Plant Functional Types on Marion Island

by

Anche Louw (nee Müller)

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Supervisor: Prof Valdon R. Smith

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Summary

A database was compiled of structural and physiological traits for 25 vascular species and 17 bryophyte species on Marion Island (sub-Antarctic). The structural traits included leaf, stem and root characteristics and the physiological traits are all associated with photosynthetic responses to light and were measured using chlorophyll fluorescence quenching analysis. The data were subjected to principal component analysis and clustering analysis to construct a suite of plant functional types (PFTs). The correspondences between the PFTs and plant habit/taxonomy (forb, graminoid, fern, moss and liverwort), status (native to the island or introduced alien) and habitat (oligotrophic, manured or saline) were investigated using correspondence analysis.

There were significant differences in most of the structural traits, but in only one of the photosynthetic traits, between sites at the same altitude and between altitudes. The between-site differences could not be explained since site characteristics were not measured, but the between site differences were often species-dependent; a particular species might show its lowest value for a particular trait at the same site where another species showed the highest value for that trait. The between-altitude differences in structural trait values could be ascribed to the effect of greater wind speed at higher altitude (lower stature, tougher leaves and stems). High altitude plants have greater specific root length, probably a response to low soil nutrient status and hence a need for foraging roots. However, plants in saline coastal habitats also show a high specific root length, probably in response to the inhibitory effect of high salt concentration on nutrient and water uptake. All the species except *Azorella selago*, the archetypical vascular species of high altitude were more stunted and showed greater signs of stress at high altitude than at low altitude.

Native species tend to show greater values for those traits indicative of structural strength (tough, thick leaves, strong stems), and allocate a greater proportion of their biomass aboveground, than human-introduced alien species. Alien graminoids also have higher stomatal densities (but lower chlorophyll concentrations on a leaf area basis) than native species. There are no consistent differences in photosynthetic capacity between natives and aliens, except that native species tend to show a sharper photosynthetic response to increasing light at low levels, possibly an adaptation to the consistently low light regime at the island.

Maximum photosynthetic electron transport rate varies greatly (by an order of magnitude) between the island's vascular species and by almost an order of magnitude between the

bryophyte species. Species with high electron transport rate also tend to have a high effective quantum yield and show electron transport saturation at high light – all indicative of high photosynthetic capacity sun species, most of which are forbs. The shade-adapted, lowest photosynthetic capacity species are mostly ferns, mosses and liverworts. Graminoids tend to be moderate photosynthetic capacity species but some of the forb species also have moderate, and even low, photosynthetic capacity.

Only two structural traits were measured on bryophytes so in grouping both the vascular and bryophyte species together into functional types only the photosynthetic traits were considered. This yielded eight photosynthetic functional groups, together representing three levels of photosynthetic capacity - high, moderate or low capacity. Forbs predominate in the two highest photosynthetic capacity groups, graminoids (with one hepatic) in the moderate to moderately high capacity groups, graminoids, ferns and some bryophytes in the low to moderate capacity groups and bryophytes and shade-adapted ferns in the very low to low capacity groups. Mosses tend to have a higher capacity than hepatics although four of the six species in the very lowest capacity group are mosses. At each level of photosynthetic capacity – the high, moderate or low capacity groups – the species are divided into subgroups based on their capability for photoprotection at high light and how sharply photosynthesis responds to increasing light at low levels.

Previous studies at the island have unequivocally shown that habitats influenced by seal and seabird manuring have higher soil and plant nutrient status, greater plant vitality and higher productivity. It was expected that species restricted to, or that attain maximum cover in manured habitats would be in the group with highest photosynthetic capacity. However, a surprising finding of the study is that those species occur in all the photosynthetic capacity groups except the highest capacity one.

Further research into plant functional traits and functional types at the island should consider phenological, reproductive, and a wider suite of physiological, traits, especially the temperature responses of, and desiccation effects on, photosynthesis, photorespiration and respiration. Since wind is such a dominant factor at the island, its effects on plant morphology, architecture, growth and physiology also need to be addressed.

Opsomming

‘n Databasis was saamgestel van strukturele en fotosintetiese eienskappe vir 25 vaatplantspesies en 17 briofietspesies op Marioneiland (sub-Antarkties). Die strukturele eienskappe het blaar, stingel en wortel eienskappe ingesluit en die fisiologiese eienskappe word geassosieer met die fotosintetiese reaksie op lig en was gemeet met behulp van chlorofilfluoressensie blussingontleding. Hierdie data was blootgestel aan beginsel komponentontledings en trosvormingsontledings om sodoende groeperings van plant funksionele tipes (PFT’s) te konstruktureer. Die ooreenkomste tussen die PFT’s en plant habitat/taksonomie (kruidagtig, grasplant, varing, mos en lewermos), status (inheems of uitheems) en habitat (oligotrofies, bioties of soutafsetting) was ondersoek deur middel van korrespondensie-ontleding.

Daar was beduidende verskille vir meeste van die strukturele eienskappe, maar slegs vir een van die fotosintetiese eienskappe, tussen liggings op dieselfde hoogte bo seevlak asook tussen liggings op verskillende hoogtes. Hierdie verskynsel kan nie tans verduidelik word nie, aangesien daar geen ligging eienskappe gemeet is nie, maar die tussen-ligging verskil was soms spesie-afhanklik; ‘n spesifieke spesie kan die laagste waarde vir ‘n sekere eienskap toon by dieselfde ligging as waar ‘n ander spesie weer die hoogste waarde vir daardie eienskap toon. Die verskille in strukturele eienskappe by verskillende hoogtes bo seevlak kan toegeskryf word aan die effek van die hoër windspoed by die hoër liggings (wat lei tot korter plante en meer geharde blare en stingels). Plante by hoër liggings het groter spesifieke wortellengtes, wat waarskynlik ‘n reaksie is op lae grondnutriëntstatusse waar voedingswortels benodig word. Daarinteendeel het plante wat in die soutryke kusgebied voorkom ook ‘n hoër spesifieke wortellengte, wat waarskynlik ‘n reaksie is op die inhiberende effek van hoë soutkonsentrasies op die absorbering van nutriënte en water. Al die spesies by die hoër liggings behalwe *Azorella selago*, wat die tipiese verteenwoordiger is van vaatplante wat op hoër hoogtes bo seevlak kan voorkom, het meer onderdrukte groei en meer tekens van stres getoon.

Inheemse spesies was geneig om groter waardes te toon vir daardie plant eienskappe wat strukturele gehardheid uitbeeld (sterk, dik blare, stingels en wotels) en wend ook proporsioneel meer biomassa bogronds aan as wat die uitheemse plante doen. Uitheemse grasplante het ook ‘n hoër huidmondjie digtheid (maar laer chlorofilkonsentrasies per blaaroppervlak) as die van inheemse spesies. Daar is geen beduidende verskille in die

fotosintetiese kapasiteit tussen inheemse en uitheemse spesies nie, behalwe dat die inheemse spesies geneig is om ‘n skerper fotosintetiese reaksie teenoor toenemende lig van lae vlakke te toon, wat moontlik die plant se aanpassing tot die konstante lae lig toestande van die eiland is.

Die maksimum fotosintetiese elektron vervoer tempo variëer grootliks tussen die eiland se vaatplantspesies en ook tussen die briofietspesies. Spesies met hoë elektron vervoer tempo’s het ook die neiging om ‘n hoër effektiewe kwantum opbrengs te hê en toon ‘n elektron vervoer versadigingspunt by hoë lig – wat ‘n aanduiding is dat hierdie spesies is met hoë fotosintetiese kapasiteit, waarvan meeste kruidagtige plante is. Spesies wat vir skadu aangepas is het die laagste fotosintetiese kapasiteit en is meestal varings, mosse en lewermosse. Die fotosintetiese kapasiteit van grasplante is oor die algemeen matig, maar sommige kruidagtige spesies het matig en selfs lae fotosintetiese kapasitiet.

Vir die groepering van briofietspesies en vaatplantspesies tesame is slegs die fotosintetiese eienskappe gebruik, aangesien slegs twee strukturele eienskappe op die briofietspesies gemeet is. Agt fotosintetiese groepe is gevorm wat lae, matige en hoë fotosintetiese kapasiteite verteenwoordig. Kruidagtige plante kom meestal in die twee groepe voor met die hoogste fotosintetiese kapasiteite, grasplante (tesame met een lewermos) val onder die matig tot matige hoë fotosintetiese kapasiteit groepe, ander grasplante, varings en sommige van die briofiete val onder die lae tot matige kapasiteit groepe en die res van die briofiete en skadu-aangepaste varings kom voor in die lae tot baie lae kapasiteit groepe. Mosse het die neiging om hoër fotosintetiese kapasiteite te toon as lewermosse, hoewel vier van die ses spesies wat voorkom in die laagste kapasiteit groep mosse is. Op elke vlak van fotosintetiese kapasiteit – hoë, matige en lae fotosintetiese kapasiteit groepe – word die spesies verder verdeel in subgroepe wat gebasseer is op hul fotobeskermingskapasiteit by hoë lig en ook hoe skerp hul fotosintese kan reageer op die verhoging van lig by lae vlakke.

Vorige studies op die eiland dui duidelik aan dat habitatte wat bemes word deur robbe en seevoëls het hoër grond-en plantnutriënt statusse, beter plant groeivermoëns en produktiwiteit. Daar was verwag dat plante wat beperk is tot, óf wat maksimum dekking bereik, in die bemesde habitatte in groepe sou voorkom wat die hoogste fotosintetiese kapasiteite besit. Inteendeel, ‘n verrassende bevinding van dié studie was dat hierdie spesies voorkom in al die fotosintetiese kapasiteit groepe behalwe die hoogste kapasiteit groep.

Verdere navorsing op die eiland oor die plant funksionele eienskappe en die funksionele groepe moet die fenologiese, voortplanting, en ‘n wyer verskeidenheid van fisiologiese eienskappe, veral die temperatuur respons of die uitdroging effek op fotosintese, fotorespirasie en respirasie, in ag neem. Aangesien wind ‘n dominante faktor op die eiland is, moet die effek daarvan op die plant morfologie, argitektuur, groei en fisiologie ook aangespreek word.

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Chapter 1.

Introduction – Aims of the Study, Marion Island and Plant Functional Traits

1.1 Aim of the study

One of the long term objectives of the biological/ecological research programme at Marion Island is to estimate, on a whole-island basis, rates of ecosystem functioning processes such as primary production, soil respiration, decomposition, nutrient cycling and carbon exchange (Smith 2008a) and how these processes will respond to perturbations. Perhaps the most important of these perturbations at the island is warming and drying (Smith 2002, Le Roux and McGeoch 2008a) and the invasive alien organisms that are continually reaching it through the agency of humans (Chown and Froneman 2008). Although some autecological and ecophysiological studies of the productivity and nutrient relations of some of the island's plant species have been carried out, it has become clear that a classical species-based approach is too complicated, and too onerous, to achieve a whole-island assessment of ecosystem functioning. Smith (2008b) suggested that the complexity of the ecosystem functioning/response models could be reduced by grouping the island plants into guilds, where species within a guild possess similar functional characteristics, or traits.
The aim of my study was to establish a data base of functional traits for the island's plants and to use that data base to identify a, hopefully small, set of plant functional types.

1.2 The island's climate, flora and vegetation

1.2.1 Climate

Marion Island (46°50′ S, 37°50′ E) and its close neighbour Prince Edward Island form part of the Prince Edward Island Group, one of four island archipelagos in the Southern Indian Ocean Province of the sub-Antarctic Region. Marion Island is 290 km^2 in area and experiences a typically hyper-oceanic, sub-Antarctic climate. Annual mean temperature is 6.4 °C, with only a small (c. 4 ºC) difference between mean temperature for the coldest (July) and warmest (January) months (Le Roux 2008). Situated in the "Roaring Forties", a belt of strong westerly atmospheric circulation, the island is subject to fierce wind (averaging > 10 m sec^{-1}; Schulze 1971). Rain (c. 2500 mm per annum) falls on more than 300 days per year and relative humidity is high (annual mean 80%; Schulze 1971). Because of this climatic wetness, soil moisture contents are high and many of the more peaty soils are permanently saturated. A

high incidence of cloud means that radiation levels are low; on average only 3.5 hours of direct sunshine reaches the island surface per day (Schulze 1971).

1.2.2 Flora

The indigenous terrestrial biota of all sub-Antarctic islands is species-poor, since they are isolated from continental landmasses and most are very young (Taylor1955; Chastain1958; Lewis-Smith and Walton 1975). This is certainly true of Marion Island, which is about 2000 km from the nearest continent, Africa, and about 500 000 years old (Mc Dougall et al. 2001). In fact, since most of the island was glaciated in the Pleistocene (Meiklejohn 2011), colonization has been possible only over about the last 11 000 years. Only 41 vascular species (of which 18 were introduced by humans) have been recorded (Gremmen and Smith 2008). The bryophyte flora (93 moss and 44 liverwort species; Ochyra 2008, Gremmen 2008) and lichen flora (128 species; Øvstedal and Gremmen 2014) are richer. The vascular plants comprise low-growing herbs, cushion plants and graminoids. There is only one semi-woody species and no trees or shrubs. Bryophytes are mainly mat-, turf or tuft-formers in the wet and mesic localities and cushion-formers in driest localities.

1.2.3 Vegetation and terrestrial habitats

In their biome/bioregion classification of South African vegetation, Smith and Mucina (2006) consider the lowland vegetation (below c. 300 m) of Marion Island (a South African territory) to belong to the s*ub-Antarctic Tundra Biome*. The highland vegetation belongs to the *Polar Desert Biome.*

Huntley (1971) classified the island's vegetation types based on floristic composition and the autecology of the dominant species. He identified 13 "noda" (abstract vegetation assemblages - roughly equivalent to plant communities) which he grouped into five "complexes" based on the main ecological forcing variables that affect them. These variables are exposure, desiccation, waterlogging, drainage, saltspray and manuring and trampling by seabirds and seals. The complexes recognized by Huntley are the Saltspray Complex, Biotic Complex, Swamp Complex, Slope Complex and Wind Desert Complex. Gremmen (1981) classified the island's vegetation using a phytosociological approach, combining floristic data with environmental information (pH, soil moisture, groundwater depth, loss-on-ignition, severity

of salt spray and of manuring and trampling). He identified 41 plant communities which he grouped into 6 community complexes. Essentially, Gremmen's complexes are the same as those proposed by Huntley, the extra one resulting from a splitting of Huntley's Slope complex into a complex comprised of fernbrakes and a complex comprised of slope drainages line, springs and flushes.

Smith and Steenkamp (2001) took a different approach - they used ordination and clustering of vegetation and soil chemistry information to define the island's terrestrial habitats, arguing that the habitat concept reflects not only just plant assemblages but also the magnitudes of the main ecological forcing variables causing those assemblages, and can be applied to ecosystem function processes. They grouped the habitats into habitat complexes that correspond closely to Gremmen's plant community complexes but added an additional complex - Polar Desert.

Gremmen and Smith (2008) drew on the two plant community classifications and the habitat classification to compile a new categorization of the plant community types of the island. They retained the term "habitat" for the categories and grouped the habitats into complexes. A brief description of the complexes defined by Gremmen and Smith (2008) is as follows:

Habitats in the **Mire Complex** occur on wet, often deep, highly organic peats. Mostly, the peats are highly oligotrophic but there are mires on the coast that are subject to saltspray and/or manuring and have a higher nutrient status. Graminoids (mainly *Agrostis magellanica, Uncinia compacta* and *Juncus scheuchzerioides)* and mat forming bryophytes are the characteristic plants of this complex. Mire communities occupy a total area of about 22 km^2 in the area where closed vegetation can develop (< 300 m altitude) but are rare higher up (Gremmen and Smith 2008).

The **Slope Complex** occupies about 25 km^2 of the area below 300 m a.s.l. and is uncommon above that altitude (Gremmen and Smith 2008). Slope Complex soils are well-drained, less organic than the mire peats and support a vegetation dominated by the fern *Blechnum penna-marina,* the woody suffruticose herb *Acaena magellanica* and the grasses *Poa cookii* and *Agrostis magellanica*. The contributions of these species to vegetation cover varies widely between the slope habitats, but *B. penna-marina* is dominant in almost all of them. Fernbrake habitats are the most common type in the complex and are overwhelmingly dominated by *B. penna-marina*. Bryophytes are unimportant in the slope complex, except in the wetter habitats where they may occur as mats or even large pillows that stand even higher than the

vascular canopy (e.g. *Racomitrium lanuginosum*) or as wefts under the vascular plants (e.g. *Brachythecium rutabulum* and *Sanionia uncinata*).

The **Fellfield Complex** occurs on skeletal mineral soils or on bare rock or volcanic ash. Plant cover is sparse, especially at mid to high altitudes. The cushion plant *Azorella selago* is always dominant and cushion- or ball-forming mosses and crustose lichens are common. Fellfield covers about 137 km^2, or 47%, of the total island area (Gremmen and Smith 2008). In Mesic fellfield (the common fellfield type at lower altitudes), *Blechnum penna-marina, Agrostis magellanica* and *Acaena magellanica* often occur with *A. selago.* Cushion and ball-forming mosses (e.g. *Ditrichum strictum, Andreaea acuminata* and *A. acutifolia)* are the most common types of bryophyte but the mat-forming liverwort *Syzygiella sonderi* and large pillows of *Racomitrium lanuginosum* are also frequently found. Total plant cover can be quite high in mesic fellfield, up to 60%, but is most commonly < 50%. Xeric fellfield occurs at mid and high altitudes and is characterized by a sparse plant cover (rarely > 10%) consisting of *A. selago,* cushion-forming mosses and crustose lichens.

The **Polar Desert Complex** comprises only one habitat, Polar Desert, and is the most extensive one at high altitudes. It comprises approximately one third of the total island area (Gremmen and Smith 2008). Plant cover is sparse, seldom >1%, and comprises of cushion mosses and crustose lichens, and sometimes also *A. selago*, which is the only vascular plant species to occur in Polar Desert.

The **Coastal Saltspray Complex** occurs in areas subjected to saltspray or inundation by seawater and occupies only about 122 ha in total (Gremmen and Smith 2008). *Crassula moschata*, alone or with *Cotula plumosa*, dominates the plant cover. Bryophytes are uncommon, except in the wettest habitat in this complex, where the salinity-tolerant liverwort *Clasmatocolea vermicularis* occurs. *A. selago* dominates in the driest habit of the complex. Shore zone boulders support halophytic lichens (e.g. *Verrucaria* spp., *Caloplaca* spp., *Turgidosculum complicatulum*). Many localities of the saltspray complex are influenced by birds and seals, but not to the same extent as the next-mentioned complex.

In the island's ecological literature, the manuring and trampling influence of seals and seabirds is commonly termed "biotic influence", and plant communities or habitats subjected to such influence have commonly been given the adjective "biotic" (Huntley 1971, Gremmen 1981, Smith and Steenkamp 2001). Found mainly near the coast, where the majority of animals occur, the **Biotic Complex** occupies about 4.5 km^2. It comprises several habitats,

such as eutrophic muds occupied by the small herb *Callitriche antarctica* or the introduced grasses *Poa annua* and *Agrostis stolonifera*, mires dominated by *Clasmatocolea vermicularis*, herbfields dominated by *C. plumosa*, and tussock grasslands dominated by *Poa cookii*. Other than *C. vermicularis*, *Brachythecium rutabulum* and *Marchantia berteroana*, bryophytes are uncommon in biotic habitats.

1.3 Plant functional types/traits

1.3.1 Plant functional types

Plant functional types (PFTs) are groupings of species that show close similarities in their resource use and response to environmental and biotic controls (Wilson 1999). Members of a PFT group sharing similar functional traits might be expected to have similar ecologies, with differences between members of a particular PFT group being smaller than the differences between groups. The groupings are generally not phylogenetic and the main rationale behind the PFT approach is to get away from a species-based approach, thereby reducing the arduousness of studying vegetation processes at community, ecosystem or landscape levels (Dormann and Woodin 2002; Diaz et al. 1998). PFTs thus offer the possibility to decrease the complexity of models of the functional responses of communities and ecosystems to perturbations such as global climate change (Gitay and Noble 1997). Duckworth et al. (2000) provide an informative account of the concept of PFTs as an alternative to a species-based approach in plant community studies.

The term “plant functional type” seems to be a relatively recent one; its introduction to the general modelling community was just before, or at, “ A Meeting on Global Vegetation Change” held in Austria in 1988 (Wullschleger et al. 2014) . However, there is a rich literature, going back to the nineteenth century, on the concept that particular groupings of plants can be recognized based on similarities in growth form, life history strategy or ecological strategy, and that these similarities suggest functional similarities. Here I give a very brief overview of that literature.

Possibly, the first recognition that plants might be considered as belonging to recognizable groups that reflect their response to the environment, and hence their function, is Von Humboldt's classification of physiognomic plant types, based on growth form (Von Humboldt 1806). Later, mainly Danish (e.g. Warming 1909, Raunkiaer 1907) and German

(e.g. Grisebach 1872, Schimper 1903) phytogeographers recognized that plants in similar climates showed similarities in their growth form, life-history and ecology, despite taxonomic and geographic differences. In other words, there is a convergence of plant form and function between plants (and hence vegetation) from climatically similar areas. This was the basis of several classification systems that grouped plants, even if only implicitly, on functional criteria. Perhaps the best known of these is Raunkiaer's life-form classification, first published in Danish (Raunkiaer 1904, 1905), but especially widely used after the English translation (Raunkiaer 1934).

In Raunkiaer's scheme, plant species are categorized into life-forms based on the position, nature and degree of protection of the dormant perennating shoot-apices, or buds. The basic life-forms are phanerophytes (carrying dormant buds on aerial shoots e.g. trees and shrubs), chamaephytes (perennating bud or shoot apices borne close - not more than 25cm - to the ground surface), hemicryptophytes (dormant buds found just below the surface, in the upper soil crust), cryptophytes (subterranean dormant parts - buds, bulbs, rhizomes) and therophytes (species living through unfavorable seasons as seeds, i.e. annuals). This classification system has been modified by various workers to make it more relevant to particular vegetation types or the particular requirements of their study. The following studies are some examples: structure and seasonality of tropical vegetation (Ellenberg and Muller-Dombois 1967), plant structure and phenology in relation to climate (Box 1981) and analyses of the functional significance of leaf morphology (Dansereau 1951; Küchler 1967), plant architecture (Hallé et al. 1978) and clonality (Klimes 2003).

An especially popular and influential classification scheme that relates in a real sense to plant function is the ecological primary strategies scheme of Grime (1977). Commonly known as the CSR (competitive – stress tolerant – ruderal) scheme, it is based on the premise that two external factors, stress and disturbance, limit plant growth. Only three of the four permutations (high or low stress versus high or low disturbance) allow plant growth (high stress together with high disturbance does not). Grime suggested that each of the three allowable permutations has been associated with the evolution of a distinct type of plant strategy, i.e., low stress/ low disturbance favours competitive plants (C), high stress/ low disturbance is associated with stress-tolerant plants (S), and low stress/ high disturbance with ruderal plants (R). Of course, these three strategies are extremes, and the Triangle Model of Ecological Primary Strategies (Grime et al. 1988) recognizes intermediate strategies, based on the relative importances of competition, stress and disturbance.

The Grime CSR model is commonly depicted as a triangle, each axis (C, S or R) of the triangle implying tradeoffs amongst plant traits. A species occupies a particular position in the triangular component space. However, in the original formulation of the CSR scheme (Grime 1977) there were no guidelines as to what plant traits should actually be used to determine a plant's position along each axis. The axes are defined by concepts that are difficult or impossible to quantify (competitor, stress tolerance and ruderal), rather than on measurable traits. This shortcoming was remedied in later variants of the scheme (Hodgson et al. 1999; Hunt et al. 2004). Simple predictor variables (each one considered to be a surrogate of a particular aspect of plant function) such as canopy height, dry matter content, flowering period, flowering start time, lateral spread, leaf dry mass and specific leaf area, are used to locate a species in the CSR component space. Based on its location in that space, the species is allocated to a specific plant functional type (Hodgson et al. 1999). If enough species in a vegetation type are considered, the functional signature of that vegetation type can be determined (Hunt et al. 2004).

Westoby (1998) proposed a LHS (leaf-height-seed) scheme that uses axes based on three easily-measured traits; specific leaf area, canopy height and seed mass and he considered that these three traits represent fundamental trade-offs controlling a plant's survival strategy. Each trait forms a single axis and the ecological strategy of a species is given by its position in the orthogonal space enclosed by the three axes.

The CSR and LHS schemes are not primarily aimed at identifying or classifying plant functional types – rather, they aim at defining the plant's primary ecological strategy, "strategy" referring to how a species sustains a population (Westoby 1998). In fact, in none of the primary expositions of the CSR scheme (Grime 1977; Grime et al. 1988) are the terms "plant functional type" or "plant functional trait" mentioned. Westoby (1998) only implies a connection between plant functional type and his LHS scheme (Page 215: "global change research urgently needs plant functional type classifications"). However, both ecological strategy schemes have become increasingly considered as plant functional type schemes.

In the past 20 years the PFT approach has progressed from these earlier life form, life-history and ecological strategy approaches, toward more explicit schemes that relate functional traits and functional types to plant responses to, and their effect on, the environment, as well as the plants' exploitation of environmental resources. For example, empirical studies have looked at whether there are consistent associations between plant traits and climatic or disturbance

gradients (Díaz et al. 1998, McIntyre et al. 1999). Other studies have attempted to identify recurrent patterns of association among plant traits within floras, to predict vegetation functional responses to a changing environment at regional (Diaz and Cabido 1997) or global (Díaz et al. 2004; Harrison et al. 2010) scales. Especially, the paper by Hobbs (1997), entitled "Can we use plant functional types to describe and predict responses to environmental change?", spurred programs such as the Global Change and Terrestrial Ecosystems (GCTE) project of the International Geosphere Biosphere Programme (IGBP) to adopt a PFT approach, with the aim being to reduce "a large number of species into a handful of manageable functional types" (Bond 1997).

The PFT concept has, in fact, proved itself useful in studies of vegetation responses to climate change and other perturbations. For instance, in Southern Africa, Skarpe (1996) related plant structural and functional characteristics of 65 savannah species to climatic data by correspondence analysis, to establish plant functional types which she used to predict possible vegetation changes in response to climate change in Southern Africa. Bond (1997) used functional types to predict the changes in Cape Fynbos due to environmental changes, and emphasized the importance of including traits related to persistence, regeneration and dispersal when constructing PFTs. More akin to the Marion Island situation, Dormann and Woodin (2002) used PFTs in a meta-analysis of field experiments to predict the impact of global temperature change on Arctic vegetation. They found a wide variation in the response of the vegetation to environmental manipulations and concluded that the main effect of increasing temperature will be on rates of nutrient cycling, which will generate feedback processes affecting plant biomass.

PFTs are now widely used in the applied plant sciences, such as agronomy, forestry, vegetation conservation and management. The following are some examples. PFTs have proved useful to assess the results of management practices (Garnier and Navas 2012; Pérez-Harguindeguy et al. 2013). A PFT approach is used at a landscape level for the management of fire-prone areas in South East Australia (Bradstock and Kenny 2003, Keith et al. 2007). Gondard et al. (2003) showed that PFTs, based on morphological, life history and regenerative traits, are a useful tool in managing and restoring land degraded by overgrazing or overlogging. Brown (2004) showed that PFTs (she termed them "functional guilds") are realistic conceptual units to use in restoration ecology and that including multiple species that represent each functional type within the community being restored provides a buffer against climate change.

Very relevant to the Marion Island situation is that an important effect of climate change is the increased possibility of plant invasion into native plant populations, communities and ecosystems. Drenovsky et al. (2012) assessed the plant functional traits driving plant invasion, the impacts and integration of those traits across multiple ecological scales, and how a trait-based approach can be used in management and restoration. By using trait-based approaches one can predict the success of invasive species and the impact on the environment. One such approach was used by Fargione et al. (2003) to investigate community assembly and invasion in prairie grasslands. In another study, Van Bodegom et al. (2012) explored the advantages of using trait-based vegetation modelling to predict global ecosystem-atmospheric fluxes.

In fact, modellers, few of which are vegetation scientists, of large scale (continental and global) biogeochemical and biophysical dynamics have been amongst the most fervent embracers of the PFT concept to represent plant diversity and function in their models (Haxeltine and Prentice 1996, Wullschleger et al. 2014). Some of these modellers have used remote sensing information to propose a new concept, "optically distinguishable functional types" (Ustin and Gamon 2010).

1.3.2 Plant functional traits

The traits used to assign a species to a PFT may relate directly ("hard" traits) or indirectly ("soft" traits) to plant function (Weiher et al. 1999; Drenovsky 2012). Hard traits (e.g. photosynthetic rate, growth rate, water use efficiency, defence against herbivory) are generally difficult or onerous to measure whereas soft traits (e.g. growth form, plant height, seed size, specific leaf area) are mostly easier to measure. Soft traits are generally measured as surrogates for hard traits, e.g. specific leaf area (area per mass of a leaf) generally correlates positively with maximum photosynthesis rate and negatively with leaf longevity and investment in leaf defence.

Plant functional traits have also been defined as 'discrete' (qualitative individual traits usually related to phylogeny – e.g. monocot/dicot) or 'continuous' (traits possessed by all or most species – e.g. specific leaf area, seed mass, stomatal density) (Drenovsky 2012). Continuous traits are most typically used for PFT groupings since they are not related to phylogeny and can be quantified.

Whether hard or soft, discrete or continuous, a wide range of traits have been proposed for use in PFT classifications. They include morphological, anatomical, physiological, life-history and phenological characteristics (Gitay and Noble 1997; Ustin and Gamon 2010).

Most often, the set of 'key traits' chosen depends on the aim and scale of the particular study. Most of the more recent attempts at grouping species into PFTs have considered many more traits than the few used in the earlier life form, life-history or ecological strategy schemes, even in their modern incarnations. Considerable effort has gone into determining which, amongst all possible traits, are the most useful ones for classifying species and vegetation on functional grounds. Lavorel et al. (2007) proposed that traits must fill four conditions if they are to be useful in global syntheses and modelling. They must: (1) bear some relationship to plant function; (2) be relatively easy to observe and quick to quantify; (3) be quantifiable using measurements that can be standardized across a wide range of species and growing conditions; (4) have a consistent ranking (not necessarily constant absolute values) across species when environmental conditions vary. Several authors (e.g. Weiher et al. 1999; Lavorel and Garnier 2002; Lavorel et al. 2007) have compiled lists of traits that meet those conditions and there are two handbooks that list the most widely used traits, define their functional significance and provide standardized protocols on how to measure them (Cornelissen et al. 2003, Pérez-Harguindeguy et al. 2013).

Several numerical techniques have been proposed for analysing functional trait data in order to define PFTs. These range from relatively simple multivariate ordination approaches, such as Principle Component Analysis (Kindscher and Wells 1995; Skarpe 1996; Díaz Barradas et al. 1999), to complex matrix analyses using algorithms designed to reveal particular PFTs whose performance in communities is maximally associated with specific environmental variables (Gitay et al. 1999; Pillar and Sosinski 2003) or to estimate functional diversity of vegetation from multiple traits (Laliberté and Legendre 2010).

1.3.3 Bryophyte functional types

Bryophytes are an important component of the island's lowland vegetation, and are dominant at high altitudes. They appear to be more effective indicators of subtle differences in environmental conditions at the island, especially moisture, than are the vascular plants (Gremmen 1981). Most effort in my study focussed on vascular species, for which a wide range of traits was measured. However I did measure some functional characteristics

(chlorophyll concentration and chlorophyll fluorescence characteristics) on 14 moss and 7 liverwort species. Worldwide, no strategy for classifying bryophytes into functional type groups has been formulated. In most accounts of vegetation ecology, bryophytes are considered as a single functional type, to distinguish them from vascular plants. In the bryophyte ecological literature, they are most usually grouped according to growth form, perichaetal position, life form or life history strategy.

Growth form is based on the direction of growth, frond length, perichaetium position, frequency and pattern of branch formation (La Farge-England 1996, Ross et al. 1998, Glime 2007). The perichaetium is a sheath of specialized leaves, together with the gametangia in the sheath and its position on the gametiphyte shoot lead to the common classification of mosses as acrocarpous, cladocarpous or pleurocarpous (Buck and Goffinet 2000).

Life form classifications consider clonal or colonial units rather than individual shoots. The life form groupings (short turfs, tall turfs, cushions, mats, wefts, pendants, etc.) are probably the most commonly used ones in bryophyte ecology and reflect adaptations to light intensity, type of substrate, CO_2 acquisition and water acquisition and retention (Mägdefrau 1982; Bates 1998).

Bryophyte life history strategy concerns mainly life cycle characteristics such as the balance between sexual and asexual reproduction, size, number and dormancy of spores, the nature of sexual reproduction (moneicious or dioecious), age at first reproduction and span of reproductive stage (During 1979, 1992; Bates 2000). Categories of life history strategy include fugitives, colonists, annual shuttle species, perennial shuttle species and perennial stayers. Kürschner and Frey (2012) provide a review of bryophyte life strategies and argue convincingly that the life strategy categories found in bryophytes are true functional groupings.

Implicit in all the above schemes is that they reflect bryophyte functional responses to environmental factors, but, except for the work by Proctor and Smith (1994) on the ecological implications of branching patterns, there have been no empirical studies on a sufficiently large range of species to test whether this is in fact so. By far the most studied aspect of bryophyte function concerns their water relations (see reviews by Proctor 1982, 2000a), which has lead to them being considered as either endohydric, mixohydric or ectohydric. These are explicitly functional groupings. A remarkable functional strategy of bryophytes is their ability to undergo complete rehydration and very quickly recover full metabolic activity

almost immediately on rehydration, a quality possessed mainly by ectohydric mosses (Proctor 2000b).

Since the exploration of functional traits has focused on vascular species, other than the bryophyte growth form, life form and life history strategy attributes discussed above, little attention has been given to what traits might be useful for assigning mosses and liverworts to functional type groups. In this respect, Cornelissen et al. (2007) is a hallmark paper, listing traits that might be useful in constructing cryptogam (mosses, liverworts and lichens) functional types. The main focus of that paper is on the role of cryptogams in biogeochemical cycling, so most of the traits concern properties such as tissue chemistry, secondary metabolites, nitrogen- fixing capacity, nutrient conservation, litter decomposability and carbon and nutrient losses. However, the authors do suggest that measurement of chlorophyll fluorescence "may be the priority candidate for multi-species screening for photosynthetic capacity" in bryophytes, a suggestion I took up in my study.

Chapter 2.

Material and Methods

2.1 Study sites

Sixty eight sampling sites were selected (Fig. 1). Between them they represented five of the six habitat complexes defined by Smith and Steenkamp (2001). Photographs of the sites and the habitat complexes they belong to are given in Appendix 1. The coordinates of the sampling sites were determined using a Garmin 60CSX GPS and their altitudes determined using ArcGIS®. Sixty one sites were at low altitude, from 2 to 150 m above sea level and within 2 kilometres of the meteorological station. Seven sites (henceforth termed "high altitude sites") were between 300 and 340 m above sea level and up to 4.5 km from the station. Twenty five vascular and 17 bryophyte species were sampled at low altitude and five vascular and six bryophyte species at high altitude. Tables 2.1 and 2.2 list the species and the sites at which they were sampled. Most species were sampled at four sites but the rare or hard to find (e.g. *Potamogeton nodosus*) were sampled at only one site.

2.2 Species identification

The taxonomy of the island's vascular species is well-resolved and the identity of the various species could be verified from voucher specimens housed on the island. Bryophyte identities were less easily to ascertain since there is no complete voucher set for mosses or liverworts on the island. In cases where bryophyte identity was uncertain, photographs (macro and micro) were sent to Dr N.J.M. Gremmen, who has over 40 years' experience with the island's bryophytes, for identification. Dr Gremmen was also on the island during the start and end of the fieldwork period and also assisted then in the identifications.

2.3 Selection and sampling of individuals for trait measurements

All traits were measured on healthy looking green plants. For species that occur in both full light and shade, the measurements were made on plants growing in full light. All measurements were made at the height of summer (December to February), except that the physiological traits measurements were also made in November. Two traits (plant height and

chlorophyll concentration) were measured in the field, the rest in the laboratory. Whole plants or portions of plants were sampled using a spade or a corer, together with a plug of soil or peat around the roots. The plants were placed in plastic bags and kept in a refrigerator at c. 4 ºC until measurement, which occurred within 48 h of sampling. The belowground portions were rinsed with tap water and dried with a paper towel before measurement. Samples taken for chlorophyll fluorescence measurements were treated differently, as described in Section 2.4.5.2.

2.4 The traits

Five types of traits were measured (Table 2.3). Four types were vegetative traits, comprising either structural (plant or organ size, mass, mass:size relationships, stomatal density, etc.) or concentration (chlorophyll) properties. The vegetative traits were measured using methods and protocols suggested by Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013). The other type of traits related to photosynthetic performance and those were measured using chlorophyll fluorescence quenching analysis (Section 2.4.5).

Not all the traits were measured on both vascular plants and bryophytes; some traits were not relevant, or could not easily be measured on the bryophytes. Also, not all the traits were measured on both high- and low altitude plants. Table 2.3 shows what traits were measured on vascular and/or bryophyte species, and on high- and /or low altitude plants. The table also shows the target number of measurements for a species at a particular site. Mostly, the target number was reached but there were some exceptions due to time constraints or limited availability of plants on which to make the measurements.

Following is a brief description of each trait; how it was measured and its functional significance.

2.4.1 Vegetative traits

2.4.1.1 Plant height

Shortest distance between the upper boundary of the main photosynthetic tissue (excluding the inflorescence) and the ground surface, measured with a ruler or a measuring staff.

Bryophyte height was measured by inserting a ruler into the fronds and until its end touched against the soil surface.

Functional relevance: Associated with competitive vigour, fecundity and above ground biomass.

2.4.2 Leaf traits

Leaf trait measurements excluded the petiole or rachis. For the leafless rush, *J. effusus*, leaf traits were measured on the photosynthetic stem.

2.4.2.1 Leaf area (LA)

The one-sided area of a leaf (mm^2). Leaves were photographed alongside a known-size sticker and photographed using a digital camera (Samsung, ES10). The areas of the leaf and sticker images were measured using Image J software (Abramoff et al. 2004; Glozer 2008).

Functional relevance: Has important consequences for leaf energy and water balances (Ackerly and Reich 1999; Moles and Westoby 2000). Related to climatic variation, wind, heat, cold, water and nutrient stresses, altitude (Perez-Harguindeguy et al. 2013).

2.4.2.2 Specific leaf area (SLA) and leaf dry mass (LDM)

SLA is the ratio of the one-sided leaf area to the oven dry mass ($mm^2\ mg^{-1}$). Leaf area was measured as described above. Leaf dry mass was measured by weighing the same leaf after oven-drying it at 100°C for at least 24 hours.

Functional relevance: SLA is one of the most commonly used surrogates of plant function for predicting plant functional responses and strategies (Wilson et al. 1999). An indicator of relative growth rate, mass-based maximum photosynthesis rate, fertility status, allocation to leaf structural and defence components, hence leaf strength or toughness (Shipley 1995; Diaz and Cabido 1997; Weiher et al. 1999, Westoby et al. 2002). Also related to leaf longevity – leaves with low SLA are mostly long lived whereas those with high SLA tend to be more ephemeral (Wright et al. 2001).

2.4.2.3 Leaf relative water content (RWC)

The ratio of the amount of water contained by a leaf to the amount of water contained when the leaf is in a fully turgid state.
Freshly collected leaves were weighed (fresh mass, FM) then placed in distilled water in a closed petri dish for 4 hours at the prevailing laboratory temperature (15 - 20 °C). The leaves were blotted dry with a paper towel and weighed (turgid mass, TM). Leaves were dried at 100°C for at least 24 hours and weighed (dry mass, DM).

RWC (%) = 100* (FM – DM)/(TM – DM)

Functional relevance: related to desiccation tolerance, leaf water status and osmoregulation (Smart and Bingham 1974; Garnier and Laurent 1994).

2.4.2.4 Leaf dry matter content (LDMC)

The ratio of the oven dry mass of a leaf to the water-saturated mass of the leaf (mg g^{-1}).

LDMC = DM/TM

Functional relevance: Related to leaf tissue density, negatively correlated with relative growth rate and hence productivity (Cornelissen et al. 1996; Niinemets 1999). Generally positively correlated with leaf lifespan (Williams et al. 1989) and leaf mechanical strength (Wright and Westoby 2002).

2.4.2.5 Chlorophyll content

Chlorophyll content (mg m^{-2}) was measured with a CCM-300 chlorophyll meter (Opti-Sciences Inc., Hudson, USA), using a fluorescence ratio technique. The meter was calibrated weekly as per the instruction manual.

Functional relevance: Correlated with photosynthetic rate, leaf nutrient status and productivity.

2.4.2.6 Stomatal density

Stomatal density is the number of stomata per leaf area. A digital microscope (ProScope Mobile, Bodelin Technologies, Lake Oswego, USA) calibrated to 100 µm was used to capture digital images of sections of the adaxial and/or abaxial leaf surface. Image J was used to measure the areas of the digital images. The counter function of Image J was used to manually count the stomata in the image.

Functional relevance: Related to transpiration rate, desiccation tolerance, photosynthesis rate and productivity.

2.4.3 Stem trait

2.4.3.1 Stem specific density (SSD)

The ratio of the oven dry mass of a stem section to the volume of that section when freshly collected (mg mm^{-3}).
SSD was measured from the thickest section of the main stem, excepting for the leafless rush *J. effuses*, where the bottom part of the stem was always measured. The diameter (D) and length (L) of the section was measured with a caliper (Insize Digital Caliper, Series 1108, Insize Inc., USA) or a ruler.

The volume (V) of the section was calculated as

$V= (0.5\ D)^2 * \pi * L$

The section was then dried at 100 ºC for at least 24 hours and weighed = DM.

SSD = DM / V

Functional relevance: Correlated with plant structural strength (Gartner 1995), represents a trade-off between relative growth rate and stem defences against pathogens or factors causing mechanical damage (Shain 1995).

2.4.4 Root traits

2.4.4.1 Root:Shoot mass ratio

The ratio of the dry root mass to the dry shoot mass of a plant (g g^{-1}). Roots were separated from shoots, dried and weighed.

Functional relevance: Indicates allocation of resources to the belowground sphere.

2.4.4.2 Specific root length (SRL)

The ratio of length to dry mass of absorptive roots (m g^{-1}). Absorptive roots were considered to be the turgid, smaller roots with a light colour and with root caps.

Two main roots were sampled per plant. Ten absorptive roots were selected from each main root. Soil was removed from the absorptive roots with fine forceps and a brush under a dissecting microscope. The combined length of each set of ten roots was measured with a ruler or caliper. Each set was dried at 100 ºC and weighed. For each set, SRL was calculated as combined length divided by combined dry mass.

Functional relevance: belowground analogue of specific leaf area, an indication of the amount of absorptive root tissue deployed per unit mass invested belowground (Perez-Harguindeguy et al. 2013). Linked to rate of root elongation and the penetrative force of roots (Cornelissen et al. 2003), rates of water and nutrient uptake (Steudle 2001), root turnover and longevity (Ryser 1996; Eissenstat et al. 2000), relative growth rate of seedlings (Reich et al. 1998) and belowground competitive ability (McCully and Canny 1989).

2.4.4.3 Root Diameter

Root diameter was measured just behind the zone of elongation in the root hair zone, using a digital microscope (Insize, ISM-PM200SA, USA).

Functional relevance: Positively related to longevity and negatively related to nutrient uptake rate (Perez-Harguindeguy et al. 2013).

2.4.5 Photosynthetic traits

2.4.5.1 Basics of the Chlorophyll fluorescence technique

Light energy absorbed by a leaf has several fates. It can result in electron transport through the thylakoid membrane to produce the ATP and NADPH that powers photosynthesis, photorespiration, nitrate reduction etc. – this fate is termed photochemistry. It can be dissipated as heat through regulated mechanisms (under the control of the plant) and unregulated mechanisms (constitutive heat dissipation, not controlled by the plant). It can also be emitted from the leaf as red light fluorescence. It is this red light emission that is actually measured in the chlorophyll fluorescence technique. Using the so-called "quenching analysis technique, also called the "saturation pulse technique" (Kraus and Weis 1991; Maxwell and Johnson 2000), the other two fates of the absorbed light energy, photochemistry and heat dissipation, can be calculated from the fluorescence signal.

2.4.5.2 Sample collection and pretreament

Vascular plants were mostly collected whole, with peat still clinging to the roots. The whole plant was placed in a jar so that the roots were in water. For larger species (e.g. *Acaena magellanica*, *Pringlea antiscorbutica*, *Juncus effusus*), individual shoots or leaves were used and the cut end of the stem or petiole was placed in a jar of water. Bryophytes were placed on wet filter paper in a petri dish. The samples were kept in an illuminated incubator (10 ºC, *c.* 200 µmol m^{-2} s^{-1} PAR for vascular plants, 50 – 100 µmol m^{-2} s^{-1} PAR for bryophytes) before carrying out the chlorophyll fluorescence measurements, which was done within 24 hours for the bryophytes and whole vascular plant samples and within 6 hours for the cut shoots/leaves.

2.4.5.3 Measurement protocol

Chlorophyll fluorescence measurements were made in a darkened incubator (10°C, RH 65-85%), using a PAM-2500 Portable Chlorophyll Fluorometer (Heinz Walz GmbH, Germany). A Heinz Walz Leaf-Clip Holder 2030-B was used for the vascular plants and a Dark Leaf Clip DLC-8 was used for the bryophytes. The Dark Leaf Clip was modified by cutting a hole in the lower part of the leaf clip directly below where the sample (comprising the distal portions of several fronds) is exposed to the fibre optic sensor held in the upper part of the

clip. A tube was attached to the lower part of the leaf clip so that its opening surrounded this hole. Air from outside the laboratory, conditioned to 10°C and ca. 80% relative humidity, passed (ca. 20 ml minute^{-1}) through the hole and over the sample to prevent CO_2 depletion during the fluorescence measurements. When using the Leaf Clip Holder 2030-B, the leaf is exposed to the surrounding air, so the end of the tube carrying the conditioned air was placed near the side of the clip so that the air was blown over both leaf surfaces.

The sample was dark adapted for 20 minutes. A measuring light of very low intensity (<1 µmol m^{-2} s^{-1}) was applied and the minimal fluorescence level (Fo) measured. A saturating light pulse of high intensity (>5000 µmol photons m^{-2} s^{-1} PAR) was applied and the maximum fluorescence level (Fm) measured. Once the fluorescence signal returned to the Fo level, photosynthesis was induced by an actinic light (AL), in six stages of increasing PAR (each lasting from 2 to 4 minutes) for vascular plants and four stages of increasing light PAR (each lasting from 1 to 4 minutes) for bryophytes (Table 2.4). The reason for inducing photosynthesis is given later.

After the induction, the AL was applied at increasing PAR levels, from 2 to 2015 µmol m^{-2} s^{-1} (for three minutes at each level) for vascular plants and 4 to 1114 µmol m^{-2} s^{-1}, (two minutes at each level) for bryophytes (Table 2.4 shows the PAR value and duration of each level). At the end of the two or three minutes exposure to a particular light level, the fluorescence signal (F) was measured, then a saturating pulse applied and Fm' (the maximum fluorescence yield of the leaf at the particular level of illumination) measured. The AL was then switched off and a far-red light applied for 4 seconds before measuring Fo', the minimum fluorescence yield of the illuminated leaf. The AL was then switched on, at the next higher PAR level.

The light response measured in this way is based on the rapid light curve (RLC) technique of Ralph and Gademann (2005). The technique offers a significant advantage for rapidly screening large number of samples in a comparative study such as the one reported on here. However, it has been criticized because it does not allow the sample to reach steady state at each PAR value. The usual technique applies the increasing PAR levels to a dark-adapted sample for a short period (20 to 40 seconds), with no pre-induction of the sample beforehand. It thus measures fluorescence yields that are influenced by the photosynthesis induction response to light, rather than only the effect of the increasing irradiation level. Inducing

photosynthesis fully before starting the RLC, and allowing the leaf to experience each new light level for two or three minutes, rather than the 20 to 40 seconds in the usual RLC procedure, minimizes the induction component and yields photosynthetic light response curves very similar to those obtained when the sample is allowed to come to full steady state at each light step (V.R. Smith, pers. comm.).

The Fo, Fm, F, Fm' and Fo' values measured at each PAR level were used to calculate the following fluorescence parameters.

2.4.5.4 Optimal quantum yield (Fv/Fm)

Fv/Fm = (Fm-Fo)/Fm

This reflects the maximum quantum yield or maximum quantum use efficiency attainable by the leaf; it reflects the maximum probability that an absorbed light photon will result in electron transport, and hence photochemistry).

2.4.5.5 Effective quantum yield (ΦPSII)

ΦPSII= (Fm'-F)/Fm'

ΦPSII is the actual quantum yield of the leaf, i.e. the probability that an absorbed photon will result in electron transport at the particular illumination level. Also known as the operative quantum yield.

2.4.5.6 Proportion of closed reaction centres (1-qL)

qL = ((Fm'-F)/(Fm'-Fo'))*(Fo'/F)

qL is commonly referred to as the photochemical quenching coefficient. It reflects the proportion of PSII reaction centres that are "open", i.e. able to accept and donate electrons. 1-qL is thus the proportion of closed reaction centres. If all reaction centres are closed, electron transport (and hence photochemistry) is not possible.

2.4.5.7 Ratio of regulated versus non-regulated excess energy dissipation (YNPQ/YNO)

In normal daylight, the leaf absorbs light energy in excess of the amount that can be used in photochemistry. This excess energy must be dissipated or it will lead to the formation of high energy reactants (triplet chlorophyll, singlet oxygen, free radicals of oxygen, H_2O_2) that cause photoinhibition and photodamage. Leaves have developed mechanisms to increase the dissipation of excess energy under photoinhibitory conditions. The most common mechanism is xanthophyll cycling, the light-dependent conversion of antheroxanthin to zeaxanthin. Zeaxanthin confers on the leaf the ability to dissipate excess absorbed light energy as heat in a regulated manner. This regulated heat dissipation causes the decline from Fm measured on the dark-adapted leaf, to Fm' measured on the illuminated leaf. In quenching analysis, non-photochemical quenching (NPQ) is represented by this decline. The yield of NPQ (ϕNPQ, or YNPQ in the terminology of Klughammer and Schreiber (2008) who first presented a consistent body of derivations for the complementary quantum yields and placed them within a sound theoretical framework) is calculated as:

YNPQ = (F/Fm')-(F/Fm)

The excess absorbed energy can also be converted to heat through non-regulated mechanisms, i.e. constitutive, or passive, dissipation not under the leaf's control.

YNO is the sum of the yield of this non-regulated energy dissipation and the yield of fluorescence emission (the red light emitted by the leaf that is measured in the chlorophyll fluorescence technique). It is calculated as:

YNO = F/Fm

Klughammer and Schreiber (2008) term YNO the "yield of primary constitutive losses" and consider that a high YNPQ:YNO ratio indicates a high capacity for protection against photoinhibition and photodamage.

2.4.5.8 Photosynthetic electron transport rate (ETR)

ETR is the rate at which electrons move through the thylakoid electron transport chain to produce NADPH and ATP, both of which are used primarily for CO_2 reduction, i.e. photosynthesis. ETR is thus a good proxy for photosynthesis rate. Since ϕPSII is the

probability that an absorbed photon will result in electron transport at the particular illumination level,

$ETR = \phi PSII * PAR_a * 0.5 * 0.84$

Where PAR_a is absorbed PAR. The factor 0.5 is introduced in the equation to account for the fact that two photons have to be absorbed for one electron to move through the electron transport chain, and the factor 0.84 is used to convert incident PAR to absorbed PAR (an "average" leaf absorbs 84% of the incident light energy). Both factors can be left out of the equation, the result is then generally termed "Relative ETR".

2.4.5.9 Traits derived from the ETR:PAR response curve

The ETR versus PAR response was subjected to a Nonlinear Estimation procedure using the Eilers and Peeters (1988) model:

$ETR=PAR/((a*PAR^2)+(b*PAR)+c)$

where a, b and c are the model coefficients used to calculate the response curve traits, which are:

2.4.5.9.1 Initial slope of the ETR:PAR response (α)

The initial slope of the ETR:PAR curve (mol electrons per mol absorbed photons) is the maximum quantum efficiency of photosynthetic electron transport.

$\alpha = 1/c$

2.4.5.9.2 Maximum electron transport rate (ETR_{max})

ETR_{max} is the maximum electron transport rate attained by the particular sample during the light response measurements.

$ETR_{max} = 1/ (b+ (2*sqrt(ac)))$.

2.4.5.9.3 PAR yielding ETR_{max} (PAR_{opt})

The minimum PAR value at which ETR_{max} is attained.

PAR_{opt} = sqrt (c/a).

2.4.5.9.4 Photoadaptation parameter (I_k)

I_k has been termed the "photoadaptation parameter" (Platt and Sathyendranath 1997) or "minimum saturating irradiance" (Ralph and Gademann 2005, Heinz Walz GmbH 2008). It is a measure of the PAR value at which photosynthesis rate switches from being light limited to becoming light saturated.

I_k = c/(b+(2*sqrt(ac))).

2.5 Data Analysis

All statistical analyses (and the nonlinear estimation modelling of the ETR:PAR response curve) were carried out using STATISTICA 12 (StatSoft Inc., OK).

Analysis of variance (ANOVA) and the Tukey's Honest Significant Difference Test were used to test the between-species, between-site and between-altitude differences in trait values. For the between-species comparisons, this mostly resulted in a confusing number of overlapping groups. Confidence interval box-plots of the species mean values were thus combined with the Tukey HSD results to rank the species into groups based on whether they show very high, high, moderate, low or very low values for a particular trait. This allowed the identification of species groupings based on trait values, considered on a trait-by-trait basis, which was useful as an initial stage of data exploration.

Principal Component Analysis (PCA) was then used to assess the overall pattern of interspecies differences across the whole suite of traits. Cluster analysis (using a weighted pair-group average amalgamation rule and City-block distance measure) of the species scores on the significant principal axes was used to group the species into functional types.

Correspondence analysis (CA) was used to evaluate if the groupings could be related to categories of habit (graminoid, forb, fern, moss, liverwort), status (indigenous or alien) or habitat (the habitat categories are described in Chapter 4).

Chapter 3.

Between-sites, between-altitude and between-species differences in trait values for the vascular plant species

In this chapter, and later chapters, frequent reference is made to three growth habits - *forb*, *fern* and *graminoid*. Strictly, ferns are also forbs; my usage of the terms follows the recommendation in the National Vegetation Classification Standard of the Federal Geographic Data Committee (FGDC 2008). In that Standard, forbs, ferns and herbs are considered as separate plant habit types, under the general growth form *herbs* (herbaceous plants, with little or no aboveground woody tissue). All the Marion Island vascular species fall in one of the three habit types, except for the submerged macrophyte *Potamogeton nodosus* which falls into two National Vegetation Classification Standard growth form categories – floating and submerged.

3.1 Between-site differences in trait values

For all the vascular species measured at three or more sites there were significant ($p \leq 0.05$) between-site differences in most of the structural traits, but in only a few cases were there differences in the photosynthetic (chlorophyll fluorescence) traits. This was true at both low altitude (Table 3.2) and high altitude (Table 3.3). Since site data (exposure, soil depth and texture, moisture, etc.) were not collected, it is not possible to relate the between-site differences to site characteristics. However, the inter-site differences are perhaps less striking than suggested by Tables 3.2 and 3.3. Tukey's HSD tests showed that, in most instances, the significant probability values in the tables can be ascribed to a particular trait having a different value at just one site (Appendix Figures A1 to A4).

Where two or more species were sampled at the same set of sites, factorial ANOVA revealed significant site x species interactions for many traits, showing that the pattern of between-site differences differed between species (Appendix Figures A1 to A4). For instance, across the four mire sites, RWC for *Juncus scheuchzerioides* was highest at sites 23 and 24, whereas for *Uncinia compacta* RWC was highest at site 25 (Fig. A1b). Similarly, at the biotic sites, *Agrostis stolonifera* was tallest at site 15 whereas *Callitriche antarctica* was tallest at site 13

(Fig. A3a). Hence, the between-site variations in a particular trait are not consistent across species and so might not be simply related to differences in site characteristics.

3.2 Differences in trait values between low altitude and high altitude plants

Only five vascular species were measured at both low and high altitude and they all showed significant between-altitude differences for most of the structural traits, with the exception of one of the photosynthetic traits (Table 3.4).
The graminoids (*Agrostis magellanica*, *Poa cookii* and *U. compacta*) and the fern (*Blechnum penna-marina*) are taller at low altitude, whereas the cushion forb, *Azorella selago* is taller at high altitude. *B. penna-marina*, especially, has a much lower stature at high than at low altitude. For all five species, mean leaf area (LA) and leaf dry mass (LDM) are higher at low altitude. Since, for three of them, specific leaf area (SLA) is greater at high altitude, the decrease in LA with altitude is proportionally less than the decrease in LDM. For the other two species the between-altitude difference in SLA is not significant.

For *A. selago* and *B. penna-marina*, leaf dry matter content (LDMC, the dry mass: turgid mass ratio) is higher at high altitude, suggesting a greater proportion of structural tissue in the high altitude leaves. However, the opposite is true for *U. compacta* and there is no difference in LDMC between high and low altitude *Ag. magellanica* and *P. cookii* plants. The between altitude differences in LDMC are opposite to the differences in leaf relative water content (RWC) for four of the species. *P. cookii* is the exception, but for that species the between-altitude differences in LDMC and RWC are not significant. Especially large between-altitude differences in RWC are shown by *B. penna-marina* (mean RWC greater at low altitude) and *A. selago* (mean RWC greater at high altitude).

For four of the five species, stem specific density (SSD) is greater at high altitude than at low altitude, suggesting a greater need for strengthening tissue in the windier higher altitude environment. Again, as was shown by the trait indicative of leaf strengthening tissue, LDMC, *U. compacta* is the exception.

Chlorophyll content per leaf area differs significantly between high and low altitude; for *Ag. magellanica*, *B. penna-marina* and *U. compacta*, chlorophyll content is greater, while for *A. selago* and *P. cookii* it is lower, at low altitude than at high altitude. Across the five species,

SLA showed the opposite pattern of altitudinal differences, although not all the differences are significant.

For all of the species, specific root length (SRL) is greater at high altitude than at low altitude. In contrast, at least for the graminoids, root diameter (RD) is greater at low altitude than at high altitude.

As what was shown by the between-site comparison, the photosynthetic trait values also did not differ significantly between high and low altitude, with the notable exception that for all five species the proportion of closed reaction centres at ETR_{max} is higher at low than at high altitude.

3.3 Between-species differences in trait values at low altitude

Appendix figures A1 to A4 show that, even within the same vegetation type and same altitudinal band, the structural traits differ significantly between-species. In several instances, the between-species difference is site dependent. Some examples are: *U. compacta* and *Ag. magellanica* showed similar leaf dry masses at mire sites 22 and 25 but at site 24 *U. compacta* leaf mass was significantly lower, and at site 23 it was significantly greater, than the *Ag. magellanica* leaf mass (Fig. A1e); *Acaena magellanica* is significantly taller than *B. penna-marina* at three of the fernbrake sites but not at the fourth (Fig. A2a); *Ac. magellanica* has less chlorophyll than *P. cookii* at fernbrake site 36, but more chlorophyll at site 34 (Fig. A2g).

To test the differences between all species, the site effect was ignored, i.e. for each species the four site values for a trait were considered as replicates. The trait values were subjected to one way anova with species as categorical variable. Species trait means, their standard errors, the *F* and *p* values from the between-species anovas and the homologous groupings from the Tukey's HSD tests are given in Appendix tables A1 to A20. As might be expected for an assemblage of plants comprising such a wide range of growth habits (from small (mm) herbaceous annual forbs, through medium-sized (cm) graminoids and perennial forbs, to a quite tall (m) rush and submerged macrophyte), the anovas showed very significant species effects for all the traits. For each trait, the Tukey's HSD tests resulted in a confusingly large number of overlapping homologous groups (Tables A1 to A20). For the sake of this presentation and discussion of the inter-species differences in trait values, a clearer picture is

provided by box plots (Figure 3.1), with the species means categorized as being very high, high, moderate, low or very low. The categorization was subjective but guided by the Tukey's HSD results.

Potamogeton nodosus is indicated as being the tallest plant on the island (Fig. 3.1a). The species is a submerged macrophyte with buoyant leaves and stems, so its height largely reflects the depth of the water in which it grows and, unsurprisingly, it has the highest leaf RWC (Fig. 3.1b). It has relatively large, but very thin, leaves and thus the largest SLA of all the species (Fig. 3.1d). It also has the lowest SSD (Fig. 3.1i) and one of the lowest leaf dry matter contents (LDMC, Fig. 3.1f), indicating structurally weak stems and leaves. *P. nodosus* possesses the lowest chlorophyll content (Fig. 3.1h) and also the lowest photosynthetic capacity, as evidenced by low maximum quantum yield (α = 0.04 electron photon^{-1}; Fig. 3.1p) and low ETR_{max} (1.73 µmol electrons m^{-2} s^{-1}; Fig. 3.1q), reached at low light (PAR_{opt} = 75 µmol photons m^{-2} s^{-1}; Fig. 3.1r). Photosynthesis also starts saturating at very low PAR (I_k = 41.47 µmol photons m^{-2} s^{-1}; Fig. 3.1s). However, these indices of photosynthetic capacity were derived from chlorophyll fluorescence measurements made on leaves in air, which is probably inappropriate for leaves that are normally submerged or floating.

The tallest terrestrial plant species is the rush *Juncus effusus*, a cosmopolitan species that occurs at only three localities on the island (Fig. 3.1a). The rest of the island's plants are all low growing; only *P. cookii*, *Poa pratensis*, *Polystichum marionense*, *Ac. magellanica*, *Cerastium fontanum* and *Ag. magellanica* have a mean height ≥ 200 mm. Of the six species with the shortest stature (≤ 50mm), four (*C. antarctica, Colobanthus kerguelensis, Crassula moschata* and *Montia fontana*) are herbaceous forbs that occur either only or predominantly in coastal habitats, and two (*Grammitis poeppigeana* and *Hymenophyllum peltatum*) are cryptic ferns that occur in sheltered situations.

J. effusus is indicated as having amongst the lowest SLA of all the island's species, but for this leafless species SLA actually refers to the area:mass ratio of the photosynthetic stems (Fig. 3.1d). Of the leafy species, the Kerguelen Cabbage, *Pringlea antiscorbutica*, has the lowest SLA. Despite this, it also has the highest LA (Fig. 3.1c), suggesting that in proportion to their area, its leaves are thicker and heavier than leaves of all the other species, which is the case (data not shown). The other species with low SLA (< 20 mm^2 mg^{-1}) comprise the island's four native graminoid species (the grasses *P. cookii* and *Ag. magellanica*, the sedge

U. compacta and the rush *J. scheuchzerioides*), the cushion plant *A. selago* and all three fern species for which SLA was measured (*B. penna-marina*, *G. poeppigeana* and *P. marionense*).

At the other end of the SLA scale, discounting *P. nodosus*, the species showing the highest mean SLA values (> 30 mm^2 mg^{-1}) are *Cotula plumosa*, *C. moschata*, *M. fontana*, *Sagina procumbens*, *C. antarctica*, *Poa annua* and *A. stolonifera*. All these attain their maximum cover and vitality in the coastal zone and the latter two are highly invasive introduced grasses.

Of the eight species with the highest LDMC (> 250 mg g^{-1}), six are graminoids, one is a rock-dwelling fern (*G. poeppigeana*) and the other a woody forb (*Ac. magellanica*) (Fig 3.1f). The six graminoids comprise the four indigenous species mentioned above, *P. pratensis* (an alien grass) and *J. effusus*, (for the latter, LDMC refers to stem dry mass per fully hydrated stem mass). Species with lowest LDMC (< 150 mg g^{-1}) are almost all forbs with succulent, or at least fleshy, leaves and most of them are restricted to, or attain maximum vitality, in coastal areas. Unsurprisingly (since LDMC is dry mass per saturated mass, and actual leaf moisture content is mostly close to saturation because of the island's high soil and atmospheric moisture contents), these species are also amongst those with the highest RWC values (Fig. 3.1b).

P. nodosus and *H. peltatum* have no stomata, and the stomata of *S. procumbens*, *Ac. magellanica* and *P. cookii* are very small and cryptic and could not be seen clearly enough under the digital microscope to count reliably. Of the 20 species for which stomata could be counted, twelve bear stomata on both leaf surfaces, three (the three fern species) on the abaxial and four (*A. selago, M. fontana, C. kerguelensis* and *J. scheuchzerioides*) on the adaxial surface. For the remaining species, *J. effusus*, stomata occur in vertical rows all around the stems.

Stomatal density (SD) for species with stomata on both leaf surfaces were within the range of values for species with stomata on only one surface. Species with abaxial stomata tended to have a lower SD than species with adaxial stomata; a notable exception is *B. penna-marina*, with abaxial stomata but the fourth highest mean SD (198 stomata mm^{-2}), Fig. 3.1g. The other two ferns showed considerably lower SD's; in fact, mean SD for *G. poeppigeana* was less than a third of the mean SD for the species with the next lowest value. Excluding *J. effusus*, graminoid species tend to have lower SD (mean 113 stomata mm^{-2}) than forbs (mean 160 stomata mm^{-2}) although the difference just fails to be significant at the 5% level

(p = 0.110). However, the most conspicuous difference in SD is between the indigenous and alien graminoid species, respectively 89 and 136 stomata mm^{-2}; p = 0.030).

Root to shoot mass ratio was measured for only ten species – for the others it was impossible to get all the roots out of the soil intact or to separate them from plant debris and soil. R:S for the indigenous graminoids *Ag. magellanica* and *U. compacta* are about half of the values for the alien graminoids *P. annua* and *A. stolonifera* (Fig. 3.1j). Other than that, no pattern could be discerned in the R:S data. For instance, of the four small herbaceous forbs, *C. moschata* and *C. plumosa* have the lowest, but *M. fontana* and *Ranunculus biternatus* the highest, R:S ratio of the ten species on which the trait was measured.

Species with the highest specific root length and lowest root diameter are *S. procumbens*, *C. moschata*, *M. fontana*, *C. antarctica*, *J. scheuchzerioides*, *P. annua* and *A. stolonifera* (Fig. 3.1k, Fig. 3.1l). All but *J. scheuchzerioides* are predominantly coastal zone species. However other coastal zone species (*P. cookii*, *C. plumosa*, *Rumex acetosella*) showed low SRL. Lowest SRL, and highest RD, was found for species occupying a variety of habitats, including wet mires (e.g. *Ag. magellanica* and *U. compacta*) and dry slopes (*B. penna-marina* and *Ac. magellanica*).

The range in mean ETR_{max} values shown by the species spanned an order of magnitude, from 9.7 µmol electrons m^{-2} s^{-1} for *H. peltatum* to 136.8 µmol electrons m^{-2} s^{-1} for *P. antiscorbutica* (Fig. 3.1q) (*P. nodosus* is not considered here since the very low ETR_{max}, < 2 µmol electrons m^{-2} s^{-1} for this submerged species is probably an artefact caused by using an inappropriate measurement technique). All species with very high mean ETR_{max} (> 100 µmol electrons m^{-2} s^{-1}) are forbs and, overall, forbs show higher ETR_{max} than graminoids, although the difference just fails to be significant at the 5% level (p = 0.066). Lowest ETR_{max} (mean < 35 electrons m^{-2} s^{-1}) were for the three ferns, *H. peltatum*, *G. poeppigeana* and *P. marionense*. *B. penna-marina*, the other fern species tested, has a mean ETR_{max} of 61 µmol electrons m^{-2} s^{-1}, exactly the same as the mean value for graminoids.

The species with the highest ETR_{max} also have a higher effective quantum yield (ΦPSII) at ETR_{max} (Fig. 3.1m), and ETR starts saturating (I_k) and becomes saturated (PAR_{opt}) at higher light levels than species with lower ETR_{max}. The only exception to this is for *P. annua*, which shows the third highest PAR_{opt} (Fig. 3.1r) of all the species, but a moderately low ETR_{max}. The three fern species that show especially low ETR_{max} start becoming ETR saturated, and

reach saturation, at lower light levels than any of the other species. The only other significant differences between taxonomic groups is that forbs have a greater mean maximum quantum yield (α, the initial slope of the ETR:PAR response) than graminoids (p = 0.035). The ferns show very similar α to the forbs (Fig.3.1p).

Unlike what was found for many of the structural traits, indigenous and alien graminoid species show no differences in any of the fluorescence traits.

3.4 Between-species differences in trait values at high altitude

Plant traits were measured on only five vascular species at high altitude. Species means and between-species anova and Tukey's HSD results for the high altitude samples are given in Appendix Tables A21 to A38.

For the structural traits, the mean values of LA, LDMC and RD differ between the five species at high altitude in the same way as they do at low altitude. For LDM, SLA, SSD and SRL, one or two species differ between high and low altitude in how they are ranked on mean values but in all such instances the differences between those species are very small and not significant at $p \leq 0.05$ at both altitudes. For example, *U. compacta* shows a slightly higher mean SLA than *A. selago* at high altitude whereas the order is reversed at low altitude, but in both instances there is a less than 10% difference in mean values.

There are some notable exceptions to this general finding that the pattern of species differences in trait values is similar at high- and low altitudes. Altitudinal stunting is more marked in *B. penna-marina* than the other species, so it is the shortest of the five species at high altitude whereas at low altitude its mean height value is in the middle of the range shown by the five species. Leaf RWC of *B. penna-marina* is also low (81%) at high altitude whereas at low altitude it showed the second highest RWC (89%) of the five species. At low altitude the fern has the highest chlorophyll content of the five species, but at high altitude its chlorophyll content is significantly lower than that of *P. cookii*. In contrast, *A. selago* has the lowest mean chlorophyll content at low altitude whereas at high altitude its chlorophyll content is in the middle of the range of values for the five species.

The between-species patterns of differences in chlorophyll fluorescence trait values at high altitude are very similar to those at low altitude. At both altitudes, ETR in *A. selago* starts saturating at about double the PAR level, ETR_{max} is also about double and occurs at a much

higher PAR, than what is shown by the other four species. At both altitudes, *B. penna-marina* shows the greatest, and *U. compacta* the smallest ETR response to light at low light levels. At both altitudes effective quantum yield is significantly higher for *Ag. magellanica* and *A. selago* than for the other three species, which between them have very similar ΦPSII values. At both altitudes, *Ag. magellanica* and *P. cookii* show the highest, and *A. selago* the lowest capacity for photoprotection (YNPQ/YNO) at ETR_{max}.

The only fluorescence trait that showed a different across-species variation between altitudes was the proportion of closed reaction centres (1-qL) at ETR_{max}. *A. selago* has the highest mean 1-qL at low altitude but the lowest one at high altitude. *B. penna-marina* at high altitude has the highest mean 1-qL whereas at low altitude its 1-qL is in the middle of the range of values shown by the other four species.

3.5. Discussion

The very high SLA, low LDMC (large, thin leaves with a low dry matter content) and very low SSD (stem with low dry mass per volume) for *P. nodosus*, indicate structural weakness, not surprising since the submerged and floating leaves require little structural support and, because the plants are surrounded by water there is less requirement for heavy water conducting xylem in the leaf or stem. It is tempting to ascribe the species' very low capacity for photosynthesis (measured as electron transport rate) and the fact that photosynthesis saturates at very low light to photosynthesis being CO_2 limited, rather than light limited, as might be expected for a submerged plant. However, the ETR measurements were made in air, on hydrated leaves in the absence of the external aqueous phase CO_2 diffusion resistance that would severely limit photosynthesis of the leaves when submerged. Hence, it might well be that the low values found for the species are, in fact, over-estimates of photosynthetic capacity. For two macrophytes (*Zostera noltii* and *Spartina maritima*) with leaves that are sometimes submerged and at other times above the water, Silva et al. (2005) found higher photosynthetic rates (measured using gas exchange and chlorophyll fluorescence) in air than in water. The low photosynthetic rate for *P. nodosus* is in keeping with the fact that it has very thin leaves (specific leaf area is nearly double that of the species with the next highest SLA) and very low chlorophyll concentration (about half of that of the species with the next lowest chlorophyll concentration). Nielson and Sand-Jensen (1989) also found that leaves of

submerged macrophytes are characterized by being thin, having low chlorophyll concentration and especially low photosynthesis rates, compared with terrestrial plant leaves.

The majority of the island's terrestrial plant species are of low stature (mean height < 200 mm), possibly ascribable to the fierce wind that occurs on the island. However, against this, most of the smaller (< 200 mm) species are restricted to coastal areas away from the fiercest winds, or to sheltered rock crevices. Also, of the six species taller than 200 mm, only *P. marionense*, is restricted to sheltered areas (under rock overhangs). The six tallest species comprise a variety of taxonomic types (and growth forms); a rush, two grasses, two perennial forbs and a fern.

This study did not address the variation in plant traits in a particular species across vegetation types. However, it is clear that even within the same vegetation type and within a narrow altitudinal band (22 to 40 m for mire, 20 to 57 m for fernbrake, 3 to 11 m for the saltspray and biotic communities, and 297 to 338 m for the fellfields), plant trait values do differ significantly from site to site. Site information, such as soil depth and texture, exposure, moisture, etc., was not obtained so the between-site differences in plant trait values cannot be attributed to site characteristics. However, even within the same vegetation types the across-site differences in plant trait values are not consistent across species, suggesting that they might not be caused by differences in site properties. Certain traits, such as plant height, leaf area and root-shoot mass ratio might well be related to properties more directly associated with the vitality of the plant species at a particular site, such as dominance or cover, but these were also not recorded.

The fact that plant height is less at high altitude than at low altitude for the four phanerophytes for which altitudinal differences were investigated can be ascribed to the greater wind speed at high altitude. In contrast, cushions of *A. selago*, the archetype vascular species of exposed, windy sites are taller at high than at low altitudes. Nyakatya (2006) also found that cushion height increases with altitude on the island. On the island's east side, near the sites investigated in this investigation, *A. selago* cushions at 588 m altitude were found to be three times taller than at 176 m altitude. Of all the island's vascular species, *A. selago* is found at the highest altitude and the structural and fluorescence trait results presented here support the suggestion by Huntley (1971) that the species attains maximum vitality at higher altitude. In fact, there are indications in the trait results that *A. selago* is stressed at low altitude. For instance, at low altitude *A. selago* shows the lowest chlorophyll content and the

highest proportion of closed reaction centres of the five species that were measured at both altitudes, whereas at high altitude both chlorophyll content and the proportion of closed reaction centres are very similar to the values shown by the other four species.

That leaf area is larger at low than at high altitude for all the species investigated can also be ascribed to the effect of wind. Huntley (1971) measured leaf size, length and breadth of four of the island's plant species at different altitudes and also found that leaves were smaller at higher altitude. The results presented here show that leaves and stems tend to be structurally tougher (have higher LDMC, SSD) at high altitude, which can also be ascribed to a wind effect. However, *U. compacta* is an exception. This species reaches maximum vitality and dominance at low altitudes (Huntley 1970, Gremmen 1981) and is actually quite rare at the high altitude sites considered in this investigation. There, *U. compacta* is strongly clonal and the plants are small, current season, ramets that do not produce inflorescences. The individual *U. compacta* clonal plants are more like annuals, rather than the perennial individuals at lower altitudes. This might explain the lower amount of strengthening tissue (low LDMC, SSD) of high altitude *U. compacta* plants than low altitude plants.

The trait results show that *B. penna-marina* is also a true lowland species. Huntley (1970) never found it above 275 m. The warming experienced at Marion Island has resulted in it extending to higher altitudes (Le Roux and McGeoch 2008b), but even today it is rare above 300 m and absent above 408 m (PC Le Roux, University of Pretoria, personal communication, June 2015). Of all the five species measured at both altitudes, the fern shows the greatest decrease in vitality with altitude, showing the largest degree of stunting, largest decreases in leaf area, leaf mass, leaf turgor and chlorophyll content. It has the highest proportion of closed reaction centres of all five species at high altitude, whereas at low altitude its 1-qL is in the range of values shown by the species. All these considerations point to the fact that *B. penna-marina* is especially stressed at higher altitudes.

Overall, the pattern of thinner (small RD) and, in relation to their mass, longer (greater SRL) roots at high altitude seems counter-intuitive considering the greater need for strengthening tissue in the windier environment of higher altitudes. However, belowground plant morphology is probably controlled primarily by the need for nutrient and water acquisition. Soil nutrient concentrations decrease markedly away from the coast, where there are dense populations of seabirds and seals and heavy deposition of seaspray (Conradie and Smith 2012). Also, the inland soils are far more mineral, are skeletal and have a lower moisture

holding capacity than the coastal peats (Smith et al. 2001). SRL is positively, and RD negatively, related to the capacity to obtain nutrients and water; the between-altitude differences in RL and RD are thus consistent with decreased soil nutrient and moisture availability going inland.

That the species show a higher proportion of closed reaction centres at low altitude than at high altitude is difficult to explain. A greater closure of reaction centres can be expected to be associated with higher saturating light levels (PAR_{opt}), lower effective quantum use efficiency (ϕPSII) and lower capacity for regulated heat dissipation (YNPQ/YNO). However, across the five species, none of these three parameters showed consistent differences in the direction in which their values changed with altitude. For some species they were greater, and for others they were smaller at high than at low altitude but none of the differences were significant at $p \leq 0.05$.

The proportion of closed reaction centres at ETR_{max} might also reasonably be expected to be positively related to chlorophyll concentration and negatively related to SLA (more chlorophyll or greater leaf thickness suggest leaves with more reaction centres, thus a lower proportion will be closed at any particular PAR). However, across the five species, there were also no consistent between-altitude differences in chlorophyll content or SLA.

The fact that for the five species the two measures of maximum quantum yield (F_v/F_m and the initial slope of the ETR:PAR response, α) were higher for low altitude plants, even though the differences were not significant, suggests that the photosynthetic apparatus of low altitude plants is less stressed than the high altitude plants. This makes the higher proportion of closed reaction centres in the low altitude plants even more puzzling.

Across species, chlorophyll content on a leaf area basis was strongly negatively correlated with SLA (r = -0.634, p = 0.001). This is unsurprising, since decreasing SLA reflects increasing leaf thickness, i.e. more leaf cells per leaf area, which would be expected to be associated with a higher chlorophyll content on a leaf area basis. All the species tested at both high and low altitude showed that the altitudinal difference in chlorophyll content was opposite to the difference in SLA (although all the species did not show the same direction in the changes in the two traits with altitude). Interestingly, although the altitudinal differences in PAR_{opt} (light level at which ETR_{max} is attained) are not significant, the overall pattern of differences across the five species investigated is the same as the pattern for chlorophyll content and opposite to the one for SLA. This suggest that photosynthesis in thicker, more

chlorophyllous leaves saturates at higher light than it does in thinner leaves having less chlorophyll, which is entirely reasonable. What cannot be explained from the available information is why the five species show differences between them in the direction in which chlorophyll content, SLA and PAR_{opt} change with altitude.

Overall, the graminoids have greater chlorophyll concentrations (mean 489 mg m^{-2}) than the forbs (407 mg m^{-2}; p = 0.017), with ferns showing intermediate values (451 mg m^{-2}). Indigenous graminoids tend to have higher chlorophyll concentrations (mean, 532 mg m^{-2}) than alien graminoids (416 mg m^{-2}; p = 0.038). In fact, a persistent theme for many of the traits is that alien graminoids show significantly different mean values than the indigenous graminoids, and for some traits this is also the case for the forbs. Especially, mean specific leaf areas of the four indigenous graminoid species (all < 20 mm^2 mg^{-1}) are lower than for the three alien grasses (*P. pratensis* 24 mm^2 mg^{-1}, *P. annua* 42 mm^2 mg^{-1}, *A. stolonifera* 47 mm^2 mg^{-1}). Similarly, leaf dry matter content, also an indicator of leaf strength, also tends to be higher for the indigenous graminoids (species means 259 – 381 mg g^{-1}) than for the alien ones (species means 184 – 268 mg g^{-1}). The cushion-forming forbs possibly show a similar pattern to the graminoids; the two indigenous species, *A. selago* and *C. kerguelensis* have lower mean SLA (12 and 24 mm^2 mg^{-1}, respectively) than the alien *S. procumbens* (47 mm^2 mg^{-1}). This is discussed in more detail in Chapter 4.

Root to shoot ratio measurements were made on only four graminoid species. The results suggest that the two indigenous graminoids, *Ag. magellanica* (R:S, 0.13 g g^{-1}) and *U. compacta* (0.17 g g^{-1}) not only form tougher leaves, but invest more in leaves than in belowground organs compared with the alien species *P. annua* (0.30 g g^{-1}) and *A. stolonifera* (0.41 g g^{-1}).

Besides the aquaphyte *P. nodosus*, the indigenous species with highest SLA (> 25 mm^2 mg^{-1}) are *C. antarctica, M. fontana, C. moschata, C. plumosa* and *R. biternatus*. All show maximum vitality and were sampled, in the coastal zone, which besides being more sheltered than the inland area, is also much more manured by seabirds and seals and thus has a higher soil and plant nutrient status (Conradie and Smith 2012, Rossouw 2014). The alien species with high (> 25 mm^2 mg^{-1}) SLA (*A. stolonifera, P. annua, S. procumbens and R. acetosella*) also attain their greatest cover (and were sampled) in the coastal zone. A high SLA is generally associated with leaves having high nitrogen concentration and high photosynthetic capacity (Shipley et al. 2005). The high SLA of the coastal zone plants might thus have more

to do with enhanced nutrient status than with shelter from wind. Leaf N concentrations (dry mass basis) for most of the island's plant species are provided in Appendix A of Rossouw (2014) and were used to test the relationship between N concentration and SLA. SLA does, in fact, correlate strongly with leaf N (r = 0.67, p = 0.004). Hence, the greater SLA of coastal plants might be associated with enhanced nutrient status at the coast, rather than shelter from the wind. However, at odds with the assertion of Shipley et al. (2005) that high SLA and high leaf N concentration is associated with high photosynthetic capacity, the greater leaf N status and high SLA of the coastal species is not accompanied by enhanced photosynthesis rate. Between them, they exhibit almost the entire range of mean values exhibited by the two strongest indicators of photosynthetic capacity, ETR_{max} (Fig. 3.1q) and maximum quantum yield (Fig. 3.1p). Across species, SLA actually shows weak negative correlations with ETR_{max} (r = -0.16, p = 0.465) and α (r = -0.19, p = 0.379).

Five of the coastal zone species (*C. antarctica*, *M. fontana*, *R. biternatus*, *P. annua* and *R. acetosella*) also show the highest leaf RWC (means all > 90%) of the terrestrial species. This shows that the species are able to maintain a high degree of leaf turgidity and this is expanded on in Chapter 4. Of the coastal species with very high leaf RWC, four of them (*C. antarctica*, *M. fontana*, *R. biternatus* and *P. annua*) have a very low or low stem specific density ($\leq$ 0.20 mg mm^{-3}), suggesting that their stems lack strengthening tissue. Possibly, most of the strength comes from being able to maintain turgid stems by the same mechanism that maintains high leaf turgidity. All four are low growing and occur in localities sheltered from wind. *R. acetosella*, the other coastal species with high leaf RWC has dryer, slightly fibrous, stems with a moderate SSD (0.28 mg mm^{-3}), is taller and not confined to sheltered localities.

There was also a strong pattern of specific root length being high, and root diameter low, for species restricted to, or reaching maximum vitality in, the coastal zone. This is discussed further in Chapter 4. That the island's graminoids tend to show a lower stomatal density than the forbs, with ferns having even lower values, accords with the pattern found globally (Willmer and Fricker 1996). It is uncertain if *J. effusus* is indigenous to the island or an introduced alien. In view of the striking difference in SD between the island's indigenous and alien graminoids, it is suggestive that the species' mean stomatal density (121 stomata mm^{-2}) is closer to the mean SD for the islands alien graminoids (136 stomata mm^{-2}) than for the indigenous graminoids (89 stomata mm^{-2}).

Across the species there is little correlation between the fluorescence trait values and the structural trait values (data not shown). Some of the cases where there is a correlation are inexplicable and possibly accidental (for instance, the positive correlations of ΦPSII and 1-qL with root diameter, and of plant height with α). The only rational, or at least intuitively understandable, correlations (some just fail to be significant at the 5% level) are that ETR_{max}, α, PAR_{opt} and I_k (together strong indicators of photosynthetic capacity) are positively correlated with chlorophyll content and stomatal density.

The overall pattern suggested by the chlorophyll fluorescence traits values is that there are species with a high photosynthetic capacity (show a high maximum electron transport rate reached at high light levels, an ability to maintain a high proportion of open reaction centres, and with a substantial effective quantum yield even at light saturation), species with very low photosynthetic capacity, and species with intermediate capacities. Broadly speaking, the high capacity group are forbs, the intermediate group comprises mainly graminoids and some forbs, and the low capacity group are ferns. Especially, the three ferns found in sheltered, shady sites (*H. peltatum*, *G. poeppigeana* and *P. marionense*) show typical shade-adaptation, with low maximum photosynthesis (ETR) rate but able to respond sharply to increasing light at low levels and to attain maximum photosynthesis in low light. The fourth fern species, *B. penna-marina*, occurs predominantly in unshaded areas but it also shows fluorescence parameter values indicative of a shade plant, although to lesser extent than the other three species. *B. penna-marina* forms carpets of tightly-packed, upright pinnate fronds and there is a great deal of self-shading. Blake (1996) found that less than 10% of the solar radiation at the surface of the carpet reaches the frond's basal pinnae. Along most of their length, therefore, the fronds are thus in a highly shaded environment.

The grouping of species into photosynthetic capacity types is explored in the next chapter.

Chapter 4.

Vascular plant functional groups

4.1. Introduction

The results of the univariate analyses presented in Chapter 3 showed that the various traits, especially the structural ones, differ from one another in how they vary across species. Also, the Tukey's HSD homologous groups of species mean values of all the traits showed large overlaps. Hence, it is difficult to recognize plant functional type groups amongst the species from the results of the univariate analyses.

The pattern of interspecies differences across the whole suite of traits was thus explored using Principal Component Analysis (PCA), and the species grouped according to their positions on the significant PC axes using a clustering algorithm. Correspondence analysis (CA) was then used to evaluate how the groupings related to plant habit (graminoid, forb, fern), status (indigenous or alien) and habitat.

PCA was applied to the structural traits and the photosynthetic traits separately, then to both. Trait values for the low altitude plants were used in the PCA.

Stomata density and root:shoot ratio were not measured on all the species so were omitted from the PCA. Also, since some of the traits used in the PCA of the structural traits were not measured on *Pringlea antiscorbutica* and *Hymenophyllum peltatum*, these species were omitted from that PCA. Preliminary analyses showed that *Potamogeton nodosus* is an extreme outlier in the PCA results, to such an extent that it influences the analyses to the point that the differences between the other species on the component axes are distorted or obscured. There are also doubts about the appropriateness of the fluorescence measurement technique for this submerged species, so it was also omitted from the PCA.

4.2. Species groupings based on structural traits

The first three principle components yielded by the PCA of the structural trait data account for 80% of the total variance in those data. Subsequent components were insignificant and

identified trait combinations peculiar to just one particular species, so were not useful in identifying groups of species showing similar overall patterns in the variation of trait values.

Six leaf traits, two root traits and plant height correlated significantly with the first principal component (PC1, which accounts for 50% of the total variance in structural trait values; Table 4.1, Fig. 4.1). The component axis represents a gradient from (positive side) tall plants with heavy, large leaves containing a high proportion of structural tissue and a high chlorophyll content, a low specific leaf area and low leaf relative water content and thick roots, to (negative side) short plants having small, light leaves with little structural tissue, a high SLA, high leaf RWC, low chlorophyll content and thin roots.

PC2 (18% of the total variance in structural trait data) is an axis of high to low leaf dry matter content and stem specific density, i.e. a gradient from (negative side) plants with tough (or non-succulent) leaves and stems, to (positive side) plants with weak (or succulent) leaves and stems. SLA is also significantly correlated with PC2.

Leaf RWC is the only trait significantly correlated with PC3, which accounts for 11% of the variance in the structural trait data. PC3 thus represents a gradient of plants with fleshy turgid leaves to plants with drier leaves. The spatial pattern of species across this gradient (not shown) is confusing and hard to interpret since, besides RWC, the species' positions on the PC3 axis are affected by several other traits that show weaker correlations with PC3 but that do not have any rational, or functionally interpretable, relationship with each other, or with RWC.

Clustering the species by their scores on the first three PC axes yielded the groups and subgroups shown in Figures 4.1 and 4.2 and described in Table 4.2. There is a clear separation of *Juncus effusus* and *Polystichum marionense* from the other species (group 1 in Table 4.2 and Figures 4.1, 4.2), based on a combination of being tall plants with large, heavy leaves with a low to moderate SLA, very low RWC (for the rush, these leaf traits refer to the photosynthetic stems), low SSD and thick roots with a very low SRL. None of the other species show this pattern.

The rest of the species are split into two groups, based on differences in mean SLA (low to moderate for group 2 species, high for group 3 species), LDMC and SSD (both are moderately high to very high in group 2 species but low or moderate for group 3 species). In each group, a particular species might show a value for particular trait that overlaps with the

values of that trait in other group. For instance, *Colobanthus kerguelensis* (group 2) has a low LDMC, *Sagina procumbens* (group 3) has a high SSD and *Cerastium fontanum* (group 3) has a moderate SLA). The two groups are distinguished on the overall pattern of differences in the three traits together (i.e. their collective behaviour in the data set) and there is no overlap of the two groups on PC2, the gradient represented mainly by LDMC, SSD and SLA. Of the ten species in group 2, nine are indigenous and they include forbs, graminoids and ferns (Fig. 4.3).

Group 2 comprises two groups (Fig. 4.1, Table 4.2), recognized on the overall pattern of differences between them in PH, LA, LDM, RD, SSD (moderately high to high in group 2.1, very low to moderate in group 2.2) and chlorophyll content (moderately high to very high in group 2.1, moderate in group 2.2). Most group 2.1 species have high or very high LDMC; overall, the group shows the highest LDMC of all groups. There is no overlap between the two groups on PC1, the component correlated with plant height, leaf size, leaf mass and root diameter (Fig. 4.1) but, again, there are instances where particular species in one group might have a value for one of those traits that overlaps with the values for the other group. The specific instances of this are that *Poa pratensis* (group 2.2) is taller than most of the group 2.1 species, *Juncus scheuchzerioides* (group 2.2) has a higher chlorophyll content than all of the group 2.1 species, *Acaena magellanica* (group 2.1) has a mean SSD that is in the middle of the range of values shown by group 2.2 species, and *Blechnum penna-marina*, with only a moderate LDMC, is an exception amongst the high LDMC group 2.1 species.

Group 2.1 thus contains moderately tall to tall species with tough, moderately large and heavy leaves possessing a high chlorophyll content, and moderately tough stems and moderately thick roots with low SRL. In leaf size and mass they are second only to group 1 species. However, their leaves contain relatively more water than do the leaves of group 1 species. Group 2.2 consists of short or prostrate species with small, light (but also relatively tough) leaves with moderate chlorophyll contents, very tough stems and thin roots with moderate SRL.

Group 2.1 comprises three indigenous graminoids, an indigenous fern and an indigenous forb (Fig. 4.3). Group 2.2 comprises all three of these plant habits but also an alien graminoid, *Poa pratensis*. For many of the traits, this species has mean values approaching those shown by the indigenous graminoid species – it is taller and has larger, heavier and tougher leaves with a higher chlorophyll content, and a lower SRL, than the other alien graminoids.

The clustering procedure showed three subgroups of group 3. One of them comprises only one species, *S. procumbens*, which has significantly lower LA, LDM and RD, and significantly higher SSD, than the other species in group 3. The other trait values for *S. procumbens* were similar to those for the species in group 3.1 than those in group 3.2 so, simply to avoid having a group containing only one species, *S. procumbens* is considered to belong to group 3.1.

Group 3.1 occurs at the extreme negative end of PC1, with no overlap with group 3.2 on that axis (Fig. 4.1). Group 3.1 species are all low growing, with small, light, weak leaves with very high SLA and moderate chlorophyll content. They have a small RD and high SRL. Group 3.2 species also have weak leaves but ones that are mostly larger and heavier, and with slightly higher chlorophyll content and lower (but still high) SLA, than group 3.1 species. However, the most conspicuous differences between groups 3.1 and 3.2 are shown by SRL (much higher in group 3.1) and RD (lower in group 3.1). In fact, mean SRL for group 3.1 is more than twice that of the group (2.2) with the next highest mean SRL and nearly six times greater than the mean for the species in all the other groups.

Correspondence analysis of plant habit (graminoid, forb, fern), status (indigenous or alien) and the plant groups based on structural traits yielded some significant associations. Group 1 was omitted from the correspondence analysis since it contained only a fern and a graminoid of unknown status. The associations are shown in the CA joint plot (Fig. 4.4) and are also obvious from Fig. 4.3. Indigenous species correspond mainly with group 2 (especially the association of indigenous graminoids with subgroup 2.1). Indigenous forbs also correspond with group 3.1, making up more than half of the species, with alien graminoids making up the rest. Most alien forbs are in group 3.2.

Gremmen (1981) provided Braun-Blanquet cover-abundance and presence values for all the island's plant species in 41 plant communities on the island. That information was used to categorize the species according to their preference for saline (influenced by saltspray), biotic (influenced by manuring and trampling of seals and seabirds) or oligotrophic ("fresh", mainly inland) habitats. Some species occur commonly, and with appreciable cover, in more than one of these habitat categories. *Cotula plumosa* was assigned to both the saline and biotic habitats. *Poa cookii*, *Ranunculus biternatus*, *Agrostis stolonifera* and *Sagina procumbens* are characteristic of biotic habitats but are also common in habitats that are not influenced by manuring. The latter two species were rare on the island when Gremmen (1981) carried out

his phytosociological study there, so the information in Table 9.5 in Gremmen and Smith (2008) was used to assign them to a habitat category.

The distribution of habitat categories across the species groups based on structural traits are shown in Fig. 4.5 and the associations of the groups with habitat in Fig. 4.6. Group 2.1 and 2.2 species are associated with fresh habitats whereas group 3.1 and 3.2 species are predominantly associated with biotic and saline habitats.

4.3. Species groupings based on photosynthetic traits

The species mean values of seven photosynthetic traits were subjected to PCA and clustering to group the plant species into photosynthetic types. Between them, the traits represent important features of the relationship between photosynthesis and the light regime. The maximum electron transport rate (ETR_{max}) and the effective quantum yield at ETR_{max} (ΦPSII) are indicators of overall photosynthetic capacity. The PAR value that yielded ETR_{max} (PAR_{opt}) shows whether the plant is a heliophyte (sun plant) or sciophyte (shade plant), or something in-between. The initial slope of the ETR response to PAR, (α), indicates the capacity to respond to light at low levels. The photoadaptation parameter (I_k) represents the light level where photosynthesis changes from being light limited to being light saturated. The proportion of closed reaction centres (1-qL) at ETR_{max} is also a measure of photosynthetic capacity; low values show an ability to maintain functional (open) PSII photosystems at ETR_{max}. YNPQ/YNO indicates the capacity for protection against photoinhibition and photodamage.

The first three components yielded by the PCA of the seven photosynthetic traits account for 92% of the total variance in their species-mean values (Table 4.3). ETR_{max}, ΦPSII, PAR_{opt} and I_k are strongly negatively correlated, and 1-qL strongly positively correlated, with PC1. PC1 thus represents a gradient of sun plants with high photosynthetic capacity to shade plants with a low capacity.

YNPQ/YNO is positively, and 1-qL and PAR_{opt} negatively, correlated with PC2. PC2 thus represents a gradient of low to high capacity for photoprotection, and also, in the same direction on the axis, of an increasing ability to maintain a high proportion of open reaction centres at ETR_{max} and to reach ETR_{max} at low PAR levels. The physiological explanation for the relationship between the three traits on the gradient is that a core function of

photoprotection is to maintain reaction centres in an open state; hence YNPQ/YNO and 1-qL occur on opposite ends of PC2. If ETR_{max} occurs at low PAR (i.e. low PAR_{opt}), ETR_{max} will likely also be low. If less electrons are flowing through the electron transport chain, then less reaction centres will be in the closed state at any one time; hence the same sign of the correlations of 1-qL and PAR_{opt} on PC2.

YNPQ/YNO and α contribute most significantly to PC3, which represents a gradient from low to high capability of photoprotection and ability to respond to increasing light at low levels.

Clustering the species on their scores on the three principal components yielded two main groups, each comprising subgroups (Figs. 4.7). The subgroups are superimposed on the species-trait biplots (Figs 4.8 and 4.9) and their main characteristics summarised in Table 4.4. Group 1 contains eight forb and five graminoid species (Fig. 4.10) and all but one are on the negative side of PC1, i.e. the high photosynthetic capacity part of the gradient (Fig. 4.8). Group 2 contains eleven species, comprising nearly equal numbers of forbs, graminoids and ferns and all occur on the low photosynthetic capacity side of PC1. The distinction between the two groups is one of overall photosynthetic capacity; group 1 species have higher effective quantum yield (ΦPSII) at PAR_{opt}, have a higher PAR_{opt}, and hence a higher photosynthetic rate (ETR_{max} =ΦPSII x PAR_{opt}), than Group 2 species. Only one group 1 species, *Poa pratensis*, overlaps with group 2 species on the PC1 axis.

The two groups are each comprised of subgroups (Fig. 4.7). Group 1.1 has only two species, *Azorella selago* and *Pringlea antiscorbutica*. Both have very high photosynthetic capacity, reached at the highest PAR of all the species (full sunlight) and the onset of light saturation is also high (>300 µmol m^{-2} s^{-1}). They have only a moderate capacity to respond to light at low levels. They characteristically occur in situations exposed to full ambient light and are the archetype sun species on the island. However, both have low capacity for photoprotection at PAR_{opt}; light energy is used in photochemistry rather than dissipated through regulated mechanisms. Because of this, and since they reach photosynthetic saturation at very high light, they have moderately high to high proportion of closed reaction centres at saturation.

Species in group 1.2 also have a high to very high photosynthetic capacity; and overlap completely with group 1.1 species on the PC1 axis (Fig. 4.8). All are forbs (Fig. 4.10). Group 1.2 species are also sun plants but tend to reach saturation at a lower PAR (about ¾ full sunlight) than group 1.1. Unlike group 1.1, they possess a high or very high capacity for

photoprotection which results in a lower proportion of closed reaction centres at light saturation, a combination resulting in the two subgroups being well separated on PC2. Photosynthesis rate also responds more sharply to light at low levels, and effective quantum yield at saturation is higher, than for group 1.1. *Rumex acetosella* clustered outside groups 1.1 and 1.2 (Fig. 4.7), mainly because it has a very high mean ΦPSII at PAR_{opt}, the highest of all the species considered in the study. Its mean values for the other six traits were very similar to the group 1.2 values so it was placed in that group simply to avoid having a group with a single species.

Group 1.3 (two forbs and two graminoids) is located closer to the origin than, and does not overlap with groups 1.1 or 1.2 on, PC1. Group 1.3 species have moderately high to high photosynthetic capacity, with saturation tending to occur at slightly lower light (mean for the four species is about $^2/_3$ full sunlight) than for the other two subgroups. Their capacity for photoprotection is moderate, higher than that for group 1.1 but substantially lower than that for group 1.2. Consequently, they have only a moderate ability to maintain open reaction centres at saturating light levels.

Group 1.4 species (three graminoids) have moderate to moderately high photosynthesis rate, reached at about ½ full sunlight, lower than for the other subgroups of group 1. The onset of saturation is also lower than for the other subgroups, on average at about 1/10 full sunlight. Group 1.4 species have a very high capability for photoprotection. Because of this, and because PAR_{opt} is relatively low, they have the lowest proportion of closed reaction centres at saturation. They show the lowest photosynthesis response to light at low levels of all the group 1 subgroups. This combination of very high photoprotection capability and a low proportion of closed reaction centres places group 1.4 at the upper extreme of PC2, with no overlap with the other subgroups.

Group 2 comprises three subgroups. Groups 2.1 and 2.2 consist of species with low to moderate photosynthetic capacity. For most of them, photosynthesis starts saturating at relatively low light level (< 200 µmol m^{-2} s^{-1}) but saturation is only reached at relatively high light (> ½ full sunlight). The main difference between the two subgroups is that 2.1 species have a low, whereas group 2.2 species have moderately high to very high, capability of photoprotection. This does not result in any difference in their ability to maintain open reaction centres at saturation, which is low or very low (i.e. 1-qL is high or very high) for both subgroups. Photosynthesis also responds more sharply to light at low levels for species

of group 2.2 than those of group 2.1. An ability to photoprotect and to respond to low light places group 2.2 with group 1.2 both at the negative end of the PC3 axis, with no overlap with the other subgroups (Fig. 4.9), but they possess very different photosynthetic capacity at high light, as shown by their complete separation on PC1 (Fig. 4.8).

Group 2.3 consists of the three species with lowest photosynthetic capacity. Maximum photosynthetic rate, effective quantum yield, onset of saturation are low or very low and photosynthetic saturation is attained at about $^1/_3$ to $^1/_2$ full sunlight. These are the archetypal shade species on the island although, unlike most shade plants, their response to light at low levels is amongst the poorest of all the species. Between them, they show different capacities for photoprotection, from low to high. Their ability to maintain open reaction centres at ETR_{max} is very low. The three species in group 2.3 are two of the ferns that occur in shady places and the alien pearlwort, *Sagina procumbens*.

Table 4.4 and the correspondence analysis joint plot (Fig. 4.11) confirms what was found from the between-species univariate comparisons of ETR_{max}, PAR_{opt}, I_k and ΦPSII; that species with high photosynthetic capacity (groups 1.1, 1.2 and 1.3) are forbs, particularly indigenous ones. However, almost half of the species in the lower photosynthetic capacity groups (2.1, 2.2, and 2.3) are also forbs. The four fern species are in the lowest capacity groups (2.2, 2.3) and occur with those groups in the same quadrant of the joint plot. Graminoids are in the moderate capacity groups, excepting for the two rush species which have a moderately high photosynthetic capacity. Unlike the groupings on structural traits, there is no differentiation between alien and indigenous graminoids in the grouping based on photosynthetic traits; both graminoid types are associated with the moderate photosynthetic capacity groups 1.4 and 2.1.

Unlike for the groups based on structural traits, the photosynthetic trait groups are poorly related to the preferred habitat of the species (Fig. 4.12). Species characteristic of fresh (non-manured, non-saline) habitat species make up a similar proportion of members in the moderate to very high photosynthetic capacity main group (group 1) as in the very low to moderate capacity main group (group 2). Similarly, species characteristic of biotic (manured) habitats are found in both main groups. For the subgroups too, almost every one contains species from manured as well as non-manured habitats. The two archetypical saline habitat species on the island, *Crassula moschata* (high photosynthetic capacity) and *Cotula plumosa*

(very high capacity) are both in group 1. Correspondence analysis (results not shown) yielded no significant photosynthetic trait group - habitat category associations.

4.4. Species groupings based on both structural and photosynthetic traits

In terms of their species membership, there is almost no correspondence between the groups yielded by PCA of the structural traits and the groups yielded by PCA of the photosynthetic traits. For instance, the five species in structural group 2.2 each occur in a different photosynthetic group, the six species in structural group 3.1 represent, between them, five photosynthetic groups, and the four species in photosynthetic group 1.3 are each in a different structural group. The only reasonably close correspondence between the groups of the two sets was that three of the four species in structural group 3.2 (plants with moderate stature, leaf area, leaf mass, chlorophyll content, low to moderate specific root length) comprised three of the four species making up photosynthetic group 1.2 (high to very high photosynthetic capacity and high photoprotective capability).

PCA of all eleven structural and all seven photosynthetic traits together (results not presented) showed the principal components to be very heavily influenced by the structural traits and clustering the species on their component scores resulted in a confusing array of small groups containing one to three species.

The separate PCA's of the structural and photosynthetic trait data sets presented in Sections 4.2 and 4.3 showed that each set contains considerable redundancy in the form of inter-correlated traits that score highly on the same principal component. Plant height, leaf area, leaf dry mass and root diameter are all significantly positively inter-correlated (large plants). Leaf RWC is significantly negatively correlated with leaf area and leaf dry matter content, but positively correlated with specific leaf area (all three traits are associated directly or indirectly to leaf toughness, thickness, succulence, longevity). Specific root length is negatively correlated with root diameter. Strong correlations also occur amongst the photosynthetic traits; ETR_{max}, ΦPSII, PAR_{opt} and I_k are positively inter-correlated and three of those four are negatively correlated with the proportion of closed reaction centres at ETR_{max}.

To avoid this redundancy a suite of less inter-correlated traits was chosen for the combined PCA of structural and photosynthetic traits. Plant height was chosen to represent plant

stature, leaf dry matter content to represent leaf strength and longevity, specific leaf area to represent leaf thickness, chlorophyll content as the structural trait representing photosynthetic capacity, and specific root length as an indication of the root's foraging ability and capability of water and nutrient absorption. Overall photosynthetic capacity is represented by maximum photosynthetic rate (ETR_{max}), the ability to respond to low light (α), and the capability of photoprotection (YNPQ/YNO). The trait weightings on the first three principal component axes yielded by this suite of structural and photosynthetic traits are shown in Table 4.5 and the positions of the traits and species on the first two principal components shown in Fig. 4.13.

Principal component 1 from the analysis accounts for 38% of the variance in the values of the eight traits and represents a gradient from (positive side) large stature plants with thick, heavy (in relation to area) and tough (not ephemeral or succulent) leaves with high chlorophyll content and roots that are short in relation to their mass (structural, rather than absorptive or foraging roots), to (negative side) low stature plants with thin, ephemeral or succulent leaves with low chlorophyll content and foraging roots. This gradient is essentially the same as that of PC1 from the PCA of the structural traits (Table 4.1).

PC2 (21% of total variance) is a gradient from (negative side) high photosynthetic capacity plants able to respond sharply to low light and very capable of photoprotection, to (positive side) low photosynthetic capacity plants with a poor photoprotective capability. This gradient is similar to that of PC1 from the PCA of the photosynthetic traits (Table 4.3), except that there photoprotective capability (YNPQ/YNO) was much less correlated with PC1.

ETR_{max} and YNPQ/YNO are oppositely correlated with PC3 (13% of total variance). In this respect it is similar to PC2 from the photosynthetic trait PCA and represents a gradient from (negative side) low photosynthetic capacity plants highly capable of photoprotection to (positive side) high photosynthetic capacity plants with poor photoprotection capability. The component space represented by PC3 and PC2 thus separates out the sun plants with high photoprotective capacity from sun plants with low such capacity, and also the shade plants capable of photoprotection from those not capable of photoprotection. The other traits, especially the structural ones, are poorly correlated with PC3.

Clustering the species on their scores on the first three principle components resulted in two large groups, one of which comprises subgroups (Fig. 4.14 and Table 4.6). The subgroups are also shown in the species-trait biplot (Fig. 4.13).

Group 1 (11 of the 13 species are forbs; Fig. 4.15) comprises very short to moderately tall species with soft, ephemeral, thin or succulent leaves having low to moderate chlorophyll content. SRL varies from moderately low to very high. Between them, group 1 species vary widely (from low to very high) in photosynthetic capacity (ETR_{max}), response to light at low levels (α) and capability of photoprotection (YNPQ/YNO). Group 2 species (six graminoids and three ferns) comprises species that are mostly moderate to tall in stature with leaves that are moderately to very tough, thick and long lived and have moderate to very high chlorophyll contents. Like for group 1, group 2 species differ widely in their photosynthetic and photoprotective capacities and ability to respond to light at low levels. However, on the whole, group 2 species have lower ETR_{max} and α, and higher YNPQ/YNO, than do group 1 species.

Group 1 comprises two subgroups, differentiated mainly on photosynthetic capacity – low to moderate ETR_{max} for group 1.1 (although one species, *C. moschata*, has a moderately high ETR_{max}) and high to very high for group 1.2. Group 1.2 species also mostly show a sharper response to low light (moderate to high mean α) than group 1.1 species (low to moderate, except for *Montia fontana*, which has a moderately high mean α). Group 1.2 species are also of moderate stature whereas group 1.1 comprises mainly small or low-growing plants.

Group 1.1 comprises two smaller groups. Group 1.1.1 (all are forbs) consists of small species with ephemeral, thin or succulent leaves (highest SLA of all the groups), foraging, absorptive roots (highest SRL), and low to moderately high photosynthetic capacity and ability to respond to low light. Group 1.1.2 comprises two low-growing graminoids and a small cushion-forming forb, also with thin or succulent leaves that tend to be slightly tougher than group 1.1.1 species. Mean specific root length for the species in group 1.1.2 is lower than for group 1.1.1 species. Like group 1.1.1, group 1.1.2 species have low photosynthetic capacity and ability to respond to low light. The biggest difference between the two groups is in their photoprotective capability, which is significantly higher for group 1.1.1.

The high photosynthetic capacity forb species in group 1.2 also comprise two smaller groups, based mainly on a difference in photoprotective capacity but also on their ability to respond to low light. Group 1.2.1 species have low to moderately high mean YNPQ/YNO and moderate or moderately high α, whereas group 1.2.2 species have high to very high YNPQ/YNO and α.

There is strong correspondence between plant habit and the groups based on the structural and photosynthetic traits (Fig. 4.15). Groups 1.1.1, 1.2.1 and 1.2.2 comprise only forbs and group 2 only graminoids and the three fern species. Group 1.1.2 contains two graminoids and a forb. Correspondence analysis (Fig. 4.16) shows these associations of plant habit, and also status (native or alien), with the various groups. Indigenous graminoids and ferns are associated with group 2. Indigenous forbs are closely associated with group 1.2.2, alien forbs with group 1.2.1, and both forb types also with group 1.1.1. Alien graminoids are most closely associated with group 1.1.2. However, much of the distinction between natives and aliens is due to structural trait differences; especially that natives have tougher (higher LDMC) and thicker (lower SLA) leaves, with a higher chlorophyll content on a leaf area basis, than do the aliens. The only photosynthetic trait difference between native and alien species that is relatively consistent is the response to light at low levels; alien species have a significantly less sharp response (0.31 ± 0.007 mol mol^{-1}) than the indigenous species (0.34 ± 0.011 mol mol^{-1}; $p = 0.038$).

Group 1.2.1 and Group 2 comprise mostly species from habitats not significantly influenced by manuring or saltspray (Figs. 4.17 and 4.18). Groups 1.1.1, 1.1.2 and 1.2.2 comprise species from manured habitats or species that primarily occur in manured habitats but can also tolerate oligotrophic and/or saline habitats.

4.5. Discussion

On structural traits the species group (into three main groups and five subgroups) primarily on stature (PH) and secondarily on traits related to leaf toughness/thickness (LDMC, SLA), leaf moisture content (RWC) and stem strength (SSD). The two root traits (SRL, RD) are important mainly in distinguishing the subgroups in two of the main groups.

Two species (*Juncus effusus* and *Polystichum marionense*) occur together in a single group well separated from all the other groups, based on a combination of being tall, with large, heavy photosynthetic organs that have a low relative water content and thick roots. The one is a rush and the other a fern. *Pringlea antiscorbutica* was not considered in the multivariate analyses of the structural traits since root traits were not measured for the species, but on the basis of its aboveground trait values it belongs to Group 1. It is a forb, so all three terrestrial vascular plant habits found on the island are represented in the group.

Four of the groups based on structural traits correspond relatively closely with plant habit. Most of the forb species occur in groups 3.1 and 3.2 (low to moderate stature plants with weak, thin, short-lived leaves with a moderate to very high leaf moisture content). Five of the eight graminoids occurred in groups 2.1 or 2.2, comprised of taller plants with thicker, tougher leaves.

However, the most striking difference between the groups based on structural traits is in the representations of alien versus native species. Of the ten species with moderately thick and tough to very thick and tough leaves, moderately strong to strong stems (group 2), nine are natives and they include forbs, graminoids and ferns. In contrast, five of the six alien species occur in group 3, characterized by thinner, weaker leaves and stems. This reinforces the suggestions based on the univariate between-species comparisons in Chapter 3 and accords with the results from an earlier comparative study at the island of the structural and functional properties of a native and an alien *Agrostis* species.

Pammenter et al. (1986) reported that the human-introduced alien, *Agrostis stolonifera*, has thinner leaves with less strengthening tissue than the native species *Agrostis magellanica* and that this determined the distribution of the two grasses on the island. The alien species, *A. stolonifera*, is a typical ruderal weed species that invests in short-lived leaves with a high proportion of photosynthetic tissue and is largely restricted to sheltered sites. The indigenous species, *A. magellanica*, is found in sheltered and exposed areas and invests in tough, long-lived leaves, a strategy that Pammenter et al. (1986) proposed evolved because of the constantly cold, low light and (especially) windy island conditions. Photosynthesis rates are low (cold, low light), so investing in large amounts of photosynthetic tissue rather than structural tissue able to withstand the high wind might be counterproductive.

In Chapter three it was suggested, on the basis of root to shoot ratios for two native and two alien graminoid species, that the indigenous species also invest more in leaves than in belowground organs compared with the alien species. Unfortunately, the multivariate comparison did not throw further light on the veracity of this suggestion since root:shoot was measured on too few species to allow it to be included in the comparison.

The univariate comparison results also suggested that species with high specific root length (foraging rather than anchoring roots), high leaf relative water content (turgid leaves) and low stem specific density (stems that get their strength from turgid parenchyma rather than from xylem or sclerenchyma) tend to be those restricted to, or reaching maximum vitality in,

manured and or saline coastal zone habitats. The multivariate comparison results show this even more strongly – species in group 3, (especially group 3.1, characterized by especially high SRL, high leaf RWC and low to moderate SSD), are mostly associated with coastal zone habitats, only one of the ten species being more restricted to "fresh" (non-saline, oligotrophic) habitats. In contrast, species of groups 2.1 and 2.2 are all characteristic of fresh habitats, although one also occurs in manured habitats.

The high leaf RWC of the coastal, saline-tolerant species, and also that most of their stem strength possibly comes from being able to maintain turgid stems, can be ascribed to the fact that they are able to maintain high leaf water potential by developing low osmotic potentials through the uptake of salts and/or the synthesis of high concentrations of organic osmolytes (Smith 1978a). The high SRL of the coastal species might also be related to salinity since it is well known that SRL of commercially cultivated species increases (and RD decreases) with salinity; for example in tomatoes (Lovelli et al. 2012), cotton (Kurth et al. 1986) and maize (Sharp et al. 1990). Also in wild species salinity results in increased SRL and decreased RD (both indicative of foraging roots), suggested to be an adaptive morphogenic response to the inhibitory effect of high salt concentration on nutrient and water uptake (Rubinigg et al. 2003).

The univariate comparisons of the individual photosynthetic trait values (Chapter 3) suggested that overall photosynthetic capacity (a combination of several photosynthetic traits, mainly maximum ETR, PAR giving maximum ETR, effective and maximum quantum yields), is strongly related to plant habit. The multivariate groupings confirm this. Forbs, particularly indigenous ones, dominate the highest photosynthetic capacity groups, ferns the lowest capacity groups and graminoids mostly occur in the moderate or moderately high capacity groups. This accords with what is found globally – that dicots, and forbs especially, show a higher photosynthetic rate than monocots, and ferns have lower rates than both (Larcher 1995).

Unlike for the forbs, the two alien graminoids did not differ from the native graminoids, regarding their photosynthetic capacity, both types being found in the two moderate capacity groups. This accords with the finding of Pammenter et al. (1986) that *Agrostis stolonifera* and *Agrostis magellanica* have similar maximum photosynthesis rates.

Surprisingly, the photosynthetic trait groups correspond poorly with habitat, despite the fact that species characteristic of biotic coastal habitats have a high SLA and a high leaf N

concentration, so might be expected to show high photosynthetic capacity (Shipley et al. 2005). However, it was shown in Chapter 3 that, although SLA and leaf N are strongly positively correlated, neither are correlated with ETR_{max} or maximum quantum yield, and in this chapter it was shown that species characteristic of manured habitats are represented in all of the photosynthetic capacity groups except the highest capacity one. This is surprising since the manured vegetation on the island shows strikingly enhanced stature, colour, vitality and nutrient status over unmanured vegetation (Huntley 1971, Smith 1978b, Gremmen 1981) and manured sites have a high productivity (Smith 2008c). In fact, sub-Antarctic island grasslands influenced by seals and seabirds have amongst the highest terrestrial primary production values shown by any vegetation type worldwide (Jenkin 1975, Lewis Smith and Walton 1975, Hnatiuk 1978). On Macquarie Island, Medek et al. (2008) found that leaf N content and photosynthetic capacity in *Stilbocarpa polaris* (megaherb) and *Poa foliosa* (tussock grass) were highest near the coast and declined going inland, but with no concurrent changes in specific leaf area; i.e. photosynthesis rate correlated significantly with leaf N but neither were correlated with SLA. That comparison was between plants of different nutrient status within the same species, not between species with different nutrient status as in the comparison made here, but the lack of correlation between photosynthetic capacity and leaf N status found on Marion Island is still surprising.

There is very poor correspondence between how the species group based on structural traits and how they group based on photosynthetic traits. Also, although the groups based on structural traits showed a correspondence with habitat (Section 4.2), those based on photosynthetic traits (Section 4.3) did not. However, multivariate analysis of both trait types together groups the species in a pattern that corresponds quite closely with their habit and habitat. The primary separation of species by the combined analysis relies on structural traits, with the result that forbs are strongly distinguished from graminoids and ferns. Overall, the forbs also have a higher photosynthetic capacity than the graminoids, although there is considerable overlap between them. The forbs are further divided into two groups based on photosynthetic capacity (low to moderate or high to very high) and each group is in turn divided into smaller groups based on the ability to photoprotect and to respond to low light.

The distinction between alien and native species in the grouping based on structural and photosynthetic traits together is less clear than the grouping on structural traits only. What distinction there is relates mainly to structural traits (native species have thicker, tougher leaves with higher chlorophyll content) but the native species also tend to show a sharper

electron transport rate response to light at low levels. The groups based on both trait types show quite a strong correspondence with habitat but even that is mainly due to the structural traits. Species of manured (and saline) habitats are mostly of short stature and have soft or succulent leaves with very low to moderate chlorophyll content and moderate to high SLA, but range widely (from low to high) in their photosynthetic capacity, photoprotective ability and response to low light.

Chapter 5.

Bryophyte traits and functional groups

5.1 Between-site differences in trait values

The only structural trait that was measured on bryophytes was plant height, which differed significantly ($p \leq 0.05$) between sites in all the species, at both high and low altitudes (Tables 5.1, 5.2). Many of the bryophytes also showed significant between-site differences in chlorophyll concentration, but, like for the vascular plants, there were few between-site differences in the photosynthetic traits. Appendix figures B1 to B4 show the site mean values of the traits for the bryophytes. Also like for the vascular species, in most instances a difference at just one site caused the significant ANOVA results and factorial ANOVA revealed significant site x species interactions. For instance, for the four mire sites, *Jensenia pisicolor* showed the highest chlorophyll concentration at site 22, whereas *Campylopus introflexus* had the lowest chlorophyll concentration at site 22 (Appendix Fig. B1b). Across the fellfield sites, chlorophyll concentration in *Bucklandiella membranaceae* was highest at site 38, whereas *Hypnum cupressiforme* showed its lowest Chl content at that site (Fig. B3b). The between-site differences in plant height showed a more consistent pattern across the species, at least for the mire sites, where eight of the ten species were shortest at site 24, although the difference was significant for only four of those eight.

5.2 Altitudinal differences in trait values

Only two bryophyte species were measured at both high and low altitudes (Table 5.3). Plant height in *H. cupressiforme* was significantly higher at high altitude than at low altitude, whereas for *Racomitrium lanuginosum* the opposite was true. Chlorophyll concentration of both species was greater at high altitude.

For both species, ETR saturated at a significantly higher light level (PAR_{opt}) at high altitude than at low altitude. The onset of saturation (I_k) also occurred at higher light, and maximum electron transport rate was also greater, at high altitude. Although few of these effects are significant at the 5% level, with the fact that both indicators of maximum quantum yield (Fv/Fm and α) were greater at high altitude, they do suggest that the both species show a

greater capacity for photosynthesis at higher altitudes, including an ability to respond to higher light levels.

5.3 Between-species differences in trait values at low altitude

Figure 5.1 and the Appendix figures B1 to B4 show that, even within the same vegetation type and same altitudinal band, there are significant between-species differences in both plant height and chlorophyll concentration. In several instances, the between-species difference is site dependent. Some examples are: *Campylopus purpureocaulis* and *Ptychomnion densifolium* showed similar plant heights at mire sites 22, 24 and 25 but at site 23 *C. purpureocaulis* is significantly taller than *P. densifolium* (Fig. B1a). *Brachythecium rutabulum* is significantly taller than *Sanionia uncinata* at fernbrake site 36, but significantly shorter at site 37 (Fig. B2a). *B. membranaceae* has significantly lower chlorophyll than *H. cupressiforme* at three of the fernbrake sites but not at fernbrake site 38 (Fig. B3b).

To test the differences between the species, the site effect was ignored, i.e. for each species the four site values for a trait are considered as replicates. The trait values were subjected to one way ANOVA with species as categorical variable. Species means, their standard errors, the *F* and *p* values from the between-species ANOVAS and the homologous groupings from the Tukey's HSD tests are given in Appendix tables A39 to A48. ANOVA revealed significant differences between bryophytes at low altitude for all the traits. For each trait, the Tukey's HSD tests resulted in a confusingly large number of overlapping homologous groups (Tables A39 to A48) and a clearer picture is given by the box plots (Fig. 5.1), with the species means categorized into classes of very high, high, moderate, low and very low.

R. lanuginosum is the tallest bryophyte and grows as large tufts or pillows on peat or rock (Fig. 5.1a). The other tall bryophytes (*S. uncinata*, *B. rutabulum*, *C. purpureocaulis*, *Dicranoloma billardierei, P. densifolium* and *Breutelia integrifolia*) are also mostly of the tuft or rough mat life forms. The shortest species (< 50 mm) represent thalloid, cushion, mat and turf life forms.

Chlorophyll concentrations of the bryophyte species (mean 65 mg m^{-2}) are very low compared with the vascular species (mean 442 mg m^{-2}); only three bryophytes (*H. cupressiforme*, *Marchantia berteroana* and *S. uncinata*) have a mean chlorophyll

concentration greater than 100 mg m^{-2} (Fig. 5.1b). *B. integrifolia*, *D. billardierei* and *R. lanuginosum* have the lowest mean chlorophyll concentration.

The hepatic *M. berteroana* showed the highest ETR_{max} of all the bryophyte species considered in the study (Fig. 5.1c). The other species with high ETR_{max} (*B. integrifolia*, *Campylopus clavatus*, *C. purpureocaulis* and *R. lanuginosum*) are turf or tuft mosses. These five species with high ETR_{max} also have a high or very high effective quantum yield at ETR_{max} (ΦPSII, Fig. 5.1f) and ETR_{max} is attained at high PAR values (PAR_{opt}, Fig. 5.1d).

The species with the lowest photosynthetic capacity (lowest ETR_{max}, attained at very low or low PAR) are mostly turf- or mat-formers in wet mires (*Blepharidophyllum densifolium*, *Distichophyllum fasciculatum*, *Syzygiella colorata*, *Clasmatocolea humilis*) or wet slopes (*B. rutabulum*, *S. uncinata*, *H. cupressiforme*). However, the species with the second lowest photosynthetic capacity, the hepatic *J. pisicolor*, also a wet mire species, shares its thallose life form with the very high photosynthetic capacity species *M. berteroana*, also a hepatic.

Most of these low photosynthetic capacity species have a moderate to high proportion of closed reaction centres (1-qL) at ETR_{max} (Fig. 5.1g) and low to moderate photoprotective capability (YNPQ/YNO, Fig. 5.1h). In contrast, the high photosynthetic capacity species, with one exception, show a low or very low 1-qL and moderate to high YNPQ/YNO. The exception is *M. berteroana*, the species with very highest photosynthetic capacity, but a high proportion of closed reaction centres and the lowest photoprotective capability of all the species. Surprisingly, the high photosynthetic capacity species have low or very low chlorophyll concentration, again excepting for *M. berteroana* which has the highest chlorophyll concentration. *R. lanuginosum* is the species with the highest capacity for photoprotection and lowest proportion of closed reaction centres at ETR_{max}.

5.4 Between-species differences in trait values at high altitude

Plant traits were measured on only six bryophyte species at high altitude. Species means and between-species ANOVA and Tukey's HSD results for the high altitude species are given in Appendix Tables A49 to A58. There are significant between-species differences in all traits, except YNPQ/YNO. Like at low altitude, *R. lanuginosum* is the tallest of the species (Fig. 5.1a). The shortest species is the cushion-forming moss *Andreaea* sp. that was not measured at low altitude. Also like at low altitude, the most shaded species (*Plagiochila heterodonta*

and *H. cupressiforme*) have significantly higher chlorophyll concentration but lower ETR_{max} and ϕPSII, and the onset of light saturation occurs at lower PAR, than the other species.

Of all the species sampled at high altitude, *R. lanuginosum* has the highest photosynthetic capacity (ETR_{max}, ϕPSII, PAR_{opt}, I_k) and, like at low altitude, is the species with highest photoprotective capability and has the lowest proportion of closed reaction centres at ETR_{max}.

5.5 Bryophyte plant functional groups based on photosynthetic traits

For all the traits the Tukey's HSD homologous groups showed large overlaps, making it difficult to recognize functional groups of species. PCA and clustering analysis were thus used to identify groups based on the photosynthetic traits. Trait values for both the low and high altitude plants were used in the PCA, excepting for the two species measured at both low and high altitude, for which the low altitude trait values were used.

The first three components yielded by the PCA account for 96% of the total variance. ΦPSII, ETR_{max}, PAR_{opt} and I_k are strongly negatively correlated, and 1-qL strongly positively correlated with PC1. PC1 thus represents a gradient of high to low photosynthetic capacity.

1-qL and α are positively, and YNPQ/YNO negatively correlated with PC2, which represents a gradient from species with high photoprotective capability and ability to maintain open reaction centres at ETR_{max}, to species with poor photoprotective capability and that have a high proportion of closed reaction centres at ETR_{max}. The main function of photoprotection is to maintain reaction centres in an open state, so it is entirely logical that YNPQ/YNO and 1-qL occur on opposite ends of PC2. The PC2 gradient is also one of a poor response (negative side) to a sharp response to increasing light at low light levels.

PC3 accounts for only 8% of the total variance in the photosynthetic trait data. YNPQ/YNO and α are most highly correlated with PC3 and occur on the same side of PC3. Thus, PC3 complements PC2 by separating species capable of responding sharply to light and able to protect the photosynthetic apparatus against excess light energy, from species with poor such abilities.

Clustering the species by their scores on the first three principal components yielded three main groups, two of which contain subgroups (Fig. 5.2). The subgroups are superimposed on

the species-trait biplot for PC1 and PC2 in Fig. 5.3. The photosynthetic characteristics of the groups and subgroups are summarised in Table 5.5.

Group 1 contains only the very high photosynthetic capacity species *M. berteroana*, which was shown in Section 5.3 to have the highest ETR_{max}, ϕPSII and I_k, and amongst the highest PAR_{opt} and response to light at low levels, of all the bryophytes considered in the study. However, it has very low photoprotective capability and ability to maintain open reaction centres. This combination of high photosynthetic capacity but low photoprotective capability is what causes it to be in a group on its own, well separated from the other groups on both PC1 and PC2 (Fig. 5.3).

Groups 2 and 3 are distinguished mainly on photosynthetic capacity - there is no overlap between them on PC1 (Fig. 5.3). Group 2 comprises ten moss and one hepatic species (Figs. 5.2, 5.4) with moderate to high ETR_{max} and that show onset of photosynthesis light saturation at moderate to very high PAR levels. The group comprises two subgroups, distinguished mainly on the overall pattern of differences in three traits; photoprotective capability, ability to maintain open reaction centres (overall, both are higher in group 2.1 than group 2.2) and response to light at low light levels (sharper in group 2.2). Group 2.2 species also tend to show photosynthetic saturation at higher light than group 2.1 species. A particular species in a subgroup might have a value for one or two of these four traits that overlaps with the values in the other subgroup, but there is clear separation of the two subgroups on PC2, the gradient that most represents the collective behaviour of the four traits.

Group 3 consists of mosses and hepatics and is located on the positive (low photosynthetic capacity) side of PC1. It comprises two subgroups of species with equally low photosynthetic capacity but that, like the subgroups of group 2, differ in their photoprotective capability, ability to maintain open reaction centres (both are greater for group 3.1) and ability to respond to light at low levels (greater for group 3.2). Hence the two subgroups are well separated on PC2 (Fig. 5.3). Group 3.1 comprises three moss and one hepatic species whereas group 3.2 comprises four hepatics and one moss.

The clear association of mosses or hepatics with particular photosynthetic groups (Fig. 5.4) is borne out by the correspondence analysis results, that show mosses to be associated with the moderate to high photosynthetic capacity groups 2.1 and 2.2 and also with the low photosynthetic capacity group with moderate to high photoprotective capability (group 3.1; Fig. 5.5). Hepatics are associated with groups 3.2 and 1.

Bryophyte life forms are discussed in Chapter 1 (Section 1.3.3). They are based on colonial or clonal architecture and are thought to reflect trade-offs to maximise photosynthesis and minimise water loss (Bates 1998, Glime 2007). The low photosynthetic capacity groups (3.1 and 3.2) comprise almost exclusively turf and mat life forms (the only exception is one thallose hepatic), whereas the moderate to high photosynthetic capacity groups (2.1, 2.2) comprise cushion, tuft and turf forms (Figs 5.6, 5.7).

With a few exceptions, bryophytes are not typical of manured habitats. Two of the exceptions were included in this study. *M. berteroana* is largely restricted to areas influenced by seals or birds and is a high photosynthetic capacity species (group 1). *Brachythecium rutabulum* is common in areas influenced by birds (especially burrowing petrels and prions; Gremmen and Smith 2008) and it occurs in the low photosynthetic capacity group 3.1.

5.6 Discussion

The relatively consistent between-site differences in bryophyte stature, especially that most of the species were tallest at one particular site, cannot be explained since site properties were not measured. Similarly, the between-site differences in chlorophyll concentration, which were mostly species-specific, cannot be explained. Bryophyte chlorophyll concentration decreases with increasing illumination (Deora and Chaudhary 1991, Marschall and Proctor 2004), so it might be that the species in a particular site experienced different light environments. The fact that chlorophyll concentration was greater at high altitude than at low altitude for both species that were measured at both altitudes also suggests that they were more shaded at high altitude. However both species showed a greater photosynthetic capacity and electron transport saturated at higher light at high altitude. This suggests that they were less, not more, shaded at high than at low altitude.

Racomitrium lanuginosum showed the greatest photoprotective capability of the species at low altitude; Marschall and Proctor (2004) also found *R. lanuginosum* to have the highest photoprotective capability (measured as NPQ) of the 55 bryophyte species they studied. Interestingly, the species has a slightly (although not significantly) greater photoprotective capacity at high than at low altitude, and the other species sampled at both altitudes (*Hypnum cupressiforme*) showed significantly greater photoprotective capability at high altitude. This is further support for the suggestion that the species are less shaded, or more adapted to high light, at high altitude.

Chlorophyll concentrations of the island's bryophytes are considerably lower than for the vascular plants, agreeing with what is found globally (Martínez-Abaigar and Núñez-Olivera 1998), and ascribed to the fact that most bryophytes have unistratose leaves and hence a higher proportion of cell wall to cell contents than vascular plants (Marschall and Proctor 2004). Photosynthetic capacity, as measured by ETR_{max}, for the bryophytes (mean 35 µmol m^{-2} s^{-1}) is about half the mean value (65 µmol m^{-2} s^{-1}) for the vascular species. Globally, bryophytes have been shown to have lower photosynthetic rates than vascular plants (Green and Lange 1995) but, as pointed out by Martin and Anderson (2001), this is an artefact of the basis for calculating photosynthetic rate, either on a dry mass or a leaf area basis: when rates are expressed on a chlorophyll concentration basis, the difference between bryophytes and vascular plants disappears. They concluded that photosynthetic capacity of bryophytes is not different to that of vascular plants. On a chlorophyll basis the island's bryophytes might be considered to have an even higher photosynthetic capacity than the vascular plants since they attain a mean ETR_{max} that is about half of the vascular species mean ETR_{max}, but with only about a seventh of the amount of chlorophyll. The difference in photosynthetic capacity between the island's bryophytes and vascular plants is considered in more detail in Chapter 6.

Although *M. berteroana* shows both the highest ETR_{max} and highest chlorophyll concentration of all the bryophytes considered in the study, the four species with the next highest ETR_{max} values all have very low or low chlorophyll concentration. In fact, if *M. berteroana* is ignored, there is a strong negative correlation between ETR_{max} and chlorophyll across the species ($r = -0.542$. $p = 0.030$). The data strongly support the finding by Marschall and Proctor (2004) of a significant negative correlation across-species between (log) chlorophyll concentration and (log) PAR at which photosynthesis is 95% saturated, suggesting that species from high light environments, although usually having a greater photosynthetic capacity, have lower chlorophyll concentrations than species from low light environments. PAR that yields 95% saturation is a trait closely akin to PAR_{opt} and for the island species (again ignoring *M. berteroana*), log chlorophyll concentration is strongly negatively correlated with PAR_{opt} ($r = -0.691$, $p = 0.003$).

The fact that the species with low ETR_{max} have a high proportion of closed reaction centres (1-qL) and low to moderate photoprotective capability at ETR_{max}, even though ETR_{max} is reached at low light, suggests that they are typical deep shade species with no need to construct the high number of reaction centres or to develop the mechanisms for dissipating excess absorbed light energy, both of which would be advantageous to a sun plant. The fact

that the high photosynthetic capacity species tend to have low or moderate 1-qL at ETR_{max}, even though ETR_{max} is attained at higher light intensity, is a typical adaptive response to a high light environment – an investment in a large number of reaction centres to ensure that there are always some oxidised (open) ones to allow photosynthetic electron transport at high light. The high photosynthetic capacity species also have substantial photoprotective capacity, which also contributes to open reaction centres. The notable exception is again *M. berteroana*, the species with the highest photosynthetic capacity, but with a high proportion of closed reaction centres and the lowest photoprotective capability at ETR_{max} of all the species. The poor photoprotective ability of *M. berteroana* agrees with the finding of Marschall and Proctor (2004) that Marchantiales liverworts have low capability for photoprotection.

The high photosynthetic capacity of *M. berteroana* is due to the fact that, like other Marchantiales species, it possesses a thick thallus with ventilated photosynthetic tissue with a high internal area to surface area ratio, more akin to vascular plant leaves than the unistratose leaves of most bryophytes, and resistance to CO_2 diffusion is low (Green and Snelgar 1982). In contrast, *Jensenia pisicolor*, also a thallose liverwort, has a very low photosynthetic capacity. In that species the thallus is solid (i.e. lacking ventilated photosynthetic tissue). A solid thallus offers considerable resistance to CO_2 diffusion into the photosynthetic centres (Green and Lange 1995), resulting in very low rates of photosynthesis and photosynthetic electron transport (Griffiths et al. 2006, Meyer et al. 2008, Raven and Edwards 2014).

Polytrichaceous mosses also have ventilated photosynthetic tissue, in the form of rows of chlorophyll-rich lamellae that increase photosynthetic surface area and reduce resistance to CO_2 diffusion (Thomas et al. 1996), and are associated with very high photosynthesis rates (Krupa 1978). None of the island's three Polytrichaceous species were included in this study.

PCA and clustering of the species on their photosynthetic characteristics yielded clear groups, with *M. berteroana* very much an outlier due to its peculiar combination of a very high photosynthetic capacity and sharp response to low light but very poor photoprotective capacity. The rest of the species fall into either a very low to low photosynthetic capacity group, consisting of four moss and five hepatic species, or a moderate to high photosynthetic capacity group made up almost entirely of mosses (one hepatic). Both groups are subdivided on the basis of differences in photoprotective capability, ability to maintain open reaction centres and ability to respond to light at low light levels. The high photosynthetic capacity

species with a high photoprotective capability and ability to maintain open reaction centres, but with a poor response to low light (group 2.1) are mosses of mesic or dry mires and fellfields. Their life form is mainly a tufted one, so they have a relatively open colony structure and the individual fronds are exposed to light. The high photosynthetic capacity species with a lower (but not low) photoprotective capacity and a poor ability to maintain open reaction centres and with a sharp response to low light (group 2.2) are mainly cushion- or turf-forming species (even the single hepatic is a turf-former), so the fronds are packed tightly together and considerably self-shaded.

The species in group 3.2 are archetypical shade species, with very low photosynthetic capacity, low to moderate photoprotective capability and an inability to maintain open reaction centres. They also show a sharp response to increasing low light. Four of the five species are hepatics of wet mires, either mat or turf formers with densely packed upright fronds or a thallose form (*J. pisicolor* - this species could also be considered as a turf hepatic; Niek Gremmen pers. comm.); in all cases there is considerable self-shading. The only moss in group 3.2 (*H. cupressiforme*) is a mat former and is restricted to very shady environments such as in rock fissures and under rock overhangs. The four species in the other group (3.1) with low photosynthetic capacity are also mat (but rough mat rather than smooth mat types, with a more open architecture) or turf formers and are also most common in shaded habitats. *Sanionia uncinata*, *Brachythecium rutabulum* and *Plagiochila heterodonta* are typical of slope areas where they occur under vascular plants and *Distichophyllum fasciculatum* (and also *S. uncinata*) occur in wet or mesic mires, often shaded by vascular plants.

The results of this study show quite strongly that mosses tend to have a higher photosynthetic capacity than liverworts on the island. If the island's Polytrichaceous moss species had been included the difference would have been even more striking. Only two of the seven liverworts occur in the groups with moderate to very high ETR_{max}; the rest are in the very low to low ETR_{max} groups. Ignoring *M. berteroana*, mean ETR_{max} for the mosses is 69% greater (p = 0.020) than the mean value for liverworts, and ETR in the mosses saturates at a 40% higher PAR level than in the liverworts (p= 0.064). Overall, the mosses also have a significantly (p = 0.001) greater photoprotective capability (mean YNPQ/YNO = 2.820 ± 0.303 (standard deviation)) than the liverworts (2.168 ± 0.505). This is probably why a significantly (p < 0.001) lower proportion of reaction centres are closed at ETR_{max} for the mosses (mean 1-qP = 0.664 ± 0.071) than for the liverworts (0.793 ± 0.042). These findings accord with those from a much more extensive survey of 39 moss and 16 liverwort species

(Marschall and Proctor 2004). Analysis of the data presented in Tables 1 and 2 of those authors showed that PAR giving 95% saturation of electron transport rate is greater (p = 0.001), photoprotective capacity is greater (p = 0.014), but the proportion of closed reaction centres is lower (p < 0.001), in the moss than the liverwort species.

Chapter 6.

Plant functional groups based on photosynthetic traits of both vascular plants and bryophytes

6.1. Introduction

Hitherto the photosynthetic traits of the vascular and bryophyte species have been analysed separately and quite clear photosynthetic functional types were identified within each of the taxa. Also, in both, the same combinations of traits define the between-group and between subgroup differences. Even a brief examination of the species data presented in chapters 3 and 5 as well as Appendix Tables A14 to A20 (for vascular species) and Appendix Tables A42 to A58 (bryophyte species) shows that, overall, bryophytes tend to have a lower photosynthetic capacity (lower ETR_{max} reached at lower PAR, photosynthetic saturation starting at lower PAR than the vascular species, lower effective quantum efficiency) but that they (mosses especially) tend to have greater capability of photoprotection. In this chapter, I analyse the two groups together to test whether bryophytes as a whole fall into entirely different photosynthetic types than vascular species or if some types contain members of both taxa. I also explore whether the various groups of species, whether they are forbs, graminoids, ferns, mosses or hepatics, or whether they are sun- or shade plants or something in between, show similar patterns in the collective behaviours of particular sets of traits, which would suggest common trade-off strategies in their response to light.

The pattern of interspecies differences across seven photosynthetic traits was determined by Principal Component Analysis and the species then clustered on their scores on the significant principal components. The groupings from the clustering analysis were then related to habit (forb, graminoid, fern, moss, hepatic) and habitat (fresh, saline, biotic) using Correspondence Analysis.

Potamogeton nodosus was omitted from the analysis because of doubts about the suitability of the fluorescence measurement technique for an aquatic species. The results from low altitude were used, excepting for the four bryophytes that were only measured at high altitude.

6.2 Results

The first three principal components account for 94% of the total variance in the seven photosynthetic trait values (Table 6.1). The various indicators of photosynthetic capacity (ETR_{max}, PAR_{opt}, I_k, α and ΦPSII) are strongly negatively correlated with PC1. PC1 thus represents a gradient of high to low photosynthetic capacity.

The electron transport response to light at low levels (α) and proportion of closed reaction centres (1-qL) are positively, and photoprotective capacity (YNPQ/YNO) negatively, correlated with PC2. PC2 thus represents a gradient of (negative side of PC2) a high photoprotective capability and good ability to maintain a high proportion of open reaction centres, but a poor response to increasing light at low levels, to (positive side of PC2) a low photoprotective capability and poor ability to maintain a high proportion of open reaction centres and a sharp response to increasing light at low levels.

Only YNPQ/YNO contributes significantly to PC3, which is interpreted as also representing a gradient of high to low photoprotective capability.

Cluster analysis of the species scores on the first three principal components yields two main groups, both comprising subgroups (Fig. 6.1 and Table 6.2). The subgroups are superimposed on the PC1/PC2 biplot in Fig. 6.2.

Group 1 contains 20 vascular and 1 bryophyte species whereas bryophytes dominate group 2 (20 bryophyte species against only four vascular species). The values of most of the photosynthetic traits for the species in each of the groups span almost the whole range found, from very low to very high. However, group 1 species tend overall to have higher values for the traits indicative of the various aspects of photosynthetic capacity (ETR_{max}, PAR_{opt}, I_k, ϕPSII at ETR_{max}, α), a lower photoprotective capacity (lower YNPQ/YNO) and a greater proportion of closed reaction centres at ETR_{max} (greater 1-qL). Despite the overlap in trait values, the two groups are quite well separated on the PC1 axis, the gradient representing the collective behaviour of the photosynthetic capacity traits. Only one group 2 species (*Agrostis magellanica*) occurs on the negative (high photosynthetic capacity) side of PC1, whereas only three group 1 species (*Montia fontana*, *Polystichum marionense* and *Sagina procumbens*) occur on the positive (low photosynthetic capacity) side of PC1. Hence, group 1 comprises species with moderate to very high, and group 2 species with very low to moderate, photosynthetic capacity. There is considerable overlap between the two groups in

photoprotective capacity and ability to maintain open reaction centres – only one of the group 2 subgroups (2.1.2) does not overlap with any of the subgroups of group 1 on PC2, the axis representative of photoprotection and reaction centre closure.

The two groups are divided into subgroups based on photosynthetic capacity or photoprotective capability or a combination of both. The subgroups are further divided into smaller groups based mainly on photoprotective capability and response to low light levels, but in one case only on photosynthetic capacity.

In total, the vascular and bryophyte species considered in this study are represented by eight photosynthetic functional types, the photosynthetic characteristics of which are described in Table 6.2. Henceforth the subgroups and sub-subgroups are referred to as groups, each representative of a photosynthetic functional type.

Groups 1.1.1 and 1.1.2 are at the extreme negative (high photosynthetic capacity) end of PC1, and comprise species (all are forbs) with the highest photosynthetic capacity. The two groups differ in that group 1.1.1 has a moderate to high capacity for photoprotection and a moderate proportion of closed reaction centres at ETR_{max}, whereas group 1.1.2 has a low capacity for photoprotection and tends to have a higher proportion of closed reaction centres. This is reflected by their separation on PC2.

At the other end of the photosynthetic capacity scale are groups 2.2.1 and 2.2.2, both with very low ETR_{max} attained at very low to low PAR, electron transport saturation commencing at very low to low light levels and very low to low quantum efficiency. They occur at the extreme positive side of the PC1 axis, with a small overlap with only one of the other groups (2.1.2). Like the distinction between the two highest photosynthetic capacity groups, these two low capacity groups differ mainly in their photoprotective capability and ability to maintain open reaction centres - there is no overlap between the two groups on PC2. Photoprotective ability is low for 2.2.1 but high for 2.2.2. Consequently, 2.2.1 species are unable to prevent most reaction centres from closing at ETR_{max}, whereas 2.2.2 species maintain a moderate proportion of open reaction centres. A further contrast between the two groups is that 2.2.1 species show a moderately sharp response, but 2.2.2 species a poor response, to light at low levels. Group 2.2.1 comprises two fern species and three hepatics, group 2.2.2 comprises four mosses and two hepatics.

Group 2.1.2 also occurs on the positive (low photosynthetic capacity) side of the PC1 axis, with some overlap with group 2.2.1. Group 2.1.2 species (all mosses) show low ETR_{max} attained at low to moderate PAR and moderate quantum efficiency. Electron transport saturation occurs at moderate PAR. They show a poor response to low light but a very high photoprotective capability (the highest of all the groups), and consequently able to maintain a considerable proportion of open reaction centres, at higher light levels.

There are two groups with low to moderate ETR_{max} (1.2.2 and 2.1.1). They occupy the middle part of the photosynthetic capacity axis (PC1), overlapping only with group 2.1.2 on that axis. Group 1.2.2 contains approximately equal numbers of forb, graminoid and fern species and group 2.1.1 contains five moss, one hepatic and two graminoid species. Group 1.2.2 species show a sharper response to low light and, on average, tend to saturate at higher PAR and have a slightly lower quantum efficiency than group 2.1.1 species. However, the biggest distinction between the two groups is that group 2.1.1 species have moderate to high photoprotection and consequently a low to moderate proportion of closed reaction centres, whereas group 1.2.2 species have low to moderate photoprotection and show high reaction centre closure. This distinction is shown by the clear separation of the two groups on PC 2.

Group 1.2.1 species have a slightly lower photosynthetic capacity than species in groups 1.1.1 and 1.1.2, but a higher capacity than species in the other groups. This is reflected in the intermediate (but well-separated) position of group 1.2.1 on PC1, between the high and low capacity groups. Species in group 1.2.1 show moderate to high ETR_{max}, attained at moderate to high PAR, and have a moderate to high quantum efficiency. They have a moderate to sharp response to low light and electron transport starts saturating at moderate PAR. They have a low to moderate photoprotective capability and are able to maintain a moderate proportion of open reaction centres – their values on both those traits overlap with the values for species in the two high capacity groups (1.1.1 and 1.1.2) and this leads to their intermediate and overlapping position on PC2. Group 1.2.1 comprises three graminoids, one forb and the high photosynthetic capacity hepatic *Marchantia berteroana*.

As was found when analysing the vascular plants and bryophytes separately, membership of the above groups is related quite strongly to plant habit and, but to a lesser extent, the moss versus hepatic distinction. This is shown in the cluster diagram (Fig. 6.3) and supported by the Correspondence Analysis joint plot (Fig. 6.4). Only forbs are found in the high to very high photosynthetic capacity groups (1.1.1 and 1.1.2). Each of those groups represents a

different capability for photoprotection; moderate to high and very low to low. Graminoids are associated mainly with the moderate to high photosynthetic capacity/ low to moderate photoprotective capability groups 1.2.1 and 1.2.2, but the latter group also contains four forbs. Mosses are associated with the very low, low or moderate photosynthetic capacity / moderately high or very high photoprotective capability groups (2.1.1, 2.1.2 and 2.2.2). Hepatics are associated most with the very low photosynthetic capacity / low photoprotective capability group 2.2.1. Of the four fern species, two occur in the very low photosynthetic capacity / low photoprotective capability group 2.2.1 and two in the low to moderate photosynthetic capacity / low to moderate photoprotective capability group 1.2.2. However, ferns from a minority in both these groups so the group-fern association is not strong, only group 1.2.2 occurring in the same quadrant of the correspondence joint plot as fern (Fig. 6.4).

The photosynthetic group/habitat correspondence analysis results are not shown, but the habitats are superimposed on the cluster diagram in Fig. 6.5. Unsurprisingly, since all but two of the bryophytes came from the oligotrophic (fresh) habitat, the photosynthetic groups comprising bryophytes associate very strongly with the fresh habitat. The vascular group/ habitat associations are the same as shown in chapter 4.

6.3 Discussion

The distribution of species across the eight photosynthetic groups found in the analysis of vascular plants and bryophytes together shows the same distinctions between vascular plant habit found in chapter 4 and between mosses and hepatics in chapter 5. Forbs predominate in the highest photosynthetic capacity groups, graminoids in moderate capacity groups, ferns in low to moderate capacity groups and bryophytes in the lowest capacity groups. Hence, the analysis clearly shows that vascular plants have a higher photosynthetic capacity than bryophytes. *Marchantia berteroana*, with ventilated mesophyll-like photosynthetic tissue, is the only bryophyte species that occurs on the negative (high photosynthetic capacity) side of PC1. All the other bryophytes are found in the low capacity groups. Hepatics, with some mosses and ferns, occur in the very lowest capacity groups.

At each level of the photosynthetic capacity hierarchy (high, moderate, low), subgroups of species are distinguishable on the basis of photoprotective capability and ability to respond to increasing light at low levels. Thus, the same combinations of traits define the between-group and between sub-group differences for both vascular species and bryophytes, but at different

levels in the ranges of trait values. This suggests a common trade-off strategy amongst the species in the way they respond to light, whether they are forbs, graminoids, ferns, mosses or hepatics.

Species in the very lowest photosynthetic capacity groups 2.2.1 and 2.2.2 (comprised of two ferns, four moss and five hepatics) are typical shade plants but with different strategies for dealing with low and high light. Group 2.2.1 species have a moderately sharp photosynthetic response to low light and a low photoprotective capability at higher light (hence are unable to prevent reaction centre closure at optimal light). This suggests that they are obligate shaded species occurring in constant shade. Group 2.2.2 species respond less sharply to low light but at higher light have a high photoprotective capability and are able to maintain a higher proportion of open reaction centres, suggesting that they occur in less shaded habitats or are sometimes exposed to brighter light. Or the distinction between the two groups might be related to growth form (Figures 6.6, 6.7). The three hepatics in group 2.2.1 form a closed turf of tightly packed upright fronds so there is considerable self-shading. The two fern species occur in constantly shaded environments. In contrast, the mosses and hepatics in group 2.2.2 are mostly mat formers, especially rough mat formers, with the fronds much less tightly packed and much less self-shaded.

Besides this distinction of turf and mat formers between the two lowest photosynthetic capacity groups, there are other correspondences between bryophyte life form and photosynthetic group (Figures 6.6, 6.7). Tuft mosses that form an even more open canopy in semi-shaded habitats (shaded by vascular plants) predominate in the low photosynthetic capacity/ very high photoprotective capacity group (2.1.2). Cushion- and turf-forming mosses, both with fronds that are more self-shaded than those of tuft mosses, but tend to occur in higher light environments, are mostly associated with the low to moderate photosynthetic capacity/ moderate to high photoprotective capacity group 2.1.1 (Fig. 6.7).

There are four photosynthetic functional groups where the species have moderate, high, or very high capabilities of photoprotection. One (1.1.1) comprises only forbs but the other three (2.1.1, 2.1.2 and 2.2.2), that have an even higher photoprotective capability, are overwhelmingly dominated by mosses (14 of the 19 species in the three groups are mosses). Thirteen of the 14 moss species studied occur on the negative (high photoprotective capacity, low proportion of closed reaction centres) side of PC2. Thus, of the species included in this study, mosses have the highest photoprotective capability. ANOVA confirms that mosses

have a significantly ($p < 0.001$) higher YNPQ/YNO (mean ± standard dev. = 2.82 ± 0.303) than hepatics, ferns, graminoids and forbs (mean for all non-moss species = 2.09 ± 0.389).

Chapter 7.

General discussion, concluding remarks and suggestions for future research

One objective of this study was to compile a database of plant structural trait values for the island plants, especially focussing on the vascular species. This was accomplished. The data are archived in a centralised data base at Stellenbosch University and will be transferred to the South African National Antarctic Programme data base once this has been established by the Department of Environment Affairs. Synopses of the trait values from the data base are given in several of the tables and figures in the various chapters and appendices of this thesis, especially Tables A1 to A57. The main patterns shown by the data (the between-site, between-altitude and between-species differences) are discussed in chapter 3 and the key findings are as follows.

Most of the island's vascular species show significant between-site differences in structural trait values, even within the same altitudinal band, but the differences cannot be ascribed to particular site characteristics since those were not recorded. However, for almost all the traits, the pattern of between-site differences in a particular trait is not consistent across species and so possibly not directly related to differences in site characteristics. Significant between-altitude differences in most structural trait values were shown for the vascular species that were measured at both low and high altitude. Largely, these differences could be ascribed to higher wind speed at high altitude - high altitude plants tend to be shorter and possess small leaves and tougher stems. High altitude plants showed greater specific root length (root length as a function of root mass) than plants of the same species at lower altitude, probably due to the greater need for foraging roots in the low nutrient status high altitude soils. However, species restricted to (or attaining maximum vitality in) coastal sites with high nutrient status soils have even greater specific root length, suggested to be a response to the inhibitory effect of high salt concentration on nutrient and water uptake.

Overall, the pattern of between-altitude differences in both structural and photosynthetic traits suggests that all of the vascular species are more stressed at higher than at lower altitude, with the exception of the cushion plant *Azorella selago*, the archetypical vascular species at high altitude.

One of the striking findings of this study is that indigenous species tend to show greater values than alien species for those traits indicative of structural strength (tough, thick leaves, strong stems) and tend to allocate a greater proportion of their biomass aboveground. At least for the graminoids, alien species also have higher stomatal densities (but lower chlorophyll concentrations on a leaf area basis) than native species. These differences in leaf traits do not translate into any consistent differences in photosynthetic capacity between natives and aliens. The only difference between the two are that indigenous species tend to show a sharper photosynthetic response to increasing light at low levels, probably an adaptation to the consistently low light regime at the island.

Maximum photosynthetic electron transport rate (a surrogate for photosynthetic rate) varies by an order of magnitude between the island's vascular species and by almost an order of magnitude between the bryophyte species. Species with high electron transport rate (most are forbs) also tend to have a high effective quantum yield and show electron transport saturation at high light – all indicative of high photosynthetic capacity sun species. At the other end of the scale are the shade-adapted, low photosynthetic capacity species; some are ferns but most are mosses and liverworts. Graminoids tend to be moderate photosynthetic capacity species but some of the forb species also have moderate, and even low, photosynthetic capacity.

The second objective of the study was to use the trait data base to group the island's species into plant functional types. First, the vascular plants were grouped based only on structural traits, then on photosynthetic traits and then on both trait types. The bryophyte species were grouped into functional types (based on photosynthetic traits), firstly on their own and then together with the vascular species.

The vascular species are separated into five groups on the structural traits, based firstly on size. One group comprises the two tallest species with the largest, heaviest leaves. The other four groups comprises smaller species and are separated on specific leaf area, leaf dry matter content and stem specific density. Two groups have moderate to high LDMC and SSD and low to moderate SLA, and two groups have low to moderate LDMC and SSD and high SLA. The former two groups are distinguished from each other by differences in plant height, leaf area and leaf mass, root diameter and stem specific density. The latter two groups are also distinguished from each other by differences in PH, LA and LM, but in addition show differences in chlorophyll concentration, specific root length and root diameter.

In these assemblages based on structural traits, indigenous graminoids predominate in the group characterized by moderately tall to tall plants with tough, moderately large and heavy leaves having a high chlorophyll content and with moderately tough stems and moderately thick roots with low SRL. Alien graminoids occur in the group characterized by low growing plants with small, light, weak leaves with very high SLA and moderate chlorophyll content and thin roots. Alien forbs are associated with a group also characterized by weak leaves (but not as weak as the aforementioned group) but with thicker roots. Indigenous forbs occur in all the groups based on the structural traits.

The groupings of vascular species based on the photosynthetic traits supported what was suggested by the univariate analyses of the individual trait values - the groups with high photosynthetic capacity (as maximum ETR, PAR giving maximum ETR, effective quantum yields, ability to maintain open reaction centres at high light) are dominated by forbs (particularly indigenous forbs), graminoids occur mostly in the moderate or moderately high capacity groups and ferns dominate the lowest photosynthetic capacity group. Unlike what was shown by the groups based on structural traits, alien and native species were not distinguished from each other in the photosynthetic trait grouping.

The biotic coastal zone habitat is nutrient rich and the plants have high nitrogen concentrations and high specific leaf areas, so might be expected to have a high photosynthetic capacity, but this was not found to be the case. Species from the biotic habitat are found in all the photosynthetic capacity groups except the highest capacity one.

In terms of species membership, there is almost no correspondence between the assemblages of vascular plants based on structural traits and those based on the photosynthetic traits. The only exception was that three of the four species in the structural group representing plants with moderate stature, leaf area, leaf mass, chlorophyll content and low to moderate specific root length, also made up three of the four species in the photosynthetic group comprised of plants with high to very high photosynthetic capacity and high capability of photoprotection.

Principal component analysis of the structural and photosynthetic traits together yielded a component space in which the species are separated first on the structural traits then on the photosynthetic traits. Clustering the species on their component scores yielded five functional groups, in which the plant habit distinction features strongly. Four of the groups are dominated by forbs and the fifth by graminoids and ferns.

The strong distinction between alien and native species shown on the structural traits is less clear when both trait types are considered but an alien-native signature is recognizable in the groups, as is habitat type (fresh, biotic or saline). Indigenous graminoids and ferns are associated with a group characteristic of non-manured, non-saline habitats and comprised of moderately tall plants with thick tough leaves with moderate to high chlorophyll content. Species in that group vary widely in their photosynthetic and photoprotective capacities. Alien graminoids occur in a group of lower stature species with thin weak leaves and with low photosynthetic and photoprotective capacities. The group is most strongly associated with the biotic (manured) habitat. Forbs dominate the remaining three groups, all comprised of low to moderate stature species with soft, thin or succulent leaves and low to moderate chlorophyll content. One of these groups comprises species with low to moderate photosynthetic and photoprotective capacities and is associated most with manured or saline habitats. Another group comprises high photosynthetic / low to moderate photoprotective capacity species and is associated with oligotrophic habitats. The remaining group comprises high photosynthetic / high photoprotective capacity species and is associated with manured habitats.

This study was focussed primarily on obtaining a functional grouping of the island's vascular plants since a separate project is addressing bryophyte functional groups at the island. However, 14 moss and 7 liverwort species were included in the photosynthetic trait measurements made in the study, mainly to see if the bryophytes formed photosynthetic functional groups of their own or if they were interspersed in the same groups as the vascular species. Also of interest was to establish whether, like the forb-graminoid-fern distinction shown in the vascular plant functional grouping, strong phylum (moss or liverwort) or life form signatures also occur in the bryophyte functional grouping.

Only two structural traits were measured on the bryophytes so the functional grouping was carried out only on the photosynthetic traits. It yielded five bryophyte functional groups. *Marchantia berteroana*, the only species included in the study that has multi-layered ventilated photosynthetic tissue, has a considerably greater photosynthetic capacity than the other bryophytes and occurs in a group of its own. There are two other high photosynthetic capacity groups, comprised entirely or almost entirely of cushion-, tuft- and turf-forming mosses, and that differ from each other in photoprotective capability, ability to maintain open reaction centres at high light and sharpness of the photosynthetic response to increasing light at low levels. Turf- and mat-forming hepatics and mosses dominate the two low

photosynthetic capacity groups, which also differ from each other in their photoprotective capability, ability to maintain open reaction centres at high light and response to increasing light at low levels. All but two of the bryophyte species included in the study are restricted to oligotrophic habitats so it was not possible to analyse the correspondence between habitat and bryophyte functional group.

Although the study included only a small number of bryophyte species, and found the species with greatest photosynthetic capacity to be a hepatic, the results otherwise strongly suggest that, overall, the mosses have a higher photosynthetic capacity and, also greater photoprotective capability than the hepatics. In fact, mosses show significantly greater photoprotective capacity than the vascular plants. The project on bryophyte functional grouping is considering a much larger number of the island's bryophyte species, including the Polytrichaceous mosses with ventilated photosynthetic tissue that are known to have very high photosynthetic capacity. It is also addressing desiccation response traits as well as light response traits.

Analysis of the photosynthetic traits for the vascular and bryophyte species together yielded eight photosynthetic functional groups. Unsurprisingly, the distinctions shown are the same as those based on analyses of only the vascular plants (forb vs graminoid vs fern) or the bryophytes (mosses vs hepatics). Forbs predominate in the two highest photosynthetic capacity groups, graminoids (with one hepatic) in the moderate to moderately high capacity groups, graminoids, ferns and some bryophytes in the low to moderate capacity groups and bryophytes and shade-adapted ferns in the very low to low capacity groups. Mosses tend to have a higher capacity than hepatics although four of the six species in the very lowest capacity group are mosses.

At each level of photosynthetic capacity – the high, moderate or low capacity groups – the species are divided into subgroups based on their capability of photoprotection at high light and how sharply photosynthesis responds to increasing light at low levels. Hence, the same combination of traits define the functional groups at all levels of photosynthetic capacity, suggesting common trade-off strategies in how the species handle very high, and very low, light, whether they are sun- or shade-adapted or whether they are forbs, graminoids, ferns, mosses or hepatics.

This study focussed on only a limited number of traits, all related to plant structure and photochemistry responses to light. Future work needs to include phenological (plant

longevity, leaf longevity, leaf bud burst, onset of flowering, tillering, ripening of seed or fruit, dormancy and senescence) and reproductive (age at reproductive maturity, pollination mode, seed size, longevity, dispersal and germination) characteristics and a wider suite of physiological traits. Throughout this thesis the arguments about differences in photosynthetic capacity have been based on rates of photochemistry and heat dissipation measured using chlorophyll fluorescence. The findings (especially the seeming lack of correlation between plant nutrient status and photosynthetic capacity) need to be tested using gas exchange measurements of photosynthesis, photorespiration and respiration rates.

Since one of the main manifestations of climate change at the island is increasing temperature, the physiological and growth responses of the island plants to warming need to be investigated. Another manifestation of climate change is that the island is becoming drier, hence aspects related to plant water relations, such as hydraulic conductance, stomatal conductance, transpiration rate, water use efficiency and desiccation tolerance, need to be addressed. A cardinal factor affecting the island vegetation is wind - the sub-Antarctic region (the “roaring 40s” and “furious 50s”) is one of the windiest on earth. The effect of wind on plant morphology, architecture, growth and the physiological characteristics mentioned in the previous sentence needs to be investigated.

A decade and a half ago, Westoby et al. (2002) described the status of plant functional type research worldwide as follows: “There is much to be done. There is also a real hope that we may be getting somewhere”. The world has since moved on – with substantial progress achieved in the field of plant functional types, at the individual species, community, ecosystem and landscape levels. So, globally, we have indeed got somewhere. I hope that as a result of this study, Westoby et al’s description befits the current status of research into plant functional types on sub-Antarctic islands and that we are at least getting somewhere.

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Appendix 1. Site photographs

Sites 1 to 4: Saltspray Complex

Species sampled: *Crassula moschata* and *Cotula plumosa*

Site Number: 1 Coordinates: S46°52.804′, E37°52.061′ 	Site Number: 2 Coordinates: S46°52.746′, E37°51.960′ 
Site Number: 3 Coordinates: S46°52.682′, E37°51.856′ 	Site Number: 4 Coordinates: S46°53.248′, E37°52.263′ 

Sites 5 to 8: Mire Complex (Wet mire habitat)

Species sampled: *Ranunculus biternatus*

Site Number: 5 Coordinates: S46°52.348′, E37°51.396′ 	Site Number: 6 Coordinates: S46°52.784′, E37°52.007′ 
Site Number: 7 Coordinates: S46°52.720′, E37°51.892′ 	Site Number: 8 Coordinates: S46°53.235′, E37°52.226′ 

Sites 9 to 12: Slope Complex (Streambank habitat)

Species sampled: *Sagina procumbens*

Site Number: 9 Coordinates: S46°52.198′, E37°51.388′  	Site Number: 10 Coordinates: S46°52.213′, E37°51.267′ 
Site Number: 11 Coordinates: S46°52.192′, E37°51.151′ 	Site Number: 12 Coordinates: S46°53.205′, E37°52.179′ 

Sites 13 to 16: Biotic Complex (Biotic mud and biotic lawn habitats)

Species: *Agrostis stolonifera*, *Callitriche antarctica*, *Montia fontana* and *Poa annua*

Site Number: 13 Coordinates: S46°53.105′, E37°52.062′  	Site Number: 14 Coordinates: S46°53.163′, E37°52.158′ 
Site Number: 15 Coordinates: S46°52.234′, E37°51.398′  	Site Number: 16 Coordinates: S46°52.654′, E37°51.684′ 

Sites 17 to 20: Biotic complex (Cotula herbfield habitat)

Species sampled: *Marchantia berteroana*

Site Number: 17 Coordinates: S46°53.086′, E37°52.063′ 	Site Number: 18 Coordinates: S46°53.044′, E37°52.121′ 
Site Number: 19 Coordinates: S46°52.211′, E37°51.392′ 	Site Number: 20 Coordinates: S46°52.231′, E37°51.374′ 

Sites 21 to 25: Mire Complex

Species sampled: *Agrostis magellanica, Blepharidophyllum densifolium, Campylopus clavatus, Campylopus introflexus, Campylopus purpureocaulis, Clasmatocolea humilis, Dicranoloma billardierei, Distichophyllum fasciculatum, Jensenia pisicolor, Juncus scheuchzerioides, Ptychomnion densifolium, Racomitrium lanuginosum Syzygiella colorata, Uncinia compacta*

Site Number: 22

Coordinates: S46°52.692′, E37°51.342′

Site Number: 23

Coordinates: S46°52.134′, E37°50.969′

Site Number: 24

Coordinates: S46°52.262′, E37°51.247′

Dicranoloma billardierei (Not found at this Mire – extra site = 21)

Site Number: 21

Coordinates: S46°52.456′, E37°51.040′

Species sampled*: Dicranoloma billardierei*

Site Number: 25

Coordinates: S46°52.872′, E37°51.539′

Site 26 to 29: Mire Complex (Drainage line habitat)

Species sampled: *Breutelia integrifolia*

Site Number: 26 Coordinates: S46°52.211′, E37°51.182′ 	Site Number: 27 Coordinates: S46°52.677′, E37°50.560′ 
Site Number: 28 Coordinates: S46°52.722′, E37°50.153′ 	Site Number: 29 Coordinates: S46°52.768′, E37°49.877′ 

Sites 30 and 33: Mire Complex

Site 31 and 32: Slope Complex

Species sampled: *Agrostis stolonifera*

Site Number: 30 Coordinates: S46°53.043′, E37°52.063′ 	Site Number: 31 Coordinates: S46°52.798′, E37°52.042′ 
Site Number: 32 Coordinates: S46°52.164′, E37°51.056′ 	Site Number: 33 Coordinates: S46°52.240′, E37°51.210′ 

Sites 34 to 37: Slope Complex (Fernbrake habitat)

Species sampled: *Acaena magellanica, Blechnum penna-marina, Brachythecium rutabulum, Poa cookii,* and *Sanionia uncinata*

<table>
<tr>
<td>Site Number: 34

Coordinates: S46°52.270′, E37°50.926′

  </td>
<td>Site Number: 35

Coordinates: S46°52.227′, E37°51.298′

  </td>
</tr>
<tr>
<td>Site Number: 36

Coordinates: S46°52.399′, E37°50.758′

  </td>
<td>Site Number: 37

Coordinates: S46°52.865′, E37°51.445′

  </td>
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</table>

Sites 38 to 41: Fellfield Complex (mesic fellfield habitat)

Species sampled: *Azorella selago, Bucklandiella membranacea* and *Hypnum cupressiforme*

Site Number: 38 Coordinates: S46°52.172′, E37°50.997′ 	Site Number: 39 Coordinates: S46°52.459′, E37°51.055′ 
Site Number: 40 Coordinates: S46°52.278′, E37°50.941′ 	Site Number: 41 Coordinates: S46°52.399′, E37°50.758′ 

Site Number: 42

Growing epiphytically on *Azorella selago*

Coordinates: S46°51.105′, E37°50.381′

Species sampled: *Colobanthus kerguelensis*

Site Number: 49

Aquatic habitat

Coordinates: S46°52.580′, E37°51.490′

Species sampled: *Potamogeton nodosus*

Site Number: 43

Rock crevice habitat

Coordinates: S46°52.994′, E37°50.956′

Species sampled: *Grammitis kerguelensis*, *Hymenophyllum peltatum*

Site Number: 44

Rock crevice habitat

Coordinates: S46°57.645′, E37°51.540′

Species sampled: *Polystichum marionense*

Site Number: 45

Rock crevice habitat

Coordinates: S46°51.307′, E37°50.574′

Species sampled: *Polystichum marionense*

Site Number: 46

Rock crevice habitat

Coordinates: S46°52.217′, E37°51.262′

Species sampled: *Polystichum marionense*

Site Number: 47

Rock crevice habitat

Coordinates: S46°57.721′, E37°44.912′

Species sampled: *Polystichum marionense*

Site Number: 48

Slope Complex

Coordinates: S46°52.416′, E37°51.439′

Species sampled: *Pringlea antiscorbutica*

Site Number: 50

Dry mire habitat

Coordinates: S46°51.136′, E37°50.367′

Species sampled: *Juncus effusus*

Site Number: 51

Biotic complex (Coastal tussock grassland habitat)

Coordinates: S46°53.043′, E37°51.150′

Species sampled: *Juncus effusus*

Site Number: 52

Slope Complex

Coordinates: S46°52.202′, E37°51.287′

Species sampled: *Juncus effusus*

Site Number: 61

Biotic Complex

Coordinates: S46°52.657′, E37°51.663′

Species sampled: *Rumex acetosella*

Site Number: 53 Slope Complex Coordinates: S46°52.700′, E37°50.504′ Species sampled: *Cerastium fontanum* 	Site Number: 54 Biotic Complex Coordinates: S46°52.433′, E37°51.432′ Species sampled: *Cerastium fontanum* 
Site Number: 55 Biotic Complex Coordinates: S46°52.434′, E37°51.433′ Species sampled: *Cerastium fontanum* 	Site Number: 56 Slope Complex Coordinates: S46°53.122′, E37°52.078′ Species sampled: *Cerastium fontanum* 

Site Number: 57 Habitat: Slope Complex Coordinates: S46°52.485′, E37°51.506′ Species sampled: *Poa pratensis* 	Site Number: 58 Habitat: Slope Complex Coordinates: S46°52.431′, E37°51.434′ Species sampled: *Poa pratensis* 
Site Number: 59 Habitat: Slope Complex Coordinates: S46°52.439’, E37°51.061’ Species sampled: *Poa pratensis* 	Site Number: 60 Habitat: Slope Complex Coordinates: S46°52.580’, E37°51.490’ Species sampled: *Poa pratensis* 

High altitude sites – Tafelberg. Sites 62 to 68: Fellfield Complex (Xeric fellfield habitat)

Species sampled: *Agrostis magellanica, Andreaea* sp., *Azorella selago, Blechnum penna-marina, Ditrichum strictum, Hypnum cupressiforme, Plagiochila heterodonta , Poa cookii, Racomitrium lanuginosum , Syzygiella sonderi* and *Uncinia compacta.*

<table>
<tr>
<td>Site Number: 62

Coordinates: S46°53.156′, E37°48.551′

  </td>
<td>Site Number: 63

Coordinates: S46°53.145′, E37°48.448′

Poa cookii not at this site – Extra site

Site Number: 64

Coordinates: S46°53.100′, E37°48.177′</td>
</tr>
<tr>
<td>Site Number: 65

Coordinates: S46°53.183′, E37°48.170′

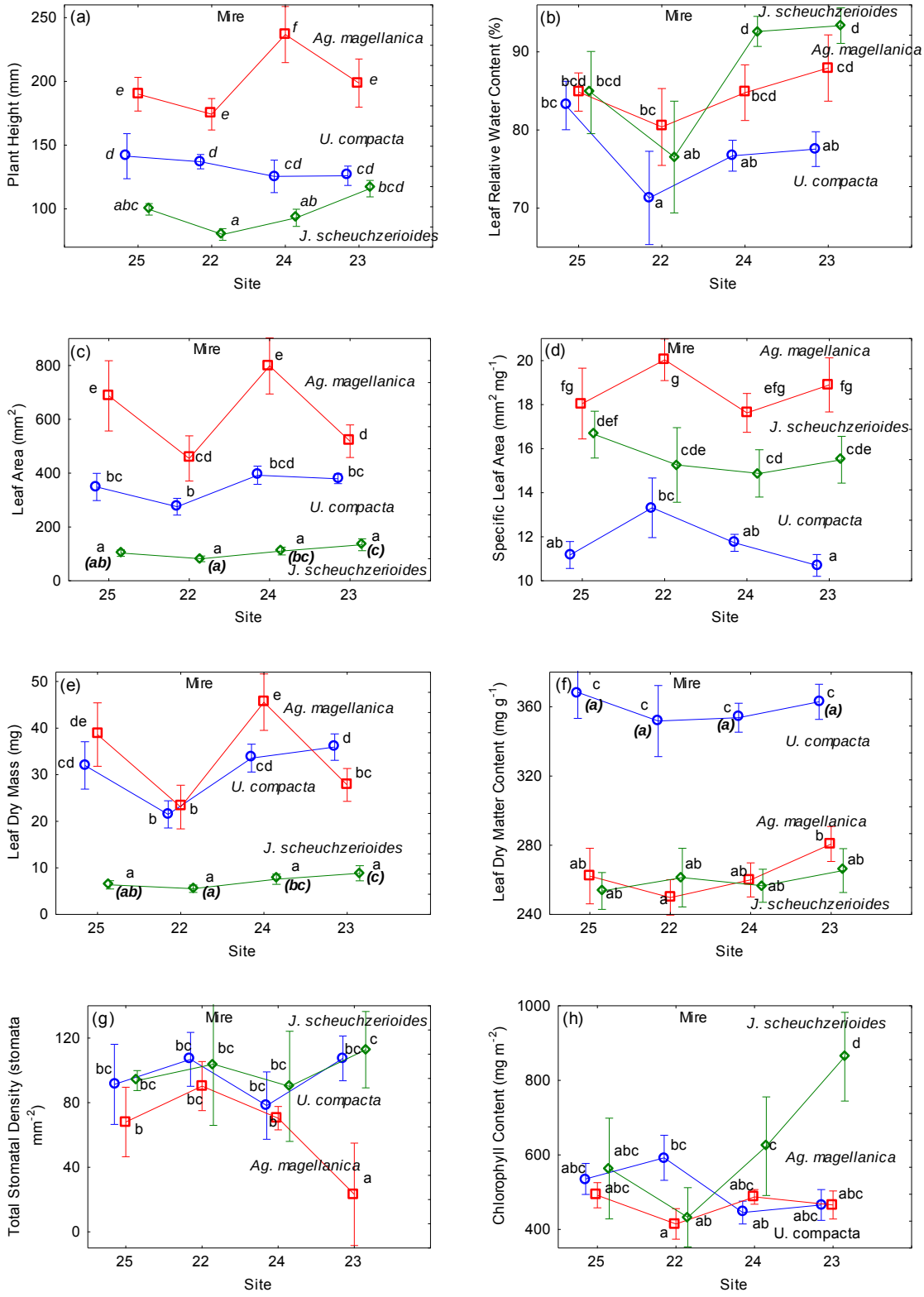
Poa cookii not at this site – Extra site:</td>
<td>Site Number: 68

Coordinates: S46°53.149′, E37°48.634′

  </td>
</tr>
</table>

Site Number: 66 Coordinates: S46°53.141′, E37°48.103′ *Uncinia compacta* not at this site – Extra site: Site Number: 67 Coordinates: S46°53.133′, E37°48.512′	

Appendix Figures



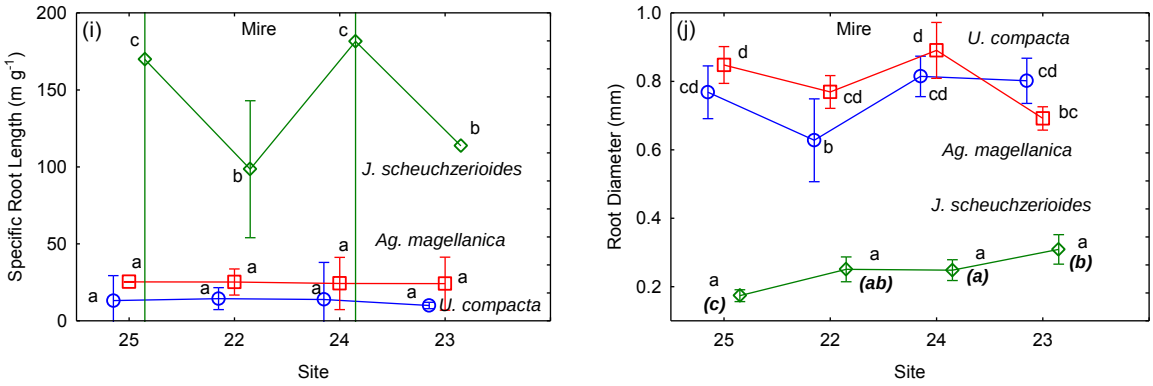
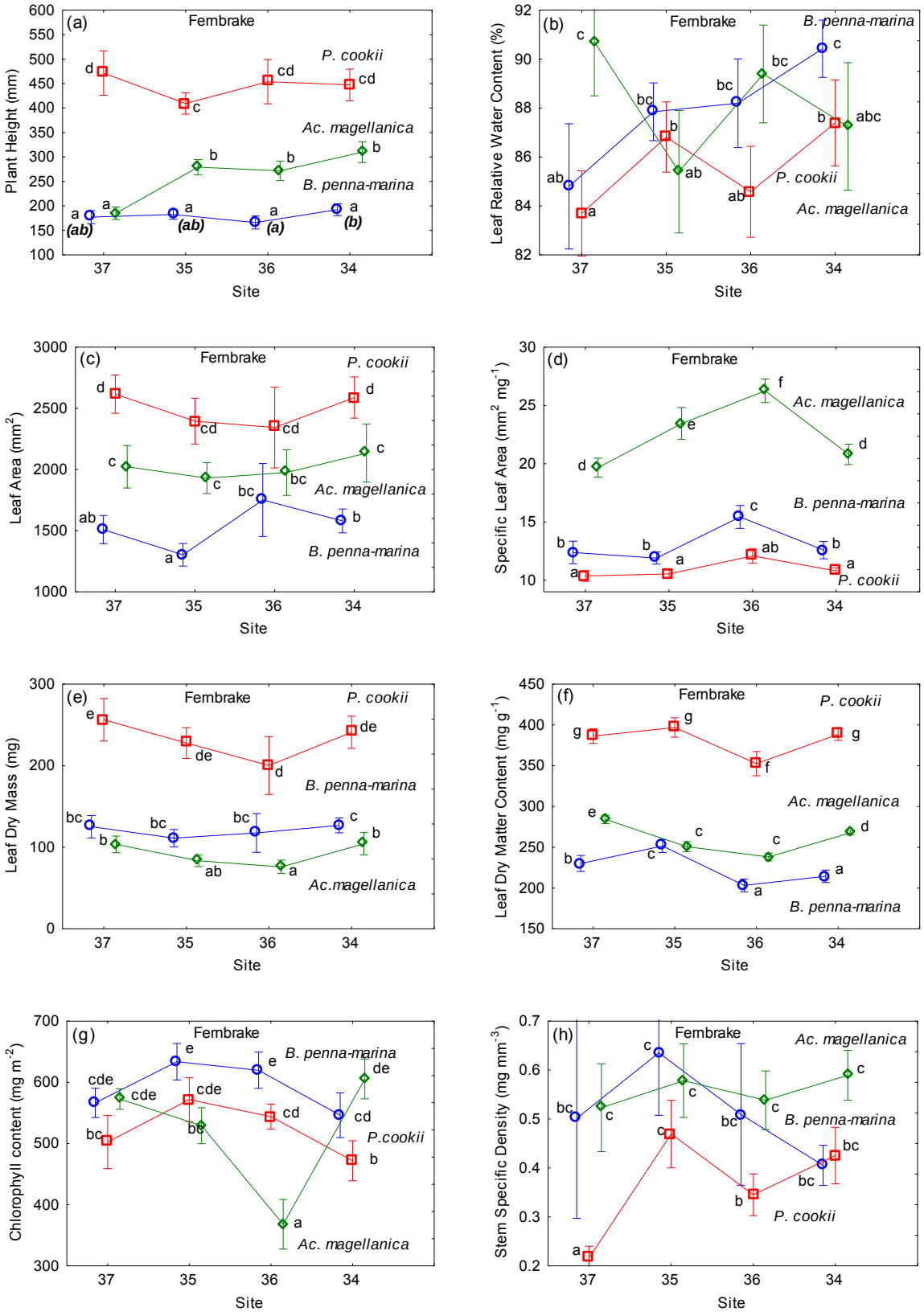


Figure A1 (a) to (j) Site x species effect for plant structural traits at four mire sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.



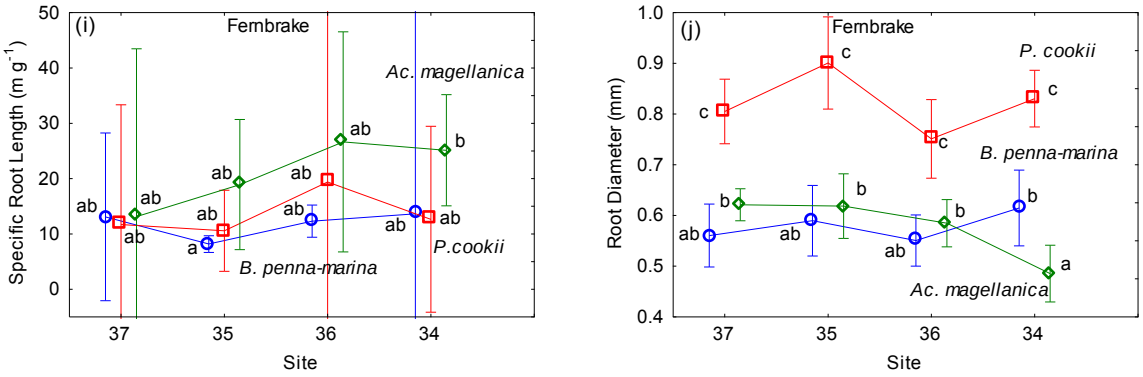
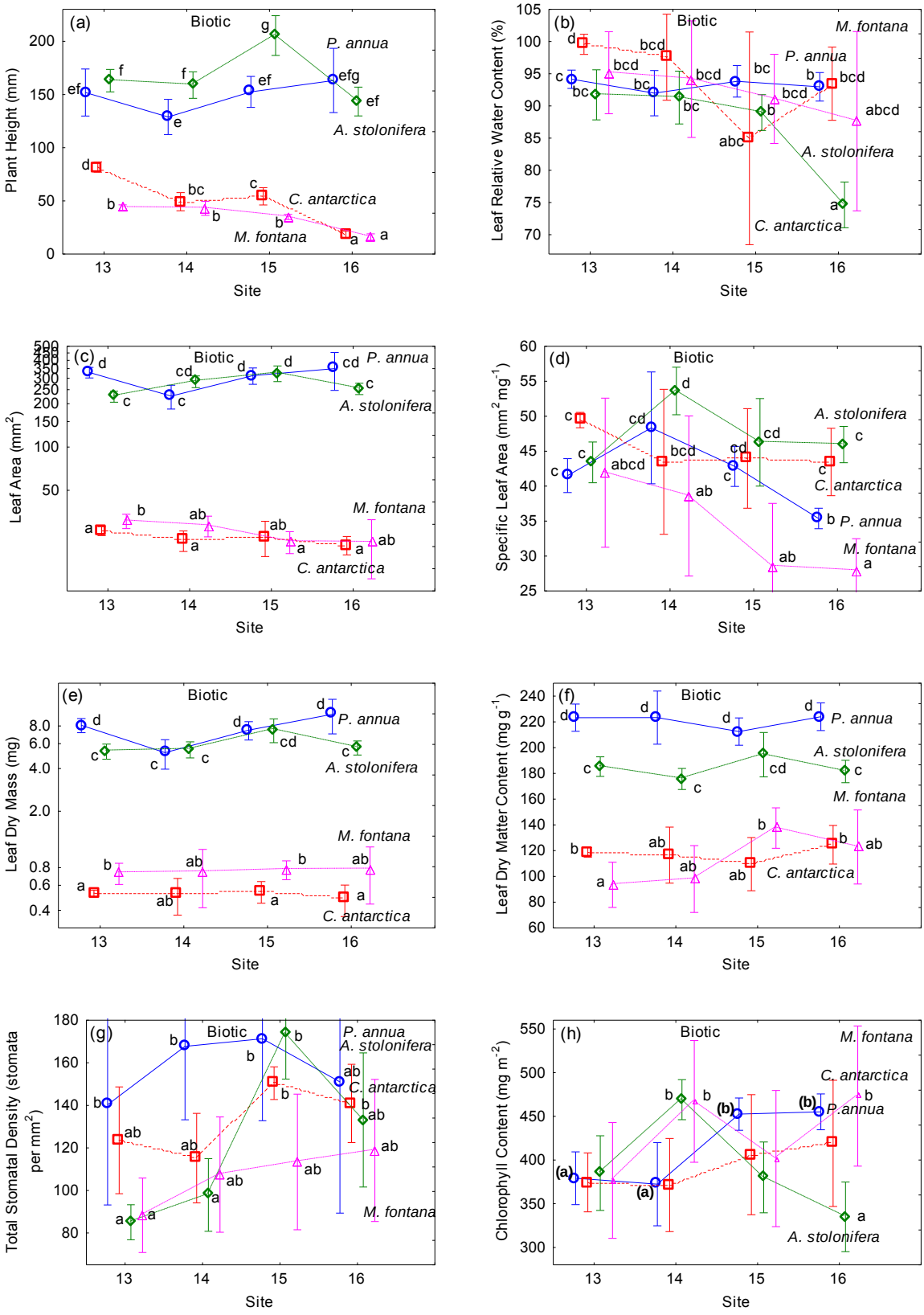


Figure A2 (a) to (j). Site x species effect for plant structural traits at four fernbrake sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.



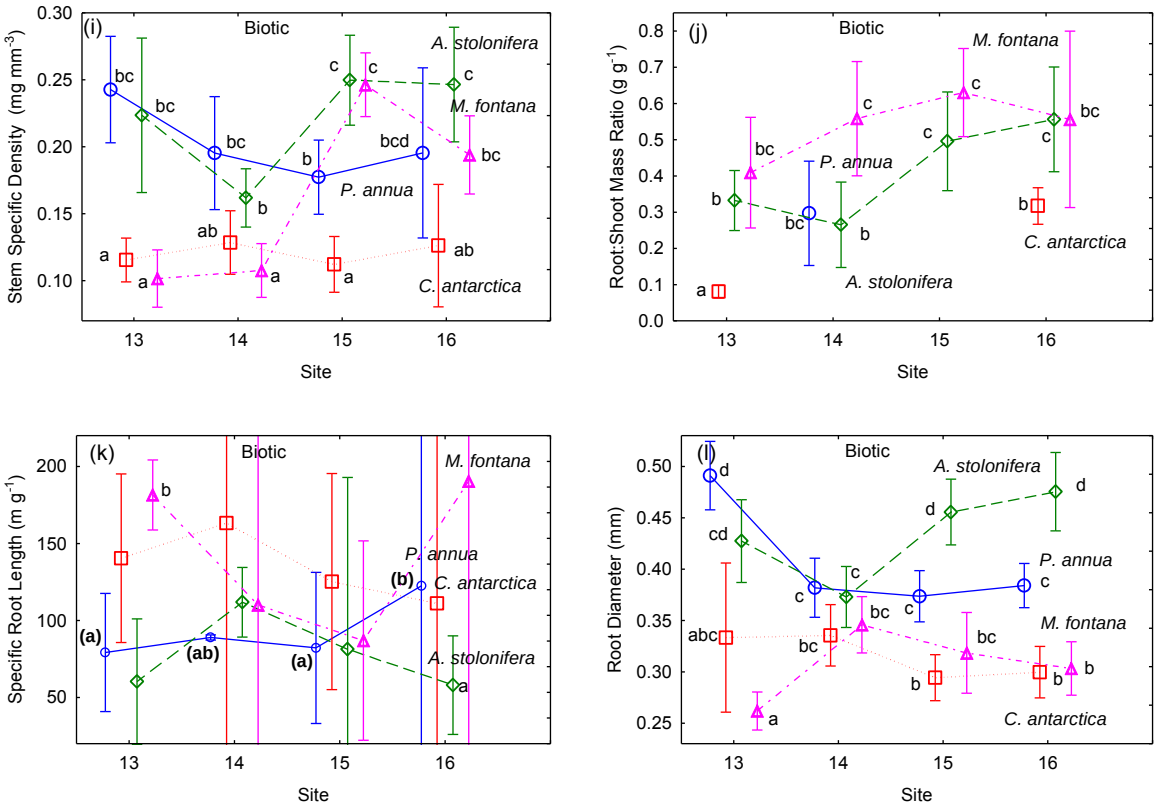
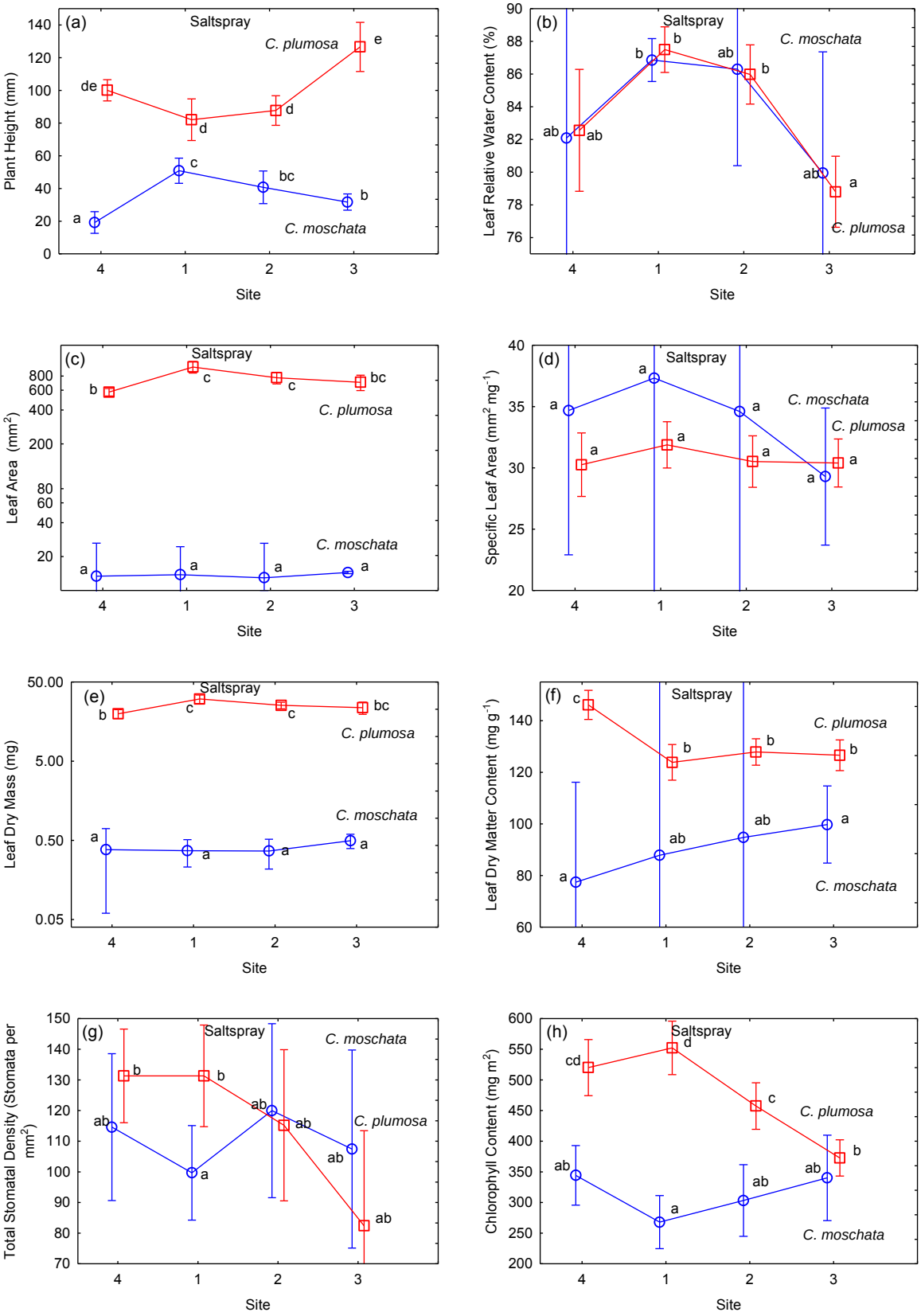


Figure A3 (a) to (l) Site x species effect for plant structural traits at four biotic sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.



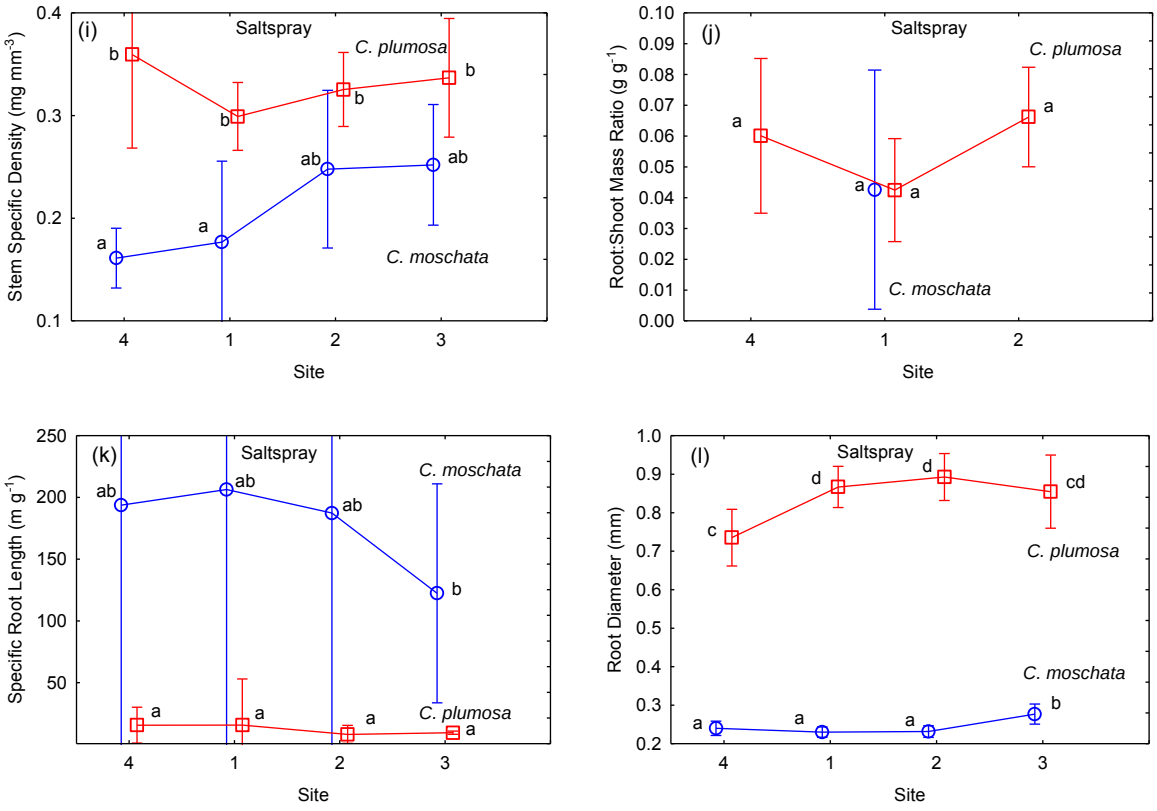


Figure A4 (a) to (l) Site x species effect for plant structural traits at four saltspray sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.

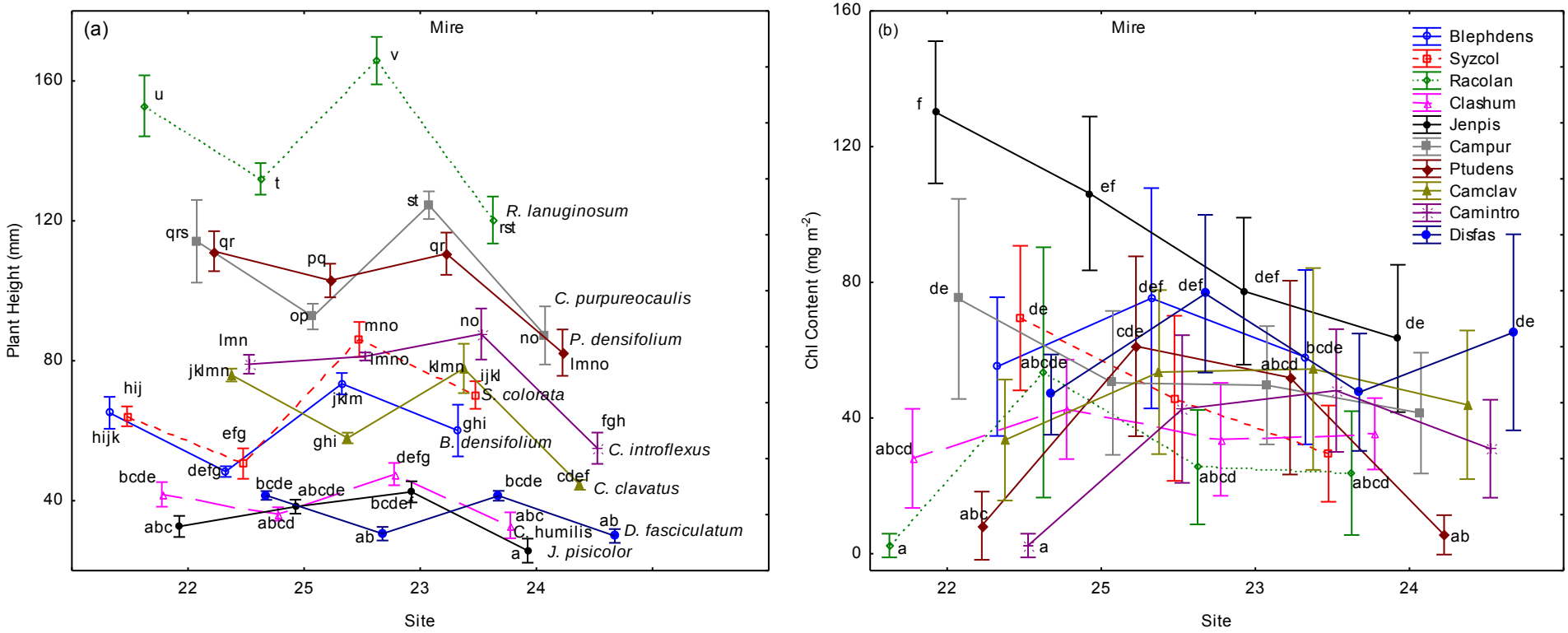


Figure B1 (a) and (b) Site x species effect for plant structural traits at four mire sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.

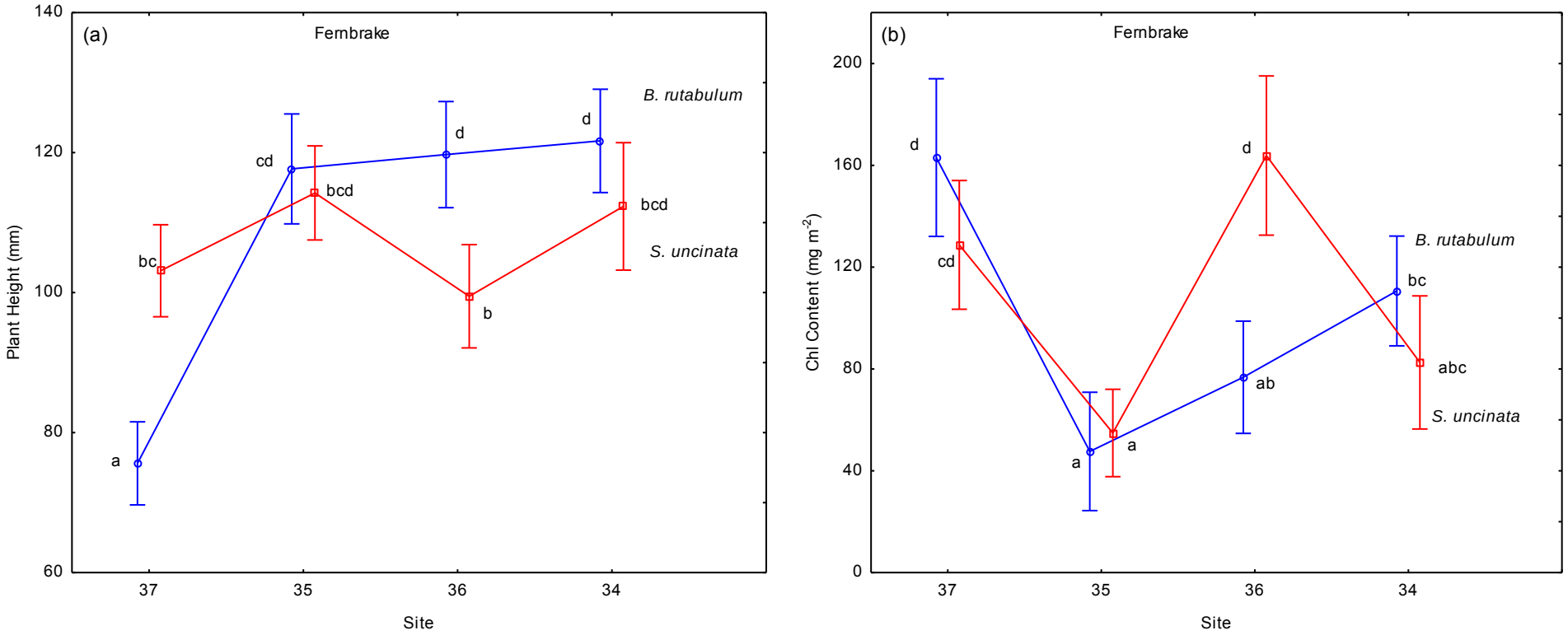


Figure B2 (a) and (b) Site x species effect for plant structural traits at four fernbrake sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.

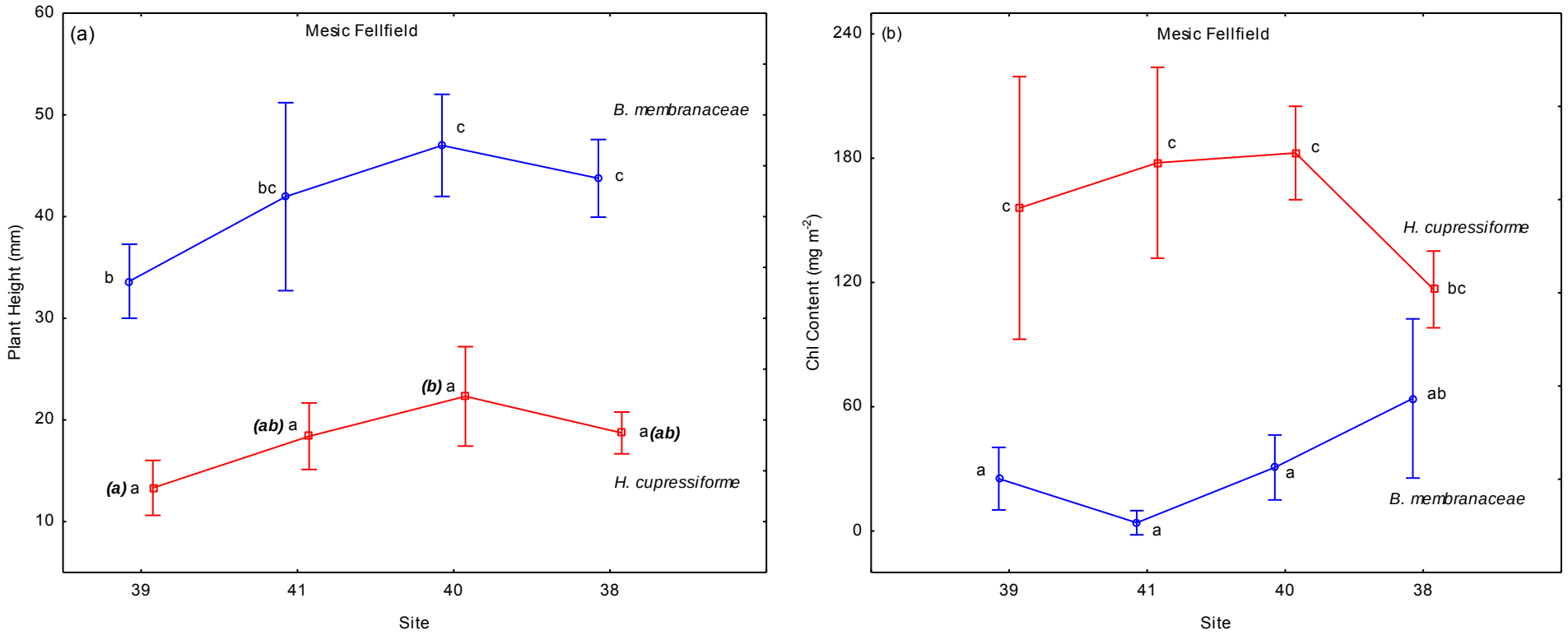


Figure B3 (a) and (b) Site x species effect for plant structural traits at fellfield sites at low altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.

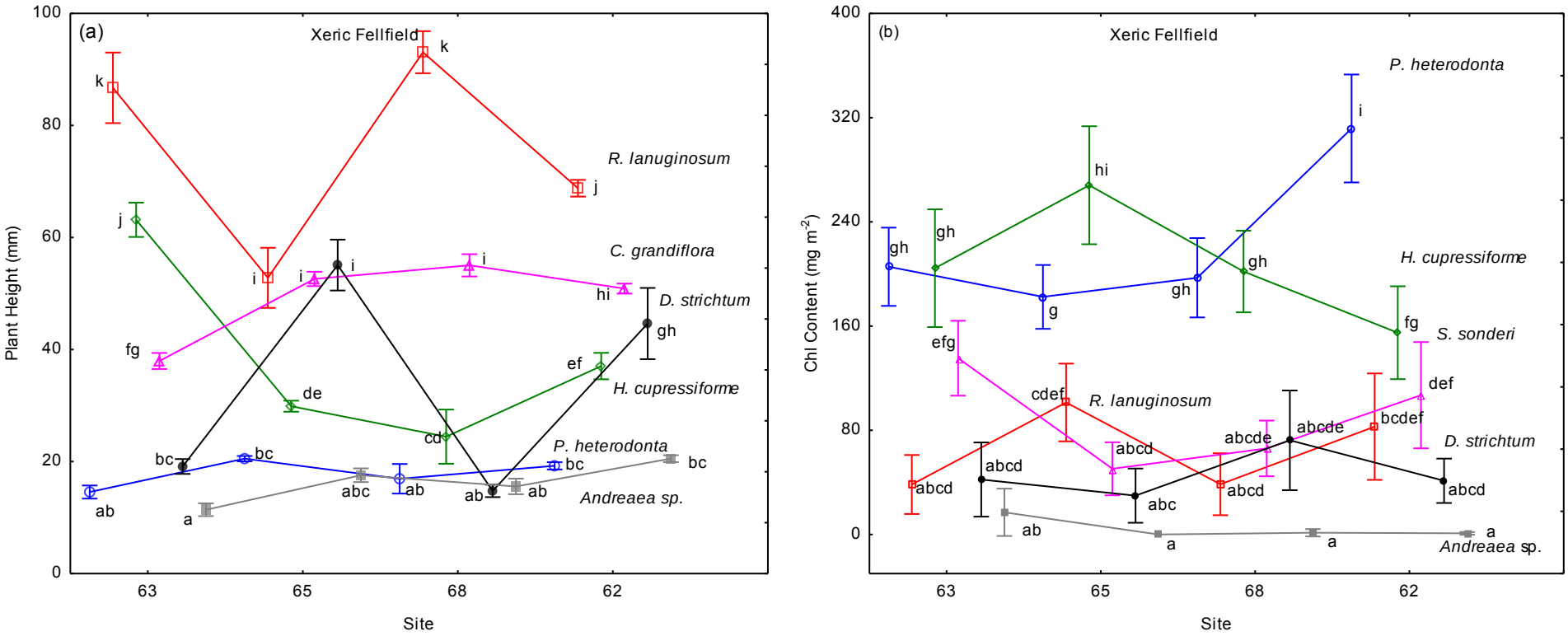


Figure B4 (a) and (b) Site x species effect for plant structural traits at four fellfield sites at high altitude. Points are species mean values at a particular site, a, b, c etc. indicate means that are significantly ($P \leq 0.05$) different from each other (from factorial ANOVA and the Tukeys HSD test). In cases where the differences between species means are so large that they obscure small, but still significant, between-site differences for a particular species, the results of a one-way anova, with site as predictor variable, for that species are shown as ***(a), (b), (c)***. Site numbers are as in Appendix 1 and Table 2.1.

Appendix Tables

Table A1. Mean (± standard error) values for plant height for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	116961417.00	4873392.37	925.59	**<0.001**
Error	10361859.24	5265.17		

Species	**n**	**PH (mm) Mean± std error**	**Ranking**
			VH ≥ 500; 500 > H ≥ 300; 300 > M ≥ 75; 75 > L ≥ 25 VL < 25
C. kerguelensis	25	11.88± 0.46^{a}	VL
H. peltatum	25	24.52± 2.75^{ab}	VL
G. poeppigeana	25	28.80± 1.53^{ab}	L
M. fontana	85	34.39± 1.48^{a}	L
C. moschata	100	35.62± 2.15^{a}	L
C. antarctica	100	50.93± 2.75^{a}	L
R. biternatus	100	90.94± 2.17^{bc}	M
J. scheuchzerioides	100	97.15± 1.88^{bcd}	M
C. plumosa	100	99.13± 3.21^{bcd}	M
S. procumbens	100	124.47± 4.99^{cde}	M
U. compacta	100	132.50± 2.92^{def}	M
R. acetosella	25	133.44± 5.25^{cdefgh}	M
P. antiscorbutica	8	138.75± 9.53^{abcdefghi}	M
P. annua	100	149.09± 5.33^{efg}	M
A. selago	100	149.58± 3.24^{efg}	M
A. stolonifera	100	167.67± 4.09^{fgh}	M
B. penna-marina	100	182.12± 2.85^{gh}	M
Ag. magellanica	100	199.94± 4.68^{h}	M
C. fontanum	85	200.61± 6.42^{h}	M
Ac. magellanica	100	262.96± 5.76^{i}	M
P. pratensis	100	301.69± 4.70^{j}	H
P. marionense	100	305.77± 6.03^{j}	H
P. cookii	100	453.38± 8.44^{k}	H
J. effusus	75	1099.76± 23.59^{l}	VH
P. nodosus	25	1339.00± 79.94^{n}	VH

Table A2. Mean (± standard error) values for leaf area for vascular species at low altitude. Column n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	2693765998.93	117120260.82	580.34	**<0.001**
Error	230067889.78	201813.94		

Species	**n**	**LA (mm^2) Mean± std error**	**Ranking**
			VH ≥ 5000; 5000 > H ≥ 1000; 1000 > M ≥ 100; 100 > L ≥ 5.0 VL < 5.0
S. procumbens	(12)	4.87± 0.26^{abc}	VL
C. moschata	(12)	13.65± 1.07^{abc}	L
A. selago	(12)	19.62± 0.72^{abc}	L
C. kerguelensis	(3)	20.69± 1.97^{abcde}	L
C. antarctica	(12)	23.35± 1.07^{abc}	L
M. fontana	(12)	25.69± 1.32^{abc}	L
J. scheuchzerioides	80	107.36± 4.16^{a}	M
G. poeppigeana	20	109.86± 6.16^{abc}	M
C. fontanum	80	133.33± 3.51^{a}	M
A. stolonifera	80	272.19± 7.90^{a}	M
R. biternatus	80	280.65± 10.30^{a}	M
R. acetosella	20	284.07± 91.22^{abcd}	M
P. annua	80	304.55± 15.21^{ab}	M
U. compacta	80	348.91± 9.73^{ab}	M
P. pratensis	80	542.43± 23.65^{bcde}	M
Ag. magellanica	80	614.76± 27.63^{cde}	M
C. plumosa	80	754.21± 26.99^{de}	M
P. nodosus	20	884.17± 91.22^{e}	M
B. penna-marina	80	1535.93± 44.43^{f}	H
Ac. magellanica	80	2015.35± 44.18^{g}	H
P. cookii	80	2485.96± 53.70^{h}	H
J. effusus	20	5196.81± 148.38^{i}	VH
P. marionense	45	6038.39± 273.80^{j}	VH
P. antiscorbutica	16	6724.94± 211.54^{k}	VH

Table A3. Mean (± standard error) values for leaf dry mass for vascular species at low altitude. Column n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	27010484.06	1174368.87	555.40	**<0.001**
Error	2410477.41	2114.45		

Species	**n**	**LDM (mg) Mean± std error**	**Ranking**
			VH ≥ 500; 500 > H ≥ 100; 100 > M ≥ 10; 10 > L ≥ 5.0 VL < 5.0
S. procumbens	(12)	0.11± 0.00^{ab}	VL
C. moschata	(12)	0.40± 0.03^{ab}	VL
C. antarctica	(12)	0.52± 0.01^{ab}	VL
M. fontana	(12)	0.76± 0.03^{ab}	VL
C. kerguelensis	(3)	0.88± 0.05^{abcd}	VL
A. selago	(12)	1.64± 0.10^{ab}	VL
A. stolonifera	80	5.98± 0.24^{a}	L
C. fontanum	80	6.86± 0.24^{a}	L
J. scheuchzerioides	80	7.07± 0.30^{a}	L
P. annua	80	7.60± 0.42^{ab}	L
G. poeppigeana	20	7.79± 0.56^{ab}	L
R. acetosella	20	10.37± 0.46^{ab}	M
R. biternatus	80	11.00± 0.44^{ab}	M
P. nodosus	20	12.19± 3.20^{ab}	M
P. pratensis	80	24.56± 1.55^{ab}	M
C. plumosa	80	24.86± 0.89^{ab}	M
U. compacta	80	30.73± 1.05^{ab}	M
Ag. magellanica	80	33.76± 1.61^{b}	M
Ac. magellanica	80	91.89± 2.75^{c}	M
B. penna-marina	80	120.28± 3.68^{d}	H
P. cookii	80	231.38± 6.49^{e}	H
P. marionense	45	393.97± 23.89^{f}	H
J. effusus	20	655.85± 34.13^{g}	VH
P. antiscorbutica	16	883.60± 40.16^{h}	VH

Table A4. Mean (± standard error) values for specific leaf area for vascular species at low altitude. Column n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	237031.66	10305.72	313.98	**<0.001**
Error	37418.27	32.82		

Species	**n**	**SLA (mm^2 mg^{-1}) Mean± std error**	**Ranking**
			VH ≥ 50; 50 > H ≥ 25; 25 > M ≥ 15; 15 > L ≥ 10 VL < 10
P. antiscorbutica	20	7.72± 0.23^{a}	VL
J. effusus	16	8.16± 0.27^{a}	VL
P. cookii	80	10.95± 0.13^{a}	L
U. compacta	80	11.73± 0.22^{a}	L
A. selago	(12)	12.19± 0.35^{abcd}	L
B. penna-marina	80	13.08± 0.25^{ab}	L
G. poeppigeana	20	14.60± 0.57^{abcd}	L
J. scheuchzerioides	80	15.57± 0.30^{bc}	M
P. marionense	45	16.57± 0.69^{bcd}	M
Ag. magellanica	80	18.65± 0.30^{cd}	M
C. fontanum	80	20.07± 0.47^{de}	M
Ac. magellanica	80	22.54± 0.38^{ef}	M
C. kerguelensis	(3)	23.51± 0.77^{abcdefghi}	M
P. pratensis	80	23.84± 0.48^{fg}	M
R. biternatus	80	26.26± 0.52^{gi}	H
R. acetosella	20	27.91± 0.97^{fghi}	H
C. plumosa	80	30.76± 0.5^{h}	H
C. moschata	(12)	33.98± 1.92^{hij}	H
M. fontana	(12)	34.23± 2.07^{hij}	H
P. annua	80	42.01± 1.17^{jk}	H
S. procumbens	(12)	43.85± 1.70^{kl}	H
C. antarctica	(12)	45.09± 1.01^{kl}	H
A. stolonifera	80	47.31± 1.04^{l}	H
P. nodosus	20	91.51± 5.08^{m}	VH

Table A5. Mean (± standard error) values for leaf dry matter content for vascular species at low altitude. Column n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	7078473.62	307759.72	256.03	**<0.001**
Error	1370310.92	1202.03		

Species	**n**	**LDMC (mg g^{-1}) Mean± std error**	**Ranking**
			VH ≥ 300; 300 > H ≥ 250; 250 > M ≥ 150; 150 > L ≥ 100 VL < 100
R. acetosella	20	77.17± 1.82^{a}	VL
C. moschata	(12)	89.96± 6.47^{ab}	VL
M. fontana	(12)	113.00± 5.90^{abc}	L
C. antarctica	(12)	117.35± 2.34^{abc}	L
P. antiscorbutica	16	119.18± 3.56^{abcd}	L
C. plumosa	80	131.13± 1.71^{bcd}	L
P. nodosus	20	142.62± 39.44^{cd}	L
C. fontanum	80	143.60± 3.22^{cd}	L
R. biternatus	80	148.09± 2.47^{cd}	L
C. kerguelensis	(3)	148.15± 6.08^{abcdefgh}	L
S. procumbens	(12)	169.39± 8.52^{def}	M
A. stolonifera	80	184.28± 2.72^{e}	M
P. marionense	45	196.81± 4.61^{efh}	M
P. annua	80	220.80± 3.29^{fghi}	M
B. penna-marina	80	224.92± 2.82^{gi}	M
A. selago	(12)	239.93± 2.71^{ghij}	M
J. effusus	20	251.22± 7.38^{ij}	H
G. poeppigeana	20	255.91± 6.65^{ij}	H
J. scheuchzerioides	80	259.19± 3.04^{j}	H
Ac. magellanica	80	260.23± 2.26^{j}	H
Ag. magellanica	80	263.14± 3.05^{j}	H
P. pratensis	80	268.46± 3.88^{j}	H
U. compacta	80	359.17± 3.44^{k}	VH
P. cookii	80	381.10± 3.23^{l}	VH

Table A6. Mean (± standard error) values for chlorophyll content for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	12533608.92	522233.71	33.64	**<0.001**
Error	24763708.42	15525.84		

Species	**n**	**Chl (mg m^{-2}) Mean± std error**	**Ranking**
			VH ≥ 600; 600 > H ≥ 500; 500 > M ≥ 350; 350 > L ≥ 200 VL < 200
P. nodosus	20	144.85± 15.25^{a}	VL
S. procumbens	80	294.84± 8.13^{b}	L
C. moschata	80	313.95± 13.56^{bd}	L
H. peltatum	20	318.90± 22.76^{bcd}	L
R. acetosella	20	365.95± 10.21^{bcdefgh}	M
C. kerguelensis	20	389.50± 38.47^{bcdefghı}	M
A. stolonifera	80	392.35± 10.31^{c}	M
C. antarctica	80	392.79± 14.01^{ce}	M
G. poeppigeana	20	406.75± 34.70^{bcdefghıj}	M
R. biternatus	80	408.40± 10.88^{cef}	M
A. selago	80	412.50± 13.10^{cef}	M
P. annua	80	414.84± 8.57^{cefg}	M
M. fontana	80	429.67± 17.90^{cefg}	M
C. fontanum	80	437.95± 10.63^{cefgh}	M
P. pratensis	80	440.05± 14.02^{cefgh}	M
P. antiscorbutica	20	445.95± 15.42^{cdefghıj}	M
Ag. magellanica	80	464.75± 8.66^{efghıj}	M
C. plumosa	80	475.57± 12.09^{fghıj}	M
P. marionense	80	485.58± 15.82^{ghıj}	M
U. compacta	80	509.62± 12.38^{hıj}	H
Ac. magellanica	80	518.86± 12.57^{ij}	H
P. cookii	80	522.53± 9.08^{ijk}	H
J. effusus	60	546.98± 15.30^{jkl}	H
B. penna-marina	80	591.54± 8.19^{kl}	H
J. scheuchzerioides	80	620.63± 32.89^{l}	VH

Table A7. Mean (± standard error) values for stomatal density (abaxial and adaxial) for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	1104819.06	58148.37	54.83	**<0.001**
Error	326615.20	1060.44		

Species	**n**	**SD (adaxial and abaxial) (stomas per mm^2) Mean± std error**	**Ranking**
			VH ≥ 200; 200 > H ≥ 150; 150 > M ≥ 100; 100 > L ≥ 50 VL < 50
G. poeppigeana	5	19.70± 2.23^{a}	VL
Ag. magellanica	19	61.57± 6.72^{ab}	L
P. marionense	20	79.54± 6.03^{abc}	L
U. compacta	20	95.95± 4.26^{bcd}	L
R. acetosella	5	96.10± 8.82^{bcdef}	L
J. scheuchzerioides	20	100.13± 5.10^{cde}	M
C. fontanum	20	101.32± 7.50^{cde}	M
M. fontana	20	106.99± 5.35^{cde}	M
C. moschata	20	110.43± 4.61^{cdeg}	M
C. plumosa	20	115.05± 5.94^{cdeg}	M
J. effusus	10	120.57± 11.18^{cdefg}	M
A. stolonifera	19	124.41± 8.86^{defg}	M
P. pratensis	20	127.88± 7.99^{defg}	M
C. antarctica	20	132.51± 4.49^{efg}	M
P. annua	20	157.58± 8.23^{f}	H
P. antiscorbutica	5	182.65± 9.12^{ghi}	H
B. penna-marina	20	198.02± 7.23^{h}	H
C. kerguelensis	5	237.56± 13.89^{hij}	VH
R. biternatus	20	253.68± 13.06^{ij}	VH
A. selago	20	260.10± 10.17^{j}	VH

Table A8. Mean (± standard error) values for leaf relative water content for vascular species at low altitude. Column n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	37356.94	1624.21	20.69	**<0.001**
Error	89485.15	78.50		

Species	**n**	**RWC (%) Mean± std error**	**Ranking**
			VH ≥ 90; 90 > H ≥ 85; 85 > M ≥ 80; 80 > L ≥ 75 VL < 75
J. effusus	20	71.27± 1.40^{a}	VL
P. marionense	45	72.81± 2.04^{a}	VL
P. pratensis	80	76.79± 1.64^{ac}	L
S. procumbens	(12)	77.03± 2.92^{abc}	L
U. compacta	80	77.17± 0.98^{ac}	L
C. kerguelensis	(3)	81.87± 1.93^{abcdefg}	M
C. plumosa	80	83.71± 0.69^{bd}	M
C. moschata	(12)	83.80± 1.08^{bcdefg}	M
Ag. magellanica	80	84.49± 0.96^{bdf}	M
C. fontanum	80	84.78± 1.10^{bdf}	M
P. antiscorbutica	16	84.87± 2.20^{bcdefg}	M
P. cookii	80	85.62± 0.44^{bdf}	H
A. stolonifera	80	86.66± 1.16^{bdef}	H
J. scheuchzerioides	80	86.82± 1.34^{bdef}	H
B. penna-marina	80	87.82± 0.47^{def}	H
G. poeppigeana	20	88.17± 2.27^{bdefg}	H
Ac. magellanica	80	88.19± 0.59^{efgh}	H
A. selago	(12)	89.07± 1.01^{bdefg}	H
R. biternatus	80	91.74± 0.75^{eg}	VH
R. acetosella	20	91.87± 1.48^{efg}	VH
M. fontana	(12)	92.02± 1.30^{defg}	VH
P. annua	80	93.24± 0.60^{g}	VH
C. antarctica	(12)	93.89± 1.93^{efg}	VH
P. nodosus	20	94.46± 3.36^{eg}	VH

Table A9. Mean (± standard error) values for stem specific density for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	34.78	1.51	8.75	**<0.001**
Error	132.94	0.17		

Species	**n**	**SSD (mg mm^{-3}) Mean± std error**	**Ranking**
			VH ≥ 1.00; 1.00> H ≥ 0.50 0.50> M ≥ 0.21 0.21 > L ≥ 0.12 VL < 0.12
P. nodosus	10	0.04± 0.00^{abcdef}	VL
R. biternatus	40	0.10± 0.00^{a}	VL
C. antarctica	40	0.12± 0.01^{a}	L
M. fontana	40	0.16± 0.01^{ab}	L
P. marionense	40	0.19± 0.01^{abc}	L
J. effusus	30	0.19± 0.01^{abcd}	L
P. antiscorbutica	3	0.20± 0.03^{abcdefgh}	L
P. annua	40	0.20± 0.01^{abc}	L
C. moschata	40	0.21± 0.02^{abc}	M
A. stolonifera	40	0.22± 0.01^{abcd}	M
C. fontanum	40	0.27± 0.01^{abcd}	M
R. acetosella	10	0.28± 0.01^{abcdefg}	M
Ag. magellanica	40	0.28± 0.01^{abcde}	M
U. compacta	40	0.31± 0.01^{abcde}	M
C. plumosa	40	0.33± 0.01^{abcde}	M
P. cookii	40	0.36± 0.02^{abcde}	M
A. selago	40	0.47± 0.02^{bcdefgh}	M
B. penna-marina	40	0.51± 0.03^{cdefgh}	H
C. kerguelensis	10	0.55± 0.03^{abcdefgh}	H
Ac. magellanica	40	0.56±0.02^{defgh}	H
J. scheuchzerioides	40	0.61±0.02^{efgh}	H
P. pratensis	40	0.71± 0.28^{fgh}	H
S. procumbens	40	0.74± 0.05^{gh}	H
G. poeppigeana	10	1.09± 0.14^{h}	VH

Table A10. Mean (± standard error) values for root:shoot mass ratio for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	7.91	0.88	19.27	**<0.001**
Error	9.12	0.05		

Species	**n**	**R:S (g g^{-1}) Mean± std error**	**Ranking**
			VH ≥ 0.60; 0.60 > H ≥ 0.40; 0.40 > M ≥ 0.20; 0.20 > L ≥ 0.10 VL < 0.10
C. moschata	3	0.04± 0.01^{abc}	VL
C. plumosa	26	0.06± 0.00^{a}	VL
U. compacta	20	0.13± 0.01^{a}	L
Ag. magellanica	30	0.17± 0.01^{a}	L
C. antarctica	20	0.20± 0.03^{ab}	M
P. annua	10	0.30± 0.06^{abc}	M
P. nodosus	1	0.32^{abcd}	M
A. stolonifera	40	0.41± 0.03^{bc}	H
M. fontana	40	0.54± 0.04^{cd}	H
R. biternatus	20	0.63± 0.10^{d}	VH

Table A11. Mean (± standard error) values for specific root length for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	408443.42	18565.61	26.43	**<0.001**
Error	77278.37	702.53		

Species	**n**	**SRL (m g^{-1}) Mean± std error**	**Ranking**
			VH ≥ 150; 150> H ≥ 80; 80> M ≥ 20; 20 > L ≥ 10 VL < 10
R. acetosella	2	10.23± 5.92^{abc}	L
J. effusus	4	10.77± 3.14^{ab}	L
P. marionense	6	11.32± 1.29^{a}	L
B. penna-marina	8	11.80± 1.07^{a}	L
C. plumosa	8	12.23± 1.43^{a}	L
U. compacta	8	12.88± 0.79^{a}	L
P. cookii	8	13.58± 1.46^{a}	L
C. kerguelensis	2	20.13± 3.60^{abc}	M
Ac. magellanica	8	20.96± 2.11^{a}	M
C. fontanum	2	21.91± 5.80^{abc}	M
Ag. magellanica	8	24.76± 0.43^{a}	M
P. pratensis	2	32.31± 0.10^{abc}	M
R. biternatus	8	32.91± 2.18^{ab}	M
G. poeppigeana	1	35.59^{abcd}	M
A. selago	8	46.03± 3.99^{abc}	M
P. nodosus	1	67.56^{abcde}	M
A. stolonifera	8	77.87± 8.38^{bc}	M
P. annua	8	93.22± 7.04^{cd}	H
J. scheuchzerioides	8	132.64± 18.22^{de}	H
C. antarctica	8	134.97± 9.68^{de}	H
S. procumbens	1	141.88^{abcde}	H
M. fontana	8	142.28± 22.45^{de}	H
C. moschata	8	177.53± 17.13^{e}	VH

Table A12. Mean (± standard error) values for root diameter for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	82.8910	3.7678	165.289	**<0.001**
Error	29.9528	0.0228		

Species	**n**	**RD (mm) Mean± std error**	**Ranking**
			VH ≥ 1.0; 1.0 > H ≥ 0.70; 0.70 > M ≥ 0.30; 0.30 > L ≥ 0.20 VL < 0.20
S. procumbens	20	0.13± 0.01^{a}	VL
C. moschata	80	0.24± 0.00^{ab}	L
J. scheuchzerioides	80	0.25± 0.01^{ab}	L
G. poeppigeana	10	0.26± 0.02^{abcde}	L
P. pratensis	20	0.28± 0.02^{abcde}	L
P. nodosus	10	0.30± 0.02^{abcde}	L
M. fontana	80	0.31± 0.01^{bd}	M
C. antarctica	80	0.32± 0.01^{bd}	M
A. selago	80	0.33± 0.01^{bcd}	M
C. kerguelensis	20	0.34± 0.02^{bcde}	M
P. annua	80	0.41± 0.01^{ce}	M
C. fontanum	20	0.43± 0.03^{cdef}	M
A. stolonifera	80	0.43± 0.01^{e}	M
Ac. magellanica	80	0.58± 0.01^{fg}	M
B. penna-marina	80	0.58± 0.02^{fg}	M
R. acetosella	17	0.71± 0.08^{gh}	H
U. compacta	80	0.75± 0.02^{h}	H
P. marionense	60	0.78± 0.03^{h}	H
R. biternatus	80	0.78± 0.02^{h}	H
Ag. magellanica	80	0.80± 0.02^{h}	H
P. cookii	80	0.82± 0.02^{h}	H
C. plumosa	80	0.84± 0.02^{h}	H
J. effusus	40	1.18± 0.06^{i}	VH

Table A13. Mean (± standard error) values for Fv/Fm for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.11	0.00	4.89	**<0.001**
Error	0.10	0.00		

Species	**n**	**Fv/Fm Mean± std error**	**Ranking**
			VH ≥ 80; 0.80> H ≥ 0.77; 0.77 > M ≥ 0.75; 0.75 > L ≥ 0.70 VL < 0.70
P. nodosus	1	0.662^{ab}	VL
H. peltatum	1	0.675^{ab}	VL
U. compacta	8	0.689± 0.02^{a}	VL
C. kerguelensis	1	0.726^{ab}	L
J. effusus	3	0.737± 0.01^{ab}	L
P. pratensis	4	0.738± 0.02^{ab}	L
P. antiscorbutica	1	0.738^{ab}	L
P. annua	4	0.751± 0.01^{ab}	M
A. selago	8	0.754± 0.02^{b}	M
S. procumbens	8	0.755± 0.01^{b}	M
G. poeppigeana	1	0.756^{ab}	M
C. antarctica	8	0.756± 0.02^{b}	M
A. stolonifera	8	0.759± 0.00^{b}	M
B. penna-marina	8	0.760± 0.01^{b}	M
J. scheuchzerioides	8	0.769± 0.01^{b}	H
M. fontana	4	0.774± 0.01^{b}	H
P. cookii	8	0.778± 0.00^{b}	H
C. fontanum	4	0.781± 0.01^{b}	H
Ag. magellanica	8	0.785± 0.00^{b}	H
R. biternatus	8	0.785± 0.01^{b}	H
C. moschata	8	0.786± 0.01^{b}	H
R. acetosella	1	0.788^{ab}	H
C. plumosa	8	0.789± 0.01^{b}	H
P. marionense	4	0.797± 0.01^{b}	VH
Ac. magellanica	8	0.808± 0.01^{b}	VH

Table A14. Mean (± standard error) values for ϕPSII for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.12	0.00	3.58	**<0.001**
Error	0.15	0.00		

Species	**n**	**ϕPSII Mean± std error**	**Ranking**
			VH ≥ 0.20; 0.20> H ≥ 0.16; 0.16 > M ≥ 0.10; 0.10 > L ≥ 0.08 VL < 0.08
H. peltatum	1	0.052^{abc}	VL
G. poeppigeana	1	0.062^{abc}	VL
P. nodosus	1	0.072^{abc}	VL
M. fontana	4	0.081± 0.02^{abc}	L
S. procumbens	8	0.093± 0.01^{a}	L
P. annua	4	0.096± 0.01^{abc}	L
P. cookii	8	0.100± 0.01^{ab}	M
B. penna-marina	8	0.104± 0.01^{ab}	M
U. compacta	8	0.105± 0.01^{abc}	M
P. marionense	4	0.106± 0.01^{abc}	M
C. kerguelensis	1	0.111^{abc}	M
C. antarctica	8	0.118± 0.01^{abc}	M
P. pratensis	4	0.127± 0.01^{abc}	M
J. scheuchzerioides	8	0.132± 0.01^{abc}	M
A. selago	8	0.132± 0.01^{abc}	M
C. moschata	8	0.139± 0.01^{abc}	M
R. biternatus	8	0.146± 0.01^{abc}	M
Ac. magellanica	8	0.150± 0.02^{abc}	M
J. effusus	3	0.160± 0.00^{abc}	H
C. fontanum	4	0.160± 0.01^{abc}	H
Ag. magellanica	8	0.165± 0.02^{bc}	H
A. stolonifera	8	0.166± 0.02^{bc}	H
P. antiscorbutica	1	0.166^{abc}	H
C. plumosa	8	0.173± 0.01^{c}	H
R. acetosella	1	0.211^{abc}	VH

Table A15. Mean (± standard error) values for 1-qL for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.35	0.01	2.79	**<0.001**
Error	0.57	0.01		
Species	**n**	**1-qL Mean± std error**		**Ranking**
				VH ≥ 0.82; 0.82 > H ≥ 0.78; 0.78 > M ≥ 0.74; 0.74 > L ≥ 0.70 VL < 0.70
Ag. magellanica	8	0.681± 0.04[a]		VL
A. stolonifera	8	0.699± 0.04[a]		VL
R. acetosella	1	0.703[abc]		L
C. plumosa	8	0.705± 0.02[ac]		L
J. effusus	3	0.720± 0.03[abc]		L
P. pratensis	4	0.731± 0.02[abc]		L
P. nodosus	1	0.746[abc]		M
R. biternatus	8	0.751± 0.01[abc]		M
P. antiscorbutica	1	0.752[abc]		M
C. moschata	8	0.755± 0.03[abc]		M
Ac. magellanica	8	0.757± 0.03[abc]		M
J. scheuchzerioides	8	0.762± 0.02[abc]		M
U. compacta	8	0.777± 0.02[abc]		M
C. fontanum	4	0.778± 0.05[abc]		M
B. penna-marina	8	0.798± 0.01[abc]		H
C. kerguelensis	1	0.801[abc]		H
C. antarctica	8	0.802± 0.01[abc]		H
P. cookii	8	0.804± 0.03[abc]		H
A. selago	8	0.811± 0.02[abc]		H
G. poeppigeana	1	0.814[abc]		H
P. marionense	4	0.821± 0.04[abc]		VH
S. procumbens	8	0.841± 0.02[b]		VH
P. annua	4	0.857± 0.05[abc]		VH
H. peltatum	1	0.859[abc]		VH
M. fontana	4	0.892± 0.02[bc]		VH

Table A16. Mean (± standard error) values for YNPQ/YNO for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	14.68	0.61	4.12	**<0.001**
Error	16.04	0.15		

Species	**n**	**YNPQ/YNO Mean± std error**	**Ranking**
			VH ≥ 2.50; 2.50> H ≥ 2.15; 2.15 > M ≥ 1.79; 1.79 > L ≥ 1.5 VL < 1.5
P. nodosus	1	1.408^{abc}	VL
P. antiscorbutica	1	1.414^{abc}	VL
P. annua	4	1.508± 0.25^{ab}	L
C. kerguelensis	1	1.542^{abc}	L
A. selago	8	1.562± 0.11^{a}	L
H. peltatum	1	1.729^{abc}	L
J. effusus	3	1.789± 0.11^{abc}	M
U. compacta	8	1.826± 0.13^{ab}	M
C. fontanum	4	1.846± 0.30^{abc}	M
G. poeppigeana	1	1.993^{abc}	M
A. stolonifera	8	2.017± 0.15^{abc}	M
B. penna-marina	8	2.077± 0.09^{abc}	M
P. marionense	4	2.100± 0.17^{abc}	M
J. scheuchzerioides	8	2.106± 0.07^{abc}	M
M. fontana	4	2.126± 0.33^{abc}	M
C. moschata	8	2.162± 0.14^{abc}	H
R. acetosella	1	2.247^{abc}	H
S. procumbens	8	2.250± 0.14^{abc}	H
C. antarctica	8	2.353± 0.14^{bc}	H
P. pratensis	4	2.364± 0.08^{abc}	H
C. plumosa	8	2.401± 0.17^{bc}	H
Ac. magellanica	8	2.501± 0.12^{bc}	VH
Ag. magellanica	8	2.570± 0.11^{c}	VH
P. cookii	8	2.603± 0.12^{c}	VH
R. biternatus	8	2.605± 0.17^{c}	VH

Table A17. Mean (± standard error) values for α for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.19	0.01	6.65	**<0.001**
Error	0.13	0.00		

Species	**n**	**α (electron photon^{-1}) Mean± std error**	**Ranking**
			VH ≥ 0.38; 0.38 > H ≥ 0.36 0.36 > M ≥ 0.30; 0.30 > L ≥ 0.20 VL < 0.20
P. nodosus	1	0.042^{a}	VL
P. pratensis	4	0.284± 0.02^{abc}	L
S. procumbens	8	0.292± 0.01^{b}	L
C. kerguelensis	1	0.297^{bcdef}	L
A. stolonifera	8	0.298± 0.01^{bc}	L
G. poeppigeana	1	0.300^{bcdef}	M
P. annua	4	0.302± 0.01^{bcdef}	M
U. compacta	8	0.305± 0.01^{bcdf}	M
R. acetosella	1	0.318^{bcdef}	M
A. selago	8	0.320± 0.01^{bcdef}	M
J. effusus	3	0.321± 0.01^{bcdef}	M
C. moschata	8	0.322± 0.00^{bcdef}	M
Ag. magellanica	8	0.325± 0.01^{bcdef}	M
J. scheuchzerioides	8	0.331± 0.01^{bcdef}	M
H. peltatum	1	0.333^{bcdef}	M
P. cookii	8	0.340± 0.02^{bcdef}	M
C. antarctica	8	0.345± 0.02^{bcdef}	M
B. penna-marina	8	0.350± 0.01^{bcdef}	M
P. antiscorbutica	1	0.352^{bcdef}	M
C. plumosa	8	0.360± 0.01^{cdef}	H
C. fontanum	4	0.362± 0.01^{bcdef}	H
R. biternatus	8	0.365± 0.01^{def}	H
M. fontana	4	0.373± 0.01^{bcdef}	H
Ac. magellanica	8	0.377± 0.01^{e}	H
P. marionense	4	0.394± 0.01^{ef}	VH

Table A18. Mean (± standard error) values for ETR_{max} for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	85550.44	3564.60	4.81	**<0.001**
Error	80066.89	741.36		

Species	**n**	**ETR_{max} (µmol electrons m^{-2} s^{-1}) Mean± std error**	**Ranking**
			VH ≥ 100; 100> H ≥ 70; 70 > M ≥ 50; 50 > L ≥ 30 VL < 30
P. nodosus	1	1.725^{abcd}	VL
H. peltatum	1	9.691^{abcd}	VL
G. poeppigeana	1	16.205^{abcd}	VL
P. marionense	4	34.679± 2.91^{ab}	L
M. fontana	4	38.209± 6.42^{abc}	L
S. procumbens	8	39.894± 6.33^{a}	L
P. pratensis	4	48.194± 8.53^{abcd}	L
C. kerguelensis	1	48.254^{abcd}	L
U. compacta	8	52.876± 7.08^{a}	M
P. cookii	8	53.683± 9.96^{a}	M
P. annua	4	58.086± 11.19^{abcd}	M
C. antarctica	8	58.300± 11.23^{abc}	M
B. penna-marina	8	60.561± 9.97^{abc}	M
A. stolonifera	8	63.854± 9.97^{abcd}	M
Ag. magellanica	8	67.656± 7.57^{abcd}	M
J. effusus	3	73.786± 7.33^{abcd}	H
J. scheuchzerioides	8	75.099± 8.86^{abcd}	H
C. moschata	8	79.890± 4.03^{abcd}	H
R. biternatus	8	87.664± 11.90^{abcd}	H
C. fontanum	4	88.916± 7.40^{abcd}	H
A. selago	8	105.664± 10.43^{bcd}	VH
Ac. magellanica	8	109.117± 17.50^{cd}	VH
C. plumosa	8	111.843± 11.67^{d}	VH
R. acetosella	1	121.739^{abcd}	VH
P. antiscorbutica	1	136.792^{abcd}	VH

Table A19. Mean (± standard error) values for PAR_{opt} for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	15713502.63	654729.28	1.91	**0.013**
Error	37028829.10	342859.53		

Species	**n**	**PAR_{opt} (µmol photons m^{-2} s^{-1}) Mean± std error**	**Ranking**
			VH ≥ 1600; 1600> H ≥ 1300; 1300 > M ≥ 1000; 1000 > L ≥ 250 VL < 250
P. nodosus	1	74.546^{ab}	VL
H. peltatum	1	422.224^{ab}	L
G. poeppigeana	1	689.285^{ab}	L
P. marionense	4	858.143± 98.42^{a}	L
C. kerguelensis	1	917.255^{ab}	L
P. pratensis	4	951.715± 170.30^{a}	L
A. stolonifera	8	1009.555± 153.61^{a}	M
S. procumbens	8	1012.170± 118.05^{a}	M
Ag. magellanica	8	1037.904± 107.97^{a}	M
J. effusus	3	1150.042± 148.36^{ab}	M
M. fontana	4	1207.559± 285.75^{ab}	M
R. acetosella	1	1246.402^{ab}	M
C. antarctica	8	1260.592± 268.42^{a}	M
P. cookii	8	1301.901± 264.48^{a}	H
C. moschata	8	1376.967± 101.80^{a}	H
B. penna-marina	8	1380.086± 205.21^{a}	H
U. compacta	8	1408.352± 280.96^{a}	H
C. fontanum	4	1435.902± 249.49^{ab}	H
R. biternatus	8	1497.160± 236.24^{a}	H
J. scheuchzerioides	8	1582.530± 300.21^{a}	H
C. plumosa	8	1771.280± 270.32^{a}	VH
Ac. magellanica	8	1792.186± 188.86^{a}	VH
P. annua	4	1807.667± 392.68^{ab}	VH
P. antiscorbutica	1	1949.332^{ab}	VH
A. selago	8	1987.245± 104.86^{ab}	VH

Table A20. Mean (± standard error) values for I_k for vascular species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	684213.00	28508.87	3.42	**<0.001**
Error	899534.93	8329.03		

Species	**n**	**I_k (µmol photons m^{-2} s^{-1}) Mean± std error**	**Ranking**
			VH ≥ 350; 350> H ≥ 250; 250 > M ≥ 150; 150 > L ≥ 100 VL < 100
H. peltatum	1	29.132^{abc}	VL
P. nodosus	1	41.474^{abc}	VL
G. poeppigeana	1	53.939^{abc}	VL
P. marionense	4	88.678± 9.62^{ab}	VL
M. fontana	4	101.323± 14.47^{abc}	L
S. procumbens	8	134.706± 19.20^{a}	L
C. kerguelensis	1	162.583^{abc}	M
P. cookii	8	164.156± 36.02^{ab}	M
P. pratensis	4	167.831± 22.71^{abc}	M
B. penna-marina	8	170.553± 25.89^{abc}	M
U. compacta	8	175.484± 24.59^{abc}	M
C. antarctica	8	178.237± 36.78^{abc}	M
P. annua	4	196.184± 40.52^{abc}	M
Ag. magellanica	8	216.936± 32.95^{abc}	M
A. stolonifera	8	219.425± 33.59^{abc}	M
J. effusus	3	231.420± 29.04^{abc}	M
J. scheuchzerioides	8	231.820± 32.26^{abc}	M
C. fontanum	4	245.267± 19.32^{abc}	M
C. moschata	8	248.667± 12.51^{abc}	M
R. biternatus	8	251.622± 42.95^{abc}	H
Ac. magellanica	8	301.300± 56.15^{abc}	H
C. plumosa	8	317.473± 41.15^{bc}	H
A. selago	8	340.149± 31.13^{c}	H
R. acetosella	1	382.373^{abc}	VH
P. antiscorbutica	1	388.371^{abc}	VH

Table A21. Mean (± standard error) values for plant height for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	p
Species	4639879.54	1159969.89	672.87	**<0.001**
Error	853331.01	1723.90		
Species	**n**	**PH (mm) Mean± std error**		
B. penna-marina	100	72.17± 2.96[a]		
U. compacta	100	109.02± 2.79[b]		
Ag. magellanica	100	139.15± 4.66[c]		
A. selago	100	172.16± 4.71[d]		
P. cookii	100	349.35± 5.07[e]		

Table A22. Mean (± standard error) values for leaf area for vascular species at high altitude. Column headed n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	p
Species	94093049.52	23523262.38	554.90	**<0.001**
Error	13862039.41	42391.56		
Species	**n**	**LA (mm^2) Mean± std error**		
A. selago	(12)	16.12± 0.50[a]		
U. compacta	80	254.16± 8.10[b]		
Ag. magellanica	80	343.68± 16.71[c]		
B. penna-marina	80	543.57± 23.10[d]		
P. cookii	80	1574.20± 36.26[e]		

Table A23. Mean (± standard error) values for leaf dry mass for vascular species at high altitude. Column headed n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**p**
Species	932538	233134.4	561.7764	**<0.001**
Error	135703	415.0		
Species	**n**	**LDM (mg) Mean± std error**		
A. selago	(12)	1.44± 0.07[a]		
Ag. magellanica	80	17.83± 0.93[a]		
U. compacta	80	20.89± 0.77[a]		
B. penna-marina	80	39.74± 2.01[b]		
P. cookii	80	146.93± 3.99[c]		

Table A24. Mean (± standard error) values for specific leaf area for vascular species at high altitude. Column headed n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**p**
Species	3804.60	951.15	171.38	**<0.001**
Error	1814.82	5.55		
Species	**n**	**SLA (mm^2 mg^{-1}) Mean± std error**		
P. cookii	80	10.90± 0.15[a]		
A. selago	(12)	11.31± 0.32[ab]		
U. compacta	80	12.49± 0.20[b]		
B. penna- marina	80	14.30± 0.30[c]		
Ag. magellanica	80	19.90± 0.36[d]		

Table A25. Mean (± standard error) values for leaf dry matter content for vascular species at high altitude. Column headed n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**p**
Species	963432.45	240858.11	413.86	**<0.001**
Error	190307.76	581.98		
Species	**n**	**LDMC (mg g^{-1}) Mean± std error**		
B. penna-marina	80	234.45± 2.74^{a}		
A. selago	(12)	253.65± 3.80^{ab}		
Ag. magellanica	80	269.24± 2.67^{b}		
U. compacta	80	326.58± 2.85^{c}		
P. cookii	80	375.97± 2.66^{d}		

Table A26. Mean (± standard error) values for chlorophyll content for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	1119830.17	279957.54	33.65	**<0.001**
Error	3286115.58	8319.28		
Species	**n**	**Chl (mg m^{-2}) Mean± std error**		
Ag. magellanica	80	433.45± 7.81^{a}		
U. compacta	80	439.22± 7.59^{a}		
A. selago	80	481.73± 14.37^{b}		
B. penna-marina	80	516.71± 11.38^{b}		
P. cookii	80	576.26± 8.07^{c}		

Table A27. Mean (± standard error) values for leaf relative water content for vascular species at high altitude. Column headed n gives the number measurements. Where n is in brackets, the leaves were small so each measurement was made on 20 leaves and the measurement value taken as being the mean for the 20 leaves. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**p**
Species	1748.01	437.00	4.05	**0.003**
Error	35247.13	107.79		
Species	**n**	**LRWC (%) Mean± std error**		
U. compacta	80	78.49± 1.65^{a}		
B. penna-marina	80	80.75± 0.46^{ab}		
Ag. magellanica	80	81.19± 2.40^{ab}		
A. selago	(12)	81.27± 1.25^{ab}		
P. cookii	80	84.99± 0.98^{b}		

Table A28. Mean (± standard error) values for stem specific density for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**p**
Species	2.60	0.65	23.70	**<0.001**
Error	5.35	0.03		
Species	**n**	**SSD (mg mm^{-3}) Mean± std error**		
U. compacta	40	0.30± 0.01^{a}		
Ag. magellanica	40	0.33± 0.02^{ab}		
P. cookii	40	0.42± 0.01^{b}		
A. selago	40	0.55± 0.03^{c}		
B. penna-marina	40	0.59± 0.05^{c}		

Table A29. Mean (± standard error) values for specific root length for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	p
Species	10565.56	2641.39	36.80	**<0.001**
Error	2512.38	71.78		
Species	**n**	**SRL (m g^{-1}) Mean± std error**		
B. penna-marina	8	12.29± 1.93^{a}		
P. cookii	8	17.83± 1.49^{a}		
U. compacta	8	20.98± 1.08^{a}		
Ag. magellanica	8	35.18± 1.94^{b}		
A. selago	8	57.54± 5.83^{c}		

Table A30. Mean (± standard error) values for root diameter for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	p
Species	5.45	1.36	68.01	**<0.001**
Error	7.92	0.02		
Species	**n**	**RD (mm) Mean± std error**		
A. selago	80	0.33± 0.01^{a}		
B. penna-marina	80	0.59± 0.02^{b}		
U. compacta	80	0.62± 0.01^{b}		
Ag. magellanica	80	0.63± 0.01^{b}		
P. cookii	80	0.63± 0.02^{b}		

Table A31. Mean (± standard error) values for Fv/Fm for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	0.06	0.01	12.85	**<0.001**
Error	0.04	0.00		
Species	**n**	**Fv/Fm Mean± std error**		
U. compacta	8	0.674± 0.02[a]		
B. penna-marina	8	0.740± 0.01[b]		
A. selago	8	0.755± 0.02[b]		
Ag. magellanica	8	0.774± 0.00[b]		
P. cookii	8	0.775± 0.01[b]		

Table A32. Mean (± standard error) values for ϕPSII for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	0.02	0.01	5.87	**<0.001**
Error	0.03	0.00		
Species	**n**	**ϕPSII Mean± std error**		
U. compacta	8	0.095± 0.01[a]		
P. cookii	8	0.113± 0.01[ab]		
B. penna-marina	8	0.116± 0.01[ab]		
A. selago	8	0.142± 0.01[bc]		
Ag. magellanica	8	0.160± 0.01[c]		

Table A33. Mean (± standard error) values for 1-qL for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	0.02	0.00	0.05	0.996
Error	2.89	0.08		
Species	**n**	**1-qL Mean± std error**		
P. cookii	8	0.456± 0.10[a]		
U. compacta	8	0.469± 0.10[a]		
A. selago	8	0.484± 0.12[a]		
Ag. magellanica	8	0.495± 0.07[a]		
B. penna-marina	8	0.513± 0.11[a]		

Table A34. Mean (± standard error) values for YNPQ/YNO for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	7.49	1.87	14.31	**<0.001**
Error	4.58	0.13		
Species	**n**	**YNPQ/YNO Mean± std error**		
A. selago	8	1.552± 0.18[a]		
B. penna-marina	8	1.929± 0.11[a]		
U. compacta	8	1.931± 0.08[a]		
P. cookii	8	2.613± 0.08[b]		
Ag. magellanica	8	2.667± 0.16[b]		

Table A35. Mean (± standard error) values for α for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	0.00	0.00	0.99	0.426
Error	0.04	0.00		
Species	**n**	**α (electron photon^{-1}) Mean± std error**		
U. compacta	8	0.303± 0.02^{a}		
P. cookii	8	0.315± 0.00^{a}		
A. selago	8	0.316± 0.01^{a}		
Ag. magellanica	8	0.317± 0.01^{a}		
B. penna-marina	8	0.336± 0.02^{a}		

Table A36. Mean (± standard error) values for ETR_{max} for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	30196.48	7549.12	13.17	**<0.001**
Error	20056.58	573.05		
Species	**n**	**ETR_{max} (µmol electrons m^{-2} s^{-1}) Mean± std error**		
U. compacta	8	50.782± 3.53^{a}		
B. penna-marina	8	62.168± 6.44^{a}		
Ag. magellanica	8	67.598± 10.28^{a}		
P. cookii	8	67.712± 7.76^{a}		
A. selago	8	129.005± 11.76^{b}		

Table A37. Mean (± standard error) values for PAR_{opt} for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	4639122.84	1159780.71	8.86	**0.001**
Error	4579910.98	130854.60		
Species	**n**	**PAR_{opt} (µmol photons m^{-2} s^{-1}) Mean± std error**		
Ag. magellanica	8	1013.524± 106.02[a]		
U. compacta	8	1290.344± 149.30[a]		
B. penna-marina	8	1297.346± 124.93[a]		
P. cookii	8	1529.699± 175.74[ab]		
A. selago	8	2029.516± 1045.33[b]		

Table A38. Mean (± standard error) values for I_k for vascular species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	503693.89	125923.47	13.74	**<0.001**
Error	320751.30	9164.32		
Species	**n**	**I_k (µmol photons $m^{-2}s^{-1}$) Mean± std error**		
U. compacta	8	170.233± 12.82[a]		
B. penna-marina	8	188.591± 20.88[a]		
P. cookii	8	215.664± 25.06[a]		
Ag. magellanica	8	217.144± 34.87[a]		
A. selago	8	474.999± 57.30[b]		

Table A39. Mean (± standard error) values for plant height for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**p**
Species	2198085.96	137380.37	374.45	**<0.001**
Error	617465.81	366.88		

Species	**n**	**PH (mm) Mean± std error**	**Ranking**
			VH ≥ 120 **120 > H ≥ 80** **80 > M ≥ 50** **50 > L ≥ 20** **VL < 20**
H. cupressiforme	100	18.19± 0.87^{a}	VL
M. berteroana	100	18.62± 0.83^{a}	VL
J. pisicolor	100	34.79± 0.94^{b}	L
D. fasciculatum	100	35.84± 0.69^{b}	L
C. humilis	100	39.64± 0.94^{b}	L
B. membranaceae	100	41.59± 1.49^{b}	L
B. densifolium	100	61.73± 1.44^{c}	M
C. clavatus	100	64.04± 1.65^{c}	M
S. colorata	100	67.75± 1.61^{cd}	M
C. introflexus	100	75.72± 1.65^{d}	M
B. integrifolia	100	100.13± 3.83^{e}	H
P. densifolium	100	101.80± 1.82^{e}	H
D. billardierei	100	104.17± 2.55^{e}	H
C. purpureocaulis	100	104.63± 2.39^{e}	H
S. uncinata	100	107.29± 1.90^{e}	H
B. rutabulum	100	108.67± 2.58^{e}	H
R. lanuginosum	100	142.73± 2.42^{f}	VH

Table A40. Mean (± standard error) values for chlorophyll content for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	2794357.39	174647.34	59.51	**<0.001**
Error	3941495.31	2934.84		

Species	**n**	**Chl (mg m^{-2}) Mean± std error**	**Ranking**
			VH ≥ 150; 150 > H ≥ 80; 80> M ≥ 55; 55 > L ≥ 30 VL < 30
B. integrifolia	80	24.53± 3.97^{a}	VL
D. billardierei	80	24.90± 4.13^{a}	VL
R. lanuginosum	80	26.28± 5.61^{a}	VL
B. membranaceae	80	31.00± 5.75^{ab}	L
C. introflexus	80	31.03± 4.24^{ab}	L
P. densifolium	80	31.71± 5.54^{ab}	L
C. humilis	80	34.93± 3.40^{ab}	L
S. colorata	80	44.76± 5.13^{ab}	L
C. clavatus	80	46.35± 5.66^{ab}	L
B. densifolium	80	53.31± 6.08^{ab}	L
C. purpureocaulis	80	54.14± 5.35^{ab}	L
D. fasciculatum	80	59.10± 5.19^{b}	M
J. pisicolor	80	94.30± 5.87^{c}	H
B. rutabulum	80	99.51± 7.55^{c}	H
S. uncinata	80	107.50± 7.61^{c}	H
H. cupressiforme	80	158.24± 10.23^{d}	VH
M. berteroana	80	175.76± 7.83^{d}	VH

Table A41. Mean (± standard error) values for Fv/Fm for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.28	0.02	5.85	**<0.001**
Error	0.36	0.00		

Species	**n**	**Fv/Fm Mean± std error**	**Ranking**
			VH ≥ 0.75; 0.75> H ≥ 0.69; 0.69> M ≥ 0.60; 0.60 > L ≥ 0.50 VL < 0.50
D. fasciculatum	8	0.584± 0.02^{a}	L
B. membranaceae	8	0.595± 0.03^{ab}	L
B. rutabulum	8	0.615± 0.02^{abc}	M
S. uncinata	8	0.615± 0.03^{abc}	M
P. densifolium	8	0.616± 0.03^{abc}	M
C. introflexus	8	0.632± 0.02^{abc}	M
C. humilis	8	0.645± 0.03^{abc}	M
S. colorata	8	0.669± 0.02^{abc}	M
J. pisicolor	8	0.669± 0.02^{abc}	M
D. billardierei	8	0.670± 0.01^{abc}	M
H. cupressiforme	8	0.672± 0.02^{abc}	M
R. lanuginosum	8	0.673± 0.01^{abc}	M
B. integrifolia	8	0.679± 0.02^{abc}	M
C. purpureocaulis	8	0.687± 0.01^{bcd}	H
C. clavatus	8	0.695± 0.01^{cd}	H
B. densifolium	8	0.700± 0.01^{cd}	H
M. berteroana	8	0.777± 0.00^{d}	VH

Table A42. Mean (± standard error) values for ϕPSII for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.12	0.01	7.86	**<0.001**
Error	0.12	0.00		

Species	**n**	**ϕPSII Mean± std error**	**Ranking**
			VH ≥ 0.160; 0.160> H ≥ 0.140; 0.140 > M ≥ 0.090; 0.090> L ≥ 0.084 VL < 0.084
C. humilis	8	0.076± 0.01^{a}	VL
J. pisicolor	8	0.083± 0.01^{ab}	VL
H. cupressiforme	8	0.084± 0.01^{ab}	L
D. fasciculatum	8	0.087± 0.02^{abc}	L
S. colorata	8	0.088± 0.01^{abc}	L
B. rutabulum	8	0.090± 0.01^{abc}	M
B. densifolium	8	0.096± 0.01^{abc}	M
S. uncinata	8	0.096± 0.01^{abc}	M
B. membranaceae	8	0.099± 0.01^{abc}	M
P. densifolium	8	0.104± 0.01^{abc}	M
C. introflexus	8	0.120± 0.01^{abc}	M
B. integrifolia	8	0.135± 0.01^{bc}	M
D. billardierei	8	0.137± 0.02^{bcd}	M
C. clavatus	8	0.140± 0.01^{cd}	H
C. purpureocaulis	8	0.140± 0.01^{cd}	H
R. lanuginosum	8	0.141±0.01^{cd}	H
M. berteroana	8	0.191±0.01^{d}	VH

Table A43. Mean (± standard error) values for 1-qL for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	1.16	0.07	9.47	**<0.001**
Error	0.91	0.01		

Species	**n**	**1-qL Mean± std error**	**Ranking**
			VH ≥ 0.80; 0.80> H ≥ 0.75; 0.75 > M ≥ 0.65; 0.65 > L ≥ 0.60 VL < 0.60
R. lanuginosum	8	0.544± 0.06^{a}	VL
C. purpureocaulis	8	0.573± 0.03^{a}	VL
C. introflexus	8	0.603± 0.03^{ab}	L
B. membranaceae	8	0.621± 0.04^{abc}	L
P. densifolium	8	0.628± 0.03^{abc}	L
C. clavatus	8	0.643± 0.02^{abcd}	L
B. integrifolia	8	0.660± 0.03^{abcde}	M
D. billardierei	8	0.675± 0.03^{abcdef}	M
S. uncinata	8	0.684± 0.03^{abcdef}	M
B. rutabulum	8	0.689± 0.03^{abcdef}	M
D. fasciculatum	8	0.752± 0.03^{bcdefg}	H
M. berteroana	8	0.759± 0.02^{cdefg}	H
C. humilis	8	0.796± 0.02^{defg}	H
H. cupressiforme	8	0.808± 0.03^{efg}	VH
J. pisicolor	8	0.813± 0.01^{efg}	VH
S. colorata	8	0.825± 0.03^{fg}	VH
B. densifolium	8	0.849± 0.01^{g}	VH

Table A44. Mean (± standard error) values for YNPQ/YNO for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	37.08	2.32	3.05	**<0.001**
Error	90.36	0.76		

Species	**n**	**YNPQ/YNO Mean± std error**	**Ranking**
			VH ≥ 3.40; 3.40> H ≥ 2.80; 2.80 > M ≥ 2.0; 2.0> L ≥ 1.40 VL < 1.40
M. berteroana	8	1.309± 0.21^{a}	VL
J. pisicolor	8	1.854± 0.19^{ab}	L
B. densifolium	8	1.920± 0.25^{abc}	L
S. colorata	8	2.220± 0.29^{abc}	M
D. fasciculatum	8	2.323± 0.38^{abc}	M
D. billardierei	8	2.544± 0.30^{abc}	M
B. integrifolia	8	2.578± 0.20^{abc}	M
C. humilis	8	2.584± 0.45^{abc}	M
C. introflexus	8	2.618± 0.36^{abc}	M
H. cupressiforme	8	2.642± 0.28^{abc}	M
S. uncinata	8	2.655± 0.36^{abc}	M
C. clavatus	8	2.858± 0.31^{bc}	H
B. rutabulum	8	3.029± 0.39^{bc}	H
B. membranaceae	8	3.039± 0.30^{bc}	H
C. purpureocaulis	8	3.120± 0.20^{bc}	H
P. densifolium	8	3.260± 0.43^{bc}	H
R. lanuginosum	8	3.403± 0.17^{c}	VH

Table A45. Mean (± standard error) values for α for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	0.12	0.01	3.65	**<0.001**
Error	0.24	0.00		

Species	**n**	**α (electron photon^{-1}) Mean± std error**	**Ranking**
			VH ≥ 0.28; 0.28> H ≥ 0.26; 0.26 > M ≥ 0.20; 0.20 > L ≥ 0.15 VL < 0.15
D. fasciculatum	8	0.187± 0.01^{a}	L
B. rutabulum	8	0.189± 0.01^{ab}	L
B. membranaceae	8	0.192± 0.02^{abc}	L
S. uncinata	8	0.205± 0.02^{abcd}	M
C. introflexus	8	0.209± 0.01^{abcd}	M
P. densifolium	8	0.211± 0.02^{abcd}	M
R. lanuginosum	8	0.221± 0.01^{abcd}	M
C. humilis	8	0.234± 0.02^{abcd}	M
B. integrifolia	8	0.239± 0.01^{abcd}	M
D. billardierei	8	0.244± 0.01^{abcd}	M
J. pisicolor	8	0.247± 0.02^{abcd}	M
H. cupressiforme	8	0.247± 0.02^{abcd}	M
S. colorata	8	0.260± 0.01^{abcd}	H
C. clavatus	8	0.264± 0.02^{abcd}	H
C. purpureocaulis	8	0.267± 0.01^{abc}	H
M. berteroana	8	0.271± 0.01^{cd}	H
B. densifolium	8	0.279± 0.01^{d}	H

Table A46. Mean (± standard error) values for ETR_{max} for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	28954.10	1809.63	12.47	**<0.001**
Error	17270.79	145.13		

Species	**n**	**ETR_{max} (µmol electrons m^{-2} s^{-1}) Mean± std error**	**Ranking**
			VH ≥ 60; 60> H ≥ 48; 48 > M ≥ 30; 30> L ≥ 20 VL < 20
D. fasciculatum	8	13.790± 2.32^{a}	VL
J. pisicolor	8	15.918± 1.74^{a}	VL
C. humilis	8	20.717± 1.50^{ab}	L
H. cupressiforme	8	22.483± 3.11^{abc}	L
B. rutabulum	8	24.470± 2.03^{abc}	L
B. densifolium	8	25.299 2.36^{abc}	L
S. uncinata	8	25.725± 3.99^{abc}	L
S. colorata	8	28.044± 1.53^{abc}	L
P. densifolium	8	33.395± 3.35^{abcd}	M
C. introflexus	8	37.452± 6.98^{bcd}	M
B. membranaceae	8	37.819± 3.97^{bcd}	M
D. billardierei	8	42.391± 5.77^{cd}	M
C. purpureocaulis	8	49.549± 6.18^{de}	H
R. lanuginosum	8	50.456± 4.42^{de}	H
C. clavatus	8	53.319± 4.75^{de}	H
B. integrifolia	8	53.745± 3.52^{de}	H
M. berteroana	8	64.962± 7.65^{e}	VH

Table A47. Mean (± standard error) values for PAR_{opt} for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	3679296.05	229956.00	5.62	**<0.001**
Error	4872334.94	40943.99		
Species	**n**	**PAR_{opt} (µmol photons m^{-2} s^{-1}) Mean± std error**		**Ranking**
				VH ≥ 900; 900> H ≥ 750; 750 > M ≥ 580; 580 > L ≥ 500 VL < 500
J. pisicolor	8	417.434± 43.50^{a}		VL
S. uncinata	8	461.395± 57.21^{a}		VL
D. fasciculatum	8	461.912± 83.16^{a}		VL
H. cupressiforme	8	537.944± 71.97^{ab}		L
C. humilis	8	563.084± 51.39^{abc}		L
B. rutabulum	8	571.324± 39.69^{abc}		L
B. densifolium	8	586.303± 60.36^{abcd}		M
C. introflexus	8	671.708± 116.53^{abcd}		M
P. densifolium	8	673.340± 64.46^{abcd}		M
S. colorata	8	697.780± 38.21^{abcd}		M
D. billardierei	8	746.176± 90.81^{abcd}		M
R. lanuginosum	8	822.376± 52.39^{bcd}		H
C. purpureocaulis	8	848.253± 75.87^{bcd}		H
B. membranaceae	8	852.863± 62.64^{bcd}		H
M. berteroana	8	874.243± 113.97^{bcd}		H
C. clavatus	8	913.175± 75.47^{cd}		VH
B. integrifolia	8	937.206± 57.73^{d}		VH

Table A48. Mean (± standard error) values for I_k for bryophyte species at low altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05). Species means are ranked as very high (VH), high (H), moderate (M), low (L) or very low (VL), according to the values shown at the top of the Ranking column.

Effect	**SS**	**MS**	**F**	**P**
species	447786.61	27986.66	10.61	**<0.001**
Error	313812.64	2637.08		

Species	**n**	**I_k (µmol photons m^{-2} s^{-1}) Mean± std error**	**Ranking**
			VH ≥ 220; 220> H ≥ 200; 200 > M ≥ 100; 100 > L ≥ 80 VL < 80
J. pisicolor	8	66.367± 8.20^{s}	VL
D. fasciculatum	8	73.021± 8.71^{a}	VL
C. humilis	8	91.170± 7.92^{ab}	L
H. cupressiforme	8	91.430± 10.75^{ab}	L
B. densifolium	8	91.618± 8.52^{ab}	L
S. colorata	8	108.625± 6.67^{abc}	M
S. uncinata	8	125.217± 15.09^{abcd}	M
B. rutabulum	8	134.202± 14.44^{abcd}	M
P. densifolium	8	165.421± 13.82^{bcde}	M
C. introflexus	8	174.269± 26.21^{bcde}	M
D. billardierei	8	176.031± 26.29^{bcde}	M
C. purpureocaulis	8	188.280± 25.44^{cde}	M
C. clavatus	8	204.248± 17.57^{de}	H
B. membranaceae	8	204.587± 19.61^{de}	H
B. integrifolia	8	226.904± 15.47^{e}	VH
R. lanuginosum	8	230.658± 21.39^{e}	VH
M. berteroana	8	244.839± 33.50^{e}	VH

Table A49. Mean (± standard error) values for plant height for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
Species	241939.67	48387.93	258.27	**<0.001**
Error	111289.25	187.36		
Species	**n**	**PH (mm) Mean± std error**		
Andreaea sp.	100	16.26± 0.43[a]		
P. heterodonta	100	17.81± 0.42[a]		
D. strictum	100	33.40± 1.95[b]		
H. cupressiforme	100	38.63± 1.67[b]		
S. sonderi	100	49.12± 0.75[c]		
R. lanuginosum	100	75.35± 1.93[d]		

Table A50. Mean (± standard error) values for chlorophyll content for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	3195871.57	639174.31	130.56	**<0.001**
Error	2320503.60	4895.58		
Species	**n**	**Chl (mg m^{-2}) Mean± std error**		
Andreaea sp.	80	4.82± 2.30[a]		
D. strictum	80	46.40± 6.66[b]		
R. lanuginosum	80	65.29± 7.72[bc]		
S. sonderi	80	89.71± 7.77[c]		
H. cupressiforme	80	207.34± 10.37[d]		
P. heterodonta	80	224.19± 9.49[d]		

Table A51. Mean (± standard error) values for Fv/Fm for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
Intercept	21.64	21.64	23001.61	**<0.001**
species	0.04	0.01	8.04	**<0.001**
Error	0.04	0.00		
Species	**n**	**Fv/Fm Mean± std error**		
P. heterodonta	8	0.614± 0.01[a]		
Andreaea sp.	8	0.668± 0.01[b]		
D. strictum	8	0.668± 0.01[b]		
S. sonderi	8	0.690± 0.01[b]		
H. cupressiforme	8	0.693± 0.01[b]		
R. lanuginosum	8	0.695± 0.01[b]		

Table A52. Mean (± standard error) values for ϕPSII for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	0.03	0.01	7.42	**<0.001**
Error	0.03	0.00		
Species	**n**	**ϕPSII Mean± std error**		
H. cupressiforme	8	0.077± 0.00[a]		
P. heterodonta	8	0.094± 0.01[ab]		
S. sonderi	8	0.105± 0.01[ab]		
Andreaea sp.	8	0.111± 0.02[ab]		
D. strictum	8	0.129± 0.01[bc]		
R. lanuginosum	8	0.155± 0.01[c]		

Table A53. Mean (± standard error) values for 1-qL for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	0.24	0.05	9.92	**<0.001**
Error	0.21	0.00		
Species	**n**	**1-qL Mean± std error**		
R. lanuginosum	8	0.582± 0.01[a]		
D. strictum	8	0.691± 0.02[b]		
Andreaea sp.	8	0.723± 0.02[bc]		
P. heterodonta	8	0.735± 0.03[bc]		
S. sonderi	8	0.782± 0.04[bc]		
H. cupressiforme	8	0.800± 0.02[c]		

Table A54. Mean (± standard error) values for YNPQ/YNO for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	SS	MS	F	P
species	9.23	1.85	2.14	0.079
Error	36.26	0.86		
Species	**n**	**YNPQ/YNO Mean± std error**		
Andreaea sp.	8	2.406± 0.26[a]		
S. sonderi	8	2.618± 0.36[a]		
P. heterodonta	8	2.670± 0.34[a]		
D. strictum	8	2.792± 0.51[a]		
H. cupressiforme	8	3.506± 0.20[a]		
R. lanuginosum	8	3.534± 0.18[a]		

Table A55. Mean (± standard error) values for α for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	0.03	0.01	5.65	**<0.001**
Error	0.05	0.00		
Species	**n**	**α (electron/photon^{-1}) Mean± std error**		
P. heterodonta	8	0.186± 0.02^{a}		
R. lanuginosum	8	0.244± 0.01^{b}		
Andreaea sp.	8	0.248± 0.01^{b}		
H. cupressiforme	8	0.253± 0.01^{b}		
D. strictum	8	0.254± 0.01^{b}		
S. sonderi	8	0.269± 0.01^{b}		

Table A56. Mean (± standard error) values for ETR_{max} for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	14361.15	2872.23	17.65	**<0.001**
Error	6833.58	162.70		
Species	**n**	**ETR_{max} (µmol electrons m^{-2} s^{-1}) Mean± std error**		
P. heterodonta	8	10.811± 2.66^{a}		
H. cupressiforme	8	27.656± 3.36^{ab}		
S. sonderi	8	33.872± 3.28^{b}		
Andreaea sp.	8	35.163± 4.85^{b}		
D. strictum	8	46.682± 5.42^{b}		
R. lanuginosum	8	67.251± 6.33^{c}		

Table A57. Mean (± standard error) values for PAR_{opt} for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	5390964.72	1078192.94	6.61	**<0.001**
Error	6848761.94	163065.76		
Species	**n**	**PAR_{opt} (µmol photons m^{-2} s^{-1}) Mean± std error**		
P. heterodonta	8	311.621± 89.98^{a}		
Andreaea sp.	8	678.691± 82.47^{ab}		
S. sonderi	8	819.942± 114.29^{ab}		
H. cupressiforme	8	888.456± 132.88^{abc}		
D. strictum	8	987.067± 189.98^{bc}		
R. lanuginosum	8	1427.522± 201.46^{c}		

Table A58. Mean (± standard error) values for I_k for bryophyte species at high altitude. Column headed n gives the number measurements. The species-effect anova results are given at the top of the table and the Tukeys HSD results as superscripts next to the standard errors. Different superscripts indicated different homologous groups (p = 0.05).

Effect	**SS**	**MS**	**F**	**P**
species	234392.17	46878.43	15.24	**<0.001**
Error	129221.33	3076.70		
Species	**n**	**I_k (µmol photons m^{-2} s^{-1}) Mean± std error**		
P. heterodonta	8	55.049± 12.17^{a}		
H. cupressiforme	8	111.819± 15.24^{ab}		
S. sonderi	8	126.496± 13.03^{ab}		
Andreaea sp.	8	140.955± 17.74^{b}		
D. strictum	8	185.476± 23.31^{b}		
R. lanuginosum	8	280.126± 29.99^{c}		

Figures

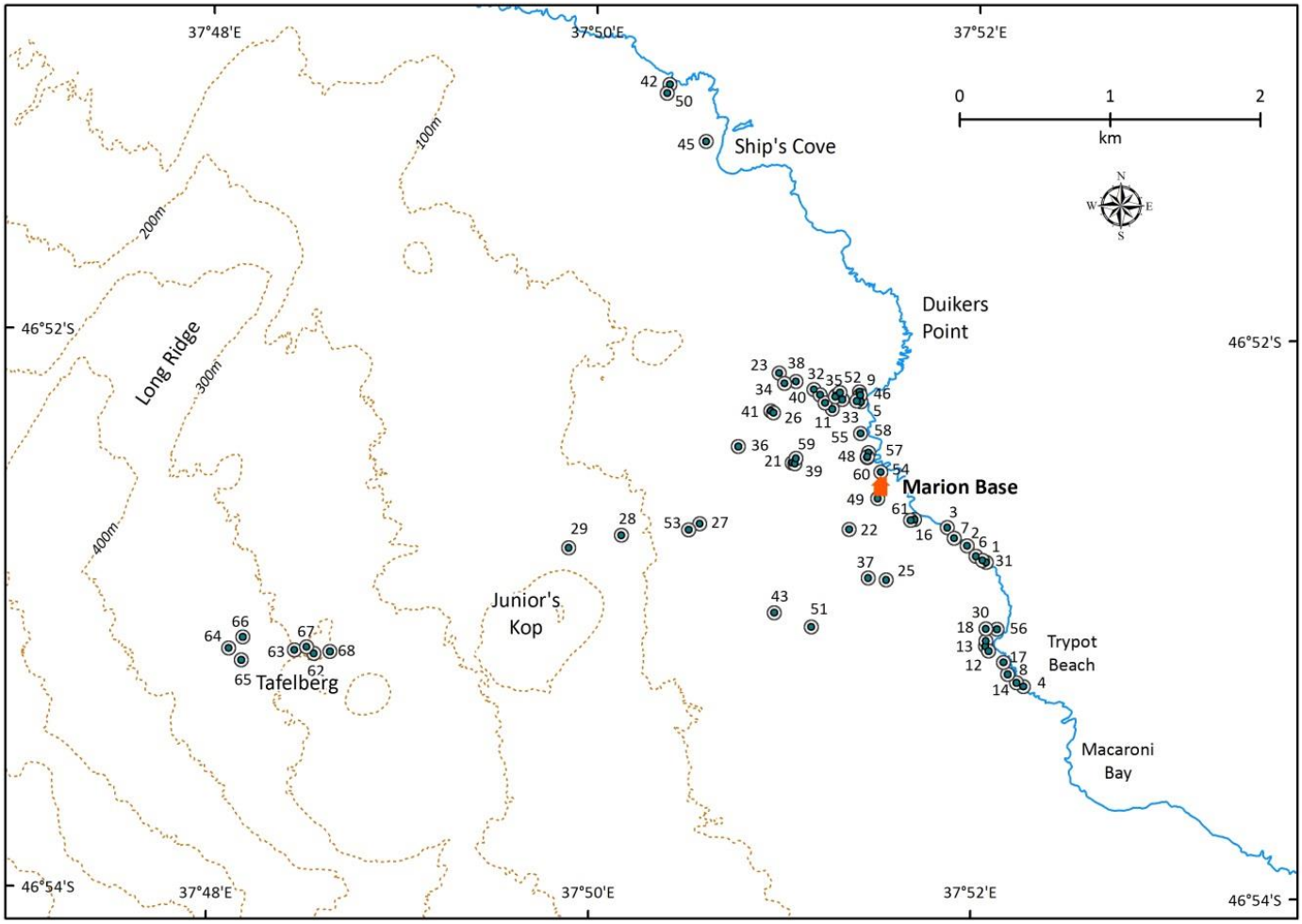
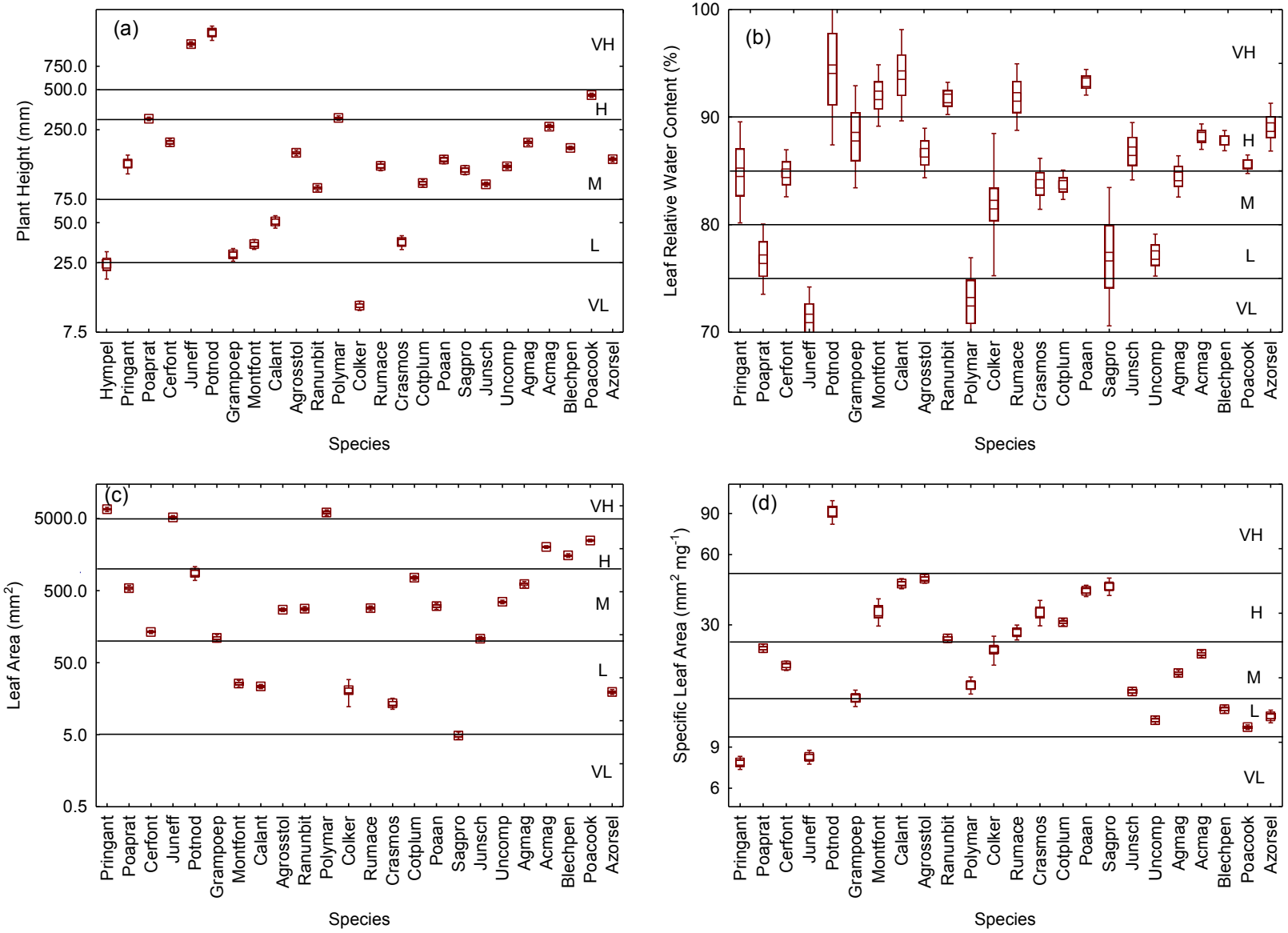
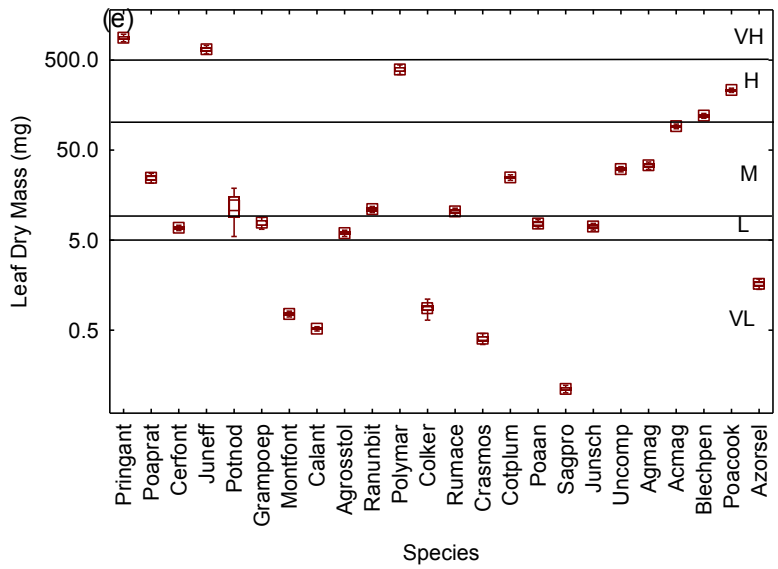
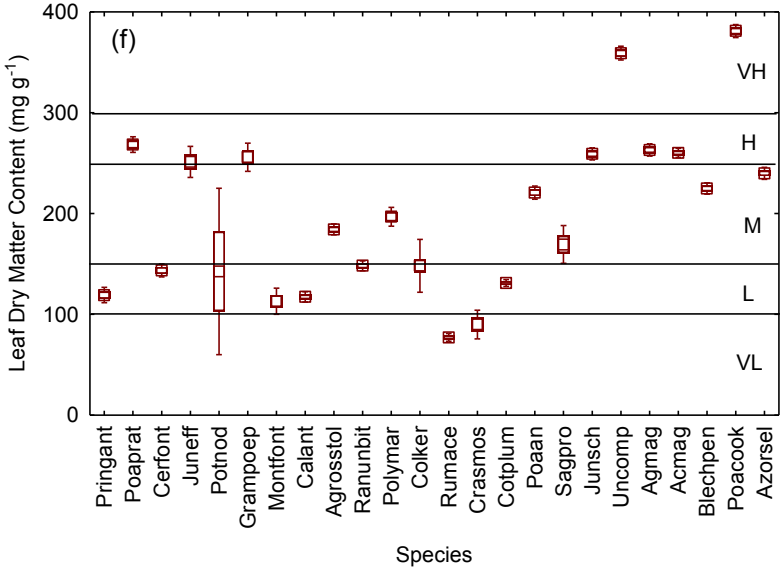
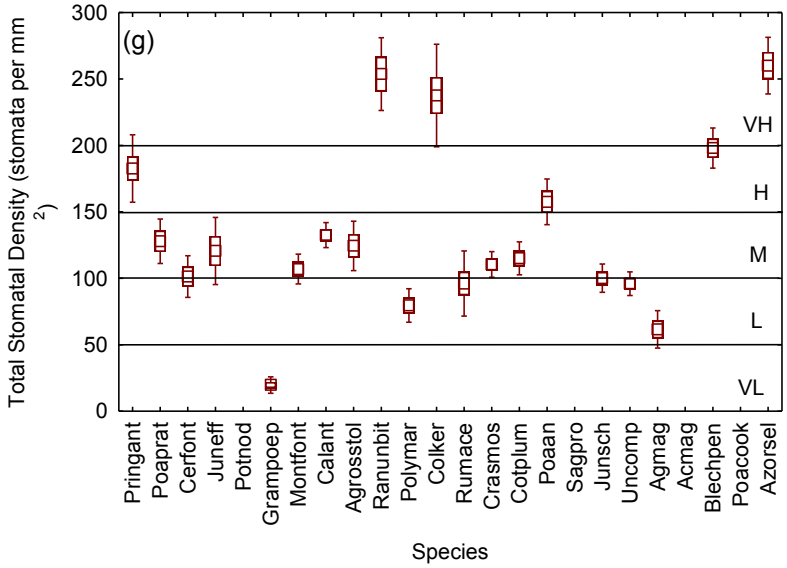


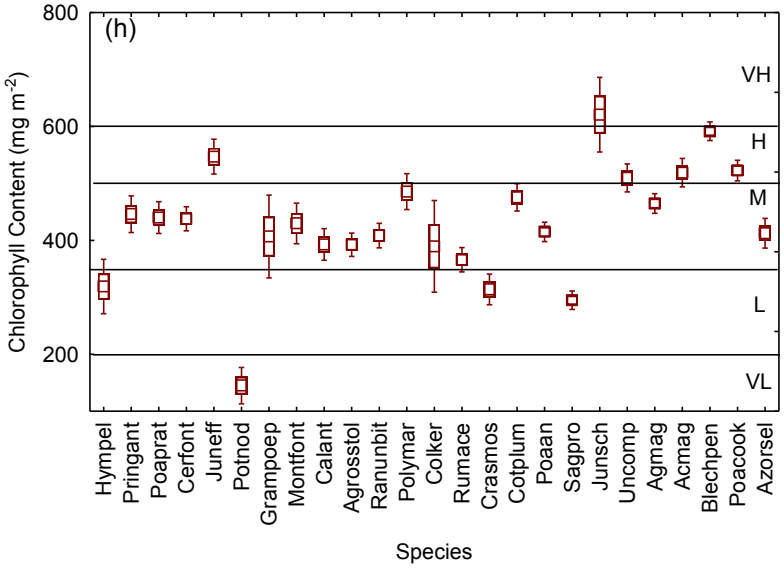
Figure 2.1. Location of sampling sites. High altitude sites are in the Tafelberg locality. Site numbers are those in Table 2.1, which also lists the species sampled at each site. Photographs and descriptions of the sites are in Appendix 1.

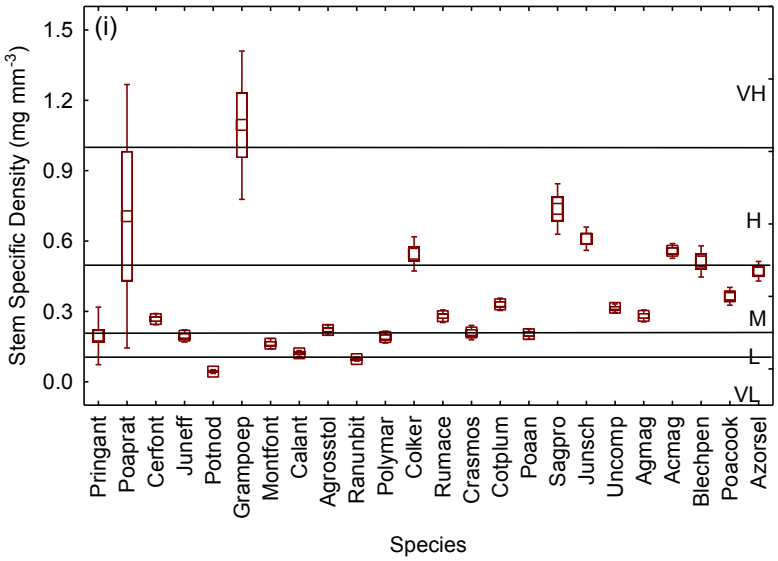


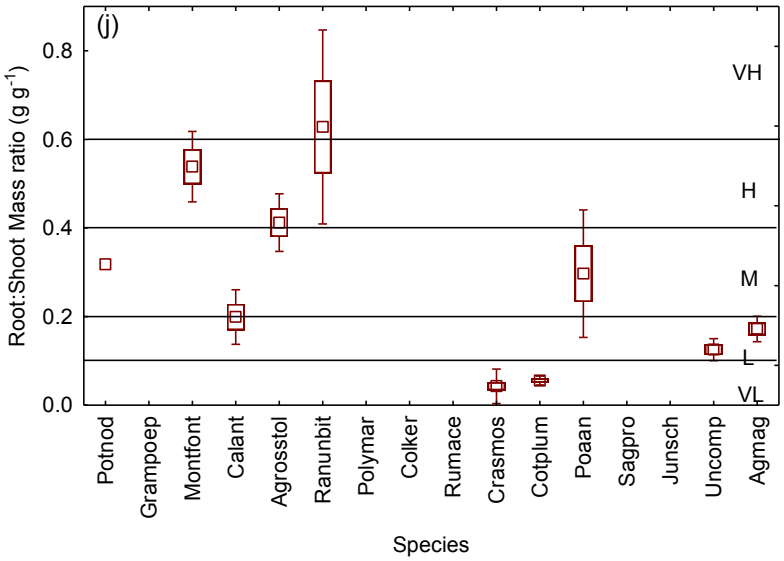


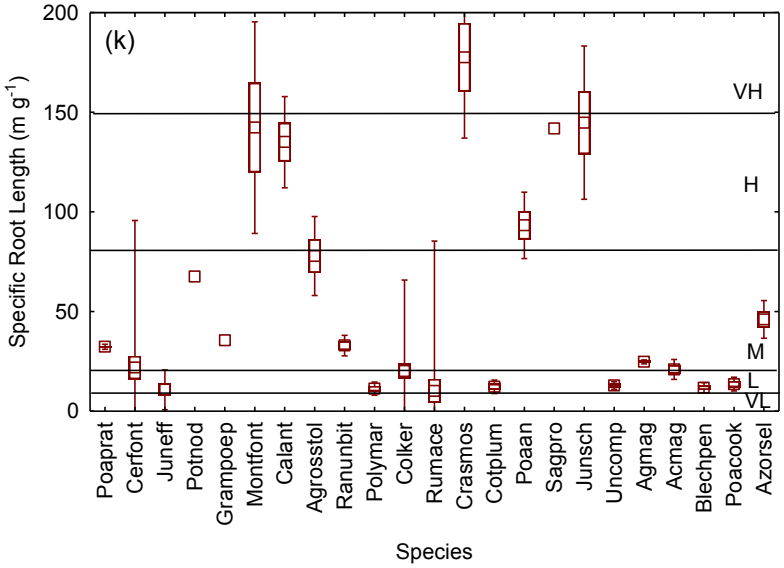


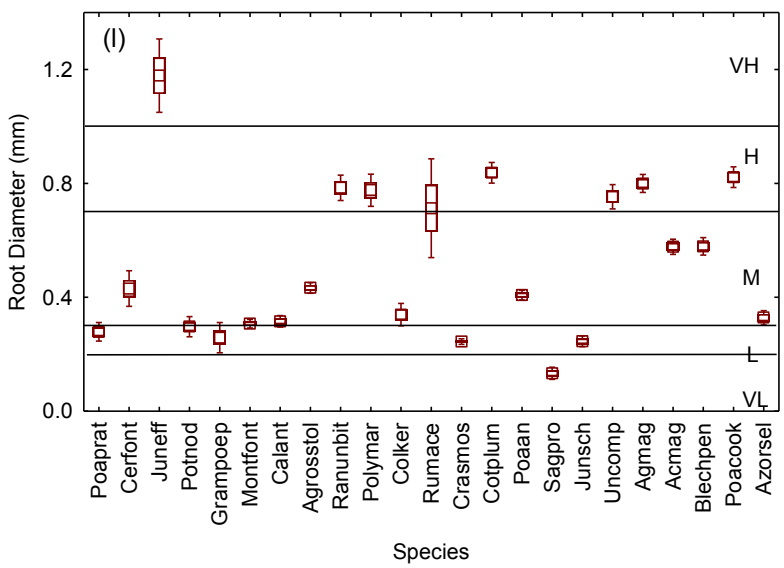


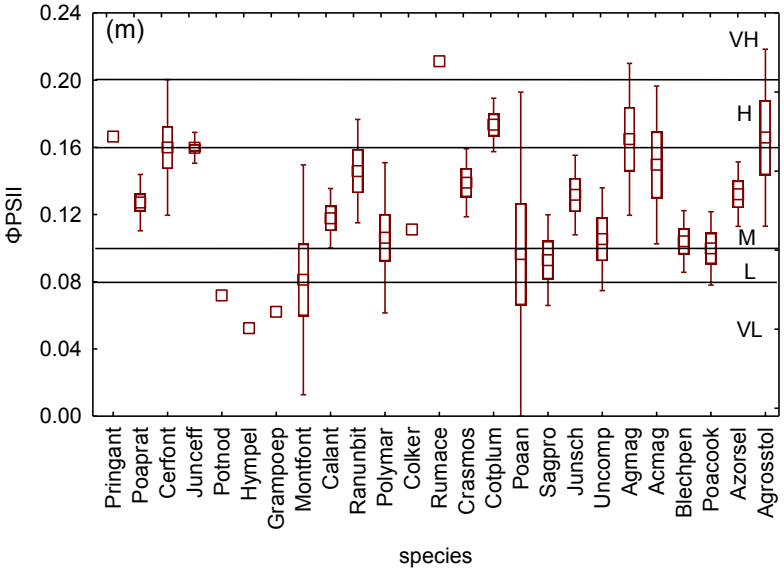


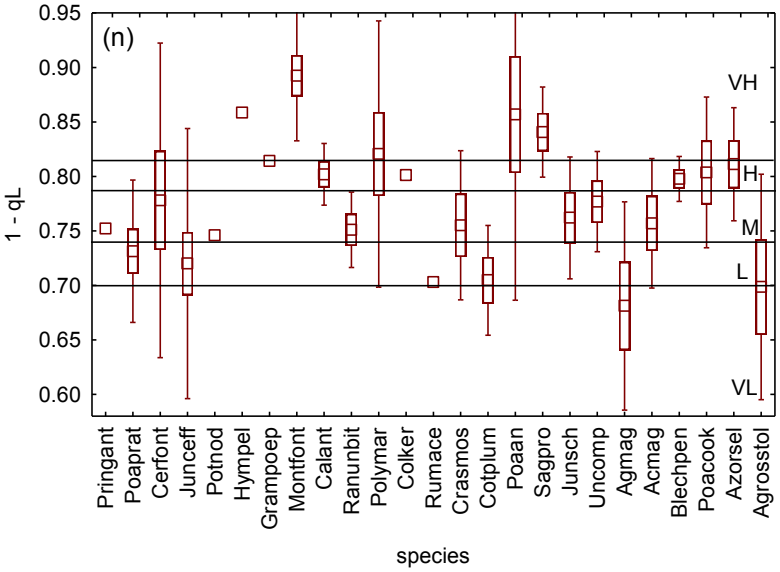


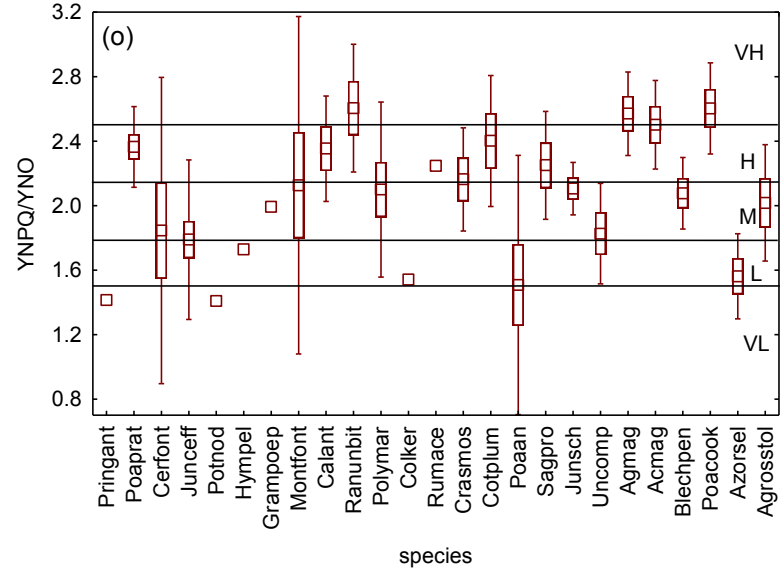


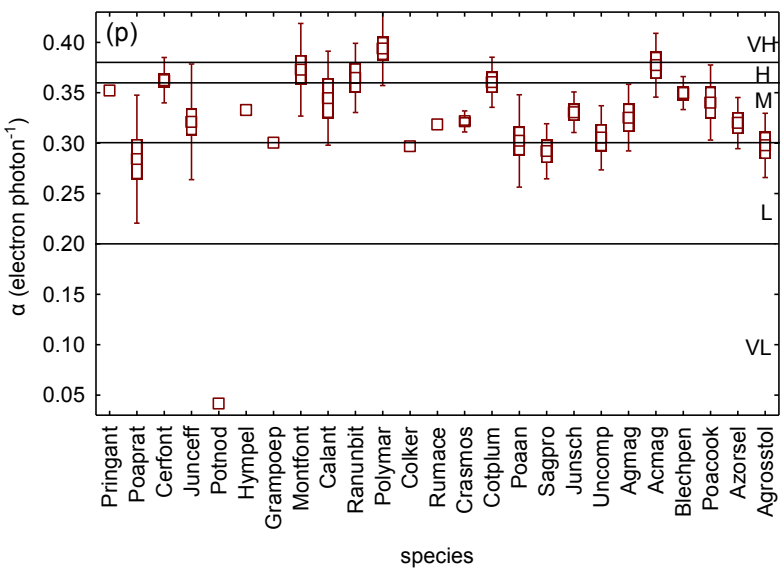












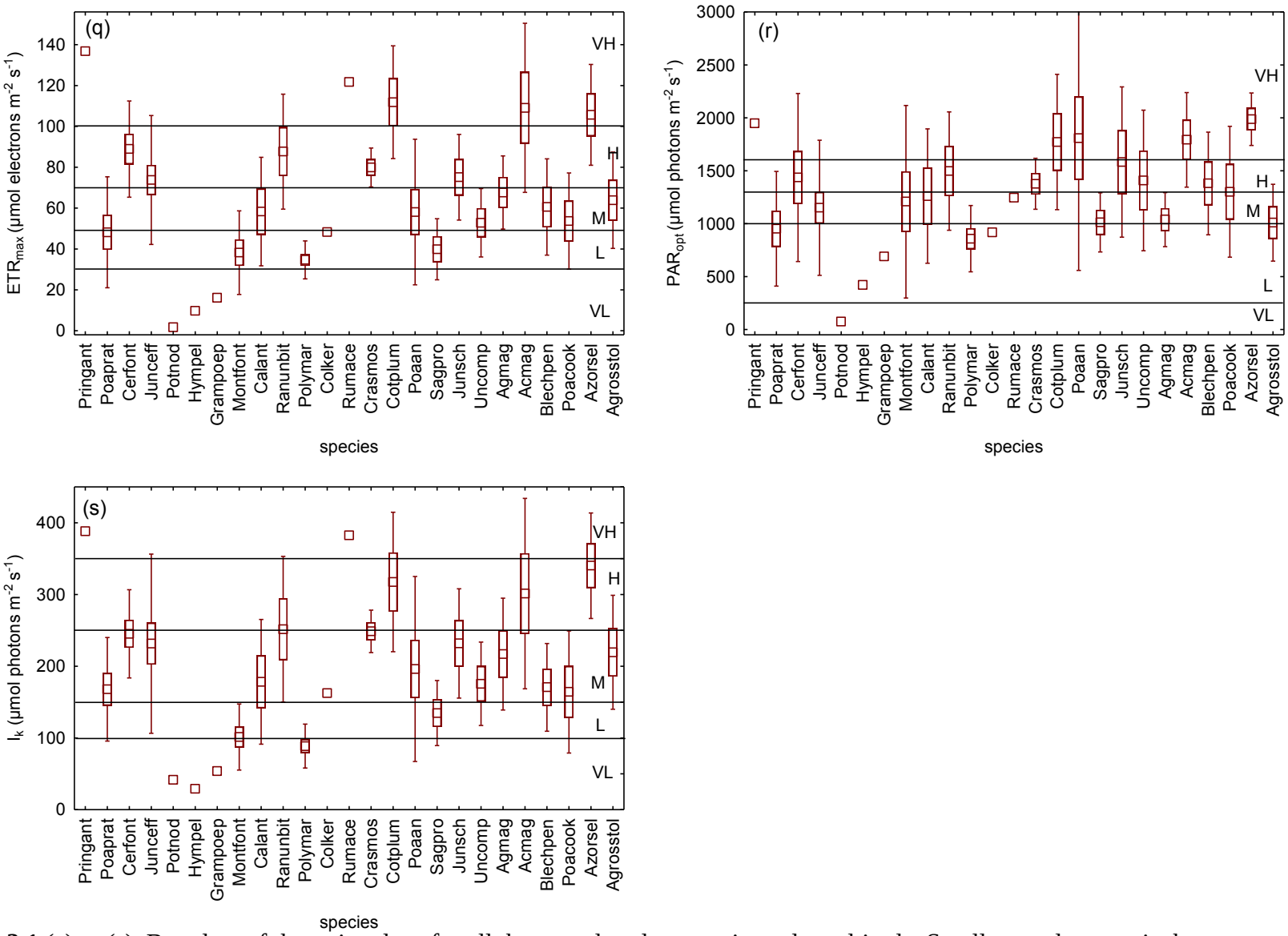


Figure 3.1 (a) to (s). Boxplots of the trait values for all the vascular plant species at low altitude. Small central square is the mean, rectangle is the standard error and whisker is the 95% confidence limits.

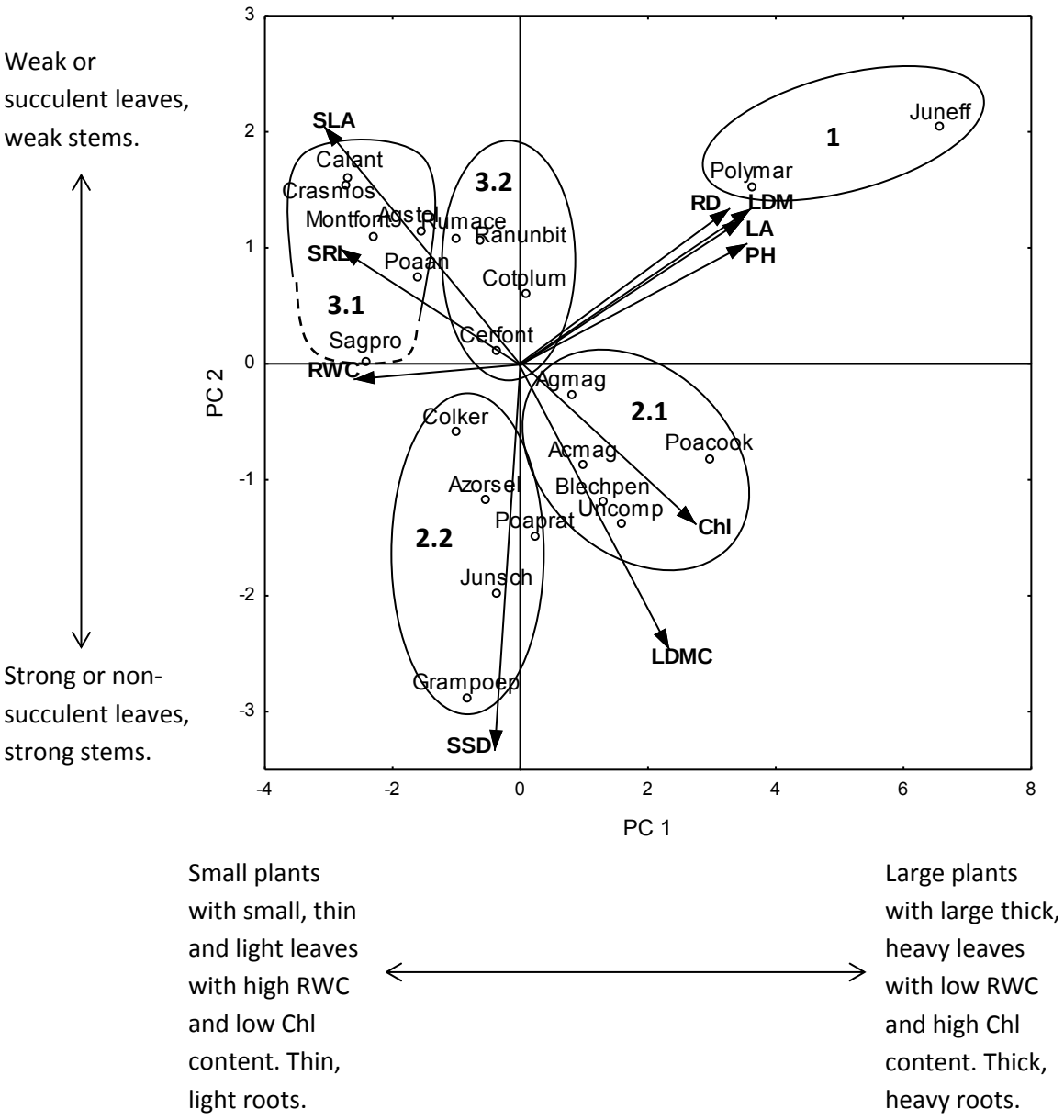


Figure 4.1. Species/ trait biplot for principal components 1 and 2 yielded by the PCA of the structural trait values.

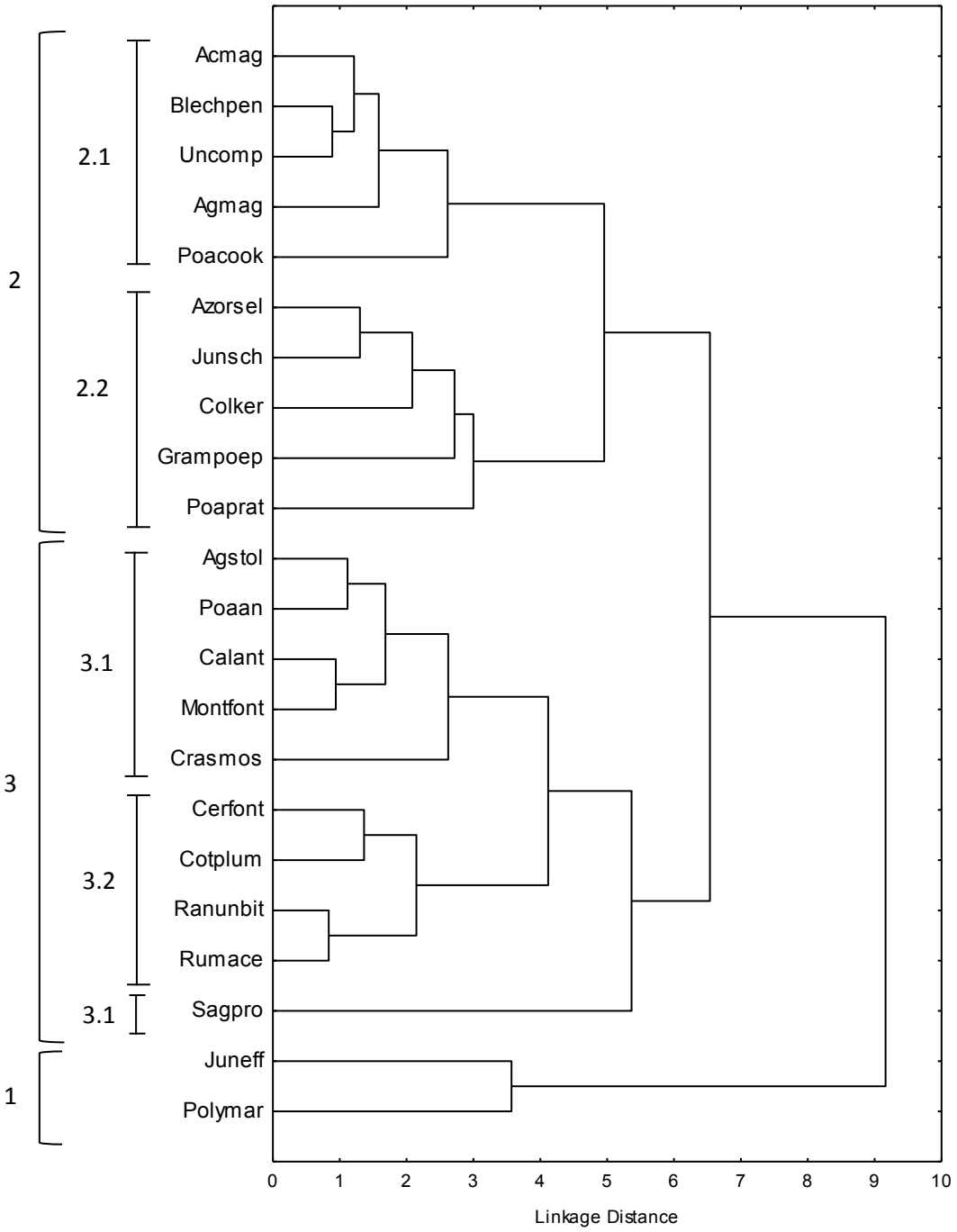


Figure 4.2. Clustering of species by their scores on the first three principal components yielded by the PCA of structural trait values.

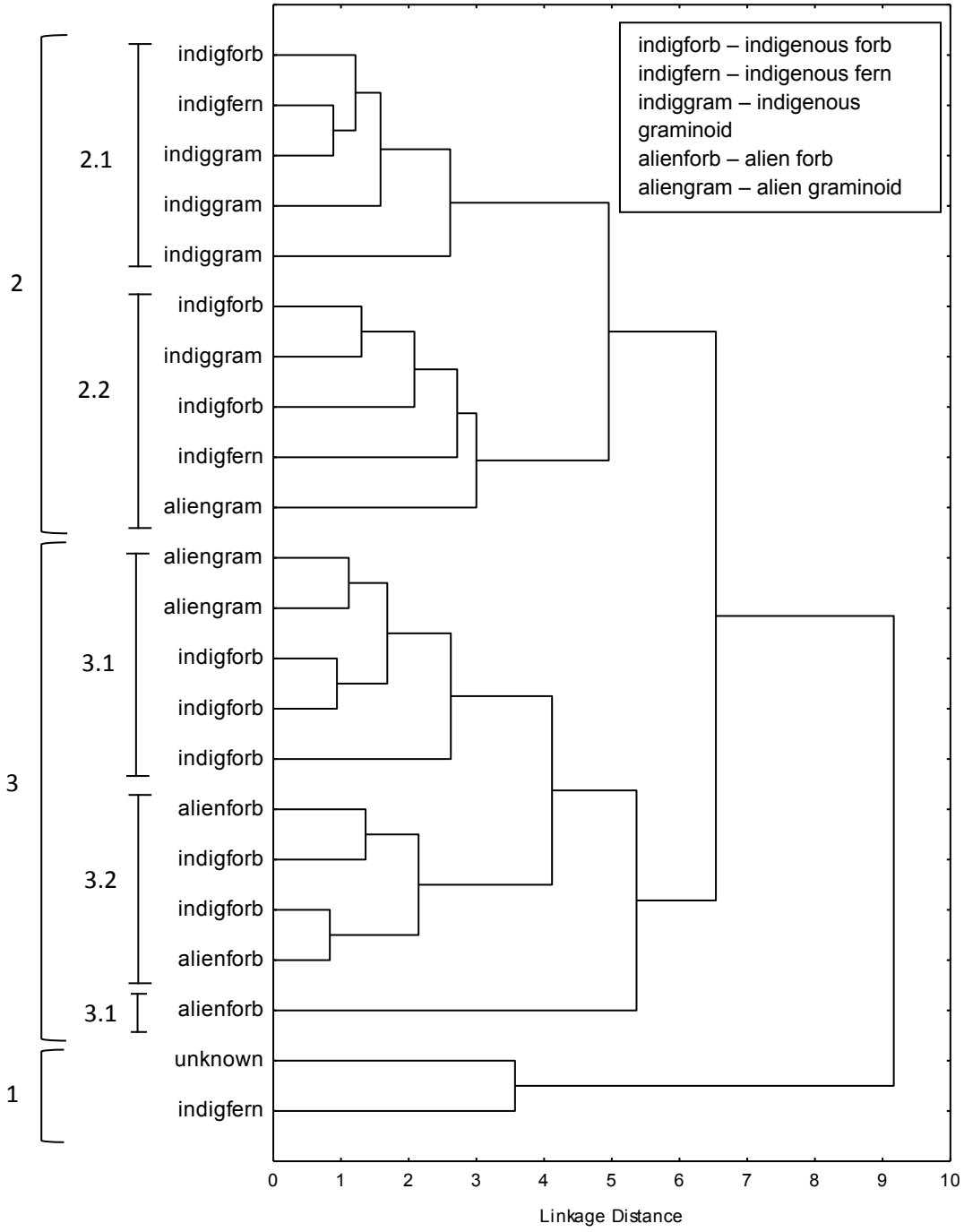


Figure 4.3. Plant habit and status of the species clustered by their scores on the first three principal components yielded by the PCA of structural trait values.

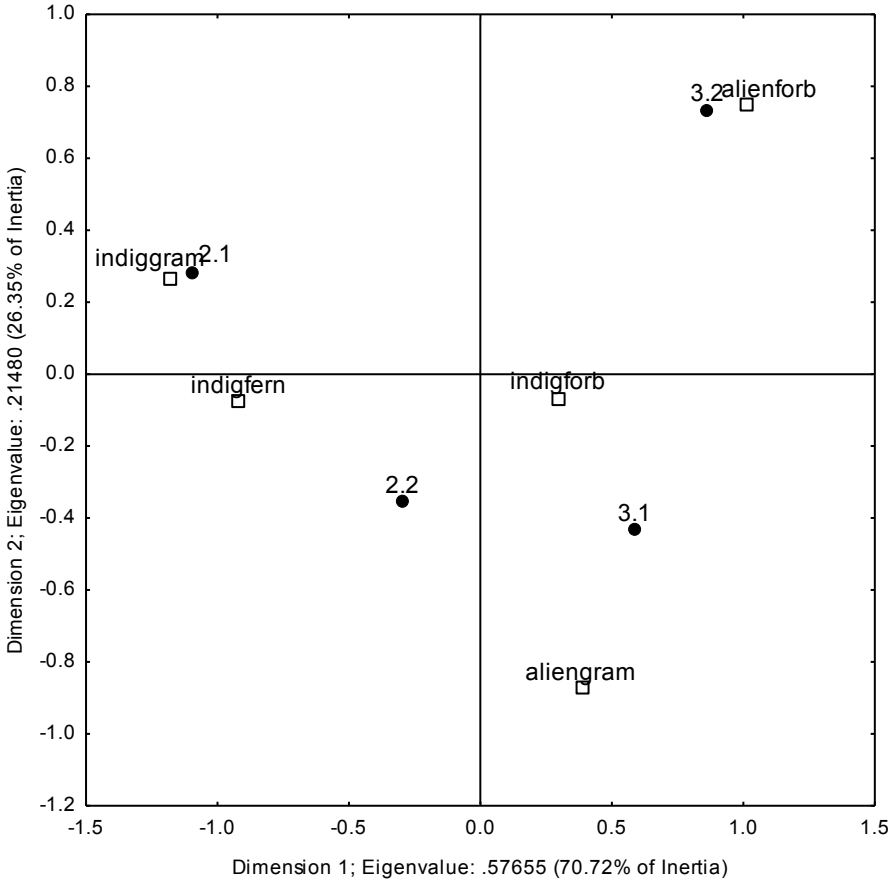


Figure 4.4. Joint plot from Correspondence Analysis of plant habit/status and groups based on structural traits. Group 1 was omitted from the analysis since it contained only two species, one of unknown status.

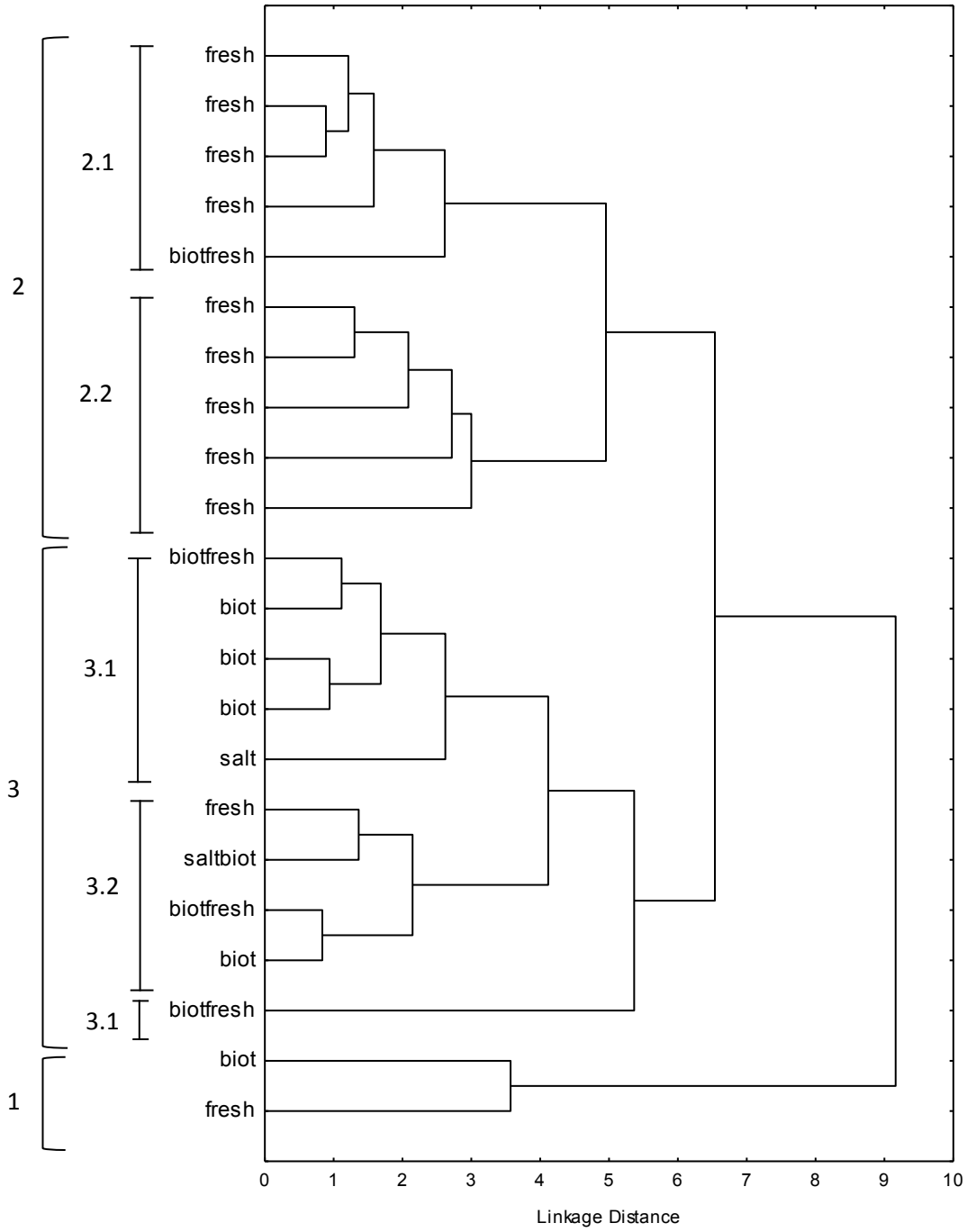


Figure 4.5. Habitat of the species clustered by their scores on the first three principal components yielded by the PCA structural trait values.

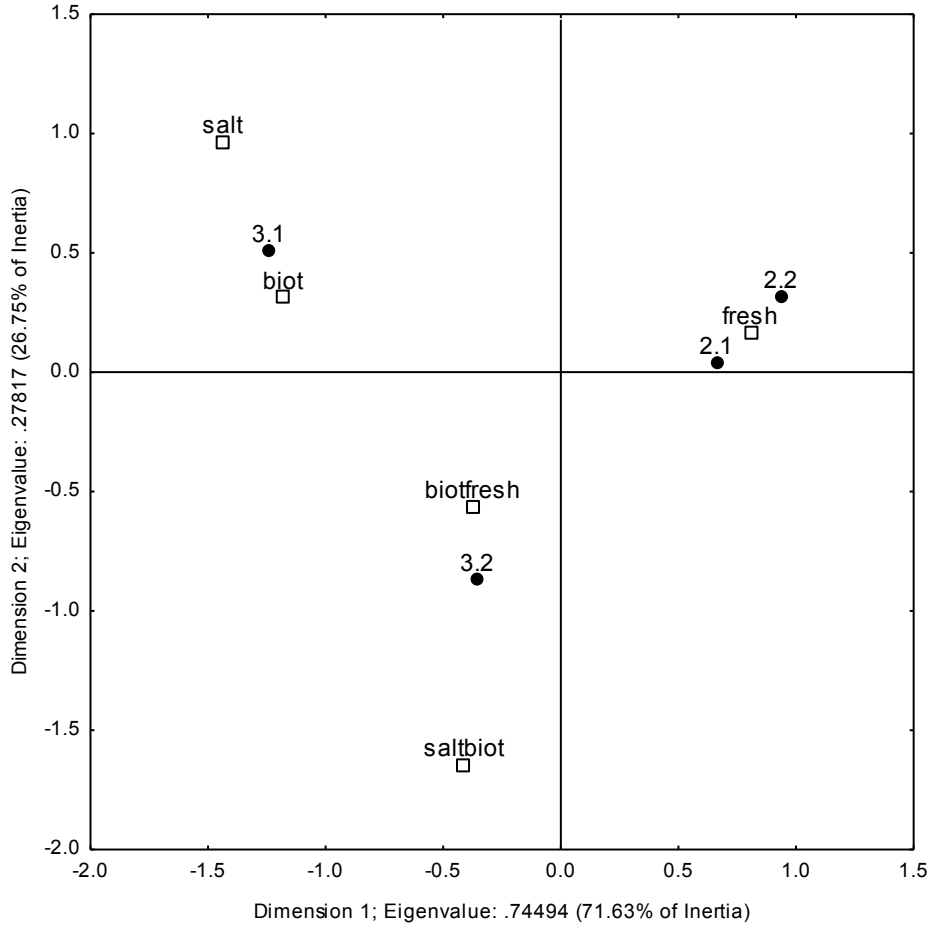


Figure 4.6. Joint plot from Correspondence Analysis of habitat and groups based on structural traits. Group 1 was omitted from the analysis since it contained only two species.

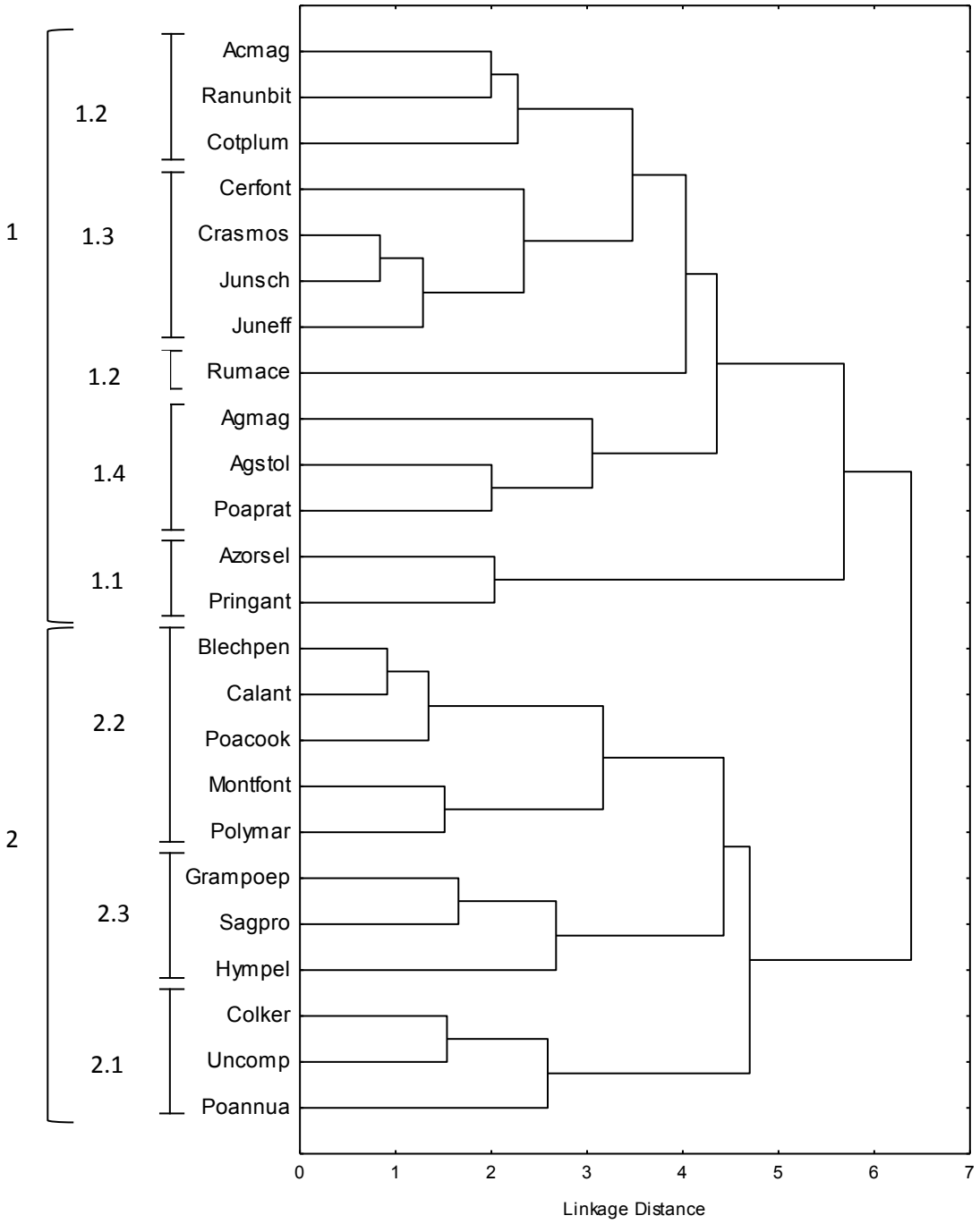


Figure 4.7. Clustering of species by their scores on the first three principal components yielded by the PCA of photosynthetic trait values.

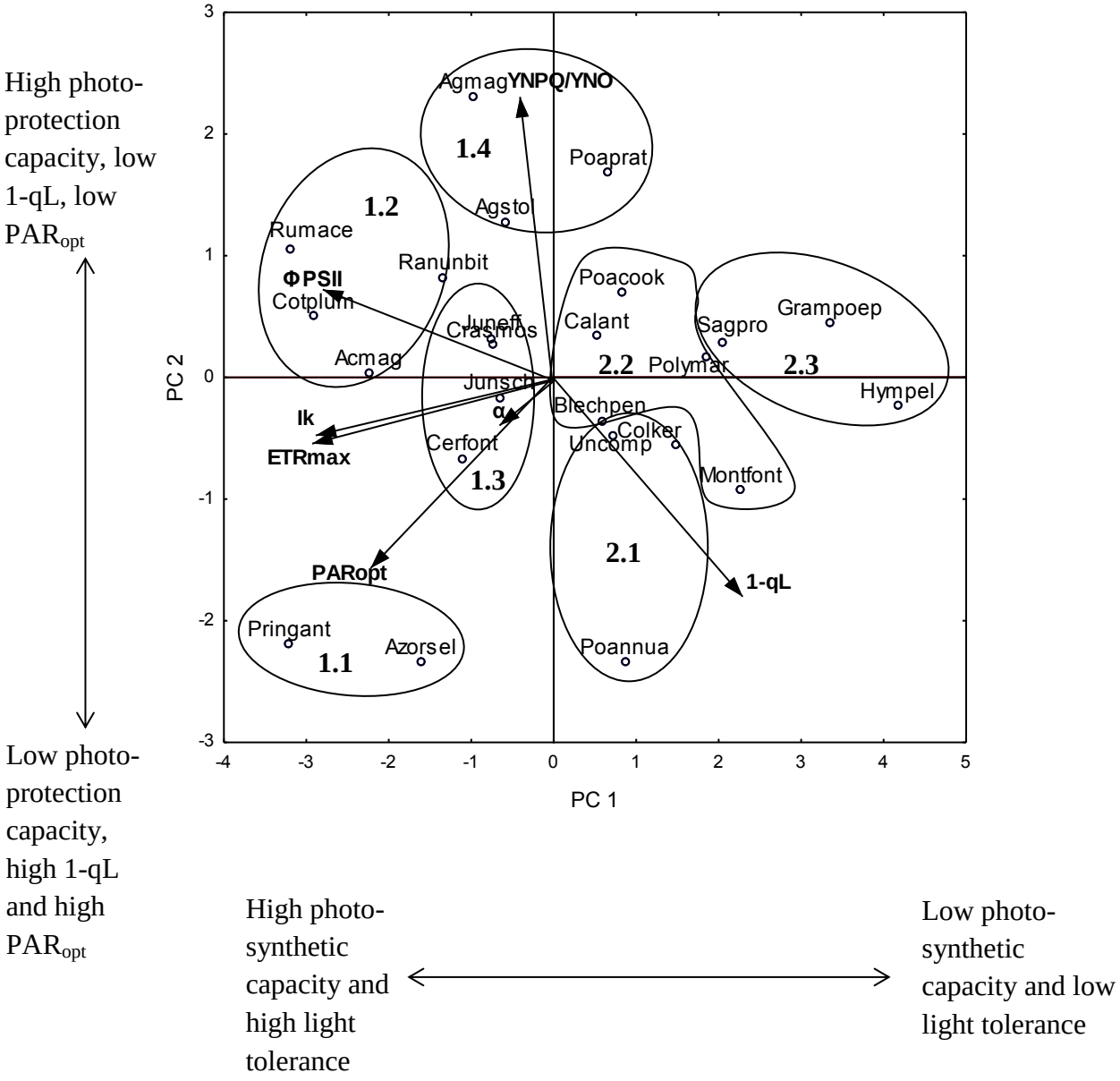


Figure 4.8. Species/ trait biplot for principal components 1 and 2 yielded by the PCA of the photosynthetic trait values.

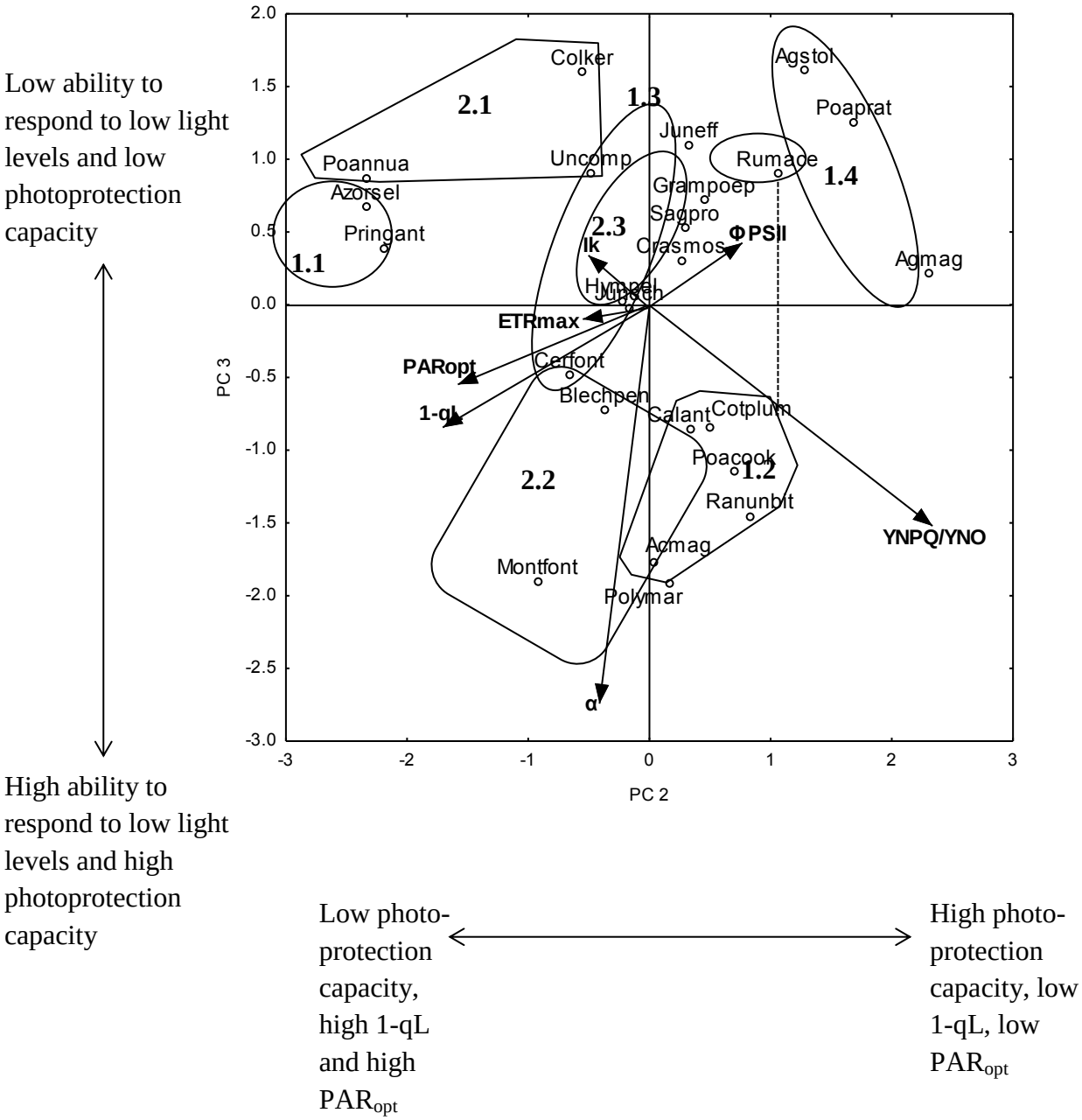


Figure 4.9. Species/ trait biplot for principal components 2 and 3 yielded by the PCA of the photosynthetic trait values.

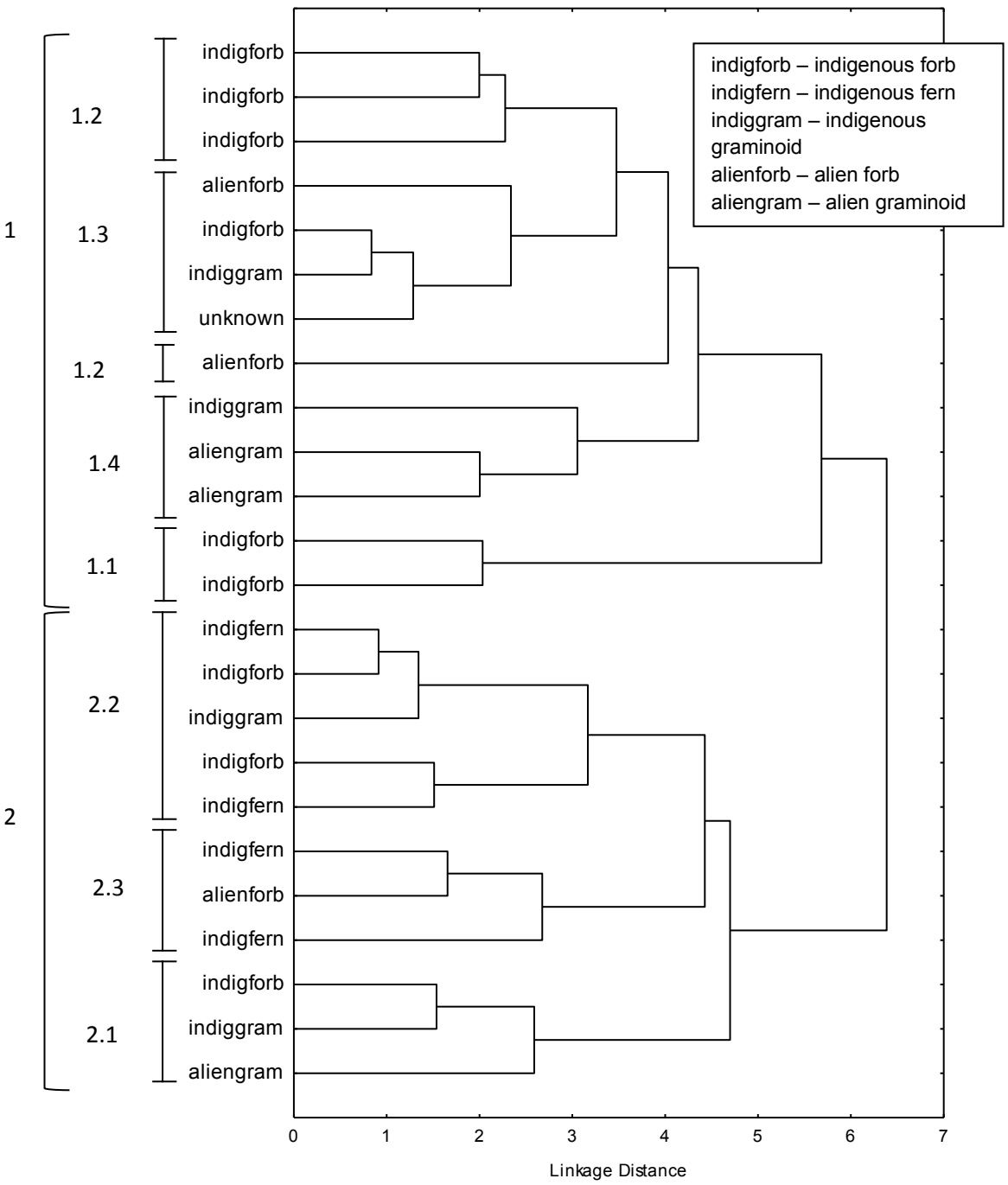


Figure 4.10. Plant habit and status of the species clustered by their scores on the first three principal components yielded by the PCA of photosynthetic trait values.

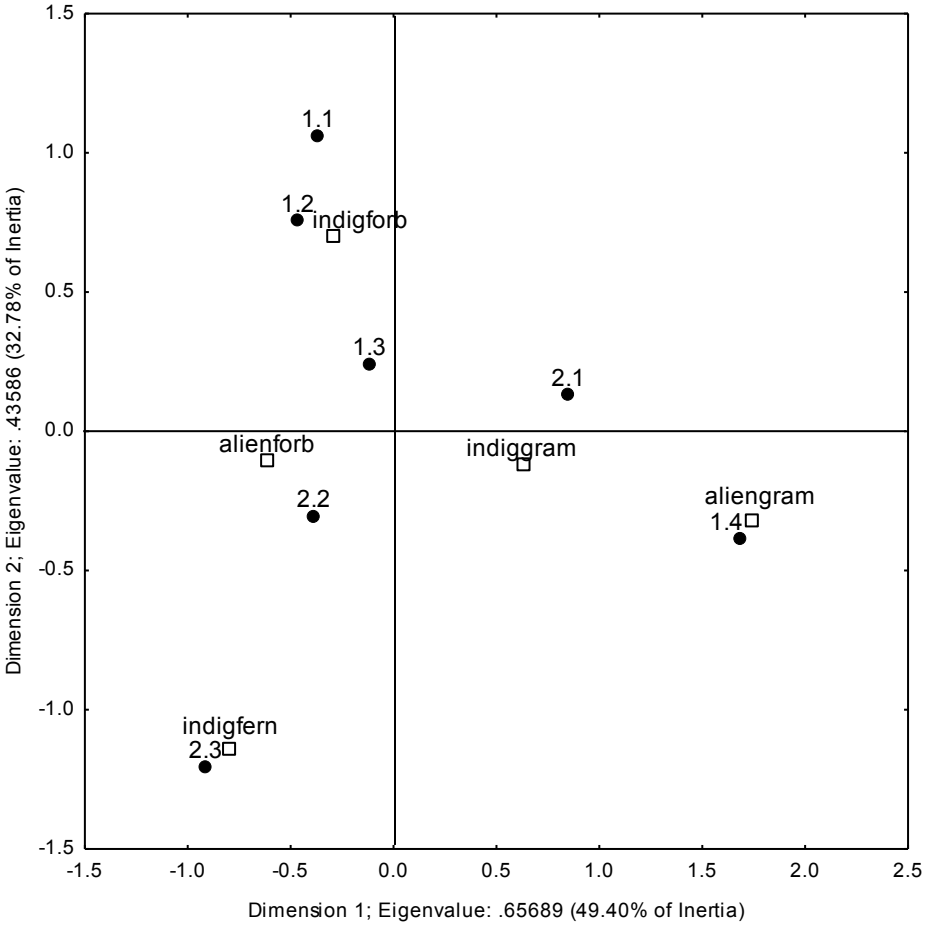


Figure 4.11. Joint plot from Correspondence Analysis of plant habit/status and sub-groups based on photosynthetic traits.

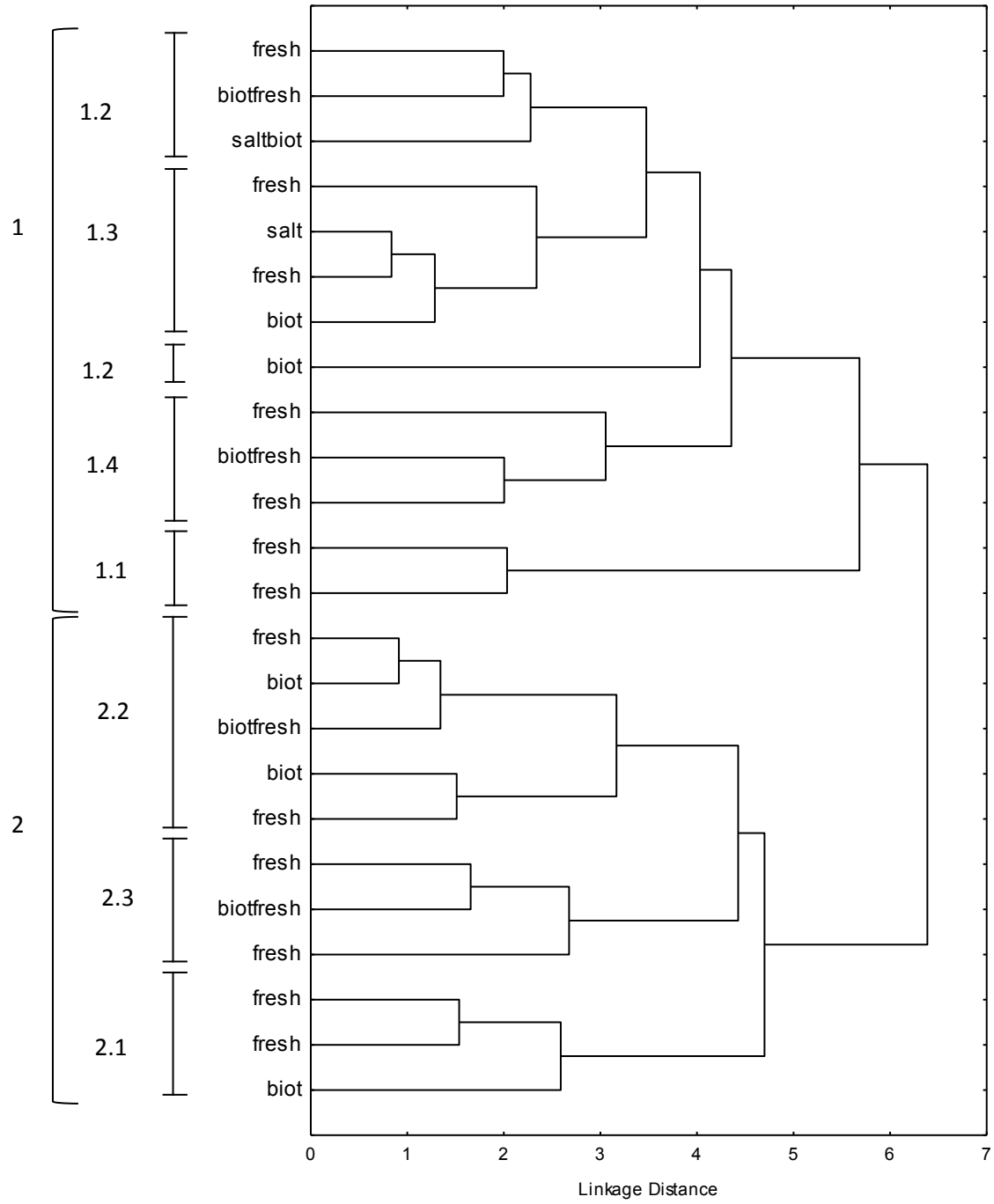


Figure 4.12. Habitat of the species clustered by their scores on the first three principal components yielded by the PCA of photosynthetic trait values.

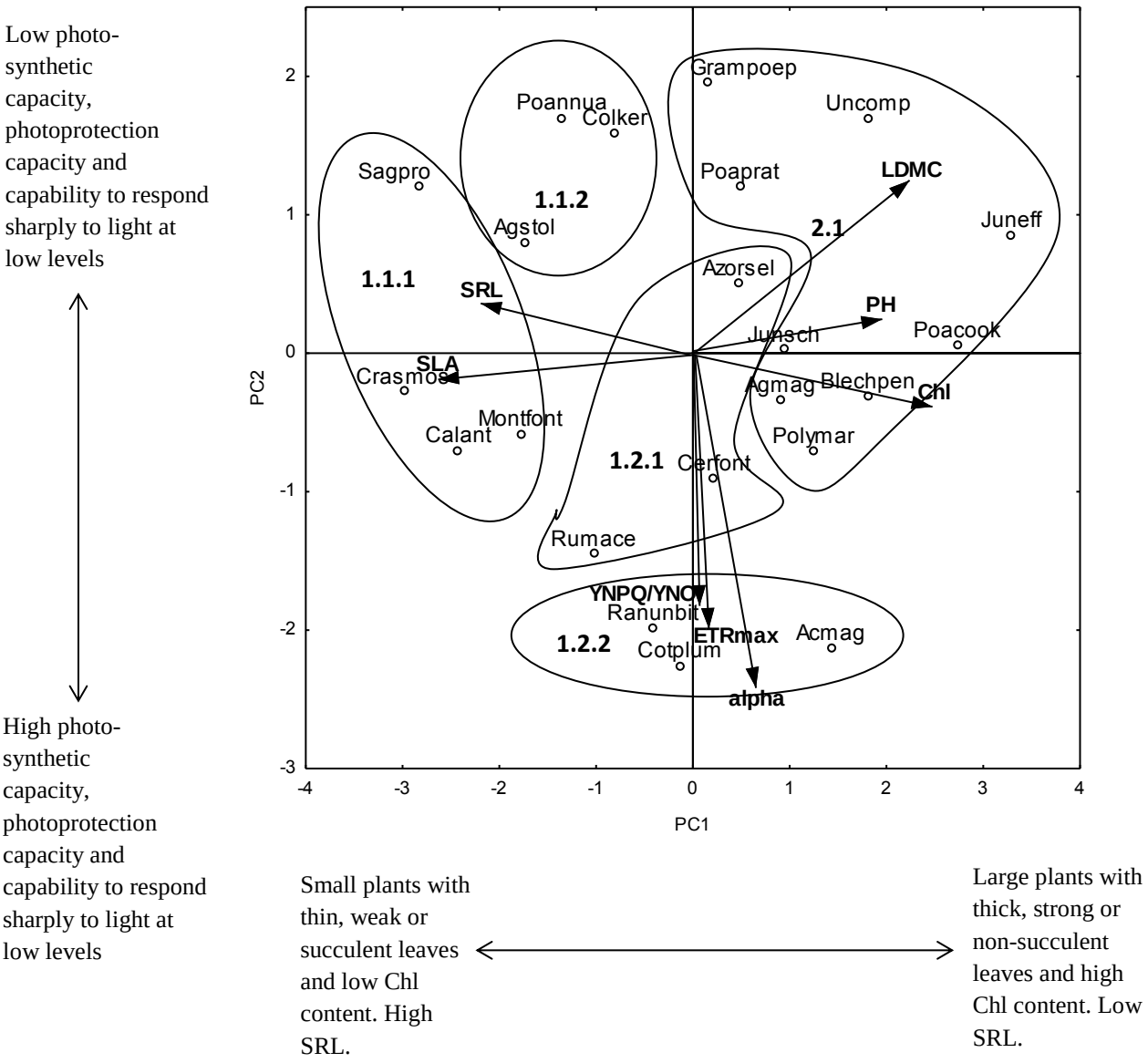


Figure 4.13. Species/trait biplot for principal component 1 and 2 yielded by the PCA of the structural and photosynthetic trait values.

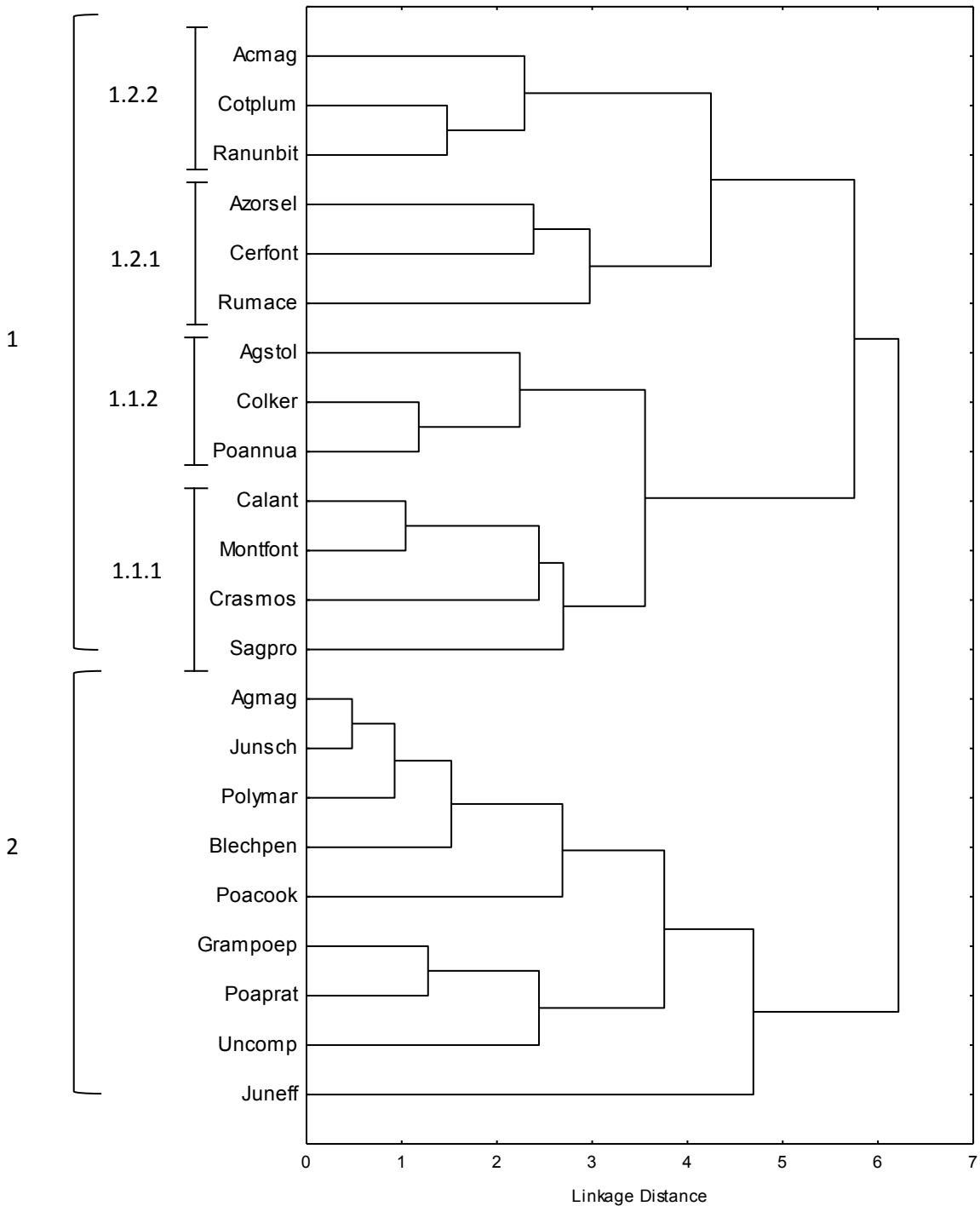


Figure 4.14. Clustering of species by their scores on the first three principal components yielded by the PCA of structural and photosynthetic trait values

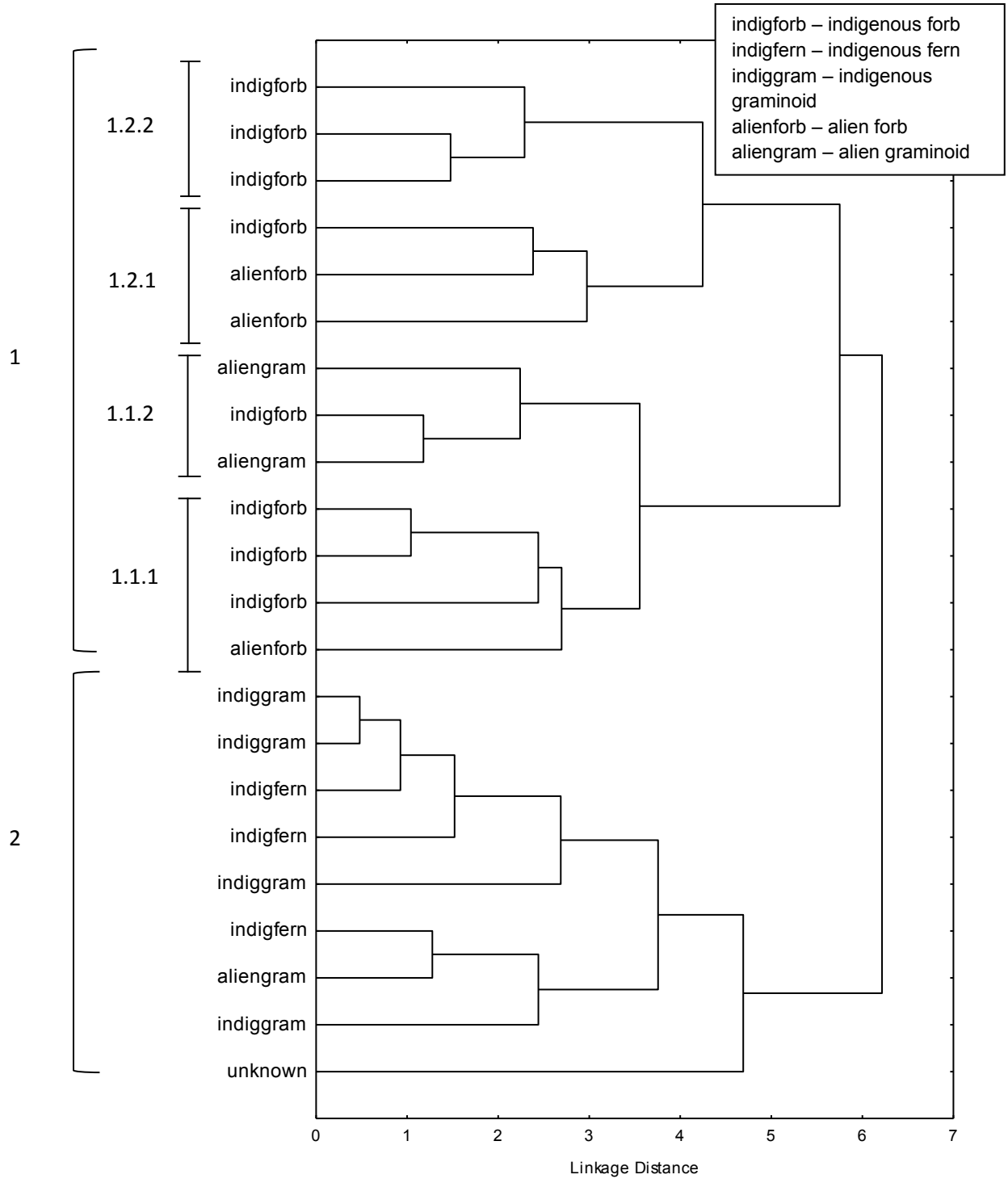


Figure 4.15. Plant habit and status of the species clustered by their scores on the first three principal components yielded by the PCA of structural trait and photosynthetic trait values.

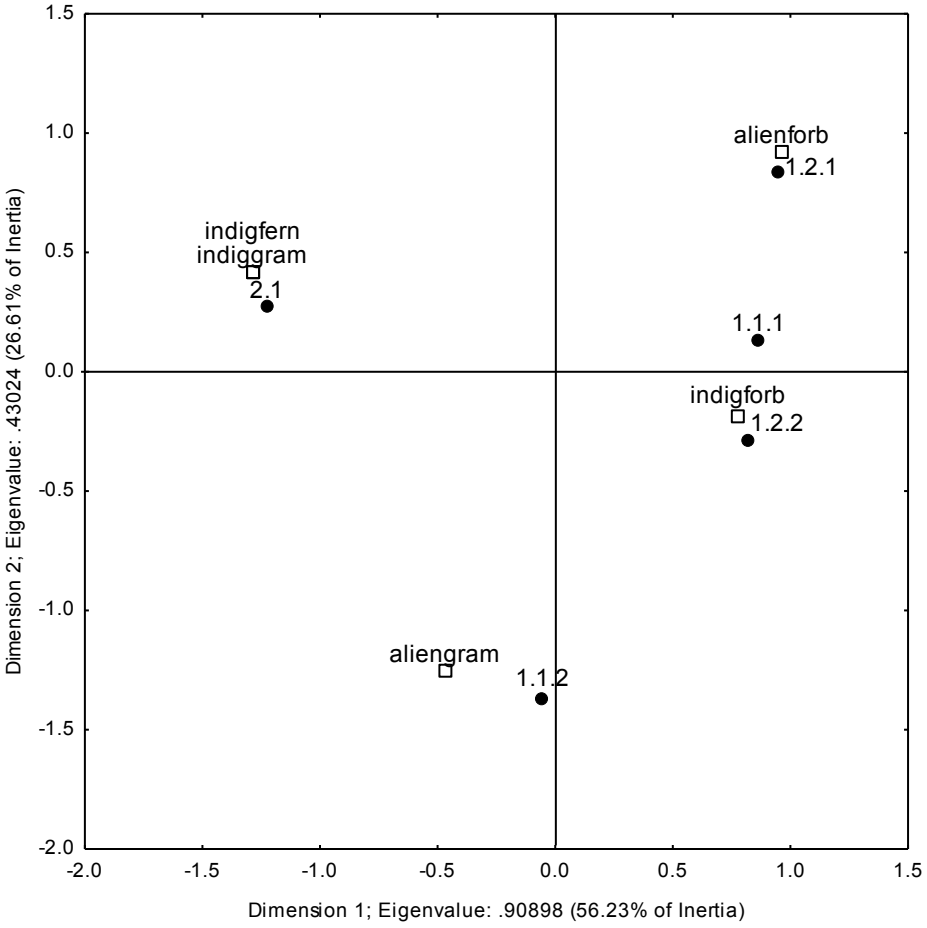


Figure 4.16. Joint plot from Correspondence Analysis of plant habit/status and sub-groups based on structural and photosynthetic traits.

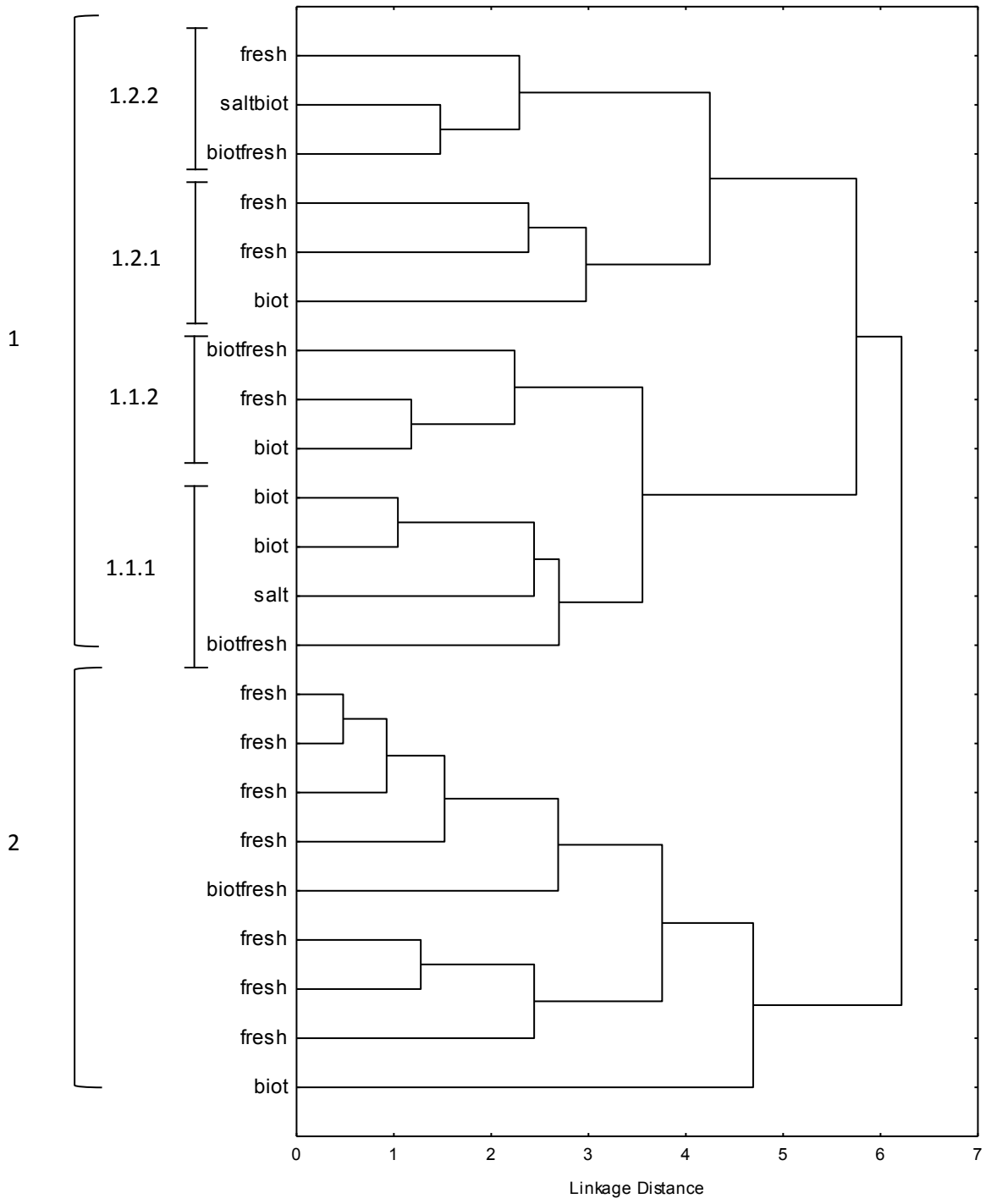


Figure 4.17. Habitat of the species clustered by their scores on the first three principal components yielded by PCA of the structural and photosynthetic trait values.

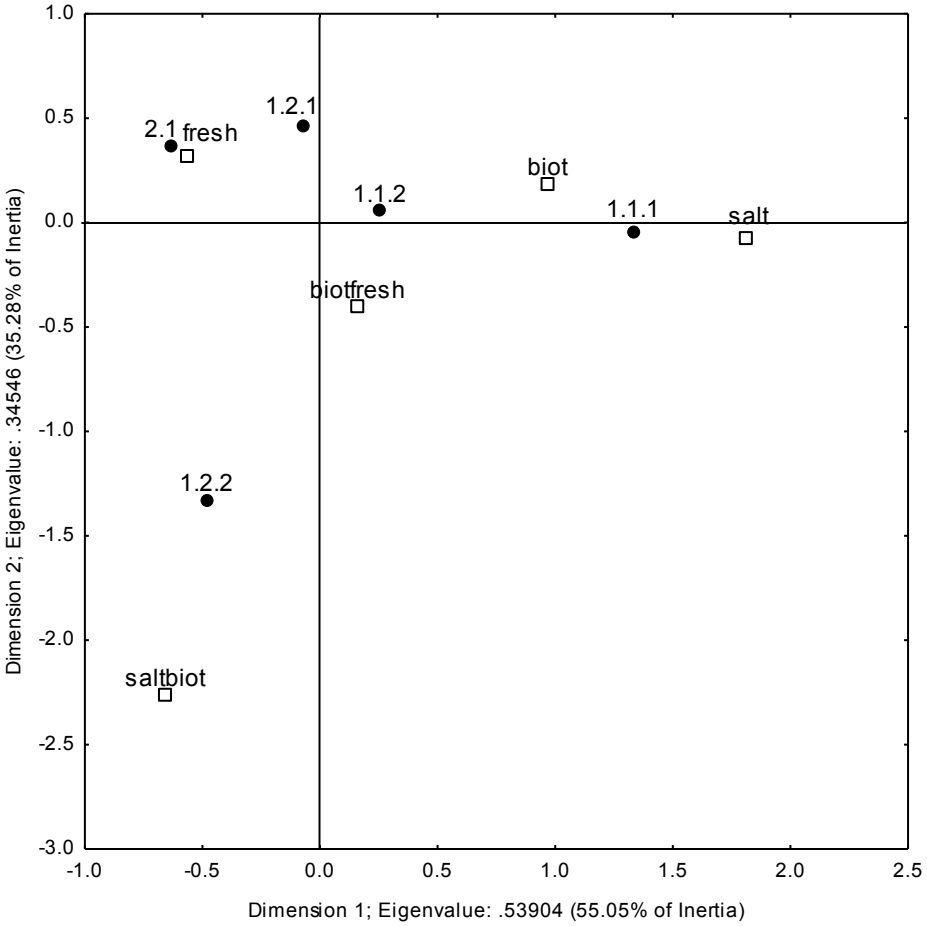
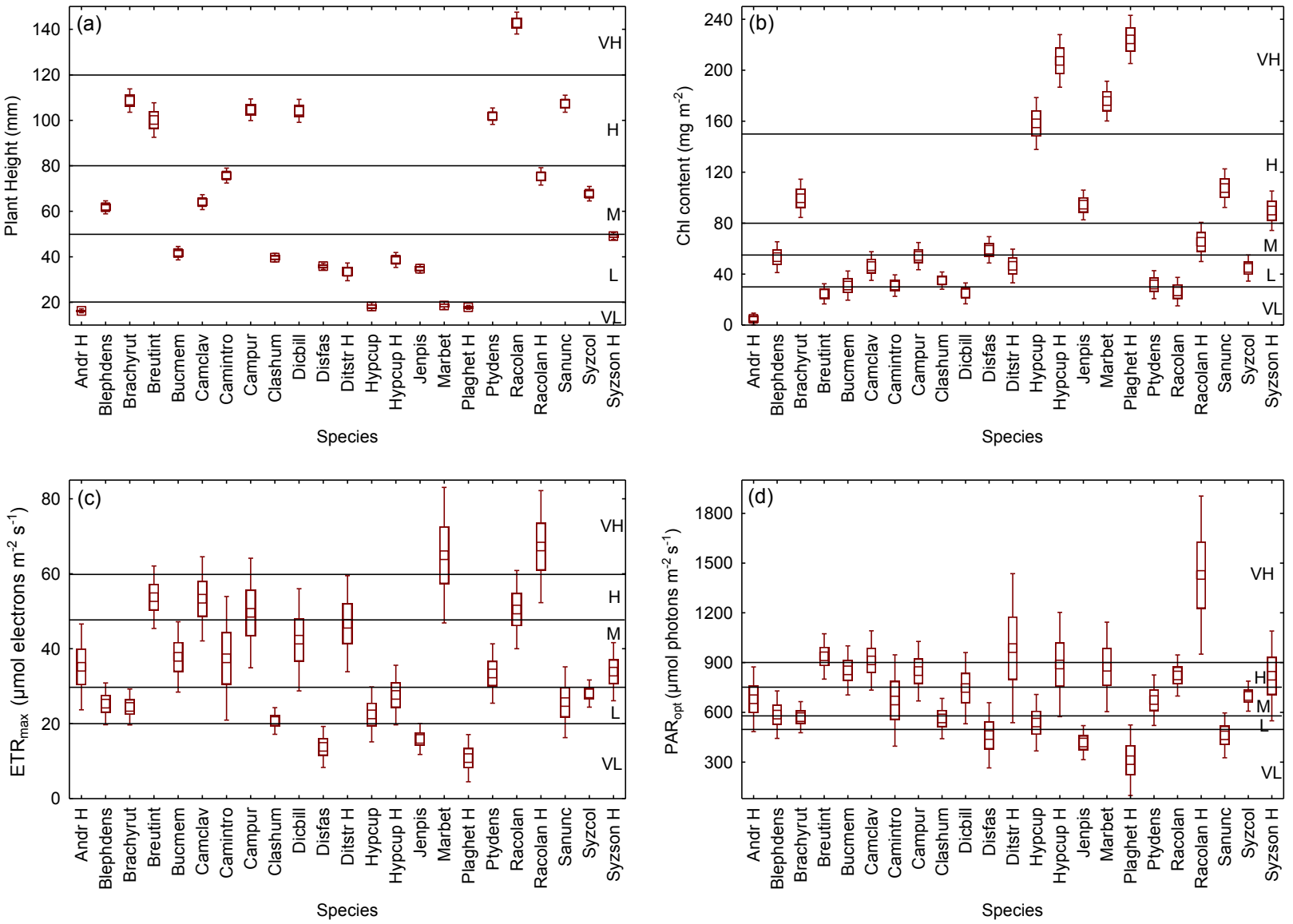
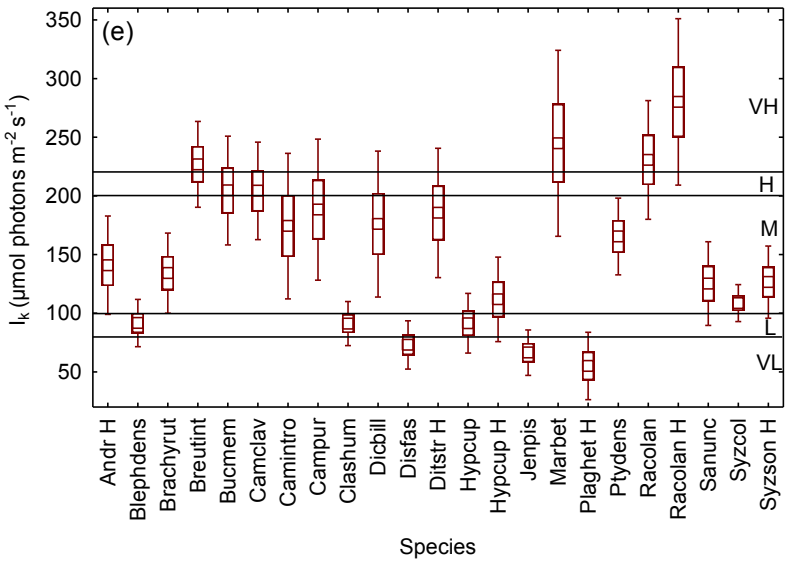
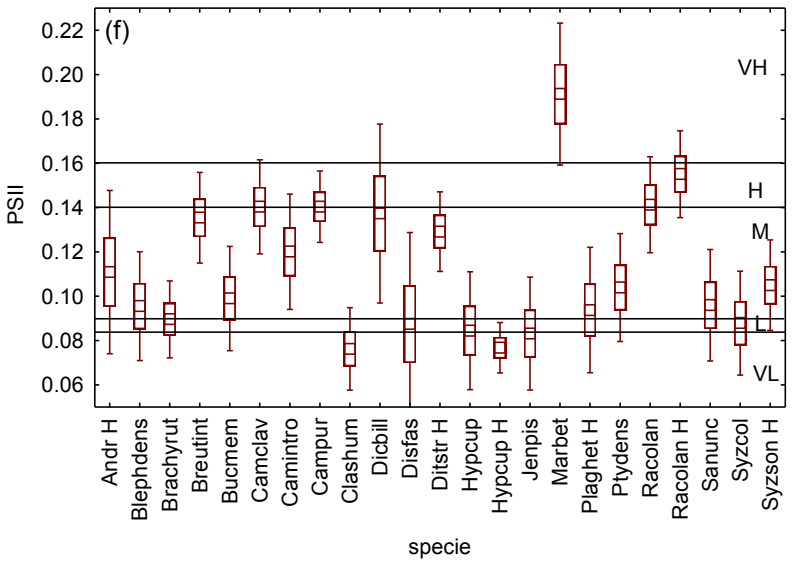
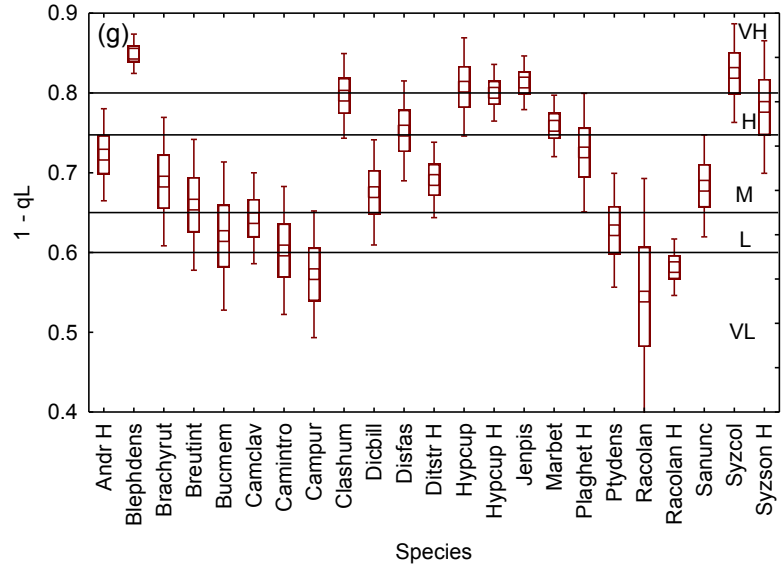


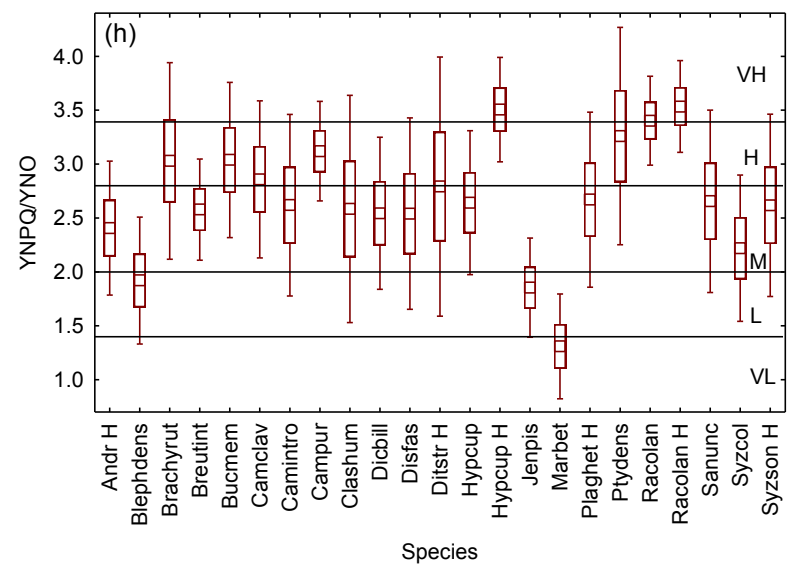
Figure 4.18. Joint plot from Correspondence Analysis of habitat and sub-groups based on structural and photosynthetic traits.











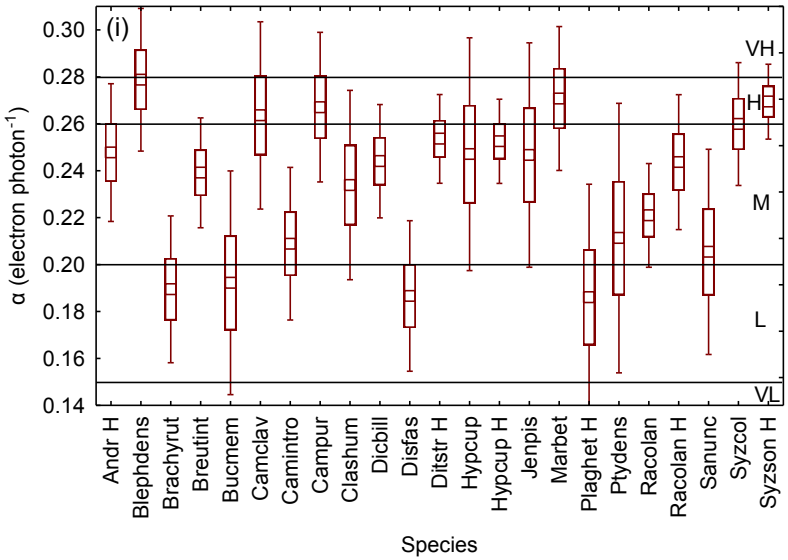


Figure 5.1 (a) to (i). Boxplots of the trait values for all the bryophyte plant species. Where H is indicated the samples were from high altitude. Otherwise samples were from low altitude. Small central square is the mean, rectangle shows the standard error and whisker shows the 95% confidence limits**.**

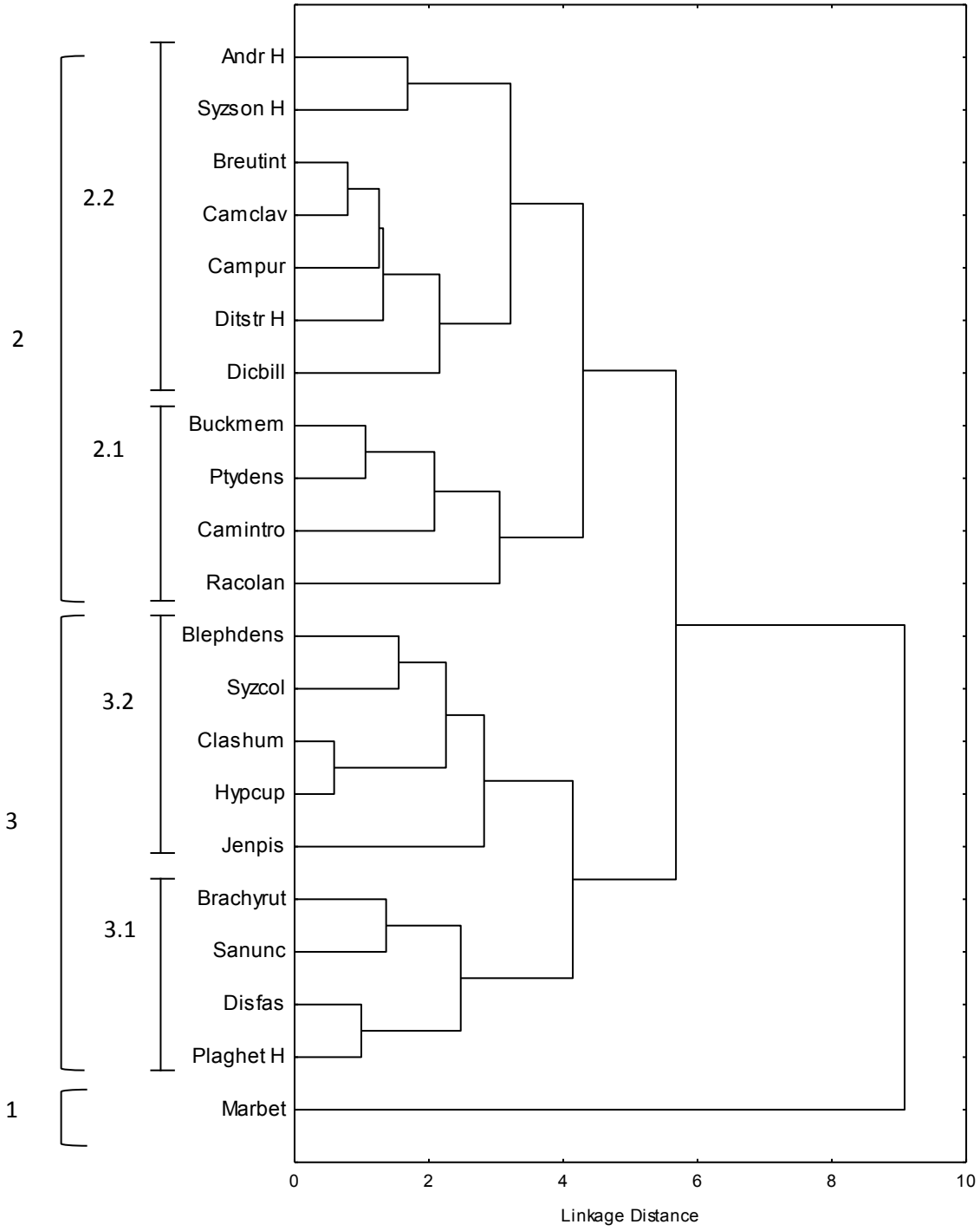


Figure 5.2. Clustering of species by their scores on the three principal components yielded by the PCA of the photosynthetic trait values.

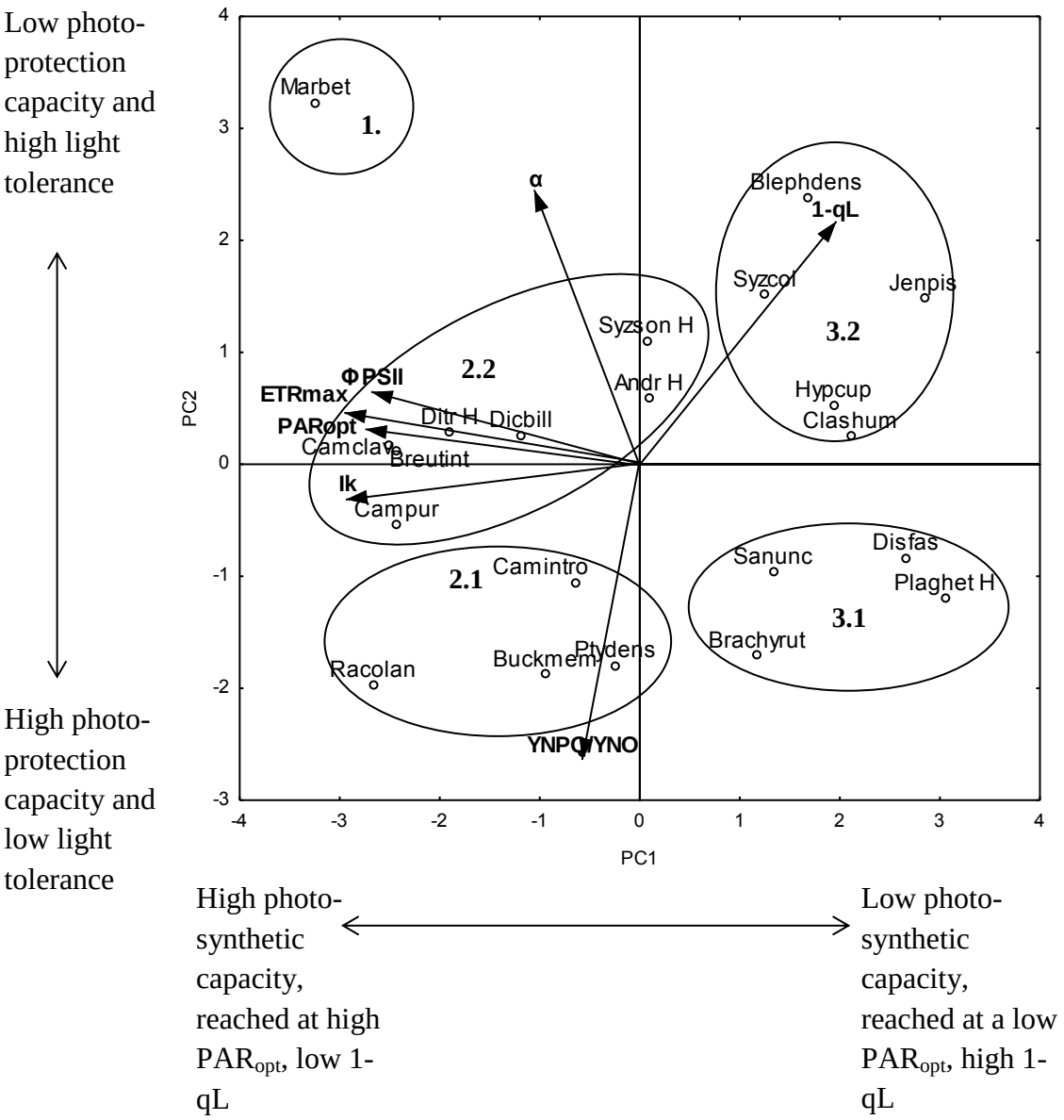


Figure 5.3. Species/ trait biplot for principal component 1 and 2 yielded by the PCA of the photosynthetic trait values.

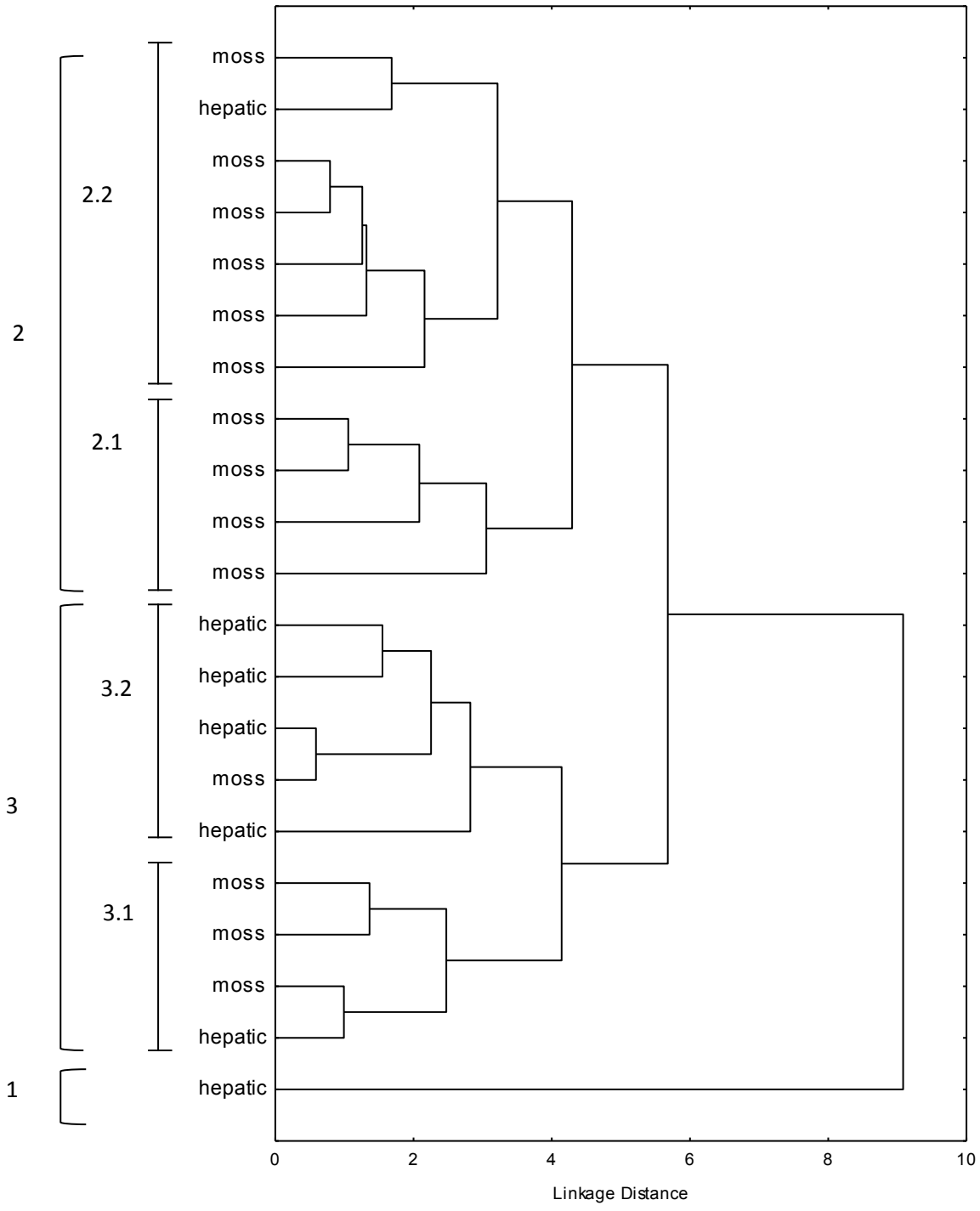


Figure 5.4. Phylum of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

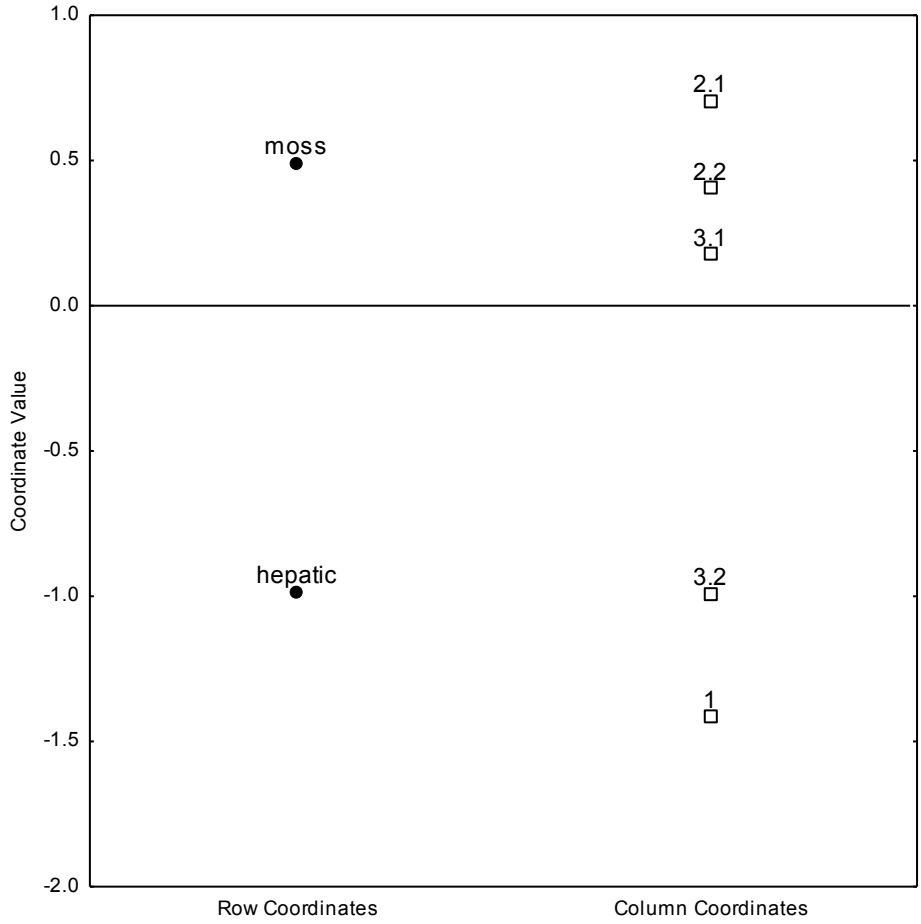


Figure 5.5. Joint plot from Correspondence Analysis of phylum and the sub-groups based on photosynthetic traits.

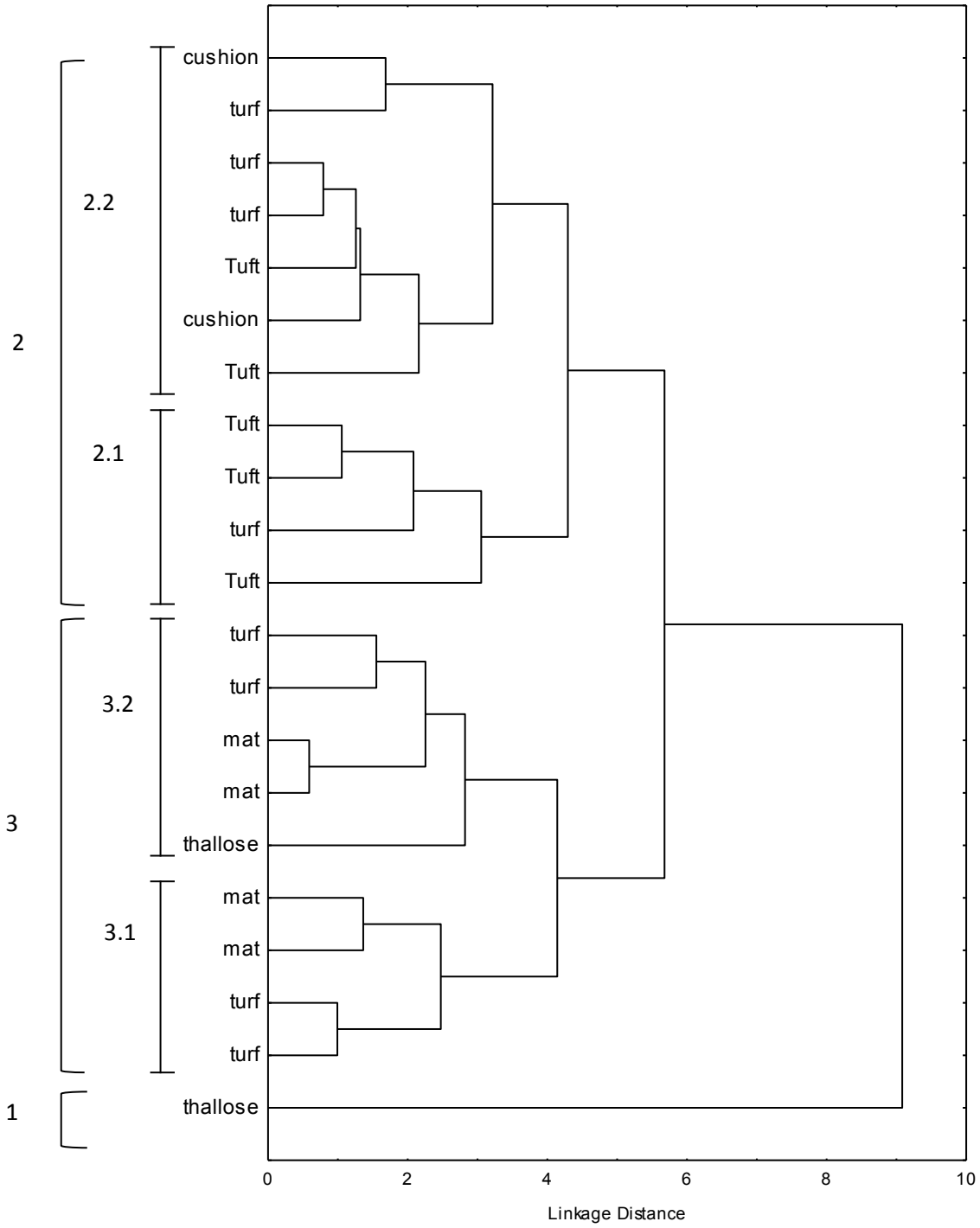


Figure 5.6. Life form of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

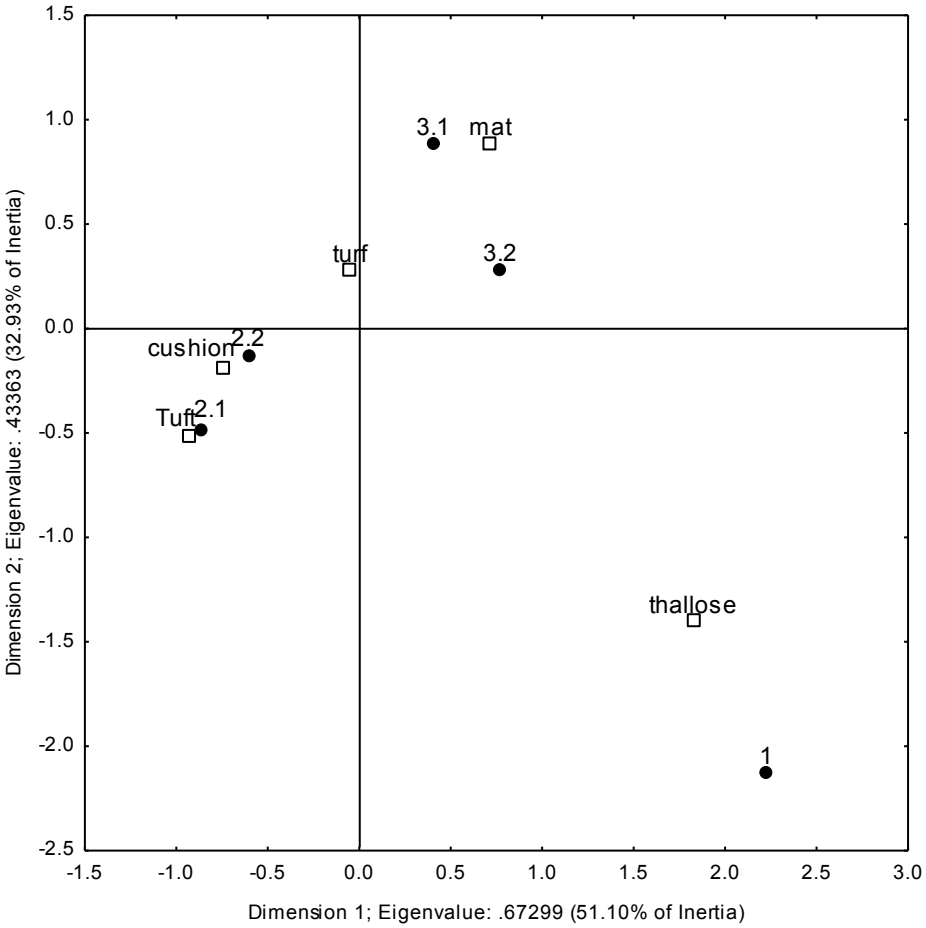


Figure 5.7. Joint plot from Correspondence Analysis of life form and the sub-groups based on photosynthetic traits.

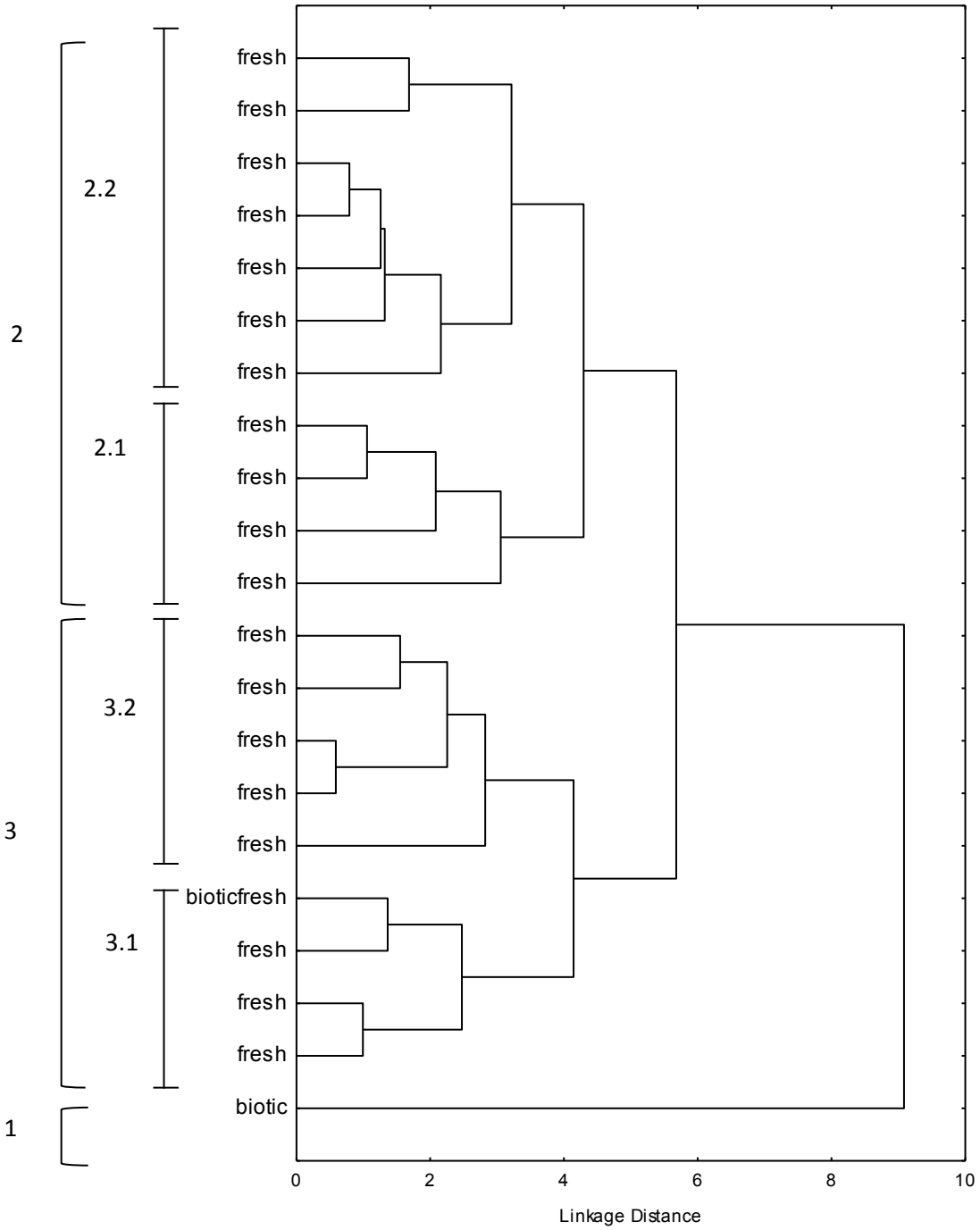


Figure 5.8. Habitat of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

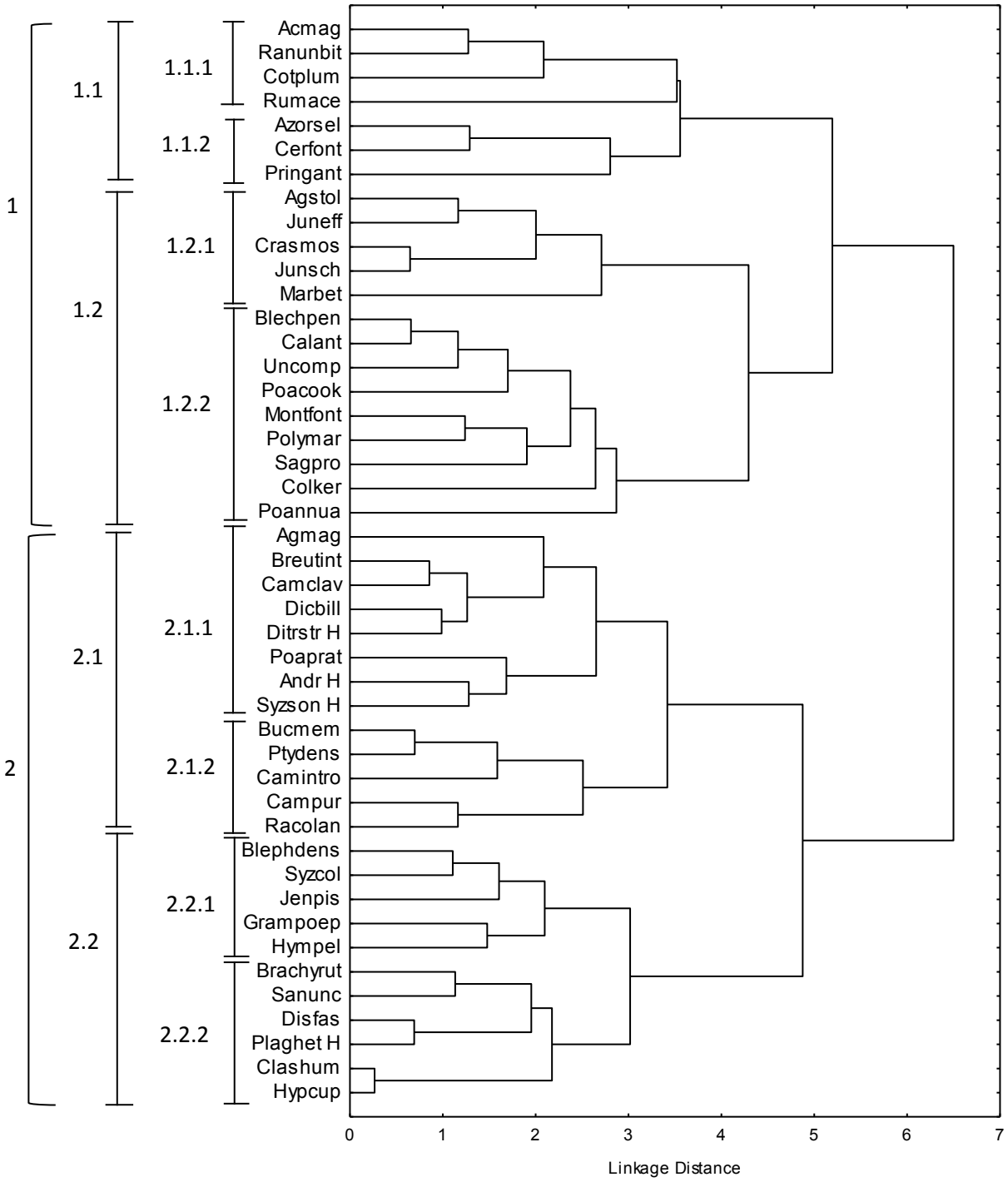


Figure 6.1. Clustering of species by their scores on the first three principal axes yielded by the PCA of the photosynthetic trait values.

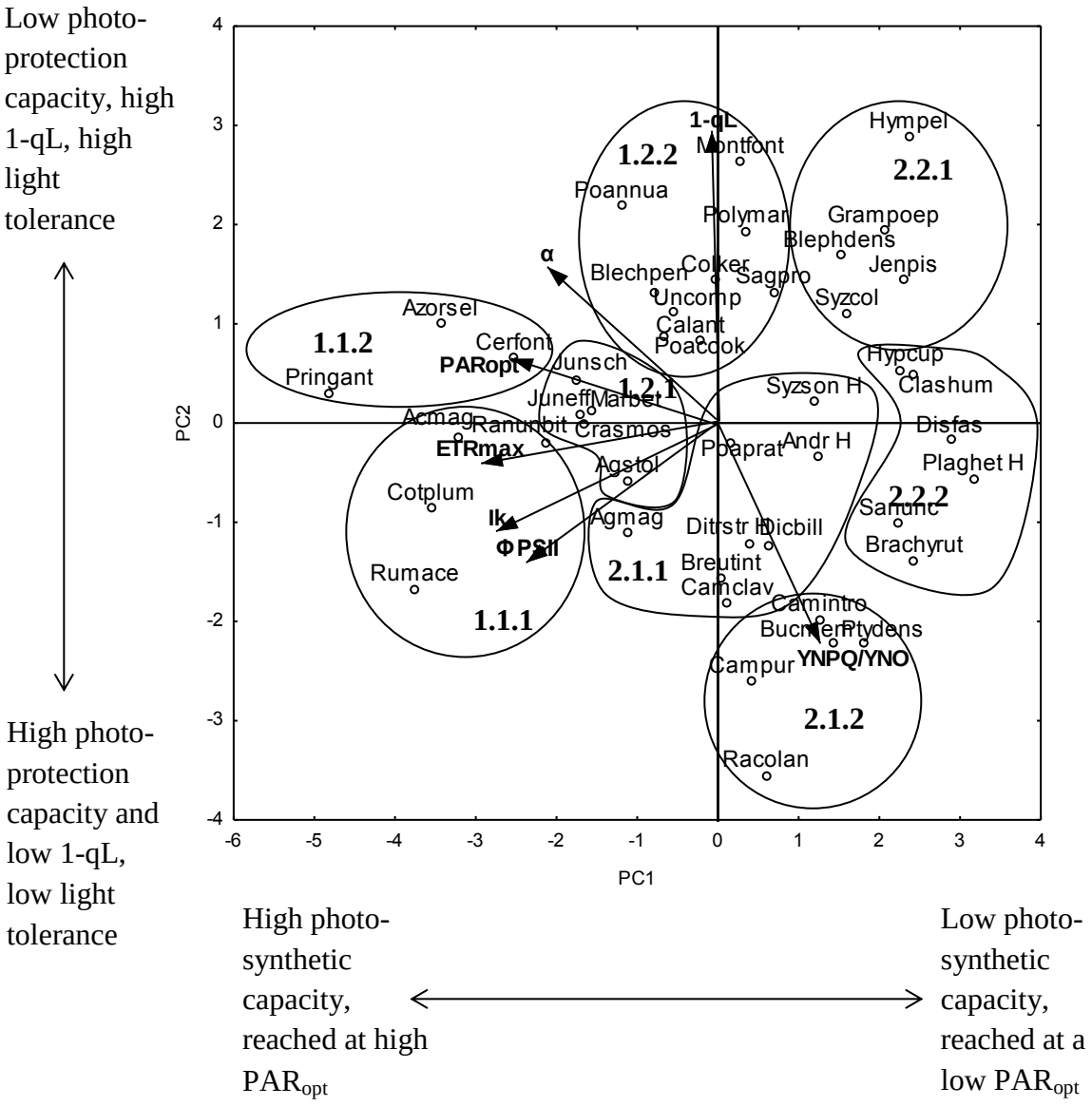


Figure 6.2. Species/ trait biplot for principal components 1 and 2 yielded by the PCA of the photosynthetic trait values.

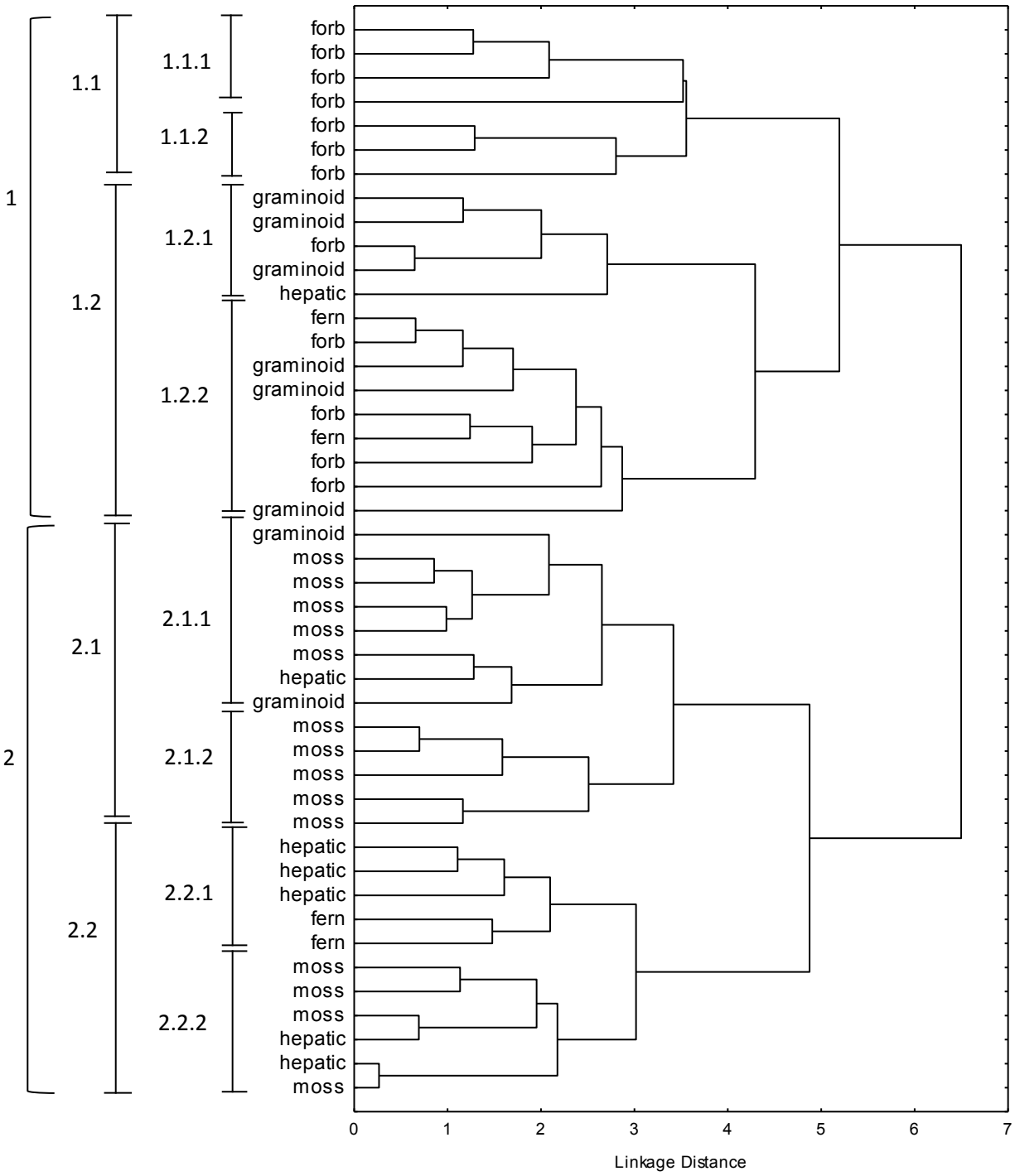


Figure 6.3. Plant habit/phylum of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

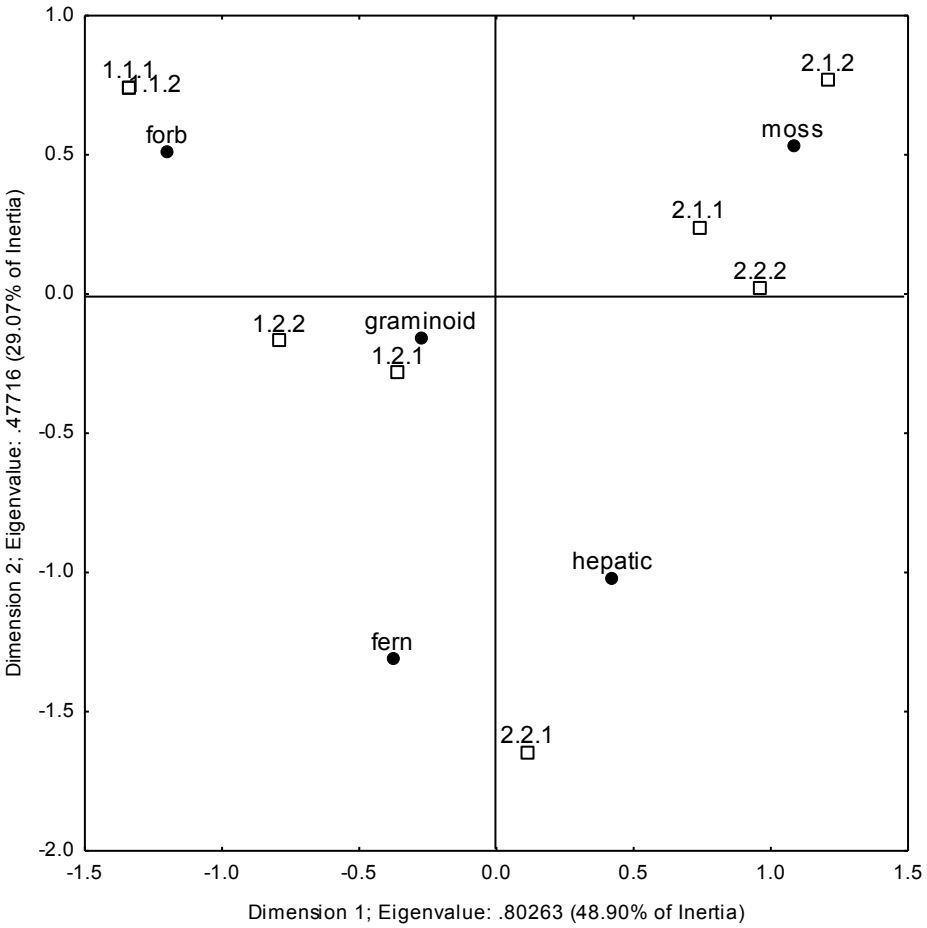


Figure 6.4. Joint plot from Correspondence Analysis of habit (vascular species) or phylum (bryophyte species) and the sub-groups based on the photosynthetic traits.

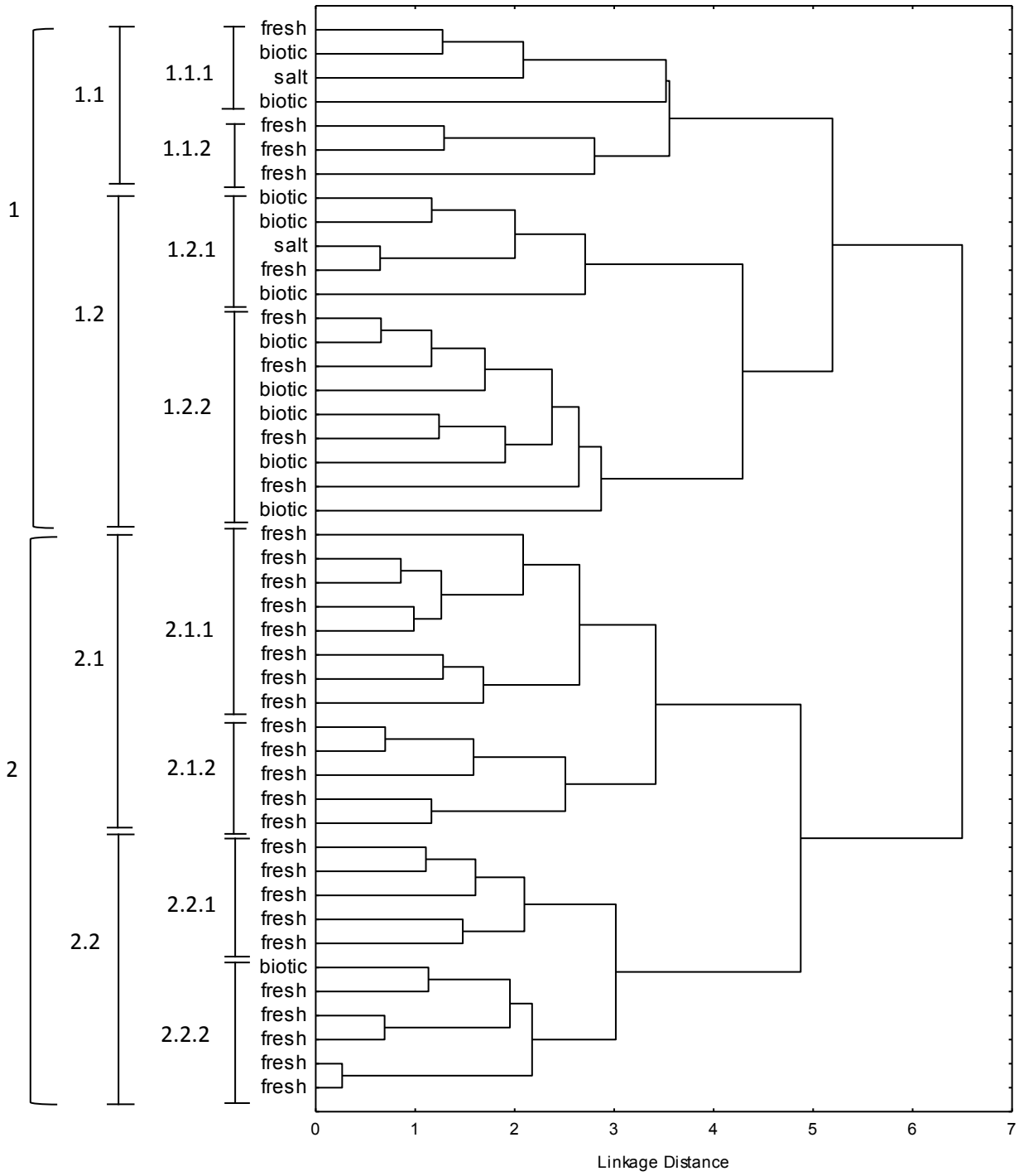


Figure 6.5. Habitat of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

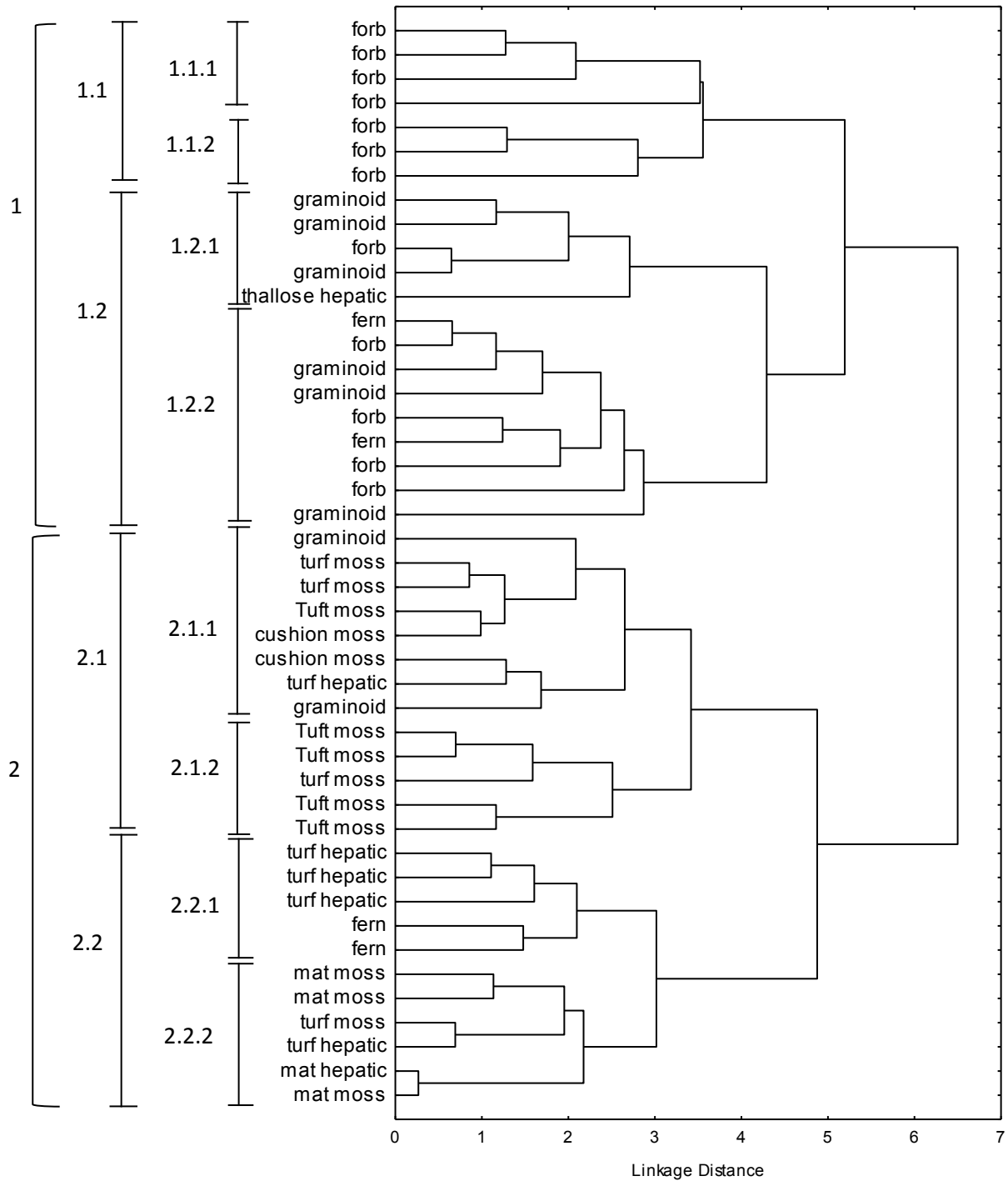


Figure 6.6. Habit/life form of the species clustered by their scores on the first three principal components yielded by the PCA of the photosynthetic trait values.

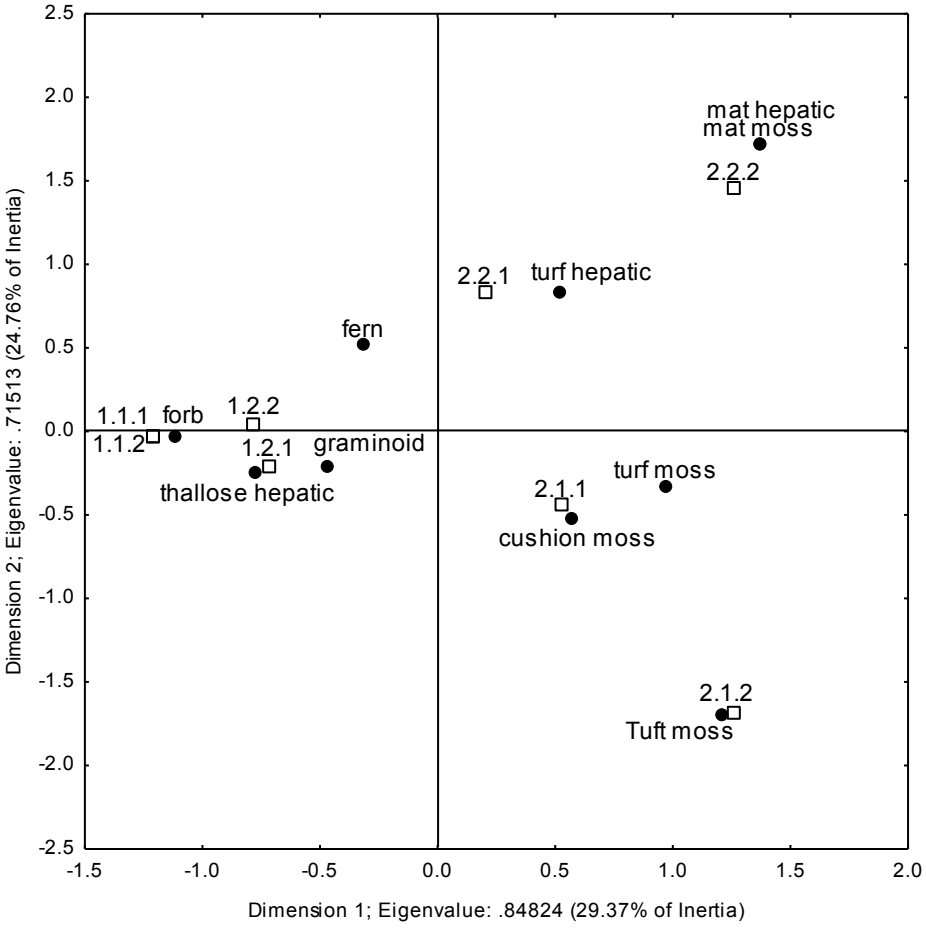


Figure 6.7. Joint plot from Correspondence Analysis of habit (vascular species) or life form (bryophyte species) and the sub-groups based on the photosynthetic traits.

Tables

Table 2.1. Vascular species sampled and sites at which they were sampled. High altitude sites are indicated in bold. Site localities are shown in Fig. 2.1.

Vascular species	Life form/habit	Sites numbers
Acaena magellanica	Forb	34, 35, 36, 37
Agrostis magellanica	Graminoid	22, 23, 24, 25, **62, 63, 65, 68**
Agrostis stolonifera	Graminoid	13,14, 15, 16, 30, 31, 32, 33
Azorella selago	Forb	38, 39, 40, 41, **62, 63, 65, 68**
Blechnum penna-marina	Fern	34, 35, 36, 37, **62, 63, 65, 68**
Callitriche antarctica	Forb	13, 14, 15, 16
Cerastium fontanum	Forb	53, 54, 55, 56
Colobanthus kerguelensis	Forb	42
Cotula plumosa	Forb	1, 2, 3, 4
Crassula moschata	Forb	1, 2, 3, 4
Grammitis poeppigeana	Fern	43
Hymenophyllum peltatum	Fern	43
Juncus effusus	Graminoid	50, 51, 52
Juncus scheuchzerioides	Graminoid	22, 23, 24, 25
Montia fontana	Forb	13, 14, 15, 16
Poa annua	Graminoid	13, 14, 15, 16
Poa cookii	Graminoid	34, 35, 36, 37, **62, 64, 66, 68**
Poa pratensis	Graminoid	57, 58, 59, 60
Polystichum marionense	Fern	44, 45, 46, 47
Potamogeton nodosus	Forb	49
Pringlea antiscorbutica	Forb	48
Ranunculus biternatus	Forb	5, 6, 7, 8
Rumex acetosella	Forb	61
Sagina procumbens	Forb	9, 10, 11, 12
Uncinia compacta	Graminoid	22, 23, 24, 25, **62, 63, 67, 68**

Table 2.2. Bryophyte species sampled, their life form and the sites at which they were sampled. High altitude sites are indicated in bold. Site localities are shown in Fig. 2.1 and Appendix 1 contains photographs and descriptions of the sites

Bryophyte Species	Life form	Sites sampled
Andreaea sp.	Cushion moss	**62, 63, 65, 68**
Blepharidophyllum densifolium	Turf hepatic	22, 23, 24, 25
Brachythecium rutabulum	Mat moss	34, 35, 36, 37
Breutelia integrifolia	Turf moss	26, 27, 28, 29
Bucklandiella membranaceae	Tuft moss	38, 39, 40, 41
Campylopus clavatus	Tuft moss	22, 23, 24, 25
Campylopus introflexus	Turf moss	22, 23, 24, 25
Campylopus purpureocaulis	Tuft moss	22, 23, 24, 25
Clasmatocolea humilis	Mat hepatic	22, 23, 24, 25
Dicranoloma billardierei	Tuft moss	21, 22, 23, 25
Distichophyllum fasciculatum	Turf moss	22, 23, 24, 25
Ditrichum strictum	Cushion moss	**62, 63, 65, 68**
Hypnum cupressiforme	Mat moss	38, 39, 40, 41, **62, 63, 65, 68**
Jensenia pisicolor	Turf hepatic	22, 23, 24, 25
Marchantia berteroana	Thallose hepatic	17, 18, 19,20
Plagiochila heterodonta	Turf hepatic	**62, 63, 65, 68**
Ptychomnion densifolium	Tuft moss	22, 23, 24, 25
Racomitrium lanuginosum	Tuft moss	22, 23, 24, 25, **62, 63, 65, 68**
Sanionia uncinata	Mat moss	34, 35, 36, 37
Syzygiella colorata	Turf hepatic	22, 23, 24, 25
Syzygiella sonderi	Turf hepatic	**62, 63, 65, 68**

Table 2.3. Plant traits measured in the study. N is the target number of individual plants of a species measured at each site. Where there are two numbers, [a] is the number of individual plants and [b] the number of leaves/roots measured on each individual.

Plant Functional traits	Measurement unit	N	High(H) and/or Low (L) altitude	Bryophytes (B) and/or Vascular (V) plants
Vegetative trait				
Plant height	mm	25	H,L	B,V
Leaf traits				
Leaf area	mm^2	$10^a,2^b$	H,L	V
Leaf dry mass	mg	$10^a,2^b$	H,L	V
Specific leaf area	$mm^2\ mg^{-1}$	$10^a,2^b$	H,L	V
Relative water content	$g\ g^{-1}$	$10^a,2^b$	H,L	V
Leaf dry matter content	$mg\ g^{-1}$	$10^a,2^b$	H,L	V
Chlorophyll content	$mg\ m^{-2}$	$10^a,2^b$	H,L	B,V
Stomatal density	stomata mm^{-2}	$5^a,1^b$	L	V
Stem trait				
Stem specific density	$mg\ mm^{-3}$	10	H,L	V
Below-ground traits				
Root :shoot mass ratio	$g\ g^{-1}$	10	L	V
Specific root length	$m\ g^{-1}$	2	H,L	V
Root Diameter	mm	$10^a,2^b$	H,L	V
Physiological traits				
Optimal quantum yield of photosynthesis (Fv/Fm)	unitless	2	H,L	B,V
Effective quantum yield of photosynthesis (ΦPSII)	unitless	2	H,L	B,V
Proportion of closed PSII reaction centers Photochemical quenching (1-qL)	unitless	2	H,L	B,V
Quantum yield of regulated heat dissipation (YNPQ/YNO)	unitless	2	H,L	B,V
Photosynthetic electron transport rate (ETR)	µmol electrons $m^{-2}\ s^{-1}$	2	H,L	B,V
Initial slope of ETR: PAR response (α)	electron $photon^{-1}$	2	H,L	B,V
Maximum ETR (ETR_{max})	µmol electrons $m^{-2}\ s^{-1}$	2	H,L	B,V
Maximum PAR (PAR_{opt})	µmol photons $m^{-2}\ s^{-1}$	2	H,L	B,V
Onset of light saturation of ETR (I_k)	µmol photons $m^{-2}\ s^{-1}$	2	H,L	B,V

Table 2.4. Photosynthetically active radiation levels and durations of the light response steps for (i) vascular plants and (ii) bryophytes. Steps marked with an asterisk form part of the induction component of the light response measurement protocol.

(i)

Step	PAR (µmol photons m^{-2} s^{-1})	Duration of exposure (sec)
1*	31	120
2*	101	180
3*	198	240
4*	363	180
5*	619	240
6*	981	180
1	2	180
2	31	180
3	64	180
4	101	180
5	141	180
6	198	180
7	271	180
8	363	180
9	619	180
10	981	180
11	1386	180
12	1663	180
13	2015	180

(ii)

Step	PAR (µmol photons m^{-2} s^{-1})	Duration of exposure (sec)
1*	10	60
2*	44	180
3*	144	180
4*	200	240
1	4	120
2	10	120
3	44	120
4	92	120
5	144	120
6	200	120
7	280	120
8	384	120
9	513	120
10	670	120
11	876	120
12	1114	120

Table 3.1. Abbreviations of plant traits used in subsequent tables.

Trait	Description
PH	Plant height
LA	Leaf area
LDM	Leaf dry mass
SLA	Specific leaf area
LDMC	Leaf dry matter content
Chl	Chlorophyll content
SD	Stomatal density (Abaxial and Adaxial)
RWC	Leaf relative water content
SSD	Stem specific density
R:S	Root:Shoot mass ratio
SRL	Specific root length
RD	Root diameter
Fv/Fm	Optimal quantum yield of photosynthesis
ϕPSII	Effective quantum yield of photosynthesis
1-qL	Proportion of closed PSII reaction centres
YNPQ/YNO	Quantum yield of regulated heat dissipation
α	Initial slope of ETR: PAR response
ETR_{max}	Maximum photosynthetic electron transport rate
PAR_{opt}	The PAR value giving ETR_{max}
I_k	Onset of light saturation of ETR

Table 3.2. Calculated probability values (*p-values*) for the between-site differences in plant trait values for vascular plant species at low altitudes. From one way anova. All degrees of freedom = 3, except where indicated otherwise in brackets. Trait abbreviations are those in Table 3.1.

Species	PH (mm)	LA (mm^2)	LDM (mg)	SLA (mm^2 mg^{-1})	LDMC (mg g^{-1})	Chl (mg m^{-2})	SD (stomas per mm^2)	LRWC (%)	SSD (mg mm^{-3})	R:S (g g^{-1})	SRL (m g^{-1})
Ac. magellanica	**<0.001**	0.406	**<0.001**	**<0.001**	**<0.001**	**<0.001**	ND	**0.007**	0.391	ND	**0.011**
Ag. magellanica	**<0.001**	**<0.001**	**<0.001**	**0.021**	**0.003**	**0.004**	**<0.001**	**0.047**	0.185	**<0.001**(2)	0.784
A. selago	**<0.001**	**0.006**	**<0.001**	**0.012**	0.404	**0.014**	**0.001**	**0.005**	**0.019**	ND	0.922
A. stolonifera	**<0.001**	**<0.001**	**0.002**	**0.003**	0.094	**<0.001**	**<0.001**	**0.000**	**0.005**	**0.001**	**0.004**
B. penna-marina	**0.003**	**0.003**	0.409	**<0.001**	**<0.001**	**<0.001**	0.394	**<0.001**	0.099	ND	0.283
C. antarctica	**<0.001**	**0.026**	0.407	0.072	0.130	0.556	**0.009**	**0.007**	0.759	**<0.001**(1)	0.291
C. fontanum	0.344	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	**0.001**	**<0.001**	0.377	ND	-
C. moschata	**<0.001**	0.978	0.226	0.576	0.704	0.156	0.463	**0.029**	0.055	-	0.360
C. plumosa	**<0.001**	**<0.001**	**<0.001**	0.661	**<0.001**	**<0.001**	**0.002**	**<0.001**	0.444	0.084(2)	0.056
J. effusus	**<0.001**(2)	-	-	-	-	0.220(2)	0.098 (1)	-	**<0.001**(2)	ND	0.267 (1)
J. scheuchzerioides	**<0.001**	**<0.001**	**<0.001**	0.195	0.539	**<0.001**	0.412	**<0.001**	**<0.001**	ND	0.057
M. fontana	**<0.001**	**0.004**	0.929	**0.004**	**<0.001**	0.145	0.205	0.149	**<0.001**	0.246	0.299
P. annua	0.136	**0.019**	**0.001**	**0.001**	0.554	**<0.001**	0.538	0.588	0.136	-	**0.034**
P. cookii	**0.027**	0.182	**0.015**	**<0.001**	**<0.001**	**<0.001**	ND	**0.005**	**<0.001**	ND	0.078
P. marionense	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.180	ND	0.130
P. pratensis	0.116	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.054**	**0.021**	**<0.001**	0.443	ND	-
R. biternatus	**<0.001**	**<0.001**	**0.008**	**<0.001**	**<0.001**	0.743	**0.006**	0.093	**<0.001**	0.346(1)	0.138
S. procumbens	**0.014**	**0.001**	**0.015**	0.071	**<0.001**	0.741	ND	**0.008**	0.092	ND	-
U. compacta	0.133	**<0.001**	**<0.001**	**<0.001**	0.280	**<0.001**	**0.027**	**<0.001**	0.188	**0.001**(1)	0.168

Table 3.2 (continued)

Species	RD (mm)	Fv/Fm	ΦPSII	1-qL	YNPQ/YNO	α (electron photon^{-1})	ETR_{max} (µmol electrons m^{-2} s^{-1})	PAR_{opt} (µmol photons m^{-2} s^{-1})	I_k (µmol photons m^{-2} s^{-1})
Ac. magellanica	**<0.001**	0.152	0.895	0.856	0.605	0.721	0.803	0.649	0.825
Ag. magellanica	**<0.001**	0.866	0.339	0.304	0.466	0.474	0.337	0.354	0.421
A. selago	**<0.001**	0.522	0.562	0.646	0.154	0.360	0.919	0.719	0.646
A. stolonifera	**<0.001**	0.356	0.883	0.265	0.163	0.262	0.956	0.289	0.994
B. penna-marina	0.453	0.839	0.733	0.664	**0.048**	0.688	0.990	0.926	0.994
C. antarctica	0.339	0.633	0.343	**0.049**	0.070	0.752	0.800	0.878	0.876
C. fontanum	-	-	-	-	-	-	-	-	-
C. moschata	**0.001**	0.512	0.879	0.935	0.703	0.196	0.698	0.396	0.933
C. plumosa	**0.010**	0.455	0.681	0.493	0.747	0.649	0.550	0.210	0.486
J. effusus	**0.004** (1)	-	-	-	-	-	-	-	-
J. scheuchzerioides	**<0.001**	0.705	0.283	0.495	0.579	0.588	0.742	0.758	0.736
M. fontana	**0.001**	-	-	-	-	-	-	-	-
P. annua	**<0.001**	-	-	-	-	-	-	-	-
P. cookii	**0.030**	0.444	0.288	0.273	0.135	0.455	0.477	0.648	0.456
P. marionense	**<0.001**	-	-	-	-	-	-	-	-
P. pratensis	0.561 (1)	-	-	-	-	-	-	-	-
R. biternatus	**<0.001**	0.105	0.898	0.970	0.331	0.444	0.455	0.265	0.391
S. procumbens	-	0.214	0.883	0.913	0.875	0.332	0.395	0.219	0.551
U. compacta	**0.006**	0.343	0.402	0.213	0.829	0.280	0.937	**0.017**	0.749

Table 3.3. Calculated probability values (*p-values*) for the between-site differences in plant trait values for vascular plant species at high altitudes. From one way anova. All degrees of freedom = 3. Trait abbreviations are those in Table 3.1.

Species	PH (mm)	LA (mm^2)	LDM (mg)	SLA (mm^2 mg^{-1})	LDMC (mg g^{-1})	Chl (mg m^{-2})	LRWC (%)	SSD (mg mm^{-3})	SRL (m g^{-1})	RD (mm)	Fv/Fm
Ag. magellanica	**<0.001**	**0.016**	**0.001**	**<0.001**	**<0.001**	**<0.001**	0.120	0.500	**0.014**	0.012	0.423
A. selago	0.987	**0.024**	**<0.001**	**0.021**	0.292	**0.016**	0.097	0.542	0.363	0.196	0.824
B. penna-marina	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.108	**<0.001**	**<0.001**	0.352	0.341	0.050	0.798
P. cookii	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.017**	0.228	0.780
U. compacta	0.231	**<0.001**	**<0.001**	**<0.001**	0.084	**0.003**	**0.027**	0.504	0.449	0.270	0.568

Species	ΦPSII	1-qL	YNPQ/YNO	α (electron $photon^{-1}$)	ETR_{max} (µmol electrons m^{-2} s^{-1})	PAR_{opt} (µmol photons m^{-2} s^{-1})	I_k (µmol photons m^{-2} s^{-1})
Ag. magellanica	0.403	0.995	0.869	0.570	0.897	0.922	0.952
A. selago	0.463	0.997	0.782	0.998	0.076	0.315	0.092
B. penna-marina	0.349	0.998	0.783	0.867	0.758	0.883	0.738
P. cookii	0.310	0.994	0.478	0.700	0.276	0.256	0.325
U. compacta	0.535	0.971	0.991	0.508	0.457	0.886	0.130

Table 3.4. Calculated probability values (*p-values*) for the between-altitude differences in plant trait values for vascular plant species. All degrees of freedom =1. H and L indicate whether the trait mean value is higher at high altitude or low altitude, respectively. See Appendix tables A1 to A20 for trait means and standard errors at low altitude and tables A21 to A38 for the means and standard errors at high altitude.

Species	PH (mm)	LA (mm^2)	LDM (mg)	SLA ($mm^2\ mg^{-1}$)	LDMC ($mg\ g^{-1}$)	Chl ($mg\ m^{-2}$)	RWC (%)	SSD ($mg\ mm^{-3}$)	SRL ($m\ g^{-1}$)
Ag. magellanica	**<0.001** (L)	**<0.001** (L)	**<0.001** (L)	**0.008** (H)	0.135 (H)	**0.008** (L)	**0.018** (L)	**0.015** (H)	**<0.001** (H)
A. selago	**<0.001** (H)	**0.001** (L)	0.115 (L)	0.076 (L)	**0.008** (H)	**<0.001** (H)	**0.007** (L)	**0.021** (H)	0.126 (H)
B. penna-marina	**<0.001** (L)	**<0.001** (L)	**<0.001** (L)	**0.002** (H)	**0.017** (H)	**<0.001** (L)	**<0.001** (L)	0.177 (H)	0.828 (H)
P. cookii	**<0.001** (L)	**<0.001** (L)	**<0.001** (L)	0.812 (L)	0.222 (L)	**<0.001** (H)	0.322 (L)	**0.017** (H)	0.062 (H)
U. compacta	**<0.001** (L)	**<0.001** (L)	**<0.001** (L)	**0.011** (H)	**<0.001** (L)	**<0.001** (L)	0.409 (H)	0.432 (L)	**<0.001** (H)

Species	RD (mm)	Fv/Fm	ΦPSII	1-qL	YNPQ/YNO	α (electron $photon^{-1}$)	ETR_{max} (µmol electrons $m^{-2}\ s^{-1}$)	PAR_{opt} (µmol photons $m^{-2}\ s^{-1}$)	I_k (µmol photons $m^{-2}\ s^{-1}$)
Ag. magellanica	**<0.001** (L)	0.059 (L)	0.833 (L)	**0.039** (L)	0.619 (H)	0.634 (L)	0.996 (L)	0.874 (L)	0.997 (H)
A. selago	0.947 (H)	0.975 (H)	0.463 (H)	**0.016** (L)	0.964 (L)	0.760 (L)	0.160 (H)	0.714 (H)	0.058 (H)
B. penna-marina	0.558 (H)	**0.043** (L)	0.364 (H)	**0.020** (L)	0.320 (L)	0.448 (L)	0.894 (H)	0.736 (L)	0.596 (H)
P. cookii	**<0.001** (L)	0.678 (L)	0.347 (H)	**0.006** (L)	0.943 (H)	0.136 (L)	0.285 (H)	0.482 (H)	0.260 (H)
U. compacta	**<0.001** (L)	0.607 (L)	0.510 (L)	**0.010** (L)	0.502 (H)	0.908 (L)	0.795 (L)	0.716 (L)	0.853 (L)

Table 4.1. Trait weightings on, and proportion of variance explained by, the first three principal components yielded by the PCA of structural trait values.

Traits	PC1 50.17%	PC2 18.15%	PC3 11.35%
LA	0.857	0.301	-0.189
PH	0.845	0.243	-0.202
LDM	0.888	0.322	-0.230
SLA	-0.731	0.494	-0.152
LDMC	0.574	-0.610	0.007
Chl	0.675	-0.336	0.325
RWC	-0.617	-0.028	0.637
SSD	-0.087	-0.823	-0.421
SRL	-0.664	0.231	-0.372
RD	0.796	0.320	0.392

Table 4.2. Characteristics of the plant groups constructed from the structural traits and shown in Figures 4.1 to 4.6.

Group and magnitudes of trait values	Sub-group and magnitudes of trait values	Species in group
1 High or very high PH, LA, LDM, RD; Moderate or high LDMC, Chl; Low or moderate SLA; Very low RWC; Low SSD, SRL;		*Juncus effusus*, *Polystichum marionense* and *Pringlea antiscorbutica*
2 Low to high PH, LA, LDM; Chl, RWC, RD, SRL; Low to moderate SLA; Moderate to very high SSD; Moderate to very high LDMC;	2.1 Moderate or high PH, LA, LDM, Chl, SSD, RD; Low to high RWC; High or very high LDMC; low to moderate SLA, SRL	*Acaena magellanica*, *Blechnum penna-marina*, *Uncinia compacta*, *Agrostis magellanica* and *Poa cookii*
	2.2 low to high PH, Chl, RWC; high to very high SSD; Moderate to high LDMC low to moderate LA, LDM, SLA, RD; SRL	*Azorella selago*, *Juncus scheuchzerioides*, *Colobanthus kerguelensis*, *Grammitis poeppigeana* and *Poa pratensis*
3 Low to moderate PH, LA, LDMC, Chl, SSD; Very low to moderate LDM; Low to high RD; Low to very high SRL; Moderate to very high RWC; high SLA	3.1 Low to moderate PH, LA, LDMC, Chl, RD, SSD; High SLA; Very low to low LDM; High to very high SRL; High to very high RWC	*Agrostis stolonifera*, *Poa annua*, *Callitriche antarctica*, *Montia fontana*, *Crassula moschata* and *Sagina procumbens*
	3.2 Moderate PH, LA, Chl, LDM; High SLA, RD; Low to moderate LDMC, SSD, SRL; Moderate to very high RWC	*Cerastium fontanum*, *Cotula plumosa*, *Ranunculus biternatus* and *Rumex acetosella*

Table 4.3. Trait weightings on, and proportion of variance explained by, the first three principal components yielded by the PCA of photosynthetic trait values.

Traits	PC1 55.29%	PC2 19.10%	PC3 17.32%
ΦPSII	-0.924	0.249	0.132
1-qL	0.723	-0.573	-0.279
YNPQ/YNO	-0.133	0.769	-0.505
α	-0.223	-0.127	-0.905
ETR_{max}	-0.973	-0.183	-0.032
PAR_{opt}	-0.731	-0.529	-0.173
I_k	-0.971	-0.160	0.106

Table 4.4. Characteristics of the plant groups constructed from the photosynthetic traits and shown in Figures 4.7 to 4.12.

Group and typical trait value	Sub-group and typical trait value	Species in group
1 Moderate to high ETR_{max}, Ik, ϕPSII, α	1.1 Very high ETR_{max}, ϕPSII, PAR_{opt}, I_k; moderate to high 1-qL; moderate α; low YNPQ/YNO	*Azorella selago, Pringlea antiscorbutica*
	1.2 High to very high $ETR_{max,}$ ϕPSII; high PAR_{opt}, I_k, YNPQ/YNO,α; moderate 1-qL	*Acaena magellanica, Ranunculus biternatus, Cotula plumosa, Rumex acetosella*
	1.3 Moderate to high ETR_{max}; moderate YNPQ/YNO, 1-qL	*Cerastium fontanum, Juncus scheuchzerioides, Crassula moschata, Juncus effusus*
	1.4 Moderate $ETR_{max,}$ $PAR_{opt,}$ Ik; very high YNPQ/YNO, 1-qL, α	*Agrostis stolonifera, Poa pratensis, Agrostis magellanica*
2 Moderate to low ETR_{max}, Ik, ϕPSII, α	2.1 Moderate ETR_{max}; low YNPQ/YNO, 1-qL; moderate α	*Poa annua, Colobanthus kerguelensis, Uncinia compacta*
	2.2 Low to moderate ETR_{max}; moderate to high YNPQ/YNO; low 1-qL; high α	*Montia fontana, Polystichum marionense, Blechnum penna-marina, Callitriche antarctica, Poa cookii*
	2.3 Very low to Low ETR_{max}, ϕPSII, 1-qL; low I_k, α; moderate YNPQ/YNO	*Hymenophyllum peltatum, Sagina procumbens, Grammitis poeppigeana*

Table 4.5. Trait weightings on, and proportion of variance explained by, the first three principal components yielded by the PCA of structural and photosynthetic trait values.

Traits	PC1 37.75%	PC2 20.69%	PC3 12.72%
PH	0.646	0.083	0.166
SLA	-0.880	-0.059	-0.078
Chl	0.831	-0.128	-0.186
LDMC	0.747	0.417	-0.304
SRL	-0.728	0.117	-0.318
ETR_{max}	0.056	-0.657	0.608
α	0.215	-0.798	-0.204
YNPQ/YNO	0.028	-0.610	-0.587

Table 4.6. Characteristics of plant groups constructed from the structural and photosynthetic traits and shown in Figures 4.13 to 4.18.

Group and typical trait value	Sub-group and typical trait value	Species in group
1 Very low to moderate PH, LDMC, Chl content; moderate to very high SLA, SRL; low to high ETR_{max}, YNPQ/YNO, α	1.1.1 Very low PH, LDMC, Chl content; very high SRL, SLA; low to moderate ETR_{max}, YNPQ/YNO, α	*Sagina procumbens, Callitriche antarctica, Crassula moschata, Montia fontana*
	1.1.2 Low PH, LDMC, Chl content; High SLA; low to high SRL; low ETR_{max}, YNPQ/YNO, α	*Poa annua, Colobanthus kerguelensis, Agrostis stolonifera*
	1.2.1 Moderate PH, LDMC, Chl content, SRL, SLA; high ETR_{max} ; low to moderate YNPQ/YNO, moderate to high α	*Rumex acetosella, Cerastium fontanum, Azorella selago*
	1.2.2 Moderate PH, LDMC, Chl content, SRL, SLA; high ETR_{max}, α; high to very high YNPQ/YNO	*Acaena magellanica, Ranunculus biternatus, Cotula plumosa*
2 Moderate to very high PH, LDMC, Chl content; low to high SLA, SRL; low to high ETR_{max}; moderate to very high YNPQ/YNO; low to very high α		*Grammitis poeppigeana, Poa pratensis, Uncinia compacta, Juncus effusus, Polystichum marionense, Agrostis magellanica, Juncus scheuchzerioides, Blechnum penna-marina, Poa cookii*

Table 5.1. Probability values from Anova testing of the between-site differences in plant trait values for bryophyte plant species at low altitudes. All degrees of freedom = 3. Trait abbreviations explained in Table 5.1.

Species	PH (mm)	Chl (mm^2)	Fv/Fm	ΦPSII	1-qL	YNPQ/ YNO	α (electron $photon^{-1}$)	ETR_{max} (µmol electrons m^{-2} s^{-1})	PAR_{opt} (µmol photons m^{-2} s^{-1})	I_k (µmol photons m^{-2} s^{-1})
B. densifolium	**<0.001**	**0.027**	0.323	0.205	0.114	0.601	0.765	0.846	0.949	0.873
B. integrifolia	**<0.001**	0.321	**0.025**	0.827	0.258	0.739	0.074	0.586	0.430	0.343
B. rutabulum	**<0.001**	**<0.001**	0.395	0.136	0.181	**0.048**	0.996	0.410	0.669	0.740
B. membranaceae	**0.010**	**0.002**	0.846	0.643	0.877	0.114	0.918	0.774	0.602	0.646
C. clavatus	**<0.001**	0.530	0.595	0.903	0.485	0.709	0.326	0.819	0.507	0.924
C. humilis	**<0.001**	0.519	0.081	0.857	0.944	0.428	0.383	0.308	0.532	0.773
C. introflexus	**<0.001**	**<0.001**	0.929	0.598	0.275	0.834	0.437	0.975	0.942	0.944
C. purpureocaulis	**<0.001**	0.135	0.188	0.500	0.472	0.120	0.610	0.104	0.173	0.517
D. billardierei	**<0.001**	**0.001**	0.537	0.750	0.105	0.753	**0.006**	0.072	0.495	0.069
D. fasciculatum	**<0.001**	0.119	0.877	0.699	0.437	0.072	0.928	0.161	**0.011**	**0.019**
H. cupressiforme	**0.003**	0.088	0.577	0.753	0.660	0.730	0.563	0.186	0.441	**0.037**
S. colorata	**<0.001**	**0.025**	**0.006**	**0.049**	0.605	0.943	0.218	0.550	0.080	0.591
J. pisicolor	**<0.001**	**<0.001**	0.774	0.742	0.840	0.745	0.670	0.916	0.551	0.678
M. berteroana	**<0.001**	**<0.001**	0.616	0.163	0.829	0.936	0.409	0.638	0.941	0.768
P. densifolium	**<0.001**	**<0.001**	0.952	0.499	0.128	0.585	0.922	0.987	0.650	0.808
R. lanuginosum	**<0.001**	**0.013**	0.884	0.240	0.275	0.842	0.406	0.555	0.720	0.745
S. uncinata	**0.012**	**<0.001**	0.736	0.827	0.136	0.305	0.919	0.289	**0.027**	**0.007**

Table 5.2. Probability values from Anova testing of the between-site differences in plant trait values for bryophyte plant species at high altitudes. All degrees of freedom = 3.

Species	PH (mm)	Chl (mg m^{-2})	Fv/Fm	ΦPSII	1-qL	YNPQ/YNO	α (electron $photon^{-1}$)	ETR_{max} (µmol electrons m^{-2} s^{-1})	PAR_{opt} (µmol photons m^{-2} s^{-1})	I_k (µmol photons m^{-2} s^{-1})
Andreaea sp.	**<0.001**	**0.021**	0.609	0.794	0.853	0.712	0.876	0.312	0.931	0.340
S. sonderi	**<0.001**	**<0.001**	0.950	0.157	0.162	0.134	0.566	0.105	0.573	**0.040**
Ditrichum sp.	**<0.001**	0.132	0.421	0.086	0.959	0.717	0.164	0.565	0.817	0.464
H. cupressiforme	**<0.001**	**0.001**	0.271	**0.035**	0.380	0.814	0.266	0.117	0.169	0.200
P. heterodonta	**<0.001**	**<0.001**	0.932	0.335	**0.043**	0.790	0.670	0.954	0.876	0.967
R. lanuginosum	**<0.001**	**0.004**	0.349	0.527	0.943	0.543	0.510	0.513	0.676	0.946

Table 5.3. Probability values from Anova testing of the between-altitude differences in plant trait values for the two bryophyte plant species that occurred at both low- and high altitude. All degrees of freedom =1. H and L indicate whether the trait mean value is higher at high or low altitude, respectively. See Appendix tables A39 to A48 for trait means and standard errors at low altitude and tables A49 to A58 for the means and standard errors at high altitude.

Species	PH (mm)	Chl (mg m^{-2})	Fv/Fm	ΦPSII	1-qL	YNPQ/YNO	α (electron $photon^{-1}$)	ETR_{max} (µmol electrons m^{-2} s^{-1})	PAR_{opt} (µmol photons m^{-2} s^{-1})	I_k (µmol photons m^{-2} s^{-1})
H. cupressiforme	**<0.001** (H)	**0.001** (H)	0.246 (H)	0.540 (L)	0.811 (L)	**0.027 (H)**	0.806 (H)	0.278 (H)	**0.036** (H)	0.293 (H)
R. lanuginosum	**<0.001** (L)	**<0.001**(H)	0.136 (H)	0.284 (H)	0.574 (H)	0.608 (H)	0.161 (H)	**0.047** (H)	**0.011** (H)	0.201 (H)

Table 5.4. Trait weightings on, and proportion of variance explained by, the first three principal components yielded by the PCA of photosynthetic trait values.

Traits	PC1 59%	PC2 29%	PC3 8%
ϕPSII	-0.892	0.221	-0.320
1-qL	0.651	0.716	0.088
YNPQ/YNO	-0.191	-0.879	0.414
α	-0.347	0.809	0.413
ETR_{max}	-0.985	0.153	-0.040
PAR_{opt}	-0.911	0.114	0.289
I_k	-0.972	-0.101	-0.106

Table 5.5. Characteristics of bryophyte groups constructed from the photosynthetic traits and shown in Figures 5.2 and 5.3.

Group and typical trait value	Sub-group and typical trait value	Species in group
1 Very high ETR_{max}, ϕPSII, I_k; High PAR_{opt}, α, 1-qL; Very low YNPQ/YNO		*Marchantia berteroana*
2 Moderate to high ETR_{max}; Moderate to very high I_k	2.1 Moderate to high PAR_{opt}; Moderate to high ϕPSII; Low to moderate α; Very low to low 1-qL; High to very high YNPQ/YNO	*Bucklandiella membranacea, Campylopus introflexus, Ptychomnion densifolium, Racomitrium lanuginosum*
	2.2 Moderate to very high PAR_{opt}; Moderate to high ϕPSII; Moderate to high α; Low to moderate 1-qL; Moderate to high YNPQ/YNO	*Andreaea* sp., *Breutelia integrifolia, Campylopus clavatus, Campylopus purpureocaulis, Dicranoloma billardierei, Ditrichum strictum, Syzygiella sonderi*
3 Very low to low ETR_{max}, Very low to moderate I_k	3.1 Very low to low PAR_{opt}; Low ϕPSII; Moderate to high YNPQ/YNO; Low to moderate α; Moderate to high 1-qL	*Brachythecium rutabulum, Distichophyllum fasciculatum, Plagiochila heterodonta, Sanionia uncinata*
	3.2 Very low to moderate PAR_{opt}: Very low to low ϕPSII; Low to moderate YNPQ/YNO; Moderate to very high α; very high 1-qL	*Blepharidophyllum densifolium, Clasmatocolea humilis, Hypnum cupressiforme, Jensenia pisicolor, Syzygiella colorata*

Table 6.1. Trait weightings on, and proportion of variance explained by, the first three principal components yielded by the PCA of photosynthetic trait values for vascular and bryophyte species.

Traits	PC1 55.66%	PC2 30.79%	PC3 7.16%
ETR_{max}	-0.980	-0.137	0.023
PAR_{opt}	-0.906	0.151	0.257
I_k	-0.909	-0.368	-0.060
α	-0.706	0.526	0.314
ϕPSII	-0.787	-0.465	-0.269
1-qL	-0.019	0.969	0.029
YNPQ/YNO	0.416	-0.739	0.509

Table 6.2. Characteristics of the plant groups constructed from the photosynthetic traits and shown in Figures 6.1 and 6.2.

1.1	High to very high ETR_{max} reached at high to very high PAR. Onset of electron transport saturation starts at high to very high PAR. Moderate to very high quantum efficiency of electron transport at ETR_{max}. Sharp to very sharp response to light at low light levels. Very low to high capacity for photoprotection. Moderate to high proportion of closed reaction centres at ETR_{max}.	1.1.1	High to very high ETR_{max} reached at high PAR. Onset of electron transport saturation starts at high to very high PAR. Moderate to very high quantum efficiency of electron transport at ETR_{max}. Very sharp response to light at low light levels. Moderate to high capacity for photoprotection. Moderate proportion of closed reaction centres at ETRmax.	*Acaena magellanica,* *Cotula plumosa,* *Ranunculus biternatus,* *Rumex acetosella*
		1.1.2	High to very high ETR_{max} reached at high to very high PAR. Onset of electron transport saturation starts at high to very high PAR. Moderate to high quantum efficiency of electron transport at ETR_{max}. Sharp response to light at low light levels. Very low to low capacity for photoprotection. Moderate to high proportion of closed reaction centres at ETR_{max}.	*Azorella selago,* *Cerastium fontanum,* *Pringlea antiscorbutica*
1.2	Low to high ETR_{max} reached at moderate to high PAR. Onset of electron transport saturation starts at low to moderate PAR. Low to high quantum efficiency of electron transport at ETR_{max}. Moderate to sharp response to light at low light levels. Low to moderate capacity for	1.2.1	Moderate to high ETR_{max} reached at moderate to high PAR. Onset of electron transport saturation starts at moderate PAR. Moderate to high quantum efficiency of electron transport at ETR_{max}. Moderate to sharp response to light at low light levels. Low to moderate capacity for photoprotection.	*Agrostis stolonifera,* *Crassula moschata,* *Juncus effusus,* *Juncus scheuchzerioides,* *Marchantia berteroana*

	photoprotection. Moderate to very high proportion of closed reaction centres at ETR_{max}.		Moderate proportion of closed reaction centres at ETR_{max}.	
		1.2.2	Low to moderate ETR_{max} reached at moderate to high PAR. Onset of electron transport saturation starts at low to moderate PAR. Low to moderate quantum efficiency of electron transport at ETR_{max}. Sharp response to light at low light levels. Low to moderate capacity for photoprotection. High to very high proportion of closed reaction centres at ETR_{max}.	*Blechnum penna-marina*, *Callitriche antarctica*, *Colobanthus kerguelensis*, *Montia fontana*, *Poa annua*, *Poa cookii*, *Polystichum marionense*, *Sagina procumbens*, *Uncinia compacta*
2.1	Low to moderate ETR_{max} reached at low to moderate PAR. Onset of electron transport saturation starts at low to moderate PAR. Moderate quantum efficiency of electron transport at ETR_{max}. Very low to moderate response to light at low light levels. Moderate to very high capacity for photoprotection. Very low to moderate proportion of closed reaction centres at ETR_{max}	2.1.1	Low to moderate ETR_{max} reached at moderate PAR. Onset of electron transport saturation starts at low to moderate PAR. Moderate quantum efficiency of electron transport at ETR_{max}. Low to moderate response to light at low light levels. Moderate to high capacity for photoprotection. Low to moderate proportion of closed reaction centres at ETR_{max}	*Agrostis magellanica*, *Andreaea* sp., *Breutelia integrifolia*, *Campylopus clavatus*, *Dicranoloma billardierei*, *Ditrichum strictum*, *Poa pratensis*, *Syzygiella sonderi*
		2.1.2	Low ETR_{max} reached at low to moderate PAR. Onset of electron transport saturation starts at moderate PAR. Moderate quantum efficiency of electron transport at ETR_{max}. Very low to low response to light at low light levels. Very high capacity for photoprotection. Very low to low proportion of closed reaction	*Bucklandiella membranaceae*, *Campylopus introflexus*, *Campylopus purpureocaulis*, *Ptychomnion densifolium*, *Racomitrium lanuginosum*

			centres at ETR_{max}	
2.2	Very low ETR_{max} reached at very low to low PAR. Onset of electron transport saturation starts at very low to low PAR. Very low to low quantum efficiency of electron transport at ETR_{max}. Very low to moderate response to light at low light levels. Low to high capacity for photoprotection. Moderate to high proportion of closed reaction centres at ETR_{max}.	2.2.1	Very low ETRmax reached at very low to low PAR. Onset of electron transport saturation starts at very low to low PAR. Very low to low quantum efficiency of electron transport at ETR_{max}. Moderate response to light at low light levels. Low capacity for photoprotection. High proportion of closed reaction centres at ETR_{max}.	*Blepharidophyllum densifolium*, *Grammitis poeppigeana*, *Hymenophyllum peltatum*, *Jensenia pisicolor*, *Syzygiella colorata*
		2.2.2	Very low ETR_{max} reached at very low to low PAR. Onset of electron transport saturation starts at very low to low PAR. Low quantum efficiency of electron transport at ETR_{max}. Very low to low response to light at low light levels. High capacity for photoprotection. Moderate proportion of closed reaction centres at ETR_{max}.	*Brachythecium rutabulum*, *Clasmatocolea humilis*, *Distichophyllum fasciculatum*, *Hypnum cupressiforme*, *Plagiochila heterodonta*, *Sanionia uncinata*