University of Wollongong

Research Online

University of Wollongong Thesis Collection
1954-2016

University of Wollongong Thesis Collections

2004

The effect of climate change on Antarctic terrestrial flora

Jane Wasley
University of Wollongong

Follow this and additional works at: https://ro.uow.edu.au/theses

University of Wollongong

Copyright Warning

You may print or download ONE copy of this document for the purpose of your own research or study. The University does not authorise you to copy, communicate or otherwise make available electronically to any other person any copyright material contained on this site.

You are reminded of the following: This work is copyright. Apart from any use permitted under the Copyright Act 1968, no part of this work may be reproduced by any process, nor may any other exclusive right be exercised, without the permission of the author. Copyright owners are entitled to take legal action against persons who infringe their copyright. A reproduction of material that is protected by copyright may be a copyright infringement. A court may impose penalties and award damages in relation to offences and infringements relating to copyright material. Higher penalties may apply, and higher damages may be awarded, for offences and infringements involving the conversion of material into digital or electronic form.

Unless otherwise indicated, the views expressed in this thesis are those of the author and do not necessarily represent the views of the University of Wollongong.

Recommended Citation

Wasley, Jane, The effect of climate change on Antarctic terrestrial flora, PhD thesis, School of Biological Sciences, University of Wollongong, 2004. http://ro.uow.edu.au/theses/275

Research Online is the open access institutional repository for the University of Wollongong. For further information contact the UOW Library: research-pubs@uow.edu.au

University of Wollongong

THESIS DECLARATION

This is to certify that I JANE WASLEY being a candidate for the degree of DOCTOR OF PHILOSOPHY am fully aware of the University of Wollongong's rules and procedures relating to the preparation, submission, retention and use of higher degree theses, and its policy on intellectual property. I acknowledge that the University requires the thesis to be retained in the Library for record purposes and that within copyright privileges of the author, it should be accessible for consultation and copying at the discretion of the Library officer in charge and in accordance with the Copyright Act (1968). I authorise the University of Wollongong to publish an abstract of this thesis.

Signature ....

Date 19.7.04

The Effect of Climate Change on Antarctic Terrestrial Flora

A thesis submitted in fulfilment of the requirements for the award of the degree

Doctor of Philosophy

from

UNIVERSITY OF WOLLONGONG

by

Jane Wasley, B.Sc. (Hons)

School of Biological Sciences

2004

Certification

I, Jane Wasley, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Jane Wasley.

22rd July 2004

Acknowledgements

I would firstly like to thank Sharon Robinson and Cath Lovelock, who have been exceptionally supportive and inspirational supervisors. Sharon and Cath have been far more than just supervisors to me, providing a wealth of support and guidance beyond the realms of this thesis - thanks to both of you, your lessons have been priceless.

Eternal thanks goes also to the other "Moss Girl", Johanna Turnbull, whose dedication to this work over three Antarctic summers and, importantly, also her friendship has made this thesis possible – I don't think I will ever be able to thank you enough Wan. Thanks too to Jodie Dunn, who also assisted with field and lab work in Antarctica, and to other ANARE members who helped with various aspects of this work. I am also very grateful to those who assisted with other analyses: Prof. Marianne Popp, Dr. Andreas Richter, Dr. Wolfgang Wanek and Sabine Maringer assisted with IRMS and GC analyses; Dr Lixia Lui performed lipid analyses; Joanne George assisted with phosphorous analyses; and Assoc. Prof. Ken Russel and Prof. David Griffith provided statistical advice. Feedback on earlier drafts, and on the manuscript that forms the basis of chapter 1, was provided by Rob Whelan, Jodie Dunn, Sue Fyfe and Margie Law. Andrew Netherwood produced Figs. 1.1 and 1.2 (and many delicious meals).

Finally a very special thank you to all my friends and family who have shown me endless love and support and who have kept me in touch with the things that really matter in life. You know who you all are… I can only list a few here…. The girls from the Gong (especially Susie Brooks and Ali Findlay), Andy Cianchi (yes, I have finally "pulled my finger out" and got this thing finished!), Rachel Cianchi (for the many life-enriching phone calls), Letitia Bright (for helping get the final stages of the "fashion parade" underway) and Margie Law (for surviving the endless "school nights"). And of course thank you Mum and Dad, for giving me the confidence, encouragement and support to "be anything I want to be".

Funding and logistic support was provided by the Australian Antarctic Division and an Australian Postgraduate Award.

Brief Table of Contents

Table of Contents

List of Figures

List of Tables

List of Appendices

List of Special Names or Abbreviations

A	Algae
ASPA	Antarctic Specially Protected Area
B	Bryophytes
C	Cyanobacteria
CA	Continental Antarctic
CV	Coefficient of Variation
CRT	Critical Recovery Time
CWC	Critical Water Content
D	Day
DR	Dark Respiration
dwt	Dry weight
ETR	Electron Transport Rate
F	Fungi
FB	Field Based
FC/L	Field Collected / Laboratory Analyses
F_v/F_m	Ratio of variable to maximum fluorescence
L	Lichen
LB	Laboratory Based
L(P)	Lichen Phycobiont
M	Moss
MA	Maritime Antarctic
M-FD	Model, based on field data
M-LD	Model, based on laboratory data
MUFA	Monounsaturated fatty acid
P_n	Net Photosynthesis
PS	Photosynthesis
PUFA	Polyunsaturated Fatty Acid
R	Review
RGR	Relative Growth Rate
S	Soil
SFA	Saturated Fatty Acid
Sn	Snow
SSSI	Site of Special Scientific Interest
temp	Temperature
TWC	Turf Water Content
V	Vascular plants
veg	Vegetation
WC	Water Content
X2, X3, X4	Unidentified soluble carbohydrate compounds
$\delta\ ^{15}N$	Abundance of ^{15}N stable isotope (relative to ^{14}N)
$\delta\ ^{13}C$	Abundance of ^{13}C stable isotope (relative to ^{12}C)
ΦPSII	Quantum yield of PSII
↑	Increasing
↓	Decreasing
‰	Parts per thousand

Abstract

Climate change is expected to affect the high latitudes first and most severely, rendering Antarctica one of the most significant baseline environments for the study of global climate change. The indirect effects of climate warming, including changes to the availability of key environmental resources, such as water and nutrients, are likely to have a greater impact upon Antarctic terrestrial ecosystems than the effects of fluctuations in temperature alone. Water availability is the focus in this thesis for two main reasons; firstly, there is a wealth of evidence to suggest water is currently limiting to Antarctic plant distributions and productivity, and secondly, availability of this key resource is predicted to change with the onset of climate change. Nutrient availability is a second variable considered in this work, as there is evidence to suggest that nutrients also play a role in determining plant species distributions, and changes to nutrient balance and turnover rates are also expected in response to climate change.

This work was conducted in the floristically important Windmill Islands region of East Antarctica, with the three Windmill Islands moss species *Bryum pseudotriquetrum*, *Ceratodon purpureus* and *Grimmia antarctici* forming its focus. A combination of field ecology, ecophysiology and laboratory studies were used to determine fine-scale patterns of present species distributions and their relationship to naturally occurring water and nutrient resource gradients, the impact of increased water and nutrients on a range of cryptogamic communities, and tolerance of desiccation biological profiles.

A survey-based approach was used to determine species level patterns in bryophyte species distributions, and identify correlations with resource availability. Ten replicate transects, along community gradients, from pure bryophyte stands, through transitional moribund bryophyte zones, to lichen-dominated communities, were surveyed at two sites. The physical environment at each site was characterised by measurement of site soil properties, along with individual transect aspects and slopes. To determine the relationship between resource gradients and community patterns water and nutrient availability, along with a range of plant biochemistry measures indicative of the growth environment, were measured using a series of quadrats along each transect. Percent abundance for each species and/or vegetation category was determined for each quadrat by microscopic examination of field samples.

The community gradient, covering the entire ecological range of past and present bryophyte occupation, was found to be accompanied by resource gradients that operated in opposing directions. Pure bryophyte communities existed under conditions of high water availability and low nutrient availability. Crustose lichen-dominated communities persisted under opposing environmental conditions, of low water availability and high nutrient availability. *Grimmia antarctici* dominated the wettest habitats but its distribution extended into the dry moribund zones, albeit in low levels of abundance. *Bryum pseudotriquetrum* occurred in consistent levels of abundance across the entire gradient, whilst *C. purpureus* was restricted to the driest habitats. Live bryophyte material was found to occur in moribund turf, supporting the potential for bryophyte regeneration under a future wetter climate. Regenerating turf showed potential to support high species diversity, as all four bryophytes survive in this zone.

To investigate the likely impacts of a wetter climate on Antarctic terrestrial communities, four cryptogamic communities, pure bryophyte, moribund bryophyte, crustose and fructicose lichen-dominated communities were subject to a multi-season manipulative field experiment. Within each community type, eight replicate quadrats received increased water and/or nutrient availability over two consecutive summer seasons. A range of physiological and biochemical measurements were conducted in order to quantify the community response to the treatments and determine the extent of any nutrient and water limitation. Few multi-season manipulative field experiments have been conducted in continental Antarctica. Whilst an overall increase in productivity in response to water and nutrient additions was supported, productivity appeared to respond more strongly to nutrient additions than to water additions. Pure bryophyte and fructicose lichen communities also showed stronger positive responses to additions, identifying some communities that may be better able to adapt and prosper under the ameliorating conditions associated with a warmer, wetter future climate.

Using a range of morphological, biochemical and physiological techniques, biological profiles related to desiccation tolerance were developed for the three bryophyte study species, providing measures of relative abilities to avoid, tolerate, recover from and survive desiccation. *Ceratodon purpureus* showed good desiccation avoidance characteristics, its photosynthetic efficiency remained high at low water contents and it was lipid rich, suggesting that this species is well adapted to survive a drying climate. *Bryum pseudotriquetrum* is also likely to survive drier conditions, as this species showed good desiccation avoidance, had a plastic response to desiccation, and contained stachyose, which is likely to assist in its survival of desiccation events. Conversely, *G. antarctici* showed poor desiccation avoidance, as photosynthetic efficiency required highest water contents and it contained few protective substances, this species is therefore least likely to survive a drying environment.

This study provides a baseline from which future changes to the Windmill Islands cryptogamic communities can be monitored. A baseline incorporating fine-scale bryophyte species patterns is particularly useful, as this component of the cryptogamic community is likely to be highly sensitive to even small shifts in water availability and detection of change is likely to be more sensitive at fine- rather than broad-scales. Both water and nutrient resource availability was found to underlie regional bryophyte species distributional patterns. The dynamics of the Windmill Islands flora is therefore likely to shift in response to climate change as the availability of these key resources is altered. Under a wetter future climate, productivity is overall likely to increase but only certain cryptogamic communities are likely to thrive. Regeneration of moribund bryophytes appears likely only if the future moisture regime creates consistently moist conditions. *Bryum pseudotriquetrum* is most likely to survive both a drying climate and also a fluctuating climate, which is a highly likely scenario for the region. Under a drier climate, the Antarctic endemic, *G. antarctici*, is likely to be most adversely affected, as it dominates only the wettest communities and generally shows poor tolerance of desiccation. Conservation issues are therefore raised for this species, if the current drying trend continues, creating overall biodiversity concerns.

Chapter 1: General introduction to plants and global change in Antarctica

This introduction has been published as part of a review paper by Robinson, Wasley and Tobin (2003).

1.1. Introduction

The Antarctic continent is the coldest, highest, driest, windiest and most isolated landmass on earth. Growth conditions are therefore extreme, and plants exist at the physiological limits of survival. Plants are confined to the few ice-free areas, which constitute ~0.5% of the Antarctic surface area. Characteristic of Antarctic growth conditions are low summer temperatures, a strongly seasonal climate, a very short growing season, continuous light in midsummer, and frequent strong winds. As a consequence of these severe conditions, the Antarctic flora is almost entirely cryptogamic, only two vascular species occur, both of which are restricted to the relatively mild Antarctic Peninsula.

1.1.1. Antarctica and the detection of climate change

Climate change is expected to impact first, and most severely, in the high latitudes (Callaghan et al. 1992, Vincent 1997, Walker 1997), rendering Antarctica one of the most significant baseline environments for the study of global climate change (Smith 1990a, Walton et al. 1997). Vegetation characteristics, such as simple community structure, and the geographic isolation of the Antarctic continent also contribute to the importance of this region in climate change research. The largely cryptogamic vegetation of continental Antarctica, dominated by bryophytes (mosses and liverworts) and lichens, constitutes one of the simplest ecosystems in the world, and therefore provides a biological study system with minimal associated ecosystem interactions (Smith 1988a). In Antarctica, where vegetation grows at the physiological limit of survival, plants would be expected to show a more marked response to changes in growth conditions than those from less extreme climates (Adamson and Adamson 1992, Callaghan et al. 1997, Melick and Seppelt 1997, Hansom and Gordon 1998) thus enhancing the suitability of this system for the detection of environmental change. The life history characteristics of polar species (Callaghan et al. 1992) and the precarious freeze-thaw balance, which influences many aspects of these ecosystems (Vincent 1997), render high latitude ecosystems vulnerable to change. In addition, the geographic isolation of the Antarctic continent further enhances the value of the vegetation of this region for climate change research, because it remains relatively free from the concurrent effects of anthropomorphic phenomena such as land use changes, weeds and pollution (Callaghan et al. 1992). It is believed that, since polar regions have been relatively undisturbed, small climatic shifts may have a significant impact on biological habitats (Melick and Seppelt 1997).

1.1.2. Vegetation and phytogeographic zones

Antarctica has been divided into three phytogeographic zones (Stonehouse 1989). The high latitude continental Antarctic zone is the most climatically severe, and is the focus of this thesis. The body of literature concerning continental Antarctic terrestrial vegetation is relatively small and I therefore also review work conducted in the maritime Antarctic, which constitutes the west coast of the Antarctic Peninsula north of c. 72°S and associated islands (including Alexander Island, King George, South Shetlands, Sandwich and Orkney and Peter I Øy). The periantarctic zone is, by contrast, relatively mild and since it is less relevant to this thesis it has not been considered here.

Despite the severe growth conditions, plants are found on the Antarctic continent although many species, including the two Angiosperms, are restricted to the relatively mild maritime zone (Table 1.1). Outside the maritime zone the remaining cryptogamic vegetation is primarily limited to a few small rocky outcrops along the coast, the dry valleys and inland nunataks (Hansom and Gordon 1998). Many of these continental areas are considered polar deserts, as the precipitation is less than 100 mm/year and is almost always delivered as snow (Kappen 1985a). Exacerbating the extremely dry conditions are the subzero summer temperatures which lock most water away as snow and ice, significantly limiting plant productivity (Hansom and Gordon 1998). Within these extremely harsh environments, lichens and algae commonly dominate the flora.

Bryophytes also occur, however, but are largely limited to favourable microclimates that receive sufficient water supply, such as the vicinity of reliable seasonal melt streams. Mosses have been reported from as far south as 84° S and although bryophyte fruiting events are rare in the continental Antarctic zone (Filson and Willis 1975), moss sporophytes have been reported as far south as 77° 55' S (Seppelt et al. 1992). In addition to the relatively conspicuous mosses and lichens, the continental Antarctic terrestrial vegetation includes groups that are often overlooked, including the chasmoendolithic algae, which occur only within rock fissures. These organisms are widespread in coastal regions of Antarctica and are believed to underlie up to 20% of the rock surface in some locations (Longton 1985, Hansom and Gordon 1998).

Table 1.1: Estimated contribution of plant groups to terrestrial plant biodiversity of Antarctica.

Phytogeographic zone	Angiosperms	Mosses	Liverworts	Lichens	Macro-fungi	References
Continental	0	25	1	150	0	Convey (2001a)
Maritime	2	100	25	250	30	Convey (2001a)

1.1.3. *Adaptations to severe conditions*

Continental Antarctic cryptogams are largely poikilohydric and as a result, during periods of low water availability or freezing temperatures, they possess the ability to enter a dormant state of physiological inactivity through controlled dehydration of their cells. The continental Antarctic flora can therefore survive frozen and desiccated, beneath a cover of snow, over the long dark winter and rehydrate during the spring thaw for the short summer growing season of 1-4 months (Melick and Seppelt 1997). Emerging from beneath the protective and insulating snow cover, these plants are exposed to the extreme conditions of the frigid Antarctic climate with frequent subzero temperatures, desiccating winds, intermittent water supply, a highly seasonal light regime, and more recently, elevated ultraviolet-B (UV-B; 290-320nm) radiation levels. Plant photosynthetic rates and consequently, growth and productivity, are greatly influenced by these environmental variables. Optimising photosynthesis over the short growing season depends on the ability of these plants to acclimate to prevailing environmental conditions in this highly seasonal and variable climate (Melick and Seppelt 1994b).

1.1.4. Distribution & community structure

Ecological distributions and aspects of community structure have been comprehensively reviewed for the Antarctic biome by Smith (1984). Antarctic plant distributions are primarily determined by environmental factors such as amount and duration of ice cover (Smith 1990b) temperature (Adamson and Adamson 1992), moisture availability (Smith 1990b, Adamson and Adamson 1992, Schwarz et al. 1992, Melick and Seppelt 1994a) and microtopography (Schwarz et al. 1992, Melick and Seppelt 1994a).

Most species occurring on continental Antarctica are restricted to either the continental or the maritime zone and only a few species are found in both (Hansom and Gordon 1998). For the cryptogamic species, lichens tend to predominate in drier, more exposed locations, while bryophytes are restricted to moist, sheltered refuges (Smith 1988a). The two maritime Antarctic vascular species have almost identical distributions across the maritime Antarctic region, with the tussock forming hairgrass, *Deschampsia antarctica*, generally more abundant than the cushion forming pearlwort, *Colobanthus quitensis* (Convey 1996b). The environmental conditions favourable to these latter species are found in sandy, mineral-rich, well-drained substrates that do not have a continuous supply of melt-water throughout the growing season but do have some moisture-holding capacity (Komarkova et al. 1985).

Antarctic terrestrial plant communities have small stature, low biomass, low productivity and low species diversity (Seppelt et al. 1988). There is, however, a wide range of growth forms, including endolithic algae and lichens (Broady 1981b, Friedmann 1982), and epiphytes (Seppelt and Ashton 1978, Broady 1981a), with communities containing multispecies assemblages that display both vertical and horizontal complexities (Seppelt et al. 1988).

A small number of ice-free coastal areas in Antarctica support relatively rich and/or extensive floristic assemblages, and as a consequence these sites have been the focus of much research. These sites include the Windmill Islands Region, which is the site of the studies described in this thesis, Ross Island and Signy Island (see Fig. 1.1).

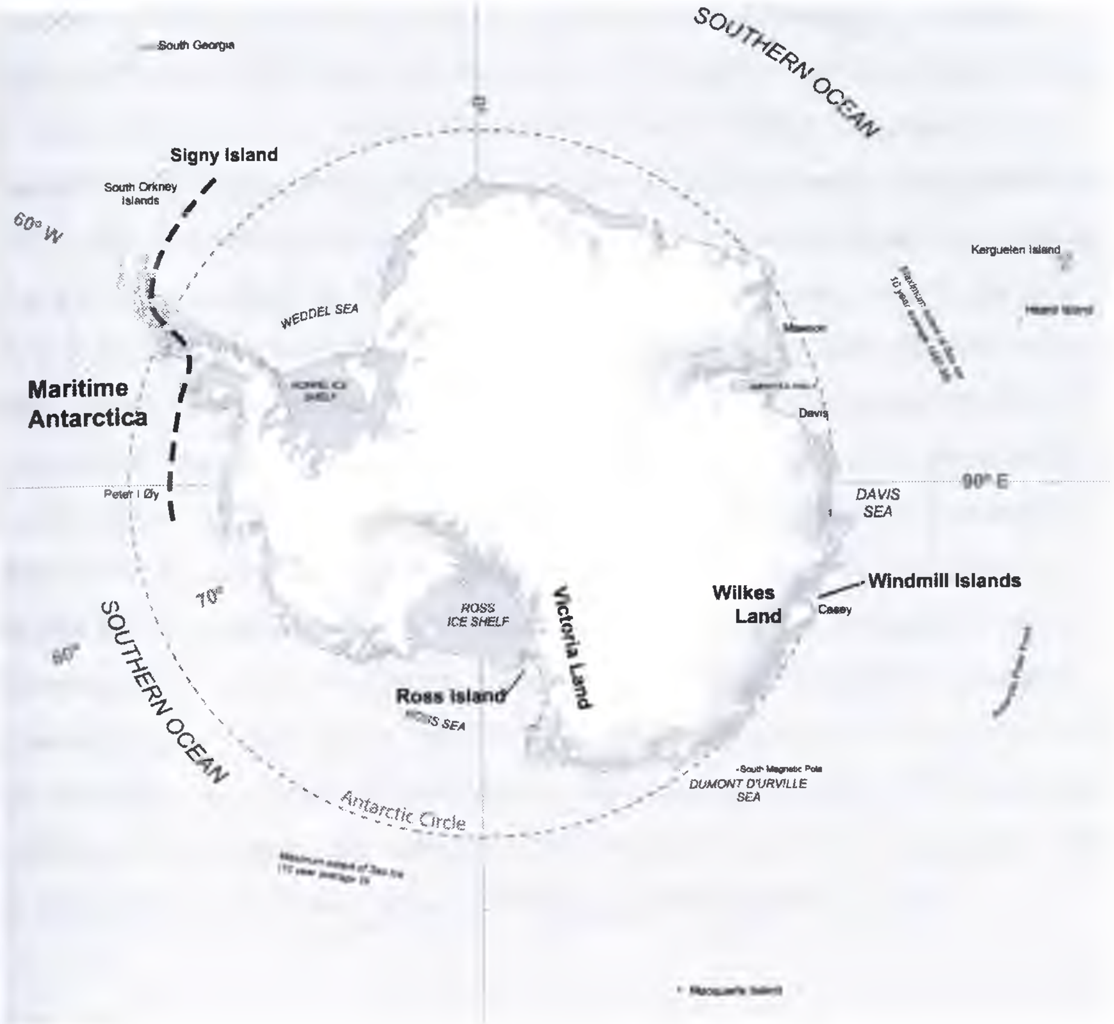


Figure 1.1: Map of Antarctica. The maritime Antarctic is the area to the left of the dashed line. The Periantarctic islands are found north of the limit of sea ice and bounded by the polar front. The bulk of the research reviewed herein was conducted at the following locations; Signy Island (maritime Antarctic), Ross Island (Victoria Land) and the Windmill Islands region (Wilkes Land), which was the location of the research presented in this thesis.

1.1.5. Antarctic research history and aims of this review

Early Antarctic terrestrial studies, prior to 1965, were limited to qualitative and taxonomic works, and are reviewed in Smith (1984). Since the 1970s, research has become both more quantitative and directed towards species autecology and community and ecosystem processes (Smith 1984). The research on vegetation patterns, life history attributes and ecosystem processes has been extensively reviewed (Lindsay 1978, Longton 1979, Pickard and Seppelt 1984, Convey 1996a, Hansom and Gordon 1998, Green et al. 1999). Only a handful of review articles have been related to climate change, with topics including: Antarctic plants as indicators of climate change (Green et al. 1999), polar desert ecosystems (Vincent 1997), the ecological considerations of Antarctic ozone depletion (Karentz 1991) and global change research strategies (Weller 1992). The most relevant works to this thesis are those discussing the potential effects of global climate change on Antarctic terrestrial ecosystems (Adamson and Adamson 1992, Kennedy 1995, Kennedy 1996, Convey 2001b, a, Convey 2003, Hennion et al. 2005). Many of these reviews have identified the need for greater research into the responses of Antarctic plants to climate change. Herein I focus on research published in the last decade and indicate where research is still required. I address how terrestrial, photosynthetic eukaryotes are likely to cope with climate change. In doing this, I identify the major factors currently influencing plant distribution and productivity in Antarctica, discuss how these factors are likely to change, and consider the potential impacts of such changes on the Antarctic flora. The likely parameters to change include UV-B radiation, CO_2, water and nutrients. In the context of this thesis CO_2, water and nutrients are considered. The impacts of UV-B radiation on Antarctic vegetation, which are beyond the scope of this thesis, are addressed in Robinson et al. (2003).

1.2. Elevated CO_2

The atmospheric concentrations of greenhouse gases, such as carbon dioxide, have been rising over the last few decades (Houghton et al. 2001). Despite considerable research effort being focussed on this issue worldwide (see for example, has been focussed on the effect of this environmental change in the Arctic and other areas worldwide (e.g. Drake and Gonzàlez-Meler 1996, Norby et al. 2001, Oechel et al. 1997). Evidence from the Arctic suggests the effects of elevated CO_2 are likely to be minimal in these nutrient-limited communities (Oechel et al. 1997). No research appears to have been conducted to investigate the ecological impact of rising CO_2 levels in Antarctic terrestrial ecosystems. Field experiments to increase CO_2 would be difficult in the continental Antarctic and were beyond the scope of this study.

The only relevant work to date is a study by Tarnawski et al. (1992) on the dominant moss species in the Windmill Islands, *Grimmia antarctici*. This showed that, whilst small cushions growing in dry sites might be CO_2 limited for much of the summer, high CO_2 levels were achieved throughout the summer in the turf form common to moist sites and making up most of the biomass of this species. Although an increase in ambient CO_2 levels, as a result of global climate change, might alleviate CO_2 limitations in certain populations, a significant increase in overall productivity seems likely only if water availability increases (see section 1.4 below).

Evidence from a non-Antarctic system, suggests that elevated CO_2 may increase the temperature optimum for photosynthesis in mosses (Silvola 1985). The interactions of increased CO_2 with increasing and decreasing water and temperature requires investigation before the effect of elevated CO_2 on these communities can be predicted.

1.3. Temperature

1.3.1. Evidence

The most recent report by the Intergovernmental Panel on Climate Change (IPCC) estimates that the global surface temperature has increased 0.6°C since the late 19th century, with a 95% confidence interval of 0.4 to 0.8°C (Houghton et al. 2001). This warming is widely accepted as being exacerbated by human intervention, with recent results from an Antarctic deep ice core supporting that, in the absence of anthropomorphic effects, the present climate is likely to remain stable well into the future (Augustin et al. 2004). Climate models predict a rise in global average surface temperatures of 1.5 to 4.5 ˚C in response to a doubling of greenhouse gas concentrations (Tokioka 1995). Temperature increases are predicted to predominately impact on the high latitudes in winter, largely due to snow- and ice-albedo feedbacks (Tokioka 1995). Other polar feedback loops, which contribute to the heightened sensitivity of the high latitude regions, include those involving sea-ice extent and temperature, have evidence provided from the Antarctic Peninsula region (King 1994, Smith et al. 1996).

Predictions for escalating temperatures are supported by meteorological evidence from the Antarctic Peninsula region, where temperatures have increased over the last half-century, by 1 °C in summer (Smith 1990a, Fowbert and Smith 1994, Smith 1994) and 4-5 °C in winter (Smith et al. 1996). The pattern of change across this region varies spatially as well as seasonally, however, with the east coast experiencing a 0.03°C annual rise across all seasons, while the west coast shows an annual rise of the same magnitude over the summer and an elevated 1°C per annum warming in winter (King et al. 2003). These substantial temperature increases appear to have already triggered ice-albedo feedback loops, evidence for which is provided from Signy Island, where there has been a 35% reduction in ice cover (Smith 1990a).

However, temperature trends for the Antarctic continent as a whole are not so clear. A recent, detailed analysis using meteorological data (1957-1998) from stations throughout the Antarctic region and satellite data (1979-1998) for the Antarctic continent found contrasting trends. The 45 y record in the meteorological data showed an overall increase of 0.012+0.008 °C y^{-1} but a decline of 0.008+0.025 °C y^{-1} over the past 20 y. The recent 20-y trend is supported by the satellite data for the same period, which showed a more severe decline in temperature of 0.042+0.067 °C y^{-1} (Comiso 2000). Similar fluctuations have been detected in the Windmill Islands region, East Antarctica; average temperatures increased 0.086 °C y^{-1} from 1960 to the mid-1980s and then declined 0.010 °C y^{-1} to the mid-1990s (Melick and Seppelt 1997). Evidence of a cooling trend for continental Antarctica has also been provided in recent studies that have analysed records throughout Antarctica for the period 1966-2000 (Doran et al. 2002) and winter temperatures (July) for the period 1980-1993 (van den Broeke and van Lipzig 2003). Contrary to the predictions of increasing global temperatures, and measured warming trends of the maritime Antarctic, these studies suggest a recent cooling trend for the Antarctic continent. However, since Antarctic temperature trends vary spatially, seasonally and interdecadally, I believe that it is impossible at this stage to confirm consistent warming or cooling of the continent and I will therefore concentrate on the likely impacts of increasing temperature since this represents the most accepted trend (see also Turner et al. 2002, Walsh et al. 2002).

1.3.2. Ecological impacts

Alien invasion

The ameliorating growth conditions provided by rising maritime Antarctic temperatures increases the threat of invasion by alien species in this region. Evidence from maritime Antarctic sites, including Signy Island, has shown that there is a continuous immigration of sporomorpha from South America (Smith 1991, Marshall 1996b) and exotic pollen and spores have also been detected on the continent (Kappen and Straka 1988, Linskens et al. 1993). Particular species (Melick et al. 1994b) and sites (Selkirk et al. 1997) have been identified as having greater potential for invasion. In addition to the potential for species from outside Antarctica to colonise the continent, expansion of species ranges within Antarctica is also a possibility as locally occurring moss (Marshall and Convey 1997) and lichen propagules (Marshall 1996a) have been collected in maritime Antarctic sites. Five native Antarctic species (Table 1.2) have been identified as potential long-distance dispersers (Convey and Smith 1993). Under ameliorating climatic conditions, alien species invasion to the Antarctic may cause detrimental disruptions to the current ecological balance in these sensitive communities (Green et al. 1999, Walther et al. 2002). Although not yet determined experimentally, sporophyte production in bryophytes is thought to be limited by the low Antarctic temperatures (Filson and Willis 1975, Seppelt et al. 1992), so an increase in temperature is likely to result in an increase in sexual reproduction events, and consequently, an increase in spore production and dispersal within continental Antarctica. Combined with ameliorating growth conditions, the likelihood of colonisation by new populations of native and alien species is projected to increase under a warmer climate.

Table 1.2: *Summary of effects of Temperature on Antarctic vascular plants, bryophytes and terrestrial algae.*

Scenario	Impact	Nature of impact	Major Results	Plant group	Location	Field / Lab	References
Increased Temperature	Increased risk of alien invasion	Physiological	Current, low, Antarctic temps limit sporophyte production.	B	CA	FB	(Seppelt et al. 1992)
			Although no causal link with increased temperature, sporophyte production higher at high latitudes than previously expected. Relatively high in micro-oases.	B	MA	FB	(Smith and Convey 2002)
		Ecological	Supply of pollen and spores to Antarctica.	VB L F	CA MA	FC/L	(Kappen and Straka 1988)
			Vestfold Hills are at greater risk of alien invasion than the Ross Sea Region.	B	CA	FC/L	(Selkirk *et al.* 1997)
			Some species have greater potential for invasion than others.	B	CA	FC/L	(Melick *et al.* 1994b)
			5 native Antarctic species identified as potential long-distance colonists.	B	MA	FC/L	(Convey and Smith 1993)
	Altered distribution	Ecological	Species-specific response to increasing summer air temps (1944-92): species distributions 1964-90 - *Deschampsia antarctica* increased in area 25-fold + increased colony numbers, *Colobanthus quitensis* increased in area 5-fold, no new colonies.	V	MA	FB	(Fowbert and Smith 1994)
			D. antarctica and *C. quitensis*: increased number of individuals and populations during 27-year monitoring period.	V	MA	FB	(Smith 1994)
			Manipulative field experiment: Warming increased *C. quitensis* growth (increased leaf production, shoot production and foliar cover). Warming decreased growth of *D. antarctica* (decreased leaf length, leaf production and foliar cover). Improved sexual reproduction in both species.	V	MA	FB	(Day *et al.* 1999)
			With up to 75% crustose lichen encrustation, moribund moss regeneration faster at 18 ˚C than at 2 ˚C.	B L	CA	FC/L	(Melick and Seppelt 1997)

Table 1.2 (continued)

		Antarctic veg often limited to sites maintaining relatively high temps which tend to be sheltered from cold winds, have high levels of solar radiation, and consequently high levels of snow and ice melt.	B L	CA	FB	(Shimizu 1977, Seppelt and Ashton 1978, Kappen 1985a)
		Lichen veg particularly rich on north facing rock sites, where temps are consistently warmer.	L	CA MA	R	(Kappen 1985a)
Increased productivity	Physiological	*D. antarctica* and *C. quitensis* grown at 7, 12 or 20 ˚C: despite P_n being highest in plants grown at 12 ˚C, all measures of growth (RGR, total biomass, leaf area, leaf area ratio and leaf mass ratio) were greatest in 20 ˚C grown plants	V	MA	LB	(Xiong *et al.* 2000)
		P_n increased with increased temp (tested up to 20 ˚C). Species differences: *Bryum argentum* > *Bryum pseudotriquetrum* > *Ceratodon purpureus*.	B	CA	FC/L	(Smith 1999)
Reduced productivity	Physiological	*D. antarctica* and *C. quitensis*: negligible midday field P_n at canopy air temp >20 ˚C, but high P_n at temps <10 ˚C. Lab tests show high temp, not visible irradiance, was responsible for P_n depression.	V	MA	FB+LB	(Xiong *et al.* 1999)
		D. antarctica pronounced decline in P_n at supra-optimal temps(>12 ˚C), P_n negligible at 35 ˚C.	V	MA	LB	(Vining *et al.* 1997)
		Increased photoinhibition with increased temp.	B	CA	FB	(Kappen *et al.* 1989)
		Sanionia uncinata: dark respiration decreased as temp increased (tested range: 0 – 20 ˚C). Low temps important for positive carbon balance: climate warming may reduce carbon gain by increasing respiratory loss.	B	MA	LB	(Nakatsubo 2002)
Morphological changes	Physiological	*D. antarctica*: leaf anatomy shows plastic response to changes in growth conditions.	V	MA	FC/ L	(Romero *et al.* 1999)
Physiological ranges	Physiological	Optimum temp for P_n: *D. antarctica* 13 ˚C, *C. quitensis* 19 ˚C.	V	MA	LB	(Edwards and Smith 1988)

Table 1.2 (continued)

		C. quitensis optimal leaf temp for P_n 14 ˚C, *D. antarctica* 10 ˚C. Continued warming: increased frequency of supraoptimal temps, but canopy temps currently average 4.3 ˚C and remain < optimal for 86% of diurnal periods during the growing season. Continued warming will usually increase P_n.	V	MA	FC/ L	(Xiong *et al.* 1999)
		Optimal temp regime (day/night) 22/15 ˚C for a moss species.	B	CA	FC/L	(Longton 1981)
		P_n highest at 15 ˚C for *B. argenteum* (measured over temp range –8 to 21 ˚C).	B	CA	LB	(Green *et al.* 2000)
		Polytrichum alpestre: optimum temp 5-10 ˚C or 15 ˚C, depending on growth conditions. *Drepanocladus uncinatus*: 15 ˚C, regardless of growth conditions. Species-specific response to temp: *P. alpestre* showed ability to acclimate to changed temps.	B	MA	LB	(Collins 1977)
		4 species: differing responses to 5-25 ˚C temp range. General trend: P_n increased with increasing temp. *D. uncinatus* shows 20-25 ˚C optimum.	B	MA	LB	(Rastorfer 1972)
		P_n maximal at 20-25 ˚C for *B. argenteum*: and 15-20 ˚C for *Umbilicaria aprina*.	BL	CA	FC/L	(Green *et al.* 1998)
		Lichen phycobionts (from 6 species of lichen): optimal temp 15 ˚C.	L(P)	CA	LB	(Schofield and Ahmadjian 1972)
Surface temps can be high, but are not sustained	Physiological	Moss surface temps measured over 13 d period: >10 ˚C 44%, >20 ˚C 24% of the time.	B	CA	FB	(Smith 1988b)
		Moss surface temp reached 17 ˚C (1 d observation).	B	CA	FB	(Seppelt and Ashton 1978)
		P. alpestre, 80% of summer: -5 to +5 ˚C.	B	MA	FB	(Collins 1977)
		B. pseudotriquetrum: field thallus temp up to 27 ˚C.	B	MA	FB	(Schlensog and Schroeter 2000)

Table 1.2 (continued)

Surface temps & fluctuations often greater than ambient	Physiological	Hourly microclimate measurements 1972-4: *Polytrichum* surface temps >+5 ˚C and <-15 C uncommon (<15% of measurements). Absolute max & min temps: +35 ˚C and –26.5 ˚C.	B	MA	FB	(Walton 1982)
		Andreaea gainii and Usnea antarctica: thallus temps in the range 0 ˚C – 15 ˚C, which is thought to be almost optimal for P_n in both species.	BL	MA	FB	(Schlensog and Schroeter 2000)
		When lichens were wet, and photosynthetically active, surface temps exceeded air temps but remained less than 10 ˚C.	L	CA	FB	(Kappen 1985c)
		Measured surface and air temps + irradiance (5 weeks), showed lichen growth conditions to be relatively warm: rock surface & hydrated lichen up to 19 ˚C higher than air, overall rock surface temp averaged 5.5 ˚C warmer than air.	LR	CA	FB	(Kappen et al. 1998)
		Within soil and plant habitats: spring/summer (Nov-Mar) minimum daily temps close to 0 ˚C.	S	MA	LB	(Davey *et al.* 1992)
		Moss and lichen summer temps higher than, and fluctuate more than, air temps (measured over 5 d). Exposed lichen surface temp fluctuates over 30 ˚C during a 5 h period.	BLE	CA	FB	(Melick and Seppelt 1994b)
		Field moss surface temps (56 d measurement): >0 ˚C >80% of the time, >10 ˚C 25% of the time.	B	CA	FB	(Smith 1999)
		Field moss surface temps (27 d measurement): < 5% of readings >13 ˚C, ~60% <2.5 ˚C.	B	CA	FB	(Longton 1974)
		Extreme surface temp diurnal fluctuation of –9.2 to 42.8 ˚C.	B	CA	FB	(Smith 1988b)
		Moss surface temp range (~17 ˚C to ~0 ˚C) greater than range of air temps (~4 ˚C to ~-2 ˚C), during 1 d of observation.	BSA	CA	FB	(Seppelt and Ashton 1978)
		Diurnal fluctuations greater at ground level than in air above or soil below.	E	CA	FB	(Longton 1974)

Table 1.2 (continued)

			Lichen temp higher (with greater fluctuations) than the relatively stable air temp (~28 h diurnal plot). Air temp ~0 ˚C, lichen temp ~0-35 ˚C.	L	CA	FB	(Inoue 1989)
			Surface temp (rock) greater, with greater fluctuations, than air temps.	E	CA	FB	(Rudolph 1966)
Increased freeze-thaw	Increased damage	Physiological	Increased loss of soluble carbohydrates, species differences in % loss.	B	CA	FC/L	(Melick and Seppelt 1992)
			P. alpestre: repeated freeze-thaw cycles caused a greater reduction in gross PS than constant freezing over the same time period. Frequency of freeze-thaw significant impact: 12h cycles, more damage than 24 or 48h cycles.	B	MA	LB	(Kennedy 1993a)
		Environmental	Spring/summer (Nov-Mar) few freeze-thaw cycles, those that occurred were not severe. Authors suggest that freeze-thaw cycling is unlikely to currently limit organism survival during summer: if freeze-thaw increases in frequency or severity, this may change.	S	MA	FB	(Davey *et al.* 1992)

Abbreviations: DR dark respiration, **d** day, **ΦPSII** quantum yield of PSII, **P_n** net photosynthesis, **PS** photosynthesis, **RGR** relative growth rate, **temp** temperature, **veg** Vegetation. **Plant group codes:** V vascular plants, B bryophytes, M moss, L lichen, L(P) lichen phycobiont, A algae, F fungi, C cyanobacteria, S soil, Sn snow. **Location codes:** CA Continental Antarctic, MA Maritime Antarctic. **Study Type:** FB Field based, LB Laboratory based, FC/L Field Collected/Laboratory analyses, R Review, M-FD Model, based on field data, M-LD Model, based on laboratory data.

Community dynamics

Substantial evidence is available to suggest that plant community dynamics are changing in response to recent warming for the maritime Antarctic (Table 1.2). On Signy Island, the steady rise in summer air temperatures since the late 1940s, and the consequent reduction in ice cover, have provided more favourable growth conditions and new areas for colonisation, respectively (Smith 1990a). There have been changes in abundance and area of the Antarctic vascular species, *D. antarctica* and *C. quitensis* (Smith 1990a, Fowbert and Smith 1994, Smith 1994).

A 26-year survey in the Argentine Islands archipelago, western Antarctic Peninsula, found a species-specific correlation with warming; *D. antarctica* showed a considerable increase in colony numbers and a 25-fold increase in area of each colony while no additional *C. quitensis* colonies were recorded and only a 5-fold increase in area was observed (Fowbert and Smith 1994). Day et al. (1999) conducted a manipulative field experiment, increasing the ambient temperatures for these species over two consecutive growing seasons. They also detected species-specific responses, but the direction was opposite to that found in the field survey. When growth was measured in terms of leaf and shoot length, leaf production and foliar cover, warming improved the growth of *C. quitensis* and reduced growth in *D. antarctica* (Day et al. 1999). Both species showed more advanced development of reproductive structures, at the time of census, as a result of the experimental warming treatment.

In the absence of long-term, field-based monitoring of plant communities on the continent, predictions for the impact of temperature change on the distribution of species can only be based on laboratory experiments and/or indirect evidence (Table 1.2). Perhaps the most direct evidence for the ecological impact of temperature on continental vegetation is provided by a controlled growth experiment from the Windmill Islands, demonstrating the regeneration potential of continental Antarctic moribund moss. This study showed that in samples with up to 75% crustose lichen encrustation, moribund moss regeneration was faster at 18 °C than at 2 °C (Melick and Seppelt 1997).

It is thought that the extremely low temperatures that are characteristic of the Antarctic environment are the primary factor limiting Antarctic terrestrial vegetation to predominantly cryptogamic. Antarctic vegetation is often limited to sites maintaining relatively high temperatures, which tend to be sheltered from cold winds, have high levels of solar radiation, and consequently high levels of snow and ice melt (Shimizu 1977, Seppelt and Ashton 1978, Kappen 1985a). Lichen vegetation, for example, tends to be particularly rich on north facing rock sites (Kappen 1985a) where temperatures are consistently warmer. Sheltered sites are also where fruiting events, which occur relatively rarely in Antarctica, have been observed (Filson and Willis 1975). Increasing temperatures on the continent are likely to see an expansion of the area suitable for reproduction, vegetation colonisation and survival. Long-term monitoring of continental Antarctic terrestrial vegetation is crucial for accurate measurement and predictions of vegetation dynamics in response to future temperature regimes.

1.3.4. Photosynthetic physiology

The response of vegetation to elevated temperatures varies across species and regions. There is evidence to suggest that both increases and decreases to productivity may occur (Table 1.2). Since the prevailing low temperatures throughout the Antarctic biome are generally considered to limit net photosynthesis (P_n) for most of the growing season, warming conditions would therefore be expected to increase primary productivity (Xiong et al. 1999). Increased P_n under elevated temperatures has been demonstrated, for example, in three continental moss species (Smith 1999) and the two maritime vascular species (Xiong et al. 2000). There is, however, a wealth of literature that suggests increasing temperatures may cause declines in P_n (Table 1.2). This has been demonstrated for both mosses and vascular plants. Laboratory experiments using the maritime moss, *Sanionia uncinata*, showed that over a temperature range of 0 to 20 °C, net photosynthesis remains low but dark respiration steadily increases (Nakatsubo 2002). Low temperatures thus appear to be important for positive net carbon balance in this species, and increasing temperatures may reduce carbon gain by increasing respiratory loss (Nakatsubo 2002). Declines in P_n with increasing temperatures also occur for those species exhibiting increased photoinhibition under conditions of increasing temperatures, as has been demonstrated by field measurements of some continental Antarctic moss species (Kappen et al. 1989).

In addition, a rise in temperature will cause an increase in the duration and frequency of supra-optimal temperature events, during which photosynthesis is often depressed. Laboratory measurements of the maritime vascular species, *D. antarctica* show a pronounced decline in photosynthetic rates at supra-optimal temperatures (>12 ˚C), with negligible photosynthesis at 35 ˚C (Vining et al. 1997). In the field, both *D. antarctica* and *C. quitensis* have negligible midday net photosynthetic rates at canopy air temperatures greater than 20 ˚C, whilst high rates of midday net photosynthesis are obtained at temperatures of less than 10 ˚C. Accompanying laboratory experiments verified that high temperatures, not visible irradiance, were responsible for the photosynthetic depression observed (Xiong et al. 1999). Currently canopy air temperatures exceed 20 ˚C for less than 1% of diurnal periods (Day et al. 1999) and midday photosynthetic depression events are uncommon. The temperature at which conditions become supra-optimal for photosynthesis varies between species (Table 1.2). Cited values of optimal temperatures range from 10 ˚C in *D. antarctica* (Xiong et al. 1999) to 20-25 ˚C in a maritime moss species (Rastorfer 1972).

Plant surface temperatures are often elevated well above air temperatures by absorption of solar radiation (Schroeter et al. 1997). The data available show that although plant surface temperatures may exceed 40 ˚C during the growing season (Smith 1986, 1988b), these elevated temperatures are not sustained (Xiong et al. 1999). A continental study recorded moss surface temperatures above 13 ˚C less than 5% of the time and below 2.5 ˚C approximately 60% of the time (Longton 1974). Exceptionally high temperatures are often accompanied by large diel fluctuations, an extreme example of which exceeded 50 ˚C (-9.2 to 42.8 ˚C) in a continental Antarctic moss species (Smith 1988b).

Despite the evidence of photosynthetic depression during elevated temperatures, it has been demonstrated that, at least in the two maritime vascular species, increasing vegetative growth outweighs declines in photosynthetic rates under these high growth temperatures (Xiong et al. 2000). The lack of experimental, field-based manipulation of temperature, due to the difficulty of performing such experiments in the severe Antarctic climate, limits our knowledge in this area. However, open-top chambers have been successfully used to increase soil temperatures by +2.2 °C at 10 cm depth and +5.2 °C at the surface (Marion et al. 1997). In addition, experimental manipulation of growth conditions has shown that some species have a greater potential for plasticity of optimal temperatures in response to elevated temperatures. Collins (1977) demonstrated that the maritime moss species, *Drepanocladus uncinatus* (now considered *Sanionia uncinata*) and *Polytrichum alpestre*, showed optimal temperatures for net photosynthesis of 15 °C and 5-10 °C, respectively when grown under a temperature regime similar to field conditions. When grown at warmer temperatures, the optimal temperature for *D. uncinatus* remained at 15 °C, whilst that for *P. alpestre* increased to 15 °C. Species such as *P. alpestre* that show a relatively plastic response to increased temperatures may be better equipped to cope with future field temperature increases (Collins 1977).

Experimental manipulation of temperature in the field has been achieved as a side effect of UV-B radiation screening experiments, thus providing an opportunity to investigate the effect of elevated temperature (e.g. Huiskes et al. 2001). Despite the challenge of conducting this kind of work in the severe Antarctic environment, well-designed experiments of this type are possible and are badly needed.

1.3.5. Impact of increased freeze-thaw

Temperature fluctuations that cause plant tissues to cyclically freeze and thaw may be more damaging than exposure to cold temperatures alone (Kennedy 1993a) and there is some evidence that these events are increasing in frequency (Lovelock et al. 1995b). Continental Antarctic species can survive repeated freeze-thaw events (Melick and Seppelt 1992), while maritime species appear to be less tolerant (Davey 1997b). Tolerance of freeze-thaw events involves interactions with other environmental parameters, such as water availability. For example, desiccation prior to freezing reduces damage to the photosynthetic apparatus and protection from freeze-thaw can be provided by snow cover, which acts as an insulator (Lovelock et al. 1995b). If climate-warming results in reductions in snow cover, Antarctic plants may be more exposed to damage by freeze-thaw events in the future. Since freeze-thaw cycles reduce plant productivity and survival (Table 1.2), increases in the frequency and/or magnitude of the temperature differential of freeze-thaw cycles on the Antarctic continent are likely to have negative impacts on the flora.

1.4. Precipitation and water relations

The predominance of extreme cold across continental Antarctica locks most water away in the form of snow and ice, resulting in the Antarctic being the largest desert on Earth. Biologically available water is in the form of melt water, and it is confined to the summer months. Melt water can be derived from freshly deposited snow, or from melting of permanent snow and ice banks. A fine balance between the snow regime and melt patterns is crucial in maintaining water availability to these exceedingly dry habitats. A discussion of precipitation and water relations must therefore also consider snow relations. Incorporating the variables of temperature, precipitation and melt, I suggest a model that predicts the impact of climate change on water availability in Antarctic ecosystems (Fig. 1.2). Three possible paths are suggested; two scenarios lead to increasing aridity, whilst the third results in either unchanged or increased water availability. If an increase in the area of permanent snow cover were the result of the final scenario, a concomitant loss of habitat for plants would occur.

1.4.1. Evidence

Climate warming is predicted to increase global precipitation and evaporation levels by 3 to 15% (Tokioka 1995). Two types of precipitation occur: (1) from cumuli-form clouds, which will increase globally in response to climate change, and (2) from strati-form clouds, which will decrease with climate change. The effect of climate change on global precipitation patterns will therefore be a decrease in precipitation area, while precipitation amount will increase (Tokioka 1995).

Antarctic snow accumulation rates have been increasing since 1960 (Morgan et al. 1991) and under a global warming scenario continued increases in accumulation rates are predicted (Ye and Mather 1997). However, measurement of continental soil moisture levels shows that continental Antarctic moisture content is decreasing (Doran et al. 2002). In the Windmill Islands, East Antarctica, the presence of moribund moss is considered indicative of a drying trend, which corresponds with glaciological and geomorphological evidence of isostatic uplift since the last glacial maximum (Melick and Seppelt 1997).

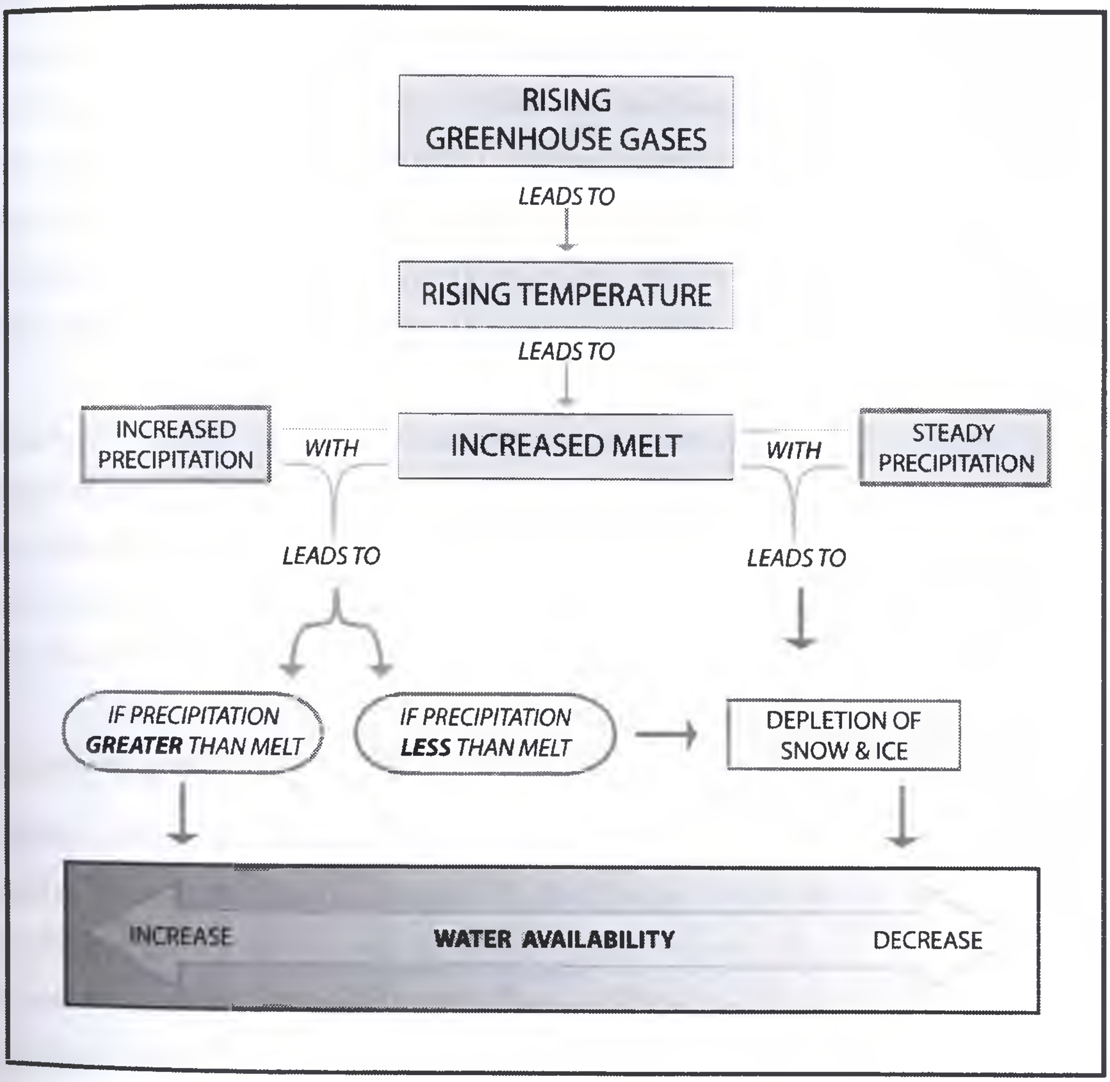


Figure 1.2: Schematic model of impact of climate change on water availability in Antarctic ecosystems.

1.4.2. Ecological impacts

Studies from across the Antarctic biome have established a correlation between water availability and species distributions (Table 1.3). The majority of these studies have investigated broad-scale patterns, covering large spatial scales and incorporating the majority of vegetation types or species (Rudolph 1963, Nakanishi 1977, Shimizu 1977, Seppelt and Ashton 1978, Smith 1986, Seppelt et al. 1988, Broady 1989, Smith 1990b, Melick et al. 1994a, Melick and Seppelt 1997, Bolter et al. 2000). Examination of broad-scale patterns may be appropriate in regions undergoing rapid change, such as the peri-Antarctic (Adamson et al. 1988, Smith and Steenkamp 1990, Frenot et al. 1997) and Antarctic Peninsula (Smith 1990a). On the continent where growth rates are slow, fine-scale studies, working with selected vegetation components such as lichens (Kappen 1985a, Inoue 1989), bryophytes (Selkirk and Seppelt 1987, Schwarz et al. 1992, Smith 1999) or single species (Kappen et al. 1998) will more likely detect change.

Relatively few studies of the relationship between water availability and vegetation distribution have included modern, quantitative statistical analyses (Table 1.3). Studies from the continent that have employed such methods have generally found positive associations between fine-scale distribution patterns and water availability (Leishman and Wild 2001) or factors affecting water availability (Ryan and Watkins 1989).

Increasing aridity

Antarctic terrestrial ecosystems will suffer increasing aridity if temperatures increase, causing elevated melts but precipitation is insufficient to counteract the increased melt, resulting in net depletion of permanent snow and ice reserves (Fig. 1.2). The ecological impact of increasing aridity on Antarctic terrestrial flora has received very little attention (Table 1.3). One exception is the work by Melick and Seppelt (1997), who suggested that the drying trend evident in the Windmill Islands, East Antarctica, is driving an expansion of lichen-dominated vegetation in the region, whilst bryophytes are contracting to lower-lying areas with more reliable moisture supply. The consequences of increasing aridity for fauna, which have some relevant implications for flora, have been investigated by Convey et al. (2002) and Convey et al. (2003).

Table 1.3: Summary of effects of precipitation and water relations on Antarctic vascular plants, bryophytes and terrestrial algae.

Scenario	**Impact**	**Nature of Impact**	**Major Results**	**Plant Group**	**Location**	**Field / Lab**	**References**
Increased Aridity	Changes to species distribution	Ecological	Presence of moribund moss is indicative of a drying trend: lichen-dominated veg is expanding in area, whilst bryophyte communities are contracting, to lower lying areas with reliable moisture supply.	BL	CA	FB	(Melick and Seppelt 1997)
	Lichens most likely to survive: adapted to dry conditions	Physiological	ΦPSII highest at intermediate WC.	L	CA	FB	(Hovenden *et al.* 1994)
			Capable of absorbing water from air. Modeled using field data.	L	CA	FB + LB	(Hovenden and Seppelt 1995b)
			Desiccated thalli able to reactivate P_n after uptake of water vapor from air.	L	CA	FC/L	(Lange and Kappen 1972)
			Metabolic activity in thalli rehydrated from snow at subzero temps (-4˚C).	L	CA	LB	(Schroeter *et al.* 1997)
	Requires extreme tolerance of desiccation	Physiological	3 bryophyte species (Windmill Islands, East Antarctica) show species-specific responses to desiccation. *Grimmia antarctici* (endemic to Antarctica) appears least tolerant of desiccation and is therefore likely to be adversely affected by an increase in frequency, duration and/or severity of desiccation events.	B	CA	FC/L	(Robinson *et al.* 2000)
			Maritime species from a variety of habitats (hydric, mesic, xeric) showed differences in gross PS: hydric species are drought sensitive.	B	MA	FC/L	(Davey 1997a)
			Recovery from desiccation faster in xeric than hydric species, but no correlation between habitat and final degree of recovery.	B	MA	FC/L	(Davey 1997c)
			Maritime moss species from a variety of habitats (hydric, mesic, xeric) showed increased penetration of light into the moss as drying occurs, reducing loss of productivity during periods of desiccation.	B	MA	FC/L	(Davey and Ellis-Evans 1996)

Table 1.3 (continued)

			Maritime liverwort (*Marchantia berteroana*) sensitive to desiccation, recovery of gross PS limited to approximately 10%.	B	MA	FC/L	(Davey 1997b)
			Continental Antarctic lichens were capable of tolerating, and recovering from, desiccation	L	CA	FC/L	(Lange and Kappen 1972)
	↑ Temperature fluctuations	Physiological	Exposed lichen thalli reached greater temps, with greater fluctuations, than moist moss bed. Measured temps only, no measurement of moisture.	B L	CA	FB	(Melick and Seppelt 1994b)
	Morphological impact	Physiological	*Bryum inconnexum*: Leaf size smaller and more diversified in dry habitats that in moist habitats. Leaf shape independent of water status.	B	CA	FC/L	(Nakanishi 1979)
			G. antarctici: comparison of wet and dry sites - differences in turf and gametophyte morphology. Dry site: shorter shoots, leaves smaller and more tightly packed, cell size and number greater.	B	CA	FC/L	(Wilson 1990)
			Growth form and water relations related to habitat occupied. *Andreaea* and *Grimmia* species (small cushions) have low evaporation rates and take up water readily from any part of shoot: occupy dry sites. *Drepanocladus uncinatus* ranges in growth form and has a wide ecological amplitude in relation to water supply.	B	MA	FC/L	(Gimingham and Smith 1971)
Increased water availability	Correlations with species distribution	Ecological	Distribution of moss species correlated with moisture availability. Quantification of % cover of species along hydrological gradient - no quantification of moisture content. Histograms of % cover along transects. Description of trends.	B	CA	FB	(Smith 1999)
			Distribution of moss species and *Nostoc* influenced by water level - e.g. *Pottia* shows significant correlation with the drier habitat of hummocks. Semi-quantitative, largely mapping of waterline on transects. Some statistical analysis performed.	B	CA	FB	(Schwarz *et al.* 1992)
			Moss community types correlated with nature of moisture supply.	B	CA	FB	(Shimizu 1977)

Table 1.3 (continued)

		Distribution of moss species correlated with moisture availability. Quantification of both species distribution and water availability.	B	CA	FB + FC/L	(Selkirk and Seppelt 1987)
		Windmill Islands: 4 major veg groups, correlated with water availability: pure bryophyte communities highest water availability, lichen communities lowest.	BL	CA	FB	(Melick and Seppelt 1997)
		Veg community types have different WCs. Quantitative measurements (moisture content in variety of community types), descriptive analysis.	BL	CA	FB	(Smith 1990b)
		Distribution of some moss sociations related to pattern of water supply (based on type of water supply: small, medium or large snow drift, lake-shore, seepage or stream). Quantification of veg patterns (development of sociations) + each veg quadrat assigned 1 of 6 water supply types. Veg + water data tabulated together - but analysis descriptive only.	BL	CA	FB	(Nakanishi 1977)
		Moss species diversity and abundance positively correlated with soil WC.	BL	CA	FB + FC/L	(Leishman and Wild 2001)
		Fine-scale (intra-transect) plant dispersion patterns determined primarily by physical factors affecting water availability (amount of drift snow available and the effects of shelter and shade on evaporation rates).	BLA	CA	FB	(Ryan and Watkins 1989)
		Soil WC highest in areas with moss veg. Quantitative measurements, no analysis of data.	BLA	CA	FB + FC/L	(Bolter *et al.* 2000)
		Buellia frigida (crustose lichen) distribution explained by frequency and duration of meltwater moistening, of rock surface. Qualitative observations and some quantification.	L	CA	FB	(Kappen et al. 1998)
Experimentally determined impact of water on species distributions	Ecological	With up to 75% crustose lichen encrustation, moribund moss regeneration potential greatest in permanently moist samples. Regeneration potential reduced in samples irrigated weekly and non-existent in samples irrigated fortnightly.	BL	CA	FC/L	(Melick and Seppelt 1997)

Table 1.3 (continued)

	Physiological	14 bryophyte species (from hydric, mesic or xeric sites): broad-scale community patterns explained by water availability, but other factors must be important in determining fine-scale patterns of species distribution (within habitats of similar water availability).	B	MA	FC/L	(Davey 1997a)
		Liverwort (*M. berteroana*), low tolerance of desiccation, therefore limited to relatively mild habitats. If conditions become wetter, might expand into new areas that are currently too severe.	B	MA	LB	(Davey 1997b)
		Water availability determines the stability of lichen symbiosis: in wet habitats the free-living algal and intermediate forms became dominant.	L A	MA	FC/L	(Huiskes et al. 1997a)
↑ P_n and growth	Physiological	Increased P_n and larger temp range for P_n in mesic versus xeric moss.	B	CA	FB + FC/L	(Kappen *et al.* 1989)
		Mesic (compared to xeric) species showed largest growth increments under a range of WCs. Generally, species-specific responses to water availability (measured growth increments, lateral shoot production, leaf density and size, optimal WC etc.).	B	MA	FC/L	(Fowbert 1996)
		13 moss species, 1 liverwort: Xeric species gross PS currently often water-limited.	B	MA	FC/L	(Davey 1997c)
		Liverwort (*M. berteroana*) desiccation had highly adverse effect on photosynthetic capacity, with only about 10% recovery after dehydration.	B	MA	LB	(Davey 1997b)
		Andreaea gainii and *Usnea antarctica*: xeric fellfield species, only water source precipitation, active only for about 40% and 31% of the time respectively.	BL	MA	FB	(Schlensog and Schroeter 2000)
↓ P_n and growth	Physiological	Field manipulations (3 lichen species): Depression of P_n at supra-optimal WC (optimum WC for P_n was 75-115% dwt). Current climate: conditions of supra-optimal WC relatively rare.	L	CA	FB	(Kappen and Breuer 1991)
No impact on P_n	Physiological	*G. antarctici*: No difference in photosynthetic physiology between wet and dry sites.	B	CA	FC/L	(Wilson 1990)

Table 1.3 (continued)

		14 moss species on Signy Is., no relationship between habitat (xeric versus hydric) and photosynthetic performance (rates of gross PS, P_n or DR).	B	MA	FC/L	(Convey 1994)
Characteristics of wet habitats (compared to dry habitats): *continental Antarctica*	Physiological	Higher concentrations of nitrogen and potassium.	VBLA	MA	FC/L	(Fabiszewski and Wojtun 2000)
		Higher turf CO_2	B	CA	FC/L	(Tarnawski *et al.* 1992)
		Higher WCs at full hydration and at 50% photosynthetic efficiency.	B	CA	FC/L	(Robinson *et al.* 2000);
		Higher production rates and a wider temp range for P_n.	B	CA	FB + FC/L	(Kappen *et al.* 1989)
		Higher chlorophyll concentrations.	BL	CA	FB + FC/L	(Kappen et al. 1989, Melick and Seppelt 1994a)
		Higher levels of soluble carbohydrates.	BL	CA	FC/L	(Melick and Seppelt 1994a, Robinson et al. 2000)
		Higher rates of nitrogen fixation.	BC	CA	FB + FC/L	(Davey 1982, Davey and Marchant 1983)
		Higher tissue freezing points.	L	CA	FC/L	(Melick and Seppelt 1994a)
Signy Is., *maritime Antarctica*	Physiological	At some sites at least water was not limiting P_n	B	MA	FB	(Collins 1977)
		P_n in xeric species, often water-limited.	B	MA	FC/L	(Davey 1997c)
		Rates of P_n for a range of xeric and hydric species showed no difference between habitats.	B	MA	FC/L	(Convey 1994)

Table 1.3 (continued)

	Species specific differences in physiological response	Physiological	Differences in species tolerance of desiccation:, *G. antarctici* was least tolerant, *Ceratodon purpureus* most tolerant and *B. pseudotriquetrum* intermediate.	B	CA	LB	(Robinson *et al.* 2000)
			Lichen (*Mastodia tesselata*) and its free-living phycobiont (*Prasiola crispa*): when occurring in symbiosis as a lichen, decline in P_n, measured when hydrated, no change in P_n in either the free-living algae, or an intermediate form of the lichen and alga.	L A	MA	FC/L	(Huiskes et al. 1997a)
			Rates of uptake and loss of water measured for 6 lichen species. Differences between species detected and thought to be due to differences in thalli morphology and anatomy.	L	MA	FB + LB	(Huiskes et al. 1997b)
Changes to snow regime	Permanent snow banks an important moisture source	Ecological	Steep decrease in moss moisture content as distance from snow patch increased.	B	CA	FB + FC/L	(Smith 1990b)
			Positive correlation between veg cover and extension and duration of shallow snow cover.	B, L	CA	FB	(Kappen *et al.* 1990)
		Physiological	Lichens photosynthetically active when moistened by snowfall or by run-off from snow melt.	L	CA	FB	(Hovenden *et al.* 1994)
	Snow cover positive impacts	Physiological	WC of lichens resulting from contact with snow was frequently near the optimum for P_n.	L	CA	FB	(Kappen and Breuer 1991)
			Lichens have total reliance on snow as a water supply.	L	CA	FB	(Hovenden *et al.* 1994)
			Quantum flux density under 15cm snow can reach light saturation for P_n of *U. sphacelata* at 0˚C.	L	CA	FB	(Kappen and Breuer 1991)
			Lichen productivity possible when snow covered: light compensation point low at low temps. Indirect quantification.	L	CA	FB + FC/L	(Lange and Kappen 1972)
			Up to 20% of the photosynthetically active radiation penetrates 20 cm of winter snow.	Sn	MA	FB	(Walton 1982)
	Snow cover negative impacts	Physiological	Snow cover deposited in winter limits lichen activity by preventing early warming.	L	CA	FB	(Pannewitz et al. 2003)

Abbreviations: DR dark respiration, **dwt** dry weight, **ΦPSII** quantum yield of PSII, **P_n** net photosynthesis, **PS** photosynthesis, **temp** temperature, **veg** vegetation, **WC** water content. ↑ increasing, ↓ decreasing. Plant group codes, location and study type as in Table 1.2

Increasing water availability

In Antarctic habitats, increases in water availability are likely to result if temperature increases are coupled with increased precipitation, equal to or exceeding the elevated melt, thus improving melt water availability and maintaining permanent snow and ice reserves (Fig. 1.2).

As is the case for increasing aridity, the ecological impacts of increasing water availability in Antarctica have received very little research attention. The regeneration potential of moribund moss (encrusted with up to 75% lichen cover) is greatest under permanently wet conditions, and regeneration potential is less under experimental irrigation regimes that provide reduced water availability (Melick and Seppelt 1997).

It appears that no experimental tests of the influence of water availability on relative species distributions in Antarctica had been published prior to this thesis. Studies that have surveyed vegetation patterns in relation to water content have tended to be short-term with most conducted during only one summer season (Table 1.3).

1.4.3. Physiological Impacts

Increasing aridity

Under a climate change scenario of increasing aridity, lichens may have a greater chance of survival than other groups of cryptogamic organisms, as they are particularly well adapted to dry conditions (Table 1.3). Uptake of water by lichen in Antarctica, is largely from snow deposited on their surfaces (Schroeter et al. 1994) which, even at subzero temperatures, is adequate for rehydration (Schroeter and Scheidegger 1995, Schroeter et al. 1997). The water relations of lichens under snow and ice have been reviewed by Kappen (1993, 2000).

Increasing aridity will subject vegetation to increasing frequency, severity, and duration of desiccation events. Levels of tolerance of desiccation vary across the Antarctic biome and between species and vegetation types (Table 1.3). Some regions and species will therefore be more severely affected than others under conditions of increasing aridity. The maritime region appears to support some desiccation-sensitive species, particularly in hydric habitats, and these might be expected to be particularly vulnerable (Davey 1997a, b, c). On the continent, lichens are likely to survive increasing aridity as they show extraordinarily high levels of tolerance of desiccation and are capable of reactivating photosynthetic activity via uptake of water vapour (Lange and Kappen 1972, Hovenden and Seppelt 1995b). Continental Antarctic bryophytes are not likely to be as tolerant of increasing aridity as lichens, but also have the ability to survive desiccation events. Morphological changes such as reduced bryophyte leaf size have been observed as a result of drying conditions (Table 1.3).

In addition to the direct effects of increasing aridity, reductions in water availability may cause alterations to other environmental parameters. For example, it has been observed that dry habitats are characterised by higher temperatures and larger temperature fluctuations than moist habitats (Melick and Seppelt 1994b).

Increasing water availability

Water is generally limiting in Antarctic terrestrial ecosystems and increases in water availability are likely to induce significant biological effects. In general the evidence suggests that net photosynthesis and growth are currently limited by water availability (Table 1.3). However certain plant groups offer exceptions to this. As previously noted, lichens can achieve physiologically optimal water contents through contact with snow, but at water contents greater than optimal, a depression of net photosynthesis occurs (Kappen and Breuer 1991, Hovenden et al. 1994). Although it is clear that water uptake directly from melting snow is a very important source of water for lichens (Schroeter et al. 1994, Schroeter et al. 1997), an increase in precipitation levels that cause more frequent periods of supra-optimal water contents may have a negative impact (Huiskes et al. 2000).

In addition to altering rates of net photosynthesis, a range of morphological, physiological and biochemical changes are likely to occur if water availability increases, as is evident in the differences that have been measured between plants from wet and dry habitats in continental Antarctica (Table 1.3). Vegetation from wet sites, for example, has been found to have higher; water contents at full hydration (Robinson et al. 2000), chlorophyll concentrations (Kappen et al. 1989, Melick and Seppelt 1994a), concentrations of soluble carbohydrates (Melick and Seppelt 1994a, Robinson et al. 2000), nitrogen and potassium (Fabiszewski and Wojtun 2000), turf CO_2 concentrations (Tarnawski et al. 1992) rates of nitrogen fixation (Davey 1982, Davey and Marchant 1983), production rates, and a wider temperature range for maximal net photosynthesis (Kappen et al. 1989). On the negative side, photosynthetic efficiency declines at higher tissue water contents (Robinson et al. 2000) and tissues freeze at higher temperatures (Melick and Seppelt 1994a) in samples collected from wet sites compared to those from dry sites.

Water may be less universally limiting in the relatively moist maritime Antarctic (Table 1.3). Whilst some xeric species from Signy Island were occasionally water-limited (Davey 1997c), there are several sites on Signy Island where photosynthesis was not water-limited (Collins 1977). When the photosynthetic rates of a range of xeric and hydric species from this island were compared, under laboratory conditions, no difference between habitats was detected (Convey 1994).

As is the case with the impact of changes to other environmental parameters, the impact of increasing water availability is likely to be species-specific and show variation across the Antarctic biome (Table 1.3). Whilst many studies have compared sites with naturally occurring variations in water content, publications produced from field manipulations of water availability are lacking. The absence of such studies is probably due to the difficulty of conducting field manipulations of this nature in the severe Antarctic environment.

One final point to consider with respect to the impact of increasing water availability in Antarctic terrestrial ecosystems, is the interaction between water content and freezing. Evidence suggests that desiccation, prior to freezing, may improve plant survival at low temperatures (Kennedy 1993a, Lovelock et al. 1995b). Increased damage during freezing events may therefore occur if Antarctic habitats receive an increase in water availability.

1.4.4. Changes to snow regime

A fine balance with respect to the snow regime may be particularly important to lichen survival in Antarctica. Although moisture from summer snowmelt is utilised by lichens (Kappen 2000), a persistent summer snow cover can cause lichen mortality (Benedict 1990, Smith 1990a, Melick and Seppelt 1997). Snow cover throughout winter, maintaining dark conditions with temperature close to zero, caused negative carbon balance in lichens (Kappen 2000). And snow cover deposited in winter limits lichen activity, by preventing early warming (Pannewitz et al. 2003). This may mean that lichens would be particularly disadvantaged by an increase in snow cover as a result of climate change (Kappen 2000, Pannewitz et al. 2003).

1.5. Interactions between water, temperature and nutrients

Changes to environmental parameters, such as temperature, CO_2 and water availability, are likely to have a synergistic effect on productivity and nutrient cycling, resulting in alterations to the current balance of the nutrient cycle. Perhaps due to the difficulties associated with detecting environmental change of this nature, there are no published studies relating nutrient availability to climate change in Antarctica.

Nutrient cycling in the Antarctic is relatively slow, due to the restraints imposed on biological activity by low temperatures and extreme aridity. Antarctic terrestrial habitats often have low nutrient availability, but the communities that they support are generally not thought to be nutrient-limited (Table 1.4). Nutrient requirements for Antarctic vegetation are exceptionally low, such that nitrogen levels in precipitation (Greenfield 1992a) are sufficient for growth of cryptogams, particularly lichens. However nutrient availability does play a role in determining patterns of species distributions in Antarctica (Table 1.4). Nutrient availability in Antarctic terrestrial

Table 1.4: Summary of effects of nutrients on Antarctic vascular plants, bryophytes and terrestrial algae.

Scenario	Impact	Nature of impact	Major Results	Plant Group	Location	Field / Lab	References
Increased nutrient availability	Relative species distribution	Ecological	Field survey of broad-scale veg patterns. Environmental influences observed and described. Crustose lichens: abundant at sites with nutrient input from skuas. Snow algae occurred in areas fertilized by birds. *Prasiola crispa* (algae) is nitrophilous and common in the vicinity of bird colonies.	BLA	CA	FB	(Broady 1989)
			Coarse-scale (inter-transect) analysis of plant dispersal patterns showed significant responses along bird-influence gradients. Quantitative statistical analysis of veg and environmental data.	BLA	CA	FB	(Ryan and Watkins 1989)
			Field observations suggested that nitrogenous debris was a major factor in influencing the distribution of the veg components. Data presented as a veg map of the study area, no quantitative statistical analysis.	BLA	CA	FB	(Rudolph 1963)
			Determined distribution of veg (using 1km grid squares). Description of field observations: nutrients (probably N & P) from bird nest sites have positive influence on distribution, biomass and species diversity of terrestrial lithic algae, mosses and lichens.	BLA	CA	FB	(Seppelt *et al.* 1988)
			Distribution of macroscopic terrestrial cryptogams determined by type of N compounds and the concentration of water-soluble salts.	BLA	CA	FB + LB	(Schofield and Ahmadjian 1972)
			Positive relationship between lichens (diversity and abundance) and soil nutrients, P more influential than N. Soil nutrients not significantly associated with moss diversity or abundance. Quantitative statistical analysis of veg and environmental data.	BL	CA	FC/L + FB	(Leishman and Wild 2001)
			Field survey of veg patterns (aerial photography + ground truthing). Quantitative analysis of soil characteristics (conductivity, pH, total N and total P). Mosses and lichens absent, and terrestrial algae *P. crispa* dominant, in eutrophic sites near bird colonies.	BL	CA	FB + FC/L	(Melick *et al.* 1994a)

Table 1.4 (continued)

			Measured nutrient contents for a range of veg samples: description of relationship between moss communities and total N and C. *P. crispa* distribution influenced by P availability. Text in Japanese, figures suggest no quantitative statistical analysis.	BA	CA	FC/L + FB	(Yamanaka and Sato 1977)
			Species composition and distribution of lichen communities influenced by organic nutrients supplied by sea bird excrement. Some quantification of veg patterns (determined sociations). Nutrient relations descriptive (related to observed vicinity of bird nests).	L	CA	FB	(Nakanishi 1977)
			Suggests nutrient enrichment from birds explains relatively rich coastal communities.	L	CA	FB	(Kappen 1985b)
			Well-developed lichens around rookeries or nests of sea birds (except where wind-blown sea-spray is significant). Based on veg mapping and observations of environment.	L	CA	FB	(Inoue 1989)
			Quantitative measurement of substratum chemistry and veg cover along a transect. Lack of effect of nutrients on distribution of major lichen species, but several minor species restricted to nutrient-rich zones (nutrient source: ancient penguin rookery). Relationship between chemical and veg data descriptive.	L	CA	FC/L + FB	(Hovenden and Seppelt 1995a)
			Species distributions within veg complexes related to factors indicating nutrient status (Cl^- and NH_4^+ concentration, distance from sea) as well as a range of microclimate variables. Although canonical correspondent analyses found a large amount of the variation could not be explained by these factors. Concentration of Cl^-, NH_4^+ and PO_4^{2-} correlated with distribution of lichen complexes: *Usnea* complex – low whilst *Mastodia-Rinodina* complex – high salt concentration.	L	MA	FB	(Gremmen *et al.* 1994)
No change to nutrient availability	Nutrients currently non-limiting	Physiological	Soil nutrients not limiting to growth of alien vascular species.	V	CA	LB	(Rudolph 1966)

Table 1.4 (continued)

			High mobility of plant nutrients in Signy Island ecosystem. K and Ca provided by rock weathering, Na and Mg from the ocean, phosphorous and nitrogen from fauna. Direct droppings and drainage particularly important for distribution of N.	VB	MA	FC/L	(Allen *et al.* 1967)
			Soils under moss favourable for soil respiration. Moss appears to act as a sink for nutrients originating from bird nests.	BS	CA	FC/L	(Cocks et al. 1998b)
			Fellfield plants and soils obtain substantial quantities of N from atmospheric precipitation. In the absence of other limitations, precipitation N would allow an annual biomass increase for *U. antarctica* of 14% at Deception Is. and 7% at Ross Is.	BLS	CA MA	FC/L	(Greenfield 1992a)
			Precipitation N major N input to fellfield biota (Cape Bird and Signy Island).		CA MA	FC/L	(Greenfield 1992b)
			U. sphacelata highly efficient at scavenging inorganic N from snow meltwater, capturing 92 and 87% of NO_3^- and NH_4^+, respectively.	L	CA	FC/L	(Crittenden 1998)
			Nutrients not limiting to veg: K, Mg and P values often extraordinarily high.	S	CA	FC/L	(Beyer *et al.* 2000)
Changed nutrient availability	Species-specific differences in nutrient relations	Physiological	Measured differences in annual nitrogen content trends for two lichen species: *U. sphacelata* and *Umbilicaria decussata*.	L	CA	FC/L	(Hovenden 2000)

Abbreviations: veg Vegetation, plant group codes, location and study type as in Table 1.2.

ecosystems is patchy with high concentration of nutrients in the vicinity of bird and seal colonies, whilst elsewhere nutrients are limited to that deposited in precipitation (Greenfield 1992a, 1992b). Two studies in particular have demonstrated positive correlations between vegetation patterns and nutrient availability associated with nutrient inputs from birds (Gremmen et al. 1994, Leishman and Wild 2001). Current nutrient availability can also be determined by site history. Abandoned penguin rookeries, for example, can produce relatively nutrient rich habitats, thus affecting local species composition (Hovenden and Seppelt 1995a). Knowledge of terrestrial site history can therefore be important in understanding current vegetation patterns.

In continental Antarctica, release of nutrients from organic matter is primarily microbial and is relatively slow (Smith and Steenkamp 1992). In the Periantarctic, rates of inorganic nutrient release from plant litter are enhanced by a suite of macroinvertebrates (Smith and Steenkamp 1992) which are absent on the continent.

Nitrogen fixation by the cyanobacteria, *Nostoc commune*, occurs during the Antarctic summer. Fixation rates are dependent on water availability and temperature conditions; fixation ceases below –7 °C (Davey and Marchant 1983), with rates highest in areas of high water content (Davey 1982). *Nostoc commune* and moist associations of moss-*Nostoc* are estimated to contribute 52 and 119 mg N m^{-2} yr^{-1} to the terrestrial ecosystem, respectively (Davey and Marchant 1983). These results suggest that warmer, wetter conditions are more favourable for nitrogen fixation.

If photosynthesis and growth rates of Antarctic plants increase, in response to greater water availability and/or temperature increases, the demand for nutrients will increase, leading to the development of a nutrient-limited system. Nutrient inputs through precipitation and biological fixation of nitrogen are known to be too small to meet the current demands of plants in Periantarctic ecosystems (Smith and Steenkamp 1992). The capacity to increase nutrient availability under future climatic conditions might also be limited by low continental soil fauna diversity.

1.6. Conclusions

Climate change has already impacted on Antarctic plants. Temperature increases in the maritime Antarctic have led to changes in the distribution of native plants and increased the opportunities for alien species to invade, with invasions already documented in the peri-Antarctic (Frenot et al. 2005).

In this review I have suggested scenarios for the Antarctic flora under global climate change. Comprehensive predictions are complicated by both the lack of certainty in the prediction of changes to abiotic variables, and by the lack of long-term studies investigating recent changes to the flora. Given the slow rate of change in these ecologically extreme communities, a commitment to long-term studies is essential to investigate both the response of key species and of key assemblages.

1.7. Objectives

The overall aim of this thesis was to investigate the likely impacts of climate change in a floristically important region of continental Antarctica. Previous studies suggest that temperature and water are likely to be key drivers of change to continental Antarctic communities. In this thesis I focus on bryoflora and concentrate on the impacts of climate change induced alterations to water and nutrient availability. As shown above (Section 1.4) changes to water availability represent one of the dominant effects of increasing temperature but have received less attention, with no manipulative field studies performed. Since the direction of change is unclear, I have considered both increasing and decreasing water availability since it is possible that either or both of these scenarios are possible in the future (Section 1.4.2). As a secondary aim, nutrients were considered since their concentration is likely to change with changing water availability and their importance in these communities was not clear from the literature.

The work is composed of three sections, which address questions from the ecological to the physiological level and considers species response to both a wetter and a drier environment. Firstly, I aimed to determine the natural variation of fine-scale patterns in bryophyte community structure, over water and nutrient availability gradients (Chapter

3) since this information is important both for building current relationships between environmental factors and species distribution (Section 1.3.3) and as a baseline for future community changes. Secondly, I manipulated these communities in the field, by increasing water and/or nutrient availability over two summer seasons, in order to assess the likely response to climate change, under a wetter climate (Chapter 4). Finally, a series of species-level laboratory-based experiments were conducted in order to investigate physiological characteristics determining tolerance of desiccation, and providing insight into the likely response of bryophyte species to a drier climate (Chapter 5). The combination of these three research areas integrates multiple biological levels, from community ecology to species physiology, to provide insight into climate change response in the Antarctic terrestrial communities investigated.

Chapter 2: General Methodologies

2.1. Study area and species

The studies described in this thesis were conducted in the Windmill Islands region of East Antarctica (Chapter 1; Fig. 1.1), centred at 66°15'S, 110°33'E. The Windmill Islands region is a 40 by 15 km area, consisting of a series of ice-free islands and peninsulas, topographically characterised by low rounded hills of altitudes generally less than 100 m. The climate is dry, with the rainfall equivalent of the mean annual snowfall less than 200 mm yr^{-1}. Temperatures are cold, with approximate mean monthly temperatures ranging from 0 °C in the warmest summer months to –15 °C in the winter. Extremes of temperature range from approximately – 40 to +10 °C. Gale force winds are common, annually averaging one day in four (Melick and Seppelt 1994b). The geology of the north of the region is dominated by metamorphics (schists, gneisses and migmatities), while the south is predominantly comprised of charnockite and porphyritic granite (Blight and Oliver 1977).

In the past, the region has been completely ice-covered (Hollin and Cameron 1961) and ice sheet thickness during the Pleistocene is estimated to have been 200 m (Goodwin 1993). The region became deglaciated during the Holocene, with the south exposed first, 8000 years ago, and the north a few thousand years later, by 5500 years ago (Goodwin 1993). Since deglaciation, the land has isostatically uplifted 53 m (Goodwin 1993). As a result of this uplift, penguin rookeries, which were once close to the sea, have been abandoned as newly exposed sites closer to the water are occupied. Abandoned penguin colonies are now common around the 30 m contour, and are frequently colonised by lichens.

The Windmill Islands is a botanically important region, supporting some of the most extensive and best-developed vegetation on continental Antarctica (Smith 1988a). The entirely cryptogamic vegetation was first described by Smith (1988a), who determined that the region supports at least 27 species of macrolichens and four bryophytes. Three bipolar lichens dominate the vegetation *Usnea sphacelata* (Hoffm.) Th. Fr., *Umbilicaria* *decussata* (Vill.) Zahlbr. and *Pseudephebe minuscula* (Nyl. Ex Arnold) Brodo & Hawksw., which is typical for continental Antarctica (Smith 1988a).

The bryoflora is restricted to low-lying, moist sites, and is composed of three moss species (*Grimmia antarctici* Card., *Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb. and *Ceratodon purpureus* (Hedw.) Brid.) and one liverwort (*Cephaloziella exiliflora* (Tayl.) Steph.). Of these species, the Antarctic endemic, *G. antarctici*, is most abundant, while the other two moss species are of widespread cosmopolitan distributions but locally less abundant. The distribution of these species is thought to be determined by water availability, as *G. antarctici* is restricted to the wettest sites, *C. purpureus* occupies the driest of sites and *B. pseudotriquetrum* co-occurs with both *G. antarctici* and *C. purpureus* (Selkirk and Seppelt 1987). The liverwort, *C. exiliflora* has a southern Australasian and scattered Antarctic distribution (Seppelt 1983) and locally is most commonly found co-occurring with *C. purpureus*.

A characteristic of the Windmill Islands vegetation is a predominance of lichen encrusted moribund moss (Fig. 2.1). Whilst this flora has yet to be accurately dated, its presence concurs with glaciological and geomorphological evidence suggesting regional isostatic uplift since deglaciation has been accompanied by long-term climatic drying, causing lichens to expand and bryophytes to become restricted to only the wettest, low-lying habitats (Melick and Seppelt 1997).

My study has focused on the bryoflora of this region, and has extended into lichen-dominated communities where moribund moss is present. My particular focus has been on the three moss species, *G. antarctici*, *B. pseudotriquetrum* and *C. purpureus*, for which taxonomic descriptions are provided by Seppelt (1986). Note, there is ongoing debate over the taxonomy of *G. antarctici*, some consider it *Schistidium antarctici* (Cardot.) L. Savicz & Smirnova, but since the most recent Windmill Islands literature has referred to it as *G. antarctici* I also will follow this convention.

Three study sites were used, each located in the north of the Windmill Islands region (Figs. 2.2 to 2.4), and containing well-developed bryophyte communities, with all three moss species present. The three study sites are referred to as: ASPA Meltlake, ASPA Meltpuddle and Robinson Ridge. The former two were located in Antarctic Specially Protected Area (ASPA) 135, formerly Site of Special Scientific Interest (SSSI) 16, on Bailey Peninsula, approximately 1 km east of Casey Station. The ASPA Meltpuddle site (Fig. 2.5A) was located in a low-lying soak area close to the northern boundary of ASPA 135, at the top of a snow slope above Thala valley (at 66°16.92'S, 110°32.36'E). The ASPA Meltlake site (Fig. 2.5B) was approximately 150 m southeast of the ASPA Meltpuddle, on the western edge of a meltlake (at 66° 16.03' S, 110° 32.53' E). The Robinson Ridge site (Fig. 2.5C) was located in the vicinity of a melt stream, on Robinson Ridge, approximately 10 km south of Casey Station (at 66°22.1'S 110°35.2'E). The Robinson Ridge and ASPA Meltpuddle sites had overall northerly aspects, while the ASPA Meltlake sites aspect was north-easterly. All three sites were in the vicinity of ancient penguin rookeries that are estimated to have been abandoned within the last 5,000 years (Goodwin 1993).

Figure 2.1: Photograph showing moribund bryophytes (undulating substrate) encrusted with various lichen species, dominated by: *Xanthoria mawsonii* (orange), *Candelariella flava* and/or *Caloplaca citrina* (yellow), *Pseudephebe minuscula* (black).

Figure 2.2: Map of the northern Windmill Islands showing Bailey Peninsula and Robinson Ridge. See Figs. 2.3 and 2.4 for study site positions within these locations. Map Source: Windmill Islands 1:50 000, Australian Antarctic Division, © Commonwealth of Australia.

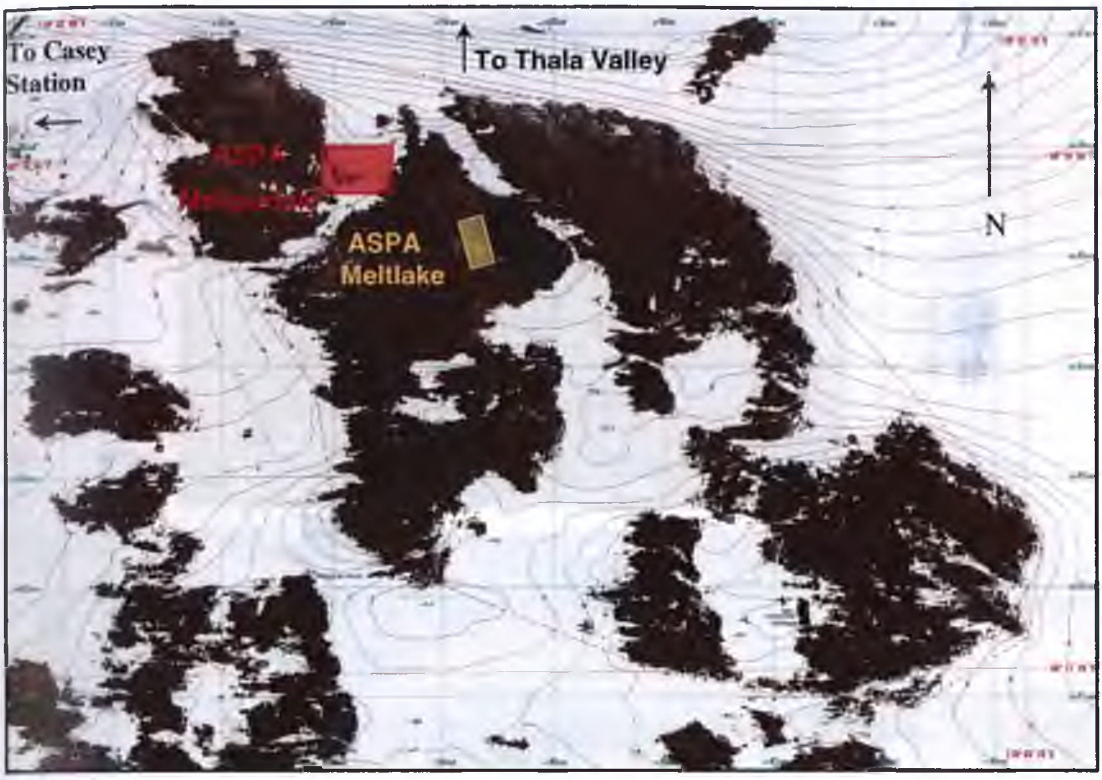


Figure 2.3: Map of Antarctic Specially Protected Area (ASPA) 135 (formerly site of special scientific interest 16), showing ASPA Meltpuddle and ASPA Meltlake study sites. ASPA 135 boundary indicated by dashed red line. Map Source: ASPA 135, 1:25 000 Ortho photo, Australian Antarctic Division, © Commonwealth of Australia.

Figure 2.4: Topographic map of Robinson Ridge, showing location of Robinson Ridge study site (shaded square). Map Source: Windmill Islands 1:50 000, Australian Antarctic Division, © Commonwealth of Australia.

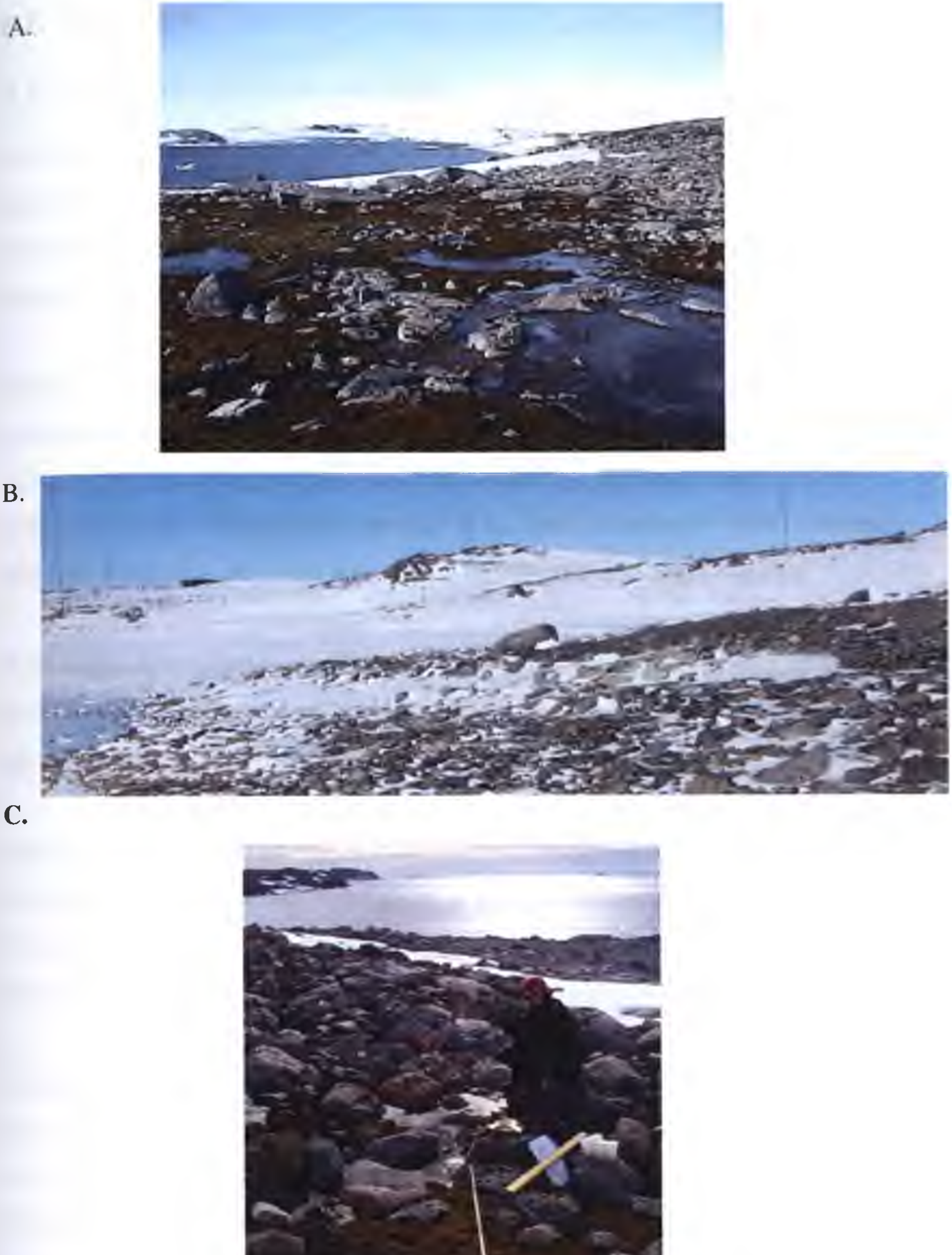


Figure 2.5: Photographs showing the three study sites: (A) ASPA Meltpuddle, (B) ASPA Meltlake and (C) Robinson Ridge.

2.2. Methods

2.2.1. *Background and rationale*

In Antarctic terrestrial communities plant growth rates are very slow, rendering detection of growth problematic. Instead of using direct measures of growth, such as biomass, I have therefore used a variety of physiological measurements that form surrogates for primary productivity and the growth environment, as described below.

Photosynthetic efficiency and electron transport rate can be measured using chlorophyll *a* fluorescence. This technique is particularly useful for measuring photosynthesis in Antarctic cryptogams, given their small size makes gas exchange measurements difficult (Lovelock et al. 1995a, Lovelock et al. 1995b, Green et al. 1998). Its non-destructive nature is also ideal where plant conservation is a major concern.

Plant tissue chlorophyll concentrations can be indicative of primary production, as chlorophyll is the major light-absorbing pigment in green plants. Reduced chlorophyll concentrations can be expected in plants subject to stresses such as nutrient-limitation.

Plant nutrient contents (such as N, P and C) can provide information to assess the nature of plant nutrient-limitations. Since plants can receive nutrients from several sources, including soil and atmospheric deposition, soil N & C characteristics were also investigated.

In addition, stable isotope methodologies can offer insight into nutrient sources (Cocks et al. 1998b, Robinson 2001) and water availability in the growth environment (Rice and Giles 1996), and therefore increase our understanding of water and nutrient relations in these ecosystems.

Specifically, fractionation of carbon isotopes provides information on access of CO_2 to the photosynthetic enzyme Rubisco. More positive $\delta^{13}C$ values are indicative of less photosynthetic isotopic fractionation, reflecting either that plants have some sort of carbon concentrating mechanism (CCM; as found in algae, C4 or Crassulacean acid metabolism (CAM) plants), or more likely that there are diffusional limitations to CO_2 reaching the site of Rubisco. In higher plants this diffusional fractionation relates to stomatal opening. However in cryptogams it likely reflects the degree to which plants are submerged in water and the consequent diffusional limitations (Proctor et al. 1992, Bottger et al. 1993, Rice and Giles 1996). Cryptogams subject to submergence are expected to show elevated (less negative) $\delta^{13}C$ signatures. Isotopic fractionation was therefore measured as an indication of degree of habitat submergence.

Fractionation of nitrogen isotopes provides information about plant nitrogen source and nutrient-use efficiency. Antarctic plants commonly have high $\delta^{15}N$, due to utilisation of nutrients derived from marine animal sources such as penguins (Cocks et al. 1998a, Cocks et al. 1998b, Robinson 2001). In many Antarctic sites plants have colonised abandoned penguin rookeries, such as described by Hovenden and Seppelt (1995a) and above (section 2.1). Nutrients deposited when these rookeries were occupied, approximately 5000 years ago (Goodwin 1993), undergo further ^{15}N fractionation as the guano passes through additional tropic levels associated with decomposition. Plants utilising this ancient nitrogen source are expected to have exceptionally high $\delta^{15}N$ values (higher than +14.6‰, the value for fresh penguin guano, Robinson 2001). Lower $\delta^{15}N$ values indicate plants are receiving a higher proportion of volatilised wind-born NH_3 (Robinson 2001) and/or plants are fixing atmospheric N.

Various soluble carbohydrates can provide protection during desiccation and freezing (Roser et al. 1992, Montiel 2000, Robinson et al. 2000). Natural variation in, and changes to, soluble carbohydrate profiles under manipulated conditions were therefore determined.

In addition to providing energy rich storage, fatty acids are important for cell membrane structure and function, and changes to fatty acid composition is known to be important in development of chilling and freezing tolerance (Taiz and Ziger 2002). I therefore determined fatty acid composition for the three moss study species.

2.2.2. *Determination of chlorophyll a fluorescence*

Measurements were performed using a MINI-PAM fluorometer equipped with a micro leaf clip (Walz, Germany). Maximum photosynthetic efficiency, determined as the ratio of variable to maximal fluorescence (F_v/F_m), was used in the laboratory-based experiments described in Chapter 5. Photosynthetic electron transport rates (ETR) were measured in the field using the MINI-PAM programmed feature, as described in Chapter 4, using the equation;

$$\mathrm{ETR} = \Phi\mathrm{PSII} * \mathrm{PAR} * 0.5 * 0.84$$

As described by Walz (2002).

2.2.3. *Determination of turf water content (TWC)*

The availability of water in the growth environment was determined for samples of bryophyte turf that were collected from the field in airtight vials. Using an analytical balance, fresh weight was determined immediately upon return to the laboratory. Dry weights were determined after oven drying at approximately 70 °C, till constant weight. The TWC of each moss sample at each time period (x) was determined as:

$$(\text{Fresh weight}_x - \text{Final dry weight}) \,/\, \text{Final dry weight}$$

after (Slatyer 1967). In higher plants where tissue is bound by an epidermis, water content (WC) of tissues can be expressed relative to the WC at full turgor. Determination of the WC at full turgor is difficult in intact mosses (Fowbert 1996) because mosses store much of their water externally, in capillary spaces, or in the cell wall apoplastic spaces (for a detailed discussion see Tuba et al. 1996). In the context of this study, the external water stored between gametophytes is biologically important to the physiological functioning of the turf as a whole. Moreover, expression of WC on a dry weight basis has been found to be repeatable in the past (Fowbert 1996, Tuba et al. 1996) it is thus used here. However, we have chosen to rename it as TWC to recognise both the inclusion of external water in these measurements and that this is a measure of the water holding capacity of the turf as a whole, rather than individual gametophytes.

2.2.4. *Determination of chlorophyll pigments*

Chlorophyll is sensitive to fluctuations in temperature and light. Samples were therefore stored on ice, in a cooler, from the time of collection in the field until they were transported to the laboratory for storage and analysis. Samples were transferred to liquid nitrogen within approximately one hour of collection and remained in liquid nitrogen while they were stored at the Casey laboratory, and during transportation back to Australia. They were transported on dry ice from the Australian Antarctic Division, Hobart (TAS) to the University of Wollongong (NSW), after which they were stored at -80 °C until analysis.

Extraction and analysis of chlorophyll pigments were undertaken at the University of Wollongong during November 2000 - January 2001. Methods follow those of Porra et al. (1989). Samples of known fresh weight (approx 0.02-0.20 g) were ground in approximately 0.75 ml of 80% acetone (in a mortar and pestle, with a small amount of sand and liquid nitrogen). Samples were then transferred to eppendorf tubes containing a small amount of $NaHCO_3$ as a buffer, reground in the eppendorf tube with a tissue homogeniser (Crown Scientific, Australia), and made up to 1.5 ml with 80% acetone. Samples were left on ice in the dark for at least 20 min before being centrifuged (13, 000 *g.* for 5 min). The supernatant was then transferred to a glass cuvette and absorbance was measured spectrophotometrically (UV-1601, UV-Visible Spectrophotometer, Shimadzu, U.S.A.) at wavelengths 750.0 nm, 663.6 nm and 646.6 nm. Chlorophyll$_{(a+b)}$ concentration was calculated from these extinction coefficients based on the equations of Porra et al. (1989).

2.2.5. *Determination of plant nitrogen and carbon*

Plant material was oven dried, as described for TWC (section 2.2.3) and ground to a fine powder (0.2 mm particles) in a ball mill (Retsch MM2). Dried, ground material was analysed using mass spectrometry methods, after Hietz et al. (1999). Aliquots of 1 to 2 mg of each sample were weighed into tin capsules and analysed by isotope ratio mass spectrometry (IRMS). The continuous-flow IRMS system consisted of an elemental analyser (EA 1110, CE Instruments, Milan, Italy), which was interfaced to an

IRMS (DeltaPLUS, Finnigan MAT, Bremen, Germany) by ConFlo II (Finnigan MAT). Reference gases (high purity CO_2 and N_2 gas, AGA, Vienna, Austria) were calibrated to the Vienna-Pee Dee Belemnite (V-PDB) standard using IAEA-CH-6 and IAEA-CH-7 and to the atmospheric N_2 standard (at-air) using IAEA-NO-3, IAEA-N-1 and –2 reference material (International Atomic Energy Agency, Vienna, Austria). Nitrogen and C isotope abundances of each sample were determined in a single run. The natural abundance of ^{15}N and ^{13}C was calculated as follows:

$$\delta^{15}N\ (‰\ \text{vs. at-air}) = (\text{Rsample/Rstandard} - 1) \times 1000$$

$$\delta^{13}C\ (‰\ \text{vs. V-VPBD}) = (\text{Rsample/Rstandard} - 1) \times 1000$$

where R is the ratio of ^{15}N / ^{14}N for nitrogen and ^{13}C / ^{12}C for carbon isotope abundance, respectively. The standard deviation of repeated measurements of a laboratory standard was 0.15‰ for $\delta^{15}N$, and 0.10‰ for $\delta^{13}C$.

Ash weight corrections

In the Crustose and *Usnea* communities (Chapters 3 and 4, respectively), it was difficult to collect pure vegetation samples that were free of soil contamination, as bryophytes occurred in this community only as a thin moribund crust, rather than a well-developed turf. Nutrient contents, calculated on a dry weight basis, therefore required correction for proportion non-organic content. This correction was conduced via determination of ash weights of samples, determined as follows. Samples (2 – 5.5 g) of the air-dried, ground material were weighed into pre-muffled (550 ˚C, 20 min) crucibles and muffled at 550 ˚C for 4 hours. Crucibles were cooled in a desiccator before weights were determined. Water content of the air-dry material was determined by weighing sub-samples (0.3-1 g) of the material onto oven dried (105 ˚C) filter papers. Samples were oven dried overnight (105 ˚C) and cooled in a desiccator before determining oven dry weights. Weight % N and C were corrected using the following formula:

$$\text{Weight \% N or C} / ((\text{air dry wt.} - \text{ash dry wt.}) / \text{air dry wt.})$$

2.2.6. *Determination of plant phosphorous*

Plant material was oven dried, as described for TWC (section 2.2.3) and ground as described for N and C (section 2.2.5). The ground material was analysed for total phosphorous during February and March 2001, at the University of Wollongong (Australia), using an acid digestion and colorimetric technique. Total phosphorous was determined in duplicate for each sample by HNO_3-H_2SO_4 digestion, followed by stannous chloride colorimetry. For each sample, ground plant material (minimum 0.25 g) was digested in 5 ml of 1:5 H_2SO_4:HNO_3 and 50 ml of milliQ water. Samples were digested on a hot plate for approximately 1 h, until the volume had reduced to less than 20 ml. Samples were allowed to cool and were filtered with MSF Borosilicate microfilter filter papers (grade GC50). To each sample, 2-3 drops of phenylphthalein indicator were added and as much 6N NaOH as was required to produce a pink colour change. Samples were made up to 100 ml volume and stored in acid washed plastic bottles at 4 ˚C until colorimetric procedures were carried out (within 3 days).

The stannous chloride colorimetric procedure was as follows. To each sample the following two reagents were added: 4.0 ml of ammonium molybdate reagent (25 g of $(NH_4)_6Mo_7O_{24}$ in 175 ml distilled water, 280 ml concentrated H_2SO_4 in 400 ml distilled water, combined and made up to 1000 ml) and 10 drops of $SnCl_2$ reagent (2.5 g $SnCl_2$ in 100 ml glycerol). Between 10-12 min after adding the $SnCl_2$ reagent, samples were measured spectrophotometrically at 690 nm (Spectronic 21D, Spectronic Instruments). A calibration curve was determined, using standards of 0.1–2.0 mg/L and a sample blank. The average of the two duplicates was used for each sample. Ash weights were corrected as described for N and C (section 2.2.5).

2.2.7. *Determination of plant soluble carbohydrates*

Plant material was oven dried, as described for TWC (section 2.2.3) and ground as described for N and C (section 2.2.5). Ground plant material was analysed for soluble carbohydrate contents using gas chromatography (GC), at the University of Vienna (Austria) in late 2000. Hot water extracts (40 mg sample in 1 mL dd H_20) were prepared and de-ionised on ion exchange resins. Low molecular weight carbohydrates and sugar alcohols in the neutral fraction were derivatised and analysed as their trimethylsilyl ethers using gas chromatography (Hewlett Packard HP 6890 Gas Chromatograph) as described in Richter et al. (1990). Calibrations were performed with a wide range of available standards. For unidentified peaks the calibration curve of the standard with the closest retention time was used. Retention times for unidentified peaks (X2, X3 and X4) were 27.98, 14.14 and 15.12 min, respectively. X2 eluted close to raffinose and is likely a relatively large compound, whilst X3 and X4 are closer in size to the hexoses (glucose and fructose).

2.2.8. *Determination of plant fatty acids*

Extraction and methylation of the samples followed Liu et al. (2000). Identification and quantification of fatty acids was conducted using gas chromatography-mass spectrometry (GC-MS), also as described in Liu et al. (2000).

2.2.9. *Determination of soil nitrogen and carbon*

Soil N and C analyses were conducted for two sites: ASPA Meltpuddle and Robinson Ridge. At each site six soil samples were collected. In order to minimise the impact to the plant communities, samples were collected from patches of bare soil within the vegetation communities. Samples were sieved (2 mm) *in situ* and stored at –20 °C until biochemical analyses were conducted.

The 12 soil samples were prepared for N and C analysis in March 2002, at the University of Wollongong. Samples were oven dried at 60 ˚C for 24 hours and stored in a desiccator overnight. Samples were ground to a fine powder in an agate mortar and pestle and 50 mg samples were weighed into tin cups. Samples were analysed for %N, %C, $\delta^{15}N$ and $\delta^{13}C$, using isotope ratio mass spectrometery (IRMS), at the University of Western Australia. The system used was a Roboprep preparation system and 20/20 IRMS from Europa PDZ, UK. Analysis precision was 0.1‰ for $\delta^{13}C$, 0.3‰ for $\delta^{15}N$.

Chapter 3: Fine-scale patterns in bryophyte community structure and relationship to resource gradients

3.1. Introduction

Broad-scale vegetation patterns in the Windmill Islands suggest the distribution of lichen-dominated vegetation is expanding, and bryophyte communities are contracting to low-lying areas with reliable moisture supply (Melick and Seppelt 1997). These vegetation patterns are thought to be a response to regional uplift and climatic drying since deglaciation (Melick and Seppelt 1997), as described in Chapter 2, section 2.1.

Evidence for these changes to broad-scale vegetation patterns is observed in the present communities. In particular, the predominance of moribund bryophytes is considered a key indicator of this regional drying trend. Moribund bryophytes are most common in transitional communities (Group 2; Melick and Seppelt 1997) that occur along a community gradient that extends from pure bryophyte-dominated communities (Group 1; Melick and Seppelt 1997) to *Usnea*-dominated communities, in which bryophytes are moribund and virtually undetectable (Group 2.5; Melick and Seppelt 1997). This latter group is considered to be the earliest indicator of the presence of bryophyte communities, when conditions were moister.

Future vegetation changes are likely to be observed along this ecologically dynamic community gradient, spanning the bryophyte-lichen interface. If regional drying persists, a continued expansion of moribund bryophytes and lichens into the present live bryophyte zone would expected. Under a wetter climate, regeneration of moribund moss, as has been experimentally demonstrated by Melick and Seppelt (1997), and expansion of present bryophyte communities, might be observed.

Detecting changes to future vegetation dynamics requires a baseline for current distributions. In this environment, where growth rates are exceedingly slow, change is more likely to be detected at fine-scales (species level) than broad-scales (community level). Previous investigations of vegetation distributions, in the Windmill Islands, have primarily examined broad-scale patterns, encompassing all vegetation types (for example, Smith 1986, 1988a, 1990a, Melick et al. 1994a, Melick and Seppelt 1997). Fine-scale patterns of individual species distributions, within bryophyte communities, have therefore been beyond the scope of most Windmill Islands studies to date. Fine-scale bryophyte species patterns have been investigated along a single transect, for which it was shown that species distributions are determined by water availability (Selkirk and Seppelt 1987, and described in Chapter 2, section 2.1). The absence of replication in this previous study limits its ability to generalise at the regional scale. The lack of comprehensive fine-scale vegetation surveys is likely to be due to the difficulties associated with field identification of cryptogamic species. Little is known about how bryophyte species distributions are influenced by environmental variables, but it appears that water is the primary factor (Selkirk and Seppelt 1987, Smith 1999) and that nutrients do not play a key role (Smith 1999).

I have examined fine-scale vegetation patterns, and measured a variety of environmental variables, along a series of transects that cross the community gradient described in Melick and Seppelt (1997), extending from pure bryophyte stands, through the transitional moribund zone, to lichen-dominated communities. I aimed to determine how fine-scale bryophyte community composition and resource availability varied across the community gradient. Three groups of hypotheses were tested.

The first group of hypotheses was associated with determining how resources vary along the community gradient, specifically:

Hypothesis 1: The community gradient is accompanied by a moisture gradient
Hypothesis 2: The community gradient is accompanied by a nutrient gradient

The presence of a moisture gradient was determined by measurement of turf water contents and plant $\delta^{13}C$, with each expected to show elevated values in wet communities (see Chapter 2, section 2.2.3. for explanation of use of $\delta^{13}C$ as an indicator of habitat submergence). In addition, if a water gradient was present, it was expected that soluble carbohydrates known to play a role in enhancing tolerance of desiccation would occur in highest concentrations in the driest communities. The presence of a nutrient gradient was determined by measurement of plant nutrient contents (percent N and C), providing an indication of nutrient availability and carbon gain. $\delta^{15}N$ was measured as an indicator of nutrient-source.

The second group of hypotheses was associated with determining how diversity varies along the community gradient. This set of hypotheses is based on the results of the Selkirk and Seppelt (1987) transect. By investigating fine-scale patterns in species distributions along replicate transects at two sites, I aimed to confirm if the following patterns are found across the region:

Hypothesis 3: *Grimmia antarctici* is restricted to the bryophyte-dominated end of the community gradient.

Hypothesis 4: The bryophyte-dominated end of the community gradient is dominated by *G. antarctici.*

Hypothesis 5: *Ceratodon purpureus* is absent from the bryophyte-dominated end of the community gradient.

Hypothesis 6: *B. pseudotriquetrum* occurs across the entire community gradient.

The final hypothesis was relevant to the future vegetation dynamics of the region. Melick and Seppelt (1997) showed that, under controlled conditions, moribund bryophytes have the potential to regenerate under conditions of high moisture availability. This suggests the moribund communities may show bryophyte regeneration if ameliorating conditions prevail in the future. This regeneration will more likely occur if live bryophyte material is present within the moribund turf, hence:

Hypothesis 7: The moribund zone contains live bryophyte material

Through testing these hypotheses in the Windmill Islands cryptogamic communities, this study provides insight into the effect of resources on plant diversity and physiology in a simple ecosystem. The work provides a baseline to monitor changes to species distributions in the future and allows the development of predictions for future species dynamics under a changing climate.

3.2. Methods

This study was conducted in the ASPA Meltpuddle and Robinson Ridge sites (Chapter 2, section 2.1). Within each of the two sites ten transects were established. The transects spanned a bryophyte community gradient; from pure bryophyte stands, at the edge of a water source (Bryophyte; group 1 described by Melick and Seppelt 1997), and away from the water source, through the moribund bryophyte zone (Moribund) to the point at which the bryophyte community is predominantly moribund and dominated by crustose lichen species (Crustose; group 2 described by Melick and Seppelt 1997). This community gradient is thought to occur along a moisture gradient, and is indicative of a drying trend, along which live bryophytes have retreated to low-lying wet habitats with reliable moisture supply (Melick and Seppelt 1997).

Characteristic of the Windmill Islands cryptogamic communities, the sites were scattered with large rocks. Bryophytes grow between the rocks, with the rock surfaces either devoid of vegetation or occupied by lichen species. In order to minimise the impact of this research, access to the bryophyte communities could only be gained by walking on bare rock surfaces. Transect locations were therefore influenced by the distribution of rocks within the sites; transects were restricted to locations that had large rocks in high enough densities for access and low enough density for quadrats (20 x 20 cm) to be placed between the rocks. Transect lengths were determined by the distance covered by the bryophyte community gradient at each location. Transect lengths varied from 1.35 to 3.10 m at the ASPA Meltpuddle site and 1.10 to 3.90 m at Robinson Ridge.

All transects were surveyed using 20 x 20 cm quadrats, one in each of the three community types described above, positioned at both ends (Bryophyte and Crustose) and the middle of each transect (Moribund).

3.2.1. *Physical environment*

Soil nitrogen and carbon

Soil N and C was determined as described in Chapter 2 (section 2.2.9).

Aspect

A compass bearing was taken along each transect (from the Crustose community end to the Bryophyte community end). Deviation from north (°) was calculated for each transect, along with the deviation direction (E or W).

Slope

Cross-sections were surveyed for each transect using a level line (taut string line fixed at horizontal using a bubble level) as a reference line. Elevation measurements from the vegetation surface to the level line (perpendicular to the level line) were recorded at known distances (measured using a tape) along each transect. Slope was calculated as the slope of the regression line, fitted to a scatter plot of the elevation and distance data.

3.2.2. *Resource patterns*

Water gradient

In order to determine if the transect community gradients were accompanied by an underlying water gradient, turf water content (TWC) was measured for each of the three community quadrats, within each of the ten transects, at the two sites. Plant samples (2-3 cm diameter and up to 3 cm depth) were collected from Robinson Ridge on 17/2/00 and from the ASPA Meltpuddle on 28/2/00. Samples were collected in airtight vials and returned to the laboratory within approximately 1 hour of collection. Upon arrival in the laboratory TWC was determined as described in Chapter 2 (section 2.2.3). Note that in the Crustose community, where well-developed bryophyte turf was absent, samples consisted of a thin moribund turf, usually encrusted with crustose lichens, and some macro-lichens, as was characteristic of the vegetation in this community.

Nutrient gradient

In order to determined if the transect community gradients were accompanied by a nutrient resource gradient, weight % nitrogen and carbon, and C/N ratio, was determined for plant material collected from each quadrat. These analyses were performed as described in Chapter 2 (section 2.2.5).

Plant biochemical characteristics

Stable isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) were determined in order to gain insight into nutrient source and degree of habitat submergence, respectively. Soluble carbohydrate contents were determined in order to provide information about the likely physiological response to stresses such as freezing and desiccation. These analyses were performed as described in Chapter 2 (sections 2.2.5 and 2.2.7, respectively).

3.2.3. Fine-scale community patterns

The quadrat (20 x 20 cm), which was divided into a 5 cm grid, was placed over each sampling position and a tweezer-pinch sample (approx. 20-50 gametophytes) was collected at nine 5 cm intervals, at the quadrat grid line intersections. Where vegetation was absent, the collection point was categorised as: bare soil, bare rock or snow and ice. Samples were returned to the laboratory, allowed to air dry, and stored at ambient laboratory conditions until microscopy analysis.

Each sample was examined using a dissecting microscope and community composition, of bryophyte and lichens, recorded. Bryophytes were categorised as either dead (brown) or live (green). Live bryophytes were identified to species level *(Bryum pseudotriquetrum, Grimmia antarctici, Ceratodon purpureus* or *Cephaloziella exiliflora*). Lichens were grouped into three taxonomic categories (crustose, fructicose or foliose).

For each sample (9 per quadrat), a relative abundance score was estimated for each species or taxonomic category using the scale described in Table 3.1. Relative abundance scores, for the 9 sub-samples for each quadrat, were then combined to obtain the quadrat relative abundance, for each species or taxonomic category. The maximum possible total score per species or taxonomic category per quadrat was 36 (i.e. for a species dominant in all nine sub-samples). The following formula was then calculated for each species or taxonomic category for each quadrat:

Percentage abundance = total score per quadrat/36 * 100.

Table 3.1: Relative abundance categories, description and score.

Category	Description of occurrence	Score
Dominant	Single species or taxonomic category occurring in highest abundance.	4
Co-dominant	Two or more species or taxonomic categories which occur in equally high abundance (with no other single species or taxonomic category occurring in higher abundance).	3
Present	Species or taxonomic categories which occur in a substantial quantity (i.e. > a few gametophytes, > a few lichen fragments), but in lower abundance than that described above.	2
Scarce	Species or taxonomic categories which occur in trace amounts only (i.e. one or two bryophyte gametophytes, a small fragment of lichen).	1
Absent	Not present in the sample	0

3.2.4. Statistical Analyses

Time constraints placed on the field season, as a result of restricted access to the sites due to snow cover and frequent periods of extreme weather, caused a reduced level of replication for the % abundance community data; seven replicate transects at each of the two sites are therefore presented. For most of the environmental variables the level of replication was ten.

Variables for which measurements were made for each quadrat were analysed using 2-way ANOVA, testing for site*community effects (sites: Robinson Ridge or ASPA Meltpuddle and communities: Crustose, Moribund or Bryophyte). Variables for which a measurement was made for a site or transect only were analysed for differences between sites using 1-way ANOVA. Tests for homoscedacity and normality were performed to ensure the assumptions of ANOVA were met, and transformations were performed as required. Transformation details, for data analysed using 2-way ANOVA, are provided in Tables 3.2 – 3.4.

Where a given variable showed a statistically similar pattern at both sites, across the three communities ($P > 0.05$ for site*community interactions; Tables 3.2 – 3.4) the significance of the two individual effects were investigated and, if significant, tested using pairwise tests (Student's t) for the significance of differences between individual pairs. These pairwise tests investigated the *overall* effect of site or community. For example, if testing for the differences between community pairs, the two sites were combined, and vice versa, effectively "lumping" site or community.

In the few cases where a significant site*community interaction was detected ($P < 0.05$ for site*community interaction; Tables 3.2 – 3.4) the significance of the two individual effects was not investigated. Pairwise tests were conducted between individual pairs of means; in the case of two sites and three communities, nine pairwise comparisons were conducted (three community pairs within each of the two sites, plus three site pairs).

The sequential Bonferroni correction was used to reduce the probability of a false result, by adjusting the table-wide p-value to keep it constant, at 0.05 (Rice 1989). As this procedure increases the risk of not detecting some biologically important differences (Moran 2003), where pairs were significant at $\alpha = 0.05$, these were also reported. Pairwise tests were therefore conducted both at $\alpha = 0.05$ and also at the Bonferroni adjusted α level if more than one pair was being tested. For the data presented in this chapter, the Bonferroni procedure altered the α to either 0.017 (in the case of three community pairs) or 0.006 (in the case of nine site and community combinations). The results of these pairwise tests are indicated by lowercase letters on the figures, with the α level provided in the respective figure legends.

3.3. Results

3.3.1. *Physical environment*

Soil properties, aspect and slope were measured in order to characterise the physical environment, which may play a role in determining vegetation patterns.

Soil properties

Soil fertility was determined by measuring soil nitrogen and carbon contents. Soil %N and %C were less than 0.1% and 1%, respectively, with no significant differences detected between the two sites (Fig. 3.1A & B). The ratio of soil C/N was however significantly lower (20%) at Robinson Ridge compared to the ASPA Meltpuddle site ($P<0.05$; Fig. 3.1C).

The two sites showed variation in nutrient source. $\delta^{15}N$ values were significantly lower (9‰) at the Robinson Ridge site than at the ASPA Meltpuddle site ($P<0.05$; Fig. 3.1D). Degree of habitat submergence appeared to be similar between sites, as indicated by statistically similar soil $\delta^{13}C$ values (1‰ variation) across the two sites (P>0.05; Fig. 3.1E).

Slope

Profiles of the seven replicate transects for which community data was collected are shown in Fig. 3.2. Transect slope was estimated as the slope of a linear regression line, calculated for each profile. The Robinson Ridge transects were significantly steeper than the ASPA Meltpuddle transects ($P<0.05$; Fig. 3.2). These slope differences were due to the community gradient occurring over an approximately 0.5 m longer distance, and 8 cm less elevation, at the ASPA Meltpuddle site than at Robinson Ridge.

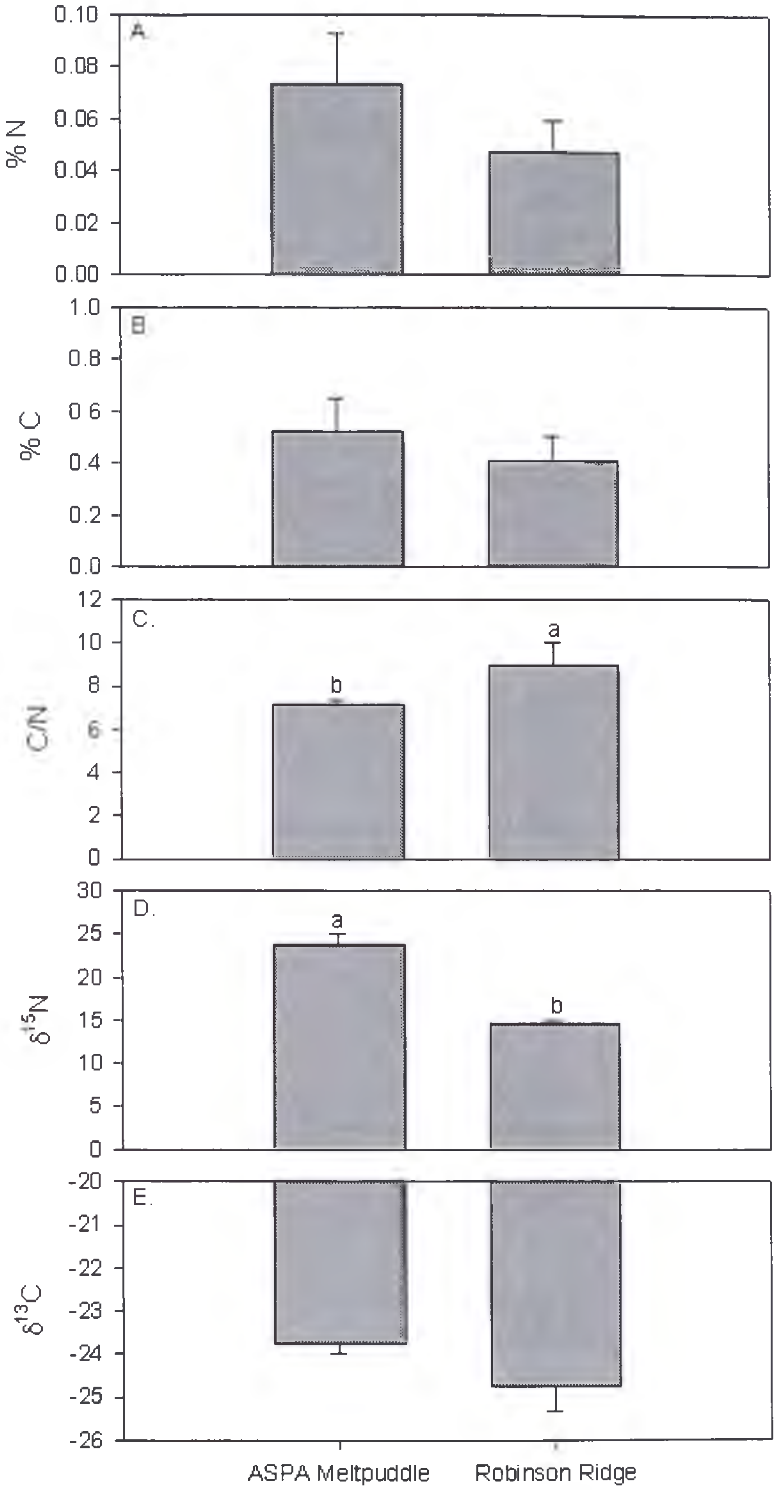


Figure 3.1: Soil nitrogen and carbon (% weight), C/N ratio and stable isotopic compositions ($\delta^{15}N$ and $\delta^{13}C$) from the two Windmill Islands sites: Robinson Ridge and ASPA Meltpuddle. Bars represent mean +/- se, n = 6. Within each plot, bars labelled with different letters are statistically different (Student's t, *P*< 0.05). Unlabeled pairs within each plot are not significantly different.

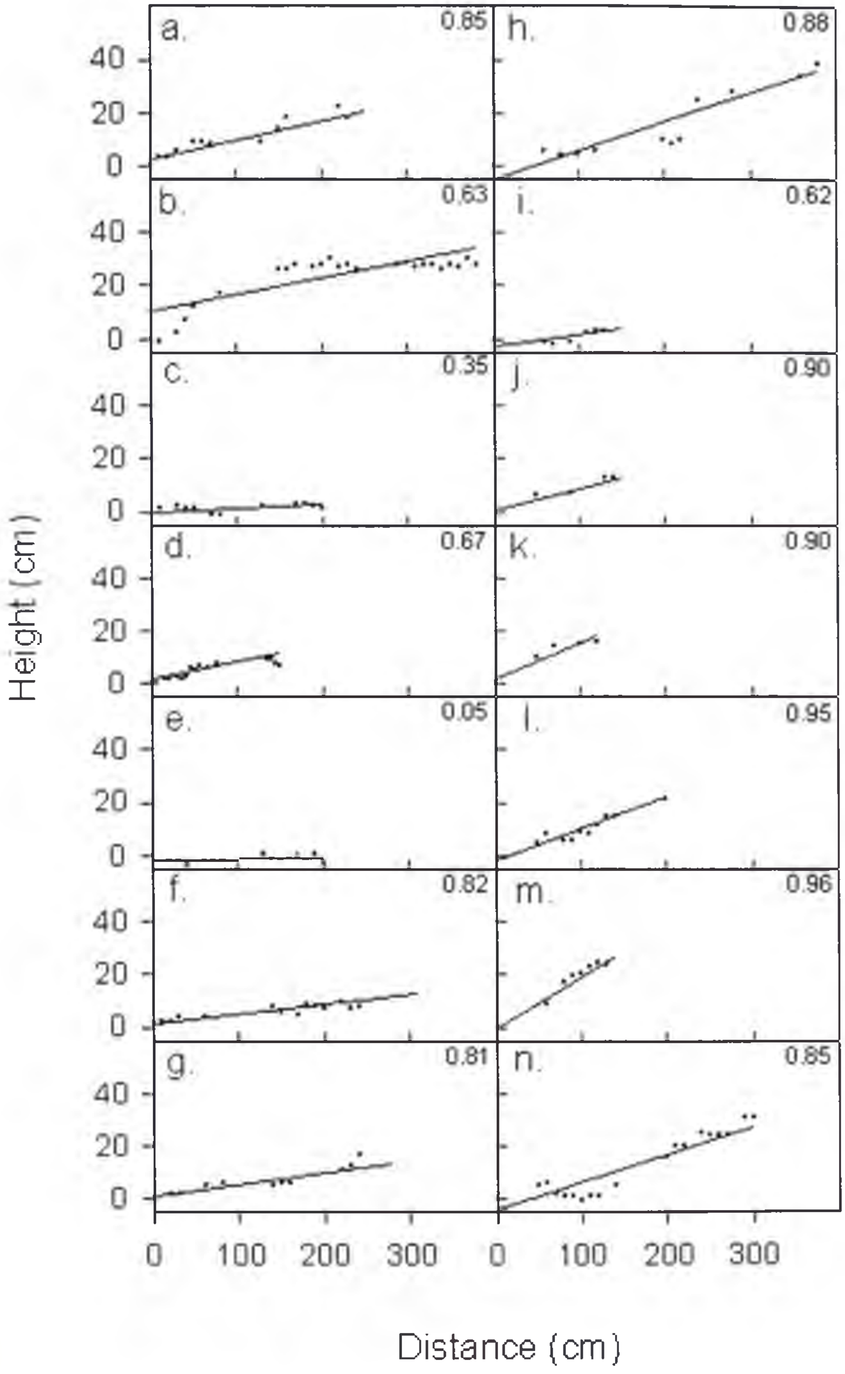


Figure 3.2: Transect profiles for seven transects at the two sites; a-g ASPA Meltpuddle, h-n Robinson Ridge. Each point represents a survey point. Bryophyte community at lower end (zero elevation and distance), Crustose community at upper end, Moribund community at approximately mid-distance. Average slope for each transect was estimated as slope of regression line, for which r^2 values are shown on each plot.

Aspect

Both sites were north facing catchments, within which microsite aspect varied. The mean deviation of transect microsite aspect from north was very similar for each site (ASPA Meltpuddle: 72±17°, Robinson Ridge: 70±12°; Fig. 3.3). The direction of the deviation from north was, however, different for the two sites. At the ASPA Meltpuddle site 8 of the 10 transects deviated from north in a westerly direction, while at Robinson Ridge 7 of the 10 transects deviated from north in an easterly direction (Fig. 3.3).

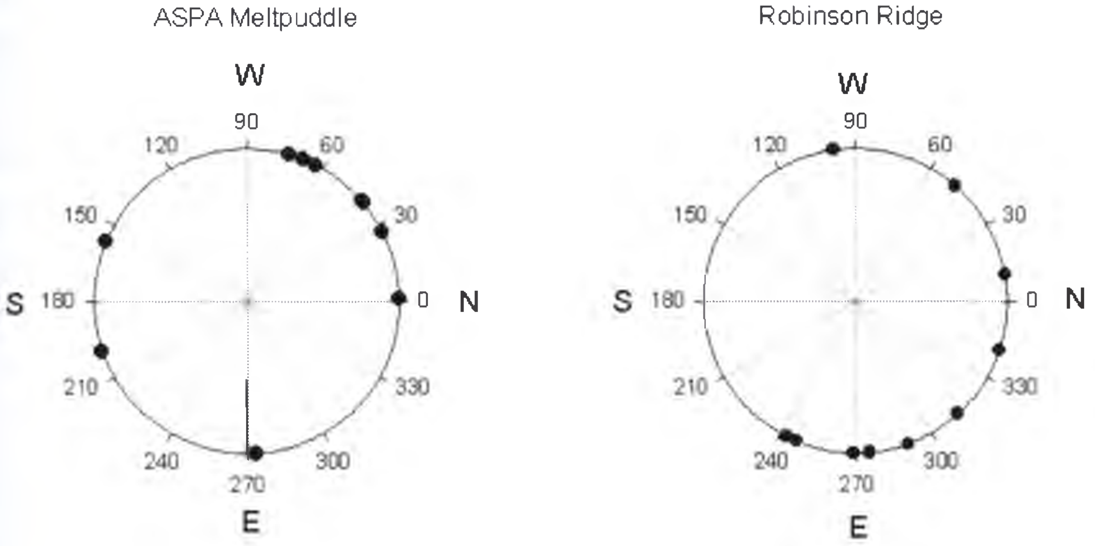


Figure 3.3: Transect aspects (°) for the two sites: ASPA Meltpuddle and Robinson Ridge. Each point indicates the aspect of one replicate transect.

3.3.2. *Growth environment*

The growth environment was characterised by quantifying availability of water and nutrients, two key environmental variables thought to play a role in determining species distributions. By measuring these variables I determined whether the community transects were accompanied by underlying water and/or nutrient gradients. Further insight into the growth environment was gained by an investigation of plant stable isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$), providing information about nutrient source and degree of habitat submergence, respectively. Natural variation in soluble carbohydrate contents were also determined, as the presence of these compounds can be used an indicator of relative plant tolerance of desiccation, and therefore may be indicative of frequency and/or severity of desiccation events the growth environment is subject to.

Water gradient

A significant water gradient accompanied the community gradient (community effect: $P = 0.0008$; Table 3.2). The Moribund and Bryophyte communities were similar at Meltpuddle, while the Moribund and Crustose communities were similar at Robinson Ridge (Fig. 3.4). Plant water availability was highest in the Bryophyte community, where TWC approached 1.5 g H_2O g^{-1} dw, and lowest in the Crustose community, where TWC was less than 1 g H_2O g^{-1} dw (Fig. 3.4). The Moribund and Bryophyte communities were overall statistically similar, containing significantly higher water contents than the Crustose community ($P<0.017$; Fig. 3.4).

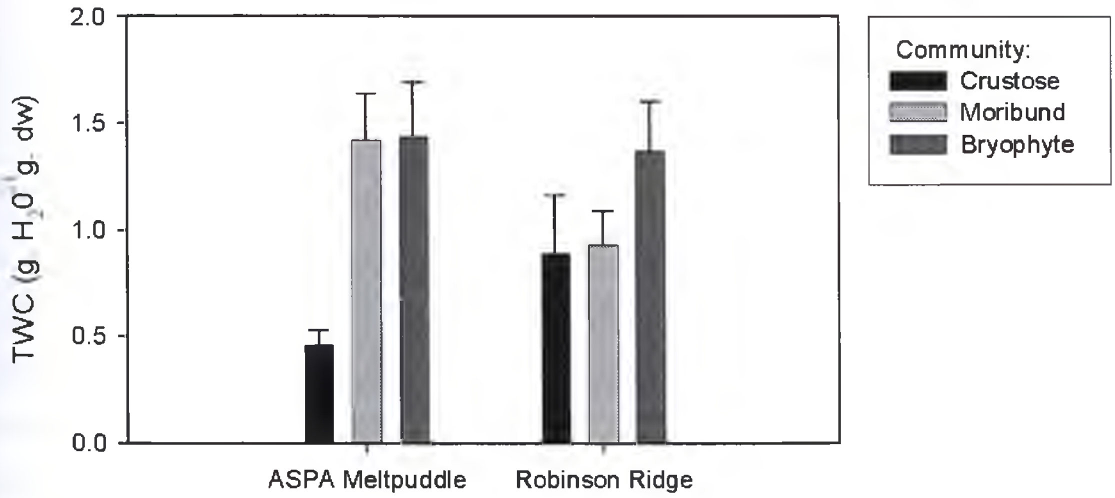


Figure 3.4: Turf Water Content (TWC; g.H_2O^{-1}g. dw) for the three communities (Crustose, Moribund and Bryophyte), and two sites (ASPA Meltpuddle and Robinson Ridge). Bars represent mean±sem, n = 10.

Table 3.2: Results of 2-way ANOVA for turf water content (TWC) and plant nitrogen and carbon variables (%N, %C, C/N, δ^{15}N and δ^{13}C). Testing for differences within the whole statistical model and the individual effects of site and community, as well as the significance of site*community interactions.

Variable	Transformation	Effect Test	Model DF	Error DF	F ratio	*P*
TWC	Square root	Whole Model	5	54	4.3496	0.0021
		Site	1		0.0572	0.8119
		Community	2		8.152	0.0008
		Site*Community	2		2.6934	0.0767
% N	None	Whole Model	5	52	3.4569	0.009
		Site	1		0.357	0.5528
		Community	2		6.4554	0.0031
		Site*Community	2		1.7731	0.1799
%C	Square root	Whole Model	5	50	3.9384	0.0043
		Site	1		13.3253	0.0006
		Community	2		1.6065	0.2108
		Site*Community	2		1.3927	0.2579
C/N	Log10	Whole Model	5	52	2.1202	0.0776
		Site	1		0.1965	0.6594
		Community	2		4.1194	0.0218
		Site*Community	2		0.9587	0.3901
δ^{15}N	None	Whole Model	5	52	28.5211	<0.0001
		Site	1		79.2131	<0.0001
		Community	2		26.5755	<0.0001
		Site*Community	2		3.7406	0.0304
δ^{13}C	None	Whole Model	5	52	4.2352	0.0026
		Site	1		0.1857	0.6683
		Community	2		8.2914	0.0007
		Site*Community	2		1.9924	0.1466

Nutrient gradient

A significant nitrogen gradient also accompanied the community gradient (community effect: $P = 0.0031$; Table 3.2). Percent N was significantly higher in the Crustose and Moribund communities than the Bryophyte community ($P<0.017$ and 0.05, respectively), where levels were approximately 1.5% (Fig. 3.5A). Nitrogen composition was not significantly different between sites (Table 3.2). Percent C, however, showed no significant difference between communities (Table 3.2), but was approximately 10% lower at the ASPA Meltpuddle site, compared to Robinson Ridge (site effect: $P<0.0006$; Table 3.2; Fig 3.5B). Higher C/N ratios were found in the Bryophyte community (community effect: $P<0.0218$; Table 3.2; Fig. 3.5C), with no significant difference between sites (Table 3.2.).

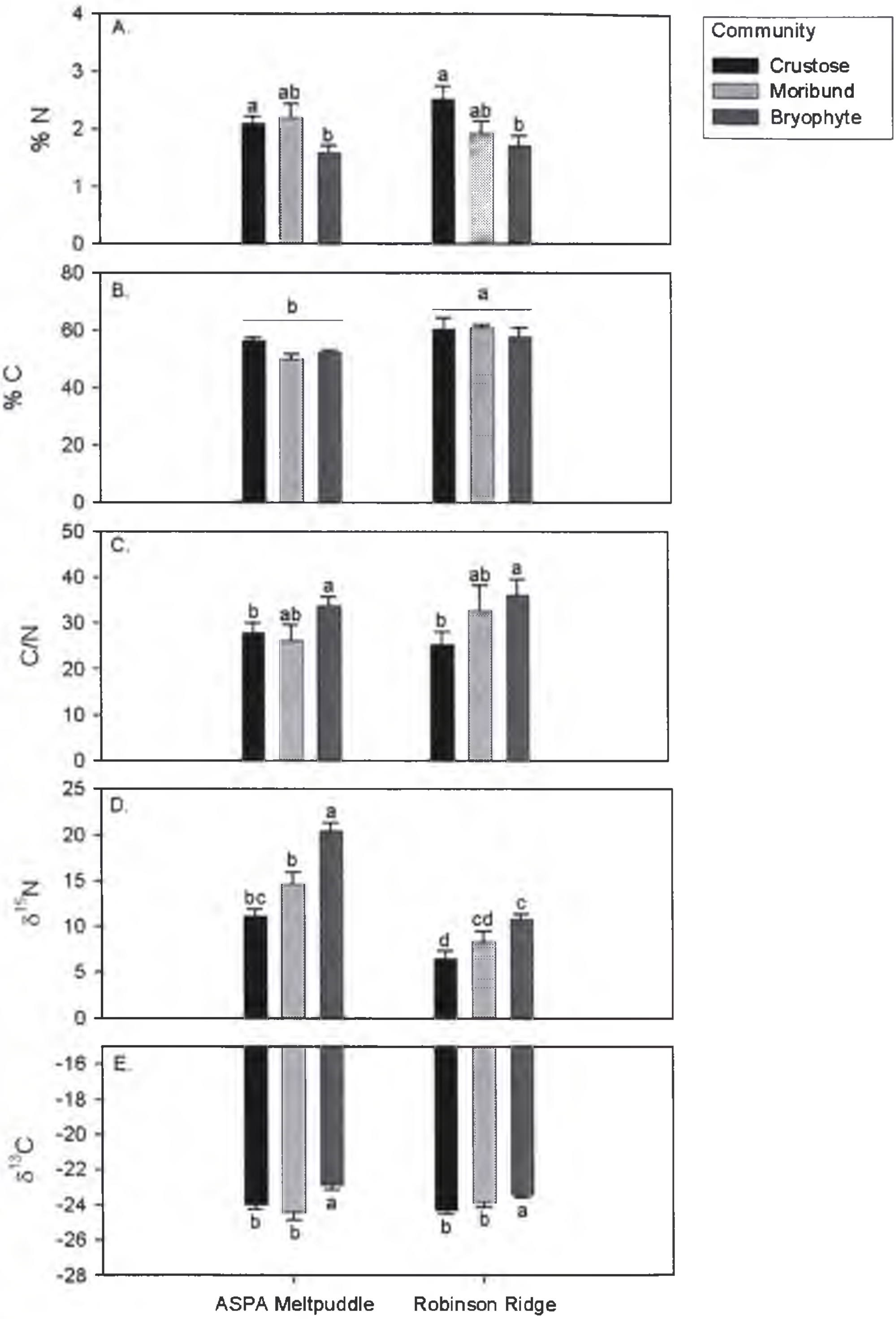


Figure 3.5: Plant nitrogen and carbon contents (% weight), C/N ratios and stable isotopic compositions for the three communities (Crustose, Moribund and Bryophyte) and two sites (ASPA Meltpuddle and Robinson Ridge). Bars represent mean±se, n = 10. Within each plot, bars labelled with different letters are statistically different (Student's t, $P< 0.006$).

Biochemical characteristics

Plant Stable Isotopes

In this environment, it is likely that high plant $\delta^{15}N$ indicates use of guano-derived nitrogen sources, and lower values indicate plants are receiving a higher proportion of urea-derived wind-born NH_3 and/or more nitrogen from atmospheric fixation (Chapter 2, section 2.2.1). A $\delta^{15}N$ gradient was found across the communities, with highest levels found in the Bryophyte community (up to 20‰) and lowest levels in the Crustose community ($P<0.006$; Fig. 3.5D). Although this pattern was observed at both sites, there were significant differences in the $\delta^{15}N$ patterns between sites (site*community interaction: $P = 0.0304$; Table 3.2). Values for $\delta^{15}N$ were higher at the ASPA Meltpuddle site than at Robinson Ridge for each community type ($P<0.006$; Fig. 3.5D), and the $\delta^{15}N$ gradient was steeper at the ASPA Meltpuddle site, where the $\delta^{15}N$ of the Bryophyte community was 9‰ greater than that of the Crustose community. The lowest $\delta^{15}N$ (less than 7‰) was found in the Robinson Ridge Crustose community.

In cryptogams, high $\delta^{13}C$ values are likely to be indicative of habitat submergence (Chapter 2, section 2.2.1). The Bryophyte community showed the greatest evidence of habitat submergence, as $\delta^{13}C$ was highest in this community ($P<0.006$; Fig. 3.5E).

Plant Soluble Carbohydrates

Plants soluble carbohydrate compositions showed natural variation across communities suggesting that their growth environments maybe subject to different frequency and/or severity of desiccation events.

Total soluble carbohydrate concentrations showed significant variation along the community gradient, with concentrations 3-fold higher in the Bryophyte community than the Crustose community (community effect: $P<0.0001$; Table 3.3; Fig. 3.6A). Individual sugar compounds which contributed most strongly to this pattern were the dominant sugars, sucrose (Appendix 1) and X2 (Fig. 3.6D), and to a lesser extent *myo*-Inositol (Fig. 3.7D) and X3 (Appendix 1).

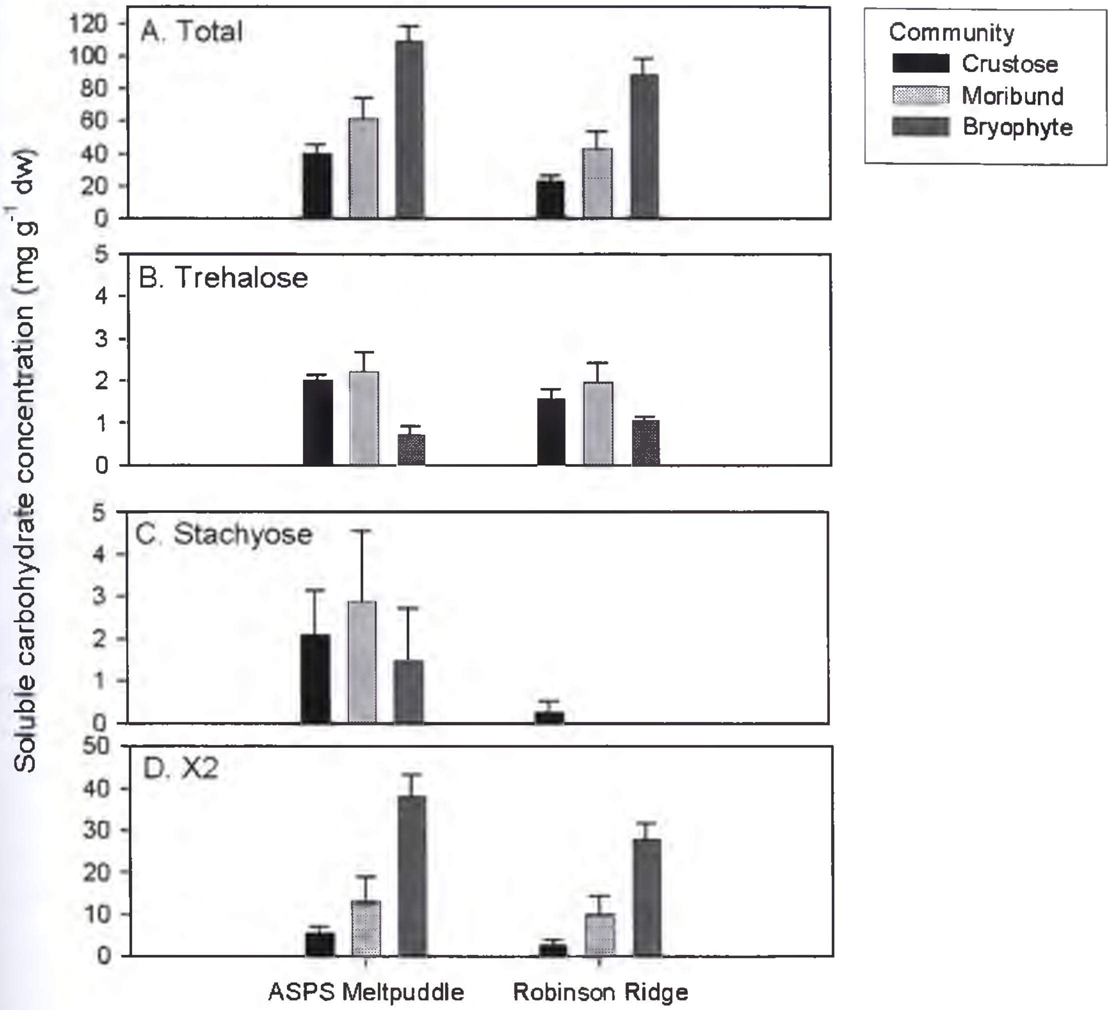


Figure 3.6: Concentration (mg g^{-1} dw) of select soluble carbohydrates: A. total, B. trehalose, C. stachyose and D. X2. Data shown for two sites: ASPA Meltpuddle and Robinson Ridge; and three communities: Crustose, Moribund and Bryophyte. Bars represent mean±sem, n = 10. Note y-axes are different.

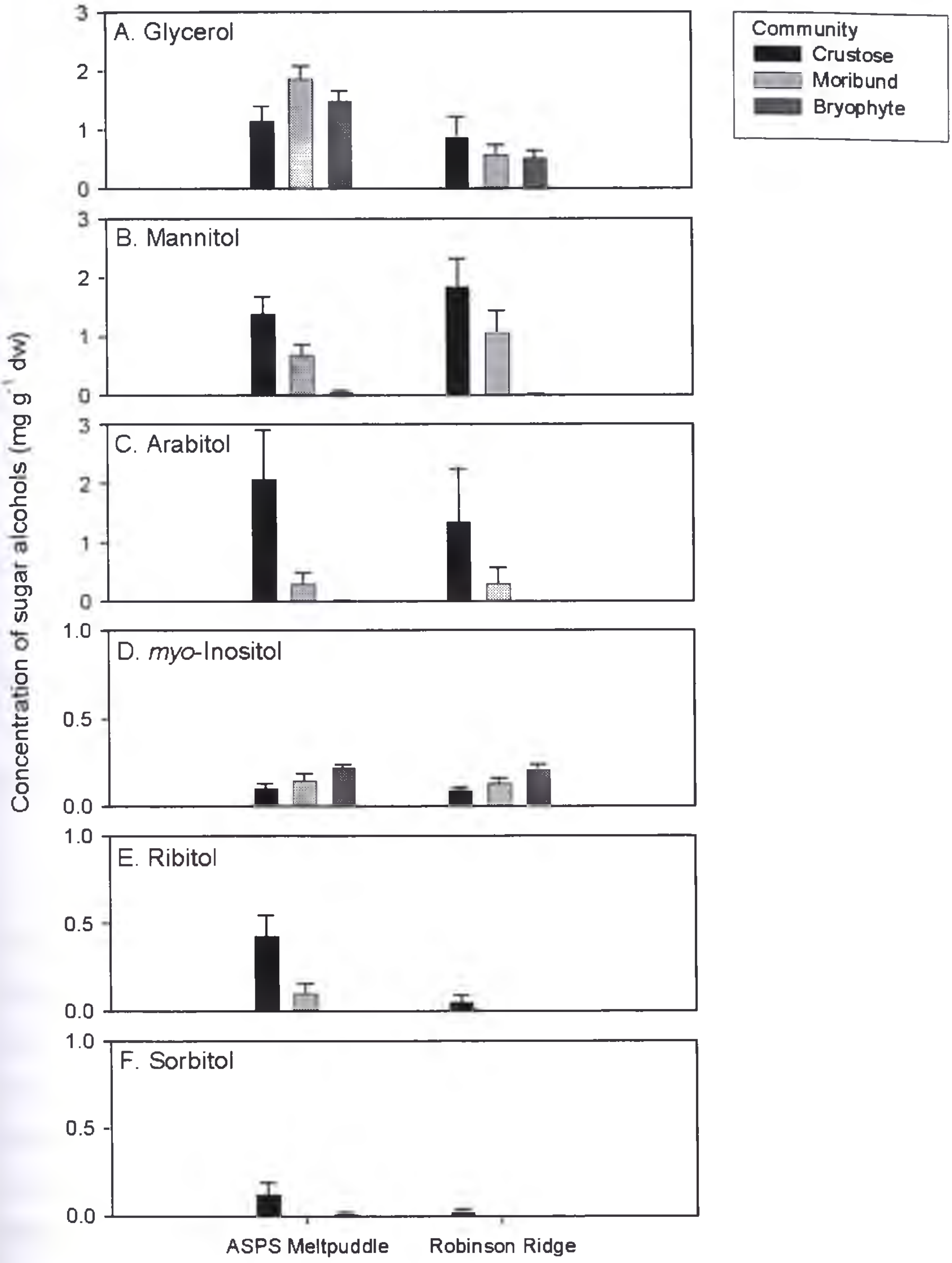


Figure 3.7: Concentration of sugar alcohols (mg g^{-1} dw): A. glycerol, B. mannitol, C. arabitol, D. *myo*-inositol, E. ribitol and F. sorbitol. Data shown for two sites: ASPA Meltpuddle and Robinson Ridge; and three communities: Crustose, Moribund and Bryophyte. Bars represent mean±sem, n = 10. Note y-axes are different.

Table 3.3: ANOVA results for the selected soluble carbohydrates and sugar alcohols in Figs. 3.6 and 3.7, respectively. Test results are for 2-way ANOVA, except for stachyose, for which 1-way ANOVA results are given. 2-way ANOVA results are for differences within the whole statistical model and the individual effects of site and community, as well as the significance of site*community interactions. Sugar alcohols not included (arabitol, ribitol and sorbitol) were not analysed using ANOVA due to predominance of zeros and/or trace concentrations.

Variable	Transformation	Effect Test	Model DF	Error DF	F ratio	*P*
Total	None	Whole Model	5	54	14.0745	<0.0001
		Site	1		6.9845	0.0107
		Community	2		31.6695	<0.0001
		Site*Community	2		0.0244	0.9759
Trehalose	Log10	Whole Model	5	54	6.8759	<0.0001
		Site	1		0.477	0.4927
		Community	2		13.1834	<0.0001
		Site*Community	2		3.7679	0.0294
Stachyose	None	Whole Model	2	27	0.2742	0.7623
		Community	2		0.2742	0.7623
X2	Square root	Whole Model	5	54	2.8327	0.0242
		Site	1		8.2534	0.0058
		Community	2		0.0363	0.9644
		Site*Community	2		2.9188	0.0626
Glycerol	None	Whole Model	5	53	8.7824	<0.0001
		Site	1		36.6678	<0.0001
		Community	2		1.8987	0.1598
		Site*Community	2		1.6118	0.2092
myo-Inositol	None	Whole Model	5	54	4.4721	0.0018
		Site	1		0.5741	0.4519
		Community	2		10.8269	0.0001
		Site*Community	2		0.0662	0.936
Mannitol	Square root	Whole Model	5	54	12.4569	<0.0001
		Site	1		0.6032	0.4407
		Community	2		30.6401	<0.0001
		Site*Community	2		0.2005	0.8189

Several sugars important in cryoprotection and desiccation tolerance were detected (e.g. trehalose, stachyose and a range of sugar alcohols; Fig. 3.6B & C and Fig. 3.7). For many of these, a significant trend in the opposite direction was observed, with concentrations significantly higher in the Crustose community than in the Bryophyte community. The concentration of mannitol, for example, was highest in the Crustose community and lowest in the Bryophyte community, with each community significantly different from one another (P<0.017; Fig. 3.7B). For trehalose, arabitol and ribitol, the trend was significant only within the ASPA Meltpuddle site (Fig. 3.6B, 3.7C & E, respectively), where the concentration of trehalose was 2.8-fold higher in the Crustose community than the Bryophyte community (P<0.006; Fig. 3.6B), and the concentrations of arabitol and ribitol were 7.2- and 4.2-fold higher in the Crustose community than the

Moribund community, respectively (*P*<0.05; Fig. 3.7C & E). The Bryophyte community contained only trace concentrations of the latter two sugars.

3.3.3. Community patterns across environmental gradients

Broad-scale patterns - lichens versus bryophytes

Patterns of percent abundance for the three broad vegetation components (dead bryophytes, live bryophytes and crustose lichen) are shown in Figure 3.8. The two other broad vegetation groups that were quantified; fructicose and foliose lichen, were either absent or occurred only in trace abundance.

Dead bryophytes, indicative of past live bryophyte presence, showed an abundance gradient (Fig.3.8A), with abundance greatest in the Crustose community (>50%) and lowest in the Bryophyte community (<10%; community effect: *P*<0.0001; Table 3.4). Crustose lichen showed a similar gradient (Fig. 3.8C), with percent abundance also highest in the Crustose community (>40%) and lowest in the Bryophyte community (approximately 5%; community effect: *P*<0.0001; Table 3.4). Live bryophytes showed an opposite pattern, occurring in highest abundance in the Bryophyte community (>90%) and declined to 50-60% in the Crustose community (community effect: *P* = 0.0001; Table 3.4; Fig. 3.8B). Live bryophytes showed the greatest percent abundance of all three of the broad vegetation components, with abundance greater than 50% in all communities. The patterns of abundance, for these three broad vegetation categories, were statistically similar between the two sites (Table 3.4).

Fine-scale patterns - bryophyte species

The four bryophyte species each showed different patterns of abundance across the community gradient. From the Bryophyte to the Crustose community, abundance of *G. antarctici* declined, *C. purpureus* increased and *B. pseudotriquetrum* remained stable (Fig. 3.9A-C). The liverwort, *C. exiliflora*, was overall least abundant, and was absent from the Bryophyte community (Fig. 3.9D).

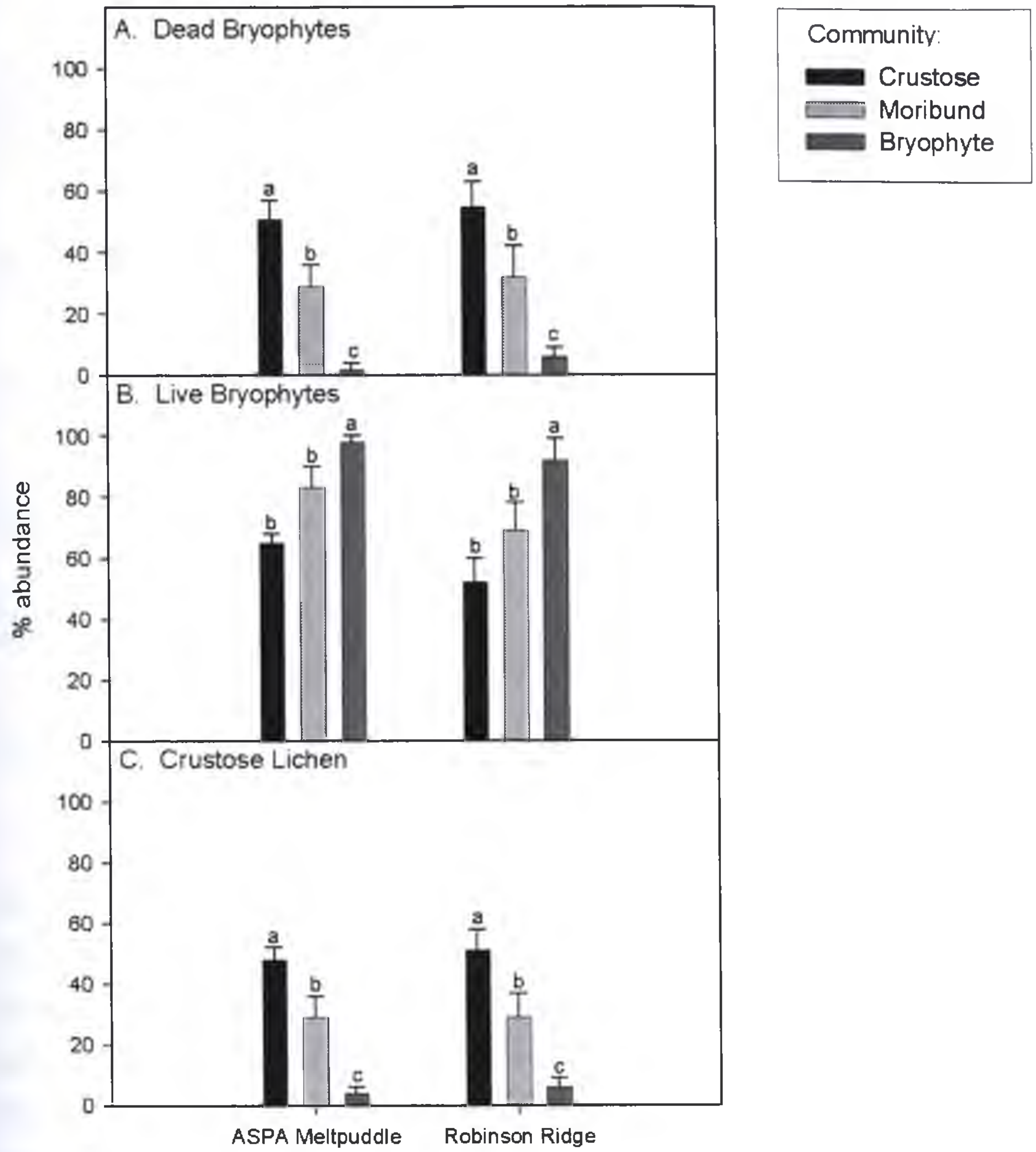


Figure 3.8: Percentage abundance of three broad vegetation components: (A) dead bryophytes, (B) live bryophytes and (C) crustose lichen, for the three communities (Crustose, Moribund and Bryophyte) and two sites (ASPA Meltpuddle and Robinson Ridge). Bars represent mean+sem, n = 7. Within each plot, bars labelled with different letters are statistically different (Student's t, *P*< 0.017).

Table 3.4: Results of 2-way ANOVA for percent abundance of broad vegetation components (dead bryophytes, live bryophytes and crustose lichen) and bryophyte species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*). Results for tests for differences within the whole statistical model, the individual effects of site and community, and the significance of site*community interactions are shown.

Percent abundance (transformation)	**Test**	**Model DF**	**Error DF**	**F ratio**	***P***
Dead Bryophytes (none)	Whole Model	5	36	7.7564	<0.0001
	Site	1		0.0495	0.8251
	Community	2		19.2332	<0.0001
	Site*Community	2		0.1332	0.8758
Live Bryophytes (none)	Whole Model	5	36	5.4484	0.0008
	Site	1		2.1445	0.1518
	Community	2		12.0039	0.0001
	Site*Community	2		0.545	0.5846
Crustose (none)	Whole Model	5	36	10.2983	<0.0001
	Site	1		0.0004	0.9845
	Community	2		25.6059	<0.0001
	Site*Community	2		0.1398	0.8700
B. pseudotriquetrum (square root)	Whole Model	5	36	1.8916	0.1201
	Site	1		5.2861	0.0274
	Community	2		1.1046	0.3423
	Site*Community	2		0.9813	0.3846
C. purpureus ($\log_{10}$)	Whole Model	5	36	6.4613	0.0002
	Site	1		2.6217	0.1141
	Community	2		14.1351	<0.0001
	Site*Community	2		0.7073	0.4997
G. antarctici (none)	Whole Model	5	36	5.2571	0.001
	Site	1		0.474	0.4955
	Community	2		12.8896	<0.0001
	Site*Community	2		0.0162	0.984

The Antarctic endemic, *G. antarctici*, was the most abundant species, with relative % abundance exceeding 20% across all communities (Fig. 3.9A). This species was least common in the Crustose community, where % abundance was less than a third of that in the Bryophyte community (community effect: $P<0.0001$; Table 3.4). *Ceratodon purpureus* was, however, most common in the Crustose community, where percent abundance was 1.5- to 2-fold greater than the Moribund community (community effect: $P<0.0001$; Table 3.4; Fig. 3.9C). This species was absent from the Bryophyte community. Abundance patterns were statistically similar between sites for both *G. antarctici* and *C. purpureus* (Table 3.4). *Bryum pseudotriquetrum* showed intermediate levels of abundance (<30%), but was 2- to 4-fold more prevalent at the ASPA Meltpuddle site than at Robinson Ridge (site effect: $P = 0.0274$; Table 3.4). This species showed no significant difference between communities (Table 3.4; Fig. 3.9B).

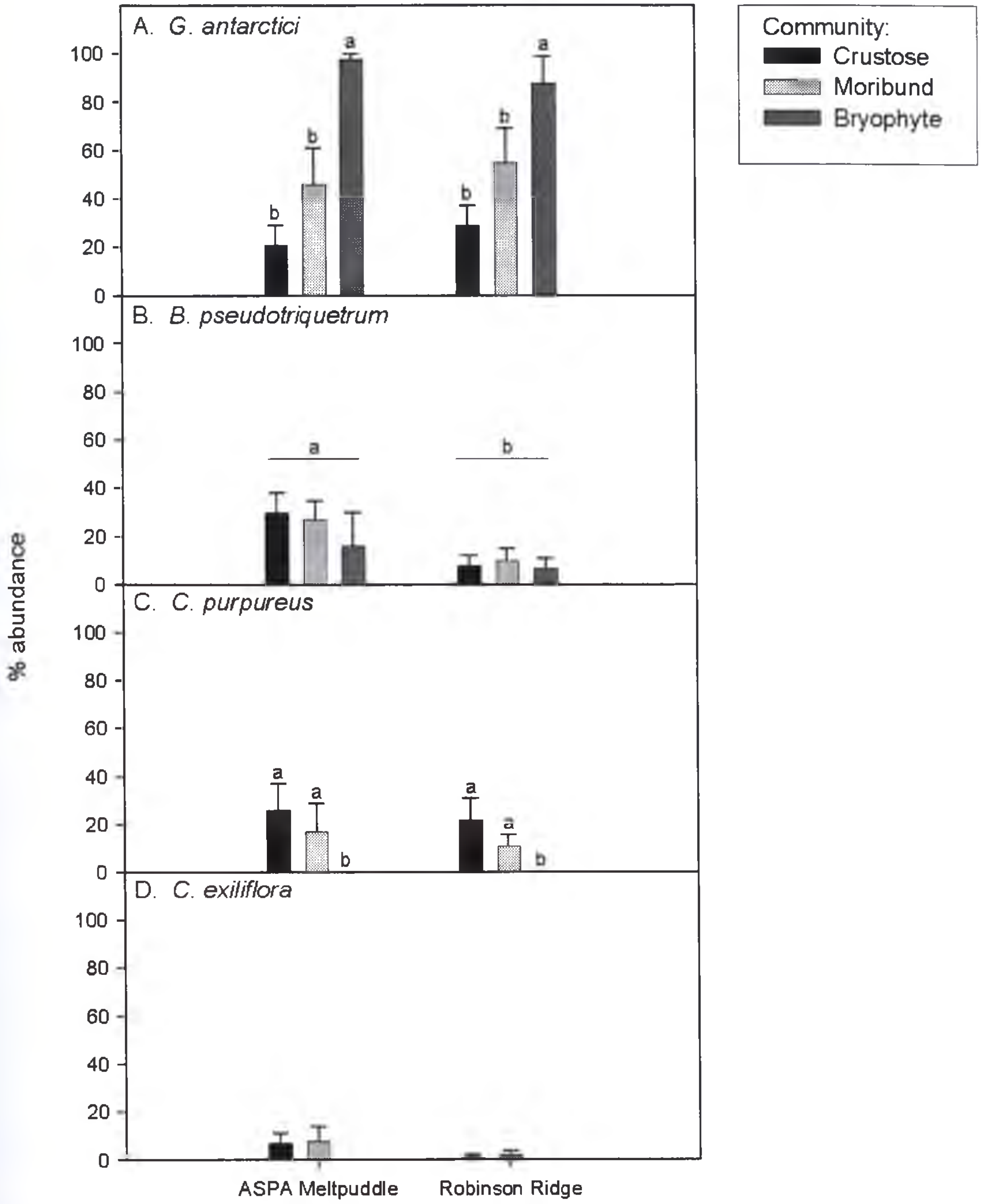


Figure 3.9: Percentage abundance of the four bryophyte species: (A) *G. antarctici*, (B) *B. pseudotriquetrum*, (C) *C. purpureus* and (D) *C. exiliflora*, for the three communities (Crustose, Moribund and Bryophyte) and two sites (ASPA Meltpuddle and Robinson Ridge). Bars represent mean±se, n = 7. Within each plot, bars labelled with different letters are statistically different (Student's t, $P < 0.017$ for A & C, 0.05 for B).

3.4. Discussion

This work has investigated fine-scale vegetation patterns and resource availability, across bryophyte communities, at two sites within the Windmill Islands region. The ecologically dynamic bryophyte-lichen interface has been investigated by including the entire ecological range of the bryophyte communities, from pure bryophyte stands, which are restricted to areas with reliable moisture supply, to moribund bryophyte communities encrusted with lichens, which are indicative of a wetter past (Melick and Seppelt 1997). The outcomes of this work will be utilised, firstly, to characterise the sites, identifying how and why the two sites are different. Secondly I discuss the evidence for resource gradients operating across the community gradient investigated. Thirdly, patterns of diversity along the community gradient are described, along with discussion of the effect of resources on plant diversity and physiology in this simple ecosystem. Finally, some predictions for future vegetation dynamics for the region are suggested. In summary, of the seven hypotheses tested, only one was rejected as shown in Table 3.5 below.

Table 3.5: Summary of the seven hypotheses tested in the present chapter.

Hypothesis	Accepted or Rejected?
1. The community gradient is accompanied by a moisture gradient	Accepted
2. The community gradient is accompanied by a nutrient gradient	Accepted
3. *Grimmia antarctici* is restricted to the bryophyte-dominated end of the community gradient.	Rejected
4. The bryophyte-dominated end of the community gradient is dominated by *G. antarctici*.	Accepted
5. *Ceratodon purpureus* is absent from the bryophyte-dominated end of the community gradient.	Accepted
6. *B. pseudotriquetrum* occurs across the entire community gradient.	Accepted
7. The moribund zone contains live bryophyte material	Accepted

3.4.1. Site characteristics

The two sites were found to be overall very similar with respect to both physical characteristics and species composition. A few site differences were detected however, which are worthy of discussion as they are common to, and underlie, other patterns discussed. Site aspect, for example, was overall northerly for both sites, but the aspect of individual transects within sites showed a predominantly easterly deviation from north at Robinson Ridge and a predominantly westerly deviation from north at the ASPA Meltpuddle. This subtle variation in aspect has the potential to underlie physiological differences between the sites, as plants along the Robinson Ridge transects will receive more light early in each diurnal period and the ASPA Meltpuddle site more light late in the diurnal period. Robinson Ridge may therefore have the opportunity to warm more quickly each day, but conversely, may be subject to increased photoinhibition as the plants may be too cold to utilise the early light. This aspect variation may underlie the site variation observed in %C, for which values were greater at Robinson Ridge than the ASPA Meltpuddle; Robinson Ridge may be fixing more carbon as a result of a more favourable temperature/light regime. Simultaneous measurements of plant surface temperatures and photosynthetic rates, throughout diurnal periods, would help determine the effect of aspect on the photosynthetic physiology of these plants.

Water availability in the Moribund community was overall statistically similar to the Bryophyte community, but at the Robinson Ridge site relatively low levels were measured, which were most similar to the Crustose community. In addition the Crustose community at the Robinson Ridge site was somewhat wetter than the corresponding community at the ASPA Meltpuddle site An explanation for this variation is an interaction with variation in slope – transect slopes were steeper at Robinson Ridge, which is likely to result in better drainage down the transects, but little accumulation except in the lowest Bryophyte community (c.f. Figs 3.2 and 3.4)

The other most noteworthy site difference was associated with nutrient source, for which insight was provided by measurement of $\delta^{15}N$. Both sites had $\delta^{15}N$ values that were relatively high compared to plant material from other environments, particularly in the Bryophyte community where values were greater than ten ‰. Enriched ^{15}N values are well documented in the Antarctic environment, due to high $\delta^{15}N$ of animal-derived nutrients entering the system and high ammonium volatilisation (Mizutani et al. 1986) leading to loss of the ^{14}N isotope and subsequent enrichment of ^{15}N. Highly positive values of $\delta^{15}N$ are indicative of organisms 'feeding' at the top of the food chain. Values for $\delta^{15}N$ of the magnitude found in the present study far exceed that found in plants from other cold environments, such as the sub-Arctic (Karlsson et al. 2000), Alaskan Boreal forest (Schulze et al. 1994) and alpine tundra (Miller and Bowman 2002) environments. The highly elevated ^{15}N values found in the present study are comparable, however, to those found in plants from the sub-Antarctic Macquarie Island at sites where plants received nutrient enrichment from the excrement of humans, seals and scavenging giant petrels (Erskine et al. 1998). The values found in the present study are also comparable to $\delta^{15}N$ values for continental Antarctic bryophytes occurring in the vicinity of bird colonies, where soil $\delta^{15}N$ is also relatively high (13.1 to 25.9‰; (Cocks et al. 1998a). The elevated $\delta^{15}N$ signatures measured in the Bryophyte community are indicative of these communities being tertiary or higher level consumers, rather than primary producers, of N (via enrichment through repeated cycling transfer between tropic levels rather than up a simple tropic chain). The results indicate that these communities do not rely on either soil derived-N or N-fixation as their primary source of N, as lower $\delta^{15}N$ values would be found. Instead they are most likely using animal-derived N, such as penguin guano and, given that penguin guano has a $\delta^{15}N$ signature of approximately 14.6‰ (Robinson 2001) the values measured in the Bryophyte community material also indicate that further enrichment has occurred. Given that the value of $\delta^{15}N$ increases with each trophic level transfer (due to loss of a portion of the lighter isotopic fraction, ^{14}N) it appears that the Bryophyte community is utilising N that has been further enriched, due to repeated plant or microbial use and therefore further loss of ^{14}N, since the guano was deposited. This is consistent with the soil N coming from penguin rookeries that have long since been abandoned. The bryophyte communities described in the present study are each situated in catchment areas containing abandoned penguin rookeries, it is expected therefore that N will now be ^{15}N enriched as it will have passed through additional tropic levels via multiple growth and decomposition cycles.

Plant and soil $\delta^{15}N$ values were greater at the ASPA Meltpuddle site than at Robinson Ridge. The reduced $\delta^{15}N$ values at the Robinson Ridge site are likely to be due to this site receiving a greater proportion of wind-born NH_3 (depleted in ^{15}N), rather than greater N-fixation, as this site is situated close to a large penguin rookery; Odbert Island, which lies approximately 1 km to the west. The closest rookery to the ASPA Meltpuddle site is the Shirley Island rookery, situated 2 km to the west. The ASPA Meltpuddle site is situated, however, very close to an abandoned penguin rookery and the drainage pattern at this site would allow this site to receive nutrients from the abandoned rookery. The combination of the ASPA Meltpuddle site being situated further from an active rookery, and closer to an abandoned rookery, relative to the Robinson Ridge site, helps explain the higher $\delta^{15}N$ values, as this site would be expected to receive less wind-born NH_3 and more ancient guano-derived N sources which have been further ^{15}N enriched via decomposition. The lower soil C/N ratio at the ASPA Meltpuddle site, due to relatively high soil nitrogen contents, suggests the abandoned penguin rookery is a more effective nutrient source.

Differences in environmental conditions between the two sites may have influenced variation in plant biochemical makeup. In particular, two soluble carbohydrates, stachyose and ribitol, which are likely to be utilised as a strategy for tolerance of desiccation and cryoprotection, were found to occur in greater concentrations at the ASPA Meltpuddle site. It may be that either more stressful environmental conditions prevail at this site, or more resources are available for plants to synthesise these compounds.

3.4.2. Resource gradients

The hypotheses that the community gradient is accompanied by moisture and nutrient gradients were supported. These resource gradients were found to operate in opposite directions across the community gradient, with water decreasing and nutrients increasing from the Bryophyte to the Crustose community.

The presence of the water gradient was supported by values for both TWC and $\delta^{13}C$. TWCs and $\delta^{13}C$ values were highest in the Bryophyte community and lowest in the Crustose community, indicating the Bryophyte community is subject to periodic submergence (Chapter 2, section 2.2.1). Periodic submergence of the Bryophyte communities is further supported by field observations.

The nutrient gradient operated in the opposite direction, with highest plant % N in the Crustose community, and lowest levels in the Bryophyte community. Low % N in the Bryophyte community may indicate this community is more nutrient-limited than the other communities. As nitrogen was measured as a percentage of plant tissue dry weight, low % N in the Bryophyte community may also indicate a productivity gradient. That is, the Bryophyte community may not necessarily receive less N, rather it may be that it is more photosynthetically active, and therefore diluting its N reserves. High C/N ratios and high concentrations of soluble carbohydrate contents in this community support the presence of this productivity gradient. The reverse is true for the Crustose community which had high %N and low C/N and soluble carbohydrate concentrations. Other environmental variables, such as water availability, are likely to be limiting carbon fixation in this community.

The combination of these two opposing resource gradients suggest that the Bryophyte community is more strongly nutrient-limited than water-limited, and vice versa for the Crustose community.

3.4.3. Effect of environmental resources on plant diversity in a simple ecosystem

Plant diversity, in this simple ecosystem, changed across the resource gradients. Conditions of high water availability and low nutrient availability, found in the Bryophyte community, supported the Antarctic endemic, *G. antarctici*, and the cosmopolitan *B. pseudotriquetrum* only. The hypothesis that *G. antarctici* is restricted to the bryophyte-dominated end of the community gradient was not supported, however, as this species was present in all three communities, albeit in low levels of abundance in the drier two communities. The hypothesis that the bryophyte-dominated end of the community gradient would be dominated by *G. antarctici* was supported, as *B. pseudotriquetrum*, the only other species found to occur in this community, was 6 and 12 time less abundant in this community at the ASPA Meltpuddle and Robinson Ridge sites, respectively. The remaining two diversity related hypothesis were also supported by the patterns measured, since *C. purpureus* was absent from the bryophyte-dominated end of the community gradient, and *B. pseudotriquetrum* was present across the entire community gradient.

Conditions of low water availability and high nutrient availability, found in the Crustose and Moribund communities, supported low, live bryophyte abundance, but highest species diversity. In these drier communities, along with the presence of crustose lichen and *C. purpureus*, the liverwort *Cephaloziella exiliflora* was also present. The wetter Bryophyte community supported only two bryophyte species.

The vegetation patterns found in my study largely concur with that described in Selkirk and Seppelt (1987). The Selkirk and Seppelt (1987) transect found the lowest, wettest positions (distance: 22.0 and 28.8 m) to have highest water contents and contain *G. antarctici* and *B. pseudotriquetrum* only. *Ceratodon purpureus* occurred only in the drier positions, which my results also support. The major difference between the results of Selkirk and Seppelt (1987) and my study is that I found *G. antarctici* to extend its distribution into relatively dry sites, although only low levels of abundance were observed in these situations. I suggest this difference in vegetation patterns is likely to be due to the very fine-scale methods employed in my study, whereby I have examined numerous small community samples in very fine detail using microscopy techniques.

3.4.4. Effect of environmental resources on plant physiology in a simple ecosystem

Plant biochemical makeup varied along the community and resource gradients. The Bryophyte community, for example, contained highest concentrations of total soluble carbohydrates. These elevated concentrations were largely due to patterns of abundance for the dominant sugars, sucrose and X2. Whilst high concentrations of these sugars are likely to create an osmotic advantage, they are unlikely to be specifically providing protection from desiccation or freezing and probably represent further evidence of the higher productivity in the wetter areas. *Myo*-Inositol was the only soluble carbohydrate, likely to be involved in tolerance of desiccation, that showed a trend toward occurring in higher concentrations in the bryophyte-dominated community. A further investigation of patterns of occurrence of this compound in individual bryophyte species, presented later in this thesis (Chapter 5), supports this compound playing a role in tolerance of desiccation in two of the three bryophyte species studied. Conversely, the Crustose community contained highest concentrations of trehalose and a range of sugar alcohols, namely mannitol, arabitol, ribitol and sorbitol, which are each likely to contribute toward increasing tolerance of desiccation.

As well as containing different soluble carbohydrate profiles, the communities appear to utilise different nutrient sources. The Bryophyte community appears to utilise soil N sources, as similar δ^{15}N values were found in both plants and soils (Figs. 3.1D and 3.5D), and the values (>15) suggest the source to both plants and soils is likely to be guano from the nearby abandoned penguin rookeries. Conversely, the Crustose communities lower δ^{15}N values indicate this community relies on alternative N sources, such as: wind-born NH_3 from active penguin rookeries, atmospheric N deposited in snow and/or nitrogen fixation.

3.4.5. Future vegetation dynamics

The final hypothesis, that the moribund zone would contain live bryophyte material, was supported. Live bryophytes were found in the moribund turf of both the Moribund and Crustose communities. Bryophyte material in moribund turf is generally not visible to the eye, but was detected using the microscopy techniques employed in this study. This study therefore documents live bryophytes occurring in habitats that would not appear to be occupied by live bryophytes upon field observations only. A surprising outcome was the presence of *G. antarctici* in the moribund turf. This species was expected to be restricted to the wettest habitats only, as has been suggested by previous studies (e.g. Selkirk and Seppelt 1987).

Predictions for species dynamics in response to climate change

If conditions become wetter, live bryophytes are likely to increase in distribution. Moribund bryophytes have the potential to regenerate (Melick and Seppelt 1997), and the presence of live bryophyte material in moribund turf further supports this possible scenario. The presence of all four bryophyte species in the moribund turf in the Crustose community provides the potential for maximum species diversity under further changing conditions. It is predicted that if wet habitats increase in area, *G. antarctici* will be advantaged and expand the area it dominates. *Ceratodon purpureus* and *C. exiliflora*, which are currently restricted to dry sites may not have the ability to survive wetter habitats and might shift their distributions out to habitats presently too dry for bryophyte occupation. Distribution of the latter species, *C. exiliflora*, may however be determined by factors other than water availability that contribute toward its overall rarity.

Under drier conditions, live bryophytes are likely to continue to retreat, increasing the moribund bryophyte zone and extent of lichen distribution. *Grimmia antarctici* is predicted to be most severely disadvantaged, as the habits it dominates will recede and potentially disappear. The relatively desiccation tolerant *C. purpureus* (Robinson et al. 2000), and possibly the liverwort, *C. exiliflora*, are most likely to survive a continuation of the present drying trend.

Bryum pseudotriquetrum, which has a relatively broad and consistent distribution, appears to be least affected by changes in resource availability. These results suggest that, regardless of which way climate shift occurs, this species is likely to survive, but will not necessarily become dominant in future communities.

3.5. Conclusions

The community gradient investigated in this study, which covers the entire ecological range of past and present bryophyte occupation, is accompanied by resource gradients. The resource gradients, of water and nutrients, operate in opposing directions across the community gradient. Pure bryophyte communities exist under conditions of high water availability and low nutrient availability. Crustose lichen-dominated communities persist under opposing environmental conditions, of low water availability and high nutrient availability.

Bryophyte species distributions across this community and resource gradient largely concur with the distributions found to occur along the Selkirk and Seppelt (1987) transect. My study has found, however that *G. antarctici* is not necessarily restricted to the wettest habitats, but extends its distribution, albeit in low levels of abundance, into the dry moribund zones. *Grimmia antarctici* is dominant in the wettest communities and likely to be most adversely affected if the current drying trend persists. This highlights conservation issues for this species, as it is endemic to the Antarctic continent.

The presence of bryophyte material in moribund turf supports bryophyte regeneration under a wetter future climate, a topic that is further explored in the following chapter. In addition regenerating turf has the potential to support high species diversity, as all four bryophytes were found to be surviving in this zone.

Chapter 4: Influence of increased water and nutrient availability in an Antarctic terrestrial community

4.1. Introduction

Species distributions, in the Windmill Islands region, coincide with the availability of water and nutrients (Chapter 3), and this appears to be a common trend in Antarctica (Tables 1.3 and 1.4). The low Antarctic temperatures cause most water to be biologically unavailable, in the forms of snow and ice, creating desert conditions. Water availability is thought to be the primary limiting factor for life on this frozen continent (Kennedy 1993b), and has been shown to be the primary determinant of vegetation patterns at both broad- (Broady 1989, Melick et al. 1994a) and fine-scales (Selkirk and Seppelt 1987, Ryan and Watkins 1989), with bryophytes generally showing greater sensitivity to water availability than lichens (Leishman and Wild 2001). Patterns of nutrient availability also play a role in determining vegetation patterns in continental Antarctica (Ryan and Watkins 1989, Hovenden and Seppelt 1995a), particularly with respect to lichens (Hovenden and Seppelt 1995a, Leishman and Wild 2001). Under a climatic warming scenario, it is arguably the indirect changes in key environmental growth variables, such as water and nutrient availability, that will be of greater influence than temperature alone (Chapin 1983, Hobbie and Chapin 1998).

The availability of these two important growth requirements is predicted to change with the onset of climate change (Chapter 1, sections 1.4 and 1.5). A likely scenario is that water, and albeit to a lesser extent, nutrient, availability will increase. A warming trend is likely to cause an increase in water and nutrient availability (Fig. 1.2), as increased ambient temperatures will, at least in the short term, result in an increase in melt-water availability in these ice-dominated environments. Conditions of elevated moisture are likely to be sustained whilst permanent snow and ice reserves, which are crucial to the supply of summer melt-water, remain. Increased precipitation for the Antarctic is predicted (Ye and Mather 1997) and if such precipitation is sufficient to offset depletion of permanent snow and ice reserves, conditions of increased water availability may be sustained (Fig. 1.2). Nutrient availability is also predicted to increase under conditions of climatic warming, as a range of variables associated with low temperatures, such as low rates of mineralisation, currently restrict the availability of nutrients (Chapin 1983). A warmer, wetter climate will thus provide ameliorating growth conditions with elevated nutrient availability and turnover.

This chapter describes a manipulative field experiment designed to test how increased water and nutrient availability affects terrestrial communities in continental Antarctica. Four community types, which occurred along an environmental gradient, from bryophyte-dominated habitat at the edge of a meltlake, to lichen-dominated habitat on the side of a ridge were investigated. The communities corresponded to those described in Chapter 3 and Melick and Seppelt (1997). The communities each received water and/or nutrient additions over two consecutive summer seasons. My main objectives were to determine if: (1) water and/or nutrient availability limits primary production, (2) the flora is more strongly water-limited than nutrient-limited, (3) the background availability of water and nutrients differs between community types and (4) some communities respond more strongly than others to water and/or nutrient additions. A number of physiological and biochemical measurements were made in order to address these questions.

Photosynthetic rates and chlorophyll concentrations were used as surrogate measures of primary productivity (as described in Chapter 2, section 2.2.1.). Under ameliorating conditions of increased water and nutrient availability, both electron transport rates and chlorophyll concentrations were expected to increase.

Nitrogen stable isotopes were investigated as a means of providing insight into nutrient sources. As described in Chapter 2 (section 2.2.2), plants with $\delta^{15}N$ values greater than 15‰ are likely to be utilising guano-derived N from abandoned penguin rookeries. Low $\delta^{15}N$ values are expected for plants receiving volatilised NH_3 from active penguin rookeries and/or fixing atmospheric N.

Degree of habitat submergence was investigated via measurement of carbon stable isotopes (see Chapter 2, section 2.2.1). Cryptogams occupying periodically submerged habitat are expected to show elevated (less negative) $\delta^{13}C$ signatures than those that are not subject to the diffusional limitations of submergence.

Present continental Antarctic communities survive under frozen, desert conditions. Plants are therefore expected to contain compounds, such as certain types of soluble carbohydrates, which provide protection during desiccation and freezing (Roser et al. 1992, Montiel 2000, Robinson et al. 2000). Under conditions of changed water and nutrient availability the soluble carbohydrate composition of these plants may shift. Increased water availability may cause a decline in compounds required for tolerating desiccation.

The overall aim of the study was to provide an insight into how Antarctic terrestrial communities are likely to respond to climate change, under a warmer, wetter climate scenario. I predict that water and nutrient additions will increase plant primary productivity in these communities. Based on the overall emphasis in the literature, I further predict that plants will respond more strongly to water-additions than nutrient-additions. The experimentally manipulated communities are likely to be differently limited by water and nutrients and show variation in the strength and nature of their response to these additions. This experiment is one of the only multi-season manipulative field experiments that has been conducted in continental Antarctica (Chapter 1 and Robinson et al. 2003) and therefore provides a particularly important contribution to our understanding of how plants in this environment are likely to respond to climate change.

4.2. Methods

4.2.1. Experimental design

This experiment was conducted at the ASPA Meltlake site (see Chapter 2, section 2.1, for site description, map and photograph). Within the site, four community types were identified based on the percentage cover of four key community components: healthy bryophytes, moribund bryophytes, crustose lichens and macrolichens of the genus *Usnea* (Table 4.1). Three communities, Bryophyte, Moribund and Crustose, correspond to the communities of the same name in Chapter 3. The fourth community, *Usnea*, extends beyond the Chapter 3 community gradient and corresponds with Group 2.5 (Transitional, Foliose lichen-dominated, *Usnea*) in Melick and Seppelt (1997). This latter community is considered to be the earliest indicator of the presence of extant bryophyte communities, which thrived when conditions were moister.

Material was comparable within each community and the dominant bryophyte was *Grimmia antarctici* across the site. *Grimmia antarctici* is increasingly overgrown by lichens along the community gradient, however, and becomes only a minor community component within the lichen-dominated *Usnea* community. Physiological natural variation is therefore expected between communities and this variation was addressed in chapter 3. The present chapter focuses on the physiological effects of a set of climate change simulation treatments across the community gradient. Differences between communities are noted, but the aim of this chapter is to compare the effect of treatments within each community. I therefore compare control quadrats between communities, establishing a baseline for each community. Treatment effects can then be compared within communities and the magnitude of treatment effects can be compared between communities.

Table 4.1: Distinguishing characteristics of the four community types used in the field water and nutrient enrichment experiment. Percent cover was estimated using a 25x25 cm quadrat.

Community	Distinguishing characteristics	Photo of typical quadrat
Bryophyte	Green, healthy bryophytes dominant (>90% cover)	
Moribund	Approximately 50% cover moribund bryophytes (predominantly ridges) and 50% cover healthy bryophytes (predominantly valleys).	
Crustose	Moribund bryophytes dominant with approximately 50% cover encrusted with crustose lichens.	
Usnea	Thin crust of moribund bryophytes with macrolichens of the genus *Usnea* dominant (>50% cover).	

The four communities occurred along a gentle slope, with an easterly aspect, between the meltlake edge and the side of a small ridge. The Bryophyte community occurred closest to the meltlake, and the other three communities were positioned with increasing distance from the meltlake edge, in the order of: Moribund community, Crustose community and, furthest from the meltlake, the *Usnea* community, which was closest to the ridge (Fig. 4.1).

Figure 4.1: Position of the four communities, within the ASPA Meltlake site, relative to the meltlake (left) and the ridge (right).

Within each community, 32 quadrats (25 x 25 cm) were randomly assigned one of the following four treatments: (1) no-treatment (NT-), (2) water only (W-), (3) nutrient only (N-), or (4) water & nutrient (WN-). The two water addition treatments (W- and WN-) had 500 ml of meltlake water applied approximately every two days during the 1998/99 and 1999/00 summer seasons (December - February). To avoid beading of the applied water off the vegetation surfaces, and therefore maximise the effectiveness of the water additions, each quadrat was first pre-soaked using a fine, firm, even spray of water from a pressurised spray bottle. The remaining treatment water was then slowly and evenly poured over the area of the quadrat.

Quadrats receiving nutrient additions (N- and WN-) had 10 g of slow release fertiliser beads (Osmocote, Scotts Australia Pty. Ltd., Castle Hill, NSW, Australia) applied at the start of the treatment period (15/12/99). A low phosphorous Osmocote variety was chosen, composed of 18% nitrogen, 4.8% phosphorous and 9.1% potassium (for a more detailed nutrient composition, refer to Table 4.2).

Table 4.2: Nutrient composition of Osmocote fertiliser used in field nutrient enrichment experiment (Variety name: Indoor, courtyard and balcony). Source: Osmocote product information.

Nutrient	% Content
Total Nitrogen (N)	18.0
Nitrogen (N) as nitrate form	7.5
Nitrogen (N) as ammonium form	10.5
Total Phosphorus (P)	4.8
Phosphorus (P) as water soluble	4.3
Phosphorus (P) as citrate soluble	0.5
Potassium (K) as potassium sulphate	9.1
Sulphur (S) as sulphate	4.0
Calcium (Ca) as calcium phosphate and calcium sulphate	1.0
Organic resin coating	9.1

4.2.2. Field measurement of chlorophyll fluorescence

Towards the end of the treatment period (14-15/2/00), measurements of PSII electron transport rates (ETR) were conducted using chlorophyll fluorescence. Measurements were taken under consistent light conditions, between 2 & 4 pm. Six measurements (each 1cm diameter) were conducted within a randomly selected quadrat from each community and treatment. Measurements were performed using a MINI-PAM equipped with a micro leaf clip (Walz, Germany). Settings were optimised for the plant material (measuring intensity 6, gain 3, damping 3, saturating pulse intensity 6 and saturating pulse width 0.8 s).

4.2.3. Laboratory analysis of chlorophyll, nutrients, stable isotopes and soluble carbohydrates

At the end of the 15-month treatment period (3–8/3/00), representative community samples were collected for pigment and nutrient analyses. From the sixteen treatment and community groups, seven replicate quadrats were sampled over a 5-day period. Samples needed to be transported to the laboratory as quickly as possible and were therefore collected in subsets of 16, each subset including one replicate from each community and treatment type (Fig. 4.2). Samples of approximately 4 cm^2 were collected from the centre of each quadrat. Each sample was divided into three; approximately 1 cm^2 area comprised the pigment and turf water content (TWC) samples for which the surface portion (top 2-3 mm) was reserved for pigment analyses and the base was used to estimate moisture content. Of the remaining larger portion (approximately 3 cm^2), the top 1 cm was divided into two for determination of soluble carbohydrate and nutrient contents.

For each sample TWC, chlorophyll, nutrient (N, P and C), stable isotope (^{15}N and ^{13}C) and soluble carbohydrate contents were determined, as described in sections 2.2.3. to 2.2.7.

4.2.4. Statistical Analysis

For each of the biological parameters measured, a two-way ANOVA was conducted, testing for community differences, treatment effects and treatment*community interactions. Transformations of the data were required in some cases to ensure an acceptable level of normality and homoscedacity (details of transformations performed are provided in Tables 4.3 – 4.6).

The significance of treatment*community interactions determined the statistical procedures performed. When the treatment*community interaction was not significant, indicating the communities are each showing a statistically similar treatment response, the effects of treatment and community alone were investigated using ANOVA. Where the interaction between treatment and community was significant, indicating that the

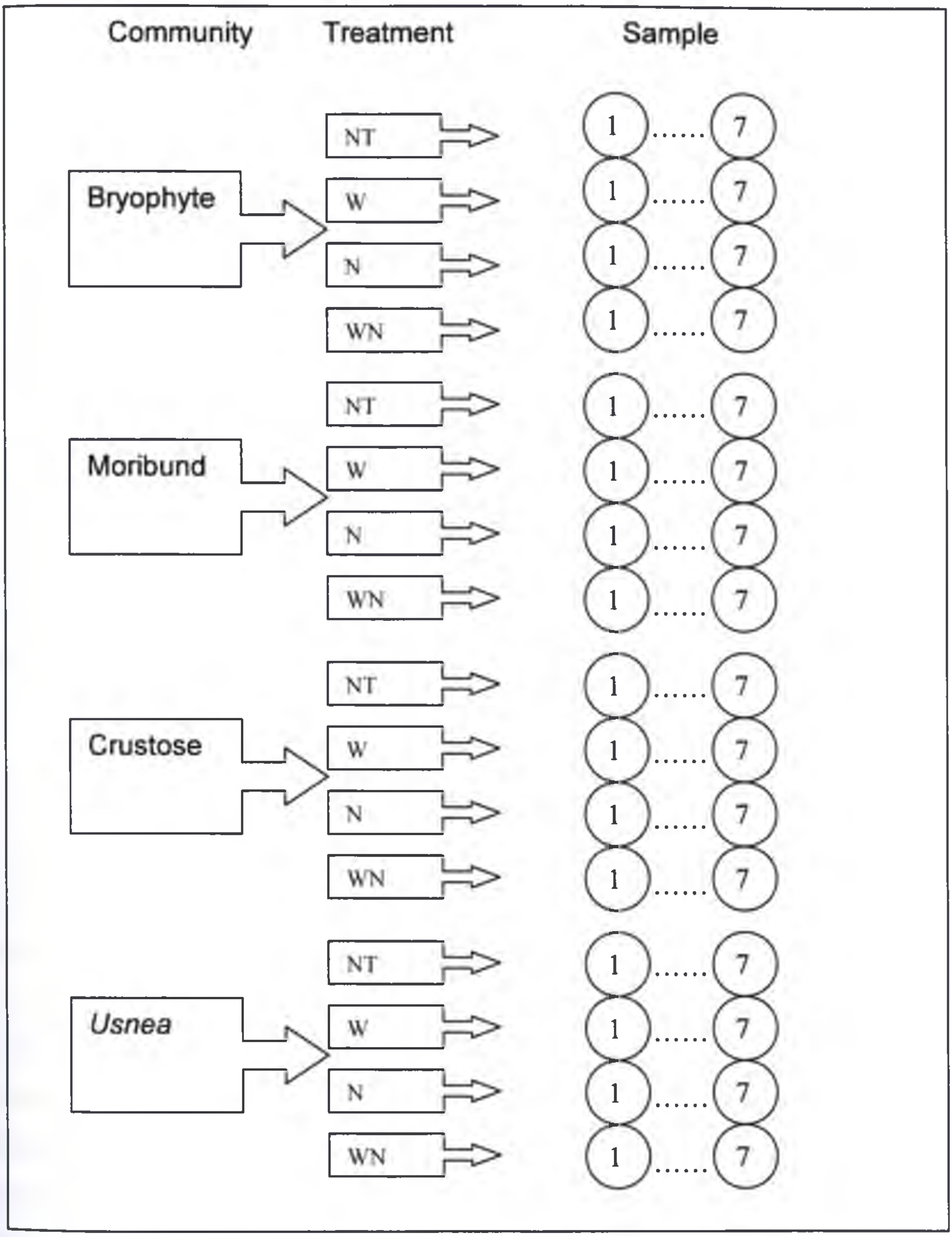


Figure 4.2: Schematic representation of sample collection. Transport of samples from the field to the laboratory needed to be conducted quickly, samples were therefore collected in subsets of sixteen, which were comprised of one replicate sample from each of sixteen treatment/community groups. Seven subsets were collected over the period 3/3/00 to 8/3/00.

communities are showing variation in their treatment response, the effects of treatment and community alone were not investigated within the ANOVA model.

In order to identify which pairs of means were significantly different, pairwise tests (Student's t tests) were conducted for data sets where significant differences were detected using ANOVA. Again, the significance of the treatment*community interaction determined the subsequent statistical procedure. Where the treatment*community interaction was significant, pairwise tests (Student's t) were conducted for individual means (sixteen groups, 24 pairwise tests; 6 treatment pairs within each of the four communities and vice versa). For situations where the treatment*community interaction was not significant, it is not valid to conduct pairwise tests for each pair. In these cases, where individual effects of treatment and/or community were significant, means within treatments and/or communities were effectively "lumped", and significant differences between overall pairs (four community groups and/or four treatment groups, 6 pairwise tests) were determined using Student's t.

The Student's t tests were used in conjunction with the Bonferroni procedure, to reduce the probability of a false result, by adjusting the table-wide p-value to keep it constant, at 0.05 (Rice 1989). The α level was adjusted according to the number of pair wise comparisons ($\alpha = 0.05$ / number of pair wise comparisons). In most cases, the number of pairs was 6, reducing the α level to 0.008. In the few cases where 24 pairs were compared, the α level was set at 0.002. As the Bonferroni procedure reduces the α level, and in turn the chance of identifying significant pairs, it is argued that the Bonferroni procedure can sometimes cause biologically important difference to be overlooked (Moran 2003). For this reason, any additional pairs of means that are significant at $\alpha = 0.05$ are reported. The results of these pairs must be interpreted with caution, but are worth noting, as they are potentially biologically significant.

The soluble carbohydrate data contained many zero values and values for trace concentrations. For carbohydrates where these type of data were common, (stachyose, arabitol, ribitol, mannitol, sorbitol, *myo*-inositol, X2 and X4) 2-way ANOVA was unable to be performed (as the residual distribution deviated significantly from normal and suitable transformations could not be found). In these cases, one-way ANOVA was conducted to investigate the effect of treatment only within each of the four communities.

A summary of the ANOVA results, including details of any transformations performed, are provided in Tables 4.3 – 4.6. Results of Student *t* tests are given in Appendix 2. Unless otherwise stated, data reported are mean values ± standard error of the mean.

4.3. Results

4.3.1. Photosynthetic efficiency

During the second summer of treatment, photosynthetic ETR was similar in the control group (NT-) across the communities, and all communities showed a positive response to the water and/or nutrient additions (Fig. 4.3). Several notable community differences were found, as the strength and nature of the treatment response differed across communities (treatment*community interaction: $P = 0.0003$; Table 4.3). The treatment response was weak (not significant) in the Moribund and *Usnea* communities, and strongest in the Crustose and Bryophyte communities. The strongest response to treatments was found in the Crustose community, where ETRs in all treatment groups were greater than 4-fold higher than the untreated control ($P<0.002$; Appendix 2). This community showed characteristics of being more strongly water-limited than nutrient-limited, as the two water-treatments (W- and WN-) had significantly higher ETRs than the nutrient-only treatment ($P<0.002$ and 0.05, respectively; Appendix 2). Conversely, the Bryophyte community, which also showed a significant treatment response, appeared to be more strongly nutrient-limited than water-limited, as ETRs were highest in the two nutrient treatments, where rates were more than 2-fold higher than the untreated control (N- $P<0.05$, WN- $P<0.002$; Appendix 2). In this community the effect of water alone was not significant ($P>0.05$; Appendix 2).

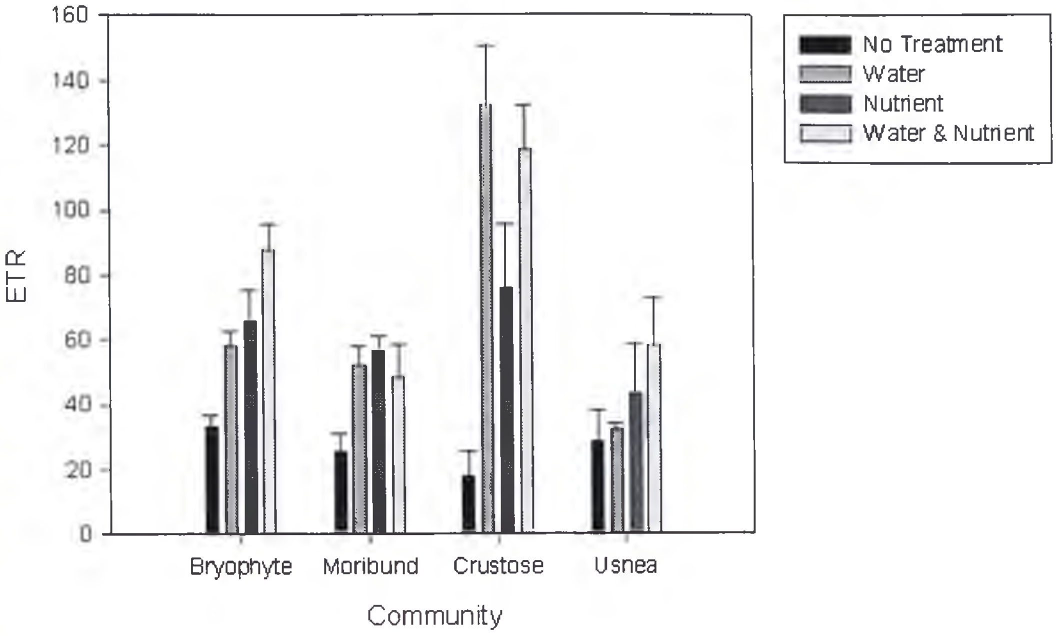


Figure 4.3: Influence of the four water and nutrient treatments on photosynthetic electron transport rate (ETR) across the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*). Measurements were made on 14-15/2/00, after 14 months of treatment. Bars represent mean ± sem, n = 6.

Table 4.3: Summary of 2-way ANOVA results for ETR, total chlorophyll concentration, chlorophyll a/b ratio and turf water content.

Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	Prob > F
ETR	None	Whole Model	15	80	8.5041	<0.0001
		Treatment	3		16.6085	<0.0001
		Community	3		13.7313	<0.0001
		Treatment*Community	9		4.0602	0.0003
Total Chi	Log10	Whole Model	15	96	5.3245	<0.0001
		Treatment	3		10.4628	<0.0001
		Community	3		13.6611	<0.0001
		Treatment*Community	9		0.8329	0.5876
Chi a/b	None	Whole Model	15	96	3.3884	0.0001
		Treatment	3		1.2177	0.3075
		Community	3		13.2301	<0.0001
		Treatment*Community	9		0.8314	0.5889
TWC	Log 10	Whole Model	15	96	1.7162	0.0602
		Treatment	3		0.9719	0.4093
		Community	3		6.0204	0.0008
		Treatment*Community	9		0.5295	0.8498

4.3.2. *Turf chlorophyll and water content*

Nutrient additions had a positive effect on concentration of total chlorophyll (nmol $ml^{-1}g^{-1}$ dry wt.), particularly in the Moss and Crustose communities (treatment effect: $P<0.0001$; Table 4.3) where total chlorophyll concentrations were 2- to 3-fold greater in the two nutrient-treatment groups (N- and WN-), compared to the corresponding non-nutrient treated groups (NT- and W-; community effect, $P<0.0001$; Table 4.3; Fig.4.4A). The Moribund and *Usnea* communities, conversely, showed a relatively weak treatment response. As well as treatment response differences between the communities, overall concentration of total chlorophyll differed between the communities, with Crustose having the highest and Moribund the lowest overall concentrations ($P<0.008$; Appendix 2).

Chlorophyll a/b ratios, which ranged from approximately 1.5 to 3.0, showed significant differences between communities, but there was no effect of treatment (Table 4.3 and Fig. 4.4B). Ratios were highest in the lichen-dominated Crustose and *Usnea* communities ($P<0.008$; Appendix 2).

Turf water content (TWC; g H_2O g^{-1} dry wt.) ranged from just less than 1 to slightly over 2 g H_2O g^{-1} dry wt. (Fig. 4.4C). Water and/or nutrient additions had no significant effect on TWC, but there was significant variation between the communities (Table 4.3), with the Crustose and Bryophyte communities having higher TWCs than the relatively dry Moribund and *Usnea* communities ($P<0.008$ and 0.05, respectively; Appendix 2).

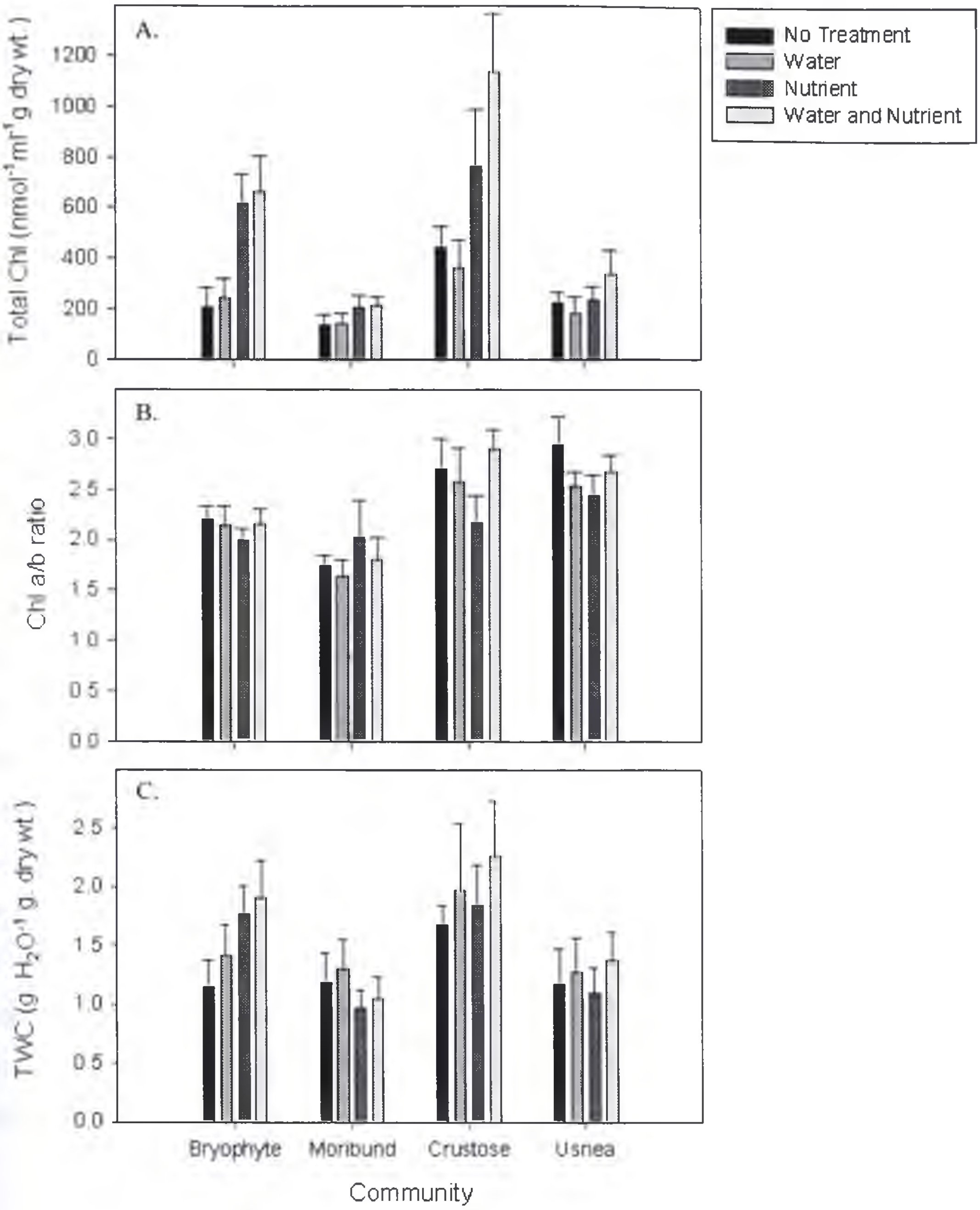


Figure 4.4: Influence of the four water and nutrient treatments on chlorophyll composition and turf water content of plant material from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*): (A) total chlorophyll concentration (nmol ml^{-1} g^{-1} dw), (B) Chlorophyll a/b ratio, (C) turf water content (TWC; g H_20 g^{-1} dw). Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Data calculated on dry weight basis. Bars represent mean ± sem, n = 7. Note y-axes are different.

4.3.3. Nutrients

Nutrient additions (N-) enhanced weight %N in all communities except the Moribund community (overall model: $P < 0.0001$; treatment* community interaction: $P = 0.0340$; Table 4.4; Fig. 4.5). In all three communities showing this response, the nutrient-only additions (N-) produced %N levels that were significantly higher than both the non-nutrient treated groups (NT- and W-, $P<0.002$ and 0.05, respectively; Appendix 2). In the Crustose community, nutrient only additions also elevated %N significantly more than the combined water and nutrient additions ($P<0.002$; Appendix 2). The *Usnea* community was the only community in which the combined water and nutrient treatment (WN-) enhanced %N to levels higher than the untreated control (NT-, $P<0.05$; Appendix 2).

Elevated water and/or nutrient availability did not significantly alter %P or %C, but significant community differences for these variables were identified (Table 4.4). Percent P showed a strong community gradient (community effect: $P<0.0001$; Table 4.4), with a greater than 20-fold increase from the Bryophyte to the *Usnea* community ($P<0.008$; Appendix 2; Fig. 4.5). Percent N was also lowest in the Bryophyte community ($P<0.002$; Appendix 2), and generally highest in the Crustose community, where control levels (NT-) were significantly higher than all communities except Moribund ($P<0.002$; Appendix 2). Community differences in %C were less well pronounced, but were significant (community effect: $P = 0.0008$; Table 4.4), with levels highest in the Moribund community and lowest in the *Usnea* community ($P<0.008$; Appendix 2).

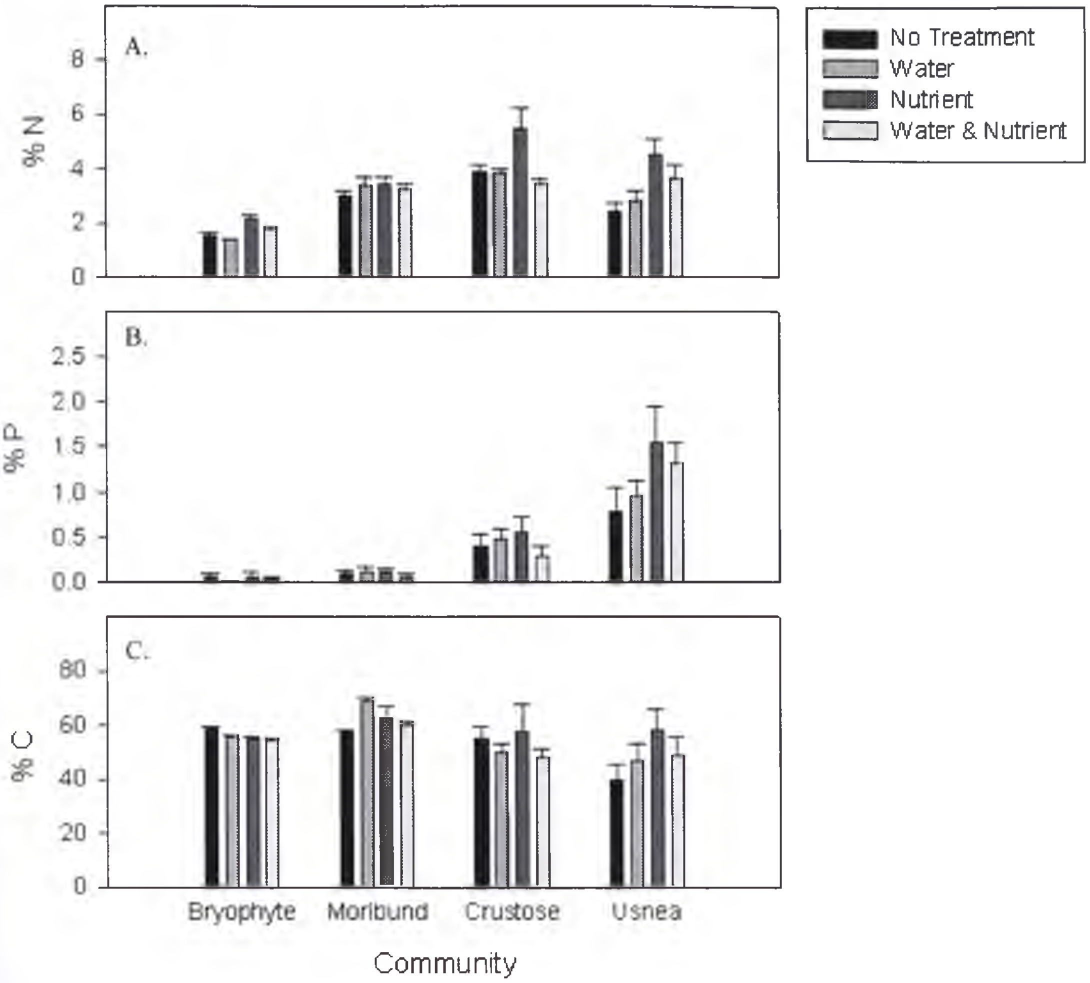


Figure 4.5: Influence of the four water and nutrient treatments on nutrient content of plant material from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*), calculated as percent dry weight: (A) nitrogen, (B) phosphorous and (C) carbon. Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Bars represent mean ± sem, n = 5-7. Note y-axes scales are different.

Table 4.4: Summary of 2-way ANOVA results for nutrient variables (%N, %P, %C, C/N, N/P, δ^{15}N and δ^{13}C).

Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	Prob > F
% N	Log10	Whole Model	15	81	17.5206	<0.0001
		Community	3		68.3384	<0.0001
		Treatment	3		12.9166	<0.0001
		Community*Treatment	9		2.1529	0.034
% P	Square Root	Whole Model	15	82	14.553	<0.0001
		Community	3		68.1251	<0.0001
		Treatment	3		1.1904	0.3186
		Community*Treatment	9		1.102	0.3707
% C	None	Whole Model	15	82	2.2188	0.0117
		Community	3		6.1293	0.0008
		Treatment	3		1.3214	0.273
		Community*Treatment	9		1.091	0.3786
δ^{15}N	Log 10	Whole Model	15	82	2.8606	0.0012
		Community	3		11.9305	<0.0001
		Treatment	3		0.6365	0.5936
		Community*Treatment	9		0.5974	0.7957
δ^{13}C	None	Whole Model	15	82	19.8089	<0.0001
		Community	3		93.0691	<0.0001
		Treatment	3		0.9378	0.4263
		Community*Treatment	9		0.7446	0.6671

4.3.4. Stable Isotopes

Water and/or nutrient additions did not significantly alter stable isotopic signatures for ^{15}N or ^{13}C (Table 4.4), indicating the fertilizer did not significantly affect δ^{15}N, nor did the watering regime significantly alter δ^{13}C (Fig. 4.6). There was, however, significant community variation in stable isotopic signatures (community effect: $P = <0.0001$; Table 4.4). Variation between communities was primarily due to distinctions in δ^{13}C, rather than δ^{15}N. The most notable community distinction found for δ^{15}N were the Crustose community values, which were significantly more positive than the other three communities ($P<0.008$; Appendix 2). Much stronger community differences occurred in δ^{13}C signatures, for which each community was significantly different to the others ($P<0.008$; Appendix 2), with values highest (least negative) in the Bryophyte community and lowest (most negative) in the *Usnea* community.

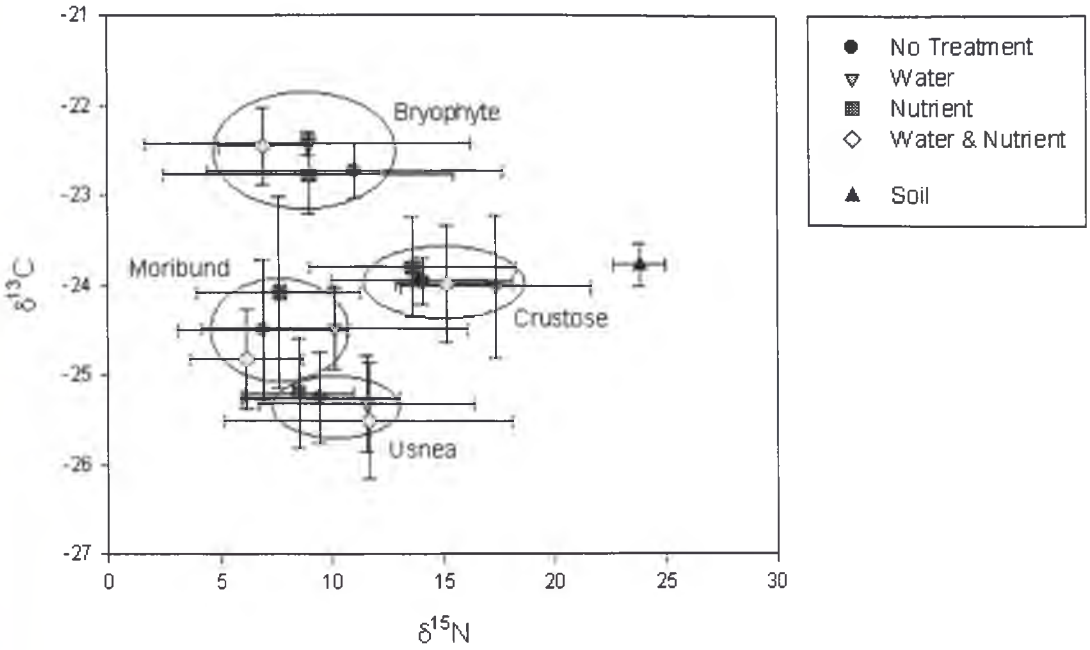


Figure 4.6: $\delta^{13}C$ and $\delta^{15}N$ values for untreated soil and plant material collected from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*). Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Data points represent mean ± sem, n = 5-7.

4.3.5. Soluble Carbohydrates

Soluble carbohydrates can provide mechanisms for cryoprotection and tolerance of desiccation in plants, and are likely to aid plant survival in this frozen desert environment. I have investigated the effect of simulated ameliorating conditions, of increased water and nutrient availability, on soluble carbohydrate contents to determine if climate change is likely to causes a shift in the composition of these compounds and therefore a change in the strategies used by these organisms to survive the dry, frozen Antarctic environment.

Eleven identified and three unidentified soluble carbohydrates were detected in the experimental plant material (Figs. 4.7 – 4.9). Two soluble carbohydrates occurred in very high concentrations (16-25 mg g^{-1} dw): arabitol and the unknown X2, four were found in high concentrations (6-15 mg g^{-1} dw): glucose, fructose, sucrose and X3, four in intermediate concentrations (3-5 mg g^{-1} dw): stachyose, glycerol, mannitol and X4, and four were found in low concentrations (0-2 mg g^{-1} dw): trehalose, ribitol, sorbitol and *myo*-inositol.

The simulated ameliorating conditions significantly altered fructose, ribitol and X2 contents (Tables 4.5 & 4.6). Water additions enhanced fructose contents (treatment effect: $P = 0.0109$; Table 4.5), with concentrations in the water-only (W-) and the combined water and nutrient (WN-) treatments significantly higher than the control group ($P<0.05$; Appendix 2). Ribitol and X2 showed significant treatment responses in the *Usnea* and Bryophyte communities, respectively ($P = 0.0268$ and 0.0273, respectively; Table 4.6). The *Usnea* community showed enhanced Ribitol concentrations in response to the combined water and nutrient additions (WN-) compared to the addition of water only ($P<0.008$; Appendix 2). In the Bryophyte community the addition of water only (W-) enhanced X2 concentrations, while nutrient additions resulted in a reduction of X2 ($P<0.008$; Appendix 2).

Soluble carbohydrate compositions varied between community types (total soluble carbohydrate community effect: $P < 0.0001$; Table 4.5; Fig. 4.7A), with total soluble carbohydrate concentrations lowest in the Crustose community and highest in the Bryophyte community ($P<0.008$; Appendix 2). Three main patterns of abundance for soluble carbohydrates were observed. Firstly, some soluble carbohydrates showed a community gradient that was highest in the moss-dominated communities and lowest in the lichen-dominated communities. Soluble carbohydrates showing this pattern included the dominant identified soluble carbohydrates, sucrose, fructose and glucose (Fig. 4.7; $P<0.008$; Appendix 2), as well as two of the unidentified soluble carbohydrates, X2 and X3 (Fig. 4.9; $P<0.008$; Appendix 2). The opposite pattern was found for a suite of sugar alcohols (arabitol, mannitol, ribitol and sorbitol; Fig. 4.8), which were each most abundant in the *Usnea* community, and either absent or found only in trace amounts in the Bryophyte and Moribund communities. Finally, a third pattern of abundance was observed for trehalose, stachyose, glycerol and X4, which occurred in highest concentrations in the two intermediate communities (Figs. 4.7-9).

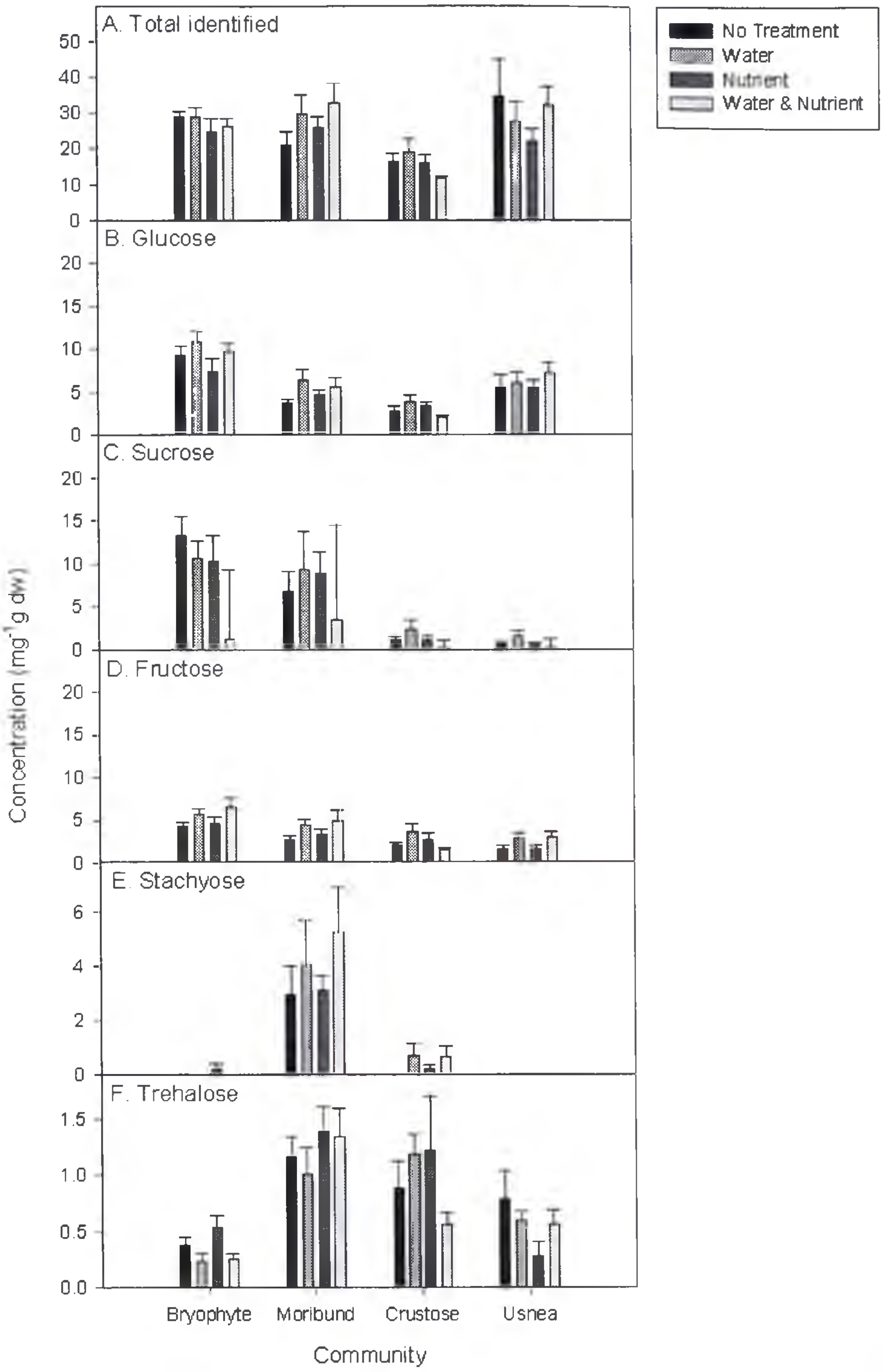


Figure 4.7: Influence of the four water and nutrient treatments on the concentration of A. total identified soluble carbohydrates, B. glucose, C. sucrose, D. fructose, E. stachyose and F. trehalose, for plant material collected from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*). Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Bars represent mean ± sem, n = 7. Y-axes are different.

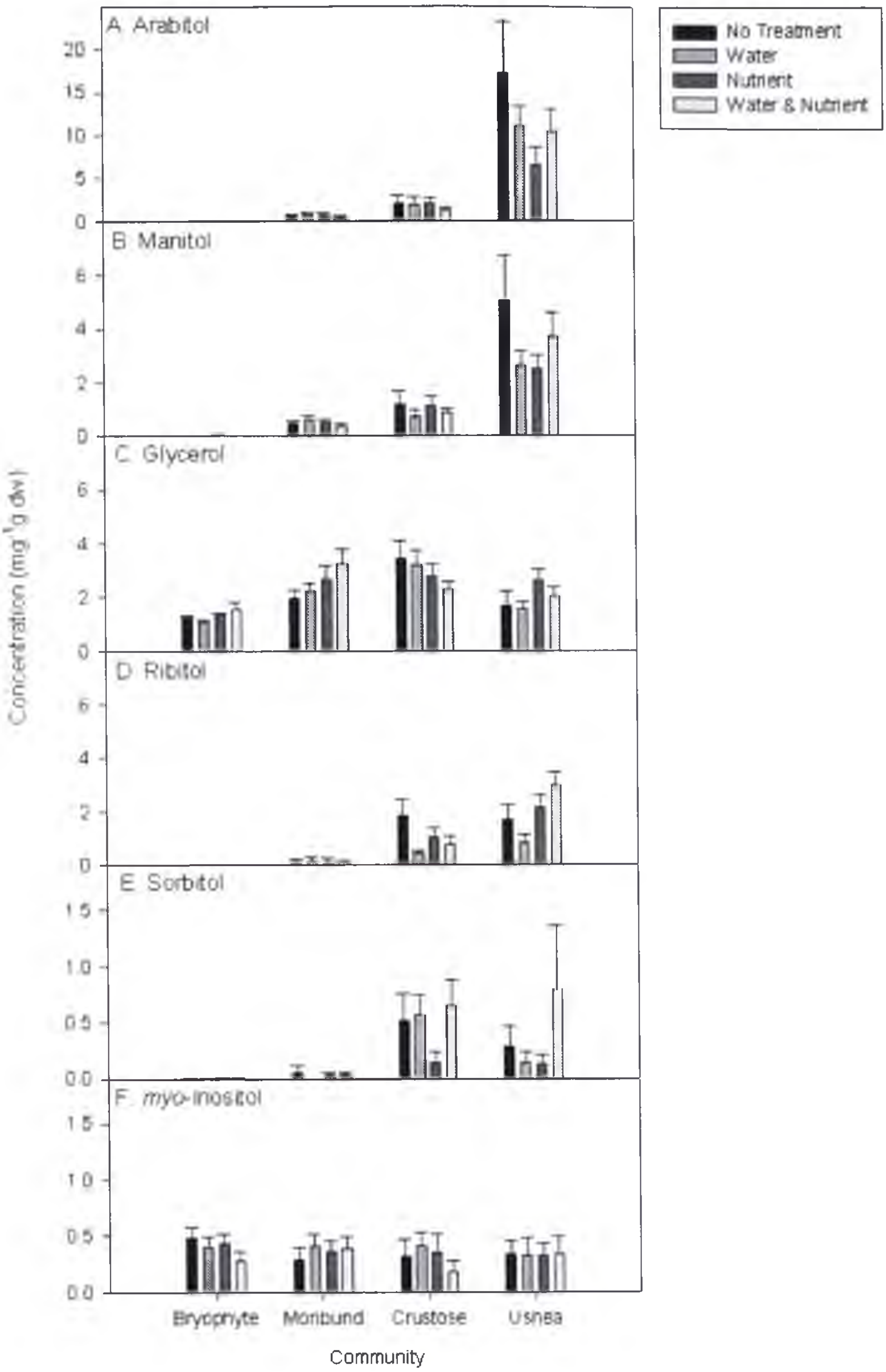


Figure 4.8: Influence of the four water and nutrient treatments on concentration of sugar alcohols: A. arabitol, B. mannitol, C. glycerol, D. ribitol, E. sorbitol and F. *myo*-Inositol, for plant material collected from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*). Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Bars represent mean ± sem, n = 7. Y-axes are different.

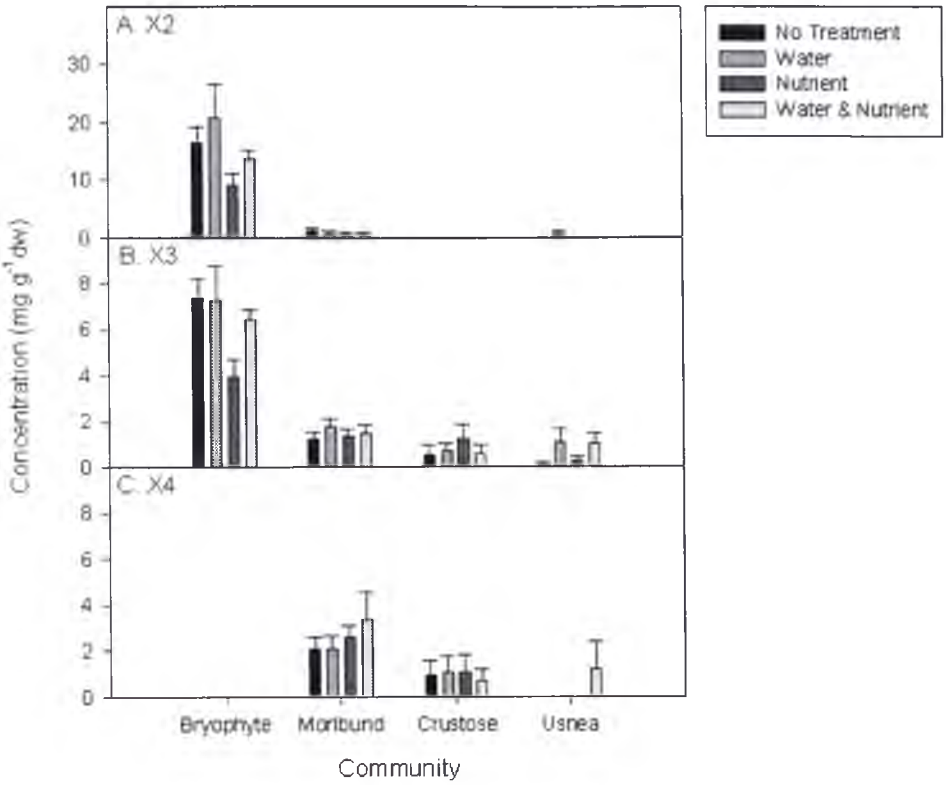


Figure 4.9: Influence of the four water and nutrient treatments on concentration of unidentified soluble carbohydrates: A. X2, B. X3, C. X4, for plant material collected from the four experimentally manipulated communities (Bryophyte, Moribund, Crustose and *Usnea*). Samples were collected after 15 months treatment with water, nutrients, water plus nutrients or no treatment. Bars represent mean ± sem, n = 7. Y-axes are different.

Table 4.5: Summary of 2-way ANOVA results for soluble carbohydrates.

Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	*P*
Glucose	Log 10	Whole model	15	96	6.1297	<0.0001
		Treatment	3		1.6806	0.1763
		Community	3		26.557	<0.0001
		Treatment*Community	9		0.8035	0.614
Fructose	Square Root	Whole model	15	96	4.7709	<0.0001
		Treatment	3		3.9211	0.0109
		Community	3		17.566	<0.0001
		Treatment*Community	9		0.7893	0.6268
Sucrose	Square Root	Whole model	15	96	9.0701	<0.0001
		Treatment	3		0.38	0.7676
		Community	3		42.703	<0.0001
		Treatment*Community	9		0.7558	0.6571
Trehalose	Square Root	Whole model	15	96	3.8426	<0.0001
		Treatment	3		0.306	0.821
		Community	3		13.873	<0.0001
		Treatment*Community	9		1.678	0.1048
Glycine	Square Root	Whole model	15	96	3.4166	0.0001
		Treatment	3		1.0603	0.3697
		Community	3		12.039	<0.0001
		Treatment*Community	9		1.3279	0.2328
X3	Square Root	Whole model	15	96	14.819	<0.0001
		Treatment	3		1.8395	0.1452
		Community	3		67.842	<0.0001
		Treatment*Community	9		1.4706	0.1699
Total ID	Square Root	Whole model	15	96	2.2875	0.0081
		Treatment	3		0.5257	0.6656
		Community	3		8.3721	<0.0001
		Treatment*Community	9		0.8466	0.5754

Table 4.6: Summary of 1-way ANOVA results for soluble carbohydrate data, testing for treatment effects in specific communities specified in parentheses.

Variable	Transformation	DF (model)	DF (error)	F Ratio	*P*
Stachyose (Mori)	None	3	24	0.6684	0.5797
Arabitol (Mori)	None	3	24	0.448	0.7210
Arabitol (Crust)	Square Root	3	24	0.1548	0.9256
Arabitol (*Usnea*)	Square Root	3	24	1.1713	0.3413
Ribitol (Crust)	Square Root	3	24	2.6507	0.0717
Ribitol (*Usnea*)	None	3	24	3.6476	0.0268
Mannitol (Mori)	None	3	24	1.0837	0.3749
Mannitol (Crust)	Square Root	3	24	0.3612	0.7815
Mannitol (*Usnea*)	Square Root	3	24	0.7039	0.5590
Sorbitol (Crust)	Square Root	3	24	1.4933	0.2416
Myo-Inositol (Bryo)	None	3	24	0.9573	0.4289
X2 (Bryo)	Log 10	3	24	3.6273	0.0273
X4 (Mori)	Square Root	3	24	0.5839	0.6313

4.4. Discussion

On this desert continent, water is considered to be the most limiting environmental parameter to plant life (Chapter 1, section 1.4), more so even than the direct limitations associated with the exceptionally low temperatures that dominate this ecosystem. It was therefore expected that increased water availability would be most influential and that the addition of nutrients, which are generally not considered limiting (Chapter 1, section 1.5; Table 1.4), would have a secondary, but possibly synergistic, effect. My study shows some support for water-limitations, but surprisingly, several indications that these communities also experience nutrient-limitations. Background availability of the two manipulated environmental variables occurred in opposing environmental gradients across the site, producing differences in availability of these resources between the communities. These gradients of resource availability were likely to have influenced the differences in treatment-response that were found across the communities.

In this discussion I will present three main aspects of the findings of this study. Firstly I will describe the environmental gradients that occurred across the site and discuss how these gradients support the hypothesis that the background availability of water and nutrients differs between community types. Secondly I will highlight community differences in treatment-response, which support the hypothesis that some communities would respond more strongly than others to water and/or nutrient additions. Finally, I will discuss how my study offers support for the hypotheses that water and/or nutrient availability limit primary production, but does not support the hypothesis that the flora is more strongly water-limited than nutrient-limited.

4.4.1. Environmental gradients

Background availability of water and nutrients differed between the communities. These differences were largely determined by two opposing environmental gradients across the site, one a water gradient, the other a nutrient gradient as shown in Chapter 3. The presence of these gradients supports the hypothesis that the background availability of water and nutrients differs between community types.

Water gradient

As the site was situated on the edge of a meltlake, a moisture gradient occurred across the site, with the Bryophyte community occupying the lowest-lying, wettest habitat and the *Usnea* community the highest and driest. Community patterns of ^{13}C support the presence of this gradient. More positive $\delta^{13}C$ values are indicative of less photosynthetic isotopic fractionation, resulting from diffusional limitations reducing the concentration of CO_2 reaching the site of Rubisco (see section 2.2.1). Diffusion is more limited when plants are submerged by water, and $\delta^{13}C$ values therefore increase, as has been shown in *Sphagnum trinitense* (Proctor et al. 1992). The relatively high $\delta^{13}C$ found in the Bryophyte community represents a cumulative signature, reflecting a tendency for periodic submergence during the summer melt. The $\delta^{13}C$ community patterns therefore likely reflect a submergence gradient, and field observations strongly support the occurrence of periodic submergence in the Bryophyte community during the growing season.

Plant soluble carbohydrate compositions also concurred with the presence of a site water gradient. Several soluble carbohydrate compounds, which are found in highly desiccation tolerant organisms, were either absent or found only in very low concentrations in the Bryophyte community (e.g. stachyose, arabitol, ribitol, mannitol and sorbitol), indicating the Bryophyte community habitat is not subject to as severely desiccating conditions as other communities in which these compounds were more abundant. Despite this latter community being less likely subject to desiccating conditions, species level investigations presented later in this thesis (Chapter 5) support bryophyte species showing a relationship between tolerance of desiccation and soluble carbohydrate concentrations (Figs. 5.6 and 5.7).

Values for $\delta^{13}C$ provided stronger support for the presence of a moisture gradient occurring across the site than did turf water contents, which did not support the presence of a water gradient. It is likely, however, that for a single measurement interval $\delta^{13}C$ is a better indicator of plant moisture availability over the season, as it provides cumulative evidence of submergence. Turf water content is an instantaneous measurement and does not necessarily reflect water availability for the majority of the growth season. I suggest that the anomaly between TWC and $\delta^{13}C$ is not due to the lack of a gradient, but instead reflects the timing of sample collection and site topography.

Timing of sample collection is likely to have reduced the effectiveness of TWC as an indicator of moisture availability. Samples were collected late in the season, by which time the level of water in the meltlake had dropped and the water had frozen; leaving the Bryophyte community relatively dry and at a seasonally low level. Moreover sample collection occurred after snowfall, and snow accumulation on the community surfaces therefore resulted in elevated moisture levels across all communities at that time.

Site topography is likely to have contributed toward the relatively high moisture contents found in the Crustose community and $\delta^{13}C$ data suggest that this represents the second most submerged community (Fig 4.6). This community was situated on a relatively flat, terraced section in the middle of the site (Fig. 4.1), causing the snowfall mentioned above to accumulate on this community. I therefore suggest that the turf water content data was collected at a time when the Bryophyte community was drier than usual and the Crustose community wetter than usual, and therefore is not necessarily representative of the water contents of these communities for the majority of the growing season. Despite the lack of support by the TWC data, the presence of a water gradient is overall supported by $\delta^{13}C$, soluble carbohydrates and field observations.

Nutrient gradient

An abandoned penguin rookery was located at the top of the low rocky ridge that the site was situated on. The rookery is similar to that described by Hovenden and Seppelt (1995a), which lies approximately 1km East of the present site. These abandoned rookeries are known to provide a significant nutrient source to plants in Antarctic terrestrial communities (Tatur and Myrcha 1989, Hovenden and Seppelt 1995a). I suggest this rookery provides a significant nutrient-source for the site and therefore underlies the nutrient gradient found to operate across the site. Nutrient source can be determined via examination of nitrogen stable isotopic values, as plant $\delta^{15}N$ is a function of the $\delta^{15}N$ of the source (Handley and Raven 1992).

Soil in the vicinity of the site of the present study also had high $\delta^{15}N$ (23.84±1.18‰, n=6, as described in Chapter 3). These high $\delta^{15}N$ values indicate that the nutrient source for this community is likely to be the nearby abandoned penguin rookery, rather than sources such as wind-blown NH_3 from present-day rookeries, from which negative $\delta^{15}N$ would be expected (Robinson 2001). Although the $\delta^{15}N$ data does not show a consistent gradient, it indicates where those nutrient inputs are likely to originate and further demonstrates that these terrestrial communities are higher trophic level consumers of N.

Plant nutrient contents show a nutrient gradient across the site and concur with the rookery being the major nutrient source underlying this gradient, as nutrient levels are highest in communities closest to the ridge rookery and decline with distance from the rookery (Fig. 4.5). This pattern was particularly strong for phosphorous, the pattern for nitrogen was less conspicuous, probably due to interactions with nitrogen fixation. Substratum nutrient concentrations in the Hovenden and Seppelt (1995a) abandoned rookery site match the patterns found in the present study; phosphorous declined 15-fold within 25m from the rookery, while nitrogen showed a less sharp decline, of less than 2-fold, over the same distance.

Site hydrology is also likely to interact with plant nutrient contents. The nearby lake drains into a stream that flows into Thala valley (Fig. 2.3). Snow melt moving down the slope, from the abandoned rookery on the ridge, to the lake is likely to be a source of nutrients, but the wetter community at the edge of the lake (i.e. Bryophyte community) is likely to be heavily leached of nutrients which flow out of the catchment. The terrace upon which the Crustose community is positioned might act to sequester nutrients for a longer period than on the steeper slopes and/or the periodically submerged lake-side positions.

The combination of the two opposing gradients is likely to strengthen them. Low nutrient contents in the Bryophyte community are thus likely to be due to both its position furthest from the abandoned rookery but are also likely to be exacerbated by leaching of nutrients when this community is submerged.

Although the Bryophyte community nitrogen contents were low, relative to other communities, they were comparable with tissue nitrogen contents of moss collected from the vicinity of penguin rookeries in the maritime Antarctic (Fabiszewski and Wojtun 2000), for mosses from the maritime Signy Island (Allen et al. 1967) and for a variety of plant types from the sub-Antarctic Macquarie Island (Erskine et al. 1998).

4.4.2. Community response to water and nutrient additions

Differences in treatment-response were found for the four experimentally manipulated communities, supporting the hypothesis that some communities would respond more strongly than others to water and/or nutrient additions. Overall, the Bryophyte and Crustose communities showed a strong treatment-response, while the Moribund and *Usnea* communities responded weakly.

The Bryophyte community showed significant nutrient-limited responses in both primary productivity measures, while the treatment response in the Crustose community was more variable. Photosynthetic rates in this latter community contrasted with the Bryophyte community by showing the strongest increases in response to water additions. Increases in total chlorophyll, however, showed a similar, nutrient-limited response to that seen in the Bryophyte community. Whilst nitrate has been found to be a limiting nutrient in other fellfield communities (e.g. Arnold et al. 2003), plant material in the present study is generally poorer in P than N (on percent weight basis; Fig. 4.5). The Arnold et al (2003) study was investigating microalgae, however, which have a greater nitrogen requirement than that of the mosses and lichens investigated in the present work.

Some of these community differences in treatment-response were likely to be related to the resource availability gradients that operated across the site, discussed in section 4.4.2. The Bryophyte community, for example, in which water contents are usually highest, appeared to be limited predominantly by nutrients. While the Crustose community, in which water availability is estimated to be relatively low for much of the growing season, showed both water- and nutrient-limited characteristics.

The lack of treatment-response in the *Usnea* community response concurs with another continental Antarctic manipulative field experiment, in which increased moisture availability was found to have no impact on photosynthetic gas exchange in *Usnea sphacelata*, the dominant lichen in this community (M. O'Brien *pers. comm.*).

The Moribund community unexpectedly showed the weakest treatment-response. This community is thought to have formed in response to a drying trend, and it was predicted that lichen encrusted moribund moss, which characterises this community, may have shown regeneration potential in response to water additions, as this has been shown to occur under controlled growth conditions (Melick and Seppelt 1997). It is possible that the water treatment was not sufficient for moss regeneration, but it may also be that the encrusting lichen species were responsible for this lack of recovery through allelopathy. Species of the genus *Buellia* are commonly found encrusting moss in this study area and it has been suggested that this species exhibits allelopathic characteristics (Melick and Seppelt 1997). It is therefore possible that the allelopathic effects of lichens, or the action of antagonistic fungi (Melick and Seppelt 1994b), were influencing the lack of response observed in this community. This finding is particularly important since it suggests that changes to water availability alone may not be sufficient to reverse the trend of drying climate producing moribund moss.

Although my results in Chapter 3 indicate that bryophyte material is present in these transitional communities (Moribund and Crustose) it is likely that only conditions of consistent soaking would allow bryophyte communities to regenerate. If this is the case, only under a future climate that produces increased frequency and intensity of water availability will regeneration be likely. Otherwise, it is likely that crustose lichens will continue to expand in distribution, encrusting bryophyte turfs.

4.4.3. Limitations to primary production

Although the hypothesis that water and/or nutrient availability limit primary production is supported, the hypothesis that the flora is more strongly water-limited than nutrient-limited is not. The evidence found for either water- and/or nutrient-limitation are summarised below.

Water-limitation

The strongest evidence for water-limitation was found in the Crustose community, where photosynthetic rates increased greater than 7-fold in response to the watering treatment (Fig. 4.3). Turf water contents suggest that, at the time of sample collection, water availability was relatively high in this community (Fig. 4.4c). Field observations and $\delta^{13}C$ values suggest, however, that this community was drier than the Bryophyte community, for the majority of the growth season, explaining why the response to water-treatment was less pronounced in the latter. Although the Crustose community showed a nutrient response (see below) the water response was the more significant.

Water additions were also associated with increased concentrations of the soluble carbohydrate fructose, across all four communities, suggesting carbohydrate metabolism may be limited by water availability across the range of vegetation types in this ecosystem. It may be that larger water additions would produce a more general trend towards increased sugar concentrations.

Nutrient-limitation

Despite the general suggestion that nutrients are non-limiting to Antarctic plant physiological processes (Table 1.4), this study provides surprisingly strong support for nutrient-limitation. Both the primary productivity variables, total chlorophyll and photosynthetic rates showed nutrient-limited characteristics. Total chlorophyll concentrations showed a nutrient-addition response, which was particularly strong in the

Bryophyte and Crustose communities, with the 3-fold increase in the Bryophyte community the most notable response to nutrient-only addition. Similarly, in the Crustose community a 4-fold increase in ETR in response to nutrient-only addition also supports the notion that these communities are nutrient-limited.

Plant tissue % nitrogen contents increased in response to the nutrient-only additions in all but the Moribund community, with the most striking increases occurring in the *Usnea* community where %N almost doubled (Fig. 4.13). These nutrient content increases indicate sufficient natural moisture availability within most communities for nutrient uptake, and that the nutrient treatments were effective.

Increasing ETR, in response to the water and nutrient additions, suggests that the plants are limited by these environmental factors and have the ability to respond by increasing photosynthesis. If increases in the concentration of N or chlorophyll had been the only response this might have indicated the plants simply absorb the nutrients and sequester them, but are in fact limited by other factors in terms of photosynthetic rate. Although ETR is not a direct measure of photosynthetic gas exchange, simultaneous fluorescence and gas exchange measurements have shown that fluorescence measurements correlate directly with CO_2 gas exchange in the moss species *Bryum argenteum* (Schroeter et al. 1995) and *Ceratodon purpureus* (J. Wasley, *unpublished data*). These results therefore support increased photosynthetic productivity as a result of nutrient additions. Further long-term studies would be required to show if growth was positively affected by nutrients.

These results, which indicate nutrient limitations in Antarctic terrestrial communities, are surprising, because the current body of literature generally supports water as being the most influential limitation to plants across this cold-desert dominated continent (Table 1.3). It has previously been suggested that sufficient nitrogen is provided in precipitation (Greenfield 1992a) but the evidence for nutrient-limitation presented here suggests this may not be the case. Other examples of nutrient-limitation in Antarctic terrestrial communities have been reported, including nutrient-limited growth of lichens situated away from bird colonies (Ryan and Watkins 1989) and nutrient-limited bryophyte carbon assimilation in the sub-Antarctic (Smith 1993). My study concurs with these latter studies suggesting that nutrient limitations may be widespread in Antarctic systems. This study does not allow me to determine which nutrients are limiting, and it is possible that nitrogen, phosphorus, or a combination of nutrients, are responsible for these strong nutrient treatment responses.

Synergistic effects

Some evidence that combined water and nutrient additions had a synergistic effect on plant community response was found in this study. The strongest examples of synergism were observed in the photosynthetic rates in the Bryophyte and *Usnea* communities, where although some increases were observed in response to water and nutrient additions when applied singularly, the highest rates occurred when both water and nutrients were added (Fig. 4.3). Also, a trend toward synergism was observed for total chlorophyll in the Crustose and *Usnea* communities, where total chlorophyll concentrations were highest in the combined water and nutrient treatments (Fig. 4.4a). This result was surprising since it shows that sufficient water is available for most communities - except perhaps the driest, *Usnea* - to take up additional nutrients when they are available, rather than water plus nutrients being required to elicit this response.

4.4.4. Study limitations

A few limitations to this study are worthy of discussion, including the level of effectiveness of the treatments, and some aspects associated with measurement of the treatment-responses.

The watering treatment increased plant water availability. The application regime, applied approximately every three days, did not keep the plant material consistently moist, however, with some drying occurring between treatment applications. The treatment may have been more effective if moisture levels could have been maintained constantly during the treatment period. Repeated cycles of dehydration and rehydration can be damaging to plants. Lichens are likely to be better adapted than bryophytes to such drying cycles. However, both mesic and xeric Antarctic bryophytes are known to utilise even short periods of rehydration (Davey 1997a), suggesting that even the bryophyte community components within the present study should have benefited from the experimental watering regime that was applied.

Further, the treatments are likely to have been least effective in the *Usnea* community, which may help explain the relative lack of treatment-response in this community. Applying effective water additions to this community was particularly difficult, since unlike the other three communities, which had a peaty bryophyte substrate, the *Usnea* community substrata is predominantly porous fellfield soil. In addition, the gross morphology of macro-lichens, which were dominant in this community, compounded the difficulties of applying effective water additions, as fructicose (shrublike) and foliose (thalloid) structures are not flush with the substrate and are prone to rapid desiccation. These morphological characteristics of the *Usnea* community may also have lessened the effectiveness of the nutrient treatment. Nutrients were applied by inserting slow-release fertilizer beads into the plant surfaces and/or substrate. In the other communities, nutrients were therefore applied relatively directly to the plants, while in the *Usnea* community the nutrient beads remained at the base of the lichen thallus structures. Nutrient uptake may therefore have been relatively poor in *Usnea* community, especially given that these lichens are adapted to obtain nutrients from precipitation/airborne nutrients.

It would have preferable to have been able to measure treatment-response via other productivity variables, including growth and community change. In other high-latitude ecosystems, ecological measures of community change (such as, biomass and species cover) have been successfully used to monitor response to environmental manipulations (Press et al. 1998, Robinson et al. 1998). The characteristically slow growth rates that occur in continental Antarctica (Green 1985), however, limit studies of this nature to using physiological methodologies such as those used in the present study. Initial attempts were made to analyse percent cover, but these measures were abandoned, as they were impractical, as rates of change are too slow to be measured over the duration available for this experiment. Hence, the productivity surrogates, of ETR and chlorophyll, were the best practical measures for productivity available.

Correlations with water availability may have been stronger if more measures of water availability were made. The single measure of turf water content, conducted at the end of the treatment period, was inadequate to support the presence of a moisture gradient across the site – which field observations and $\delta^{13}C$ values suggest is present for the majority of the growth season. Measures of water availability generally require destructive collection of samples, which must be avoided wherever possible in this fragile ecosystem. Water contents were therefore only determined for samples that were also being collected for other analyses at the end of the experimental period. The moisture gradient described in Chapter 3 was measured very close to the site used for the present study, and included comparable community types. It is most likely that a similar moisture gradient occurred across the ASPA Meltlake site for the majority of the growth season.

Despite these limitations, this study represents one of the only manipulative field experiments to be conducted in continental Antarctica, and illustrates both that such studies are possible and produce valuable results.

4.5. Conclusions

This experiment has provided some surprising results regarding the way in which Antarctic terrestrial communities are likely to respond to climate change. Whilst an overall increase in productivity in response to water and nutrient additions was supported, productivity appeared to respond more strongly to nutrient additions than to water additions. Certain communities are likely to thrive under a wetter future, providing nutrient availability increases with increasing water availability. Increased productivity was most pronounced in the Crustose and Bryophyte communities, suggesting these community types may be most able to adapt and prosper under the ameliorating conditions associated with a warmer, wetter future climate. However, if nutrient availability does not increase along with wetter conditions, bryophyte communities may be nutrient-limited and fail to thrive.

Chapter 5: Predicting response to climate change for three continental Antarctic moss species, based on biological profiles of desiccation tolerance

5.1. Introduction

Although an increase in water availability for continental Antarctica is likely in the short-term (Chapter 1, section 1.4 and Chapter 4), a drying trend is an alternative scenario that is likely in the longer-term (Chapter 1, section 1.4; Fig. 1.2). The region of the present study, the Windmill Islands (66°17'S, 110°32'E) has been undergoing a drying trend, due to isostatic uplift, since the onset of deglaciation 6-8 000 years ago (Melick and Seppelt 1997, see Chapter 2, section 2.1, for more details). This region may continue to dry unless future increases in water availability are great enough to offset this trend. Around continental Antarctica, in general, if increased melt, as a result of rising temperatures, is not accompanied by the predicted increases in precipitation (Tokioka 1995, Ye and Mather 1997), permanent snow and ice reserves are likely to reduce causing, in the long term, a drying of the Antarctic terrestrial environment (Chapter 1, section 1.4).

Environmental shifts affecting water availability are likely to alter plant distributions, particularly with respect to bryophytes, which require free water availability for photosynthesis and growth. Bryophytes are known to be particularly sensitive to their growth environment and have been successfully used as indicators of climatic fluctuations in other habitats (Frahm and Klaus 2001). The distribution of the four Windmill Islands bryophyte species, at both broad- (Smith 1988a) and fine-scales (Selkirk and Seppelt 1987, Smith 1999), are thought to be dictated primarily by water availability (Chapter 2, section 2.1) and my research supports this pattern (Chapter 3). Alterations to distributions, in response to environmental shifts, are likely to be species-specific, as has been observed in other cold-climate communities, such as Alaskan tussock tundra (Hobbie and Chapin 1998) and subarctic heath (Press et al. 1998).

Species-specific responses may be determined by variation in species morphology and physiology. This section of my study investigates various aspects of bryophyte species morphology and physiology that are related to tolerance of desiccation, and therefore species chances of survival under a drying climate. Characteristics that contribute toward increased tolerance of drier conditions include the ability to: (1) avoid desiccation, (2) tolerate drying, (3) survive desiccation, and (4) recover from desiccation. The overall aim of the study was to determine whether such biological characteristics are correlated with the observed field distributions. A better understanding of the relationship between species physiology and ecology will contribute toward developing more informed predictions for the future of these organisms under a changing climate.

The ability to avoid desiccation is limited in bryophytes. Bryophytes are non-vascular and therefore do not possess many of the mechanisms for desiccation avoidance that characterise vascular plants, such as epidermal layers and stomata. Some aspects of bryophyte turf structure can however alter a species' ability to retain moisture. A tightly packed turf, with few inter-gametophyte spaces will be less prone to drying than a loosely packed turf that has large spaces between gametophytes. Gametophyte size and density was therefore determined for turf samples of each of the three Windmill Island moss species.

The ability to tolerate drying is a characteristic that enhances a species' tolerance of desiccation, and ultimately survival under a drying climate. The ability to tolerate drying can be determined by measurements of metabolism during desiccation of plant tissues. The ability to metabolise at relatively low TWCs will allow a plant to perform better under drying conditions. TWC at which photosynthetic efficiency declines was therefore determined, for each of the three species, in a series of experiments that were conducted over the course of a summer season.

The ability to survive desiccation is often due to the presence of compounds which protect membrane structure during the desiccation / rehydration process. Such compounds include particular types of soluble carbohydrates and lipids. Since the quantity and type of soluble carbohydrate and lipid compounds can be important factors for protection during desiccation in plants (Koster and Leopold 1988, Ghasempour et al. 1998), concentrations of these biochemical factors were determined for the study species.

The ability to recover from desiccation will contribute toward a species' tolerance of desiccation. Species which are able to recover from complete desiccation of tissues will have a greater chance of surviving a drying climate. Further, species which are able to recovery quickly from desiccation will have greater productivity under a drying climate where plants will need to take full advantage of short periods of water availability. Recovery time, after complete desiccation of plant material, was therefore measured for the study species, using chlorophyll fluorescence.

Since plants occupying relatively wet habitats are less likely than those that occupy dry environments to survive a drying trend, information about the current and past climates is also important. Carbon isotopic fractionation was compared between species to determine degree of current submergence (see Chapter 2, section 2.2.4 for an explanation of the use of $\delta^{13}C$ as an indicator of habitat submergence). In addition, for *G. antarctici*, the changes in fractionation with depth (and age) of gametophytes were examined to determine historic changes.

The main focus of this study was to investigate the response to water, however nutrient availability is also predicted to change with climate (Chapter 1, section 1.5) and therefore nutrient content of the three species was investigated, including fractionation of nitrogen isotopes, which provides information about nitrogen source.

Species which are phenotypically plastic have a greater survival potential under a changing environment (Valladares et al. 2000a, Valladares et al. 2000b, Agrawal 2001). For the suite of biological characteristics measured for each species a plasticity index (CV; sem/mean) was calculated to identify the relative plasticity of each species. In addition, the biological characteristics that contribute most toward species plasticity were identified.

The suite of characteristics investigated, which are thought to contribute toward species survival under a drying climate, builds upon the community level work presented in the previous two chapters by producing species level biological profiles. These biological profiles helped identify the nature of likely species-specific responses to a drying climate. The overall aim of the study was to determine whether the biological profiles, related to tolerance of desiccation, are able to help explain the observed field distributions, in relation to water availability. A better understanding of the relationship between species physiology and ecology will contribute toward developing more informed predictions for the future of these organisms under a changing climate. This study builds on the work of Robinson et al. (2000), in which the desiccation tolerance of these species from the Windmill Islands was first investigated.

5.2. Methods

5.2.1. Study site and plant material

Sample material of the three study species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*) was collected from the ASPA Meltpuddle site, described in Chapter 2 (section 2.1; see Fig. 2.3 for location). The collection site was approximately 10 m from the edge of a meltpool, where all three species occurred within a 4 m^2 area.

Material was collected at three times over the Southern Hemisphere summer season of 1999-2000: early-season (2/12/99), mid-season (24/1/00) and late-season (27/2/00). The early- and late-season collections were before and after the summer-melt period, respectively, and as a consequence the plant material was frozen and relatively dry. In contrast, the mid-season collection coincided with the height of the summer melt, during which the material was relatively warm and wet, allowing assessment of bryophyte response to seasonal changes in water availability. Morphological measurements, fatty acid determination and isotopic analysis were performed on only one set of samples over the season, whilst desiccation tolerance parameters, including carbohydrate analysis, were measured on all samples.

At each collection time, a turf sample of approximately 50 mm x 30 mm was collected for each of the three species and transported immediately to the laboratory. In the laboratory, the turf samples were sprayed with water and allowed to hydrate overnight. Eight replicate plugs of moss (approximately 13 mm diameter and 10 mm depth) for each species were cut from the rehydrated material. Excess surface water was removed by blotting samples with paper towel. The samples, which weighed approximately 1.5 g (fresh weight), were placed in small pre-weighed foil capsules.

In order to investigate longer-term changes (over decades) of nutrient source and habitat water availability, stable isotopic signatures along long gametophyte sections were measured. A set of 5 samples of *G. antarctici* was collected from the edge of a melt lake behind the Casey Station accommodation building on Bailey Peninsula (66˚15.9'S, 110˚31.6'E). The moss turf here contained continuous intact gametophytes up to 4 cm long. These samples were sectioned at 1 cm intervals and C and N isotopic determinations performed on each individual section as described in section 2.2. The short gametophyte length of the other species prevented this experiment being performed for *C. purpureus* and *B. pseudotriquetrum.*

5.2.2. Morphology

Morphology was determined for material collected in association with the final experiment of the season only.

Gametophyte density

Using a dissecting microscope, a quadrat (2 x 2 mm) was placed in three random locations on each replicate moss plug, and all gametophytes within the quadrat were counted. The median value of the three counts was used for analysis. The method was conducted on both desiccated and hydrated turf samples.

Gametophyte width

Material was stored at –20 °C until the time of measurement, in August 2001. Samples were air-dried in a desiccator, at –4 °C, before measurements were taken. Measurement of gametophyte widths was conducted on dry plant material.

Eight single gametophytes, for each of the three species, were randomly selected, with juvenile and/or dead gametophytes excluded from the selection. Measurements were conducted using binocular microscopes (Leica MS5 and Leica Wild M3C) with a graticule. Gametophytes were measured at the widest part of the gametophyte tip. Measurements were repeated three times for each gametophyte and the median value was used for analysis.

5.2.3. Physiological and Biochemical determinations

Response to desiccation

Chlorophyll fluorescence was used to assess the ability to photosynthesise during desiccation and the recovery of photosynthesis following desiccation for the three species throughout the season (methods adapted from Robinson et al. 2000). Photosynthetic efficiency for each sample (1 cm diameter) was determined as the ratio of variable to maximal fluorescence (F_v/F_m), measured after a 10 min dark adaption period, using a Mini PAM chlorophyll fluorometer (H. Walz, Germany). Dark adapted F_v/F_m has been shown to be a good indicator of the maximum photon-use efficiency of photosynthesis in a broad range of plant taxa (Bjorkman and Demming 1987). Settings on the Mini PAM were optimised for the three species at the start of the first experiment (measuring light 3, gain 2, damping 2, saturating pulse 4 s, saturating pulse intensity 0.8 s). Moss samples were then allowed to desiccate slowly in the laboratory under low light conditions (approximately 10 μmol photons m^{-2} s^{-1}), air temperature 18°C, and relative humidity 22%.

Change in the turf water content (TWC) of each sample was determined from changes in weight. The weight of each sample plus capsule was determined immediately after measurement of chlorophyll fluorescence. The TWC (grams of water per gram dry weight of sample) was calculated for each measurement point after subtraction of the capsule weight. The TWC of each moss sample at each time period (x) was determined as described in section 2.2.1

In the context of this experiment, the external water stored between gametophytes is biologically important to the physiological functioning of the turf as a whole. A species that is better able to retain external water will have a slower drying rate and therefore be able to delay desiccation compared to a species that has little external water and a fast drying rate.

Dark adapted F_v/F_m and sample weights were determined periodically for each sample until F_v/F_m declined to zero and/or minimal fluorescence (F_o) values were too low to consider reliable. The samples were then stored at low light (approx 10 μmol photons m^{-2} s^{-1}) until the recovery phase of the experiment was conducted.

Recovery from desiccation

Recovery from desiccation was measured approximately 1 week after desiccation commenced. Replication was half that of the desiccation phase of the experiment due to some samples being randomly removed after desiccation for biochemical analyses (see below). Recovery from desiccation was conducted in the dark for approximately 1 hour and in low light conditions (approx 10 μmol photons m^{-2} s^{-1}) thereafter. The desiccated moss samples were dark adapted for 10 min, sprayed with a fine mist of water, and chlorophyll fluorescence measurements were commenced immediately. Since recovery of chlorophyll fluorescence was too fast to measure TWC simultaneously, recovery was therefore measured over time alone.

Determination of plant biochemical characteristics

In order to identify whether the study species contain compounds that might assist in tolerance of desiccation, soluble carbohydrate and fatty acid compositions were determined. Samples for soluble carbohydrate analysis were collected in association with each of the three desiccation experiments described above (n = 8 for early- and late-season, 6 mid-season). Samples were hydrated overnight, microwaved on high power for 2 min to preserve organic compounds (Popp et al. 1996) and analysed following the methods described in Chapter 2 (section 2.2). Samples for determination of fatty acid composition were collected in association with the late-season desiccation experiment (28/2/00) only. Fatty acid composition was determined for three replicate samples of each of the three species using the methods described in Chapter 2 (section 2.2).

Nitrogen and carbon contents, along with N and C stable isotopic signatures, constituted the final suite of biological characteristics that were determined for the three study species. These analyses were performed in order to identify species differences in nutrient availability, nutrient source and degree of habitat submergence. Plant nitrogen and carbon was determined for material collected in association with the late-season desiccation experiment (28/2/00). Eight replicates for each of the three species were hydrated overnight and analysed following the methods described in Chapter 2 (section 2.2).

It should be noted that although the study area is small (4 m^2), within this environment slight changes in microtopography have large impacts on water (and potentially nutrient) availability. Within the 4 m^2 area from which these samples were collected differences in levels of submergence occurred (supported by field observations). These small-scale changes are further supported by the data presented in chapter 3, note in particular Fig. 3.2 (a-g) which shows transect lengths for Meltpuddle site (where the material for the present chapter was collected). Transects c-e (Fig. 3.2) for example, were $\leq$ 2 m in length and over this small distance the community changed from bryophyte dominated to lichen dominated (Fig. 3.8), coinciding with the presence of a moisture gradient (Fig. 3.4). Given this information I suggest that interspecific differences in nutrient source, availability and submergence are likely and thus have been investigated here.

5.2.4. Statistical Analyses

Desiccation and recovery from desiccation was analysed using non-linear regression. Each replicate was analysed by plotting (1) photosynthetic efficiency (F_v/F_m) against turf water content (g H_2O^{-1} g dw), during desiccation and (2) photosynthetic efficiency (F_v/F_m) against time (h), during recovery from desiccation. Non-linear regression analysis was performed for each plot, as represented schematically in Figure 5.1. The point of intercept between the two regression lines in each plot are the points of further statistical analysis and are referred to as (1) Critical Water Content (CWC) during desiccation and (2) Critical Recovery Time (CRT) from desiccation.

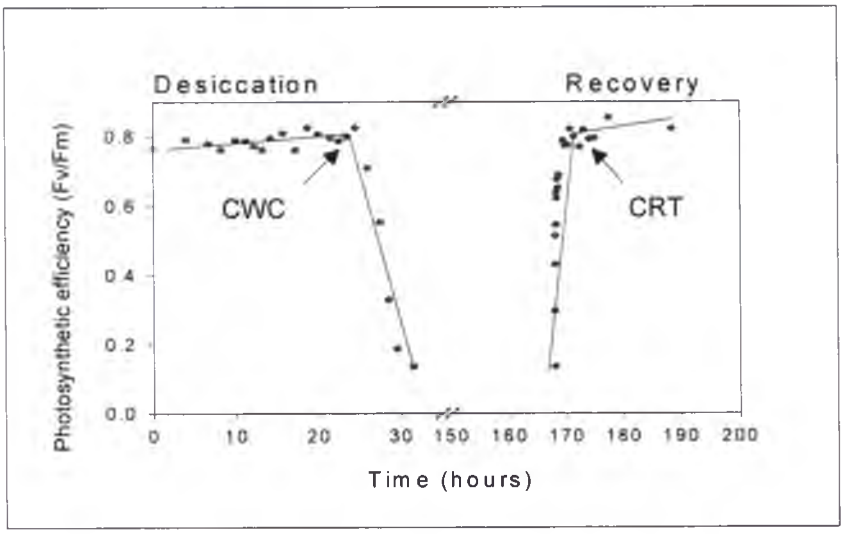


Figure 5.1: Schematic representation of desiccation and recovery analysis methods, used to determine critical water content (CWC) during desiccation and critical recovery time (CRT) from desiccation, using non-linear regression. Data points displayed are data for a representative sample; regression lines and critical points are schematic representations of regression analysis.

Statistically significant differences within each of the following data sets: critical water content during desiccation; critical time to recovery from desiccation; soluble carbohydrate levels; and nitrogen and carbon concentration and isotopic fractionation data, were tested using ANOVA. Where required, the data sets were transformed to normalise the variance of the data and thereby satisfy the assumptions of the ANOVA model. Pairwise comparisons (using Student's t test) were used to identify pairs of means which are significantly different. All statistical operations were conducted using JMP (SAS Inc., Cary, NC, USA) statistical analysis software.

5.3. Results

5.3.1. Morphology

Gametophyte widths were significantly different between the three species (Table 5.1), with approximately 0.1 mm difference between each of the three species; *B. pseudotriquetrum* was the largest and *G. antarctici* the smallest (Fig. 5.2A). In turn, gametophyte density was lower in *B. pseudotriquetrum* than *C. purpureus* (Fig. 5.2B). However *G. antarctici*, which had the smallest gametophyte widths, had a similar gametophyte density to the relatively large gametophytes of *B. pseudotriquetrum* (Fig. 5.2B). Gametophyte densities were significantly greater in desiccated turf than hydrated turf (Table 5.2 and Fig. 5.2B).

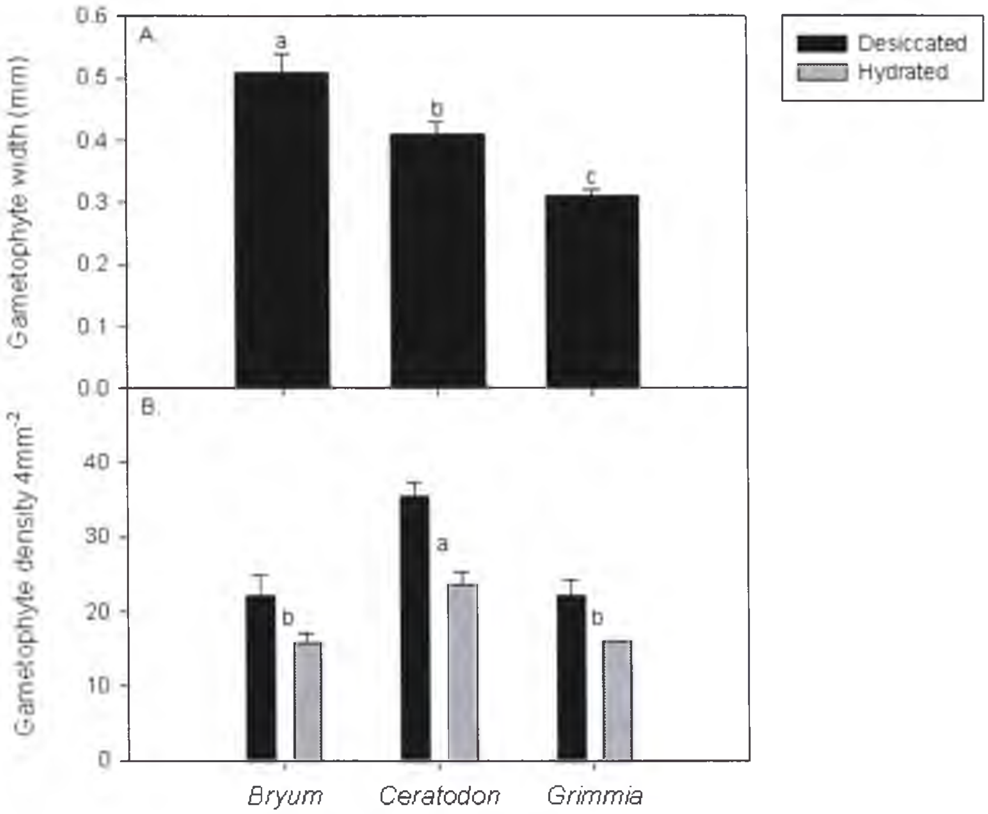


Figure 5.2: Morphological characteristics of the three moss species: *Bryum pseudotriquetrum*, *Ceratodon purpureus* and *Grimmia antarctici*. (A). Gametophyte width (mm) of desiccated samples. Bars represent mean±se, n = 8. (B). Turf gametophyte density (gametophytes per 4 mm^2 area) for desiccated and hydrated samples. Bars represent mean±se, n = 4. Samples collected from ASPA Meltpuddle site at the end of the season (28/2/00). Lowercase labels represent results of pair-wise Student's t tests: same letters indicate pairs of means that are not significant. Pair-wise tests are significant at $\alpha = 0.017$. Gametophyte densities: desiccated significantly higher than hydrated ($P<0.05$).

Table 5.1: Summary of 1-way ANOVA results for gametophyte width and nitrogen and carbon measurements (%N, %C, C/N, $\delta^{15}N$ and $\delta^{13}C$), testing for difference between the three species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*), and changes in $\delta^{15}N$ and $\delta^{13}C$ along long *G. antarctici* gametophytes.

Variable	Transformation	DF (model)	DF (error)	F Ratio	Prob > F
Gametophyte width	None	2	21	20.0948	<0.0001
%N	Log Log	2	21	320.1024	<0.0001
%C	None	2	21	64.4086	<0.0001
C/N	Square	2	21	237.7468	<0.0001
$\delta^{15}N$	None	2	21	19.0723	<0.0001
$\delta^{13}C$	None	2	21	228.5490	<0.0001
$\delta^{15}N$ long gametophyte	None	3	16	10.9915	0.0004
$\delta^{13}C$ long gametophyte	None	3	16	1.0022	0.4173

Table 5.2: Summary of 2-way ANOVA results for gametophyte density and tolerance of desiccation variables (turf water content at full hydration, drying rate, critical water content, critical recovery time).

Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	Prob > F
Gametophyte Density	None	Whole Model	5	18	15.3226	<0.0001
		Species	2		22.0628	<0.0001
		Desiccated / Hydrated	1		29.0700	<0.0001
		Species * D / H	2		1.7085	0.2092
Turf water content at full hydration	None	Whole Model	8	54	69.2648	<0.0001
		Time	2		164.0236	<0.0001
		Species	2		70.7114	<0.0001
		Time * Species	4		22.0305	<0.0001
Drying Rate	None	Whole Model	8	54	6.9573	<0.0001
		Time	2		10.9743	<0.0001
		Species	2		14.6578	<0.0001
		Time * Species	4		1.6356	0.1787
Critical Water Content	None	Whole Model	8	50	9.3006	<0.0001
		Time	2		2.8956	0.0646
		Species	2		18.2650	<0.0001
		Time * Species	4		7.8908	<0.0001
Critical Recovery Time	None	Whole Model	8	30	31.9097	<0.0001
		Time	2		39.8003	<0.0001
		Species	2		36.9061	<0.0001
		Time * Species	4		28.6313	<0.0001

5.3.2. *Physiology and Biochemistry*

Response to desiccation

Turf water content (TWC) in fully hydrated plant material was significantly different between the three species (Table 5.2). Levels were generally lower in *C. purpureus* (4.0±0.2 to 6.2±0.3 g H_2O^{-1}dw) than the other species (*B. pseudotriquetrum*, 5.7±0.2 to 8.7±0.2 g $H_2O^{-1}dw^{-1}$, *G. antarctici*, 3.9±0.1 to 7.7±0.3 g $H_2O^{-1}dw^{-1}$ respectively).

Drying rate was slowest in *C. purpureus* (-0.06±0.00 to -0.12±0.01 g H_2O^{-1} h) compared to the other two species (*B. pseudotriquetrum*, -0.12±0.01 to -0.19±0.01 and *G. antarctici*, -0.14±0.03 to -0.17±0.01; Table 5.2). Drying rate was largely a reflection of TWC at T_0: *B. pseudotriquetrum* for example, had significantly higher TWC and faster drying rate than *C. purpureus*.

Critical water content (CWC) showed significant variation across the three species, and three experimental intervals (whole model and time*species interaction: *P*<0.0001; Table 5.2; Fig. 5.3). CWC was highest in *B. pseudotriquetrum* in the early-season (December) experimental interval, for which mean CWC approached 2 g H_2O^{-1}g dw, but declined by half over the course of the season. *Grimmia antarctici* was consistently high throughout the season whilst *C. purpureus* was consistently lowest (Fig. 5.3). By the end of the season, CWCs of *B. pseudotriquetrum* and *C. purpureus* had reached similar low levels and were significantly lower than those for *G. antarctici* at this time of year (*P*<0.003; Appendix 3; Fig. 5.3).

The three species showed significantly different critical recovery time (CRT) patterns across the season (whole model and time*species interaction: *P*<0.0001; Table 5.2). A significant seasonal increase in CRT occurred for *B. pseudotriquetrum* and *C. purpureus*, taking 2.4- and 4.3-fold longer to recover from desiccation, respectively, over the course of the season (*P*<0.003; Appendix 3; Fig. 5.3D). Conversely, *G. antarctici* showed a significant decline in CRT over the season, with CRT declining by more than 10 min over the course of the season (*P*<0.003; Appendix 3; Fig. 5.3).

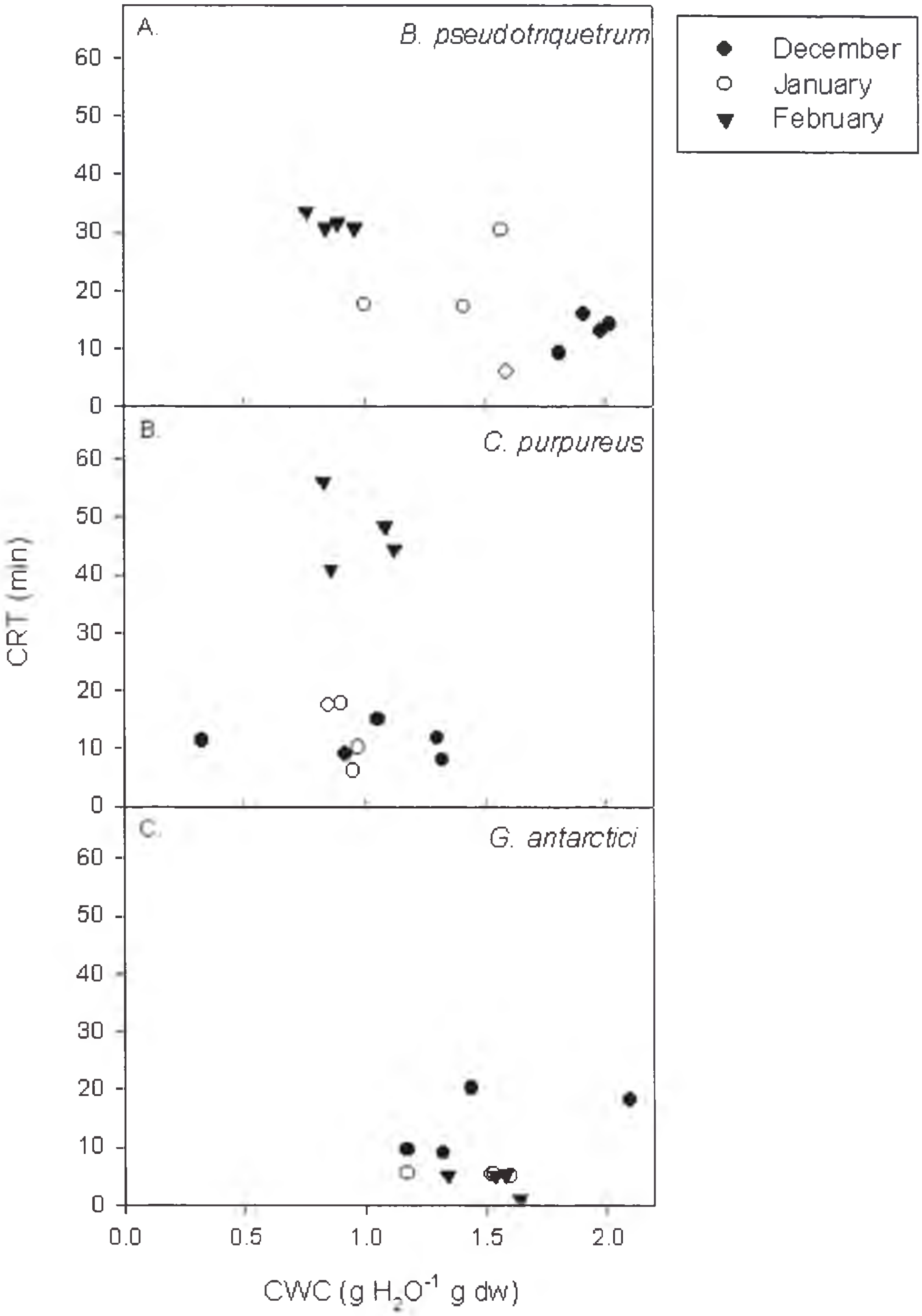


Figure 5.3: Desiccation response across a summer season (December, January and February) for the three species: *Bryum pseudotriquetrum*, *Grimmia antarctici* and *Ceratodon purpureus*. The relationship between critical recovery time (CRT; min) and critical water content (CWC; g H_2O^{-1}g dw) is shown for early (filled circles), mid (open circles) and late (filled triangles) season samples.

Nitrogen and Carbon determinations

In order to determine if nutrient contents differ between the species, percent N and C were measured. Percent N was in the 1 to 2% range for all species (Fig. 5.4A). *Bryum pseudotriquetrum* had highest N contents, 73% greater than *C. purpureus* and 16% greater than the intermediate *G. antarctici* ($P<0.0001$; Table 5.1).

In contrast to the %N pattern, %C was relatively uniform; varying only 5% between species. Significant species differences were however detected ($P<0.0001$; Table 5.1). *Bryum pseudotriquetrum* had the greatest %C, close to 50% (Fig. 5.4B). Also in contrast to the %N pattern, the lowest %C values were found in *G. antarctici*, in which carbon contents were approximately 45%. For this variable, *C. purpureus* was the intermediate species (Fig. 5.4B).

Since the between species variation for %C was much smaller than the variation in %N, the C/N ratio primarily reflected the patterns in %N. *Ceratodon purpureus* had the lowest %N and therefore C/N was much higher in this species, exceeding 50% greater than the other two species, which were statistically similar ($P<0.0001$; Table 5.1; Fig. 5.4C).

Nitrogen stable isotopic values were measured to determine if the three species utilise similar nutrient sources, while carbon isotopic values were investigated to determine whether the species are subject to differing levels of habitat submergence (Chapter 2, section 2.2.4). *Grimmia antarctici* had a significantly lower $\delta^{15}N$ value and a significantly higher (less negative) $\delta^{13}C$ value than the other two species ($P<0.0001$; Table 5.1; Fig. 5.4D&E).

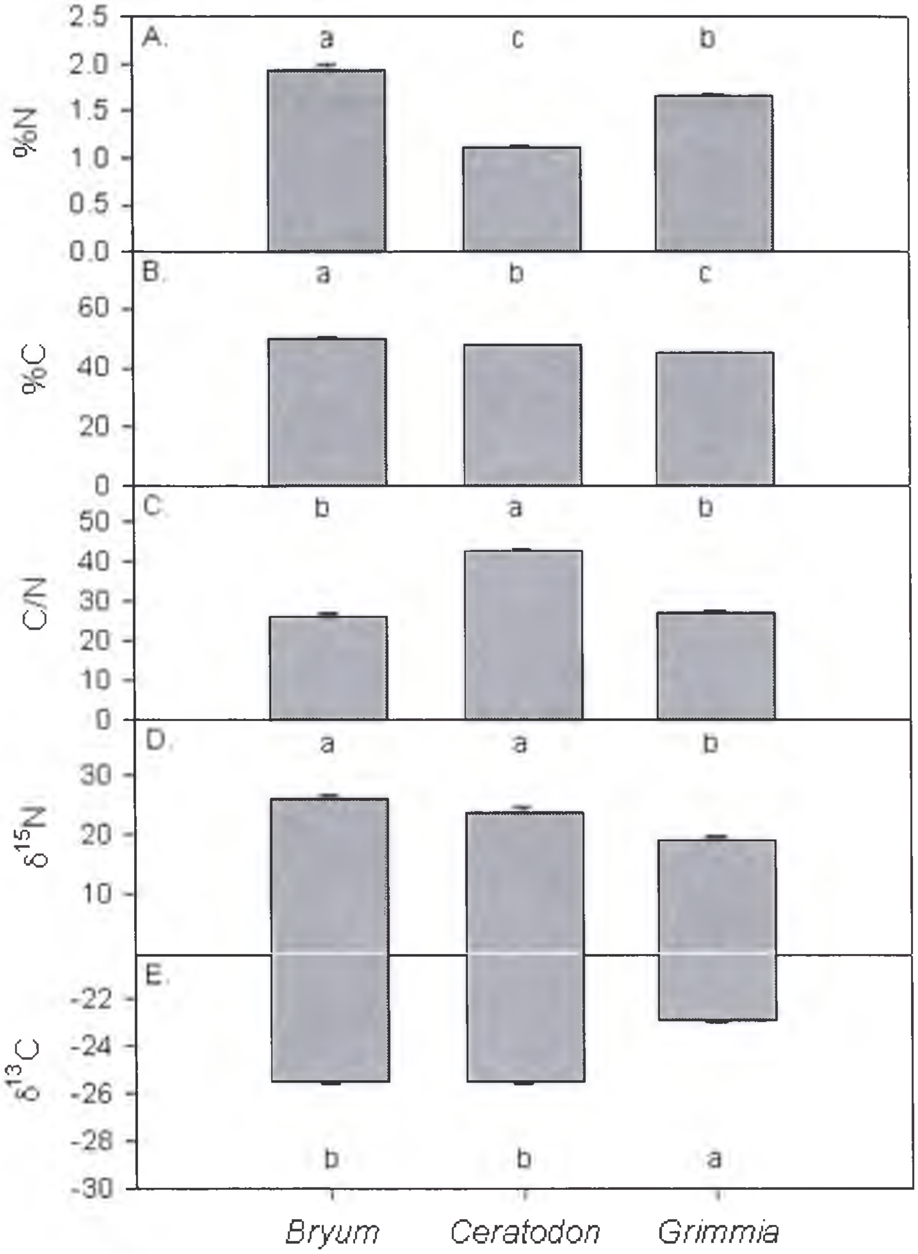


Figure 5.4: Nitrogen and carbon composition of the three species: *Bryum pseudotriquetrum*, *Grimmia antarctici* and *Ceratodon purpureus*. (A) weight %N, (B) weight %C, (C) C/N ratio, (D) δ^{15}N, (E) δ^{13}C. Samples collected from ASPA Meltpuddle site at the end of the season (28/2/00). Bars represent mean±se, n = 8. Labels a-c represent results of pair-wise Student's t tests: same letters indicate pairs of means that are not significant. Pair-wise tests are significant at α = 0.017 (Bonferroni adjusted α level).

Changes in N and C stable isotopic signatures over time (decades) were investigated in *G. antarctici*, for which sufficiently long gametophytes were available from a nearby site. The value of $\delta^{13}C$ increased significantly from the growing tip to the oldest and deepest tissue ($P = 0.0004$; Table 5.1; Fig. 5.5). There was no significant gradient in $\delta^{15}N$ values (Table 5.1). However, the $\delta^{15}N$ values from this site were much lower than those measured within the ASPA Meltpuddle site (compare Fig. 5.4D and Fig. 5.5).

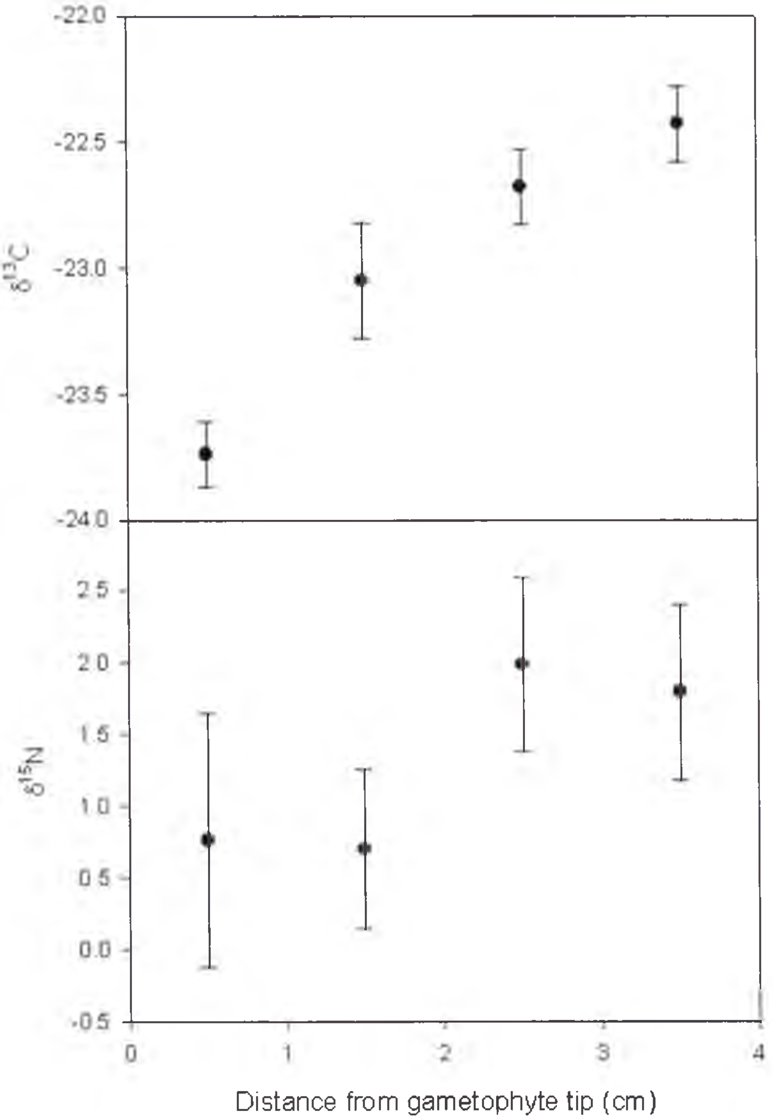


Figure 5.5: Changes in $\delta^{13}C$ and $\delta^{15}N$ with depth for 4 cm long gametophytes of *Grimmia antarctici* collected from Bailey Peninsula (samples numbered from top of gametophyte). Data are mean±se, n = 5.

Seasonal variation in soluble carbohydrate contents

Soluble carbohydrate contents of the three species were determined in order to ascertain whether the species contain soluble carbohydrate compounds that might assist in tolerance of desiccation. Soluble carbohydrate concentrations were therefore plotted against the tolerance of desiccation variables CWC and CRT in order to investigate this relationship (Figs. 5.6 and 5.7 and Appendices 4 - 6). Eight identified soluble carbohydrates were detected: sucrose, fructose, glucose, stachyose, trehalose, glycerol, mannitol and *myo*-inositol. This suite of soluble carbohydrates is similar to that previously detected for these species (Robinson et al. 2000). In the previous work, five unidentified soluble carbohydrates were also detected and designated X1-5. In the current study only X2, X3 and X4 were found (Appendices 4 - 6).

Several of the soluble carbohydrates detected in these species are known to play a role in tolerance of desiccation, particularly stachyose, trehalose and the sugar alcohols (glycerol, mannitol and *myo*-inositol). The concentration of these compounds showed significant species and temporal variation (Table 5.3). The relationship of these compounds (and total soluble carbohydrates) with the tolerance of desiccation characteristics; CWC and CRT, are shown in Figures 5.6 and 5.7 (for full regression results see Appendix 7).

The three species showed variation in their relationships between total soluble carbohydrates and tolerance of desiccation. CWC and CRT were positively correlated with total soluble carbohydrates in *B. pseudotriquetrum* ($r^2 = 0.43$; Fig. 5.6) and *G. antarctici* ($r^2 = 0.40$; Fig. 5.7), respectively. *Ceratodon purpureus* showed poor correlations between both CWC and CRT and total soluble carbohydrates, as concentrations were consistently low throughout the season (Figs. 5.6 and 5.7).

Two compounds known to play a role in tolerance of desiccation are stachyose and trehalose. Stachyose was detected in *B. pseudotriquetrum* only, in which it was positively correlated with CWC and negatively correlated with CRT ($r^2 = 0.22$; Fig. 5.6 and 0.35; Fig. 5.7, respectively). Trehalose was detected in all three species, but

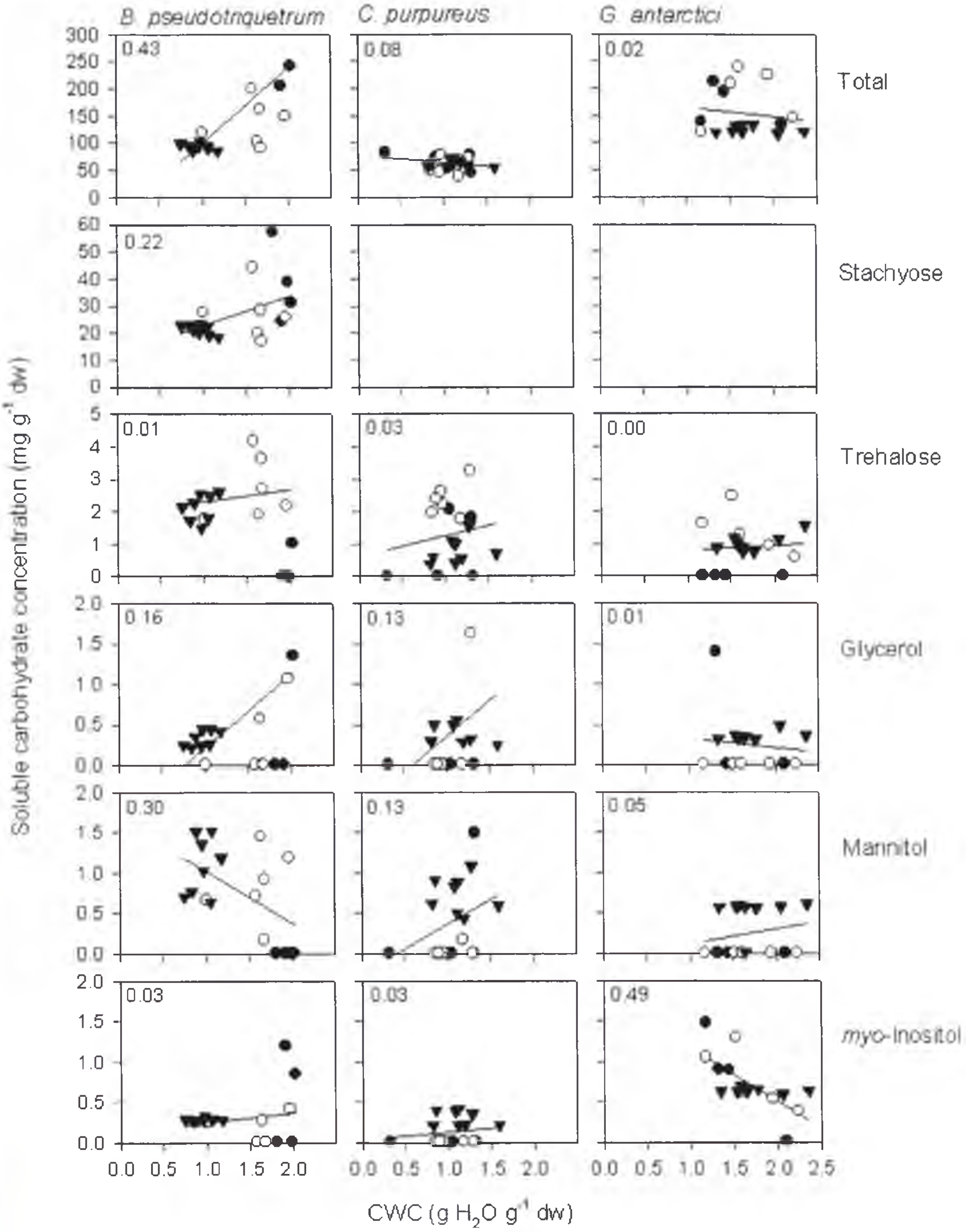


Figure 5.6: Relationship between soluble carbohydrate concentrations (mg g^{-1} dw) and critical water content (CWC; g H_2O g^{-1} dw) for three experimental intervals: December (filled circles), January (empty circles) and February (filled triangles), for the three study species (*B. pseudotriquetrum, C. purpureus* and *G. antarctici*). Lines indicate results of linear regression analysis of all data in each plot, values indicate r^2. Full regression results are provided in Appendix 7. Note, y-axes are different.

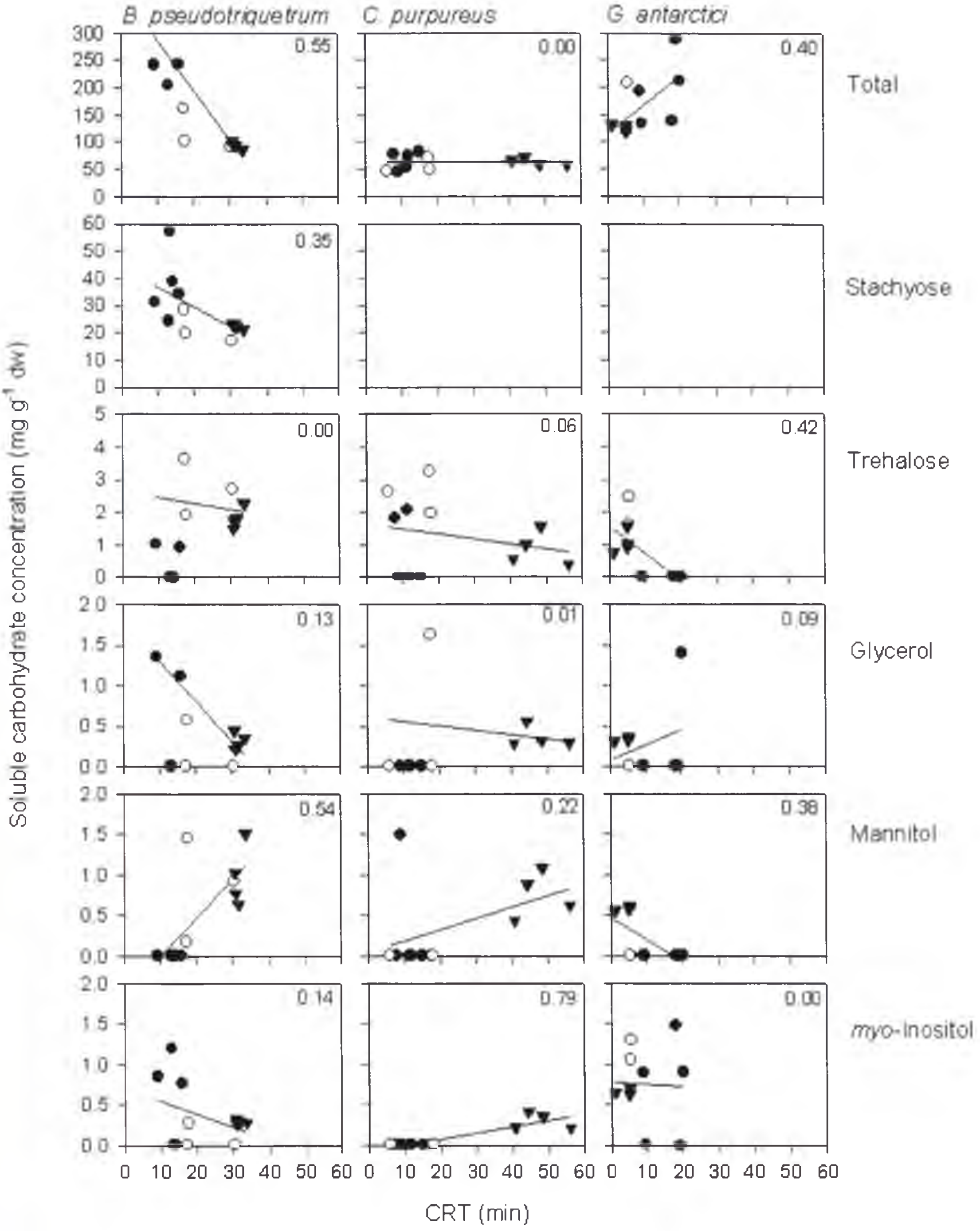


Figure 5.7: Relationship between soluble carbohydrate concentrations ($mg^{-1}g$ dw) and critical recovery time (CRT; min) for three experimental intervals: December (filled circles), January (empty circles), February (filled triangles) for the three study species (*B. pseudotriquetrum, C. purpureus* and *G. antarctici*). Lines indicate results of linear regression analysis of all data in each plot, values indicate r^2. Full regression results are provided in Appendix 7. Note, y-axes are different.

was correlated with tolerance of desiccation in G. *antarctici* only, where the relationship with CRT was negative ($r^2 = 0.42$; Fig. 5.7).

The three sugar alcohols (glycerol, mannitol and *myo*-inositol) also showed variation between the three species in patterns of correlation with the tolerance of desiccation variables (Figs. 5.6 and 5.7). The concentration of glycerol and mannitol was most strongly correlated with the tolerance of desiccation variables in *B. pseudotriquetrum*. In this species, glycerol showed a similar positive relationship to CWC as that found for total soluble carbohydrates, while mannitol showed the opposite pattern of a negative relationship with CWC ($r^2 = 0.30$; Fig. 5.6) and a positive relationship with CRT ($r^2 = 0.54$; 5.7). Conversely, *myo*-Inositol was most strongly correlated with the tolerance of desiccation variables in *G. antarctici* with respect to CWC (negative relationship, $r^2 = 0.49$; Fig. 5.6) and *C. purpureus* with respect to CRT (positive relationship, $r^2 = 0.79$; Fig. 5.7).

Table 5.3: Summary of ANOVA results testing for differences in concentration of soluble carbohydrates (total, trehalose, glycerol, stachyose and mannitol) and fatty acids (total, % total SFA, % total MUFA, % total PUFA). 2-way ANOVA results are presented for whole model and the effects of experiment (Dec, Jan and Feb) and species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*) and the significance of the experiment interval * species interaction. 1-way ANOVA results are presented where indicated.

	Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	Prob > F
	Total soluble carbohydrates	None	Whole Model	8	57	52.8409	<0.0001
			Experimental interval	2		36.3488	<0.0001
			Species	2		147.7512	<0.0001
			Expt * Species	4		13.8552	<0.0001
	Trehalose	None	Whole Model	8	56	9.5312	<0.0001
			Experimental interval	2		17.9724	<0.0001
			Species	2		14.1848	<0.0001
			Expt * Species	4		2.7020	0.0395
	Glycerol	Log	Whole Model	8	57	3.8781	0.0010
			Experimental interval	2		12.2053	<0.0001
			Species	2		1.9747	0.1482
			Expt * Species	4		0.7057	0.5913
1-way	Stachyose	Log Log	Expt (Bryum only)	2	19	8.9308	0.0018
	Mannitol	None	Species (Feb only)	2	21	9.3420	0.0013
	Total fatty acids	None	Species	2	6	23.0608	0.0015
	% total SFA	None	Species	2	6	4.0891	0.0758
	% total MUFA	None	Species	2	6	27.1981	0.0010
	% total PUFA	None	Species	2	6	4.2556	0.0707

Species differences in fatty acid composition

Fatty acids are important for membrane function and they may also provide protection during desiccation and freezing. The fatty acid composition of the three species was therefore determined in order to investigate if they possess different mechanisms for surviving these stresses. Significant differences in fatty acid compositions were found between the three species ($P = 0.0015$; Table 5.3). The concentration of total fatty acids was greatest in *C. purpureus* (more than 25 mg^{-1}g dw) with concentrations in the other two species less than 15 mg^{-1}g dw (Fig. 5.8A).

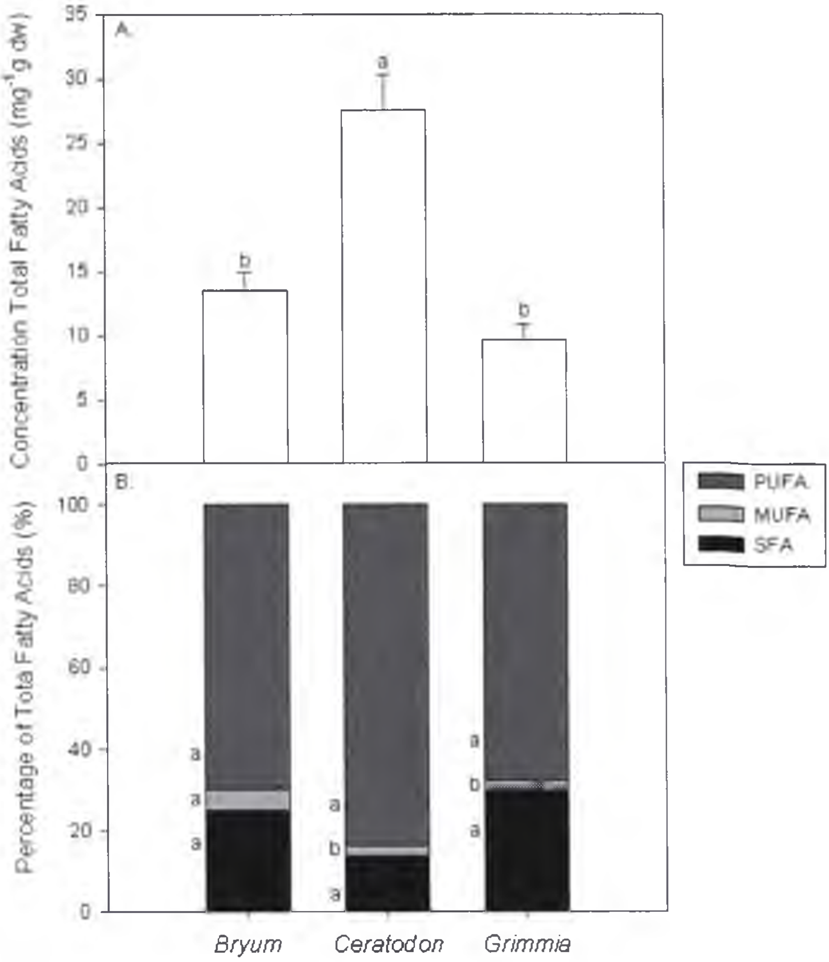


Figure 5.8: Fatty acid composition for the three species: *B. pseudotriquetrum*, *G. antarctici* and *C. purpureus*. Bars represent mean, n = 3. (A). Concentration of total fatty acids (mg^{-1}g dw), error bars indicate sem, (B). Saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA), expressed as a percentage of total fatty acids. Samples collected from ASPA Meltpuddle site at the end of the season (28/2/00), sem (not shown) = SFA: 6.5, 0.3, 6.9, MUFA: 0.8, 0.0, 0.8 and PUFA: 2.3, 0.4, 2.4, for the three species respectively. Letters a & b denote results of pairwise comparisons (student's t), testing for differences between species, $\alpha = 0.017$.

The most abundant fatty acids in all species were the saturated fatty acid (SFA) 10:00, and the polyunsaturated fatty acids (PUFAs) 18:2 and 18:3, which each occurred in relatively high concentrations (> 1 $mg^{-1}g$ dw) in each of the three species (Table 5.4). Other relatively abundant fatty acids included SFAs 16:0 and 18:0, the monounsaturated fatty acid (MUFA) 18:1 and a suite of PUFAs (18:2, 18:3 n-6, 20:2, 20:3 n-6, 20:4, 20:3 n-3, 20:5 and 22:5; Table 5.4).

Table 5.4: Fatty acid composition of *B. pseudotriquetrum*, *C. purpureus* and *G. antarctici* ($mg^{-1}g$ dw). Values in parentheses indicate sem, n = 3. Lipids are grouped into three types: Saturated Fatty Acids (SFAs), Monounsaturated Fatty Acids (MUFAs) and Polyunsaturated Fatty Acids (PUFAs). Only fatty acids detected in concentrations of >0.1 $mg^{-1}g$ dw are listed. Additional fatty acids detected in concentrations of <0.1 only include: 12:0, 14:0, 14:1, 15:0, 15:1, 16:1, 17:1, 20:0, 22:0, 22:1, 24:0, 24:1.

Fatty acid			*B. pseudotriquetrum*	*C. purpureus*	*G. antarctici*
SFA	10:0	Capric	1.85 (0.58)	2.04 (0.13)	2.01 (0.07)
	16:0	Palmitic[b]	1.12 (0.11)	1.51 (0.16)	0.67 (0.05)
	18:0	Stearic[b]	0.08 (0.01)	0.12 (0.01)	0.08 (0.01)
MUFA	18:1	Oleic[b]	0.41 (0.03)	0.42 (0.04)	0.12 (0.03)
	18:1	Elaidic (trans)	0.12 (0.01)	0.13 (0.01)	0.05 (0.01)
PUFA	18:2	Linoleic[b]	4.71 (0.98)	7.4 (0.83)	1.33 (0.08)
	18:3 n-6	γ-Linolenic	0.22 (0.07)	0.28 (0.03)	0.03 (0.00)
	18:3	Linoleic	3.37 (0.66)	7.09 (0.72)	4.02 (0.74)
	20:2	Dienoic	0.05 (0.01)	0.37 (0.05)	0.04 (0.00)
	20:3 n-6	Dihomo-γ-linolenic	0.37 (0.08)	0.13 (0.02)	0.03 (0.01)
	20:4	Arachidonic	0.89 (0.01)	1.17 (0.12)	0.43 (0.04)
	20:3 n-3	Eicosatrienoic	0.00 (0.00)	5.45 (0.63)	0.12 (0.02)
	20:5	Eicosapentaenoic	0.04 (0.00)	0.98 (0.10)	0.61 (0.14)
	22:5	Docosapentaenoic	0.00 (0.00)	0.23 (0.01)	0.00 (0.00)

[b] common principal constituents of membrane fatty acids others mainly storage

Within each of the three species the fatty acid composition was dominated by PUFAs, constituting greater than 68% of the total (Fig. 5.8B). The relative proportion of PUFAs tended to be different between species ($P = 0.0707$; Table 5.3). *Ceratodon purpureus* had the highest and *G. antarctici* the lowest relative PUFAs (Fig. 5.8B). MUFAs were a relatively minor constituent of the total fatty acid composition, $\leq$ 5% across all species. However, significant species differences were observed, ($P = 0.0010$; Table

5.3), with MUFAs 2-fold greater in *B. pseudotriquetrum* than that in the other two species ($P<0.017$; Appendix 3). The remaining lipids were SFAs, constituting up to 30% of the total fatty acid composition. Evidence of differences between species was found ($P = 0.0758$; Table 5.3), with saturated fatty acids possibly more common in *G. antarctici* than in *C. purpureus* ($P<0.05$; Appendix 3; Fig. 5.8B).

The ratio of unsaturated fatty acid (UFA) to SFA was greatest in *C. purpureus* (3.77±0.24), intermediate in *B. pseudotriquetrum* (3.21±0.49) and lowest in *G. antarctici* (2.82±0.13).

Fatty acid / soluble carbohydrate ratio

Soluble carbohydrate and fatty acid concentrations indicate that *C. purpureus* has relatively low soluble carbohydrate content and relatively high fatty acid composition (Figs. 5.6-5.8). In order to quantify this difference in biochemical make-up, and to identify differences in physiological strategies available for tolerance of desiccation, the ratio of total fatty acids: identified soluble carbohydrates was calculated for the three species. The ratio was approximately 5-fold higher in *C. purpureus* (0.756) than the other two species: *B. pseudotriquetrum* (0.158) and *G. antarctici* (0.145).

5.3.3. Plasticity

Phenotypic plasticity is likely to increase survival potential in changing environments (Valladares et al. 2000b, Agrawal 2001). In order to quantify species' relative plasticity, and the variables contributing most toward plasticity, a plasticity index (CV; sem/mean) was calculated for each of the biological characteristics presented in sections 5.3.1. and 5.3.2. Biological variables measured over the course of the season, that is, the tolerance of desiccation variables (CWC and CRT) and the soluble carbohydrates, are shown in Figure 5.9. Variables measured only once are shown in Figure 5.10.

Of the three species, *B. pseudotriquetrum* was found to show the greatest degree of phenotypic plasticity. In 60% of the biological variables shown in Figures 5.9 and 5.10, *B. pseudotriquetrum* had the highest level of plasticity of the three species. The sum

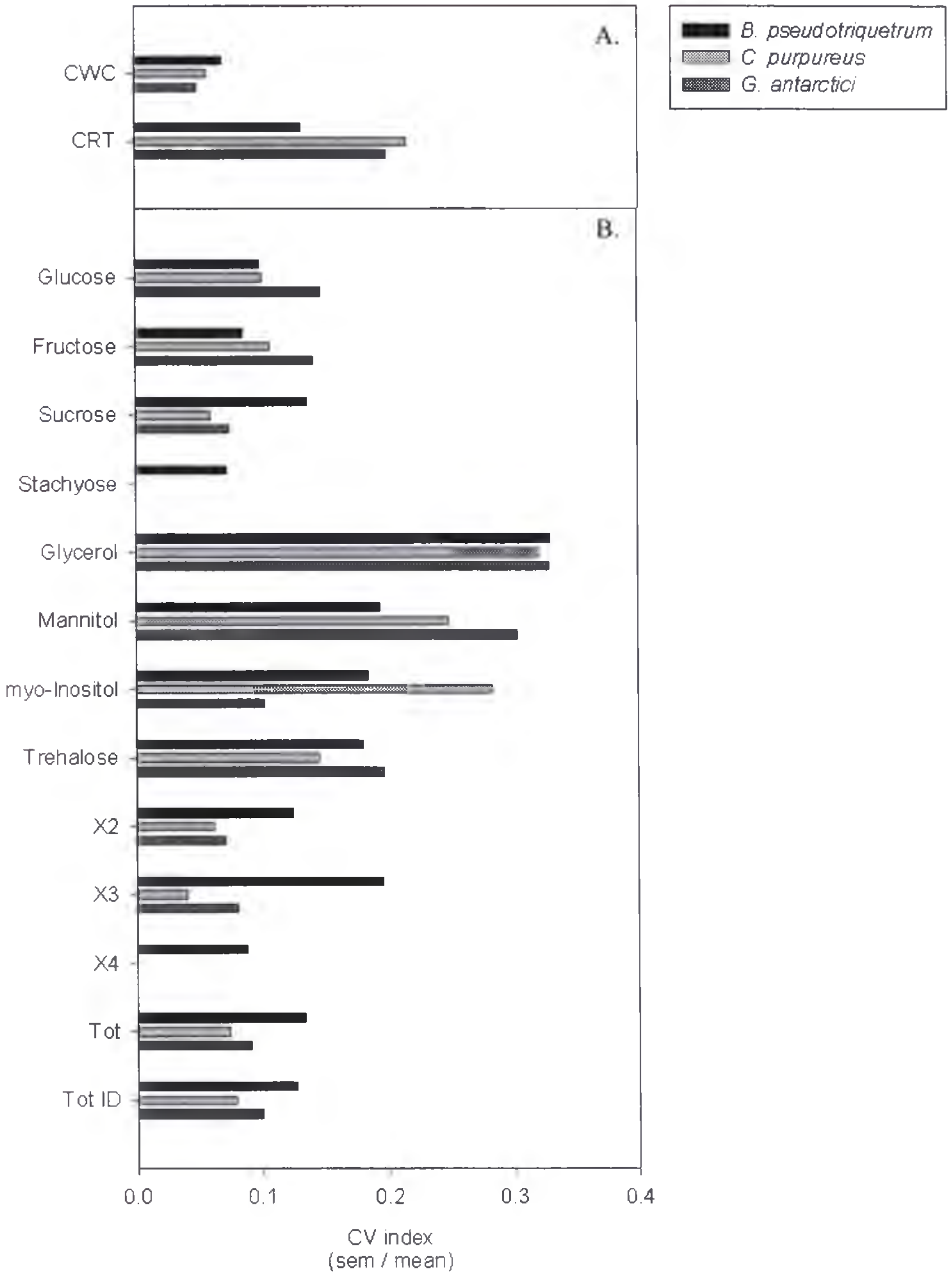


Figure 5.9: Coefficient of variation (CV) index for biological variables measured at three intervals across a summer season: (A) physiological tolerance of desiccation (CWC and CRT) and (B) soluble carbohydrate concentrations, for the three species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*).

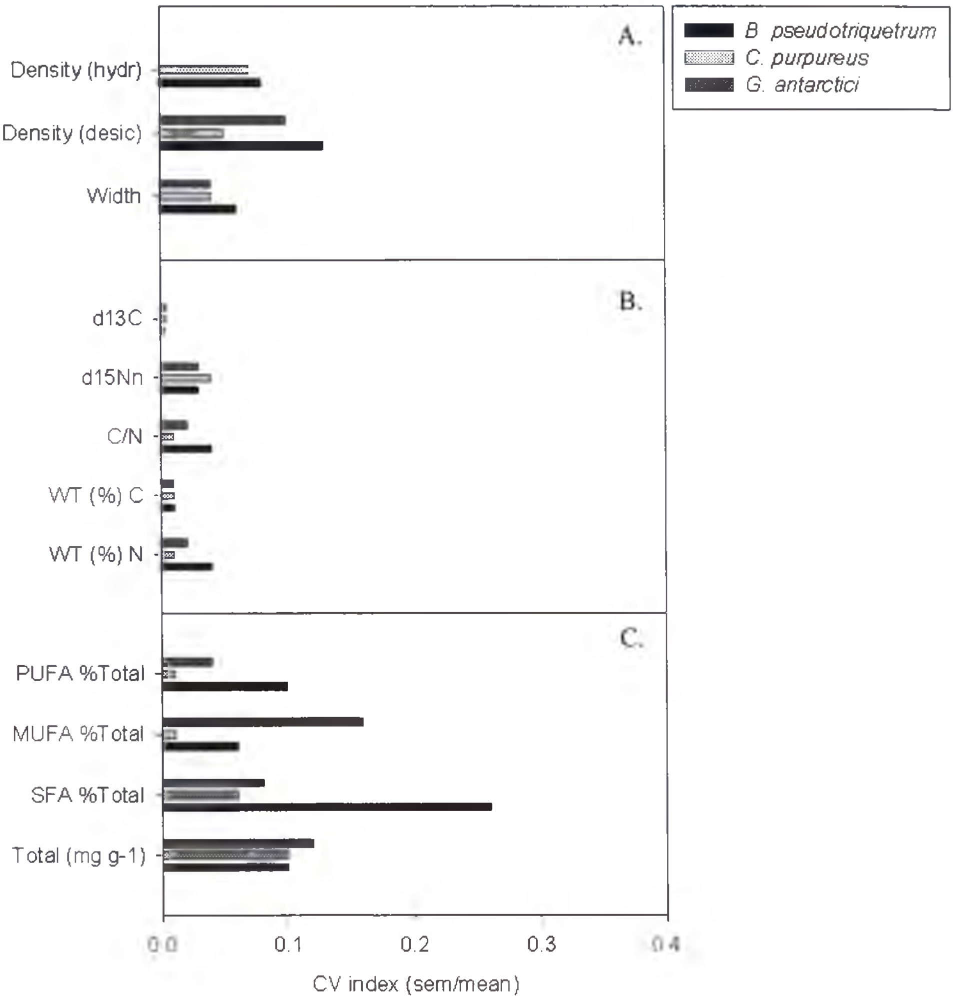


Figure 5.10: Coefficient of variation (CV) index for biological variables measured for a single interval during the summer season: (A) morphology, (B) nitrogen and carbon and (C) fatty acids for the three species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*).

CV, across all variables, was approximately 20 and 30% lower than *B. pseudotriquetrum*, in *G. antarctici* and *C. purpureus*, respectively (*B. pseudotriquetrum* = 3.05, *C. purpureus* = 2.21 and *G. antarctici* = 2.49). *Bryum pseudotriquetrum* was the most phenotypically plastic species in all three of the morphological variables and in eight of the thirteen soluble carbohydrates.

Overall, greatest levels of plasticity were found in the soluble carbohydrate variables, particularly the sugar alcohols (glycerol, mannitol and *myo*-inostiol) which each had CV values exceeding 0.2 for at least one species (Fig. 5.9B). For the tolerance of desiccation variables, CRT showed greater plasticity than CWC (Fig. 5.9A). The nitrogen and carbon variables showed the lowest plasticity values for all species (Fig. 5.10B).

5.4. Discussion

5.4.1. Biological profiles underpinning tolerance of desiccation

The study species relative chances of surviving a drying climate were investigated through the development of biological profiles that relate to tolerance of desiccation. Increased tolerance of drying conditions was considered as the ability to (1) avoid desiccation, (2) tolerate drying, (3) recover from desiccation, and (4) survive desiccation. The biological profiles of the three species are discussed in terms of their relationship to these characteristics.

Avoidance of desiccation

The turf morphology measures showed that *G. antarctici* had a relatively loosely packed turf, as it had smallest gametophyte widths and similar gametophyte densities to the large *B. pseudotriquetrum* (Fig. 5.2). These characteristics indicate this species has a reduced desiccation avoidance potential. The other two species had more densely packed turf, and therefore greater desiccation avoidance potential, due to larger gametophytes and higher gametophyte densities, for *B. pseudotriquetrum* and *C. purpureus*, respectively. Other morphological characteristics that influence desiccation avoidance are also likely to be adopted by these species, such as degree of leaf curling toward stem (Longton 1988), which may cause addition variation between species. Rates of water loss at the individual shoot or leaflet level have not been investigated in this thesis and would be a useful topic for future work.

Despite differences in turf gametophyte packing between *B. pseudotriquetrum* and *G. antarctici*, these two species have similar TWC at full hydration. *Bryum pseudotriquetrum* therefore stores a greater proportion of its turf water internally than the loosely packed turf of *G. antarctici*, which has relatively high external water storage. Since external water is lost more quickly than internal water, this provides further support for *G. antarctici* having the lowest desiccation avoidance potential.

Turf densities in the present study were exceptionally high, with *C. purpureus* exceeding 500 gametophytes per cm^2, a density which is 75% great than that measured in European populations of this species (Simon 1987). Given the prevailing severe Antarctic growth conditions, Antarctic ecotypes of these cosmopolitan species may therefore be better adapted to avoid desiccation than populations of the same species growing under more ameliorating conditions.

Tolerance of desiccation

Tolerance of desiccation was quantified as the ability for a species to continue to metabolise at low water contents. Low CWC was therefore considered to be indicative of high tolerance of desiccation.

The three study species show different levels of tolerance of desiccation. Highest tolerance of desiccation was found in *C. purpureus*, in which photosynthetic activity was maintained at relatively low water contents throughout the season (Fig. 5.3). Conversely, the consistently high CWC values for *G. antarctici*, with photosynthesis always ceasing once water contents dropped below 1.17 g H_2O^{-1}g dw (Fig. 5.3C), suggests that this species is relatively intolerant of desiccation. A third response pattern was observed in *B. pseudotriquetrum*, which showed considerable plasticity in its response to desiccation, with a significant seasonal decline in CWC occurring (Fig. 5.3

and 5.9A). Early in the season photosynthetic activity in *B. pseudotriquetrum* ceased at relatively high water contents (similar to that in *G. antarctici*), while late in the season it was able to maintain photosynthetic activity until a relatively low water content (similar to that in *C. purpureus*). This suggests that Antarctic *B. pseudotriquetrum* has inherent plasticity. A previous study has shown that plants of this species collected from dry sites maintained metabolism to lower CWC than plants from wet sites (Robinson et al. 2000), perhaps indicating the presence of ecotypes. My study has shown, however, that plants from the same site demonstrate a seasonal CWC response to desiccation.

Recovery from desiccation

Recovery from desiccation was quantified by measuring critical recovery time (CRT), the time taken from rehydration to the point at which photosynthetic activity had largely recovered and the rate of increase had begun to plateau (Fig. 5.1).

B. pseudotriquetrum and *C. purpureus*, had similar seasonal trends for CRT; critical recovery times were significantly longer in the late-season desiccation experiment, compared to those measured in the early- and mid-season experiments (Fig. 5.3), suggesting that these species are undoing any cold acclimation that may have been obtained during the previous winter.

The particularly large increase in CRT over the season for *C. purpureus* suggests a reduction in overall tolerance to desiccation throughout the season (Fig. 5.3). This slower recovery late in the season could be an acclimation response related to temperature and not simply water availability. Since *C. purpureus* occupies the most xeric habitats, relative to the other study species (Chapter 3), this result is in contrast to a maritime Antarctic study in which recovery was found to be faster in xeric species than hydric species (Davey 1997c).

Grimmia antarctici was the only species to show a seasonal decline in CRT, and an overall increase in tolerance of desiccation across the season, with the fastest recovery of all species occurring in this species in the late-season experiment, taking only 4.2±1.0

min to reach the critical recovery point (Fig. 5.3). This result, for this hydric species (Chapter 3), is again in contrast that found in the maritime Antarctic, where recovery has been found to be slower in hydric than xeric species (Davey 1997c).

It should be noted that recovery from desiccation occurred within an hour, in all species and across the season. The advantage gained by a quicker CRT is thus in the order of minutes. In contrast, the ability to metabolise at low TWC is likely to allow photosynthetic carbon gain to occur over periods of hours. As such, CWC is probably a more important indicator of overall tolerance of desiccation in these species than CRT.

Survival of desiccation

An important characteristic that assists in survival of desiccation is the ability to regain membrane function, quickly and efficiently, after a desiccation event. Many compounds are important in promoting membrane integrity, during desiccation and rehydration, including a suite of soluble carbohydrates and fatty acids. Ways in which these compounds appear to be related to tolerance of desiccation, and recovery from desiccation, in the three species is discussed.

Bryum pseudotriquetrum is the most likely of the three species to be utilising soluble carbohydrates as a mechanisms for tolerance of desiccation, as correlations between soluble carbohydrate concentrations and the CWC and CRT measures of tolerance of desiccation were strongest in this species (regression r^2 and slope values highest in most sugars; Appendix 7). For most sugars, photosynthesis in *B. pseudotriquetrum* was able to occur at low water contents when concentrations of soluble carbohydrates were low. Although high concentrations of soluble carbohydrates are likely to assist in osmotic stabilisation of tissues and counteract freezing or desiccation damage, the response pattern observed in *B. pseudotriquetrum* indicates high concentrations may be producing osmotic conditions unfavourable to photosynthesis during desiccation. Conversely, photosynthesis recovers quickly at high soluble carbohydrate concentrations in this species, indicating there is a trade-off in overall tolerance of desiccation, in relation to soluble carbohydrate concentrations, when both desiccation and recovery from desiccation are considered. For both desiccation and recovery, mannitol is the exception to these trends, with concentrations exhibiting an opposite pattern to most other soluble carbohydrates. This may mean that mannitol plays a specific role in tolerance of dry conditions in *B. pseudotriquetrum.*

Bryum pseudotriquetrum contains a high proportion of soluble carbohydrates which are known to play an important role in desiccation and freezing tolerance. For example it was the only species in which stachyose was detected and this sugar was a substantial component of the overall pool (Fig. 5.6). Stachyose is known to play a role in desiccation tolerance and is commonly found in other desiccation tolerant organisms such as invertebrates and vascular plant seeds (Koster and Leopold 1988, Pukacka and Pukacki 1997). Whilst stachyose was absent from the other two species, it has been previously detected in these species, albeit in trace concentrations (Robinson et al. 2000). The unidentified X4, also found in *B. pseudotriquetrum*, is a small soluble carbohydrate similar in size to glucose and fructose (Chapter 2, section 2.2.5) and its function is unknown at this stage. However, the high concentration of X4 would also contribute toward the overall total soluble carbohydrate concentrations in this species, and therefore is likely to promote overall osmotic stabilisation of tissues, counteracting damage, during a desiccation event.

Grimmia antarctici generally showed a weaker or an opposing pattern to *B. pseudotriquetrum*, with respect to correlations of soluble carbohydrate concentrations with the tolerance of desiccation measures. In this species, *myo*-inositol appears to be the most likely sugar to be playing a role in tolerance of desiccation, while trehalose and mannitol may be important in promoting fast recovery from desiccation (Fig. 5.6 & 5.7).

High levels of soluble carbohydrates occurred early in the season in both *B. pseudotriquetrum* and *G. antarctici*, which probably reflects active photosynthesis early in the season, as photosynthetic activity occurs while plants are still snow covered (Collins and Callaghan 1980). The highest soluble carbohydrate concentrations occurred in *B. pseudotriquetrum*, as did the largest seasonal decline. By late season the concentration of total identified soluble carbohydrates in *B. pseudotriquetrum* had declined to less than half the concentration that occurred early in the season (Fig. 5.6). This is in contrast to other Antarctic studies, from both the maritime (Davey 1999) and continental (Melick and Seppelt 1994b) regions, which found no significant seasonal change in carbohydrate contents, or found concentrations to increase during the summer (Zuniga et al. 1996). Despite Melick and Seppelt (1994b) reporting no significant annual cycle in soluble carbohydrate contents for *B. pseudotriquetrum*, or *G. antarctici*, concentrations in these species, collected from the same peninsula a decade earlier, showed similar concentrations and a similar decline to that found in the present study over the same collection period (December to February). The seasonal decline in soluble carbohydrates in both species may reflect a lag between the start of photosynthesis early in the season and the onset of growth, however *B. pseudotriquetrum* has also been reported to lose a greater portion of its sugar pool during freeze-thaw events over the summer season, relative to the other study species (Melick and Seppelt 1992).

A soluble carbohydrate that is likely to be important in promoting desiccation tolerance is trehalose, as it is a cryoprotective carbohydrate commonly found in polar biota (Montiel 1998, 2000, Weinstein et al. 2000), and in this study was detected in all three species, despite not being detected in these species in a previous study from the same region (Melick and Seppelt 1992). In contrast to patterns of abundance across the season for other sugars, trehalose accumulated highest concentrations mid-season (Fig. 5.6), when growth temperatures and moisture availability were greatest. This compound is common in many organisms capable of withstanding near-complete desiccation, including cyanobacteria, fungi, yeast, arthropods and plant seeds, as it is very effective at stabilizing proteins and other macromolecules during dehydration (Crowe et al. 1992). It has been suggested that caution should be exercised, however, regarding the detection of trehalose in field-collected, continental Antarctic bryophytes; as it occurs only in low levels, and is absent from laboratory grown *C. purpureus* and temperate moss species (Roser et al. 1992). Roser et al. 1992 suggests it is possible that the source is derived from epiphytic fungi rather than bryophyte tissue, however if this is the case it would indicate high fungal contamination.

An alternative strategy for coping with severe growth conditions appears to be adopted by *C. purpureus*. This species contained the lowest soluble carbohydrate concentrations and showed poor correlations between soluble carbohydrate content and the desiccation variables (Fig. 5.6 & 5.7). The other two species in this study have, however, very high levels of soluble carbohydrates and the concentrations in *C. purpureus* are within the range found for the three study species in a previous continental Antarctic study (Roser et al. 1992) and in arctic *Polytrichum* (Sveinbjornsson and Oechel 1991, Barsig et al. 1998). Conversely, *C. purpureus* had the highest concentration of fatty acids. Since this is unlikely to indicate this species has more membrane material, the elevated fatty acid concentrations are likely to indicate greater use of fatty acids for storage. Fatty acids formed a substantial proportion of the total carbohydrate pool, with the fatty acid/soluble carbohydrate ratio 5-fold higher in this species. *Ceratodon purpureus* is therefore converting a greater proportion of its carbon into fatty acids, while the other two species retain significantly more in the form of soluble carbohydrates. A similar increase in the relative concentration of fatty acids to carbohydrates is seen in evergreen trees growing at altitude compared with lowland trees (Li et al. 2002) and in herbaceous biomass along an altitudinal gradient on Mt Olympus, Greece (Pantis et al. 1987). Lipids are suggested to form an efficient, osmotically neutral form of carbohydrate storage in these alpine plants and it maybe that in *C. purpureus* this strategy allows the plants to maintain a low CWC throughout the season. It seems likely that *C. purpureus* relies more on its large lipid pool, than its sugar pool, for protection from freezing and desiccation. Carbon storage in this energy rich, but insoluble form may reduce the loss of soluble carbon during desiccation and freeze-thaw events. Temperate *C. purpureus* has also been shown to contain a relatively high concentration of lipids, often contained in lipid droplets (Swanson et al. 1976). The acetylenic acid triglyceride 9,12,15–Octadecatrien–6-ynoic acid occurs in large amounts in *C. purpureus* and its concentration correlates with presence of these cytoplasmic droplets. Nutrient stressed axenic cultures of *C. purpureus* showed an almost 4 fold increase in triglycerides especially 9,12,15–Octadecatrien–6-ynoic acid (Andersson et al. 1974). The presence of fatty acids with 4 and 5 double bonds (such as arachidonic and eicosapentaenoics) is not unusual in mosses (Anderson et al. 1974), but these fatty acids are uncommon in higher plants (Gellerman et al. 1972, Anderson et al. 1974).

Along with a higher concentration of total lipids, *C. purpureus* contains a different lipid composition to the other two species, with more PUFAs and less SFA. This species had the highest UFA:SFA ratio, within the upper range typically found for chilling-resistant plants (Taiz and Ziger 2002). This is in contrast to *G. antarctici*, in particular, which was found to have a low UFA:SFA ratio, within the range considered to be typical of chilling-sensitive plants (Taiz and Ziger 2002). The high proportion of UFAs found for *C. purpureus* indicates that this species may have different membrane composition to the other species, and this may in turn be advantageous in allowing it to compete better in an environment with frequent freeze-thaw or desiccating events. Since photosynthesis and respiration are both membrane based processes it seems likely that this unusual lipid composition may explain the ability of this species to maintain photosynthesis under the driest conditions of the three species.

5.4.2. Species variation in growth conditions

The distribution of the three species along an environmental gradient of opposing water and nutrient availability (Chapter 3) indicates that the three species are likely to have different biological requirements of the growth environment. Under a drying climate, the availability of both these variables is likely to decline (Chapter 1, sections 1.4 and 1.5). The present status of the species water and nutrient relations is therefore of interest in order to understand how they might respond to future altered conditions.

Habitat submergence

Species that are presently restricted to wet sites are less likely, than species occupying dry sites, to survive a drying climate. The $\delta^{13}C$ signature for the three species concurs with the trends presented in Chapter 3 and Selkirk and Seppelt (1987), suggesting that the two cosmopolitan species occupy drier sites and *G. antarctici* is subject to greater diffusional limitations due to its occupation of wetter sites (Chapter 2, section 2.2.4). The habitat occupied by this latter, endemic, species is therefore less likely to persist under a drying climate than the conditions presently occupied by the former two species.

The changes in $\delta^{13}C$ with depth of gametophyte support the current drying trend, described by Melick and Seppelt (1997) and suggests that submergence was more common in the past than it is at the present time (Fig 5.5). The gametophytes used were entire and the lower sections represent growth that occurred in previous years. Given the lack of transport tissues, it is unlikely that much mixing occurs between the various layers. Unfortunately, an independent quantification of the age of the various sections was not possible in this study, but based on estimates of growth rates of 0.6 mm per year for this species in the Windmill Island (Melick and Seppelt 1997) these gametophytes are likely to be over 60 years old, predating the availability of meteorological data for the region.

Nutrient availability

Nitrogen contents of the three species suggest that *B. pseudotriquetrum* is nutrient rich and *C. purpureus* nutrient-poor (Fig. 5.4A). *Ceratodon purpureus* grows on nutrient-poor growth mediums (Seppelt and Hancock 1991) and readily colonises nutrient-poor substrates (Carvey et al. 1977, Engelmann and Weaks 1985). If nutrient availability is reduced under a future drying climate, this species, with apparently low-nutrient requirements, may gain a competitive advantage over the other two species.

Given that the soil inputs in this area are heavily fractionated ($\delta^{15}N$ value from chapter 4) *B. pseudotriquetrum* and *C. purpureus* would appear to be obtaining nitrogen directly from the input source. The relatively low $\delta^{15}N$ found for *G. antarctici* suggests that it is utilising inputs with a lower fractionation signature, which might include fresh inputs of bird guano, or a greater proportion of its nitrogen being obtained from cyanobacterial fixing of N, under these wetter conditions (Davey and Marchant 1983). It may also be a feature of relative moisture availability since, at large spatial scales at least, $\delta^{15}N$ declines as ecosystem water availability increases along rainfall gradients (e.g. Robinson 2001).

5.5. Conclusions

These biological desiccation tolerance profiles highlight many important differences between the species that are likely to influence their relative chance of survival under a drying climate.

The ability to both avoid desiccation and also tolerate drying was lowest in *G. antarctici* and these factors are likely to be of major importance in relation to maintaining a positive carbon balance in these environments. *Grimmia antarctici* showed improved recovery from desiccation across the season, while recovery rates slowed over the season for the other two species. Despite this, long term data from $\delta^{13}C$ values along with evidence from Chapter 3 still suggests that *G. antarctici* does better in the wet sites and is less competitive in dry sites. The ability to tolerate drying was consistently high in *C. purpureus* and plastic in *B. pseudotriquetrum*. Different strategies for survival of desiccation are likely to be utilised by these cosmopolitan species, with *B. pseudotriquetrum* likely to rely on sugars for efficient osmoregulation, whilst *C. purpureus* utilises its extensive suite of lipids to provide tolerance of drying and freeze-thaw events.

Chapter 6: General discussion and conclusions

The main aim of this thesis was to explore the likely impacts of two opposing scenarios for the future of the Windmill Islands region, namely increased and decreased water availability. The major findings in relation to these opposing environmental conditions are listed in Table 6.1 and illustrated in Fig. 6.1.

Under a wetter future climate, my work suggests that productivity is overall likely to increase but only certain cryptogamic communities are likely to thrive (Chapter 4). Community types such as the Bryophyte and Crustose communities examined in this study are examples of communities that are likely to flourish under wetter conditions. In contrast, communities such as the Moribund and *Usnea* communities investigated in this work, showed a relatively inert response to ameliorating growth conditions. I concluded that, although gametophytes are present in the Moribund communities examined (Chapter 3) regeneration is only likely if the future moisture regime creates consistently moist conditions (Chapter 4) and providing allelopathy is not a major inhibitor of growth.

A wetter climate may allow expansion of bryophyte communities, and *G. antarctici* is most likely to dominate future wetter bryophyte communities. The relatively plastic *B. pseudotriquetrum* is likely to be present at levels of abundance expected to be similar to those found in present day communities. Of the three study species, *C. purpureus* is most likely to decline in abundance under future wetter conditions and/or its distribution will incorporate habitats presently too dry for bryophyte occupation. These predicted changes to abundance patterns and species distributions, based on present distributions and physiological characteristics, are illustrated in the schematic model below (Fig. 6.1B).

Table 6.1: Summary of main results.

Main Results	
Primary production	Increased in response to water and/or nutrient availability.
Limitations	The flora was more nutrient-limited than expected. In some cases nutrient-limitations exceeded water-limitations (e.g. total Chlorophyll).
Natural variation in resource availability	The availability of water and nutrients differed between community types (e.g. the Bryophyte community had low nutrient and high water availability, and vice versa for *Usnea* community).
Community response to resource availability	Some communities respond more strongly than others to water and/or nutrient additions (Crustose and Bryophyte communities showed strongest response, Moribund community weakest response).
Crustose community	High potential for increased productivity under wetter climate.
Usnea community	Low response to water and nutrient treatments. Background environmental conditions: high nutrient availability, low water availability. Evidence of desiccation stress - highest concentration of sugar alcohols.
Moribund community	Low response to water and nutrient treatments. High concentration of trehalose and stachyose.
Bryophyte community	High potential for increased productivity under wetter climate if nutrient availability increases. Strongest nutrient response. Background environmental conditions: low nutrient availability, high water availability. Evidence of current high productivity from sugar content.
Ceratodon purpureus	Most likely to survive a drying climate: presently restricted to the driest bryophyte sites, avoids desiccation via tightly packed turf, metabolise at consistently low water contents and is lipid rich. Lowest nutrient requirement of bryophyte species.
Grimmia antarctici	Least likely to survive a drying climate: presently dominant in low-lying wet sites only, poor ability to avoid desiccation, requires high water content for metabolism, contains no stachyose, lowest trehalose and low lipid content.
Bryum pseudotriquetrum	Most likely to survive a changing environment (but unlikely to dominate, abundance likely to remain intermediate): widely distributed, avoids desiccation via tightly packed turf, plastic desiccation response (requiring less water for metabolism over the course of the season), high soluble carbohydrate content, only species containing stachyose.
Predicted impact of a wetter climate	Increased primary productivity, particularly in "Bryophyte" and "Crustose" type communities. *Grimmia antarctici* may increase in abundance, *C. purpureus* likely to shift distribution to sites presently too dry for bryophytes.
Predicted impact of a drier climate	Primary productivity likely to decrease, with "Bryophyte" and "Crustose" type communities particularly disadvantaged. *Bryum pseudotriquetrum* and *C. purpureus* most likely species to survive. Conservation issues for *G. antarctici.*

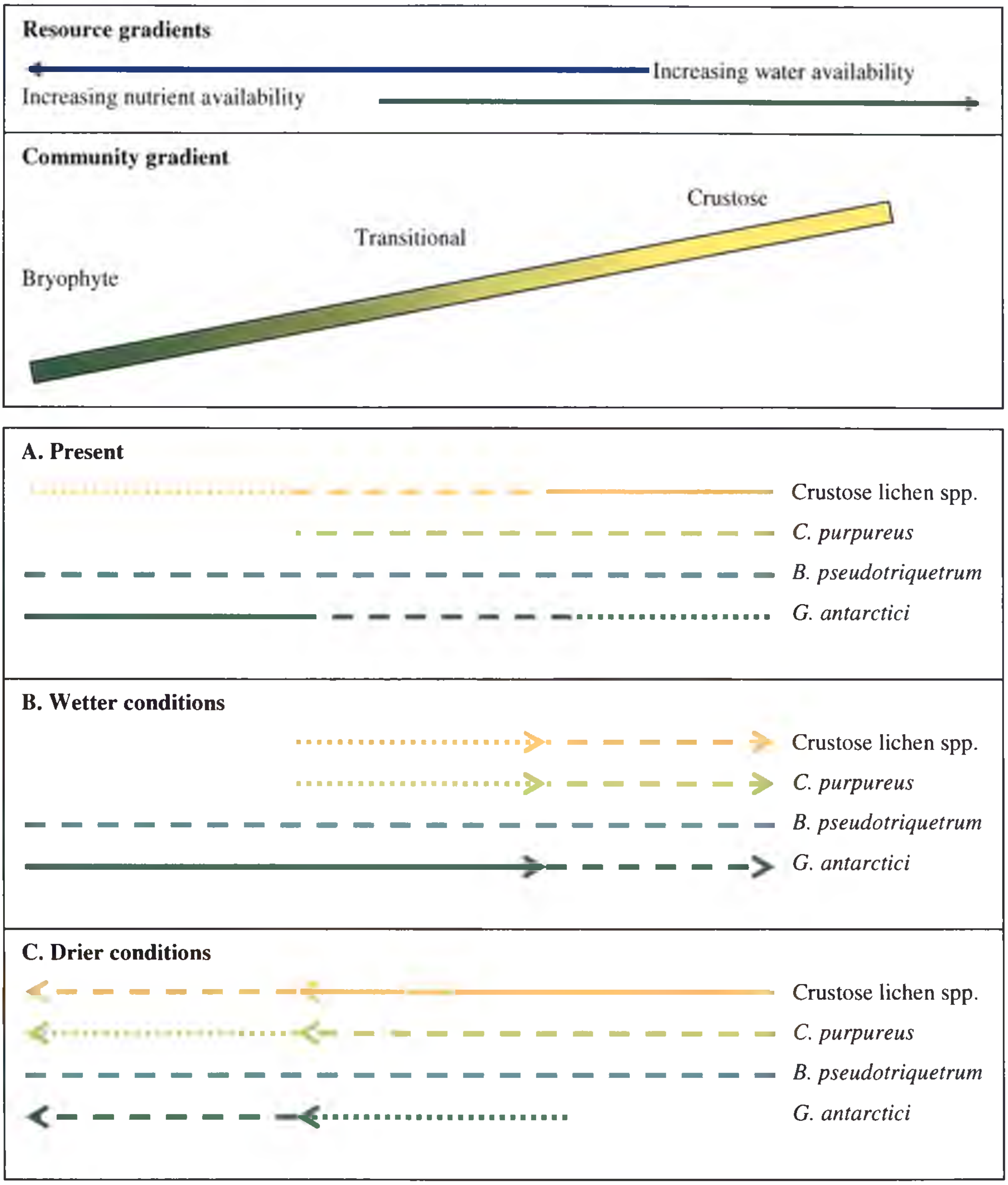


Figure 6.1: Schematic model of the Windmill Islands' bryophyte and crustose lichen community dynamics. The model shows three communities (Bryophyte, Moribund and Crustose) occurring along a slope that has underlying, opposing, water and nutrient resource gradients. Three levels of relative abundance: dominant (solid line), present (dashed line) and rare (dotted line) are shown for four vegetation categories (crustose lichen, and three bryophyte species: *C. purpureus*, *B. pseudotriquetrum* and *G. antarctici*). The three models represent (A) present distributions and that predicted for two future scenarios; (B) wetter conditions and (C) drier conditions.

Conversely, under a drier climate, there is likely to be a continued bryophyte contraction and lichen expansion. The Antarctic endemic, *G. antarctici*, is likely to be most adversely affected by increased aridity, as it presently dominates only the wettest communities (Chapter 3) and generally shows poor tolerance of desiccation (Chapter 5). Conservation issues are therefore raised for this species, if the current drying trend continues, creating overall biodiversity concerns. The bryoflora of a future drier climate is likely to be dominated by the two cosmopolitan species only, the relatively desiccation tolerant *C. purpureus* and the highly plastic *B. pseudotriquetrum*. These predicted changes to abundance patterns and species distributions under conditions of increasing aridity are illustrated in the schematic model (Fig. 6.1C).

The physiological plasticity observed in *B. pseudotriquetrum* indicates that this species has the greatest chance of survival under a fluctuating climate, regardless of which way climate may shift. Despite its generalist characteristics, this species does not appear to be a strong competitor, particularly with *G. antarctici* in wet habitats. It is therefore concluded that this species is likely to persist in the future, with little change to its present distributions, but is unlikely to achieve dominance (Fig. 6.1).

This study represents one of the only field manipulations of water and nutrients to be conducted in continental Antarctica. It demonstrates that such experiments are possible, and worthwhile for the advancement of our understanding of community dynamics in this model ecosystem. Perhaps the most surprising outcome of this research was the clear evidence that nutrients play a relatively large role in the functioning of Antarctic terrestrial communities. It was concluded, from the field manipulations of water and nutrient availability, that the communities studied were more nutrient- than water-limited (Chapter 4). This indicates that the nutrient resource availability gradient, found to underlie patterns of species distributions in the cryptogamic communities studied (Chapter 3), may be as important as, or even exceed, the role played by the opposing water resource gradient. The strength of this nutrient effect was unexpected because it is incongruent with the current body of literature, which indicates water availability is more important to the functioning of these communities than that of nutrients (Tables 1.3 and 1.4). The literature does suggest nutrients influence species distributions in

Antarctic cryptogamic communities, but only at the extremes, for example, in the occurrence of nitrophilous lichens in the vicinity of animal-derived nutrient sources (e.g. Broady 1989, Hovenden and Seppelt 1995a, Leishman and Wild 2001). In addition, the focus cryptogamic components of this thesis, the bryophytes, are considered in the literature to be primarily influenced by the availability of water (Selkirk and Seppelt 1987, Schwarz et al. 1992, Smith 1999, Leishman and Wild 2001) with very little reference to nutrients influencing species distributions in this vegetation sector.

My results have important implications for predictions of future distributional patterns. Although a warmer, wetter climate would support better nutrient cycling there is probably little likelihood of increased nutrient inputs, given that the present primary source appears to be ancient penguin colonies. Unless bird populations increased markedly, terrestrial Antarctic communities could become increasingly nutrient-limited. Although this work did not address the relative nutrient requirements of the three bryophyte species, *C. purpureus* is known to thrive in nutrient-poor conditions and might be at an advantage if nutrient limitations develop in this system. It is also likely that those lichens with either reduced nutrient requirements or the potential to fix atmospheric nitrogen would be favoured under such conditions

6.1. Study limitations and future research directions

The primary limitation encountered in this study was the restrictions associated with measurement of water availability. Since destructive sampling methods were used for the measurement of water availability (determination of wet versus dry weight for turf samples), single measurements only were conducted in order to keep environmental impacts to a minimum. The implementation of alternative non-destructive measures of water availability would have been useful, as this would have allowed multiple measures to be conducted over the course of the experimental period. Multiple measures would have both improved understanding of patterns of water availability over the course of the growth season and determined if my single measurement intervals were indicative of the conditions prevailing over the course of the season.

I have therefore conducted work in subsequent field seasons that has utilised non-destructive methodologies for this application. Methods that have proved useful include the insertion of small sponge cores into the moss turf (approx 1cm diameter). These sponges form an inert medium, with similar water holding properties to the bryophyte turf (J. Wasley, *unpublished data*). In addition, they can be removed and reinserted multiple times throughout the season, providing an indication of seasonal bryophyte water availability, with negligible impacts to the turf. Other methodologies I have investigated in subsequent seasons include the use of purpose-built moisture sensors that provide a relative indication of water availability (P. Johnson and J. Wasley *unpublished data*). Similar to the sponge method, multiple measures can be performed without causing damage to the turf. With conservation of these fragile ecosystems in mind, methodologies such as these latter suggestions are superior to those methods requiring destructive sampling.

The survey component of my work (Chapter 3) provides a baseline for future monitoring of these communities. It has allowed optimisation of the methods, which have now been utilised in the establishment of a series of permanent transects, installed during the summer of 2002/3. These transects are registered as State of the Environment Indicator sites, due to be resurveyed at 5-yearly intervals. An improvement to the methodologies employed in the installation of the permanent transects included more frequent water availability measures, as discussed above. Further improvements planned for the next survey interval include identification of encrusting lichen species on areas of moribund turf, as regeneration is less likely for turf encrusted with lichen species known to inhibit regeneration, such as *Buellia* spp. (Melick and Seppelt 1997).

My work has highlighted several new research directions that will increase our understanding of climate change effects on Antarctic terrestrial communities. For example, whilst the present body of literature directed my research toward a water-relations focus, the surprisingly strong influence of nutrient availability found in my study suggests future research attention is warranted in the nutrient-relations arena. Specifically, experiments investigating species-specific nutrient-relations for the bryoflora of this region are recommended. My study indicates *C. purpureus* has low nutrient requirements, experiments measuring productivity, under a range of controlled nutrient regimes, would allow confirmation of species-specific responses to future changes to these environmental factors. Another area of research, regarding nutrient-relations, which requires attention, is an investigation of nitrogen-fixation rates across species and communities under a range of controlled environmental conditions. If future environmental conditions exacerbate the present nutrient limitations, nitrogen-fixation may become increasingly important as a nitrogen source.

A focus of this thesis has been tolerance of desiccation, which has provided an explanation for species distributions in the field, however this is unlikely to be the whole story. Future research to examine the other water-relations extreme, namely tolerance of submergence, would be useful to increase our understanding of the mechanisms determining the dominance of *G. antarctici* in wet habitats. Such experiments would help to determine if this species is a better competitor in this environment, or whether the other species are intolerant of submergence, and are therefore excluded from those habitats that suffer frequent submergence in the summer months.

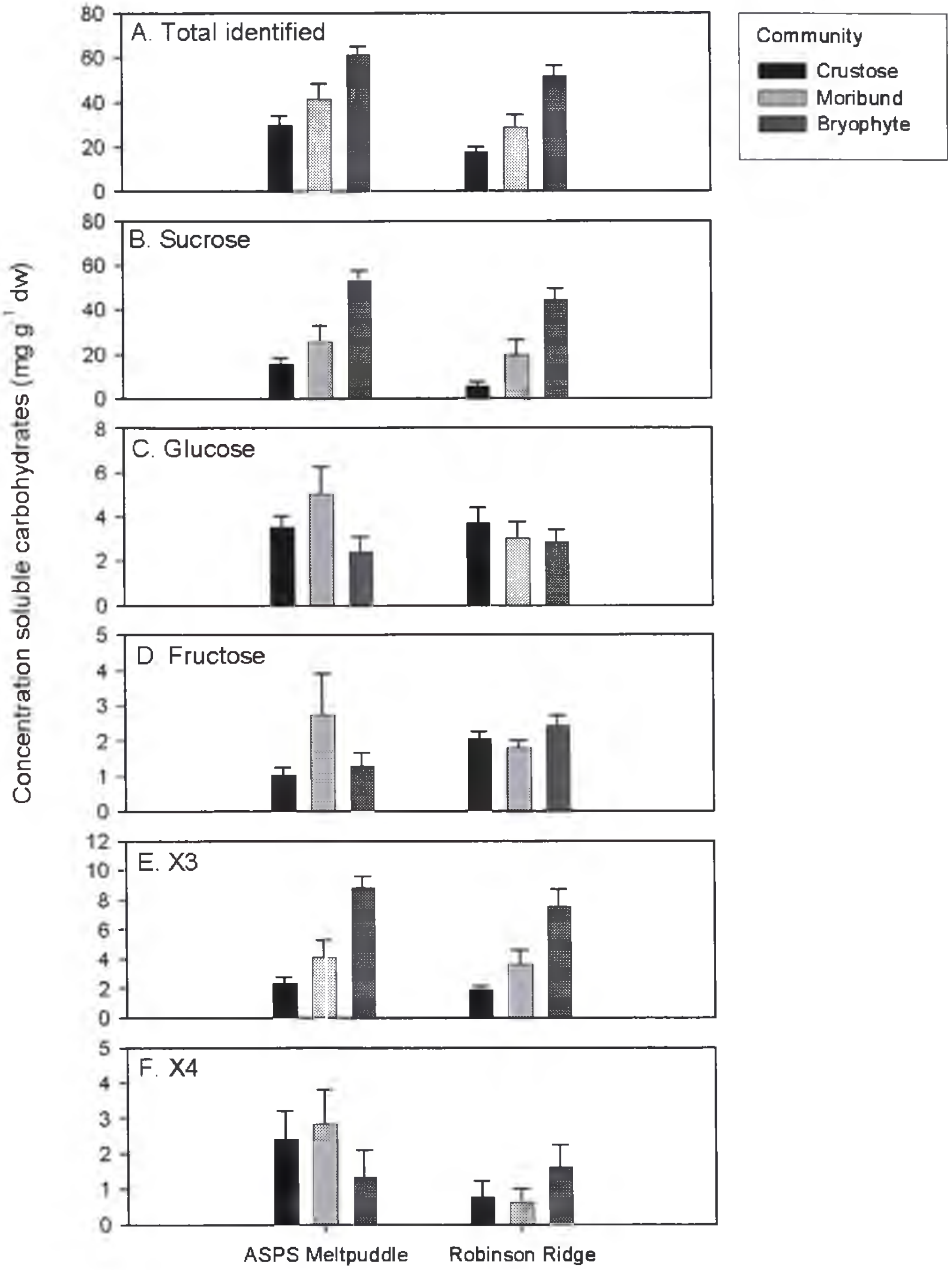
6.2. Conclusions

This study has provided a baseline for future monitoring of these Antarctic terrestrial communities, by establishing fine-scale distributions for the Windmill Islands' bryoflora. In addition, I have demonstrated that field manipulation experiments are possible in these extreme environments and can provide unexpected and important results. I have confirmed that although *G. antarctici* is most abundant in the wettest environments it is not restricted to these areas but appears to be less competitive, probably due to its reduced ability to tolerate frequent desiccation events. This species appears to be most at threat from a drying climate. *Ceratodon purpureus* is limited to dry areas and showed the highest ability to tolerate desiccation, its low nutrient content suggests it is likely to out perform the other bryophyte species under drying conditions, even if nutrient availability remains low. Under a wetter environment this species would shift its distribution into drier areas. A generalist response was observed in *B. pseudotriquetrum*, with this species occurring across a broad range of habitats and showing a plastic, physiological response to desiccation. Although this species appears highly adaptable to a range of conditions and is highly likely to survive the future climate, it appears to be a poor competitor with *G. antarctici* in the wettest habitats. Regardless of the direction of any future shift in climatic conditions, *B. pseudotriquetrum* is likely to survive but remain present at intermediate levels of abundance only.

Overall, this work has provided a significant contribution to our understanding of the functioning of Antarctic terrestrial communities and how they are likely to respond to the changes to environmental conditions, which are predicted to occur in response to future climatic change. This work has developed a baseline for the monitoring of community change and the combination of field- and laboratory-controlled experiments have provided a greater understanding of community and species-specific water and nutrient relations. Since the direction of change for environmental factors is currently unclear, a range of likely future scenarios have been considered by this work, rendering the findings applicable, regardless of the nature of future climatic shifts.

Appendices

Appendix 1: Concentration (mg^{-1}g dw) of select soluble carbohydrates: A. total identified, B. sucrose, C. glucose, D. fructose, E. X3 and F. X4. Data shown for two sites: ASPA Meltpuddle and Robinson Ridge; and three communities: Crustose, Moribund and Bryophyte. Bars represent mean±sem, n = 10. Note y-axes are different.



Results of 2-way ANOVA for soluble carbohydrates shown in graph above. Testing for differences within the whole statistical model and the individual effects of site and community, as well as the significance of site*community interactions.

Variable	Transformation	Effect Test	Model DF	Error DF	F ratio	*P*
Total ID	**None**	**Whole Model**	**5**	**54**	**11.4761**	**<0.0001**
		Site	1		8.7375	0.0046
		Community	2		24.2548	<0.0001
		Site*Community	2		0.0666	0.9356
Sucrose	**None**	**Whole Model**	**5**	**54**	**13.9611**	**<0.0001**
		Site	1		4.3522	0.0417
		Community	2		32.6208	<0.0001
		Site*Community	2		0.1059	0.8997
Glucose	**Log10**	**Whole Model**	**5**	**54**	**1.8244**	**0.1236**
		Site	1		0.3707	0.5452
		Community	2		2.6189	0.0821
		Site*Community	2		1.7567	0.1823
Fructose	**None**	**Whole Model**	**5**	**52**	**7.3205**	**<0.0001**
		Site	1		26.4043	<0.0001
		Community	2		0.2959	0.7451
		Site*Community	2		4.6561	0.0138
X3	**None**	**Whole Model**	**5**	**54**	**11.2374**	**<0.0001**
		Site	1		1.0926	0.3006
		Community	2		27.3994	<0.0001
		Site*Community	2		0.1477	0.863
X4	**Square root**	**Whole Model**	**5**	**54**	**2.8327**	**0.0242**
		Site	1		8.2534	0.0058
		Community	2		0.0363	0.9644
		Site*Community	2		2.9188	0.0626

Appendix 2: Summary tables of Student's t pair-wise comparison results

Pair-wise comparisons (Student's t) for variables showing significant treatment * community interactions: N% and ETR. Number of comparisons: 24 treatment and 24 community. Community abbreviations: Bryo = Bryophyte, Mori = Moribund, Crust = Crustose. Treatment codes: NT = No Treatment, W = Water, N = Nutrient, WN = Water & Nutrient.

% N			ETR		
Group	$\alpha = 0.05$	$\alpha = 0.002$	Group	$\alpha = 0.05$	$\alpha = 0.002$
Crust-N	1	1	Crust-W	1	1
Usnea-N	1, 2	1, 2	Crust-WN	1	1,2
Crust-NT	2, 3	1, 2, 3	Bryo-WN	2	1,2,3
Crust-W	2, 3	1, 2, 3	Crust-N	2,3	2,3,4
Mori-N	2, 3, 4	2, 3	Bryo -N	2,3,4	3,4,5
Crust-WN	2, 3, 4	2, 3, 4	*Usnea*-WN	2,3,4,5	3,4,5
Usnea-WN	2, 3, 4	2, 3, 4	Bryo –W	2,3,4,5	3,4,5
Mori-W	3, 4	2, 3, 4	Mori-N	2,3,4,5,6	3,4,5
Mori-WN	3, 4	2, 3, 4	Mori-W	3,4,5,6	3,4,5
Mori-NT	3, 4, 5	2, 3, 4, 5	Mori-WN	3,4,5,6,7	3,4,5
Usnea-W	4, 5, 6	3, 4, 5	*Usnea*-N	4,5,6,7	3,4,5
Usnea-NT	5, 6	4, 5, 6	Bryo –NT	5,6,7	4,5
Bryo-N	6, 7	5, 6, 7	*Usnea*-W	5,6,7	4,5
Bryo-WN	7, 8	6, 7, 8	*Usnea*-NT	5,6,7	4,5
Bryo-NT	8	7, 8	Mori-NT	6,7	5
Bryo-W	8	8	Crust-NT	7	5

Community pair-wise comparisons (Student's t) for variables showing significant community differences and no significant treatment * community interaction: %P, %C, C/N, N/P, Total Chl, Chi a/b, TWC, $\delta^{15}N$, $\delta^{13}C$, Glucose, Fructose, Sucrose, Trehalose, Glycine, X3, Total (-X) and Total (+X). Communities that share the same number are not significantly different from each other. Conducted at $\alpha = 0.05$ and the Bonferroni adjusted $\alpha = 0.008$.

Community	% P		%C		C/N		N/P		Total Chl		Chi a/b	
	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$
Bryophyte	3	3	1,2	1,2	1	1	1	1	2	1,2	2	2
Moribund	3	3	1	1	2	2	1	1	3	3	3	2
Crustose	2	2	2	1,2	3	3	2	2	1	1	1	1
Usnea	1	1	3	2	3	3	3	3	2,3	2,3	1	1

Community	TWC		$\delta^{15}N$		$\delta^{13}C$		Glucose		Fructose		Sucrose	
	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$
Bryophyte	1	1,2	2,3	2	1	1	1	1	1	1	1	1
Moribund	2	2	3	2	3	3	2	2	2	2	1	1
Crustose	1	1	1	1	2	2	3	3	3	3	2	2
Usnea	2	2	2	2	4	4	2	2	3	3	2	2

Community	Trehalose		Glycine		X3		Total (-X)		Total (+X)	
	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$	$\alpha = 0.05$	$\alpha = 0.008$
Bryophyte	2	2	2	3	1	1	1	1	1	1
Moribund	1	1	1	1,2	2	2	1	1	2	2
Crustose	1	1	1	1	3	3	2	2	3	3
Usnea	2	2	2	2,3	3	3	1	1	2	2

Treatment pair-wise comparisons (Student's t) for variables showing significant treatment effects and no significant treatment * community interaction: C/N, Total Chlorophyll, Fructose, Ribitol (*Usnea*) and X2 (Bryo). Treatments that share the same number are not significantly different from each other. Conducted at $\alpha = 0.05$ and the Bonferroni adjusted $\alpha = 0.008$.

Treatment	C/N		Total Chi		Fructose		Rib (*Usnea*)		X2 (Bryo)	
	α = 0.05	α = 0.008	α = 0.05	α = 0.008	α = 0.05	α = 0.008	α = 0.05	α = 0.008	α = 0.05	α = 0.008
No Treatment	1,2	1	2	2,3	2	1	1,2	1,2	1	1,2
Water	1	1	2	3	1	1	2	2	1	1
Nutrient	2	1	1	1,2	1,2	1	1,2	1,2	2	2
Water & Nutrient	1,2	1	1	1	1	1	1	1	1,2	1,2

Appendix 3: Results of Student's t pairwise tests conducted for data presented in Chapter 5.

Student's t pairwise test results testing for differences between the three study species (*B. pseudotriquetrum, C. purpureus* and *G. antarctici*) with respect to: %N, %C, C/N, $\delta^{15}N$ and $\delta\ ^{13}C$, mannitol. For each variable, species denoted different letters are significantly different. The results at both $\alpha = 0.05$ and the Bonferroni corrected 0.017 are shown.

Variable	$\alpha = 0.05$			$\alpha = 0.017$		
	Bryum	*Ceratodon*	*Grimmia*	*Bryum*	*Ceratodon*	*Grimmia*
Gametophyte density	B	A	B	B	A	B
Gametophyte width	A	B	C	A	B	C
%N	A	C	B	A	C	B
%C	A	B	C	A	B	C
C/N	B	A	B	B	A	B
$\delta^{15}N$	A	A	B	A	A	B
$\delta\ ^{13}C$	B	B	A	B	B	A
Mannitol	A	B	B	A	B	B
Total fatty acids	B	A	B	B	A	B
% total SFA	AB	B	A	A	A	A
% total MUFA	A	B	B	A	B	B
% total PUFA	AB	A	B	A	A	A

Student's t pairwise test results, testing for differences between the experimental intervals (Dec, Jan and Feb) with respect to: Stachyose and Glycerol. For each soluble carbohydrate and experimental interval denoted different letters, differences are significant. The results at both $\alpha = 0.05$ and the Bonferroni corrected 0.017 are shown.

Variable	$\alpha = 0.05$			$\alpha = 0.017$		
	Dec	Jan	Feb	Dec	Jan	Feb
Stachyose	A	B	B	A	AB	B
Glycerol	B	C	A	B	B	A

Student's t pairwise test results testing for differences between the three study species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*) and three experimental intervals (Dec, Jan and Feb) with respect to: water content at full hydration (WC @ T0), critical water content (CWC) and critical recovery time (CRT). For each variable, species (and experimental intervals) denoted different letters are significantly different. The results at both $\alpha = 0.05$ and the Bonferroni corrected 0.003 are shown.

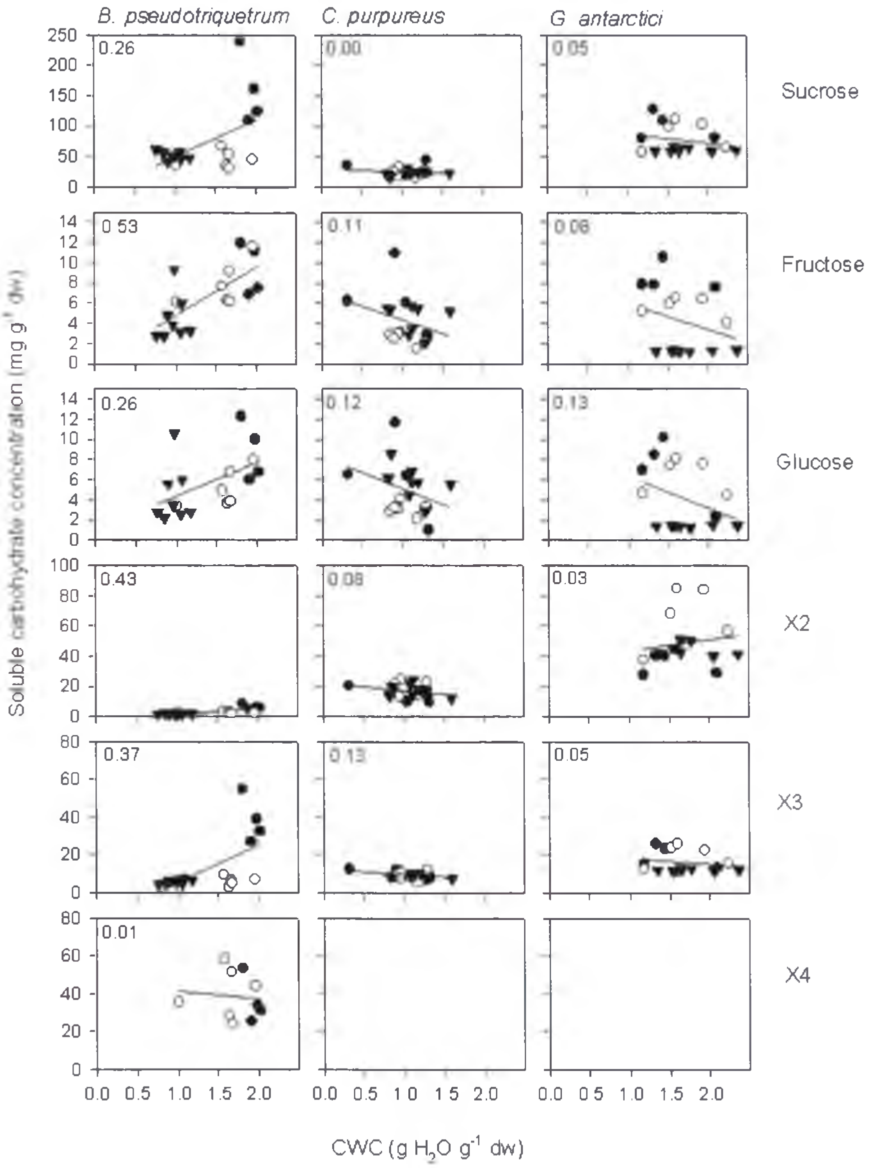
Species (Expt)	WC @ T0		CWCs		CRT	
	$\alpha = 0.05$	$\alpha = 0.003$	$\alpha = 0.05$	$\alpha = 0.003$	$\alpha = 0.05$	$\alpha = 0.003$
Bryum (Dec)	C	C	AB	A	CD	CDE
Bryum (Jan)	A	A	B	AB	C	C
Bryum (Feb)	C	C	C	C	B	B
Ceratodon (Dec)	D	D	C	C	DE	CDE
Ceratodon (Jan)	C	C	C	BC	CD	CDE
Ceratodon (Feb)	D	D	C	BC	A	A
Grimmia (Dec)	B	B	B	ABC	CD	CD
Grimmia (Jan)	B	B	AB	A	EF	DE
Grimmia (Feb)	D	D	AB	A	F	E

Student's t pairwise test results testing for differences between the three study species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*) and three experimental intervals (Dec, Jan and Feb) with respect to: glucose, fructose, sucrose, trehalose, X2, X3, total and total identified. For each carbohydrate, species (and experimental interval) denoted different letters are significantly different. The results at both α = 0.05 and the Bonferroni corrected 0.003 are shown.

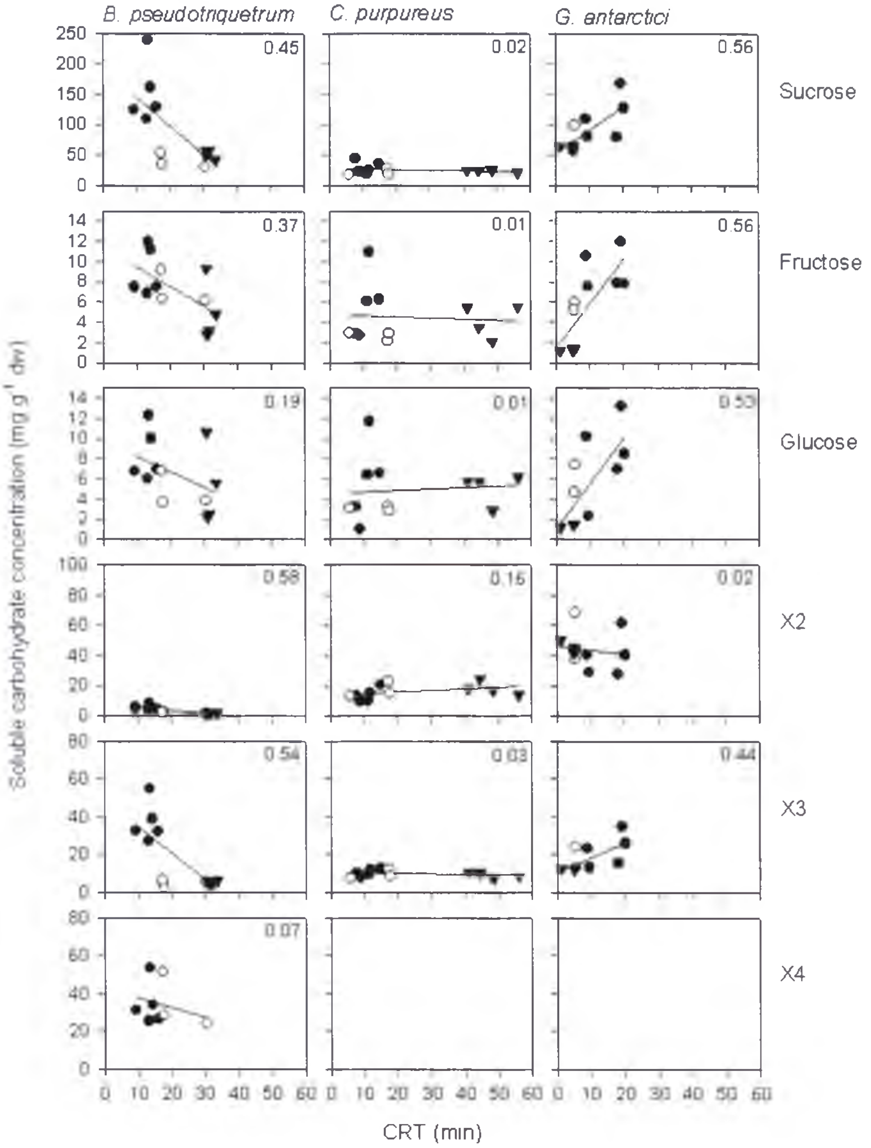
Species (Expt)	Glucose		Fructose		Sucrose		Trehalose	
	α=0.05	α=0.003	α=0.05	α=0.003	α=0.05	α=0.003	α=0.003	α=0.05
Bryum (Dec)	AB	A	A	A	A	A	C	B-E
Bryum (Jan)	CDE	AB	AB	AB	D	DE	A	A
Bryum (Feb)	DE	B	D	C	CD	D	AB	ABC
Ceratodon (Dec)	CD	AB	CD	BC	E	EF	C	BCD
Ceratodon (Jan)	E	BC	E	D	F	F	A	AB
Ceratodon (Feb)	BCD	AB	CD	C	EF	F	C	DE
Grimmia (Dec)	A	A	A	A	AB	AB	D	E
Grimmia (Jan)	ABC	AB	BC	ABC	B	BC	BC	BCD
Grimmia (Feb)	F	C	F	E	C	CD	C	CDE

Species (Expt)	X2		X3		Total		Total ID	
	α=0.05	α=0.003	α=0.05	α=0.003	α=0.05	α=0.003	α=0.05	α=0.003
Bryum (Dec)	E	D	A	A	A	A	A	A
Bryum (Jan)	F	E	E	D	C	BC	C	CD
Bryum (Feb)	F	E	E	D	D	C	C	CD
Ceratodon (Dec)	D	C	CD	C	E	D	E	E
Ceratodon (Jan)	C	C	D	CD	E	D	F	E
Ceratodon (Feb)	C	C	D	C	E	D	EF	E
Grimmia (Dec)	B	B	B	B	B	A	B	B
Grimmia (Jan)	A	A	B	B	B	AB	C	BC
Grimmia (Feb)	B	B	C	C	C	C	D	D

Appendix 4: Relationship between soluble carbohydrate concentrations (mg g^{-1} dw) and critical water content (CWC; g H_2O g^{-1} dw) for three experimental intervals: December (filled circles), January (empty circles), February (filled triangles) for the three study species (*B. pseudotriquetrum, C. purpureus* and *G. antarctici*). Lines indicate results of linear regression analysis of all data in each plot, values indicate r^2. Full regression results are provided in Appendix 7. Note, y-axes are different.



Appendix 5: Relationship between soluble carbohydrate concentrations (mg g^{-1} dw) and critical recovery time (CRT; min) for three experimental intervals: December (filled circles), January (empty circles), February (filled triangles) for the three study species (*B. pseudotriquetrum, C. purpureus* and *G. antarctici*). Lines indicate results of linear regression analysis of all data in each plot, values indicate r^2. Full regression results are provided in Appendix 7. Note, y-axes are different.



Appendix 6: Summary of ANOVA results testing for differences in concentration of soluble carbohydrates for data presented in Appendix 4 and 5. 2-way ANOVA results are presented for whole model and the effects of experiment (Dec, Jan and Feb) and species (*B. pseudotriquetrum*, *C. purpureus* and *G. antarctici*) and the significance of the experiment interval * species interaction. 1-way ANOVA results are presented where indicated.

Variable	Transformation	Test	DF (model)	DF (error)	F Ratio	*P*
Sucrose	**Log**	**Whole Model**	**8**	**57**	**61.4490**	**<0.0001**
		Experimental interval	2		48.1448	<0.0001
		Species	2		170.4756	<0.0001
		Expt * Species	4		11.8211	<0.0001
Fructose	**Log**	**Whole Model**	**8**	**56**	**30.9118**	**<0.0001**
		Experimental interval	2		53.5032	<0.0001
		Species	2		19.7145	<0.0001
		Expt * Species	4		26.0839	<0.0001
Glucose	**Square root**	**Whole Model**	**8**	**57**	**9.9168**	**<0.0001**
		Experimental interval	2		16.8846	<0.0001
		Species	2		1.1859	<0.0001
		Expt * Species	4		10.8072	<0.0001
X2	**Log**	**Whole Model**	**8**	**57**	**225.2844**	**<0.0001**
		Experimental interval	2		7.4738	<0.0001
		Species	2		849.3556	<0.0001
		Expt * Species	4		29.0607	<0.0001
X3	**Log**	**Whole Model**	**8**	**57**	**51.1753**	**<0.0001**
		Experimental interval	2		86.5921	<0.0001
		Species	2		45.4447	<0.0001
		Expt * Species	4		38.3121	<0.0001
X4 (1-way)	**Log**	**Expt (Dec & Jan)**	**1**	**12**	**1.9907**	**0.1837**

Appendix 7: Regression results (y-intercept, slope and r^2 values) for soluble carbohydrate versus CWC or CRT linear regressions presented in Figures 5.6 and 5.7 and Appendices 5 and 6, for the three study species.

Soluble	CWC	*B. pseudotriquetrum*			*C. purpureus*			*G. antarctici*		
Carbohydrate	/ CRT	y-intercept	Slope	r^2	y-intercept	Slope	r^2	y-intercept	Slope	r^2
Total	CWC	-38.53	138.86	0.43	76.01	12.94	0.08	180.72	-16.27	0.02
Stachyose	CWC	12.25	10.64	0.22						
Trehalose	CWC	1.95	0.36	0.01	0.63	0.63	0.03	0.67	0.13	0.00
Glycerol	CWC	-0.71	0.92	0.16	-0.55	0.91	0.13	0.45	-0.12	0.01
Mannitol	CWC	1.69	-0.66	0.30	-0.25	0.62	0.13	-0.04	0.17	0.05
myo-Inositol	CWC	0.13	0.12	0.03	0.02	0.10	0.03	1.83	-0.66	0.49
Sucrose	CWC	-11.25	60.69	0.26	26.64	-1.76	0.00	102.05	-14.38	0.05
Fructose	CWC	-0.05	4.86	0.53	7.06	-2.74	0.11	8.48	-2.52	0.08
Glucose	CWC	1.00	3.36	0.26	8.37	-3.27	0.12	9.59	-3.22	0.13
X2	CWC	-0.90	2.83	0.43	22.11	-4.91	0.08	35.81	7.68	0.03
X3	CWC	-14.15	19.78	0.37	11.98	-2.51	0.13	21.88	-3.35	0.05
X4	CWC	45.63	-4.18	0.01						
Total	CRT	378.35	-9.15	0.55	61.92	0.03	0.00	114.68	5.20	0.40
Stachyose	CRT	44.04	-0.72	0.35						
Trehalose	CRT	2.65	-0.02	0.00	1.63	-0.01	0.06	1.54	-0.08	0.42
Glycerol	CRT	1.80	-0.05	0.13	0.62	-0.01	0.01	0.08	0.02	0.09
Mannitol	CRT	-0.48	0.05	0.54	0.06	0.01	0.22	0.48	-0.03	0.38
myo-Inositol	CRT	0.70	-0.02	0.14	-0.07	0.01	0.79	0.77	0.00	0.00
Sucrose	CRT	192.00	-4.71	0.45	26.70	-0.06	0.02	51.83	3.89	0.56
Fructose	CRT	11.38	-0.19	0.37	4.67	-0.01	0.01	1.54	0.44	0.56
Glucose	CRT	9.80	-0.16	0.19	4.54	0.01	0.01	1.08	0.45	0.53
X2	CRT	7.76	-0.19	0.58	13.58	0.10	0.16	46.53	-0.26	0.02
X3	CRT	49.58	-1.45	0.54	10.19	-0.02	0.03	10.84	0.77	0.44
X4	CRT	42.17	-0.49	0.07						

References

Adamson, D. A., P. Whetton, and P. M. Selkirk. 1988. An analysis of air temperature records for Macquarie Island: decadal warming, ENSO cooling and Southern Hemisphere circulation patterns. Papers and Proceedings of the Royal Society of Tasmania **122**:107-112.

Adamson, H., and E. Adamson. 1992. Possible effects of global climate change on Antarctic terrestrial vegetation. Pages 52-62 *in* P. G. Quilty, editor. Impact of climate change: Antarctica-Australia. Daset, Canberra.

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolutions of species. Science **294**:321-326.

Allen, S. E., H. M. Grimshaw, and M. W. Holdgate. 1967. Factors affecting the availability of plant nutrients on an Antarctic island. Journal of Ecology **55**:381-396.

Anderson, W. H., J. Hawkins, J. L. Gellerman, and H. Schlenk. 1974. Fatty acid composition as a criterion in the taxonomy of mosses. J. Hattori Bot. Lab. **38**:99-103.

Andersson, B., W. H. Anderson, J. Chipault, E. Ellison, S. Fenton, J. L. Gellerman, J. Hawkins, and H. Schlenk. 1974. 9,12,15-Octadecatrien-6-γnoic acid, a new acetylenic acid from mosses. Lipids **9**:506-511.

Arnold, R. J., P. Convey, K. A. Hughes, and D. D. Wynn-Williams. 2003. Seasonal periodicity of physical factors, inorganic nutrients and microalgae in Antarctic fellfields. Polar Biology **26**:396-403.

Augustin, L., C. Barbante, P. R. F. Barnes, J. M. Barnola, M. Bigler, E. Castellano, O. Cattani, J. Chappellaz, D. Dahl-Jensen, B. Delmonte, G. Dreyfus, G. Durand, S. Falourd, H. Fischer, J. Fluckiger, M. E. Hansson, P. Huybrechts, R. Jugie, S. J. Johnsen, J. Jouzel, P. Kaufmann, J. Kipfstuhl, F. Lambert, V. Y. Lipenkov, G. V. C. Littot, A. Longinelli, R. Lorrain, V. Maggi, V. Masson-Delmotte, H. Miller, R. Mulvaney, J. Oerlemans, H. Oerter, G. Orombelli, F. Parrenin, D. Peel, J. Petit, D. Raynaud, C. Ritz, U. Ruth, J. Schwander, U. Siegenthaler, R. Souchez, B. Stauffer, J. P. Steffensen, B. Stenni, T. F. Stocker, I. E. Tabacco, R. Udisti, R. S. W. van de Wal, M. van den Broeke, J. Weiss, F. Wilhelms, J. G.

Winther, E. W. Wolff, and M. Zucchelli. 2004. Eight glacial cycles from an Antarctic ice core. Nature **429**:623-628.

Barsig, M., K. Schneider, and C. Gehrke. 1998. Effects of UV-B radiation on fine-structure carbohydrates and pigments in *Polytrichum commune*. Bryologist **101**:357-365.

Benedict, J. B. 1990. Lichen mortality due to late lying snow: results of a transplant study. Arctic and Alpine Research **22**:81-89.

Beyer, L., M. Bolter, and R. D. Seppelt. 2000. Nutrient and thermal regime, microbial biomass, and vegetation of Antarctic soils in the Windmill Islands region of east Antarctica (Wilkes Land). Arctic, Antarctic and Alpine Research **32**:30-39.

Bjorkman, O., and B. Demming. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. Planta **170**:489-504.

Blight, D. F., and R. L. Oliver. 1977. The metamorphic geology of the Windmill Islands, Antarctica: a preliminary account. Journal of the Geological Society of Australia **24**:239-262.

Bolter, M., R. D. Seppelt, L. Beyer, and K. Pingpank. 2000. Studies on floristic diversity, soil organic matter, and soil microbes from the Windmill Islands, East Antarctica. Bibliotheca Lichenologica **75**:421-432.

Bottger, T., M. Schidlowski, and U. Wand. 1993. Stable carbon isotope fractionation in lower plants from the Schirmacher and Untersee oases (Central Dronning Maud Land, East Antarctica) - (Preliminary Report). Isotopenpraxis **29**:21-25.

Broady, P. A. 1981a. Ecological and taxonomic observations on subaerial epilithic algae from Princess Elizabeth Land and MacRobertson Land, Antarctica. British Phycological Journal **16**:257-266.

Broady, P. A. 1981b. The ecology of chasmolithic algae at coastal locations of Antarctica. Phycologia **20**:259-272.

Broady, P. A. 1989. Broadscale patterns in the distribution of aquatic and terrestrial vegetation at three ice-free regions on Ross Island, Antarctica. Hydrobiologia **172**:77-95.

Callaghan, T. V., B. A. Carlsson, M. Sonesson, and A. Temesvary. 1997. Between-year variation in climate-related growth of circumarctic populations of the moss *Hylocomium splendens*. Functional Ecology **11**:157-165.

Callaghan, T. V., M. Sonesson, and L. Somme. 1992. Response of terrestrial plants and invertebrates to environmental change at high latitudes. Philosophical Transactions of the Royal Society of London **338**:279-288.

Carvey, K., D. R. Farrar, and D. C. Glenn-Lewis. 1977. Bryophytes and revegetation of coal spoils in southern Lowa. The Bryologist **18**:630-637.

Chapin, F. S., III. 1983. Direct and indirect effects of temperature on Arctic plants. Polar Biology **2**:47-52.

Cocks, M. P., D. A. Balfour, and W. D. Stock. 1998a. On the uptake of ornithogenic products by plants on the inland mountains of Dronning Maud Land, Antarctica, using stable isotopes. Polar Biology **20**:107-111.

Cocks, M. P., I. P. Newton, and W. D. Stock. 1998b. Bird effects on organic processes in soils from five microhabitats on a nunatak with and without breeding snow petrels in Dronning Maud Land, Antarctica. Polar Biology **20**:112-120.

Collins, N. J. 1977. The growth of mosses in two contrasting communities in the maritime Antarctic: measurement and prediction of net annual production. Pages 921-933 *in* G. A. Llano, editor. Adaptations within Antarctic ecosystems. Gulf Publishing, Houston Texas.

Collins, N. J., and T. V. Callaghan. 1980. Predicted patterns of photosynthetic production in maritime Antarctic mosses. Annals of Botany **45**:601-620.

Comiso, J. C. 2000. Variability and trends in Antarctic surface temperatures from *in situ* and satellite infrared measurements. Journal of Climate **13**:1674-1696.

Convey, P., and R. I. L. Smith. 1993. Investment in sexual reproduction by Antarctic mosses. Oikos **68**:293-302.

Convey, P. 1994. Photosynthesis and dark respiration in Antarctic mosses - an initial comparative study. Polar Biology **14**:65-69.

Convey, P. 1996a. The influence of environmental characteristics on the life history attributes of Antarctic terrestrial biota. Biological Review **71**:191-225.

Convey, P. 1996b. Reproduction of Antarctic flowering plants. Antarctic Science **8**:127-134.

Convey, P. 2001a. Antarctic Ecosystems. Pages 171-184 *in* S. Levin, editor. Encyclopeadia of Biodiversity. Academic Press, San Diego.

Convey, P. 2001b. Terrestrial ecosystem responses to climate changes in the Antarctic. *in* Walther, editor. "Fingerprints" of Climate Change. Kluwer Academic/Plenum Publishers, New York.

Convey, P., P. J. A. Pugh, C. Jackson, A. W. Murray, C. T. Ruhland, F. S. Xiong, and T. A. Day. 2002. Response of Antarctic terrestrial microarthropods to long-term climate manipulations. Ecology **83**:3130-3140.

Convey, P. 2003. Maritime Antarctic climate change: signals from terrestrial biology. Pages 145-158 *in* E. Domack, A. Burnett, A. Leventer, P. Convey, M. Kirby, and R. B. (eds.), editors. Antarctic Peninsula Climate Variability: Historical and Palaeoenvironmental Perspectives. American Geophysical Union, Washington, D.C.

Convey, P., W. Block, and H. J. Peat. 2003. Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? Global Change Biology **9**:1718-1730.

Corner, R. W. M. 1971. Studies in *Colobanthus quitensis* (Kunth) and *Deschampsia antarctica* Des. IV. Distribution and reproductive performance in the Argentine Islands. British Antarctic Survey Bulletin **26**:41-50.

Crittenden, P. D. 1998. Nutrient exchange in an Antarctic macrolichen during summer snowfall snow melt events. New Phytologist **139**:697-707.

Crowe, J. H., F. A. Hoekstra, and L. M. Crowe. 1992. Anhydrobiosis. Annual Review of Physiology **54**:579-599.

Davey, A. 1982. *In situ* determination of nitrogen fixation in Antarctica using a high sensitivity portable gas chromatograph. Australian Journal of Ecology **7**:395-402.

Davey, A., and H. Marchant. 1983. Seasonal variation in nitrogen fixation in *Nostoc commune* Vaucher at the Vestfold Hills, Antarctica. Phycologia **22**:377-385.

Davey, M. C. 1997a. Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia **110**:25-31.

Davey, M. C. 1997b. Effects of physical factors on photosynthesis by the Antarctic liverwort *Marchantia berteroana*. Polar Biology **17**:219-227.

Davey, M. C. 1997c. Effects of short-term dehydration and rehydration on photosynthesis and respiration by Antarctic bryophytes. Environmental and Experimental Botany **37**:187-198.

Davey, M. C. 1999. The elemental and biochemical composition of bryophytes from the maritime Antarctic. Antarctic Science **11**:157-159.

Davey, M. C., and J. C. Ellis-Evans. 1996. The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. Journal of Bryology **19**:235-242.

Davey, M. C., J. Pickup, and W. Block. 1992. Temperature variation and its biological significance in fellfield habitats on a maritime Antarctic island. Antarctic Science **4**:383-388.

Day, T. A., C. T. Ruhland, C. W. Grobe, and F. Xiong. 1999. Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. Oecologia **119**:24-35.

Doran, P. T., J. C. Priscu, W. Berry Lyons, J. E. Walsh, A. G. Fountain, D. M. McKnight, D. L. Moorhead, R. A. Virginia, D. H. Wall, G. D. Clow, C. H. Fritsen, C. P. McKay, and A. N. Parsons. 2002. Antarctic climate cooling and terrestrial ecosystem response. Nature **415**:517-520.

Drake, B. G., and M. A. González-Meler. 1996. More efficient plants: a consequence of rising atmospheric CO_2? Annual Review of Plant Physiology and Plant Molecular Biology **48**:609-639.

Edwards, J. A., and R. I. L. Smith. 1988. Photosynthesis and respiration of *Colobanthus quitensis* and *Deschampsia antarctica* from the maritime Antarctic. British Antarctic Survey Bulletin **81**:43-63.

Engelmann, M. H., and T. E. Weaks. 1985. An analysis of the effects of strip-mining on bryophyte species diversity. The Bryologist **88**:344-349.

Erskine, P. D., D. M. Bergstrom, S. Schmidt, G. R. Stewart, C. E. Tweedie, and J. D. Shaw. 1998. Subantarctic Macquarie Island - a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. Oecologia **117**:187-193.

Fabiszewski, J., and B. Wojtun. 2000. Chemical composition of some dominating plants in the maritime Antarctic tundra (King George Island). Bibliotheca Lichenologica **75**:79-91.

Filson, R. B., and J. H. Willis. 1975. A fruiting occurrence of *Bryum algens* Card. in East Antarctica. Muelleria **3**:112-116.

Fowbert, J. A. 1996. An experimental study of growth in relation to morphology and shoot water content in maritime Antarctic mosses. New Phytologist **133**:363-373.

Fowbert, J. A., and R. I. L. Smith. 1994. Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. Arctic and Alpine Research **26**:290-296.

Frahm, J.-P., and D. Klaus. 2001. Bryophytes as indicators of recent climate fluctuations in Central Europe. Lindbergia **26**:97-104.

Frenot, Y., S. L. Chown, J. Whinam, P. Selkirk, P. Convey, M. Skotnicki, and D. Bergstrom. 2005. Biological invasions in the Antarctic: extent, impacts and implications. Biological Reviews **80**:45-72.

Frenot, Y., J.-C. Gloaguen, and P. Tréhen. 1997. Climate change in Kerguelen Islands and colonisation of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. Pages 358-366 *in* B. Battaglia, J. Valencia, and D. W. H. Walton, editors. Antarctic Communities: Species, Structure and Survival. Cambridge University Press, Cambridge.

Friedmann, E. I. 1982. Endolithic microorganisms in the Antarctic cold desert. Science **215**:1045-1053.

Gellerman, J. L., W. H. Anderson, and H. Schlenk. 1972. Highly unsaturated lipids of *Mnium*, *Polytrichum*, *Marchantia* and *Matteuccia*. Bryologist **75**:550-557.

Ghasempour, H. R., D. F. Gaff, R. P. W. Williams, and R. D. Gianello. 1998. Contents of sugars in leaves of drying desiccation tolerant flowering plants, particularly grasses. Plant Growth Regulation **24**:185-191.

Gimingham, C. H., and R. I. L. Smith. 1971. Growth form and water relations of mosses in the maritime Antarctic. British Antarctic Survey Bulletin **25**:1-21.

Goodwin, I. D. 1993. Holocene deglaciation, sea level change, and the emergence of the Windmill Islands, Budd Coast, Antarctica. Quaternary Research **40**:70-80.

Green, T. G. A. 1985. Dry Valley terrestrial plant communities. The problem of production and growth. New Zealand Antarctic Record **6**:40-44.

Green, T. G. A., B. Schroeter, L. Kappen, R. D. Seppelt, and K. Maseyk. 1998. An assessment of the relationship between chlorophyll *a* fluorescence and CO_2 gas exchange from field measurements on a moss and lichen. Planta **206**:611-618.

Green, T. G. A., B. Schroeter, and L. G. Sancho. 1999. Plant life in Antarctica. Pages 495-543 *in* F. I. Pugnaire and F. Valladares, editors. Handbook of Functional Plant Ecology. Marcel Dekker, New York.

Green, T. G. A., B. Schroeter, and R. D. Seppelt. 2000. Effect of temperature, light and ambient UV on the photosynthesis of the moss *Bryum argenteum* Hedw. in continental Antarctica. Pages 165-170 *in* W. Davison, C. Howard-Williams, and P. Broady, editors. Antarctic ecosystems: modes for wider ecological understanding. New Zealand natural sciences, Christchurch.

Greenfield, L. G. 1992a. Retention of precipitation nitrogen by Antarctic mosses, lichens and fellfield soils. Antarctic Science **4**:205-206.

Greenfield, L. G. 1992b. Precipitation nitrogen at maritime Signy Island and continental Cape Bird, Antarctica. Polar Biology **11**:649-653.

Gremmen, N. J. M., A. H. L. Huiskes, and J. W. Francke. 1994. Epilithic macrolichen vegetation of the Argentine Islands, Antarctic Peninsula. Antarctic Science **6**:463-471.

Handley, L. L., and J. A. Raven. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. Plant, Cell and Environment **15**:965-985.

Hansom, J. D., and J. E. Gordon. 1998. Antarctic environments and resources: geographical perspective. Addison Wesley Longman Ltd, Harlow, Essex.

Hennion, F., Huiskes, A, Robinson, S., Convey, P. (2005). Physiological traits of organisms in a changing environment. Antarctic Ecosystems and Global Change (Bergstrom, Huiskes, Convey eds). Kluwer Dordrecht (in press).

Hietz, P., W. Wanek, and M. Popp. 1999. Stable isotopic composition of carbon and nitrogen and nitrogen content in vascular epiphytes along an altitudinal transect. Plant, Cell and Environment **22**:1435-1443.

Hobbie, S. E., and F. S. Chapin, III. 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO2 flux to experimental warming. Ecology **79**:1526-1544.

Hollin, J. T., and R. L. Cameron. 1961. I.G.Y. glaciological work at Wilkes Station, Antarctica. Journal of Glaciology **3**:833-843.

Houghton, J. T., Y. Ding, D. J. Griggs, and e. al. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, UK.

Hovenden, M. J. 2000. Seasonal trends in nitrogen status of Antarctic lichens. Annals of Botany **86**:717-721.

Hovenden, M. J., A. E. Jackson, and R. D. Seppelt. 1994. Field photosynthetic activity of lichens in the Windmill Islands oasis, Wilkes Land, continental Antarctica. Physiologia Plantarum **90**:567-576.

Hovenden, M. J., and R. D. Seppelt. 1995a. Exposure and nutrients as delimiters of lichen communities in continental Antarctica. Lichenologist **27**:505-516.

Hovenden, M. J., and R. D. Seppelt. 1995b. Uptake of water from the atmosphere by lichens in continental Antarctica. Symbiosis **18**:111-118.

Hovenden, M. J., and R. D. Seppelt. 1995a. Exposure and nutrients as deliminitors of lichen communities in continental Antarctica. Lichenologist **27**:505-516.

Huiskes, A. H. L., N. J. M. Gremmen, and J. W. Francke. 1997a. The delicate stability of lichen symbiosis: comparative studies on the photosynthesis of the lichen *Mastodia tesselata* and its free-living phycobiont, the alga *Prasiola crispa*. Pages 234-240 *in* B. Battaglia, J. Valencia, and D. W. H. Walton, editors. Antarctic Communities: Species, Structure and Survival. Cambridge University Press, Cambridge.

Huiskes, A. H. L., N. J. M. Gremmen, and J. W. Francke. 1997b. Morphological effects on the water balance of Antarctic foliose and fructicose lichens. Antarctic Science **9**:36-42.

Huiskes, A. H. L., D. Lud, and T. C. W. Moerdijk-Poortvliet. 2001. Field research on the effects of UV-B filters on terrestrial Antarctic vegetation. Plant Ecology **154**:75-.

Huiskes, A. H. L., T. C. W. Moerdijk-Poortvliet, and D. Lud. 2000. Responses to UV-B radiation in terrestrial Antarctic vegetation. Pages 252-257 ***in*** W. Davison, C. Howard-Williams, and P. Broady, editors. Antarctic ecosystems: Models for wider ecological understanding. New Zealand natural sciences, Christchurch.

Inoue, M. 1989. Factors influencing the existence of lichens in the ice-free areas near Syowa Station, East Antarctica. Proc. NIPR Symp. Polar Biology. **2**:167-180.

Kappen, L. 1985a. Lichen-habitats as micro-oases in the Antarctic - the role of temperature. Polarforschung **55**:49-54.

Kappen, L. 1985b. Vegetation and ecology of ice-free areas of Northern Victoria Land, Antarctica. 1. The lichen vegetation of Birthday Ridge and an inland mountain. Polar Biology **4**:213-225.

Kappen, L. 1985c. Vegetation and ecology of ice-free areas of Northern Victoria Land, Antarctica. 2. Ecological conditions in typical microhabitats of lichens at Birthday Ridge. Polar Biology **4**:227-236.

Kappen, L. 1993. Plant activity under snow and ice, with particular reference to lichens. Arctic **46**:297-302.

Kappen, L. 2000. Some aspects of the great success of lichens in Antarctica. Antarctic Science **12**:314-324.

Kappen, L., and M. Breuer. 1991. Ecological and physiological investigations in continental Antarctic cryptogams. II. Moisture relations and photosynthesis of lichens near Casey Station, Wilkes Land. Antarctic Science **3**:273-278.

Kappen, L., M. Meyer, and M. Bolter. 1990. Ecological and physiological investigations in continental Antarctic cryptograms. I. Vegetation pattern and its relation to snow cover on a hill near Casey station, Wilkes Land. Flora **184**:209-220.

Kappen, L., B. Schroeter, T. G. A. Green, and R. D. Seppelt. 1998. Microclimatic conditions, meltwater moistening, and the distributional pattern of *Buellia frigida* on rock in a southern continental Antarctic habitat. Polar Biology **19**:101-106.

Kappen, L., R. I. L. Smith, and M. Meyer. 1989. Carbon dioxide exchange of two ecodemes of *Schistidium antarctici* in continental Antarctica. Polar Biology **9**:415-422.

Kappen, L., and H. Straka. 1988. Pollen and spores transport into the Antarctic. Polar Biology **8**:173-180.

Karentz, D. 1991. Ecological considerations of Antarctic ozone depletion. Antarctic Science **3**:3-11.

Karlsson, P. S., R. L. Eckstein, and M. Weih. 2000. Seasonal variation in ^{15}N natural abundance in subarctic plants of different life forms. Ecoscience **7**:365-369.

Kennedy, A. D. 1993a. Photosynthetic response of the Antarctic moss *Polytrichum alpestre* Hoppe to low temperatures and freeze-thaw stress. Polar Biology **13**:271-279.

Kennedy, A. D. 1993b. Water as a limiting factor in the Antarctic terrestrial environment: a biogeographical synthesis. Arctic and Alpine Research **25**:308-315.

Kennedy, A. D. 1995. Antarctic terrestrial ecosystem response to global environmental change. Annual Review of Ecology and Systematics **26**:683-704.

Kennedy, A. D. 1996. Antarctic fellfield response to climate change: a tripartite synthesis of experimental data. Oecologia **107**:141-150.

King, J. C. 1994. Recent climate variability in the vicinity of the Antarctic peninsula. International Journal of Climatology **14**:357-369.

King, J. C., J. Turner, G. J. Marshall, W. M. Connolley, and T. A. Lachlan-Cope. 2003. Antarctic peninsula climate variability and its causes as revealed by analysis of instrumental records. Pages 17-30 *in* E. Domack, A. Burnett, A. Leventer, P. Convey, M. Kirby, and R. B. (eds.), editors. Antarctic Peninsula Climate Variability: Historical and Palaeoenvironmental Perspectives. American Geophysical Union, Washington, D.C.

Komarkova, V., S. Poncet, and J. Poncet. 1985. Two native Antarctic vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis*: a new southernmost locality and other localities in the Antarctic Peninsula area. Arctic and Alpine Research **17**:401-416.

Koster, K. L., and A. C. Leopold. 1988. Sugars and dessication tolerance in seeds. Plant Physiology **88**:829-832.

Lange, O. L., and L. Kappen. 1972. Photosynthesis of lichens from Antarctica. Pages 83-95 *in* G. A. Llano, editor. Antarctic Terrestrial Biology. American Geophysical Union, Washington, D.C.

Leishman, M. R., and C. Wild. 2001. Vegetation abundance and diversity in relation to soil nutrients and soil water content in Vestfold Hills, East Antarctica. Antarctic Science **13**:126-134.

Li, M. H., G. Hoch, and C. Körner. 2002. Source/sink removal affects mobile carbohydrates in *Pinus cembra* at the Swiss treeline. TREES-STRUCTURE AND FUNCTION **16**:331-337.

Lindsay, D. C. 1978. The role of lichens in Antarctic Ecosystems. The Bryologist **81**:268-276.

Linskens, H. F., R. Bargagli, M. Cresti, and S. Focardi. 1993. Entrapment of long-distance transported pollen grains by various moss species in coastal Victoria Land, Antarctica. Polar Biology **13**:81-87.

Liu, L. X., P. Howe, Y. F. Zhou, Z. Q. Xu, C. Hocart, and R. Zhang. 2000. Fatty acids and β-carotene in Australian pursulane (*Portulaca oleracea*) varieties. Journal of Chromatography A **893**:207-213.

Longton, R. E. 1974. Microclimate and biomass in communities of the *Bryum* association on Ross Island, continental Antarctica. The Bryologist **77**:109-127.

Longton, R. E. 1979. Vegetation ecology and classification in the Antarctic Zone. Canadian Journal of Botany. **57**:2264-2278.

Longton, R. E. 1981. Inter-population variation in morphology and physiology in the cosmopolitan moss *Bryum argenteum* Hedw. Journal of Bryology **11**:501-520.

Longton, R. E. 1985. Terrestrial Habitats - Vegetation. Pages 73-105 *in* D. W. H. Walton, editor. Key Environments Antarctica. Pergamon Press, Oxford.

Longton, R. E. 1988. The Biology of Polar Bryophytes and Lichens. Cambridge University Press, Cambridge.

Lovelock, C. E., A. E. Jackson, D. R. Melick, and R. D. Seppelt. 1995a. Reversible photoinhibition in Antarctic moss during freezing and thawing. Plant Physiology **109**:955-961.

Lovelock, C. E., C. B. Osmond, and R. D. Seppelt. 1995b. Photoinhibition in the Antarctic moss *Grimmia antarctica* Card. when exposed to cycles of freezing and thawing. Plant, Cell and Environment **18**:1395-1402.

Marion, G. M., G. H. R. Henry, D. W. Freckman, J. Johnstone, G. Jones, M. H. Jones, E. Levesque, U. Molau, P. Molgaard, A. N. Parsons, J. Svoboda, and R. A. Virginia. 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology **3**:20-32.

Marshall, W. A. 1996a. Aerial dispersal of lichen soredia in the maritime Antarctic. New Phytologist **134**:523-530.

Marshall, W. A. 1996b. Biological particles over Antarctica. Nature **383**:680.

Marshall, W. A., and P. Convey. 1997. Dispersal of moss propagules on Signy Island, maritime Antarctic. Polar Biology **18**:376-383.

Melick, D. R., M. J. Hovenden, and R. D. Seppelt. 1994a. Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, continental Antarctica. Vegetatio **111**:71-87.

Melick, D. R., and R. D. Seppelt. 1992. Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. Antarctic Science **4**:399-404.

Melick, D. R., and R. D. Seppelt. 1994a. The effect of hydration on carbohydrate levels, pigment content and freezing point of *Umbilicaria decussata* at a continental Antarctic locality. Cryptogamic Botany **4**:212-217.

Melick, D. R., and R. D. Seppelt. 1994b. Seasonal investigations of soluble carbohydrates and pigment levels in Antarctic bryophyte and lichens. The Bryologist **97**:13-19.

Melick, D. R., and R. D. Seppelt. 1997. Vegetation patterns in relation to climatic and endogenous changes in Wilkes Land, continental Antarctica. Journal of Ecology **85**:43-56.

Melick, D. R., M. G. Tarnawski, K. D. Adam, and R. D. Seppelt. 1994b. Isozyme variation in three mosses from the Windmill Islands oasis, Antarctica: a preliminary study. Biodiversity Letters **2**:21-27.

Miller, A. E., and W. D. Bowman. 2002. Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition by nitrogen form? Oecologia **130**:609-616.

Mizutani, H., H. Hasegawa, and E. Wada. 1986. High nitrogen isotope ratio for soils of seabird rookeries. Biogeochemistry **2**:221-247.

Montiel, P. O. 1998. Profiles of soluble carbohydrates and their adaptive role in maritime Antarctic terrestrial arthropods. Polar Biology **19**:250-256.

Montiel, P. O. 2000. Soluble carbohydrates (trehalose in particular) and cryoprotection in polar biota. CryoLetters **21**:83-90.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos **100**:403-405.

Morgan, V. I., I. D. Goodwin, D. M. Etheridge, and C. W. Wookey. 1991. Evidence from Antarctic ice cores for recent increases in snow accumulation. Nature **354**:58-60.

Nakanishi, S. 1977. Ecological studies of the moss and lichen communities in the ice-free areas of Syowa Station, Antarctica. Antarctic Record **59**:68-96.

Nakanishi, S. 1979. On the variation of leaf characters of an Antarctic moss, *Bryum inconnexum*. Memoirs of the National Institute of Polar Research. Proceedings of the Symposium on Terrestrial Ecosystems in the Syowa Station Area (Special Issue). **11**:47-57.

Nakatsubo, T. 2002. Predicting the impact of climatic warming on the carbon balance of the moss *Sanionia uncinata* on a maritime Antarctic island. Journal of Plant Research **115**:99-106.

Norby, R. J., K. Kobayashi, and B. A. Kimball. 2001. Rising CO2 - future ecosystems. New Phytologist **150**:215-221.

Oechel, W. C., A. C. Cook, S. J. Hastings, and G. L. Vourlitis. 1997. Effects of CO2 and climate change on arcitc ecosystems. Pages 255-273 *in* S. J. Woodin and M. Marquiss, editors. Ecology of Arctic Environments. Blackwell Science, Oxford.

Pannewitz, S., M. Schlensog, T. G. A. Green, L. G. Sancho, and B. Schroeter. 2003. Are lichens active under snow in continental Antarctica? Oecologia **135**:30-38.

Pantis, J. D., S. Diamantoglon, and N. S. Margaris. 1987. Altitudinal variation in total lipids and soluble sugar content in herbaceous plants on Mount Olympus (Greece). Vegetatio **72**:21-25.

Pickard, J., and R. D. Seppelt. 1984. Phytogeography of Antarctica. J. Biogeog. **11**:83-102.

Popp, M., W. Lied, A. J. Meyer, A. Richter, P. Schiller, and H. Schwitte. 1996. Sample preservation for determination of organic compounds: microwave versus freeze-drying. Journal of Experimental Botany **47**:1469-1473.

Porra, R. J., W. A. Thompson, and P. E. Kriedemann. 1989. Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls *a* and *b* extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochimica et Biophysica Acta **975**:384-394.

Press, M. C., J. A. Potter, M. J. W. Burke, T. V. Callaghan, and J. A. Lee. 1998. Response of a subarctic dwarf shrub heath community to simulated environmental change. Journal of Ecology **86**:315-327.

Proctor, M. C. F., J. A. Raven, and S. K. Rice. 1992. Stable carbon isotope discrimination measurements in *Sphagnum* and other bryophytes: physiological and ecological implications. Journal of Bryology **17**:193-202.

Pukacka, S., and P. M. Pukacki. 1997. Changes in soluble sugars in relation to desiccation tolerance and effects of dehydration on freezing characteristics of *Acer platanoides* and *Acer pseudoplatanus* seeds. Acta Physiologiae Plantarum **19**:147-154.

Rastorfer, J. R. 1972. Comparative physiology of four west Antarctic mosses. Pages 143-161 *in* G. A. Llano, editor. Antarctic Terrestrial Biology. American Geophysical Union, Washington , D.C.

Rice, S. K., and L. Giles. 1996. The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. Plant Cell and Environment **19**:118-124.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Richter, A., B. Thonke, and M. Popp. 1990. id-1-*O*-methyl-*muco*-inositol in *Viscum album* and members of the Rhizophoraceae. Phytochemistry **29**:1785-1786.

Robinson, C. H., P. A. Wookey, J. A. Lee, T. V. Callaghan, and M. C. Press. 1998. Plant community response to simulated environmental change at a high arctic polar semi-desert. Ecology **79**:856-866.

Robinson, D. 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends in Ecology and Evolution **16**:153-162.

Robinson, S. A., J. Wasley, M. Popp, and C. E. Lovelock. 2000. Desiccation tolerance of three moss species from continental Antarctica. Australian Journal of Plant Physiology **27**:379-388.

Robinson, S. A., J. Wasley, and A. K. Tobin. 2003. Living on the edge - plants and global change in continental and maritime Antarctica. Global Change Biology **9**:1681-1717.

Romero, M., A. Casanova, G. Iturra, A. Reyes, G. Montenegro, and M. Alberdi. 1999. Leaf anatomy of *Deschampsia antarctica* (Poaceae) from the maritime Antarctic and its plastic response to changes in the growth conditions. Revista Chilena de Historia Natural **72**:411-425.

Roser, D. J., D. R. Melick, H. U. Ling, and R. D. Seppelt. 1992. Polyol and sugar content of terrestrial plants from continental Antarctica. Antarctic Science **4**:413-420.

Rudolph, E. D. 1963. Vegetation of Hallett Station Area, Victoria Land, Antarctica. Ecology **44**:585-586.

Rudolph, E. D. 1966. Terrestrial vegetation of Antarctica: past and present studies. Pages 190-124 *in* J. C. F. Tedrow, editor. Antarctic soils and soil forming processes. American Geophysical Union, Washington, D.C.

Ryan, P. G., and B. P. Watkins. 1989. The influence of physical factors and ornithogenic products on plant and arthropod abundance at an inland nunatak group in Antarctica. Polar Biology **10**:151-160.

Schlensog, M., and B. Schroeter. 2000. Poikilohydry in Antarctic cryptogams and its influence on photosynthetic performance in mesic and xeric habitats. Pages 175-182 *in* W. Davidson, C. Howard-Williams, and P. Broady, editors. Antarctic Ecosystems: models for wider ecological understanding. New Zealand Natural Sciences.

Schofield, E., and V. Ahmadjian. 1972. Field observations and laboratory studies of some Antarctic cold desert cryptogams. Pages 97-142 *in* G. A. Llano, editor. Antarctic Terrestrial Biology. American Geophysical Union, Washington, D.C.

Schroeter, B., T. G. A. Green, L. Kappen, and R. D. Seppelt. 1994. Carbon dioxide exchange at subzero temperatures. Field measurements on *Umbilicaria aprina* in Antarctica. Cryptogamic Botany **4**:233-241.

Schroeter, B., T. G. A. Green, L. Kappen, R. D. Seppelt, and K. Maseyk. 1995. The relationship between electron transport rate through PSII and CO_2 gas exchange in Antarctic cryptogams. Pages 959-962 *in* P. Mathis, editor. Photosynthesis: from light to biosphere. Kluwer Academic Publishers.

Schroeter, B., L. Kappen, T. G. A. Green, and R. D. Seppelt. 1997. Lichens and the Antarctic environment: Effects of temperature and water availability on photosynthesis. *in* W.B. Lyons, C. Howard-Williams, and I. Hawes, editors. Ecosystem processes in Antarctic ice-free landscapes. A.A. Balkema, Rotterdam, Brookfield, Christchurch, New Zealand.

Schroeter, B., and C. Scheidegger. 1995. Water relations in lichens at subzero temperatures: structural changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental Antarctica. New Phytologist **131**:273-285.

Schulze, E.-D., F. S. Chapin, III., and G. Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia **100**:406-412.

Schwarz, A. M. J., T. G. A. Green, and R. D. Seppelt. 1992. Terrestrial vegetation at Canada Glacier, Southern Victoria Land, Antarctica. Polar Biology **12**:397-404.

Selkirk, P. M., and R. D. Seppelt. 1987. Species distribution within a moss bed in Greater Antarctica. Symp. Biol. Hung. **25**:279-284.

Selkirk, P. M., M. Skotnicki, K. D. Adam, M. B. Connett, T. Dale, T. W. Joe, and J. Armstrong. 1997. Genetic variation in Antarctic populations of the moss *Sarconeurum glaciale*. Polar Biology **18**:344-350.

Seppelt, R. D. 1983. *Cephaloziella exiliflora* (Tayl.) Steph. from the Windmill Islands, continental Antarctica. Lindbergia **9**:27-28.

Seppelt, R. D. 1986. Bryophytes of the Vestfold Hills. Pages 221-245 *in* J. Pickard, editor. Antarctic Oasis: Terrestrial environment and the history of the Vestfold Hills. Academic Press, Sydney.

Seppelt, R. D., and D. H. Ashton. 1978. Studies on the ecology of the vegetation at Mawson Station, Antarctica. Australian Journal of Ecology **3**:373-388.

Seppelt, R. D., P. A. Broady, J. Pickard, and D. A. Adamson. 1988. Plants and landscape in the Vestfold Hills, Antarctica. Hydrobiologia **165**:185-196.

Seppelt, R. D., T. G. A. Green, A.-M. J. Schwarz, and A. Frost. 1992. Extreme southern locations for moss sporophytes in Antarctica. Antarctic Science **4**:37-39.

Seppelt, R. D., and T. J. Hancock. 1991. Growth responses of *Ceratodon purpureus* in culture. Journal of the Hattori Botanical Laboratory **69**:133-145.

Shimizu, H. 1977. Vegetational distribution and habitats on West Ongul and Teoya Islands, Antarctica. Antarctic Record **59**:97-107.

Silvola, J. 1985. CO_2 dependence of photosynthesis in certain forest and peat mosses and simulated photosynthesis at various actual and hypothetical CO_2 concentrations. Lindbergia **11**:86-93.

Simon, T. 1987. The leaf-area index of three moss species (*Tortula ruralis, Ceratodon purpureus,* and *Hypnum cupressiforme*). Symposia Biologica Hungarica **35**:699-706.

Slatyer, R. O. 1967. Plant-water relationships. Academic Press, London.

Smith, R. C., E. Stammerjohn, and K. S. Baker. 1996. Surface air temperature variations in the western Antarctic Peninsular region. Pages 105-121 *in* R. M. Ross, E. E. Hofmann, and L. B. Quetin, editors. Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington, D.C.

Smith, R. I. L. 1984. Terrestrial plant biology of the sub-Antarctic and Antarctic. Pages 61-162 *in* R. M. Laws, editor. Antarctic Ecology. Academic Press, London.

Smith, R. I. L. 1986. Report on Antarctic fieldwork: Plant ecological studies in the fellfield ecosystem near Casey Station, Australian Antarctic Territory, 1985 - 86. Br. Antarct. Surv. Bull. **72**:81-91.

Smith, R. I. L. 1988a. Classification and ordination of cryptogamic communities in Wilkes Land, continental Antarctica. Vegetatio **76**:155-166.

Smith, R. I. L. 1988b. Recording bryophyte microclimate in remote and severe environments. Pages 275-284 *in* J. M. Glime, editor. Bryological Methods Workshop. The Hattori Botanical Laboratory, Mainz, Germany.

Smith, R. I. L. 1990a. Signy Island as a paradigm of biological and environmental change in Antarctic terrestrial ecosystems. Pages 32-50 *in* K. R. Kerry and G. Hempel, editors. Antarctic ecosystems, ecological change and conservation. Springer-Verlag, Heidelberg.

Smith, R. I. L. 1990b. Plant community dynamics in Wilkes Land, Antarctica. Proc. NIPR Symp. Polar Biol. **3**:229-244.

Smith, R. I. L. 1991. Exotic sporangia as indicators of potential immigrant colonists in Antarctica. Grana **30**:313-324.

Smith, R. I. L. 1994. Vascular plants as bioindicators of regional warming in Antarctica. Oecologia **99**:322-328.

Smith, R. I. L. 1999. Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. Journal of Vegetation Science **10**:231-242.

Smith, R. I. L., and P. Convey. 2002. Enhanced sexual reproduction in bryophytes at high latitudes in the maritime Antarctic. Journal of Bryology **24**:107-117.

Smith, V. R. 1993. Effect of nutrients on CO_2 assimilation by mosses on a sub-Antarctic Island. New Phytologist **123**:693-697.

Smith, V. R., and M. Steenkamp. 1990. Climate change and its ecological implications at a subantarctic island. Oecologia **85**:14-24.

Smith, V. R., and M. Steenkamp. 1992. Macroinvertebrates and litter nutrient release on a sub-Antarctic Island. South African Journal of Botany **58**:105-116.

Stonehouse, B. 1989. Polar Ecology. Blackie, Glasgow.

Sveinbjornsson, B., and W. C. Oechel. 1991. Carbohydrate and Lipid-Levels in 2 *Polytrichum* Moss Species Growing on the Alaskan Tundra. Holarctic Ecology **14**:272-277.

Swanson, E. S., W. H. Anderson, J. L. Gellerman, and H. Schlenk. 1976. Ultrastructure and Lipid-Composition of Mosses. Bryologist **79**:339-349.

Taiz, L., and E. Ziger. 2002. Plant Physiology. Sinauer Associates, Sunderland, Mass.

Tarnawski, M., D. Melick, D. Roser, E. Adamson, H. Adamson, and R. Seppelt. 1992. *In situ* carbon dioxide levels in cushion and turf forms of *Grimmia antarctici* at Casey Station, East Antarctica. Journal of Bryology **17**:241-249.

Tatur, A., and A. Myrcha. 1989. Soils and vegetation in abandoned penguin rookeries (maritime Antarctica). Proc. NIPR Symp. Polar Biol. **2**:181-189.

Tokioka, T. 1995. Climate changes predicted by climate models for the increase of greenhouse gases. Progress in Nuclear Energy **29**:151-158.

Tuba, Z., Z. Csintalan, and M. C. F. Proctor. 1996. Photosynthetic response of a moss, *Tortula ruralis*, ssp. *ruralis*, and the lichens *Cladonia convoluta* and *C. furcata* to water deficit and short periods of desiccation, and their ecophysiological significance: a baseline study at present-day CO_2 concentration. New Phytologist **133**:353-361.

Turner, J., J. C. King, T. A. Lachlan-Cope, and P. D. Jones. 2002. Recent temperature trends in the Antarctic. Nature **418**:291-292.

Valladares, F., E. Martinez-Ferri, L. Balaguer, E. Perez-Corona, and E. Manrique. 2000a. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservation resource-use strategy? New Phytologist **148**:79-91.

Valladares, F., S. J. Wright, E. Lasso, K. Kitajima, and R. W. Pearcy. 2000b. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology **81**:1925-1936.

van den Broeke, M. R., and N. P. M. van Lipzig. 2003. Response of wintertime Antarctic temperatures to the Antarctic oscillation: results of a regional climate model. Pages 43-58 *in* E. Domack, A. Burnett, A. Leventer, P. Convey, M. Kirby, and R. B. (eds.), editors. Antarctic Peninsula Climate Variability: Historical and Palaeoenvironmental Perspectives. American Geophysical Union, Washington, D.C.

Vincent, W. F. 1997. Polar desert ecosystems in a changing climate: a north-south perspective. Pages 3-14 *in* Lyons, Howard-Williams, and Hawes, editors. Ecosystem processes in Antarctic ice-free landscapes. Balkema, Rotterdam.

Vining, E. C., S. J. Crafts-Brandner, and T. A. Day. 1997. Photosynthetic acclimation of antarctic hair grass (*Deschampsia antarctica*) to contrasting temperature regimes. Bulletin of the Ecological Society of America **78**:327.

Vuori, K.-M., H. Luotonen, and P. Liljaniemi. 1999. Benthic macroinvertebrates and aquatic mosses in pristine streams of the Tolvajarvi region, Russian Karelia. Boreal Environment Research **4**:187-200.

Walker, B. H. 1997. Preface: Global Change and Terrestrial Ecosystems: The GCTE Research Programme for the Arctic. Pages v-xii *in* W. C. Oechel, T. V. Callaghan, T. Gilmanov, J. I. Holten, B. Maxwell, U. Molau, and B. Sveinbjornsson, editors. Global Change and Arctic Terrestrial Ecosystems. Springer, New York.

Walsh, J. E., P. T. Doran, J. C. Priscu, and e. al. 2002. Climate change - recent temperature trends in the Antarctic. Nature **418**:292.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Walton, D. H., W. F. Vincent, M. H. Timperley, I. Hawes, and C. Howard-Williams. 1997. Synthesis: Polar deserts as indicators of change. Pages 275-279 *in* Lyons, Howard-Williams, and Hawes, editors. Ecosystem processes in Antarctic ice-free landscapes. Balkema, Rotterdam.

Walton, D. W. H. 1982. The Signy Island terrestrial reference sites. XV. Microclimate monitoring, 1972-4. British Antarctic Survey Bulletin **55**:111-126.

Walz, H. 2002. MINI-PAM user manual. Heinz Walz GmbH, Germany.

Weinstein, R. N., P. O. Montiel, and K. Johnstone. 2000. Influence of growth temperature on lipid and soluble carbohydrate synthesis by fungi isolated from fellfield soil in the maritime Antarctic. Mycologia **92**:222-229.

Weller, G. 1992. Antarctica and the detection of environmental change. Phil. Trans. R. Soc. Lond. B **338**:201-208.

Wilson, M. E. 1990. Morphology and photosynthetic physiology of *Grimmia antarctici* from wet and dry habitats. Polar Biology **10**:337-341.

Xiong, F. S., E. C. Mueller, and T. A. Day. 2000. Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. American Journal of Botany **87**:700-710.

Xiong, F. S., C. T. Ruhland, and T. A. Day. 1999. Photosynthetic temperature response of the Antarctic vascular plants *Colobanthus quitensis* and *Deschampsia antarctica*. Physiologia Plantarum **106**:276-286.

Yamanaka, M., and K. Sato. 1977. Distribution of terrestrial plant communities near Syowa Station in Antarctica, with special reference to water supply and soil property. Antarct. Rec. **59**:54-67.

Ye, H., and J. R. Mather. 1997. Polar snow cover changes and global warming. International Journal of Climatology **17**:155-162.

Zuniga, G. E., M. Alberdi, and L. J. Corcuera. 1996. Non-structural carbohydrates in *Deschampsia antarctica* Desv. from South Shetland Islands, maritime Antarctic. Environmental and Experimental Botany **36**:393-399.