration was slightly higher for *A. selago* than reported in Smith, 1976, 1977).

Treatment effects on micro-environment

The rainout shelters and the shade treatments had little effect on soil nutrients. Soil nutrient concentration generally did not differ between treatments (Appendix A). Potassium concentration differed between control (highest concentration) and half-shade-dry treatments (lowest concentration; all other treatments did not differ from each other; ANOVA across all treatments: $F_{24, 5} = 3.978$, $p = 0.009$). Phosphorus also differed between treatments with a significantly lower concentration in the shade treatment compared to the control and half-shade and shade-shade-dry treatments (all other treatments did not differ significantly from each other; ANOVA across all treatments: $F_{24, 5} = 2.880$, $p = 0.036$). However, after sequential Bonferroni adjustment (Rice 1989) the concentration of the soil nutrients (also soil resistance and pH) did not differ between treatments.

Rainout shelters blocked direct rainfall to the experimental plants (primary shelter effect), but also caused other unwanted changes in microclimate (secondary shelter effects; altering relative humidity, temperature and light). However, as outlined in the methods, the procedural control enabled the effect of reduced rainfall to be separated from the secondary shelter effects. The warm-dry treatment lowered relative humidity (RH) significantly during two (out of three) sampling periods (both periods $t > 27.00$, d.f. = 131, bootstrap $p < 0.001$; RH (mean \pm S.E.) 1.88 ± 0.07 % and 4.66 ± 0.10 % lower), but had no effect on the range of RH experienced by cushions (all comparisons $p > 0.05$). The procedural control had a similar effect (control RH – treatment RH = 3.60 %; $t = 41.47$, d.f. = 65, bootstrap $p < 0.001$). Cushion core moisture ($F_{134, 5} = 8.749$, $p < 0.001$) differed between sampling dates,

but not between treatments ($F_{130, 9} = 0.449$, $p = 0.906$; high d.f. because multiple cores were taken from half-shade and half-shade-dry cushions). Soil moisture also differed between sampling dates (although only warm-dry treatment: $F_{41, 2} = 7.054$, $p = 0.002$; other treatments: $p > 0.05$) and not between treatments ($F_{72, 6} = 0.772$, $p = 0.595$) or between paired samples (i.e. from under and adjacent to the rainout shelters; $p \geq 0.02$, all comparisons non-significant after sequential Bonferroni correction).

Rainout shelters also altered the temperatures experienced by treatment cushions (Fig. 3). The shelters consistently reduced the range of temperatures experienced by plants (mean annual daily temperature range > 0.65 °C narrower in the treatments: Appendix B). Mean temperatures were higher under the rainout shelters than in control plants. Plants in the warm-dry treatment were warmer than controls in all seasons (warming relative to control plants: mean \pm S.E. = 0.25 ± 0.01 °C: Appendix B). In the procedural control, mean warming was experienced in three of the four sampling periods (Appendix B). The magnitude of temperature enhancement under the rainout shelters was negatively related to plant temperature in all treatments (across seasons and within days). Therefore, treatments were cooler than control plants during the hottest part of the day and generally warmer during the coldest part of the day (simple linear regression of size of warming against control temperature: all treatments $p < 0.001$, $R^2 = 14 - 46$ %, slope = -0.08 to -0.17 ; Fig. 3). This was supported by examination of the seasonal temperatures where, for a given treatment, during the hottest season cushions tended to be warmed the least, and during the coldest season cushions tended to be warmed the most (Pearson correlation: all treatments $r < -0.18$, although $p > 0.25$).

Plants under rainout shelters received lower intensity light than control plants. Transmission by the rainout shelters at the end of the experiment was lower than expected at 61.5 ± 4.5 % (mean \pm S.E., $n = 14$) for warm-dry treatment and 61.0 ± 6.8 % (mean \pm S.E., $n = 4$) for the procedural control, despite an initial transmissivity of approximately 85 %. This was due to superficial damage (wind abrasion), and condensation on the shelters. Light transmission, however, differed significantly between sampling days, with proportionally lower transmission on the sunnier day ($F_{1, 16} = 35.970$, bootstrap $p < 0.001$). Transmission declined with increasing light intensity in all treatments, although only significantly so in the warm-dry treatment (Spearman rank correlation; all treatments: $r = -0.79$, $p < 0.001$).

Under the shading treatments, light intensity was significantly reduced (mean transmission \pm S.E. = 15.8 ± 1.8 %, $n = 9$). The plants in the half-shade-dry treatment experience an 89 % reduction in light intensity on their shaded portion relative to control plants (mean transmission \pm S.E. = 11.2 ± 1.47 %, $n = 6$). Similar to results from the rainout shelters, the transmissivity of the shade cloth varied between sunny and overcast conditions (shade and half-shade treatments: $F_{1,9} = 6.196$, bootstrap $p < 0.001$). In addition, shade and half-shade treatments consistently experienced lower temperatures than control cushions (cooling relative to control plants: mean \pm S.E. = 0.30 ± 0.01 and 0.44 ± 0.01 respectively: Appendix B). Plants under the half-shade-dry treatment experienced mean cooling in three seasons, and the effect of slight warming during the autumn sampling period is assumed to be negligible, particularly since the plants were senescent over most of that period (Appendix B). As reported for the rainout shelters, temperature enhancement was greatest during the coolest periods. Shading did not alter cushion or soil moisture ($t = -0.47$, d.f. = 65, bootstrap $p > 0.31$), but did increase RH in both sampling periods. Relative humidity was 2.12 – 2.79 % higher in the shade treatment for the two sampling period showing significant differences ($t = 11.08$, d.f. = 131, bootstrap $p < 0.001$ and $t = -8.94$, d.f. = 40, bootstrap $p < 0.001$ respectively; no significant difference in RH during third sampling period). Data were not available for the half-shade-dry treatment. Because these changes in relative humidity were small (< 3 %) and inconsistent, their effects were considered to be negligible in comparison with the large reductions in light, temperature and wind.

Growth rate and leaf morphology

Whole-cushion treatments

Cushion growth rate and leaf morphology differed between treatments. Shade cushions grew significantly more during the experimental year than control, procedural control and warm-dry cushions ($F_{3,61} = 31.365$, $p < 0.001$; Fig. 4). Leaf area, green leaf (leaflet) area and sheath area (and their associated measurements of length, width and perimeter) all differed in a similar way between treatments, with shade leaves differing most from control leaves than the other treatments (Table 1; Fig. 5). Leaves from the shade treatment were always significantly larger (i.e. had a

greater area and perimeter and were longer and wider, for the whole leaf, the leaflets and the sheath) and heavier than control leaves (Table 1; Fig. 5a, b). Leaves from the procedural control and warm-dry treatment tended to be larger (but not significantly so) than control leaves, although smaller than shade leaves (Fig. 5a).

The fraction of leaf area comprising leaflets and leaf shape differed significantly between treatments (Table 1). Leaflets comprised a lower proportion of total leaf area in the shade treatment compared to the other treatments (Fig. 5c). Leaf shape differed between some treatments, with shade leaves having a significantly lower shape factor (i.e. less circular) than leaves from the other treatments (Table 1; Fig. 5d).

Numbers of leaflets and trichomes were similar across treatments (Table 1). However, trichome density differed significantly between treatments with significantly lower densities in the shade and warm-dry treatments than in the control plants (Table 1; Fig. 5e). Specific leaf area (SLA) also varied significantly between treatments (Table 1), with a significantly higher ratio for shade leaves, but no difference between control, procedural control and warm-dry leaves (Fig. 5f).

Half-cushion treatments

Similar to the whole cushions, partial shading also increased growth rate (Fig. 4). The shaded halves of the half-cushion treatments grew significantly more than the exposed halves (half-shade: $t = -5.709$, d.f. = 5, $p = 0.002$; half-shade-dry: $t = -10.734$, d.f. = 12, $p < 0.001$).

The differences between shaded and exposed leaves from the half treatments were also similar to the differences between leaves from the shade treatment and the other whole-cushion treatments. Leaves from the shaded halves were always significantly larger than exposed leaves (Table 1; Fig. 6a). Shade leaves also had a greater mass than exposed leaves, although the difference was small and non-significant for the half-shade-dry treatment (Table 1; Fig. 6b). Similar to leaves from the whole shade cushions, leaf sheath made up a significantly larger proportion of total leaf area in shade leaves (Table 1; Fig. 6c). Leaf shape was similar between halves, except when considering total leaf area, where shade leaves had a significantly less circular (i.e. more indented) shape (Table 1; Fig. 6d). Trichome density was also consistently lower on shaded than exposed leaves (Fig. 6e). SLA was higher in the

shaded leaves in the half-shade-dry treatment, but not for the half-shade treatment (no difference: Table 1; Fig. 6f).

Leaf nutrient content

Whole-cushion treatments

Foliar nutrient concentration differed between treatments (Appendix C). Concentrations were determined on a per leaf mass and per leaf area basis, but since the area – mass relationship (i.e. SLA) did not differ much between treatments (except when comparing shaded leaves to exposed leaves), results were similar (although the significance of some patterns changed). Foliar concentrations of N, P, K and B were higher in shade leaves than in other treatments (significantly so for N and P on a per mass basis; Appendix C). In contrast, leaves from the shade treatment had lower Na and Ca concentrations than other treatments (significantly so for Ca on a per area basis: Fig. 7a; Appendix C). Leaf nutrient concentration also differed between the rainout shelters (procedural control and warm-dry treatment; which never differed significantly: Appendix C) and the other treatments. For example, foliar concentration of Na, Fe and Zn tended to be higher in the procedural control and/or warm-dry treatments than in shade or control leaves (significantly so for Zn on a per area basis: Fig. 7b; Appendix C).

Half-cushion treatments

The nutrient results of the half-cushion treatments were similar to their whole-cushion treatment equivalents (Appendix D). Foliar concentrations of P, Zn and B were higher under shading (on a per mass basis, and the difference in B concentration only significant in the half-shade-dry treatment), and those of Ca and Na higher in exposed portions of cushions (only significant in the half-shade treatment, Fig. 7a; similar pattern on a per area basis: Appendix D).

Cushion surface

Whole-cushion treatments

Cushion cover differed significantly between treatments (Table 2). The proportion of each cushion covered by green leaves (hereafter green fraction) was significantly lower under the warm-dry treatment than under the procedural control or shade treatment (Table 2; Fig. 8a). Similarly, the proportion of cushion surface area comprising dead tissue (hereafter dead fraction) was lower in warm-dry and shade cushions than in control plants (Table 2; Fig. 8b). Therefore, cushion surface cover was responsive to the treatments imposed, changing in both the green and dead fraction.

The senescent fraction of treatment cushions was significantly higher in the warm-dry treatment than in the procedural control or shade treatment (Table 2; Fig. 9). The senescent fraction of the other treatments (i.e. control, procedural control and shade treatment) did not differ significantly.

Agrostis magellanica responded strongly to shading (Fig. 10). Over the course of the experiment, the number of *A. magellanica* individuals increased by a similar proportion on control, procedural control and warm-dry cushions, but declined in shade cushions (Fig. 10a). Average *A. magellanica* size did not differ between control, procedural control and warm-dry treatments, but was significantly larger in the shade treatment (Fig. 10b). The fraction of cushion surface covered by *A. magellanica* increased significantly under the shade treatment, and slightly (albeit non-significantly) under the procedural control (Table 2; Fig. 10c). Therefore, epiphyte load increased under shading, despite reduced numbers of grasses, due to increased average individual size. Other epiphyte species occurred on only a few treatment cushions (mostly *Ditrichum spp.* and *Sagina procumbens* mosses, and also liverworts and lichens on the shaded cushions), and never covered more than a small proportion of cushion surface area (maximum cover 4 %). Epiphyte load from all these other species did not differ between treatments (Table 2).

Agrostis magellanica epiphyte load (measured as proportional cover) also differed significantly between quarters in all treatments, and was always highest in the SE quarter and lowest in the NW quarter (Table 3; Fig. 11a). After adjusting cushion fractions for this unequal distribution of epiphyte load, only the warm-dry treatment

showed any other differences in surface cover between quarters (Table 3). The warm-dry treatment had a significantly lower green fraction in the SW than the NE quarters (SE and NW quarters intermediate; Fig. 11b). The inverse pattern was observed for the senescent fraction in the warm-dry treatment, with the greatest proportion of senescent area in the SW quarter and the lowest in the NE (Fig. 11c). Other cushion surface cover variables did not differ between quarters (e.g. Fig. 11d). Therefore, in all treatments epiphyte load differed between cushion quarters and, in the warm-dry treatment, quarters differed in their degree of autumnal senescence.

Half-cushion treatments

The responses of the shaded portions of the half cushions were similar to those of the shade cushions. Green fraction was significantly lower in the shaded halves of the half-shade treatment, and tended to be lower (although not significantly) in the half-shade-dry treatment (Fig. 8c). In contrast, the gap fraction (i.e. the proportion of each cushion's surface covered by gaps between stems) was significantly higher in the shaded sections (half-shade treatment: exposed halves; mean \pm S.E. = 0.50 ± 0.15 %, shaded halves; 2.14 ± 0.52 %; half-shade-dry treatment: exposed halves; 0.13 ± 0.05 %, shaded halves; 1.84 ± 0.66 %; Table 2), while dead fraction did not differ between halves (Fig. 8d).

Proportional cover by *A. magellanica* was strongly and significant higher in the shaded portion of the half-shade treatment, although there was no difference in the half-shade-dry treatment (Fig. 10c). The mean size of *A. magellanica* individuals did not differ between shaded and exposed halves, although tended to be slightly greater in the shaded portions of the half-shade treatment (Fig. 10b). Changes in numbers of *A. magellanica* grasses were less clear in the half cushions than in the whole cushions, because the two halves were analysed together ("before" counts were not split into the two halves; Fig. 10a).

Other vascular epiphyte species increased their proportional cover under shading (although only significant in the half-shade treatment after removing *A. magellanica* cover: $t = -2.10$, d.f. = 13, $p = 0.020$). Total cover by epiphyte species (excluding *Agrostis magellanica*) still though never exceeded 7 % of the cushion surface. The size of the senescent fraction did not differ between shaded and unshaded halves (Table 2), although there was a trend for slightly higher senescence in both the

shaded halves (compared to the exposed halves) and the half-shade-dry treatment (compared to the half-shade treatment: Fig. 9).

Discussion

Significant and striking differences were observed between treatments in cushion growth rate, leaf morphology, phenology and epiphyte cover, despite the short duration of the experiment.

Responses to reduced precipitation

Reduced rainfall strongly altered cushion phenology, but had a limited effect on leaf morphology, leaf nutrient concentrations and stem growth rate of *A. selago*. Few previous studies have examined the effects of reduced rainfall in mesic high latitude areas, because rainfall is predicted to increase in the Arctic (where most high latitude climate change research has been conducted). However, most reviews stress the importance of changes in rainfall to vegetation, particularly in fellfield habitats (e.g. Callaghan and Emanuelsson, 1985; Kennedy, 1995b; Callaghan and Carlsson, 1997; see also Callaghan and Jonasson, 1995).

The most striking effect of reduced rainfall in this study was that it accelerated autumnal senescence, shortening the growing season of *A. selago*. Cushion senescence in the half-cushion treatments also supported this result because senescence was greater under drying and shading than under shading alone. Therefore, rainfall potentially constrains the length of the *A. selago* growing season, as has been suggested for Arctic vegetation (Callaghan and Emanuelsson, 1985). Further reductions in rainfall on Marion Island could thus shift autumnal senescence to earlier in the season and possibly reduce *A. selago* productivity as a consequence of the shorter growing season (Myneni et al., 1997; Perfors et al., 2003; although see Walker et al., 1995; Chapin and Shaver, 1996; Starr et al., 2000).

In this study, reduced rainfall had little effect on leaf morphology (i.e. leaf responses in the procedural controls and warm-dry treatment, and half-shade and half-shade-dry treatments were similar), in broad agreement with results from the Arctic, where simulated increases in rainfall had little effect on plants (Dormann and Woodin, 2002). However, one notable exception was the contrasting responses of

shade leaf weight and thickness in the half-shade treatments. Shaded leaves were heavier than exposed leaves in the half-shade treatment, but not in the half-shade-dry treatment. In contrast, shade leaves were thinner (i.e. higher SLA) than exposed leaves in the half-shade-dry treatment, but SLA did not differ between leaves in the half-shade treatment. This result highlights the importance of considering the interactive effects of multiple simultaneous changes in environmental factors (e.g. the effect of a reduction in rainfall on a species might differ if shading increases or remains constant over the same period: Cavender-Bares et al., 2000; Sack and Grubb, 2002; Dole et al., 2003).

Changes in rainfall may also affect the growth of epiphytes on this species. Comparing *A. magellanica* cover between the procedural control and the warm-dry treatment suggests that the species' growth may be limited by rainfall (the trend was consistent, although differences were non-significant). Its cover under the procedural control was greater than that of the controls, although the difference between *A. magellanica* cover between the warm-dry treatment and the controls was much smaller. Similarly, comparing the half-cushion treatments, *A. magellanica* cover was highest under the shaded portion of half-shade treatment than its exposed portion, but did not differ between the exposed and shaded portions of the half-dry-shade treatment. This suggests that drying could also constrain the response of *A. magellanica* to shade. Therefore, reduced rainfall could alter both the timing of autumnal senescence in, and the epiphyte cover of, *A. selago*.

Effects of shading

Shading brought about large changes in *A. selago* leaf morphology, foliar nutrient concentrations, growth rate and surface cover. As expected, *A. selago* cushions produced larger (lamina area and petiole length) and thinner (increased SLA) shade leaves (Salisbury and Ross, 1992; Niklas, 1996; Gutschick, 1999; Cavender-Bares et al., 2000; high latitude studies: Michelsen et al., 1996; Dormann and Woodin, 2002; but see also Havström et al., 1993). These changes increase leaf light interception area (as expected for shaded leaves), while increasing potential water loss (due to higher surface – volume ratio: Larcher, 1980). The lower leaf shape factor (i.e. shape becoming less circular) of shaded leaves also suggests a shift towards higher moisture loss under shade conditions, since it represents an increase in leaf perimeter to volume

ratio. Similarly, due to their lower trichome density, shade leaves have a higher potential for light interception (trichomes can reduce light interception: Gutschick, 1999; Press, 1999), but also for water loss (trichomes can reduce water loss: Gutschick, 1999; Press, 1999). Another difference between shade and exposed leaves was the disproportionately large area of sheath tissue in shade leaves (i.e. supporting structure). Shade leaves had less leaflet area (i.e. photosynthesising area) per unit leaf area than exposed leaves (i.e. leaflets comprised $\pm 55\%$ of exposed leaves, but only $\pm 45\%$ of shaded leaves), and therefore increased their light interception area as well as their sheath area.

Leaf nutrient concentrations also differed between shaded and exposed leaves. Because the treatments did not affect soil nutrient concentrations, these differences in foliar nutrient concentrations were not a result of changes in the soil-availability of nutrients. In agreement with other studies, foliar nitrogen, potassium and phosphorus concentrations (also boron and zinc; not measured in other studies) were generally higher in the shade leaves of *A. selago* in this study (e.g. Michelsen et al., 1996; Shaver et al., 1998; Jonasson et al., 1999; Cavender-Bares et al., 2000). Higher nutrient concentrations in shaded plants have been attributed to these plants maintaining their nutrient uptake despite their lower productivity, i.e. they maintain the same nutrient content as unshaded plants, but at higher concentrations because the nutrients are not diluted by growth (Dormann and Woodin, 2002). However, because production was not measured in this study, the contribution of nutrient dilution to the changes in plant nutrients observed could not be assessed. Nonetheless, since nutrients did not show a uniform pattern of dilution (i.e. in the shade treatment the concentration of all nutrients did not increase), other mechanisms (i.e. controlling nutrient allocation and accumulation) must also be important.

Stem growth rate was much higher in shaded treatments than exposed controls. Increased shoot length is a common response to reduced light in Arctic plants (Havström et al., 1993; Dormann and Woodin, 2002). This response has been attributed to reduced foliar thermal stress (Danner and Knapp, 2003), and also as an attempt to increase light interception (Grime, 1979). In addition, the effect of reduced wind may also be important, as strong winds can alter plant growth and morphology (Ennos, 1997). Indeed, observations by Ashton and Gill (1965) and Huntley (1972) suggest that *A. selago* and *A. macquariensis* have higher stem growth rates in

sheltered areas. Therefore, rapid changes in stem growth rate are likely in response to changes in shading.

The increased gap fraction in shaded plants is likely to be the result of two changes in stem characteristics. First, if increased stem growth rate under the shading treatment was not matched by increased branching, the tight packing of stems on the surface of cushions would not be maintained, resulting in gaps between stems. Second, shading may have increased stem mortality (Chapin and Shaver, 1996). In this study, some stems grew more under shading, while others appeared to not have grown at all (pers. obs), thereby leading to increased gap fractions in shaded cushions. The implication of increases in gap fraction is a reduction in cushion surface integrity and regularity, and therefore potentially increased rates of temperature change and moisture loss. In general, the overall loss of compactness of the shaded cushions could make them more vulnerable to the effects of climatic extremes (e.g. strong winds, extended dry periods, very cold temperatures, although increased epiphyte cover will also buffer plants against these extremes: e.g. Freiberg, 2001; Hsu et al., 2002).

Shading also affected an increase in epiphyte cover and a reduction in senescent fraction in some treatments. Shading increased the proportional cover of *A. magellanica*, despite a reduction in the total number of individuals on cushions. The fewer *A. magellanica* individuals are possibly a result of *A. selago* shade-growth overwhelming small *A. magellanica* individuals. This also potentially explains why average *A. magellanica* size was larger in the shaded treatments (i.e. mean grass size increased because smallest individuals were removed), although increases in *A. magellanica* leaf size under shading (pers. obs) probably also contributed to this result. This result also suggests that *A. selago*'s response to shading can reduce the number of epiphyte individuals successfully establishing on a cushion (i.e. *A. selago* is not just a passive host, but can offer resistance to epiphyte establishment). The effect of shading on senescence was less consistent. Shading delayed senescence in the shade treatment, in agreement with previous studies (e.g. Cavender-Bares et al., 2000), but had no effect on senescence in the half-cushion treatments.

Previous studies and field observations suggest the longer-term effects of shading are different from the responses observed after one year. Short- and longer-term responses to environmental manipulations can differ greatly (e.g. Chapin et al., 1995; Michelsen et al., 1996; Arft et al., 1999; Rustad et al., 2001; Melillo et al.,

2002), and therefore extrapolations from short-term manipulations must be made cautiously. Cushion structure under heavy *A. magellanica* cover usually comprises dead, loosely-packed *A. selago* stems with large leaves (pers. obs; see also Bergstrom et al., 1997). This suggests that increased growth in response to shading is probably a short-term response, and that ultimately reduced light conditions lead to stem mortality (Bergstrom et al., 1997; Shaver et al., 1998).

Therefore, the short-term response of *A. selago* to shading includes greater stem elongation, larger leaves, raised foliar nitrogen and phosphorus concentrations and increased gap fraction. Additionally, the cover of *A. magellanica* increases, despite a reduction in the number of epiphytically growing individuals. However, these responses may be transient, with different longer-term responses expected to reductions in light intensity.

Responses to warming

Some plant responses differed strikingly between the procedural controls and the control plants. Since only temperature, light intensity and relative humidity differed between the control and procedural controls, differences in plant responses were attributable to these three secondary rainout shelter effects. Relative humidity differed little between control and procedural control plants (2 – 5 % higher for control plants), and therefore its effect on the plants was considered negligible in comparison with the differences in temperature and light (following Havström et al., 1993). Therefore, since the short-term effects of shading on *A. selago* are known, and some (cautious) inferences could be made about the effect of warming, despite the effects of reduced light and increased temperatures being confounded in these treatments. For example, if a given parameter increased under shading but decreased in the procedural control (i.e. when plant responses in the two treatments were in opposite directions), then the effect of warming could be inferred to be negative, and that of reduced light to be positive. Further evidence of the consequences of drying was obtained by comparing the half-shade and half-shade-dry treatments. While the effects of reduced rainfall were also confounded by shelter effects in this treatment, the relative influence of shelter effects was assumed to be much lower than in the warm-dry treatment. This assumption was made because the additional reduction in light intensity by the rainout shelter was small relative to that of the shade cloth, and

differences in temperature (particularly during the growing season) and relative humidity between the half treatments were similar.

Leaf nutrient concentrations responded to warming. Sodium, iron and zinc concentrations were higher under the procedural control, but did not differ between the shade treatment and control cushions. Therefore, the reduction in light under the rainout shelters is not responsible for the changes in foliar nutrient concentration, suggesting therefore that increased temperatures are responsible instead. This is supported by previous studies that have shown changes in temperature to alter foliar nutrient concentrations. For example, Jonasson et al. (1999) found higher concentrations of nitrogen and potassium in warmed *Cassiope tetragona*-dominated communities (see also Dormann and Woodin, 2002). However, comparisons with these studies are limited, as they have generally only considered nitrogen, phosphorus and potassium.

Warming may also favour the growth of *A. magellanica* (assuming that changes in rainfall do not constrain the grass' response). While this study does not provide convincing evidence for warming affecting the species (since its cover in the procedural control was not significantly higher than that in the control), strong evidence from other studies suggest that it is likely. For example, recent experimental work showed a congener (*Agrostis curtisii*) to increase shoot mass in response to warming (under laboratory conditions; Norton et al., 1999). More generally, grasses are amongst the most responsive plant groups (e.g. Zhang and Welker, 1996; Dormann and Woodin, 2002) probably due to their rapid biomass turn-over (Dormann and Woodin, 2002). Increases in *A. magellanica* could have large long-term implications for *A. selago*, particularly a reduction the cushion plant's photosynthetic area and increased shading of adjacent areas. Epiphytes potentially also ameliorate their host's environment by buffering against changes in temperature and moisture (by extending the cushion boundary layer) and sheltering the plant from strong winds. The net effect of a change in epiphyte load is therefore unknown, although large long-term increase in epiphyte load will probably negatively affect cushion plants because of their sensitivity to shading.

Therefore, while future warming on Marion Island may alter *A. selago* foliar nutrient concentrations, changes in the distribution and cover of the epiphyte *A. magellanica* in response to the same factor could have greater effects on *A. selago*. These results agree with Scott's (1985) pollen analyses, which suggested that fellfield

vegetation is probably not directly negatively affected by warming, but is rather susceptible to replacement by other vegetation types when temperature and moisture availability increase.

Inferred effects of wind

Previous authors have suggested the importance of wind in determining plant growth and stature in fellfield ecosystems (e.g. Ashton and Gill, 1965; Smith, 1978). Wind patterns on Marion Island are characterized by strong, warm north-westerly winds and weaker, colder, drier south-westerlies (Schulze, 1971). South-easterly winds are the most rare (< 10 % of the time) and weakest (Schulze, 1971). While the influence of wind was not experimentally tested, its effects can be inferred (e.g. Belyea and Lancaster, 2002). Indeed, analysis of cushion quarters suggests that wind speed, temperature and humidity might influence the distribution of epiphyte cover and cushion senescence.

The most striking difference between cushion quarters was the unequal distribution of *A. magellanica*. This was the result of *a priori* differences in *A. magellanica* distribution (since control and experimental cushions did not differ in distribution of epiphyte cover). The grass dominated the southeastern quarter of cushions, with lowest cover in the northwest quarter. Since this is the inverse of wind speed (and frequency) patterns, it suggests that strong winds may negatively affect *A. magellanica*. Winds can cause mechanical damage and reduce photosynthetic performance (van Gardingen et al., 1991; Ennos, 1997). Indeed, reduced photosynthetic performance under windy conditions has already been shown for another grass species (*Poa cookii*) on Marion Island by Bate and Smith (1983). Additionally, as *A. magellanica* carbon assimilation rate is temperature dependent (Pammenter et al., 1986), it may be suppressed by wind-driven cooling. The abundance and distribution patterns of *A. magellanica* on Marion Island (Chapter 3), and the relatively low cover of this species on the top of *A. selago* cushions (pers. obs; where winds is predicted to be strongest: Warren-Wilson 1959) provides additional support for the importance of wind in influencing the distribution of this species. However, alternative explanations for the unequal distribution of grasses exist (e.g. *A. magellanica* seeds are unequally dispersed, tending to accumulate on the leeward side of cushions, etc.).

Through its effect on *A. magellanica*, wind may indirectly affect cushion plant morphology, since the distribution of *A. magellanica* has implications for the growth of *A. selago* cushions. Under long-term heavy epiphyte load *A. selago* suffers increased stem mortality (pers. obs), and therefore stem growth is likely to be slower in the SE than NW quarter. Accumulated difference in cushion growth (as well as stem and epiphyte mortality) could then lead to the sickle-shape shown by many larger cushions (“cushions... develop an arcuate shape, advancing into the wind”: Huntley, 1972; see also Ashton and Gill, 1965). These patterns had previously been attributed to abiotic factors such as differential erosion patterns or needle-ice formation (e.g. Ashton and Gill, 1965; Boelhouwers et al., 2003), but could be complemented by this indirect effect of wind.

Autumnal senescence also differed in its distribution between cushion quarters, although only under the warm-dry treatment (possibly since senescence had progressed further in this treatment than in any other). Greatest senescence occurred in the SW quarter, and least in the NE (pattern weakly mimicked by the procedural control), consistent with wind temperature and humidity patterns on Marion Island (coldest and driest winds from the SW). This suggests that cold and/or dry winds can accelerate senescence in *A. selago*.

Therefore, *A. magellanica* cover and autumnal senescence (the latter only in the warm-dry treatment) are not equally distributed within cushions, probably due to the differences in speed, temperature and humidity of winds from different directions. Considering that wind patterns are changing at high latitudes in the southern hemisphere (strengthening of the circumpolar westerlies: Gillet and Thompson, 2003; although on Marion easterly winds are becoming stronger and more common: Smith et al., 2001), these results suggest that the distribution of senescence and of epiphytes on *A. selago* could change in the future.

Conclusion

Azorella selago showed rapid vegetative responses to changes in temperature, rainfall and shading, despite its slow growth and the short duration of the experiment. Plant responsiveness differed between treatments and plant characteristics, and demonstrates the differing sensitivities of the species' morphology, phenology and physiology to changes in its environment. The potential for interactions between

simultaneous environmental changes was illustrated by the effects of reduced rainfall (on certain *A. selago* characteristics) not being independent of other environmental factors. This suggests that the effects of a change in one factor (e.g. shading) can only be predicted accurately with knowledge of how other factors (e.g. rainfall) will change over the same period. Finally, this study highlights the importance of indirect effects of climate change. Epiphyte cover (particularly the dominant epiphyte *A. magellanica*) responded to shading and appears to be affected by wind strength patterns. Given the high responsiveness of grasses in general, and the sensitivity of *A. selago* to shading, it is possible that changes in epiphyte load could overshadow the direct effects of changes in climate. Therefore, ongoing climate changes on Marion Island will affect *A. selago* and its epiphytes, with likely repercussions for fellfield communities.

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TABLE 1

Differences in Azorella selago leaf morphology between treatments. All p-values bootstrapped. ‡ no longer significant after column-wide sequential Bonferroni correction (Rice, 1989). See text and Fig. 2 for explanation of measurements.

	Whole cushions			Half-shade			Half-shade-dry		
	d.f.	F	p	d.f.	t	p	d.f.	t	p
Total leaf area	3, 64	51.16	< 0.001	13	-8.80	< 0.001	8	-8.09	< 0.001
Leaf length	3, 64	73.61	< 0.001	13	-9.94	< 0.001	8	-7.91	< 0.001
Leaf width	3, 64	3.66	0.013‡	13	-7.30	< 0.001	8	-3.75	0.006‡
Leaf perimeter	3, 64	45.98	< 0.001	13	-7.06	< 0.001	8	-4.85	0.001
Leaf shape factor	3, 64	6.22	< 0.001	13	1.99	0.069	8	2.75	0.025‡
Green leaf area (GA)	3, 64	39.62	< 0.001	13	-7.10	< 0.001	8	-3.75	0.006‡
GA length	3, 64	28.86	< 0.001	13	-6.96	< 0.001	8	-3.38	0.010‡
GA width	3, 64	57.45	< 0.001	13	-7.23	< 0.001	8	-4.27	0.003
GA perimeter	3, 64	24.73	< 0.001	13	-5.26	< 0.001	8	-3.13	0.014‡
GA shape factor	3, 64	2.49	0.066	13	-1.17	0.263	8	0.69	0.511
Sheath area (SA)	3, 64	51.13	< 0.001	13	-9.17	< 0.001	8	-12.08	< 0.001
SA length	3, 64	59.10	< 0.001	13	-8.84	< 0.001	8	-8.17	< 0.001
SA width	3, 64	10.91	< 0.001	13	-3.78	< 0.001	8	-0.74	0.482
SA perimeter	3, 64	37.73	< 0.001	13	-7.88	< 0.001	8	-7.96	< 0.001
SA shape factor	3, 64	3.67	0.008	13	1.68	0.117	8	1.60	0.148
Leaflets	3, 64	0.83	0.603	13	-0.55	0.591	7	-0.53	0.609
Trichomes	3, 64	2.29	0.086	13	0.10	0.919	7	0.48	0.646
Mass	3, 59	18.30	< 0.001	12	-6.92	< 0.001	5	-1.00	0.362
GA/total leaf area	3, 64	19.02	< 0.001	13	6.76	< 0.001	8	7.59	< 0.001
Specific leaf area	3, 63	3.47	0.015‡	12	-0.94	0.367	5	-3.09	0.027‡
Trichome density	3, 64	11.07	< 0.001	13	6.26	< 0.001	7	4.28	0.004

TABLE 2

Differences in Azorella selago surface cover between treatments. Analyses were repeated after excluding cushion areas covered by Agrostis magellanica. Gap fraction was only measured for shaded cushions, and therefore a test for differences in gap fraction between whole cushions was not performed. † bootstrapped p-values, ‡ no longer significant after column-wide sequential Bonferroni correction (Rice, 1989).

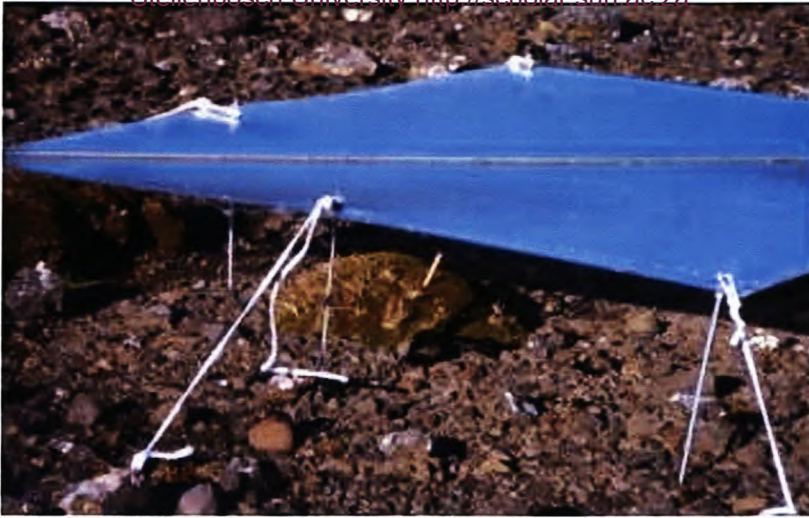
Surface cover (% of cushion surface)	d.f.			without <i>A. magellanica</i>	
		F	p	F	p
Whole cushions					
Green fraction	3, 62	3.41	0.023 ‡	7.11	< 0.001 †
Dead fraction	3, 62	9.83	< 0.001	9.14	< 0.001
<i>A. magellanica</i> cover	3, 62	7.75	< 0.001		
Other epiphyte cover	3, 62	0.02	0.688 †	0.74	0.691 †
Senescent fraction	3, 62	8.35	< 0.001	6.78	< 0.001
Half-shade					
		t		t	
Green fraction	13	3.31	0.006 ‡	2.16	0.019 ‡†
Dead fraction	13	0.22	0.832	0.11	0.913
<i>A. magellanica</i> cover	13	-2.19	0.048 ‡		
Other epiphyte cover	13	-2.09	0.056	-2.10	0.020 ‡†
Senescent fraction	13	-0.86	0.403	-1.14	0.274
Gap fraction	13	-4.54	0.001	-5.05	< 0.001
Half-shade-dry					
Green fraction	8	0.78	0.460	1.52	0.082 †
Dead fraction	8	-1.08	0.313	0.13	0.450 †
<i>A. magellanica</i> cover	8	0.43	0.682		
Other epiphyte cover	8	-1.32	0.222	-1.33	0.095 †
Senescent fraction	8	-1.49	0.173	-1.32	0.111 †
Gap fraction	8	-3.78	0.005 ‡	-2.55	0.008 †

TABLE 3

Comparison of *Azorella selago* cushion cover distribution between cushion quarters (north-east, north-west, south-east and south-western quarters). Analyses were repeated after excluding cushion areas covered by *Agrostis magellanica*. Proc. Con. = procedural control. † bootstrapped *p*-values, ‡ no longer significant after column-wide sequential Bonferroni correction (Rice 1991).

Treatment	Surface cover (% of cushion surface)	d.f.			without <i>A. magellanica</i>	
			F	p	F	p
Control	Green fraction	3, 96	10.19	< 0.001	1.04	0.374 †
	Dead fraction	3, 96	0.35	0.827 †	0.35	0.827 †
	<i>A. magellanica</i> cover	3, 96	11.15	< 0.001		
	Other epiphyte cover	3, 96	2.22	0.072 †	2.03	0.101 †
	Senescent fraction	3, 96	2.73	0.048 ‡	1.11	0.352 †
Proc. Con.	Green fraction	3, 44	12.78	< 0.001	1.33	0.267 †
	Dead fraction	3, 44	0.40	0.827 †	0.74	0.592 †
	<i>A. magellanica</i> cover	3, 44	12.05	< 0.001		
	Other epiphyte cover	3, 44	1.32	0.126 †	1.22	0.305 †
	Senescent fraction	3, 44	1.26	0.299	1.56	0.213 †
Warm-dry	Green fraction	3, 56	5.68	0.002	5.57	0.003 †‡
	Dead fraction	3, 56	0.15	0.950 †	0.16	0.944 †
	<i>A. magellanica</i> cover	3, 56	5.29	0.003		
	Other epiphyte cover	3, 56	1.28	0.275 †	1.14	0.332 †
	Senescent fraction	3, 56	4.60	0.006 ‡	5.68	0.002 †‡
Shade	Green fraction	3, 52	3.90	0.014 ‡	0.44	0.74 †
	Dead fraction	3, 52	1.24	0.303 †	1.74	0.164 †
	<i>A. magellanica</i> cover	3, 52	3.67	0.018 ‡		
	Other epiphyte cover	3, 52	0.79	0.604 †	0.81	0.641 †
	Senescent fraction	3, 52	0.19	0.902	0.41	0.764 †
	Gap fraction	3, 52	0.58	0.628	0.15	0.926

a)



b)



c)



FIGURE 1. The a) warm-dry, b) procedural control, and c) half-shade treatments.

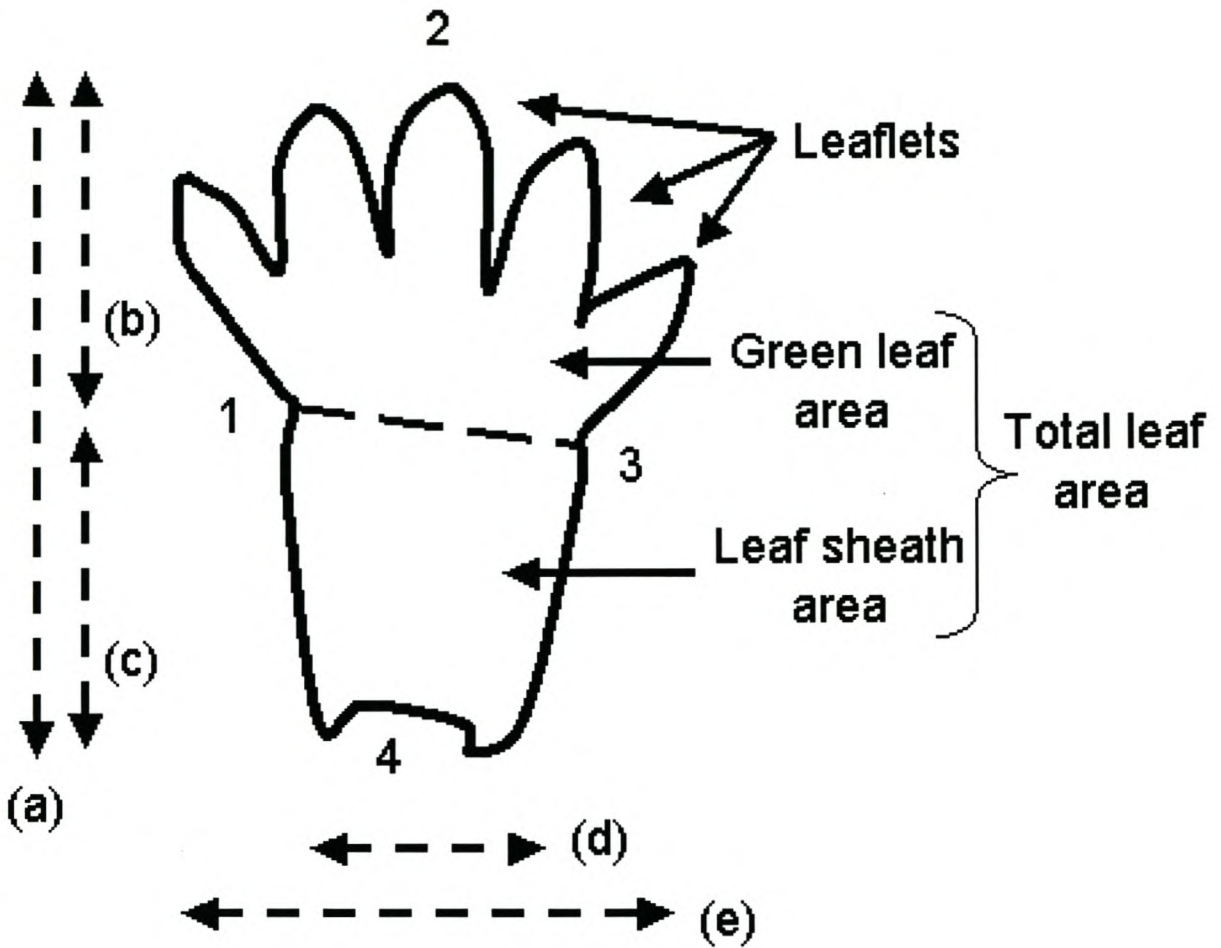


FIGURE 2. Schematic diagram of an *Azorella selago* leaf, indicating the measurements taken in this study. Leaflets comprised part of the green leaf area. The boundary between “green leaf area” and “leaf sheath area” (line 1-3) was determined by leaf colour, but always lay approximately between the notches in either side of the leaf. a = leaf length, b = green leaf length, c = leaf sheath length, d = leaf sheath width, e = green leaf width. Leaf width was the maximum of (d) and (e) . Leaf perimeter was measured as the distance along the leaf edge from 1-2-3-4-1, green leaf perimeter from 1-2-3-1, and leaf sheath perimeter from 1-3-4-1.

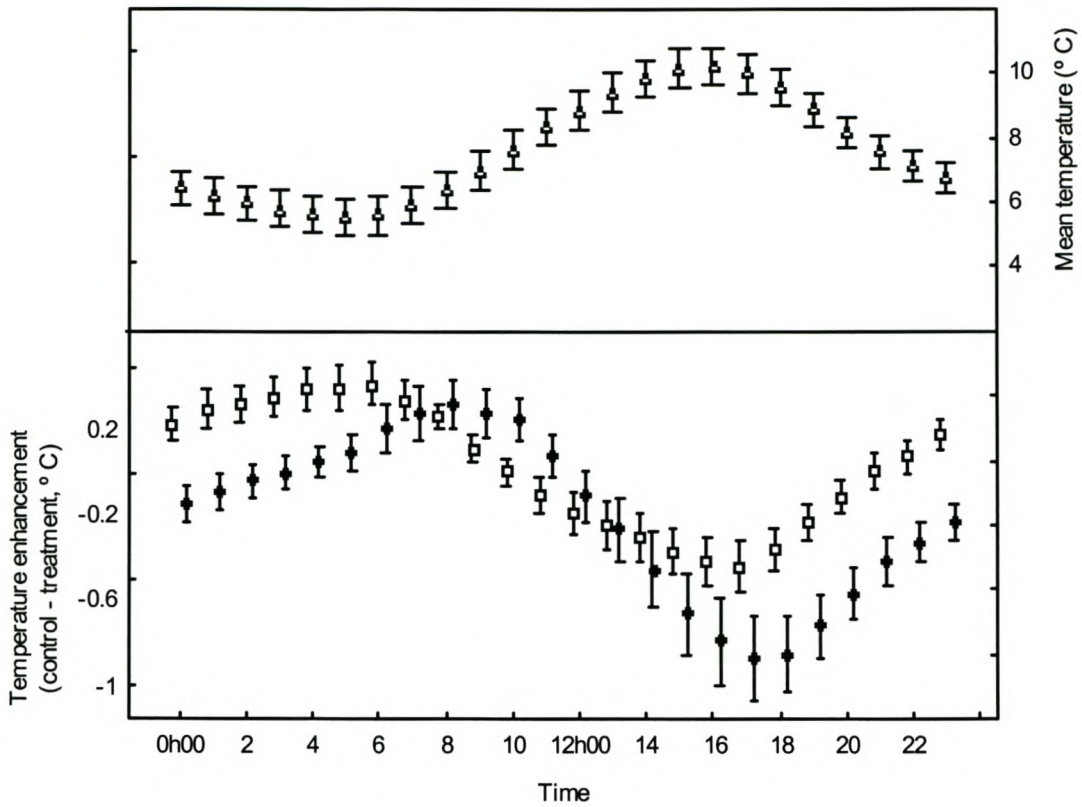


FIGURE 3. Daily temperature cycle (mean \pm 95 % C.I.) as recorded between 7 December 2002 and 24 January 2003 (“spring” sampling period) inside control *Azorella* selago plants (top), and temperature deviations (i.e. difference between control and treatment temperatures, °C) affected by the procedural control (● closed circles) and warm-dry (□ open squares) treatment during the same period (bottom). Negative temperature enhancement values indicate the treatments were cooler than the controls (see Appendix B).

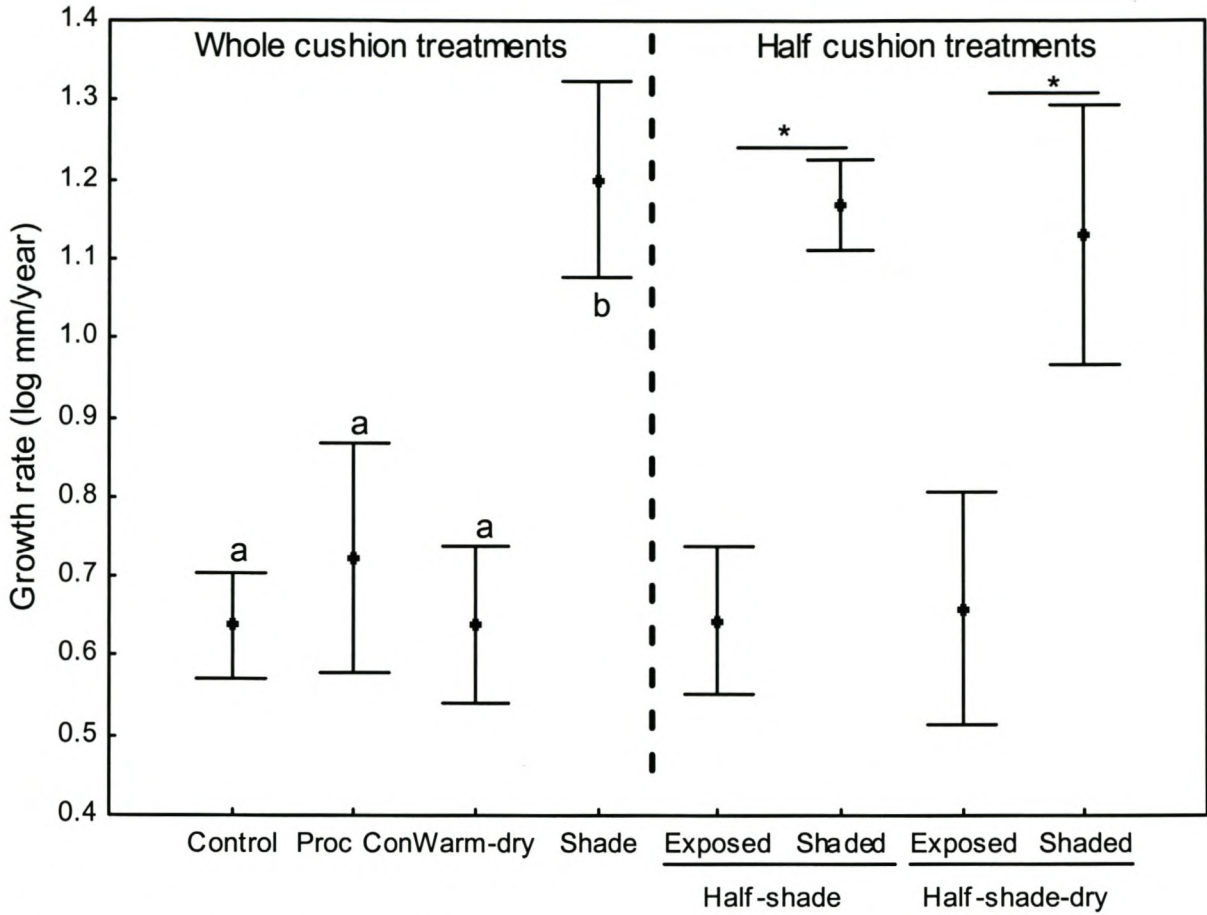


Figure 4. Growth rate (mean \pm 95 % confidence intervals) of *Azorella selago* plants exposed to different treatments. Whole cushion treatments not sharing a letter differ at $p < 0.05$ (details in text). Paired samples (i.e. exposed and shaded portions of the half-cushion treatments) differing at $p < 0.05$ indicated with an asterisk (*). Proc Con = procedural control.

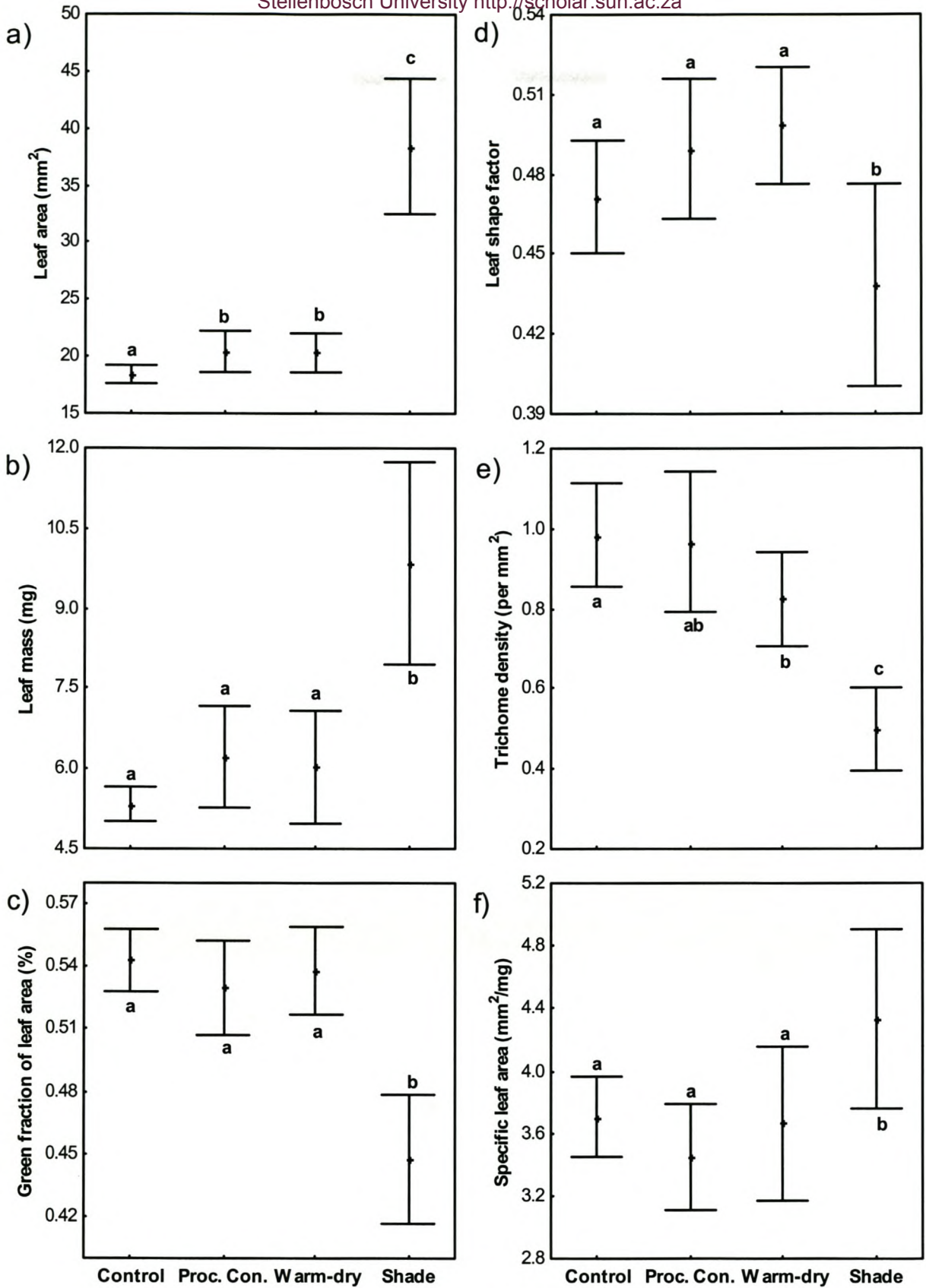


FIGURE 5. Morphological characteristics of *Azorella selago* leaves from the whole cushion treatments. All plots show mean \pm 95 % confidence intervals. Treatments not sharing letters differ at $p < 0.05$ (see Table 1). Proc. Con. = procedural control.

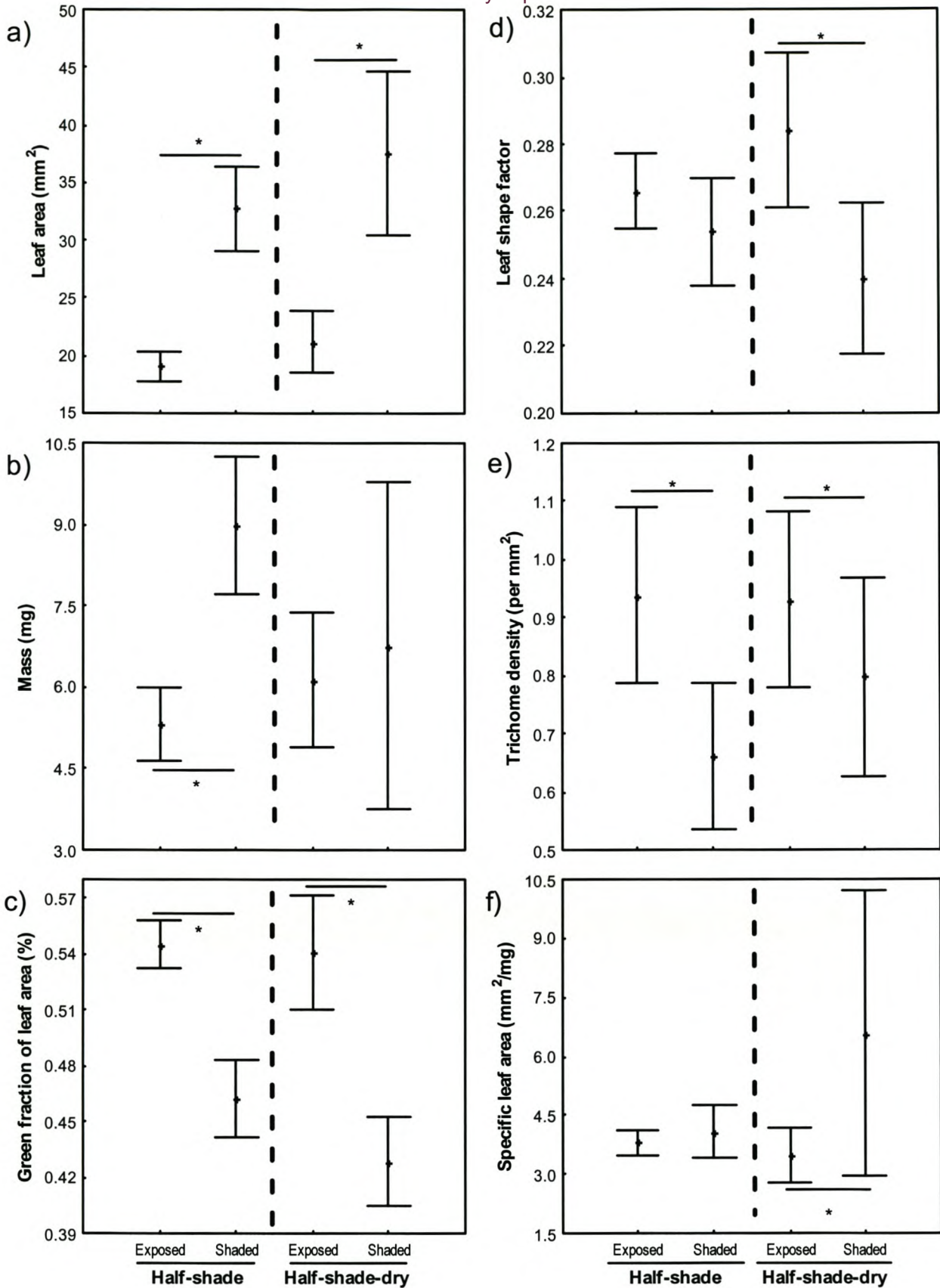


FIGURE 6. Morphological characteristics of exposed and shaded *Azorella selago* leaves in the half-shade and half-shade-dry treatments. All plots show mean \pm 95% confidence intervals. Paired samples differing at $p < 0.05$ indicated with an asterisk (*; see Table 1).

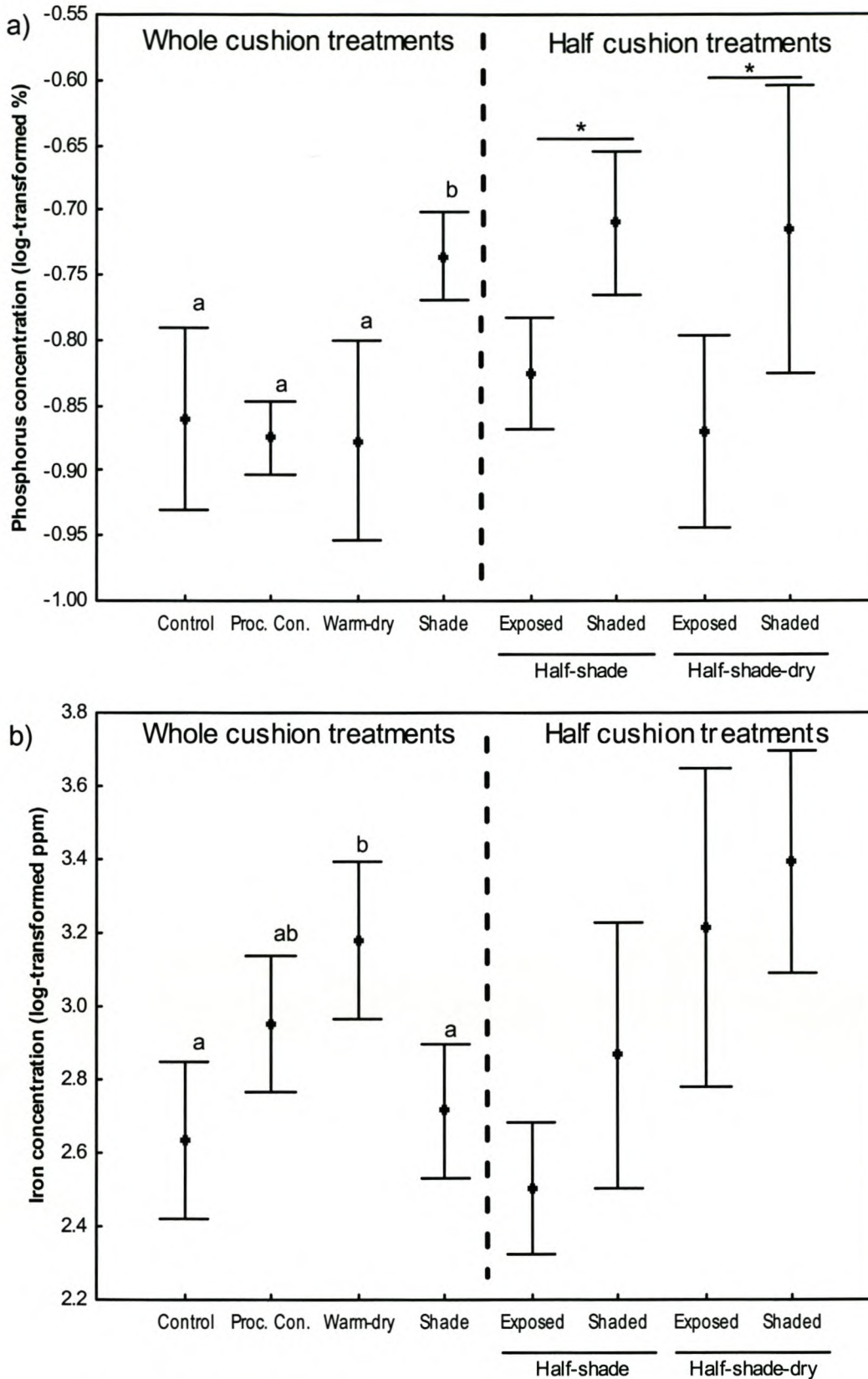


FIGURE 7. Foliar a) phosphorus, b) iron concentration (mass per mass basis; mean \pm 95 % confidence intervals) in the treatments. Whole-cushion treatments not sharing letters differ at $p < 0.05$. Paired samples (i.e. exposed and shaded portions of the half-cushion treatments) differing at $p < 0.05$ indicated with an asterisk (*; See Appendices C and D). Proc. Con. = procedural control.

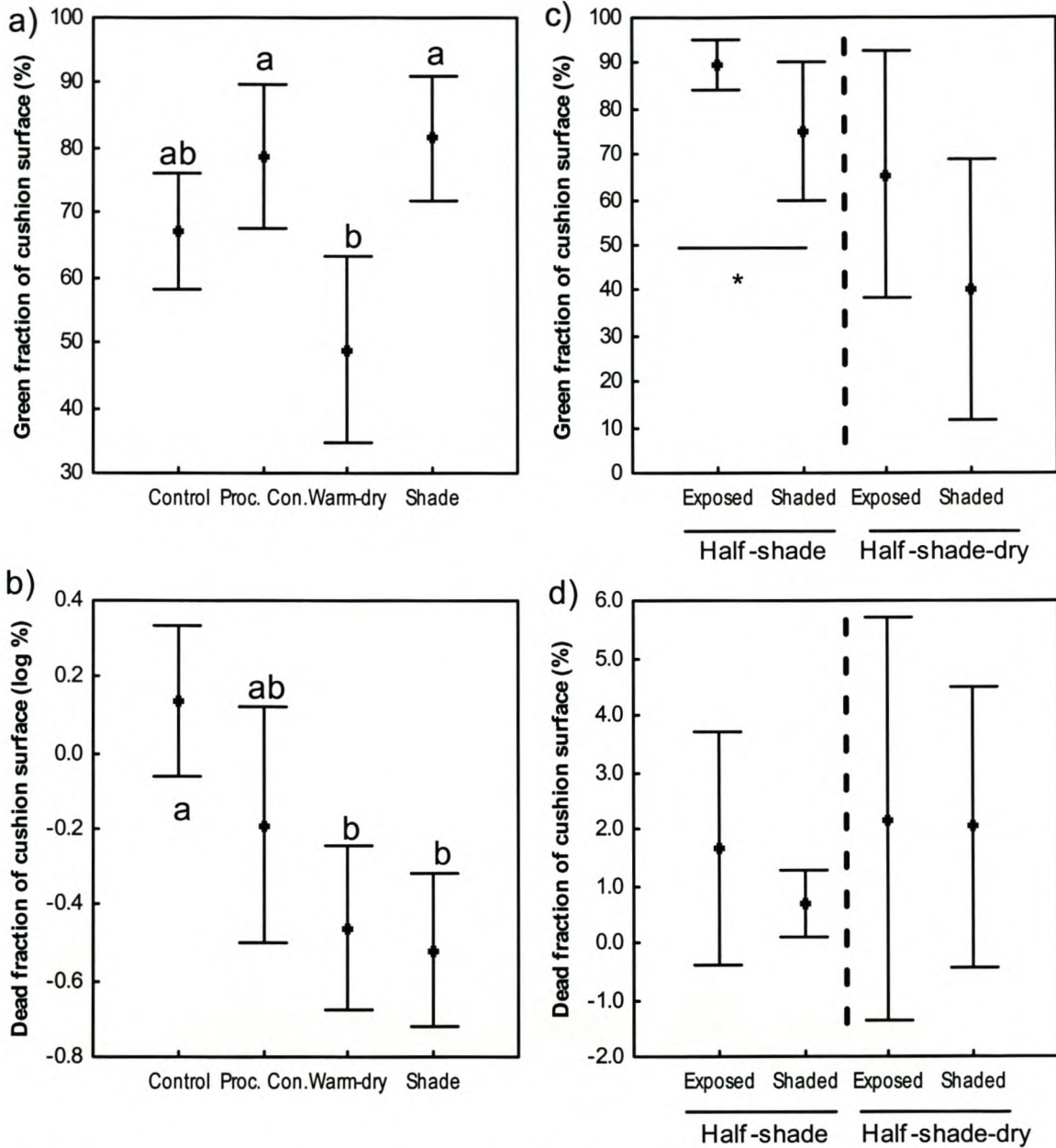


FIGURE 8. Green fraction (mean \pm 95 % confidence intervals) and dead fraction of *Azorella selago* cushion surface under different treatments, after removing *Agrostis magellanica* covered areas. Whole-cushion treatments not sharing a letter differ at $p < 0.05$. Paired samples (i.e. exposed and shaded portions of the half-cushion treatments) differing at $p < 0.05$ indicated with an asterisk (*; see Table 2). Proc. Con. = procedural control.

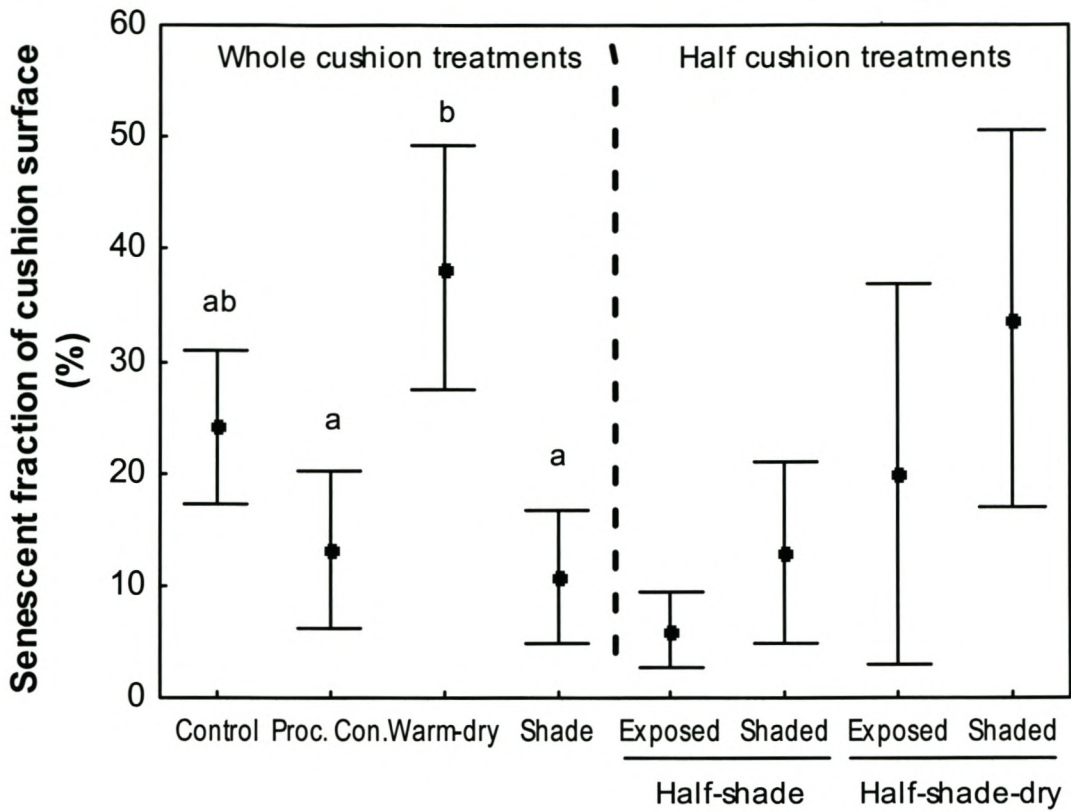


FIGURE 9. Senescent fraction (mean \pm 95 % confidence intervals) of *Azorella selago* cushion surface under different treatments. Whole-cushion treatments not sharing a letter differ at $p < 0.05$. Paired exposed and shaded portions did not differ significantly (see Table 2). Proc. Con. = procedural control.

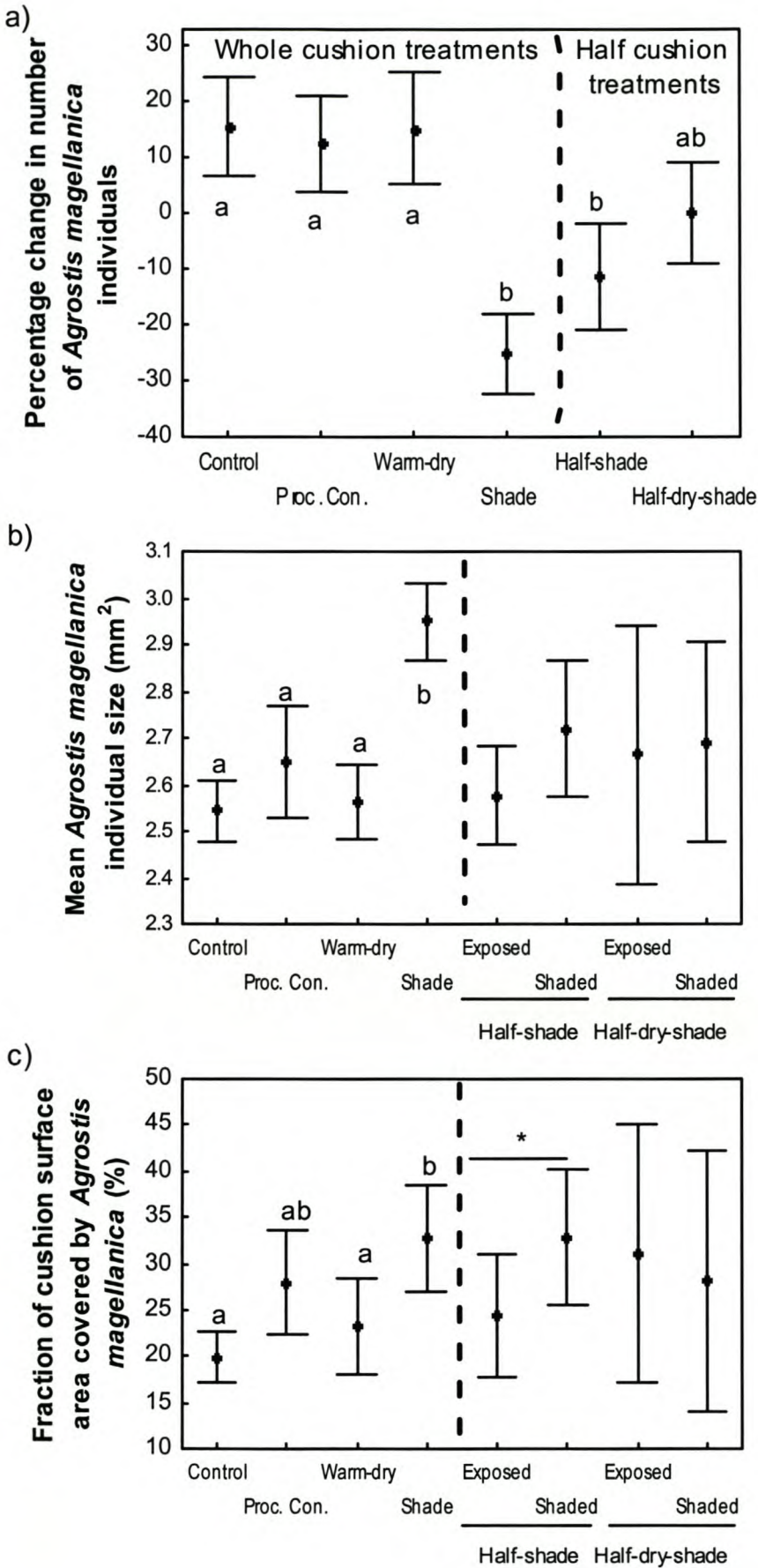


FIGURE 10. *Agrostis magellanica* epiphyte load (mean \pm 95 % confidence intervals) on *Azorella selago*. Proportional change in number of *A. magellanica* individuals during the experimental year (a), mean size of *A. magellanica* individuals at the end of the experiment (b), and proportion of *Azorella selago* surface covered by *A. magellanica* (c) for the treatments. As only total *A. magellanica* counts were available for the half-shade and half-shade-dry treatments the exposed and shaded halves cannot be evaluated individually in the first graph, and therefore are combined. Whole-cushion treatments not sharing a letter differ at $p < 0.05$. Paired samples (i.e. exposed and shaded portions of the half-cushion treatments) differing at $p < 0.05$ indicated with an asterisk (*; see Table 2). Proc. Con. = procedural control.

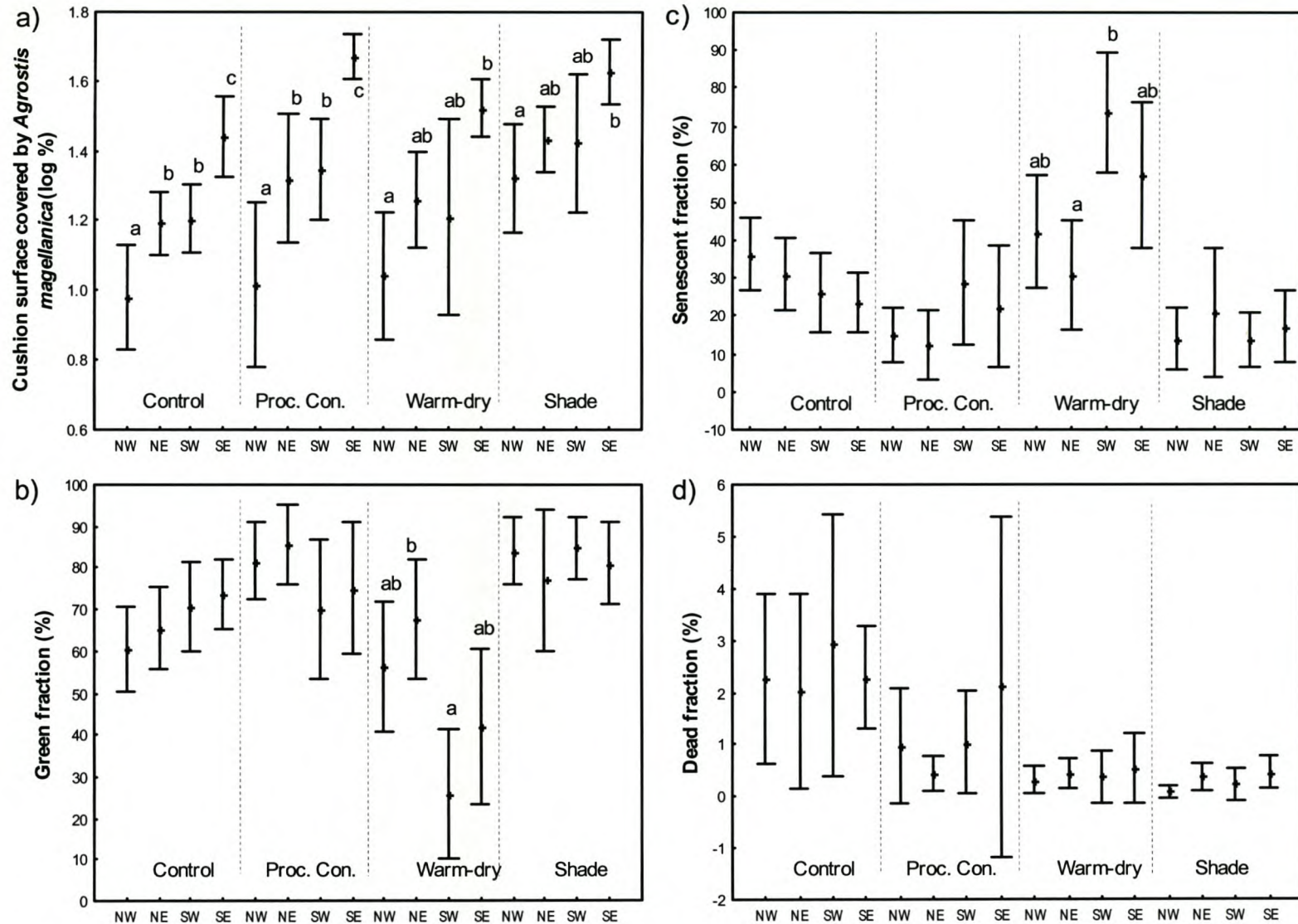


FIGURE 10. *Azorella selago* surface cover (mean \pm 95 % confidence intervals) for the north-west (NW), north-east (NE), south-west (SW) and south-east (SE) quarter of cushions in each treatment: a) *Agrostis magellanica* cover, b) green fraction, c) senescent fraction, and d) dead fraction. Quarters not sharing a letter differ at $p < 0.05$. Where all quarters in a treatment lack letters no significant difference was found between quarters (see Table 3).

APPENDIX A

Soil properties of the treatments after experiment. Only potassium and phosphorus differed significantly between treatments (details in text). ¹ used by Smith (1978).

	Control	Proc. Con.	Warm-dry	Full shade	Half-shade	Half-shade-dry
pH	4.68 ± 0.06	4.76 ± 0.04	4.64 ± 0.10	4.68 ± 0.04	4.78 ± 0.08	4.66 ± 0.04
Resistance (Ohm)	1764.00 ± 142.78	2022.00 ± 223.59	1670.00 ± 136.71	1724.00 ± 97.24	1660.00 ± 151.86	1968.00 ± 243.57
Organic C (%)	4.46 ± 0.79	3.81 ± 0.48	6.64 ± 2.07	4.15 ± 0.46	6.10 ± 1.38	6.43 ± 1.61
P (ppm)	25.40 ± 6.92	23.80 ± 8.00	17.4 ± 6.07	28.80 ± 5.21	8.40 ± 5.44	12.80 ± 7.70
Exchangeable cations (cmol/kg)						
H	2.66 ± 0.27	2.41 ± 0.10	3.23 ± 0.59	2.66 ± 0.10	2.72 ± 0.35	2.91 ± 0.31
Na	0.29 ± 0.04	0.27 ± 0.04	0.46 ± 0.12	0.32 ± 0.04	0.36 ± 0.06	0.33 ± 0.07
K	0.21 ± 0.03	0.14 ± 0.02	0.33 ± 0.12	0.19 ± 0.03	0.19 ± 0.04	0.25 ± 0.06
Ca	0.45 ± 0.14	0.38 ± 0.09	0.76 ± 0.22	0.77 ± 0.19	0.62 ± 0.15	0.49 ± 0.10
Mg	0.76 ± 0.21	0.76 ± 0.15	1.54 ± 0.52	1.18 ± 0.25	1.13 ± 0.31	0.99 ± 0.21
(Mg + Na)/Ca ¹	2.87 ± 0.51	2.87 ± 0.30	2.62 ± 0.15	2.45 ± 0.17	2.05 ± 0.13	2.87 ± 0.20
Percentage base saturation (%)						
Na	6.84 ± 0.35	6.65 ± 0.54	7.23 ± 0.35	6.32 ± 0.42	7.24 ± 0.23	6.45 ± 0.47
K	4.94 ± 0.23	3.58 ± 0.31	4.86 ± 0.46	3.80 ± 0.37	3.72 ± 0.14	4.76 ± 0.43
Ca	9.23 ± 1.94	9.04 ± 1.36	11.36 ± 1.25	14.32 ± 1.82	11.85 ± 0.97	9.43 ± 1.33
Mg	15.86 ± 2.62	18.51 ± 1.92	21.92 ± 2.77	22.17 ± 1.91	21.38 ± 1.71	19.02 ± 1.83

APPENDIX B

Thermal environment (°C) experienced within experimental Azorella selago cushions. Mean temperatures and mean daily temperature ranges experienced by control cushions are provided. The differences between the temperature and range experienced by control and treatment cushions are presented (negative values show treatment experienced a lower temperature or reduced daily temperature range). Maximum and minimum temperatures experienced in each treatment also presented. Data presented combined ("All") and separately for the four sampling periods. n = number of hourly recordings of temperature, N = number of recording of daily temperature range and daily maximum and minimum temperatures.

Treatment	Season	n	Temperature ± S.E.	N	Range ± S.E.	Max. ± S.E.	Min. ± S.E.
Control	All	4824	5.42 ± 3.13	201	4.75 ± 0.16	7.97 ± 0.23	3.23 ± 0.17
	Autumn	1680	4.08 ± 2.19	70	3.59 ± 0.17	5.98 ± 0.23	2.39 ± 0.19
	Winter	1440	3.98 ± 2.8	60	4.97 ± 0.35	6.74 ± 0.39	1.77 ± 0.25
	Spring	1080	7.63 ± 2.46	45	5.77 ± 0.28	10.79 ± 0.30	5.01 ± 0.23
	Summer	624	8.52 ± 2.57	26	5.57 ± 0.42	11.32 ± 0.38	5.74 ± 0.49
			Temperature difference ± S.E.		Range difference ± S.E.		
Proc. Con.	All	4824	0.08 ± 0.01	201	-0.66 ± 0.06	7.65 ± 0.2	3.56 ± 0.16
	Autumn	1680	0.33 ± 0.01	70	-0.30 ± 0.06	6.12 ± 0.21	2.83 ± 0.19
	Winter	1440	-0.02 ± 0.02	60	-0.96 ± 0.13	6.09 ± 0.32	2.08 ± 0.24
	Spring	1080	-0.20 ± 0.02	45	-0.68 ± 0.10	10.16 ± 0.27	5.07 ± 0.22
	Summer	624	0.16 ± 0.02	26	-0.91 ± 0.15	11.03 ± 0.32	6.37 ± 0.4
Warm-dry	All	4824	0.25 ± 0.01	201	-0.77 ± 0.05	7.78 ± 0.21	3.81 ± 0.16
	Autumn	1680	0.37 ± 0.01	70	-0.68 ± 0.08	5.92 ± 0.21	3.02 ± 0.19
	Winter	1440	0.29 ± 0.02	60	-0.78 ± 0.11	6.55 ± 0.32	2.37 ± 0.22
	Spring	1080	0.04 ± 0.01	45	-0.90 ± 0.08	10.33 ± 0.26	5.46 ± 0.21
	Summer	624	0.21 ± 0.02	26	-0.78 ± 0.12	11.23 ± 0.36	6.44 ± 0.38
Shade	All	4824	-0.30 ± 0.01	201	-1.48 ± 0.08	6.77 ± 0.18	3.51 ± 0.17
	Autumn	1680	-0.04 ± 0.01	70	-0.68 ± 0.06	5.51 ± 0.21	2.60 ± 0.18
	Winter	1440	-0.31 ± 0.02	60	-1.42 ± 0.14	5.54 ± 0.33	1.99 ± 0.24
	Spring	1080	-0.69 ± 0.03	45	-2.20 ± 0.16	8.78 ± 0.23	5.20 ± 0.21
	Summer	624	-0.30 ± 0.04	26	-2.56 ± 0.24	9.56 ± 0.31	6.55 ± 0.39
Half-shade	All	4824	-0.44 ± 0.01	201	-1.15 ± 0.08	6.78 ± 0.20	3.19 ± 0.17
	Autumn	1680	-0.08 ± 0.01	70	-0.58 ± 0.08	5.49 ± 0.23	2.48 ± 0.19
	Winter	1440	-0.68 ± 0.02	60	-1.44 ± 0.18	5.10 ± 0.33	1.58 ± 0.24
	Spring	1080	-0.74 ± 0.02	45	-1.50 ± 0.14	9.10 ± 0.26	4.83 ± 0.23
	Summer	624	-0.33 ± 0.02	26	-1.43 ± 0.15	10.14 ± 0.36	6.00 ± 0.47
Half-shade- dry	All	4824	-0.19 ± 0.01	201	-1.38 ± 0.08	6.93 ± 0.18	3.57 ± 0.16
	Autumn	1680	0.18 ± 0.01	70	-0.82 ± 0.08	5.67 ± 0.2	2.90 ± 0.19
	Winter	1440	-0.14 ± 0.02	60	-1.37 ± 0.17	5.69 ± 0.3	2.09 ± 0.24
	Spring	1080	-0.82 ± 0.03	45	-1.94 ± 0.17	8.77 ± 0.24	4.94 ± 0.21
	Summer	624	-0.26 ± 0.03	26	-1.96 ± 0.19	10.01 ± 0.32	6.40 ± 0.38

APPENDIX C. Azorella selago foliar nutrient concentrations (mean ± S.E.) for the control, procedural control, warm-dry and shade treatments (whole-cushion treatments), expressed on a per mass and per area basis. Differences were tested using ANOVA, with $\mu\text{mol}/\text{m}^2$ Na, Mn, Fe, Cu and Zn concentrations log-transformed prior to analysis (to achieve normal distribution), although untransformed mean values provided. Sample size = 10 per treatment, except for $\mu\text{mol}/\text{m}^2$ concentration of warm-dry treatment ($n = 9$). Degrees of freedom = 3, 36 for mg/kg data, and 3, 35 for $\mu\text{mol}/\text{m}^2$ data.

Units	Control		Proc. Con.		Warm-dry		Shade		F	p
Mass per mass										
N %	1.33 ± 0.06	a	1.27 ± 0.05	a	1.20 ± 0.07	a	1.67 ± 0.06	b	12.28	<0.001
P %	0.14 ± 0.01	a	0.13 ± 0.01	a	0.14 ± 0.01	a	0.19 ± 0.01	b	7.39	0.001
K %	1.79 ± 0.15	a	1.89 ± 0.08	ab	1.60 ± 0.10	a	2.29 ± 0.08	b	7.21	0.001
Ca %	0.75 ± 0.03	b	0.71 ± 0.03	ab	0.78 ± 0.03	b	0.61 ± 0.03	a	5.32	0.004
Mg %	0.30 ± 0.01		0.33 ± 0.03		0.32 ± 0.02		0.28 ± 0.02		1.04	0.385
Na mg/kg (ppm)	5691.00 ± 489.44	ab	7244.40 ± 454.88	b	7582.00 ± 734.03	b	5075.40 ± 400.71	a	5.08	0.005
Mn mg/kg (ppm)	191.30 ± 23.61		225.10 ± 26.99		316.90 ± 65.63		162.20 ± 24.28		2.74	0.057
Fe mg/kg (ppm)	549.20 ± 143.34	a	1103.70 ± 306.26	ab	1790.40 ± 310.28	b	599.30 ± 112.57	a	7.73	<0.001
Cu mg/kg (ppm)	11.80 ± 0.44		12.00 ± 0.83		13.00 ± 0.58		14.10 ± 0.60		2.85	0.051
Zn mg/kg (ppm)	12.60 ± 0.60	a	30.70 ± 4.01	c	23.80 ± 2.64	bc	17.00 ± 1.14	b	16.27	<0.001
B mg/kg (ppm)	16.80 ± 0.36	a	18.70 ± 0.65	ab	17.40 ± 0.73	a	20.80 ± 0.83	b	7.22	0.001
Mols per area										
N ($\mu\text{mol}/\text{m}^2$)	2.76 ± 0.17		2.71 ± 0.13		2.45 ± 0.29		2.92 ± 0.23		0.87	0.466
P ($\mu\text{mol}/\text{m}^2$)	0.14 ± 0.01		0.13 ± 0.01		0.13 ± 0.02		0.15 ± 0.01		0.79	0.505
K ($\mu\text{mol}/\text{m}^2$)	1.34 ± 0.12		1.46 ± 0.10		1.16 ± 0.15		1.44 ± 0.11		1.21	0.322
Ca ($\mu\text{mol}/\text{m}^2$)	0.54 ± 0.03	b	0.53 ± 0.04	b	0.57 ± 0.06	b	0.37 ± 0.03	a	5.30	0.004
Mg ($\mu\text{mol}/\text{m}^2$)	0.36 ± 0.02	ab	0.40 ± 0.03	b	0.37 ± 0.04	ab	0.28 ± 0.02	a	3.57	0.024
Na ($\mu\text{mol}/\text{m}^2$)	75.27 ± 7.64	ab	99.40 ± 8.30	b	101.42 ± 14.43	ab	55.47 ± 4.80	a	3.96	0.016
Mn ($\mu\text{mol}/\text{m}^2$)	1.04 ± 0.15	ab	1.29 ± 0.19	ab	1.76 ± 0.44	b	0.78 ± 0.16	a	3.74	0.020
Fe ($\mu\text{mol}/\text{m}^2$)	2.85 ± 0.71	a	6.09 ± 1.70	ab	9.85 ± 2.08	b	2.81 ± 0.71	a	7.19	0.001
Cu ($\mu\text{mol}/\text{m}^2$)	0.05 ± 0.01		0.06 ± 0.01		0.06 ± 0.01		0.05 ± 0.00		0.05	0.985
Zn ($\mu\text{mol}/\text{m}^2$)	0.06 ± 0.01	a	0.14 ± 0.02	b	0.10 ± 0.02	b	0.06 ± 0.01	a	13.40	<0.001
B ($\mu\text{mol}/\text{m}^2$)	0.45 ± 0.02		0.52 ± 0.03		0.45 ± 0.04		0.47 ± 0.03		1.34	0.277

APPENDIX D. Azorella selago foliar nutrient concentrations (mean ± S.E.) for the half cushion treatments, expressed on a per area and per mass basis. Ten samples per treatment.

Units	Half-shade				Half-shade-dry			
	Exposed portion	Shaded portion	t	p	Exposed portion	Shaded portion	t	p
Mass per mass								
N %	1.43 ± 0.16	1.42 ± 0.13	0.08	0.942	1.26 ± 0.18	1.36 ± 0.33	-1.04	0.355
P %	0.15 ± 0.01	0.20 ± 0.02	-5.66	0.005	0.14 ± 0.02	0.20 ± 0.04	-5.07	0.007
K %	2.10 ± 0.23	2.32 ± 0.16	-1.54	0.197	1.61 ± 0.28	2.07 ± 0.29	-2.58	0.061
Ca %	0.79 ± 0.10	0.66 ± 0.08	4.66	0.010	0.73 ± 0.12	0.69 ± 0.14	0.92	0.408
Mg %	0.35 ± 0.10	0.34 ± 0.05	0.46	0.669	0.34 ± 0.09	0.37 ± 0.05	-0.92	0.411
Na mg/kg (ppm)	6245.60 ± 1459.77	5304.20 ± 1380.96	4.44	0.011	7113.40 ± 1448.27	6503.20 ± 883.13	0.70	0.520
Mn mg/kg (ppm)	129.00 ± 27.47	133.60 ± 42.16	-0.36	0.738	275.20 ± 57.49	274.80 ± 84.49	0.01	0.989
Fe mg/kg (ppm)	329.40 ± 88.98	889.00 ± 653.31	-1.89	0.132	2170.40 ± 1986.58	2746.40 ± 1233.00	-0.57	0.599
Cu mg/kg (ppm)	17.20 ± 13.88	13.80 ± 3.11	0.62	0.568	13.40 ± 3.13	17.20 ± 3.03	-2.54	0.064
Zn mg/kg (ppm)	14.40 ± 2.30	17.00 ± 2.92	-2.80	0.049	22.00 ± 6.40	28.8 ± 5.45	-3.67	0.021
B mg/kg (ppm)	16.80 ± 0.45	20.00 ± 2.83	-2.58	0.061	16.60 ± 2.61	24.60 ± 4.16	-4.40	0.012
Mols per area								
N (μmol/m ²)	3.11 ± 0.70	2.77 ± 0.48	0.78	0.482	2.78 ± 0.82	1.98 ± 1.37	2.55	0.064
P (μmol/m ²)	0.15 ± 0.02	0.18 ± 0.03	-3.12	0.035	0.14 ± 0.04	0.13 ± 0.09	0.42	0.694
K (μmol/m ²)	1.62 ± 0.09	1.61 ± 0.16	0.13	0.902	1.23 ± 0.10	1.02 ± 0.53	0.89	0.425
Ca (μmol/m ²)	0.60 ± 0.09	0.45 ± 0.05	2.84	0.047	0.57 ± 0.19	0.33 ± 0.21	5.35	0.006
Mg (μmol/m ²)	0.46 ± 0.19	0.39 ± 0.08	0.97	0.385	0.45 ± 0.21	0.30 ± 0.18	5.73	0.005
Na (μmol/m ²)	86.82 ± 25.05	65.96 ± 20.61	3.48	0.025	98.37 ± 24.04	56.57 ± 28.79	2.53	0.065
Mn (μmol/m ²)	0.72 ± 0.17	0.67 ± 0.21	0.72	0.512	1.55 ± 0.38	0.91 ± 0.42	3.41	0.027
Fe (μmol/m ²)	1.84 ± 0.62	4.40 ± 3.47	-1.90	0.130	13.65 ± 15.1	9.48 ± 6.59	0.39	0.716
Cu (μmol/m ²)	0.09 ± 0.09	0.06 ± 0.02	0.66	0.545	0.07 ± 0.03	0.05 ± 0.03	2.19	0.094
Zn (μmol/m ²)	0.07 ± 0.01	0.07 ± 0.02	-0.78	0.481	0.11 ± 0.04	0.08 ± 0.04	2.47	0.069
B (μmol/m ²)	0.47 ± 0.07	0.51 ± 0.11	-0.97	0.387	0.46 ± 0.06	0.41 ± 0.16	0.70	0.521

Chapter 5: General conclusion

Large and rapid changes in climate are predicted for high latitude ecosystems over the next 100 years (IPCC, 2001). These changes will have diverse effects on communities and their constituent species due to species-specific sensitivity to different environmental parameters (Chapin et al., 1997). However, due to the disproportionately large influence of dominant and/or keystone species on community structure and function (Begon et al., 1996), understanding their responses can greatly improve predictions of the ecological consequences of climate change. In many sub-Antarctic fellfield habitats, the cushion plant *Azorella selago* is both a dominant and keystone species (Huntley, 1971, 1972), and thus its response will strongly influence the entire fellfield community.

The three complementary approaches used in this study showed that *A. selago* is sensitive to changes in climate, despite expectations for the species to be relatively unresponsive (as a stress-tolerator; *sensu* Grime, 1979). First, experimental microclimate modifications demonstrated that *A. selago* could show rapid vegetative responses to changes in environmental conditions (Chapter 4). Second, altitudinal trends in *A. selago* morphology suggested that the species also shows a vegetative response to more gradual changes in climate (Chapter 3). Finally, the age structure of *A. selago* populations suggested that the establishment of seedlings is dependent on specific environmental conditions, and therefore that species' population dynamics may be affected by changes in climate (Chapter 2). While adult plants survived the climate manipulation experiment, it is possible that reproductive and establishment processes of *A. selago* are more vulnerable to shifts in climate. Therefore, further changes in climate are likely to have both (rapid) vegetative and (gradual) demographic effects on the species.

The epiphytes growing on the cushion plants also appeared responsive to changes in environmental conditions. Changes in epiphyte cover can alter the environmental conditions experienced by the cushion plants (particularly because of shading by the epiphytes), and climate change may thus indirectly affect *A. selago* through its effects on the epiphytes. The abundance and cover of the cushion plant's dominant epiphyte, *Agrostis magellanica*, was affected by microclimate

modifications, and observations across the island suggest that its distribution is also strongly dependent on climatic conditions. Furthermore, the altitudinal zonation of epiphyte species suggests that changes in climate could cause elevational shifts in the distribution of these species, leading to changes in epiphyte cover and composition across the island. Therefore, considering the sensitivity of *A. selago* to shading, the indirect effects of climate change on *A. selago* (i.e. climate change-driven shifts in epiphyte abundance, cover and distribution) could overshadow any direct effects.

Bioindicators of climate change

Due to their short-term sensitivity to environmental conditions, *A. selago* and its epiphytes may be good bioindicators of climate change in the sub-Antarctic (environmental bioindicator: *sensu* McGeoch, 2002; see also e.g. Smith, 1994; Molau, 1997). *Azorella selago* trichome density, leaf size and timing of autumnal senescence proved sensitive to changes in climate (in agreement with other species: Halloy and Mark, 1996; Walther et al., 2002), and these characteristics could be used to monitor the progression of climate change. Because the duration of *A. selago*'s growing season influences the dynamics of fellfield ecosystems, a change in this parameter will indicate the effects of climate change on ecosystem functioning. Changes in *A. selago* leaf size and trichome density are less easily related to changes in ecosystem dynamics, but still indicate the response of the cushion plant to climate change. The altitudinal distribution of epiphyte species also appeared to be strongly related to climate, and could also be potential indicators of changes in climate. Since species may be limited by different environmental factors, monitoring a suite of epiphyte species can indicate changes in a range of environmental factors (e.g. *A. magellanica* to indicate shifts in wind patterns, and *Sanionia* mosses to monitor changes in rainfall: see McGeoch, 2002). Continued monitoring of these species (as well as further experimentation) would enable the improvement and refinement of these biomonitoring systems.

Implications for fellfield ecosystems

Under a scenario of warmer and drier conditions, Smith et al. (2001) predicted that mesic fellfield and polar desert habitats would be succeeded by xeric fellfield

vegetation. The results of this study agree with this broad prediction since lower rainfall is likely to reduce epiphyte cover (at least of *Agrostis magellanica*) in mesic fellfield and higher temperatures will favour the increase of *A. selago* in polar desert (if low temperatures limit the establishment of the species). Further, results from this study predict lower fellfield (both mesic and xeric) plant production under this scenario due to a shortened *A. selago* growing season (assuming the onset of the species' growing season is not altered) and lower epiphyte abundance. At the same time higher temperatures, and the associated decline in the frequency of freeze-thaw events (Boelhouwers et al., 2003), will potentially favour the production of larger *A. selago* leaves with lower trichome densities at mid altitudes. In turn, the invertebrate communities within *A. selago* cushions are affected by changes in the cushion plants and their epiphytes (as well as directly by the shifts in climate: E.A. Hugo, M.A. McGeoch, P.C. le Roux, M. Nyakatya & S.L. Chown, unpublished data). Changes in foliar nutrient concentrations (in response to changes in temperature) will also have an effect on the composition and abundance of invertebrate communities (Callaghan and Jonasson, 1995), although this effect will be diluted by the presence of many previous years' leaves.

Under a slightly different climate change scenario, where the island's rainfall stops declining but temperatures continue to rise, vastly different outcomes are predicted. Under such a scenario, epiphyte cover is likely to increase, leading to greater shading of cushion plants. In turn, shading strongly affects *A. selago* morphology (increased stem growth rate, leaf size and leaf mass, decreased leaf thickness and trichome density) and physiology (higher foliar concentrations of nitrogen, potassium, phosphorus, boron and zinc). As a result, increased epiphyte cover could potentially cause a short-term increase in the quantity and quality of *A. selago* biomass produced, favouring detritivorous invertebrates (Callaghan et al., 1992; Callaghan and Jonasson, 1995). However, as *A. selago* stem mortality occurs and cushions lose compactness over the longer-term, a decline in cushion abundance and production is expected. Any such reduction in cushion abundance will negatively affect their associated epiphytes and invertebrates, particularly where conditions outside *A. selago* cushions are unfavourable for those species (see e.g. Barendse and Chown, 2001). All predictions, however, concur that further changes in climate will cause changes in *A. selago* and its epiphytes, potentially with repercussions for the entire fellfield ecosystem on Marion Island.

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