Marion Island bryophytes: evidence for functional types based on traits related to photosynthesis and desiccation tolerance

by Jacqueline Nicole Tonkie

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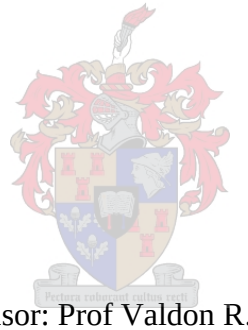

Supervisor: Prof Valdon R. Smith

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Summary

There is currently a worldwide interest in grouping species on the basis of their functional characteristics into plant functional types (PFTs). This reduces the complexity of models that predict the effects of global change on vegetation and ecosystem processes. Marion Island has vegetation dominated by bryophytes and is experiencing intense climate change. However, there is no accepted scheme and no consensus on the most useful traits for a bryophyte PFT classification. This study aimed at grouping 38 of the island bryophyte species into functional groups. A suite of 14 photosynthetic traits related to light or desiccation response were obtained from chlorophyll fluorescence quenching analysis and water relations. The characteristics were subjected to analysis of variance, box plot rankings, principal component and clustering analyses to group the species into functional types. Seven light response groups and nine desiccation response groups were recognized. Six groups were recognized in the combined analysis of light and desiccation traits. The species with the highest photosynthetic capacity and lowest photoinhibition had low or moderate saturated moisture content, dried out slowly, low or moderate photoprotection capability in high light and when desiccated and moderate recovery of photochemistry upon rehydration. The species with the lowest photosynthetic capacity and highest photoinhibition had the highest saturated moisture content, dried out very fast, had low photoprotective capability in high light and when desiccated and showed very low to moderate recovery. The group of species with low photosynthetic capacity was distinguished from the group with the lowest photosynthetic capacity by having a higher quantum yield of electron transport at the optimal photosynthetically active radiation (PAR). The two groups consisting of moderate or high photosynthetic capacity species were distinguished by the fraction of open reaction centres in high light and the ability to recover photochemistry upon rehydration. The group consisting of species with moderate photosynthetic capacity had a moderate fraction of open reaction centres in high light, moderate photoprotective capability when desiccated and high recovery of photochemistry upon rehydration. Correspondence analysis shows that the groupings are related to phylogeny, especially at the phylum level, and the species belonging to the same genus mostly had similar light and desiccation response characteristics. There is a strong correspondence between functional groupings, light regime and habitat moisture. The light response traits, particularly photoinhibition, are strongly associated with light regime. Photosynthetic capacity, moisture content and ability to recover photochemistry upon

rehydration, correspond to habitat moisture. Life form was also strongly associated with functional groupings, particularly with the desiccation response traits.

Opsomming

Daar is tans 'n wêreldwye belangstelling in die groepering van spesies in Plantfunksie Tipes (PFTs) volgens hul funksionele karaktereienskappe. Dit verminder die kompleksiteit van modelle wat die uitwerkings van aardverandering op plantegroei en ekosisteemprosesse voorspel. Marioneiland se plantegroei word oorheers deur briofiete, en ervaar intense klimaatverandering. Daar is egter geen aanvaarde skema en geen konsensus wat die mees nuttige eienskappe vir 'n briofiet PFT klassifikasie betref nie. Hierdie studie is daarop gemik om 38 van die eiland se briofietspesies in funksionele groepe te groepeer. 'n Suite van 14 fotosintetiese eienskappe water verband hou met lig- of uitdrogingreaksies is verkry vanaf chorofilflouressensie blus-ontleding en water-verwantskappe. Die karaktereienskappe is aan die ontleding van variansie, boksgrafiek-ranglyste en hoofkomponent- en groeperings-ontledings onderwerp om die spesies in funksionele tipes te groepeer. Sewe ligreaksie- en nege uitdrogingsreaksie-groepe is bevestig. Ses groepe is bevestig in die gesamentlike ontleding van lig- en uitdrogings-eienskappe. Die spesie met die hoogste fotosintetiese kapasiteit en die laagste fotoinhibisie (photoinhibition) het ‘n lae of matige versadigde voginhoud. Hierdie spesie het ook stadig uitgedroog, het lae of matige fotobeskermingsvermoë in skerp lig (high light) en wanneer dit uitgedroog is, en het matige herstel van fotochemie getoon wanneer dit gerehidreer is. Die spesie met die laagste fotosintetiese kapasiteit en hoogste fotoinhibisie het die hoogste versadigde voginhoud gehad en het baie vinnig uitgedroog. Hierdie spesie het ook ‘n lae fotobeskermingsvermoë in skerp lig wanneer dit uitgedroog is en het baie lae tot matige herstel getoon. Die groep wat bestaan uit spesies met lae fotosintetiese kapasiteit is onderskei van die groep met die laagste fotosintetiese kapasiteit deur 'n hoë kwantumopbrengs van elektronvervoer by die optimale Fotositeties Aktiewe Bestraling (FAB). Die twee groepe wat bestaan uit spesies met 'n matige of hoë fotositetiese kapasiteit was onderskei deur die breukdeel van oop reaksie-sentrums in skerp lig en die vermoë om fotochemie te herstel met rehidrasie. Die groep wat bestaan uit spesies met matige fotosintetiese kapasiteit het 'n matige breukdeel van oop reaksie-sentrums in skerp lig, matige fotobeskermingsvermoë en 'n hoë herstel van fotochemie met rehidrasie gehad. Ooreenkomsontleding het gewys dat die groeperings wel ooreenstem met filogenie, veral op die filumvlak, en die spesies wat aan dieselfde genus behoort het meestal soortgelyke lig- en uitdrogings-reaksie karaktereienskappe gehad. Daar is 'n sterk ooreenstemming tussen funksionele groeperings, ligtoestande en habitat vogtigheid. Die

ligreaksie-eienskappe, veral fotoinhibisie, hou sterk verband met lig regime (light regime). Fotosintetiese kapasiteit, voginhoud en die vermoë om fotochemie te herstel met rehidrasie stem ooreen met habitat vogtigheid. Lewensvorm het ook sterk ooreengestem met funksionele groeperings, veral met die uitdrogingsreaksie-eienskappe.

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Chapter 1

Marion Island, study aims and thesis overview

Marion Island (46°54'S, 37°45'E, area 293km²) is situated just north of the Antarctic Convergence in the Southern Indian Ocean, about 2000km southeast of Cape Town. Together with its smaller neighbour, Prince Edward Island, it forms the Prince Edward Island group, one of six island groups in the Southern Ocean recognized as a true sub-Antarctic islands on the basis of climate (Holdgate 1964), vegetation (Wace 1965) or both (Lewis Smith 1984). Both islands are volcanic and geologically young (c. 450 000 years old; McDougall et al. 2001). They have a typical cold, wet and windy sub-Antarctic climate. Mean annual temperature at Marion Island is 5.5°C, with very small seasonal (4.4°C) and diurnal (3°C) variations (Schulze 1971). The westerly winds bring heavy precipitation; annual total rainfall is *c.* 2500mm, spread more or less evenly across the months. Mean wind speed is 32km per hour and gale force winds (>55 $km.h^{-1}$) lasting for at least 1 hour occur on average for 100 days a year (Schulze 1971). Mean relative humidity is 80%, again with little seasonal or monthly variation. Because of the constant wetness and lack of a bitterly cold winter, the islands' vegetation experiences a long growing season and total annual primary production is high (Smith 1987a, b). However, it is cloudy for most of the time and only 29% of solar radiation at the top of the atmosphere reaches the vegetation, so primary productivity (measured as the rate of plant growth or biomass accumulation) is low (Smith 2008a).

The Prince Edwards Islands' lowland vegetation has been classified as *tundra* and its upland vegetation as *polar desert* (Smith and Mucina 2006). Due to both the remoteness of the islands, and their young age Marion Island was heavily glaciated in the Pleistocene so has only been open to plant colonization and establishment for the past 15 000 years), plant species diversity is low. On Marion Island there are only 23 indigenous vascular plant species and 12 introduced species (Gremmen and Smith 2008). Cryptogams are more diverse, with 94 moss (Ochyra 2008), 44 hepatic/liverwort (Gremmen 2008) and 128 lichen (Øvstedal and Gremmen 2008, 2014) species. Both mosses and hepatics form an important component of the lowland vegetation and mosses and lichens are overwhelmingly dominant in the upland vegetation (Gremmen 1981). Bryophytes have been shown to contribute significantly to vegetation biomass and primary production (Russell 1985; Smith 1987a). They are important in nutrient cycling since they sequester nutrients from rainfall and dry-deposition and form associations with epiphytic nitrogen-fixing cyanobacteria (Smith and Russell 1982).

A goal of the ecological research program on Marion Island is to quantify ecosystem functioning on a whole island basis (Smith 2008b). This entails the construction of whole island stocks and flows of energy, carbon and nutrients in order to estimate primary production and nutrient cycling for the island's ecosystem. Intensive studies over the last 40 years, focused on individual plant species, have yielded production and nutrient cycling estimates for only 8 of the island's 42 plant communities (Smith 1987a,b, 2008a). Smith (2008c) suggested that a more efficient approach might be to group the plant species into what he termed "guilds", based on similarities in their functional characteristics. He suggested that this would reduce the arduousness of data collection for, and complexity of, a whole island model.

Other workers in systems ecology have made similar suggestions, generally preferring the term "Plant Functional Type" (PFT), rather than guild. Workers involved in large international research efforts, such as the International Geosphere-Biosphere Program's project of Global Change in Terrestrial Ecosystems (Smith et al. 1997), are especially interested in the PFT concept.

My study explored the prospect of grouping the island's bryophytes into functional types relevant to primary production. Its objectives were:
1. To establish whether Marion Island bryophyte species can be grouped into functional types on the basis of their photosynthetic responses to light and desiccation, determined by chlorophyll fluorescence quenching analysis.
2. If functional type groups can be so identified, to assess how they relate to life form, phylogeny, light regimes and habitat moisture.

Chapter 2 provides a brief conspectus of bryophyte morphology and physiology and of the concept of plant functional types, especially concerning bryophytes. A description of the chlorophyll fluorescence quenching analysis technique and the information it can provide what about the photosynthetic performance of a plant, is also provided.

Chapter 3 provides a thorough description of the sampling and pretreatment protocols, chlorophyll fluorescence techniques used, the parameters that were calculated for the light and desiccation response characteristics, the statistical analyses used to group bryophytes into PFTs and test their relationship to life form, phylogeny, light regime and habitat moisture.

Chapter 4 provides the results obtained from the light response of bryophytes and the light response groupings that were achieved through univariate and multivariate analyses and shows how these light response groupings relate to life form, phylogeny, light regime and habitat moisture.

Chapter 5 provides the results obtained from the desiccation response of bryophytes and the desiccation response groupings that were achieved through univariate and multivariate analyses and shows how these desiccation response groupings relate to life form, phylogeny, habitat moisture and light regime.

Chapter 6 provides the results obtained from the combined analyses of light and desiccation response traits and discusses how the overall functional groupings relate to life form, phylogeny, habitat moisture and light regime.

Chapter 7 provides a comprehensive discussion of the overall results, how they compare with previous findings, the limitations of this study and suggested future research.

Chapter 2

Bryophytes, plant functional types and chlorophyll fluorescence quenching analysis

2.1 Bryophytes – their morphology and physiology

Bryophytes are a highly successful primitive group of terrestrial plants consisting of mosses (Bryophyta), hepatics (Marchantiophyta) and hornworts (Anthocerotophyta) (Shaw and Goffinet 2000). Mosses are the second most diverse phylum of land plants, with approximately 13 000 species worldwide. Mosses are structurally diverse but are commonly distinguished by their growth form into three major moss types. Acrocarpous mosses are erect, have unbranched shoots and sporophytes borne on tips of stems. In contrast, pleurocarpous mosses have monopodially-branched creeping shoots with sporophytes borne on specialized lateral branches and cladocarpous mosses have monopodially-branched creeping shoots with sporophytes borne on unspecialized lateral branches (Goffinet et al. 2009). The mosses of Marion Island are largely represented by the families Grimmiaceae, Bryaceae and Dicranaceae (10, 12 and 13 species respectively; Ochyra 2008). On the island, Grimmiaceae consists of cushion-forming and tuft- forming mosses which are mostly xerophytic and colonize dry, acidic exposed surfaces at high and low altitudes. Bryaceae and Dicranaceae mosses occur mostly as tuft or turf growth forms on peat or rock surfaces at low to medium altitudes on the island.

Hepatics are small, herbaceous plants with a flattened appearance. The 5000 species of hepatics worldwide are also divided into three groups on the basis of their gametophyte growth form: simple thalloid (Metzgeriales), complex thalloid (Marchantiales) and leafy hepatics (Jungermanniales). Simple thalloids lack significant tissue differentiation, unlike the complex thalloids which have well-differentiated photosynthetic and storage tissues. Leafy hepatics have two rows of lateral leaves and one row of ventral leaves, the latter sometimes lacking (Shaw et al. 2011). Hepatics tend to prefer more moist and shady habitats than mosses. Only one species belonging to Marchantiales occurs on Marion Island, *Marchantia berteroana*, which grows on moist soil and rocks in biotic habitats and has a thallose growth form. Jungermanniales and Metzgeriales are represented by 32 and 11 species, respectively, on the island. The Jungermanniales mostly grow on damp soil and moist rocks with a mat (smooth and rough) and turf growth form. The Metzgeriales hepatics on the island also inhabit moist, shady areas and mainly have a turf growth form.

Hornworts have a thalloid gametophyte and are typically separated from the hepatics on the basis that the sporophyte is shaped like a tapered horn and the sporophyte has an intercalary meristem which allows it to grow indeterminately (Shaw et al. 2011). Only 200 to 240 species occur worldwide (Villarreal et al. 2010) and none occur on Marion Island.

The laminar boundary layer is highly significant to bryophytes as they spend much of their time living within this layer. Water vapor moves slowly through the boundary layer, creating an ideal zone of humidity for bryophytes. The slow diffusion of CO_2 into the boundary layer can lead to a higher concentration than that of ambient air which aids in bryophyte photosynthesis. The laminar boundary layer thus affects physiological characteristics of bryophytes such as water movement, gas exchange, CO_2 uptake and capillary storage (Proctor 2007).

Bryophytes absorb water and nutrients from rainwater, clouds and mist droplets. Because most bryophytes lack internal conducting tissues (i.e. ectohydric), water and nutrients are carried externally through capillary spaces around the hairs at the bases of leaves and stems and in paraphilia on stems (Slack 2013). Diffusion then occurs within the cell walls and/or through cells. Bryophytes are also poikilohydric, meaning they are unable to regulate water loss and water is freely lost and gained across the membrane (Oliver et al. 2005). The exceptions include Polytrichaceae which have an internal conducting system composed of a central strand of hydroids, and Marchantiales, which conduct water internally around and within cell walls (Slack 2013). The external capillary water is physiologically important as it relates to water storage which is a major determinant of tissue turgidity and the ability to photosynthesize and grow (Proctor 2008).

Since bryophytes are poikilohydric and their small size results in a high surface area to volume ratio, desiccation tolerance is vital. Desiccation tolerance is the ability of a plant to completely dry out and survive by suspending metabolic processes such as photosynthesis and then resume normal functioning upon rehydration (Proctor 2000; Alpert 2000). Most bryophytes can survive moderate levels of desiccation (-20 to -40 MPa) for short periods and some bryophytes can tolerate severe desiccation for extended periods such as desert species (-540 MPa for 6 years) (Oliver et al. 1993). Bryophytes can also survive extremely rapid desiccation (to -540 MPa in less than 30 min) (Oliver et al. 2005).

Photosynthesis and respiration may recover within seconds or minutes, but full recovery generally takes a few hours (Proctor 2001; Proctor and Pence 2002). In many species there is a lag time between re-wetting and the beginning of photosynthesis recovery (Proctor 2010). Protein synthesis also recovers within minutes, however, there is a change in the pattern of protein synthesis that occurs without a change in the pool of mRNA used for translation (Oliver and Bewley 1984; Scott and Oliver 1994). Therefore bryophytes are able to recover from desiccation because they prepare for water loss by activating pre-existing repair mechanisms. These pre-existing repair mechanisms rely on translational controls (Scott and Oliver 1994; Oliver and Bewley 1997), not transcription, which allows for a very rapid gene expression response and rapid recovery. Some of the genes expressed are responsible for the biosynthesis of abscisic acid (ABA). In the moss *Physcomitrella patens*, the binding of bZIP transcription factors to ABA-responsive *cis*-elements (ABREs) induces ABA (Wang et al. 2009). The accumulation of ABA triggers gene products that play a role in cellular protection prior to desiccation. *Tortula ruralis* employs a constitutive protection mechanism that is independent of ABA and constitutively expresses dehydrins- a sub-class of LEA proteins (Bewley et al. 1993). Genes that encode LEA proteins are amongst the most abundant transcripts for protecting cellular components during rehydration in bryophytes (Oliver et al. 2004; Wang et al. 2012). In addition to ABA, dehydrins and LEA proteins, osmotically active sugars (mainly sucrose) (Buitink et al. 2002) and Early Light Inducible Proteins (ELIPS) (Wood et al. 1999) are associated with desiccation tolerance in bryophytes.

All bryophytes have some degree of shade plant characteristics in their photosynthetic physiology (Marschall and Proctor 2004). These characteristics include very thin leaves or thalli (commonly only one cell thick) and low chlorophyll a:b ratios (Rastorfer 1972; Rao et al. 1979; Martin 1980; Kershaw and Webber 1986). Light saturation of photosynthesis occurs at relatively low irradiances, typical for C_3 plants, but some mosses are able to grow over a relatively wide range of light intensities, up to full sunlight (Glime 2007). Hepatics seem to be more adapted to shade, generally exhibiting lower chlorophyll a:b ratios and lower light saturation points than mosses (Marschall and Proctor 2004).

2.2 The concept of Plant Functional Types

A plant functional type (PFT) usually comprises a non-phylogenetic grouping of species exhibiting any or all of the following: they have similar responses to their environment, they

exploit the environment in a similar way and they have similar effects on ecosystem processes such as productivity and nutrient cycling (Landsberg et al. 1999; Walker et al. 1999; Duckworth et al. 2000; Gitay and Noble 1997). PFTs have been used for vegetation management, e.g. to determine the optimal fire regime for biodiversity planning in a national park (Bradstock and Kenny 2003), and for range management (Díaz et al 2002). PFTs have also proved useful in predicting changes in plant communities in response to climate change (Box 1996; Esther et al. 2010) and understanding and predicting successional changes, for example in tropical forests (Chazdon et al. 2010) and grasslands (Kahmen 2004). In addition, a significant advantage of PFTs is that they can be applied at community (Pla et al. 2012; Kuiper et al. 2014), ecosystem (Breshears and Barnes 1998; Paruelo et al. 2001; Diaz and Cabido 2009) and global (Poulter et al. 2011; Arneth et al. 2014) scales.

The concept behind PFTs is, in fact, not a new one. In the 19th and early 20th centuries, plant geographers recognized that plants in similar climates showed similarities in their growth form, life-history and ecology, despite taxonomic and geographic differences (von Humboldt 1806; Grisebach 1872; Schimper 1903; Warming 1909), leading to a realization that there is a convergence of plant form and function between plants from climatically similar areas. This formed the basis for various classification systems that grouped plants implicitly on functional criteria, the best known example of which is the life form system of Raunkiaer (1907), which became widely used after the English translation (Raunkiaer 1934). This system distinguishes between plants on the basis of their perennating bud. Since this characteristic represents a plant adaptation to climatic conditions, Raukiaer's life form classification may be considered to be a functional one, and his life form groups to represent PFTs.

The C-S-R Ecological Primary Strategies Scheme (Grime 1977) and the L-H-S Plant Ecology Strategy Scheme of Westoby (1998) both reflect the emphasis since the 1970's on plant strategies and life history attributes. Both schemes have a functional basis and can be used to explain species ecology and predict vegetation patterns. The indicator values system of Ellenberg (1979) is also essentially a functional type approach. Species are assigned a score for light, moisture, pH, temperature, continentality, salinity and nutrient status and these values are then used to group species.

These earlier schemes relied on a limited number of plant attributes, or characteristics, for grouping plants on the basis of their function. The focus of PFT research has since become increasingly focused on identifying characteristics most useful for constructing PFTs (Duckworth et al. 2000; Lavorel et al. 2007; Harrison et al. 2010). These are usually termed "plant functional traits", i.e. observable properties linked to biophysical or physiological mechanisms that enable a plant to cope with its abiotic and biotic environment (Harrison et al. 2010).

There is currently no consensus on what plant characteristics represent the most useful functional traits - different ones have been used for different vegetation types, different plant types and different objectives. Anatomical, morphological, physiological and phenological characteristics and life history strategies have all been proposed as a basis for defining plant functional types (Woodward and Cramer 1996; Smith et al. 1997). The nature of these characteristics in a particular species is considered to reflect trade-offs among different plant designs and functions that have evolved to enable the species to function optimally in their environment (Grime 2001; Kùrschner and Frey 2012). There have been some efforts towards a global "recipe sheet" of plant functional traits, with reasons why certain traits are especially useful and giving standardized protocols for measuring them (Weiher et al. 1999; Lavorel and Garnier 2002; Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). However, there is still great disparity in the traits used in plant functional type studies.

Similarly, there is no consensus on what are the cardinal plant functional types. Indeed, amongst plant ecologists, the search for a single, parsimonious, functionally comprehensive plant functional classification has been likened to the search for the 'Holy Grail' (Lavorel et al. 2007). Almost all efforts toward this elusive Holy Grail have involved vascular plants; little attention has been paid to bryophytes and none to sub-Antarctic bryophytes. Cornelissen et al. (2007) suggest that this may be due to an unfamiliarity of most comparative plant ecologists with bryophytes, to taxonomic identification problems and to methodological hurdles, rather than a lack of appreciation that bryophytes are particularly important determinants of ecosystem functioning in many ecosystems.

Most PFT schemes that have included bryophytes have grouped them into a single functional type, simply to distinguish them from vascular plants (e.g. Chapin et al. 1996; Hudson and Henry 2009. Ward et al. 2009). Chapin et al. (1996) did suggest that bryophytes might be

subdivided into Sphagnum and non-Sphagnum groups on the basis of peat-forming ability, but Gordon et al. (2001) pointed out that the major division in the Chapin et al. (1996) ordination of the data is actually between *Polytrichum* species and other bryophyte species, a distinction also made by Potter et al. (1995) based on growth responses of sub-Arctic bryophytes to simulated environmental change.

Several studies have shown functional trait differences between mosses and hepatics, for example in their UV-B response (Martínez- Abaigar et al. 2003), distribution across altitude and topography (Brunn et al. 2006) and cyanobacteria-associated nitrogen fixation (Gavazov et al. 2010). Some of these studies included only one moss and one liverwort species and so could not address variation within, or overlap between, groups. There have also been some investigations of a wider range of bryophyte species that suggest that a range of PFTs is represented amongst bryophytes. For instance, Gordon et al. (2001) found that Arctic bryophytes show a range of responses to increased nutrient supply. Dormann and Woodin (2002) carried out a meta-analysis of the results of many studies of the responses of Arctic plants to artificial manipulations of environmental factors (shading, moisture availability, nutrients, temperature, CO_2 concentration and UV-B level) that clearly showed that bryophytes were not coherently different from the other (vascular) PFTs and that the patterns of responses differ widely between bryophyte species. None of these accounts explicitly defined bryophyte functional type groupings, they simply conclude that bryophytes cannot be regarded as belonging to a single PFT.

Similar to the ecological schemes of Raunkier (1907, 1934), Grime (1977) and Westoby (1998) that are implicitly functional type classifications for vascular plants, there are various growth form and life form classifications for bryophytes which in essence reflect functional differences and similarities between species. Growth form (Meusel 1935) is the morphological characteristics of the plant (branching patterns, leaf orientation etc.) and refers to the individual shoot, while life form (Gimingham and Robertson 1950; Mägdefrau 1982) includes growth form and the assembly of the individual shoots into colonies. Therefore, in the life form approach the colony rather than the individual is regarded as the functional unit.

Ten life forms were recognized by Mägdefrau (1982): annuals, short turfs, tall turfs, cushions, mats, wefts, pendants, tails, fans and dendroids. In her very comprehensive treatise on bryophytes, Glime (2013) added another: streamer. The life forms are considered to reflect

adaptations that minimize water loss while maximizing photosynthetic light capture. For instance, the smooth surfaces of cushion and turf life forms increase aerodynamic resistance to water loss while the dense packing of shoots results in capillaries in which water is stored (Proctor 1981, 1982), whereas light has been found to penetrate quite deep into the cushions or turfs so the self-shading effect is less than predicted (Davey and Ellis- Evans 1996). Weft and pendant life forms have a more open architecture, with less possibility of capillary water storage and they dry out more rapidly. They are also more exposed to light and thus more prone to photoinhibition, especially during desiccation. Thus they often possess biochemical adaptations (anti-oxidant enzymes and enhanced chlorophyll a:b ratios) to combat oxidative stress (Dhindsa 1991; Seel et al. 1992a, b). These open weft and pendant life forms generally occupy shadier habitats than turf or cushion forms (Birse 1958a, b; Dilks and Proctor 1979). This implies that there is some concordance of life form with the environment. Bates (1998) reviewed the usefulness of life forms in bryophyte ecology and concluded that the major bryophyte life forms have strong correlations to gradients of moisture and irradiance, although no formal model exists to express the exact nature of the relationships.
Joenje and During (1977) demonstrate that there is a strong correlation between bryophyte growth form and bryophyte life history strategy (the balance between sexual and asexual reproduction, the reproductive effort spent on both kinds of reproduction, the size and number of the spores, and annual production and standing crop) to bryophyte ecology. During (1992) suggested that growth form and life history strategy might meaningfully be combined to construct bryophyte functional groupings that relate well to environmental factors and show strong affinities to particular habitats. Baldwin and Bradfield (2005) followed that suggestion; they grouped forest bryophytes on growth form and life history strategy and found that species' composition and abundance within the groups differed between edge and interior habitats and before and after logging.

Kürschner and Frey (2012) describe how life history strategies have been used in bryophyte ecological studies and models. They also analyzed 140 communities of bryophytes grouped according to life history strategy, to show that co-evolved adaptive traits have developed under similar environmental pressures to ensure the successful dispersal and establishment of species. They conclude that life strategy groupings are therefore functional groupings.

The most comprehensive data set on bryophyte comparative ecology, and one that most represents a functional classification of bryophytes, is the *BRYOATT* system of Hill et al.

(2007). *BRYOATT* is a compilation of attribute data for 1057 British bryophyte species. It is a sequel to *PLANTATT* (Hill et al. 2004), which contains attribute information for British vascular species. Both works have greatly enhanced the ability to interpret plant distribution patterns, and in particular to interpret changes in those patterns in response to environmental changes. *BRYOATT* lists attributes such as taxonomy and native status, size and life history attributes (including life form, lifespan and reproduction), geographic attributes, substrates and habitats. *BRYOATT* also lists "habitat indicator values", comprised of six of Ellenberg's et al. (1991) seven major indicator scales and modified by Hill et al. (2007). These indicator values are light, moisture, reaction, nitrogen, salt tolerance and heavy metal tolerance. All of these are important variables determining plant function.

Cornelissen et al. (2007), from a consideration of cryptogam (bryophyte and lichen) morphology, physiology, life form and life history strategy, proposed a list of traits that they consider are directly relevant to understanding and predicting the functional responses of cryptogams to their environment, as well as their control over ecosystem functional processes. The traits should thus be useable for an explicitly functional classification of cryptogams, and thus of bryophytes. Since the major focus of Cornelissen et al. (2007) was on the role of cryptogams in biogeochemical cycling, most of the traits relate to aspects such as tissue chemistry, secondary metabolites, nitrogen- fixing capacity, nutrient conservation, litter decomposability and carbon and nutrient losses. However, Cornelissen et al. (2007) do suggest that measurement of chlorophyll fluorescence "may be the priority candidate for multi-species screening for photosynthetic capacity", a suggestion that was taken up in my study.

2.3 Chlorophyll fluorescence quenching analysis

Lavorel et al. (2007) stipulated four conditions that a functional trait must meet in order to be useful for grouping plants into PFTs. The trait must (1) bear some relationship to plant function, (2) be easy and quick to quantify (Hodgson et al. 1999), (3) use measurements that can be standardized across a wide range of species and growing conditions, and (4) have a consistent ranking across species when environmental conditions vary. Chlorophyll fluorescence measurement yields a suit of traits that meet all these stipulations and has been extensively used in bryophyte studies, especially of desiccation tolerance (e.g. Deltoro et al.

1998; Csintalan et al. 1999; Proctor et al. 2007; Cruz de Carvalho et al. 2011), including Antarctica (Robinson et al. 2000).

In my study I used chlorophyll fluorescence, specifically chlorophyll fluorescence quenching analysis, to gain a suite of parameters for grouping the island's bryophytes into functional types. Comprehensive descriptions of the quenching analysis technique are given by Maxwell and Johnson (2000), Schreiber (2004) and Baker (2008) but the account of Klughammer and Schreiber (2008) is especially informative since it presents the derivations of the quantum yields (see below) obtained from quenching analysis in an understandable way. Here, I give a brief description of the quenching analysis technique and the information it can provide regarding a plant's photosynthetic performance.

Light energy absorbed by the leaf can be dissipated by four pathways, each associated with its particular rate constant:

(1) It can be converted to chemical energy in the form of ATP and NADPH, through electron transport in the chloroplast. Since the ATP and NADPH are used to reduce CO_2 (photosynthesis), this fate is termed photochemistry and the rate constant is k_P.

(2) It can be dissipated as heat through regulated dissipation of thermal energy, this serves to protect the chloroplast from photoinhibition and photodamage and is known as non-photochemical quenching, with rate constant k_{NPQ}.

(3) It can be dissipated by so-called "radiationless" decay, i.e. dissipation as thermal energy by non-regulated mechanism, with rate constant k_D.

(4) It can be emitted from the chloroplast as red light, known as chlorophyll fluorescence, associated with rate constant k_F. Only this red light emission is measured directly in the chlorophyll fluorescence technique.

The four pathways compete for the same substrate, which is absorbed light energy.
Each of the pathways has a rate (r), which is a function of the rate constant k and the quantity of absorbed light energy I_a:

$r = k \times I_a$

Each pathway has a quantum yield (Y) which is a function of the rate and Ia:

$Y = r/I_a = (k \times I_a) / I_a$

Hence, at a particular I_a, the yield of each competing pathway is proportional to k.
In the chlorophyll fluorescence quenching analysis technique, red light emission is measured immediately before and after the application of a saturating pulse of light (a subsecond application of light at an intensity several times stronger than that of full sunlight). The yields of photochemistry (termed ϕPSII; since at physiological temperatures most fluorescence is from photosystem II) and regulated heat dissipation (YNPQ) are calculated. Also calculated is a yield, YNO, which is the sum of the yields of non-regulated heat dissipation (YD) and of fluorescence (YF).

The saturating pulse (SP) induces the maximum possible fluorescence yield for the sample (i.e. maximal diversion of absorbed energy to fluorescence). It reduces all the components of the electron transport pathway (they thus cannot accept electrons and are said to be “closed”), so electron flow to NADPH is halted (no photochemistry, ϕPSII = 0). The fluorescence value at the end of the SP is termed F_m or F_m' depending on whether the leaf had been dark adapted (generally for ≥ 20 minutes in total darkness; F_m), or was illuminated at the time of the SP (F_m'). The yield of regulated energy dissipation (YNPQ) during the SP is assumed to remain at what it was immediately before the SP (Klughammer and Schreiber 2008).

During dark adaptation, electron transport will have ceased and all the components of the transport pathway will be oxidized (“open”). Regulated heat dissipation mechanisms will have relaxed (no NPQ). Hence, YNPQ at F_m would be zero, but at F_m' YNPQ will be what it was prior to the SP.

At F_m, fluorescence yield (ϕPSII =0, YNPQ=0) will reflect the maximum fluorescence yield, whereas at F_m' it will reflect maximum fluorescence yield at the current NPQ yield (ϕPSII =0, YNPQ>0). The difference between F_m and F_m', with the appropriate normalization, is thus a measure of non-photochemical quenching NPQ.

At any time between SPs the level of fluorescence can be measured. If the leaf has been dark adapted (and is still in the dark), the fluorescence value is the minimum fluorescence value for the leaf and is termed F_o. The potential for electron flow, i.e. photochemistry, at F_o is maximal. A stated above, NPQ is also zero after dark adaptation, (i.e. at F_o). Since at F_m there can be no photochemistry (all pathway components are closed), and NPQ is also zero (dark adapted leaf), the normalized difference between the fluorescence values at F_m and F_o indicates the maximum quantum yield, or maximum quantum efficiency, of photochemistry for that leaf. This is the most commonly reported value in the chlorophyll fluorescence literature, F_v/F_m.

For an illuminated leaf, the florescence value measured at any time between SPs is termed F (sometimes termed F_s if the leaf has reached a steady state fluorescence value at the particular illumination level). At F, there will be both photochemistry and NPQ. At the F_m' value given by a SP, photochemistry will be zero but NPQ will be unchanged. Hence, the normalized difference between F_m' and F indicates the actual, or effective, quantum yield (or efficiency) of the leaf at the particular illumination level.

An illuminated leaf can also be momentarily darkened for a few seconds, during which a far-red light is applied. This stimulates electron flow through PSI and relaxes, or oxidizes, the electron transport chain – a quasi-dark adaptation that opens the transport chain. The fluorescence value measured at the end of this dark period is termed F_o', the minimal fluorescence for the leaf at the particular illumination level.

Genty et al. (1996) derived expressions based on the basic fluorescence parameters F_m, F_m' and F, that describe, in terms of quantum yields, the partitioning of absorbed light energy between (1) photochemistry, (2) regulated heat dissipation and (3) the sum of non-regulated heat dissipation plus fluorescence emission:

$\phi PSII = (F_m' - F)/ F_m'$ (Effective quantum yield of photochemistry)

$YNPQ = (F/ F_m')-(F/ F_m)$ (Yield of regulated thermal energy dissipation)

YNO = F/ F_m (Sum of the yields of non-regulated heat dissipation and fluorescence emission), termed the yield of "primary constitutive losses" by (Klughammer and Schreiber 2008).

Kramer et al. (2004) derived different expressions for YNPQ and YNO, based on F_m, F_m', F_o, F_o' and also a quenching coefficient (qL) that describes the fraction of open PSII centers in a "lake" model (PSII reaction centers assumed to share light harvesting antennae in the thylakoid pigment bed). The inclusion of qL complicates the use of the Kramer et al. (2004) expressions since calculation of qL depends a reliable determination of F_o', which is problematical. However, (Klughammer and Schreiber 2008) elegantly showed that the more simple expressions of Genty et al. (1996) can be deduced from the more complex ones of Kramer et al. (2004), and that they are not only valid in the lake model but also in the alternative "puddle" model (each PSII reaction center possesses its own antenna).
In my study I used the Genty et al. (1996) expressions.

Since ϕPSII is the effective quantum yield of photochemistry (i.e. of photosynthetic electron transport), electron transport rate (ETR) is half of the product of ϕPSII and absorbed Photosynthetically Active Radiation (PAR) (half since two photons need to be absorbed for the transport of one electron). Absorbed PAR was taken to be 84% of incident PAR (Schrieber et al. 2011). Other parameters considered in my study were calculated from the ETR:PAR response are described in Chapter 3, section 3.2.2.

Chapter 3
Materials and Methods

3.1 Sampling and Pre-treatment

Bryophytes were sampled in April and May of 2013 and 2014. The shoots of 38 bryophyte species (25 were mosses, 13 were liverworts) were collected from various habitats (*sensu* Gremmen and Smith 2008). Eight or more samples of each species were collected, each from a different locality. Between them, the species (Table 3.1) represent 13 Orders and 22 Families based on the phylogenetic classifications of Buck and Goffinet (2000) and Crandall-Stotler and Stotler (2000), and 12 of the bryophyte life forms defined by Hill et al. (2007). There were two varieties of Bucklandiella membranacea (Bmem1 and Bmem2). During the field and laboratory work they were thought to be different species since they occur in different habitats and show a different growth form, but their identity as the same species (*B. membranacea*) was later confirmed by R. Ochyra (Polish Institute of Botany, Cracow) the authority on sub-Antarctic Bucklandiella species.

At each sampling site, light measurements were made, at the level of the bryophyte fronds and also above the canopy, using a ULM-500 light meter and logger connected to two MQS-B cosine-corrected mini quantum sensors (Heinz Walz GmbH). The difference between the above- and below- canopy PAR (photosynthetically active radiation) percentage were used to rank the sampling sites from low to very high light regime (Table 3.2) At each locality, the habitat was noted in order to rank the habitat moisture from very wet to very dry (Table 3.3).

Within a few (1 to 4) hours of collection the samples were hydrated (water added) and placed under a LED light bank in an incubator (10°C, 70-90% R.H., 50 to 80 µmol photons m^{-2} s^{-1} PAR) for at least one hour prior to carrying out the chlorophyll fluorescence measurements. All chlorophyll fluorescence measurements were carried out within 48 hours, and most within 24 hours of collection.

3.2 Photosynthetic light response

3.2.1 Chlorophyll fluorescence measurements

The chlorophyll fluorescence measurements were made in the incubator at 10°C. A sample (distal ends of several fronds) was placed in a DLC-8 dark adaptation leaf clip (Heinz Walz GmbH). The clip was modified by cutting a hole in the lower part of the leaf clip directly below where the sample is exposed to the fibre optic sensor of a PAM-2500 fluorimeter (Heinz Walz GmbH) attached to 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 sample to prevent CO_2 depletion during the fluorescence measurements. The sample was dark adapted for 30 minutes to oxidize the electron transport chain components. A weak modulated light (c 0.5 µmol photons m^{-2} s^{-1}) was used to measure minimal fluorescence yield (F_o) followed by a saturating pulse (c. 5000 µmol photons m^{-2} s^{-1} for 0.8 sec) to measure maximum fluorescence yield (F_m). Two minutes after the light pulse, the actinic light source was used to induce photosynthesis (10 µmol photons m^{-2} s^{-1} for one minute, followed by 44 µmol photons m^{-2} s^{-1} for 3 minutes, 144 µmol photons m^{-2} s^{-1} for 3 minutes and 200 µmol photons m^{-2} s^{-1} for 4 minutes). Reasons for this induction are given below. Immediately after this induction period, fluorescence (F), maximum fluorescence (F_m') and minimum fluorescence (F_o') were measured at 12 PAR levels (4, 10, 44, 92, 144, 200, 280, 384, 513, 670, 876 and 1114 µmol photons m^{-2}s^{-1}), each applied for 2 minutes.

The induction period before the light response determination was necessary because of the prior dark adaptation. A "Rapid Light Curve" (RLC) technique (White and Critchley 1999; Ralph and Gademann 2005) measures the light response of fluorescence yield where the sample is exposed for very short times (generally 10 - 40 sec) to increasing PAR levels. This does not allow the various photosynthetic reactions to reach steady state. During initial dark adaption these reactions will have been inactivated, so measuring fluorescence yields during the course of the RLC measurements will reflect not only the response to each new PAR level, but also an increasing degree of activation of photosynthesis and heat dissipation mechanisms (Rascher et al. 2000).

Inducing photosynthesis and heat dissipation before the light response measurement, plus the fact that the samples were illuminated for 120 sec at each PAR level, 3 to 12 times longer than usual for the RLC technique, alleviates some of these shortcomings. Obviously, the induction period adds to the time needed for the RLC. In a preliminary study, V.R. Smith (pers. comm.) measured RLCs on some of the island's bryophytes, using different induction and equilibration times, and compared the results with those from conventional light response measurements (where fluorescence yield was allowed to come to steady state at each PAR level). His findings were used to draw up the protocol employed in this study. The protocol offers the advantage that many samples (up to 24 in this study) can be screened per day, compared with up to two hours needed to measure a single light response using conventional protocols that allow full equilibration at each light level.

3.2.2 Calculations of fluorescence and light response parameters

The F_o, F_m, F, F_m' and F_o' values were used to calculate the effective quantum yield of photochemistry (ϕPSII), the yield of regulated photoprotective excess energy dissipation as heat (YNPQ) and the yield of non-regulated heat dissipation plus fluorescence (YNO), see chapter 2, Section 2.3 and Table 3.4 for an explanation of the fluorescence parameters and their equations.

The ratio of YNPQ to YNO at 876 µmol m^{-2} s^{-1} PAR was used as the measure of photoprotective capacity through regulated heat dissipation mechanisms (Klughammer and Schreiber 2008). The reason for using the YNPQ and YNO values at 876 µmol m^{-2} s^{-1} PAR is given below.

ΦPSII and PAR were used to calculate electron transport rate (ETR). The response of ETR to PAR was then fitted using the model of Eilers and Peeters (1988):

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

where a, b and c are regression coefficients.

Several additional light response parameters can be calculated from the Eilers and Peeters equation coefficients (Table 3.2):

α; Initial slope of the ETR:PAR response - the maximum or optimum quantum yield of photosynthetic electron transport.

ETR_{max}; Maximum electron transport rate.

PAR_{opt}; the PAR value at which the maximum electron transport rate is attained.

I_k: a "light adaptation parameter" (Kasai et al. 1998) or "photoadaptation parameter" (Platt and Sathyendranath 1997). It is the PAR value where the linear part of the ETR:PAR response intersects with the plateau of the response (i.e. with a line drawn at ETR_{max} parallel to the x axis. Talling (1957) consider Ik/2 to be the PAR value at the onset of light saturation. In the PAM-2500 fluorimeter instruction manual Ik is called the "minimum saturating irradiance" (Heinz Walz GmbH 2008).

$Inhib_{876}$: For many species, ETR declined after PAR_{opt}, indicating photoinhibition. For a measure of photoinhibition, the ETR value at the second highest PAR (876 µmol m^{-2} s^{-1}) was compared with ETR_{max}.

The photoinhibition and regulated photoprotection (YNPQ/YNO) parameters were calculated from the fluorescence data at 876 µmol m^{-2} s^{-1} PAR, rather than at the highest PAR level applied in the light response measurements, for two reasons. Some samples showed such severe photoinhibition above 876 µmol photons m^{-2} s^{-1} that F_m' was equal to or lower than F, so most of the fluorescence parameters could not be calculated. Other samples showed the opposite; ETR reached light saturation below 1000 µmol photons m^{-2} s^{-1} and then increased again at higher PAR. This is a known phenomenon in bryophytes and is unexplained, possibly being due to electron flow to water (Marschall and Proctor 2004). It leads to a poor fit with the Eilers and Peters model and large variances in the regression coefficients.

3.3 Photosynthetic desiccation response

3.3.1 Desiccation

Chlorophyll fluorescence was used to assess the changes in photosynthesis during desiccation and the recovery of photosynthesis following desiccation. Several (up to 16) samples (distal ends of several fronds) were placed into bulldog clips, dipped in water for 1 minute, flicked and blotted lightly to remove excess water. The samples were then placed in the dark in the incubator (10°C, 70-90% R.H.) for at least 20 minutes before measuring F_o and F_m. The samples (still in the bulldog clips) were then dipped again in water, flicked, blotted and weighed to obtain the saturated mass. They were allowed to adapt to light under the LED light bank in the incubator (10°C, 70-90% R.H., 50 to 80 µmol photons m^{-2} s^{-1} PAR, supplied by two LED light strips) for at least 30 minutes. One sample at a time was then exposed to the fibre optic sensor of the PAM-2500 fluorimeter for 2 minutes at 100 or 200 µmol photons m^{-2} s^{-1} PAR. The lower PAR was used for the shade adapted species (*Cratoneuropsis chilensis, Distichophyllum fasciculatum, Leptoschyphus expansus* and *Lepidozia laevifolia*. After the two minutes exposure to the particular PAR, fluorescence (F), maximum fluorescence (F_m') and minimum fluorescence (F_o') were measured and the sample then weighed. These measurements were repeated periodically (the samples being held under the 50 to 80 µmol photons m^{-2} s^{-1} PAR light bank during the intervals) until the difference between F and F_m' was too small to be reliably measured.

3.3.2 Recovery

Once the difference between F and F_m' became unreliable, the sample was rehydrated by dipping it in water for one minute. After flicking and blotting it was placed under the light bank in the incubator. F, F_m' F_o', and the sample mass was measured after 15 and 30 minutes. After the 30 minute measurement the sample was dried at 100°C and weighed.

3.3.3 Calculation of moisture content and drying rate

Sample moisture content on a dry mass basis (MC) was calculated as:

$$MC = ((\text{fresh mass} - \text{dry mass}) / \text{dry mass}) \times 100$$

where fresh mass is the mass of the sample at any time during the desiccation period and dry mass is the oven-dried mass of the sample.

Sample relative water content (RWC) was calculated as:

RWC= ((fresh mass-dry mass)/(saturated mass-dry mass)) × 100

where saturated mass is the mass of the fully hydrated sample as measured at the start of the desiccation period.

An exponential decay function fitted exactly or almost exactly the decrease in RWC during desiccation:

$RWC_t = RWC_i\ e^{-kt}$

where RWC_t is the RWC at a particular time during desiccation, RWC_i is the RWC at the start of desiccation (=100%), t is the time since start of desiccation (in minutes) and k is the exponential decay rate constant.

The time taken from RWCi to RWC=50% (minutes) is thus given by:

Halftime = log(2)/k

The average rate of water loss during the time to reach half saturated moisture content (percent moisture content on a dry mass basis per minute) was calculated as:

Rate = $(MC_{sat}/2)$/Halftime

where MC_{sat} is the saturated moisture content on a dry mass (i.e. corresponding to RWC=100%)

The relative water content when the sample was so desiccated that the fluorescence measurements became unreliable was recorded (RWC_{final}).

MC_{sat}, Rate and RWC_{final} were the water relation parameters used to compare desiccation responses between species. More details on these, and other desiccation response parameters considered in the study, are given in Table 3.5.

3.3.4 Desiccation response parameters calculated from fluorescence variables

Various parameters relating to desiccation response were determined from the ΦPSII desiccation response values (Table 3.5). The maximum ΦPSII ($\Phi PSII_{max}$), the ΦPSII when the difference between F and F_m' became zero or unreliable ($\Phi PSII_{final}$), the ΦPSII after 30 minutes of recovery ($\Phi PSII_{30recov}$), the ΦPSII at a similar RWC as the $\Phi PSII_{30recov}$ ($\Phi PSII_{RWC30}$) and the YNPQ/YNO ratio at the end of desiccation ($YNPQ/YNO_{final}$) were determined. The RWC where ΦPSII started decreasing ($RWC\Phi PSII_{max}$), i.e. after the maximum ΦPSII, could also be determined. The recovery of ΦPSII was calculated from the ΦPSII after 30 minutes of recovery ($\Phi PSII_{30recov}$) relative to the ΦPSII at a similar RWC as the $\Phi PSII_{30recov}$ ($\Phi PSII_{RWC30}$).

3.4 Data analysis

All statistical analyses were carried out using STATISTICA 12 software package (StatSoft, Inc. 2013). Fitting of the ETR:PAR response according to the Eilers and Peeters (1988) model was done using the nonlinear estimation module in STATISTICA 12.

3.4.1 Grouping the species into PFTs based on the light response and desiccation response parameters

One-way Analysis of Variance and Tukey's Honest Significant Difference testing were used to assess the interspecies differences in each of the parameters. The HSD test yielded many, largely overlapping, homologous groups and so was not directly useful for categorizing the species. Box plots of species means and confidence intervals were thus constructed for each parameter and the species ranked into five categories: very low, low, moderate, high and very high values of the particular parameter. The upper and lower boundaries of the categories were set subjectively, but guided by the Tukey's HSD results.

To assess the across species patterns of the light response or desiccation response or both sets of characteristics, Principal Component Analysis (PCA) was carried out on the species mean values for the eight light (ETR_{max}, PAR_{opt}, $\Phi PSIIPAR_{opt}$, Ik, α, YNPQ/YNO876, Inhib876 and qL_{876}) and six desiccation (MC_{sat}, Rate, RWC_{final}, $RWC\Phi PSII_{max}$, $\Phi PSII_{recov}$ and $YNPQ/YNO_{final}$) response traits separately and also in a combined analysis of all the traits.

Clustering was used to identify homogenous clusters in the response characteristics in the principal component space using the mean species scores on the principal component axes.

3.4.2 Relating the PFTs to phylogeny, life form, light regime and habitat moisture

Cluster analysis and correspondence analysis (CA), using STATISTICA 12 software package (StatSoft, Inc. 2013), was used to evaluate how the light response and desiccation response groups identified by PCA and clustering analysis related to phylogeny, life form, light regime and habitat moisture.

Chapter 4
Results: Bryophyte response to light

4.1 Photosynthetic types based on univariate analyses of the fluorescence parameters

The species means and standard deviations for the light response traits are given in Appendix Table A1. Analysis of Variance and Tukey's Honest Significant Difference testing (results not shown) yielded confusing sets of overlapping homologous groups (up to 14 for some traits). For each trait, the species mean values were thus ranked as being very low, low, moderate, high or very high. The upper and lower boundaries of the categories were chosen subjectively, but guided by the 95% confidence intervals of the species means and the Tukey's HSD results. For this preliminary exploration of the light response results, reducing the mean values to just five categories gives a clearer picture of the overall pattern of between-species differences across all the light response traits.

The rankings of species by their values of the eight photosynthetic parameters are shown in Table 4.1. ETR_{max} (the maximum, or light saturated, electron transport rate), PAR_{opt} (the PAR value at which ETR_{max} is attained), $\phi PSII_{PARopt}$ (the effective, or operative, quantum yield at PAR_{opt}), α (the maximum quantum yield, indicates how sharply ETR responds to increasing light at low levels), Ik (onset of light saturation of electron transport rate) and qL_{876} (the fraction of open reaction centres at 876 PAR) are together indicative of photosynthetic capacity. $Inhib_{876}$ is the photoinhibition experienced at 876 PAR (the decrease from ETR_{max} to ETR at 876 µmol photons m^{-2} s^{-1}) and $YNPQ/YNO_{876}$ indicates the capacity for photoprotective regulated heat dissipation at 876 PAR.

Table 4.1 shows that there are five species (*Polytrichum juniperinum*, *Notologitrichum australe*, *Marchantia berteroana*, *Campylopus purpureocaulis* and *Racomitrium lanuginosum*) with high or very high photosynthetic capacity (maximum ETR >40 µmol m^{-2} s^{-1}, mostly $\phi PSII_{PARopt}$, PAR_{opt}, Ik and α are high), and they are not photoinhibited at supra-optimal PAR even though four of them have only low or moderate capability for photoprotection via regulated heat dissipation. Their ability to maintain open reaction centres at supra-optimal PAR ranges from moderate to very high. Of the five species, all but one is a moss (*M. berteroana* is a hepatic). In fact, only two of the 21 species with an ETR_{max} over 20

µmol m^{-2} s^{-1} are hepatics. In contrast, hepatics comprise 11 of the 17 species with low or very low maximum ETR (< 20 µmol m^{-2} s^{-1}).

Of the 16 species with moderate ETR_{max} (20 - 40 µmol m^{-2} s^{-1}), *Bucklandiella membranacea* var.1, *Guembelia kidderi*, *Muelleriella crassifolia* and *Philonotis tenuis* have high or very PAR_{opt} whereas the other 12 species (*Andreaea acutifolia*, *Brachythecium subplicatum, Breutelia integrifolia, Bryum laevigatum, Bucklandiella membranacea* var.2, *Bucklandiella ochracea, Campylopus clavatus*, *Dicranoloma billardieri*, *Ditrichum strictum*, *Ptychomion densifolium, Sanonia uncinata* and *Syzygiella sonderi*) have moderate or low PAR_{opt}. ETR in the first mentioned set of species starts saturating at low to moderate PAR, whereas the second set saturates at moderate to high PAR. Both sets, but especially the second one, show low photoinhibition.

Species with low ETR_{max} (10-20 µmol m^{-2} s^{-1}; *Blepharidophyllum densifolium, Brachythecium rutabulum, Campylopus subnitens, Clasmatocolea humilis, Clasmatocolea vermicularis, Hypnum cupressiforme, Jensenia pisicolor, Jungermannia coniflora*, *Lepidozia laevifolia, Leptoscyphus expansus, Lophocolea randii, Plagiochila heterodonta*, *Riccardia prehensilis* and *Syzygiella colorata*) mostly also have low or very values for PAR_{opt}, Ik and qL_{876}. They are thus typical shade plants and have very low to moderate capability for photoprotection. However, they vary widely in their effective quantum yield ($\phi PSII_{PARopt}$ very low to high), ability to respond to light at low levels (α low to high), and the degree to which they become photoinhibited ($Inhib_{876}$ very low to very high).

The species with the very lowest photosynthetic capacity (lowest ETR_{max}, PAR_{opt}, and Ik) are *Brachythecium paradoxum, Cratoneuropsis chilensis* and *Distichophyllum fasciculatum*. The three species do have a low $\phi PSII_{PARopt}$, but some species in the medium and low photosynthetic capacity groups show even lower $\phi PSII_{PARopt}$ values. They have a very low capacity for photoprotective regulated energy dissipation, are unable to prevent most reaction centres from closing at supra-optimal PAR and become very highly photoinhibited. They are thus highly shade adapted plants, without the typical shade plant's ability to respond sharply to light at low levels.

The rankings in Table 4.1 were used to group the species into ten photosynthetic light response types (Table 4.2). Type A comprises the four mosses and the single hepatic species, with the highest photosynthetic capacity and ability to respond to light at high levels. Although they show little photoinhibition, they have different capabilities for photoprotection. Mostly, they show only a moderate response to light at low levels.

Type B and C comprise nine mosses and one hepatic species (*S. grandiflora*, in type C) with moderate photosynthetic capacity and that show little photoinhibition. Type B species maintain a higher fraction of open reaction centres, have a greater photoprotective capability and, mostly, a sharper response to light at low levels than type C species. Type D comprises only *B. subplicatum* which shares most of its characteristics (ETR_{max}, Ik, α, qL_{876} and $YNPQ/YNO_{876}$) with types B and C but differs from them by having a lower optimal PAR, higher effective quantum yield at the optimal PAR and is more photoinhibited.

Type E, F and G species have a low or moderate photosynthetic capacity, moderate fraction of open reaction centres and experience low or moderate photoinhibition. Type E (one moss and one hepatic) species are distinguished from types F (one moss, three hepatics) and G (four mosses) in having a very low effective quantum yield at the optimal PAR. A high capability for photoprotection at supra-optimal PAR distinguishes Type G from types E and F.

Types H and I comprise mainly hepatics (three hepatics and one moss in each) with low photosynthetic capacity, low or moderate response to light at low levels, low or moderate fraction of open reaction centres and very low to moderate photoprotective capability at supra-optimal PAR. Type H species have a high effective quantum yield at the optimal PAR and become highly or very highly photoinhibited, whereas type I species have a moderate effective quantum yield and (mostly) become less photoinhibited.

Type J comprises the three mosses and the one hepatic species with very low photosynthetic capacity, very low or low fraction of open reaction centres, have no photoprotective capability at supra-optimal PAR and therefore experience very high photoinhibition. These are the archetypical shade adapted species.

4.2 Light response groups based on multivariate analysis of the fluorescence parameters

The light response types in Table 4.2 are a subjective evaluation of the overall between-species differences in the eight traits individually, based on a subjective categorization of the trait values. For a less subjective grouping of species based on their light response, the species means for the eight traits were subjected to Principal Components Analysis (PCA) and the species clustered by their scores on the significant components. Preliminary analyses showed that *Polytrichum juniperinum* with an ETR_{max}, PAR_{opt} and Ik almost double that found for the species with the next highest values, and is such an outlier that it distorts the component axes and obscures the differences between the other species in how they occupy the component space. The species was thus excluded from these analyses.

The first three PCA axes account for 91% of the total variance in the species light response trait data (Table 4.3). $Inhib_{876}$ was positively, and ETR_{max}, PAR_{opt}, Ik, α and qL_{876} negatively, correlated with PC1. The axis represented by PC1 is thus interpreted as a gradient from species with a low photosynthetic rate attained at low PAR, onset light saturation of ETR at low PAR, low response to light at low levels, low fraction of open reaction centres and high photoinhibition, to species with a high photosynthetic rate attained at high PAR, the onset light saturation of ETR at high PAR, sharp response to light at low levels, high fraction of open reaction centres and low photoinhibition.

$\phi PSII_{PARopt}$ shows the only significant correlation with PC2. The axis thus represents a gradient from high to low effective quantum yield at optimal PAR. PC3 represents a gradient from high to low photoprotective capability ($YNPQ/YNO_{876}$).

Clustering of the species on their scores on PC1, PC2 and PC3 (Figure 4.1) results in two well defined superclusters, comprised of clusters and groups. Figure 4.2a is a species/trait PCA biplot showing the superclusters and cluster while Figure 4.2b and 4.2c are trait/species PCA biplots showing the light response groups. Supercluster 1 contains 11 moss and 12 hepatic species, while Supercluster 2 contains 14 mosses and only one hepatic species. The two Superclusters overlap almost completely on PC2. Supercluster 2 consists of species with moderate to very high photosynthetic capacity (ETR_{max}, PAR_{opt} and Ik), sharper response to low light (α), and are capable of maintaining open reaction centres (qL_{876}). Supercluster 2 species thus occur on the negative side of PC1, whereas Supercluster 1, comprised of species

with very low to moderate photosynthetic capacity mostly occupy the positive side of PC1. On PC3, Supercluster 2 species are capable of photoprotection ($YNPQ/YNO_{876}$) while Supercluster 1 species have a very low or low photoprotective capability and mostly occur on the negative side of PC3.

Supercluster 1 comprises two clusters (Figures 4.1). Cluster 1 contains five mosses and two hepatics and cluster 2 six mosses and ten hepatics. Cluster 1 comprises moderate photosynthetic capacity species that lie further toward the high photosynthetic capacity side of PC1, with almost no overlap with cluster 2, which comprises species with low or very low photosynthetic capacity. ANOVA (results not shown) confirmed that the cluster mean values of ETR_{max}, $PAR_{opt,}$ α, Ik and qL_{876}, are all significantly (p<0.001) higher for cluster 1 than for cluster 2.

There is no variation of light response traits within cluster 1 and so the species form group 1 (Figure 4.1, 4.2b and 4.2c). Cluster 2 comprises three groups of species (Figure 4.1, 4.ba and 4.2c). Group 2 contains five hepatics and one moss, group 3 four hepatics and two mosses and group 4 three mosses and one hepatic species. These groups consist of low photosynthetic capacity species but group 4 species are the lowest of all, and they show the greatest photoinhibition. Hence, group 4 is at the positive extreme of PC1, with no overlap with the other groups. There is complete overlap of group 2 and group 3 on PC1 (they have similar photosynthetic capacities) and on PC3 (they have similar photoprotective capabilities) but they are well separated on PC2, based on differences in their effective quantum yield at PAR_{opt}; mean $\phi PSII_{PARopt}$ for group 3 species is significantly greater than for the other two groups (p=0.001).

Supercluster 2 comprises three groups (Figures 4.1, 4.2b and 4.2c). Group 5 and group 6 each contain five moss species and group 7 contains three mosses and a hepatic.

Group 7 species have the highest photosynthetic capacity of all the bryophytes considered in the study, except for *Polytrichum juniperinum*. They especially show high ETR_{max}, Ik and $\phi PSII_{PARopt}$. However, they tend to show lower capability for photoprotection than species in the other two groups in Supercluster 2. *P. juniperinum* would, on the basis of its very high ETR_{max}, PAR_{opt} and Ik values, and its low photoprotective capability, occupy the component space to the left of the group 7 in Figure 4.2b and 4.2c.

Group 5 overlaps with group 7 on PC1, as group 5 species have a high ETR_{max}, PAR_{opt}, Ik and qL_{876} , and a very sharp response to light at low levels and experience very little photoinhibition. However, group 5 species have a lower effective quantum yield at optimal PAR and higher photoprotective capability than group 7 species. Hence, group 5 occupies the negative side of PC2 and positive side of PC3 (Figure 4.2b and 4.2c). Group 6 is distinguished from group 5 and 7 on PC1, as species have a lower photosynthetic capacity (moderate ETR_{max}, PAR_{opt}, α, Ik and qL_{876}) than the other groups. Group 6 species also have a higher photoprotective capability than group 7 species but lower than group 5 species.

Clustering the species on their PCA scores thus distinguishes seven functional groups of bryophyte species based on their light response traits. The distinguishing characteristics and species membership of the groups are listed in Table 4.4.

There is a good deal of correspondence between these functional groups and the photosynthetic light response types found from the univariate analyses (see Table 4.2). Group 7 are the very high photosynthetic capacity (very high ETR_{max}, PAR_{opt}, $\phi PSII_{PARopt}$, α and Ik) species that have a sharp response to low light, show no photoinhibition and have a moderate photoprotective capability. This group is comprised of species that are in univariate type A.

Group 5 are the high photosynthetic capacity species (high ETR_{max}, PAR_{opt}, $\phi PSII_{PARopt}$, α and Ik) that show no photoinhibition, have the sharpest response to low light and have the highest photoprotective capability. This group comprises univariate type B.

Group 6 is comprised of univariate types D and G. These species have moderate photosynthetic rate, experience little photoinhibition and have high photoprotective capability. Group 1 species also have a moderate photosynthetic rate but they achieve this at high PAR, saturate at high PAR, have low effective quantum yield, and do not become photoinhibited while having a low photoprotective capability. Group 1 comprises univariate types C and E.

Group 2 and 3 are both comprised of species with low photosynthetic rates achieved at low PAR, have low responses to low light and low photoprotective capabilities. Group 2 species saturate at low PAR, have moderate effective quantum yield and become moderately photoinhibited, while Group 3 species saturate at moderate PAR, have very high effective

quantum yield and become highly photoinhibited. Group 2 is mainly comprised of univariate types I and F, while Group 3 is mainly composed of type H.

Group 4 are the very low photosynthetic capacity species (very low ETR_{max}, PAR_{opt} and Ik with moderate $\phi PSII_{PARopt}$) that are unable to respond to low light, do not have photoprotective capabilities and become very highly photoinhibited. This group is comprised of univariate type J.

The multivariate groupings of species, based on their light response traits, yields two thirds the number of groups as the univariate analysis and represents the same grouping of species as the univariate analysis, therefore the multivariate groups were used for all further analyses.

4.3 Relating light response groups to phylogeny, life form, light regime and habitat moisture

There are some affinities between light response groups and bryophyte phylogeny. Clustering of the species phylum based on their PCA scores (Figure 4.3) shows that species, in Supercluster 2, with moderately high to very high photosynthetic capacities that experience very little or no photoinhibition and are able to photoprotect themselves are almost exclusively mosses (13 out of 14 species). Supercluster 1, with very low to moderate photosynthetic capacity species that experience moderate to very high photoinhibition and are unable to photoprotect themselves, is comprised of almost equal numbers of mosses as hepatics (11 mosses and 12 hepatics).
Beyond the relationship between light response groups and phylogeny at the phylum level, clustering based on PCA scores (Figure 4.4) and correspondence analysis (Figure 4.5) shows some of the light response groups are dominated by certain orders. Some orders are only represented by one or two species so Andreaeales, Orthotrichales, Hookeriales, Ptychomniales, Marchantiales, Metzgeriales and Polytrichales are excluded from the correspondence analysis (CA). The Jungermanniales is the most well represented order and is strongly associated with the low photosynthetic capacity, low response to low light, low photoprotective capability, low fraction of open reaction centres and moderate or high photoinhibition groups. Three of six species in group 2 are Jungermanniales and four of six species in group 3 are Jungermanniales. Grimmiales is mainly associated with high photosynthetic capacity, highest response to low light, highest photoprotective capability and highest fraction of open reaction centres group (three of five species in group 5 are

Grimmiales). The Dicranales are associated with moderately high to very high: photosynthetic capacity, photoprotective capability and fraction of open reaction centres with very low or low photoinhibition groups (All in Supercluster 2; two in group 6 and one each in group 5 and 7). Bryales is mainly associated with the moderate photosynthetic capacity, low photoprotective capability group, with two Bryales species in group 1, while the other Bryales species has a high photosynthetic capacity and occurs in group 5. Hypnales are mainly associated with the lowest photosynthetic capacity group (two species in group 4 out of four species) and the moderate photosynthetic capacity group with high effective quantum yield (two species in group 6 out of five species).

CA analysis relating the light response groups to phylogeny at the Family level did not show any significant associations, as many of the Families were represented by only one or two species.

Five genera included in the study are represented by more than one species. The clustering of the species based on their PCA scores (Figure 4.1) show that most species of the same genus have similar light response traits. *Syzygiella colorata* (Scol) and *Syzygiella sonderi* (Sson) are both in group 1, having moderate photosynthetic capacity with low effective quantum yield and low photoprotective capability. The *Campylopus* species (*C. clavatus* (Cclav), *C. subnitens* (Csub) and *C. purpureocaulis* (Cpur)) generally have similar light responses with all three occurring in Supercluster 2, the highest photosynthetic capacity groups, but these species occur in different groups. *C. clavatus* occurs in group 5, *C. subnitens* in 6 and *C. purpureocaulis* in 7. *Clasmatocolea humilis* (Chum) and *Clasmatocolea vermicularis* (Cver) are both low photosynthetic capacity species, however, *C. humilis* is in group 2 while *C. vermicularis* is in group 3. *Brachythecium rutabulum* (Brut), *Brachythecium paradoxum* (Bpar) and *Brachythecium subplicatum* (Bsub) have quite different light responses with species occurring in both Superclusters. *B. rutabulum* occurs in group 3, *B. paradoxum* in 4 and *B. subplicatum* in 6. Interestingly, *Bucklandiella membranacea* var. 1 (Bmem1) and *Bucklandiella membranacea* var. 2 (Bmem2) both occur in group 5 even though they have very different life forms and do not occur in the same type of habitat. *Bucklandiella ochracea* (Boch) occurs in group 3 as it has a low photosynthetic capacity and low photoprotective capability while the other *Bucklandiella* species have very high or high values for those light response traits.

The results of the clustering of life form based on PCA scores and CA of the association between life form and light response groups are shown in Figure 4.6 and Figure 4.7. Life forms that are poorly represented (i.e. one or two species in a life form) are excluded from the analysis, such as aquatic trailing moss, weft moss, weft hepatic and thallose hepatic. The cushion moss life form is associated with the moderate photosynthetic capacity and low photoprotective capability group (three cushion mosses in group 1) but is also associated with the high photosynthetic capacity, very high photoprotective capability group (two species in group 5). The turf hepatics are associated with Supercluster 1, not surprisingly as it comprises all but one hepatic. However, the turf hepatics do not dominate a particular group, with two turf hepatics each in group 1, 2 and 3. All seven tuft mosses occur in Supercluster 2, and dominate group 6 with three of five species being tuft mosses. The turf moss life form does not dominate any particular group or Supercluster, with two turf mosses in group 1 and one each in group 4, 5, 6 and 7. The mat mosses and mat hepatics are associated with Supercluster 1. The mat life forms dominate group 2 which has two mat mosses and two mat hepatics out of six species, and group 3 which has two mat hepatics and one mat moss out of six species in the group.

Clustering of light regime based on PCA scores (Figure 4.8) and the CA plot (Figure 4.9) shows there is a very strong association between light regime and light response groups. The highest photosynthetic capacity group (group 7) is only comprised of species that occupy very high light regimes while the low photosynthetic capacity groups (group 2 and 3) are only comprised of species that occupy moderate light regimes. The high photosynthetic capacity species (group 5) mostly occupy a very high light regime; four of five species have very high light regimes. The moderate photosynthetic capacity groups (group 1 and 6) are highly associated with species that occupy high light regimes, with four of seven species in group 1 and four of five species in group 6 having high light regimes. The lowest photosynthetic capacity species (group 4) are highly associated with a low light regime; three of four species occupy low light regimes.

Clustering of the habitat moisture (Figure 4.10) and the CA plot (Figure 4.11) shows that the very low and low photosynthetic capacity species come from very wet or wet habitats. Group 2 comprises four species from wet habitats and two from very wet habitats, while group 3 comprises five of six species from wet habitats. The lowest photosynthetic capacity group, group 4, is comprised of two species from very wet and two species from wet habitats. Group

1, the moderate photosynthetic capacity species also occupy very wet and wet habitats but in contrast some species occupy very dry habitats. In general though, the species in supercluster 1 occupy wetter habitats (very wet or wet) than species in supercluster 2. The other moderate photosynthetic capacity species (group 6) mainly occupy a mesic habitat, with three of five species from mesic habitats. The highest photosynthetic capacity species come from dry habitats, with three of four species in group 7 from dry habitats. Species in group 5 come from a range of habitats; two species from very dry, two from mesic and one from very wet habitats.

Chapter 5
Results: Bryophyte response to desiccation

5.1 Photosynthetic response to desiccation

The species means and standard deviations for the six desiccation response traits are given in Appendix Table A2. Analysis of Variance and Tukey's Honest Significant Difference testing (results not shown) yielded confusing sets of overlapping homologous groups. For each trait, the species mean values were thus categorized as being very low, low, moderate, high or very high (Table 5.1). The upper and lower boundaries of the categories were subjective but guided by the 95% confidence intervals of the species mean values and the Tukey's HSD results.

MC_{sat} is the moisture content when fully hydrated, Rate is the rate that the species dries out (at 10 °C and 70-90% RH). $RWC\phi PSII_{max}$ is the relative water content at which photochemistry starts to starts to decline. RWC_{final} is the RWC when photochemistry ceases $YNPQ/YNO_{final}$ is the photoprotective capability at RWC_{final}. $\phi PSII_{recov}$ is the recovery of photochemistry 30 minutes after rehydration.

Clasmatocolea humilis, *Clasmatocolea vermicularis*, *Distichophyllum fasciculatum*, *Leptoscyphus expansus*, *Lophocolea randii* and *Marchantia berteroana* have a very high saturated moisture content (Table 5.1), low or moderate relative water content when photochemistry ceases, very low or low capacity for photoprotective regulated heat dissipation when dry and very low or low recovery of photochemistry upon rehydration ($\phi PSII_{recov}$), except for *M. berteroana* which has moderate $\phi PSII_{recov}$. These very high moisture content species experience slow to very fast rates of drying (2 to >10 % MC per min) and photochemistry starts to decline at very low to very high RWC.

Species that are slightly less wet (MC_{sat} 1000-1300%) when fully hydrated (*Blepharidophyllum densifolium*, *Brachythecium paradoxum*, *Brachythecium rutabulum*, *Brachythecium subplicatum*, *Lepidozia laevifolia*, *Riccardia prehensilis* and *Sanonia uncinata*) dry out fast or very fast, have very low or low RWC when photochemistry ceases, very low to moderate RWC when photochemistry starts to decline, very low to moderate photoprotective capability and experience very low to moderate recovery of photochemistry

on rehydration. However, some species show small deviations in particular components of this pattern. *B. subplicatum* dries out moderately fast and *B. densifolium* dries out slowly, in *R. prehensilis* photochemistry ceases at a moderate RWC in *B. densifolium* photochemistry starts to decline at a high RWC.

The species that are moderately wet when fully hydrated have low or moderate rates of water loss, very low to moderate RWC when photochemistry ceases, low or moderate photoprotective capability when desiccated and experience very low to moderate recovery of photochemistry on rehydration. These moderate MC_{sat} species either have a high RWC (*Breutelia integrifolia*, *Dicranoloma billardieri*, *Jungermannia coniflora*, *Philonotis tenuis*) or a low to moderate RWC (*Bryum laevigatum*, *Bucklandiella ochracea*, *Cratoneuropsis chilensis*, *Hypnum cupressiforme*, *Jensenia pisicolor*, *Ptychomion densifolium*) when photochemistry starts to decline. Again, particular species show deviations in one or two traits making up this general pattern. *C. chilensis* has a high rate of water loss, *B. ochracea* has a high photoprotective capability when desiccated and high ability of photochemistry recovery on rehydration, *H. cupressiforme* also has a high ability to recover photochemistry upon rehydration and *B. laevigatum* has a very high photoprotective capability when dry.

Species that are dry when fully hydrated have a very low or low rate of water loss (except *Plagiochila heterodonta* which has a moderate rate). They can be divided into two groups based on RWC when photochemistry ceases; in *Andreaea acutifolia*, *Bucklandiella membranacea* var. 1, *Campylopus purpureocaulis*, *Ditrichum strictum*, *Guembelia kidderi*, *Muelleriella crassifolia*, *Syzygiella colorata* and *Syzygiella sonderi* photochemistry ceases at moderate to very high RWC whereas in *Bucklandiella membranacea* var. 2, *Campylopus clavatus*, *Campylopus subnitens*, *Notologitrichum australe*, *Plagiochila heterodonta* and *Racomitrium lanuginosum* it ceases at very low or low RWC. For the group as a whole, photochemistry starts to decline at a wide range of RWCs, from very low to high (<65 to >85%), and also photoprotective capability when desiccated and the ability to recover photochemistry on rehydration both range from low to very high.

Polytrichum juniperinum has very low saturated moisture content when fully hydrated, a very low rate of water loss, very high RWC when photochemistry ceases, very high photoprotective capability, moderate RWC when photochemistry starts to decline and moderate recovery of photochemistry on rehydration.

5.2 Desiccation response groups based on multivariate analysis of fluorescence and water relation parameters

Although this ranking of species based on how wet (or dry) they are when fully saturated explains some of the variation in the desiccation response traits, it does not yield a coherent picture of the pattern in which the traits behave collectively across the 38 species studied. This makes it difficult to recognize desiccation response functional groups amongst the species.

Principal Component Analysis of the species means for all six desiccation response traits was therefore used to elucidate patterns in the collective behaviour of the traits. Clustering of the species by their scores on the significant components was used to construct desiccation response functional groups.

The first three PCA axes accounted for 83% of the total variance in the data (Table 5.2). MC_{sat} and Rate are positively correlated with PC1, which thus represents a gradient from species that are very wet when fully hydrated and dry very fast, to species that are very dry when fully hydrated and dry very slowly. $\phi PSII_{recov}$ and $YNPQ/YNO_{final}$ are negatively correlated with PC1. The gradient is one of species with very low photoprotective capability when desiccated and that do not recover photochemistry on rehydration, to species with very high photoprotective capability and good recovery of photochemistry.

$RWC\phi PSII_{max}$ is positively correlated with PC2, so it represents a gradient from species in which photochemistry starts to decline at high RWC, to species in which photochemistry starts to decline at low RWC. RWC_{final} is positively correlated with PC3 so it represents a gradient from species that cease photochemistry at high RWC to those that cease photochemistry at low RWC.

Clustering of the species on their scores on PC1, PC2 and PC3 yielded two well defined superclusters, each comprised of smaller groups (Figure 5.1). The superclusters and clusters are superimposed on the species-traits PCA biplot in Figure 5.2a and the groups are superimposed on Figure 5.2b and 5.2c. Their desiccation response characteristics and species membership given in Table 5.3. The distribution of phyla (moss or hepatic) across the groups is shown in Figure 5.3.

Supercluster 1 species (19 mosses, three hepatics) are mainly on the negative side (low saturated moisture content, low rate of water loss, high photoprotective capability when desiccated and good recovery of photochemistry on rehydration) of PC1 (Figure 5.2a). All but one of the supercluster 2 species (six mosses and 10 hepatics) is on the positive side of PC1 (high saturated moisture content, high rate of water loss, low photoprotective capability when desiccated and poor recovery of photochemistry on rehydration).

Supercluster 1 is comprised of two clusters (Figure 5.1). Cluster 1.1 contains five mosses and one hepatic species that are very dry or dry when fully hydrated, dry out slowly or very slowly, have a moderate to high photoprotective capability when desiccated and show moderate to very good recovery of photochemistry on rehydration. Cluster 1.2 contains 14 moss and two hepatic species that are slightly wetter (but still dry) when fully hydrated, dry out slightly faster and recovery of photochemistry not as good as cluster 1.1 species. Hence, cluster 1.2 lies further towards the positive side of PC1 than cluster 1.1, but there is considerable overlap (Figure 5.2a). The two clusters overlap totally on PC2. They overlap less on PC3 (Figure 5.2c); cluster 1.1 species cease photochemistry at a high or very high RWC and cluster 1.2 species cease photochemistry at a very low to moderate RWC.

Cluster 1.1 comprises two groups. Group 1 comprises four mosses and one hepatic species and Group 2 comprises two mosses. These groups overlap almost completely on PC1 (Figure 5.2b), with both groups containing species with very low moisture contents when saturated, lowest rate of water loss, are capable of photoprotection when desiccated and are able to recover well on rehydration. The two groups lie on opposite sides of PC2 (Figure 5.2b); species in group 1 have a very low to moderate RWC, whereas group 2 species have a high RWC, when photochemistry starts to decline. Both groups have a high or very high RWC when photochemistry ceases.

Cluster 1.2 comprises four groups (3 to 6), all with species in which photochemistry ceases at very low to moderate RWC. Groups 3 and 4 lie further towards the positive side of PC2 (Figure 5.2b) than groups 5 or 6. This is largely because in groups 3 and 4 photochemistry starts to decline at a moderate or high RWC, whereas in groups 5 and 6 it starts declining at very low to moderate RWC.

The main difference between groups 3 and 4 is explained by their separation on PC1; group 3 species (one moss and two hepatics) have high or very high photoprotective capability when desiccated and photochemistry recovers well on rehydration, whereas group 4 (five mosses) species have a moderate to moderately high photoprotective capability and recover more poorly on rehydration.

Groups 5 and 6 (each comprising four moss species) both contain species that are dry or moderately wet and dry out slowly or moderately fast. Group 5 species lie more towards the negative side of PC1 (Figure 5.2b) as they have a greater photoprotective capability and better recovery of photochemistry on rehydration than group 6 species. Although there is some overlap, Group 5 species also lie further towards the negative side of PC2 (Figure 5.2b), mainly because photochemistry ceases at a higher RWC than it does in group 5 species.

Supercluster 2 comprises three groups (7, 8, 9; Figure 5.1). Group 7 comprises of three mosses and five hepatics, group 8 three mosses and two hepatics, and group 9 three hepatics The three groups overlap completely on the positive (wet, fast-drying) side of PC1 (Figure 5.2b). Photochemistry in group 9 starts to decline at a much higher RWC than in groups 7 or 8, hence the separation of group 9 from groups 7 and 8 on PC2. Group 8 is clearly separated from groups 7 and 9 on PC3 (Figure 5.2c); species in group 8 dry out faster and tend to attain lower RWC when photochemistry ceases than those in groups 7 or 9.

5.3 Relationship of desiccation response groups to phylogeny, life form, light regime and habitat moisture

The association between desiccation response groups and phylogeny, at the phylum level, is a strong one. Of the 22 species in Super-cluster 1 (low saturated moisture content, low rate of water loss, high photoprotective capability when desiccated and good recovery of photochemistry on rehydration), 19 are mosses - four of the functional groups in the super cluster comprise only mosses. Hepatics predominate (10 out of 16 species) in supercluster 2 (high saturated moisture content, high rate of water loss, low photoprotective capability and poor recovery of photochemistry). The six mosses are shared between groups 7 and 8 but group 9, comprising very wet species in which photochemistry starting to decline at very high RWC consists only of hepatics.

The cluster diagram also suggests that certain of the desiccation response groups are dominated by particular orders (Figure 5.4) confirmed by the correspondence analysis results (Figure 5.5). Orders represented by only one or two specie (Andreaeales, Orthotrichales, Ptychomniales, Marchantiales, Hookeriales, Metzgeriales and Polytrichales) were excluded from the analysis.

Seven of the 10 Jungermanniales species occur in supercluster 2 (high saturated moisture content, high rate of water loss, low photoprotective capability when desiccated and poor recovery of photochemistry on rehydration) –all species in group 9 of that supercluster are Jungermanniales. Hypnales is mainly associated with another group (8) of that supercluster. Grimmiales is mainly associated with group 5 (low saturated moisture contents, low or moderate RWC when photochemistry ceases and moderate or high photoprotective capability when desiccated). Bryales and Dicranales are mainly associated with the two groups (4 and 6) with a low to moderate rate of drying and a moderate to high photoprotective capability and in which photochemistry ceases at very low to low RWC.

Some desiccation response groups show no correspondence to phylogeny at the order level. The four species in group 1 and the four species in group 6 each represent a different order. The two species in group represent different orders.

The cluster diagram (Figure 5.6) shows few striking associations between phylogeny at the family level and desiccation response groups. There are too few representatives of the families to perform a meaningful correspondence analysis so, although the CA joint plot (Figure 5.7) shows some strong correspondences some of them are spurious. However, there are some strong correspondences at the supercluster level. Three of the four Geocalycaceae species are in group 9, and the other in group 8. Hence, Geocalycaceae associate with supercluster 2 (high saturated moisture content, high rate of water loss, low photoprotective capability when desiccated and poor recovery of photochemistry on rehydration). Three of the five Grimmiaceae species are in group 5, and one in each of group 2 and 3. Hence, there is a strong association between the Grimmiaceae and Super-cluster 1 (low saturated moisture content, low rate of water loss, high photoprotective capability when desiccated and good recovery of photochemistry on rehydration species). The group correspondences for Dicranaceae and Jungermanniaceae extend across superclusters and are dubious, ascribable to the low number of species being considered. Two of the four Dicranaceae species are in

group 4 while the other two are either in group 6 or 7. Of the three Jungermanniaceae species, two occur in supercluster 1 (one in each of group 1 and 3) and the other in group 7.

Five genera were represented by more than one species in the study. *Clasmatocolea humilis* and *Clasmatocolea vermicularis* are very high saturated moisture content, very fast drying species with very high RWC when photochemistry starts to decline and both occur in group 9. *Syzygiella colorata* and *Syzygiella sonderi* occur in supercluster 1 but they differ in that *S. colorata* (group 1) has a lower moisture content when fully saturated and lower RWC when photochemistry starts to decline than *S. sonderi* (group 3).

Bucklandiella membranacea var. 1 occurs in group 3, whereas *Bucklandiella membranacea* var. 2 and *Bucklandiella ochracea* occur in group 5. The Bucklandiella species are thus both in cluster 1.2. *Campylopus subnitens* is in group 4, *Campylopus clavatus* in group 6 and *Campylopus purpureocaulis* in group 7. The Campylopus species are thus represented in both superclusters. Likewise the three Brachythecium species occur in different superclusters; *Brachythecium subplicatum* occurs in group 4. *Brachythecium rutabulum* and *Brachythecium paradoxum* in group 8.

Clustering of life forms based on the PCA scores and the CA joint plot for life form and desiccation response group are in Figure 5.8 and Figure 5.9, respectively. Life forms that were poorly represented in the study, such as aquatic trailing moss, weft moss, weft hepatic and thallose hepatic, are excluded from the analysis,. Cushion mosses are associated with groups 1, 2 and 3, tuft mosses with groups 4, 5 and 6 and turf mosses with group 4. Cushion, tuft and turf mosses are thus strongly associated with supercluster 1 – supercluster 2 contains only one tuft and one turf moss species. The mat life form is highly associated with supercluster 2, mat mosses with group 8 and mat hepatics with group 9. The only life form that does not occur predominantly in one or other of the superclusters is the turf hepatic one – three turf hepatic species occur in supercluster 1 (groups 1 and 3) and three in supercluster 2 (group 7).

The pattern shown by the life form– desiccation CA is thus where the cushion moss life form is associated with the very low or low saturated moisture content, very low to moderate rate of water loss groups that cease photochemistry at moderate to very high RWC and have a moderate to very high ability to recover their effective quantum efficiency upon rehydration.

Turf and tuft mosses are associated with the low or moderate saturated moisture content groups that have very low to moderate RWC when photochemistry starts declining and moderate or high photoprotection capability when desiccated. Mat hepatics and mat mosses are associated with the groups the highest saturated moisture content and rates of water loss that have very low to moderate recovery of photochemistry on rehydration. The mat mosses are most associated with the group where photochemistry starts to decline at very low to moderate RWC, whereas the mat hepatics are mostly associated with the group where photochemistry starts to decline at high or very high RWC. The turf hepatics are associated with groups with very low or low saturated moisture content, very low to moderate rate of water loss and have high ability to recover photochemistry on rehydration or associated with groups with low to very high saturated moisture content, very low or low photoprotective capability when desiccated and very low to moderate ability to recover photochemistry on rehydration.

There is a strong correspondence between light regime and the desiccation response groups, especially at the supercluster level (Figures 5.10 and 5.11). The higher light regimes are associated with desiccation response groups in supercluster 1, comprising the drier species that lose water slowly, have good photoprotective capability when desiccated and mostly (species in group 4 are the exception) show good recovery of photochemistry on rehydration. Only three of the 20 species from regimes with high or very high light are in supercluster 2. Conversely, only 5 of the 18 species from regimes with low to moderate light are in supercluster 1, the majority are in supercluster 2, characterized by wetter species that dry out faster and have poor photoprotective capacity when desiccated and show poor to moderate recovery of photochemistry on rehydration.

Surprisingly, the correspondence between the desiccation response groups and habitat moisture (Figures 5.12 and 5.13) is less clear, or harder to explain, than between the groups and habitat light regime. Groups 1, 2 and 3 (species with very low or low moisture contents when fully hydrated, that dry out slowly and show moderately good to very good recovery of photochemistry on rehydration) are associated with dry or very dry habitats. Group 5 (low to moderate saturated moisture content, low to moderate drying rate, low to high recovery on rehydration) seems also to be weakly associated with dry habitat (two of the four species in group 5 are from dry habitat).

At the other end of the scale, group 8 (species with high or very high moisture contents when fully hydrated and that dry out fast) are mostly associated with habitats with a very wet moisture regime. Surprisingly, group 4, in which some species have low saturated moisture contents and dry out slowly, also shows a strong association with a very wet moisture regime Groups 4 and 8 do have two desiccation response characteristics in common – in both photochemistry ceases at very low to low RWC and recovery of photochemistry on rehydration is very low to moderate.

Groups 7 and 9 are associated with wet habitats. In the case of group 9 this is understandable – the group comprises species with very high saturated moisture contents that dry out fast, photochemistry starts to decline at high RWC and there is little or no recovery from desiccation. Group 7 contains some species with low saturated moisture contents, that dry slowly and where photochemistry starts declining only at low RWC and recovers moderately well on rehydration. The common characteristic of the two groups is that both have very low to low photoprotective capability when desiccated. The correspondence between group 6 and mesic habitat is probably spurious, or at least weaker than suggested by the joint plot. Two of the four species in group 6 are from a mesic habitat, the other two are from wet or very wet habitats, which is possibly why the group occurs in the same quadrant of the joint plot as very wet habitat. Group 6 does have affinities with groups associated with wetter habitats, especially group 4, with which it shares the desiccation response characteristics of drying out slowly or moderately fast, having a low RWC when photochemistry ceases and a moderate to high photoprotective capability when desiccated.

Chapter 6

Bryophyte functional groups based on the photosynthetic response to light and desiccation and the relationship to phylogeny, life form, light regime and habitat moisture

Principal component analysis and clustering analysis of the species scores on the component axes, were performed on both the light response and the desiccation response trait values, to see if bryophyte functional groups can be recognized on the basis of both responses together. As was found in the analysis of only the light response traits, *Polytrichum juniperinum* is such an extreme outlier that it distorts the component axes and obscures the differences between the other species. The data for *P. juniperinum* were therefore excluded from the combined analysis.

The first three PC axes account for 73% of the total variance in the light- and desiccation-response traits data (Table 6.1). ETR_{max}, PAR at ETR_{max} (PAR_{opt}), onset light saturation of photosynthetic electron transport rate (Ik), proportion of open reaction centres in high light (qL_{876}) and response to light at low levels (α) are all negatively correlated with PC1 (Table 6.1). These are the indicators of photosynthetic capacity, PC1 represents a gradient from high (negative side) to low (positive side) photosynthetic capacity. The two traits indicative of photoprotective capability, either in high light when fully hydrated ($YNPQ/YNO_{876}$), or at more moderate light when desiccated ($YNPQ/YNO_{final}$), are also negatively correlated with PC1, so the gradient is also one of high to low photoprotective capability in the same direction. In the opposite direction (positive to negative), PC1 represents a gradient from low to high severity of photoinhibition in high light and from species that are very wet when fully hydrated (MC_{sat}) and dry out very fast (Rate), to species that are relatively dry when fully hydrated and dry out slowly. Overall, the gradient is one of wet species that desiccate fast and are poorly capable of photosynthesis and photoprotection to drier species that desiccate slowly and with good capabilities for photosynthesis and photoprotection.

Thallus moisture content at saturation (MC_{sat}), RWC when photochemistry starts to decline ($RWC\phi PSII_{max}$), quantum yield at PAR_{opt} ($\phi PSII_{PARopt}$) and photoprotection in high light ($YNPQ/YNO_{876}$) are positively correlated with PC2. RWC when photochemistry ceases

during desiccation (RWC_{final}) and the ability of photochemistry to recover on rehydration ($\phi PSII_{recov}$) are negatively correlated with PC2. The gradient represented by PC2 is thus primarily one of (positive side) wet species in which photochemistry starts decreasing at a high RWC, ceases when RWC becomes low, and recovery of photochemistry on rehydration is poor, to (negative side) drier species in which photochemistry starts declining at a lower RWC, but ceases at a relatively high RWC, and which show good recovery of photochemistry on rehydration. PC2 also represents, although weakly, a gradient from (positive side) high photosynthetic capacity (especially the ability to maintain open reaction centres in high light) and good photoprotective capability in high light, to low photosynthetic and photoprotective capacities.

Like PC1, PC3 also represents a gradient in photosynthetic capacity (especially ETR_{max} and the PAR values at which electron transport starts becoming saturated, Ik, and at which it is saturated, PAR_{opt}) and in photoprotective capability (both against high light and when desiccated). However, unlike for PC1, on PC3 the correlations for ETR_{max}, PAR_{opt} and Ik have opposite signs to the correlations of $YNPQ/YNO_{876}$ and $YNPQ/YNO_{final}$. Hence PC3 distinguishes between species with high (or low) photosynthetic capacity and low (or high) photoprotective ability.

Clustering species based on their score on the first three principal component axes yielded three large clusters, each comprising smaller groups (Figure 6.1). The groups are superimposed on the species-traits PCA biplot in Figure 6.2a, 6.2b and 6.2c, the light- and desiccation response characteristics of the groups are given in Table 6.2. The distribution of phyla (moss or hepatic) across the groups is shown in Figure 6.3.

Clusters 1 (six mosses, two hepatics) and 2 (11 mosses, one hepatic) are on the negative (high photosynthetic capacity, low or moderate saturated moisture content, dry slowly or moderately slowly) side of PC1 (Figure 6.2a). There is total overlap of the two clusters on PC1 but not on PC2, cluster 1 comprises species in which photochemistry ceases at moderate to high RWC, photochemistry recovers well on rehydration and that have good capability for photoprotection when desiccated, whereas cluster 2 species photochemistry ceases at very low to moderate RWC and recovers much more poorly on rehydration.

Cluster 3 species (seven mosses, 10 hepatics) are all on the positive side of PC1 – they have moderately high to very high saturated moisture contents, dry out fast, have low photosynthetic capacity, poor capability of photoprotection when desiccated and poor to moderate photochemistry recovery on rehydration.

Cluster 1 is comprised of two groups (group 1 and 2, Figure 6.1), each comprised of three mosses and one hepatic species. The two groups occur in the lower left quadrant of the biplot (Figure 6.2b; low saturated moisture contents, dry slowly, good recovery of photochemistry on rehydration, moderate to high photosynthetic capacity). Group 2 species tend to have greater photosynthetic capacity (higher ETR max reached at higher PAR and onset of light saturation at higher PAR), and show a sharper response to light at low levels than group 1 species. Group 2 species also tend to have greater photoprotection in high light and are thus able to maintain a higher proportion of open reaction centres than group 1 species. Although there are some overlaps between the two groups of species on one or more of these photosynthetic and photoprotective capacity traits, the groupings reflect the collective behaviour of those traits and there is no overlap between them on PC1 or PC2. The greatest differences between the two groups are that photochemistry ceases at much lower RWC in group 1 (hence the separation of the two groups on PC2) and that photoprotection when photochemistry ceases is greater for group 2 than group 1. However, the greater photoprotective capability of group 2 species does not translate into a significantly better recovery of photochemistry on rehydration, which is high for both groups.

Cluster 2 comprises two groups of species (groups 3 and 4, Figure 6.1), both on the negative side of PC1 and positive side of PC2 (Figure 6.2b). Group 3 contains eight moss species, while Group 4 contains three mosses and one hepatic species. Although the groups overlap considerably, especially on PC2, group 4 species tend to score more negatively on PC1 since they exhibit higher mean values for most of the photosynthetic capacity traits (especially ETR_{max}) than group 3 species. In fact, group 4 species have the highest ETR_{max} of all the species. They also tend to have a lower rate of water loss and experience less photoinhibition when dry than group 3 species, which also places them further toward the negative side of PC1. Group 4 is well separated from group 3 (and all the other groups) on PC3 (Figure 6.2c), based on the combination of group 4 having a higher photosynthetic capacity (ETR_{max}, attained at higher PAR), but lower photoprotective capability (both when desiccated and in high light when hydrated) than group 3. *Polytrichum juniperinum*, on the basis of its very

high photosynthetic capacity, very low saturated moisture content and very low drying rate, is an extreme outlier on the negative side of PC1 and would be included in group 4. Cluster 3 comprises two groups (group 5 and 6, Figure 6.1), both on the positive side of PC1 (Figure 6.2b). Group 6 species (three mosses and two hepatics) occur at the extreme positive end of PC1 and are the wettest species when saturated, show the highest rate of drying, have the lowest photosynthetic capacity and show very low capability for photoprotection when desiccated. When hydrated, they are also the least capable of photoprotection in high light and thus are most severely photoinhibited. Group 5 species (four moss and eight hepatics) are less wet when fully hydrated, tend to dry out more slowly, have a higher photosynthetic capacity and a higher photoprotective capability both in high light and when desiccated, than group 6 species. The two groups do not overlap on PC1.

Hence, six bryophyte functional groups are recognized based on their photosynthetic responses to light and to desiccation. The groups fall into three main clusters. There is a strong correspondence between phylogeny and functional grouping at the phylum level. Of the 20 species in clusters 1 and 2 (low to moderate saturated moisture content, dry out slowly or moderately fast, moderate to very high photosynthetic capacity), 17 are mosses (Figure 6.3). Hepatics are predominant (10 out of 17 species) in cluster 3, comprised of species with higher saturated moisture contents and which dry out fast and have a low photosynthetic capacity. However, mosses are also well represented in the cluster and in group 6, which comprises the wettest species that dry out fastest and have the lowest photosynthetic capacity, three of the five species are mosses.

There is also quite a strong correspondence between functional groups and phylogeny at the order level (Figure 6.4 and 6.5; orders represented by less than three species were excluded from the correspondence analysis). Groups 5 and 6 (cluster 3, wettest species with low photosynthetic and photoprotection capacity and poor recovery of photochemistry on rehydration) are dominated by Jungermanniales and Hypnales (13 of the 17 species in cluster 3 belong to these two orders). Of the seven species in group 3, Bryales and Dicranales are each represented by three species. Three of the five Grimmiales species are in group 2 (low saturated moisture content, high response to low light, high fraction of open reaction centres at supra-optimal PAR and good photoprotection when desiccated).

For some groups there is little or no correspondence with phylogeny at the order level. Group 4 (moderately low saturated moisture content, highest photosynthetic capacity and a very low photoinhibition despite a low to moderate photoprotective capability) is represented by five species, in four orders. The four species in group 1 (dry species that dry out very slowly, with moderate photoprotection when desiccated and low photoprotection in high light) each represent a different order.

Twenty-one families are represented by the 38 species considered in the study, 17 of the families by two or less species (Figure 6.6). The 17 families were excluded from the correspondence analysis that yielded the family/functional group joint plot in Figure 6.7. Three of the four Dicranaceae species are in group 3, and the other is in group 4. Hence, Dicranaceae are in cluster 2 (low to moderate saturated moisture content, very low RWC when photochemistry ceases, moderate to very high photosynthetic capacity, moderate to high photoprotection in high light). Three of the four species in group 2 (low saturated moisture content, dry slowly, moderate to high photosynthetic capacity, sharp response to light at low levels, very good photoprotective capability and ability to maintain a high proportion of open reaction centres at supra-optimal PAR) belong to the Grimmiaceae. Two other Grimmiaceae species were included in the study; one is in group 4 and the other in group 5.

Three of the four Geocalycaceae species are in group 5 (moderate to very high saturated moisture content, low photosynthetic capacity, but with a moderate to high quantum yield at saturating PAR and a moderate to high photoprotective capability in high light). The other Geocalycaceae species is in group 6, so all four species considered in the study are in cluster 3, which comprises the wettest, fastest drying, lowest photosynthetic and photoprotective capacity species. Of the three Jungermanniaceae species, one occurs in group 1 and another in group 2, hence the correspondence with cluster 1 in Figure 6.7. This correspondence is surprising since cluster 1 comprises dry species that dry slowly and have moderate or high photosynthetic capacity, moderate to very high photoprotection when desiccated and show good recovery of photochemistry on rehydration. At the order level, the Jungermanniales are associated with cluster 3 – the wettest species with low photosynthetic and photoprotective capacity and poor photochemistry recovery on rehydration. The family Jungermanniaceae thus seems to be, functionally, an anomaly within the Jungermanniales.

Other than for the above three families, there are no other correspondences between functional group and phylogeny at the family level. For instance, the 13 non- Geocalycaceae species in cluster 3 represent 11 different families. Groups 1 and 4 each comprise four species and in both instances the species are from four different families. Similarly, the five species in group 6 are each from a different family.

Five genera included in the study are represented by more than one species. Overall, species within a genus showed similar light and desiccation response characteristics and in many instances occurred in the same cluster (Figure 6.2a, b and c). The three Campylopus species (Cclav, Cpur and Csub) are in cluster 2, the two Syzygiella species (Scol and Sson) are in cluster 1 and the two Clasmatocolea (Chum and Cverm) species are in group 6 of cluster 3. Two of the three Brachythecium species (Brut and Bpar) are also in cluster 3, while the third (Bsub) is in cluster 2. Bucklandiella is represented by two species; Boch in cluster 3 and Bmem in cluster 1. Two varieties of Bmem were included in the study (Bmem1 and Bmem2 in Figure 6.2a, b and c). Despite differences in habitat and life from (Bmem1 forms cushions on dry exposed rocks whereas Bmem2 is a tuft former on dry peat), both occur in group 2.

However, this example of the same functional group being represented by two life forms is the exception to an otherwise strong correspondences between functional group and life form (Figures 6.8 and 6.9). Except for Bmem2, most of the other tuft (and all the turf) mosses are in groups 3 and 4 (cluster 2). Three of the five cushion mosses are in group 1 and the other two are in group 2, i.e. a strong association with cluster 1. Mat mosses, mat hepatics and turf hepatics are associated with groups 5 and 6, i.e. cluster 3. The weft moss, weft hepatic and aquatic trailing moss life forms are represented by less than three species, and were therefore excluded from the correspondence analysis.

There is a strong correspondence between light regime of the species and the functional group in which they occur (Figures 6. 10 and 6.11a). Species in groups 1 to 4 are mostly associated with high or very high light environments and show very low or low inhibition of photochemistry in high light. This low photoinhibition is not necessarily related to an enhanced capacity for regulated energy dissipation – species in groups 1 and 4 have only low to moderate YNPQ/YNO_{876}, thus they must have other mechanisms to dissipate excess light energy. Groups 2 and 4 are associated with particularly high light environments and comprise the most light-adapted species, based on the PAR level at which electron transport becomes

light saturation (PAR_{opt}), the ability to maintain open reaction centres in high light and a complete, or almost complete, absence of photoinhibition in high light. Groups 1 and 3 are associated with environments with slightly lower (but still high) light and for both groups photochemistry saturates at moderate PAR, the capacity to maintain open reaction centres in high light is moderate and photoinhibition in high light, whilst low, is higher than for groups 2 and 4. Group 5 species are associated with a moderate light environment, have only low or moderate photoprotective capacity, show moderate to high photoinhibition and have a poor ability to maintain open reaction centres in high light. Group 6 species are the most shade-adapted of all. They occur in low light environments, have very low or low photoprotective capacity, are highly photoinhibited in high light and have very poor ability to maintain open reaction centres in high light. Thus, several key light response traits account for the correspondence between functional group and light environment in Figure 6.11a. However, the cardinal trait is the degree to which photochemistry is inhibited by high light. This is shown by the strong correspondences between functional group, the most prevalent light environment for the groups and the degree of photoinhibition shown by the species in each group (Figure 6.11b).

There is also a strong pattern of correspondences between functional group and habitat moisture content (Figures 6.12 and 6.13a). Groups 1 and 2 are associated mostly with very dry habitats, group 4 with dry habitats, group 3 with mesic or very wet habitats, group 5 with wet habitats and group 6 with very wet habitats. Unsurprisingly, saturated moisture content of the species (an important trait determining the functional grouping) is related to habitat moisture – wettest species come from the wettest habitats and vice versa – but there are anomalies; for example, four of the eight species in group 3 come from very wet habitats but have only moderate saturated moisture contents. Rather, the functional trait most related to habitat moisture is the ability to recover photochemistry on rehydration after desiccation. This is very clearly demonstrated in the joint plot in Figure 6.13b, which shows a direct relationship between increasing habitat moisture and a decreasing ability to recover from desiccation. This trait thus explains most of the pattern shown in the habitat moisture – functional group joint plot.

Chapter 7

General discussion, concluding remarks and suggestions for future research

The first aim of this study was to establish whether Marion Island bryophyte species can be grouped into functional types on the basis of their photosynthetic responses to light and desiccation. Overall, the bryophytes on Marion Island exhibit a wide range of responses to light and desiccation. Seven main light response (see Chapter 4) and nine main desiccation response (see Chapter 5) groups can be recognized amongst the 38 Marion Island bryophyte species studied. The combined analysis of the light and desiccation response traits (see Chapter 6) yielded six functional groups of Marion Island species.

The light response characteristics of the island's bryophytes resemble those of shade adapted vascular plants, as has been shown for most bryophytes worldwide. With a few exceptions, they have unistratose leaves and thus lack an internal ventilated photosynthetic tissue and this leads to high resistance to CO_2 diffusion and low rates of photosynthesis (Proctor 1981; Meyer et al. 2008). Maximum photosynthesis rate is also attained at low light levels compared with most vascular plants (Marschall and Proctor 2004; Proctor 2005). Of the bryophytes studied here, *Brachythecium paradoxum*, *Cratoneuropsis chilensis*, *Distichophyllum fasciculatum* and *Lepidozia laevifolia*, are the archetypical shade-adapted species, with the lowest photosynthetic capacity (lowest maximum ETR, optimum PAR, effective quantum yield at optimum PAR and onset light saturation of ETR) and are unable to photoprotect themselves in high light and are severely photoinhibited.

In contrast to these under-performers, the 'super-stars' are mostly species with ventilated photosynthetic tissue in the form of rows of chlorophyll-rich lamellae (*Polytrichum juniperinum* and *Notologitrichum australe*) or as a thick multi-celled thallus open to the atmosphere by pores (*Marchantia berteroana*). These arrangements increase photosynthetic surface area and reduce resistance to CO_2 diffusion (Green and Snelgar 1982; Thomas et al. 1996; Proctor 2005) and are associated with high photosynthetic rates (Krupa 1978). *P. juniperinum* showed the highest photosynthetic capacity of all the species studied.

High levels of photoprotective heat dissipation are typically associated with high photosynthetic capacity bryophytes, especially mosses (Marschall and Proctor 2004). *R. lanuginosum* and *Campylopus purpeocaulis* are capable of high levels of photoprotection but the bryophytes belonging to the Polytrichales and Marchantiales possess little photoprotection (measured as non-photochemical quenching) in high light, something that has also been reported by Proctor and Smirnoff (2010). This suggests that there are other photoprotection mechanisms in play, other than heat dissipation, mediated by xanthophyll cycling. In the Polytrichales, many species show anatomical and behavioural (leaf movement) mechanisms that possibly help to protect them from high light intensity. For example, the lamellae of several Polytrichum species are enclosed (shaded) by the inrolled lamina of the leaf and leaf curling and orientation changes also lessen exposure of the photosynthetic tissue to light (Glime 2007). *Marchantia berteroana* thalli, especially those exposed to high light, show a marked purple colouration. *Syzygiella colorata* also exhibits red colouration and shows low photoinhibition despite having low photoprotective heat dissipation. Red forms of hepatics are due to anthocyanic pigmentation that has been suggested to contribute to photoprotection by intercepting the excess light which may lead to photodamage (Post and Vesk 1992).

Other (non-Polytrichales) mosses included in this study also show low levels of photoinhibition in high light but are without appreciable photoprotective heat dissipation. *Andreaea acutifolia*, *Ditrichum strictum* and *Muelleriella crassifolia* are all cushion mosses that occur in high light environments. Their cushion life form may be an avoidance type photoprotective mechanism through self-shading within the cushion, or it may aid in surface reflectance (Lovelock and Robinson 2002).

Bryophyte species in high light environments that are not capable of thermal energy dissipation are able to use oxygen as an electron sink to maintain electron transport and contribute to photoprotection (Proctor and Smirnoff 2011). Cyclic electron flow, photorespiration and the Mehler reaction have been shown to play a role in photoprotection (Shikanai 2007; Takahashi and Badger 2011). Cyclic electron flow and photorespiration dissipate excess energy preventing the over-reduction of photosystem I (Asada 2006) and the Mehler reaction, in which electrons to flow to O_2 via PSI, reduces the need for photoprotection as it supports electron flow (Osmond and Grace 1995). The modulation of gene expression, protein content and physiological properties may also aid in a species'

acclimation to high light (Walters 2005; Eberhard et al. 2008). These mechanisms were not addressed in the study and it is possible that a proportion of the electron transport rate measured by the chlorophyll fluorescence technique went to oxygen reduction and so would have served a photoprotective (consumption of excess energy in the chloroplast to prevent the formation of reactive oxygen species), not photochemical, function.

The poikilohydric nature of bryophytes means that they are subjected to large variations in water content (Glime 2007; Elumeeva et al. 2011). High water content can limit CO_2 diffusion and low water content can inhibit photosynthetic activity (Williams and Flanagan 1996; Tuittila 2000). Therefore, there is an optimum water content for photosynthesis, measured as the RWC at the maximum quantum yield (i.e. maximum ETR, since PAR was held constant). This optimum RWC varies greatly between species studied.

The decline in photosynthesis below critical water content can occur rapidly or gradually. Some bryophytes dry out over a long period before photochemistry ceases while other bryophytes dry out quickly and photochemistry ceases rapidly (Proctor and Tuba 2002). Slow rates of drying in bryophytes provide the time necessary to induce dissipation mechanisms that protect the plant from the inhibitory effects of excess light during desiccation or facilitate recovery (Oliver et al. 1998, 2000a, 2000b). *Guembelia kidderi* is a good example of this. This species dries very slowly and is highly capable of photoprotection when desiccated, so photosynthesis recovers rapidly upon rehydration. Some species such as *Racomitrium lanuginosum* can recover photochemistry well upon rehydration without having a high capability for photoprotection when desiccated because it dries very slowly over a long period of time. On the other hand, some species, such as *Sanonia uncinata* and *Brachythecium paradoxum*, can tolerate a rapid rate of water loss and recover moderately well despite a low photoprotective capability when desiccated.

The morphological differences of the Polytrichales and Marchantiales not only aid in their high photosynthetic capacities but also in their ability to tolerate desiccation. The Polytrichales lose water slowly because their lamellae create capillary spaces between the stem and the leaf bases for external conduction and the leaf lamina enclosing the lamellae acts like an epidermis by retarding water loss (Proctor and Tuba 2002; Glime 2015). In addition, the leaf arrangement changes as water availability changes, so that the leaves are spread away from the stem in moist conditions and are curled around the stem in dry

conditions, thus retarding water loss and protecting the photosynthetic apparatus (Glime 2015).

The pores in *Marchantia berteroana* reduce rates of water loss. However, photosynthesis in the species is highly susceptible to desiccation in that photochemistry ceases at high RWC and does not recover well on rehydration; this has also been reported for *M. berteroana* on Signy Island, Antarctica (Davey 1997).

The species with the lowest photosynthetic capacities and highest saturated moisture contents, and that dry out rapidly, also cope poorly with desiccation. Not only do they desiccate rapidly, but when dehydrated they have poor photoprotective capability and poor recovery when rehydrated.

The second aim of this study was to assess how the functional type groups that were obtained relate to phylogeny, life form, habitat moisture and light regime. The results show that the functional grouping strongly related to phylogeny at the phylum and order level.

At the phylum level, mosses tend to be drier when saturated and have a higher photosynthetic capacity, than hepatics. Mean ETR_{max} for the mosses is nearly double (p= 0.033) and saturates at nearly double the PAR level (p = 0.013), than for the hepatics. The mosses also have a greater photoprotective capability at supra-optimal light (mean $YNPQ/YNO_{876}$= 2.83) than the hepatics (2.51) although the difference is not significant at the 5% level (p= 0.200). This is probably why mosses maintain a significantly higher fraction of reaction centres at ETR_{max} (mean qL_{876}= 0.21) than the hepatics (mean qL_{876} = 0.11; p= 0.001). These findings accord with those from a much more extensive survey of 39 moss and 16 hepatic 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), and the fraction of open reaction centres is higher (p< 0.001), in the moss than the hepatic species.

The mosses also tend to have a greater photoprotective capacity when desiccated (mean $YNPQ/YNO_{final}$ is 4.30 for mosses versus 3.03 for hepatics; p=0.020) and their photochemistry tends to recover better 30 minutes after rehydration than hepatics ($\phi PSII_{recov}$ for mosses 0.41, for hepatics 0.24; p=0.097).

Some exceptions to this pattern include the three moss species (*Brachythecium paradoxum*, *Cratoneuropsis chilensis* and *Distichophyllum fasciculatum*), that show the lowest photosynthetic capacity, and are the wettest when fully saturated, of all the bryophytes included.

Desiccation tolerance was identified by Wood (2007) to occur in all the bryophyte orders represented in this study. The mechanism of this desiccation tolerance, as shown, varies between species and functional groups. However, there are strong affinities at the order level with the functional groups based on the responses to light and desiccation. The Dicranales and Bryales species show some differences in light response and occur in different light response groups but are very similar in desiccation response and so they occur in the same functional grouping in the combined analysis of light and desiccation response. Overall, these orders are desiccation tolerant, using their photoprotective capability to aid in recovery upon rehydration and avoid photoinhibition in high light. The other moss order, Grimmiales, is also associated with species that have a low moisture content, experience very little photoinhibition, and have the highest response to light at low levels. As mentioned previously the Marchantiales contrast sharply with most of the other bryophytes. Hepatics in the Jungermanniales and Metzgeriales both occur in groups with low photosynthetic capacity that are not able to recover rapidly after desiccation. However, too few species of some of the hepatic orders were included in the study (one Marchantiales and two Metzgeriales) to unambiguously conclude anything about their correspondence to the light and desiccation response groups. The Hypnales mosses have much the same response to light and desiccation as the hepatic orders, having the highest moisture content at full saturation and the lowest photosynthetic capacity of all. For some groupings, there is little or no correspondence with phylogeny at the order level.

There was little correspondence between phylogeny at the family level and the functional groupings. The lack of correspondence at the family level is not surprising considering that the number of families was less than half of the species studied. Possibly if more species are studied so that the species: family ratio becomes more suitable for correspondence analysis, stronger associations will be shown between family and functional group.

In most cases, species belonging to the same genera had similar light and desiccation responses. The species in the genus *Syzygiella* have similar light responses but slightly different desiccation responses, so species in this genus fall within the same cluster in the combined analysis but not the same group. This is also the case with the species in the genus *Campylopus*. The *Clasmatocolea* species have similar light and desiccation responses and fall within the same group. Both *Bucklandiella membranacea* varieties occur within the same group, despite differences in their desiccation response, while *Bucklandiella ochracea* has a completely different light and desiccation response. The three *Brachythecium* species have different light and desiccation responses and do not fall within the same group or cluster.

Bryophyte life form (how shoots are assembled into colonies) has been suggested to reflect adaptations related to water relations (especially the rate of water loss) and to photosynthesis (Mägdefrau 1982; Bates 1988), but the suggestion has not been rigorously tested. The results show a correspondence between life form and desiccation response groups but not with the light response groups. In the combined analysis of light and desiccation response, there was a very strong correspondence between life form and the resultant groupings. The cushion mosses have the lowest rate of water loss, high photoprotection capability when desiccated and show good recovery on rehydration in this study, which shows this life form, is adapted to tolerate desiccation by losing water slowly. The mat mosses, mat hepatics and turf hepatics have a slightly different desiccation response and correspond to different desiccation response groups within one cluster, but their close similarity in light response means that they occur in the same groups in the combined analysis. These life forms are thus associated with low photosynthetic capacity, experience high inhibition in high light even with some level of photoprotection, moderate to very high saturated moisture content, moderate to very high rate of water loss and experience very low to moderate recovery on rehydration. The tuft and turf moss life forms are suggested to retard water loss and therefore prolong the time available to photosynthesize (Deltoro et al. 1998). This is reflected by their low or moderate rate of water loss and the very low to moderate RWC when photochemistry ceases.

The light response trait values (especially regarding the degree to which photochemistry is inhibited by high light) are closely associated to light regime, so there is a close correspondence between functional group and light regime. Species in the highest photosynthetic capacity, very low photoinhibition groups occupy open exposed environments and are not shaded by vascular species to any great extent (exposed fellfield expanses, tops of

rocks, drainage lines in mires that lack vascular species, areas denuded of vascular plants by seal and seabird trampling). Species with moderate photosynthetic capacity and that also experience low levels of photoinhibition, but higher photoinhibition than the highest photosynthetic capacity species, tend to occupy habitats where light levels are also high. There is some shading by vascular plants (mires and bogs) or the plant can lessen the light load it receives by occupying sides of rocks not in full sunlight (fellfields, streambanks).

Species with low photosynthetic capacity and moderate or high photoinhibition are in well vegetated mires whereas the lowest photosynthetic and highest photoinhibition species are the archetype shade plants on the island, occurring under closed canopies or in deep crevices and holes. The shade adapted species are not capable of photoprotection when desiccated and thus are more quickly and severely damaged during desiccation, also found by Demming-Adams and Adams (1992) and Proctor (2003). These differences in light response characteristics may be due to plasticity or genetic differentiation of the species occurring in different light regimes (Waite and Sack 2010).

There is also a strong correspondence between functional groupings and habitat moisture. The species' photosynthetic capacity, moisture content and ability to recover photochemistry on rehydration are the main traits that correspond to habitat moisture. Bryophytes from wet habitats are less likely to experience water stress and so have not developed efficient photoprotective mechanisms against excess light induced by desiccation (Deltoro et al. 1998). The groups that are associated with very wet and wet habitats do have very low to moderate photoprotection capability when desiccated and are the wettest species with the lowest photosynthetic capacity. The species from dry sites have been shown to recover rapidly and have enhanced photoprotective capability than species of mesic or wet habitats (Deltoro et al. 1998; Proctor and Tuba 2002). The species of groups associated with dry and very dry habitats have the highest recovery of photochemistry on rehydration, are the driest, mostly have higher photoprotection capabilities than species of wetter habitats and high photosynthetic capacity. The species of mesic habitats have moderate photosynthetic capacity, are moderately wet and have a moderate recovery.
Bryophyte life form shows good correspondence with functional group and is associated especially with traits related to desiccation tolerance, especially saturated moisture content and retention (rate of drying). This confirms the suggestion of Russell (1987) that bryophyte growth form on the island appears to related to field water content and water retention.

The fact that the functional groups on the light and desiccation response characteristics relate so well to life form and environmental factors (light and moisture, both of which are changing as a result of general climate change at the island) suggests that bryophyte life form might be a profitable unit for use in whole island functional ecology models. The island is warming up and the bryophytes' photosynthetic response to temperature needs to be addressed.

Future research into the relationship between phylogeny and bryophyte functional groups should include a molecular phylogeny. The traits for the functional groupings can then be subjected to a phylogenetic analysis (e.g. phylogenetic linear model) to test whether the functional groupings remain when the phylogenetic difference between species are accounted for. In addition, more species representing the different orders, families and life forms on the island need to be included, since many of them were poorly represented in this study. Bryophytes from habitats that were poorly represented in this study also need to be included. Only three bryophytes restricted to, or attaining maximum vitality in, manured sites were included in this study, and only three cushion forming species characteristic of extremely dry situations such as rock faces and boulders.

Sampling was only done on one side of the island and only at low altitudes. There are important ecological differences between the different sides of the island, related to substrate age, soil nutrient status, nutrient composition of precipitation and climate (especially wind, with its chilling and drying effects). Altitudinal zonation is a striking feature of the island and bryophytes are the dominant plant form (even more so than lichens) at high altitude. Any future bryophyte functional type research on the island should include samples from a much wider range of localities than in the study reported on here.

8 References

Alpert P (2000) The discovery, scope, and puzzle of desiccation tolerance in plants. Plant Ecology 151: 5– 17

Alpert P, Oliver MJ (2002) Drying without dying. In Black M, Pritchard HW (eds.) Desiccation and survival in plants: Drying without dying. CABI Publishing, Wallingford, Oxon, pp 3– 43

Arneth A, Brown C, Rounsevell MDA (2014) Global models of human decision-making for land-based mitigation and adaptation assessment. Nature Climate Change 4: 550– 557

Asada K (2006) Production and scavenging of Reactive Oxygen Species in chloroplasts and their functions. Plant Physiology 141: 391–396

Baker NR (2008) Chlorophyll Fluorescence: a probe of photosynthesis in vivo. Annual Review of Plant Biology 59: 89-113

Baldwin LK, Bradfield GE (2005) Bryophyte community differences between edge and interior environments in temperate rain-forest fragments of coastal British Columbia. Canadian Journal of Forest Research 35: 580– 592

Bates JW (1998) Is 'life-form' a useful concept in bryophyte ecology? Oikos 82: 223-237

Birse EM (1958a) Ecological studies on growth-form in bryophytes. IV. Growth-form distribution in a deciduous wood. Journal of Ecology 46: 29- 42

Birse EM (1958b) Ecological studies on growth-form in bryophytes. III. The relationship between the growth-form of mosses and ground-water supply. Journal of Ecology 46: 9- 27

Bewley JD, Reynolds TL, Oliver MJ (1993) Evolving strategies in the adaptation to desiccation. In: Close TJ, Bray EA (eds.) Plant responses to cellular dehydration during environmental stress. Current Topics in Plant Physiology 10: 193-201

Box EO (1996) Plant functional types and climate at a global scale. Journal of Vegetation Science 7: 309- 320

Bradstock RA, Kenny BJ (2003) An application of plant functional types to fire management in a conservation reserve in southern Australia. Journal of Vegetation Science 14: 345- 354

Breshears DD, Barnes FJ (1998) Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology 14: 465- 478

Brunn HH, Moen J, Virtanen R, Grytnes JA, Oksanen L, Angerbjorn A (2006) Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science 17: 37- 46

Buck WR, Goffinet B (2000) Morphology and classification of mosses. In: Shaw A J, Goffinet B (eds.) Bryophyte Biology, Cambridge University Press, Cambridge, pp 71–123

Buitink J, Hoekstra FA, Leprince O (2002) Biochemistry and biophysics of tolerance systems. In: Black M, Pritchard HW (eds.) Desiccation and Survival in Plants Drying without Dying. CABI Publishing, Wallingford, U.K., pp 293-318

Chapin FS III, Bret-Harte MS, Hobbie SE, Zhong H (1996) Plant functional types as predictors of the transient response of arctic vegetation to global change. Journal of Vegetation Science 7: 347– 358

Charron AJ, Quatrano RS (2009) Between a rock and a dry place: the water-stressed moss. Molecular Plants 1- 9

Chazdon RL, Finegan B, Capers RS, Salgado-Negret B, Casanoves F, Boukili V, Norden N (2010) Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. Biotropica 42: 31- 40

Cornelissen JHC, Lavorel S, Garnier E et al. (2003) Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian journal of Botany 51: 335–308

Cornelissen JHC, Lang SI, Soudzilovskaia NA, During HJ (2007) Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biochemistry. Annals of Botany 99: 987-1001

Crandall-Stotler B, Stotler RE (2000) Morphology and classification of the Marchantiophyta. In: Shaw AJ, Goffinet B (eds.) Bryophyte Biology. Cambridge University Press, Cambridge, pp 1-54

Cruz de Carvalho R, Branquinho C, Marques da Silva J (2011). Physiological consequences of desiccation in the aquatic bryophyte *Fortinalis antipyretica*. Planta 234: 195- 205

Csintalan Z, Proctor MCF, Tuba Z (1999). Chlorophyll fluorescence during drying and rehydration in mosses *Rhytidiadelphus loreus* (Hedw.) Warnst, *Anamodon viticulosus* (Hedw.) Hook. and Tayl. and *Grimmia pulvinata* (Hedw.) Sm. Annals of Botany 84: 235-244

Davey MC (1997) Effects of continuous and repeated dehydration on carbon fixation by bryophytes from the maritime Antarctic. Oecologia 110: 25-31

Davey MC, Ellis-Evans JC (1996) The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. Journal of Bryology19: 235- 242

Deltoro VI, Calatayud A, Gimeno C, Barreno E (1998) Water relations, chlorophyll fluorescence, and membrane permeability during desiccation in bryophytes from xeric, mesic, and hydric environments. Canadian Journal of Botany 76: 1923- 1929

Demmig-Adams B, Adams WW (1992) Photoprotection and other responses of plants to high light stress. Annual Review of Plant Physiology and Plant Molecular Biology 43: 599- 626

Dhindsa RS (1991) Drought stress, enzymes of glutathione metabolism, oxidation injury, and protein synthesis in *Tortula ruralis*. Plant Physiology 95: 648- 651

Díaz S, Briske D, McIntyre S (2002) Range management and plant functional types. In: Hodkingson K, Grice AC (eds.) Global Rangelands: Progress and Prospects. CAB International, Wallingford, pp 81–100

Díaz S, Cabido M (2009) Plant functional types and ecosystem function in relation to global change. Journal of Vegetation Science 8: 463- 474

Dilks TJK, Proctor MCF (1979) Photosynthesis, respiration and water content in bryophytes. New Phytologist 82: 97- 114

Dormann CF, Woodin SJ (2002) Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. Functional Ecology 16: 4– 17

Duckworth JC, Kent M, Ramsay PM (2000) Plant functional types: an alternative to taxonomic plant community description in biogeography? Progress in Physical Geography 24: 515-542

During HJ (1992) Ecological classifications of bryophytes and lichens. In: Bates JW, Farmer AM (eds.) Bryophytes and lichens in a changing environment. Claren- don Press, Oxford, pp 1- 31

Eberhard S, Finazzi G, Wollman FA (2008) The dynamics of photosynthesis. Annual Review of Genetics 42: 463–515

Eilers PHC, Peeters JCH (1988) A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. Ecological Modelling 42: 199–215

Ellenberg H (1979) Zeigerwerte von Gefässpflanzen Mitteleuropas. Scripta Gobotanica 9: 1-122

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18: 1-248

Elumeeva TG, Soudzilovskaia NA, During HJ, Cornelissen JHC (2011) The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. Journal of Vegetation Science 22: 152–164

Esther A, Groenveld J, Enright NJ, Miller BP, Lamont BB, Perry GLW, Blank FB, Jeltsch F (2010) Sensitivity of plant functional types to climate change: classification tree analysis of simulation model. Journal of Vegetation Science 21: 447– 461

Gavazov KS, Soudzilovskaia NA, van Logtestijn RSP, Braster M, Cornelissen JHC (2010) Isotopic analysis of cyanobacterial nitrogen fixation associated with subarctic lichen and bryophyte species. Plant Soil 333: 507– 517

Genty B, Harbinson J, Cailly AL and Rizza F (1996) Fate of excitation at PS II in leaves: the non-photochemical side. Presented at The Third BBSRC Robert Hill Symposium on Photosynthesis, March 31 to April 3, 1996, University of Sheffield, Department of Molecular Biology and Biotechnology, Western Bank, Sheffield, UK, Abstract no. P28

Gimingham CH, Robertson ET (1950) Preliminary investigations on the structure of bryophytic communities. Trans. Br. Bryol. Soc. 1: 330- 344

Gitay H, Noble IR (1997) What are functional types and how should we seek them? In: Smith TM, Shugart HH, Woodward FI (eds.) Plant functional types. Their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, pp 3- 19

Glime JM (2007) Bryophyte Ecology. Volume 1. Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists, http://www.bryoecol.mtu.edu/. Accessed March 2013

Glime JM (2013) Adaptive Strategies: Growth and Life Forms, Chapter 4-5. In: Glime JM (ed.) Bryophyte Ecology: Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. http://www.bryoecol.mtu.edu/. Accessed June 2014

Glime JM (2015) Water Relations: Leaf Strategies – Structural, Chapter 7-4a. In: Glime JM (ed.) Bryophyte Ecology: Physiological Ecology. Ebook sponsored by Michigan Technological University and the International Association of Bryologists, http://www.bryoecol.mtu.edu/. Accessed June 2013

Goffinet B, Buck WR, Shaw AJ (2009) Morphology, anatomy and classification of Bryophyta. In: Goffinet B, Shaw AJ (eds.) Bryophyte biology. Cambridge University Press, Cambridge, pp 55-126

Gordon C, Wynn JM, Woodin SJ (2001) Impacts of increase nitrogen supply in high Arctic Heathlands: The importance of bryophytes and phosphorus availability. New Phytologist 149: 461- 471

Green TGA, Snelgar WP (1982) A comparison of photosynthesis in two thalloid liverworts. Oecologia 54: 275-280

Gremmen NJM (1981) The vegetation of the Subantarctic Islands Marion and Prince Edward. Dr W. Junk, The Hague, pp 145

Gremmen NJM (2008) Hepatics of the Prince Edward Islands. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 379- 382

Gremmen NJM, Smith VR (2008) Terrestrial vegetation and dynamics. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 215-244

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111: 1169-1194

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd ed. Wiley, Chichester, UK

Grisebach A (1872) Die vegetation der Erde nach ihrer klimatischen Anordnung: Ein Abriss der vergleichende Geographie der Pflanzen. Wilhelm Engelmann, Leipzig

Harrison SP, Prentice IC, Barboni D, Kohfeld KE, Ni J, Sutra JP (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. Journal of Vegetation Science 21: 300–317

Hill MO, Preston CD, Bosanquet SDS, Roy DB (2007) BRYOATT attributes of British and Irish mosses, liverworts and hornworts. The Saxon Print Group, Norwich, pp 1-88

Hill MO, Preston CD, Roy DB (2004) PLANTATT - attributes of British and Irish Plants: status, size, life history, geography and habitats. Centre for Ecology and Hydrology, Huntingdon, pp 1-71

Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. Oikos 85: 282- 294

Holdgate MW (1964) Terrestrial ecology in the Maritime Antarctic. In: Carrick R, Holdgate MW, Prévost J (eds.) Biologie Antarctique. Herman, Paris, pp 181-194

Hudson JMG, Henry GHR (2009) Increased Plant Biomass in a High Arctic Heath Community from 1981 to 2008. Ecology 90: 2657- 2663

Joenje W, During HJ (1977) Colonisation of a desalinating Wadden-polder by bryophytes. Vegetation 35: 177-185

Kahmen S (2004) Plant trait responses to grassland management and succession. Dissertationes Botanicae 382: 123

Kasia H, Saito H, Tsuda A (1998) Estimation of standing stock of chlorophyll a and primary production from remote-sensed ocean color in the Oyashio region, the Western subarctic Pacific, during the spring bloom in 1997. Journal of Oceanography 54: 527-537

Kershaw KA, Webber MR (1986) Seasonal changes in the chlorophyll content and quantum efficiency of the moss *Brachythecium rutabulum*. Journal of Bryology l4: 151-158

Klughammer C, Schrieber U (2008) Complementary PS II quantum yields calculated from simple fluorescence parameters measured by PAM fluorometry and the Saturation Pulse method. PAM Application Note 1: 27 -35

Kramer DM, Johnson G, Kiirats O and Edwards GE (2004) New fluorescence parameters for the determination of QA redox state and excitation energy fluxes. Photosynthesis Research 79: 209-218

Krupa J (1978) Photosynthesis rate in moss leaves of various anatomical structure. *Acta Societatis Botanicorum Poloniae* 4: 391-402

Kuiper JJ, Mooij WM, Bragazza L, Robroek BJM (2014). Plant functional types define magnitude of drought response in peatland CO_2 exchange. Ecology 95: 123- 131

Kürschner H, Frey W (2012) Life strategies in bryophytes – a prime example for the evolution of functional types. Nova Hedwigia 96: 83– 116

Landsberg J, O'Connor T, Freudenberger D (1999) The impacts of livestock grazing on biodiversity in natural ecosystems. In: Jung HG, Fahey GC (eds.) Nutritional Ecology of Herbivores. Proc. Vth International Symposium on the Nutrition of Herbivores. American Society of Animal Science, Savoy, Illinois, pp 752–777

Lavorel S, Diaz S, Cornelissen JHC, Garnier E, Harisson SR, McIntyre S, Pausas JG, Perez-Harguindeguy N, Roumet C, Urcelay C (2007) Plant functional types: are we getting any closer to the holy grail? In: Canadell JG, Pataki D, Pitelka L (eds.) Terrestrial Ecosystems in a Changing World. The IGBP Series, Springer-Verlag, Berlin Heidelberg, pp 149-165

Lavorel S, Garnier E (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. Functional Ecology 16: 545–556

Lewis Smith RI (1984) Terrestrial plant biology of the sub-Antarctic and Antarctic. In: Laws RM (ed.) Antarctic ecology 1. Academic Press, London, pp 61-161

Lovelock CE, Robinson SA (2002) Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. Plant Cell Environ 25: 1239–1250

Mägdefrau K (1982) Life-forms of bryophytes. In: Smith AJE (ed.) Bryophyte Ecology. Chapman and Hall, London, pp 45-58

Marschall M, Proctor MCF (2004) Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll b and total carotenoids. Annals of Botany 94: 593- 603

Martin CE (1980) Chlorophyll a : b ratios of eleven North Carolina mosses. Bryologist 83: 84–87

Martínez- Abaigar J, Núñez- Olivera E, Beaucourt N, García- Álvaro MA, Tomás R, Arróniz M (2003) Different physiological responses of two aquatic bryophytes to enhanced ultraviolet-B radiation. Journal of Bryology 25: 17- 30

Maxwell K, Johnson GN (2000) Chlorophyll fluorescence- a practical guide. Journal of Experimental Botany 51: 659- 668

McDougall I, Verwoed W, Chevallier L. 2001. K-Ar geochronology of Marion Island, Southern Ocean. Geological magazine 138: 1- 17

Meyer M, Seibt U, Griffiths H (2008) To concentrate or ventilate? Carbon acquisition, isotope discrimination and physiological ecology of early land plant life forms. Philosophical Transactions of the Royal Society B 363: 2767–2778

Meusel H (1935) Wuchsformen und Wuchstypen der europais- chen Laubmoose. Nova Acta Leopoldina 3: 123- 277

Ochyra R (2008) Mosses on the Prince Edward Islands. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 383- 389

Oliver MJ, Bewley JD (1984) Plant desiccation and protein synthesis VI. Changes in protein synthesis elicited by desiccation of the moss *Tortula ruralis* are effected at the translational level. Plant Physiology 74: 923-927

Oliver MJ, Bewley JD (1997) Desiccation-tolerance of plant tissues: a mechanistic overview. Horticultural Reviews 18: 171–213

Oliver MJ, Mishler BD, Quisenberry JE (1993) Comparative measures of desiccation tolerance in the *Tortula ruralis* complex. I. Variation in damage control and repair. American Journal of Botany 80: 127– 136

Oliver MJ, Tuba Z, Mishler BD (2000a) The evolution of vegetative desiccation tolerance in land plants. Plant Ecology 151: 85– 100

Oliver MJ, Velten J, Wood AJ (2000b) Bryophytes as experimental models for the study of environmental stress tolerance: *Tortula ruralis* and desiccation-tolerance in mosses. Plant Ecology 151:73–84

Oliver MJ, Dowd SE, Zaragoza J, Mouget SA, Payton PR (2004) The rehydration transcriptome of the desiccation tolerant bryophyte *Tortula ruralis*: transcript classification and analysis. BMC Genomics 5: 89

Oliver MJ, Velten J, Mischler BD (2005). Desiccation tolerance in bryophytes: A reflection of the primitive strategy for plant survival in dehydrating habitats? Integrative and Comparative Biology 45: 788- 799

Oliver MJ, Wood AJ, O'Mahony P (1998) ''To dryness and beyond''- preparation for the dried state and rehydration in vegetative desiccation-tolerant plants. Plant Growth Regulation 24:193–201

Osmond CB, Grace SC (1995) Perspectives on photoinhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis? Journal of Experimental Botany 46: 13511362

Øvstedal DO, Gremmen NJM (2008) Lichens of the Prince Edward Islands. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 215-244

Øvstedal DO, Gremmen NJM (2014) Additional lichen records from Subantarctica III, Marion Island. Australian Lichenology 74: 2- 7

Paruelo JM, Jobba´gy EG, Sala OE (2001) Current Distribution of Ecosystem Functional Types in Temperate South America. Ecosystems 4: 683– 698

Pérez-Harguindeguy N, Díaz S, Garnier E et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61: 167– 234

Pla L, Casonoves F, Di Reinzo J (2012) Quantifying Functional Biodiversity. Springer, Berlin, pp 98

Platt T, and Sathyendranath S (1997) Modelling primary production – 2. Aquabiology 19: 68-71

Post A, Vesk M (1992) Photosynthesis, pigments and chloroplast ultrastructure of an Antarctic liverwort from sun-exposed and shaded sites. Canadian Journal of Botany 70: 2259-2264

Potter JA, Press MC, Callaghan TV, Lee JA (1995) Growth responses of Polytrichum commune and *Hylocomium splendens* to simulated environmental change in the sub-arctic. New Phytologist 131: 533- 541

Poulter B, Ciais P, Hodson E, Lischke H, Maignan E, Plummer S, Zimmermann NE (2011) Plant functional type mapping for earth system models. Geoscientific Model Development 4: 993– 1010

Proctor MCF (1981) Diffusion resistances in bryophytes. In: Grace J, Ford ED, Jarvis PG (eds.) Plants and their atmospheric environment. Blackwell Scientific, Oxford, pp 219- 229

Proctor MCF (1982) Physiological ecology: water relations, light and temperature responses, carbon balance. In: Smith AJE (ed.) Bryophyte ecology. Chapman and Hall, London, pp 333-381

Proctor MCF (2000) The bryophyte paradox: tolerance of desiccation, evasion of drought. Plant Ecology 151: 44–49

Proctor MCF (2001) Patterns of desiccation tolerance and recovery in bryophytes. Plant Growth Regulation 35: 147–156

Proctor MCF (2003) Experiments on the effect of different intensities of desiccation on bryophyte survival, using chlorophyll fluorescence as an index of recovery. Journal of Bryology 25: 201-210

Proctor MCF (2005) Why do Polytrichaceae have lamellae? Journal of Bryology 27: 221–229

Proctor MCF (2007) Ferns, evolution, scale and intellectual impedimenta. New Phytologist 176: 504- 506

Proctor MCF (2008) Physiological ecology. In: Goffinet B, Shaw AJ (eds.) Bryophyte biology, 2nd ed. Cambridge University Press, pp 237– 268

Proctor MCF (2010) Trait correlations in bryophytes: exploring an alternative world. New Phytologist 185: 1-3

Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL, Mishler BD (2007) Desiccation-tolerance in bryophytes: a review. The Bryologist 110: 595- 621

Proctor MCF, Pence VC (2002) Vegetative tissues: bryophytes, vascular resurrection plants and vegetative propagules. In: Black M, Pritchard H (eds.) Desiccation and survival in plants: drying without dying. CABI Publishing, Wallingford, pp 207–237

Proctor MCF, Smirnoff N (2011) Ecophysiology of photosynthesis in bryophytes: major roles for oxygen photoreduction and non-photochemical quenching? Physiologia Plantarum 141: 130–140

Proctor MCF, Tuba Z (2002) Poikilohydry and homoihydry: antithesis or spectrum of possibilities? New Phytologist 156: 327–349

Ralph PJ, Gademann R (2005) Rapid light curves: A powerful tool to assess photosynthetic activity. Aquatic Botany 82: 222-237

Rao KR, Kumar NR, Reddy AN (1979) Studies of photosynthesis in some liverworts. Bryologist 82: 286– 289

Rascher, U, Liebig M, Luttge U (2000) Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. Plant Cell Environment 23: 1397– 1405

Rastorfer JR (1972) Comparative physiology of four west Antarctic mosses. Antarctic Research Series 20: 143– 161

Raunkiaer C (1907) Planterigets livsformer og deres betydning for geografien. Copenhagen, Munksgaard

Raunkiaer C (1934) The life-forms of plants and statistical plant geography. Oxford, Oxford University Press.

Robinson SA, Wasley J, Popp M, Lovelock CE (2000) Desiccation tolerance of three moss species from continental Antarctica. Australian Journal of Plant Physiology 27: 379-388

Russell S (1985) Bryophyte production at Marion Island. In: Siegfried WR, Condy PR, Laws RM (eds.) Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Belin, Heidelberg, pp 200-203

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

Schimper AFW (1903) Plant geography upon a physiological basis. Oxford University Press, Oxford

Schreiber U (2004) Chlorophyll a fluorescence: A signature of photosynthesis. In: Papageorgiou G, Govindjee (eds.) An overview: Pulse-amplitude-modification (PAM) fluoremetry and saturation pulse method. Springer, Dordrecht, The Netherlands, pp 279-319

Schreiber U, Klughammer C, Kolbowski J (2011) High end chlorophyll fluorescence analysis with MULTI-COLOR-PAM. PAM Application Notes 1: 1-21

Schulze BR (1971) The climate of Marion Island. In: Van Zinderen Bakker EM, Winterbottom JM, Dyer RA (eds.) Marion and Prince Edward Islands. Report on the South African Biological and Geological Expedition 1965-1966. A.A. Balkema, Cape Town, pp 16-31

Shikanai T (2007) Cyclic electron transport around photosystem I: genetic approaches. Annual Review of Plant Biology 8:199-217

Seel WE, Hendry GAF, Lee JA (1992a) The combined effects of desiccation and irradiance on mosses from xeric and hydric habitats. Journal of Experimental Botany 43: 1023- 1030

Seel WE, Hendry GAF, Lee JA (1992b) Effects of desiccation on some activated oxygen processing enzymes and anti-oxidants. Journal of Experimental Botany 43: 1031- 1037

Shaw J, Goffinet B (2000) Bryophyte biology. Cambridge University Press, Cambridge, UK, pp 476

Shaw AJ, Szövényi P, Shaw B (2011) Bryophyte diversity and evolution: Windows into the early evolution of land plants. American Journal of Botany 98: 352- 369

Slack NG (2013) The ecological value of bryophytes as indicators of climate change. In: Tuba Z, Slack NG, Starck LR (eds.) Bryophyte ecology and climate change. Cambridge University Press, Cambridge, pp 1- 11

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

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

Smith VR (2008a) Energy flow and nutrient cycling in the Marion Island terrestrial ecosystem: 30 years on. Polar Record 44: 211-226

Smith VR (2008b) Terrestrial and freshwater primary production and nutrient cycling. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 181-214

Smith VR (2008c) Whole-island estimate of production and nutrient cycling on a sub-Antarctic island: are plant guilds the way to go? In: Mucina L, Kalwij J, Smith VR et al. (eds.) Frontiers of Vegetation Science - An Evolutionary Angle, Proceedings of the 51st Annual Symposium of the International Association for Vegetation Science, Stellenbosch, South Africa. Keith Phillips Images, Somerset West, pp 176-177

Smith VR, Mucina L (2006) Vegetation of subantarctic Marion and Prince Edward Islands. In: Chown SL, Froneman PW (eds.) The Prince Edward Islands: Land-Sea Interactions in a Changing Ecosystem. African Sun Media, Stellenbosch, pp 698-723

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

Smith TM, Shugart HH, Woodward FI (1997) Plant functional types, their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge

Takahashi S, Badger MR (2011) Photoprotection in plants: A new light on photosystem II damage. Trends in Plant Science 16: 53–60

Talling JF (1957) The phytoplankton population as a compound photosynthetic system. New Phytologist 56: 29-50

Thomas R J, Ryder SH, Gardner MI, Sheetz JP, Nichols SD (1996) Photosynthetic function of leaf lamellae in Polytrichum commune. Bryologist 99: 6-11

Tuittila ES (2000) Restoring vegetation and carbon dynamics in a cut-away peatland. Faculty of Science, Department of Ecology, University of Helsinki

Villarreal JC, Cargill DC, Hagborg A, Söderström LS, Renzaglia KS (2010). A synthesis of hornwort diversity: Patterns, causes and future work. Phytotaxa 9: 150- 166

von Humboldt A (1806) Ideen zu einer Physiognomik der Gewachse. Englisg Translation by E.C. Otté and H.G. Bohn, as Ideas for a physiognomy of plants. In Von Humboldt A, Views of Nature. H.G. Bohn, London, pp 210-352

Wace NM (1965) Vascular Plants. In: Van Miegham J, Van Oye P (eds.) Biogeography and ecology in Antarctica. Junk, The Hague, pp 201-266

Waite M, Sack L (2010) How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. New Phytologist 185: 156–172

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity resilience and ecosystem function: the nature and significance of dominant and minor species. Ecosystem 2: 95- 113

Walters RG (2005) Towards an understanding of photosynthetic acclimation. Journal of Experimental Botany 56: 435–447

Wang X, Liu Y, Yang P (2012) Proteomic studies of the abiotic stresses response in model moss- *Physcomitrella patens*. Frontiers in Plant Science 3: 258

Ward SE, Bardgett RD, McNamara NP, Ostle NJ (2009) Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. New Phytologist 23: 454- 462

Warming E (1909) Oecology of plants: an introduction to the study of plant communities. Oxford University Press, Oxford

Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999) Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science 10: 609–620

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199: 213-227

White AJ, Critchley C (1999) Rapid light curves: a new fluorescence method to assess the state of the photosynthetic apparatus. Photosynthesis Research 59: 63–72

Williams TG, Flanagan LB (1996) Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in Pleurozium and Sphagnum. Oecologia 108: 38–46

Wood AJ (2007) The nature and distribution of vegetative desiccation-tolerance in hornworts, liverworts and mosses. The Bryologist 110:163-177

Wood AJ, Duff JR, Oliver MJ (1999) Expressed sequence tags (ESTs) from desiccated *Tortula ruralis* identify a large number of novel plant genes. Plant, Cell and Physiology 40: 361-368

Woodward FI, Cramer W (1996) Plant functional types and climatic changes: introduction. Journal of Vegetation Science 7: 306- 308

9 Appendix

Table A1. Species means and standard deviations (mean±std.dev) for the eight light response traits: ETR_{max} (µmol m^{-2} s^{-1}), PAR_{opt} (µmol photons $m^{-2}s^{-1}$), $\phi PSII_{PARopt}$ (µmol m^{-2} s^{-1}), α (µmol photons $m^{-2}s^{-1}$), Ik (µmol m^{-2} s^{-1}), $Inhib_{876}$ (%), $YNPQ/YNO_{876}$ (ratio) and qL_{876} (fraction).

Species	ETR_{max}	PAR_{opt}	$\phi PSII_{PARopt}$	α	Ik	$Inhib_{876}$	$YNPQ/YNO_{876}$	qL_{876}
Andreaea acutifolia	26.35±5.40	661.69±150.14	0.10±0.02	0.24±0.04	121.84±23.87	7.53±9.99	2.33±0.71	0.19±0.02
Blepharidophyllum densifolium	14.09±3.43	286.09±95.18	0.12±0.02	0.28±0.04	52.66±9.19	24.32±16.93	1.88±0.19	0.07±0.02
Brachythecium paradoxum	7.49±1.80	168.60±32.86	0.11±0.02	0.23±0.06	34.32±12.56	41.56±22.78	1.63±0.30	0.06±0.05
Brachythecium rutabulum	12.07±2.23	202.09±46.55	0.15±0.03	0.22±0.07	58.96±18.32	41.28±26.67	2.60±0.76	0.08±0.04
Brachythecium subplicatum	28.43±6.62	394.18±104.50	0.17±0.01	0.26±0.03	107.46±18.16	19.44±12.76	3.95±0.79	0.22±0.09
Breutelia integrifolia	37.29±8.86	760.41±321.79	0.13±0.03	0.29±0.02	124.89±37.16	1.86±2.75	2.50±0.67	0.24±0.07
Bryum laevigatum	36.01±9.19	697.08±129.91	0.12±0.02	0.31±0.01	117.00±30.52	2.18±2.98	3.59±0.25	0.26±0.06
Bucklandiella membranacea var.1	35.24±8.20	1214.43±608.31	0.08±0.03	0.28±0.02	126.56±31.73	2.19±4.28	4.08±0.80	0.32±0.06
Bucklandiella membranacea var.2	27.80±4.46	774.32±273.00	0.09±0.03	0.37±0.04	75.99±16.37	0.98±1.42	4.22±0.71	0.32±0.05

Bucklandiella ochracea	23.65±7.47	414.60±163.47	0.14±0.01	0.25±0.05	92.69±17.57	17.31±16.19	1.61±0.30	0.17±0.09
Campylopus clavatus	34.22±5.13	596.22±101.19	0.14±0.03	0.38±0.05	94.11±17.65	5.25±5.28	3.67±0.74	0.29±0.07
Campylopus purpureocaulis	42.82±6.44	752.64±182.38	0.14±0.02	0.29±0.04	144.98±20.51	3.26±5.47	2.72±0.61	0.29±0.7
Campylopus subnitens	19.47±3.23	378.47±52.45	0.12±0.00	0.30±0.04	60.49±12.11	13.43±4.17	3.21±0.69	0.16±0.04
Clasmatocolea humilis	12.26±3.09	258.06±70.92	0.11±0.02	0.22±0.05	57.27±11.03	26.41±15.43	2.96±0.16	0.07±0.03
Clasmatocolea vermicularis	18.29±2.17	322.07±70.88	0.14±0.02	0.26±0.05	72.05±8.88	21.09±12.61	2.68±0.28	0.12±0.02
Cratoneuropsis chilensis	6.53±1.71	139.49±37.53	0.12±0.04	0.17±0.05	38.75±4.85	55.10±20.94	1.59±0.16	0.02±0.02
Dicranoloma billardieri	21.26±5.27	476.46±203.11	0.11±0.03	0.28±0.04	75.11±12.75	10.06±9.33	3.26±0.47	0.17±0.08
Distichophyllum fasciculatum	8.79±1.86	189.63±33.73	0.11±0.03	0.17±0.02	47.49±7.20	41.65±13.58	1.80±0.17	0.06±0.03
Ditrichum strictum	24.95±6.72	521.94±146.65	0.12±0.02	0.27±0.02	90.66±21.90	6.83±9.21	2.58±0.53	0.24±0.04
Guembelia kidderi	38.87±10.37	851.48±262.59	0.11±0.02	0.36±0.07	115.60±50.85	0.00±0.00	3.59±0.81	0.38±0.13
Hypnum cupressiforme	12.74±2.81	246.07±85.26	0.13±0.03	0.26±0.06	49.36±7.02	27.83±19.33	2.26±0.52	0.07±0.05
Jensenia pisicolor	14.64±3.72	352.62±38.84	0.10±0.02	0.21±0.07	70.81±11.13	15.75±5.87	2.98±0.68	0.12±0.05
Jungermannia coniflora	15.35±3.84	248.50±62.62	0.15±0.02	0.26±0.05	59.14±10.53	32.60±5.75	2.48±0.82	0.11±0.06

Lepidozia laevifolia	10.02±1.77	172.29±26.53	0.14±0.02	0.23±0.07	46.49±11.57	46.43±10.19	1.87±0.54	0.05±0.02
Leptoscyphus expansus	10.66±4.44	219.29±73.13	0.11±0.03	0.23±0.06	44.59±15.33	34.67±22.10	2.28±0.42	0.06±0.04
Lophocolea randii	12.89±2.74	214.85±54.59	0.14±0.01	0.25±0.04	52.62±9.29	36.59±12.04	2.53±0.49	0.10±0.05
Marchantia berteroana	45.99±6.55	680.39±62.21	0.16±0.02	0.34±0.03	131.17±21.41	1.18±0.89	2.47±0.28	0.22±0.04
Muelleriella crassifolia	25.29±5.04	805.79±335.39	0.09±0.03	0.26±0.03	97.00±15.72	1.98±2.83	2.27±0.63	0.20±0.04
Notologitrichum australe	58.35±15.52	996.39±321.20	0.14±0.01	0.29±0.01	189.14±55.55	0.38±.67	2.04±0.19	0.23±0.04
Philonotis tenuis	31.64±14.21	1050.38±701.40	0.08±0.03	0.31±0.02	102.20±43.00	2.56±4.22	2.59±0.69	0.18±0.07
Plagiochila heterodonta	13.77±2.65	228.65±53.32	0.15±0.02	0.23±0.06	62.63±16.56	38.98±24.42	2.95±0.71	0.09±0.06
Polytrichum juniperinum	101.58±32.44	1745.92±345.59	0.14±0.03	0.28±0.02	369.57±116.31	0.00±0.00	2.18±0.62	0.35±0.12
Ptychomion densifolium	20.97±3.70	460.97±126.24	0.11±0.01	0.28±0.04	75.80±18.30	8.24±7.45	3.40±0.45	0.22±0.06
Racomitrium lanuginosum	45.46±6.33	803.88±275.78	0.15±0.04	0.26±0.04	173.12±29.06	3.09±5.19	3.67±0.82	0.38±0.12
Riccardia prehensilis	14.34±3.48	344.60±60.99	0.10±0.02	0.24±0.04	61.17±18.91	13.32±5.95	2.45±0.56	0.11±0.06
Sanonia uncinata	20.36±3.57	371.98±68.36	0.13±0.01	0.28±0.04	72.86±15.06	13.29±8.06	3.27±0.30	0.19±0.07
Syzygiella colorata	15.98±5.02	551.05±187.04	0.07±0.02	0.24±0.04	68.38±16.12	5.31±7.11	2.37±0.44	0.09±0.03
Syzygiella sonderi	24.68±7.00	601.03±213.64	0.10±0.02	0.27±0.02	98.41±16.54	6.37±8.39	2.77±0.56	0.16±0.09

Table A2. Species means for the six desiccation response traits: MC_{sat} (%), Rate (% MC per min), $RWC\phi PSII_{max}$ (%), RWC_{final} (%), $YNPQ/YNO_{final}$ (ratio) and $\phi PSII_{recov}$ (%).

Species	**MC_{sat}**	**Rate**	**$RWC\phi PSII_{max}$**	**RWC_{final}**	**$YNPQ/YNO_{final}$**	**$\phi PSII_{recov}$**
Andreaea acutifolia	344.62±61.48	1.25±0.27	64.06±9.22	31.83±10.86	3.85±1.42	63.00±33.37
Blepharidophyllum densifolium	1090.59±162.14	4.31±2.62	67.79±15.07	22.66±4.89	1.70±1.55	17.89±36.44
Brachythecium paradoxum	1048.63±294.69	11.87±3.05	73.41±31.10	4.22±1.82	2.07±0.93	22.17±14.20
Brachythecium rutabulum	1038.64±403.39	8.32±3.41	64.33±29.71	8.22±3.90	3.52±1.96	21.24±14.98
Brachythecium subplicatum	1091.45±246.40	5.07±2.00	81.86±16.62	4.99±1.10	4.16±2.07	7.91±6.82
Breutelia integrifolia	779.46±294.62	3.61±0.72	85.95±15.66	8.33±3.34	4.15±2.26	13.16±9.83
Bryum laevigatum	940.74±359.68	4.68±1.49	76.27±17.16	6.67±3.65	5.56±1.26	6.60±8.19
Bucklandiella membranacea var.1	379.72±48.86	1.73±0.44	80.80±21.92	12.29±3.72	6.05±2.86	88.17±13.41
Bucklandiella membranacea var.2	488.80±53.55	2.50±0.60	71.28±19.61	8.56±2.68	5.90±1.69	56.28±7.55
Bucklandiella ochracea	665.82±428.57	4.91±3.56	72.04±22.63	14.45±11.00	4.56±3.25	64.50±37.06
Campylopus clavatus	522.61±79.77	3.32±0.40	72.32±4.35	6.92±1.21	4.86±0.86	24.67±7.57
Campylopus purpureocaulis	564.61±117.18	1.93±0.97	76.00±12.18	13.24±4.74	3.09±1.21	16.31±17.10

Campylopus subnitens	576.44±178.67	2.68±0.75	82.27±21.58	6.11±1.59	4.98±0.89	22.60±32.30
Clasmatocolea humilis	1544.47±348.65	3.95±2.05	97.73±4.49	10.52±4.11	2.74±0.86	4.65±11.59
Clasmatocolea vermicularis	1721.81±360.57	9.11±2.63	90.72±13.58	11.87±5.24	2.84±1.30	10.13±26.08
Cratoneuropsis chilensis	765.86±345.88	10.22±4.46	74.16±25.18	14.11±7.56	2.21±1.09	59.08±41.34
Dicranoloma billardieri	704.75±113.43	2.62±1.30	89.40±11.80	7.83±2.45	4.98±2.68	23.17±33.05
Distichophyllum fasciculatum	2368.88±753.02	5.69±2.10	73.95±8.27	15.57±9.63	1.69±1.34	2.58±5.58
Ditrichum strictum	306.25±99.43	0.90±0.32	84.04±11.90	21.21±4.75	3.81±2.08	66.70±18.53
Guembelia kidderi	339.76±89.70	1.57±0.97	87.35±11.11	21.68±8.12	5.59±3.85	89.21±16.33
Hypnum cupressiforme	884.63±125.96	5.04±1.86	74.69±22.47	5.52±2.63	4.10±1.81	53.06±22.61
Jensenia pisicolor	961.55±345.28	4.23±2.30	73.78±25.21	12.48±7.10	2.82±1.80	11.92±15.16
Jungermannia coniflora	779.21±367.46	2.92±2.05	79.51±9.02	18.33±7.36	2.73±1.39	6.68±26.43
Lepidozia laevifolia	1054.76±199.11	11.89±4.78	74.47±30.07	10.00±5.63	2.19±1.04	3.19±7.01
Leptoscyphus expansus	1505.71±408.03	11.71±4.69	58.69±24.17	11.13±5.44	2.48±0.78	4.25±1554.51
Lophocolea randii	1392.62±341.41	9.75±3.61	95.20±9.45	13.56±4.85	1.19±0.64	13.03±15.28
Marchantia berteroana	1571.00±266.19	3.47±1.29	80.85±16.93	13.82±9.25	2.49±1.26	20.29±12.75
Muelleriella crassifolia	402.49±62.98	1.46±0.37	68.43±23.05	20.28±4.01	4.61±1.75	89.65±66.86

Notologitrichum australe	458.96±205.93	3.75±1.35	65.30±10.56	10.17±3.39	4.17±2.51	30.92±37.03
Philonotis tenuis	722.98±359.57	4.88±2.22	86.86±16.77	9.67±2.09	4.08±2.39	1.80±3.08
Plagiochila heterodonta	530.14±202.61	4.06±2.43	84.53±13.56	8.86±4.77	5.09±1.02	78.44±27.82
Polytrichum juniperinum	154.13±48.41	1.48±0.91	61.50±29.27	27.08±5.39	8.41±3.21	60.30±22.86
Ptychomion densifolium	853.34±180.31	4.78±2.46	63.42±32.01	4.04±1.35	4.54±1.16	30.15±19.71
Racomitrium lanuginosum	385.28±84.48	2.18±0.38	61.97±10.43	9.61±2.71	3.47±1.32	73.92±20.97
Riccardia prehensilis	1098.02±243.07	10.34±4.59	76.66±18.97	16.58±5.14	1.60±0.57	0.14±0.28
Sanonia uncinata	1259.95±285.55	10.61±3.62	67.54±33.54	6.09±3.37	3.15±0.66	28.19±12.86
Syzygiella colorata	416.58±70.34	3.09±1.14	59.99±12.02	24.12±7.78	3.63±2.03	70.08±18.44
Syzygiella sonderi	369.00±28.05	1.89±0.37	80.27±18.07	11.88±4.50	7.88±2.42	71.20±17.12

Figures

Figure 4.1. Clustering of species based on their scores for light response traits on PC1, PC2 and PC3 from PCA analysis.

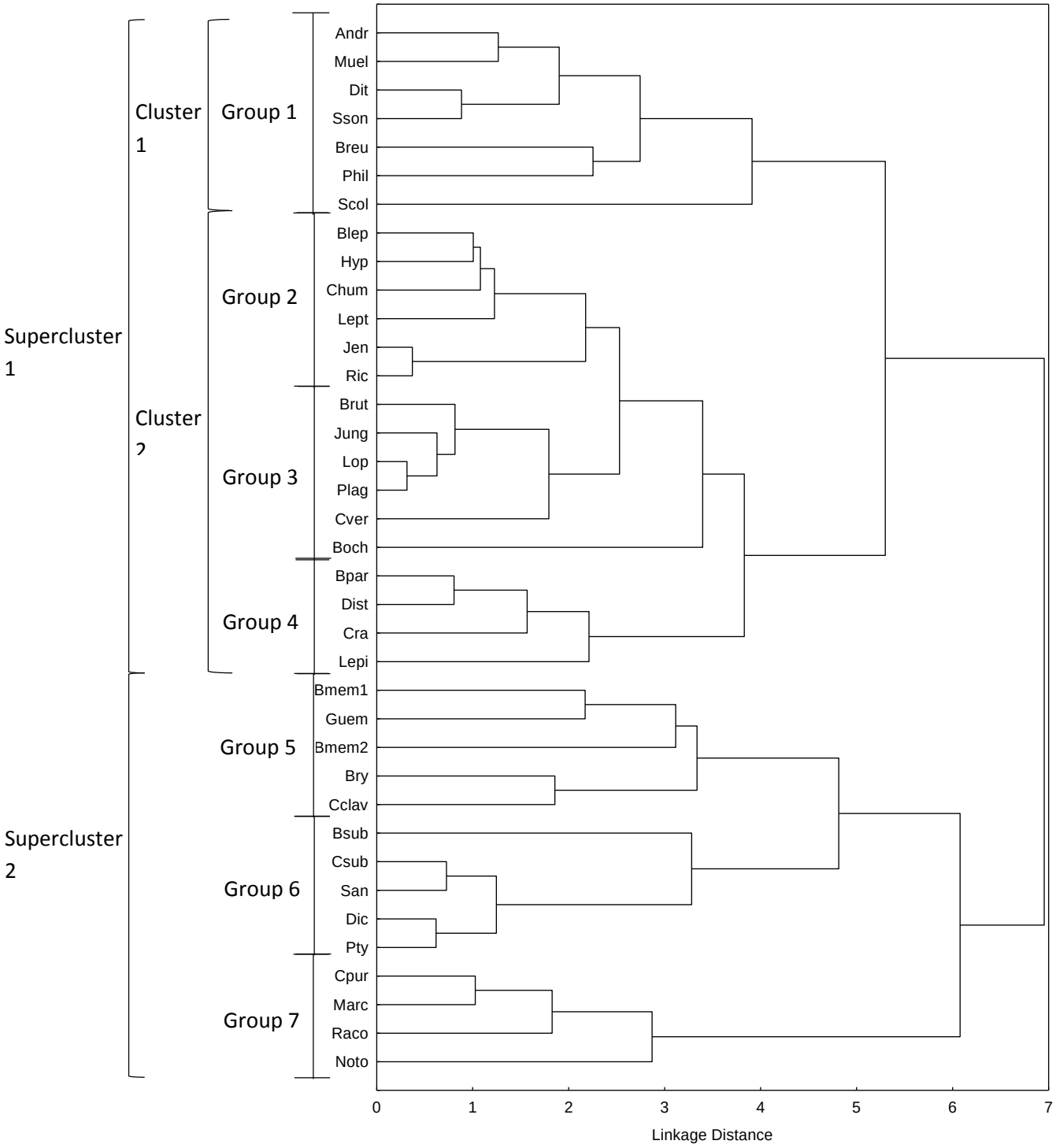


Figure 4.2a. Biplot showing the light response trait gradients and mean species scores on PC1 and PC2. The superclusters and clusters are shown.

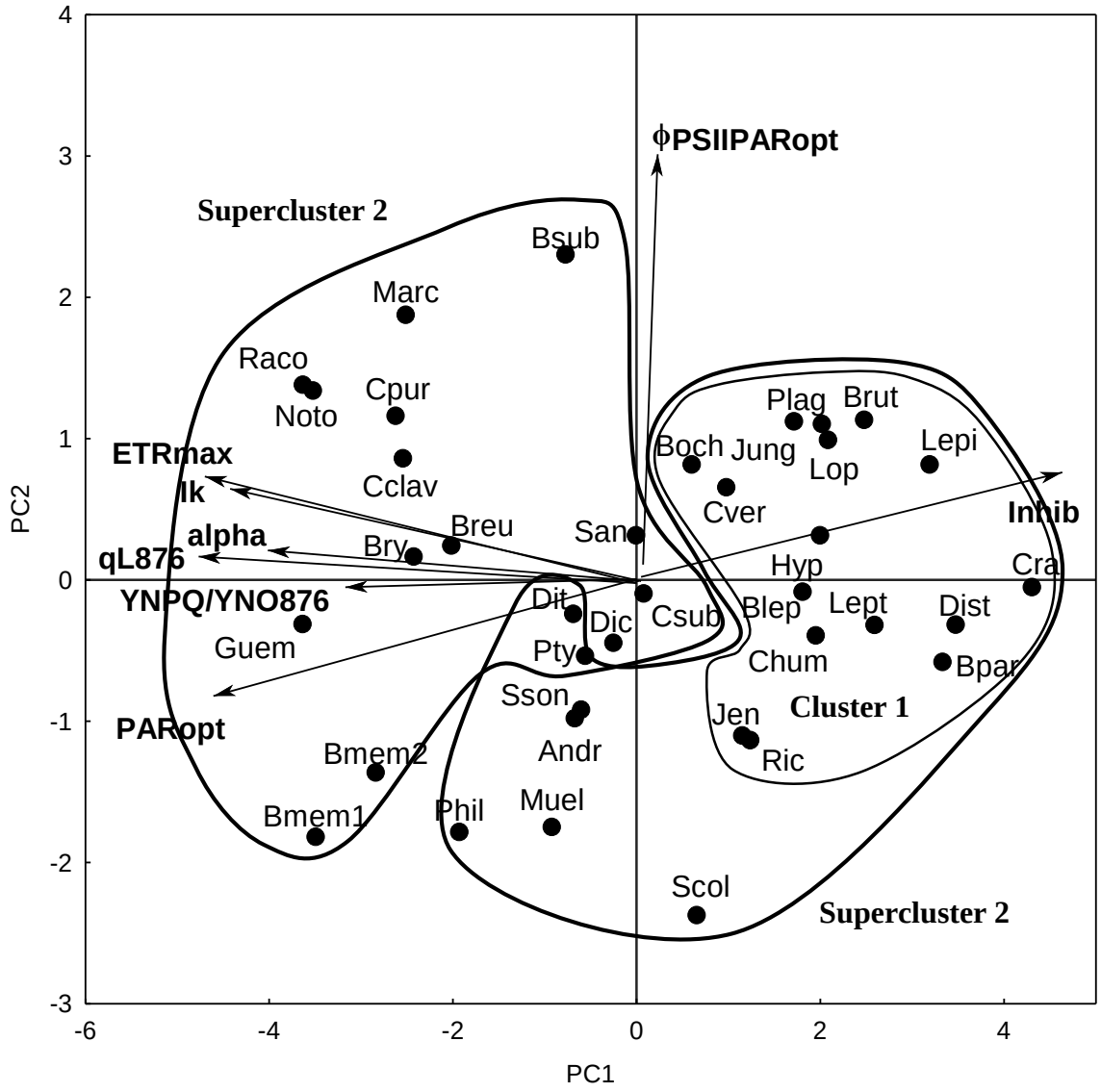


Figure 4.2b. Biplot showing the light response trait gradients and mean species scores on PC1 and PC2. The seven groups are shown.

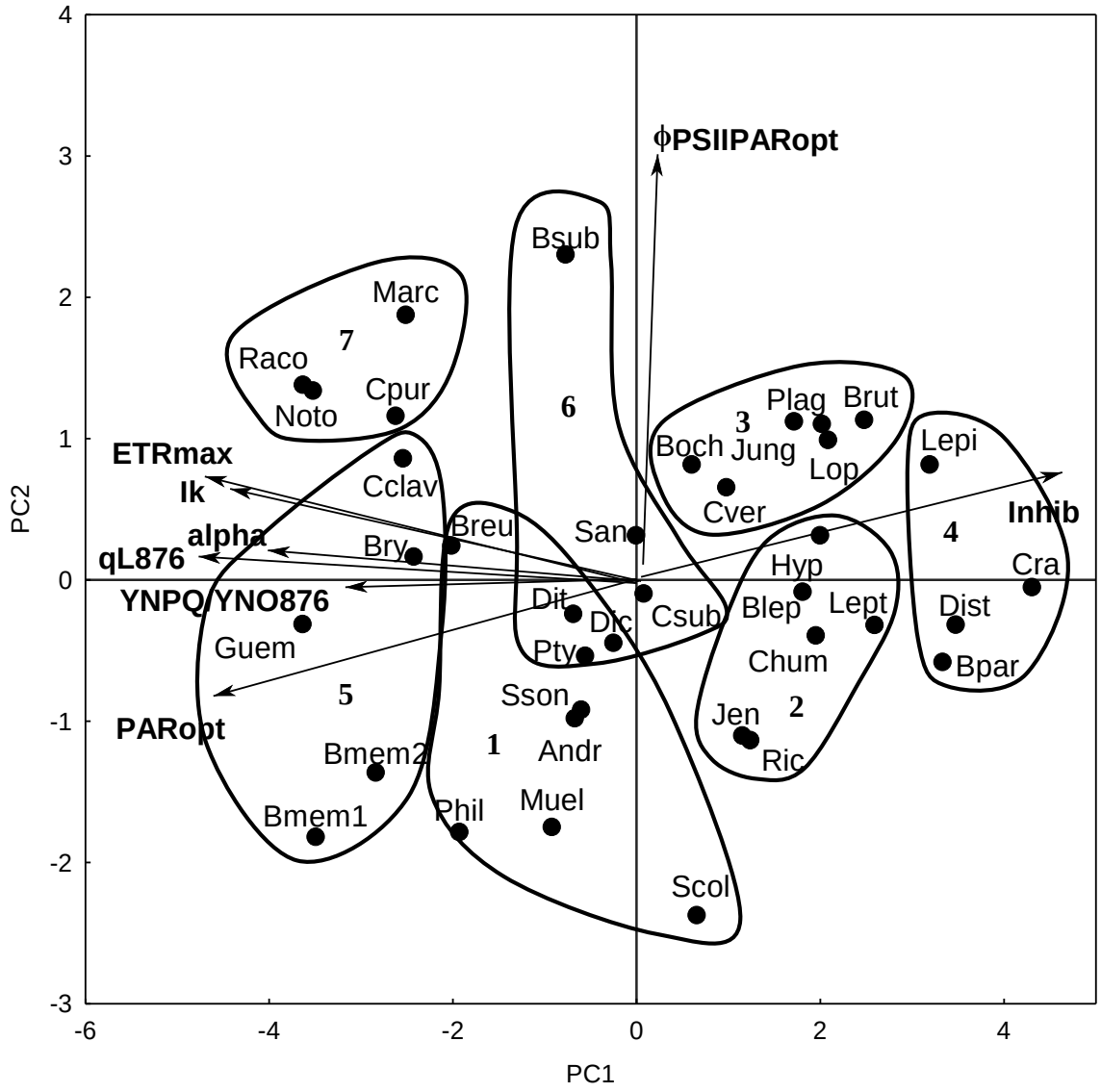


Figure 4.2c. Biplot showing the light response trait gradients and mean species scores on PC1 and PC3. The seven groups are shown.

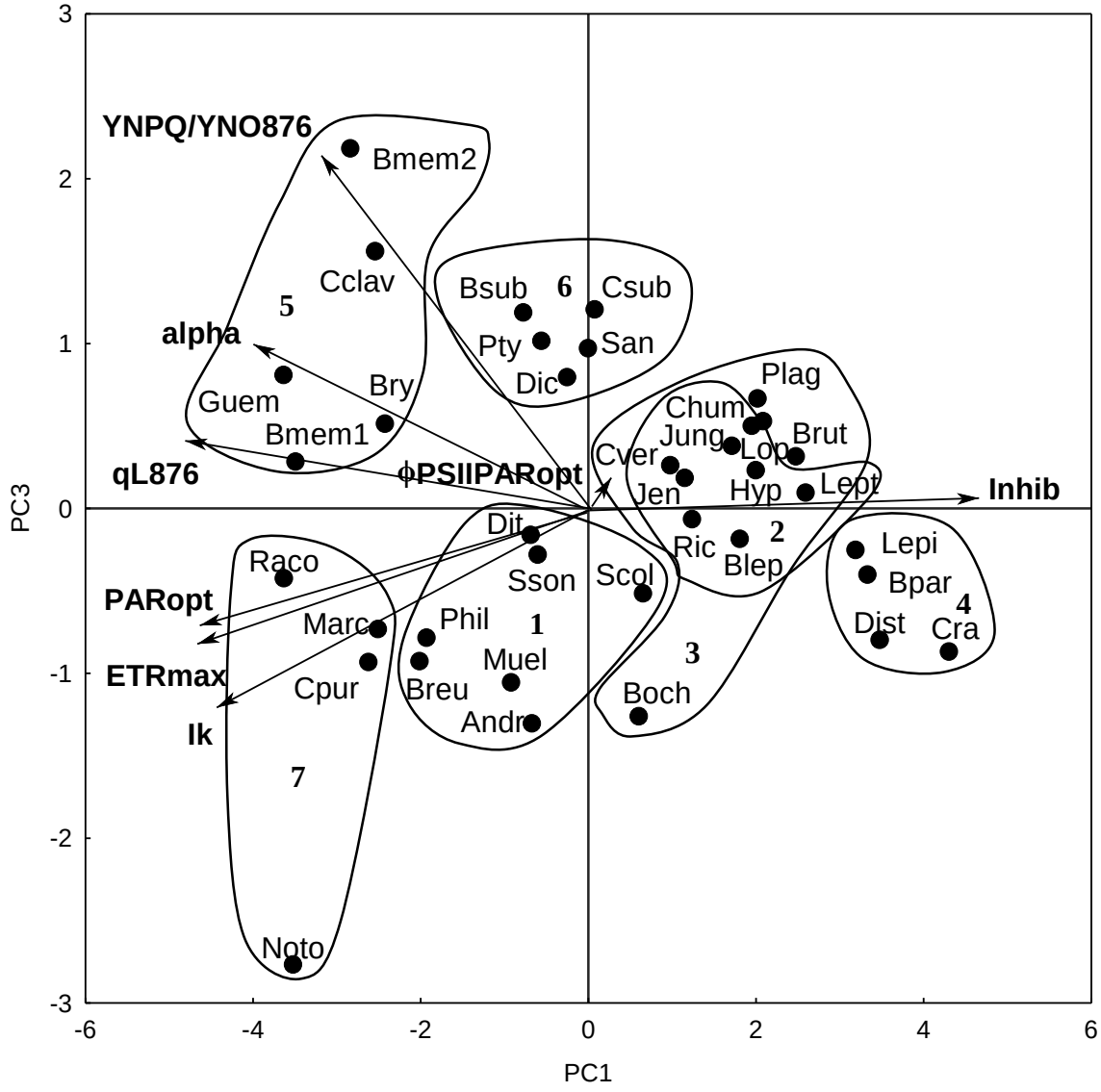


Figure 4.3. Clustering of phylum based on the species scores on the first three components yielded by the PCA on light response traits. 'M' indicates that it is a moss species while 'H' indicates it is a hepatic species.

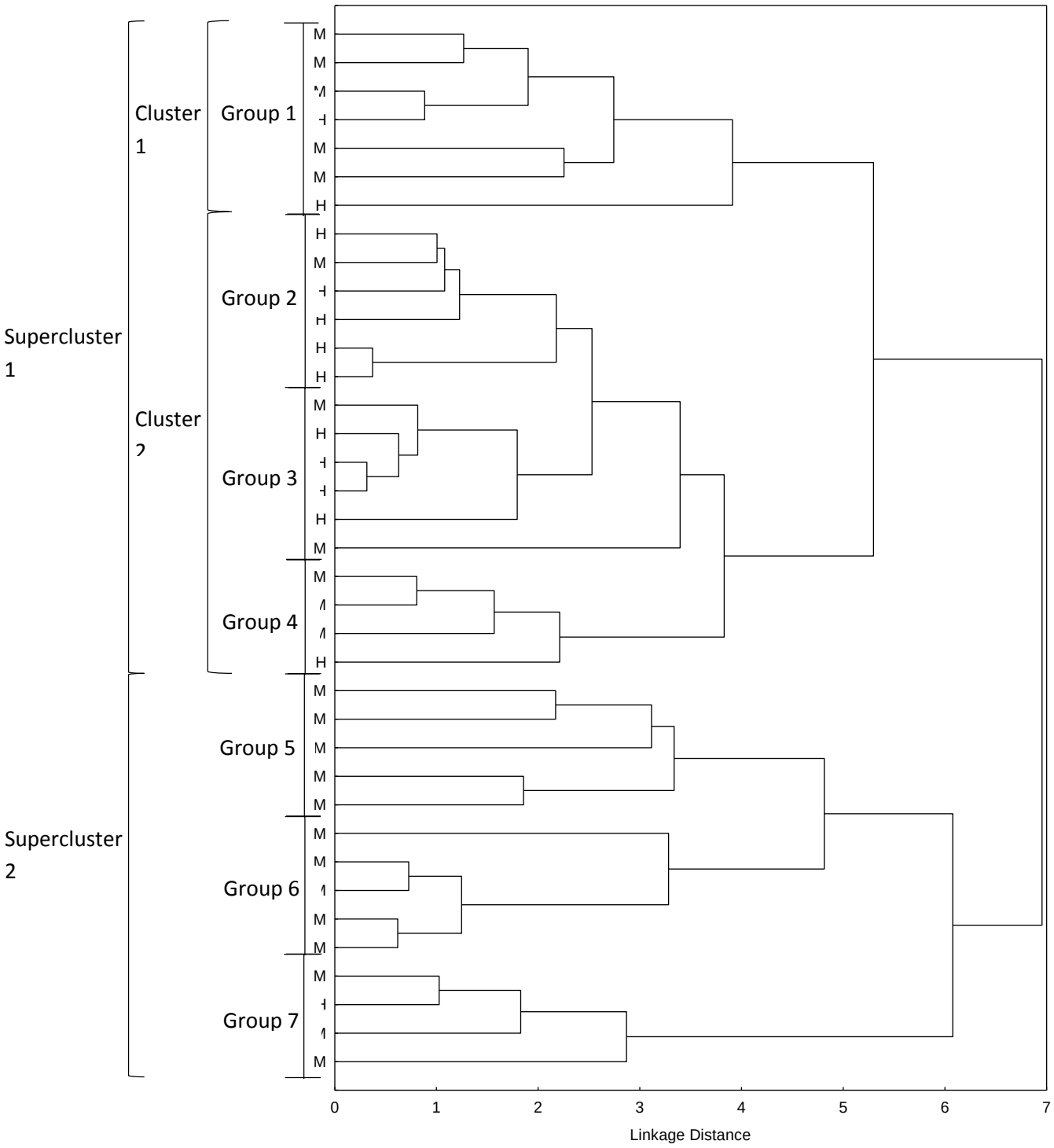


Figure 4.4. Clustering of order based on the species scores on the first three components yielded by the PCA on light response traits.

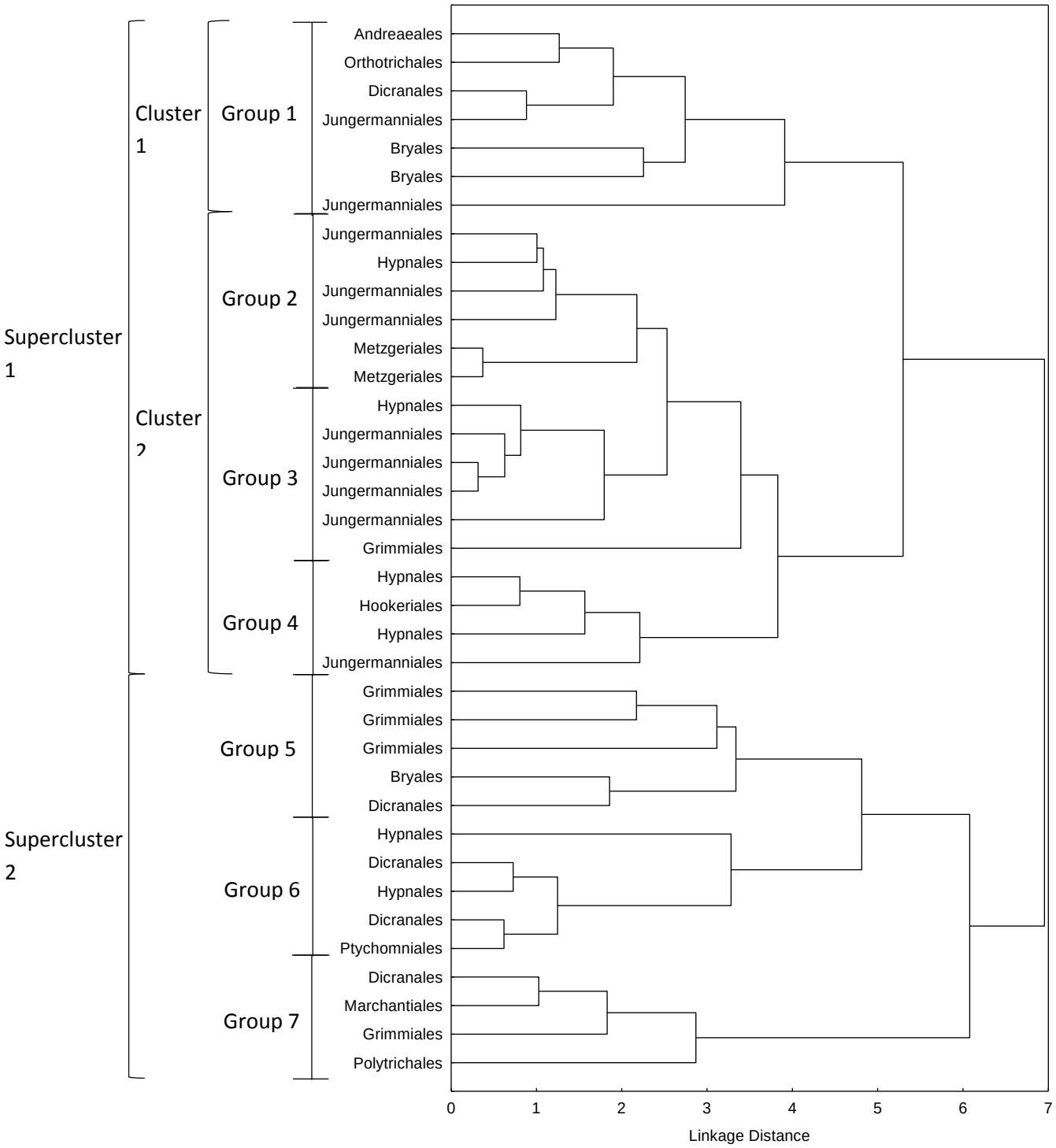


Figure 4.5. CA joint plot showing the centroids of the seven light response groups and the association of the bryophyte orders on the principal axes.

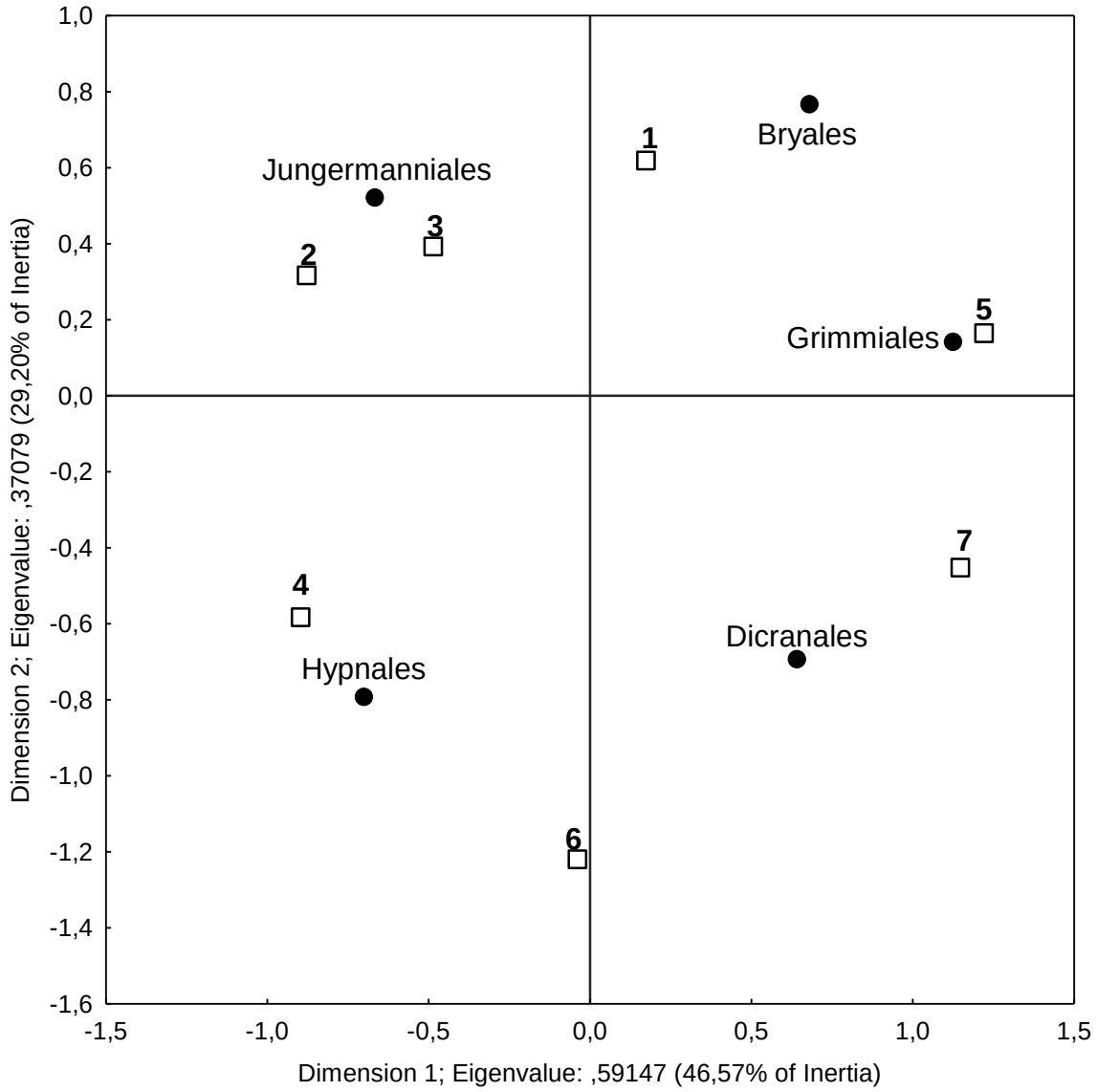
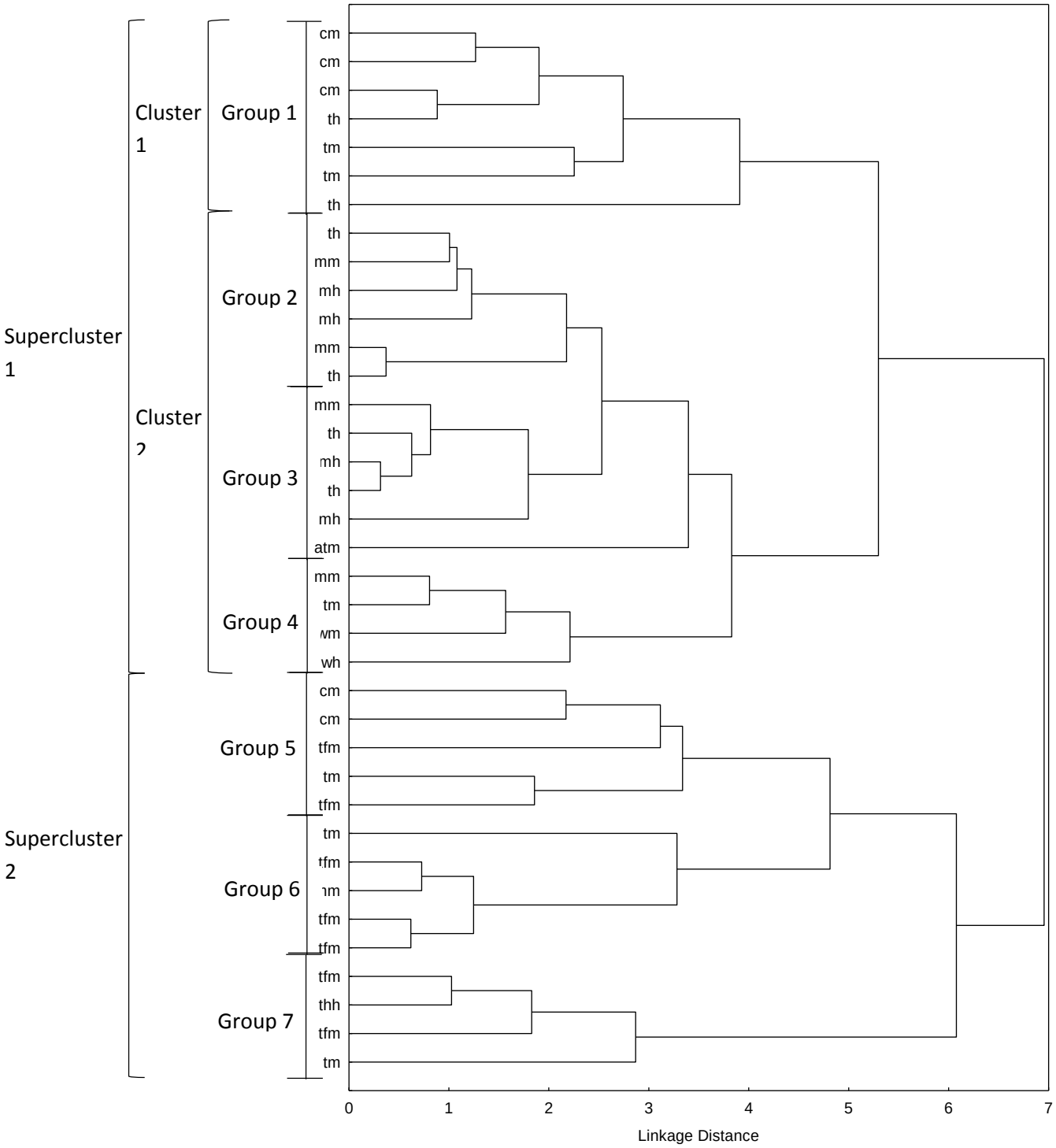


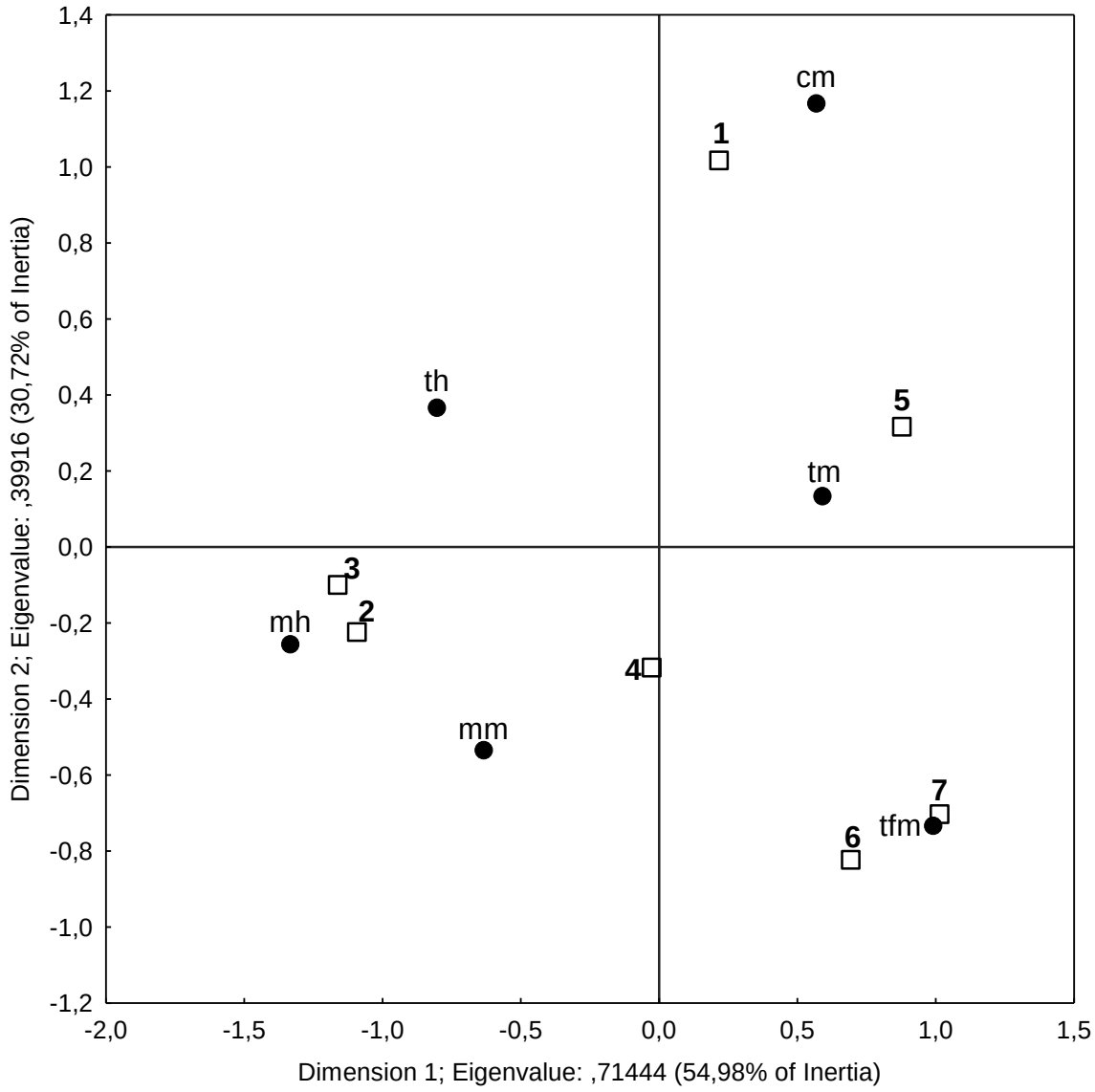
Figure 4.6. Clustering of life form based on the species scores on the first three components yielded by the PCA on light response traits.



Abbreviations

cm-	cushion moss	tm-	turf moss	tfm-	tuft moss
mm-	mat moss	mh-	mat hepatic	th-	turf hepatic

Figure 4.7. CA joint plot showing the centroids of the seven light response groups and the association of the bryophyte life forms on the principal axes.



Abbreviations

cm-	cushion moss	tm-	turf moss	tfm-	tuft moss
mm-	mat moss	mh-	mat hepatic	th-	turf hepatic

Figure 4.8. Clustering of light regime based on the species scores on the first three components yielded by the PCA on light response traits.

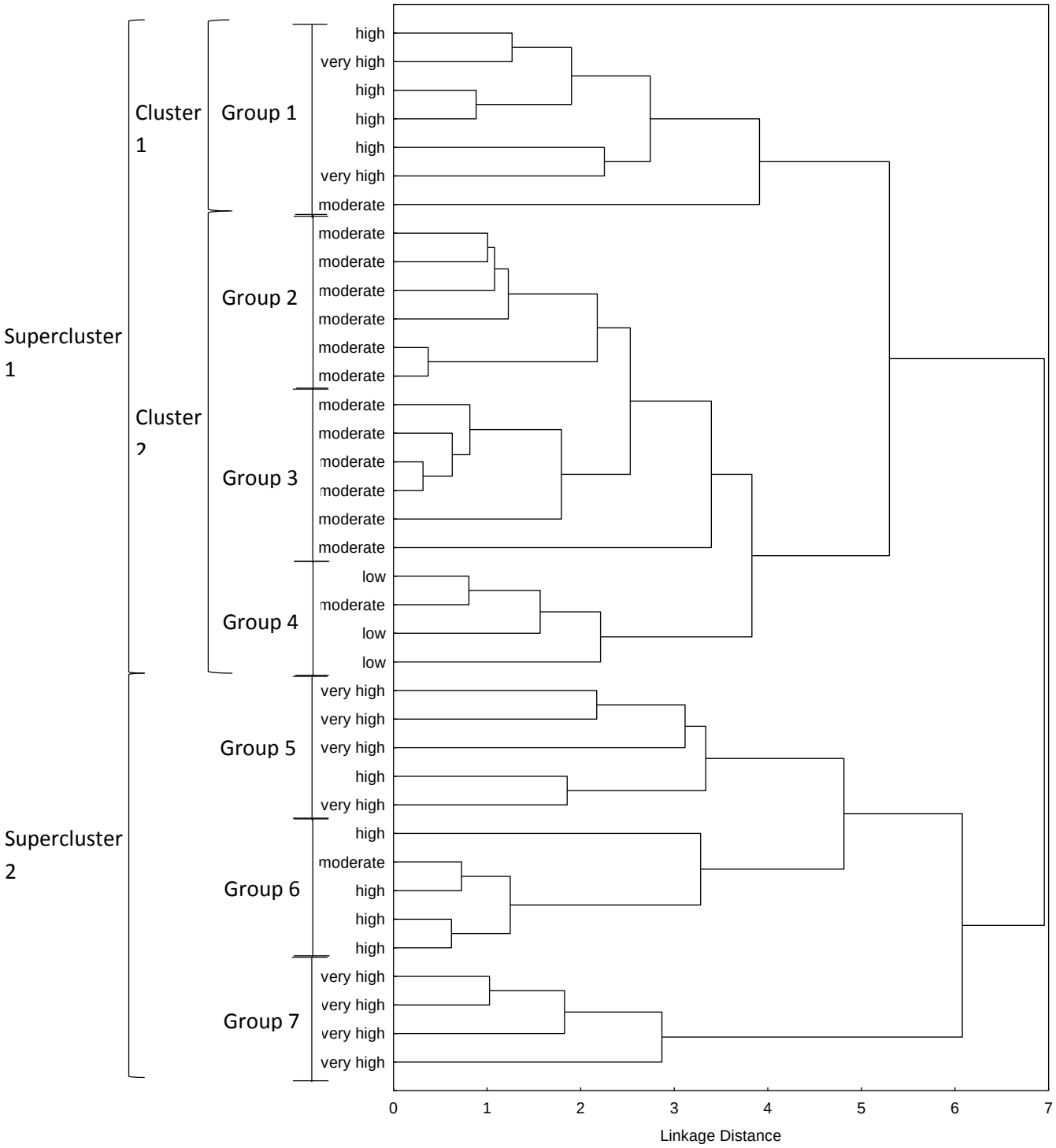


Figure 4.9. CA joint plot showing the centroids of the seven light response groups and the association of the bryophyte light regime on the principal axes.

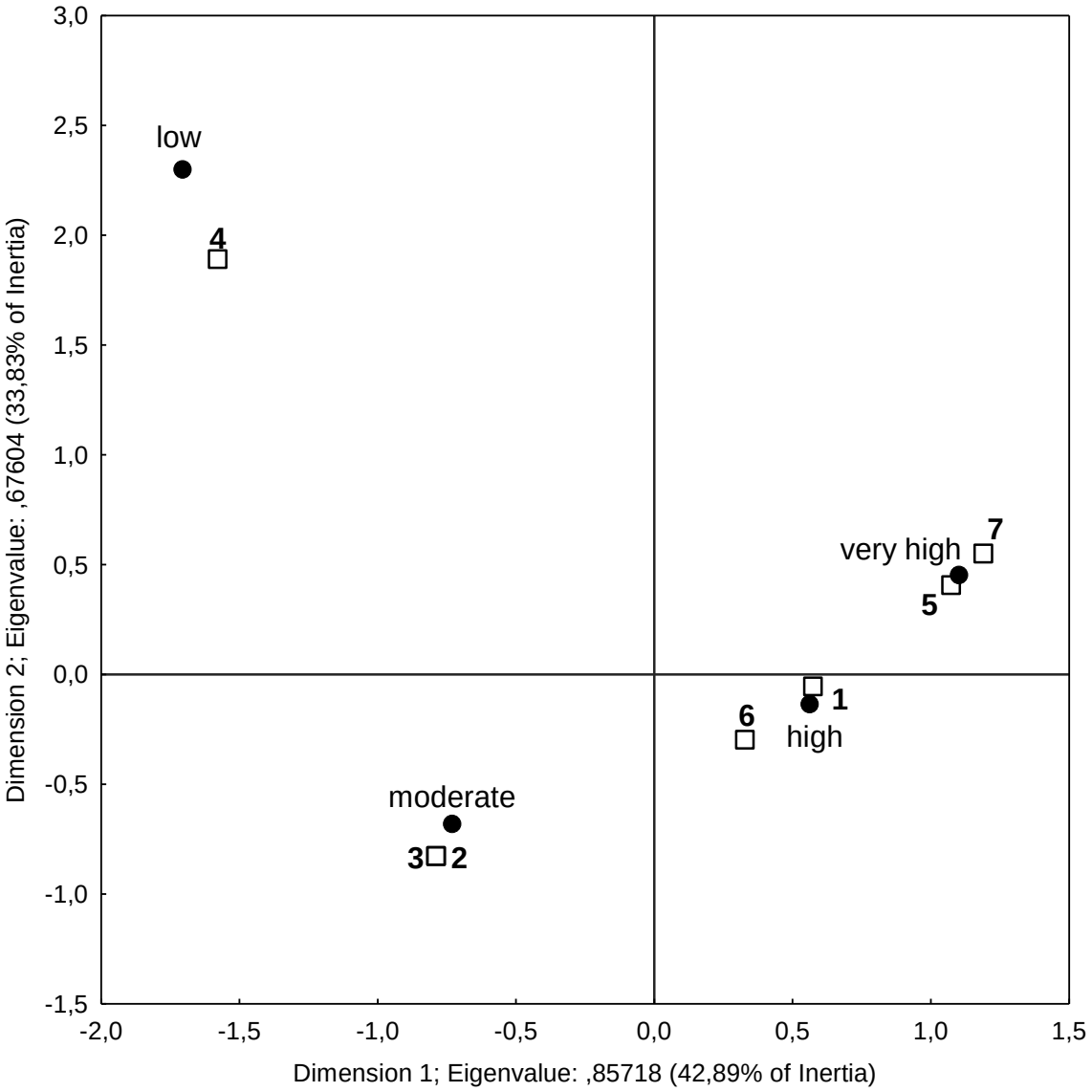


Figure 4.10. Clustering of habitat moisture based on the species scores on the first three components yielded by the PCA on light response traits.

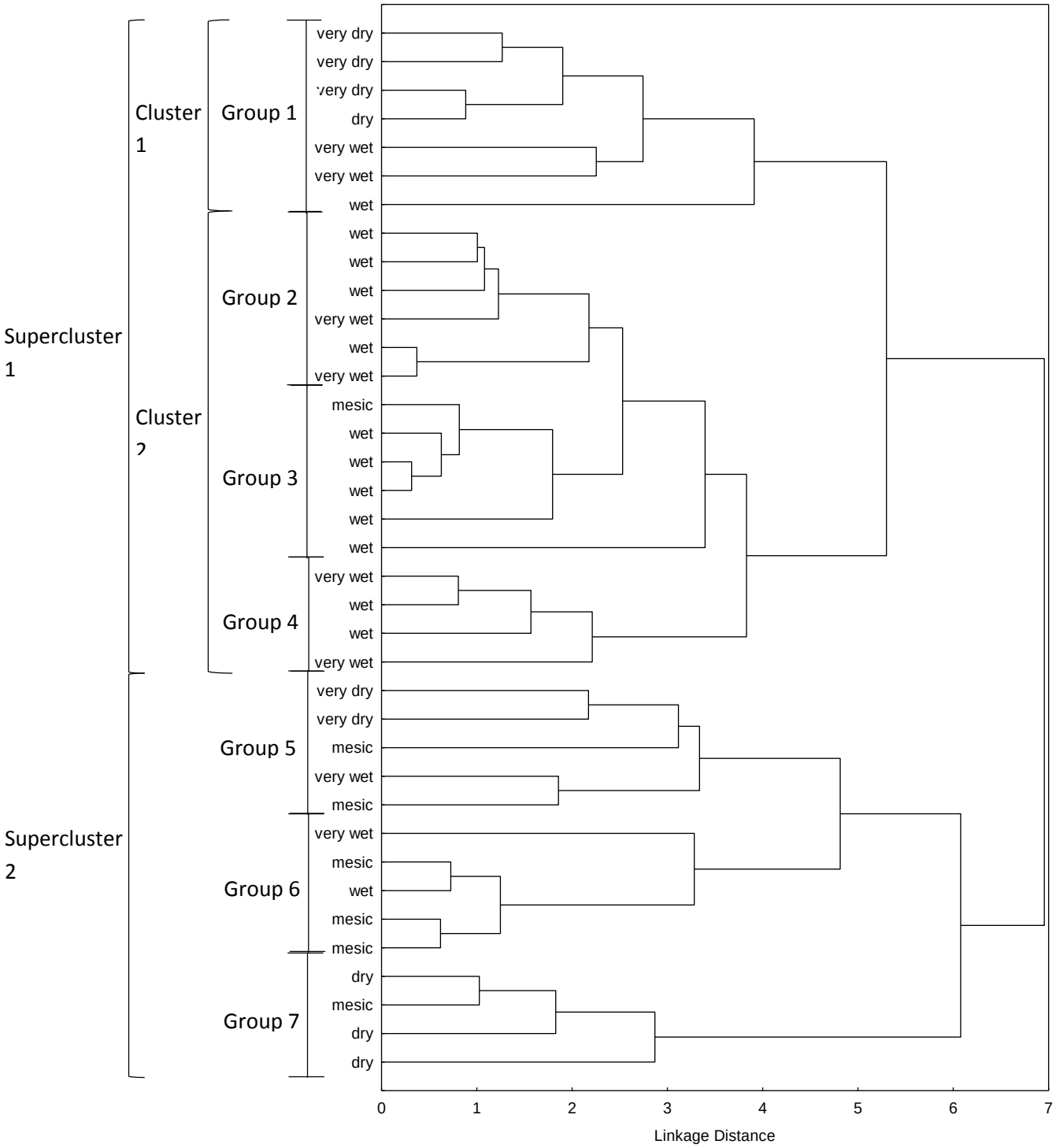


Figure 4.11. CA joint plot showing the centroids of the seven light response groups and the association of the bryophyte habitat moisture on the principal axes.

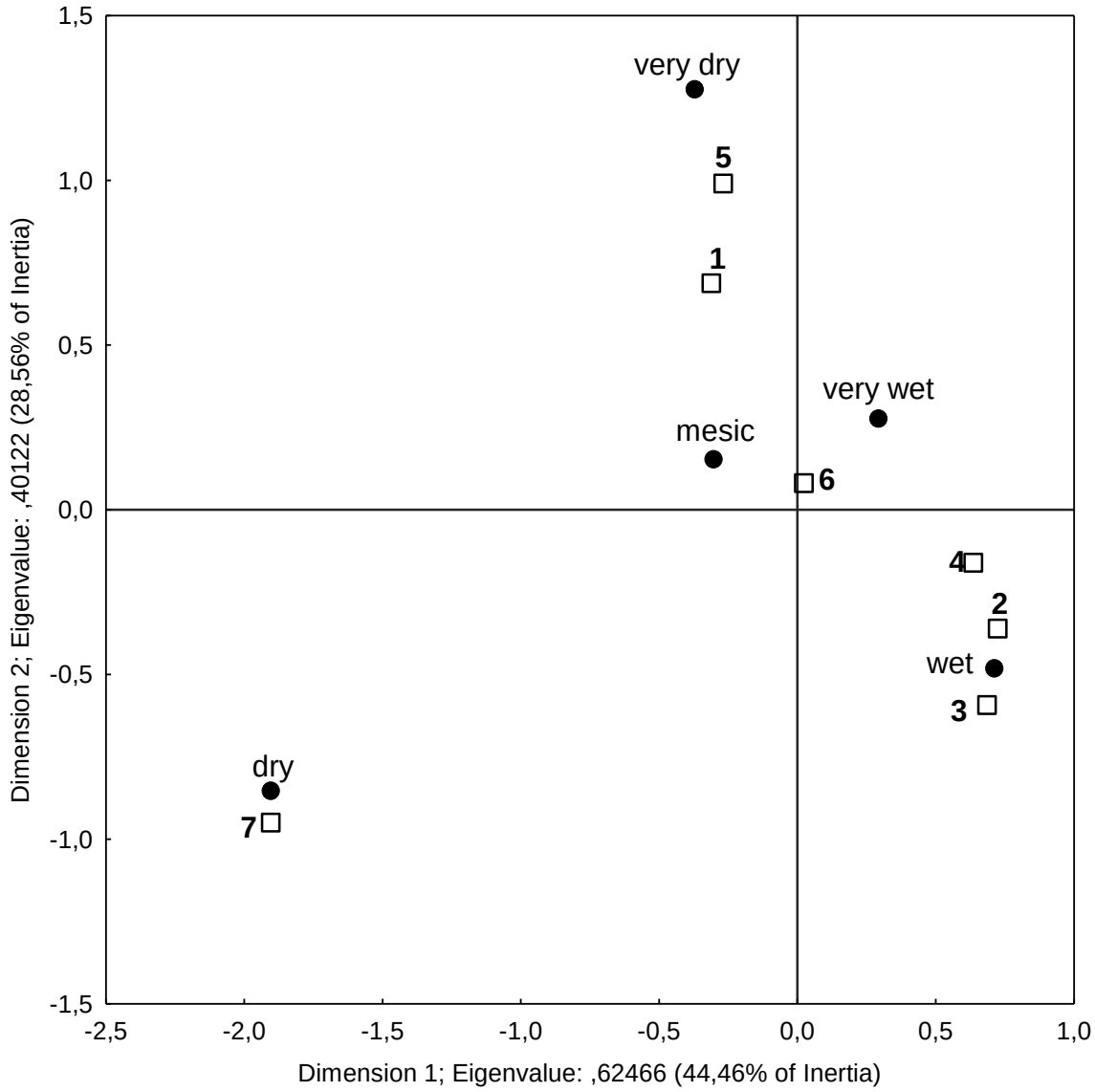


Figure 5.1. Clustering of species based on their scores for desiccation response traits on PC1, PC2 and PC3 from PCA analysis.

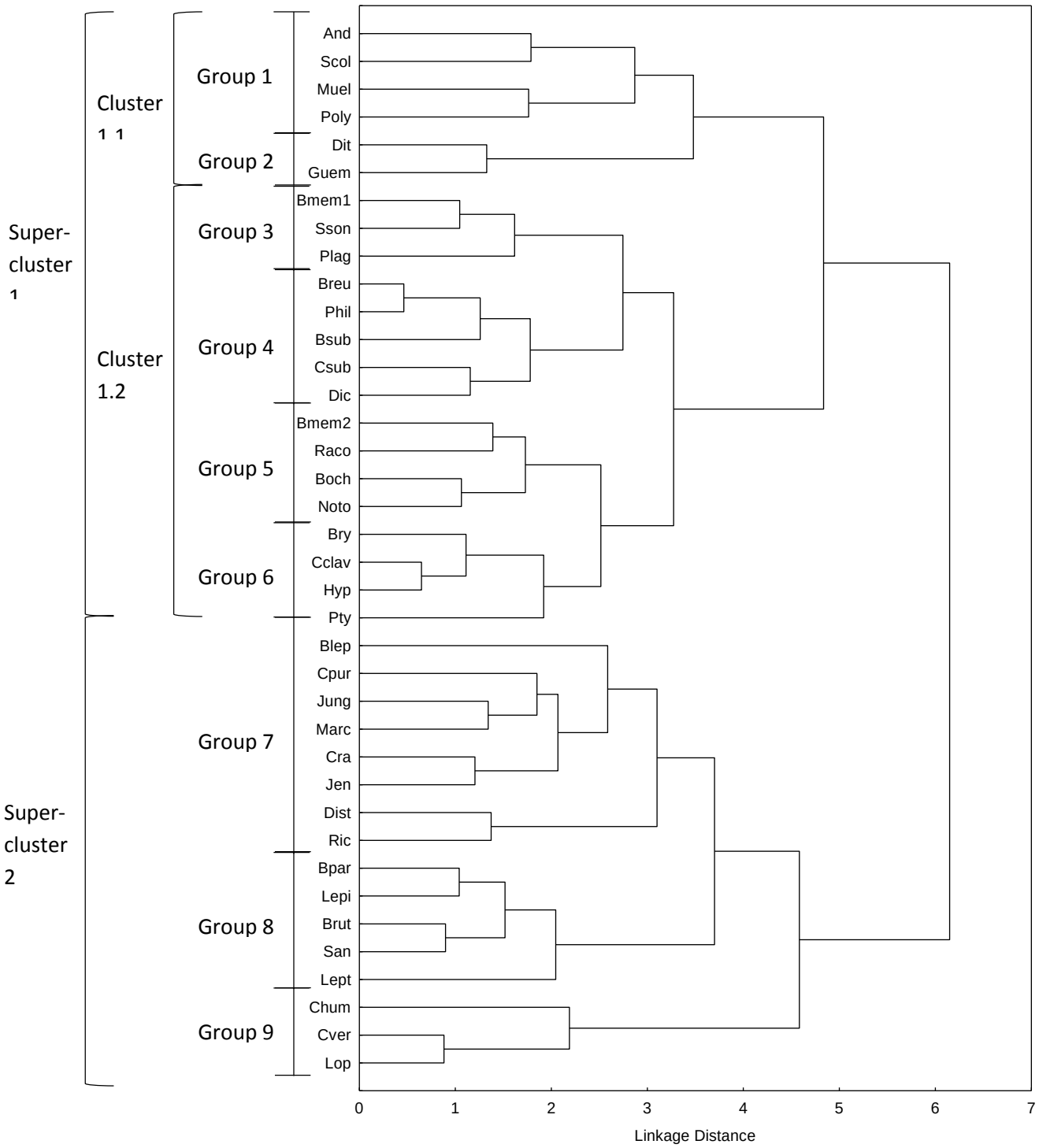


Figure 5.2a. Biplot showing the desiccation response trait gradients and mean species scores on PC1 and PC2. The two superclusters and the two clusters within supercluster 1 are shown.

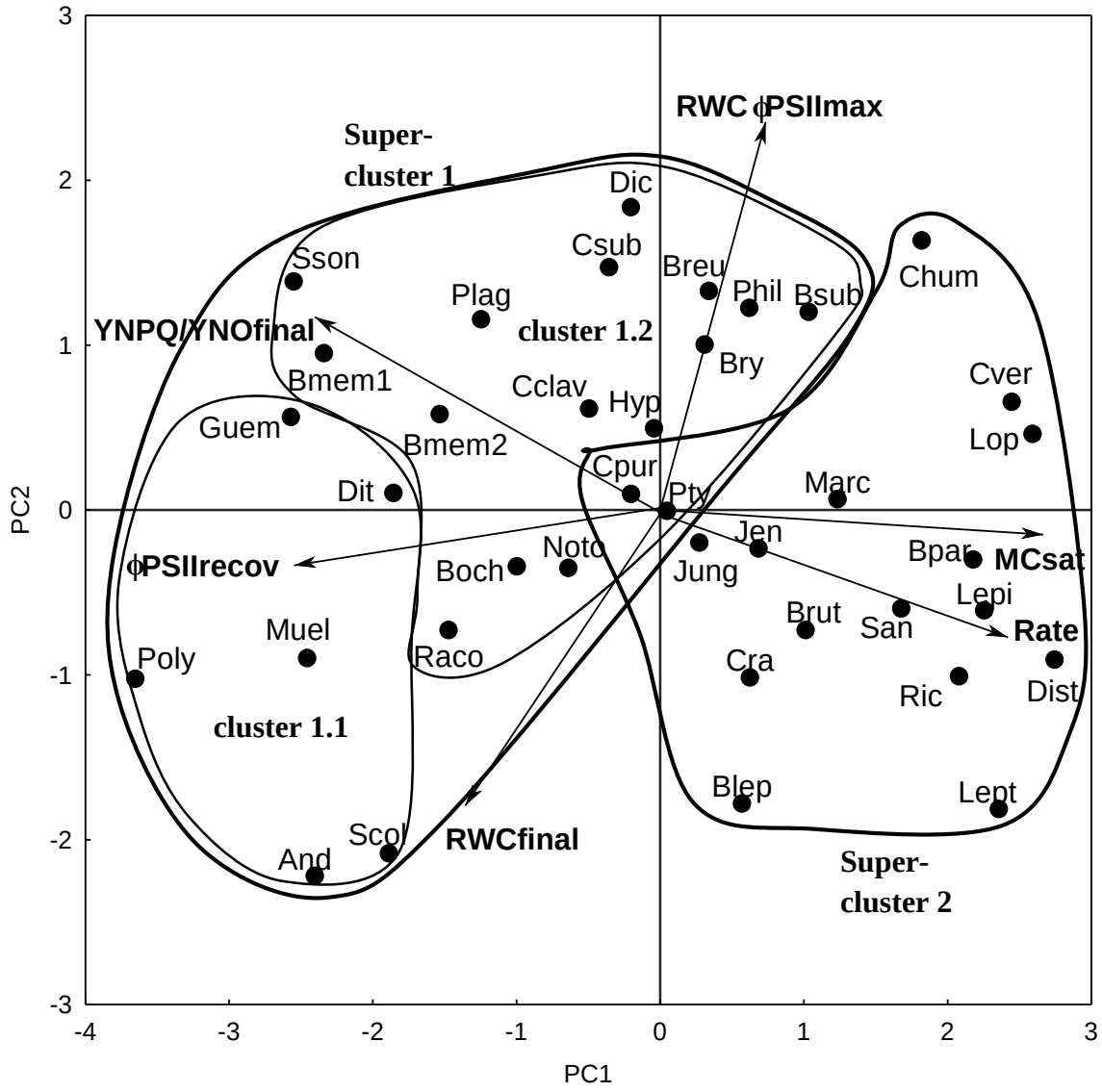


Figure 5.2b. Biplot showing the desiccation response trait gradients and mean species scores on PC1 and PC2. The nine groups are shown.

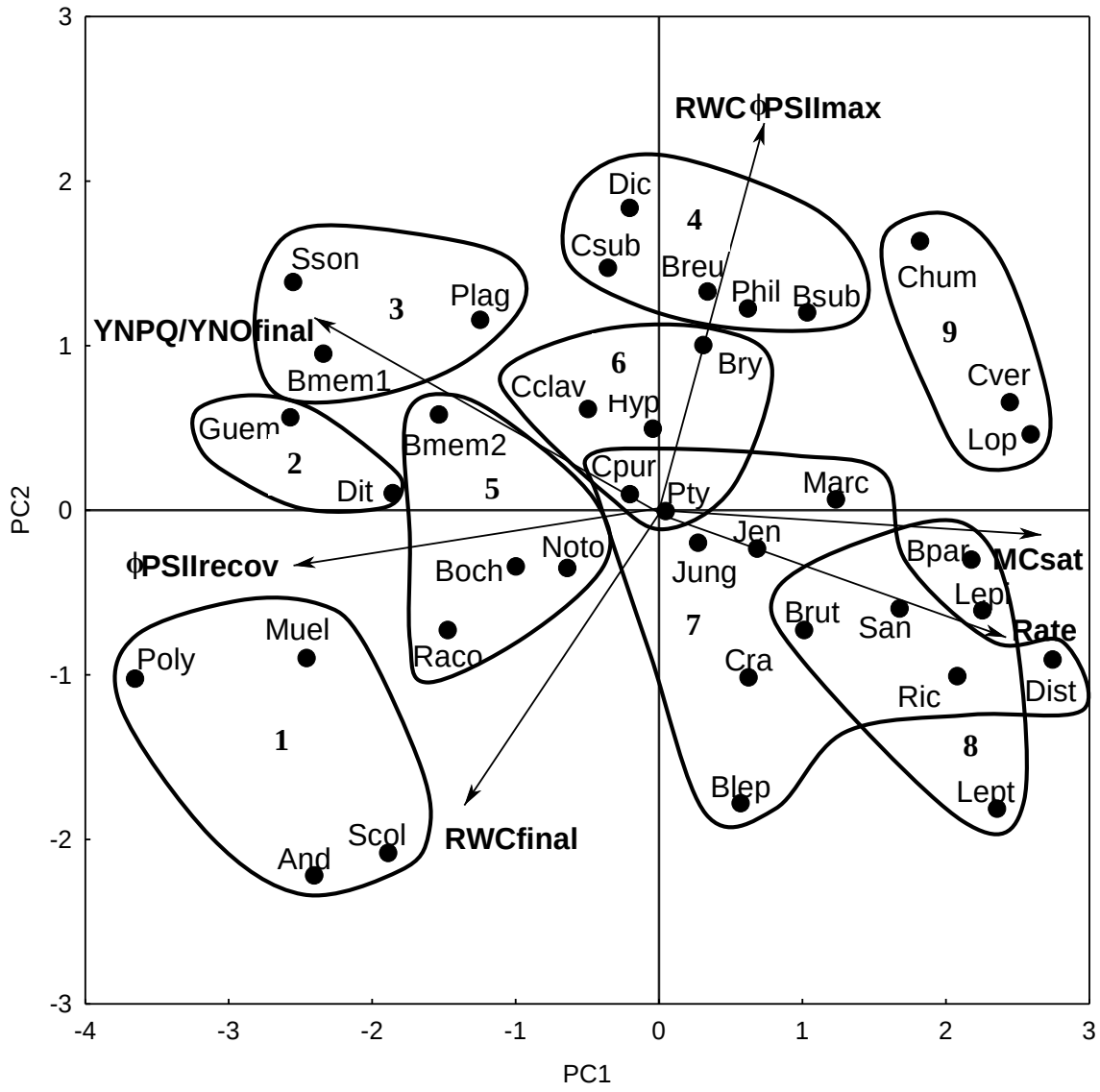


Figure 5.2c. Biplot showing the desiccation response trait gradients and mean species scores on PC1 and PC3. The nine groups are shown.

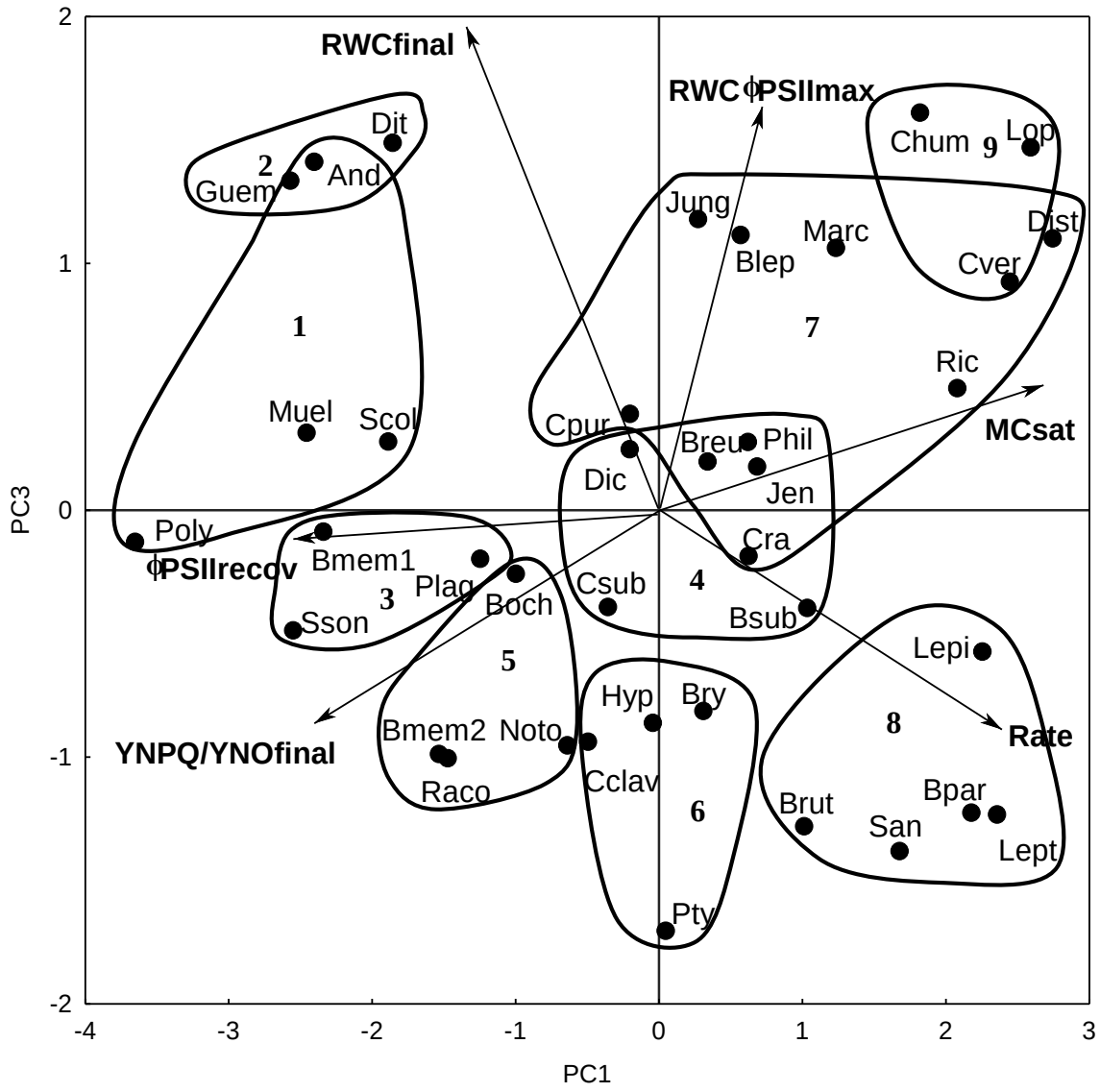


Figure 5.3. Clustering of phylum based on the species scores on the first three components yielded by the PCA on desiccation response traits. 'M' indicates that it is a moss species while 'H' indicates it is a hepatic species.

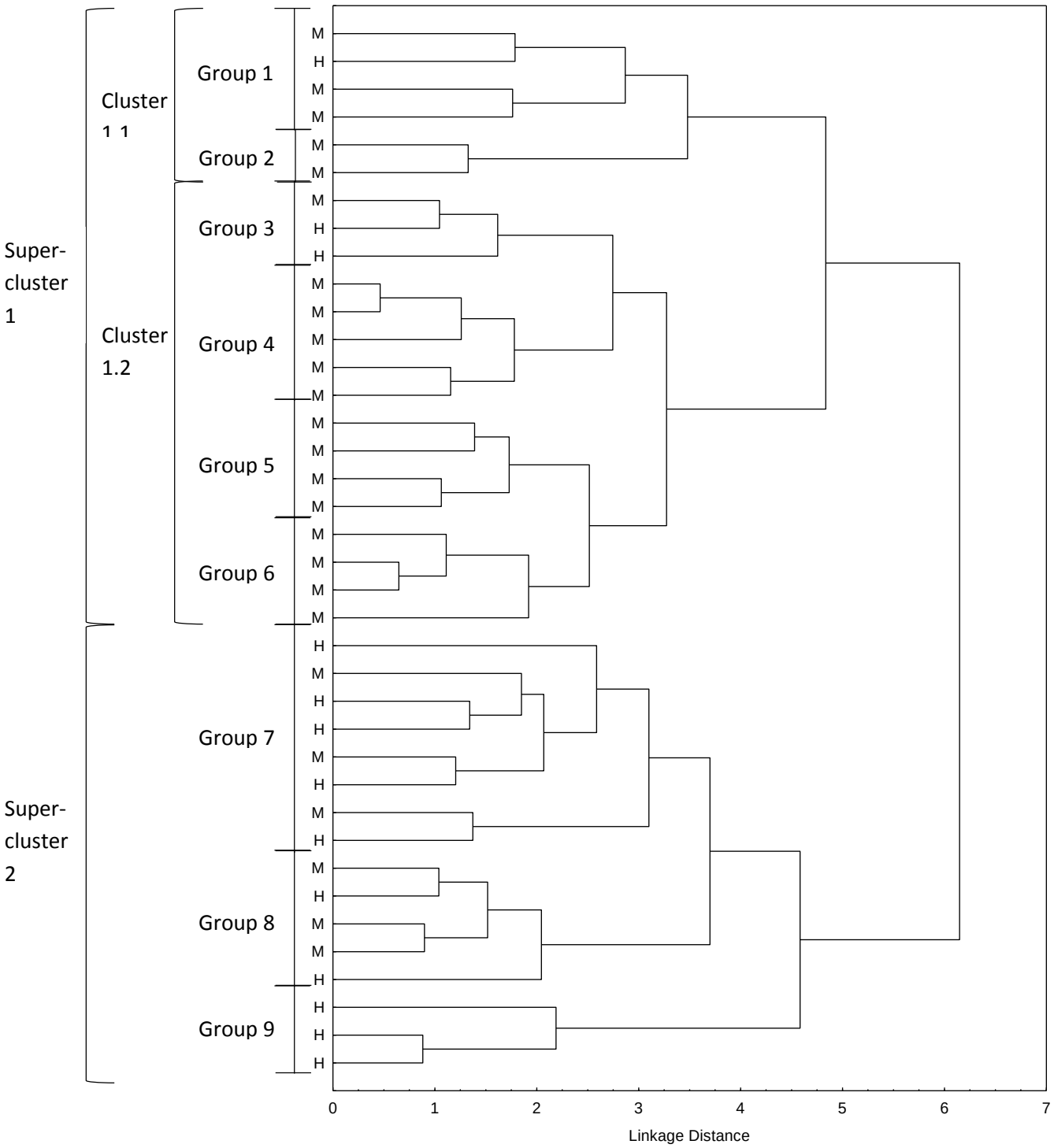


Figure 5.4. Clustering of order based on the species scores on the first three components yielded by the PCA on the desiccation response traits.

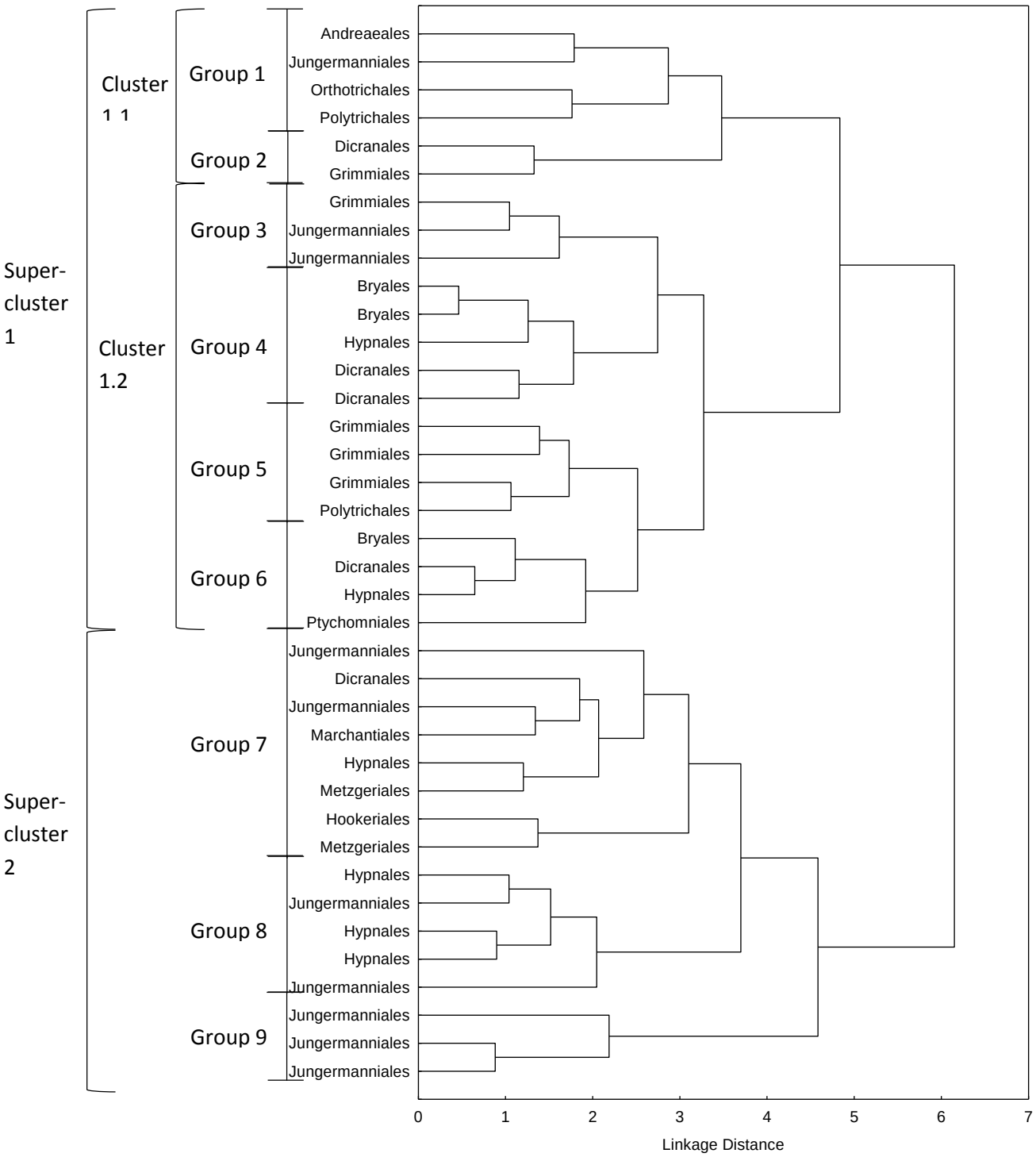


Figure 5.5. CA joint plot showing the centroids of the nine desiccation response groups and the association of the bryophyte orders on the principal axes.

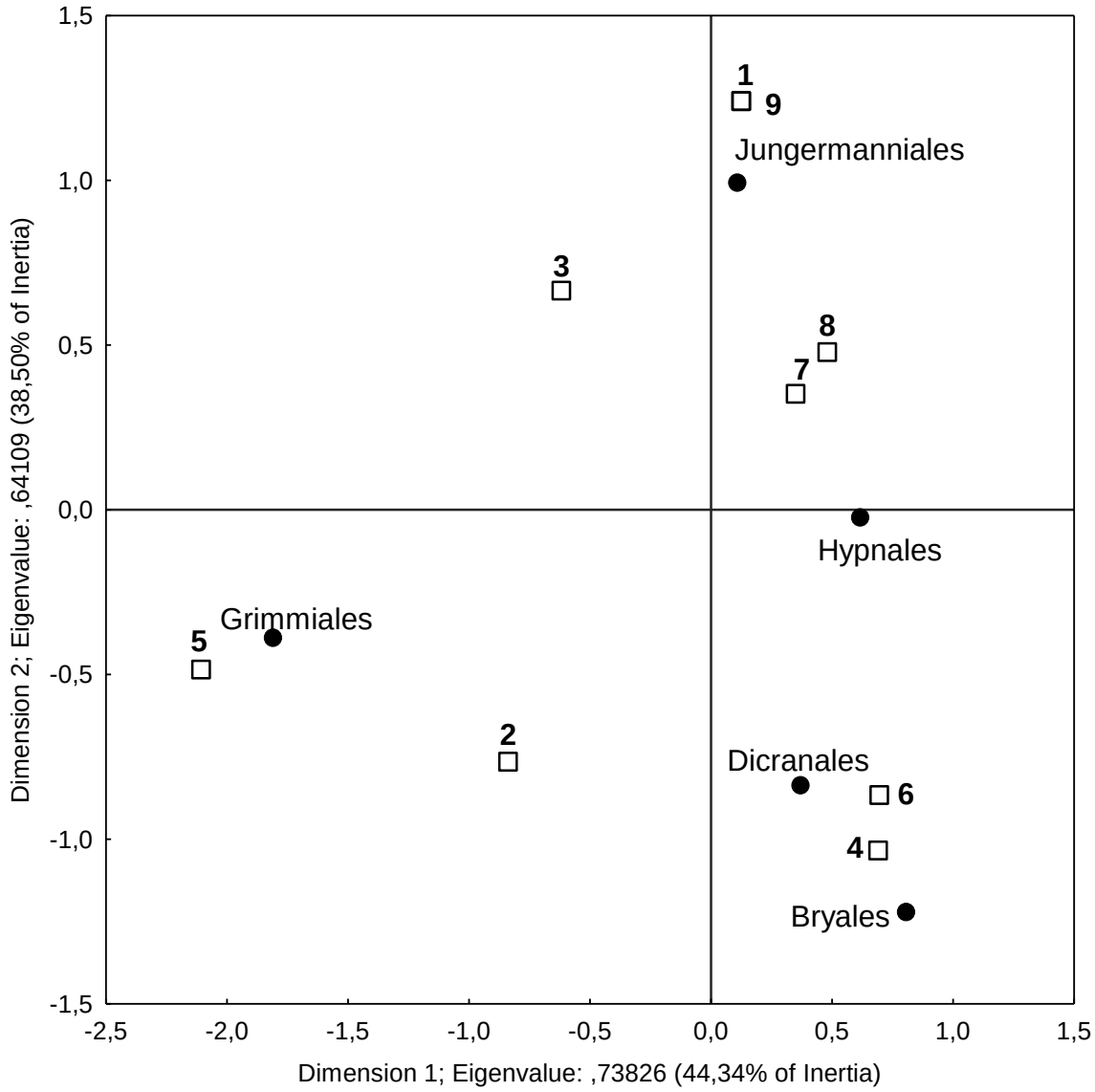


Figure 5.6. Clustering of family based on the species scores on the first three components yielded by the PCA on the desiccation response traits.

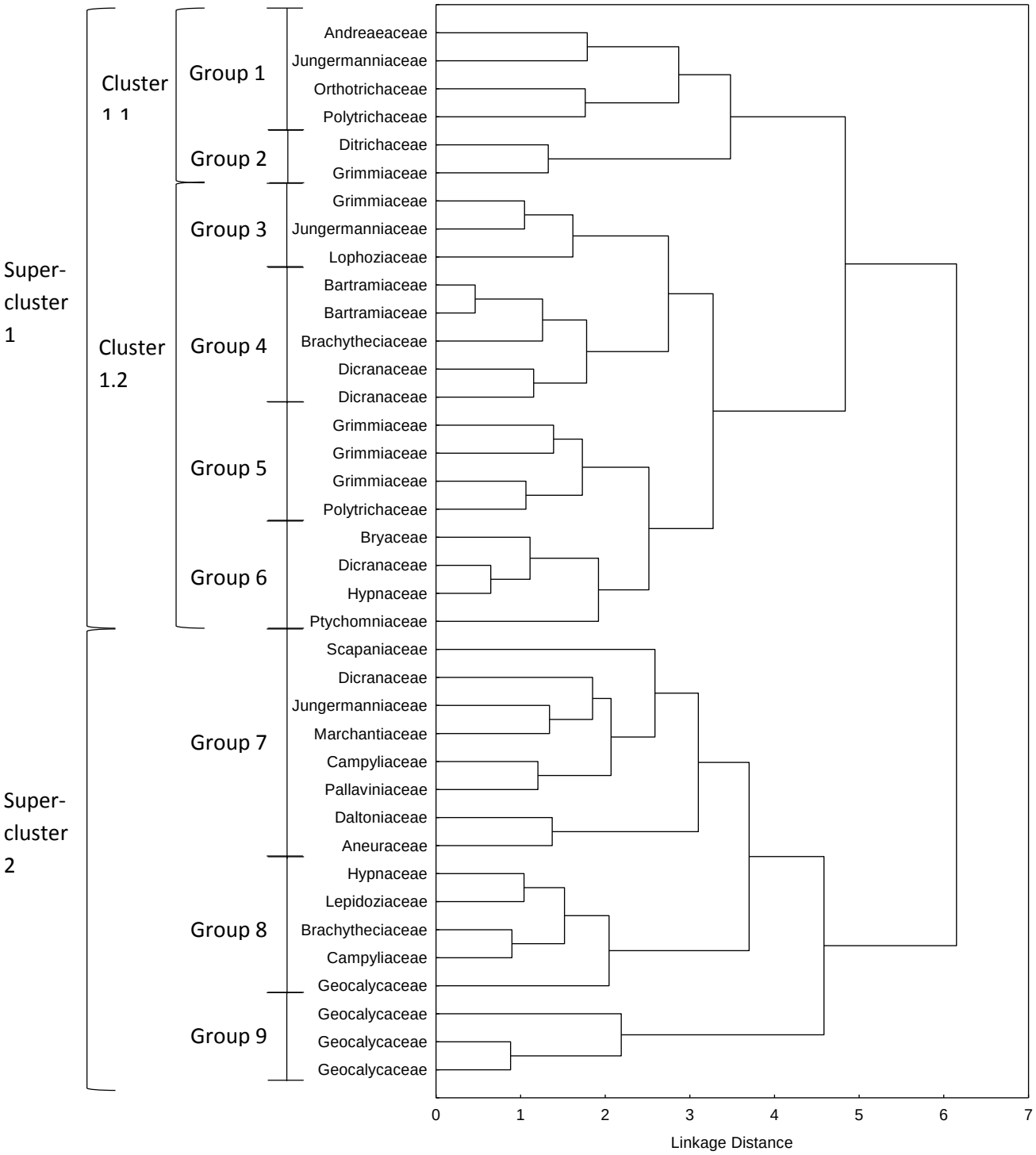


Figure 5.7. CA joint plot showing the centroids of the nine desiccation response groups and the associations of the bryophyte family the on the principal axes.

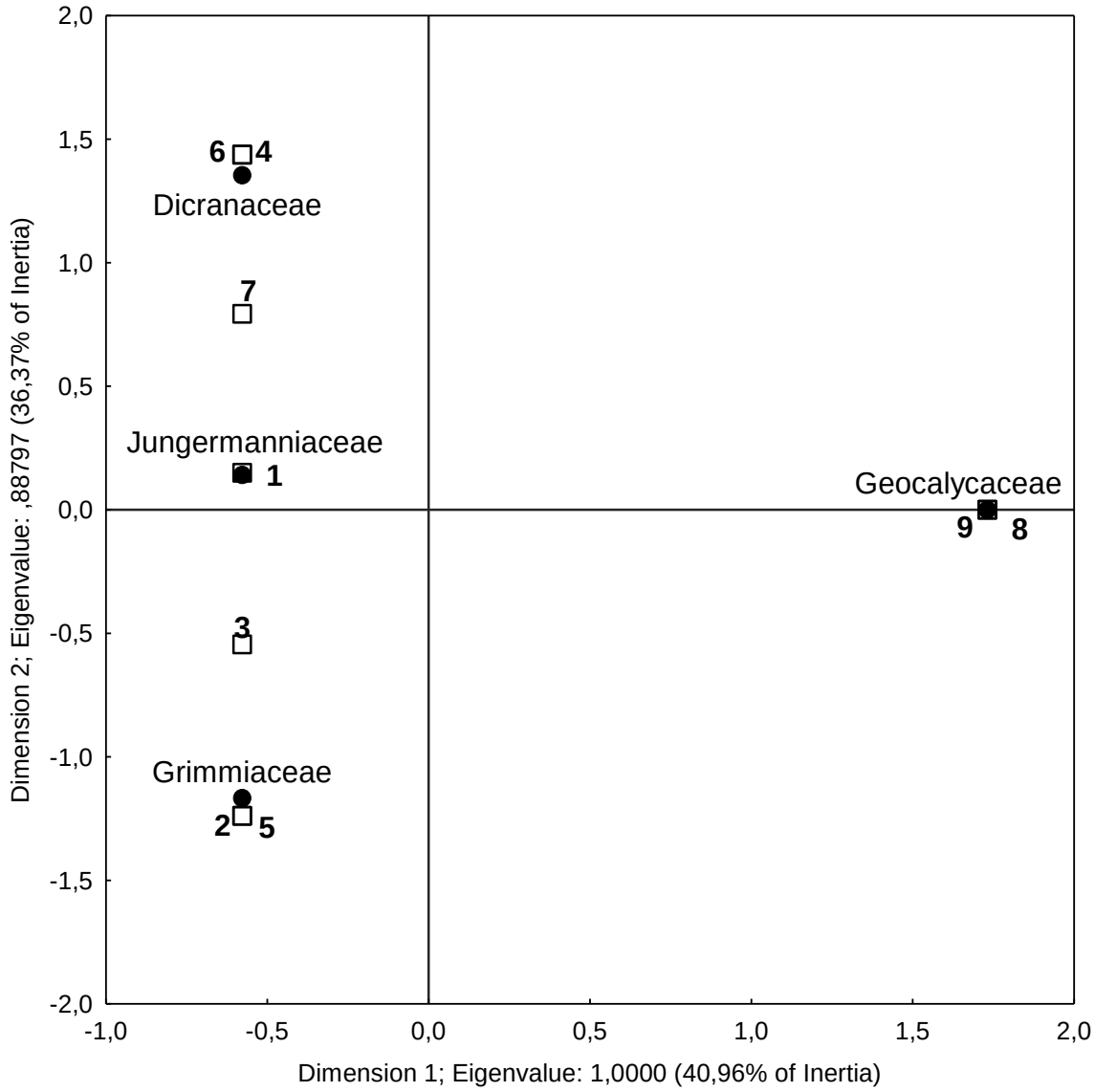
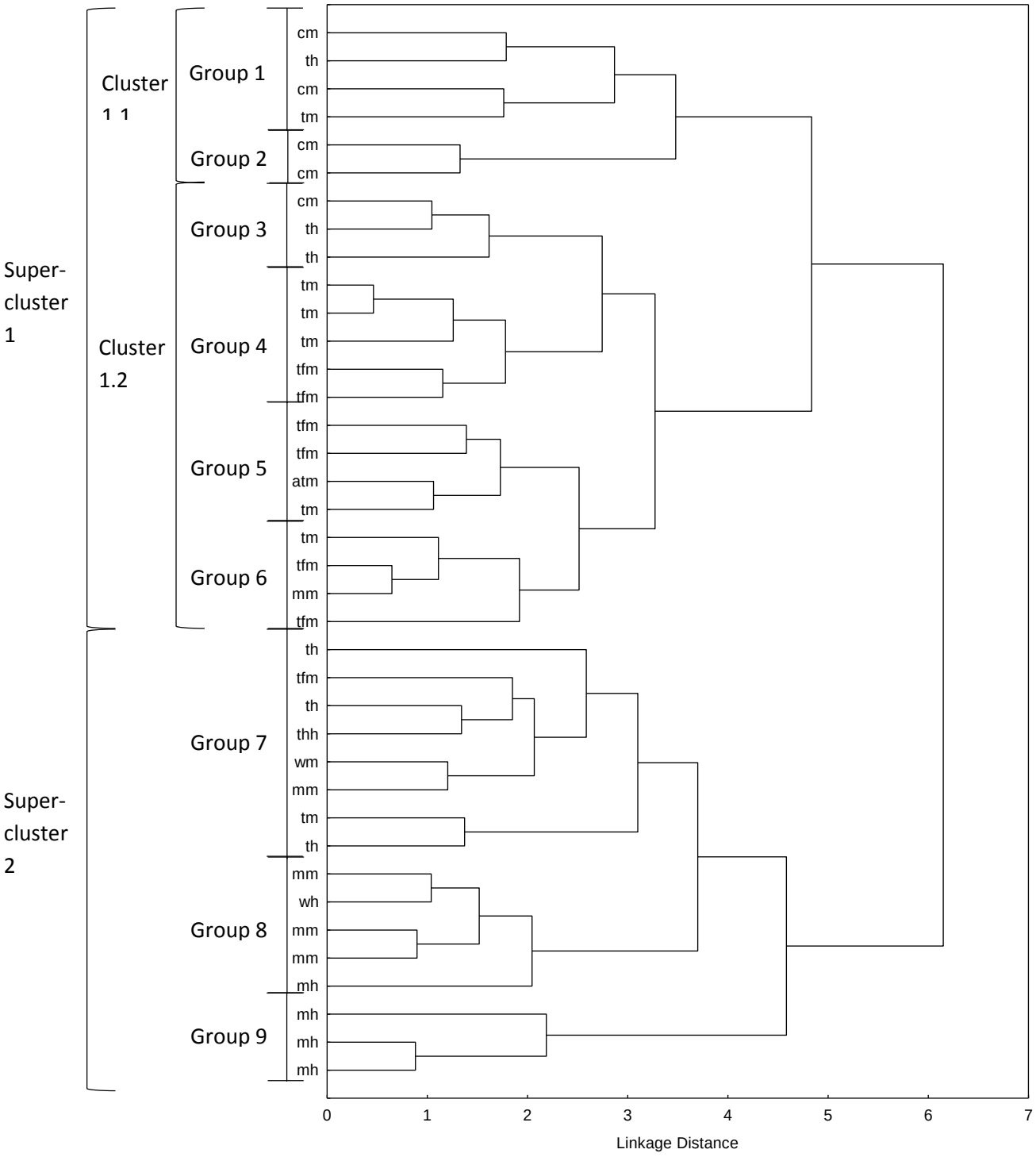


Figure 5.8. Clustering of life form based on the species scores on the first three components yielded by the PCA on desiccation response traits.

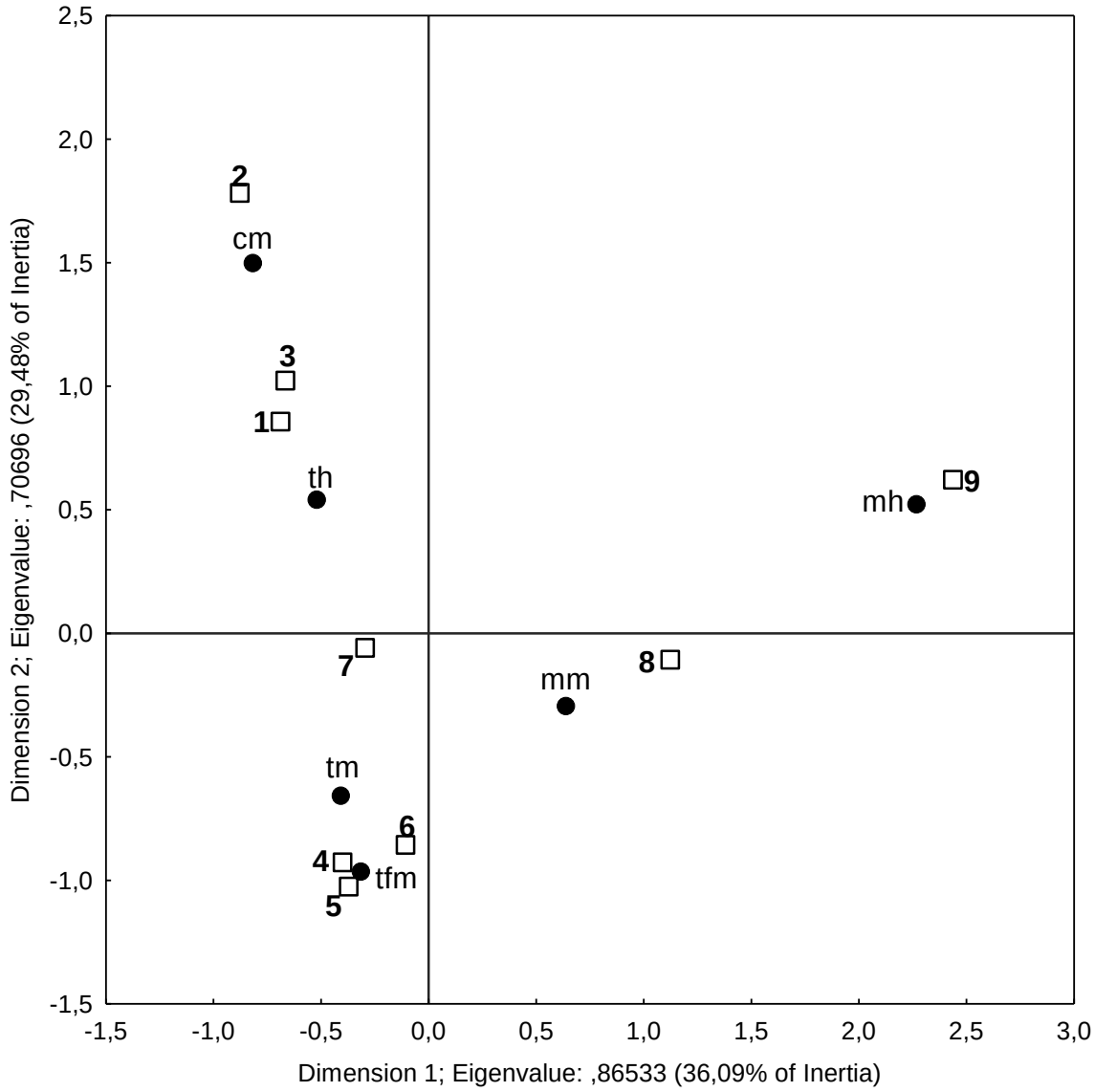


Abbreviations

cm= cushion moss tfm= tuft moss tm= turf moss

mm= mat moss mh= mat hepatic th= turf hepatic

Figure 5.9. CA joint plot showing the centroids of the nine desiccation response groups and the association of the bryophyte life forms on the principal axes.



Abbreviations

cm= cushion moss

tfm= tuft moss

tm= turf moss

mm= mat moss

mh= mat hepatic

th= turf hepatic

Figure 5.10. Clustering of light regime based on the species scores on the first three components yielded by the PCA on desiccation response traits.

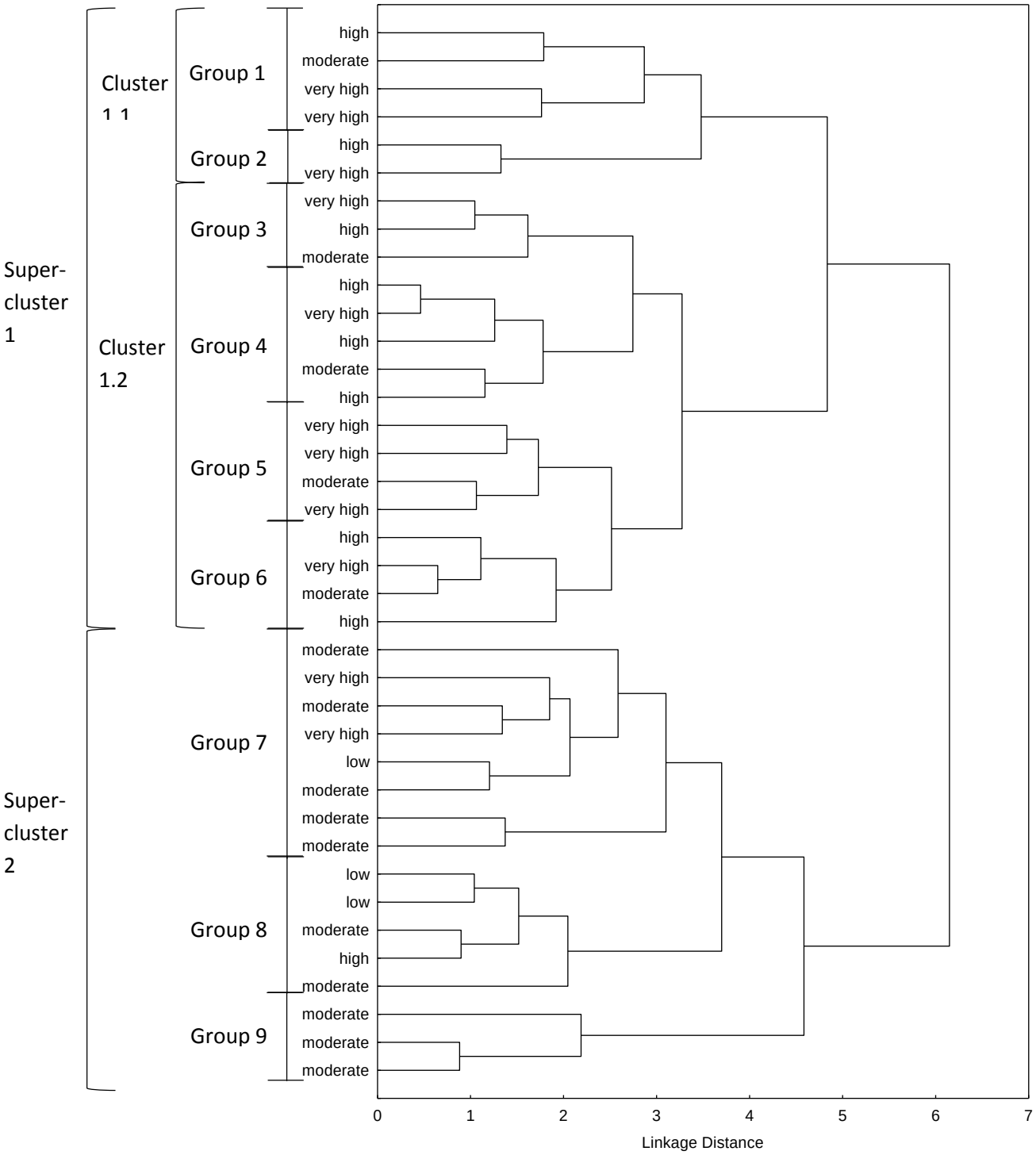


Figure 5.11. CA joint plot showing the centroids of the nine desiccation response groups and the association of the bryophyte light regime the on the principal axes.

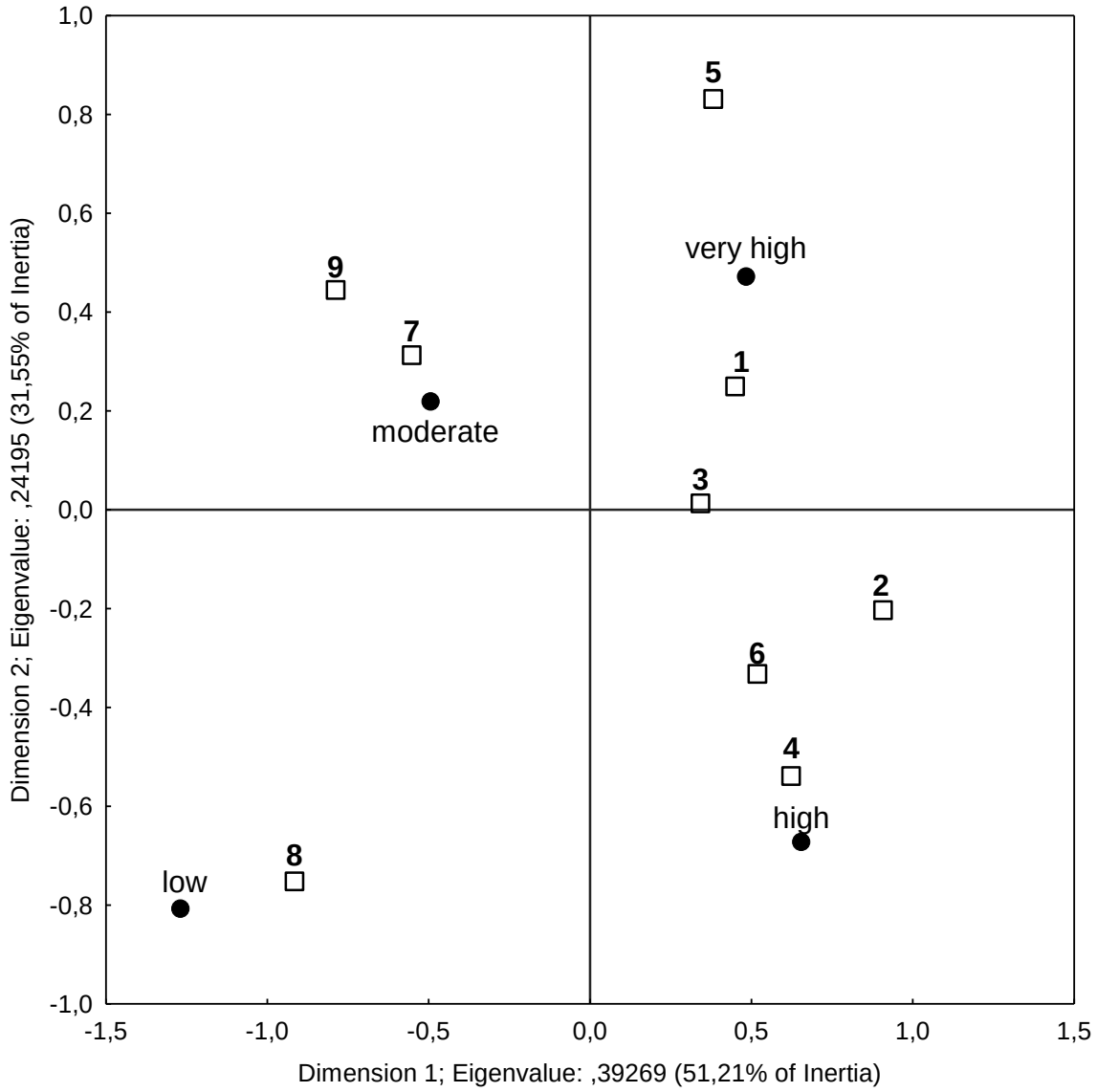


Figure 5.12. Clustering of habitat based on the species scores on the first three components yielded by the PCA on desiccation response traits.

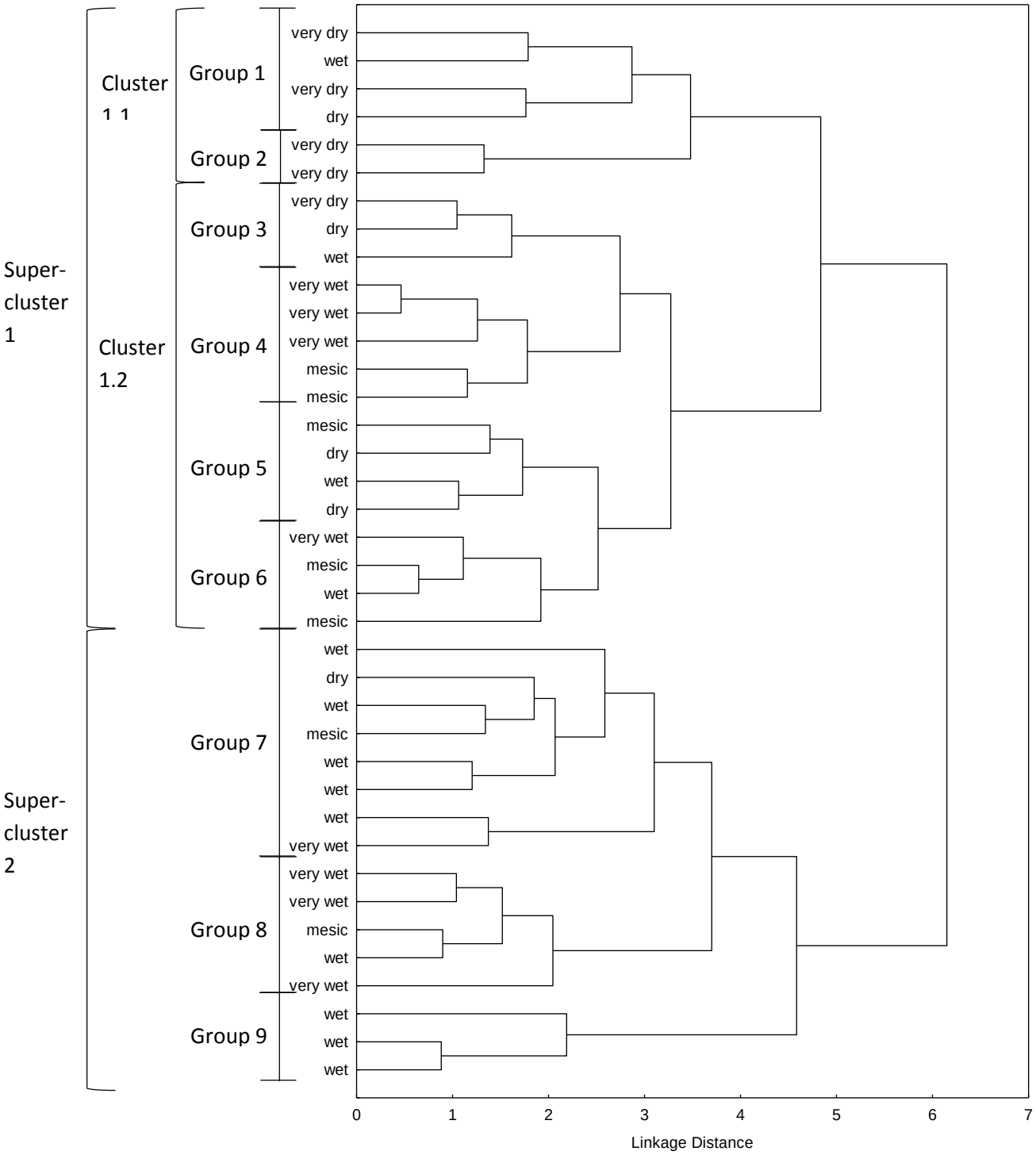


Figure 5.13. CA joint plot showing the centroids of the nine desiccation response groups and the association of the bryophyte habitat moisture on the principal axes.

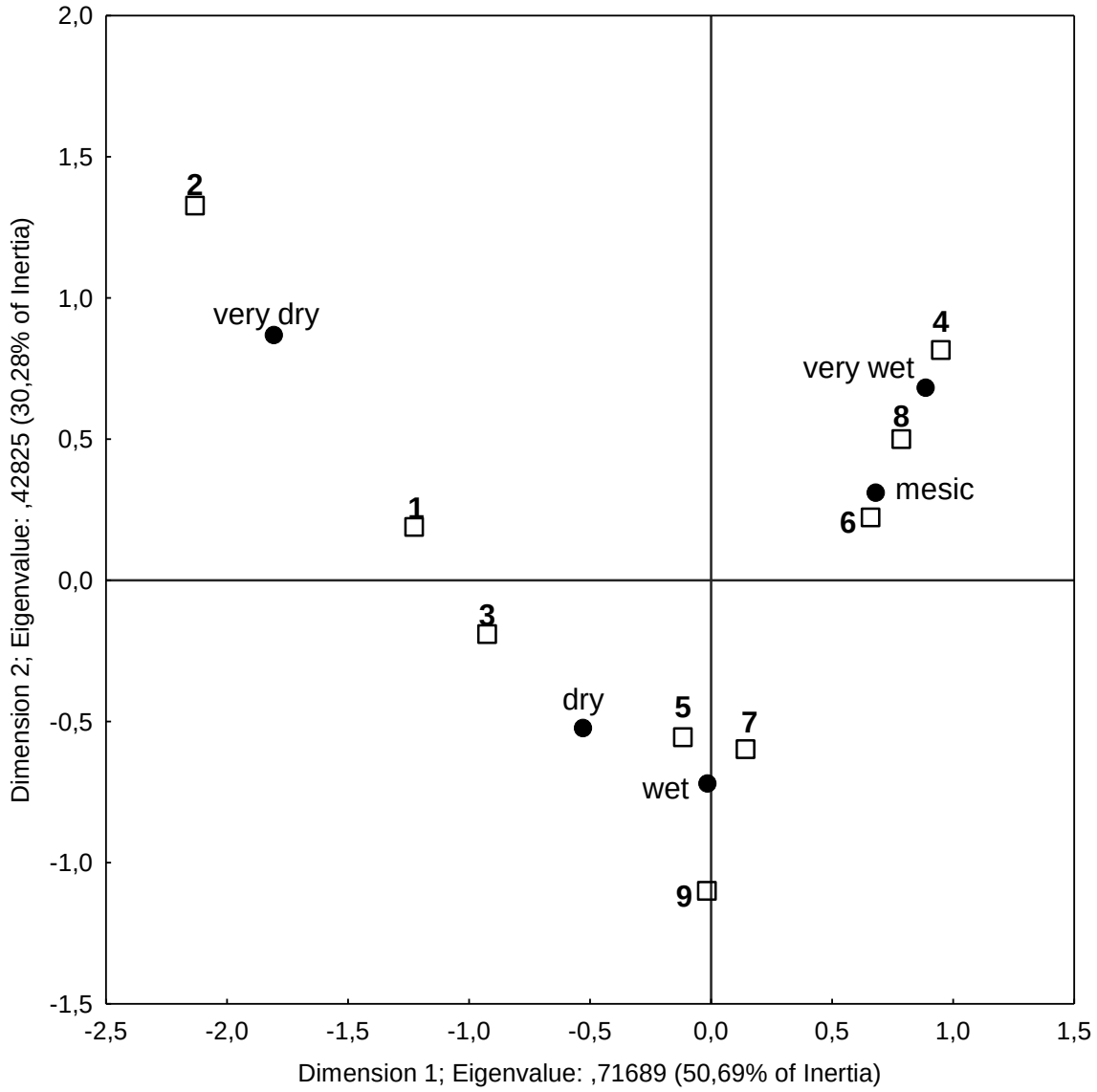


Figure 6.1. Clustering of species based on their scores for both light- and desiccation-response traits on PC1, PC2 and PC3 from PCA analysis.

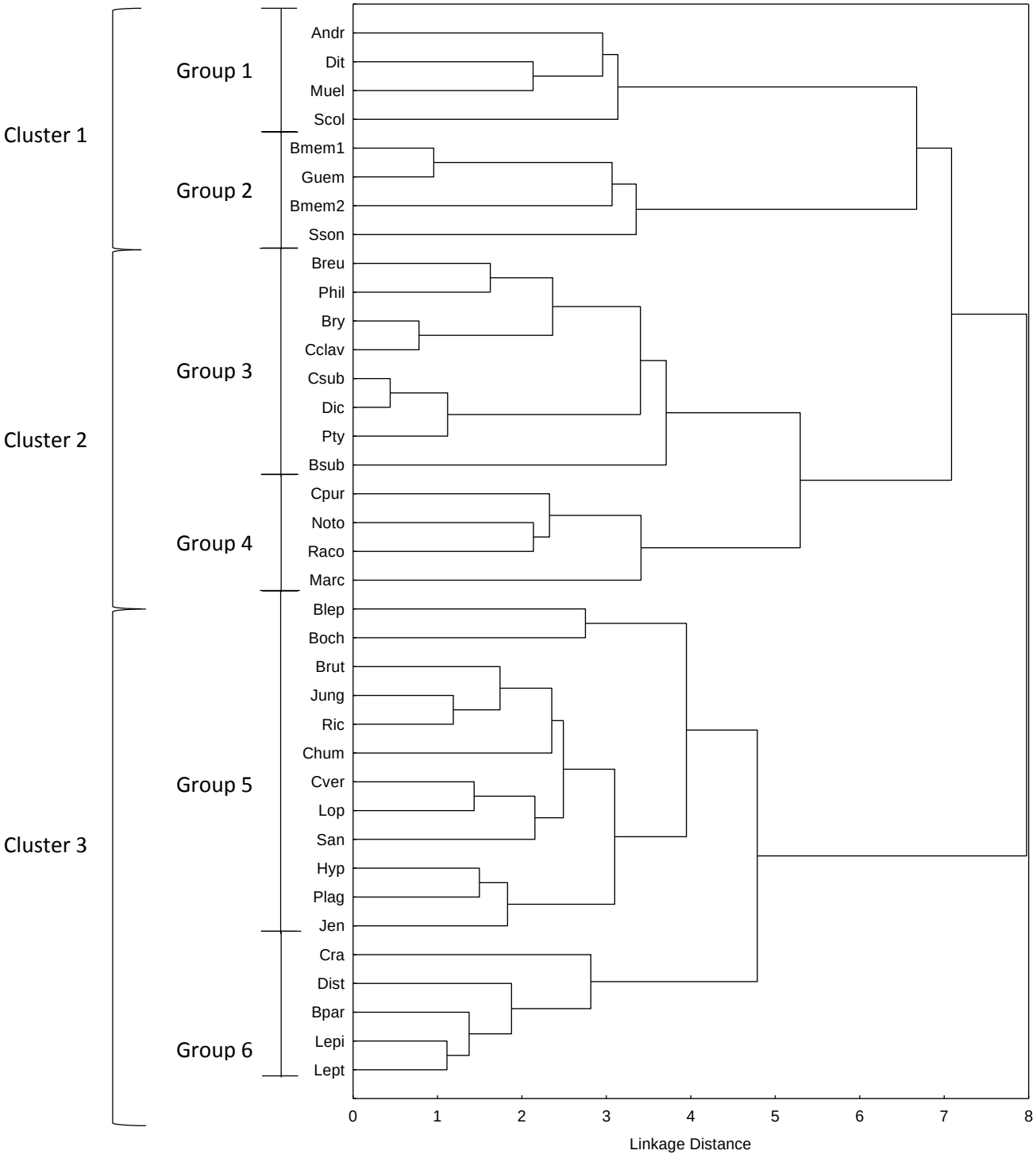


Figure 6.2a. Biplot showing the light- and desiccation- response trait gradients and mean species scores on PC1 and PC2. The three clusters are shown.

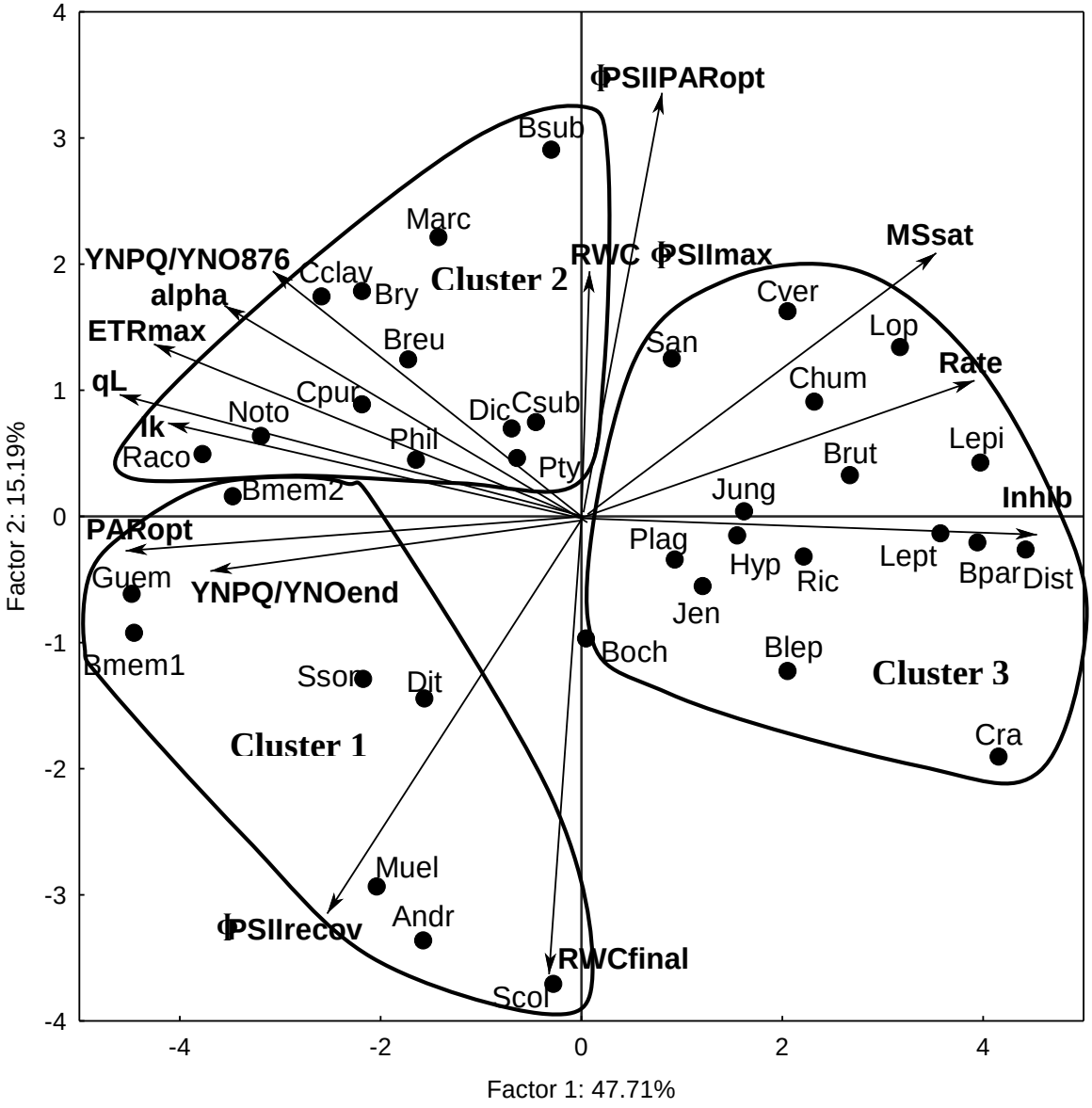


Figure 6.2b. Biplot showing the light- and desiccation- response trait gradients and mean species scores on PC1 and PC3. The six groups are numbered.

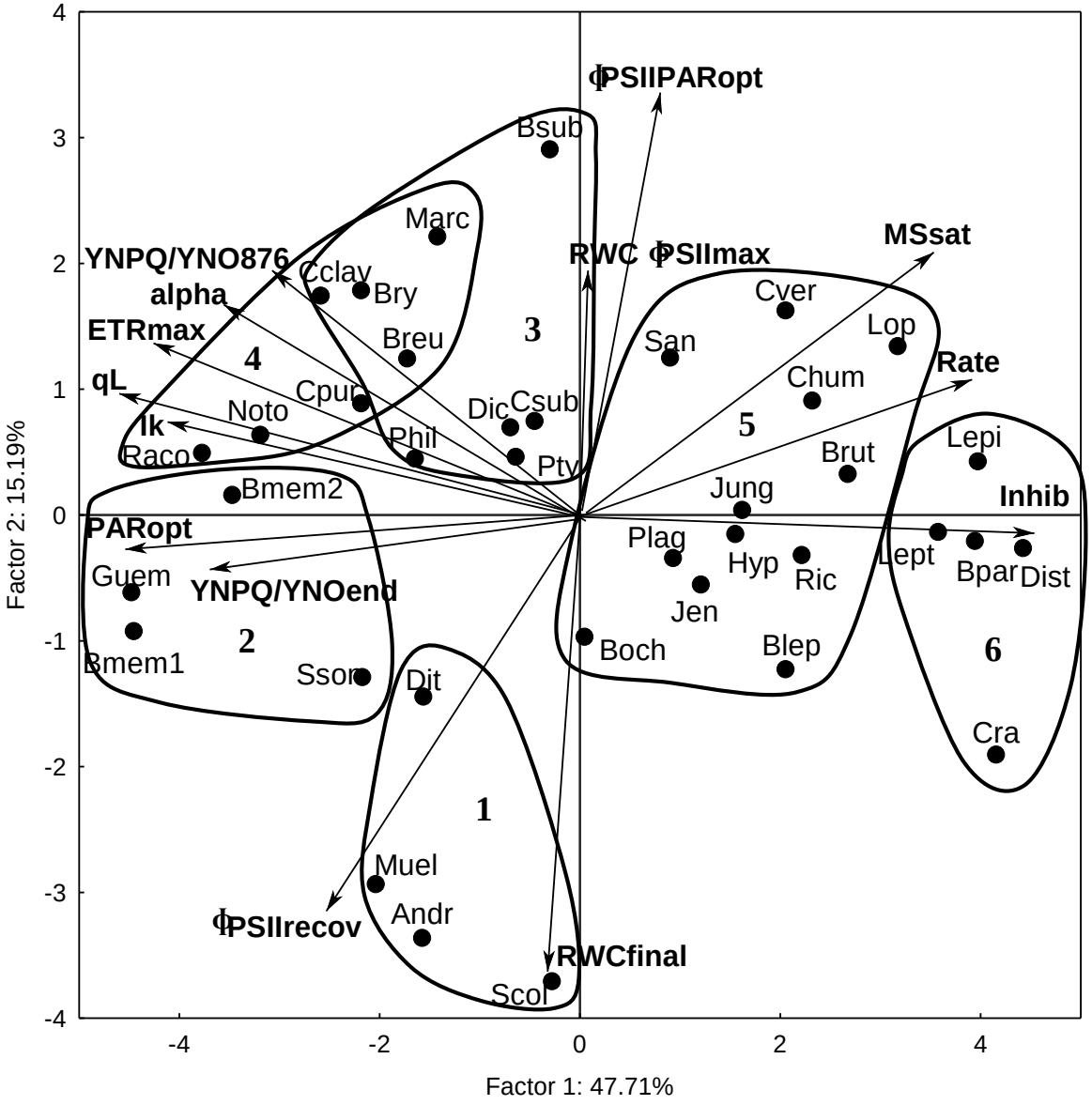


Figure 6.2c. Biplot showing the light- and desiccation- response trait gradients and mean species scores on PC1 and PC3. The six groups are numbered.

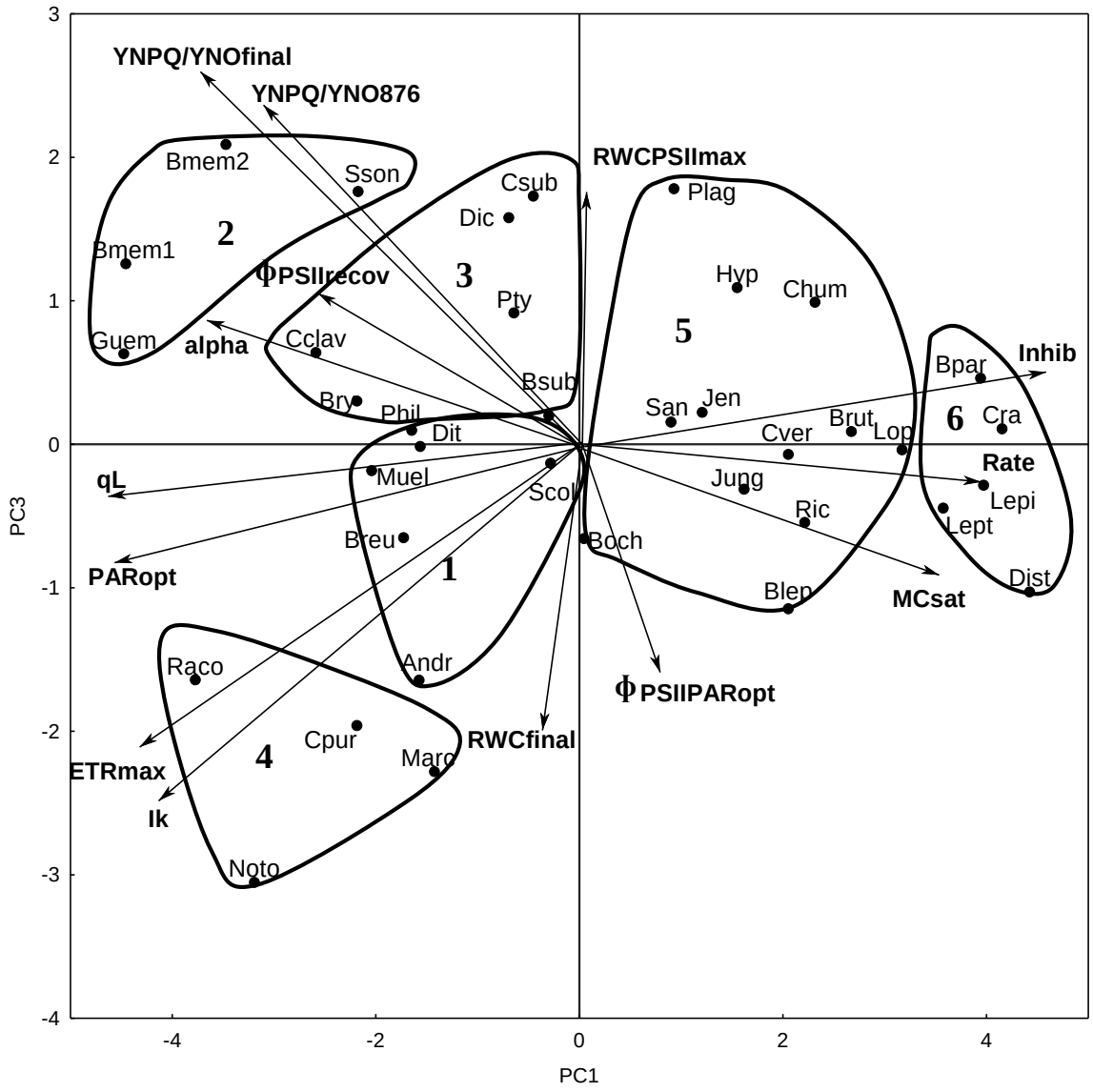


Figure 6.3. Clustering of phylum based on the species scores on the first three components yielded by the PCA on both light and desiccation traits. 'M' indicates that it is a moss species while 'H' indicates it is a hepatic species.

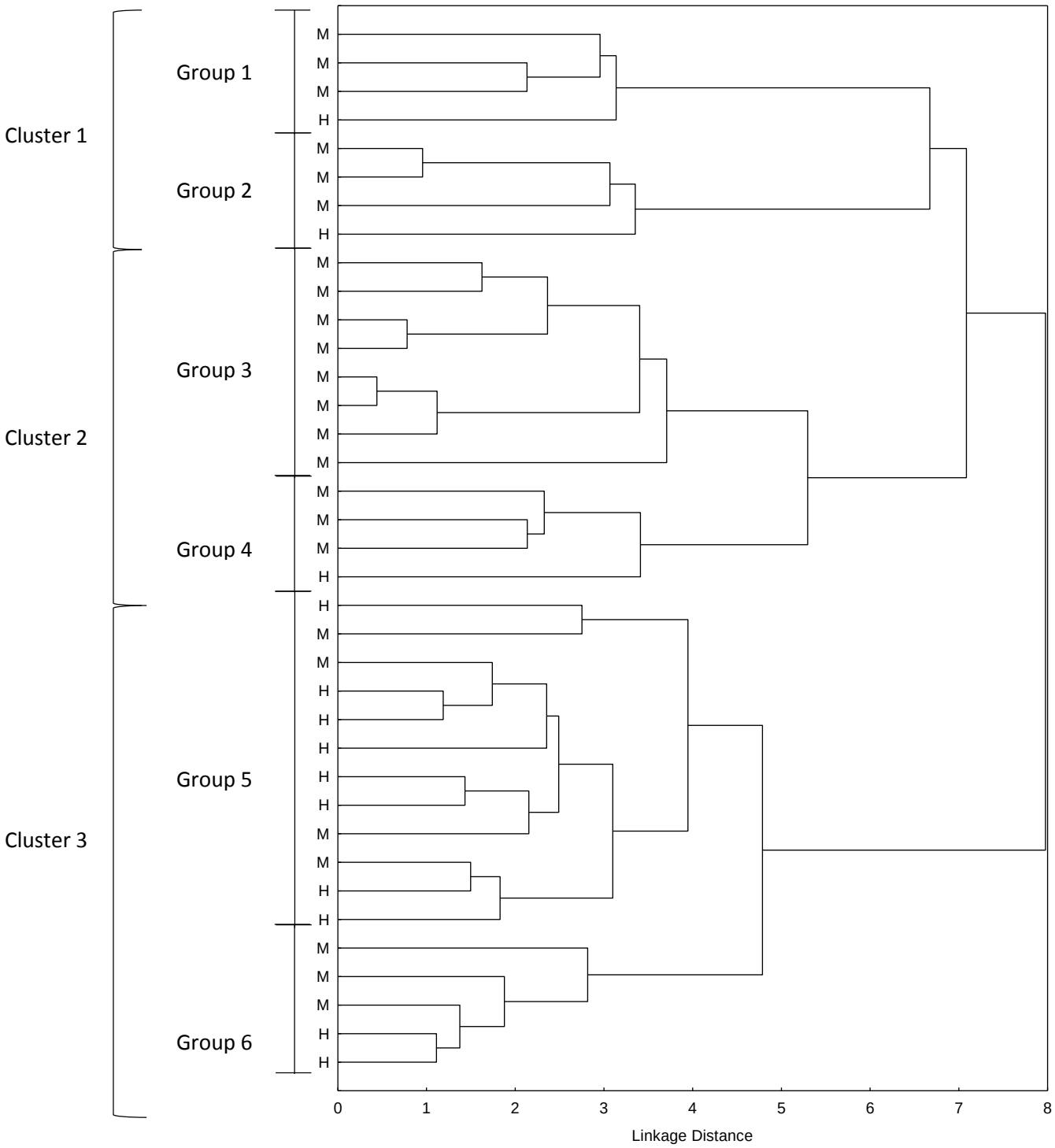


Figure 6.4. Clustering of order based on the species scores on the first three components yielded by the PCA on both light and desiccation traits.

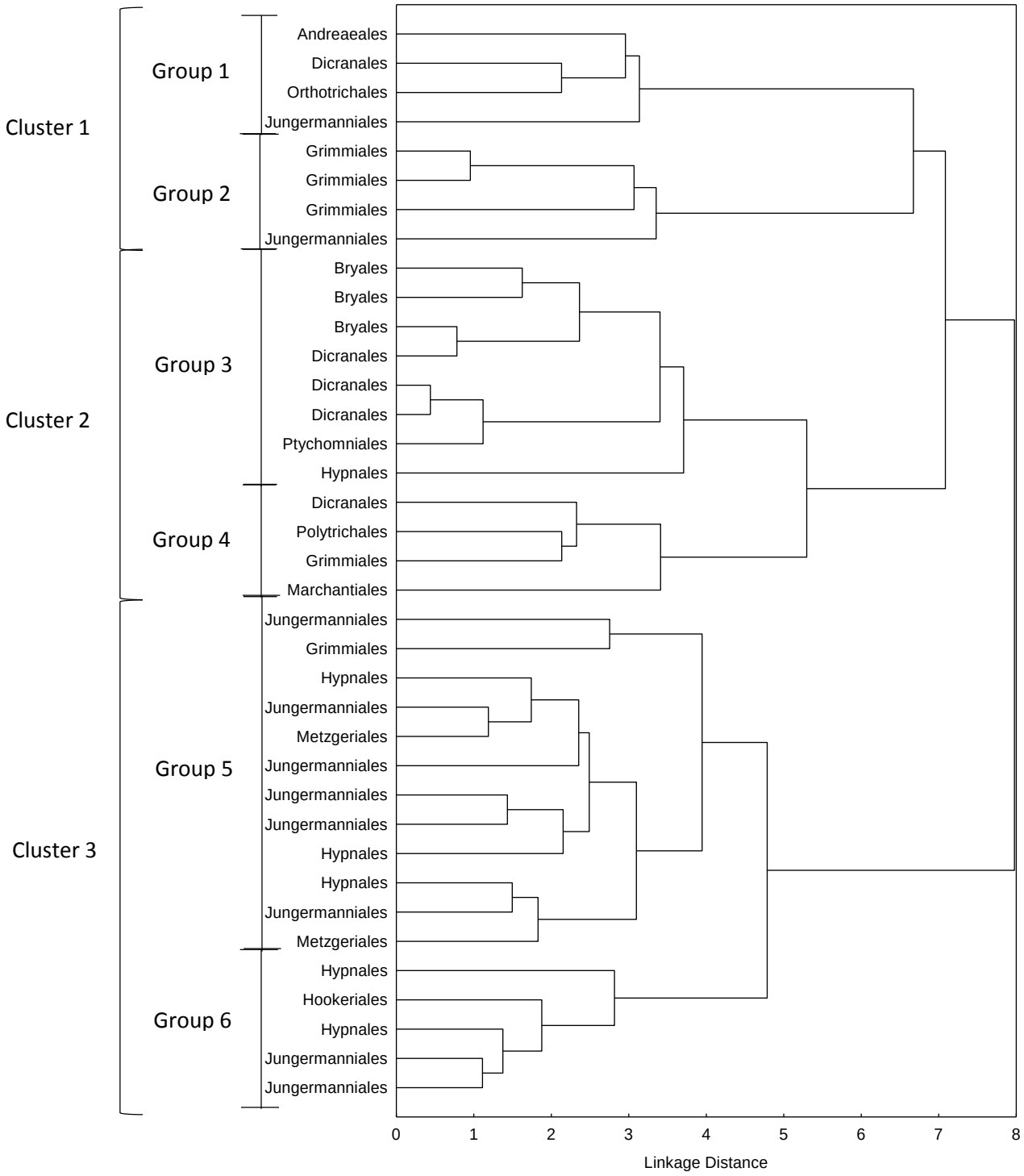


Figure 6.5. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte orders on the principal axes.

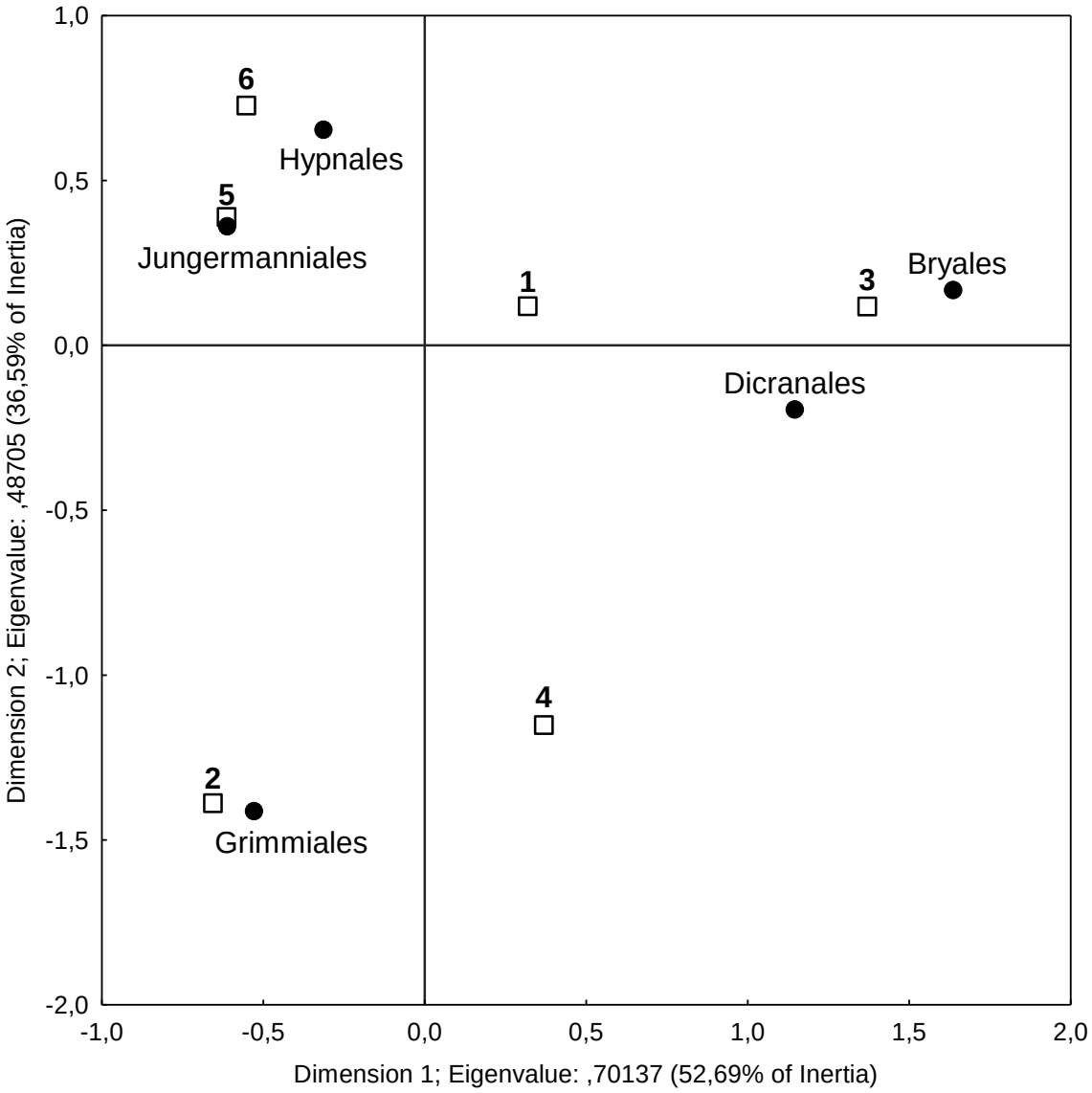


Figure 6.6. Clustering of family based on the species scores on the first three components yielded by the PCA on both light and desiccation traits.

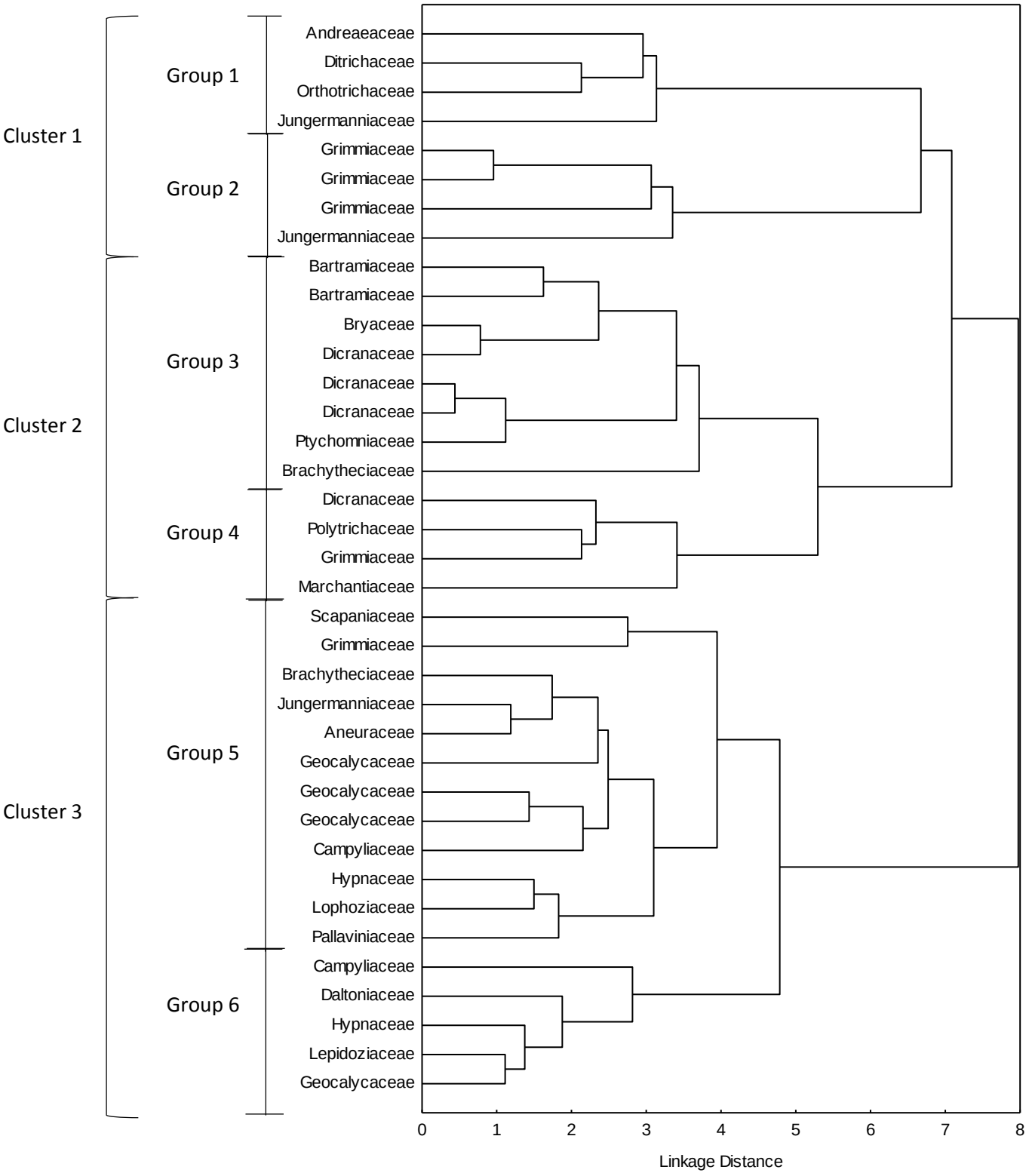


Figure 6.7. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte family on the principal axes.

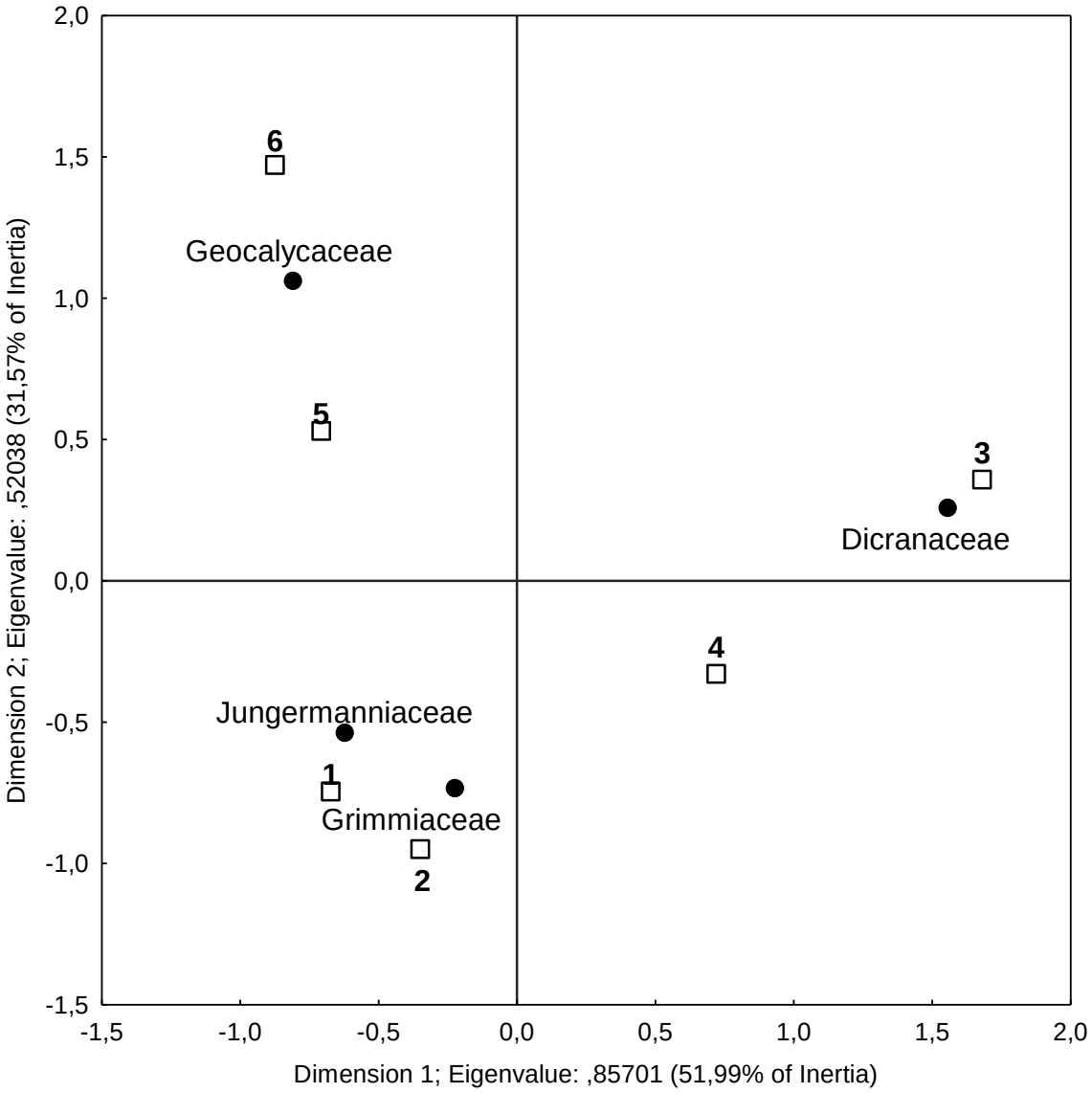
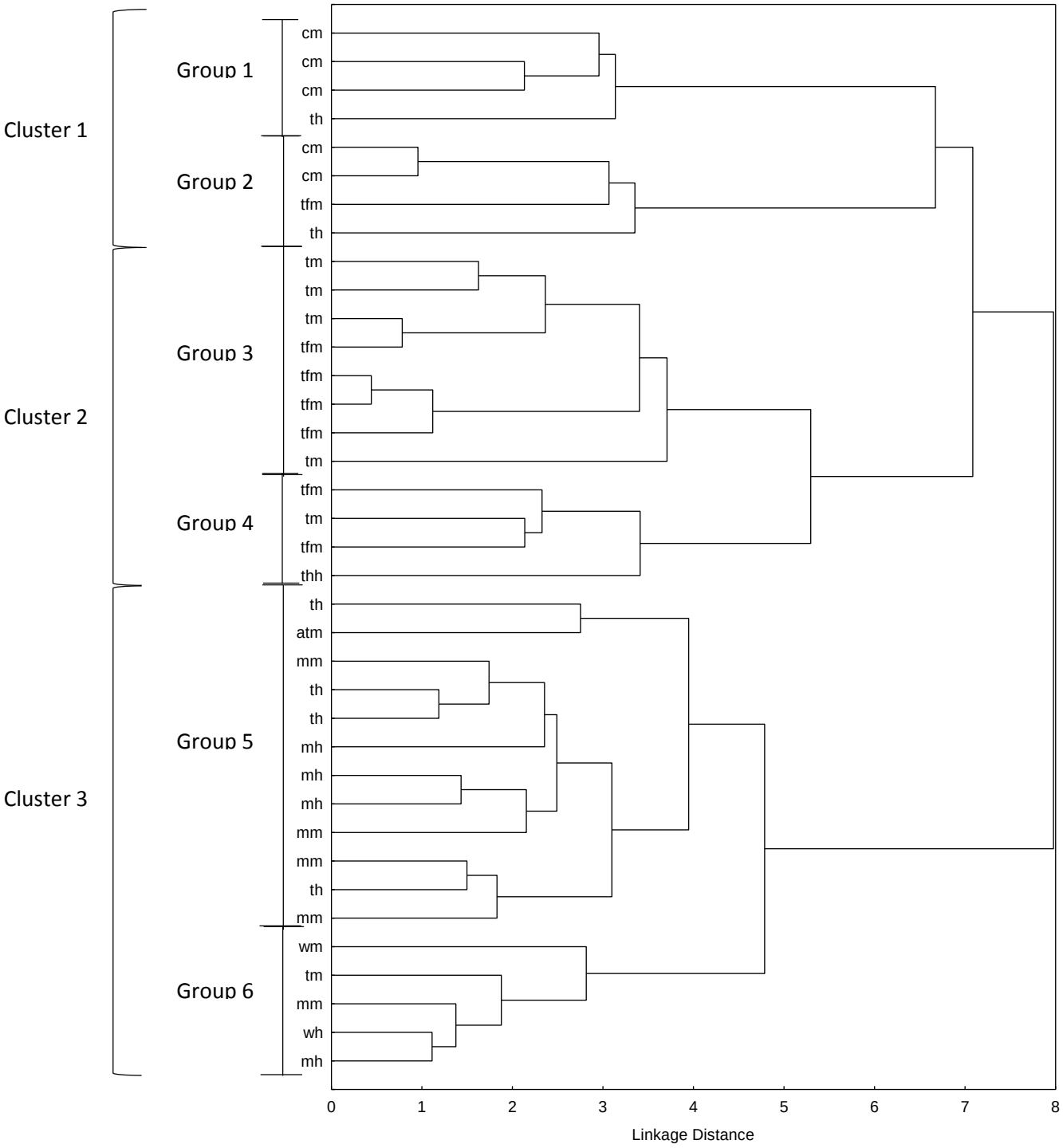


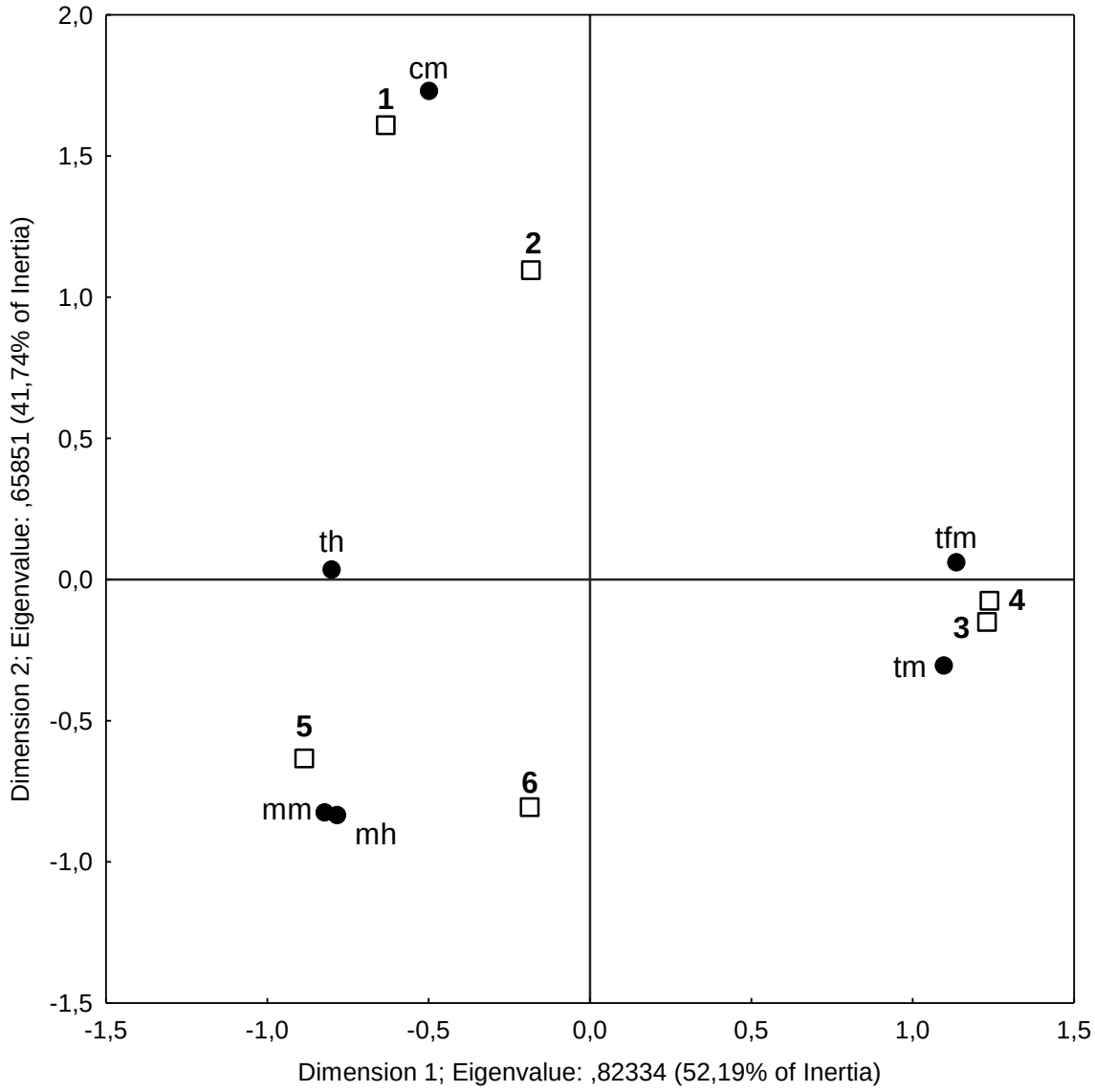
Figure 6.8. Clustering of life form based on the species scores on the first three components yielded by the PCA on both light and desiccation traits.



Abbreviations

cm-	cushion moss	tm-	turf moss	tfm-	tuft moss
mm-	mat moss	mh-	mat hepatic	th-	turf hepatic

Figure 6.9. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte life forms on the principal axes.



Abbreviations

cm-	cushion moss	tm-	turf moss	tfm-	tuft moss
mm-	mat moss	mh-	mat hepatic	th-	turf hepatic

Figure 6.10. Clustering of light regime based on the species scores on the first three components yielded by the PCA on both light and desiccation traits.

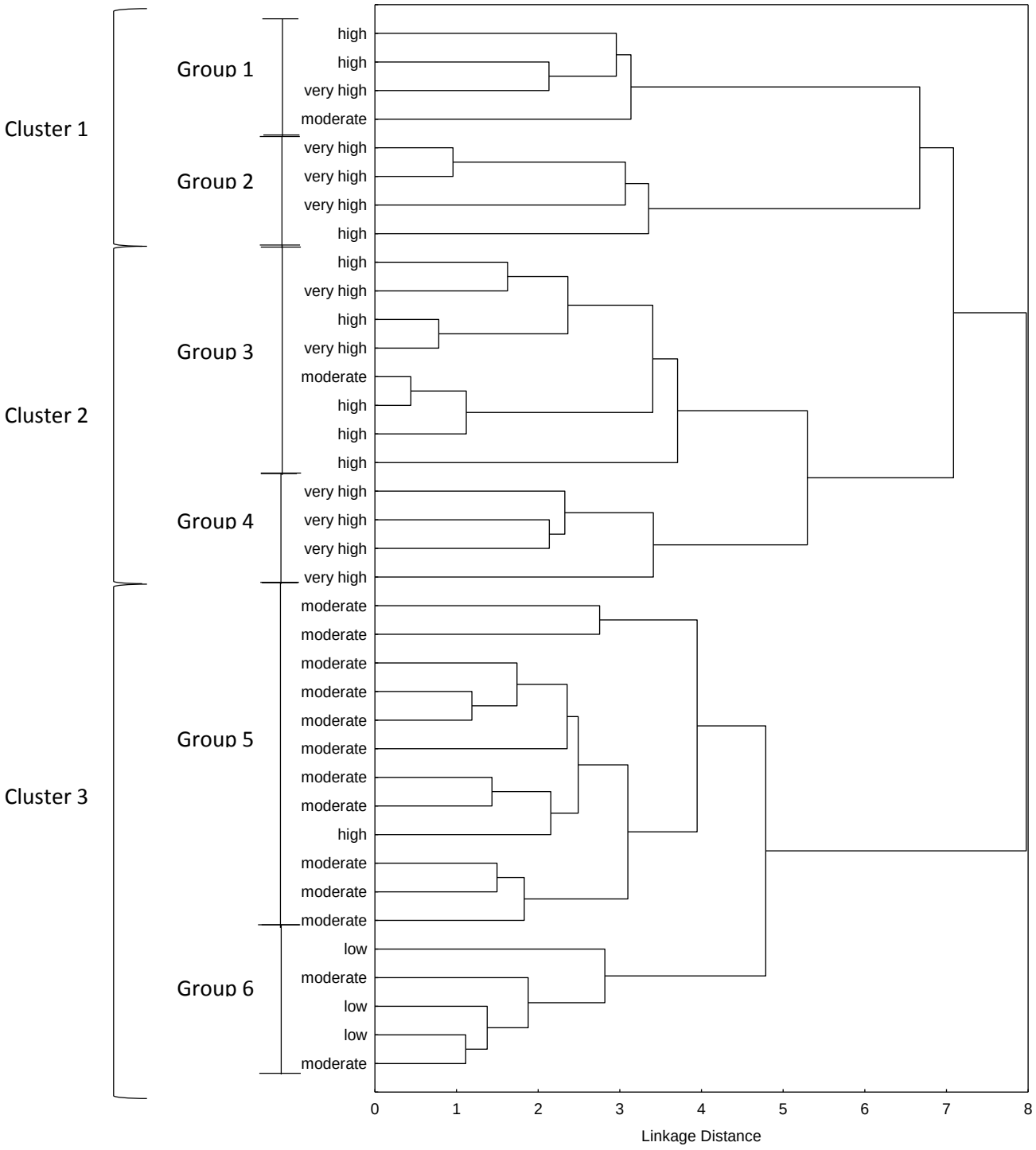


Figure 6.11a. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte light regime on the principal axes.

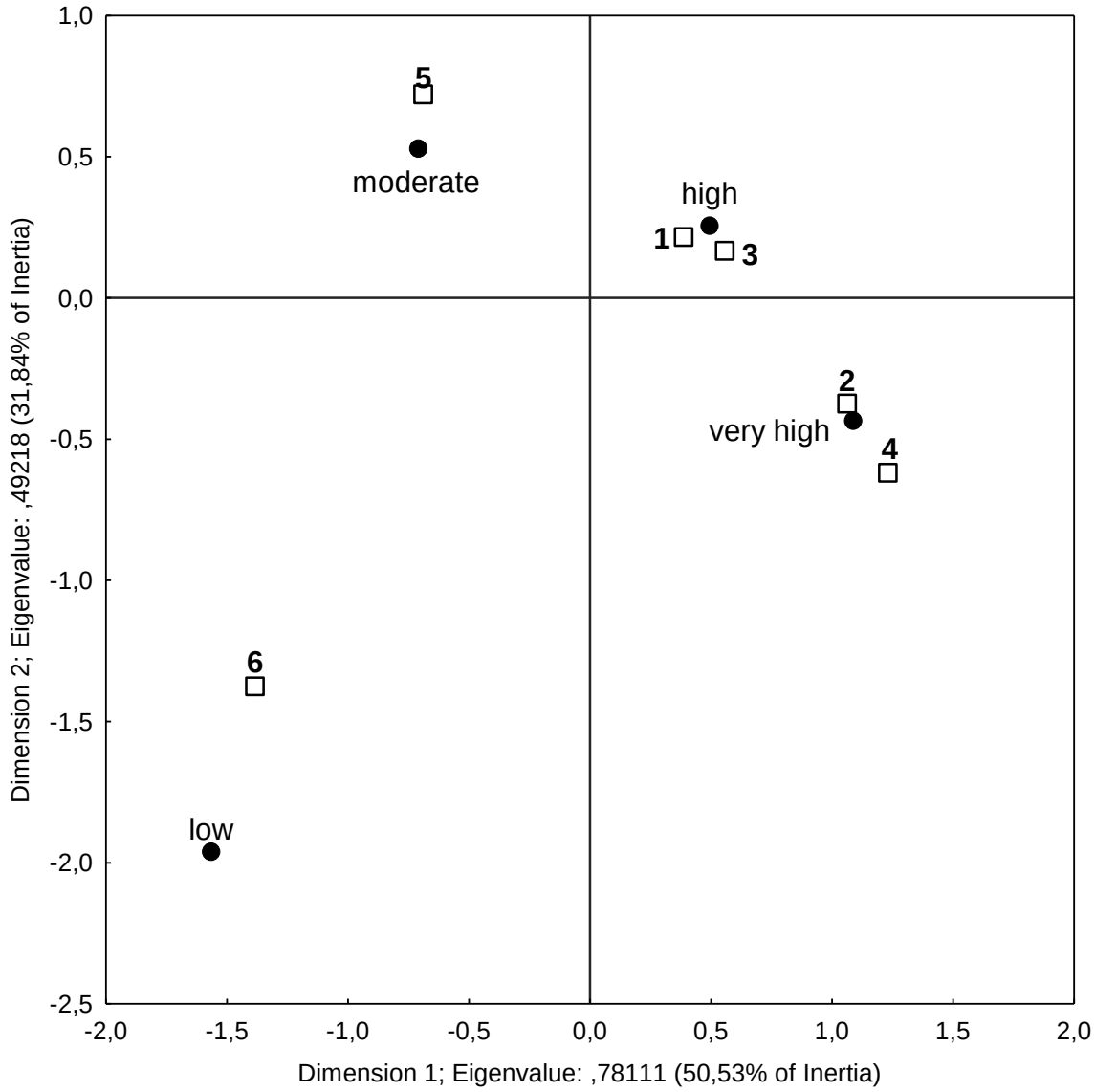


Figure 6.11b. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte light regime and degree of photoinhibition on the principal axes.

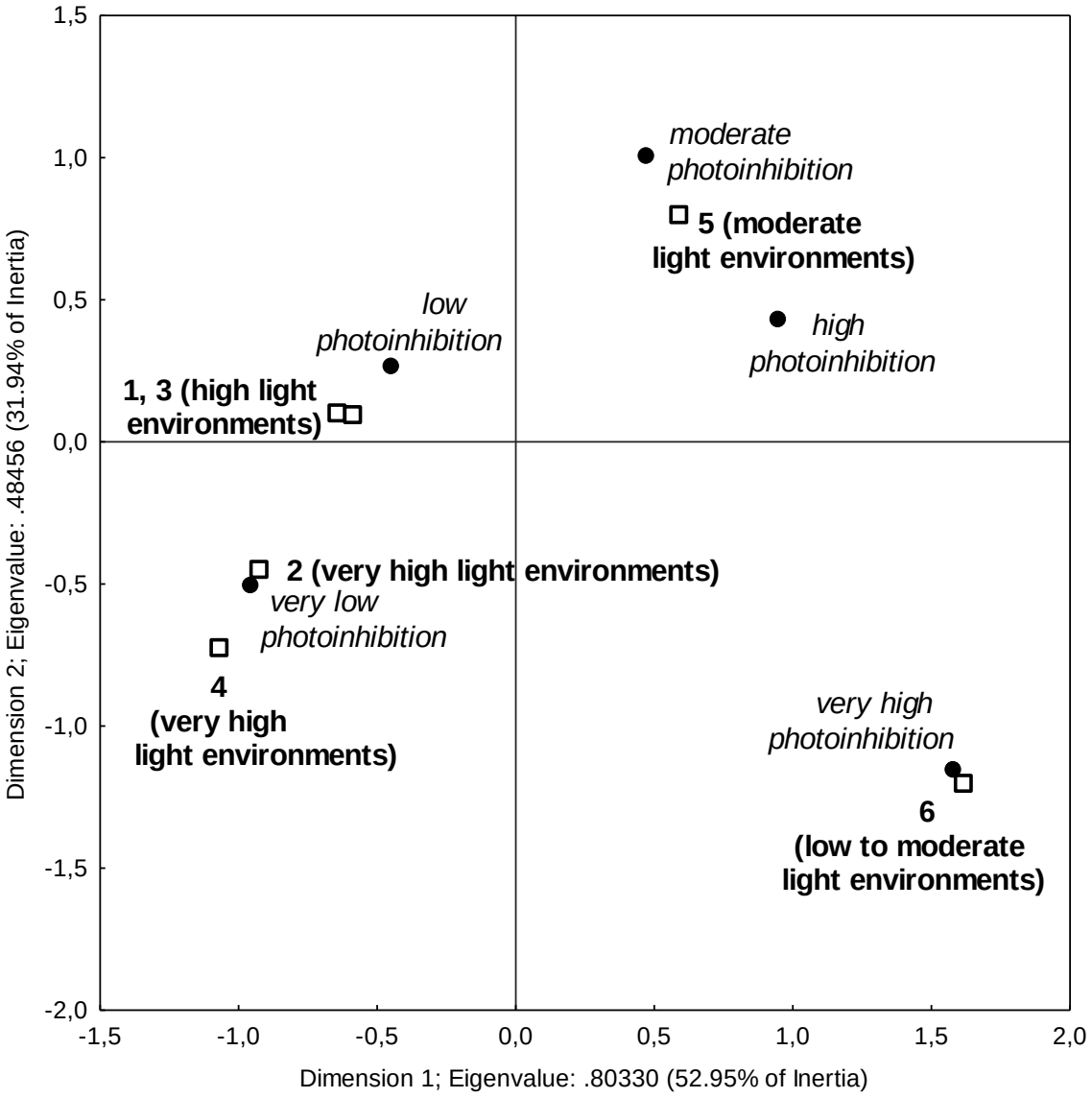


Figure 6.12. Clustering of habitat moisture based on the species scores on the first three components yielded by the PCA on both light and desiccation traits.

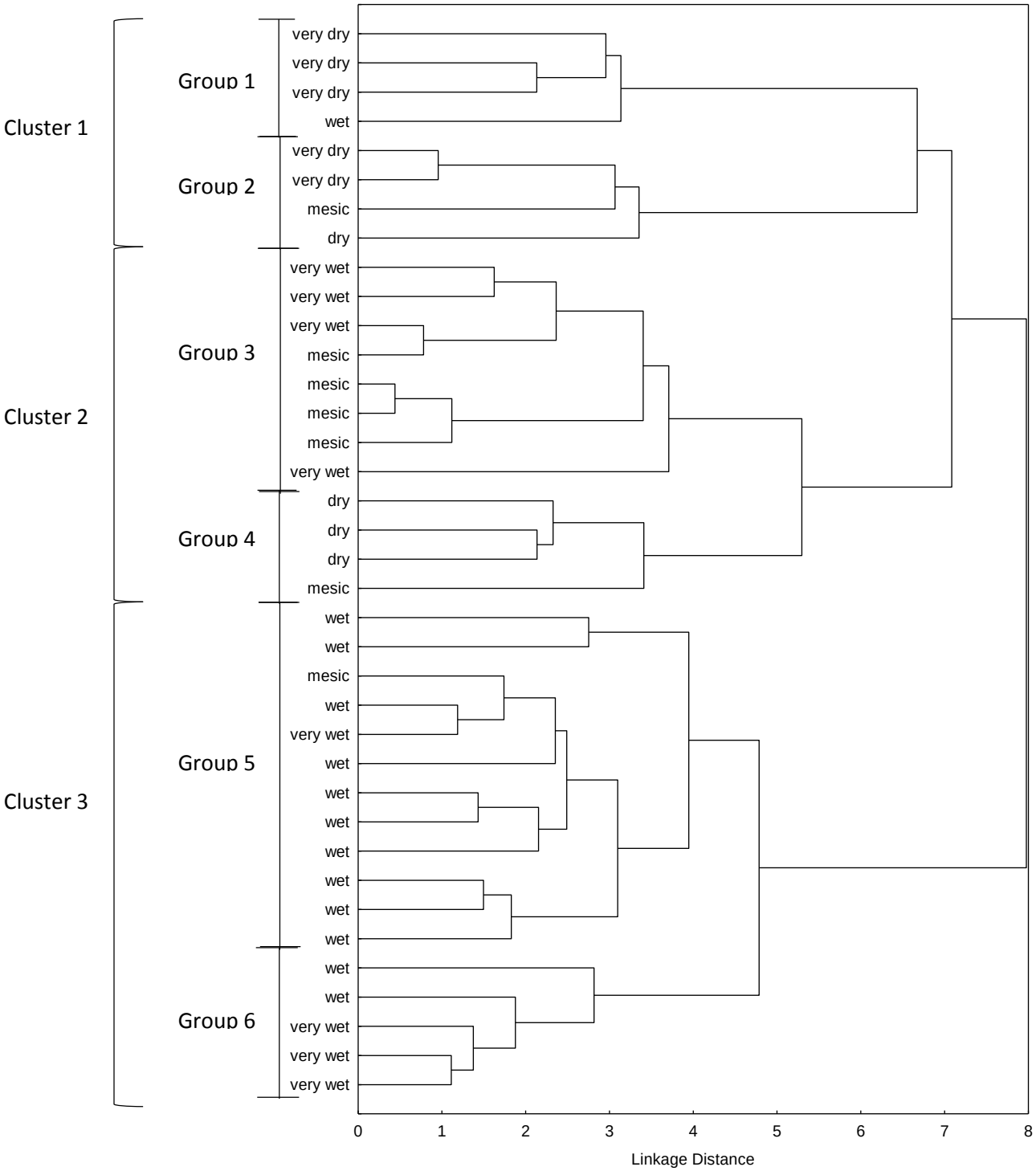


Figure 6.13a. CA joint plot showing the centroids of the six response groups, based on light and desiccation traits, and the association of the bryophyte habitat moisture on the principal axes.

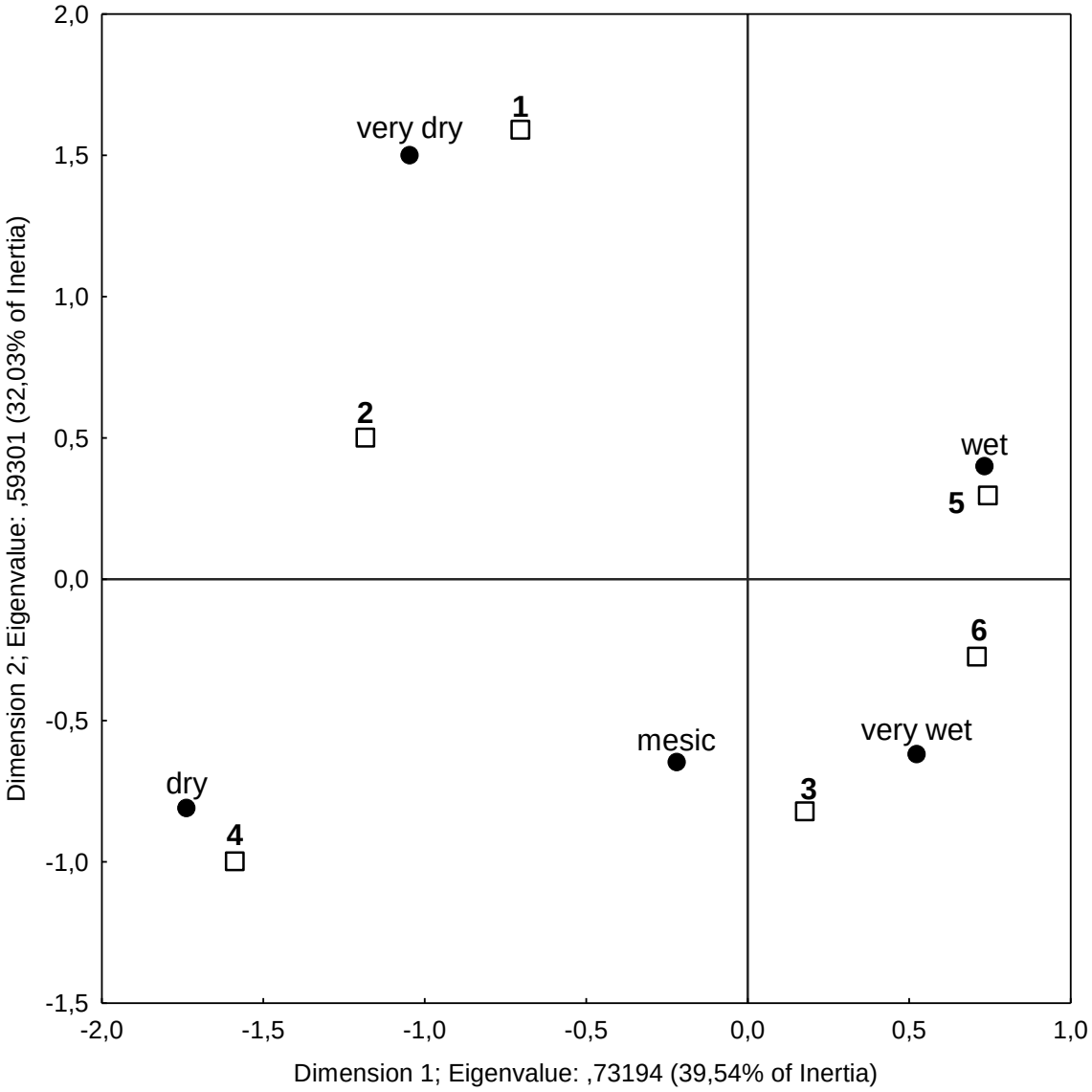
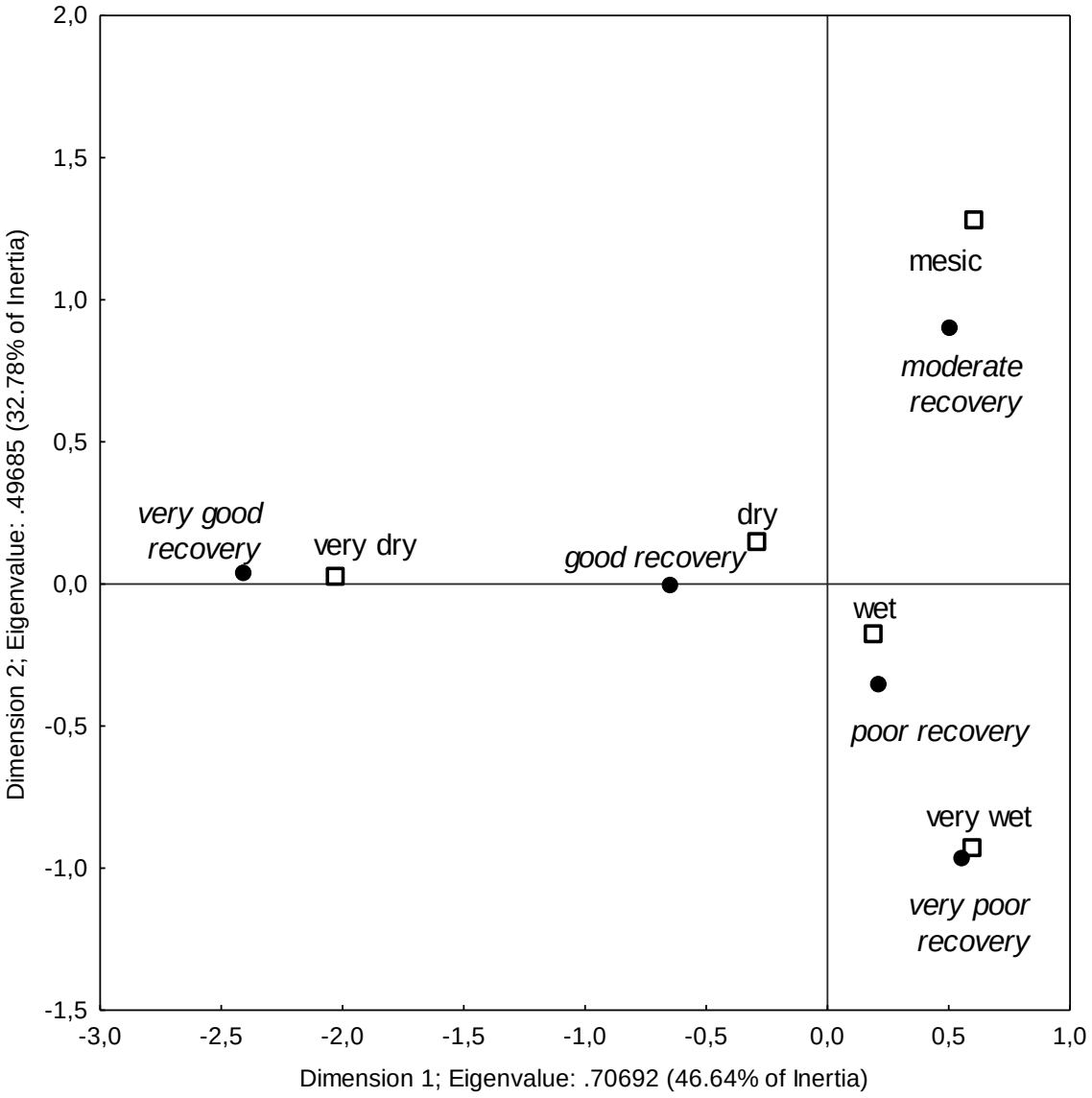


Figure 6.13b. CA joint plot showing the centroids of bryophyte habitat moisture, and the association of the ability to recover photochemistry on rehydration after desiccation on the principal axes.



Tables

Table 3.1. Bryophyte species sampled, their taxonomy and life form. N light is the number of samples for the photosynthetic response and N desic is the number of samples in the response to desiccation.

Species	Abbr-evia-tion	Phylum	Order	Family	Life form	N light	N desic
Andreaea acutifolia	And	Bryophyta	Andreaeales	Andreaeaceae	cushion moss	8	8
Breutelia integrifolia	Breu	Bryophyta	Bryales	Bartramiaceae	turf moss	8	8
Bryum laevigatum	Bry	Bryophyta	Bryales	Bryaceae	turf moss	8	8
Brachythecium rutabulum	Brut	Bryophyta	Hypnales	Brachytheciaceae	rough mat moss	8	9
Brachythecium paradoxum	Bpar	Bryophyta	Hypnales	Hypnaceae	rough mat moss	8	8
Brachythecium subplicatum	Bsub	Bryophyta	Hypnales	Brachytheciaceae	turf moss	8	8
Bucklandiella membranacea var.1	Bmem1	Bryophyta	Grimmiales	Grimmiaceae	cushion moss	8	10
Bucklandiella membranacea var.2	Bmem2	Bryophyta	Grimmiales	Grimmiaceae	tuft moss	9	9
Bucklandiella ochracea	Boch	Bryophyta	Grimmiales	Grimmiaceae	aquatic trailing moss	8	9
Campylopus subnitens	Csub	Bryophyta	Dicranales	Dicranaceae	tuft moss	11	8
Campylopus clavatus	Cclav	Bryophyta	Dicranales	Dicranaceae	tuft moss	8	8
Campylopus purpureocaulis	Cpur	Bryophyta	Dicranales	Dicranaceae	tuft moss	8	8
Cratoneuropsis chilensis	Cra	Bryophyta	Hypnales	Campyliaceae	weft moss	8	8
Dicranoloma billardieri	Dic	Bryophyta	Dicranales	Dicranaceae	tuft moss	8	8
Distichophyllum fasciculatum	Dist	Bryophyta	Hookeriales	Daltoniaceae	turf moss	8	8
Ditrichum strictum	Dit	Bryophyta	Dicranales	Ditrichaceae	cushion moss	8	8

Guembelia kidderi	Guem	Bryophyta	Grimmiales	Grimmiaceae	cushion moss	8	8
Hypnum cupressiforme	Hyp	Bryophyta	Hypnales	Hypnaceae	smooth mat moss	8	8
Muelleriella crassifolia	Muel	Bryophyta	Orthotrichales	Orthotrichaceae	cushion moss	8	9
Notoligotrichum australe	Noto	Bryophyta	Polytrichales	Polytrichaceae	scattered turf moss	8	8
Philonotis tenuis	Phil	Bryophyta	Bryales	Bartramiaceae	turf moss	8	9
Polytrichum juniperinum	Poly	Bryophyta	Polytrichales	Polytrichaceae	scattered turf moss	9	10
Ptychomion densifolium	Pty	Bryophyta	Ptychomniales	Ptychomniaceae	tuft moss	8	8
Racomitrium lanuginosum	Raco	Bryophyta	Grimmiales	Grimmiaceae	tuft moss	8	8
Sanonia uncinata	San	Bryophyta	Hypnales	Campyliaceae	rough mat moss	8	11
Blepharidophyllum densifolium	Blep	Marchantiophyta	Jungermanniales	Scapaniaceae	turf hepatic	8	7
Clasmatocolea humilis	Chum	Marchantiophyta	Jungermanniales	Geocalycaceae	smooth mat hepatic	8	8
Clasmatocolea vermicularis	Cver	Marchantiophyta	Jungermanniales	Geocalycaceae	smooth mat hepatic	8	8
Lepidozia laevifolia	Lepi	Marchantiophyta	Jungermanniales	Lepidoziaceae	weft hepatic	8	7
Leptoscyphus expansus	Lept	Marchantiophyta	Jungermanniales	Geocalycaceae	rough mat hepatic	8	9
Lophocolea randii	Lop	Marchantiophyta	Jungermanniales	Geocalycaceae	rough mat hepatic	8	8
Jensenia pisicolor	Jen	Marchantiophyta	Metzgeriales	Pallaviniaceae	scattered turf hepatic	8	9
Jungermannia coniflora	Jun	Marchantiophyta	Jungermanniales	Jungermanniaceae	turf hepatic	8	8
Marchantia berteroana	Marc	Marchantiophyta	Marchantiales	Marchantiaceae	thallose hepatic	8	8
Plagiochila heterodonta	Plag	Marchantiophyta	Jungermanniales	Lophoziaceae	turf hepatic	8	8
Riccardia prehensilis	Ric	Marchantiophyta	Metzgeriales	Aneuraceae	thallose hepatic	8	9
Syzygiella colorata	Scol	Marchantiophyta	Jungermanniales	Jungermanniaceae	turf hepatic	8	8
Syzygiella sonderi	Sson	Marchantiophyta	Jungermanniales	Jungermanniaceae	turf hepatic	8	8

Table 3.2. Ranking of light regime from low to very high based on species measured percentage of light in the canopy.

Percentage	**Light regime**
85-100	Very high
70-80	High
40-60	Moderate
20-30	Low

Table 3.3. Ranking of habitat moisture from very dry to very wet based on species habitat.

Habitat	**Habitat moisture**
Open fellfield	Very dry
Closed fellfield Biotic grassland Dry mire	Dry
Mesic mire	Mesic
Biotic mire	Wet
Drainage line mire Wet mire Streambank	Very wet

Table 3.4. Important measured and calculated chlorophyll fluorescence parameters from light response curves (Genty et al. 1996).

Light response parameters	**Describes**	**Equation**
$YNPQ/YNO_{876}$	Photoprotective capability at 876 PAR, indicates the capacity for regulated photoprotective heat dissipation in high light	$YNPQ/YNO_{876}= F((F_m/F_m')-1)$
qL_{876}	The fraction of open reaction centres at 876 PAR	$qL_{876}= ((F_m'-F)\times F_o')/((F_m'-F_o')\times F$
$\phi PSII$	Effective quantum yield of photochemistry in PSII	$\phi PSII = (F_m'-F)/F_m'$
ETR	Electron transport rate	$ETR= \phi PSII\times PAR$
α	Initial slope of the RLC, indicates the response to light at low levels	$\alpha = 1/c$
ETR_{max}	Maximum electron transport rate, a measurement of maximum photosynthetic rate	$ETR_{max} = 1/(b+2(ac)^{0.5})$
PAR_{opt}	Optimal PAR, PAR value yielding ETR_{max}	$PAR_{opt} = (c/a)^{0.5}$
$\phi PSII_{PARopt}$	The effective quantum yield of photochemistry at the optimal PAR	
I_k	Minimum saturating irradiance, the PAR at the onset of ETR saturation	$I_k = c/(b+2(ac)^{0.5}) = ETR_{max}/\alpha$

$Inhib_{876}$	Photoinhibition, indicates the decrease from ETR_{max} to ETR_{876} (relative electron transport rate at 876 PAR)	$Inhib_{876} = 100((ETR_{max}-ETR_{876})/ETR_{max})$

* a, b and c are the Eilers and Peeters (1988) equation coefficients.

Table 3.5. Important calculated moisture content, drying rate and chlorophyll fluorescence parameters for desiccation response.

Desiccation response parameters	**Describes**	**Equation**
MC_{sat}	Saturated moisture content on a dry mass basis before desiccation, indicates how wet/dry species initially are	MC_{sat}= ((saturated mass-dry mass)/dry mass) × 100
Halftime	The time it takes to reach half of the saturated moisture content	HT= log2/k
Rate	The rate of water loss from 100% RWC to 50% RWC, indicates how slow or fast drying out takes place	Rate= (MC_{sat}/2)/Halftime
RWC_{final}	The final relative water content, indicates at what moisture content photosynthetic activity stops	RWC_{final}= ((final mass-dry mass)/(saturated mass-dry mass)) × 100
$RWC\phi PSII_{max}$	The relative water content at the maximum quantum yield of photochemistry in PSII, indicates the critical RWC after which photochemistry declines	
$\phi PSII_{recov}$	Recovery of photochemistry on rehydration, indicates to what extent photosynthesis recovers upon rehydration relative to the ϕPSII at the same relative water content during desiccation	$\phi PSII_{recov}$= ($\phi PSII_{30recov}$-$\phi PSII_{final}$)/($\phi PSII_{RWC30}$-$\phi PSII_{final}$)
$YNPQ/YNO_{final}$	Photoprotection capability at the end of desiccation, indicates the capacity for regulated photoprotective heat dissipation when desiccated	$YNPQ/YNO_{final}$= $F((F_m/F_m')-1)$

Table 4.1. Rankings of 38 bryophyte species from very low (VL) to very high (VH) based on their values of ETR_{max} (µmol m^{-2} s^{-1}), PAR_{opt} (µmol photons $m^{-2}s^{-1}$), $\phi PSII_{PARopt}$ (µmol m^{-2} s^{-1}), α (µmol photons $m^{-2}s^{-1}$), Ik (µmol m^{-2} s^{-1}), $Inhib_{876}$ (%), $YNPQ/YNO_{876}$ (ratio), and qL_{876} (fraction). From ANOVA and Tukey's Honest Significant Differences.

Species	**ETR_{max}** **VH**: > 50 **H:** 40- 50 **M:** 20- 40 **L:** 10-20 **VL:** < 10	**PAR_{opt}** **VH:** > 1100 **H:** 800- 1100 **M:** 500- 800 **L:** 300- 500 **VL:** < 300	**$\phi PSII_{PARopt}$** **VH:** > 0.16 **H:** 0.14-0.16 **M:** 0.12-0.14 **L:** 0.1-0.12 **VL:** < 0.1	**α** **VH:** > 0.32 **H:** 0.28- 0.32 **M:** 0.24- 0.28 **L:** 0.2- 0.24 **VL:** <0.2	**Ik** **VH:** > 140 **H:** 110- 140 **M:** 80- 110 **L:** 50- 80 **VL:** < 50	**$Inhib_{876}$** **VH:** > 40 **H:** 30- 40 **M:** 20- 30 **L:** 10- 20 **VL:** < 10	**$YNPQ/YNO_{876}$** **VH:** > 4 **H:** 3.5- 4 **M:** 2.5- 3.5 **L:** 2- 2.5 **VL:** < 2	**qL_{876}** **VH:** > 0.3 **H:** 0.25- 0.3 **M:** 0.15- 0.25 **L:** 0.06- 0.15 **VL:** < 0.06
Polytrichum juniperinum	VH	VH	M	H	VH	VL	L	VH
Notologitrichum australe	VH	H	H	H	VH	VL	L	M
Racomitrium lanuginosum	H	H	H	M	VH	VL	H	VH
Marchantia berteroana	H	M	VH	VH	H	VL	L	M
Campylopus purpureocaulis	H	M	H	H	VH	VL	M	H
Bucklandiella membranacea var.1	M	VH	VL	H	H	VL	VH	VH
Guembelia kidderi	M	H	L	VH	H	VL	H	VH
Philonotis tenuis	M	H	VL	H	M	VL	M	M
Muelleriella crassifolia	M	H	VL	M	M	VL	L	M
Campylopus clavatus	M	M	M	VH	M	VL	H	H
Bryum laevigatum	M	M	M	H	H	VL	H	H
Breutelia integrifolia	M	M	M	H	H	VL	M	M
Syzygiella sonderi	M	M	L	M	M	L	M	M
Ditrichum strictum	M	M	L	M	M	VL	M	M
Bucklandiella membranacea var.2	M	M	VL	VH	L	VL	VH	VH
Andreaea acutifolia	M	M	VL	L	H	VL	L	M
Brachythecium subplicatum	M	L	VH	M	M	L	H	M
Bucklandiella ochracea	M	L	M	M	M	L	VL	M
Sanonia uncinata	M	L	M	M	L	L	M	M
Dicranoloma billardieri	M	L	L	H	L	L	M	M
Ptychomion densifolium	M	L	L	M	L	VL	M	M
Syzygiella colorata	L	M	VL	M	L	VL	L	L
Campylopus subnitens	L	L	M	H	L	L	M	M
Clasmatocolea vermicularis	L	L	M	M	L	M	M	L
Jensenia pisicolor	L	L	VL	L	L	L	M	L

Riccardia prehensilis	L	L	VL	L	L	L	L	L
Lophocolea randii	L	VL	H	M	L	H	M	L
Jungermannia coniflora	L	VL	H	M	L	H	L	L
Brachythecium rutabulum	L	VL	H	L	L	VH	M	L
Plagiochila heterodonta	L	VL	H	L	L	H	M	L
Blepharidophyllum densifolium	L	VL	M	H	L	M	VL	L
Hypnum cupressiforme	L	VL	M	M	VL	M	L	L
Lepidozia laevifolia	L	VL	M	L	VL	VH	VL	VL
Clasmatocolea humilis	L	VL	L	L	L	M	M	L
Leptoscyphus expansus	L	VL	L	L	VL	H	L	L
Brachythecium paradoxum	VL	VL	L	L	VL	VH	VL	VL
Cratoneuropsis chilensis	VL	VL	L	VL	VL	VH	VL	VL
Distichophyllum fasciculatum	VL	VL	L	VL	VL	VH	VL	VL

Table 4.2. The 10 Types of bryophytes and their rankings based on ANOVA and Tukey's Honest Significant Difference test of their light response traits. Rankings 1= very low, 2= low, 3= moderate, 4= high and 5= very high.

Light response types	**Species**	**ETR_{max}**	**PAR_{opt}**	**$\phi PSII_P$ ARopt**	**α**	**Ik**	**$Inhib_{876}$**	**YNPQ/ YNO_{876}**	**qL_{876}**
Type A. Very high or high photosynthetic rate achieved at moderate to very high PAR, moderate to very high effective quantum yield at the optimal PAR, moderate to high response to light at low levels, high or very high onset light saturation of ETR, little or no photoinhibition experienced at super-optimal PAR, low to high photoprotective capability at super-optimal PAR, moderate to very high fraction of open reaction centres at super-optimal PAR.	Mosses								
	Campylopus purpureocaulis,	4	3	4	3	4	2	3	4
	Notologitrichum australe,	4	4	4	3	4	1	2	3
	Polytrichum juniperinum,	5	5	3	3	5	1	2	4
	Racomitrium lanuginosum	4	3	4	3	4	2	4	5
	Hepatics								
	Marchantia berteroana	4	3	5	4	4	1	2	3
Type B. Moderate photosynthetic rate achieved at moderate to high optimal PAR very low to high effective quantum yield at the optimal PAR, moderate to very high response to light at low levels, , moderate to high onset light saturation of ETR, very low or low photoinhibition experienced at super-optimal PAR, high or very high photoprotective capability at super-optimal PAR, high or very high fraction of open reaction centres at super-optimal PAR.	Mosses								
	Bucklandiella membranacea var. 1,	3	4	1	3	4	2	5	4
	Bucklandiella membranacea var. 2,	3	3	2	5	3	1	5	4
	Campylopus clavatus,	3	3	4	5	3	2	4	4
	Guembelia kidderi,	3	4	3	5	3	1	4	5
	Bryum laevigatum	3	3	3	4	3	2	4	4

Type C. Moderate photosynthetic rate achieved at moderate optimal PAR, very low to moderate effective quantum yield at the optimal PAR, low to moderate response to light at low levels, moderate onset light saturation of ETR, very low or low photoinhibition experienced at super-optimal PAR, low or moderate photoprotective capability at super-optimal PAR, moderate fraction of open reaction centres at super-optimal PAR.	<u>Mosses</u> *Andreaea acutifolia*, *Muelleriella crassifolia*, *Ditrichum strictum*, *Breutelia integrifolia* <u>Hepatics</u> *Syzygiella sonderi*	3 3 3 3 3	3 3 3 3 3	2 1 3 3 2	2 3 3 3 3	3 3 3 3 3	2 1 2 1 2	2 2 3 3 3	3 3 3 3 3
Type D. Moderate photosynthetic rate achieved at low optimal PAR, very high effective quantum yield at the optimal PAR, moderate response to light at low levels, moderate onset light saturation of ETR, low photoinhibition experienced at super-optimal PAR, high photoprotective capability at super-optimal PAR, moderate fraction of open reaction centres super-optimal PAR.	<u>Mosses</u> *Brachythecium subplicatum*	3	2	5	3	3	3	4	3
Type E. Moderate or low photosynthetic rate achieved ay moderate or high optimal PAR, very low effective quantum yield at the optimal PAR, moderate or low response to light at low levels, low or moderate onset light saturation of ETR, low photoinhibition experienced at super-optimal PAR, low or moderate photoprotective capability at super-optimal PAR, low or moderate fraction of open reaction centres at super-optimal PAR.	<u>Mosses</u> *Philonotis tenuis* <u>Hepatics</u> *Syzygiella colorata*	3 2	4 3	1 1	4 2	3 2	2 2	3 2	3 2

Type F. Moderate or low photosynthetic rate achieved at low or moderate optimal PAR, low to high effective quantum yield at the optimal PAR, low or moderate response to light at low levels, low or moderate onset light saturation of ETR, moderate photoinhibition experienced at super-optimal PAR, very low to moderate photoprotective capability at super-optimal PAR, moderate fraction of open reaction centres at super-optimal PAR.	Mosses *Bucklandiella ochracea* Hepatics *Clasmatocolea vermicularis*, *Jensenia pisicolor*, *Riccardia prehensilis*	3 2 2 2	3 2 2 2	4 3 2 2	3 3 2 2	3 2 2 2	3 3 3 3	1 3 3 2	3 3 3 3
Type G. Moderate or low photosynthetic rate achieved at low or moderate optimal PAR, moderate effective quantum yield at the optimal PAR, moderate or high response to light at low levels, low or moderate onset light saturation of ETR, low or moderate photoinhibition experienced at super-optimal PAR, high photoprotective capability at super-optimal PAR, moderate fraction of open reaction centres at super-optimal PAR.	Mosses *Dicranoloma billardieri*, *Ptychomion densifolium*, *Sanonia uncinata*, *Campylopus subnitens*	3 3 3 2	3 3 2 2	3 3 3 3	3 3 3 4	3 3 2 2	3 2 3 3	4 4 4 4	3 3 3 3
Type H. Low photosynthetic rate achieved at low optimal PAR, high effective quantum yield at the optimal PAR, low or moderate response to light at low levels, low onset light saturation of ETR, highly or very highly photoinhibited at super-optimal PAR, low or moderate photoprotective capability at super-optimal PAR, low or	Mosses *Brachythecium rutabulum*, *Lophocolea randii* Hepatics *Plagiochila heterodonta*, *Jungermannia coniflora*	2 2 2 2	2 2 2 2	4 4 4 4	2 3 2 3	2 2 2 2	5 4 4 4	3 3 3 2	2 2 2 3

moderate fraction of open reaction centres at super-optimal PAR.									
Type I. Low photosynthetic rate achieved at low optimal PAR, moderate effective quantum yield at the optimal PAR, low to moderate response to light at low levels, very low or low onset light saturation of ETR, moderately to highly photoinhibited at super-optimal PAR, very low to moderate photoprotective capability at super-optimal PAR, low fraction of open reaction centres at super-optimal PAR.	<u>Mosses</u> *Hypnum cupressiforme*, *Leptoscyphus expansus* <u>Hepatics</u> *Blepharidophyllum densifolium*, *Clasmatocolea humilis*	2 2 2 2	2 2 2 2	3 3 3 3	3 2 3 2	1 1 2 2	3 4 3 3	2 2 1 3	2 2 2 2
Type J. Very low photosynthetic rate achieved at very low optimal PAR, low or moderate effective quantum yield at optimal PAR, very low or low response to light at low levels, very low onset light saturation of ETR, very highly photoinhibited at super-optimal PAR, very low photoprotective capability at super-optimal PAR, very low or low fraction of open reaction centres at super-optimal PAR.	<u>Mosses</u> *Brachthecium paradoxum*, *Cratoneuropsis chilensis*, *Distichophyllum fasciculatum* <u>Hepatics</u> *Lepidozia laevifolia*	1 1 1 1	1 1 1 1	2 3 3 3	2 1 1 2	1 1 1 1	5 5 5 5	1 1 1 1	2 1 2 2

Table 4.3. Factor loadings, eigenvalues and explained variance of PC1, PC2 and PC3 for the eight light response traits.

	Factor 1	**Factor 2**	**Factor 3**
ETR_{max}	-0.929	0.234	-0.263
PAR_{opt}	-0.910	-0.260	-0.222
$\phi PSII_{PARopt}$	0.040	0.994	0.060
α	-0.795	0.066	0.325
Ik	-0.872	0.215	-0.388
$Inhib_{876}$	0.913	0.244	0.035
$YNPQ/YNO_{876}$	-0.624	-0.0.13	0.706
qL_{876}	-0.945	0.055	0.128
Expl.Var	65%	15%	11%
Eigenvalue	5.202	1.225	0.894

Table 4.4. Characteristics and species memberships of the seven light response functional groups. Numbering of the groups corresponds to the cluster or sub-cluster numbering in Figures 4.1 and 4.2.

Group	Species
Group 1. Moderate maximum ETR. ETR_{max} attained at high PAR. Low quantum yield at PAR_{opt}. High onset light saturation of photosynthetic ETR. Moderate response to light at low levels. Very little photoinhibition experienced at high light. Low photoprotective capability at high light. Moderate fraction of open reaction centres at high light.	*Andreaea acutifolia*, *Breutelia integrifolia*, *Ditrichum strictum*, *Muelleriella crassifolia*, *Philonotis tenuis*, *Syzygiella colorata*, *Syzygiella sonderi*
Group 2. Low maximum ETR. ETR_{max} attained at low PAR. Moderate quantum yield at PAR_{opt}. Low onset light saturation of photosynthetic ETR. Low response to light at low levels. Moderate photoinhibition experienced at high light. Low photoprotective capability at high light. Low fraction of open reaction centres at high light.	*Blepharidophyllum densifolium*, *Clasmatocolea humilis*, *Hypnum cupressiforme*, *Jensenia pisicolor*, *Leptoscyphus expansus*, *Riccardia prehensilis*
Group 3. Low maximum ETR. ETR_{max} attained at low PAR. Very high quantum yield at PAR_{opt}. Moderate onset light saturation of photosynthetic ETR. Low response to light at low levels. Highly photoinhibited at high light. Low photoprotective capability at high light. Low fraction of open reaction centres at high light.	*Brachythecium rutabulum*, *Bucklandiella ochracea*, *Clasmatocolea vermicularis*, *Jungermannia coniflora*, *Lophocolea randii*, *Plagiochila heterodonta*
Group 4. Very low maximum ETR. ETR_{max} attained at very low PAR. Moderate quantum yield at PAR_{opt}. Low onset light saturation of photosynthetic ETR. Very low response to light at low levels. Very highly photoinhibited at high light. Very low photoprotective capability at high light. Very low fraction of open reaction centres at high light.	*Brachythecium paradoxum*, *Cratoneuropsis chilensis*, *Distichophyllum fasciculatum*, *Lepidozia laevifolia*

Group 5. High maximum ETR. ETR_{max} attained at high PAR. Moderate quantum yield at PAR_{opt}. High onset light saturation of photosynthetic ETR. Very high response to light at low levels. Very little photoinhibition experienced at high light. Very high photoprotective capability at high light. Very high fraction of open reaction centres at high light.	*Bryum laevigatum*, *Bucklandiella membranacea* var. 1, *Bucklandiella membranacea* var. 2, *Campylopus clavatus*, *Guembelia kidderi*
Group 6. Moderate maximum ETR. ETR_{max} attained at moderate PAR. High quantum yield at PAR_{opt}. Moderate onset light saturation of photosynthetic ETR. Moderate response to light at low levels. Little photoinhibition experienced at high light. High photoprotective capability at high light. Moderate fraction of open reaction centres at high light.	*Brachythecium subplicatum*, *Campylopus subnitens*, *Dicranoloma billardieri*, *Ptychomion densifolium*, *Sanonia uncinata*
Group 7. Very high maximum ETR. ETR_{max} attained at very high PAR. Very high quantum yield at PAR_{opt}. Very high onset light saturation of photosynthetic ETR. High response to light at low levels. Very little photoinhibition experienced at high light. Moderate photoprotective capability at high light. High fraction of open reaction centres at high light.	*Campylopus purpureocaulis*, *Marchantia berteroana*, *Notologitrichum australe*, *Racomitrium lanuginosum*, *Polytrichum juniperinum*

Table 5.1. Rankings of 38 bryophyte species from very low (VL) to very high (VH) based on their values of MC_{sat} (%), Rate (% MC per min), RWC_{final} (%), $RWC\phi PSII_{max}$ (%), $\phi PSII_{recov}$ (%) and $YNPQ/YNO_{final}$ (ratio) from ANOVA and 95% confidence limit box plots.

Species	**MC_{sat}** **VH**: > 1300 **H:** 1000-1300 **M:** 600-1000 **L:** 200-600 **VL:** <200	**Rate** **VH:** >10 **H:** 6-10 **M:** 4-6 **L:** 2-4 **VL:** <2	**$RWC\phi PSII_{max}$** **VH:** >85 **H:** 80-85 **M:** 73-80 **L:** 65-73 **VL:** <65	**RWC_{final}** **VH:** >25 **H:** 20-25 **M:** 13-20 **L:**7-13 **VL:** <7	**$YNPQ/YNO_{final}$** **VH:** > 6 **H:** 5-6 **M:** 3.5-5 **L:** 2-3.5 **VL:** <2	**$\phi PSII_{recov}$** **VH:** >80 **H:** 50-80 **M:** 20-50 **L:** 10-20 **VL:** <10
Lophocolea randii	VH	VH	H	M	VL	L
Leptoscyphus expansus	VH	VH	VL	L	L	VL
Clasmatocolea vermicularis	VH	H	VH	L	L	VL
Distichophyllum fasciculatum	VH	M	M	M	VL	VL
Marchantia berteroana	VH	L	H	M	L	M
Clasmatocolea humilis	VH	L	H	L	L	VL
Riccardia prehensilis	H	VH	M	M	VL	VL
Sanonia uncinata	H	VH	L	VL	L	M
Lepidozia laevifolia	H	VH	L	L	L	L
Brachythecium paradoxum	H	VH	M	VL	L	M
Brachythecium rutabulum	H	H	VL	L	M	M
Brachythecium subplicatum	H	M	H	VL	M	VL
Blepharidophyllum densifolium	H	L	VL	H	L	L

Cratoneuropsis chilensis	M	H	L	M	L	M
Jensenia pisicolor	M	M	L	L	L	L
Bucklandiella ochracea	M	M	L	M	H	H
Bryum laevigatum	M	M	M	VL	VH	VL
Hypnum cupressiforme	M	M	L	VL	M	H
Ptychomion densifolium	M	M	L	VL	M	M
Philonotis tenuis	M	M	H	L	M	VL
Jungermannia coniflora	M	L	H	M	L	L
Dicranoloma billardieri	M	L	H	L	M	L
Breutelia integrifolia	M	L	H	L	M	L
Plagiochila heterodonta	L	M	H	L	H	H
Syzygiella grandiflora	L	L	M	M	VH	H
Bucklandiella membranacea var.2	L	L	M	L	H	L
Racomitrium lanuginosum	L	L	VL	L	M	H
Campylopus clavatus	L	L	VL	VL	H	M
Campylopus subnitens	L	L	M	VL	H	M
Syzygiella colorata	L	L	VL	H	M	H
Notologitrichum australe	L	L	L	L	M	M
Campylopus purpureocaulis	L	VL	M	M	L	L
Guembelia kidderi	L	VL	H	VH	H	VH
Andreaea acutifolia	L	VL	L	VH	M	H
Ditrichum strictum	L	VL	H	H	M	H
Muelleriella crassifolia	L	VL	M	H	M	VH
Bucklandiella membranacea var.1	L	VL	M	M	H	L

Polytrichum juniperinum	VL	VL	M	VH	VH	M

Table 5.2. Factor loadings, eigenvalues and explained variance on PC1, PC2 and PC3 for the six desiccation response traits.

	Factor 1	**Factor 2**	**Factor 3**
MC_{sat}	0.881	-0.045	0.165
$RWC\phi PSII_{max}$	0.236	0.772	0.539
Rate	0.794	-0.244	-0.287
RWC_{final}	-0.445	-0.586	0.644
$YNPQ/YNO_{final}$	-0.787	0.378	-0.276
$\phi PSII_{recov}$	-0.836	-0.105	-0.029
Expl. Var	49%	19%	15%
Eigenvalue	2.97	1.15	0.89

Table 5.3. Characteristics and species memberships of the nine desiccation response groups, based on clustering of the PCA scores of the six desiccation response traits.

Group	Species
Group 1. Very low or low moisture content when fully hydrated. Very low or low rate of water loss. Very low to moderate RWC when photochemistry starts to decline. High or very high RWC when photochemistry ceases during desiccation. Moderate photoprotective capability when desiccated. Moderate to very high ability of photochemistry to recover on rehydration.	*Andreaea acutifolia* *Muelleriella crassifolia* *Polytrichum juniperinum* *Syzygiella colorata*
Group 2. Low moisture content when fully hydrated. Very low rate of water loss. High RWC when photochemistry starts to decline. High or very high RWC when photochemistry ceases during desiccation. Moderate or high photoprotective capability when desiccated. High or very high ability of photochemistry to recover on rehydration.	*Ditrichum strictum* *Guembelia kidderi*
Group 3. Low moisture content when fully hydrated. Very low to moderate rate of water loss. Moderate or high RWC when photochemistry starts to decline. Low or moderate RWC when photochemistry ceases during desiccation. High or very high photoprotective capability when desiccated. High ability of photochemistry to recover on rehydration.	*Bucklandiella membranacea* var. 1 *Plagiochila heterodonta* *Syzygiella sonderi*
Group 4. Low to high moisture content when fully hydrated. Low or moderate rate of water loss. Moderate or high RWC when photochemistry starts to decline. Very low or low RWC when photochemistry ceases during desiccation.	*Brachythecium subplicatum* *Breutelia integrifolia* *Campylopus subnitens* *Dicranoloma billardieri* *Philonotis tenuis*

Moderate or high photoprotective capability when desiccated. Very low to moderate ability of photochemistry to recover on rehydration.	
Group 5. Low or moderate moisture content when fully hydrated. Low or moderate rate of water loss. Very low to moderate RWC when photochemistry starts to decline. Low or moderate RWC when photochemistry ceases during desiccation. Moderate or high photoprotective capability when desiccated. Low to high ability of photochemistry to recover on rehydration.	*Bucklandiella membranacea* var. 2 *Bucklandiella ochracea* *Notologitrichum australe* *Racomitrium lanuginosum*
Group 6. Low or moderate moisture content when fully hydrated. Low or moderate rate of water loss. Very low to moderate RWC when photochemistry starts to decline. Very low RWC when photochemistry ceases during desiccation. Moderate to very high photoprotective capability when desiccated. Moderate or high ability of photochemistry to recover on rehydration.	*Bryum laevigatum* *Campylopus clavatus* *Hypnum cupressiforme* *Ptychomion densifolium*
Group 7. Low to very high moisture content when fully hydrated. Very low to very high rate of water loss. Very low to high RWC when photochemistry starts to decline. Low to high RWC when photochemistry ceases during desiccation. Very low or low photoprotective capability when desiccated. Very low to moderate ability of photochemistry to recover on rehydration.	*Blepharidophyllum densifolium* *Campylopus purpureocaulis* *Cratoneuropsis chilensis* *Distichophyllum fasciculatum* *Jensenia pisicolor* *Jungermannia coniflora* *Marchantia berteroana* *Riccardia prehensilis*
Group 8. High or very high moisture content when fully hydrated. High or very high rate of water loss. Very low to moderate RWC when photochemistry starts to decline.	*Brachythecium paradoxum* *Brachythecium rutabulum* *Lepidozia laevifolia* *Leptoscyphus expansus* *Sanonia uncinata*

Very low or low RWC when photochemistry ceases during desiccation. Low or moderate photoprotective capability when desiccated. Very low to moderate ability of photochemistry to recover on rehydration.	
Group 9. Very high moisture content when fully hydrated. High or very high rate of water loss. High or very high RWC when photochemistry starts to decline. Low or moderate RWC when photochemistry ceases during desiccation. Very low or low photoprotective capability when desiccated. Very low or low ability of photochemistry to recover on rehydration.	*Clasmatocolea vermicularis* *Clasmatocolea humilis* *Lophocolea randii*

Table 6.1. Factor loadings, eigenvalues and explained variance of PC1, PC2 and PC3 for the eight light and six desiccation response traits.

	PC 1	**PC 2**	**PC 3**
ETR_{max}	-0.853	0.272	-0.412
PAR_{opt}	-0.904	-0.047	-0.162
$\phi PSII_{PARopt}$	0.155	0.670	-0.304
α	-0.720	0.337	0.164
Ik	-0.817	0.151	-0.483
$Inhib_{876}$	0.900	-0.021	0.103
$YNPQ/YNO_{876}$	-0.616	0.388	0.463
qL_{876}	-0.919	0.195	-0.070
MC_{sat}	0.694	0.421	-0.171
Rate	0.776	0.217	-0.040
$RWC\phi PSII_{max}$	0.011	0.389	0.344
RWC_{final}	-0.073	-0.716	-0.383
$YNPQ/YNO_{final}$	-0.735	-0.075	0.513
$\phi PSII_{recov}$	-0.510	-0.619	0.206
Expl.Var	48%	15%	10%
Eigenvalue	6.679	2.126	1.381

Table 6.2. Characteristics and species memberships of the three main clusters and the six groups based on light and desiccation response traits.

Cluster	Description	Group	Description	Species
1	Moderate or high ETR_{max}, attained at moderate or high PAR. Light saturation of photosynthesis starts at moderate or high PAR. Very low or low quantum yield of electron transport at optimal PAR. Moderate, high or very high response to low light. Low, moderate or high photoprotection and very low photoinhibition at supra-optimal PAR. Moderate, high or very high fraction of open reaction centres at supra-optimal PAR. Low moisture content when saturated. Dry very slowly or slowly. Photosynthesis ceases at moderate or high RWC. Moderate, high or very high photoprotection when desiccated. High or very high photosynthesis recovery from desiccation.	1	Moderate ETR_{max}, attained at moderate PAR. Light saturation of photosynthesis starts at moderate PAR. Very low quantum yield of electron transport at optimal PAR. Moderate response to low light. Low photoprotection and very low photoinhibition at supra-optimal PAR. Moderate fraction of open reaction centres at supra-optimal PAR. Low moisture content when saturated. Dry very slowly. Photosynthesis ceases at high RWC. Moderate photoprotection when desiccated. High photosynthesis recovery from desiccation.	*Andreaea acutifolia* *Ditrichum strictum* *Muelleriella crassifolia* *Syzygiella colorata*
		2	Moderate to high ETR_{max}, attained at high PAR. Light saturation of photosynthesis starts at high PAR. Low or very low quantum yield of electron transport at optimal PAR.	*Bucklandiella membranacea* var.1 *Bucklandiella membranacea* var.2 *Guembelia kidderi* *Syzygiella sonderi*

			High or very high response to low light. Moderate or high photoprotection and very low photoinhibition at supra-optimal PAR. Very high fraction of open reaction centres at supra-optimal PAR. Low moisture content when saturated. Dry slowly or very slowly. Photosynthesis ceases at moderate RWC. High or very high photoprotection when desiccated. High or very high photosynthesis recovery from desiccation.	
2	Moderate, high or very high ETR_{max}, attained at moderate or high PAR. Light saturation of photosynthesis starts at moderate, high or very high PAR. Moderate or high quantum yield of electron transport at optimal PAR. Moderate or high response to low light. Low, moderate or high photoprotection and very low or low photoinhibition at supra-optimal PAR. Moderate or high fraction of open reaction centres at supra-optimal PAR . Low or moderate moisture content when saturated. Dry slowly or moderately fast.	3	Moderate to high ETR_{max}, attained at moderate PAR. Light saturation of photosynthesis starts at moderate or high PAR. Moderate quantum yield of electron transport at optimal PAR. High response to low light. Moderate or high photoprotection and very low or low photoinhibition at supra-optimal PAR. Moderate fraction of open reaction centres at supra-optimal PAR. Moderate moisture content when saturated. Dry moderately slow or slowly.	*Brachythecium subplicatum* *Breutelia integrifolia* *Bryum laevigatum* *Campylopus clavatus* *Campylopus subnitens* *Dicranoloma billardieri* *Philonotis tenuis* *Ptychomion densifolium*

	Photosynthesis ceases at very low, low or moderate RWC. Moderate or high photoprotection when desiccated. Very low, low or moderate photosynthesis recovery from desiccation.		Photosynthesis ceases at very low RWC. Moderate or high photoprotection when desiccated. Very low, low or moderate photosynthesis recovery from desiccation.	
		4	Very high ETR_{max}, attained at moderate or high PAR. Light saturation of photosynthesis starts at very high PAR. High quantum yield of electron transport at optimal PAR. Moderate or high response to low light. Low or moderate photoprotection and very low photoinhibition at supra-optimal PAR. Moderate or high fraction of open reaction centres at supra-optimal PAR. Low or moderate moisture content when saturated. Dry slowly. Photosynthesis ceases at low or moderate RWC. Moderate photoprotection when desiccated. Moderate photosynthesis recovery from desiccation.	*Campylopus purpureocaulis* *Marchantia berteroana* *Notoligotrichum australe* *Racomitrium lanuginosum* *Polytrichum juniperinum?*

3	Very low or low ETR_{max}, attained at very low PAR. Light saturation of photosynthesis starts at very low or low PAR. Low, moderate or high quantum yield of electron transport at optimal PAR. Low or moderate response to low light. Very low or moderate photoprotection and moderate, high or very high photoinhibition at supra-optimal PAR. Very low or low fraction of open reaction centres at supra-optimal PAR. Moderate, high or very high moisture content when saturated. Dry moderately fast, fast or very fast. Photosynthesis ceases at low or moderate RWC. Low photoprotection when desiccated. Very low, low or moderate photosynthesis recovery from desiccation.	5	Low ETR_{max}, attained at very low PAR. Light saturation of photosynthesis starts at low PAR. Moderate or high quantum yield of electron transport at optimal PAR. Low or moderate response to low light. Low or moderate photoprotection and moderate or high photoinhibition at supra-optimal PAR. Low fraction of open reaction centres at supra-optimal PAR. Moderate, high or very high moisture content when saturated. Dry moderately fast, fast or very fast. Photosynthesis ceases at low or moderate RWC. Low photoprotection when desiccated. Low or moderate photosynthesis recovery from desiccation.	*Brachythecium rutabulum* *Blepharidophyllum densifolium* *Bucklandiella ochracea* *Clasmatocolea humilis* *Clasmatocolea vermicularis* *Hypnum cupressiforme* *Jensenia pisicolor* *Jungermannia coniflora* *Lophocolea randii* *Plagiochila heterodonta* *Riccardia prehensilis* *Sanonia uncinata*
		6	Very low or low ETR_{max}, attained at very low PAR. Light saturation of photosynthesis starts at very low PAR. Low quantum yield of electron transport at optimal PAR. Low response to low light.	*Brachythecium paradoxum* *Cratoneuropsis chilensis* *Distichophyllum fasciculatum* *Lepidozia laevifolia* *Leptoscyphus expansus*

			Very low photoprotection and very high photoinhibition at supra-optimal PAR. Very low fraction of open reaction centres at supra-optimal PAR. High or very high moisture content when saturated. Dry very fast. Photosynthesis ceases at low or moderate RWC. Low photoprotection when desiccated. Very low, low or moderate photosynthesis recovery from desiccation.	