Spatial variation in plant nutrient composition on Marion Island

by
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Dissertation presented for the degree of *Masters in Botany in the Faculty of Botany and Zoology at Stellenbosch University*

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April 2014

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March 2014

Summary

To estimate nutrient budgets and model nutrient cycling at a whole ecosystem level on sub-Antarctic Marion Island requires information on the spatial variability of plant nutrient concentrations on the island. The complexity of constructing budgets and models will also be reduced if, instead of considering each plant species individually, the species can be grouped on the basis of their similarities/differences in nutrient concentrations. This thesis presents the results of an investigation into both these aspects.

Altitude and distance from the sea are highly correlated with each other and thus influence the concentrations of all the nutrients considered (N, P, K, Ca, Mg and Na) very similarly. Concentrations of N, P and Na in living leaves, dead leaves, stems and roots decrease going inland, due to a decline in the influence of animal manuring and of sea spray. Ca concentration increases going inland, away from the organic peats characteristic of the lowland regions toward the mineral rawmark inland soils. Declining sea spray and increasing soil minerality going inland both affect plant Mg concentration; the net effect is a slight decrease in Mg concentration going away from the coast. K concentration in living leaves and roots did not change going inland; dead leaf and stem K concentrations showed a weak decline. Bryophyte shoot nutrient concentrations do not show such marked patterns of change going inland. Considering the bryophyte species as a whole, the only significant effect is that shoot Na concentration decreases, and Ca concentration increases, going inland.

Although information on nutrient concentrations in all plant organs from all four (N, E, W and S) sides of the island was available for only a few species, and in many instances the between-side effect was not significant for individual species, the pattern of between-side differences is quite clear. Living leaf N, P and Mg concentrations are higher in west side than east side plants, with south and north side plants having intermediate concentrations. Leaf K concentrations are highest on the north and lowest on the west side, with east and south side concentrations being intermediate. Leaf Ca concentrations are highest on the south side and lowest on the north side, with east and west side Ca concentrations being intermediate. Leaf Na concentration declines more sharply with distance inland on the island's western and southern sides than on its eastern and northern sides, so that closer than 450 m from the shore leaf Na concentration is higher on the west and south than on the east or north sides, but further inland than that the difference lessens. There was sufficient information for dead leaf,

stem and root nutrient concentrations only for the west and east sides of the island. West-east differences in nutrient concentrations of dead leaves are the same as for living leaves. Stem and root west-east concentration differences are also similar to those for living leaves, except for P and Mg concentrations, which were similar on the two sides. All organs showed the same steeper decline in Na concentration on the west than on the east side of the island. Bryophytes show somewhat different between-side nutrient concentration patterns to the vascular plants. South side (not west) bryophytes have highest N and P concentrations but, like for the vascular plants, east side bryophytes have the lowest N and P concentrations. Also similar to the vascular plants, bryophyte K concentration is highest on the north side and lowest on the west side, although south side concentrations are nearly as high as the north side ones. Unlike the vascular plant leaves, bryophyte Mg concentration is highest on the south (not west) side and lowest on the north (not east) side, with east and west side concentrations being intermediate. South side bryophytes have highest Ca and Na concentrations, similar to the vascular plant pattern.

Ordination and clustering analyses of leaf nutrient concentrations suggested five nutrient type clusters amongst the island's plant species. The clusters differ in the amount (low, moderate or high) of N, P, K and Na versus the amount of Ca and Mg. Species membership of the clusters is strongly related to what major taxonomic group (bryophyte, pteridophyte, monocot or dicot) the species belongs to, but habitat factors, especially the intensity of animal manuring, also play a role. Plant guilds compiled previously for the island and which have been suggested might prove useful for modeling nutrient standing stocks on a whole island basis associate poorly with the clusters. Where a particular guild does associate closely with a cluster it is mostly an effect of taxonomic group (the guild members are all from a single taxonomic group) or habitat (the guild members are typical for a particular habitat).

It is suggested that in order to reduce the complexity and arduousness of constructing whole island plant nutrient standing stock budgets, the species should be grouped according to their taxonomy – as bryophytes, dicots, monocots, club mosses or pteridophytes (the ferns proper). Subgroups of these taxonomic groups can be constructed on the basis of habitat. Mostly, this will be necessary to distinguish plants from manured habitats from plants of the same species from unmanured ones.

Opsomming

Ten einde die voedingstofvoorrade en modelvoedingstofsiklus op die sub-Antarktiese Marioneiland op ’n algehele ekosisteemvlak te raam, word inligting oor die ruimtelike variasie in plantvoedingstofkonsentrasies op die eiland benodig. Die raming van voorrade en die konstruksie van modelle sal ook minder ingewikkeld wees indien plantspesies op grond van hul ooreenkomste/verskille in voedingstofkonsentrasies gegroepeer word eerder as om elke spesie individueel te beskou. Hierdie tesis bied ’n uiteensetting van die ruimtelike variasie (hoogte, afstand van die see én kant van die eiland) in die chemiese samestelling (N, P, K, Ca, Mg en Na) van plante, en probeer die plantspesies op grond daarvan in voedingstoftipes klassifiseer.

Hoogte en afstand van die see is nou verwant en beïnvloed dus voedingstofkonsentrasies op feitlik dieselfde manier. N-, P- en Na-konsentrasies in lewende blare, dooie blare, stingels en wortels neem af in die rigting van die binneland weens ’n afname in die invloed van dierebemesting en seesproei. Ca-konsentrasies styg weer namate daar vanaf die organiese veengrondkenmerke van die laagliggende streke na die mineraalryke binnelandse grond beweeg word. Sowel die afname in seesproei as die toename in grondmineraalgehalte in die rigting van die binneland beïnvloed die Mg-konsentrasie in plante; die netto uitwerking is ’n effense afname in Mg-konsentrasie namate daar wegbeweeg word van die kus. Die K-konsentrasie in lewende blare en wortels verander nie in die rigting van die binneland nie, terwyl dié in dooie blare en stingels ’n geringe afname toon. Die voedingstofkonsentrasies in briofietspruite toon egter nie dieselfde merkbare veranderingspatrone in die rigting van die binneland nie. Wat die briofietspesie in die geheel betref, is die enigste beduidende uitwerking dat die Na-konsentrasie in spruite afneem en die Ca-konsentrasie toeneem namate daar na die binneland beweeg word.

Die N-, P- en Mg-konsentrasies in lewende blare is hoër by plante in die weste as in die ooste van die eiland, en plante in die suide en noorde toon tussenkonsentrasies. K-konsentrasies in blare is die hoogste in die noorde en die laagste in die weste, met tussenkonsentrasies in die ooste en suide. Ca-konsentrasies in blare is weer die hoogste in die suide en die laagste in die noorde, met tussenkonsentrasies in die ooste en weste. Aan die weste- en suidekant van die eiland toon Na-konsentrasies in blare ’n skerper afname namate daar verder van die see beweeg word as aan die ooste- en noordekant. Verskille in die voedingstofkonsentrasies van

dooie blare in die weste en ooste is dieselfde as vir lewende blare. Konsentrasieverskille in stingels en wortels in die weste en ooste is ook soortgelyk aan dié in lewende blare, buiten P- en Mg-konsentrasies, wat dieselfde was aan albei kante. Alle plantorgane toon dieselfde skerper afname in Na-konsentrasies in die weste as in die ooste van die eiland. Die voedingstofkonsentrasiepatrone tussen die verskillende kante van die eiland was ietwat anders vir briofiete as vir vaatplante. Briofiete in die suide (nie die weste nie) het die hoogste N- en P-konsentrasies. Soos die vaatplante, het die briofiete in die ooste die laagste N- en P-konsentrasies. Óók soortgelyk aan die vaatplante, is die K-konsentrasie van briofiete die hoogste in die noorde en die laagste in die weste, hoewel konsentrasies in die suide bykans so hoog is as dié in die noorde. In teenstelling met die blare van vaatplante, is die Mg-konsentrasie van briofiete die hoogste in die suide (nie die weste nie) en die laagste in die noorde (nie die ooste nie), met tussenkonsentrasies in die ooste en weste. Briofiete in die suide het die hoogste Ca- en Na-konsentrasies, wat weer ooreenstem met die vaatplantpatroon.

Ordinasie- en trosvormingsontledings van voedingstofkonsentrasies in blare dui op vyf voedingstoftipes onder die plantspesies op die eiland, op grond van die (klein, matige of groot) hoeveelheid N, P, K en Na teenoor die hoeveelheid Ca en Mg. Die klas waartoe ’n spesie behoort, hou sterk verband met sy hoof- taksonomiese groep (briofiet, pteridofiet, monokotiel of dikotiel), hoewel habitatfaktore (veral die intensiteit van dierebemesting) ook ’n rol speel. Die plantgildes wat voorheen vir die eiland opgestel is, toon weinig ooreenkoms met die klasse wat uit hierdie studie na vore kom.

Acknowledgements

I would like to thank the National Research Foundation for funding this project and providing me with a bursary. The Department of Environmental Affairs provided logistical support. The Department of Botany and Zoology at the University of Stellenbosch provided facilities and logistic support.

I would also like to thank Prof. V.R. Smith for his guidance over the past 5 years and the opportunity to experience Marion Island. I have learned much from him. Dr. Martin Kidd instructed me on the statistical tests I used in my study. Prof. Ian Meiklejohn constructed Fig. 2.1.

To all my Gogga colleagues, especially Tanya Haupt, thank you for the late nights we worked together and your encouragement. I would also like to thank Dr Aleysia Kleinert for technical help and encouragement.

To my parents, who were a source of unyielding support and compassion during my study, and other times of my life - thank you for patiently listening to me complain about statistics and helping me with my tables. I would also like to thank my girlfriend, Rocille Korf, for her support, understanding and patience over the past year.

This thesis is dedicated to David Gold, Ronnie James Dio, Peter Steele and Jeff Hannemann, who all passed away while this thesis was being written.

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Chapter 1

Introduction and aim of the study

1.1 The Marion Island environment, vegetation and nutrient ecology

1.1.1. Geology and climate

Marion Island (47° S, 38° E) is situated in the sub-Antarctic region about 1800 km SSE of Cape Town (Fig 1.1). It is 290 km^2 in area and its highest peak is 1242 m above sea level. It is a young island (c. 500 000 years old) made up of the peak of a Hawaiian type shield volcano (Mc Dougall et al. 2001). Holocene black basaltic lavas and scoria cover older Pleistocene grey basaltic lavas although there are places on the island where the latter are on the surface (Verwoerd 1971, Hall 1978). McDougall et al. (2001) state that the lavas belong to an alkaline oceanic island basalt suite and suggest that there were as many as eight periods of volcanic activity and at least five glacial events.

The island has a cool maritime thermal regime, with an annual mean temperature of 6 ºC and small seasonal and diurnal variations (difference in mean temperature of the warmest and coldest month is only about 4 ºC and between warmest and coldest hours in a day only 3 ºC; le Roux 2008). The island's maritime setting also ensures an almost constant cloud cover and a high rainfall (between 2000 and 2500 mm per year), evenly spread over the year (Schulze 1971). The extensive cloud cover limits the amount of solar radiation received by the island surface to about 30% of the amount that would occur in the absence of clouds (Smith and Steenkamp 1990). Winds are predominantly from the North West and South West and can be strong. Annual mean wind speed at the meteorological station 20 m above sea level is c. 29 km h^{-1} with annual maximum wind speeds from 65 to 151 km h^{-1}. Much stronger winds occur at higher altitudes (V.R. Smith pers. comm.).

1.1.2. The island biome and its terrestrial flora

Traditionally, sub-Antarctic island vegetation has been considered to be *tundra* or, at least, *tundra-like* (Rosswall and Heal 1975), because it shows many physiognomic similarities to Northern Hemisphere tundra vegetation (low-growing shrubs, herbs, graminoids and cushion

plants, cryptogams prominent) and it occurs on typically tundra-type soils (either skeletal, dry and mineral rawmarks or wet and organic peats). Smith and Mucina (2006) recognize two distinct biomes on the island, the *sub-Antarctic Tundra Biome* and the *Antarctic Polar Desert Biome*. The island differs from true tundra of the Northern Hemisphere mainly because of its hyperoceanicity (Boelhouwers et al. 2003 provide a detailed account of the maritime climate of the sub-Antarctic islands).; it does not experience the bitterly cold winters and relatively warm summers so characteristic of true tundra, and water is available throughout the year. This lack of a severely cold or dry period results in a long (c. 300 days) growing season for the plants.

Another factor that distinguishes the island biome from most Northern Hemisphere tundras also relates to its hyperoceanicity and its recent origin. The island is isolated from continental sources of colonizing organisms and there has not been much time for colonization to occur. In fact, most of the island was under ice during the Pleistocene and its extant terrestrial biota could only have colonized it during the past c 10 000 years (Boelhouwers et al. 2008). Consequently its biota is species-poor. For instance, only 23 indigenous vascular species occur on the island, although 18 human-introduced alien vascular species have been recorded (Gremmen and Smith 2008a). Bryophyte and lichen diversity is somewhat higher, with 93 moss (Ochyra 2008), 43 liverwort (Gremmen 2008), and 116 lichen species (Øvstedal and Gremmen 2008).

1.1.3. Vegetation and terrestrial habitats

The island's vegetation has been classified and described by Huntley (1971) and by Gremmen (1981). Based on floristic composition of the vegetation and autecological characteristics of the dominant species, Huntley (1971) used a process of successive approximation to arrive at an ecological classification that recognizes 13 "nodal" plant communities, grouped into 5 complexes based on the most important factor controlling their distribution (salt-spray, manuring and trampling, exposure, and drainage). The complexes are: Salt Spray Complex, Swamp Complex, Slope Complex, Wind Dessert Complex and Biotic Complex. (In the ecological literature of Marion Island the term "biotic" has been commonly used when referring to plants, communities or habitats influenced by seals or seabirds, through manuring and trampling).

Gremmen (1981) used a more rigorous phytosociological approach to define 41 plant communities within the island's vegetation and used the floristic data with environmental information (soil depth, moisture content, pH, loss-on-ignition, depth of groundwater,

severity of manuring and trampling by animals and of salt spray) to group the communities in 6 community complexes. These complexes are essentially similar to Huntley's ones, the additional (6^{th}) complex arising as a result of distinguishing two complexes in Huntley's Slope Complex (dry fernbrakes are separated from springs, flushes and drainage lines, based on floristics and environmental parameters, especially moisture).

Smith and Steenkamp (2001) applied ordination and clustering methods to vegetation and soil chemistry information to compile a classification of the terrestrial habitats of the island. Although the habitats were not based on floristics (other than cover values of the main plant guilds), most of them are analogues of the floristic-based communities and they form habitat complexes very similar to the plant community complexes. The habitats were found to closely reflect with differences in the magnitudes of the main ecological forcing variables (exposure, moisture, saltspray and manuring by seals and seabirds) that determine succession and ecosystem structure and function on the island. The habitat classification has thus provided a useful framework against which to explain the patterns of variation in aspects of ecological functioning at the island (Smith 2003, 2005, 2008a). Smith et al. (2001) also showed that the classification can be used to detect and evaluate structural and functional responses of the plant communities to the marked climate change the island has experienced over the past 4 decades (le Roux 2008). In fact, the classification has been used to predict some of the responses (Smith et al. 2001, Gremmen and Smith 2008, Smith 2008b).

More recently, Gremmen and Smith (2008a) hybridized the ecological classification of Huntley (1971), the floristic classification of Gremmen (1981) and the habitat classification of Smith and Steenkamp (2001), retaining the term "habitat" to describe the resultant categories. What follows is a very brief synopsis of the complexes, based on all the above classifications but especially on the most recent one of Gremmen and Smith (2008a).

The Mire Complex consists of graminoid and bryophyte-dominated communities on wet, mostly oligotrophic, peats. Within the complex, water table depth and its variation, the source of soil water (ombrotrophic or minerotrophic) and moisture content determine the type of mire community. In some of the classifications referred to above, mire communities strongly influenced by saltspray or manuring are considered as part of the Saltspray and the Biotic Complexes, respectively. The most common graminoids are *Agrostis magellanica*, *Juncus scheuchzerioides* and *Uncinia compacta*. Other vascular species are the buttercup *Ranunculus biternatus* in the wetter, and the fern *Blechnum penna-marina* in the drier mires. Many

bryophyte species occur, the most common ones of oligotrophic/ombrotophic mires being *Blepharidophyllum densifolium*, *Clasmatocolea humilis*, *Ptychomnion densifolium*, *Jamesoniella colorata*, *Racomitrium lanuginosum*, *Sanionia uncinata* and several *Campylopus* species. *Breutelia integrifolia*, *Bryum laevigatum* and, sometimes, *Cryptochila grandiflora* dominate minerotrophic mires.

Mire communities are a conspicuous feature of the area where closed vegetation can develop (< 300 m altitude), occupying a total area of about 22 km^2 but above this they are rare, occupying about 0.06 km^2 in total (Gremmen and Smith 2008).

The Slope Complex occupies about 25 km^2 of the area below 300 m a.s.l. but above this only about 0.2 km^2 (Gremmen and Smith 2008). Slope Complex soils are well-drained and less organic than the mire soils and support a vegetation dominated by *B. penna-marina* (fernbrakes), the woody dwarf shrub *Acaena magellanica* (drainage lines, streambanks, springs and flushes), or both (dwarf shrub fernbrake). Fernbrakes are by far the most common type of habitat in the complex, and are distinguished mainly by their moisture regime. Brypohytes have low cover in fernbrake communities, except in the driest ones where they may occur as moss balls (e.g. *Ditrichum strictum*, *Andaea acuminata*) and in the wetter ones where they may occur as large pillows standing higher that the vascular canopy (*Racomitrium lanuginosum* in mesic fernbrake) or as an understorey to the vascular plants (e.g. *Brachythecium rutabulum* and *Sanionia uncinata* in dwarf shrub fernbrake and drainage lines and streambanks).

The Fellfield Complex consists of open cover vegetation on skeletal mineral soils, generally with a high rock cover. The cushion plant *Azorella selago* is always dominant, often also cushion-forming mosses, and crustose lichens are common. Fellfield vegetation covers about 137 km^2, or 47%, of the total area of Marion Island; it occupies 72% of the area between 100 and 300 m a.s.l. (Gremmen and Smith 2008).

The Polar Desert Complex comprises only one type of habitat or community, mainly because it has been poorly studied, especially regarding its floristics. It occupies 32% of the area between 300 and 500m a.s.l. (second only to fellfield vegetation) and 85% of the area above that (Gremmen and Smith 2008). Only one vascular species, *A. selago*, occurs in polar desert. Bryophytes (mainly ball- or cushion-forming mosses, but in snow-melt patches short turf- or mat-forming mosses and liverworts) are common, but total plant cover rarely exceeds 1%. There are no soils in polar desert, only volcanic rock or gravel-sized scoria. In some areas,

bryophytes grow on the undersurfaces of the scoria rocks, protected from the desiccating and chilling effects of wind.

The Coastal Saltspray Complex occurs in areas subjected to saltspray and inundation by waves and, because of the prevailing wind direction, it extends further inland on the north and west sides than on the east and south sides of the island. In total, the complex occupies only about 1.22 km^2 (Gremmen and Smith 2008). The moisture regimes of the various habitats/plant communities making up the complex extend across almost the complete wet-dry gradient found at the island, from shore-zone rocks dominated by halophytic lichens (e.g *Verrucaria* spp., *Caloplaca* spp., *Mastodia tesselata*) and mosses (e.g. *Eriopus apiculatus* and *Muelleriella crassifolia*), through coastal fellfields dominated by *A. selago* and *Crassula moschata* and herbfields dominated by *C. moschata* and/or *Cotula plumosa*, to saline mires dominated by the liverwort *Clasmatocolea vermicularis* and where characteristic species of the mire complex (e.g. *Agrostis magellanica* and *Ranunculus biternatus*) also occur.

The Biotic Complex occupies about 4.5 km^2 of the island, predominantly on the coastal lowlands but also further inland around albatross nests and on slopes occupied by burrowing birds species (Gremmen and Smith 2008). The manuring effect of the animals is to significantly enhance plant and soil nutrient status, stimulate plant vigour and growth and also rates of soil heterotrophic activity. Manuring and its effects will be discussed in the next section.

Several communities/habitats make up the Biotic Complex, ranging from eutrophic muds occupied by the small herb *Callitriche antarctica* or the grasses *Poa annua* and *Agrostis stolonifera*, mires dominated by *C. vermicularis* and herbfields by *C. plumosa*, through to tussock grasslands dominated by *Poa cookii*, including a pedestalled type where the *P. cookii* tussocks occur on peat pedestals up to a meter high, making it the tallest vegetation type on the island. Bryophytes are uncommon; other than *C. vermicularis*, mentioned above as being the dominant plant in biotic mires, *B. rutabulum*, *Marchantia berteroana*, *Leptodontium gemmascens*, *Lophocolea randii* and *Schizymenium campylocarpum* are the most frequently found bryophytes in tussock grasslands and the first mentioned may be abundant, especially in the more inland grasslands.

1.1.4. Biomass, primary production and soil and plant nutrient concentrations at the island

In 1971, the South African Scientific Committee for Antarctic Research initiated a project on energy flow and nutrient cycling at the island (van Zinderen Bakker 1973). The project was heavily influenced by the International Biological Program (IBP) which dominated ecological research at the time. The aims of the IBP were to quantify primary productivity and nutrient cycling of representative ecosystems of all Earth's biomes, and to investigate the relationships between primary productivity and the factors that influence it (Heal 1981). Two sub-Antarctic islands were included in the Tundra Biome component of the IBP, but for political reasons Marion Island was not. However, the project on the island was carried out in the spirit of the IBP and had identical objectives – to quantify biomass, primary production and nutrient cycling of the whole island ecosystem.

The IBP is now part of ecological research history. Although it yielded many valuable insights into particular aspects of ecosystem functioning at community levels, in not one of the more than 150 terrestrial IBP sites was the goal of a whole ecosystem model of production and nutrient cycling achieved. Perhaps its greatest achievement was to make ecologists aware of just how complex ecological interactions are at the functional level, and the intensity of sampling required to reveal the details of the interactions, especially at a whole ecosystem level. The feeling at the time of the IBP wrap-up regarding the feasibility of quantifying energy flow and nutrient cycling of whole ecosystems is reflected in the title of the paper on ecological functioning in the IBP Tundra Biome final synthesis volume – " Ecosystem synthesis – a 'fairytale'" (Bunnell 1981).

The project at Marion Island was no different – after nearly 30 years all that could be shown were production and nutrient budgets for five of the island's 42 plant communities (Smith 1987a,b,c, 1988a,b). More recently, production and nutrient cycling information has been published for three more communities (Smith 2008a). Quantifying the production and nutrient budgets for the eight communities necessitated the harvesting and sorting of plants and soils from nearly 1800 quadrats and chemical analysis of 28 000 soil/plant samples (V.R. Smith, pers. comm.).

The results show that aboveground plant biomasses (live material) in the lowland communities are high (330 to 1245 g m^{-2}) compared with most other tundra communities. Because there is a lack of macroherbivores, and even meso- and micro-herbivory are limited (Smith 2008b), almost all of the produced plant matter becomes necromass (dead material) that decomposes only slowly

under the cold island conditions. Hence, above- plus belowground standing crops (living and dead plant matter) are very high (2519 to 7494 g m^{-2}) in the lowland plant communities. Primary production (amounts of plant matter produced per year are also high (685 to 2178 g m^{-2} y^{-1}, above- plus belowground). This is because of the long growing season, not because the plants are particularly productive. In fact, productivity (the rate of dry matter production) is low (0.9 to 2.9 g m^{-2} day^{-1}) compared with most tundra communities (2.2 to 10.0 g m^{-2} day^{-1}). This is because of the low amount of sunlight energy due to high cloudiness (Smith 2008b).

Nutrient concentrations have been measured for a whole growing season for the dicotyledonous species *Acaena magellanica* and *Azorella selago*, the fern *Blechnum penna-marina* and four graminoid species, *Agrostis magellanica*, *Juncus scheuchzerioides*, *Poa cookii* and *Uncinia compacta* (Smith 1987d,e). All these measurements were on plants from a restricted locality about 450 m inland on the island's eastern coastal plain. Nutrient concentrations have also been measured for some other species (*Callitriche antarctica*, *Cotula plumosa*, *Crassula moschata*, *Montia fontana* and *Agrostis stolonifera*), on an *ad hoc* basis and mostly connected with studies on the influence of seabirds or seals on plant nutrient status (Smith 1976a, 1978a).

Leaves of the dicotyledonous species (and fronds of *B. penna-marina*, which on the island behaves as a deciduous shrub) possess higher concentrations of N, P, Ca and Mg than do leaves of graminoid species, whereas leaf K and Na concentrations are similar in the two life-forms (Smith 1987d). Concentrations of all nutrients, especially K, are mostly higher in leaves than in stems or roots, and N, P, K and Na concentrations are higher in living leaves than in dead leaves. For most species, Mg concentrations are similar in living and dead leaves whereas Ca concentrations are always higher in the latter.

Ca concentrations in the leaves of the island's graminoid species are lower than Ca concentrations in graminoid plants in Northern Hemisphere tundra or tundra-like vegetation such as montane and alpine grasslands and oceanic moorlands (Smith 1987d). Concentrations of N, P and Mg in the island's graminoid species are in the lower part of the range of concentrations exhibited by the tundra graminoids. Leaf K concentrations in the island's graminoids are similar to those of Arctic and sub-Arctic tundra graminoids but higher than most alpine grasslands and oceanic moorlands. Na concentrations in the island's graminoid are higher than in tundra graminoids. For the dicotyledonous species, and *B. penna-marina*, leaf concentrations of N, P and K are similar to, but Mg and Na concentrations are higher than, the concentrations in Northern Hemisphere tundra dwarf shrubs and shrubs (Smith 1987e). Like the graminoids, the

island's dicotyledonous plants have considerably lower Ca levels than tundra shrubs or cushion plants.

Because of the high standing crops, the plants contain large standing stocks of nutrients (the amount of nutrients contained in the plant matter, in g m^{-2}) and because the amount of plant matter produced per year is large, the vegetation requires substantial amounts of nutrients. Up to 27 g N m^{-2} y^{-1}, 3.2 g P m^{-2} y^{-1}, 10.2 g K m^{-2} y^{-1}, 10.1 g Ca m^{-2} y^{-1}, and 9.6 g Mg m^{-2} y^{-1} are taken up by the vegetation, higher amounts than are taken up by most other tundra vegetation types.

1.1.5. Nutrient inputs to the island's terrestrial ecosystem

Considerable research has concentrated on identifying and quantifying the sources of nutrients for the island's terrestrial ecosystem. The predominant source is the ocean, through sea spray and volatiles of seawater that are entrained in rain or deposited directly onto the island's surface, and through seabirds and seals that feed in the ocean and deposit excreta, feathers, eggshells and carcasses on land, Terrestrial sources are less important, comprising weathering of the basalts and biological nitrogen fixation.

The nutrient composition of the rainwater on Marion Island resembles that of a very dilute solution of seawater (Smith 2008a). Very low concentrations of NH_4-N and NO_3-N, but no PO_4-P, have been detected in the rainwater (Smith 1987a). The NH_4-N in rainwater most likely originates as volatised ammonia from the coastal penguin rookeries and seal wallows (Lindeboom 1984) and the NO_3-N is probably blown inland as an aerosol of seawater (Smith 1987a). At about 450 m inland on the island's eastern side, the annual inputs of nutrients through rainfall and dry deposition were measured as being (in g m^{-2} y^{-1}): 0.21g N, 0.39g K, 0.37 g Ca, 1.24 g Mg, 10.35 g Na, 16.40 g Cl and 2.11 g S (Smith 1987a). For N, K, and Ca these quantities represent a small fraction (e.g, only 1 to 3% of the N) of the amounts taken up annually by one square meter of vegetation 450 inland (Smith 1988b, 2008b). No P reached the sites through rainfall or dry deposition.

The island's plants do not have nitrogen fixing rhizobia, but there is N fixation by heterotrophic soil bacteria (Smith 1985) and phototrophic cyanobacteria (Smith and Russell 1982). However, the input of N through biological fixation is only c. 0.1 g m^{-2} (Smith 2008b).

Weathering of lava as a nutrient source for the plants has not been measured but it is likely to be unimportant in the closed plant communities at lower altitudes, which occur mainly on blanket peats that isolate the vegetation from the lava. At higher altitudes, rock weathering may be a significant source of some nutrients, but not of N or P.

In 2002/03, 694 tonnes N, 107 t P, 85 t K, 223 t Ca and 22 t Mg were deposited as seabird guano and moulted feathers in the island's terrestrial ecosystem (Smith 2008b). Elephant Seal excreta and moulted fur represented an additional input of 7382 kg N, 392 kg P, 82 kg K, 62 kg Ca and 73 kg Mg (Smith 2008b). Fur Seals are far more numerous than Elephant Seals at the island but there is no information on their contribution to nutrient input. Thus, seals and seabirds are important sources of nutrients for the island's terrestrial ecosystem as whole, and they greatly enhance soil and plant nutrient status (Smith 1976a, 1978a) and stimulate ecological functioning processes (Smith 2003) in the localities where they occur. However, their importance to the nutrient budgets of the island's plant communities in general is less clear. Most birds and seal occur within a few hundred meters of the coast; in fact, most guano is deposited on the bare beach surfaces of King Penguin and Macaroni Penguin rookeries and much of the guano and mineralized products of the guano washes down to the sea. Smith (2008b) estimated that only about 560 ha of the island's surface is directly influenced (occupied and manured by) by birds or seals, representing only 4% of the area below 300 m, the upper limit of closed plant communities.

1.1.6. Spatial variation in nutrient concentrations

The primary production and nutrient cycling studies have yielded information for only 8 plant communities, all below 50 m altitude on the island's eastern coastal plain- a far cry from the early aspirations of a whole island model of energy flow and nutrient cycling. There is some nutrient-related information for some other communities, mostly instantaneous values of plant and soil chemical composition (Panagis 1984, Smith 1976a,b, 1977, 1978a,b). Nothing is known about how plant nutrient concentrations vary spatially at the island, for example with increasing distance from the sea, or with altitude. There is some information on the spatial variation in soil nutrient concentrations, from a recent study on how soil chemical composition changes with distance inland and altitude, and how it differs between the eastern and western sides of the island (Conradie and Smith 2012). On the east side, total C, total N and soil moisture content all decrease, and soil bulk density increases, significantly as one moves away from the sea, whereas

on the west side this is not the case. The eastern coastal plain is wide (a few km) and slopes gently up to the mountainous interior so that there is a gradual transition from wet organic to dry mineral soils as one moves inland, causing the decrease in moisture, C and N and increase in bulk density (which is related to soil minerality). The western coastal plain is narrow (a few hundred meters) and bounded by an escarpment that rises up very steeply to the interior highlands. Sampling on the west was largely restricted to the coastal plain, since soils are rare on the escarpment and interior. Most of the west side soils were thus coastal plain peats and there was little change in organic matter or mineral content with increasing distance inland. On the east side total soil Mg concentration increased, but on the west side it decreased, with distance inland and altitude. The mineral fraction comprises most of the total Mg in the soil, with a lesser contribution by organic, exchangeable and soil solution forms of Mg. On the east side the gradual transition from organic peats to mineral soils going inland results in the increase in total Mg, whereas on the west side there is no corresponding change in soil minerality so the total Mg concentration depends mostly on the intensity of sea spray, which decreases going inland. Total Ca concentrations of both east and west side soils increased with increasing distance inland, reflecting a change in soil minerality. In contrast, total Na and exchangeable Na, Mg and K concentrations decreased, reflecting the decrease in intensity of sea spray deposition going inland.

Once these between-side differences in the influence of altitude and distance from the sea on soil chemical composition are accounted for, there are significant differences in soil chemical composition between the two sides of the island (Conradie and Smith 2012). West side soils are much more mineral and influenced by the parent volcanic rock (causing higher concentrations of total Ca, Mg and K) than are east side soils. Because the wind (especially strong wind) is predominantly westerly, west side soils are also more influenced by sea spray (manifested as higher total Na and exchangeable and soluble forms of Na, Ca and Mg) than are the east side soils. In contrast, west side soils have lower exchangeable K concentrations than do east side soils, possibly because the mineral-rich west side soils fix K in an unavailable form to a greater extent than do the more organic east side soils, or because the high concentrations of Na displaces exchangeable K in the western soils (Conradie and Smith 2012).

1.2. Aims of the study

To date, information on the between-species similarities/differences in nutrient concentrations has been limited to only a few species, and nothing is known about the spatial variation in plant chemical composition. The habitat classification referred to earlier (Smith and Steenkamp 2001) relied on grouping plant species into plant guilds, based on a combination of morphological, taxonomical and ecological traits. Recently Smith (2008c) showed that the plant guilds can be considered as analogues of plant functional types and suggested that they can be used to estimate nutrient budgets at the whole island scale. The first approach would be to assess the spatial variations (with distance inland and with altitude) in plant nutrient concentrations (analogous to the soil nutrient study described above), to see whether the plant species within guilds possess similar nutrient concentrations and to establish whether or not their nutrient concentrations vary spatially in a similar way.

My study represents a start in this approach; the main aim is to assess the spatial and between-species variations in plant nutrient composition on the island. A secondary aim is to establish whether between-species differences in nutrient concentration can be related to particular plant guilds or broad taxonomic groups. A third aim is to use the much more detailed plant nutrient information (from more species, sampled across a greater spatial range) from my study to refine the comparisons, made in the 1970s and 1980s, of the nutrient status of the island's plants with those of polar and subpolar plants from other tundra and tundra-like vegetations.

Chapter 2

Materials and Methods

2.1. Sampling and sample treatment

A total of 774 plant samples across 171 localities (Figure 2.1) were collected in April/May of each year from 2008, to 2012., representing 20 vascular and 15 bryophyte species. The position of each sampling locality was recorded with a GPS and its altitude and nearest distance to the sea determined using a digital elevation model in ArcGIS 8 (ESRI, California). ArcGIS 8 was also used to construct Figure 2.1. Prof. Ian Meiklejohn carried out these ArcGIS determinations.

Most of the species were chosen for sampling because they are ubiquitous (and common) over the island, a few are dominant only in coastal or in inland areas. The species sampled are listed in Table 2.1.

Aboveground vascular plant parts were cut with secateurs to ground level and sorted into organ (living leaves, dead leaves, stems). A 7 cm diameter soil core containing roots or rhizomes was collected and the plant material separated from the soil by sieving and washing. Obviously decomposing material was discarded; otherwise no attempt was made to distinguish living from dead belowground plant material. Bryophytes were collected by plucking or cutting material from the acrotelm. Otherwise, no attempt was made to distinguish living from dead shoots.In the rare cases where sporophytes were found they were discarded.

All plant material was rinsed with tapwater (tapwater on the island is ultra-oligotrophic, with very low conductivity (<30 μSiemens cm^{-1}), dried at 100 ºC and then ground (40 mesh) with a Micro-Wiley mill (Thomas Scientific, NJ, USA).

2.2. Chemical analysis

A subsample of the ground plant material was analysed for nitrogen with a TruSpec CHN analyser (Leco Corporation, MI, USA.). Phosphorus, calcium, potassium, magnesium and sodium were determined by dry-ashing another subsample, dissolving the ash in dilute HCl

and measuring their concentrations by Inductively Coupled Plasma–Optical Emission Spectrometry using a Vista ICP-OES Spectrometer (Varian Inc., CA, USA.).

2.3. Statistical analyses

All statistical analyses were performed using the Statistica 10 software package (StatSoft, Inc. 2011).

Linear regression analysis was used to test the relationship between the plant nutrient concentrations and the two location variables, altitude and nearest distance from the sea. Because the relationships were approximately negative exponential ones, the concentration and positional data were natural log-transformed for the regression analyses.

To test the differences in plant nutrient concentrations between sides of the island, a homogeneity-of-slopes analysis was used to test if the slopes of the (natural log) concentration versus (log) altitude (or distance inland) differed significantly between sides. If the slopes were not different, the between-sides difference in concentrations was tested by analysis of covariance; if they were different, a separate-slopes test was used. In both instances altitude or distance to the sea was the covariate. Where mean concentrations are reported subsequent to an analysis performed on logged values, the means and their variances were calculated according to Zhou and Gao (1997). The 95% confidence intervals about the means were calculated using a modification of the Cox method proposed by Olsson (2005).

The analyses of the effect of side of island, distance inland and altitude on nutrient concentrations were done on individual species where sample number allowed this. To increase sample size, the analyses were also performed on a data set comprising all the vascular species, or all the bryophytes. To compile these data sets, the concentrations of each nutrient were standardized within species (and within organ for the vascular species), by dividing them by the mean concentration for the particular nutrient. This made the means of all the species/organ/nutrient combinations equal to one, allowing an assessment of the general influence of distance inland, altitude or side of island on nutrient concentrations.

To see if species could be grouped based on similarities/differences in their nutrient concentrations, two approaches were used.

In a univariate approach the species were ordered by concentration, for each nutrient separately. Using box-plots of mean concentrations and their 95% confidence limits, assisted by analysis of variance and Tukeys Honest Significant Difference testing, the species were divided into five groups: very high, high, moderate, low and very low concentration. The similarities/dissimilarities in how the species grouped on the individual nutrients were examined to see if "nutrient types" could be identified and how these types related to major taxonomic group (dicot, monocot, pteridophyte, bryophyte), habitat, or the plant guilds used by Smith and Steenkamp (2001) to construct the habitat classification (see Section 1.1.3, with more details on the guilds in Chapter 6, Section 6.1).

A multivariate approach was then used to see if there were patterns in the nutrient concentration data that could not be found by analyzing the patterns of nutrient concentration similarities/differences for each nutrient separately. Principal Components Analysis (PCA) was used to elucidate the main gradients in the overall nutrient concentration data. Ward's Clustering of the raw nutrient data was carried out and the clusters yielded at various linkage distances examined. The clusters yielded at different linkage distances were examined. A linkage distance of 50 yielded five clusters with a clear pattern regarding their coherence and interpretability (on the basis of taxonomic group, guild, habitat and what is known about the species' autecologies). Clustering on the raw data was repeated using non-hierarchical (K-Means) clustering and specifying five clusters. Non-hierarchical clustering maximises the ratio of between-cluster to within-cluster variance and produced an even clearer pattern across the five clusters, especially at the guild level. The results of the K-Means clustering were superimposed on the PCA sample biplot and the clusters interpreted according to their two main PC axis gradients. Correspondence Analysis was then used to test the association between the five clusters and species, taxonomic group, guild and habitat.

Where necessary, further details of how the statistical methods were applied are provided when discussing their results.

Chapter 3

Variation in plant nutrient concentrations with increasing distance from the sea and with altitude

3.1. Vascular plants

Thirteen vascular species were sampled at localities across a wide altitudinal range and from near the coast to far inland. The standardized concentrations of all 13 species were used together to determine if there was a general influence of altitude and nearest distance from the sea on nutrient concentrations. No distinction was made between data from the different sides of the island in analyzing the overall effect of distance from sea or altitude on nutrient concentrations.

The means, standard deviations, minima and maxima of the nutrient concentrations for living leaves of the vascular species are given in Appendix A.

3.1.1 Vascular plant living leaf nutrient concentrations

Figure 3.1 shows the relationships of standardized N concentration in living leaves of all the 13 species to distance from sea and to altitude. N concentration declined significantly with both spatial variables (Table 3.1). Considering each species separately, 11 of the 13 showed negative correlations of N concentration in leaves with distance from sea, but only for five species was the relationship significant (Table 3.1). For 11 species leaf N concentration was negatively correlated with altitude, the correlations being significant for the same five species.

Thus, the overall pattern for live leaf N concentrations shown in Table 3.1 is that they declined with increasing distance away from the sea and with increasing altitude. The notable exception was for *Lycopodium saururus*, where leaf N concentration increased significantly with both distance inland and altitude. However, it is interesting that in the case of the other club moss, (*Lycopodium magellanicum*) and the three ferns (*Blechnum penna-marin*a, *Grammitis poeppigeana* and *Polystichum marionense*), leaf N concentration is not significantly correlated with either distance inland or altitude.

The spatial pattern shown by leaf P concentration is very similar to that of leaf N; for the vascular species overall, leaf P concentrations declined with both distance inland and altitude (Figure 3.2), and the correlations were significant for even more species (e.g. also for *B. penna-marina*, *L. magellanicum* and *Montia fontana*) than is the case for N (Table 3.1). Again, the exception was that for *L. saururus* leaf P increased with both distance inland and altitude.

Considering all the vascular species together, leaf K concentration did not change significantly with either distance inland or altitude (Figure 3.3). Considering the individual species, leaf K in *M. fontana* declined significantly with both distance inland and altitude while in *Acaena magellanica* and *P. marionense* it declined significantly with altitude (Table 3.1).

Leaf Na concentration decreased markedly with both distance inland and altitude (Figure 3.4) and 12 of the 13 species showed this, the effect being significant in eight (distance inland) or seven (altitude) instances (Table 3.1). The exception was *G. poeppigeana*, where leaf Na increased with increasing distance inland and altitude.

For the vascular species as a whole, leaf Mg was only weakly related to (it declined) distance inland or altitude (Figure 3.5), the effect being significant only for distance inland (Table 3.1). However, considering the species individually, leaf Mg increased significantly with distance inland and altitude for *G. poeppigeana* and *L. magellanicum* whereas it decreased significantly for *Azorella selago* and *B. penna-marina* (it also decreased for M. *fontana* and *P. marionense* but the effects just failed to be significant at P=0.05.

Ca was the only element where the concentration in live leaves of the vascular species as a whole increased with distance inland and altitude (Figure 3.6) and this was true of nine of the 13 species, although the correlations were significant for only four of them (Table 3.1). *Poa cookii* leaves showed no change, whereas *P. marionense*, *M. fontana* and *Ranunculus biternatus* leaves showed a decrease in Ca concentration with distance inland and altitude, although the effect was significant only in the case of *P. marionense* and then only with distance inland.

3.1.2 Vascular plant dead leaf nutrient concentrations

Dead leaf material was collected for eight of the 13 vascular plant species that occur across a wide range of localities. Dead leaves do not accumulate to any extent in the cases of *L. magellanicum*, *L saururus*, *M. fontana* and *R. biternatus*. Of three samples were taken of *P. marionense* dead leaves so the dead leaf nutrient concentrations data for that species are not considered here.

As was the case with living leaves, N concentration in dead leaves of the vascular plant species showed an overall decline in N concentration with increasing distance inland and altitude (Fig. 3.7) but the relationships are not significant at $P \leq 0.05$ and the N concentration versus altitude relationship is especially weak (Table 3.2). Of the eight species, only for *P. cookii* was the decrease in N concentration with distance inland or altitude significant.

Across all species, dead leaf P concentration declined significantly with distance inland and altitude (Fig. 3.8, Table 3.2). Most of the species individually showed this pattern but the effect was significant only for *A. selago* (distance inland and altitude) and *P. cookii* (distance inland).

Dead leaf K concentration for the vascular species as a whole declined with both distance inland and altitude (Fig. 3.9, Table 3.2) but for individual species the effect was significant only for *A. selago*.

For seven of the eight species, dead leaf Na concentration was negatively correlated with both distance inland and altitude, for five of them the effect was significant, so that the effect for vascular species overall is highly significant (Fig. 3.10, Table 3.2). The only exception was for dead leaves of *G. poeppigeana*, where Na concentration (and that of all the other elements) increased with both distance inland and altitude.

Magnesium concentration in dead leaves showed a similar pattern to Na concentration, mostly decreasing with both distance inland and altitude (Fig. 3.11, Table 3.2), although the decline was significant for only three of the species.

Unlike for the living leaves, where Ca concentration was generally strongly positively correlated with distance inland and altitude, Ca concentration in dead leaves of the vascular species as a whole did not change with either (Fig. 3.12). Amongst the individual species, there were only two significant responses of dead leaf Ca concentration to the two location

variables; for *Acaena magellanica* it increased, and for *A. selago* it decreased, with distance inland and altitude (Table 3.2).

3.1.3 Vascular plant stem nutrient concentrations

Of the species studied, only *Acaena magellanica* and *A. selago* possess large, woody stems. The other two species with above-ground stems, *R. biternatus* and *M. fontana*, are herbaceous annuals with stems that have small internodes and are of a much smaller mass than the leaves they support, so they were included with the leaf material in the chemical analysis. For some other species (especially the ferns and club mosses) the "stems" are actually belowground rhizomes and were included in the belowground component.

For both *Acaena magellanica* and *A. selago*, stem N concentration was positively correlated with both distance inland and altitude, although the effect was only significant in the case of *Acaena magellanica* (Table 3.3). In contrast to stem N, stem P concentration in both species decreased with distance inland and altitude, but here the effect was significant only for *A. selago*. For both species, K and Na concentrations both showed a weak, mostly insignificant, decline with distance inland and altitude. For *A. selago*, stem Mg concentration decreased with distance inland and altitude whereas for *Acaena magellanica* stem Mg concentration was poorly correlated with both spatial variables. Stem Ca showed a different pattern – it increased with distance inland and altitude in the case of *Acaena magellanica*, although this was not significant, but no significant change was detected in *A. selago*.

3.1.4 Vascular plant belowground organ nutrient concentrations

Belowground organs were collected for ten of the 13 vascular plant species. The root masses of *L. saururus*, *P. marionense* and *R. biternatus* are very low and in only a few instances did the samples yield enough material for chemical analysis, so belowground nutrient concentrations are not given for these species. Roots and rhizomes that were obviously dead (i.e. detached and decomposing) were not sampled, but even the material that was sampled could not be reliably differentiated into living or dead tissue. Hence, nutrient concentrations reported here are for the belowground standing crop as a whole (biomass and necromass).

The only significant change in belowground organ N concentration with distance inland or altitude was for *Acaena magellanica* (Fig. 3.13, Table 3.4), where, like in the stems, root N concentration increased with altitude (N concentration also increased with distance inland but the effect just fails significance at P=0.05). N concentrations in *Grammitis poeppegiana* and *Lycopodium magellanicum* roots also showed strong positive relationships with distance inland and altitude, but in both instances sample sizes are low and the effect not significant at $p \leq 0.05$.

Belowground P concentration showed a highly significant decrease with both distance inland and altitude when considered across all the vascular species (Fig. 3.14) and seven of the ten species showed this pattern. The effects are significant for *J. scheuchzerioides* and *P. cookii* (Table 3.4) and almost significant for *Agrostis magellanica* (P=0.065), *A. selago* (P=0.055) and *B. penna-marina* (P=0.069).

Belowground K concentration did not change conspicuously with distance inland or altitude, for the vascular species as whole (Fig. 3.15) or for any of the individual species, with the exception of *Agrostis magellanica*, where root K concentration declined significantly with altitude and almost significantly (P=0.073) with altitude (Table 3.4).

Root/rhizome Na concentrations were negatively correlated with distance inland and altitude for eight of the ten species but significantly so only in the case of *B. penna-marina* and *P. cookii*. Considering the vascular species together, the decline in Na concentration with both distance inland and altitude is highly significant (Fig. 3.16, Table 3.4).

Unlike in living leaves and dead leaves, where, for a particular species, Mg concentration changed with distance inland or altitude in the same direction as did Na concentration, this was not always the case in the belowground concentrations. For five of the species where Na concentration was negatively correlated with distance inland or altitude, Mg was positively correlated with both. Considered across all the vascular species, belowground Mg concentration was positively correlated with distance inland and altitude (Fig. 3.17) but in both instances the effects just fail to be significant at the 5% level (Table 3.4). Of the individual species, the only significant relationships between Mg concentration and distance inland or altitude are the positive ones shown by *M. fontana*.

The overall pattern of belowground Ca concentration across the vascular species was a weak increase with both distance inland and altitude (Fig. 3.18, Table 3.4). Amongst the individual

species the only significant changes (an increase) belowground Ca concentration with distance inland or altitude were for *B. penna-marina* and *M. fontana* (Table 3.4).

3.2. Bryophytes

Nine species of bryophytes (Table 3.5) were sampled across a wide range of altitudes and distances inland (Table 2.1). Six other species were sampled across much narrower spatial ranges. *Campylopus arboricola*, *Clasmatocolea vermicularis* and *Marchantia berteroana* are mostly restricted to the coastal areas; 15 of the 17 samples were collected < 1000 m from the sea and <50 m a.s.l.. *Andraea acutifolia*, *Ditrichum strictum* and *Cryptochila grandiflora* were sampled mainly towards the island's interior (24 of 26 samples were from >2000 m inland and >100 m a.s.l.). *A. acutifolia* and *D. strictum* occur on rocks and are characteristic high altitude species (Gremmen 1981). *C. grandiflora* occurs mainly on scoria which is far more common at higher than at lower altitudes, explaining the sampling distribution for this species.

The means, standard deviations, minima and maxima of the shoot nutrient concentrations for the bryophyte species are given in Appendix A.

Figure 3.19 to 3.24 show the relationships of standardized nutrient concentration to distance inland and to altitude for shoots of the nine bryophyte species that were sampled over a wide spatial range. Table 3.5 gives the correlation statistics for the all-species relationships, and also those for the individual species.

On both an all-species and individual species basis, bryophyte N, P and K concentrations seem unrelated to either distance inland or altitude (Figs. 3.19 – 3.21), excepting for *Clasmatocolea humilis*, where P and K decreased significantly with distance inland and K also decreased with altitude (Table 3.5).

Considering all nine bryophytes together, shoot Na concentration decreased significantly with distance inland and its decrease with altitude is only marginally insignificant (P= 0.068) (Fig. 3.22, Table 3.5). Of the individual species, Na concentrations in *Breutelia integrifolia* and *Sanionia uncinata* shoots decreased significantly with both distance inland and altitude (Table 3.5).

Shoot Mg concentration was unrelated to distance inland when considering all species together (Fig. 3.23a). This was mainly due to quite strong opposing trends amongst individual species. Mg concentration in *B. integrifolia* decreased, whereas in *S. uncinata* it increased with distance inland (Table 3.5). The same opposite trend was found for *Brachythecium rutabulum* (decreased) and *Blepharidophyllum densifolium* (increased) although in both instances the effects are not significant at the 5% level. A similar effect of species showing opposing patterns of Mg concentration was found for altitude. For *B. rutabulum* and *B. integrifolia*, Mg concentration decreased, whereas for *B. densifolium*, *Jamesoniella colorata*, *Racomitrium lanuginosum* and *S. uncinata* it increased, with altitude. Although in most instances these effects were marginally insignificant (0.05<P>0.10), the net result is that the all-species effect is one of a weak, but significant increase in Mg concentrations with altitude (Fig. 3.23b, Table 3.5).

The most conspicuous change in bryophyte shoot nutrient concentration with distance inland and altitude was for Ca. As was the case with vascular plant leaves, bryophyte Ca concentration on an all-species basis increased significantly with both distance inland and altitude (Fig. 3.24). Almost all the bryophyte species individually showed this pattern, although the effect was not always significant (Table 3.5).

Some remarks on the shoot nutrient concentrations of those bryophytes with a restricted distribution (either closer to the coast or further inland) are made in the discussion (3.3.).

3.3 Discussion

On the island, altitude and nearest distance to the sea are strongly correlated, so it is not surprising that changes in both yielded very similar patterns of nutrient concentration changes. The major source of Na, to the island' terrestrial ecosystem is via sea spray and Conradie and Smith (2012) showed that both total and exchangeable Na concentrations in the island's soils decline exponentially with both distance from the sea and altitude. The results presented here show this to be also the case for Na concentrations in living leaves, dead leaves, stems and roots of the vascular plants. The only species that seems an exception to this is *Grammitis poeppigeana, w*here Na concentrations in living leaves, dead leaves and roots were positively correlated with distance inland. The reason for this is not known. *G. poeppigeana* occurs in the crevices of lava rocks, anchored in a very skeletal mat of root and

frond litter, rather than in peat or soil as is the case for the other vascular plant species. The morphology, configuration and orientation of the crevices all differ greatly, influencing how much sea spray is deposited in them, the amount of rainwater channeled to them, and also the rate of water evaporation from the litter mat. The salinity of the mat might thus be more than a simple function of distance from the sea; rather it depends on the regime of salt deposition versus rainwater leaching versus evaporation regime of a particular crevice.

Sea spray is also an important source of Mg to the island ecosystem but the changes in Mg concentrations in the various plant organs were much less clear than for Na. Mostly, Mg concentrations in living leaves, dead leaves and stems decreased slightly going inland but, if any pattern could be discerned for root/rhizomes, it was that seven of the ten species showed a weak positive correlation between root Mg concentration and distance inland or altitude. Parent mineral substrate (volcanic rock and scoria) also contributes to the Mg status of the soils and vegetation, and Conradie and Smith (2012) ascribed changes in soil Mg levels going inland to the net effect of a decrease in the amount of sea spray received, and a gradual change from organic peats nearer the coast to highly mineral soils further inland. This buffered the changes in soil Mg and the different forms of soil Mg showed different patterns. Total Mg concentration mostly increased (although this was site dependent), whereas exchangeable Mg (the component available for plant uptake) decreased, with increasing distance inland and with altitude. Mg has an important functional role in photosynthesis and is mostly accumulated into the aboveground plant parts. The slight decrease in Mg concentration in these parts with distance inland mirrors the decrease in plant-available soil Mg. The reason for the apparent insensitivity of root/rhizome Mg concentration to, or the possibility that it may even increase with, distance inland, is not clear. However, belowground concentrations are low and are perhaps not as dependent on Mg availability as are the aboveground concentrations. Belowground, the main function of Mg in a plant is in taking up and transporting nutrients, especially P. Perhaps the suggestion from the data that root/rhizome Mg concentration increases with increasing distance from the sea reflects the decreasing nutrient (especially P) status of the soils going inland (Conradie and Smith 2012, and see below).

Mostly, Ca concentration in the different plant organs (dead leaves are possibly an exception) showed the same pattern of change (an increase) going inland, and most of the species fitted into this pattern. There are no calcareous rocks such as limestones, dolostones or marbles on the island, and the soils are poor in Ca (Huntley 1971). However, the volcanic rocks (alkaline

trachybasalts) are still the main source of Ca, and their influence becomes stronger moving away from the acid peats of the coastal region to the skeletal, mineral soils further inland and at higher elevations. The increase in leaf, stem and root/rhizome Ca concentrations with distance inland and altitude probably reflects this increasing influence of parent rock.

Dead leaf Ca concentration showed only a very weak response, or in some cases no response at all, to increasing distance inland. This can be ascribed to the fact that dead leaves possess high Ca concentrations, the result of mobilization (retranslocation and leaching) of soluble organic compounds and most other nutrients during and after leaf senescence (Smith 1988b). Ca concentration increases long after the leaf dies, as even more mobile elements are leached out of the dead leaf (Smith 1987c, 1988a). In some species dead leaves remain attached to the plant for several years. This causes the dead leaf component to be far more heterogeneous than the living leaf, stem and even the root/rhizome components; a particular dead leaf sample might consist of a population of leaves with a very different time-since-senescence profile (and hence Ca concentration) than another sample. This will tend to obscure the spatial changes in dead leaf Ca concentrations.

Seabirds and seals are the main source of N and P to the island's terrestrial system (Smith and Froneman 2008) and plants and soils influenced by these animals show enhanced N and P status compared with uninfluenced souls (Smith 1976a, 1978a). The animals have a direct, (deposition of excreta, feathers and carcasses) and indirect (deposition of ammonia volatilized from rookeries and wallowing areas on the coast; Lindeboom 1984) influence on soil and plant nutrient status. The ammonia reaches the inland vegetation either through dry deposition or entrained in rainwater. Both direct and indirect influences decrease sharply going inland, since most seabirds and seals occur on the coast and also the rainwater becomes more diluted going inland (Smith 1987f). This explains the decline in N and P concentrations in most of the plant organs with increasing distance from the sea and with altitude. Stem and belowground N concentrations seem an exception, not changing, or perhaps in some instances (notably stems and roots of *Acaena magellanica*) perhaps even increasing, with distance inland. However, especially in woody species like *A. magellanica*, N occurs at much lower concentrations (and mainly as a structural element) in stems and roots, than in leaves (where it has predominantly a functional role). Only a certain amount of N is needed for structural purposes, and any extra N taken up from N-rich soils will be used for functional purposes such as photosynthesis, growth and reproduction, and hence affect mainly leaf N concentrations.

Overall for the vascular species, K concentrations in living leaves, stems and roots/rhizomes did not change with increasing distance inland or altitude, and this was the pattern shown by most of the individual species. This is surprising, since Conradie and Smith (2012) showed that available soil K (i.e. exchangeable K) does decrease strongly inland, and manuring does significantly increase leaf K concentration, even though this might simply be an effect of enhanced nutrient status in general, i.e. enhanced N and P uptake might "force" greater K accumulation by the plants (Smith 1976a). Hence, one might expect that leaf K concentration should show the same pattern as N and P concentrations and decrease going inland. Two other considerations strengthen this expectation. (1) K is an important osmoticum in plants and so might be expected to accumulate more in coastal than in inland plants. (2) Prinsloo et al. (2011) have shown that the island soils contain crystalline minerals such as biotite and muscovite, both of which weather into K-fixing clays. This lead Conradie and Smith (2012) to suggest that K-fixation by clay is an important determinant of K availability on the island. If this is so, then the inland plants on more mineral soils might be expected to take up less K than the coastal plants on organic soils.

This surprising lack of response of K concentration in the living organs of the island's vascular plants to increasing distance inland might be explained, although not convincingly so with the information at hand, by either assuming that soil K levels are adequate throughout (sea spray, animal manuring and parent rock are all sources of K), or that there is an antagonistic effect between K uptake and Na uptake or Mg uptake, or both (Russell 1961). High exchangeable Na and Mg concentrations will lower K uptake closer to the coast, even though coastal soils might have high available K levels. This effect will lessen as both exchangeable Na and Mg concentrations decrease. going inland, but perhaps be counteracted by a lesser availability of K due to fixation by clay minerals.

Even more surprising perhaps, is the fact that while K concentration in living organs of the vascular plants did not change, that in dead leaves decreased, going inland, and it suggests that the inland plants have a greater need to conserve assimilated K. K is a very mobile element and large amounts are lost from the leaf through backtranslocation and leaching during leaf senescence. Smith (1988b) showed that more K is removed from the leaves of the island plants during senescence than any other element and my results show the same – for the vascular species as whole, comparison of the live leaf and dead leaf nutrient concentrations show that, on average, 90% of K but only 17% of N, 63% of P and 73% of Na was lost from the leaves during senescence. The fact that live leaf K concentration did not

decrease with increasing distance inland whereas dead leaf K concentration did do so, suggests that, going inland, an increasing proportion of the leaf K is backtranslocated or leached during senescence. This was indeed the case. For the vascular plants as whole, the ratio of K concentration between living and dead leaves correlated positively with both distance inland (r=0.241, p=0.002) and with altitude (r=0.264, p=0.001). Since Na is at least as soluble an element (and as readily leached from a senescing leaf) as K, it can be argued that the greater mobility shown by K during leaf senescence is due mainly to backtranslocation rather than leaching. Hence, leaves conserve K to a greater extent, indicating that soil K concentration may indeed become more limiting when moving away from the highly manured coastal area to the inland region with its highly mineral soils.

Shoot nutrient concentrations in those bryophytes that occur over a wide range of distances from sea or altitude mostly did not change with distance from the sea or with altitude. The exceptions were for Na, which mostly decreased, and Ca, which mostly increased, in concentration going inland. All of the bryophytes with a widespread range are oligotrophs and do not occur to any great extent at manured localities. They are characteristic of the islands nutrient-poor bogs and mires. Hence, even close to the sea, they were mainly sampled infertile sites, explaining why shoot N and P concentrations did not change appreciably going inland.

Bryophytes are efficient "scavengers" of nutrients received as sea spray or precipitation. They possess strong cation exchange sites on their cell walls that efficiently adsorb nutrients from very dilute solutions (Bates 2000), and this is especially so for bryophytes of nutrient poor bogs and mires (Malmer 1988). On the island sea spray and rainwater are the main sources of nutrients for the bryophytes, hence the decrease in Na going away from the sea is not surprising. The increase in Ca, the same pattern shown by the vascular plants, is perhaps unexpected. It suggests an increasing influence of mineral soil or rock going inland and that, nutrient-wise, the bryophytes are not entirely divorced from the substrate on which they occur.

There were also no significant correlations detected between nutrient concentrations and distance inland or altitude for any of the bryophytes sampled mainly at coastal, or mainly at inland localities (data not shown), but those species did have different shoot nutrient concentrations to the widespread species. The three species found mainly at coastal sites (*Campylopus arboricola*, *Clasmatocolea vermicularis* and *Marchantia berteroana*) were all

sampled at manured localities (the latter two are restricted to such localities) and they possessed significantly higher N, P, K, Mg and Na concentrations than the species with a wider distribution, or than those found only further inland at higher altitudes. Ca concentration, on the other hand, tended to be higher in the inland species (especially *A. acutifolia* and *D. strictum*, both of which are attached directly to rocks or scoria) than in the widespread or coastal bryophyte groups.

Chapter 4

Differences in plant nutrient concentration between sides of the island

4.1. Vascular plants

4.1.1. Vascular living leaves

Since distance from sea and altitude were so highly correlated, only distance from sea was considered as covariate when assessing whether plant nutrient concentrations differed between sides of the island. The (natural log) standardized nutrient concentrations for the 13 vascular species were subjected to analysis of covariance with side of island as categorical variable and (natural log) distance from sea as covariate. For four species (*Acaena magellanica, Agrostis magellanica, Azorella selago and Blechnum penna-marina*) there were sufficient samples to assess the effect of island side on a per species basis, using ANCOVA with species and island side as categorical variables and (natural log) distance from the sea as covariate. The (natural log) actual nutrient concentrations (not the standardized values) were used for this species x side ANCOVA. Each of the four species is an example of an important plant guild (*sensu* Smith and Steenkamp 2001) in the island's vegetation, and each contributes significantly to the cover (Gremmen 1981) and biomass (Smith 1987a,b) of the vegetation. *Agrostis magellanica* is a mire graminoid, *Acaena magellanica* a deciduous shrub, *A. selago* a cushion dicotyledonous plant and *B. penna-marina* a fern.

Considered across all 13 vascular species and accounting for the effect of distance inland, leaves of west side plants possessed significantly higher N concentrations than leaves of east side plants, with north and south side leaves being intermediate (Table 4.1). Of the four species for which the effect of island side could be individually assessed, *B. penna-marina* showed this pattern, but the other three species deviated slightly from it. In *A. selago*, east and north side leaves had significantly lower N concentrations than west side leaves, with south side leaves being intermediate. In *Acaena magellanica* north side leaves had significantly lower N concentrations than west side leaves with east and south side leaves being intermediate. In *Agrostis magellanica*, N concentrations in west and north side leaves were significantly greater than in east side leaves, with south side leaves being intermediate.

Leaf P concentration showed the same overall pattern between island side as leaf N, west side leaves having higher P concentrations than east side leaves and north and south side leaves having intermediate concentrations (Table 4.1). For the individual species, west side leaves always showed highest P concentrations but the effect was only significant in the case of *Acaena magellanica*. Also with *Acaena magellanica*, as was the case with N, the lowest mean P concentration was for north side, not east side, leaves.

For the vascular species as a whole, the highest mean K concentration was in north side leaves, not west side leaves as was the case for N and P (Table 4.1). In fact, west side plants showed the lowest mean K concentration, with east and south side leaves intermediate between north and west side values. *Agrostis magellanica* and *B. penna-marina* showed this pattern, but for *Acaena magellanica* and *A. selago* there were no significant between-side differences found in leaf K concentration.

Leaf Ca concentration in the vascular species as a whole declined significantly between sides in the sequence south > east> north, with west side leaves intermediate between east and north side leaves (Table 4.1). All four species showed this but the effect was significant only for *Agrostis magellanica* and *A. selago*.

Considered across all 13 vascular species, Mg concentration was highest in west side, and lowest in east side, leaves (Table 4.1). North and south side leaves showed intermediate Mg concentrations. However, of the four vascular species, only *A. selago* showed this pattern. *Agrostis magellanica* and *B. penna-marina* showed no significant between-side differences in leaf Mg concentration. For *Acaena magellanica* a different pattern occurred; north side leaves had the highest, and east side leaves the lowest, mean K concentration, west and north side concentrations being intermediate.

Leaf Na concentration for the vascular species as a whole declined more sharply with distance inland on the island's western and southern sides than on its eastern and northern sides (Figure 4.1). Closer than 450 m from the shore, leaf Na concentration was higher on the west than the east or north sides but further inland than that the situation reversed. Because of this difference in the Na concentration relationship with distance inland, a separate slope covariance analysis was used to test the between-side differences at 100m and at 1600m inland. These distances were chosen because these positions are in the overlapping part of the sampling ranges for the four sides.

At 100 m inland, south side leaves possessed significantly higher Na concentrations than leaves on the other three sides, and west side leaves possessed higher concentrations than east or north side leaves (Table 4.1). At 1600 m inland, south side Na concentration was still higher than the other three sides. West side leaves at 1600 m showed a lower, not higher, Na concentration than east or north side leaves, although the difference was not significant at $p \leq 0.05$. Further inland than 1600 m, the separate slope analysis shows that leaf Na concentration on the west side becomes progressively lower than on the east or north sides, but the reliability of the results is poor since few west side samples were taken so far inland.

Qualitatively, the four individual species showed the same trend in leaf Na concentration shown by the vascular species as a whole; south side and west side leaf Na concentrations were higher than east and north side concentrations at 100m inland, whereas at 1600 m inland, while south side concentrations remained highest, west side concentrations were similar to east and north side ones. However, only for *Agrostis magellanica* and *B. penna-marina* were the effects significant, and then only for the comparison at 1600 m inland (Table 4.1).

4.1.2. Vascular plant dead leaves

Only the east and west sides of the island are considered here, since few dead leaf samples were collected from the other two sides. Again, only for four species were sufficient samples collected to enable an assessment of the effect of island side on an individual species basis. The results are given in Table 4.2.

Similar to what was shown by living leaves, for the 13 vascular species as a whole, N concentration in west side dead leaves was significantly higher than in east side ones (Table 4.2). This was true for all four species for which enough dead leaf samples were collected to test them individually, although the effect is marginally insignificant in the case of *Acaena magellanica.* Across all vascular species, dead leaf P concentration was also higher on the west side than the east side. Qualitatively, this was the pattern for the individual species, but in no instances is the effect significant at $p \leq 0.05$.

In contrast to N and P, and as was the case for living leaves, west side dead leaves possessed lower K concentrations than east side ones when considered across all the vascular species. Three of the individual species tested showed this pattern but the effect was significant only

for *B. penna-marina*. For the vascular species as a whole, west side dead leaves also had lower Ca concentrations than east side ones. Although three of the four species individually showed this pattern, again the effect was significant only for *B. penna-marina*.

Dead leaf Mg concentration was higher on the west than on the east side. Of the four species tested individually, this pattern was shown only by *Agrostis magellanica* and *A. selago*.

As was the case with living leaves, dead leaf Na concentration for the vascular species as a whole declined more sharply with distance inland on the island's western than on its eastern side (Figure 4.2). Closer than 200 m from the shore, leaf Na concentration was higher on the west than the east side but further inland the situation reversed. Separate slope covariance analysis suggested that at 100 m inland west side dead leaves possess higher Na concentrations than east side ones The differences are not significant at $p \leq 0.05$, for individual species or for the vascular species as a whole, mainly because few dead leaf samples were collected so close to the coast on the west side, leading to large variance in the estimation of the west coast Na concentrations 100m inland. At 1600 m inland, east side dead leaf concentrations were higher than west side ones. Hence, the overall pattern for Na concentration in dead leaves between west and east sides and with distance inland closely resembles that shown by the living leaves.

4.1.3. Vascular plant stems

For both *Acaena magellanica* and *Azorella selago*, stems on the island's west side had higher N concentrations than stems on its east side, once the effect of distance inland on N concentration is accounted for (Table 4.3). For neither species did stem P or Mg concentrations differ between the two sides. As was the case for K and Ca in living and dead leaves, east side stems possessed higher K and Ca concentrations than west side stems (Table 4.3), although the differences are marginally insignificant in the case of *Acaena magellanica* (K, p=0.086; Ca, p=0.095).

Stem Na concentration declined much more with distance inland on the west than on the east side. Separate slopes analysis of covariance yielded adjusted Na concentrations for 100 m inland that have high variances, so although the west side values for both species were nearly double the east side ones (table 4.3), the effect is not significant at $p \leq 0.05$. For *A. selago*, adjusted stem Na concentration 1600 m inland was higher for east side than west side stems.

4.1.4. Vascular belowground organ nutrient concentrations

For the 13 vascular species as a whole, root/rhizome mean N concentration on the west side was higher than on the east side (Table 4.4). All four species for which sufficient belowground samples were collected to make this comparison showed this pattern but the effect was significant only for *Acaena magellanica* and *Agrostis magellanica*.

Belowground P or Mg concentrations did not differ significantly between west and east sides, for the vascular species as a whole or for the individual species. On an all-species basis, belowground K concentration also did not differ between the two sides, but for three of the species K concentration was significantly higher on the east than on the west side. Belowground Ca concentration was, overall for the vascular species, also higher on the east side. Qualitatively, all four species showed this pattern in Ca concentration but the effect is significant only for *Acaena magellanica*.

Like for the other plant organs, root/rhizome Na concentration declined more sharply with distance inland on the west than the east side. Separate slope covariance analysis was used to determine the distance-inland corrected Na concentrations at 300 m and 1600 m inland (the overlapping part of the ranges for belowground samples from the two sides). For the vascular species as a whole, Na concentration at 300 m inland was higher on the west than the east side, whereas at 1600 m inland the opposite was true (Table 4.4). Variances in the distance inland-adjusted means are large, especially for the 300 m ones, so these west-east differences are not significant at $p \leq 0.05$. It seems, though, that the overall pattern of belowground Na concentration differences between west side and east side plants is the same as that shown by living leaves, dead leaves and stems; west side concentrations are higher than east side concentrations closer to the coast but are lower than east side concentrations further inland. Of the individual species, this effect is significant for *Agrostis magellanica* and *Azorella selago*.

4.2. Bryophytes

The standardized nutrient concentrations for the nine bryophyte species with a widespread distribution were used together to compare concentrations between sides. For only one

species (*Racomitrium lanuginosum*) were enough samples taken on all four sides of the island to enable the between-side comparison to be made for an individual species.

Since the N, P, K and Mg concentrations did not change going inland, simple ANOVAs of the standardized concentrations were used for the between-side comparisons. For Ca and Na, both of which are significantly affected by distance inland, ANCOVAs of the log standardized concentrations, with the natural log of distance inland as covariate, were used.

Bryophytes from the south side had highest, and east side bryophytes lowest N and P concentrations (Table 4.5); north and west side concentrations were intermediate. K concentration was higher in south and north side bryophytes than east or west side ones, whereas Mg concentration was highest on the south side and lowest on the north side, with east and west side concentrations being intermediate. The distance inland–corrected concentrations of Ca and Na in south side bryophytes were also higher than in bryophytes from the other three sides. *R. lanuginosum* comprised 28% of the bryophyte samples and showed very similar patterns of between-side concentration differences as those described above for the nine species together (Table 4.5).

4.3. Discussion

Sample sizes were sufficient to enable a comparison of nutrient concentrations between all four sides of the island only in the case of living leaves; for dead leaves, stems and roots/rhizomes only the west and east sides could be compared.

For the vascular species as a whole, live leaf N concentrations were highest on the west side and lowest on the east side, with north and south side leaves mostly having intermediate concentrations (for some species, south side leaf N concentrations were close to west side concentrations). Dead leaf, stem and root/rhizome N concentrations were also greater on the west than on the east side of the island. All four species for which individual between-side comparisons could be made showed this pattern. Living and dead leaf P concentrations were also higher on the west side than the east side, and again, all four species showed this. However, stem and root/rhizome P concentrations did not differ between the two sides.

Like for the vascular plants, bryophyte shoot N and P concentrations were also higher on the west than on the east side, but south side concentrations were highest.

Plant-available N and P concentrations have not been measured for west side soils. Since manuring by seabirds and seals is the dominant source of both elements, and the highest densities of those animals is on the west side (also, much of the ammonia volatilized there is blown inland, rather than out to sea as on the east side), soil N and P status might be expected to be greater for west side than for east side soils. Certainly, this is the case for the island's freshwaters - west coast water bodies have higher N and P concentrations than east coast ones (Grobbelaar 1974). On the whole, the west side vegetation shows an enhanced vitality (stature, luxuriance and colour) compared with east side vegetation, attesting to a greater intensity of manuring on the side and the greater N and P status of west side plants, especially the aboveground parts, can confidently be ascribed to a greater influence of animal manuring.

Na concentration of all the plant organs declined more sharply with distance inland on the west than the east side. Strongest winds at the island are the westerly ones so the west side receives more sea spray than does the east side. Close to the coast, up to about 400-500 m inland, plant Na concentrations are higher on the west than on the east coast and further inland the difference disappears, or is even reversed. Soil exchangeable Na levels also decrease much more markedly going inland on the west than the east side of the island (Conradie and Smith 2012). Figure 4.2 compares the relationships between altitude and distance-from-sea up to 2000 m inland for plant samples collected from the two sides (the separate slopes analysis comparisons of Na concentrations were carried out for this range; only 2% of west side plant samples were collected further inland). The east side of the island comprises a wide coastal plain that increases slowly in altitude up to about 3 to 4 km inland, and only then starts rising more sharply toward the mountainous interior. In contrast, the western coastal plain is narrow, meeting a steep escarpment about 1 km inland. This difference in how altitude changes going inland possibly explains the difference in the rate of decrease in soil and plant Na status between west and east sides of the island.

In the case of leaves, which were also sampled on the south and north side of the island, south side Na concentrations were even higher than west side ones, especially close to the coast. Nothing is known regarding soil Na concentrations on the south side but since southwesterly winds are very fierce and are the predominant saltspray-bearing winds at the island (Huntley 1971), they are likely to be high.

Unlike for the vascular plants, there were no between-side differences in the rate at which bryophyte shoot Na concentration declined going inland. Like for vascular plant leaves, the

distance inland–corrected bryophyte Na concentrations were highest for south side plants. Unlike for the vascular plant leaves, west side bryophytes did not show different Na concentrations to east or north side bryophytes.

K concentrations in living leaves, dead leaves, stems and root/rhizomes were higher on the east than on the west side, opposite to what was shown by N and P but consistent with the finding by Conradie and Smith (2012) that plant-available K is higher in east than in west side soils. Conradie and Smith (2012) ascribed this to the fact that west side soils are more mineral and thus fix K into an unavailable form to a greater extent than do east side soils, and/or to a greater substitution of K by Na on the soil cation exchange complex caused by heavier sea spray deposition on the west side than on the east side.

The above comparison of leaf K concerns the east and west sides. For the vascular species as a whole, living leaf K concentration was, in fact, highest for north side plants, and for some of the species, south side leaf K concentrations were as high as north side ones. The reason for this is not apparent. Nothing is known about soil K concentrations on the north and south sides. Based on the fact that saltspray deposition is likely to be heaviest on the south side of the island, and following the argument made in chapter 3 that Na depresses K uptake, the high K concentration of south side leaves is surprising. For the bryophytes too, shoot K concentration was higher in south and north side bryophytes than east or west side ones.

Ca concentrations in live leaves were not different between west and east side plants (like Na, highest leaf Ca concentrations were from the south side of the island). Dead leaf, stem and root Ca concentrations tended to be higher on the east than on the west side, which is unexpected since west side soils are more mineral and have considerably higher exchangeable Ca (and total soil Ca) concentrations than east side soils (Conradie and Smith 2012). The reason for the higher Ca status of east side dead leaves, stems and roots is not known.

Like with vascular plant leaves, the distance inland–corrected Ca concentrations in bryophyte shoots were highest for south side plants.

West side living leaves had highest, and east side leaves lowest, Mg concentrations (although for some species south side, or even northern side, leaves were as high in Mg as west side ones). Dead leaf Mg concentration was also higher on the west than on the east side. There was no difference found in stem or root Mg concentrations between the two sides. Conradie

and Smith (2012) found that west side soils have much higher exchangeable (and total) Mg concentrations. Perhaps Mg's role in photosynthesis accounts for the fact that leaf concentrations and not stem or root concentrations respond to the higher Mg status of west side soils.

Bryophyte shoot Mg concentration showed a somewhat different between-side pattern to the one for vascular plant leaves. Bryophyte Mg concentration was highest on the south side and lowest on the north side, with east and west side concentrations being intermediate.

Overall, bryophytes from the south side tended to have higher concentrations for all nutrients than those from the other three sides. This is most probably due to the dependence of bryophytes on aerial nutrient input, which is likely to be greatest on the southern side of the island.

Chapter 5

Comparisons of plant nutrient concentrations: between island species and between island plants and those of tundra and tundra-like vegetations.

5.1 Comparisons of plant nutrient concentrations: Between the four species sampled most extensively

In chapters 3 and 4 it was shown that the concentrations of certain nutrients in the island plants depends on distance inland and side of island. These two factors thus need to be taken into account when comparing nutrient concentrations between species. Only four vascular species (*Acaena magellanica*, *Agrostis magellanica*, *Azorella selago* and *Blechnum penna-marina*) were sampled sufficiently to enable the effect of both spatial variables to be taken into account when comparing their nutrient concentration values. The results of the comparisons are presented in Table 5.1.

Of the four species, once the effect of distance from sea is accounted for, *Acaena magellanica* tended to have the highest living leaf N concentration on all four sides of the island, although on the north and south sides, *Agrostis magellanica* leaf N values were almost as high (Table 5.1). *A. selago* and *B. penna-marina* had the lowest N concentration. Dead leaf, stem and root N concentrations could only be compared for the west and east sides. Dead leaf N concentration was also mostly higher (although not always significantly so) for *Acaena magellanica* than for the other three species but there were no consistent, or significant, between-species differences in stem N or root N concentrations.

Living leaf P concentration was significantly higher for *Acaena magellanica* than for the other three species on the east and west sides, but not on the north and south sides. *Acaena magellanica* also possessed higher dead leaf P concentrations than did the other three species. As was the case for N, there were no between-species differences found in stem or root P concentrations.

A. selago had higher living leaf, stem and root K concentrations than the other three species. In contrast, K concentrations in dead leaves of *A. selago* were similar to, or even lower than, in dead leaves of the other three species. This shows that *A. selago* translocates a large proportion of K out of its leaves during senescence, which was also found in the nutrient cycling studies of the species by Smith (1988a).

Acaena magellanica possessed highest, and *Agrostis magellanica* lowest, living and dead leaf Ca concentrations, with *A.selago* and *B. penna-marina* having intermediate concentrations. The pattern was somewhat different for roots and stems. *A.selago* and *B. penna-marina* roots had higher Ca concentrations than *Acaena magellanica* or *Agrostis magellanica* roots. *A. selago* stems had higher Ca concentrations than *Acaena magellanica* stems.

B. penna-marina living leaves, dead leaves and roots had considerably higher Mg concentrations than did those of *Agrostis magellanica* and *A.selago*, and mostly they were also higher than for *Aceana magellanica*. Previous studies (Smith 1977, 1987e) also reported that the Mg status of *B. penna-marina* is high compared with other plants on the island.

Living leaves, stems and roots of *A.selago* had higher Na concentrations than did those of *Acaena magellanica* but, like with the K concentrations, the opposite was true for dead leaves. *Agrostis magellanica* and *B. penna-marina* had particularly low living leaf and dead leaf Na concentrations, and *Acaena magellanica* particularly low root Na concentrations.

Overall, these nutrient concentration differences between the four species, which take into account the effect of distance inland and side of island, are similar to the differences found by previous comparisons which did not consider the influence of the two spatial variables (Smith 1977, 1987e,f). Mostly, the differences can be ascribed to the plants belonging to different major taxonomical groups (dicot, monocot and fern), and this is explored in the next section.

5.2 Comparisons of plant nutrient concentrations: between the main taxonomic groups

Table 5.2 (compiled from the species data in Appendix A) gives the ranges in species-mean leaf nutrient concentrations for all the species considered in my study, per taxonomic group.

The ranges in species-mean leaf N, P and K concentrations for dicots largely overlap those for monocots, whereas Ca, Mg and Na concentrations are mostly higher for dicots than for monocots. Much of the dicot-monocot difference in Na concentration is because saline communities of the shore zone tended to be dominated by indigenous halophytic dicotyledonous species such as *Cotula plumosa* (mean Na concentration, 1.68%), *Callitriche antarctica* (1.27%), *Montia fontana*, (1.13%) and *Crassula moschata* (1.08%). Their only real monocot counterparts (also common on the shore, mainly in biotic muds of seal wallows, but also occurring inland) are two non-indigenous grasses with considerably lower, but still

appreciable, leaf Na concentrations. They are *Poa annua* (mean Na concentration, 0.75%) and *Agrostis stolonifera* (0.44%). Indigenous monocot species are more characteristic of less saline sites.

Ferns (Pteridophytes) mostly have lower N and P concentrations than, but similar K concentrations to, monocots and dicots. Fern Ca and Mg concentrations are greater than those for monocots but similar to, or slightly lower than those for dicots. Fern Na concentrations are low, similar to those in monocots but less than in dicots. Bryophyte shoot N and P concentrations are similar to those in fern fronds and lower than in dicots or monocots. Bryophyte K concentrations are the lowest of all the groups Bryophyte Ca, Mg and Na concentrations are similar to those for ferns, mostly higher than those for monocots but considerably lower than those for dicots.

The same patterns of differences in the concentrations of the various nutrients between the main taxonomic groups have been found in other studies, not only those concerning plants of tundra or tundra-like vegetations (Rodin and Bazilevich 1967, Allen 1974, Pilbeam and Morley 2007).

5.3 Comparisons of plant nutrient concentrations: With previous values reported for the island and between the island plants and plants of other Southern Ocean islands and tundra or tundra-like vegetations

Table 5.2 also compares the leaf nutrient concentrations found in my study with those reported previously for the island plants with those for plants from other tundra and tundra-like vegetations. The conclusions from the previous studies (Smith 1978b, 1987d,e,) were that the Marion Island plants have lower N, P, K and Ca status, but a higher Na status, than plants of South Georgia Island, Signy Island or northern hemisphere tundra and tundra-like vegetations.

These previous studies considered only a few plant species at very restricted localities, all within 500 m of the seashore on the east side of the island). Manured coastal sites were not sampled; in fact almost all samples in previous studies were from highly oligotrophic sites. In my study a wider range of plant species was sampled, on all four sides of the island and from the coast up to 760 m altitude and 6.5 km inland. The inclusion of samples from a wide range of localities, especially shore zone manured sites, and of more species than previously,

explains why the ranges of species-mean N, P and K values for all the taxonomic groups found in my study extend to much higher values than found previously at the island (Table 5.2). They are similar to values reported for other southern ocean island and tundra plants, disaffirming the earlier conclusion that the island's plants have a comparatively low N, P and K status.

My study also yielded considerably higher species-mean leaf Ca concentrations than found previously. Again, this is because plants were sampled over a much wider area, especially inland (leaf Ca status increases going inland; Fig. 3.6, Table 3.1). No samples were taken more than 500 m inland in previous studies whereas 75% of samples taken in my study were further inland than that. However, for all the groups, the species-mean leaf Ca concentrations found are in the lower part of the range reported for plants on South Georgia Island or Signy Island. The soils and plants of both those islands are influenced by calcareous parent materials such as marble bands or quartz- and feldspar-rich veins (Allen et al. 1967, Headland 1984), whereas calcareous rocks are lacking on Marion Island. *Acaena magellanica* showed the highest species-mean Ca concentration (1.21%) – the next highest was for *Azorella selago* (0.80%). If the *Acaena magellanica* value is excluded, the suggestion from previous studies that the island plants have a low Ca status compared with plants from the other two Southern Ocean islands and tundra or tundra-like vegetations is supported by the results of my study.

Previous results also suggested that dicot and monocot leaf Mg concentrations at the island are similar to (or perhaps slightly lower), but that pteridophyte and bryophyte Mg concentrations are higher, than at South Georgia Island, Signy Island or northern hemisphere tundra or tundra-like vegetations. This is supported by the results presented here. The highest leaf Mg concentration (0.86%) in Table 5.2 was for *Cerastium fontanum* (an introduced dicot species) but represented only a single sample, not a species mean (the highest species mean Mg concentration was 0.63%, for *Acaena magellanica*). Hence, excepting for the *C. fontanum* value, leaf Mg concentrations of the island's dicots and monocots are in the lower part of the ranges shown by their counterparts on the other two Southern Ocean islands or by northern hemisphere tundra plants. In contrast, Marion Island ferns and bryophytes tend to have high leaf Mg concentrations compared with ferns and bryophytes from the other islands or northern hemisphere tundras.

My study confirms previous conclusions that leaf Na concentrations for all the plant groups at the island are higher than for their counterparts on South Georgia Island, Signy Island or in northern hemisphere tundra and tundra-like vegetation.

Chapter 6

Can "plant nutrient types" be recognized in the Marion Island flora?

6.1. The *plant guild* and *plant functional type* concepts and their use in previous research at the island

The second main aim of my study was to see whether the island plant species can be grouped according to similarities in their nutrient concentrations, at a finer level than the broad taxonomic one discussed above. This would simplify constructing nutrient standing stock budgets for nutrient cycling models on a whole island basis, compared with having to include each species as a separate component in the model. It is consonant with the growing interest worldwide in defining functional traits in order to classify species into plant functional types (Lavorel et al. 2007, Harrison et al. 2010). A plant functional type (PFT) thus contains species with similar functional traits, meaning that it represents a (usually non-phylogenetic) grouping of species that respond to, and exploit, their environment in a similar way (Duckworth et al. 2000). Focusing on PFTs, rather than species, reduces the complexity of models for monitoring and predicting the effect of climatic change or management on vegetation distribution and ecosystem processes (Diaz et al. 2004).

In my study, the functional trait of interest is plant nutrient composition and I tested the plant guilds that Smith and Steenkamp (2001) used to classify the island's terrestrial habitats. The habitat classification was based on canonical correspondence ordinations of plant cover and soil chemistry information. The ordinations were carried out reiteratively, first on the plant species and subsequently on increasingly broader groupings of species, until further grouping resulted in a significant decrease in the variance explained by the ordination axes (i.e. significance of the plant group-soil chemistry relationships). The final groupings of species in the ordination space were the plant guilds on which (with the soil chemistry information) the habitat classification was based. Motivation for testing those guilds as being representative of plant (nutrient) functional types is as follows:

The rationale for the classification was that it should serve as the framework against which to detect and evaluate biological and ecological responses to climate change at the island, and

that it could be used in models to predict what those responses might be. To some extent, these aspirations have been met. Smith et al. (2001) and Gremmen and Smith (2008a) used the classification, with the ordinations on which is based, to predict how the various terrestrial habitats might respond (change into another habitat) under various scenarios such as the the island becoming warmer and drier more (or less) affected by sea spray, more (or less) influenced by manuring. Smith (2003) showed that the habitat classification (more specifically the distribution patterns of the habitats on the ordination axes on which they were based) explains much of the variation in laboratory-measured soil respiration rate at the island; for example, habitat-mean respiration rate correlates positively ($r = 0.76$; $P<0.001$) with habitat-mean score on the first ordination axis. More recently, Lubbe and Smith (2012) examined a variety of predictors (soil chemistry, microbiology, moisture and botanical) of soil respiration rate and found that the relative covers of five of the plant guilds sensu Smith and Steenkamp (2001) formed the best suite of predictors, accounting for 94% of the total variation in field-measured soil respiration rate.

The basic criterion for the habitat classification was that it should emphasize variation between habitats in ecological attributes, especially functional ones (e.g. primary production, decomposition and nutrient cycling), related to differences in the relative magnitudes of the important environmental forcing variables. These are wetness/dryness, temperature, parent substrate, sea spray and manuring. Plant nutrient composition is related to most of these forcing variables, and can also be regarded as a component of ecosystem functioning (nutrient cycling). Smith (2008c) suggested that the plant guilds on which the habitats are based are analogues of plant functional types and can potentially be used to estimate biomass and nutrient composition of the vegetation on a whole island basis. It is for this reason that the plant guilds are used as the basis for exploring the nutrient composition affinities of the plants considered in my study.

The guilds *sensu* Smith and Steenkamp (2001) are; Tussock Graminoid, Mire Graminoid, Epiphytic Graminoid, *Poa annua*, Deciduous Shrub, Mat Dicot, Cushion Dicot, Rosette Dicot, Erect Dicot, Pteridophyte, Cushion Bryophyte, Mire Bryophyte, *Brachythecium* Mosses, and *Bryum/Breutelia* Mosses. The latter two guilds comprise bryophytes most characteristic of drainage line habitats; *Brachythecium* Mosses occur drainage lines of more-or-less steep slopes, and *Bryum/Breutelia* Mosses occur in drainage lines through more-or-less level mires. The two guilds are thus termed here "Slope drainage line bryophytes" or "Mire drainage line bryophytes", respectively. The Epiphytic Graminoid guild was used by Smith and Steenkamp to distinguish *Agrostis magellanica*

plants growing on cushions of *Azorella selago* from *A. magellanica* plants rooted in peat (when it was considered a Mire Graminoid); without this distinction, fellfield habitats were poorly differentiated from mire habitats. Here, *A. magellanica* is considered a Mire Graminoid.

The introduced grass, *Poa annua* was placed in its own guild (*Poa annua*) since it did not group with any other graminoid in the ordinations from which the habitats were constructed. Rather, its position in the ordination space was such that it formed the basis of just one habitat, Biotic lawn, and is thus considered here, with another introduced grass, *Agrostis stolonifera*, as a Biotic graminoid. *A. stolonifera* was not in the data set used by Smith and Steenkamp (2001) since when they carried out the fieldwork for their study (in the 1970s, 1980s and early 1990s), the species was far less common on the island than it is today. It has since become very much more widespread (Le Roux et al. 2013) and reaches maximum abundance in three quite disparate habitats; biotic lawns, streambanks and wet mires. It is considered here to be, with *P. annua*, a Biotic graminoid.

Other species included in my study were also not considered by Smith and Steenkamp (2001). The Pteridophyte guild in Smith and Steenkamp's classification comprised only one species, *Blechnum penna-marina*, which dominates large areas on the island. Four other vascular cryptogams (seedless vascular plants)were considered in my study; none of them are dominant, or even important, in the habitats they occur in and all have a very different ecology to *B. penna-marina*. *Polystichum marionense* is found in shallow caves and rock overhangs, especially on streambanks, and *Grammitis poeppigeana* occurs in rock crevices. For both species, there is not enough information (on relative cover, chemical composition and moisture content of the substrate) to determine their positions in the ordination spaces and hence what plant guilds they represent. Almost certainly they do not belong to the same guild, but simply for convenience they are both considered here as Rock substrate ferns. Similarly, *Lycopodium magellanicum* (restricted to mires) and *L. saururus* (restricted mainly to fellfields) will certainly not belong to the same guild. There might be a case for including *L. magellanicum* with *B. penna-marina*, in the Pteridophyte guild, on the basis that the mire community (at the association level in the syntaxonomic hierarchy formulated by Gremmen 1981) in which *L. magellanicum* is most frequent is also the mire community in which *B. penna-marina* is most common. There is not enough data to test this, so, again simply for convenience, the two *Lycopodium* species are placed in the same guild, Club moss.

Several of the bryophytes in my study were not included in the Smith and Steenkamp (2001) study. Most are characteristic mire species and thus in the Mire bryophyte guild. *Cryptochila grandiflora* is considered here to be a Drainage line bryophyte. *Marchantia berteroana* differs from all other

hepatics in that it occurs on heavily trampled and manured peats. It is thus considered as a Biotic bryophyte.

Two approaches were taken to assess the patterns of similarities/differences in nutrient concentrations between plant species, between plant guilds, between taxonomic groups or between characteristic species of the various habitats.

6.2. Univariate approach

In Table 6.1 the species are listed in descending order of their living leaf nutrient concentrations. For each element they are divided into five groups, based on their mean concentrations found in this study: very high, high, moderate, low and very low concentration. The groupings are primarily based box-plots of mean concentrations and their 95% confidence limits, assisted by analysis of variance and Tukeys Honest Significant Difference testing. However, since the HSD tests resulted in many homogenous groups that overlapped considerably in concentration values, the upper and lower limits of the groups in Table 6.1 were mostly determined arbitrarily. The two species sampled only once (*Cerastium fontanum* and *Colobanthus kerguelensis*) were not considered in this analysis.

The ordering of the species is very similar whether based on N or P concentration. The very high and high groups for both elements contain the same species and comprised dicots, monocots, a pteridophyte and even a bryophyte. Of the plant guilds (*sensu* Smith and Steenkamp 2001 and the additional ones established here), mat dicots occur only in the very high or high N/P groups. The other members of the very high and high N and P groups are: a mire bryophyte, a pteridophyte, a tussock graminoid, the two Biotic lawn graminoids, a cushion dicot, a rosette dicot and a deciduous shrub. The other end of the N or P range of values (the low and very low concentration groups) is occupied by bryophytes (the low P group also contains a pteridophyte), comprising representatives of three bryophyte guilds. Species with moderate N and P concentrations comprise six different plant guilds.

The species groupings on K concentration largely resembles the N and P groupings – species in the very high and high K groups are mostly in the very high or high N/P groups and low and very low K group species are mostly in the low or very low N/P groups. This not surprising since it has been shown that although animal manuring significantly enhances soil N and P, but not K, concentration, the greater plant vitality caused by the N and P fertilization

effect includes enhanced K uptake by the plants (Smith 1976a, 1978a). Particular plant guilds are not restricted to just one K concentration group but, like for the N and P groupings, mat dicots are in the high or very high K groups and the very low and low K groups comprise only bryophytes, with the exception of the erect dicot *Crassula moschata*.

The three mat dicots are also in the very high Na group. Two of them, *Callitriche antarctica* and *Montia fontana* are characteristic coastal zone species but the other, *Ranunculus biternatus*, while common on the coast also occurs further inland. The remaining two species in the very high Na concentration group, *C. moschata* and *Cotula plumosa*, are both restricted to the coastal zone. The high Na group contains two characteristic coastal zone species, the grass *Poa annua* and the liverwort *Marchantia berteroana*. However, it also contains three species (a cushion dicot, a mire graminoid and a club moss) that are more characteristic of non-saline inland sites. The very low Na concentration group comprises only bryophytes. Overall then, the grouping on Na concentration shows some resemblance, but to a lesser extent than does the grouping on K concentration, to the N and P groupings. Again, this is not surprising, since saltspray and manuring are both most intense near the coast.

Grouping of the species on Ca or Mg concentration results in quite different patterns to the groupings on N and P, and the various guilds are distributed across the Ca and Mg groups to a greater extent than they are across the N and P groups. The most striking difference is that while bryophytes fall mainly in the moderate to very low N and P groups, they are well represented in all the Ca and Mg concentration groups; even (with several dicot guilds) the very high and high ones. Dicots are absent from the low and very low Ca and Mg groups, which contain only monocots (mainly mire graminoids), club mosses and bryophytes (mostly mire bryophytes).

Table 6.1 also lists the community complex or complexes each species predominantly occurs in, extracted from Table 32 in Gremmen (1981). Gremmen listed six complexes and two have been added here. Mire drainage lines, which Gremmen considered as part of the mire complex, are considered here to belong to a mire drainage line complex. The rock substrate complex was constructed to incorporate *Polystichum marionense* and *Grammitis poeppigeana*.

Unsurprisingly, species in the very high and high N and P groups were those characteristic of the biotic complex. The association between K and complex is not as strong but the biotic complex species are in the middle to upper part of the range of K concentrations. Vascular

species characteristic of the saltspray complex are in the very high Na group but, since most animal manured communities occur near the coast, biotic complex species also tend to be in the mid to upper range of Na concentrations. *Clasmatocolea vermicularis* is characteristic of the saltspray and biotic complexes and has the highest Na concentration of all the bryophytes studied, *except Marchantia berteroana* (also a coastal species but restricted to manured sites).

The very low and low N, P, K and Na concentration groups comprise species characteristic of mire, mire drainage line and fellfield, complexes, although certain mire species are also found in the moderate and even the high concentration groups.

Mire drainage line species occur in the high or very high Ca concentration groups, whereas mire species are almost exclusively in the moderate or low Ca concentration groups. This accords with the finding that drainage lines in mire areas are more minerotrophic than the surrounding mire (Smith et al. 2001). Character species of the other complexes are scattered throughout the Ca concentration groups.

The arrangement of complex character species on Mg concentration shows little pattern. In some respects, the grouping resembles the groupings on N, P and K, excepting that like with Ca, mire drainage line species are in the high Mg concentration group.

6.3. Multivariate approach

The groupings described above are largely subjective, based on separate orderings of species-mean concentration values for each of the nutrients, with somewhat arbitrarily set upper and lower limits for the categories. In reality, for each of the nutrients, the species means formed a continuum across the concentration range. ANOVA and Tukey's HSD testing mostly showed that the only significant difference was between species with very low and those with very high concentrations. However, the results are revealing. They suggest that there are differences between species that are definitely related to major taxonomic group and, but much less closely, to some of the plant guilds of Smith and Steenkamp (2001) or to community complex. Henceforth, the terms habitat and community complex will be used interchangeably.

Multivariate approaches were used to see if there were patterns in the nutrient concentration data that could not be found by analyzing each variable separately. The first two axes from a

Principal Components Analysis (PCA) accounted for 73% of the total variance in the concentration data (Table 6.2). N, P, K and Na were significantly correlated with PC1 whereas Ca and Mg were significantly correlated with PC2. PC1 is thus interpreted as a gradient of plants with high leaf N, P, K and Na concentrations (mostly these will be from manured, coastal peats) to plants with low N, P, K and Na concentrations (mostly from more mineral soils further inland). PC2 is interpreted as a gradient of plants with high leaf Ca and Mg concentrations (mostly on mineral soils) to plants with low concentrations (mostly on peats).

Further principal components did not add significantly to the explained variance in the data set (data not shown). Each one tended to identify particular anomalous combinations of nutrient concentrations, in all instances associated with only one species. For example, PC3 distinguished the (unusual) very high K/very high Ca concentration combination in *Azorella selago*.

Fig. 6.1 shows a PC biplot with the positions of all the leaf samples on the N, P, K, Na (termed here the NPKNa) gradient and the Ca, Mg (the CaMg) gradient. A hierarchical (Ward) clustering of the raw concentration data for the six elements was carried out and the clusters yielded at various linkage distances examined. Low linkage distances (<30) yielded many small clusters throughout which the species, guilds, major taxonomic groups and habitat types were incoherently grouped. Large linkage distances yielded fewer clusters (only three at a l.d. of 70) that contained a wide range of different species, guilds, and habitats; with only taxonomic group being grouped coherently. A linkage distance of 50 yielded five clusters with clear patterns for taxonomic group and habitat, and reasonably clear patterns for guild. Having accepted that five groups offered the best compromise regarding the resolution, clarity and interpretability of the clustering, the clustering on the raw data was repeated using non-hierarchical (K-Means) clustering and specifying five clusters. Non-hierarchical clustering maximises the ratio of between-cluster to within-cluster variance and produced an even clearer pattern across the five clusters, especially at the guild level. The results of the K-Means clustering are superimposed on the PC sample biplot (Fig. 6.1), with the samples distinguished according to what K-mean cluster they belonged to. The 0.5 alpha ellipse (a confidence ellipse encompassing 50% of the samples) for each of the five groups is also shown.

From the positions of the ellipses on the NPKNa and CaMg gradients, the five nutrient concentration clusters are interpreted as: (1) average NPKNa/average CaMg cluster, (2) average NPKNa/low CaMg cluster, (3) average NPKNa/high CaMg cluster, (4) high NPKNa/average CaMg cluster, (5) lowNPKNa/low to average CaMg cluster.

Correspondence analysis (CA) was used to see how the five K-mean clusters relate to species, taxonomic group, guild or habitat. There are strong associations with taxonomic group (Fig. 6.2). The low NPKNa/low to average CaMg cluster (5) is separated from all the other groups by being on the positive side of axis 1 and negative side of axis 2 (in the lower right quadrant of the joint plot), as are bryophytes. Pteridophytes and dicots are in the lower left quadrant, as are the average NPKNa/average CaMg (1) and average NPKNa/high Ca (3) clusters. Monocots are associated with the average NPKNa/ low CaMg cluster (2), both being on the positive side of both axes. This pattern of association of the taxonomic groups with the nutrient concentration clusters accords well with the patterns of differences for the individual nutrients shown by the univariate analyses (Table 6.1) and also with the between-taxonomic group differences at other tundra and tundra-like sites in Table 5.2.

The joint plots showing the association between species and clusters (Fig. 6.3), or between plant guild and clusters (Fig. 6.4) both show a pronounced arch effect. This is commonly observed in ordinations obtained by linear scaling methods such as PCA and Correspondence Analysis and is due to the fact that the underlying relationship between dissimilarity (Euclidean distance in PCA, chi square distance in CA) and the particular gradient axis is nonlinear. The biplot (PCA) or joint plot (CA) is thus trying to display a potentially complex and non-linear relationship between dissimilarity and the distance along the gradient in a simple (linear, 2D) form. Particularly, the second axis is affected; it becomes a quadratic distortion of the first axis, rather than reflecting a linear gradient (Legendre and Legendre 1998). In the words of Podani and Miklós (2002), "The appearance of arches is a mathematical necessity".

Despite the pronounced arch effect, the joint plots do show some credible associations between the clusters and species or guilds. The sedge *U. compacta*, rush *J. scheuchzerioides* and the two grasses *Agrostis magellanica* and *P. cookii* are associated with the average NPKNa/low CaMg cluster (Fig. 6.3). The other two grass species, *Poa annua* and, but to a lesser extent, *A stolonifera* are associated with the high NPKNa, average CaMg cluster (4), indicative of manuring. Also associated with cluster 4 are some dicots (*R. biternatus, M.*

fontana, C. antarctica) and the hepatic M. *berteroana*. Other dicots (*A. selago*, *Acaena magellanica*, *C. plumosa*) and the pteridophyte *B. penna-marina* are associated with the average NPKNa/ high CaMg or the average NPKNa/average CaMg clusters (3 and 1 respectively). Of these species, all but *C plumosa* are characteristic of the more mineral soils of lowland slopes and fellfields not appreciably influenced by animal manuring. *C. plumosa* is characteristic of saltspray and/or manured areas and might be expected to associate more with cluster 4 than clusters 1 or 3. As might be expected from the pattern shown from the univariate analysis results, almost all of the bryophytes are in the same quadrant as the low NPKNa/low to average CaMg cluster. The position of the *C. moschata*, the most typical salt spray vascular species on the island in this low nutrient quadrant is surprising since it has very high Ca and high Mg concentrations; possibly it is due to the species showing the unusual combination of low K, but very high Na, concentrations (Table 6.1).

Most of the associations between the plant guilds and the nutrient concentration clusters (fig. 6.4) seem plausible, or at least can be interpreted from what is known of their ecology. Mire graminoids and tussock graminoids associate with the average NPKNa/low CaMg cluster (2). Club moss is in the same quadrant but much less associated with cluster 2. The club moss guild comprises two species associated with different clusters. *Lycopodium magellanicum* is associated with cluster 2; and *L. saururus* is associated with cluster 5 (Fig 6.3), which accounts for its position in the guild joint plot (Fig 6.4). Four of the five bryophyte guilds are associated with cluster 5, as is erect dicot. This guild comprises only *C. moschata* and a possible reason for its anomalous position in the joint plot is given in the previous paragraph. The guilds associated with manuring (mat dicot, biotic lawn, biotic bryophyte) are associated with the highNPKCa/low CaMg cluster (4). The cushion dicot, deciduous shrub and pteridophyte guilds are in the same quadrant as the average NPKNa, high CaMg cluster. Rosette dicot comprises only *C. plumosa* and its anomalous association with cluster 3 rather than the biotic cluster 4 was remarked on above.

Both axes of the habitat cluster joint plot (Fig. 6.5) clearly separate fellfield and cluster 1 from other habitats/clusters, suggesting that fellfield comprises species with average NPKNa/average CaMg concentrations. This is surprising since fellfields have the most mineral soils and so the species would be expected to have high CaMg concentrations. In Fig. 6.4, mire graminoid was associated with cluster 2 and mire bryophytes with cluster 5. The mire habitat is associated with both clusters (Fig. 6.5), more closely to cluster 5 because more mire bryophytes than mire graminoid species are represented in the data set. Thus the mire

habitat may be regarded as possessing species with low to average NPKNa/low to average CaMg. The mire drainage line habitat is associated with cluster 5 – it comprises species with higher CaMg concentrations than the does the mire habitat. Biotic habitats are associated with the high NPKNa/average CaMg cluster (4) and the slope drainage line and lowland slope habitats with the average NPKNa/high CaMg cluster (3).

There might be an element of circular argument when comparing the guild-cluster joint plot with the habitat-cluster one. Smith and Steenkamp (2001) found that certain species could be grouped together (in guilds) because they affected the ordinations used to construct the habitat classification similarly. In some cases the guilds were given the name of the habitat they were characteristic of (e.g. mire bryophyte, mire graminoid) simply because they grouped together in the habitat classification ordinations. However those ordinations did not consider plant chemical composition and comparison of Figs 6.4 with Fig 6.5 show that it is bryophyte versus graminoid, rather than the mire habitat that determines what clusters the two guilds are associated with. In other instances, the habitat factor is more important, e.g. manuring greatly influences plant chemical composition, so species of manured habitats (biotic bryophytes, mat dicots, biotic graminoids group more closely to each other than they do to the non-biotic members of the respective taxonomic groups.

In summary, the results presented in this chapter suggest that the Smith and Steenkamp(2001) plant guilds do not reflect the inter-species nutrient concentration similarities/differences as closely as does major taxonomic group or habitat. The few instances where the guilds are associated with a particular nutrient type (cluster) are due to the effect of taxonomic group (e.g. all bryophyte guilds except Biotic bryophytes, most dicot guilds, most monocot guilds) or habitat (most especially, the distinction between manured and unmanured habitats).

Chapter 7

Conclusions and a suggested approach for a whole island model of nutrient standing stocks.

One main aim of my study was to establish whether plant nutrient concentrations varied spatially on Marion Island. I showed that they vary with distance from the sea and altitude in almost an identical pattern, which is unsurprising since the two spatial variables are highly correlated. The concentrations of N, P and Na in living leaves, dead leaves, stems and roots decrease going inland, due to a decline in the influence of animal manuring and of sea spray. Ca concentration increases going inland, away from the organic peats characteristic of the lowland regions toward the mineral rawmark inland soils. Declining sea spray and increasing soil minerality going inland both affect plant Mg concentration; the net effect is a slight decrease in Mg concentration away from the coast. K concentration in living leaves and roots did not change going inland; dead leaf and stem K concentrations showed a weak decline.

Information on nutrient concentrations in all plant organs from all four sides of the island was available for only a few species; for dead leaves, stems and roots there was information only for the east and west sides. Although in many instances the island side effect was not significant for individual species, the pattern of between-side differences is quite clear. Living leaf N, P and Mg concentrations are higher in west side than east side plants, with south and north side plants having intermediate concentrations. Leaf K concentrations are highest on the north and lowest on the west side, with east and south side concentrations being intermediate. Leaf Ca concentrations are highest on the south side and lowest on the north side, with east and west side Ca concentrations being intermediate.

Only for the west and east sides of the island were there sufficient dead leaf, stem and root samples to enable a between-side comparison. The dead leaf west-east differences in nutrient concentration are the same as for living leaves. Stem and root west-east concentration differences are also similar to those for living leaves, except for P and Mg concentrations, which were the same on the two sides. Leaf Na concentration declines more sharply with distance inland on the island's western and southern sides than on its eastern and northern sides, so that closer than 450 m from the shore, leaf Na concentration is higher on the west

and south than the east or north sides but further inland the difference lessens. All organs showed this steeper decline in Na concentration on the west than on the east side of the island.

Bryophytes show somewhat different patterns of between-side nutrient concentration differences to the vascular plants. South side (not west) bryophytes have highest N and P concentrations. Like for vascular plant leaves, east side bryophytes have the lowest N and P concentrations. Also like with vascular plants, bryophyte K concentration is highest on the north side and lowest on the west side, although south side concentrations are nearly as high as the north side ones. Unlike the vascular plant leaves, bryophyte Mg concentration is highest on the south (not west) side and lowest on the north (not east) side, with east and west side concentrations being intermediate. South side bryophytes also have highest Ca and Na concentrations, similar to the vascular plant pattern.

The second main aim of my study was to see if the island's plant species can be grouped on the basis of similarities/differences in nutrient concentrations. The between-species differences in nutrient concentrations can largely be explained by what taxonomic group they belong to – bryophyte, pteridophyte, monocot or dicot. Habitat factors, particularly the intensity of manuring, are also a determinant of nutrient concentration.

Ordination and clustering analyses of leaf nutrient concentrations suggested five nutrient type clusters, differing in the amount (low, moderate or high) of N, P, K and Na, and the amount of Ca and Mg. The clusters are: (1) average NPKNa/average CaMg cluster, (2) average NPKNa/low CaMg cluster, (3) average NPKNa/high CaMg cluster, (4) high NPKNa/average CaMg cluster, (5) low NPKNa/ low to average CaMg cluster.

Clusters 1,2,3 and 5 correspond well with taxonomic group; 5 with bryophytes, 3 with pteridophytes, 2 with monocots and 1 with dicots. The clusters also correspond quite clearly with habitat (plant community complexes) ; 1 with fellfields, 3 with lowland slopes and slope drainage lines, 5 with mires and mire drainage lines and 4 with animal influenced (manured) habitats. The clusters associate less closely with the plant guilds compiled previously for the island, which have been suggested might prove useful for modeling nutrient standing stocks on a whole island basis. Where a particular guild is associated with a particular cluster, it can mostly be ascribed to either taxonomic group or habitat, i.e. the guild represents plants from one taxonomic group or from a particular habitat.

From these findings it is suggested that in order to reduce the complexity and arduousness of constructing whole island plant nutrient standing stock budgets, the species should be grouped first according to their taxonomy – as bryophytes, dicots, monocots and pteridophytes (the ferns proper). (However, the two club mosses cannot be considered as belonging to the same group). Where necessary (e.g. a particular species is common in several, nutrient-wise very different habitats), subgroups of these taxonomic groups can be constructed on the basis of habitat. Mostly, this will be necessary to distinguish plants from manured habitats from plants of the same species from unmanured ones. However, it might also be necessary to distinguish mire habitat plants from slope habitat plants (e.g., the club mosses), and, at least for the bryophytes, fellfield bryophytes from mire bryophytes.

This suggestion can be tested using the plant chemistry data for the eight communities for which nutrient standing stocks are accurately known. The community level standing stocks are based on species-level nutrient concentration data. Taxonomic group-level concentrations can be calculated from the appendix tables in this thesis and the nutrient standing stocks recalculated. The concentrations can then be calculated at the level of habitat subgroup within the taxonomic group to yield another estimate of nutrient standing stocks. Comparing the three estimates will show how viable the various levels of grouping are.

To incorporate the effect of distance from sea, altitude and side of island into the estimate of nutrient standing stocks, it is suggested the similarities/differences in slopes between the groups/subgroups, and between sides of the island within groups/subgroups, be tested to see if a single regression function can be applied to a particular group/subgroup on all four sides of the island, or if the sides must be modeled separately. This testing cannot be done with the data presented here since there were insufficient samples taken of all the members of a group/subgroup.

This testing falls outside the scope of my study and will be addressed in an honours project in 2014.

8 References

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

Allen, S.E. (1974) Chemical Analysis of Ecological Materials. Blackwell, Oxford: 565.

Babb, T.A., Whitfield, D.W.A. (1977) Mineral nutrient cycling and limitations of plant growth in the Truelove Lowland ecosystem. In: Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. (ed.) Bliss, L.C. University Alberta Press, Edmonton, Canada: 589 - 606.

Bates, J.W. (2000) Mineral nutrition, substratum ecology and pollution. In: Bryophyte Ecology. (eds) Shaw, A.J. and Goffinet, B. Cambridge University Press, Cambridge, United Kingdom: 248 -311.

Boelhouwers, J., Holness, S., Sumner, P. (2003) The Maritime Subantarctic: a distinct periglacial environment. *Geomorphology.* **52**: 39–55.

Boelhouwers, J.C., Meiklejohn, K.I., Holness, S.D., Hedding, D.W. (2008) Geology, Geomorphology and Climate Change. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.) Chown, S.L and Froneman, P.W. African SunMedia, Stellenbosch: 65 - 96.

Boyd, C.E. (1978) Chemical composition of wetland plants. In: Fresh Water Wetlands. (eds.) Good, R.E., Whigham, D.F. and Simpson, R.L. Academic Press, New York, San Francisco, London: 155-167.

Bunnell, F. L. (1981) Ecosystem Synthesis - a "fairytale". In: Tundra Ecosystems: A Comparative Analysis. (eds.) Bliss, L.C., Heal, O.W. and Moor, J.J. Cambridge University Press, Cambridge: 637-646.

Chapin , F.S. III, Van Cleeve, K., Trietszen, L.L. (1975) Seasonal dynamics of tundra vegetation at Barrow, Alaska. *Arctic Alp Research.* **7**: 209 -226.

Chepurko, N.L. (1972) The biological productivity and the cycle of nitrogen and ash elements in the dwarfshrub tundra ecosystems of the Khibini Mountains (Kola Peninsula). In: Proc. Fourth International Meeting on the Biological Productivity of Tundra, Leningrad, OCT 1971. (eds) Wielgolaski, F.E. and Rosswall, T. Tundra Biome Steering Committee, Stockholm, Sweden: 236 - 247.

Collins, N.J., Baker, J.H., Tillbrook, P.J. A. (1975) Signy Island, Maritime Antarctic. In: Structure and Function of Tundra Ecosystems. (eds.) Rosswall, S T. and Heal, O.W. *Ecology* (Stockholm) **20**: 345 -374.

Conradie, E.C., Smith, V.R. (2012) Spatial Variation in Soil Chemistry on a sub-Antarctic Island. *Open Journal of Soil Science* **2**: 111-115.

Díaz, S.; Hodgson, J.G.; Thompson, K.; et al. (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15**: 295-304.

Dowding, P., Chapin FS III, Wielgolaski, FE, Kilfeather, P. (1981) Nutrients in Tundra Ecosystems. In: Tundra Ecosystems: A Comparative Analysis. (eds) Bliss, L.C., Heal, O.W. and Moor, J.J. Cambridge University Press, Cambridge: 647-683.

Duckworth, J.C., Kent, M., Ramsay, P.M. (2000) Plant functional types: an alternative to taxonomic plant community description in biogeography. *Progress in Physical geography* **24**: 515-542.

Gremmen, N.J.M. (1981) The Vegetation of the sub-Antarctic Islands Marion and Prince Edward. Junk, W. The Hague.

Gremmen, N.J.M. (2008) Appendix II: Hepatics of the Prince Edward Islands. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.) Chown, S.L. and Froneman, P.W. African SunMedia, Stellenbosch: 181-214.

Gremmen, N.J.M, Smith V.R. (2008a) Appendix IV: Vascular Plants of the Prince Edward Islands. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.) Chown, S.L and Froneman, P.W. African SunMedia, Stellenbosch: 390-392.

Gremmen, N.J.M, Smith V.R. (2008b) Terrestrial vegetation and dynamics. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.) Chown, S.L and Froneman, P.W. African SunMedia, Stellenbosch: 215 - 244.

Grobbelaar, J.U. (1974). A contribution to the limnology of the sub-Antarctic island Marion. Unpublished D. Sc. Thesis. Univ. of the Free State, South Africa.

Hall, K. (1978). Evidence for Quaternary glaciation of Marion Island (sub-Antarctic) and Some Implications. In: Van Zinderen-Bakker, E.M. (ed.) Antarctic Glacial History and World Palaeoenvironments. Balkema, Rotterdam: 137–147.

Harrison, S.P., Prentice, I.C., Barboni, D., et al. (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. *Journal of Vegetation Science* **21**: 300–317.

Headland, R. (1984) The Island of South Georgia. Cambridge: Cambridge University Press.

Heal, O.W. (1981) Introduction. In: Tundra Ecosystems: A Comparative Analysis. (eds.) Bliss, L.C., Heal, O.W. and Moore, J.J. Cambridge. Cambridge University Press: xxvii–xxxvii.

Heal, O.W., Smith R.A.H. (1978) The Moorhouse Programme - Introduction and site description. In: Prodution Ecology of British Moors and Montane Grasslands. (eds.) Heal, O.W. and Perkins, D.F. Spinger-Verlag Berlin, Heidelberg, New York: 3-16.

Huntley, B.J. (1971) Vegetation. In: Marion and Prince Edward Islands. (eds.) Van Zinderen-Bakker, E.M., Winterbottom, J.M. and Dyer, R.A. A.A. Balkema, Cape Town: 98-160.

Jenkin, J.F. (1972) Studies on plant growth in a sub-Antarctic environment. Unpublished Ph.D. thesis, University of Melbourne, Australia.

Kilfeather, P. (1973) Nutrient circulation in relation to primary productivity of western blanket bog in Ireland. PhD thesis, University of Ireland, 178 pp.

Lavorel, S., Diaz, S., Cornelissen, J.H.C., et al. (2007) Plant functional types: are we getting any closer to the holy grail? In: Terrestrial Ecosystems in a Changing World. (eds) Canadell, J.G., Pataki, D., Pitelka, L. The IGBP Series, Springer-Verlag, Berlin Heidelberg: 149-165.

Lawson, G.J. (1985) Decomposition and nutrient cycling in Rostcovia Magellanica from two contrasting bogs on South Georgia. In: Antarctic Nutrient Cycles and Food Webs. (eds.) Siegfried, W. R., Condy, P.R. and Laws, R.M. Springer-Verlag. Heidelberg: 211- 220.

Legendre, P., Legendre, L. (1998) Numerical Ecology. Second edition. Elsevier, Amsterdam, The Netherlands.

Le Roux, P.C., McGeoch, M.A. (2008) Changes in climate extremes, variability and signature on sub-Antarctic Marion Island. *Climatic Change* **86**: Issue 3-4, February 2008, 309-329.

Le Roux, P.C., Ramaswiela, T., Kalwij, J.M., Shaw, J.D., Ryan, P.G., Treasure, A.M., McClelland, G.T.W., McGeoch, M.A., Chown, S.L. (2013) Human activities, propagule pressure and alien plants in the sub-Antarctic: Tests of generalities and evidence in support of management. *Biological Conservation* **161**: 18-27.

Lewis-Smith, R.I., Walton, D.W.H. (1975) South Georgia, Subantarctic. In: T. Rosswall and O.W. Heal (editors). *Structure and function of tundra ecosystems* Swedish Natural Science Research Council Stockholm 399–423.

Lindeboom, H.J. (1984) The nitrogen pathway in a penguin rookery. *Ecology* **65**: 269–277.

Loach, K (1968) Relations between soil nutrients and vegetation in wet heaths II: nutrient uptake by the major species in the field and in controlled conditions *Journal of Ecology* **56**: 117-127.

Lubbe, A., Smith,V.R. (2012) Field Soil Respiration Rate on a sub-Antarctic Island: Its Relation to Site Characteristics and Response to Added C, N and P. *Open Journal of Soil Science* **2**:187-195.

Malmer, N. (1988): Patterns in the growth and the accumulation of inorganic constituents in the Sphagnum-cover on ombrotrophic bogs in Scandinavia. *Oikos* **53**: 105-120.

McDougal, I., Verwoerd, W., Chevalier, L. (2001). K–Ar geochronology of Marion Island, Southern Ocean. *Geological Magazine* **138**: 1–17.

Muc, M. (1977) Ecology and primary production of sedge moss meadow communities, Truelove Lowland. In: Truelove Lowland Devin Island Canada: A High Arctic Ecosystem (ed.) Bliss, L. C. University of Alberta Press, Edmonton, Canada:157-184.

Ochyra, R. (2008) Appendix III: Mosses of the Prince Edward Islands. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.). Chown, S.L, Froneman, P.W. African SunMedia, Stellenbosch: 383-389.

Olsson, U. (2005) Confidence intervals for the mean of a log-normal distribution. *Journal of Statistics Education* Volume 13, Number 1. Published online at www.amstat.org/publications/jse/v13n1/olsson.html.

Øvstedal, D.O., Gremmen, N.J.M. (2008) Appendix V: Lichens of the Prince Edward Islands. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.).. Chown, S.L., Froneman, P.W. African SunMedia, Stellenbosch: 393-397.

Panagis, K. (1984). The influence of southern elephant seals *Mirounga leonina* (Linnaeus) on the coastal terrestrial ecology of Marion Island. Unpublished M.Sc Thesis. University of Pretoria, Pretoria, South Africa

Perkins, D.F, Jones V., Millar, R.O., Neep, P. (1978) Primary production, mineral nutrients and litter decomposition in grassland ecosystem In: Production Ecology of British Moors and Montane Grasslands. (eds) Heal, O.W. and Perkins, D.F. Spinger- Verlag Berlin, Heidelberg, New York: 304- 331.

Pilbeam, D.J, Morley, P.S.(2007) Calcium. In: Handbook of Plant Nutrition. (eds.) Barker, A.V. and Pilbeam, D.J. CRC Press: 121–144.

Podani J., Miklós, I. (2002) Resemblance coefficients and horseshoe effect in principal coordinates analysis. *Ecology* **83**: 3331–3343.

Pratt, R.M., Lewis Smith, R.I. (1982) Seasonal trends in chemical composition of Reindeer forage plants on South Georgia. *Polar Biology* **1**: 13-31.

Prinsloo, L. C., Colomban, P., Brink, J. D., Meiklejohn, K. I. (2011) A Raman Spectroscopic Study of the Igneous Rocks on Marion Island: A Possible Terrestrial Analogue for the Geology on Mars. *Journal of Raman Spectroscopy* **42**: 626-632.

Rodin, L.E., Bazilevich, N.I. (1967) Production and Mineral Cycling in Terrestrial Vegetation (English translation by Fogg GE). Oliver and Boyd, Edinburgh London.

Rosswall, T., Heal, O.W. (editors). (1975) Structure and function of tundra ecosystems. Stockholm: Swedish Natural Science Research Council (*Ecological Bulletins* **20**).

Russell, E. W. *(*1961*).* Soil Conditions and Plant Growth. 9th edition. Longmans, London .

Russell, S. (1987) Water relations and Nutrient status of bryophyte communities at Marion Island (sub Antarctic). *Symposia Biologica Hungarica* **35**: 39-57.

Schulze, B.R. (1971) The climate of Marion Island. In: Marion and Prince Edward Islands. (eds.) Van Zinderen Bakker, E.M., Winterbottom, J.M. and Dyer, R.A. A.A. Balkema, Cape Town: 16-31.

Smith, V.R.: (1976a) The effect of burrowing species of *Procellariidae* on the nutrient status of inland tussock grasslands on Marion Island. *Journal of South African Botany* **42**: 265-272.

Smith, V.R. (1976b). Standing crop and nutrient status of Marion Island (sub-Antarctic) vegetation. *Journal of South African Botany* **42**: 231-263.

Smith, V.R. (1977) The chemical composition of Marion Island soils, plants and vegetation. *Journal of Antarctic Research* **7**: 28-39.

Smith, V.R. (1978a). Animal-plant-soil nutrient relationships on Marion Island (sub-Antarctic). *Oecologia* **32**: 239- 253.

Smith V.R. (1978b) Plant ecology of Marion Island: a review. *South African Journal of Antarctic Research* **8**: 2130.

Smith, V.R. (1985) Heterotrophic acetylene reduction in soils at Marion Island. In: Siegfied, W.R., P.R. Condy, and R.M. Laws (editors). *Antarctic nutrient cycles and food webs*. Heidelberg: Springer: 186–191.

Smith, V.R. (1987a) Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 1. Standing crop and primary production of mire-grasslands. *Polar Biology* **7**: 57-75.

Smith, V.R. (1987b) Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 2. Standing crop and primary production of fjaeldmark and fernbrakes. *Polar Biology* **7**: 125-144.

Smith, V.R. (1987c) Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 3. Standing stocks, uptake and loss of nutrients in mire-grasslands. *Polar Biology* **8**: 135-153.

Smith V.R (1987d) Seasonal changes in plant and soil chemical composition at Marion Island (sub Antarctic): I Mire-grasslands. *South African Journal of Antarctic Research* **17**: 117-132.

Smith V.R (1987e) Seasonal changes in plant and soil chemical composition at Marion Island (sub Antarctic): II Fjaeldmark and Fernbrakes. *South African Journal of Antarctic Research* **17**: 133-154.

Smith, V.R. (1987f). Chemical composition of precipitation at Marion Island (sub-Antarctic). *Atmospheric Environment* **21**: 1159–1165.

Smith, V.R. (1988a). Production and nutrient dynamics of plant communities on a sub-Antarctic Island. 4. Standing stocks, uptake and loss of nutrients in fjaeldmark and fernbrakes *Polar Biology* **8**: 191-211.

Smith, V.R. (1988b) Production and nutrient dynamics of plant communities on a sub-Antarctic sub-AntarcticIsland. 5. Nutrient budgets and turnover times for mire-grasslands, fjaeldmark and fernbrakes. *Polar Biology* **8**: 255-269.

Smith, V.R. (2003) Soil respiration and its determinants on a sub-Antarctic sub-Antarcticisland. *Soil Biology and Biochemistry* **35**: 77–91.

Smith, V.R. (2005) Moisture, carbon and inorganic nutrient controls of soil respiration at a sub-Antarctic island. *Soil Biology and Biochemistry* **37**: 81–91.

Smith, V.R. (2008a) Terrestrial and freshwater primary production and nutrient cycling. In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.). S.L. Chown and P.W. Froneman, African SunMedia, Stellenbosch: 181-214.

Smith, V.R. (2008b) Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. *Polar Record* **44**: 211-226.

Smith, V.R. (2008c) Whole-island estimate of production and nutrient cycling on a sub-Antarctic island. Are plant guilds the way to go? In: Frontiers of Vegetation Science – An Evolutionary Angle. *(*eds.) Mucina, L., Kalwij, J, Smith, V.R., et al. Keith Phillips Images, Somerset West: 176 – 177.

Smith, V.R., Froneman, P.W. (2008) Nutrient dynamics in the vicinity of the Prince Edward Islands. . In: The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. (eds.). S.L. Chown and P.W. Froneman, African SunMedia, Stellenbosch: 165 - 179

Smith, V.R., Mucina, L. (2006) Vegetation of sub Antarctic Marion and Prince Edward Islands . In: The Vegetation of South Africa, Lesotho and Swaziland (eds.) Mucina, L. and Rutherford, M.C.. SANBI, Pretoria: 698-723.

Smith, V.R., Russell, S. (1982) Acetylene reduction by bryophyte–cyanobacteria associations on a sub- Antarctic Island. *Polar Biology* **1**: 153–157.

Smith, V.R., Steenkamp, M. (2001) Classification of the terrestrial habitats on sub-Antarctic Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science* **12**: 181-198.

Smith, V.R., Steenkamp, M. (1990) Climatic change and its ecological implications at a sub-Antarctic island. *Oecologia* **85**: 14–24.

Smith V.R., Steenkamp M., Gremmen, N.J.M. (2001) Terrestrial habitats on sub-Antarctic Marion Island: their vegetation, edaphic attributes, distribution and response to climate change. *South African Journal of Botany* **67**: 641–654.

Van Zinderen Bakker, E.M. Sr. (1973) The second South African biological expedition to Marion Island 1971–72. *South African Journal of Antarctic Research* **13**: 60–63.

Vassiljevskaya, V.D., Ivanov, V.V., Bogatyrev, L.G., Pospelova, E.B., Schalaeva, N.M., Grushina, L.A. (1975) Abapa, USSR. In: Structure and function of tundra ecosystems (eds) Rosswall, T., Heal, O.W. *Ecology* **20**: 141-158.

Verwoerd, W.J. (1971) The glaciation(s) of Marion Island (sub-Antarctic). In: Palaeoecology of Africa and the Surrounding Islands and Antarctica. (ed.) Van Zinderen Bakker, E.M. A. A. Balkema, Cape Town: 161–178.

Vitt, D.H., Pakarinen, P. (1977) The bryophyte vegetation, production and organic compounds of Truelove Lowland. In:Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem. (ed.) Bliss, L.C. University of Alberta Press, Edmonton, Canada: 225-244.

Walton, D.W.H., Lewis Smith, R.I. (1980) Chemical composition of South Georgian vegetation. *British Antarctic Survey Bulletin* **49**: 117–135.

Wielgolaski, F.E., Kjelvik, S., Kallio, P. (1975) Mineral content of tundra and forest tundra plants in Fennoscandia. In: Fennoscandian Tundra Ecosystems. Part 1. Plants and Micro-organisms. (eds.) Wielgolaski, FE. Springer, Berlin, Heidelberg, New York: 316-332.

Zhou, X-H., Gao, S. (1997) Confidence intervals for the log-normal mean. *Statistics in Medicine* **16**: 783-790.

Appendix A. Nutrient concentrations in vascular plant living leaves and bryophyte shoots.

	Nutrient	Mean ± std dev. (min. – max.)
Monocotyledonous species		
Agrostis magellanica	N	1.99 ± 0.470 (1.40 - 4.19)
	P	0.19 ± 0.074 (0.07 - 0.44)
N=84	K	1.59 ± 0.401 (0.71 - 2.46)
	Ca	0.11 ± 0.035 (0.04 - 0.20)
	Mg	0.21 ± 0.063 (0.06 - 0.37)
	Na	0.30 ± 0.161 (0.06 - 0.91)
Agrostis stolonifera	N	2.83 ± 1.417 (1.03 - 4.43)
	P	0.35 ± 0.132 (0.16 - 0.46)
N=4	K	1.19 ± 0.463 (0.66 - 1.79)
	Ca	0.13 ± 0.039 (0.09 - 0.18)
	Mg	0.23 ± 0.095 (0.09 - 0.31)
	Na	0.44 ± 0.290 (0.13 - 0.70)
Juncus scheuchzerioides	N	1.95 ± 0.300 (1.53 - 2.59)
	P	0.17 ± 0.049 (0.11 - 0.27)
N=15	K	1.24 ± 0.241 (0.90 - 1.75)
	Ca	0.14 ± 0.031 (0.09 - 0.18)
	Mg	0.26 ± 0.033 (0.20 - 0.30)
	Na	0.55 ± 0.269 (0.24 - 1.23)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Uncinia compacta	N	1.62 ± 0.427 (1.03 - 2.61)
	P	0.16 ± 0.128 (0.09 - 0.64)
N=17	K	1.51 ± 0.190 (1.27 - 1.92)
	Ca	0.11 ± 0.025 (0.07 - 0.16)
	Mg	0.17 ± 0.044 (0.11 - 0.23)
	Na	0.11 ± 0.021 (0.08 - 0.15)
Poa cookii	N	2.06 ± 0.457 (1.22 - 3.35)
N=28	P	0.21 ± 0.066 (0.08 - 0.37)
	K	1.12 ± 0.239 (0.73 - 1.70)
	Ca	0.10 ± 0.026 (0.04 - 0.17)
	Mg	0.12 ± 0.054 (0.05 - 0.22)
	Na	0.20 ± 0.149 (0.03 - 0.63)
Poa annua	N	5.23 ± 1.428 (4.22 - 6.24)
N=2	P	0.46 ± 0.078 (0.40 - 0.51)
	K	2.46 ± 1.775 (1.20 - 3.71)
	Ca	0.16 ± 0.028 (0.14 - 0.18)
	Mg	0.22 ± 0.035 (0.19 - 0.24)
	Na	0.75 ± 0.516 (0.39 - 1.12)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Dicotyledonous species		
Acaena magellanica	N	2.47 ± 0.453 (1.57 - 3.55)
	P	0.22 ± 0.086 (0.12 - 0.47)
N=67	K	1.42 ± 0.495 (0.58 - 3.01)
	Ca	1.21 ± 0.254 (0.63 - 1.88)
	Mg	0.63 ± 0.112 (0.45 - 0.92)
	Na	0.46 ± 0.203 (0.17 - 1.59)
Callitriche antarctica	N	3.21 ± 0.917 (1.88 - 4.64)
	P	0.58 ± 0.194 (0.35 - 1.03)
N=9	K	1.82 ± 0.613 (1.11 - 3.10)
	Ca	0.38 ± 0.065 (0.30 - 0.49)
	Mg	0.56 ± 0.118 (0.39 - 0.74)
	Na	1.27 ± 0.285 (0.84 - 1.60)
Azorella selago	N	1.67 ± 0.370 (1.02 - 3.54)
	P	0.18 ± 0.065 (0.10 - 0.42)
N=93	K	2.10 ± 0.710 (0.83 - 5.11)
	Ca	0.80 ± 0.211 (0.30 - 1.34)
	Mg	0.26 ± 0.072 (0.14 - 0.51)
	Na	0.64 ± 0.308 (0.19 - 2.07)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Cerastium fontanum	N	4.37
	P	0.68
N=1	K	2.44
	Ca	0.77
	Mg	0.86
	Na	1.03
Colobanthus kerguelensis	N	2.53
	P	0.23
N=1	K	2.44
	Ca	0.19
	Mg	0.21
	Na	0.51
Cotula plumosa	N	2.28 ± 0.627 (1.50 - 3.68)
	P	0.31 ± 0.061 (0.20 - 0.41)
N=24	K	1.21 ± 0.300 (0.65 - 2.00)
	Ca	0.44 ± 0.073 (0.32 - 0.65)
	Mg	0.40 ± 0.083 (0.24 - 0.56)
	Na	1.68 ± 0.377 (0.87 - 2.30)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Crassula moschata	N	1.22 ± 0.343 (0.86 - 2.01)
	P	0.16 ± 0.056 (0.10 - 0.30)
N=9	K	0.48 ± 0.266 (0.29 - 1.13)
	Ca	0.66 ± 0.093 (0.58 - 0.83)
	Mg	0.46 ± 0.070 (0.39 - 0.59)
	Na	1.08 ± 0.729 (0.61 - 1.92)
Ranunculus biternatus	N	2.68 ± 0.198 (2.49 - 3.01)
	P	0.29 ± 0.094 (0.20 - 0.44)
N=5	K	1.52 ± 0.291 (1.12 - 1.92)
	Ca	0.30 ± 0.069 (0.21 - 0.39)
	Mg	0.55 ± 0.105 (0.41 - 0.66)
	Na	1.01 ± 0.366 (0.52 - 1.38)
Montia fontana	N	3.72 ± 0.604 (2.79 - 4.83)
	P	0.61 ± 0.117 (0.36 - 0.79)
N=9	K	2.19 ± 0.799 (1.23 - 3.81)
	Ca	0.29 ± 0.059 (0.22 - 0.38)
	Mg	0.47 ± 0.059 (0.39 - 0.55)
	Na	1.13 ± 0.438 (0.33 - 1.53)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Pteridophytes		
Blechnum penna-marina	N	1.53 ± 0.234 (1.10 - 2.12)
	P	0.19 ± 0.071 (0.07 - 0.48)
N=108	K	1.23 ± 0.361 (0.47 - 2.09)
	Ca	0.59 ± 0.060 (0.44 - 0.75)
	Mg	0.83 ± 0.109 (0.61 - 1.11)
	Na	0.30 ± 0.126 (0.10 - 0.97)
Lycopodium magellanicum	N	1.51 ± 0.195 (1.15 - 1.79)
	P	0.14 ± 0.036 (0.10 - 0.19)
N=8	K	0.77 ± 0.228 (0.45 - 1.08)
	Ca	0.13 ± 0.051 (0.06 - 0.21)
	Mg	0.14 ± 0.073 (0.06 - 0.25)
	Na	0.44 ± 0.210 (0.16 - 0.67)
Lycopodium saururus	N	1.03 ± 0.089 (0.88 - 1.10)
	P	0.11 ± 0.020 (0.08 - 0.13)
N=5	K	0.76 ± 0.088 (0.68 - 0.87)
	Ca	0.08 ± 0.011 (0.06 - 0.09)
	Mg	0.17 ± 0.073 (0.08 - 0.26)
	Na	0.62 ± 0.183 (0.42 - 0.82)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Polystichum marionense	N	2.31 ± 0.157 (2.14 - 2.48)
	P	0.23 ± 0.008 (0.22 - 0.24)
N=4	K	2.30 ± 0.093 (2.21 - 2.43)
	Ca	0.17 ± 0.041 (0.14 - 0.23)
	Mg	0.34 ± 0.056 (0.28 - 0.41)
	Na	0.16 ± 0.075 (0.07 - 0.24)
Grammitis poeppigeana	N	1.31 ± 0.128 (1.17 - 1.48)
	P	0.09 ± 0.006 (0.08 - 0.09)
N=4	K	0.90 ± 0.056 (0.83 - 0.96)
	Ca	0.27 ± 0.283 (0.11 - 0.69)
	Mg	0.51 ± 0.169 (0.36 - 0.75)
	Na	0.49 ± 0.263 (0.27 - 0.87)
Bryophytes		
Andreaea acuminata	N	0.73 ± 0.299 (0.32 - 1.10)
	P	0.07 ± 0.020 (0.05 - 0.10)
N=6	K	0.05 ± 0.008 (0.04 - 0.06)
	Ca	0.07 ± 0.049 (0.02 - 0.15)
	Mg	0.27 ± 0.174 (0.15 - 0.58)
	Na	0.05 ± 0.047 (0.02 - 0.12)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Blepharidophyllum densifolium	N	0.68 ± 0.234 (0.39 - 1.34)
	P	0.03 ± 0.013 (0.01 - 0.06)
N=18	K	0.61 ± 0.259 (0.33 - 1.25)
	Ca	0.24 ± 0.081 (0.12 - 0.39)
	Mg	0.32 ± 0.053 (0.21 - 0.40)
	Na	0.14 ± 0.029 (0.10 - 0.21)
Brachythecium rutabulum	N	1.24 ± 0.387 (0.70 - 1.81)
	P	0.14 ± 0.058 (0.04 - 0.25)
N=15	K	0.58 ± 0.113 (0.44 - 0.80)
	Ca	0.38 ± 0.042 (0.30 - 0.46)
	Mg	0.35 ± 0.036 (0.28 - 0.41)
	Na	0.09 ± 0.035 (0.04 - 0.15)
Breutelia integrifolia	N	0.84 ± 0.341 (0.41 - 1.39)
	P	0.02 ± 0.010 (0.01 - 0.05)
N=25	K	0.12 ± 0.072 (0.00 - 0.30)
	Ca	0.54 ± 0.118 (0.34 - 0.90)
	Mg	0.45 ± 0.073 (0.37 - 0.68)
	Na	0.07 ± 0.041 (0.03 - 0.18)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Bryum laevigatum	N	0.94 ± 0.339 (0.58 - 1.37)
	P	0.06 ± 0.054 (0.02 - 0.15)
N=6	K	0.22 ± 0.105 (0.09 - 0.35)
	Ca	0.63 ± 0.134 (0.44 - 0.78)
	Mg	0.37 ± 0.094 (0.26 - 0.53)
	Na	0.10 ± 0.036 (0.04 - 0.13)
Campylopus purpureocaulis	N	1.38 ± 1.400 (0.56 - 3.87)
	P	0.07 ± 0.093 (0.02 - 0.24)
N=5	K	0.37 ± 0.464 (0.11 - 1.20)
	Ca	0.11 ± 0.048 (0.04 - 0.16)
	Mg	0.15 ± 0.036 (0.10 - 0.20)
	Na	0.08 ± 0.055 (0.04 - 0.12)
Clasmatocolea humilis	N	1.11 ± 0.216 (0.72 - 1.45)
	P	0.10 ± 0.043 (0.03 - 0.17)
N=19	K	1.09 ± 0.249 (0.56 - 1.50)
	Ca	0.20 ± 0.075 (0.11 - 0.39)
	Mg	0.27 ± 0.074 (0.17 - 0.41)
	Na	0.22 ± 0.108 (0.07 - 0.38)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Clasmatocolea vermicularis	N	1.36 ± 0.446 (0.95 - 2.04)
	P	0.15 ± 0.037 (0.12 - 0.21)
N=6	K	0.86 ± 0.400 (0.54 - 1.64)
	Ca	0.24 ± 0.038 (0.19 - 0.28)
	Mg	0.33 ± 0.067 (0.21 - 0.41)
	Na	0.47 ± 0.321 (0.08 - 0.90)
Cryptochila grandiflora	N	0.71 ± 0.250 (0.46 - 1.20)
	P	0.05 ± 0.018 (0.03 - 0.08)
N=7	K	0.18 ± 0.038 (0.11 - 0.22)
	Ca	0.32 ± 0.148 (0.14 - 0.61)
	Mg	0.39 ± 0.177 (0.23 - 0.76)
	Na	0.12 ± 0.090 (0.05 - 0.30)
Ditrichum strictum	N	0.55 ± 0.136 (0.40 - 0.66)
	P	0.03 ± 0.012 (0.02 - 0.04)
N=3	K	0.12 ± 0.056 (0.07 - 0.18)
	Ca	0.16 ± 0.114 (0.08 - 0.29)
	Mg	0.21 ± 0.116 (0.09 - 0.32)
	Na	0.11 ± 0.074 (0.06 - 0.16)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Jamesoniella colorata	N	0.64 ± 0.152 (0.42 - 1.20)
	P	0.04 ± 0.013 (0.02 - 0.08)
N=56	K	0.24 ± 0.099 (0.08 - 0.53)
	Ca	0.26 ± 0.070 (0.14 - 0.45)
	Mg	0.30 ± 0.049 (0.19 - 0.44)
	Na	0.10 ± 0.036 (0.02 - 0.18)
Marchantia berteroana	N	2.59 ± 1.009 (1.42 - 3.73)
	P	0.33 ± 0.110 (0.14 - 0.45)
N=6	K	1.72 ± 0.365 (1.34 - 2.23)
	Ca	0.26 ± 0.113 (0.14 - 0.42)
	Mg	0.53 ± 0.168 (0.36 - 0.78)
	Na	0.79 ± 0.474 (0.30 - 1.65)
Ptychomnion densifolium	N	1.00 ± 0.543 (0.51 - 1.77)
	P	0.04 ± 0.010 (0.03 - 0.06)
N=11	K	0.14 ± 0.030 (0.08 - 0.18)
	Ca	0.25 ± 0.126 (0.12 - 0.59)
	Mg	0.25 ± 0.098 (0.15 - 0.50)
	Na	0.06 ± 0.037 (0.03 - 0.14)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Racomitrium lanuginosum	N	0.36 ± 0.094 (0.20 - 0.63)
	P	0.02 ± 0.008 (0.01 - 0.05)
N=60	K	0.07 ± 0.034 (0.00 - 0.15)
	Ca	0.10 ± 0.032 (0.05 - 0.19)
	Mg	0.12 ± 0.046 (0.06 - 0.27)
	Na	0.05 ± 0.019 (0.01 - 0.10)
Sanionia uncinata	N	1.28 ± 0.423 (0.65 - 1.99)
	P	0.10 ± 0.032 (0.06 - 0.19)
N=24	K	0.29 ± 0.142 (0.00 - 0.57)
	Ca	0.32 ± 0.155 (0.14 - 0.70)
	Mg	0.28 ± 0.042 (0.20 - 0.37)
	Na	0.07 ± 0.041 (0.03 - 0.18)

Appendix B. Nutrient concentrations in vascular plant dead leaves.

	Nutrient	Mean ± std dev. (min. – max.)
Monocotyledonous species		
Agrostis magellanica	N	1.35 ± 0.277 (0.79 - 1.80)
	P	0.14 ± 0.036 (0.06 - 0.23)
N=23	K	0.57 ± 0.051 (0.26 - 0.92)
	Ca	0.35 ± 0.020 (0.16 - 0.70)
	Mg	0.27 ± 0.052 (0.18 - 0.40)
	Na	0.06 ± 0.034 (0.02 - 0.17)
Juncus scheuchzerioides	N	1.37 ± 0.287 (0.70 - 2.18)
	P	0.14 ± 0.032 (0.05 - 0.41)
N=14	K	0.44 ± 0.098 (0.16 - 0.70)
	Ca	0.08 ± 0.081 (0.04 - 0.18)
	Mg	0.18 ± 0.106 (0.06 - 0.30)
	Na	0.12 ± 0.067 (0.03 - 0.34)
Poa cookii	N	1.52 ± 0.332 (0.88 - 1.97)
	P	0.1 ± 0.046 (0.02 - 0.17)
N=21	K	0.18 ± 0.094 (0.06 - 0.39)
	Ca	0.15 ± 0.046 (0.05 - 0.24)
	Mg	0.16 ± 0.066 (0.03 - 0.34)
	Na	0.12 ± 0.123 (0.02 - 0.44)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Uncinia compacta	N	2.28 ± 0.495 (1.42 - 2.90)
	P	0.13 ± 0.060 (0.09 - 0.19)
N=13	K	0.17 ± 0.066 (0.05 - 0.31)
	Ca	0.11 ± 0.053 (0.07 - 0.16)
	Mg	0.11 ± 0.037 (0.09 - 0.14)
	Na	0.11 ± 0.020 (0.02 - 0.15)
Dicotyledonous species		
Acaena magellanica	N	2.47 ± 0.399 (1.57 - 3.55)
	P	0.22 ± 0.056 (0.12 - 0.47)
N=21	K	1.42 ± 0.156 (0.58 - 3.01)
	Ca	1.21 ± 0.255 (0.63 - 1.88)
	Mg	0.63 ± 0.099 (0.45 - 0.92)
	Na	0.46 ± 0.098 (0.17 - 1.59)
Azorella selago	N	1.25 ± 0.292 (0.65 - 1.68)
	P	0.12 ± 0.011 (0.06 - 0.19)
N=36	K	0.43 ± 0.062 (0.18 - 0.72)
	Ca	0.19 ± 0.169 (0.10 - 0.38)
	Mg	0.22 ± 0.101 (0.13 - 0.29)
	Na	0.03 ± 0.096 (0.01 - 0.07)

Cont.	Nutrient	Mean ± std dev. (min. – max.)

Pteridophytes		
Blechnum penna-marina	N	1.99 ± 0.423 (1.40 - 4.19)
	P	0.19 ± 0.032 (0.07 - 0.44)
N=50	K	1.59 ± 0.067 (0.71 - 2.46)
	Ca	0.11 ± 0.133 (0.04 - 0.20)
	Mg	0.21 ± 0.093 (0.06 - 0.37)
	Na	0.3 ± 0.051 (0.06 - 0.91)
Grammitis poeppigeana	N	1.14 ± 0.282 (0.73 - 1.57)
	P	0.05 ± 0.123 (0.02 - 0.13)
N=4	K	0.11 ± 0.428 (0.04 - 0.21)
	Ca	0.12 ± 0.754 (0.08 - 0.15)
	Mg	0.17 ± 0.240 (0.04 - 0.26)
	Na	0.06 ± 0.489 (0.02 - 0.14)
Polystichum marionense	N	2.83 ± 0.096 (1.03 - 4.43)
	P	0.35 ± 0.010 (0.16 - 0.46)
N=3	K	1.19 ± 0.191 (0.66 - 1.79)
	Ca	0.13 ± 0.131 (0.09 - 0.18)
	Mg	0.23 ± 0.227 (0.09 - 0.31)
	Na	0.44 ± 0.427 (0.13 - 0.70)

Appendix C. Nutrient concentrations in vascular plant stems.

	Nutrient	Mean ± std dev. (min. – max.)
Acaena magellanica	N	1.35 ± 0.32 (0.79 - 1.80)
	P	0.14 ± 0.04 (0.06 - 0.23)
N=22	K	0.57 ± 0.21 (0.26 – 0.92)
	Ca	0.35 ± 0.15 (0.16 – 0.70)
	Mg	0.27 ± 0.06 (0.18 – 0.40)
	Na	0.06 ± 0.04 (0.02 – 0.17)
Azorella selago	N	1.27 ± 0.35 (0.83 – 2.04)
	P	0.13 ± 0.05 (0.07 – 0.26)
N=36	K	0.76 ± 0.16 (0.45 - 1.01)
	Ca	0.48 ± 0.10 (0.23 - 0.64)
	Mg	0.38 ± 0.05 (0.30 - 0.53)
	Na	0.13 ± 0.05 (0.04 - 0.25)

Appendix D. Nutrient concentrations in vascular plant roots.

	Nutrient	Mean ± std dev. (min. – max.)
Agrostis magellanica	N	1.37 ± 0.380 (0.70 - 2.18)
	P	0.14 ± 0.091 (0.05 - 0.41)
N=24	K	0.77 ± 0.146 (0.45 - 1.08)
	Ca	0.13 ± 0.031 (0.06 - 0.21)
	Mg	0.14 ± 0.055 (0.06 - 0.25)
	Na	0.12 ± 0.077 (0.03 - 0.34)
Juncus scheuchzerioides	N	1.41 ± 0.148 (1.17 - 1.61)
	P	0.10 ± 0.049 (0.05 - 0.23)
N=15	K	1.12 ± 0.110 (0.73 - 1.70)
	Ca	0.10 ± 0.035 (0.04 - 0.17)
	Mg	0.12 ± 0.075 (0.05 - 0.22)
	Na	0.21 ± 0.136 (0.05 - 0.47)
Poa cookii	N	1.53 ± 0.293 (1.03 - 2.07)
	P	0.20 ± 0.090 (0.08 - 0.38)
N=22	K	0.90 ± 0.312 (0.33 - 1.44)
	Ca	0.07 ± 0.021 (0.03 - 0.11)
	Mg	0.12 ± 0.064 (0.01 - 0.21)
	Na	0.18 ± 0.127 (0.03 - 0.46)

Cont.	Nutrient	Mean ± std dev. (min. – max.)

Uncinia compacta	N	1.52 ± 0.562 (0.75 - 2.61)
	P	0.15 ± 0.114 (0.05 - 0.49)
N=13	K	0.31 ± 0.194 (0.19 - 0.53)
	Ca	0.38 ± 0.080 (0.29 - 0.53)
	Mg	0.46 ± 0.082 (0.27 - 0.71)
	Na	0.06 ± 0.012 (0.04 - 0.08)
Acaena magellanica	N	1.25 ± 0.336 (0.65 - 1.68)
	P	0.12 ± 0.035 (0.06 - 0.19)
N=18	K	0.45 ± 0.179 (0.26 - 0.59)
	Ca	0.09 ± 0.075 (0.04 - 0.14)
	Mg	0.28 ± 0.054 (0.18 - 0.37)
	Na	0.03 ± 0.017 (0.01 - 0.07)
Azorella selago	N	1.19 ± 0.307 (0.77 - 1.82)
	P	0.14 ± 0.079 (0.06 - 0.37)
N= 13	K	0.82 ± 0.175 (0.61 - 1.02)
	Ca	0.08 ± 0.126 (0.04 - 0.12)
	Mg	0.08 ± 0.067 (0.03 - 0.18)
	Na	0.14 ± 0.107 (0.04 - 0.55)

Cont.	Nutrient	Mean ± std dev. (min. – max.)

Callitriche antarctica	N	2.35 ± 0.326 (2.07 - 2.97)
	P	0.16 ± 0.102 (0.08 - 0.35)
N=6	K	0.76 ± 0.150 (0.68 - 0.87)
	Ca	0.08 ± 0.067 (0.06 - 0.09)
	Mg	0.17 ± 0.110 (0.08 - 0.26)
	Na	0.61 ± 0.525 (0.28 - 1.21)
Cotula plumosa	N	1.30 ± 0.566 (0.51 - 2.37)
	P	0.19 ± 0.039 (0.15 - 0.26)
N=15	K	0.33 ± 0.202 (0.07 - 0.59)
	Ca	0.27 ± 0.077 (0.10 - 0.54)
	Mg	0.25 ± 0.096 (0.06 - 0.69)
	Na	0.63 ± 0.249 (0.16 - 0.97)
Crassula moschata	N	1.38 ± 0.311 (1.01 - 1.73)
	P	0.10 ± 0.018 (0.08 - 0.13)
N=8	K	2.46 ± 0.064 (1.20 - 3.71)
	Ca	0.16 ± 0.257 (0.14 - 0.18)
	Mg	0.22 ± 0.155 (0.19 - 0.24)
	Na	0.54 ± 0.056 (0.50 - 0.58)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Montia fontana	N	2.57 ± 0.446 (1.92 - 3.36)
	P	0.19 ± 0.086 (0.09 - 0.35)

N=9	K	0.15 ± 0.193 (0.00 - 0.44)
	Ca	0.13 ± 0.150 (0.01 - 0.26)
	Mg	0.13 ± 0.197 (0.03 - 0.22)
	Na	0.52 ± 0.213 (0.30 - 0.77)
Ranunculus biternatus	N	2.05 ± 0.530 (1.67 - 2.42)
	P	0.20 ± 0.042 (0.17 - 0.23)
N=3	K	2.30 ± 1.344 (2.21 - 2.43)
	Ca	0.17 ± 0.000 (0.14 - 0.23)
	Mg	0.34 ± 0.007 (0.28 - 0.41)
	Na	0.40 ± 0.045 (0.37 - 0.43)
Blechnum penna-marina	N	1.32 ± 0.378 (0.75 - 2.11)
	P	0.16 ± 0.091 (0.05 - 0.56)
N=50	K	1.38 ± 0.122 (1.13 - 1.63)
	Ca	0.08 ± 0.154 (0.04 - 0.12)
	Mg	0.05 ± 0.084 (0.04 - 0.05)
	Na	0.08 ± 0.055 (0.02 - 0.30)

Cont.	Nutrient	Mean ± std dev. (min. – max.)
Grammitis poeppigeana	N	1.29 ± 0.228 (0.98 - 1.46)
	P	0.12 ± 0.095 (0.06 - 0.26)
N=4	K	0.20 ± 0.804 (0.20 - 0.20)
	Ca	0.15 ± 0.313 (0.15 - 0.15)
	Mg	0.05 ± 0.207 (0.05 - 0.05)

Na	0.15 ± 0.133 (0.07 - 0.34)

Figures

Fig 1.1. Location of Marion and Prince Edward Islands, and of all other sub-Antarctic islands.

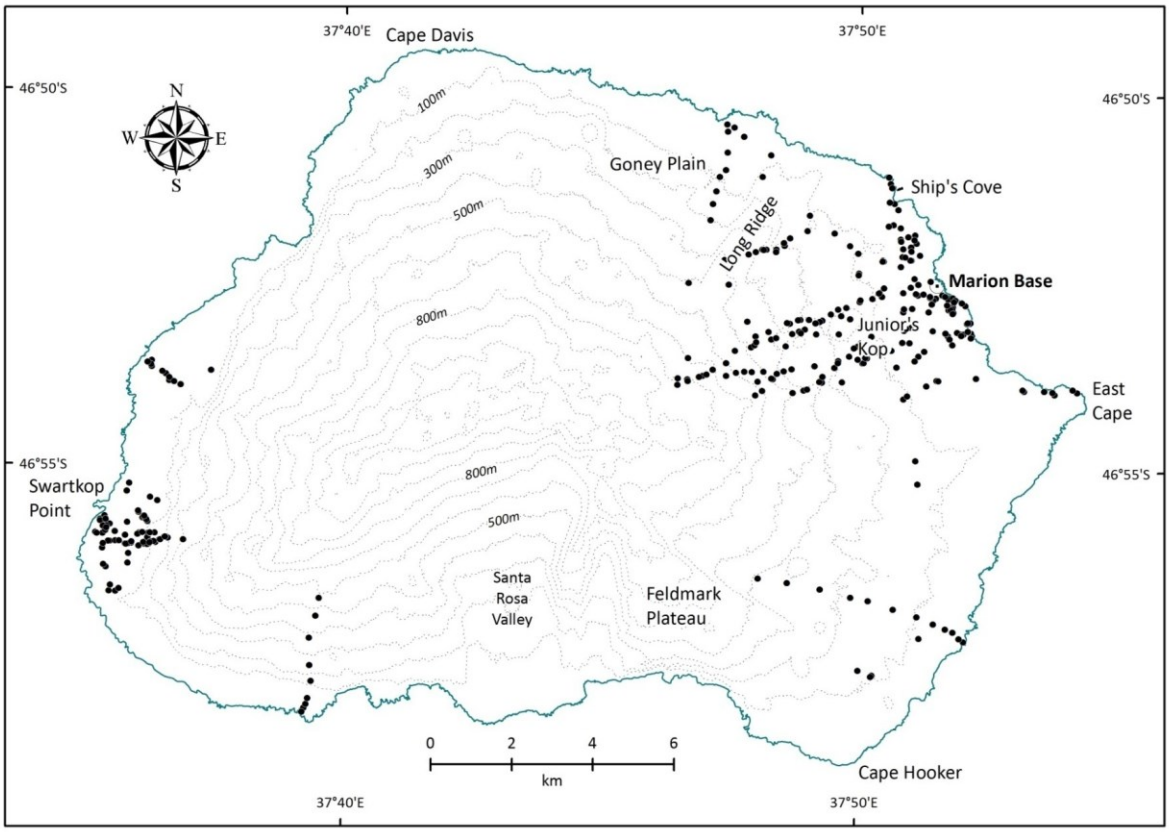

Figure 2.1 The sampling locations of this study. Samples were collected in April/May from 2009 to 2011.

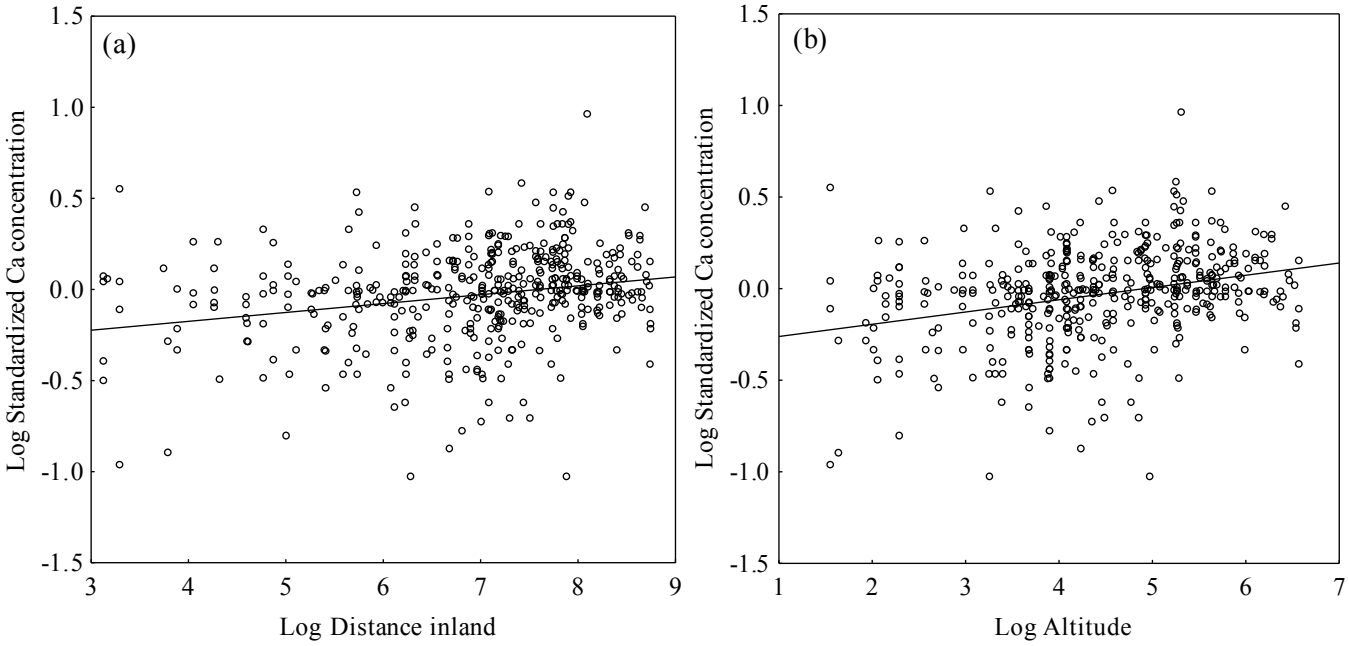

Figure 3.1. The relationship of log standardised N concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1.

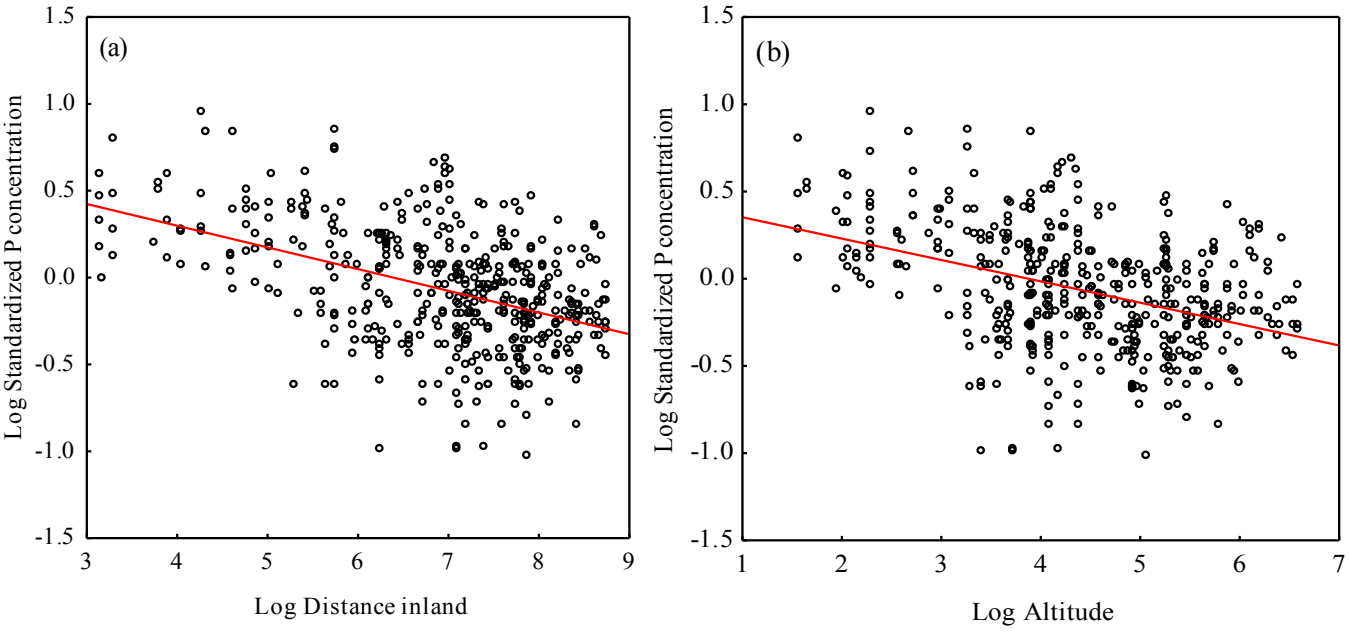

Figure 3.2. The relationship of log standardised P concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1.

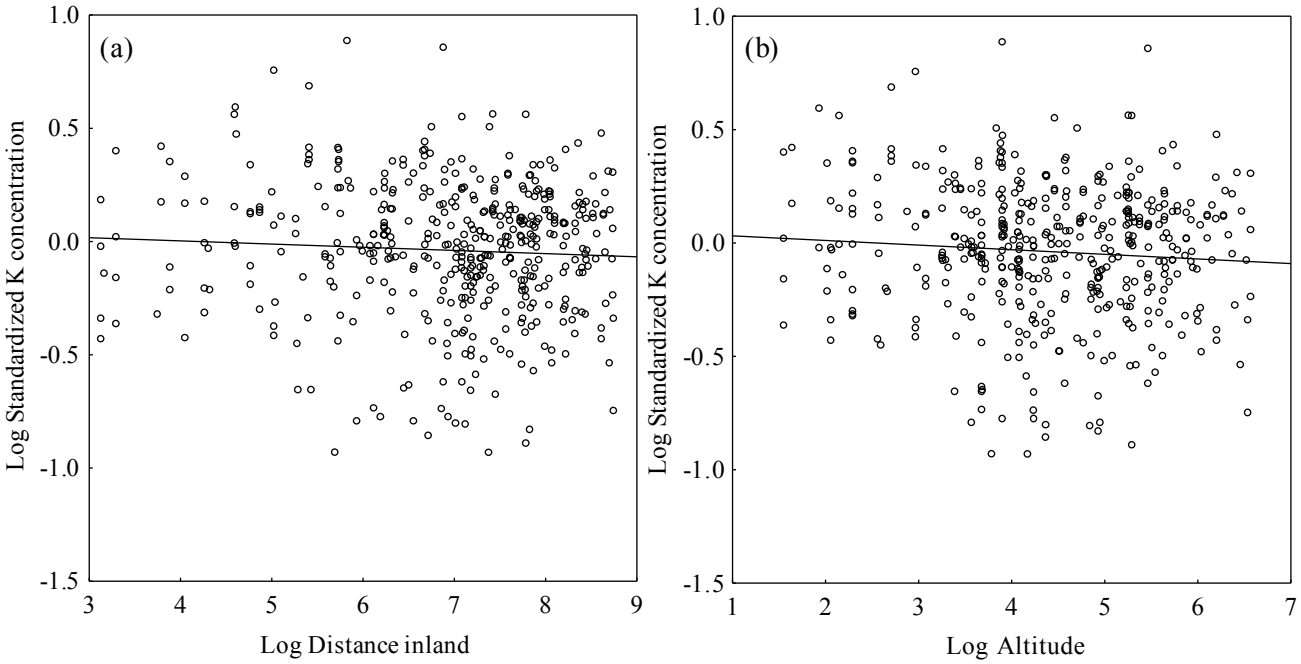

Figure 3.3. The relationship of log standardised K concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1.

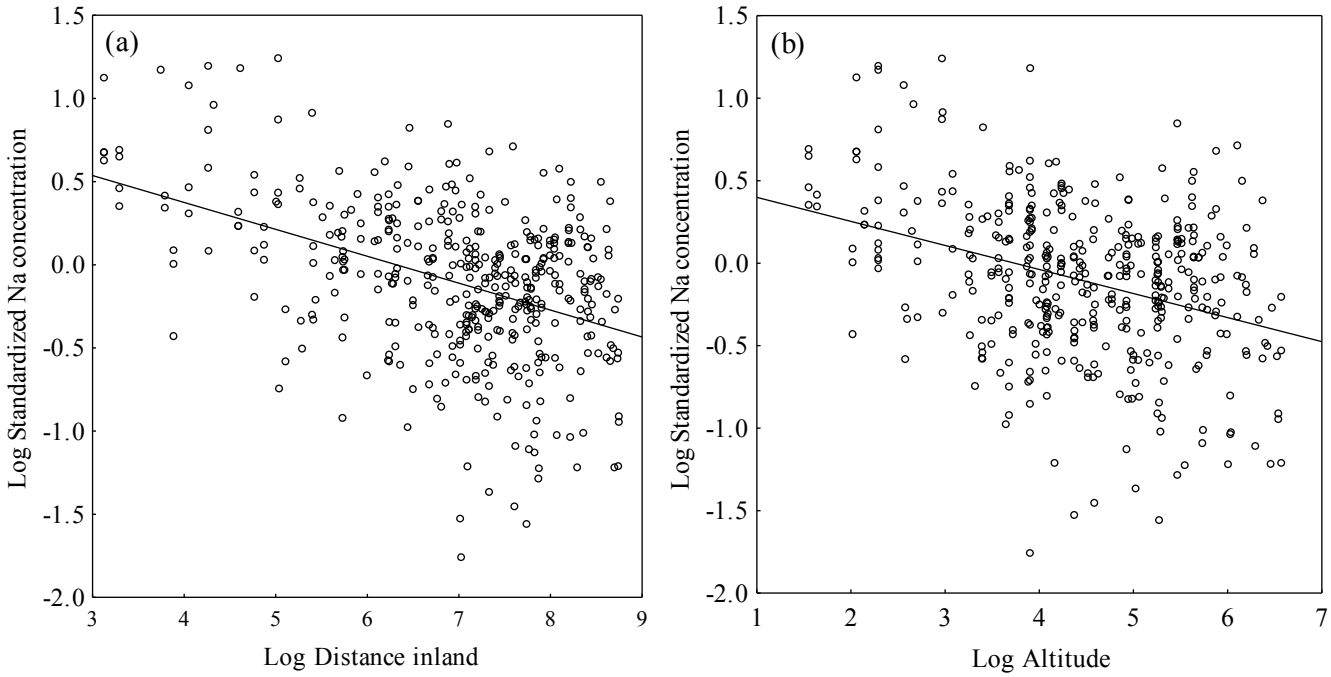

Figure 3.4. The relationship of log standardised Na concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1.

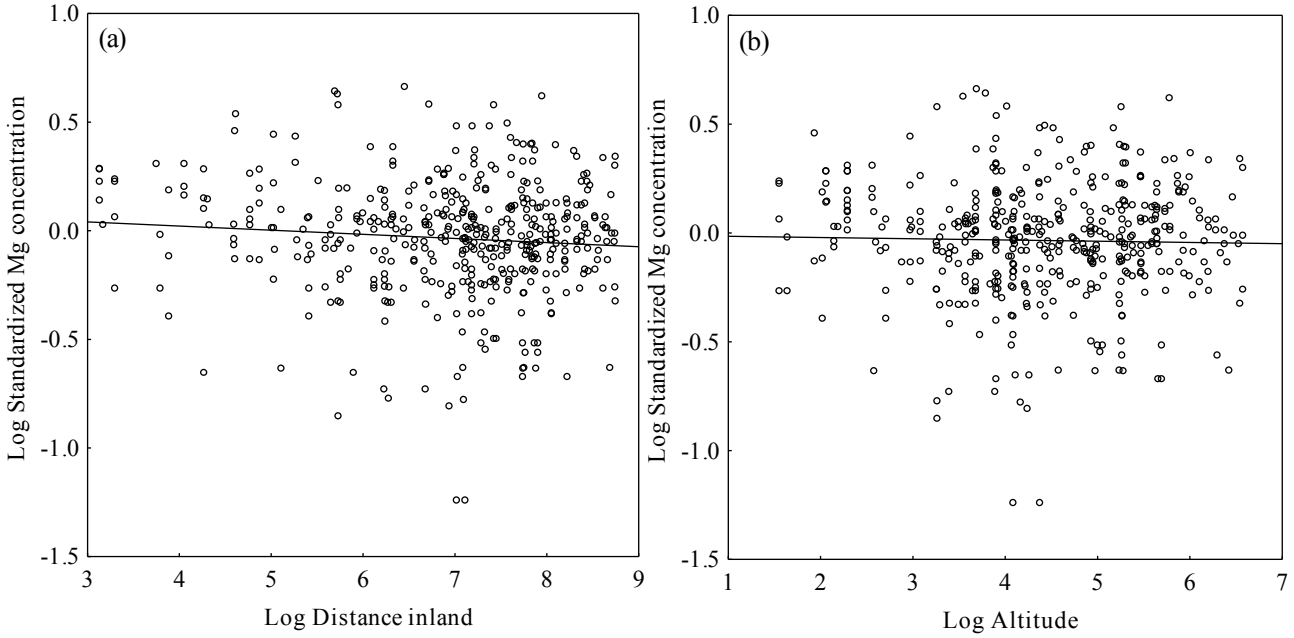

Figure 3.5. The relationship of log standardised Mg concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1

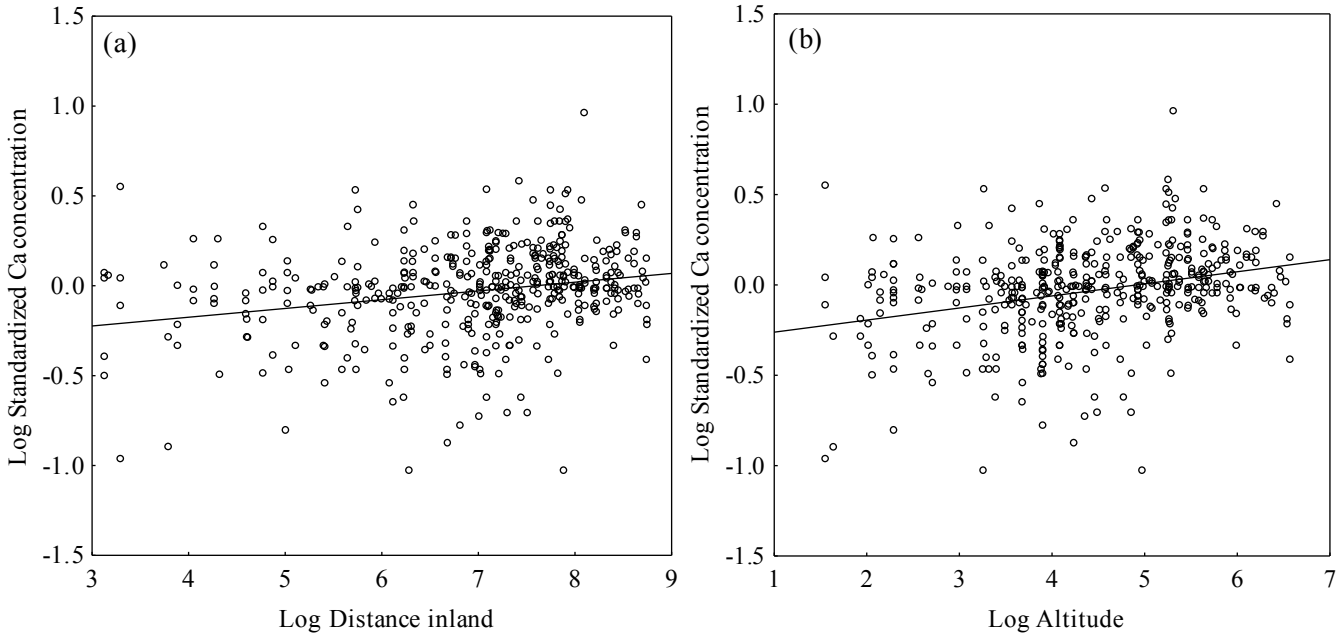

Figure 3.6. The relationship of log standardised Ca concentrations in the live leaves of 13 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.1

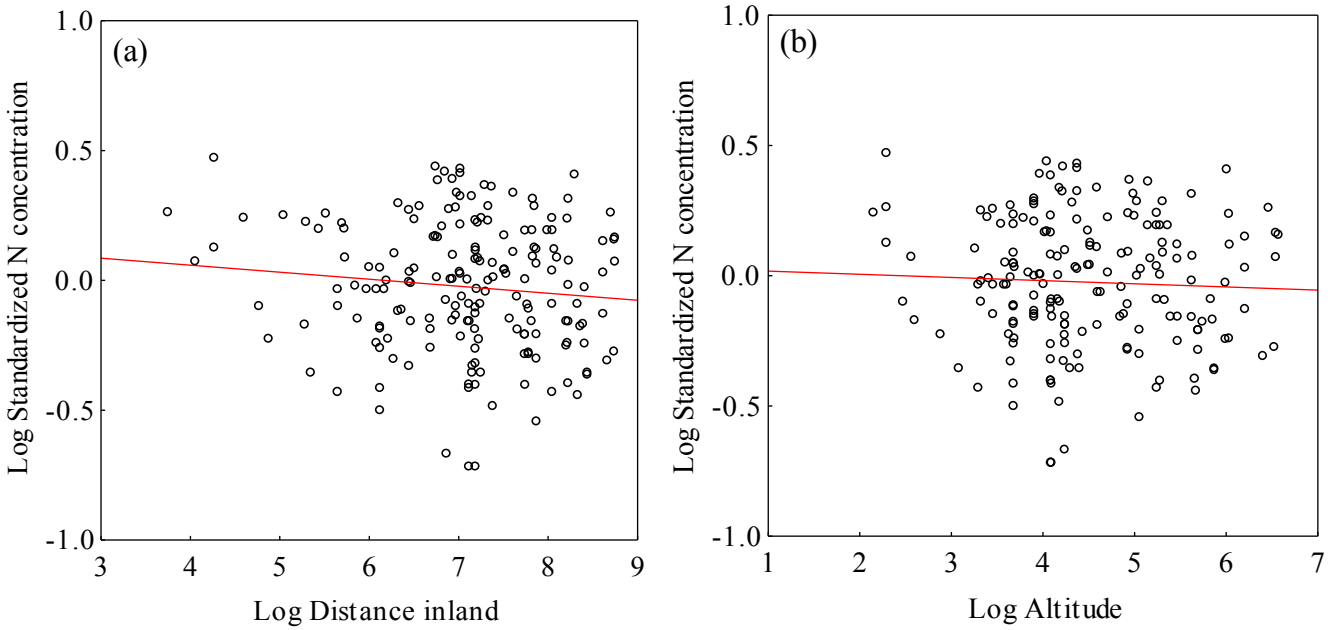

Figure 3.7 The relationship of log standardised N concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2

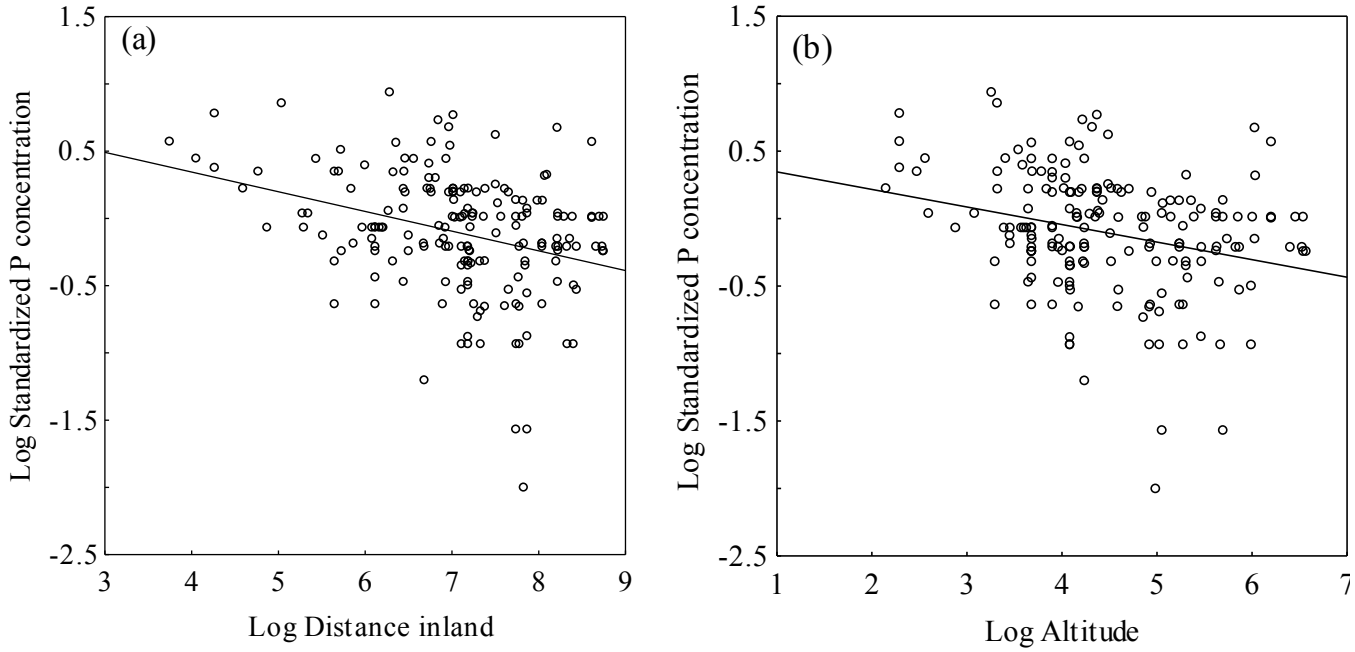

Figure 3.8 The relationship of log standardised P concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2

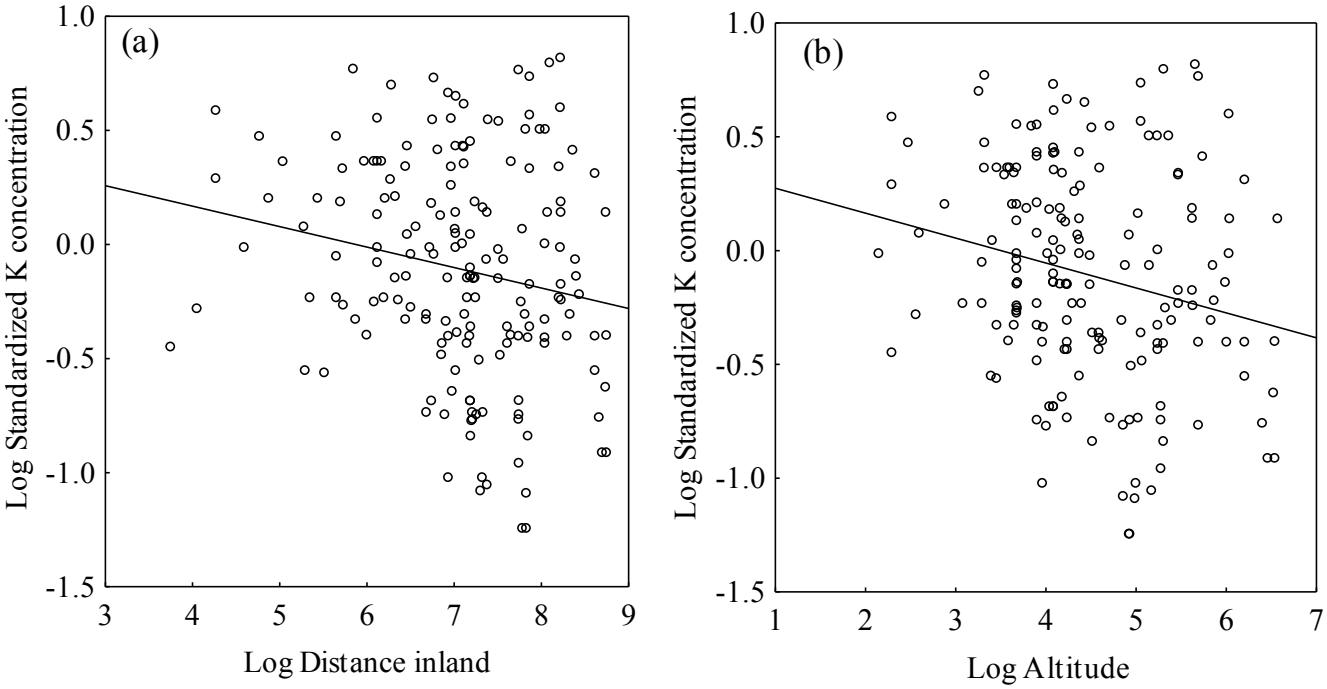

Figure 3.9 The relationship of log standardised K concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2

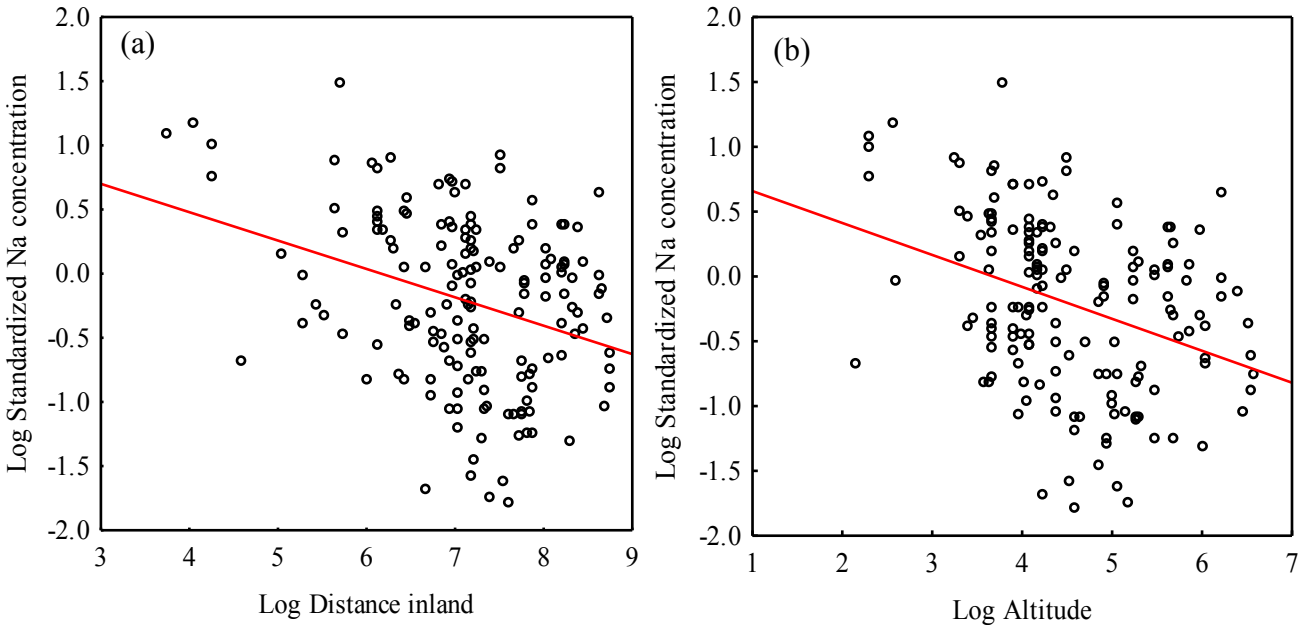

Figure 3.10 The relationship of log standardised Na concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2

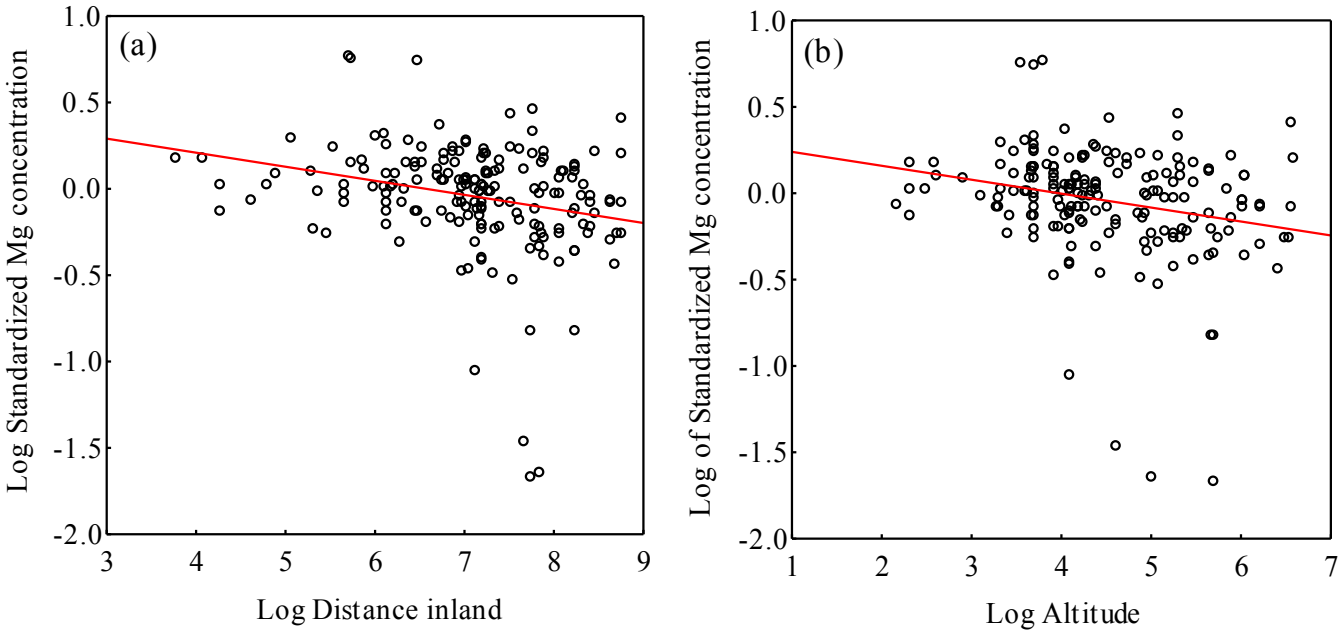

Figure 3.11 The relationship of log standardised Mg concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2.

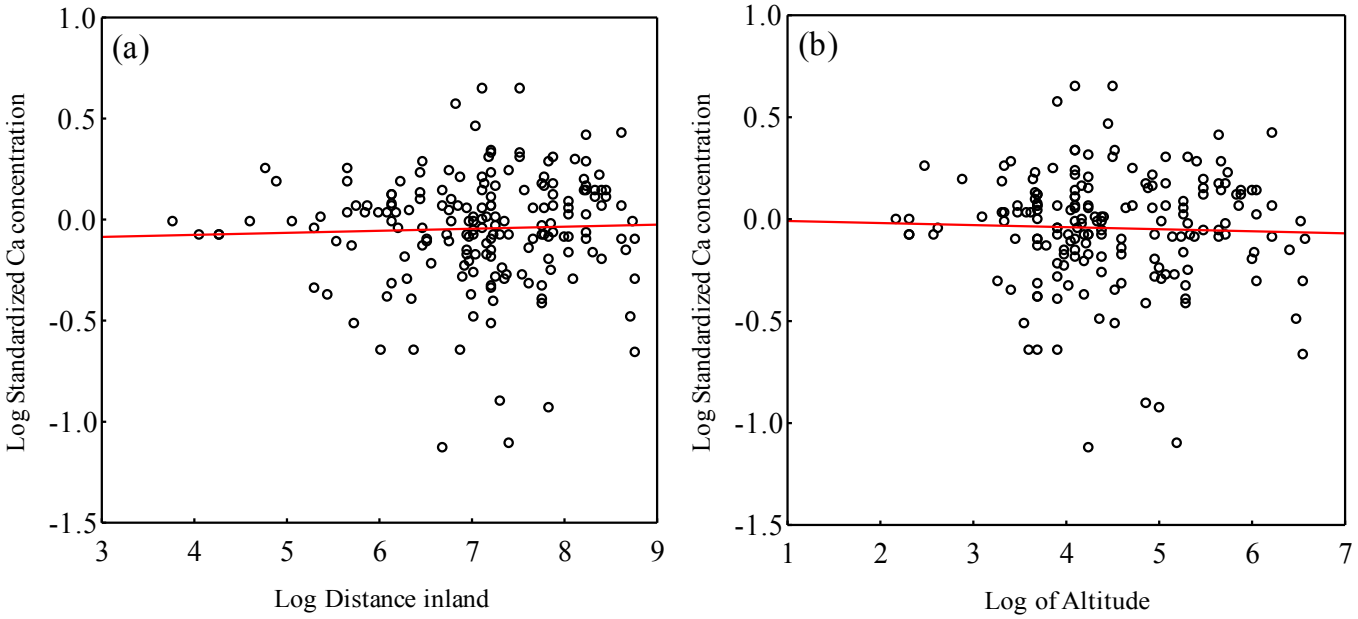

Figure 3.12 The relationship of log standardised Ca concentrations in the dead leaves of eight vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.2.

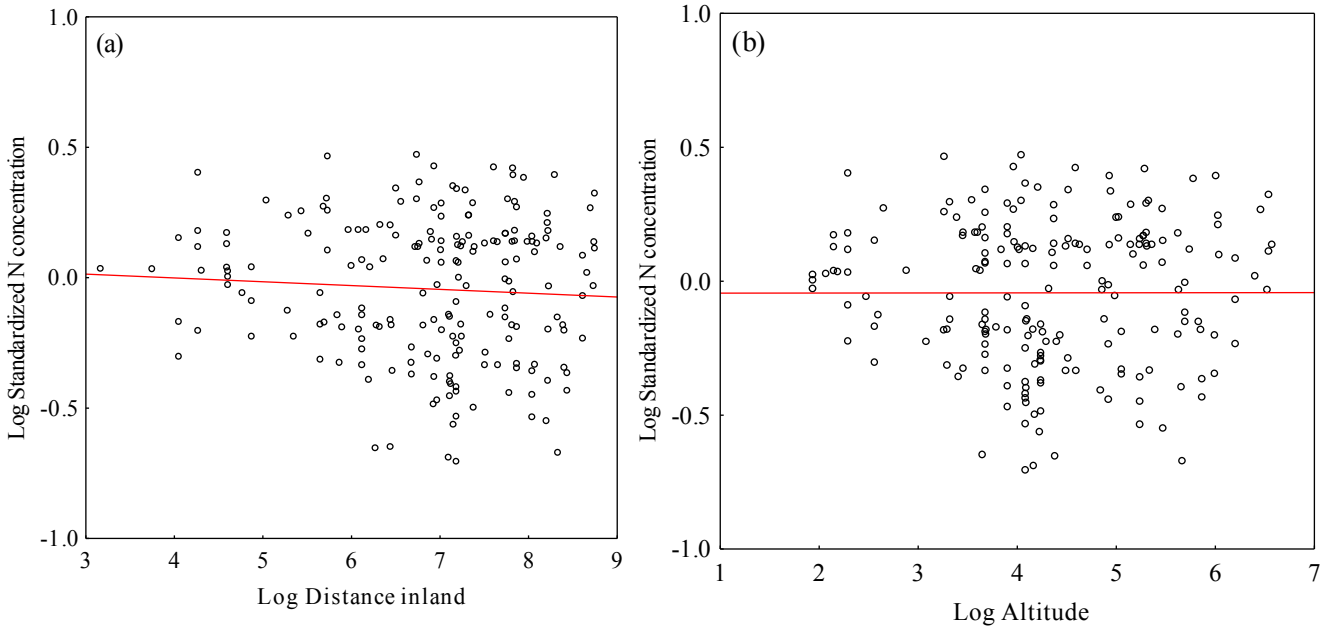

Figure 3.13 The relationship of log standardised N concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4

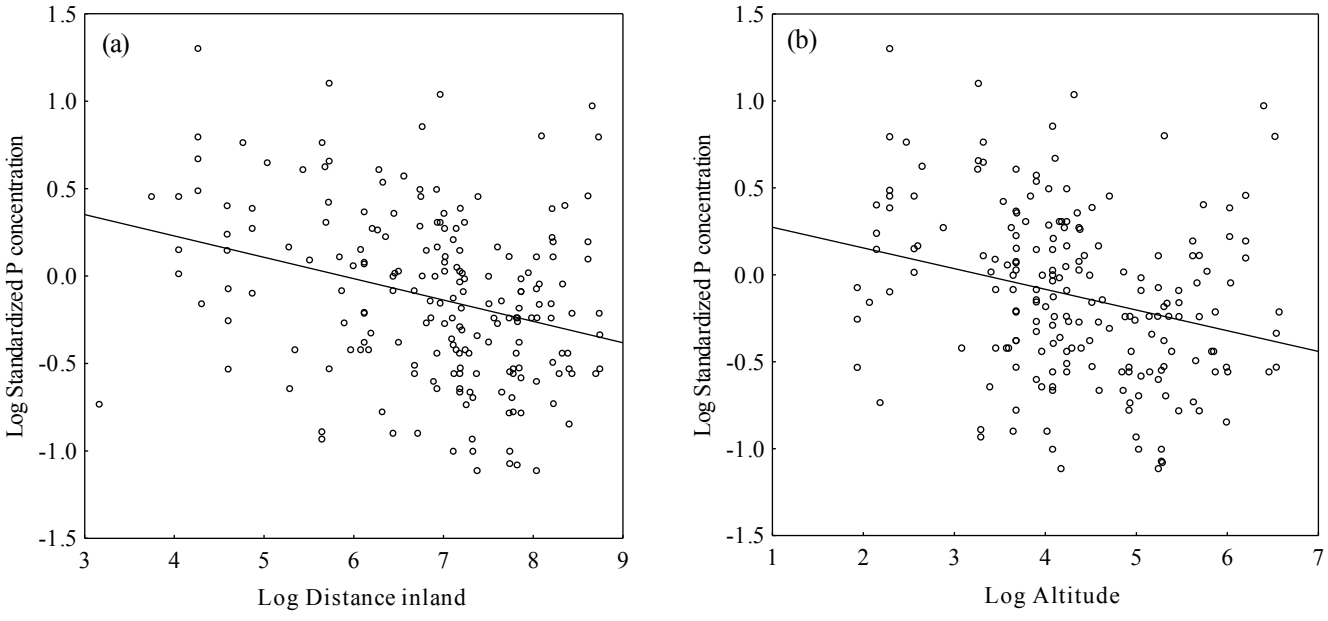

Figure 3.14 The relationship of log standardised P concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4

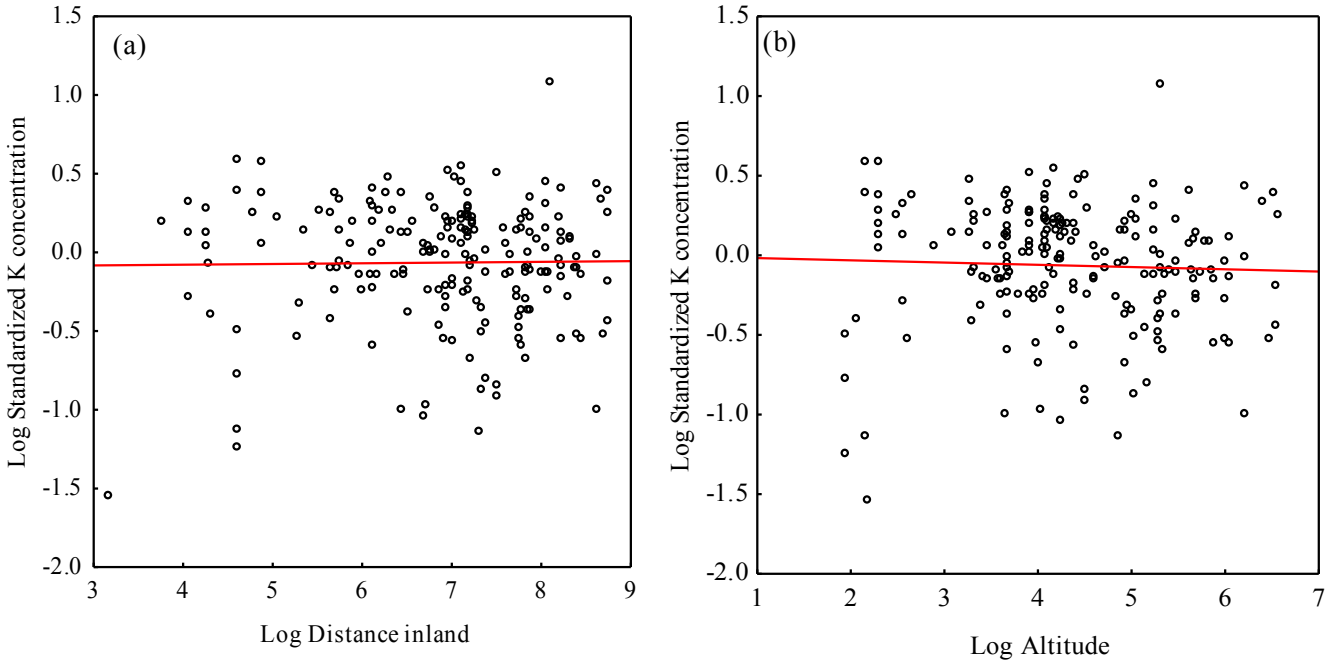

Figure 3.15 The relationship of log standardised K concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4

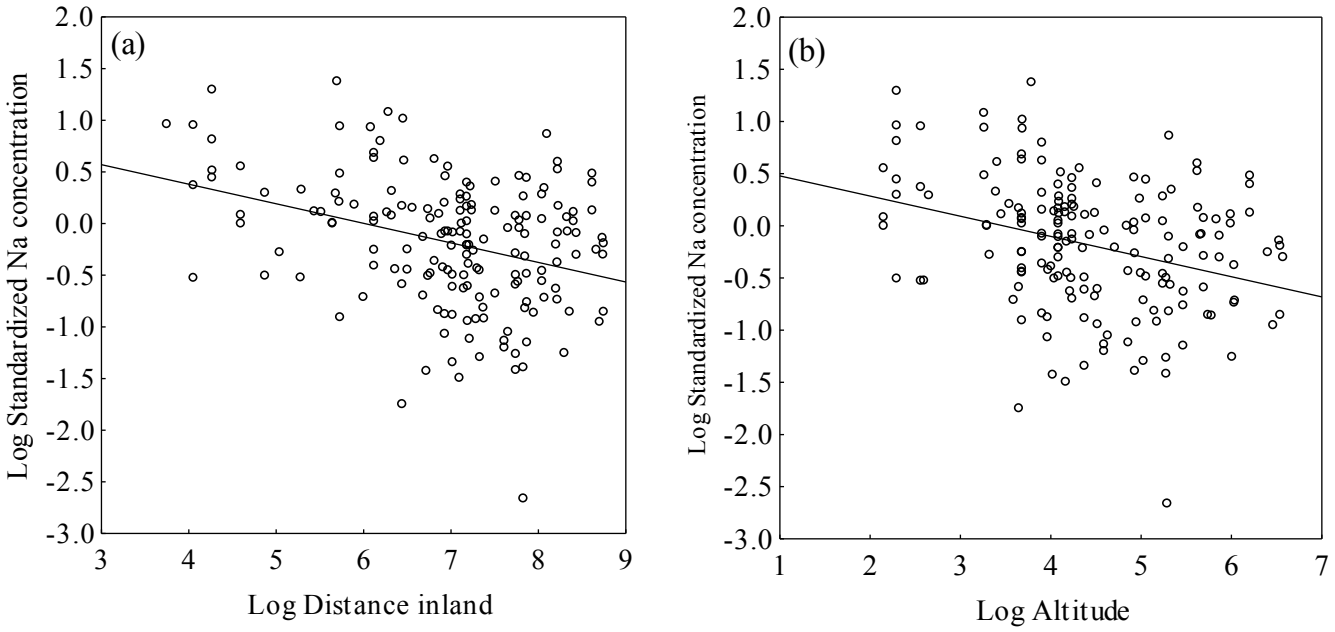

Figure 3.16 The relationship of log standardised Na concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4.

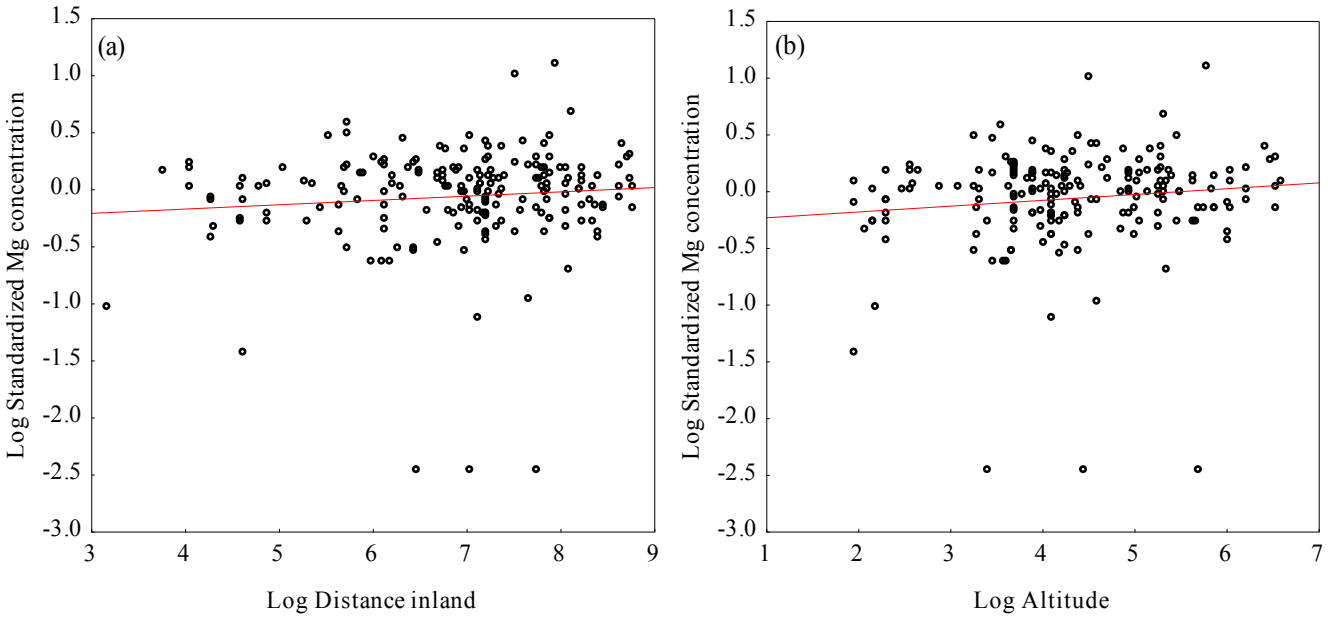

Figure 3.17 The relationship of log standardised Mg concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4.

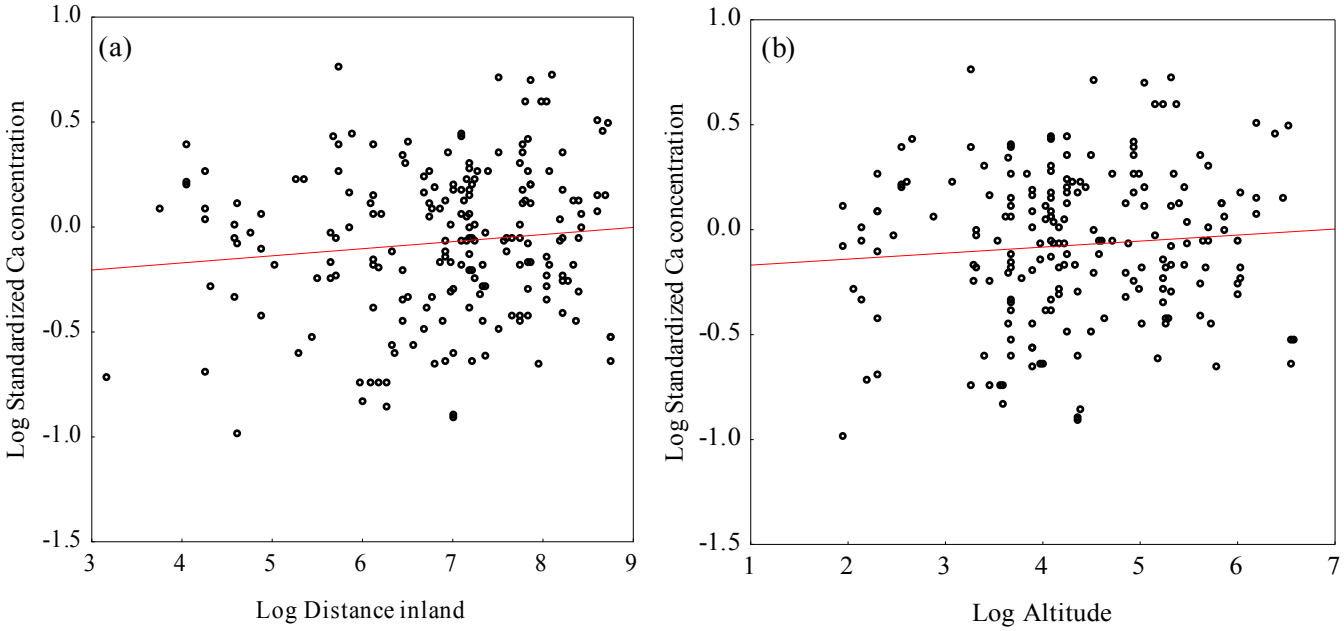

Figure 3.18 The relationship of log standardised Ca concentrations in the belowground tissue of 10 vascular species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.4.

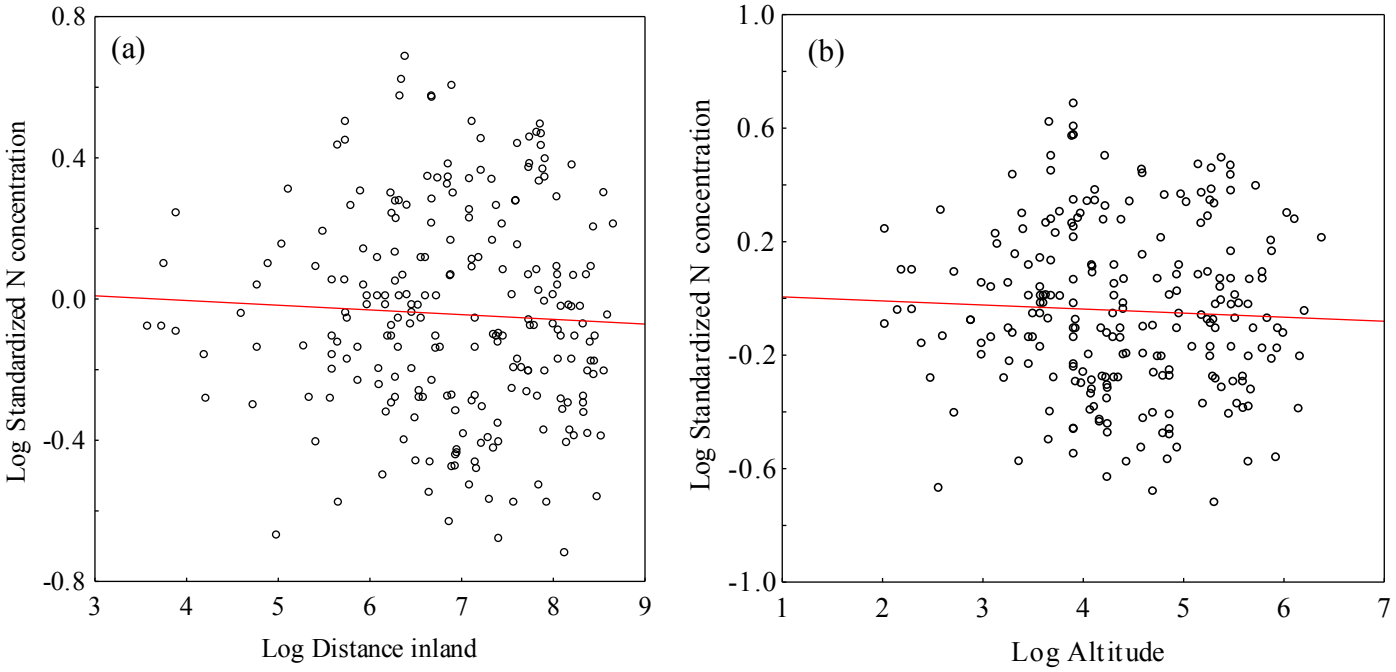

Figure 3.19 The relationship of log standardised N concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.5

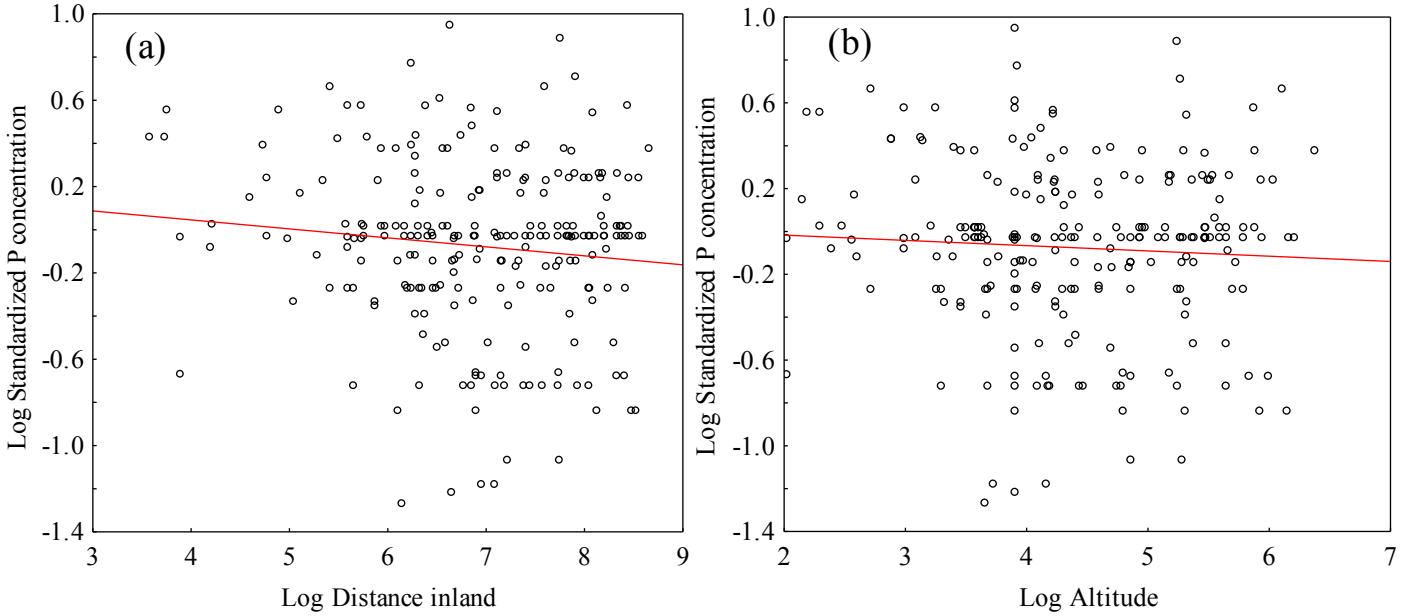

Figure 3.20 The relationship of log standardised P concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.5

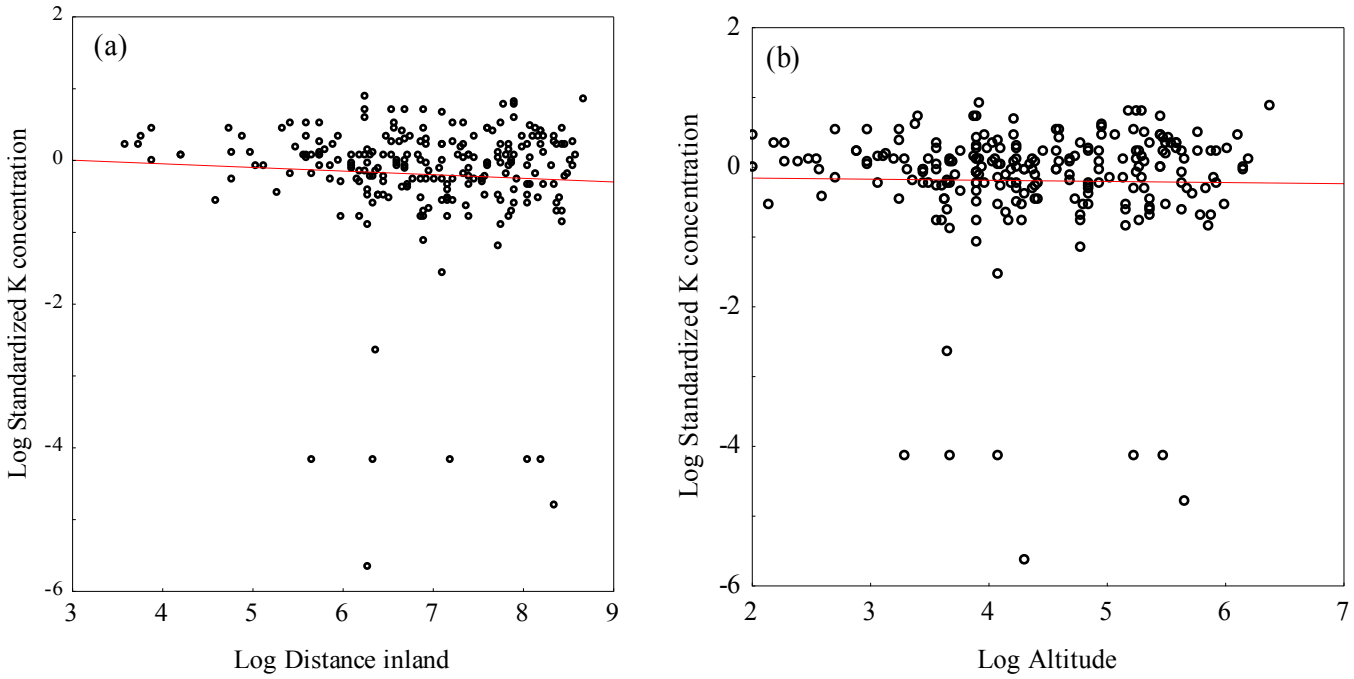

Figure 3.21 The relationship of log standardised K concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.5

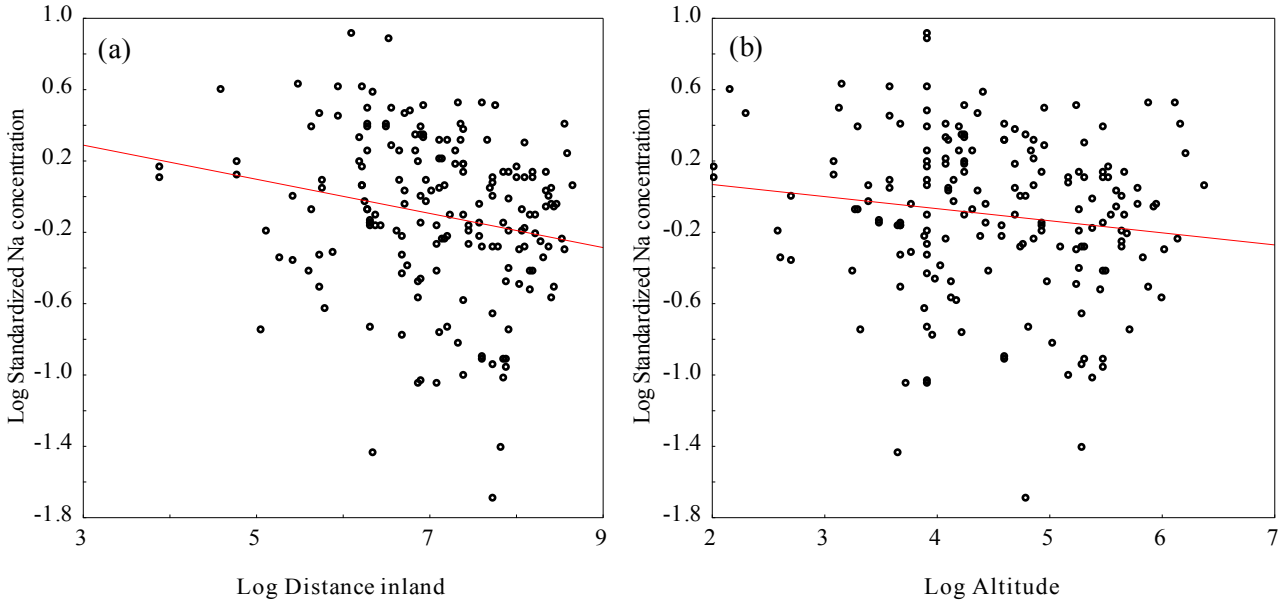

Figure 3.22 The relationship of log standardised Na concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.5

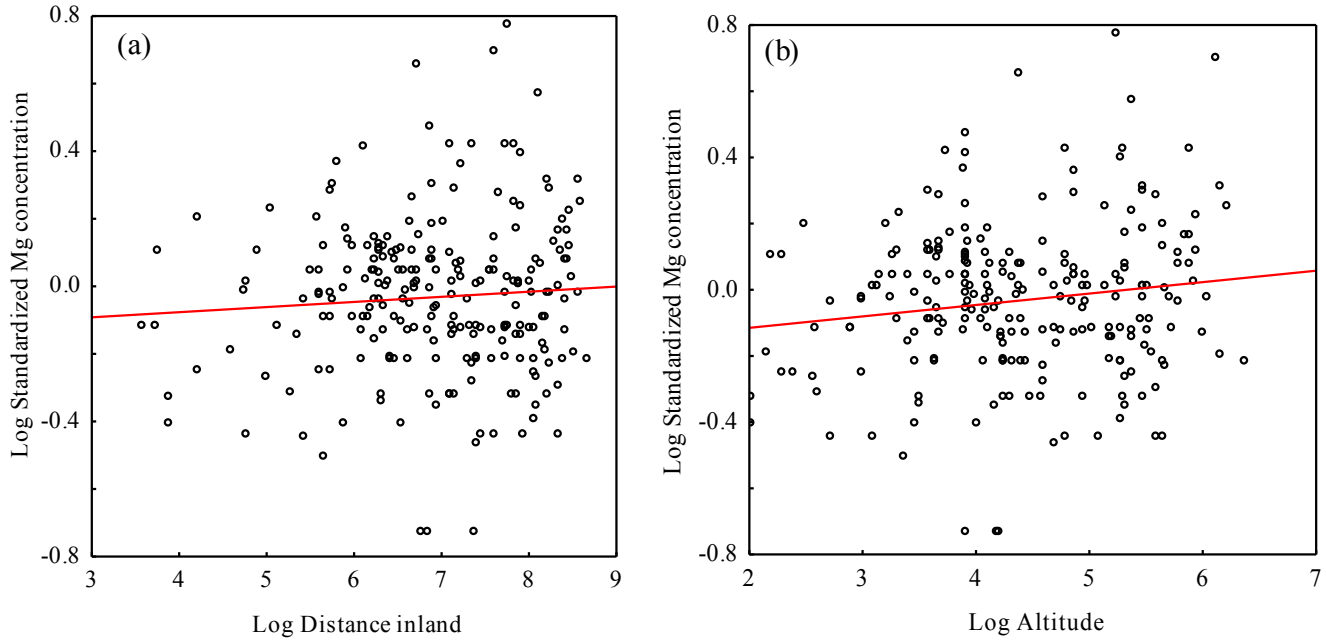

Figure 3.23 The relationship of log standardised Mg concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.5

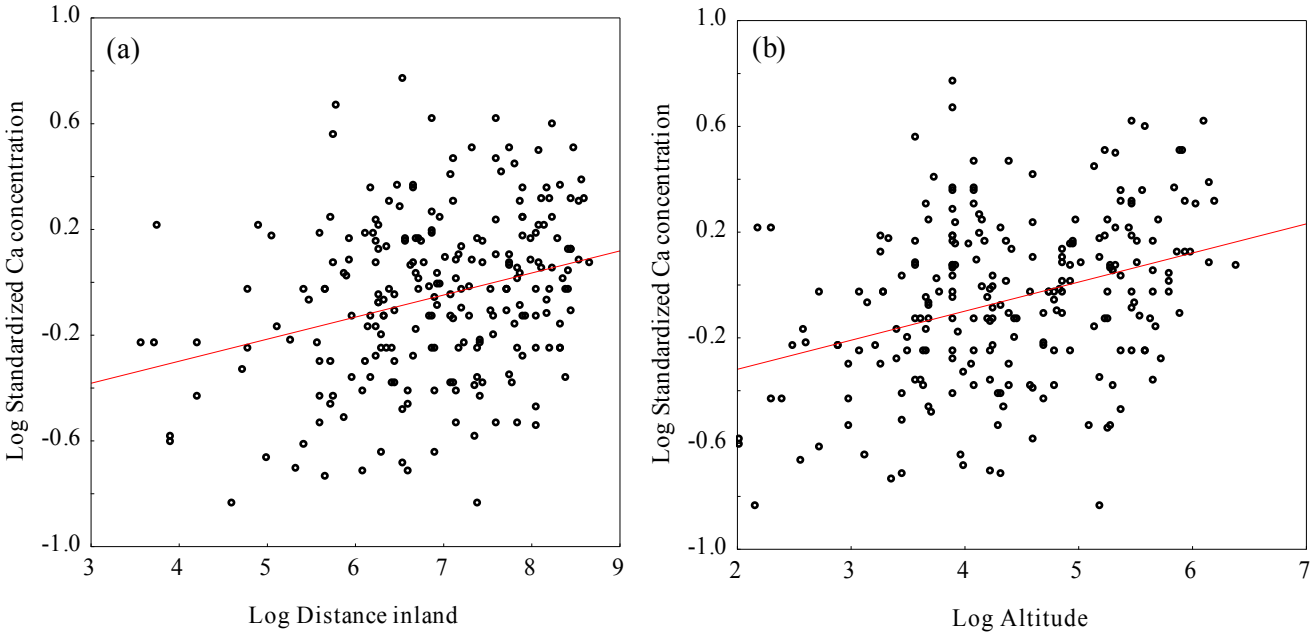

Figure 3.24 The relationship of log standardised Ca concentrations in shoots of 9 bryophyte species to (a) log distance inland and (b) log altitude. The correlation coefficient (*r*) and its significance (*p*) for each relationship are in Table 3.

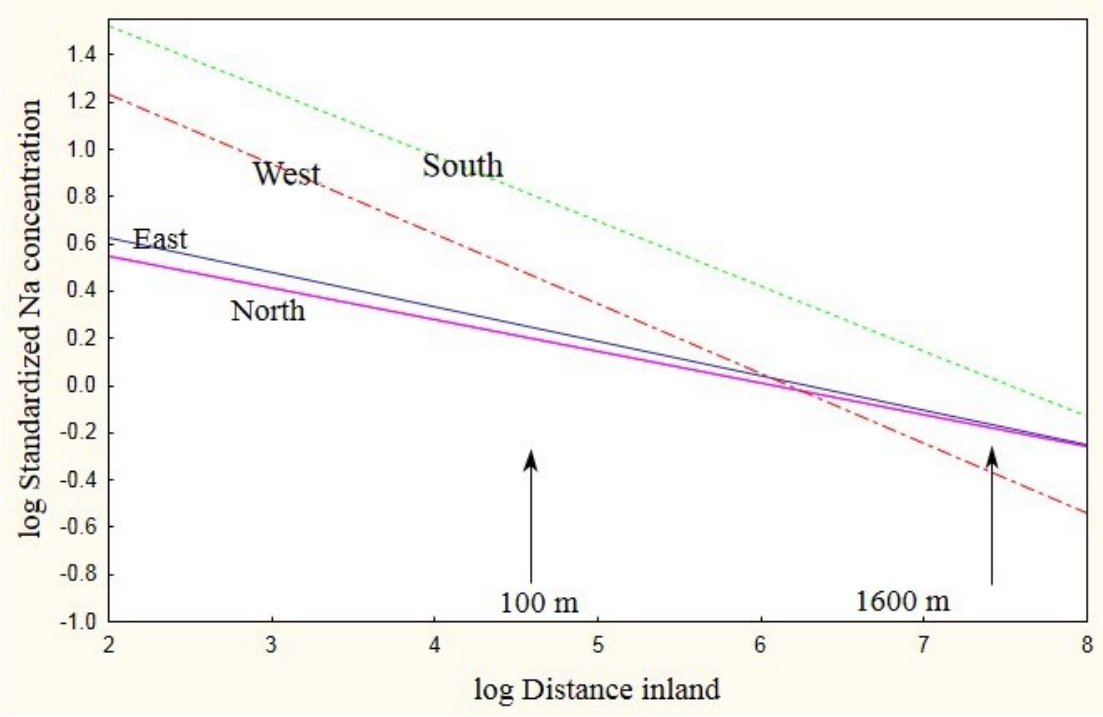

Figure 4.1. Slopes of the relationship between log standardized Na concentrations in living leaves of 13 vascular plant species and log distance inland for different sides of the island. The between-side differences in Na concentration given in Table 4.1 were calculated for 1000 m and 100 m inland.

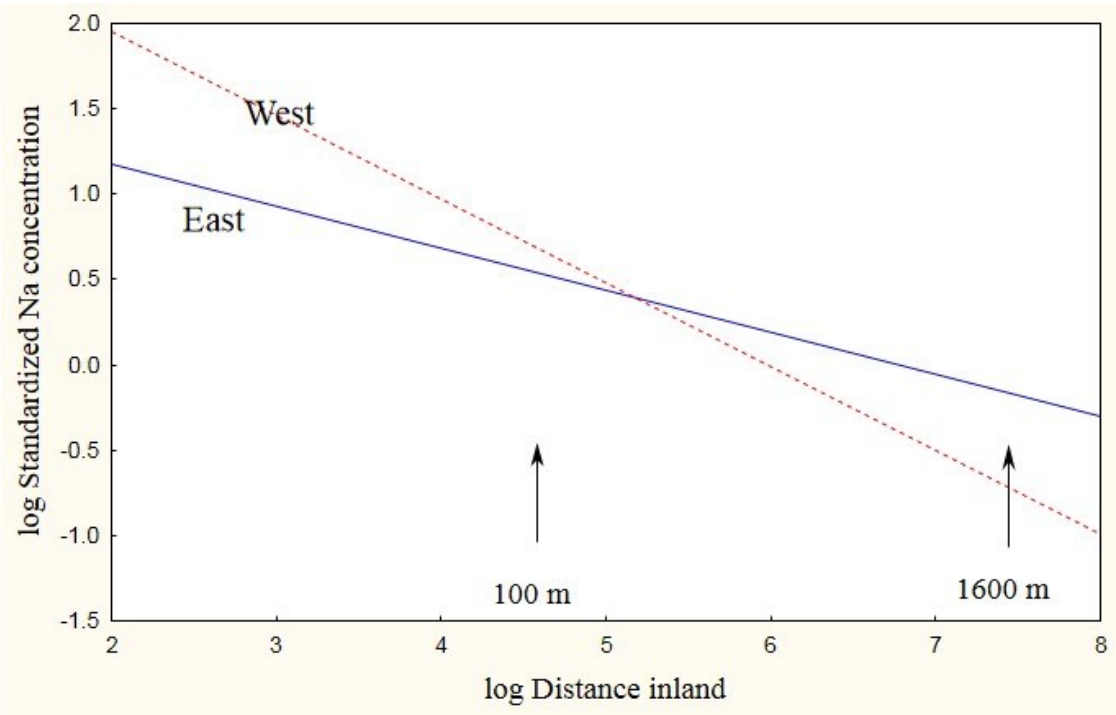

Figure 4.2. Slopes of the relationship between log standardized Na concentrations in dead leaves of 13 vascular plant species and log distance inland for different sides of the island. The between-side differences in Na concentration given in Table 4.1 were calculated for 1000 m and 100 m inland.

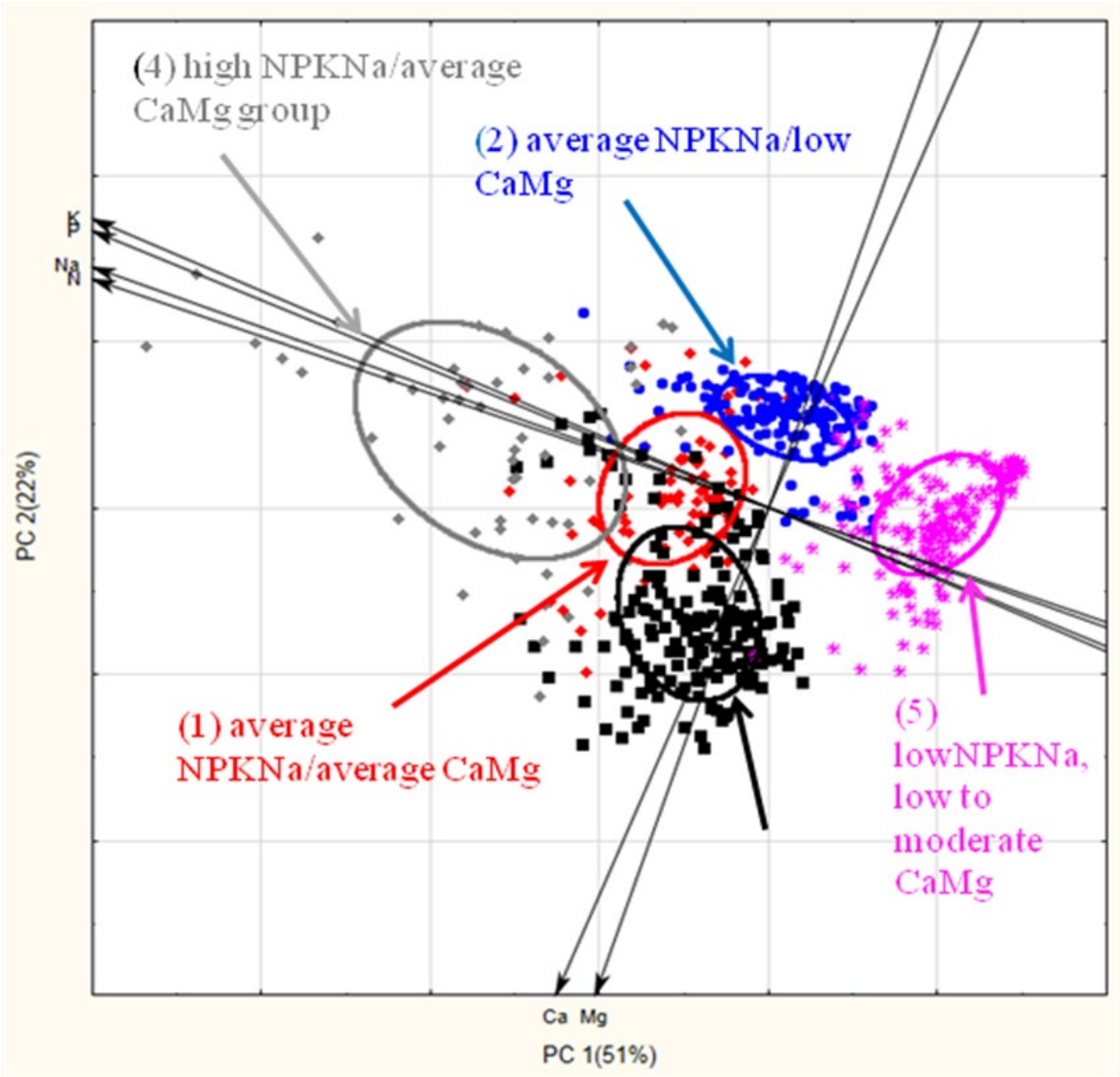

Figure 6.1 Biplot from PCA of leaf nutrient concentrations. Points are samples, colour coded by K-mean cluster membership. The 0.5 alpha ellipses encompassing 50% of the members of a particular cluster are shown.

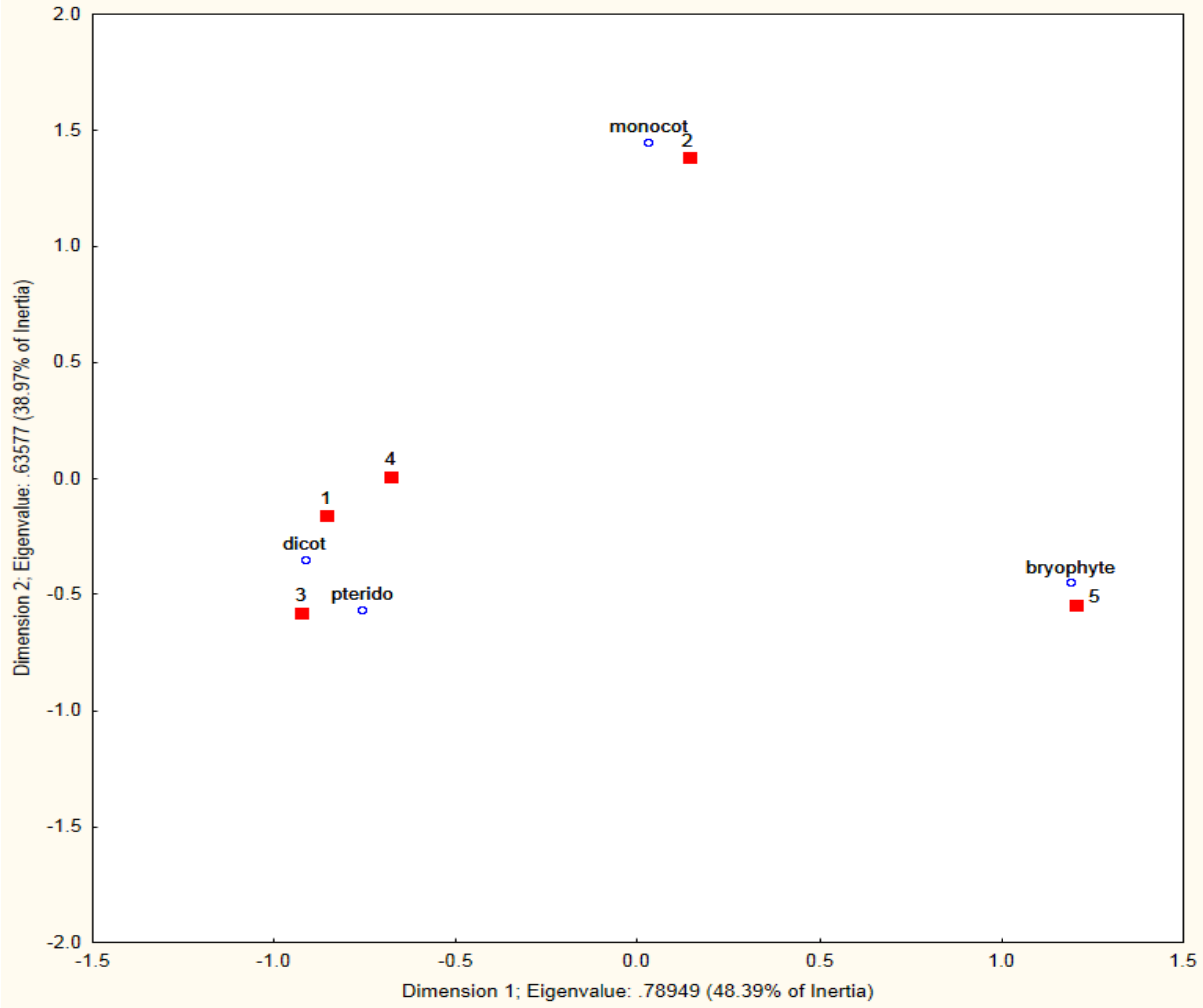

Figure 6.2 Joint plot of taxonomic group and K-mean plant nutrient concentration clusters. Clusters are: (1) average NPKNa/average CaMg concentrations, (2) average NPKNa/low CaMg concentrations, (3) average NPKNa/high CaMg concentrations, (4) high NPKNa/average CaMg concentrations, (5) lowNPKNa/low to average CaMg concentrations.

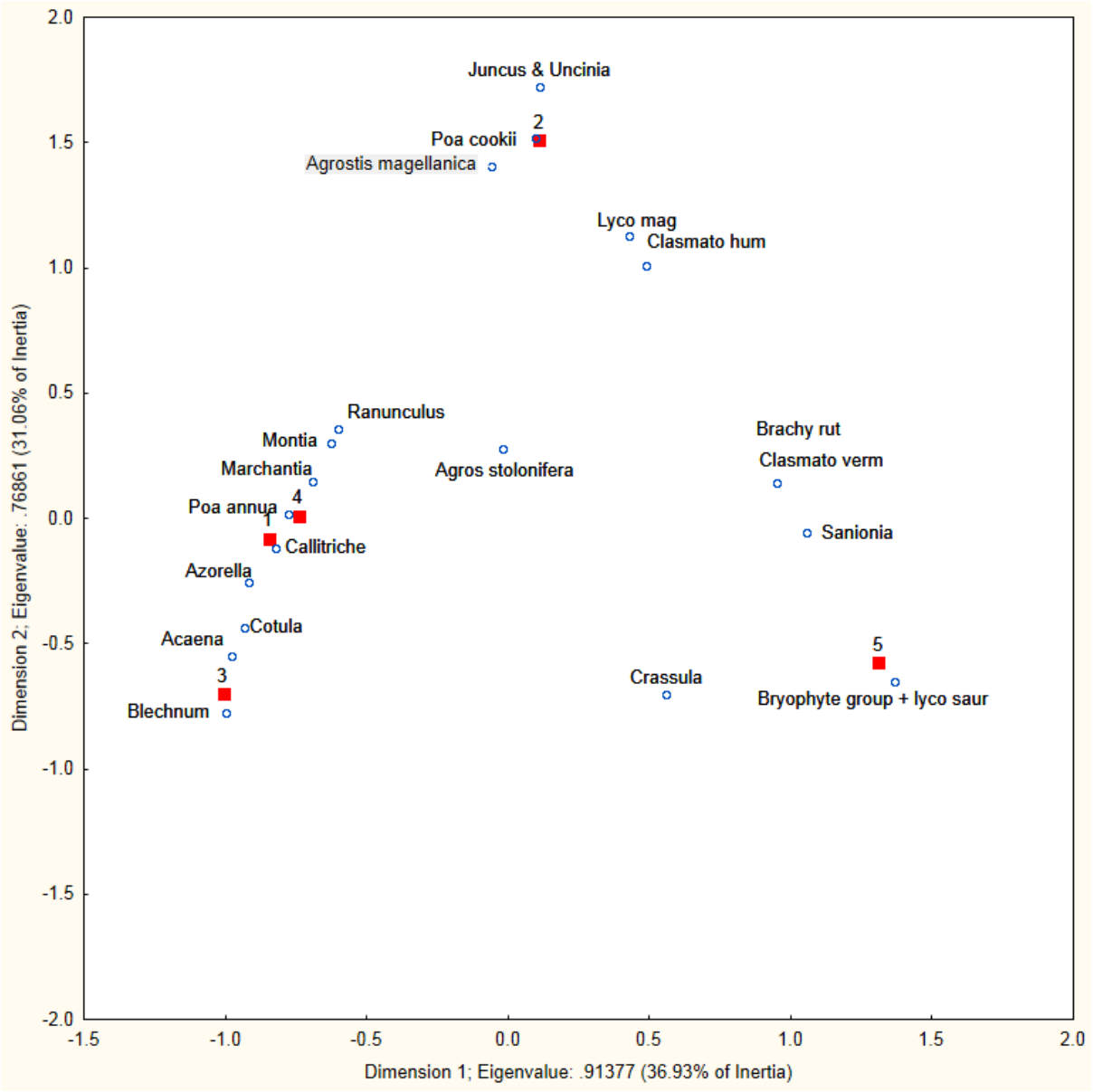

Figure 6.3 Joint plot of species and K-mean plant nutrient concentration clusters. Clusters are: (1) average NPKNa/average CaMg concentrations, (2) average NPKNa/low CaMg concentrations, (3) average NPKNa/high CaMg concentrations, (4) high NPKNa/average CaMg concentrations, (5) lowNPKNa/low to average CaMg concentrations.

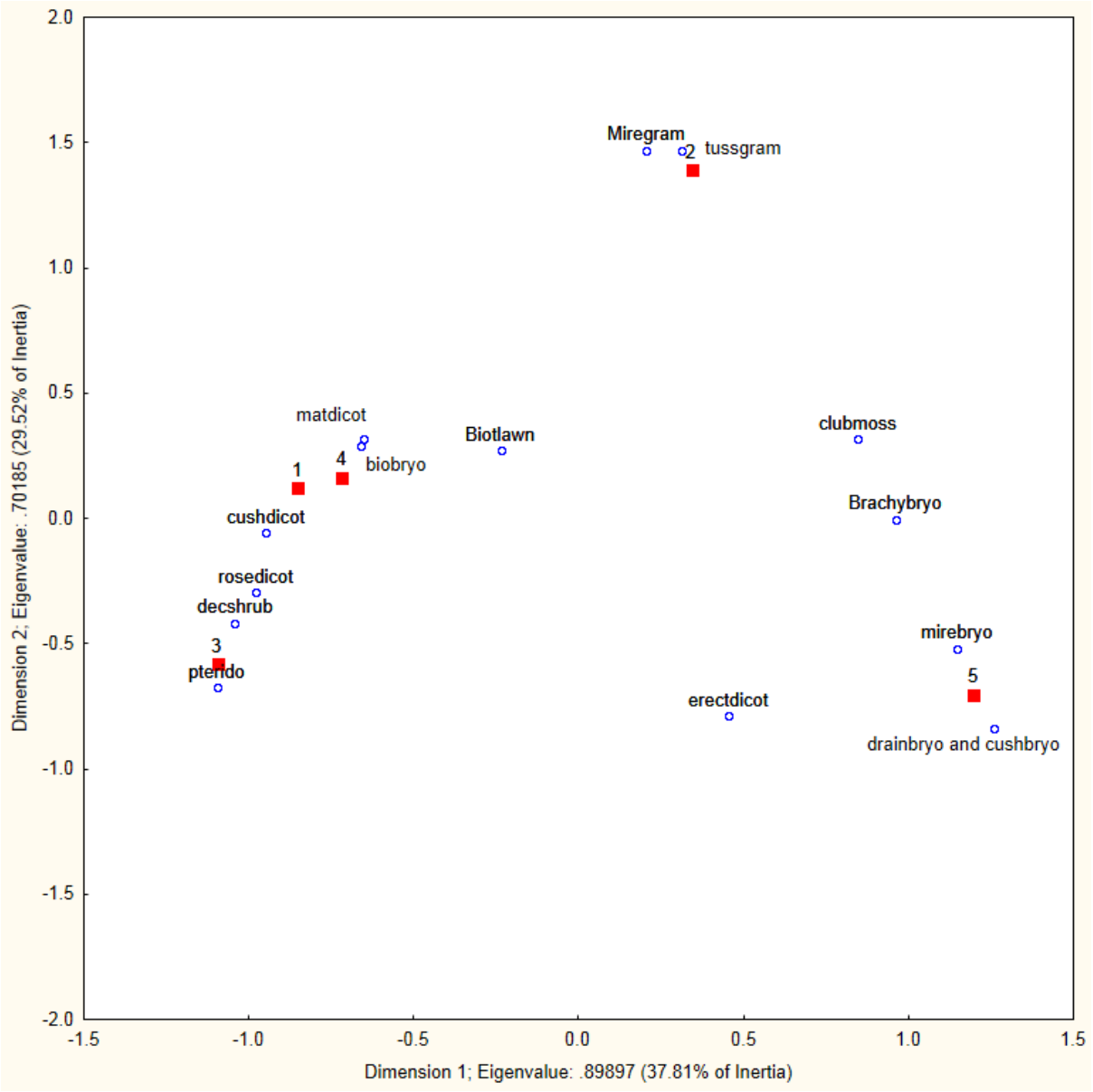

Figure 6.4 Joint plot of the Smith and Steenkamp (2001) guilds and K-mean plant nutrient concentration clusters. Clusters are: (1) average NPKNa/average CaMg concentrations, (2) average NPKNa/low CaMg concentrations, (3) average NPKNa/high CaMg concentrations, (4) high NPKNa/average CaMg concentrations, (5) lowNPKNa/low to average CaMg concentrations.

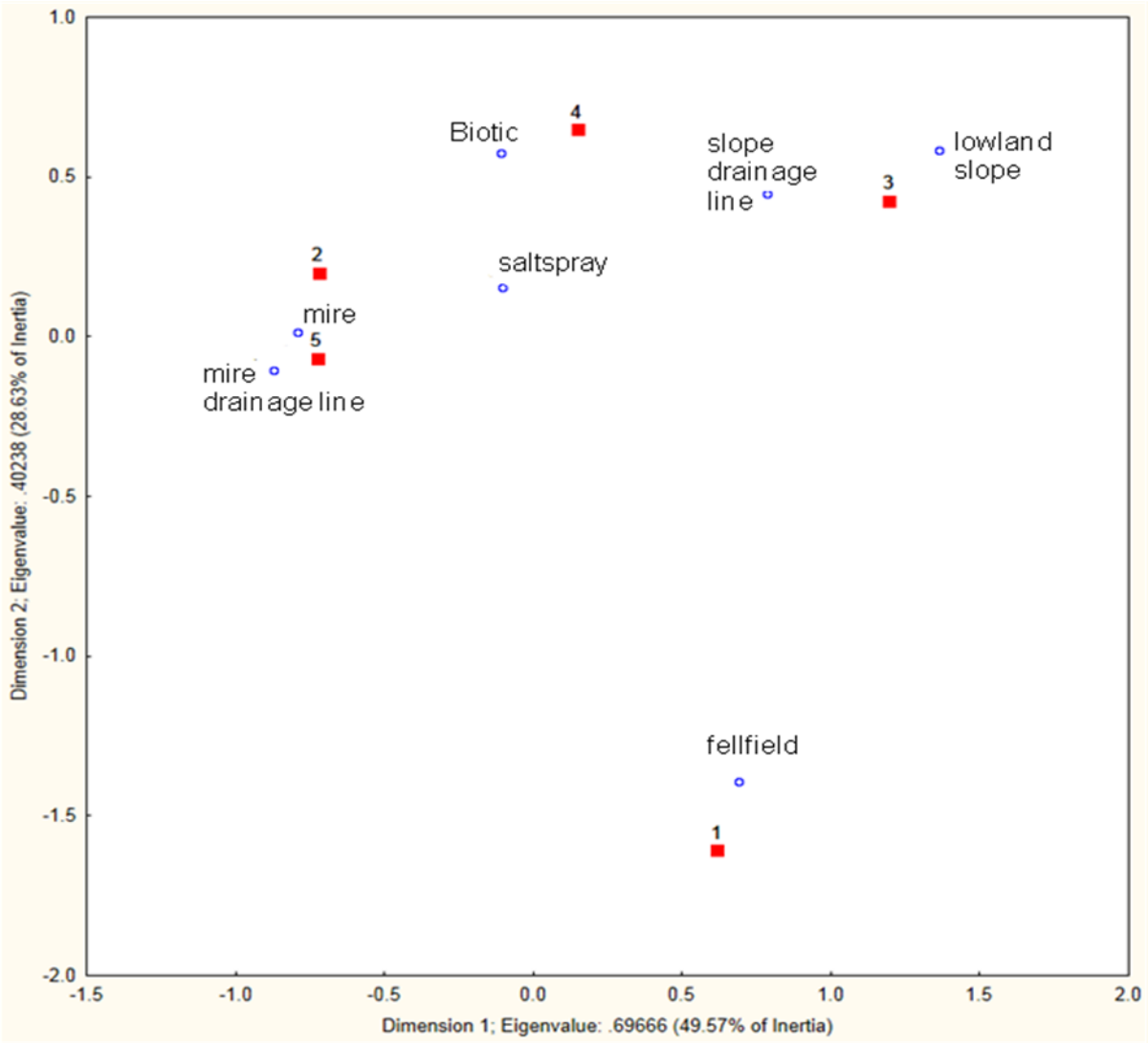

Figure 6.5 Joint plot of habitat and K-mean plant nutrient concentration clusters. . Clusters are: (1) average NPKNa/average CaMg concentrations, (2) average NPKNa/low CaMg concentrations, (3) average NPKNa/high CaMg concentrations, (4) high NPKNa/average CaMg concentrations, (5) lowNPKNa/low to average CaMg concentrations.

Tables

Table 2.1 The list of species that were sampled, as well as the altitudinal range and the range of distances from the sea that was sampled.

Species	Organ	N	Distance (m) from sea range	Altitudinal range (m.a.s.l.)
Acaena magellanica	Live leaf	68	23 - 5571	8 - 500
	Dead leaf	21	442 - 5571	39 - 500
	Stem	22	311 - 5571	26 - 500
	Root	18	442 - 5571	39 - 500
Agrostis stolonifera	Live leaf	4	58 - 1220	7 - 65
	Dead leaf	1	1220 - 1220	65 - 65
	Root	4	58 - 1220	7 - 65
Agrostis magellanica	Live leaf	89	23 - 6363	5 - 722
	Dead leaf	23	156 - 6363	26 - 722
	Root	24	156 - 6363	26 - 722
Andreaea sp.		11	2169 - 6508	167 - 760
Azorella selago	Live leaf	94	23 - 6363	5 - 722
	Dead leaf	36	119 - 6363	12 - 700
	Stem	36	119 - 6363	12 - 700
	Root	36	119 - 6363	12 - 700
Blechnum penna-marina	Live leaf	106	23 - 4819	5 - 388
	Dead leaf	50	72 - 3770	10 - 280
	Root	50	72 - 3770	10 - 280
Blepharidophyllum densifolium		19	114 - 4047	13 - 285
Brachythecium rutabulum		15	357 - 3759	32 - 289
Breutellia intergrifolia		25	311 - 5071	40 - 471
Bryum laevigatum		6	766 - 3276	50 - 206
Callitriche antarctica	Live leaf	9	27 - 151	2 - 13
	Root	6	27 - 132	2 - 13
Campylopus sp.		5	151 - 1531	10 - 82
Cerastium fontanum	Live leaf	1	1841 - 1841	90 - 90
Clasmatocolea humilus		19	36 - 1657	8 - 110
Clasmatocolea vermicilaris		6	43 - 541	8 - 44
Colobanthus kerguelensis	Live leaf	1	5571 - 5571	500 - 500
Cotula plumosa	Live leaf	25	20 - 600	1 – 70
	Root	15	20 - 600	1 - 70

Table 2.1 cont.

Species	Organ	N	Distance from Sea range	Altitudinal range (m.a.s.l.)
Crassula moschata	Live leaf	9	4 - 636	1 - 44
	Root	8	4 - 636	1 - 44
Cryptochila grandifolia (Now called *Syzigiella sonderi* but in text old name is retained for comparison with previous literature)		7	1208 - 5696	98 - 540
Ditrichum strictum		5	1436 - 6508	82 - 760
Grammitis poeppigeana	Live leaf	4	806 - 3319	70 - 204
	Dead leaf	4	806 - 3319	70 - 204
	Root	4	806 - 3319	70 - 204
Jamesoniella colorata (Now called *Syzigiella colorata* but in text old name is retained for comparison with previous literature)		56	119 - 5219	15 - 420
Juncus scheuchzerioudes	Live leaf	17	49 - 3787	8 - 282
	Dead leaf	14	194 - 3787	36 - 282
	Root	15	72 - 3787	10 - 282
Lycopodium magellanicum	Live leaf	9	72 - 3231	37 - 327
	Root	9	72 - 3231	37 - 327
Lycopodium saurus	Live leaf	5	537 - 2334	26 - 190
	Root	2	918 - 2334	50 - 133
Marchantia berteroana		6	45 - 1849	5 - 92
Montia fontana	Live leaf	9	24 - 2651	7 - 259
	Root	9	24 - 2651	7 - 259
Poa annua	Live leaf	2	53 - 1138	8 - 104
	Root	1	1138 - 1138	104 - 104
Poa cookii	Live leaf	28	27 - 3759	5 - 300
	Dead leaf	21	43 - 3759	9 - 300
	Root	22	43 - 3759	9 - 300
Polystichum marionense	Live leaf	4	515 - 1883	51 - 160
	Dead leaf	3	1147 - 1883	92 - 160
Ptychomnion densifolium		11	147 - 3276	13 - 239
Racomitrium lanuginosum		59	119 - 5798	15 - 592

Table 2.1 cont.

Species	Organ	N	Distance from Sea range	Altitudinal range (m.a.s.l.)
Ranunculus biternatus	Live leaf	5	100 - 1240	9 - 60
	Root	3	100 - 1240	9 - 60
Sanionia uncinata		24	49 - 3783	8 - 271
Uncinia compacta	Live leaf	16	250 - 3138	26 - 204
	Dead leaf	13	250 - 3138	27 - 204
	Root	13	250 - 3138	27 - 204

Table 3.1. Correlation coefficients (r) and their significances (p) for the relationships between (log) standardized nutrient concentrations of living vascular plant leaves and (log) distance inland or (log) altitude shown in Figures 3.1 to 3.6. Significant relationships ($p \leq 0.05$) are marked in **bold**. Particular relationships that deviate markedly form the overall pattern are shown in ***bold italics***.

Species		Nitrogen				Phosphorous				Potassium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	451	**-0.33**	**<0.001**	**-0.26**	**<0.001**	**-0.45**	**<0.001**	**-0.40**	**<0.001**	-0.06	0.220	-0.08	0.108
Acaena magellanica	67	**-0.31**	**0.010**	**-0.36**	**0.003**	**-0.39**	**0.001**	**-0.44**	**<0.001**	-0.17	0.162	**-0.25**	**0.038**
Agrostis magellanica	84	**-0.44**	**0.000**	**-0.34**	**0.001**	**-0.49**	**<0.001**	**-0.39**	**<0.001**	-0.13	0.249	-0.12	0.278
Azorella selago	93	**-0.40**	**<0.001**	**-0.28**	**0.007**	**-0.56**	**<0.001**	**-0.43**	**<0.001**	-0.03	0.776	0.04	0.678
Blechnum penna-marina	108	-0.02	0.856	0.08	0.405	**-0.38**	**<0.001**	**-0.37**	**<0.001**	0.15	0.121	0.09	0.368
Grammitis poeppigeana	4	-0.32	0.681	-0.65	0.345	-0.80	0.198	-0.44	0.565	0.43	0.574	-0.03	0.975
Juncus scheuchzerioides	15	**-0.56**	**0.031**	-0.46	0.085	**-0.72**	**0.002**	**-0.76**	**0.001**	0.27	0.335	0.18	0.528
Lycopdium magellanicum	8	-0.25	0.553	0.08	0.985	**-0.72**	**0.045**	-0.58	0.133	-0.10	0.810	0.13	0.756
Lycopodium saurus	5	***0.93***	***0.022***	***0.90***	***0.036***	***0.96***	***0.008***	***0.99***	***0.002***	0.80	0.101	0.79	0.115
Montia fontana	9	-0.35	0.357	-0.53	0.140	**-0.69**	**0.040**	**-0.75**	**0.020**	**-0.70**	**0.036**	**-0.75**	**0.020**
Poa cookii	28	**-0.65**	**<0.001**	**-0.61**	**0.001**	**-0.62**	**<0.001**	**-0.60**	**0.001**	-0.05	0.790	-0.14	0.488
Polystichum marionense	4	-0.91	0.092	-0.63	0.370	-0.85	0.147	-0.50	0.500	-0.93	0.066	**-0.99**	**0.016**
Ranunculus biternatus	5	-0.82	0.090	-0.77	0.127	-0.81	0.093	0.85	0.070	0.74	0.155	0.71	0.182
Uncinia compacta	17	0.09	0.739	0.22	0.421	-0.23	0.384	-0.13	0.626	-0.49	0.056	-0.36	0.174

Table 3.1 cont.

		Sodium				Magnesium				Calcium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*P*	*r*	*p*	*r*	*p*	*r*	*p*
All species	451	**-0.42**	**<0.001**	**-0.35**	**<0.001**	**-0.10**	**0.045**	-0.03	0.484	**0.24**	**<0.001**	**0.29**	**<0.001**
Acaena magellanica	67	**-0.42**	**<0.001**	**-0.33**	**0.007**	-0.08	0.507	-0.05	0.688	**0.62**	**<0.001**	**0.63**	**<0.001**
Agrostis magellanica	84	**-0.28**	**0.011**	-0.17	0.134	0.04	0.727	0.14	0.195	**0.28**	**0.009**	**0.39**	**<0.001**
Azorella selago	93	**-0.59**	**<0.001**	**-0.61**	**<0.001**	**-0.30**	**0.004**	**-0.23**	**0.033**	**0.26**	**0.012**	**0.29**	**0.006**
Blechnum penna-marina	108	**-0.35**	**0.001**	-0.21	0.053	**-0.20**	**0.042**	-0.08	0.435	0.14	0.153	0.16	0.096
Grammitis poeppigeana	4	***0.98***	***0.023***	0.87	0.130	**0.95**	**0.050**	**0.96**	**0.041**	0.84	0.151	0.87	0.129
Juncus scheuchzerioides	15	-0.35	0.204	-0.33	0.228	0.08	0.768	0.14	0.614	0.21	0.460	0.36	0.194
Lycopdium magellanicum	8	-0.26	0.527	-0.21	0.619	***0.74***	***0.036***	***0.88***	***0.004***	0.18	0.665	0.66	0.142
Lycopodium saurus	5	**-0.94**	**0.016**	**-0.90**	**0.042**	0.53	0.356	0.61	0.270	0.62	0.263	0.73	0.163
Montia fontana	9	-0.80	0.055	**-0.89**	**0.018**	-0.59	0.094	-0.43	0.247	-0.24	0.537	-0.02	0.969
Poa cookii	28	**-0.71**	**<0.001**	**-0.63**	**<0.001**	-0.24	0.215	-0.20	0.298	0.03	0.869	0.08	0.702
Polystichum marionense	4	-0.71	0.290	-0.76	0.240	-0.92	0.075	-0.93	0.073	***-0.98***	***0.025***	-0.81	0.193
Ranunculus biternatus	5	**-0.88**	**0.050**	-0.78	0.119	-0.74	0.154	-0.62	0.263	-0.39	0.516	-0.39	0.511
Uncinia compacta	17	**-0.51**	**0.043**	**-0.58**	**0.019**	0.25	0.343	0.35	0.178	**0.60**	**0.014**	**0.67**	**0.005**

Table 3.2. Correlation coefficients (*r*) and their significances (*p*) for the relationships between (log) standardized nutrient concentrations of dead vascular plant leaves and (log) distance inland or (log) altitude shown in Figures 3.7 to 3.12. Significant relationships ($p \leq 0.05$) are marked in **bold**.

Species		Nitrogen				Phosphorous				Potassium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	186	-0.11	0.146	-0.05	0.534	**-0.32**	**<0.001**	**-0.27**	**<0.001**	**-0.19**	**0.013**	**-0.22**	**0.004**
Acaena magellanica	20	-0.16	0.502	-0.23	0.325	-0.19	0.407	-0.24	0.307	0.25	0.286	0.32	0.163
Agrostis magellanica	23	-0.14	0.517	0.05	0.835	-0.30	0.161	-0.17	0.451	-0.23	0.392	-0.11	0.606
Azorella selago	36	-0.11	0.516	-0.06	0.707	**-0.54**	**<0.001**	**-0.44**	**0.007**	**-0.64**	**<0.001**	**-0.69**	**<0.001**
Blechnum penna-marina	53	0.03	0.833	0.12	0.400	-0.28	0.052	-0.20	0.154	-0.24	0.089	-0.21	0.137
Grammitis poeppigeana	4	0.82	0.180	0.50	0.501	0.81	0.188	0.44	0.561	0.81	0.186	0.59	0.412
Juncus scheuchzerioides	11	0.03	0.926	-0.04	0.903	-0.55	0.083	-0.46	0.154	-0.28	0.404	-0.46	0.150
Poa cookii	21	**-0.54**	**0.011**	**-0.49**	**0.020**	**-0.65**	**0.002**	-0.26	0.248	0.05	0.841	0.02	0.943
Uncinia compacta	14	0.01	0.974	0.16	0.591	-0.37	0.219	-0.27	0.381	-0.34	0.250	-0.39	0.186

Table 3.2 cont.

		Sodium				Magnesium				Calcium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	186	**-0.33**	**<0.001**	**-0.35**	**<0.001**	**-0.25**	**<0.001**	**-0.24**	**0.001**	0.04	0.626	-0.03	0.644
Acaena magellanica	20	**-0.52**	**0.019**	**-0.53**	**0.017**	**-0.52**	**0.020**	**-0.54**	**0.014**	**0.62**	**0.003**	**0.55**	**0.011**
Agrostis magellanica	23	-0.21	0.330	-0.34	0.115	-0.05	0.832	0.17	0.440	-0.01	0.968	-0.05	0.810
Azorella selago	36	**-0.46**	**0.013**	**-0.44**	**0.017**	**-0.54**	**<0.001**	**-0.52**	**0.001**	**-0.31**	**0.058**	**-0.38**	**0.024**
Blechnum penna-marina	53	**-0.34**	**0.047**	**-0.35**	**0.046**	**-0.19**	**0.180**	-0.26	0.072	-0.02	0.894	-0.12	0.400
Grammitis poeppigeana	4	0.76	0.237	0.37	0.609	0.57	0.614	-0.11	0.928	0.77	0.234	0.37	0.632
Juncus scheuchzerioides	11	-0.13	0.695	-0.33	0.317	-0.45	0.170	-0.32	0.333	0.25	0.461	0.11	0.743
Poa cookii	21	**-0.62**	**0.003**	**-0.50**	**0.019**	-0.36	0.110	-0.27	0.224	-0.03	0.890	0.04	0.858
Uncinia compacta	14	**-0.47**	**0.108**	**-0.52**	**0.070**	-0.17	0.572	-0.07	0.824	-0.21	0.501	-0.27	0.367

Table 3.3. *Correlation* coefficients (*r*) and their significances (*p*) for the relationships between (log) standardized stem nutrient concentrations and (log) distance inland or (log) altitude for *Acaena magellanica* and *Azorella selago*. Significant relationships ($p \leq 0.05$) are marked in **bold**..

Species		Nitrogen				Phosphorous				Potassium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Acaena magellanica	22	**0.52**	**0.012**	**0.55**	**0.008**	-0.2	0.363	-0.19	0.391	-0.04	0.866	-0.03	0.908
Azorella selago	36	0.19	0.255	0.22	0.206	**-0.63**	**<0.001**	**-0.62**	**<0.001**	-0.15	0.380	-0.27	0.110

		Sodium				Magnesium				Calcium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Acaena magellanica	22	-0.39	0.076	**-0.44**	**0.039**	0.03	0.884	-0.09	0.699	0.46	0.067	0.30	0.171
Azorella selago	36	-0.22	0.247	-0.23	0.233	**-0.33**	**0.047**	-0.24	0.167	-0.02	0.923	0.03	0.877

Table 3.4. Correlation coefficients (*r*) and their significances (*p*) for the relationships between (log) standardized nutrient concentrations in belowground organs (living material was not distinguished from dead material) of vascular plants and (log) distance inland or (log) altitude shown in Figures 3.13 to 3.18. Significant relationships ($p \leq 0.05$) are marked in **bold**.

Species		Nitrogen				Phosphorous				Potassium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	179	-0.06	0.370	0.00	0.987	**-0.30**	**<0.001**	**-027.**	**<0.001**	0.01	0.847	-0.04	0.584
Acaena magellanica	18	0.40	0.097	**0.50**	**0.035**	0.08	0.748	0.10	0.707	-0.25	0.323	-0.29	0.244
Agrostis magellanica	24	-0.30	0.152	-0.11	0.611	-0.38	0.065	-0.30	0.148	-0.37	0.073	**-0.41**	**0.047**
Azorella selago	34	0.12	0.514	0.13	0.456	-0.33	0.055	-0.27	0.119	-0.21	0.233	-0.31	0.072
Blechnum penna-marina	52	-0.17	0.231	-0.12	0.417	-0.26	0.069	-0.24	0.097	0.14	0.337	0.13	0.361
Grammitis poeppigeana	4	0.91	0.090	0.65	0.349	0.80	0.192	0.76	0.235	0.81	0.187	0.81	0.190
Juncus scheuchzerioides	11	-0.32	0.341	-0.197	0.652	**-0.87**	**<0.001**	**-0.92**	**<0.001**	-0.11	0.747	-0.25	0.466
Lycopdium magellanicum	7	0.41	0.366	0.60	0.153	-0.60	0.155	-0.38	0.403	-0.29	0.532	-0.44	0.345
Montia fontana	8	-0.33	0.430	-0.59	0.123	0.36	0.385	0.11	0.797	0.09	0.837	-0.21	0.617
Poa cookii	22	-0.42	0.052	-0.32	0.141	**-0.64**	**0.002**	**-0.59**	**0.004**	-0.25	0.259	-0.24	0.280
Uncinia compacta	14	-0.05	0.877	-0.00	0.993	-0.33	0.267	-0.33	0.273	-0.09	0.774	-0.03	0.912

Table 3.4 cont.

		Sodium				Magnesium				Calcium			
		Distance from sea		Altitude		Distance from sea		Altitude		Distance from sea		Altitude	
	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	176	**-0.34**	**<0.001**	**-0.32**	**<0.001**	0.10	0.165	0.13	0.082	0.11	0.115	0.09	0.224
Acaena magellanica	18	-0.42	0.082	-0.43	0.072	0.04	0.862	0.11	0.652	-0.02	0.937	-0.03	0.918
Agrostis magellanica	24	-0.16	0.468	-0.26	0.221	-0.25	0.234	-0.08	0.704	-0.09	0.668	-0.09	0.668
Azorella selago	34	-0.36	0.060	-0.35	0.069	0.11	0.550	0.18	0.297	0.16	0.355	0.17	0.342
Blechnum penna-marina	52	**-0.43**	**0.012**	-0.33	0.064	0.27	0.060	0.27	0.064	**0.33**	**0.020**	0.28	0.055
Grammitis poeppigeana	4	0.82	0.178	0.90	0.091	0.85	0.150	0.90	0.111	0.81	0.185	0.90	0.102
Juncus scheuchzerioides	11	-0.34	0.308	-0.36	0.275	0.11	0.753	0.10	0.773	0.09	0.783	0.07	0.846
Lycopdium magellanicum	7	-0.50	0.258	-0.51	0.244	0.10	0.870	0.42	0.480	-0.33	0.467	-0.31	0.505
Montia fontana	8	0.81	0.099	0.62	0.260	**0.74**	**0.040**	**0.82**	**0.013**	**0.73**	**0.040**	**0.78**	**0.022**
Poa cookii	22	**-0.62**	**0.002**	**-0.55**	**0.008**	-0.12	0.619	-0.08	0.744	-0.14	0.547	-0.13	0.550
Uncinia compacta	14	-0.40	0.179	-0.44	0.131	-0.06	0.843	-0.07	0.813	0.07	0.823	-0.23	0.450

Table 3.5. The relationship between the standardised concentrations in bryophytes and distance to the sea or altitude. Significant interactions ($p \leq 0.05$) are marked in **bold.**

		Nitrogen				Phosphorous				Potassium			
		Distance inland		Altitude		Distance inland		Altitude		Distance inland		Altitude	
Species	N	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	234	-0.05	0.409	-0.05	0..447	-0.11	0.086	-0.06	0.375	-0.07	0.322	-0.02	0.767
Blepharidophyllum densifolium	18	-0.06	0.828	-0.18	0.484	-0.30	0.220	-0.23	0.363	-0.33	0.176	-0.19	0.450
Brachythechium rutabulum	15	0.05	0.850	0.02	0.941	0.14	0.623	0.17	0.542	0.30	0.285	0.45	0.090
Breutelia integrifolia	25	-0.23	0.271	-0.21	0.306	-0.13	0.523	-0.27	0.187	-0.23	0.260	-0.24	0.245
Bryum laevigatum	6	0.08	0.874	-0.21	0.700	-0.18	0.729	-0.53	0.276	-0.10	0.853	-0.16	0.759
Clasmatocolea humilis	19	0.00	0.999	-0.00	0.990	**-0.53**	**0.018**	-0.35	0.137	**-0.71**	**<0.001**	**-0.70**	**0.001**
Jamesoniella colorata	57	-0.07	0.620	-0.09	0.526	-0.02	0.905	-0.01	0.914	-0.24	0.074	-0.15	0.282
Ptychomnion densifolium	10	0.17	0.630	0.27	0.457	0.05	0.893	0.11	0.765	-0.07	0.845	-0.10	0.778
Racomitrium lanuginosum	60	-0.21	0.116	-0.09	0.512	-0.03	0.814	0.15	0.248	0.11	0.388	0.22	0.099
Sanionia uncinata	24	0.14	0.504	0.10	0.657	-0.11	0.609	-0.11	0.616	0.07	0.744	0.03	0.885

Table 3.5 (cont.)

Species	N	Sodium				Magnesium				Calcium			
		Distance inland		Altitude		Distance inland		Altitude		Distance inland		Altitude	
		r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
All species	234	**-0.20**	**0.007**	-0.14	0.068	0.07	0.290	**0.14**	**0.030**	**0.29**	**<0.001**	**0.34**	**<0.001**
Blepharidophyllum densifolium	18	0.30	0.280	0.30	0.275	0.41	0.095	0.40	0.096	**0.52**	**0.027**	0.37	0.127
Brachythechium rutabulum	15	-0.26	0.417	0.05	0.887	-0.45	0.089	**-0.66**	**0.008**	0.08	0.768	0.13	0.655
Breutelia integrifolia	25	**-0.49**	**0.034**	**-0.48**	**0.036**	**-0.41**	**0.039**	-0.39	0.054	**0.44**	**0.029**	**0.42**	**0.039**
Bryum laevigatum	6	-0.01	0.989	-0.03	0.961	-0.53	0.276	-0.25	0.628	0.16	0.768	-0.05	0.929
Clasmatocolea humilis	19	0.01	0.971	0.03	0.924	0.04	0.881	0.07	0.765	0.34	0.154	0.44	0.062
Jamesoniella colorata	57	-0.23	0.142	-0.17	0.300	0.12	0.401	0.25	0.070	0.16	0.236	**0.27**	**0.050**
Ptychomnion densifolium	10	-0.01	0.980	-0.21	0.620	0.02	0.950	0.12	0.743	0.56	0.089	0.62	0.056
Racomitrium lanuginosum	60	-0.14	0.337	0.07	0.611	0.11	0.425	0.24	0.071	0.21	0.115	**0.38**	**0.003**
Sanionia uncinata	24	**-0.51**	**0.023**	**-0.57**	**0.009**	**0.41**	**0.048**	0.34	0.100	**0.46**	**0.025**	**0.42**	**0.039**

Table 4.1. Comparison of nutrient concentrations in vascular plant living leaves between sides of the island, and between four species. The comparisons were done by Ancova (for the between-sides comparison of Na concentration, a separate slopes analysis was used), with side of island and species as categorical predictors and distance inland as covariate. Means and 95% confidence intervals (C.I.) were calculated from the corresponding log statistics using the method of Olsson (2005). The all-species, between-side comparisons were based on standardized leaf nutrient concentrations. For the individual species comparisons (between sides and between species) the actual nutrient concentrations were used. Differences in superscripts left of mean indicate differences ($p \leq 0.05$) between sides.

		All species		*Acaena magellanica*		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nut-rient	Side	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)
N	East	316	^{b}0.97 (0.96-0.92)	42	^{ab}2.50 (2.38-2.63)	58	^{b}1.90 (1.82-1.98)	60	^{b}1.61^{c} (1.55-1.68)	75	^{b}1.49^{c} (1.44-1.55)
	West	78	^{a}1.12 (1.08-1.16)	13	^{a}2.79 (2.55-3.06)	13	^{a}2.17 (1.99-2.38)	18	^{a}1.99^{bc} (1.84-2.15)	18	^{a}1.76^{c} (1.63-1.90)
	North	27	^{ab}0.98 (0.92-1.04)	7	^{b}2.15 (1.90-2.43)	7	^{a}2.24 (1.98-2.54)	6	^{b}1.48^{b} (1.30-1.69)	7	^{ab}1.60^{b} (1.41-1.81)
	South	23	^{ab}1.00 (0.94-1.08)	5	^{ab}2.27 (1.96-2.63)	6	^{ab}2.12 (1.86-2.43)	8	^{ab}1.76^{ab} (1.57-1.97)	4	^{ab}1.49^{b} (1.26-1.75)
P	East	316	^{b}0.97 (0.94-1.03)	42	^{b}0.22 (0.20-0.24)	58	^{a}0.18 (0.17-0.20)	60	^{a}0.19^{ab} (0.17-0.20)	75	^{a}0.18^{b} (0.16-0.19)
	West	78	^{a}1.17 (1.09-1.25)	13	^{a}0.29 (0.25-0.35)	13	^{a}0.20 (0.17-0.24)	18	^{a}0.22^{ab} (0.19-0.25)	18	^{a}0.21^{b} (0.18-0.25)
	North	27	^{ab}0.99 (0.88-1.11)	7	^{b}0.19 (0.15-0.24)	7	^{a}0.21 (0.17-0.27)	6	^{a}0.16^{a} (0.12-0.20)	7	^{a}0.21^{a} (0.16-0.26)
	South	23	^{ab}0.95 (0.84-1.08)	5	^{ab}0.20 (0.15-0.26)	6	^{a}0.19 (0.14-0.24)	8	^{a}0.19^{a} (0.15-0.24)	4	^{a}0.14^{a} (0.10-0.19)
K	East	316	^{ab}1.02 (0.99-1.06)	42	^{a}1.41 (1.28-1.55)	58	^{ab}1.60 (1.48-1.74)	60	^{a}2.09^{a} (1.92-2.27)	75	^{b}1.27^{c} (1.19-1.37)
	West	78	^{b}0.95 (0.89-1.01)	13	^{a}1.60 (1.35-1.90)	13	^{b}1.34 (1.13-1.59)	18	^{a}2.04^{a} (1.77-2.36)	18	^{c}0.95^{c} (0.83-1.10)
	North	27	^{a}1.16 (1.04-1.30)	7	^{a}1.27 (1.00-1.60)	7	^{a}2.04 (1.62-2.57)	6	^{a}2.25^{a} (1.75-2.90)	7	^{a}1.78^{ab} (1.41-2.25)
	South	23	^{ab}0.99 (0.87-1.12)	5	^{a}1.11 (0.84-1.46)	6	^{ab}1.96 (1.53-2.52)	8	^{a}2.30^{a} (1.85-2.86)	4	^{bc}0.95^{b} (0.70-1.30)
Ca	East	316	^{b}1.00 (0.97-1.03)	42	^{a}1.19 (1.11 -1.27)	58	^{b}0.11 (0.10-0.12)	60	^{ab}0.78^{b} (0.73-0.83)	75	^{a}0.60^{c} (0.57-0.63)
	West	78	^{bc}0.97 (0.92-1.03)	13	^{a}1.15 (1.01 -1.30)	13	^{ab}0.11 (0.10-0.13)	18	^{ab}0.75^{b} (0.67-0.83)	18	^{a}0.59^{c} (0.53-0.65)
	North	27	^{c}0.85 (0.77-0.93)	7	^{a}1.21 (1.02 -1.44)	7	^{c}0.08 (0.07-0.09)	6	^{b}0.62^{b} (0.52-0.74)	7	^{a}0.54^{b} (0.46-0.64)
	South	23	^{a}1.15 (1.04-1.27)	5	^{a}1.31 (1.07 -1.60)	6	^{a}0.14 (0.12-0.17)	8	^{a}0.88^{b} (0.75-1.03)	4	^{a}0.68^{b} (0.54-0.85)
Mg	East	316	^{b}0.98 (0.95-1.00)	42	^{b}0.61 (0.57-0.66)	58	^{a}0.20 (0.19-0.22)	60	^{b}0.25^{c} (0.23-0.27)	75	^{a}0.85^{a} (0.81-0.90)
	West	78	^{a}1.09 (1.03-1.16)	13	^{ab}0.66 (0.58-0.75)	13	^{a}0.21 (0.18-0.24)	18	^{a}0.32^{c} (0.29-0.36)	18	^{a}0.80^{a} (0.72-0.90)
	North	27	^{ab}1.04 (0.94-1.15)	7	^{a}0.79 (0.66-0.94)	7	^{a}0.19 (0.16-0.23)	6	^{ab}0.26^{c} (0.22-0.32)	7	^{a}0.82^{a} (0.69-0.98)
	South	23	^{ab}1.06 (0.95-1.18)	5	^{ab}0.64 (0.52-0.79)	6	^{a}0.23 (0.19-0.27)	8	^{ab}0.26^{c} (0.22-0.30)	4	^{a}1.02^{a} (0.81-1.29)
Na 1600 m	East	316	^{b}0.84 (0.80-0.91)	42	^{a}0.41 (0.37 - 0.45)	58	^{b}0.25 (0.22 – 0.29)	60	^{a}0.58 (0.53 – 0.64)	75	^{b}0.26 (0.23 – 0.28)
	West	78	^{b}0.68 (0.57 – 0.83)	13	^{a}0.35 (0.26-0.48)	13	^{b}0.16 (0.10 – 0.27)	18	^{a}0.44 (0.36 – 0.56)	18	^{ab}0.30 (0.21 – 0.41)
	North	27	^{b}0.84 (0.76-0.92)	7	^{a}0.43 (0.31-0.59)	7	^{b}0.20 (0.14 – 0.27)	6	^{a}0.63 (0.54 – 0.71)	7	^{b}0.23 (0.20 – 0.26)
	South	23	^{a}1.04 (0.92-1.35)	5	^{a}0.45 (0.18-0.72)	6	^{a}0.55 (0.39 – 0.77)	8	^{a}0.71 (0.49 – 0.87)	4	^{a}0.36 (0.30 – 0.43)
Na 100 m	East	316	^{c}1.48 (1.41 – 1.56)	42	^{a}0.91 (0.63 – 1.31)	58	^{a}0.48 (0.38 – 0.60)	60	^{a}1.59 (1.15 – 2.21)	75	^{a}0.48 (0.39 – 0.61)
	West	78	^{b}1.79 (1.63 – 1.97)	13	^{a}1.36 (0.92 – 2.02)	13	^{a}0.62 (0.26 – 1.48)	18	^{a}2.58 (1.87 – 3.57)	18	^{a}0.72 (0.27 – 1.92)
	North	27	^{c}1.33 (1.13 – 1.56)	7	^{a}0.54 (0.30 – 1.00)	7	^{a}0.40 (0.20 – 0.82)	6	^{a}1.76 (1.01 – 3.09)	7	^{a}0.64 (0.21 – 1.89)
	South	23	^{a}2.68 (2.25 – 3.19)	5	^{a}2.13 (0.79 – 3.73)	6	^{a}1.02 (0.37 – 2.81)	8	^{a}2.05 (1.46 – 2.88)	4	^{a}0.84 (0.24 – 3.01)

Table 4.2. Comparison of nutrient concentrations in vascular plant dead leaves between sides of the island, and between four species. The comparisons were done by Ancova (for the between-side comparison of Na concentration, a separate slopes analysis was used), with side of island and species as categorical predictors and distance inland as covariate. Means and 95% confidence intervals (C.I.) were calculated from the corresponding log statistics using the method of Olsson (2005). The all-species, between-side comparisons were based on standardized nutrient concentrations. For the individual species comparisons (between sides and between species) the actual nutrient concentrations were used. Differences in superscripts left of mean indicate differences ($p \leq 0.05$) between sides.

		All species		*Acaena magellanica*		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nutrient	Side	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)
N	East	130	^{b}0.93 (0.90 - 0.97)	13	^{a}1.77 (1.57 - 1.99)	16	^{b}1.00 (0.90 - 1.12)	26	^{b}1.06 (0.97 - 1.15)	36	^{b}1.50 (1.40 - 1.61)
N	West	52	^{a}1.19 (1.12 - 1.27)	7	^{a}2.25 (1.92 - 2.64)	7	^{a}1.44 (1.23 - 1.70)	10	^{a}1.47 (1.28 - 1.68)	14	^{a}1.82 (1.62 - 2.04)
P	East	130	^{b}0.94 (0.87 - 1.02)	13	^{a}0.13 (0.11 - 0.16)	16	^{a}0.04 (0.03 - 0.05)	26	^{a}0.05 (0.04 - 0.06)	36	^{a}0.09 (0.08 - 0.11)
P	West	52	^{a}1.14 (1.01 - 1.28)	7	^{a}0.17 (0.12 - 0.22)	7	^{a}0.06 (0.04 - 0.07)	10	^{a}0.06 (0.05 - 0.07)	14	^{a}0.11 (0.09 - 0.13)
K	East	130	^{a}1.07 (0.98 - 1.17)	13	^{a}0.57 (0.45 - 0.74)	16	^{a}0.14 (0.10 - 0.19)	26	^{a}0.16 (0.13 - 0.19)	36	^{a}0.14 (0.12 - 0.16)
K	West	52	^{b}0.88 (0.77 - 1.01)	7	^{a}0.43 (0.31 - 0.60)	7	^{a}0.08 (0.06 - 0.12)	10	^{a}0.16 (0.12 -0.21)	14	^{b}0.10 (0.08 - 0.13)
Ca	East	130	^{a}1.04 (0.99 - 1.09)	13	^{a}1.10 (0.99 - 1.22)	16	^{a}0.12 (0.11 - 0.14)	26	^{a}0.85 (0.79 - 0.91)	36	^{a}0.90 (0.84 - 0.95)
Ca	West	52	^{b}0.89 (0.82 - 0.96)	7	^{a}0.89 (0.78 - 1.03)	7	^{a}0.12 (0.11 - 0.14)	10	^{a}0.73 (0.65 - 0.82)	14	^{b}0.75 (0.68 - 0.83)
Mg	East	130	^{b}0.98 (0.92 - 1.03)	13	^{a}0.55 (0.49 - 0.63)	16	^{b}0.15 (0.14 - 0.17)	26	^{b}0.31 (0.28 - 0.34)	36	^{a}0.69 (0.64 - 0.74)
Mg	West	52	^{a}1.11 (1.02 - 1.21)	7	^{a}0.55 (0.46 - 0.66)	7	^{a}0.20 (0.17 - 0.24)	10	^{a}0.38 (0.33 - 0.44)	14	^{a}0.62 (0.55 - 0.70)
Na	East	130	^{a}0.99 (0.86 – 0.90)	13	^{a}0.25 (0.18 – 0.34)	16	^{a}0.08 (0.06 – 0.12)	26	^{a}0.14 (0.10 – 0.20)	36	^{a}0.09 (0.07 – 0.12)
1600 m	West	52	^{b}0.64 (0.54 – 0.75)	7	^{b}0.15 (0.12 – 0.18)	7	^{b}0.03 (0.02 – 0.04)	10	0.10^{a} (0.07 - 0.15)	14	^{a}0.07 (0.05 – 0.10)
Na	East	130	^{a}1.72 (1.22 – 2.34)		^{a}0.63 (0.88 – 1.73)	16	^{a}0.07 (0.04 – 0.12)	26	^{a}1.30 (0.39 – 2.92)	36	^{a}0.09 (0.03 – 0.34)
100 m	West	52	^{a}1.97 (1.05 – 4.95)		^{a}0.90 (0.35 – 2.64)	7	^{a}0.22 (0.07 – 0.66)	10	^{a}2.47 (0.45 – 4.81)	14	^{a}0.18 (0.10 – 0.31)

Table 4.3. Comparison of nutrient concentrations in vascular plant stems between the west and the east sides of the island, and between two species. The comparisons were done by Ancova (for the between-side comparison of Na, a separate slopes analysis was used), with side of island and species as categorical predictors and distance inland as covariate. Means and 95% confidence intervals (C.I.) were calculated from the corresponding log statistics using the method of Olsson (2005). The all-species, between-side comparisons were based on standardized stem nutrient concentrations. For the individual species comparisons (between sides and between species) the actual nutrient concentrations were used. Differences in superscripts left of mean indicate differences ($p \leq 0.05$) between sides.

		Acaena magellanica		*Azorella selago*	
Nutrient	Side	N	Mean (C.I.)	N	Mean (C.I.)
N	East	15	^{b}1.23 (1.11 - 1.36)	26	^{b}1.17 (1.06 - 1.29)
	West	7	^{a}1.54 (1.33 - 1.78)	10	^{a}1.49 (1.27 - 1.74)
P	East	15	^{a}0.14 (0.12 - 0.17)	26	^{a}0.14 (0.12 - 0.15)
	West	7	^{a}0.13 (0.10 - 0.17)	10	^{a}0.14 (0.11 - 0.16)
K	East	15	^{a}0.64 (0.52 - 0.80)	26	^{a}0.81 (0.74 - 0.88)
	West	7	^{a}0.45 (0.33 - 0.62)	10	^{b}0.66 (0.58 - 0.76)
Ca	East	15	^{a}0.37 (0.30 - 0.46)	26	^{a}0.52 (0.48 - 0.57)
	West	7	^{a}0.28 (0.21 - 0.38)	10	^{b}0.39 (0.35 - 0.44)
Mg	East	15	^{a}0.27 (0.24 - 0.31)	26	^{a}0.38 (0.36 - 0.40)
	West	7	^{a}0.26 (0.22 - 0.31)	10	^{a}0.39 (0.36 - 0.42)
Na	East	15	^{a}0.07 (0.05 - 0.09)	26	^{a}0.17 (0.13 - 0.23)
1600 m	West	7	^{a}0.05 (0.02 - 0.19)	10	^{b}0.08 (0.05 - 0.13)
Na	East	15	^{a}0.67 (0.15 - 2.94)	26	^{a}1.41 (0.70 - 3.82)
100 m	West	7	^{a}1.22 (0.07 - 2.62)	10	^{a}2.68 (0.58 - 8.76)

Table 4.4. Comparison of nutrient concentrations in vascular belowground organs (roots and rhizomes) between the west and the east sides of the island, and between two species. The comparisons were done by Ancova (for the between-side comparison of Na, a separate slopes analysis was used) on the log concentrations, with side of island and species as categorical predictors and (log) distance inland as covariate. Means and 95% confidence intervals (C.I.) were calculated from the corresponding log statistics using the method of Olsson (2005). The all-species, between-side comparisons were based on standardized nutrient concentrations. For the individual species comparisons (between sides and between species) the actual (log) nutrient concentrations were used. Differences in superscripts left of mean indicate differences ($p \leq 0.05$) between sides.

		All species		*Acaena magellanica*		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nutrient	Side	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)
N	East	147	[b]0.95 (0.91 - 0.99)	13	[b]1.08 (0.95 - 1.23)	17	[b]1.29 (1.11 - 1.50)	25	[a]1.14 (1.02 - 1.27)	35	[a]1.26 (1.15 - 1.39)
N	West	50	[a]1.13 (1.05 - 1.22)	5	[a]1.60 (1.31 - 1.95)	7	[a]1.68 (1.35 - 2.09)	9	[a]1.32 (1.11 - 1.57)	14	[a]1.51 (1.29 - 1.76)
P	East	147	[a]0.97 (0.90 - 1.05)	13	[a]0.13 (0.10 - 0.15)	17	[a]0.15 (0.11 - 0.21)	25	[a]0.15 (0.12 - 0.19)	35	[a]0.15 (0.12 - 0.18)
P	West	50	[a]1.04 (0.91 - 1.19)	5	[a]0.12 (0.09 - 0.16)	7	[a]0.14 (0.08 - 0.22)	9	[a]0.13 (0.10 - 0.19)	14	[a]0.18 (0.13 - 0.24)
K	East	147	[a]1.04 (0.97 - 1.11)	13	[a]0.50 (0.41 - 0.61)	17	[a]0.44 (0.37 - 0.54)	25	[a]0.80 (0.72 - 0.88)	35	[a]0.54 (0.50 - 0.58)
K	West	50	[a]0.94 (0.84 - 1.05)	5	[b]0.27 (0.19 - 0.38)	7	[a]0.44 (0.32 - 0.59)	9	[b]0.61 (0.52 - 0.72)	14	[b]0.46 (0.41 - 0.52)
Ca	East	147	[a]1.03 (0.97 - 1.09)	13	[a]0.22 (0.18 - 0.26)	17	[a]0.09 (0.07 - 0.11)	25	[a]0.52 (0.46 - 0.58)	35	[a]0.46 (0.41 - 0.51)
Ca	West	50	[b]0.87 (0.79 - 0.97)	5	[b]0.13 (0.10 - 0.18)	7	[a]0.08 (0.06 - 0.11)	9	[a]0.44 (0.37 - 0.53)	14	[a]0.37 (0.31 - 0.45)
Mg	East	143	[a]1.02 (0.95 - 1.10)	13	[a]0.23 (0.20 - 0.27)	17	[a]0.17 (0.14 - 0.21)	25	[a]0.36 (0.33 - 0.39)	35	[a]0.45 (0.42 - 0.48)
Mg	West	49	[a]1.08 (0.95 - 1.23)	5	[a]0.19 (0.15 - 0.24)	7	[a]0.24 (0.18 - 0.31)	9	[a]0.36 (0.32 - 0.41)	14	[a]0.44 (0.39 - 0.49)
Na	East	120	[a]1.626 (1.35 - 1.95)	13	[a]0.12 (0.04 - 0.31)	17	[b]0.09 (0.05 - 0.17)	19	[b]0.48 (0.19 - 1.25)	19	[a]0.14 (0.09 - 0.22)
300 m	West	50	[a]2.566 (1.66 - 3.98)	5	[a]0.29 (0.08 – 0.60)	7	[a]0.46 (0.22 - 0.95)	9	[a]1.22 (0.44 - 3.36)	4	[a]0.13 (0.07 - 0.24)
Na	East	120	[a]0.984 (0.88 - 1.10)	13	[a]0.03 (0.02 - 0.04)	17	[a]0.15 (0.11 - 0.19)	19	[a]0.15 (0.11 - 0.20)	19	[a]0.07 (0.06 - 0.10)
1600 m	West	50	[a]0.788 (0.59 - 1.05)	5	[a]0.02 (0.01 - 0.07)	7	[a]0.08 (0.04 - 0.15)	9	[b]0.07 (0.04 - 0.11)	4	[a]0.06 (0.04 - 0.09)

Table 4.5. Comparison of nutrient concentrations in bryophytes between sides of the island. For N, P, K, and Mg the comparisons were by anova. For Ca and Na, comparisons were by ancova of the log concentrations with log distance inland as covariate, and the means and 95% confidence intervals (C.I.) calculated from the corresponding log statistics using the method of Olsson (2005). The all-species, between-side comparisons were based on standardized leaf nutrient concentrations. The between-side comparisons for *Racomitrium lanuginosum* were done on the actual nutrient concentrations. Differences in superscripts indicate differences ($p \leq 0.05$) between sides.

		All bryophytes		*R. lanuginosum*	
Nutrient	Side	N	Mean (95% CL)	N	Mean (95% CL)
N	East	169	^{a}0.95 (0.91 - 0.99)	45	^{a}0.34 (0.31 - 0.36)
N	West	46	^{b}1.12 (0.99 - 1.25)	3	^{ab}0.32 (0.18 - 0.46)
N	North	7	^{ab}1.24 (0.92 - 1.57)	6	^{ab}0.41 (0.27 - 0.55)
N	South	11	^{b}1.33 (1.15 - 1.51)	6	^{b}0.43 (0.40 - 0.46)
P	East	169	^{a}0.99 (0.93 - 1.04)	45	^{ab}0.02 (0.02 - 0.02)
P	West	46	^{ab}0.99 (0.85 - 1.13)	3	^{a}0.01 (0.00 - 0.03)
P	North	7	^{ab}0.91 (0.60 - 1.22)	6	^{a}0.02 (0.01 - 0.03)
P	South	11	^{b}1.30 (1.09 - 1.51)	6	^{b}0.03 (0.02 - 0.04)
K	East	169	^{a}0.95 (0.89 - 1.02)	45	^{a}0.06 (0.05 - 0.07)
K	West	46	^{a}0.97 (0.86 - 1.07)	3	^{a}0.04 (0.01 - 0.07)
K	North	7	^{b}1.58 (1.21 - 1.95)	6	^{b}0.11 (0.08 - 0.13)
K	South	11	^{b}1.46 (1.28 - 1.64)	6	^{b}0.10 (0.09 - 0.10)
Mg	East	169	^{ab}0.98 (0.94 - 1.01)	45	^{a}0.13 (0.11 - 0.14)
Mg	West	46	^{ab}1.04 (0.97 - 1.11)	3	^{a}0.11 (0.09 - 0.31)
Mg	North	7	^{a}0.75 (0.66 - 0.85)	6	^{a}0.09 (0.08 - 0.11)
Mg	South	11	^{b}1.22 (1.01 - 1.43)	6	^{a}0.16 (0.11 - 0.21)
Ca	East	169	^{b}0.95 (0.91 - 0.99)	45	^{a}0.10 (0.09 - 0.11)
Ca	West	46	^{b}1.10 (1.01 - 1.19)	3	^{a}0.10 (0.07 - 0.14)
Ca	North	7	^{a}0.80 (0.65 - 0.99)	6	^{a}0.09 (0.07 - 0.11)
Ca	South	11	^{c}1.40 (1.16 - 1.69)	6	^{b}0.17 (0.13 - 0.21)
Na	East	169	^{a}1.00 (0.92 - 1.09)	45	^{a}0.05 (0.04 - 0.06)
Na	West	46	^{a}0.90 (0.79 - 1.03)	3	^{ab}0.05 (0.03 - 0.09)
Na	North	7	^{a}0.92 (0.66 - 1.28)	6	^{a}0.04 (0.03 - 0.06)
Na	South	11	^{b}1.58 (1.18 - 2.13)	6	^{b}0.09 (0.06 - 0.14)

Table 5.1. Comparison of living leaf nutrient concentrations between four vascular plant species in between sides of the island, and. The comparisons were done by ancova with log concentration as dependent variable, species and side of island as categorical predictors ,and log distance inland as covariate. Means and 95% confidence intervals (C.I.) were calculated from the corresponding log statistics using the method of Olsson (2005). Differences in superscripts left of mean indicate differences ($p \leq 0.05$) in row means, i.e. between species.

			Acaena magellanica		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nutrient	Organ	Side	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)	N	Mean (C.I.)
Nitrogen	Living leaf	East	42	^{a}2.50 (2.38-2.63)	58	^{b}1.90 (1.82-1.98)	60	^{c}1.61 (1.55-1.68)	75	^{c}1.49 (1.44-1.55)
		West	13	^{a}2.79 (2.55-3.06)	13	^{b}2.17 (1.99-2.38)	18	^{bc}1.99 (1.84-2.15)	18	^{c}1.76 (1.63-1.90)
		North	7	^{a}2.15 (1.90-2.43)	7	^{a}2.24 (1.98-2.54)	6	^{b}1.48 (1.30-1.69)	7	^{b}1.60 (1.41-1.81)
		South	5	^{a}2.27 (1.96-2.63)	6	^{a}2.12 (1.86-2.43)	8	^{ab}1.76 (1.57-1.97)	4	^{b}1.49 (1.26-1.75)
	Dead leaf	East	13	^{a}1.77 (1.57 - 1.99)	16	^{b}1.00 (0.90 - 1.12)	26	^{b}1.06 (0.97 - 1.15)	36	^{a}1.50 (1.40 - 1.61)
		West	7	^{a}2.25 (1.92 - 2.64)	7	^{b}1.44 (1.23 - 1.70)	10	^{b}1.47 (1.28 - 1.68)	14	^{ab}1.82 (1.62 - 2.04)
	Stem	East	15	^{a}1.23 (1.11 - 1.36)	26	^{a}1.17 (1.06 - 1.29)				
		West	7	^{a}1.54 (1.33 - 1.78)	10	^{a}1.49 (1.27 - 1.74)				
	Root	East	13	^{a}1.08 (0.95 - 1.23)	17	^{a}1.29 (1.11 - 1.50)	25	^{a}1.14 (1.02 - 1.27)	35	^{a}1.26 (1.15 - 1.39)
		West	5	^{a}1.60 (1.31 - 1.95)	7	^{a}1.68 (1.35 - 2.09)	9	^{a}1.32 (1.11 - 1.57)	14	^{a}1.51 (1.29 - 1.76)
Phosphorus	Living leaf	East	42	^{a}0.22 (0.20-0.24)	58	^{b}0.18 (0.17-0.20)	60	^{ab}0.19 (0.17-0.20)	75	^{b}0.18 (0.16-0.19)
		West	13	^{a}0.29 (0.25-0.35)	13	^{b}0.20 (0.17-0.24)	18	^{ab}0.22 (0.19-0.25)	18	^{b}0.21 (0.18-0.25)
		North	7	^{a}0.19 (0.15-0.24)	7	^{a}0.21 (0.17-0.27)	6	^{a}0.16 (0.12-0.20)	7	^{a}0.21 (0.16-0.26)
		South	5	^{a}0.20 (0.15-0.26)	6	^{a}0.19 (0.14-0.24)	8	^{a}0.19 (0.15-0.24)	4	^{a}0.14 (0.10-0.19)
	Dead leaf	East	13	^{a}0.13 (0.11 - 0.16)	16	^{c}0.04 (0.03 - 0.05)	26	^{c}0.05 (0.04 - 0.06)	36	^{b}0.09 (0.08 - 0.11)
		West	7	^{a}0.17 (0.12 - 0.22)	7	^{b}0.06 (0.04 - 0.07)	10	^{b}0.06 (0.05 - 0.07)	14	^{a}0.11 (0.09 - 0.13)
	Stem	East	15	^{a}0.14 (0.12 - 0.17)	26	^{a}0.14 (0.12 - 0.15)				
		West	7	^{a}0.13 (0.10 - 0.17)	10	^{a}0.14 (0.11 - 0.16)				
	Root	East	13	^{a}0.13 (0.10 - 0.15)	17	^{a}0.15 (0.11 - 0.21)	25	^{a}0.15 (0.12 - 0.19)	35	^{a}0.15 (0.12 - 0.18)
		West	5	^{a}0.12 (0.09 - 0.16)	7	^{a}0.14^{a}(0.08 - 0.22)	9	^{a}0.13 (0.10 - 0.19)	14	^{a}0.18 (0.13 - 0.24)
Potassium	Living leaf	East	42	^{bc}1.41 (1.28-1.55)	58	^{b}1.60 (1.48-1.74)	60	^{a}2.09 (1.92-2.27)	75	^{c}1.27 (1.19-1.37)
		West	13	^{ab}1.60 (1.35-1.90)	13	^{b}1.34 (1.13-1.59)	18	^{a}2.04 (1.77-2.36)	18	^{c}0.95 (0.83-1.10)
		North	7	^{b}1.27 (1.00-1.60)	7	^{a}2.04 (1.62-2.57)	6	^{a}2.25 (1.75-2.90)	7	^{ab}1.78^{b} (1.41-2.25)
		South	5	^{b}1.11 (0.84-1.46)	6	^{a}1.96 (1.53-2.52)	8	^{a}2.30 (1.85-2.86)	4	^{b}0.95 (0.70-1.30)

(Table 5.1 cont.)			*Acaena magellanica*		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nutrient	*Organ*	*Side*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*
	Dead leaf	East	13	[a]0.57 (0.45 - 0.74)	16	[b]0.14 (0.10 - 0.19)	26	[b]0.16 (0.13 - 0.19)	36	[b]0.14 (0.12 - 0.16)
		West	7	[a]0.43 (0.31 - 0.60)	7	[c]0.08 (0.06 - 0.12)	10	[b]0.16 (0.12 -0.21)	14	[c]0.10 (0.08 - 0.13)
	Stem	East	15	[b]0.64 (0.52 - 0.80)	26	[a]0.81 (0.74 - 0.88)				
		West	7	[b]0.45 (0.33 - 0.62)	10	[a]0.66 (0.58 - 0.76)				
	Root	East	13	[b]0.50 (0.41 - 0.61)	17	[b]0.44[b] (0.37 - 0.54)	25	[a]0.80 (0.72 - 0.88)	35	[b]0.54 (0.50 - 0.58)
		West	5	[c]0.27 (0.19 - 0.38)	7	[abc]0.44 (0.32 - 0.59)	9	[a]0.61 (0.52 - 0.72)	14	[b]0.46 (0.41 - 0.52)
Calcium	Living leaf	East	42	[a]1.19 (1.11 -1.27)	58	[d]0.11 (0.10-0.12)	60	[b]0.78 (0.73-0.83)	75	[c]0.60 (0.57-0.63)
		West	13	[a]1.15 (1.01 -1.30)	13	[d]0.11 (0.10-0.13)	18	[b]0.75 (0.67-0.83)	18	[c]0.59 (0.53-0.65)
		North	7	[a]1.21 (1.02 -1.44)	7	[c]0.08 (0.07-0.09)	6	[b]0.62 (0.52-0.74)	7	[b]0.54 (0.46-0.64)
		South	5	[a]1.31 (1.07 -1.60)	6	[c]0.14 (0.12-0.17)	8	[b]0.88 (0.75-1.03)	4	[b]0.68 (0.54-0.85)
	Dead leaf	East	13	[a]1.10 (0.99 - 1.22)	16	[c]0.12 (0.11 - 0.14)	26	[b]0.85 (0.79 - 0.91)	36	[b]0.90 (0.84 - 0.95)
		West	7	[a]0.89 (0.78 - 1.03)	7	[b]0.12 (0.11 - 0.14)	10	[a]0.73 (0.65 - 0.82)	14	[a]0.75 (0.68 - 0.83)
	Stem	East	15	[b]0.37 (0.30 - 0.46)	26	[a]0.52 (0.48 - 0.57)				
		West	7	[b]0.28 (0.21 - 0.38)	10	[a]0.39 (0.35 - 0.44)				
	Root	East	13	[b]0.22 (0.18 - 0.26)	17	[c]0.09 (0.07 - 0.11)	25	[a]0.52 (0.46 - 0.58)	35	[a]0.46 (0.41 - 0.51)
		West	5	[b]0.13 (0.10 - 0.18)	7	[c]0.08 (0.06 - 0.11)	9	[a]0.44 (0.37 - 0.53)	14	[a]0.37 (0.31 - 0.45)
Magnesium	Living leaf	East	42	[b]0.61 (0.57-0.66)	58	[d]0.20 (0.19-0.22)	60	[c]0.25 (0.23-0.27)	75	[a]0.85 (0.81-0.90)
		West	13	[a]0.66 (0.58-0.75)	13	[d]0.21 (0.18-0.24)	18	[c]0.32 (0.29-0.36)	18	[a]0.80 (0.72-0.90)
		North	7	[a]0.79 (0.66-0.94)	7	[c]0.19 (0.16-0.23)	6	[c]0.26 (0.22-0.32)	7	[a]0.82 (0.69-0.98)
		South	5	[b]0.64 (0.52-0.79)	6	[c]0.23 (0.19-0.27)	8	[c]0.26 (0.22-0.30)	4	[a]1.02 (0.81-1.29)
	Dead leaf	East	13	[b]0.55 (0.49 - 0.63)	16	[d]0.15 (0.14 - 0.17)	26	[c]0.31 (0.28 - 0.34)	36	[a]0.69 (0.64 - 0.74)
		West	7	[a]0.55 (0.46 - 0.66)	7	[c]0.20 (0.17 - 0.24)	10	[b]0.38 (0.33 - 0.44)	14	[a]0.62 (0.55 - 0.70)
	Stem	East	15	[b]0.27 (0.24 - 0.31)	26	[a]0.38 (0.36 - 0.40)				
		West	7	[b]0.26 (0.22 - 0.31)	10	[a]0.39 (0.36 - 0.42)				
	Root	East	13	[c]0.23 (0.20 - 0.27)	17	[d]0.17 (0.14 - 0.21)	25	[b]0.36 (0.33 - 0.39)	35	[a]0.45 (0.42 - 0.48)
		West	5	[c]0.19 (0.15 - 0.24)	7	[c]0.24 (0.18 - 0.31)	9	[b]0.36 (0.32 - 0.41)	14	[a]0.44 (0.39 - 0.49)

(Table 5.1 cont.)			*Acaena magellanica*		*Agrostis magellanica*		*Azorella selago*		*Blechnum penna-marina*	
Nutrient	*Organ*	*Side*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*	*N*	*Mean (C.I.)*
Sodium	Living leaf	East	42	^{b}0.45 (0.40 – 0.50)	58	^{c}0.28 (0.25 – 0.31)	53	^{a}0.63 (0.57 – 0.70)	59	^{c}0.28 (0.25 – 0.31)
		West	13	^{ab}0.50 (0.38 – 0.66)	13	^{c}0.19 (0.15 – 0.25)	18	^{a}0.61 (0.48 – 0.77)	18	^{b}0.32 (0.26 – 0.41)
		North	7	^{b}0.44 (0.38 – 0.51)	7	^{c}0.23 (0.19 – 0.26)	6	^{a}0.69 (0.59 – 0.82)	7	^{c}0.25 (0.21 – 0.29)
		South	5	^{a}0.75 (0.57 – 0.99)	6	^{a}0.65 (0.50 – 0.83)	8	^{a}0.66 (0.53 – 0.82)	4	^{b}0.38 (0.27 – 0.51)
	Dead leaf	East	13	^{a}0.21 (0.16 – 0.27)	16	^{c}0.07 (0.06 – 0.09)	19	^{b}0.13 (0.10 – 0.16)	20	^{c}0.08 (0.07 – 0.10)
		West	7	^{a}0.20 (0.13 – 0.31)	7	^{c}0.04 (0.02 – 0.06)	10	^{ab}0.13 (0.09 – 0.19)	14	^{b}0.08 (0.06 – 0.11)
	Stem	East	15	^{b}0.06 (0.05 – 0.08)	26	^{a}0.16 (0.12 – 0.20)				
		West	7	^{b}0.06 (0.04 – 0.08)	10	^{a}0.11 (0.08 – 0.14)				
	Root	East	13	^{c}0.03 (0.02 - 0.04)	17	^{a}0.14 (0.11 - 0.18)	19	^{a}0.15 (0.11 - 0.19)	19	^{b}0.07 (0.05 - 0.09)
		West	5	^{c}0.02 (0.01 - 0.04)	7	^{b}0.07 (0.04 - 0.10)	9	^{a}0.14 (0.10 - 0.21)	14	^{b}0.08 (0.06 - 0.11)

Table 5.1. Comparison of leaf nutrient concentrations (% of dry mass) of the major taxonomic plant groups found in this study with values reported previously for the island and with those found for other tundra and tundra-like vegetations. Values are the range of mean values found for species within each group.

	Locality/Vegetation	N	P	K	Ca	Mg	Na
Monocots	Marion Island (this study)	1.61-5.23	0.16-0.46	1.12-2.45	0.09-0.16	0.12-0.25	0.11-0.75
	Marion Island[a]	0.76-2.77	0.10-0.22	1.00-1.72	0.08-0.19	0.08-0.23	0.09-0.62
	Marion Island[b,c]	0.70-1.47	0.08-0.17	1.08-1.70	0.07-0.14	0.08-0.25	0.09-0.64
	South Georgia Island[d]	1.0-4.9	0.10-0.58	0.4-4.3	0.02-0.65	0.02-0.34	0.01-0.35
	Macquarie Island[e]	1.78					
	Signy Island[f]	2.22	0.29	0.48	0.47	0.51	0.11
	Arctic tundra[g]	1.15-3.12	0.12-0.33	0.77-1.88	0.08-0.53	0.11-0.29	0.03
	Cool temperate bogs, heaths and montane	1.32-2.69	0.06-0.26	0.45-1.47	0.02-0.44	0.04-0.53	0.01-0.22
	Temperate freshwater and estuarine wetlands[i]	1.46-3.95	0.08-0.63	0.42-4.56	0.20-8.03	0.08-0.95	0.07-1.52
Dicots	Marion Island (this study)	1.22-4.37	0.09-0.68	0.48-2.44	0.19-1.21	0.21-0.86	0.46-1.68
	Marion Island[a]	2.01-2.91	0.13-0.25	1.00-1.50	0.12-0.68	0.33-0.51	0.41-1.80
	Marion Island[c]	1.8-2.2	0.19-0.22	1.2-1.7	0.5-0.7	0.3-0.4	0.3

Table 5.2 cont.

	South GeorgiaIsland[d]	1.5-4.0	0.2-0.7	0.6-5.0	0.3-3.1	0.1-0.8	0.05-0.80
	Arctic tundra[j]	0.8-3.2	0.09-0.41	0.3-2.3	0.2-1.0	0.1-0.7	0.01-0.23
	Cool temperate bogs, heaths and montane grasslands[k]	0.8-2.4	0.04-0.13	0.21-0.90	0.2-0.8	0.1-0.4	0.06
Pteridophytes	Marion Island (this study)	1.03-2.31	0.09-0.23	0.76-2.30	0.08-0.59	0.14-0.83	0.16-0.62
	Marion Island[a]	2.36	0.24	1.55	0.43	0.71	0.28
	Marion Island[c]	1.5	0.19	1.5	0.6	0.9	0.5
	South GeorgiaIsland[l]	1.5-2.2	0.2-0.3	1.5-2.5	0.3-0.6	0.3-0.4	0.1-0.3
Bryophytes	Marion Island (this study)	0.36-2.59	0.02-0.33	0.05-1.72	0.07-0.63	0.12-0.53	0.05-0.79
	Marion Island[a]	0.47-1.55	0.03-0.23	0.15-0.87	0.19-0.83	0.17-0.43	0.06-0.87
	Marion Island[m]	0.41-1.28	0.06-0.22	0.10-1.87	0.13-0.51	0.10-0.67	0.04-0.86
	Arctic tundra[n]	0.03-2.0	0.01-0.15	0.1-0.6	0.06-2.1	0.12-0.18	0.07

[a]Smith (1978b), [b]Smith (1987d,e), [c]Smith (1987e), [d]Lewis Smith and Walton (1975), Walton and Lewis Smith (1980), Pratt and Lewis Smith (1982), Lawson (1985), [e]Jenkin (1972), [f]Collins et al. (1975), [g]Babb and Whitfield (1977), Chapin et al. (1975), Dowding et al. (1981), Muc (1977), Wielgolaski et al. (1975), [h]Heal and Smith (1978), Kilfeather (1973), Perkins et al. (1978), [i]Boyd (1978), [j]Chapin et al. (1975), Chepurko (1972), Vassiljevskaya et al. (1975), Wielgolaski et al. (1975), [k] Heal and Smith (1978), Kilfeather (1973), Loach (1968), [l] Walton and Lewis Smith (1980), [m]Russell (1987), [n]Rodin and Bazilevich (1967), Vitt and Pakarinen (1977), Wielgolaski et al. (1975)

Table 6.1. Rankings of species-mean nutrient concentrations into very high (vh), high (h), moderate (m), low (l) and very low (vl) groups, based on concentration ranges given in footnote. Community complexes: B=biotic, SS = saltspray, SDL = springs and drainage lines, M = mire, MDL = mire drainage line, LS = lowland slopes, F = fellfield, RS = Rock substrate

Species	Guild	Community complex	N	P	K	Na	Mg	Ca
Poa annua	Poa annua	B	vh	vh	vh	h	l	m
Montia fontana	Mat dicot	B	vh	vh	vh	vh	h	m
Callitriche antarctica	Mat dicot	B	vh	vh	h	vh	vh	h
Agrostis stolonifera	Mire Graminoid	B, SDL, M,	h	h	m	m	l	l
Ranunculus biternatus	Mat dicot	B, M, SS	h	h	h	vh	vh	h
Marchantia berteroana	Biotic bryophyte	B	h	h	h	h	vh	m
Acaena magellanica	Dwarf Shrub	SDL, LS	h	h	m	m	vh	vh
Polystichum marionense	Pteridiophyte	RS	h	h	vh	l	m	m
Cotula plumosa	Rosette dicot	B,SS	h	h	m	vh	h	h
Poa cookii	Tussock grass	B	h	h	m	l	vl	vl
Agrostis magellanica	Mire Graminoid	M	m	m	h	m	l	l
Juncus scheuchzerioides	Mire Graminoid	M	m	m	m	h	m	l
Azorella selago	Cushion dicot	F	m	m	vh	h	m	vh
Uncinia compacta	Mire Graminoid	M	m	m	h	l	l	l
Blechnum penna-marina	Pteridiophyte	LS	m	m	m	m	vh	vh
Lycopodium magellanicum	Club moss	M	m	m	m	m	vl	l
Campylopus sp	Mire bryophyte	M	m	l	l	vl	vl	l
Clasmatocolea vermicularis	Mire bryophyte	B, SS	m	m	m	m	m	m
Grammitis poeppigeana	Pteridiophyte	RS	m	l	m	m	vh	m
Sanionia uncinata	Mire bryophyte	M	m	m	l	vl	m	h
Brachythechium rutabulum	*Brachythechium* moss	SDL	m	m	m	vl	h	h
Crassula moschata	Erect dicot	SS	m	m	l	vh	h	vh
Clasmatocolea humilis	Mire bryophyte	M	m	l	m	m	m	m
Lycopodium saururus	Club moss	F	m	m	m	h	l	vl
Ptychomnion densifolium	Mire bryophyte	M	l	l	vl	vl	l	m
Bryum laevigatum	Drainage Line Bryophyte	MDL	l	l	l	vl	h	vh
Breutelia integrifolia	Drainage Line Bryophyte	MDL	l	vl	vl	vl	h	vh
Andreaea sp	Cushion Bryophyte	F	l	l	vl	vl	m	vl
Cryptochila grandifolia	Mire bryophyte	MDL, F	l	l	vl	l	h	h
Blepharidophyllum densifolium	Mire bryophyte	M	l	vl	m	l	m	m
Jamesoniella colorata	Mire bryophyte	M	l	vl	l	vl	m	m
Ditrichum strictum	Cushion Bryophyte	F	l	vl	vl	l	l	m
Racomitrium lanuginosum	Mire bryophyte	M	vl	vl	vl	vl	vl	l

N: vh (> 3%), h (2-3%), m (1-2%), l (0.5-1%), vl (<0.5%).
P: vh (> 0.4%), h (0.2-0.4%), m (0.1-0.2%), l (0.05-0.1%), vl (<0.05%).
K: vh (> 2%), h (1.5-2%), m (0.5-1.5%), l (0.5-1%), vl (<0.5%).
Na: vh (> 1%), h (0.5-1%), m (0.2-0.5%), l (0.1-0.2%), vl (<0.1%).
Mg: vh (> 0.5%), h (0.35-0.5%), m (0.25-0.35%), l (0.15-0.25%), vl (<0.15%).
Ca: vh (> 0.5%), h (0.3-0.5%), m (0.15-0.3%), l (0.1-0.15%), vl (<0.1%).

Table 6.2. Eigenvalues of first two components derived from the PCA and correlations of nutrient variables on the components.

Nutrient	PC1	PC2
N	-0.877*	0.209
P	-0.886*	0.234
K	-0.767*	0.211
Ca	-0.482	-0.722*
Mg	-0.415	-0.777*
Na	-0.727*	0.161
Eigenvalue	3.076	1.295
Proportion explained variance	0.513	0.216