

A study of the ecology of Tasmanian *Sphagnum* peatlands

by

Jennifer Whinam B.A. (Hons.)

Submitted in fulfilment of the
requirements for the degree of
Doctor of Philosophy

University of Tasmania
Hobart
August 1990

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and contains no copy or paraphrase of material previously published or written by another person, except where due reference is made in the text.

J. Whinam

Acknowledgements

Many people made the completion of this thesis possible. I thank my supervisor Prof J.B. Kirkpatrick for his enthusiastic and supportive encouragement and assistance throughout the duration of this project. I am also grateful to Neil Gibson, Rod Fensham and Pierre Horwitz for critically reading parts of this thesis and providing helpful discussions. I thank Dr G.S. Hope for initially stimulating my interest in peatlands.

I am most grateful to the many friends who helped during the course of my fieldwork. I particularly thank Russell Bauer, Kate Brown, Neil Gibson and Malcolm Robb who all provided companionship and assistance on numerous field trips.

The Tasmanian Government Analyst conducted all nutrient analyses. Darryl Mummery provided assistance with BIOCLIM. Airlie Alam kindly provided graphic assistance with figs. 3.8, 7.11 and 8.1. Glen McPherson freely gave statistical advice. Dr A.E. Orchard and the staff of the Tasmanian Herbarium provided assistance with plant identifications. Fred Koolhof printed plates 1 and 2.

Rodney Rich of the Forestry Commission of Tasmania and Jayne Balmer of Tasmanian Department of Parks, Wildlife and Heritage provided bureaucratic assistance and support. Many of the costs associated with fieldwork and experiments were defrayed by a National Estate grant from the Australian Heritage Commission. Financial support was provided by the Australian Postgraduate Research Award.

Members of the Department of Geography and Environmental Studies provided a pleasant and friendly work environment, for which I am most appreciative.

Finally, I gratefully acknowledge the assistance and encouragement provided by Russell Bauer, Shirley Grosvenor and Louise Gilfedder in the production stage of the thesis.

ABSTRACT

A study of the ecology of Tasmanian *Sphagnum* peatlands

The ecology of *Sphagnum* peatlands in the southern hemisphere has been poorly understood. Comparisons with northern hemisphere literature suggest that Tasmanian *Sphagnum* peatlands are limited in their morphology and geomorphic expression, possibly due to relatively low effective precipitation. While *Sphagnum* bogs tend to occupy nutrient poor situations in the northern hemisphere, in Tasmania they do not occur on the poorest substrates, despite climatic suitability.

To provide data on spatial variability of Tasmanian *Sphagnum* mires, a survey of 137 sites across Tasmania was carried out. Plant species composition and cover, peat depths and height of hummocks were recorded. Climatic data were generated by using the computing package BIOCLIM. Peats from a subset of samples were analysed for their nutrient composition. Eight ecologically distinct groups spanning an almost continuous gradient from high to low altitude sites were recognised. Floristic variation between sites along this gradient can largely be explained by location along secondary gradients of nutrient availability and disturbance (fire).

In a glasshouse experiment, the dry matter biomass of *S. cristatum* showed no significant relative effects when subjected to drought, fertiliser or shade treatments, either singularly or interactively. Shade resulted in a reduced biomass of *Sphagnum*-associates, suggesting that shade affects the competitive ability of other species.

Monitoring of exclosure and control plots provided data which suggest that grazing may result in the maintenance of conditions suitable for *Sphagnum* by altering inter-specific competition. The effects of grazing appear to be more pronounced at lower altitude, high productivity sites than at higher altitudes. There was no evidence to suggest that marsupials graze *Sphagnum* moss.

Monitoring of a site subjected to a low intensity burn provided some short-term data on this disturbance event. Initial effects varied according to the vegetation present, which influenced the local severity of the fire. The most significant change appears to be a drying out of the peatland, which has resulted in a decline of *Sphagnum*.

Macrofossils from peat cores have enabled a possible model of *Sphagnum* peatland succession in Tasmania to be developed. Succession appears to be multi-directional, with micro-successional changes occurring across mires in response to extremely local events. While the major successional pathway suggested by these cores is from *Sphagnum/Restiad* to *Sphagnum* mires, progression to sites dominated by herbs and shrubs is possible.

<u>Table of Contents</u>	<u>Page No.</u>
Acknowledgements	(i)
Abstract	(ii)
List of figures	(vii)
List of tables	(x)
List of plates	(xii)
List of appendices	(xiii)
 <u>Chapter 1 - Introduction</u>	
1.1 Preamble	1
1.2 Distribution and typology of <i>Sphagnum</i> peatlands	4
1.3 Spatial variation in vegetation	6
1.4 Resource constraints	8
1.5 Disturbance	9
1.6 Temporal trends	10
 <u>Chapter 2 - Tasmanian <i>Sphagnum</i> peatlands in an international context</u>	
2.1 Introduction	13
2.2 Methodology	14
2.2.1 Field methods	14
2.2.2 Data analyses	16
2.3 Description of Tasmanian <i>Sphagnum</i> peatlands	16
2.3.1 Distribution	16
2.3.2 Species composition	18
2.3.3 Morphology of the Tasmanian <i>Sphagnum</i> mires	18
2.3.4 Geology	20
2.4 The geomorphic context of Tasmanian <i>Sphagnum</i> mires	20
2.5 Climatic Parameters	22
2.6 Environmental relationships of geomorphic types of <i>Sphagnum</i> mire	24
2.7 Australasian floristic and structural affinities	27
2.8 Comparisons with global data	28
2.8.1 Climate	28
2.8.2 Nutrients	29
2.8.3 Species richness	32
2.8.4 Mire complex types	33
2.8.5 Historical land-use practices	33
2.9 Conclusions	34

Chapter 3 - Vegetation of Tasmanian *Sphagnum* mires

3.1 Introduction	36
3.2 Methods	37
3.2.1 Data analysis	37
3.3 Results	39
3.3.1 The communities	39
3.3.2 Environmental variables and site characteristics	46
3.3.3 Species attributes of communities	46
3.4 Environmental relationships	48
3.4.1 Climate and altitude	48
3.4.2 Ability to regenerate after fire	50
3.4.3 Geomorphology	51
3.4.4 Peat depth and rock type	51
3.4.5 Height of hummocks	52
3.4.6 Nutrients	53
3.4.7 Ordination	53
3.5 Discussion and conclusions	56

Chapter 4 - The effects of drought, shade and nutrients on *Sphagnum cristatum* and associated species

4.1 Introduction	59
4.2 Methods	61
4.3 Results and discussion	64
4.3.1 <i>Sphagnum</i>	64
4.3.2 <i>Sphagnum</i> -associated species	66
4.3.3 Humified <i>Sphagnum</i>	67
4.4 Conclusions	70

Chapter 5 - The effects of marsupial grazing on Tasmanian *Sphagnum* peatlands

5.1 Introduction	71
5.2 Methods	72
5.3 Results and discussion	74
5.4 Conclusions	80

Chapter 6 - Effects of fire on a *Sphagnum* peatland

6.1 Introduction	82
6.2 Methods	83
6.2.1 Field methods	83
6.2.2 Data analyses	85

6.3 Results	86
6.3.1 Comparison of burnt and unburnt plots	86
6.3.2 Rate of change post-fire	89
6.3.3 Natalities/Mortalities	90
6.3.4 <i>Asperula gunnii</i> and <i>Celmisia asteliifolia</i>	91
6.3.5 0.25 m ² plot with bare peat	91
6.4 Discussion and conclusions	93

Chapter 7 - Medium term successional processes in Tasmanian *Sphagnum* peatlands

7.1 Introduction	97
7.2 Description of the sites	98
7.3 Methods	98
7.4 Results	99
7.4.1 Pine Valley cores	100
7.4.2 Little Fisher River	105
7.4.3 Excavations	111
7.4.4 Surface trends	111
7.5 Discussion	116
7.6 Conclusion	120

Chapter 8 - Conclusions

8.1 Summary of findings	121
-------------------------	-----

Appendices

List of Figures

	<u>Page No.</u>
Fig. 1.1 Distribution of the main types of mire complex on a world scale. Primary mires are found throughout the world.	2
Fig. 1.2 Location of all sites in Tasmania referred to in text.	5
Fig. 2.1 Distribution of surveyed <i>Sphagnum</i> peatlands.	17
Fig. 2.2 Size and depth of <i>Sphagnum</i> pillows at the Little Fisher River.	19
Fig. 2.3 Limits of Pleistocene ice in Tasmania (1) according to Lewis; (2) according to Banks.	21
Fig. 2.4 Mean annual rainfall of Tasmania (mm).	23
Fig. 2.5 Dissimilarities between geomorphic types of statistically significant environmental variables.	24
Fig. 2.6 Mean precipitation of the wettest month for the different geomorphic types.	25
Fig. 2.7 Temperature and precipitation profiles for Europe, Canada and Tasmania.	29
Fig. 2.8 Total K (mg g ⁻¹) and total N (mg g ⁻¹) for Tasmanian <i>Sphagnum</i> peatlands and European mires.	31
Fig. 2.9 Total P ₀₄ (µg g ⁻¹) and total N (mg g ⁻¹) for Tasmanian <i>Sphagnum</i> peatlands and European mires.	31
Fig. 3.1 Dendrogram showing indicator species at each division.	44
Fig. 3.2 Differences in environmental and floristic variables between TWINSPAN groups.	47
Fig. 3.3 (a) Precipitation and (b) temperature variables (with standard errors of the mean, S.E.M.) for each TWINSPAN group.	49
Fig. 3.4 Species' ability to recover from fire within TWINSPAN groups (mean scores and S.E.M.).	50
Fig. 3.5 Mean peat depths and S.E.M. for each of the TWINSPAN groups.	51
Fig. 3.6 Height of hummocks (above hollows) and S.E.M. for each of the TWINSPAN groups.	52
Fig. 3.7 Nutrient analysis of the peat samples from a subset of 26 quadrats (with S.E.M.).	54

Fig. 3.8	Vectors of environmental and vegetational variables in the normalised space of the two-dimensional non-metric multidimensional scaling solution for (a) the subsample of 47 quadrats and (b) the subsample of 26 quadrats for which nutrient data were available.	55
Fig. 3.9	(a) Total Nitrogen (%) and (b) organic matter (%) from Tasmanian <i>Sphagnum</i> peatlands at different altitudes.	57
Fig. 4.1	Summary of different treatments for glasshouse experiment.	62
Fig. 4.2	Mean values of humified <i>Sphagnum</i> moss as a fraction of total moss weight under different experimental treatments (a) Nutrients combined with droughting treatments; (b) Nutrients combined with shading treatments.	69
Fig. 5.1	Growth in height of species at different locations over time.	79
Fig. 6.1	Layout of burnt (B) and unburnt (U) plots at Kenneth Lagoon.	84
Fig. 6.2	Mean total overlapping cover (with standard error of the mean S.E.M.) on burnt and unburnt plots at different times post-fire.	87
Fig. 6.3	Mean percentage cover (with S.E.M.) on burnt and unburnt plots at different times post-fire (note different vertical scales).	88
Fig. 6.4	Total number of individual tussocks/rosettes of <i>Asperula gunnii</i> and <i>Celmisia asteliifolia</i> on burnt and unburnt plots.	91
Fig. 6.5	Total overlapping cover of species on a 0.25m ² plot, where both vegetation cover and peat were burned.	92
Fig. 7.1	Cross-section of cores taken at 50 metre intervals across Pine Valley. (L.O.I.) values are bulked organic values (except where otherwise indicated) at 550°C.	101
Fig. 7.2	Pine Valley (a) surface cross-section and (b) % cover of species and lifeforms on surface of core sites.	102
Fig. 7.3	Details of eight cores extracted at 50 metre intervals across Pine Valley.	103
Fig. 7.4	1.5 m core extracted from Pine Valley	106
Fig. 7.5	Percentage cover of species and lifeforms on surface of core sites at the Little Fisher River.	107
Fig. 7.6	Details of eight cores extracted from the Little Fisher River.	108
Fig. 7.7	Peat cores from a heterogeneous <i>Sphagnum</i> mire at the Little Fisher River. Loss-on-ignition (L.O.I.) values are bulked organic values (except where otherwise indicated) at 550°C.	112
Fig. 7.8	Details of four excavations made at Pine Valley.	113

Fig. 7.9 (a) surface transect and (b) species presence/absence on hummocks and hollows along a 130 m transect at Paradise Plains.	114
Fig. 7.10 (a) surface transect and (b) species presence/absence on hummocks and hollows along a 270 m transect at the Walls of Jerusalem.	115
Fig. 7.11 Model of successional changes from 50 cm cores from Pine Valley and the Little Fisher River.	118
Fig. 8.1 Model of the possible development and regulating mechanisms of Tasmanian <i>Sphagnum</i> peatlands.	125

<u>List of Tables</u>	<u>Page No.</u>
Table 2.1 Nutrient data (N, P, K and organic matter) from a subset of 26 quadrats.	26
Table 3.1 Sorted two-way table of species by classificatory groups.	40
Table 4.1 Analysis of variance of biomass index for different experimental treatments for <i>S. cristatum</i> .	65
Table 4.2 Analysis of variance of biomass index for different experimental treatments for <i>Sphagnum</i> -associated species.	66
Table 4.3 Ratios of <i>Sphagnum</i> to <i>Sphagnum</i> -associated species for different shade treatments, based on final dry weights.	66
Table 4.4 Analysis of variance of the effects of the different experimental treatments on the fraction of live:humified <i>S. cristatum</i> (dry weight).	67
Table 5.1 Mean growth in height over 22 months (with S.E.M.) for grazed and ungrazed plots (2 plots each) at Mt Field and the Walls of Jerusalem.	76
Table 5.2 Results of Kruskal-Wallis analysis of variance tests for total growth rates over 22 months of species for grazed and ungrazed plots at the Walls of Jerusalem and Mt Field.	76
Table 5.3 BIOCLIM data (climatic values interpolated from known stations as functions of latitude, longitude and elevation, Busby 1986) for Mt Field and the Walls of Jerusalem.	77
Table 5.4 Growth in grazed plots as a percentage of ungrazed plots for vascular plants at Mt Field and the Walls of Jerusalem, both separately and combined.	78
Table 5.5 Results of Kruskal-Wallis analysis of variance tests for variation in growth of <i>S. cristatum</i> , <i>E. minus</i> and <i>E. serpyllifolia</i> at all locations during different seasons.	78
Table 5.6 Mean number of natalities and mortalities for all species at grazed and ungrazed sites at the Walls of Jerusalem and Mt Field at different measurement times.	80
Table 6.1 Species and lifeforms recorded from Kenneth Lagoon plots.	86
Table 6.2 Mean percentage cover of species with significantly different cover on burnt and unburnt plots at different times post-fire.	87
Table 6.3 Changes in cover abundance in the lifeform (l/f) categories occurring on burnt and unburnt plots, 22 months post-fire, with H values.	89
Table 6.4 Number of instances where species were recorded in quadrats occurring above the median, equal to the median and below the median growth rate, in periods since the fire.	89
Table 6.5 Numbers of quadrats in which lifeform classes are above, equal to (=) and below the median on burnt and unburnt plots.	90

Table 6.6	Numbers of natalities and mortalities on burnt and unburnt plots over the periods of measurement.	91
Table 7.1	Numbers of instances each lifeform recorded on hummocks and hollows.	116

List of plates

Page No.

Plate 1 Surface morphology of Tasmanian *Sphagnum* mires

19(a)

(a) strings of parallel hummocks

(b) mosaic of hummocks and hollows.

Plate 2 Grazing exclosure plots at

73(a)

(a) the Walls of Jerusalem

(b) Mt Field

<u>List of appendices</u>	<u>Page No.</u>
Appendix 1. Species codes, family, status and lifeform.	138
Appendix 2. Descriptions of the locations and general details of surveyed <i>Sphagnum</i> sites.	142
Appendix 3. Distribution of each of the eight TWINSPAN groups.	147
Appendix 4. The frequency of taxa in communities.	151
Appendix 5. Chemical composition of 'Aquasol'	153
Appendix 6. Mean dry weights for different experimental treatments.	154

CHAPTER 1 - INTRODUCTION

1.1 Preamble

In terms of its total mass, live and dead, *Sphagnum* is regarded as one of the most important of all plants (Andrus 1986, Clymo and Duckett 1986). It is estimated that there are approximately 300 species world-wide, with the greatest biomass of *Sphagnum* (probably fewer than 30 species) in the north temperate and boreal zones (Clymo and Hayward 1982). At lower latitudes it usually grows at high altitudes (Clymo and Hayward 1982). *Sphagnum* is considered a dominant and important peatland taxon (Clymo 1970).

The terms 'mire' and 'peatland' are generally taken to be synonymous and are used to describe all types of peat accumulating ecosystems (Gore 1983). Moore and Bellamy's (1974) generalised map (fig. 1.1) shows the global distributions of the main types of lowland mire complex. This small-scale map shows mires as being largely confined to the northern hemisphere. The only peatlands shown in the southern hemisphere are the domed Tertiary mires located at the southern tip of South America and in Indonesia, with *Sphagnum* on the southern oceanic islands.

The ecology, evolution and utilisation of *Sphagnum* peatlands have been the focus of many studies, particularly in the temperate, boreal and subarctic regions of the northern hemisphere, where they occupy a significant portion of the landscape and are of some economic importance. The ecologic importance of *Sphagnum* relates not only to its dominance of northern hemisphere peatlands, but also to its acidifying properties (Clymo and Hayward 1982) and hence to its influence on habitat successional trends (Andrus 1986).

Recent literature has focused on the relationship of acid rain and the decline of *Sphagnum* moss (Gorham *et al.* 1987, Lee *et al.* 1987), the effects of heavy metals on *Sphagnum* (Pakarinen 1978b), the nutrient enrichment effects of sewage (Sanville 1988) and the relationship of *Sphagnum* peat mining (for burning and horticulture) to atmospheric carbon (Clymo 1987). Peat mining, *Sphagnum* moss harvesting (Elling and Knighton 1984) and *Sphagnum* mire use for tree plantations (Blain *et al.* 1987, Caron and Joyal 1987) have resulted in conflict between economic use and nature conservation (Thompson D. 1987).

Vascular species names follow Buchanan *et al.* (1989), and *Sphagnum* names follow Scott *et al.* (1976), except where otherwise stated. Vegetation terminology follows Kirkpatrick (1983).

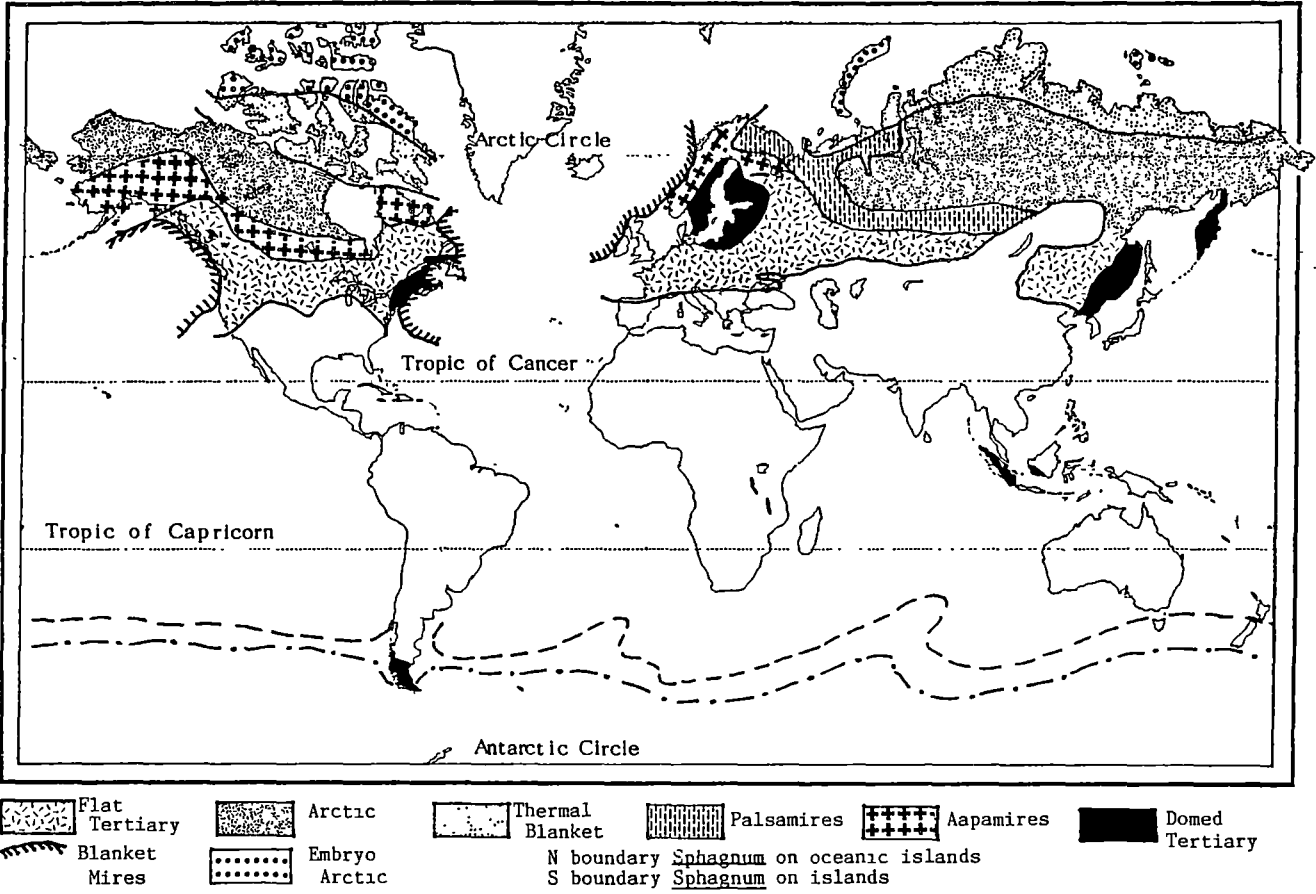


Fig. 1.1 Distribution of the main types of mire complex on a world scale. Primary mires are found throughout the world (from Moore and Bellamy 1974).

The areas dominated by *Sphagnum* in the cooler part of the southern hemisphere, including Australia, New Zealand, South America and the subantarctic islands, are not as extensive as in the northern hemisphere. In the southern hemisphere much peatland vegetation is dominated by Restionaceae species (Campbell 1983), terrestrial sedges such as *Gymnoschoenus sphaerocephalus* (Jarman *et al.* 1988), cushion plants (Gibson and Hope 1986) or wetland species, such as *Phragmites australis* (Kirkpatrick and Harwood 1983). Thus, *Sphagnum* occupies a smaller proportion of peatland than in the northern hemisphere. While all these peatland types occur in Tasmania, buttongrass moorland is the most extensive peatland type (Jarman *et al.* 1988).

The northern hemisphere research experience offers many potential lines of inquiry for the study of Tasmanian *Sphagnum* peatlands. Northern hemisphere studies have focused on the autecology of *Sphagnum* (Hayward and Clymo 1983), vegetation floristics (Vitt and Bayley 1984), history of *Sphagnum* peatlands (Frenzel 1983), partitioning of *Sphagnum* species along environmental gradients (Gignac & Vitt 1990, Slack *et al.* 1980), interactions with other species (Ovenden & Brassard 1989, van Baaren *et al.* 1988), effects of environment (Clymo 1973, 1987), successional trends (Walker and Walker 1961) and effects of disturbance (Rawes 1983).

Northern hemisphere studies have produced much information, but the ecology of *Sphagnum* peatlands in the southern hemisphere is poorly understood. This is particularly true in Australasia where the limited area of *Sphagnum* peatlands is reflected by the paucity of literature directed towards these ecosystems (see Thompson K. 1987). Papers generally refer to new species or new distributions for species (Rodway 1914, Crocker and Eardley 1939, Smith 1969, Scott 1971), although some discuss aspects of peatland ecology (Millington 1954, Cockayne 1958, Campbell 1964, 1983, Ashton and Hargreaves 1983, Clarkson 1984).

There are eight species of *Sphagnum* recorded in Australia. These are:

1. *S. cristatum* : the most common, found throughout eastern Australia and New Zealand;
2. *S. australe* : much rarer, although probably overlooked, found in Tasmania, Victoria, New South Wales, South America, South Africa and New Zealand;
3. *S. subsecundum* : found down to sea level in swampy country, in Tasmania, Western Australia, South Australia, Victoria, New South Wales, Australian Capital Territory, South America, New Zealand and widely distributed in the northern hemisphere;

4. *S. falcatulum* : common floating in ponds, found in Tasmania, Victoria, New South Wales, Queensland, South America and New Zealand;
5. *S. beccarii* : found in Victoria and New South Wales, India, S.E. Asia, Africa and America;
6. *S. compactum* : not common, found in Tasmania;
7. *S. dominii* : found in Queensland; and
8. *S. cuspidatum* : not common, found in Tasmania (Scott *et al.* 1976). A recent taxonomic revision of *Sphagnum* in Australia has resulted in a further six species being recognised (Streimann and Curnow 1989).

In Tasmania, *Sphagnum* species occur over a wide geographic, altitudinal and geomorphic range. Patches of *Sphagnum* occur from sea level on the Bass Strait islands (Kirkpatrick and Harwood, unpubl. data; fig. 1.2), to high in the mountains of south-west Tasmania. However, while *Sphagnum* is a widespread genus in Tasmania, mires in which *Sphagnum* is the dominant taxon are much less frequent (Watts 1912, Pemberton 1986, Jarman *et al.* 1988, Kirkpatrick and Whinam 1988, Whinam *et al.* 1989). It could be expected that the ecology of Tasmanian *Sphagnum* peatlands would differ from that of the northern hemisphere, given their restricted distribution, the relatively maritime nature of the climate, the small number of *Sphagnum* species, and the isolated evolution of the Australian flora.

This thesis concentrates on some aspects of *Sphagnum* mire ecology which northern hemisphere literature suggests could be useful in understanding the contemporary distribution of *Sphagnum* in Tasmania. As a first step towards understanding spatial variation in Tasmania, the *Sphagnum* mires are classified by geomorphic type and floristics. Investigations of the dynamics of mire ecology concentrate on the interaction of *Sphagnum* with other species. These interactions are examined under varying moisture/light/nutrient levels, and in areas subjected to marsupial grazing and after fire. An attempt is made to determine the historical dynamics of *Sphagnum* and other species by examining macrofossils from peat cores.

1.2 Distribution and typology of *Sphagnum* peatlands

The vast majority of peatlands are located in the subarctic regions and in mountainous areas, but usually at high latitudes (Moore and Bellamy 1974, Clymo and Hayward 1982). Mire ecosystems are, however, also found in the tropics (Anderson 1983, Thompson and Hamilton 1983). The general requirements for the development of *Sphagnum* mires are thought to be an assured water supply, moderate aeration and minimal nutrient input (Moore and Bellamy 1974, Clymo and Hayward 1982).

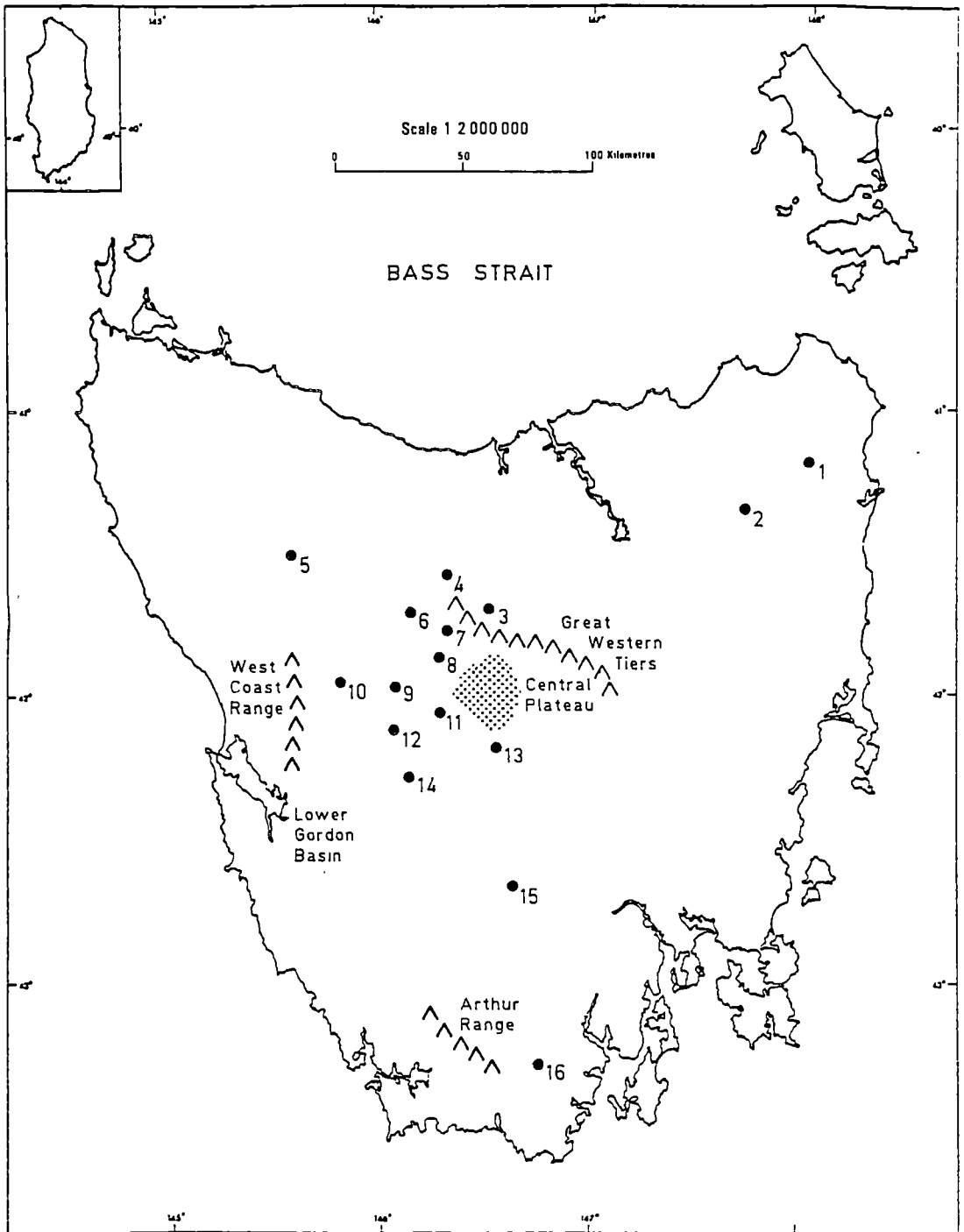


Fig. 1.2 Location of all sites in Tasmania referred to in text. Key to locations: 1=Blue Tier, 2=Paradise Plains, 3=Mother Cummings Peak, 4=Mole Creek sinkholes, 5=Netherby Plains, 6=Mersey River Valley, 7=Little Fisher River, 8=Walls of Jerusalem, 9=Pine Valley, 10=Eldon Range, 11=Kenneth Lagoon, 12=Mt Rufus, 13=Browns Marsh, 14=King William Plains, 15=Mt Field, 16=Birds Plain.

Sphagnum peatlands appear to be confined within a distinct climatic/topographic/edaphic envelope (Moore and Bellamy 1974, Clymo 1983, Frenzel 1983, Tallis 1983). Within that environmental envelope the recognised types of mire appear to be broadly correlated with precipitation (Moore and Bellamy 1974, Clymo and Hayward 1982, Ingram 1983). In climates where evaporation does not exceed precipitation for long periods, *Sphagnum*-dominated vegetation may blanket the whole countryside on slopes up to 20° (blanket bog) (Moore and Bellamy 1974). In regions with summer drought *Sphagnum* may be more localised in basins where the accumulated peat is sufficient to provide a reservoir that insulates *Sphagnum* from fluctuations in the regional watertable (raised bog) (Moore and Bellamy 1974). Valleys allow extensive *Sphagnum* growth where the water has flowed through solute-poor rocks (valley bog) (Clymo and Hayward 1982). Less commonly, a carpet of *Sphagnum*, often with sedges, grows out over a deep pool (schwingmoor) (Moore and Bellamy 1974). In the boreal zone, string bogs (aapamires) are widespread. This mire type has a distinctive surface appearance, with ridge and pool surfaces oriented along the contours (Gore 1983).

Chapter 2 addresses the question : to what extent do Tasmanian *Sphagnum* peatlands conform in their location and variability to the patterns described for the northern hemisphere?

1.3 Spatial variation in vegetation

The term 'plant community' has been used to define the 'units' (characterised by strong internal floristic, physiognomic and structural affinities) that comprise the vegetation of a landscape area (Zimmerman and Thom 1982). Conversely, plant communities have been described as arbitrary sections of a gradient of continuous compositional change (Ritchie 1986). Three major elements of community theory are response of species to habitat conditions, interactions between species (competition, facilitation), and chance and random processes, both in the environment (disturbance) and in populations (dispersal) (Noy-Meir and van der Maarel 1987).

Phytosociology concerns the structure of plant communities, the pattern or order that may be found in the co-occurrence and co-abundance of the various plant species and its variation in space (Noy-Meir and van der Maarel 1987). The Braun-Blanquet phytosociologic approach has been summarised (Noy-Meir and van der Maarel 1987) as :

1. Plant communities are conceived as types of vegetation recognised by their floristic composition, which better expresses their relationships to one another and to the environment than any other characteristic.
2. Amongst the species that make up the floristic composition of a plant community some are more sensitive indicators of environmental relationships; these diagnostic species include character-species with an occurrence largely confined to one community type, differential-species characterising a few types towards related other types, and constant companions.

In contrast, while using mainly floristic criteria, Clements and Tansley both classified communities into types on the basis of dominant species or dominant species groups (Mueller-Dombois and Ellenberg 1974). The wider ecological amplitudes of dominant species resulted in larger communities and a more heterogeneous environment (Mueller-Dombois and Ellenberg 1974).

It became clear, using modern quantitative methods of vegetation analysis, that the pattern of variation shown by the distribution of species hovers between the continuous and the discontinuous (Noy-Meir and van der Maarel 1987). The concept of a nodum, or centre of variation, was introduced to acknowledge the occurrence of relative discontinuities in the vegetational continuum (Noy-Meir and van der Maarel 1987).

Much of current vegetation theory has been described as simply a set of descriptive propositions with a lack of process-orientation (Austin 1987). Current directions in vegetation research include the modelling of vegetation dynamics (e.g. Hobbs and Hobbs 1987, van Hulst 1987) and new methods of analysis (e.g. Faith *et al.* 1987, Jongman *et al.* 1987, ter Braak 1987). Analytical methods have been used to test theory as well as examining vegetation-environment correlations (Austin 1987).

An early example of a phytosociologic study of peatlands is by Katz (1926) who used this approach to separate and describe floristic associations of Russian *Sphagnum* mires. Much of the more recent phytosociological literature on *Sphagnum* mires relates to separating mires into nutrient-poor bogs and minerotrophic fens (International Peat Society 1979, Sims *et al.* 1982, Rybníček 1985). Fens can range from poor, through various intermediate and transitional types, to rich fens (Slack *et al.* 1980). Ordination has been used as a means of positioning sites from fen to bog extremes (Clymo 1983). Other phytosociologic studies have focused on the distribution of *Sphagnum* and allied vascular species along various environmental gradients associated with the transition

from bog to fen. The gradients most commonly examined are pH, light, peat depth and nutrient concentration (Vitt and Slack 1975, Luken 1985, Ovenden and Brassard 1989, Gignac and Vitt 1990).

Chapter 3 addresses the questions : what phytosociological communities can be distinguished within Tasmanian *Sphagnum* peatlands and how do they relate to environmental conditions?

1.4 Resource constraints

Species abundances and distributions are controlled by the independent variables of physical environment factors and attributes of individual species (Diamond 1986), as well as chance and random processes (Noy-Meir and van der Maarel 1987). Species compete for the resources of light, moisture, nutrients and space (Roughgarden and Diamond 1986). Both extrinsic and intrinsic factors control the growth of plants. The principal extrinsic factors controlling the distribution of *Sphagnum* are thought to be atmospheric conditions, with precipitation probably being the most effective and insolation also being important (Hayward 1980). Intrinsic factors, such as the anatomy and physiology of the plants, serve to modify the external factors, resulting in the plants influencing their own growth and that of their neighbours and competitors (Hayward 1980).

Many observations and some experimental data have led to generalisations about the effects of external environmental factors on the growth of *Sphagnum* and its associated species. For example, an assured water supply is considered decisive for the growth of *Sphagnum* (Clymo and Hayward 1982), with the distribution over time of the moisture likely to be more important than mean values for a certain period (Backeus 1988). The separation of some *Sphagnum* species between hummocks and hollows is thought to represent differential utilisation of the moisture gradient, which probably co-varies with other microhabitat gradients, such as pH (Vitt and Slack 1984, Andrus 1986).

A frequently made observation is that *Sphagnum* is intolerant of climatic conditions which threaten the moss with dessication (Godley 1978, Vitt and Slack 1984), the most common cause of mortality (Clymo and Hayward 1982). Shade is thought to give protection from dessication, with light and moisture interacting (Vitt and Slack 1975). However, while some shade gives protection from dessication, dense shade normally excludes *Sphagnum* (Clapham 1940, Godwin and Turner 1933). The relationship is unlikely to be simple, as temperature and light interact with yet other

factors, and environmental history, to produce the daily photosynthetic curve (Billings and Mooney 1968).

The applicability of these generalisations on the effects of the principal external factors affecting growth of several northern hemisphere *Sphagnum* species can be tested for their relevance to *S. cristatum*, the dominant Australian and New Zealand *Sphagnum* species. Chapter 4 addresses the questions : do shading, nutrient status and moisture availability affect the growth rate of *Sphagnum cristatum*? Do these environmental factors affect the growth rate of *Sphagnum* by altering its competitive relationships with other Tasmanian *Sphagnum* peatland species?

1.5 Disturbance

Three factors causing vegetation changes have been identified as: disturbance, stress and competition (Grime 1979). Ecologists have separated two aspects of the response of ecosystems to disturbance: the ability of a system to resist displacement from its initial state when subject to perturbation ('inertia' or 'resistance') and the ability to recover to the initial state after disturbance ('resilience', 'elasticity' or 'stability') (Hill 1975, Gignon 1983).

Every ecosystem is subject to differing types of disturbance, of varying intensities (Noble and Slatyer 1980). Grazing and fire are considered as disturbance events in peatlands (Ratcliffe and Walker 1958). However, it has been suggested that continuous grazing, which may have a significant impact, cannot be strictly classified as a disturbance, as it is part of the normal environment (Noble and Slatyer 1980). Changes resulting from a disturbance event may be simply fluctuations (short-term reversible changes) or successional changes (directional changes operating on very short to very long timescales) (Miles 1979). The sub-optimal conditions encountered by many wetland species subjected to flooding mean that an additional stress such as grazing, burning or pollution can result in the elimination of those species from the regional bog flora (Crawford 1983).

While little is known about the interaction of Tasmanian marsupials and *Sphagnum* peatlands, large numbers of herbivore droppings suggest that marsupials frequent *Sphagnum* mires. The hollows and the edges of hummock mounds are often clearly marked by animal trails. None of the literature reviewed contains any suggestion that vertebrates eat *Sphagnum*. However, it is likely that marsupials graze the palatable herbs, grasses and shrubs that are associated with *Sphagnum*, and therefore favour the survival of *Sphagnum* by altering inter-specific competition.

The few studies that have been carried out on the effects of grazing in Australian peatlands have concentrated on the effects of cattle grazing (Carr and Turner 1959b, McDougall 1989). The influence of fire on *Sphagnum* peatlands globally is poorly understood (Andrus 1986).

Chapter 5 addresses the question : does marsupial grazing significantly alter the competition and productivity of plants in *Sphagnum* peatlands? Chapter 6 addresses the question : what effect has fire had on species composition and survival in a Tasmanian *Sphagnum* peatland?

1.6 Temporal trends

The use of analogue analysis, where temporal trends are inferred from spatial patterns, is common practice in vegetation studies. Analogues are used to gain insight into the nature of possible long-term compositional changes in a community (Orloci 1981). Pollen and macrofossil profiles have been recorded from numerous mires in an attempt to determine changes in species composition over time (Heinselman 1970, Moore 1977, Glaser and Janssens 1986, Heathwaite and Ross 1987, Nicholson 1989). The study of pattern and process in vegetation may enable the mutual connections between 'variety-in-space' (pattern) and 'variety-in-time' (process) within plant communities to be examined (van Leeuwen 1966).

Northern hemisphere *Sphagnum* peatlands often consist of a pattern of hummocks with intervening hollows (Moore and Bellamy 1974, Luken *et al.* 1985). The hummocks and hollows often exhibit distinctive segregation of species, including both bryophytes and vascular species (Vitt *et al.* 1975, Slack *et al.* 1980, Vitt and Slack 1984). There has been some suggestion that this spatial patterning expresses the successional processes (Ashton and Hargreaves 1983, van Baaren *et al.* 1988). Interpretation of successional sequences from stratigraphic evidence involves comparison with this current day analogue (e.g. Ashton and Hargreaves 1983, Svensson 1986).

Under some conditions, *Sphagnum* may direct wetland succession through acidification and paludification (Andrus 1986). The physiologically active roots of woody mire plants are generally restricted to the uppermost few centimetres of peat, where there is sufficient oxygen to maintain aerobic respiration, and are quickly killed when the accumulation of *Sphagnum* raises the water table (Andrus 1986, Glaser and Janssens 1986).

One aspect to receive much attention in peat stratigraphic studies has been predictability, particularly whether cyclic trends or directionality exist in peatland development. There have been contradictory findings from these studies. Stratigraphic information, as well as pollen and rhizopod analyses, have been used to demonstrate that peatland development is not cyclic (Casparie 1969, Walker and Walker 1961). There is, however, evidence to suggest that cycles may occur within longer term trends ('persistent changes', Sjors 1980). Examples from boreal peatlands show both convergence from different origins and divergence in the local development of mires (Sjors 1980). American examples show no consistent trend towards mesophytism, terrestrialisation or even uniformity, but rather changes in the direction of succession due to local or regional events (Heinselman 1970).

Perhaps the most commonly cited example of succession has been the hydrosere, commencing from shallow water and leading to fen and eventually to bog or wooded bog (Sjors 1980, Moore and Bellamy 1974). However, this is no longer considered to be the dominant origin of mires (Sjors 1980). The most common mode of origin for northern hemisphere peatlands is thought to be paludification (Sjors 1980, 1983; Gore 1983).

The term paludification describes the formation of peat over a landscape. Paludification most commonly occurs on terrestrial humus, podsolised soils or even on bare rock surfaces (Gore 1983). *Sphagnum* is known as a paludifier in cool humid areas because of the expansion of carpets from mires into the surrounding forest (Heinselman 1970, Andrus 1986). Sjors (1980) has suggested that nearly all sloping peatlands (including most 'aapa mires' or string bogs), were formed by paludification in post-glacial time. Sjors (1980) also postulates that much of the peatlands on the plains of the north and interior of Eurasia and North America were once covered by woodland, or in some cases grasslands.

Chapter 7 addresses the questions : is spatial variation a reflection of temporal trends in Tasmanian *Sphagnum* peatlands? Are temporal trends uniform and unidirectional?

Chapter 8 attempts to integrate the findings of this study by addressing the question : what are the major factors influencing the distribution and types of Tasmanian *Sphagnum* mires?

Table 1.1 Summary of questions posed in Chapter 1 and the chapters in which they are addressed.

Chapter 2 : Distribution and typology of Tasmanian <i>Sphagnum</i> peatlands
To what extent do Tasmanian <i>Sphagnum</i> peatlands conform in their location and variability to the patterns described for the northern hemisphere?
Chapter 3 : Vegetation of Tasmanian <i>Sphagnum</i> mires
What phytosociological communities can be distinguished within Tasmanian <i>Sphagnum</i> peatlands and how do they relate to environmental conditions?
Chapter 4 : Glasshouse experiment testing the effects of drought, shade and addition of nutrients on <i>Sphagnum cristatum</i>
Do shading, nutrient status and moisture availability affect the growth rate of <i>Sphagnum cristatum</i> ? Do these environmental factors affect the growth rate of <i>Sphagnum</i> by altering its competitive relationships with other Tasmanian peatland species?
Chapter 5 : The effects of marsupial grazing on Tasmanian <i>Sphagnum</i> peatlands
Does marsupial grazing significantly alter the competition and productivity of plants in <i>Sphagnum</i> peatlands?
Chapter 6 : Effects of fire on a <i>Sphagnum</i> peatland
What effect has fire had on species composition and survival in a Tasmanian <i>Sphagnum</i> peatland?
Chapter 7 : Succession in Tasmanian <i>Sphagnum</i> peatlands
Is spatial variation a reflection of temporal trends in Tasmanian <i>Sphagnum</i> peatlands? Are temporal trends uniform and unidirectional?
Chapter 8 : Conclusion
What are the major factors influencing the distribution and types of Tasmanian <i>Sphagnum</i> mires?

CHAPTER 2 - TASMANIAN *SPHAGNUM* PEATLANDS IN AN INTERNATIONAL CONTEXT

2.1 Introduction

Many different classifications of peat-forming systems exist, using various attributes and methods (e.g. International Peat Society 1979). Most classifications recognise the fundamental importance of plant nutrition and source of water (Clymo 1983). The first division of mires is generally between fen and bog, with the latter being acid and mineral-poor and the former being less acid, or even alkaline, and mineral-rich (Gore 1983). Bogs and fens are distinguished by the origin and chemistry of their respective water supplies. Bogs are ombrotrophic, influenced solely by water that falls directly on them as rain or snow, while fens are minerotrophic, influenced by water derived predominantly from outside their own immediate limits (Gore 1983). The general floristic differences between northern hemisphere fen, poor fen, and bog may be widely accepted, but it is more doubtful that there are clear chemical limits (Waughman 1980).

On a global scale the definitions attached to ombrotrophic bogs and subdivisions of ombrotrophic vegetation have been easier than the subdivision of fens, due to the extensive, uniform (or regularly recurring) vegetation and habitat conditions of bogs (Gore 1983). The diversity of fen types has led to further classification into poor fen, fen and rich fen (Sjors 1983), and treed and treeless fens (Ruuhijarvi 1983). In the boreal and north temperate zones plant communities are often distinctly related to mire formations so that descriptions of vegetation can give a reliable measure of the mire ecosystem and its variants (Gore 1983). It appears more difficult to make clear distinctions between fens and bogs in Tasmania (and Australasia generally). This is partly because *Sphagnum* is not a prominent indicator of bog conditions, as it is in the northern hemisphere (Campbell 1983).

The other major global subdivision of mires is based on the topographic setting and position in relation to the watertable. Moore and Bellamy (1974) describe three major categories:-

1. primary mire systems: form in basins or depressions found in all except the most hot and arid areas of the earth. The key feature which restricts primary mire development is the dry season, coupled with high temperatures which result in high moisture loss by evapotranspiration;

2. secondary mire systems: develop beyond the physical confines of the basin or depression, with the peat acting as a reservoir and increasing the surface retention of the landscape unit; and
3. tertiary mire systems: which develop above the physical limits of the groundwater, with the peat acting as a reservoir holding a volume of water by capillary action up above the groundwater. The tertiary peat reservoir is fed by the precipitation falling directly on it. Both secondary and tertiary mire systems show distinct zonation related to macroclimatic factors (Moore and Bellamy 1974).

The aim of this chapter is to document the distribution and possible environmental controls of *Sphagnum* peatlands in Tasmania. Little benefit is likely to be gained by a comparison of the floristics of Tasmanian peatlands with those of the northern hemisphere, as they have evolved isolated from each other, with few vascular peatland species in common. A comparison of geomorphic types, however, may provide insights into comparative environmental relationships. This chapter compares the distribution, characteristics and ecology of Tasmanian *Sphagnum* peatlands with *Sphagnum* mires located in the northern hemisphere.

2.2 Methodology

2.2.1 Field methods

For the purposes of this survey, a *Sphagnum* peatland was taken to be any peatland 1000 m² or more in size, where *Sphagnum* moss covered no less than 30% of the mire surface. In addition, any *Sphagnum* deposits in unusual locations, regardless of size, were recorded (e.g. sinkholes, rainforest floors). The various geomorphic types of *Sphagnum* mires which occur in Tasmania and are discussed in this chapter are raised bog, linear mire, lakeside/streamside mires, valley mires, pillow mires, shelf peatlands, kettlehole/sinkhole and snowpatch mires. With the exception of raised bogs, all *Sphagnum* mires are minerotrophic.

All available colour aerial photographs at 1:20,000 scale were examined to identify sites likely to have *Sphagnum* peatlands. Where colour aerial photographs were not available, black and white aerial photographs were used. The reliability of colour aerial photographs was much greater than that of black and white photographs. *Sphagnum* peatlands can be discerned by orange-brown to orange-yellow shades on colour photographs. When using black and white photographs, possible *Sphagnum* sites can only be inferred from geographic setting and identification of vascular species normally associated with *Sphagnum*. *Sphagnum* sites previously identified by the Tasmanian Forestry Commission, the Tasmanian Herbarium and the Department of Parks, Wildlife and Heritage were located. Potential sites identified by all these methods (with some inaccessible exceptions) were visited for ground-truthing.

Data from 137 sites were collected. At each site at least one 100 m² quadrat was sampled. The quadrats were located away from the margins of the bog to minimise edge effects (Godwin and Conway 1939) and were subjectively located in an area that visually appeared representative of the vegetation of the bog. Floristic data are presented in chapter 3.

Three peat depth measurements were taken from the base of hummocks within each quadrat. As it became evident during the course of the survey that the micro-topography within the bogs varied, three measurements of the height of hummocks above hollows were also taken. Surface peat was collected from each quadrat and measured in the field for pH using an Inoculo CSIRO colorimetric test kit. Measuring of pH ceased after 66 quadrats because of the poor resolution of the technique. At all sites investigated the watertable was observed to be at or near the surface. The area and depth (using a peat probe) of 10 *Sphagnum* pillows were measured.

The vast majority of sites are located in areas remote from climatic stations. Estimates of the broad climatic parameters of each site were obtained using BIOCLIM, which interpolates estimates of climatic values from known stations as functions of latitude, longitude and elevation (Busby 1986). There are some limitations in using the climatic parameters generated by BIOCLIM. No account is taken of topographic position or

local orographic influences on precipitation patterns in the climate analysis (Busby 1986). It is, however, the best available method for estimating temperature and precipitation at remote sites.

The nutrient composition of the peats (total N, P, K and organic content) was determined for a subset of the data (26 quadrats), based on TWINSPAN classification of floristic data (chapter 3). Total concentrations were used to avoid the assumptions associated with using available concentrations (Crane 1978). Percentage organic matter was indicated by weight loss on ignition (550°C). Total nitrogen was determined by Kjeldahl digestion. Analysis of phosphorus was by the vanado-molybdate method on a digest of 1 g of sample with HNO₃/HClO₄. Potassium was determined by flame emission measurement of the above digest on an EEL flame photometer.

2.2.2 Data analyses

The various geomorphic types were tested against the environmental variables and site characteristics. As the data were not normally distributed non-parametric statistics were used (Sokal and Rohlf 1969). Kruskal-Wallis one way analysis of variance was used to test the relationships between geomorphic types and climatic parameters, altitude and peat depths (results presented have been adjusted for ties). When there was a relationship between types and an environmental parameter, differences between each classificatory group were considered significant when there was a difference of 2.0 units in Z value (McPherson 1990). Chi-squared tests were used on geologic data.

Comparative global data are presented. Temperature and precipitation profiles for mire types in Canada and Europe (Moore and Bellamy 1974) were plotted against BIOCLIM profiles for Tasmanian *Sphagnum* mires. Chemical analyses of European peats (Waughman 1980) were plotted against those available for Tasmanian *Sphagnum* mires.

2.3 Description of Tasmanian *Sphagnum* peatlands

2.3.1 Distribution

The largest area of *Sphagnum* peatlands in Tasmania occurs on the Central Plateau and in the Mersey River catchment (fig. 2.1). There are occasional *Sphagnum* mires in the south-east, north-east and north-west. Although small patches of *Sphagnum cristatum* have been observed from sea level on the south coast to 1200 m in the Arthur Range,

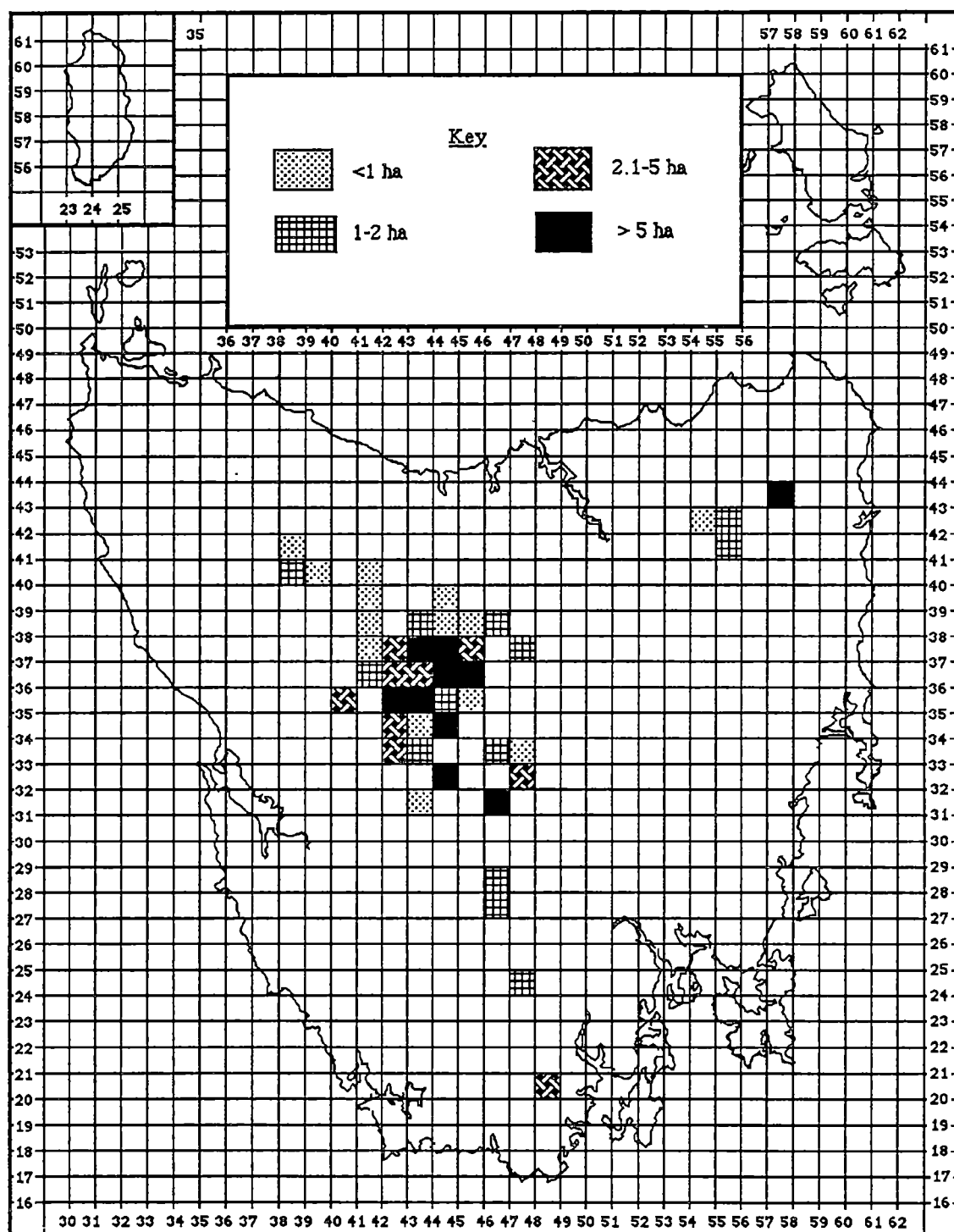


Fig. 2.1 Distribution of surveyed *Sphagnum* peatlands.

large peatlands dominated by this species are largely absent from the south-west region of the State. This absence of large *Sphagnum* mires from the south-west of Tasmania is of some interest, given that there appears to be ample climatic and topographic opportunity for their development. This region experiences one of the highest rainfalls in Australia (Bureau of Meteorology 1986). The south-west is dominated by acidic skeletal organic soils typically underlain by Pre-Cambrian metamorphic rocks, such as quartzite (Brown *et al.* 1982).

2.3.2 Species composition

With the exception of *Sphagnum* and possibly *Richea gunnii*, species found in Tasmanian *Sphagnum* peatlands are not confined to this vegetation type. Twenty-one per cent of species described as dominant species in the Tasmanian treeless high altitude vegetation (Kirkpatrick 1983), 24.6% of Tasmanian rainforest species (Jarman *et al.* 1984), 27.3% of species listed as typical of Tasmanian buttongrass moorland (Jarman *et al.* 1988) and 50.8% of species with more than 20% frequency in Tasmanian grasslands and grassy woodlands (Kirkpatrick *et al.* 1988), occur in *Sphagnum* peatland. Of the 183 species recorded in Tasmanian *Sphagnum* mires, 26.8% are endemics (appendix 1).

2.3.3 Morphology of the Tasmanian *Sphagnum* mires

Where *Sphagnum* moss is dominant it demonstrates four distinct surface morphologies. In floating mires the moss surface is smooth. This mire type is uncommon in Tasmania. It occurs when *Sphagnum* forms a floating mat over a quaking bog of liquid peat in sinkholes. The best examples of this type are near Mole Creek.

Where *Sphagnum* mires form under rainforest there is often a development of large *Sphagnum* pillows, both on flat and sloping terrain. These pillows are characteristic of relatively pure moss beds, with the pillows acting as a propagation medium for seedlings of rainforest species. The size of the pillows is closely correlated with the depth of peat ($r=0.97$, $p<0.001$, fig. 2.2). The boundaries of moss mounds were observed to merge at a rainforest-*Sphagnum* site at the Little Fisher River, suggesting that smaller pillows can coalesce over time. Occasionally, small *Sphagnum* pillows are found on sloping ground (up to 45° slope), usually below cliff-lines and cave overhangs with constant seepage of moisture. Similar 'hanging' *Sphagnum* bogs have been described from New Zealand (Campbell 1983).

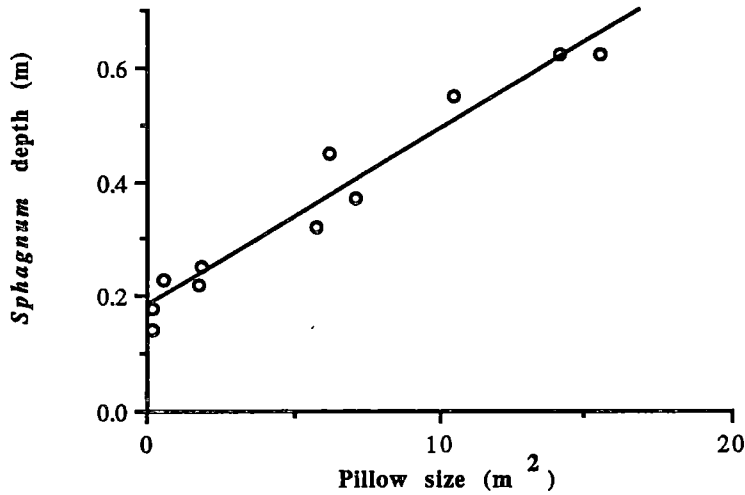


Fig. 2.2 Size and depth of *Sphagnum* pillows at the Little Fisher River.

The third type consists of strings of hummocks, running in parallel series (plate 1). These linear mires are an unusual mire type, also described from New South Wales (Young 1983). They seem to be best developed on sloping ground. They are similar in appearance to the string bogs of the northern hemisphere (Boatman *et al.* 1981, Foster and Fritz 1987), although the hollows do not generally contain water, and the formation is confined to geographically small areas. The most pronounced development of the type occurs on the Central Plateau.

The fourth and most common type consists of a jumble of hummocks and hollows (plate 1). The hollows may be dominated by moss or by Cyperaceae and Restionaceae. The mounds are formed largely of *Sphagnum*, but may have shrubs protruding above the moss.

The most common geomorphic type of *Sphagnum* peatland in Tasmania is the lakeside/streamside mire (37% of sites), with valley mires (31.4%) and shelf mires (23.4%) also being common (appendix 2). Unlike in the northern hemisphere, true raised or ombrotrophic *Sphagnum* bogs are rare, with few examples recorded, at the Walls of Jerusalem and the Eldon Range. These are similar to the ombrotrophic bogs described for the northern hemisphere (Damman 1977, Foster and Glaser 1985). The snowpatch *Sphagnum* mire is another uncommon mire type, occurring as moss mats on the lee side of ridges in the nival zone.

(a)



(b)

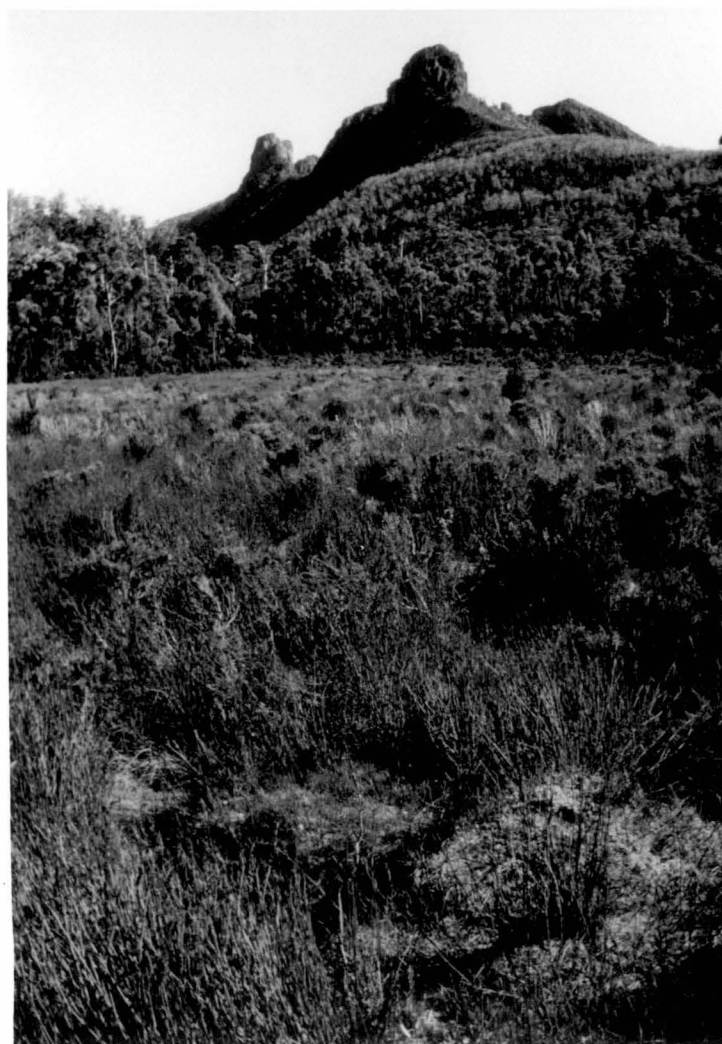


Plate 1. Surface morphology of Tasmanian *Sphagnum* mires
(a) strings of parallel hummocks, (b) mosaic of hummocks and hollows.

Patterned fens (string bogs or aapamires) dominated by *Sphagnum* are restricted in Tasmania to the Central Plateau. String bogs are rare in Tasmanian peatlands generally, with only occasional, poorly developed examples in mires dominated by cushion plants (Kirkpatrick and Gibson 1984) or alpine heath (Whinam 1985). All the Tasmanian patterned fens are limited in extent, with smaller strings and over smaller areas than the expanses described for the northern hemisphere (Boatman and Tomlinson 1977, Glaser *et al.* 1981, Foster *et al.* 1988).

Peat depths in *Sphagnum* mires varied from 0.17 m to more than 3.10 m (note that some peat measurements of 2.5-2.6 m are minimum depths, because that was the length of the peat probe most commonly used) (appendix 2). The height of hummocks varied considerably between sites. At sites dominated by floating mats of *Sphagnum* moss there were no hummocks. At other sites the height of hummocks varied from 0.10 m to a maximum of 1.33 m (appendix 2).

2.3.4 Geology

Sphagnum peatlands occur over a wide range of country rock including limestone, granodiorite and basalt (appendix 2). However, *Sphagnum* peatlands are most commonly found on unconsolidated sediments (30.7%) and dolerite (26.3%). There was only one recorded occurrence of *Sphagnum* on limestone (a sinkhole). *Sphagnum* was not observed occurring directly on quartzite during this survey. Wherever *Sphagnum* was observed in a location where quartzite was the dominant country rock, the moss was usually found growing on streamside alluvium, and only covered small areas.

2.4 The geomorphic context of Tasmanian *Sphagnum* mires

A considerable area of Tasmania has been subject to glaciation in the past. Comparisons of the locations of *Sphagnum* mires (fig. 2.1) with the boundaries of glaciation (fig. 2.3) show a high degree of correlation. Tasmania is thought to have been ice free for the past 10 000 years (Kiernan 1985). Both erosion and deposition in glacial landscapes lead to impeded drainage, which creates many opportunities for *Sphagnum* mire formation.

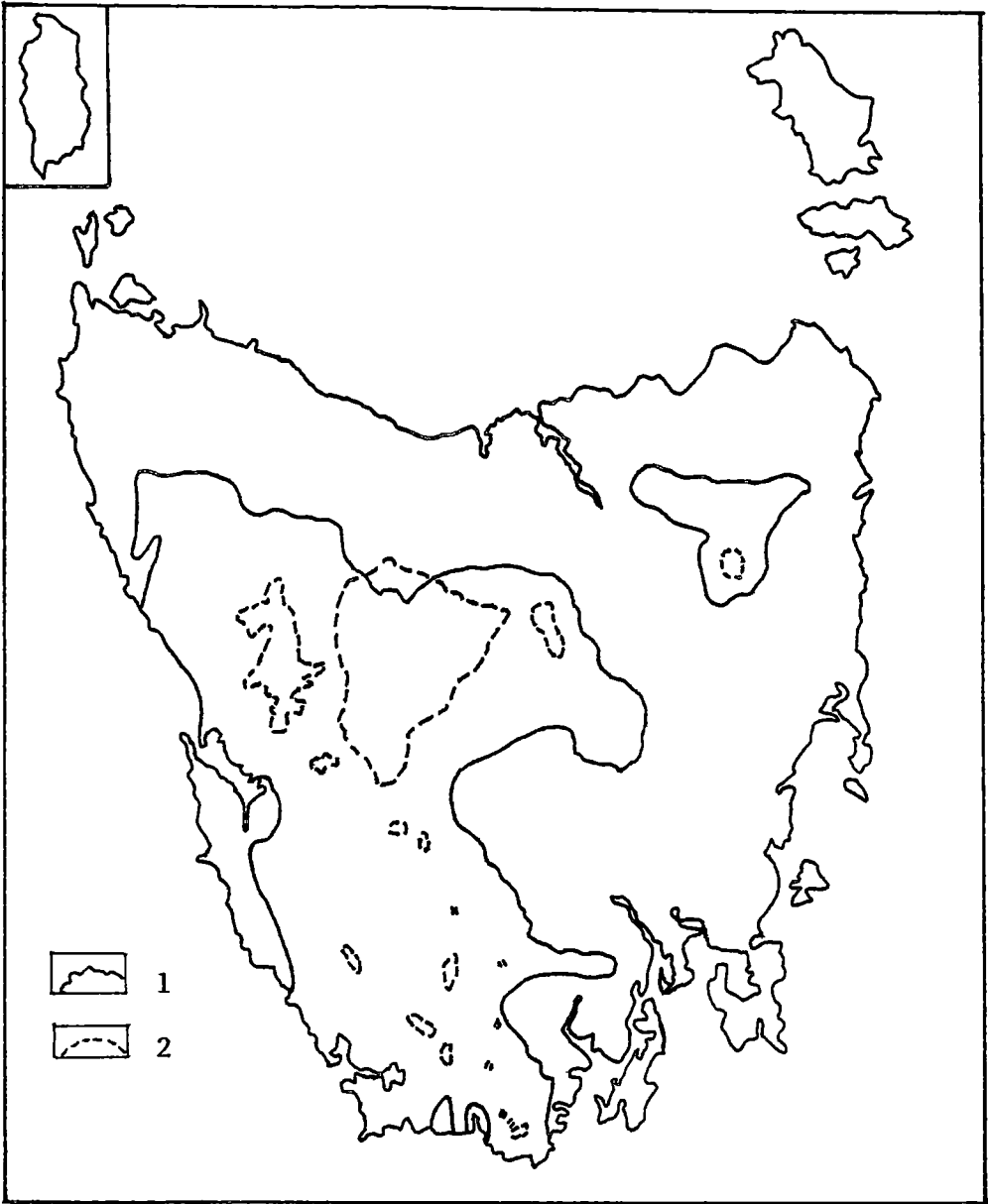


Fig. 2.3 Limits of Pleistocene ice in Tasmania (1) according to Lewis; (2) according to Banks (after Kiernan 1985).

Edaphic conditions in the more elevated eroded areas are not as suitable for mire formation as they are in the many hollows created by the uneven deposition of moraine and the melting of large masses of ice within the moraine. The kettle holes and moraine-dammed valleys of the depositional zone contain a large proportion of the area of Tasmanian *Sphagnum* peatlands. Glaciofluvial outwash deposits also create numerous situations in which drainage is slowed or blocked, and in which *Sphagnum* mires have formed.

Conditions suitable for *Sphagnum* mires can be created by wind deflation and, in locations where drainage is impeded, by sediment deposition. Peat can be locally removed by fast or slow oxidation (Pemberton 1986), resulting in altered drainage conditions, thereby creating an environment suitable for *Sphagnum* growth.

Horizontally-bedded sandstone shelves occur in the moist montane zone throughout much of Tasmania. A slight dip or a history of deflation is often sufficient to allow the establishment of shelf peatlands. *Sphagnum* mires are localised along the margins of many lakes and streams on the Central Plateau, where moisture is constantly present, forming lakeside/streamside mires. In some cases mires run linearly alongside the levee banks of streams. Valley mires occur on the floors of valleys. These mires receive water and nutrients from the surrounding slopes.

2.5 Climatic Parameters

The climate of Tasmania is generally considered to be maritime (Gentili 1972), with distinct climatic zones occurring longitudinally across the State. The west and south-west region of the island experiences some of the highest rainfalls in Australia, while the east and south-east coast has rainfall amounts and patterns akin to the adjacent eastern mainland (Bureau of Meteorology 1986). Precipitation patterns for Tasmania are shown in fig. 2.4.

While *Sphagnum* moss does occur at all altitudes, the altitudinal range of *Sphagnum* peatlands is 360 metres to 1360 metres a.s.l., with only seven sites below 600 metres (appendix 2). The estimated mean annual temperature at Tasmanian *Sphagnum* peatland sites is between 5.7° and 8.6°C; the mean minimum temperature of the coldest month ranges from -1.6° to 1.1°C; the mean maximum temperature of the

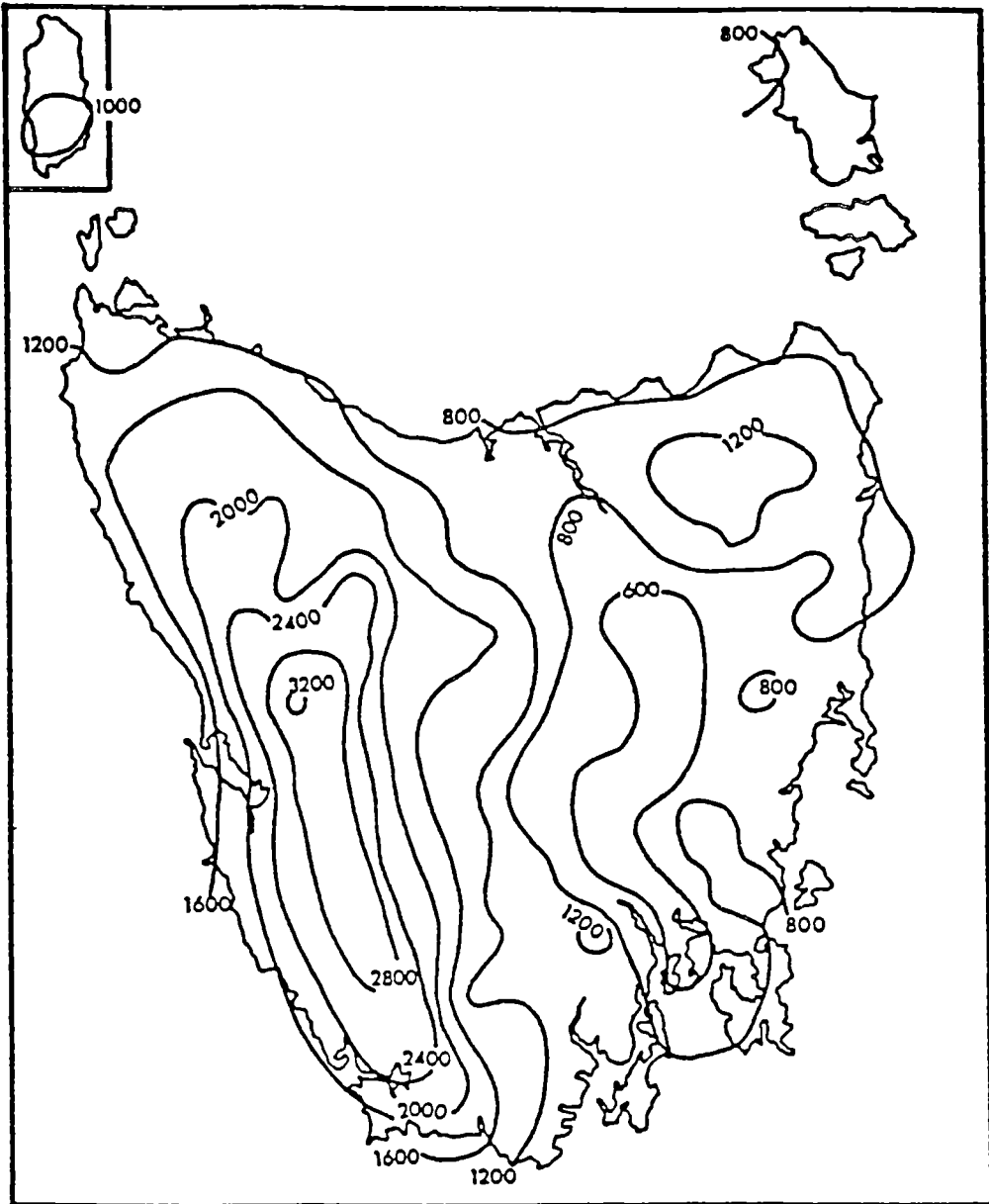


Fig. 2.4 Mean annual rainfall of Tasmania (mm). Reproduced from the Tasmanian Year Book (1986).

warmest month ranges from 16.2° to 19.5°C. Mean annual precipitation varies between 1547 and 2028 mm. Mean precipitation for the wettest month ranges between 194 and 201 mm and mean precipitation for the driest month ranges between 68 and 101 mm.

S. cristatum, like most *Sphagnum* species, cannot tolerate dry conditions (Costin 1954, Campbell 1983). Sites in relatively drier areas of Tasmania tend to be located alongside watercourses, receiving waterflow from the surrounding countryside. Pan evaporation rates (Nunez, unpubl. data) suggest that even in the driest month the Tasmanian *Sphagnum* sites are probably not subjected to a significant moisture deficit. The lower maximum temperatures and lower evaporation rates at the altitudes at which the majority of *Sphagnum* peatlands occur promote the constant availability of moisture postulated to be necessary for the survival of *Sphagnum* mires (Moore and Bellamy 1974, Backeus 1988).

2.6 Environmental relationships of geomorphic types of *Sphagnum* mire

The distribution of geomorphic types was most strongly associated with peat depth, rock type and precipitation of the wettest month (fig. 2.5).

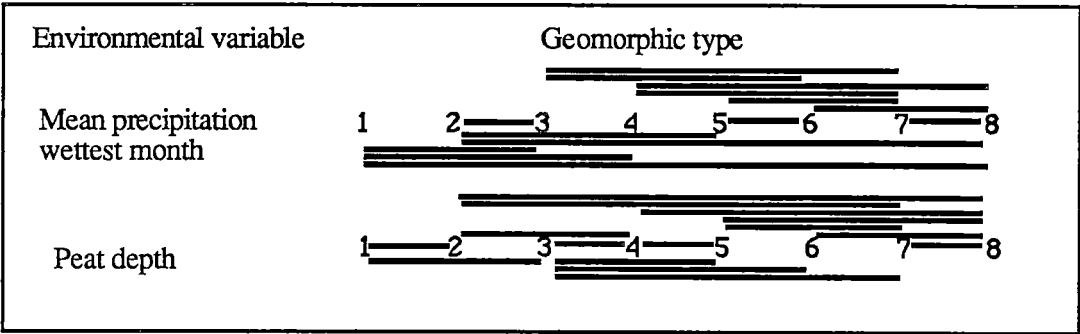


Fig. 2.5 Dissimilarities between geomorphic types of statistically significant ($p<0.01$) environmental variables. Geomorphic types are:- 1=raised bog, 2=linear, 3=lakeside/streamside, 4=valley, 5=pillow, 6=shelf, 7=kettle hole/sinkhole, and 8=snowpatch. Lines are drawn between (above and below) geomorphic types which are significantly different (Z values > 2.0 units) from each other.

Geomorphic type was correlated with peat depth ($H=20.08$, $p<0.01$). The main differences are between the snowpatch peatlands which tend to be on relatively shallow peat (mean 0.21 m) compared to the pillow mires which have greater peat depths (mean 0.87 m). Also, peat depths for shelf mires tend to be shallower (mean 1.05 m) than sinkholes/kettleholes (mean 2.10 m).

Several geomorphic types were preferentially located on specific types of rock, with lakeside/streamside *Sphagnum* peatlands being preferentially located on granite or granodiorite ($\chi^2=15.8$, $p<0.001$) and valley mires being preferentially located on unconsolidated deposits (alluvium, marsh and till) ($\chi^2=6.7$, $p<0.05$). However, these results may be partly due to geographic coincidence, with most unconsolidated deposits being located in valleys.

The only climatic parameter distinguishing the geomorphic types is mean precipitation of the wettest month ($H=16.98$, $p<0.05$). The major differences are between the relatively wetter rainfalls of the snowpatch type compared with the relatively drier linear and kettle hole/sinkhole types (fig. 2.6).

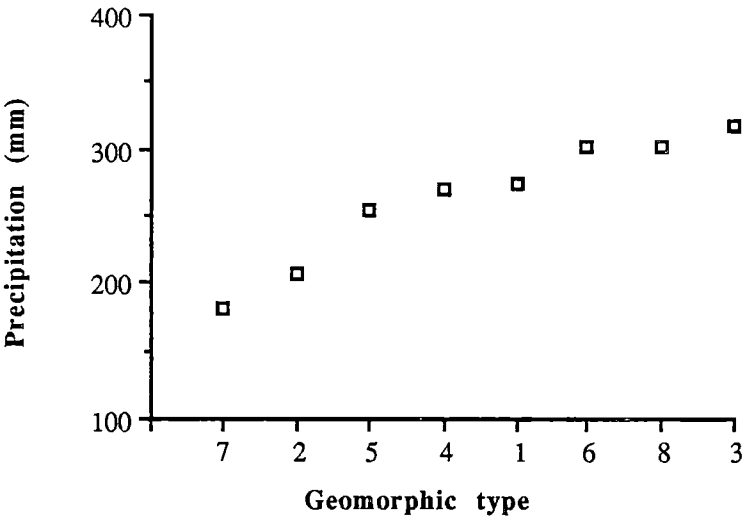


Fig. 2.6 Mean precipitation of the wettest month for the different geomorphic types. Geomorphic types are:- 1=raised bog, 2=linear, 3=lakeside/streamside, 4=valley, 5=pillow, 6=shelf, 7=kettle hole/sinkhole, and 8=snowpatch.

The results of nutrient analyses on a subset of Tasmanian *Sphagnum* peatlands are shown in table 2.1.

Table 2.1 Nutrient data (N, P, K and organic matter) from a subset of 26 quadrats. Geomorphic types are:- 1=raised bog, 2=linear, 3=lakeside/streamside, 4=valley, 5=pillow, 6=shelf, 7=kettle hole/sinkhole, and 8=snowpatch. n.a.=not available.

N (%)	P ($\mu\text{g g}^{-1}$)	K ($\mu\text{g g}^{-1}$)	organic matter (%)	Geomorphic type
0.5	70	380	20	4
0.6	770	11000	25	7
0.8	950	1100	30	6
0.9	1200	9900	39	4
1.0	350	3700	49	4
1.2	260	7900	49	8
1.3	240	5800	54	5
1.4	750	600	94	4
1.4	900	770	76	4
1.5	520	130	91	4
1.6	780	1200	94	7
1.6	400	91	98	1
1.7	490	1000	94	9
1.8	970	460	80	1
1.8	1200	710	98	4
1.8	810	1400	n.a.	7
2.0	980	650	92	7
2.0	360	120	93	5
2.0	550	590	94	4
2.1	770	330	92	7
2.2	520	290	97	7
2.2	950	470	90	4
2.3	900	490	94	8
2.3	720	440	90	1
2.4	870	330	90	7
2.7	2100	580	89	6

2.7 Australasian floristic and structural affinities

In mainland Australia, the closest vegetation affinities to the Tasmanian *Sphagnum* mires lie with the sub-alpine areas of Victoria (Carr and Turner 1959a, Ashton and Hargreaves 1983) and New South Wales (Costin 1954). The most prominent plants of the *Sphagnum* moss beds in south-eastern Australia, including Tasmania, belong to the families Cyperaceae, Epacridaceae, Juncaceae, Liliaceae, Myrtaceae, Poaceae, and Restionaceae (Costin 1954, Carr and Turner 1959a, Farrell and Ashton 1973, Ashton and Hargreaves 1983, Whinam *et al.* 1989).

At Echo Flat, Lake Mountain, the bog heath is described as an open heath of *Epacris paludosa* patterned with hummocks of *S. cristatum* and *Astelia alpina* (Ashton and Hargreaves 1983). Hollows are occupied by *S. subsecundum*, a species tolerant of submergence. This is in contrast to the sedge swards of *Carex gaudichaudiana*, typical of the single species *Sphagnum* bogs common in drier or colder parts of Victoria (Ashton and Hargreaves 1983). Occasional hummocks of *S. cristatum* occur along drainage areas on the Bennison High Plains, Victoria (Farrell and Ashton 1973). These 30-60 cm high hummocks are interspersed with gravel and mud-filled hollows colonised by *Carex gaudichaudiana* (Farrell and Ashton 1973). Pure mounds of *Sphagnum* are rare, with the mounds mostly being supported by the shoots of the bog-heath shrubs.

Two floristic associations with *Sphagnum cristatum* have been described for the Monaro Region of New South Wales (Costin 1954). One is the *Carex gaudichaudiana*-*S. cristatum* alliance, a physiographically controlled groundwater community, which occurs independent of rock type in strongly acid situations in the alpine and subalpine tracts of the Monaro (Costin 1954). The main families represented in this valley bog alliance are Poaceae, Cyperaceae, Restionaceae and Juncaceae, with a total of 31 species and varieties recorded. An *Epacris paludosa*-*S. cristatum* alliance occurring on a raised bog is described as a physiographic climax in the Monaro Region. Its occurrence is favoured by uneven terrain, and is best

developed in the alpine and subalpine tracts of the Monaro Region, but is found in montane environments under favourable moisture conditions (Costin 1954). The greater number of species (77 recorded) is reflected in the greater number of families represented - Gramineae, Cyperaceae, Restionaceae, Juncaceae, Epacridaceae, Umbelliferae and Compositae.

The Tasmanian *Sphagnum* peatlands also seem to be floristically and structurally similar to the *Sphagnum* peatlands of New Zealand. The most common peatland type in New Zealand is the shrub mire, with *Leptospermum scoparium*, *Gleichenia dicarpa*, *Empodisma minus* and *Sphagnum cristatum* being the major species with few examples of pure *Sphagnum* bogs (Knox 1969, Campbell 1983). In New Zealand *Empodisma minus* is the most frequently encountered peat former (Davoren 1978). The recorded pH of New Zealand mires varies from 3.0 to 4.5, and these mires tend to occur in nutrient poor situations (Knox 1969). The Tasmanian rainforest-*Sphagnum* mires appear to be similar to the New Zealand 'bog forests' (Campbell 1983). In New Zealand the overstorey is dominated by *Dacrydium* or *Nothofagus*, with dense mats of *Sphagnum*, which can combine with other mosses and lichens to form hummocks (Campbell 1983).

2.8 Comparisons with global data

2.8.1 Climate

Data for mire types in Canada and Europe vary from the temperature and precipitation profiles of *Sphagnum* peatlands in Tasmania (fig. 2.7). While precipitation at Tasmanian *Sphagnum* mires is generally greater than that shown for either European or Canadian mires (Moore and Bellamy 1974), the Tasmanian temperatures are all clustered at the warmer end of the temperature range recorded from European and Canadian mires.

A map depicting "radiational index of dryness" on a global scale has been produced (Budyko 1958). A ratio is calculated by relating the net radiation available to evaporate water vapour from a wet surface to the heat required to evaporate the mean annual precipitation. It has a value of less than unity in humid areas, greater than unity in dry areas (Lockwood 1974). Using Moore and Bellamy's map of mire locations as a guide

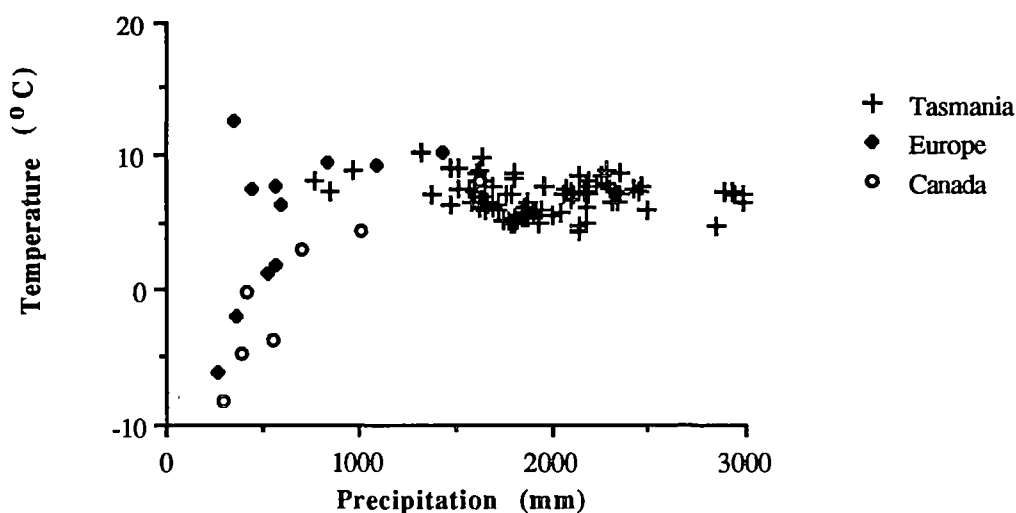


Fig. 2.7 Walter Klimadiagrams for Europe and Canada (from Moore and Bellamy 1974) and temperature and precipitation profiles for Tasmania. Note: it is assumed that the mean annual rainfall in Moore and Bellamy (1974, fig. 2.5) should read 'mm' not 'cm'.

(fig. 1.1), the radiation index of dryness values for most areas depicted in the northern hemisphere is most commonly between 0.33 and 0.66 (Budyko 1958). In contrast, the Tasmanian *Sphagnum* mires have values of between 0.50 to 1.4, with most values being greater than 0.75 (Nunez 1978). Thus, while precipitation is generally greater in Tasmanian *Sphagnum* mires than northern hemisphere mires (fig. 2.7), the warmer temperatures result in less effective precipitation.

The generally drier conditions of Tasmanian sites compared to northern hemisphere sites probably explain the limited number of ombrotrophic Tasmanian *Sphagnum* mires. The only two large (>0.5 ha) ombrotrophic *Sphagnum* mires recorded (at the Walls of Jerusalem and the Eldon Range) have radiation index of dryness values at the lower end of the range recorded (approximately 0.50 and 0.75).

2.8.2 Nutrients

There has been considerable discussion in the literature as to which chemical elements best reflect the variations in mires. Some studies have shown that the total contents of N, Ca and Fe in peats show a similar trend to that of pH - in general, an increase in nutrient content from bog to fen (Wells 1981, Sjors 1983). However, a combination of the above chemical elements with the metallic cations (K, Mg, Ca, Fe, Al, etc.) is likely to be important for the supply of inorganic plant nutrients to mires (Malmer 1986).

The amount of total N in *Sphagnum* peats can vary considerably. For example, total N varies from 0.8% to 2.7% for Newfoundland (Wells 1981). Total N varies in Alaskan peatlands between 0.9% and 1.6% of dry weight (Murray et al. 1989). Total N from Tasmanian *Sphagnum* peatlands varies between 0.5% to 2.4% of dry weight (table 2.1). This is higher than total N values recorded from peats with sedgeland vegetation on the west coast of Tasmania of between 0.4% and 0.5% of dry weight (Kirkpatrick 1984).

The percentage of organic matter in the Tasmanian *Sphagnum* peats is variable, but generally quite high (20-98%, table 2.1), and consistent with global data (Clymo 1983). Results of chemical analysis of Tasmanian *Sphagnum* peats show a correlation between total N and percentage organic matter ($r=0.844$, $p<0.001$). The Tasmanian *Sphagnum* peats generally have a considerably higher organic content than sedgeland peats on the west coast of Tasmania, which range between 21.1% and 24.3% (Kirkpatrick 1984) and Tasmanian peats generally where organic content can reach 50-70% (Pemberton, unpubl. data). Thus, in European terms, Tasmanian peatlands generally are minerotrophic fens.

While total N in Tasmanian *Sphagnum* peatlands generally lies within the range of total N recorded in European peatlands, total K covers a greater range than that recorded for European peatlands (Waughman 1980, Clymo 1983, fig. 2.8). The great variation in K (0.09 to 11.0 mg g⁻¹) in Tasmanian *Sphagnum* peats can largely be explained by the fact that K is present in the form of a weatherable mineral, which is confirmed by the negative correlation between K and percentage organic matter ($r=-0.675$, $p<0.001$). However, total K from Tasmanian west coast sedgeland peats does not show the same variability (0.43 to 1.80 mg g⁻¹, Kirkpatrick 1984).

Total P for the Tasmanian *Sphagnum* peatlands varies considerably (between 70 and 2100 mg g⁻¹, table 2.1). The figures are markedly higher than West Coast sedgeland peats which have 27 to 41 mg g⁻¹ (Kirkpatrick 1984). Phosphate figures for Tasmanian *Sphagnum* peatlands (214 to 6434 mg g⁻¹, converted from P, Jackson 1958, table 2.1), are generally higher than figures available for Europe (fig. 2.9), but this may be due in part to differences in extraction methods (Waughman 1980) and possible discrepancies in phosphate fixation capacity (Jackson 1958).

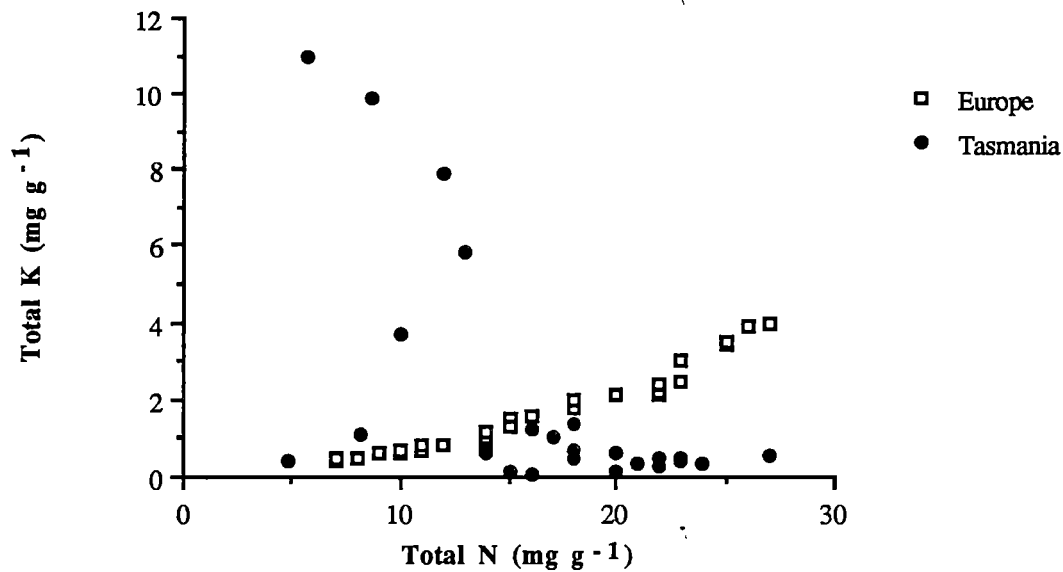


Fig. 2.8 Total K (mg g⁻¹) and total N (mg g⁻¹) for Tasmanian *Sphagnum* peatlands and European mires. European data from Waughman (1980).

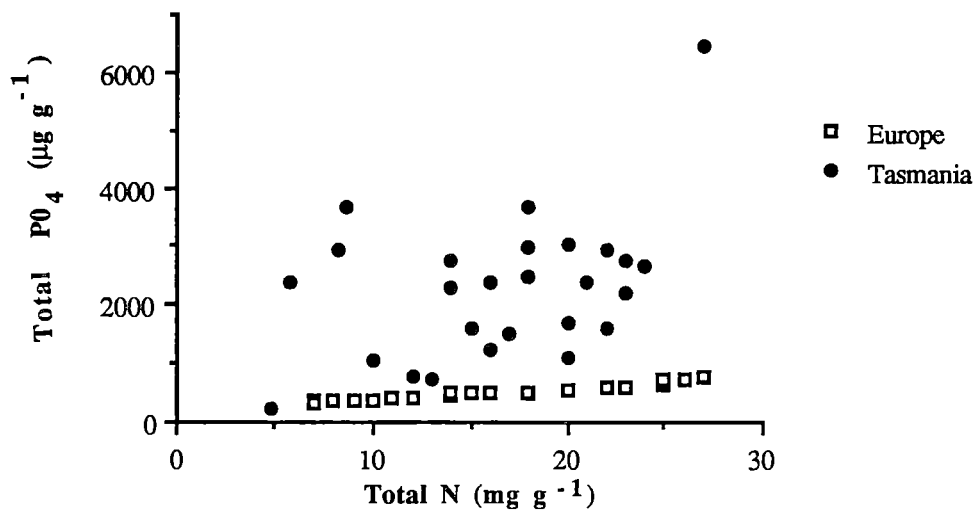


Fig. 2.9 Total P₀₄ (µg g⁻¹) and total N (mg g⁻¹) for Tasmanian *Sphagnum* peatlands and European mires. European data from Waughman (1980).

It has been suggested (Heinselman 1970) that pH alone distinguishes ombrotrophic waters from other types (Heinselman 1970). The acidity of a peatland site is also thought to represent differences in chemical and nutrient status. The lower acidity and higher base status of the minerotrophic waters of fens promotes microbial activity, recycling of nutrients and increased availability of P and N, in contrast to ombrotrophic bogs (Heinselman 1970). Northern hemisphere fens are characterised by pH of greater than 5.5, while bogs, at least during the summer, are below 4 (Heinselman 1970, Moore and Bellamy 1974, Malmer 1986). Extremely rich fen sites are characterised by a pH of greater than 6.8 (Moore and Bellamy 1974) to 7.0 (Malmer 1986), with some sites attaining values of 7.9 (Slack *et al.* 1980). Poor fens, or transitional fens, tend to have a pH of around 4.1 to 6.0 (Heinselman 1970, Kenkel 1988). The pH of surface peats from comparable mires in Victoria ranges between 4.5 and 5.6 (Farrell and Ashton 1973, Ashton and Hargreaves 1983), while comparable mires on the Monaro Plateau N.S.W vary between 4.1 and 5.0 (Costin 1954). Thus, on the basis of global data, the pH of Tasmanian *Sphagnum* peatlands (3.5-4.5 (6.0)) lies within the range commonly considered indicative of bogs or poor fens. The range of pH recorded in Tasmanian *Sphagnum* peatlands lies within the recorded range of other peatland vegetation communities in Tasmania. Buttongrass (*Gymnoschoenus sphaerocephalus*) sedgeland most commonly range from 3.5 to 4.5 (Jarman *et al.* 1988) with heathy sedgeland ranging from 4.3 to 4.4 (Kirkpatrick 1984), organic soils of the Central Plateau being <5 (Pemberton 1986) and the fibrous peats of the south-west generally ranging from 4.2 to 4.7 (Pemberton 1989).

2.8.3 Species richness

Most authors agree that minerotrophic fens support a diverse vegetation while bog vegetation is poor in species (Heinselman 1970). The Tasmanian *Sphagnum* peatlands exhibit a broad range of species diversity (5 to 28 species in 100 m² quadrats, appendix 2). Some sites obviously support a rich vegetation, although comparisons with the northern hemisphere literature are difficult because of the generally smaller size of quadrat used (Clymo and Reddaway 1971, Slack, *et al.* 1980, Kenkel 1988). Glaser *et al.* (1981) record between 11 and 17 vascular species in 100 m² quadrats in Minnesotan *Sphagnum* mires, while vascular species diversity in *Sphagnum* mires in kettleholes in northern Michigan ranges between 23 and 58 species (Vitt and Slack 1975).

2.8.4 Mire complex types

Moore and Bellamy (1974) have classified the mire complex types found throughout Europe into nine major zonal types (with three sub-types). The zones are geographic, passing northwards and northwestwards across Europe, with each zone defining the location of types of tertiary mire complexes. The complex types are :

1. Primary and Secondary Mire Systems of Zone 1 (valley bogs, fens);
2. Tertiary Mire Systems (Hochmoore, raised bog);
3. Tertiary Valley Mires of Zone 2;
4. Tertiary Basin Mires of Zone 3 (karst raised bogs and continental raised bogs, basin bogs);
5. Plateau Domed Mires of Zone 4;
6. Concentric Domed Mires of Zone 5 (Baltic raised bog);
- 7(a). Excentric Mires of Zone 6 (excentric raised bogs);
- 7(b). Ridge Raised Mires Zone 7B (continental ridge raised bogs);
- 8(a). Aapamires (string bogs and patterned fens);
- 8(b). Blanket Mires, Zone 8b (blanket bogs);
- 9(a). Palsamires;
- 9(b). Unconfined Arctic Mires, Zone 9 (thermal blanket mire, in part unconfined muskeg);

Using the above European classification, primary and secondary mire systems of zone 1 and tertiary valley mires of zone 2 are the most commonly found *Sphagnum* mire complexes in Tasmania, with an occasional example of tertiary basin mires of zone 3.

2.8.5 Historical land-use practices

Frenzel (1983) has postulated that the triggering effect for peat accumulation in the northern hemisphere may have been the extensive clearing of forest for agricultural purposes. It has been suggested that burning and clearing of forests from catchment hillslopes altered run-off and sediment load, with consequent impediment of local drainage (Moore 1973, 1975, Frenzel 1983, Tallis 1983, Taylor 1983). The simultaneous increase in accumulation of various types of peat with the earliest indications of clearing by humans for agricultural purposes has been cited as supporting evidence (Frenzel 1983, Taylor 1983). Historical land-use practices in Tasmania do not mirror those of the northern hemisphere. Burning by Tasmanian Aborigines is likely to have had different effects from the long-term clearing of tree

cover for pastoral and agricultural purposes in Europe. These differences are in part due to the fire adapted nature of the vegetation (Bureau of Flora and Fauna 1981) and the fire-stick farming methods of the Aborigines, where fire was used to clear undergrowth, for hunting and to enable regeneration of plant food (Jones 1969).

2.9 Conclusions

The greatest areas of *Sphagnum* mire occur on the Central Plateau and in the Mersey River valley. Glacial activity in both these areas has created a surface topography with areas of impeded drainage suitable for the growth of *Sphagnum*. The many lakes and watercourses of the Central Plateau have created moist edaphic conditions. The uneven deposition of moraine in the Mersey River valley has created areas of impeded drainage. The combination of suitable geomorphology and a climate with relatively high precipitation and low evaporation has created conditions suitable for the growth of *Sphagnum* in these areas. The structure and floristics of the Tasmanian *Sphagnum* mires appear to have close affinities with those of mire types described for mainland Australia and New Zealand.

Tasmanian *Sphagnum* peatlands appear to be confined to the lower range of mire complex types described from the northern hemisphere. The comparatively drier climate may be a factor limiting morphologic expression of Tasmanian *Sphagnum* mires. The limiting effects of these drier conditions on the extent and expression of *Sphagnum* peatlands in Tasmania is supported by their topographic location. Tasmanian *Sphagnum* mires are commonly located besides lakes/streams and in valleys, locations favoured in drier climates to give amplification or stabilisation of the water supply (Clymo 1983).

It appears, therefore, that the distribution of *Sphagnum* peatlands in Tasmania is strongly influenced by climatic and edaphic factors. The nutrient status of the *Sphagnum* peats appears to be considerably higher than Tasmanian peats dominated by other vegetation types. *Sphagnum* peatlands are absent from the nutrient poor south-west of Tasmania, despite ample geomorphic and climatic opportunity.

Unlike in the northern hemisphere, there seems to be no clear distinction between bog and fen in Tasmanian *Sphagnum* mires, although nutrients play a role in determining mire floristics. While the nutrient status of Tasmanian *Sphagnum* peats falls within the global range, *Sphagnum* mires do not generally occupy the poorest end of the nutrient gradient in Tasmania. This is most commonly occupied by buttongrass moorland

(*Gymnoschoenus sphaerocephalus*). However, although the extent and expression of *Sphagnum* peatlands in Tasmania may be limited by climatic and nutrient factors, they have many features in common with *Sphagnum* mires described from other parts of the southern hemisphere and the northern hemisphere.

CHAPTER 3 - VEGETATION OF TASMANIAN *SPHAGNUM* MIRES

3.1 Introduction

Phytosociological methods have been widely used to classify community complexes in mires (Diersson 1979) and to describe mire types (Dobson 1979, Jeglum 1987). In formulating classifications, floristic attributes have often been combined with other attributes of the peatlands, such as nutrient/chemical composition of the peat (Damman 1986, Lewis Smith 1979), or environmental type (Jurkovskaja 1979). Other classifications of the vegetation of peatlands have been based on physiognomy (Sims *et al.* 1982).

In some cases, phytosociological units in peatlands have been found to be an indicator of the nutrient status of the mire, with particular species or suites of species being associated with a particular nutrient status and acidity. For example, in northern Minnesota, contrasting assemblages of plant species are associated with spring-fen channels and poor fen *Sphagnum* lawns (Gorham *et al.* 1987).

The results from research in the northern hemisphere suggest that many geographic, environmental, climatic and nutrient characteristics influence the species composition of *Sphagnum* peatlands. Hydrology is cited as a critical parameter (Ivanov 1981), with many peatland vegetation types being apparently related to drainage patterns (Heinselman 1970).

In north-west European mires, floristic gradients within and between mires have been related to:

- ombrotrophy and minerotrophy
- distance from the sea
- oscillations in the water level
- origin and flow of water
- supply of minerals (Malmer 1986).

In this chapter a floristic typology of Tasmanian *Sphagnum* peatlands is developed, and an attempt is made to determine the environmental variables that influence the distribution of the component plant communities.

3.2 Methods

The methods for site selection are detailed in chapter 2. The vegetation details recorded from each site included species cover abundance in 100 m² quadrats (determined as the minimal area) on the Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974).

Data on several environmental variables were collected. These included peat depth (chapter 2), altitude, height of *Sphagnum* hummocks (chapter 2), geomorphic type (chapter 2) and rock type. The ability to regenerate after fire (Kirkpatrick 1984, Kirkpatrick and Dickinson 1984, Jarman *et al.* 1988, Kirkpatrick pers. comm.), was scored on a one to three scale for all species for which data were available in the order vegetative recovery, seed recovery, neither seed nor vegetative recovery (appendix 1). The total scores for each quadrat were divided by the number of species per quadrat for which fire recovery data are available and multiplied by 100. Climatic parameters were generated using BIOCLIM (Busby 1986, see methods chapter 2). Peat samples from a subset of 26 sites were analysed for organic content, N, P and K (see methods, chapter 2).

3.2.1 Data analysis

The polythetic divisive computer program TWINSpan (Hill 1979) was used to obtain an initial sorting of quadrats and species. Geophytes were excluded from the analyses. Due to problems of identification at species level, particularly with infertile monocotyledons, some taxa were used in the analyses at genus level. Species presence/absence data and species cover abundance data were analysed separately. As the inclusion of species cover abundance appeared to make little difference to the classification (possibly as most species had <5% cover), only the results from the species presence/absence data are presented.

Problems identified with detrended correspondence analysis (DCA) (Hill and Gauch 1980) concern the lower order axes, with the third axis generally exhibiting a curvilinear relationship to a combination of the first two axes (M.J. Brown, pers. comm.). Whilst DCA and TWINSpan are both based on reciprocal averaging, the classification produced by TWINSpan is based on the first two axes and natural breaks in the data (M.J. Brown, pers. comm.).

The TWINSpan groups were tested against the environmental variables and site characteristics. As the data were not normally distributed non-parametric statistics were used (Sokal and Rohlf 1969). Kruskal-Wallis one-way analysis of variance was used to test the relationships between TWINSpan groups and species richness, peat depth, altitude, precipitation and temperature data, percentage of rainforest species in quadrats, and height of hummocks. Results were adjusted for ties. When there was a relationship between typology and an environmental parameter, differences between each classificatory group were considered significant if there was a difference of 2.0 or more units of Z value (McPherson 1990). Chi-squared tests were used on geology and typology data. Correlations were tested using Pearson's correlation coefficient.

Computing restrictions prevented an analysis of the complete data set by non-metric multidimensional scaling (NMDS) ordinating technique using KYST (Minchin 1987). A subset of 47 samples, representing a minimum of two quadrats from the ultimate level of division displayed by TWINSpan, was extracted and a matrix of compositional dissimilarities between these sites was calculated, using the Bray-Curtis coefficient. It was used here on species presence-absence in the subset of 47 samples in two, three and four dimensions with ten starts, and using uniform random numbers to provide initial configurations. Studies have shown that NMDS with the Bray-Curtis coefficient is more robust and reliable as a technique of indirect gradient analysis than alternative methods such as DCA and principal components analysis (PCA) (Clymo 1980, Minchin 1987, Jongman *et al.* 1987). However the Bray-Curtis coefficient is sensitive to outliers (Clymo pers. comm.).

The same subset of 26 quadrats from which peat was collected for nutrient analysis was separately ordinated using KYST, in an attempt to determine the possible effects of nutrients.

Because there is no necessary correspondence between variation in environmental variables and the NMDS axes, trend surface analysis was used to describe the direction and strength of the variation in environmental and vegetation variables within the ordination space (Bowman and Minchin 1987, Kirkpatrick *et al.* 1988), for both subsets of data (26 and 47 quadrats). Cosines between vectors were calculated to determine the degree of correspondence in directionality between these variables.

3.3 Results

3.3.1 The communities

The distribution of each of the TWINSPAN groups is shown in appendix 3. A sorted two-way table is shown in table 3.1. The eight ecologically distinct groups selected are perceivable communities spanning a largely continuous gradation, from high altitude (group 1, snowpatch-*Sphagnum* mires) to low altitude sites (group 8, aquatic *Sphagnum* bogs). Species frequency in each of the eight communities is shown in appendix 4. A vascular plant species list is given in appendix 1. A dendrogram shows indicator species at each division (fig. 3.1). The characteristics of the eight communities are summarised below :

1. Snowpatch-*Sphagnum* community

Helichrysum backhousii, *Leptospermum rupestre* and *Podocarpus lawrencei* distinguish the high altitude (1360 metres) snowpatch community (group 1). This group consists of only 2 quadrats, both sheltered below a ridge at Mt Rufus. Both quadrats are less than 100 m². Occasional dwarf and prostrate shrubs protrude from the mossbeds of this group.

2. Sub-alpine coniferous mires

Athrotaxis cupressoides, *Celmisia asteliifolia*, *Epacris serpyllifolia* and *Gleichenia* spp. distinguish the sub-alpine coniferous *Sphagnum* mires (group 2). This community generally occurs in fire-protected sites and is most commonly found on the Central Plateau and in the Walls of Jerusalem National Park. In these locations it often occurs in small mires (10 m² to 500 m²) around lake margins and alongside streams.

This group is easily discerned by the upper stratum of pencil pines over mounds of *Sphagnum*. The cover abundance of *Sphagnum* generally decreases from the margins towards the denser, central grove of the pencil pines. Other studies have found that *Sphagnum* tends to decrease in abundance under dense canopy cover, probably due to variation in shade, litter and moisture (Clapham 1940, Vitt and Slack 1975).

Table 3.1 Sorted two-way table of species by classificatory groups.

	1	2	3	4	5	6	7	8
	11111	11	111	11111111	111	1 1 1111111	1 11	1 11 11
2277	11148	12455555677778888822222	1127800224666666690231111234447889900011113	356778911135633390112222	9334501 33993	5290032593323444		
2356256811395901245802494580245678		180108956160012345613312347866787672447801672973	9133935886700600490129674749591253468377329598557412234					
35 heli back	11	-----1-----	-----	-----	-----	-----	-----	-----
11 celm saxi	11	-----1-----	-----	-----	-----	-----	-----	-----
146 micr tetr	11	-----1-----	-----	-----	-----	-----	-----	-----
36 hier fras	1	-----1-----	-----	-----	-----	-----	-----	-----
18 cyat deal	1	-----1-----	-----	-----	-----	-----	-----	-----
47 micr niph	11	-----1-----	-----	-----	-----	-----	-----	-----
54 ouri inte	1	-----1-----	-----	-----	-----	-----	-----	-----
20 dipl cord	1	-----1-----	-----	-----	-----	-----	-----	-----
67 sene spp.	1	-----1-----	-----	-----	-----	-----	-----	-----
22 dros arct	1	-----1-----	-----	-----	-----	-----	-----	-----
30 euph spp.	1	-----1-----	-----	-----	-----	-----	-----	-----
26 epac serp	1	-----1-----	-----	-----	-----	-----	-----	-----
13 carp alpi	1	-----1-----	-----	-----	-----	-----	-----	-----
188 spha aust	1	-----1-----	-----	-----	-----	-----	-----	-----
53 oreo pumi	1	-----1-----	-----	-----	-----	-----	-----	-----
64 rich spre	1	-----1-----	-----	-----	-----	-----	-----	-----
4 athr cupp	1	-----1-----	-----	-----	-----	-----	-----	-----
63 rich scop	1	-----1-----	-----	-----	-----	-----	-----	-----
142 mono aff.	1	-----1-----	-----	-----	-----	-----	-----	-----
25 epac lanu	1	-----1-----	-----	-----	-----	-----	-----	-----
48 mitr arch	1	-----1-----	-----	-----	-----	-----	-----	-----
32 gent diem	1	-----1-----	-----	-----	-----	-----	-----	-----
164 Cent mono	1	-----1-----	-----	-----	-----	-----	-----	-----
180 rest comp	1	-----1-----	-----	-----	-----	-----	-----	-----
84 cras spp	1	-----1-----	-----	-----	-----	-----	-----	-----
91 pent pumi	1	-----1-----	-----	-----	-----	-----	-----	-----
3 aste alpi	1	-----1-----	-----	-----	-----	-----	-----	-----
17 copr moor	1	-----1-----	-----	-----	-----	-----	-----	-----
141 gnep coli	1	-----1-----	-----	-----	-----	-----	-----	-----
57 plan glab	1	-----1-----	-----	-----	-----	-----	-----	-----
10 celm aste	1	-----1-----	-----	-----	-----	-----	-----	-----
68 spre inca	1	-----1-----	-----	-----	-----	-----	-----	-----
98 poa spp	1	-----1-----	-----	-----	-----	-----	-----	-----
19 deye mont	1	-----1-----	-----	-----	-----	-----	-----	-----
94 care spp	1	-----1-----	-----	-----	-----	-----	-----	-----
71 Erig stel	1	-----1-----	-----	-----	-----	-----	-----	-----
160 dipl lati	1	-----1-----	-----	-----	-----	-----	-----	-----
33 glei spp.	1	-----1-----	-----	-----	-----	-----	-----	-----
158 Gymn spha	1	-----1-----	-----	-----	-----	-----	-----	-----
76 ehrh tasm	1	-----1-----	-----	-----	-----	-----	-----	-----
43 lept rupe	1	-----1-----	-----	-----	-----	-----	-----	-----
79 pult subu	1	-----1-----	-----	-----	-----	-----	-----	-----
167 dich rara	1	-----1-----	-----	-----	-----	-----	-----	-----
82 card spp	1	-----1-----	-----	-----	-----	-----	-----	-----
60 rest aust	1	-----1-----	-----	-----	-----	-----	-----	-----
23 empo minu	1	-----1-----	-----	-----	-----	-----	-----	-----
62 rich gunn	1	-----1-----	-----	-----	-----	-----	-----	-----
46 Mela squa	1	-----1-----	-----	-----	-----	-----	-----	-----
74 baum spp.	1	-----1-----	-----	-----	-----	-----	-----	-----
81 euca rodw	1	-----1-----	-----	-----	-----	-----	-----	-----
163 mitr mont	1	-----1-----	-----	-----	-----	-----	-----	-----
101 Mill dens	1	-----1-----	-----	-----	-----	-----	-----	-----
165 acti moor	1	-----1-----	-----	-----	-----	-----	-----	-----
65 rubu gunn	1	-----1-----	-----	-----	-----	-----	-----	-----

	11111	11	111	11111111	111	1 1 1111111	1 11	1	11	11
2277 11148 12455555677778888822222	1127800224666666690231111234447889900011113	356778911135633390112222	9334501 33993	52900325933233444						
22562568113959012458024945802456781	1801089561600123456133123478667876724478016729739133935886700600490129674749591253468377329598557412234									
128 isol spp	1	1	1	1	1	1	1	1	1	1
189 spha subs	1	1	1	1	1	1	1	1	1	1
137 spha falc	1	1	1	1	1	1	1	1	1	1
80 heli hook	1	1	1	1	1	1	1	1	1	1
122 junc spp	1	1	1	1	1	1	1	1	1	1
42 lept lani	1	1	1	1	1	1	1	1	1	1
120 gera pote	1	1	1	1	1	1	1	1	1	1
39 holc lana	1	1	1	1	1	1	1	1	1	1
14 come retu	1	1	1	1	1	1	1	1	1	1
21 tasm lanc	1	1	1	1	1	1	1	1	1	1
85 gunn cord	1	1	1	1	1	1	1	1	1	1
116 cyat parv	1	1	1	1	1	1	1	1	1	1
175 styl gram	1	1	1	1	1	1	1	1	1	1
153 liss mont	1	1	1	1	1	1	1	1	1	1
171 oxal corn	1	1	1	1	1	1	1	1	1	1
31 gahn gran	1	1	1	1	1	1	1	1	1	1
51 noth cunn	1	1	1	1	1	1	1	1	1	1
115 cyat juni	1	1	1	1	1	1	1	1	1	1
88 hist inci	1	1	1	1	1	1	1	1	1	1
106 phyl aspl	1	1	1	1	1	1	1	1	1	1
126 pitt bico	1	1	1	1	1	1	1	1	1	1
107 blec wats	1	1	1	1	1	1	1	1	1	1
103 troc cunn	1	1	1	1	1	1	1	1	1	1
105 pime drup	1	1	1	1	1	1	1	1	1	1
135 libe pulc	1	1	1	1	1	1	1	1	1	1
104 athe mosc	1	1	1	1	1	1	1	1	1	1
138 telo trun	1	1	1	1	1	1	1	1	1	1
129 gono mont	1	1	1	1	1	1	1	1	1	1
134 lept scop	1	1	1	1	1	1	1	1	1	1
179 lepy tasm	1	1	1	1	1	1	1	1	1	1
119 deye spp	1	1	1	1	1	1	1	1	1	1
155 lyco late	1	1	1	1	1	1	1	1	1	1
156 rume spp	1	1	1	1	1	1	1	1	1	1
168 ehrh dist	1	1	1	1	1	1	1	1	1	1
173 bill long	1	1	1	1	1	1	1	1	1	1
174 tetr tasm	1	1	1	1	1	1	1	1	1	1
176 gono teuc	1	1	1	1	1	1	1	1	1	1
177 viol hede	1	1	1	1	1	1	1	1	1	1
182 carp curv	1	1	1	1	1	1	1	1	1	1
170 leuc coll	1	1	1	1	1	1	1	1	1	1
172 zier arbo	1	1	1	1	1	1	1	1	1	1
178 deye acce	1	1	1	1	1	1	1	1	1	1
12 cent musc	1	1	1	1	1	1	1	1	1	1
90 hypo rugo	1	1	1	1	1	1	1	1	1	1
109 athr sela	1	1	1	1	1	1	1	1	1	1
123 olea myrs	1	1	1	1	1	1	1	1	1	1
145 lept squa	1	1	1	1	1	1	1	1	1	1
147 orit acic	1	1	1	1	1	1	1	1	1	1
166 lepi filii	1	1	1	1	1	1	1	1	1	1
181 boro citr	1	1	1	1	1	1	1	1	1	1
125 poa annu	1	1	1	1	1	1	1	1	1	1
130 Acti suff	1	1	1	1	1	1	1	1	1	1
132 cera glom	1	1	1	1	1	1	1	1	1	1
72 vero grac	1	1	1	1	1	1	1	1	1	1

		11111	11	111	11111111	111	1 1 1111111	1	11	1	11	11	
	2277	11148	12455555677778888822222	1127800224666666690231111234447889900011113	3567789111135633390112222	9334501	33993	52900325933233	4444				
	2356256811395901245802494580245678	180108956160012345613312347866787672447801672973	9133935886700600490129	6747495912534683	77329598557412234								
77 mono glau								1					
69 colo apet												1	
56 oxyl elli			-1-										
102 drym cyp												-1-	
161 oreo oxyc				-1-									
110 brac spp							1						
154 pers sp												1	
34 grev aust					1								
136 picr hier													1
92 podo lawr	1-												
144 lila brow							1		1				
183 pult dent													
184 deye quad													
185 ehrh acum													
186 cent cord													
187 scle sp.													
190 olea pers												-1-	
191 gaul hisp												-1-	
192 pern tasm							-1-						

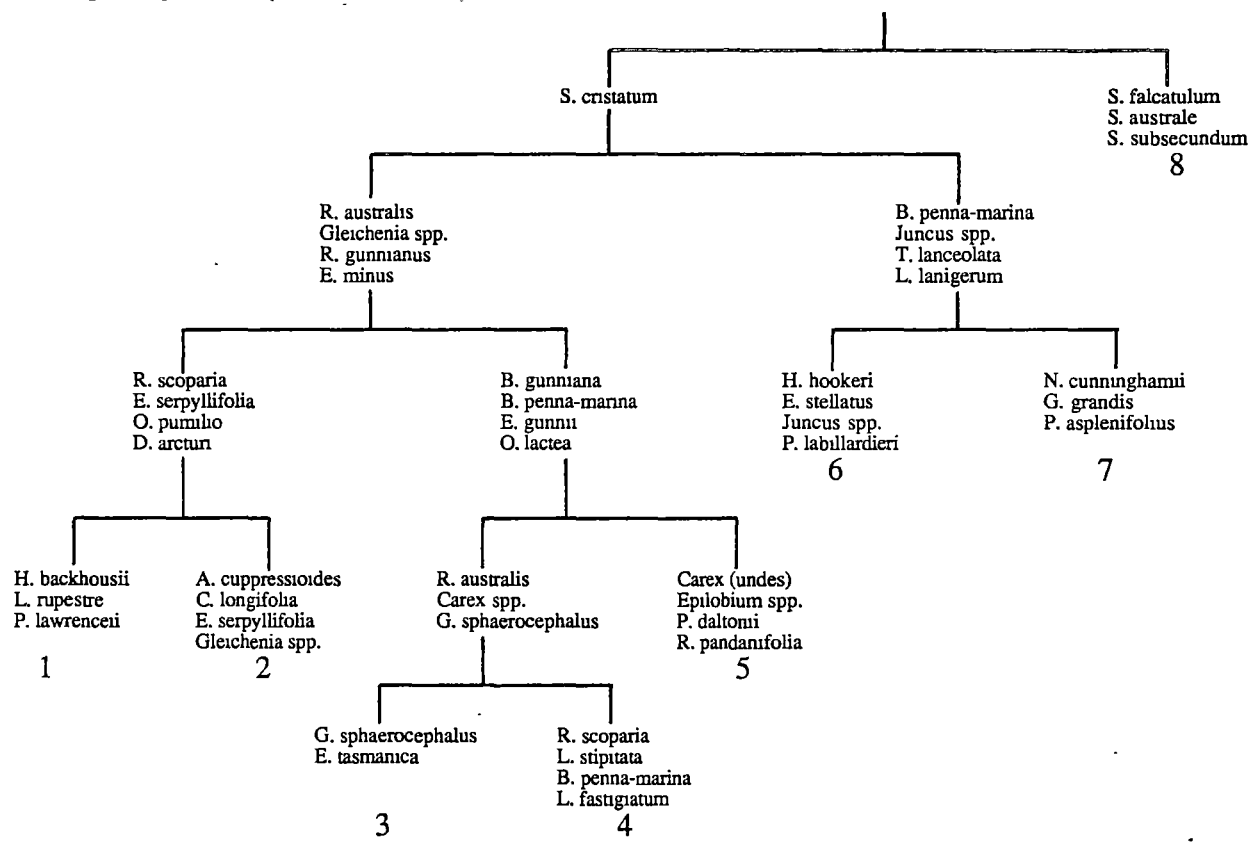


Fig. 3.1 Dendrogram showing indicator species at each TWINSpan division.

3. Buttongrass-*Sphagnum* bogs

Gymnoschoenus sphaerocephalus and *Ehrharta tasmanica* are the distinguishing species in the generally infertile buttongrass-*Sphagnum* bogs. This community usually occurs where there is glacial moraine or alluvium over a largely infertile substrate, such as near Lake Ewart in the Eldon Range and King William Plains. This mire type can cover large areas (as in the Eldon Range) or occur as isolated patches near grassland and buttongrass dominated moorland, or as line boundaries between these vegetation types and forest. The buttongrass tussocks are separated by *Sphagnum*.

The relative percentage cover of *S. cristatum* may be inversely related to the cover of *G. sphaerocephalus* (Kirkpatrick and Whinam 1988). Floristics and apparent fire boundaries suggest that the relationship between buttongrass and *Sphagnum* is largely fire governed. The variation in percentage cover of both species on relatively fertile sites appears to represent a fire degradation sequence, with *Sphagnum* bogs at one end, degrading to buttongrass vegetation at the other with increasing fire frequency (Jarman, *et al.* 1988).

4. *Richea*-*Sphagnum* bogs

Richea scoparia, *Lagenifera stipitata*, *Blechnum penna-marina* *Lycopodium fastigiatum* and *Richea acerosa* are indicator species for this type of *Sphagnum* peatland. These bogs are the most frequent type found in this survey, occurring throughout Tasmania. This community is found on poorly drained sites, often on old riverine and lacustrine sediments. Both the overstorey of shrubs and the understorey of ferns and herbs can vary from occasional to dense.

5. *Richea pandanifolia* -*Sphagnum* mires

Carex sp. nov., *Epilobium* spp., *Plantago daltonii* and *Richea pandanifolia* distinguish group 5. The Pandani-*Sphagnum* mires have an unusual appearance, with tall *R. pandanifolia* towering over the short shrubs and herbs growing out of hummocky mounds of *Sphagnum*. This is a small group, the outstanding example of which is located at Birds Plain.

6. Tussock grassland-*Sphagnum* mires

Helichrysum hookeri, *Erigeron stellatus*, *Juncus* spp. and *Poa labillardieri* are the species which distinguish this community. Group 6 occurs at moderate altitudes on generally fertile sites, which appear to have been subjected to fire in the past. This community is found in the north-east, at Blue Tier and Paradise Plains. At most sites this group tended to occur on the open fringes of *Nothofagus cunninghamii* rainforest.

Occasional shrubs form an overstorey, with *Juncus* and *Poa* tussocks, over a herb-moss understorey.

7. Rainforest-*Sphagnum* mires

Nothofagus cunninghamii, *Gahnia grandis* and *Phyllocladus aspleniifolius* are the distinguishing species of the rainforest-*Sphagnum* community. This is usually found at lower altitudes than the communities listed above, and is typified by peatlands in the west (Little Fisher River, Mother Cummings Peak) and north-west (Netherby Plains). In this community *Sphagnum* can occur in mats with emergent rainforest species, or as small discrete patches on a humic layer below a rainforest canopy.

8. Aquatic *Sphagnum* bogs

The absence of *S. cristatum* and the presence of *Sphagnum falcatum*, *S. australe* and *S. subsecundum* are the distinguishing features of this uncommon community. This group is only recorded at limestone sinkholes near Mole Creek and at streamside soaks under a rainforest canopy at the Little Fisher River. At the limestone sinkholes *S. falcatum* occurs as a floating mat over liquid peat under an overstorey of occasional shrubs and graminoids.

3.3.2 Environmental variables and site characteristics

As well as a particular species or suite of species (fig. 3.1), the various communities have distinctly different environmental ranges. The differences between the communities are summarised in fig. 3.2, and discussed below. Fig. 3.2 shows that TWINSpan groups 4 and 6 are the most dissimilar from each other, while TWINSpan groups 3 and 4 are the most similar in environmental variables and site characteristics. TWINSpan group 1 - restricted to patches of snowlie - is, not surprisingly, different in some aspects from all other groups.

3.3.3 Species attributes of communities

The number of rainforest species (Jarman *et al.* 1984) as a percentage of the total number of species per quadrat, was found to be significantly different between the TWINSpan groups ($H=39.15$, $p<0.001$). As might be expected, the major difference is between the relatively low number of rainforest species in the buttongrass bogs compared with the higher number of rainforest species in the rainforest-*Sphagnum* mires.

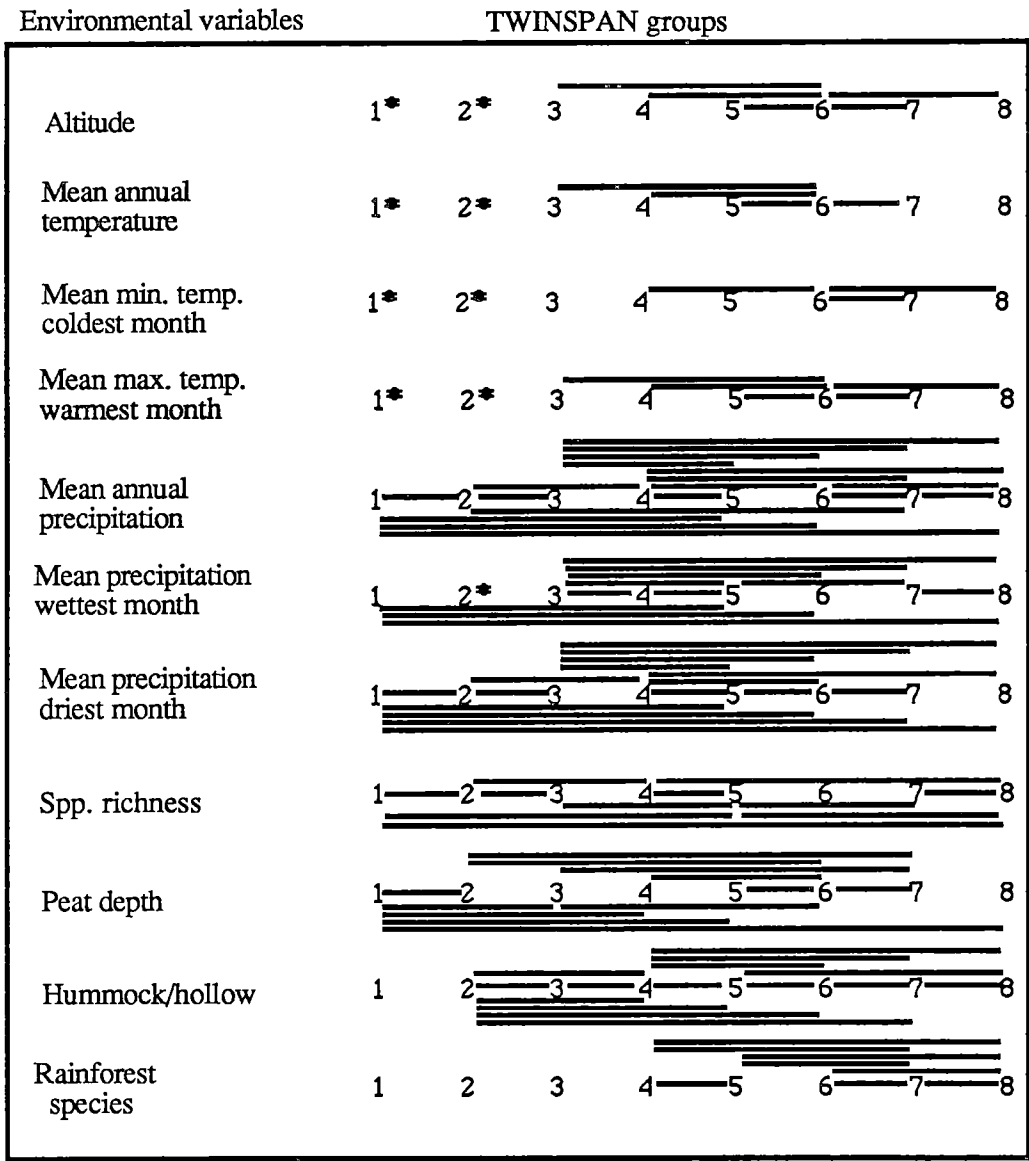


Fig. 3.2 Differences in environmental and floristic variables between TWINSPAN groups. * denotes different from all other TWINSPAN groups. Solid lines indicate significant difference between groups ($p < 0.01$). 'Rainforest species' indicates number of rainforest species as a percentage of total number of species per quadrat. 'Species richness' denotes number of species per quadrat. 'Hummock/hollow' denotes height of hummocks above hollows. TWINSPAN group 1=snowpatch-*Sphagnum* mires, 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

Not surprisingly, altitude is found to be strongly negatively correlated with all three measures of temperature ($r=0.94$ to 0.99 , $p<0.001$). Altitude was not, however, correlated with any of the three measures of precipitation ($r=0.06$ to 0.15). The close relationship between temperature and altitude is reflected in the significant altitudinal partitioning of the TWINSPAN groups ($H=68.11$, $p<0.001$).

It is possible that this variation in rainforest species between communities may represent a difference in fire regimes, with rainforest *Sphagnum* peatlands representing the least frequently burned type, and buttongrass-*Sphagnum* peatlands being the result of frequent fire and equating with the degradational end of the peatland succession (Jarman *et al.* 1988).

There are statistically significant differences in the species richness of the different communities ($H=18.98$, $p<0.01$). The low number of species in the aquatic *Sphagnum* quadrats (mean 7 species) contrasts with the species rich pandani-*Sphagnum* peatlands (mean 19.5 species).

3.4 Environmental relationships

3.4.1 Climate and altitude

There are statistically significant differences in the main climatic parameters between the different communities (fig. 3.3, $p<0.001$ for all three temperature measures; $p<0.001$ for all three precipitation measures). All three temperature parameters were highly correlated with each other ($r=0.92$ to 0.97), as were the three precipitation parameters ($r=0.85$ to 0.94), although temperature and precipitation parameters were not correlated.

The major climatic distinctions between the communities are that the relatively high altitude snowpatch *Sphagnum* peatlands (group 1) and the sub-alpine coniferous mires (group 2) tend to have the lowest mean annual temperature (4.8 and 5.6°C), mean minimum temperature of the coldest month (-2.5 and -1.7°C) and mean maximum temperature of the warmest month (14.9 and 16.1°C). In contrast, the tussock-*Sphagnum* mires (group 6) of the north-east and lowland aquatic *Sphagnum* bogs (group 8) tend to have the warmest mean annual temperature (8.2 and 8.1°C), mean minimum temperature of the coldest month (0.4 and 0.6°C) and mean maximum temperature of the warmest month (both 18.9°C).

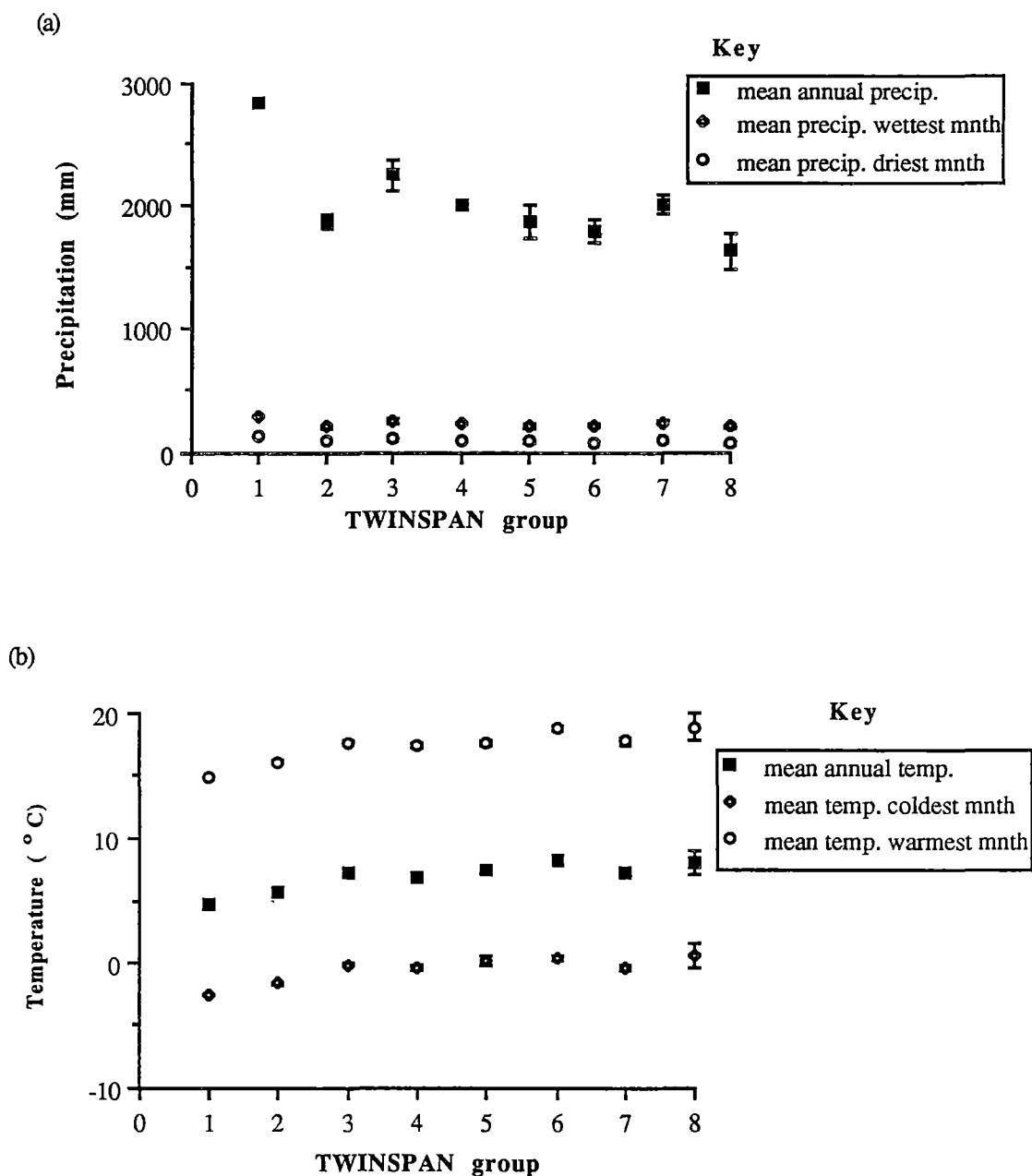


Fig. 3.3 (a) Precipitation and (b) temperature variables (with standard error of the means, S.E.M.) for each TWINSpan group. TWINSpan group 1=snowpatch-*Sphagnum* mires, 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

The community receiving the greatest amount of precipitation on a mean annual basis (2251 mm), in the wettest month (251 mm) and in the driest month (112 mm) is the buttongrass-*Sphagnum* peatland (group 3), located in the west of Tasmania. In contrast, the driest community in terms of mean annual precipitation is the lowland aquatic *Sphagnum* bogs (group 8), with sub-alpine coniferous mires (group 2), pandani-*Sphagnum* mires (group 5) and aquatic *Sphagnum* bogs (group 8) all having the lowest precipitation in the wettest month (207-210 mm). Tussock-*Sphagnum* mires (group 6) and aquatic *Sphagnum* bogs (group 8) have the lowest precipitation in the driest month (74-81 mm).

3.4.2 Ability to regenerate after fire

Plant species in the different communities have a differential ability to regenerate after fire ($H=25.95$, $p<0.001$, fig. 3.4). Buttongrass-*Sphagnum* bogs (group 3) had the highest percentage of plants per site able to regenerate after fire, with very few species unable to regenerate after fire (mean score 124 - see methods section for details), followed by Pandani-*Sphagnum* mires (group 5, mean score 128) and *Richea-Sphagnum* bogs (group 4, 130). These communities contrast with the obligate seed and fire sensitive species of the rainforest-*Sphagnum* mires (group 7, 161). Other aspects of the effects of fire on *Sphagnum* peatlands are discussed in chapter 6.

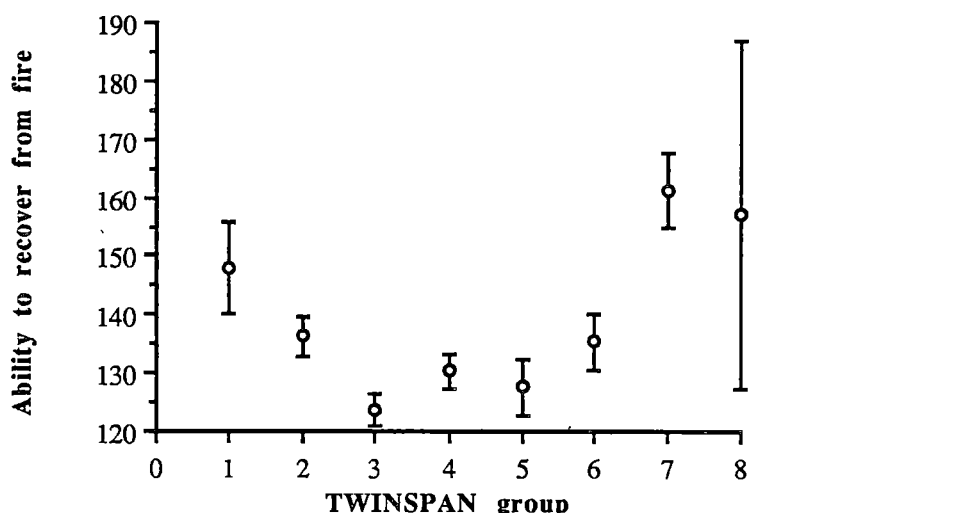


Fig. 3.4 Species' ability to recover from fire within TWINSpan groups (mean scores and S.E.M.). Low scores suggest an ability for vegetative recovery, medium scores suggest an ability for seed recovery, and high scores suggest neither seed nor vegetative recovery ability (see methods for details). TWINSpan group 1=snowpatch-*Sphagnum* mires, 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

3.4.3 Geomorphology

Some of the different TWINSPAN floristic communities are preferentially located at sites with a particular geomorphic type (chapter 2). As would be expected, the snowpatch community is restricted to places of snowlie and the aquatic *Sphagnum* bogs are located in sinkholes. Tussock-*Sphagnum* mires are preferentially located in lakeside/streamside locations (chi square = 12.3, $p < 0.001$).

3.4.4 Peat depth and rock type

Peat depths vary significantly for the different TWINSPAN groups ($H = 25.81$, $p < 0.001$), with the snowpatch community being located on relatively shallow peats, and *Richea-Sphagnum* mires, buttongrass-*Sphagnum* bogs and sub-alpine coniferous mires being located on the deeper peats (fig. 3.5).

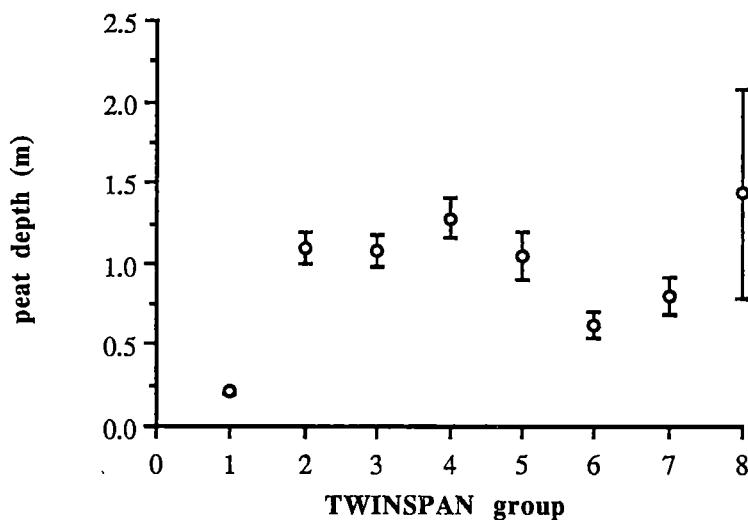


Fig. 3.5 Mean peat depths and S.E.M. for each of the TWINSPAN groups. TWINSPAN group 1=snowpatch-*Sphagnum* mires, 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

The different rock types were preferentially distributed between the different TWINSPAN groups. The sub-alpine coniferous mires were preferentially located on dolerite (chi square=61.7, $p < 0.001$); buttongrass-*Sphagnum* mires were preferentially located on siltstone/sandstone (chi square=26.3, $p < 0.001$); *Richea-Sphagnum* bogs were preferentially located on marsh deposits (chi square=7.1, $p < 0.001$); *Pandani-*

Sphagnum mires were preferentially located on alluvium (chi square=19.6, $p<0.001$); and tussock-*Sphagnum* mires were preferentially located on granodiorite (chi square=18.4, $p<0.001$).

Peat depths varied with rock type ($H=25.95$, $p<0.001$, with the omission of the lone limestone sinkhole site). The deeper peats of the alluvium and marsh deposits (mean 1.11 m), the sedimentary rocks (1.29 m) and till (1.16 m) contrast with the shallower peats associated with granite and granodiorite (0.46 m). Dolerite (mean 0.99 m) and basalt (0.80 m) tended to have intermediate peat depths. Rock type and peat depth are two factors influencing floristic variation between TWINSPAN groups.

3.4.5 Height of hummocks

Although data were not available from all sites, the height of hummocks above hollows varies between TWINSPAN groups ($H=29.86$, $p<0.001$). The relatively large hummocks of the buttongrass-*Sphagnum* bogs and tussock grassland-*Sphagnum* mires contrast with the smaller pillow-hummocks of the rainforest-*Sphagnum* mires (fig. 3.6).

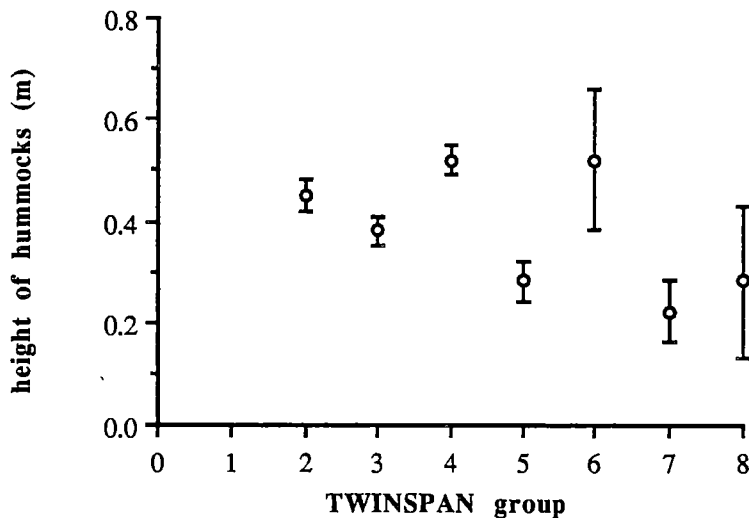


Fig. 3.6 Height of hummocks (above hollows) and S.E.M. for each of the TWINSPAN groups. Data not available for TWINSPAN group 1 (snowpatch-*Sphagnum* mires). TWINSPAN group 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

3.4.6 Nutrients

The nutrient analysis of the peats from a subset of 26 quadrats is shown in fig. 3.7. The amount of total nitrogen was significantly correlated with percentage organic matter ($r=0.844$, $p<0.001$) and total potassium was negatively correlated with percentage organic matter ($r=-0.675$, $p<0.001$). Total N increases with altitude ($r=0.442$, $p<0.05$), as does percentage organic matter ($r=0.515$, $p<0.01$).

3.4.7 Ordination

A preliminary ordination of the complete data set by DCA showed only one discernible axis, which was closely related to altitude.

The maximum correlation between any environmental property and the projections of the vectors fitted to the two dimensional NMDS solution for the subsample of 47 sites was that of mean maximum temperature of the warmest month ($r=0.56$). Peat depth, ability to recover from fire, mean precipitation in the driest month, altitude ($p<0.01$) and rock type ($p<0.05$) also have significant values in declining order of magnitude. The relationships between the vectors for various descriptive attributes of the vegetation and environmental variables for this subsample of sites are shown in fig. 3.8(a). This figure shows that peat depth varies almost orthogonally from altitude and ability to resprout after fire.

The maximum correlation between any peat nutrient property and the projections of the vectors fitted to the two dimensional NMDS solution for the subsample of 26 sites was that of percentage organic matter ($r=0.73$). Total K and N also have significant ($p<0.01$) values in declining order of magnitude. The relationships between the vectors for various descriptive attributes of the vegetation and environmental variables for this subsample of sites are shown in fig. 3.8(b). This figure shows that peat depth varies almost orthogonally from percentage organic matter and total K, suggesting that fertility and organic content are independent of peat depth.

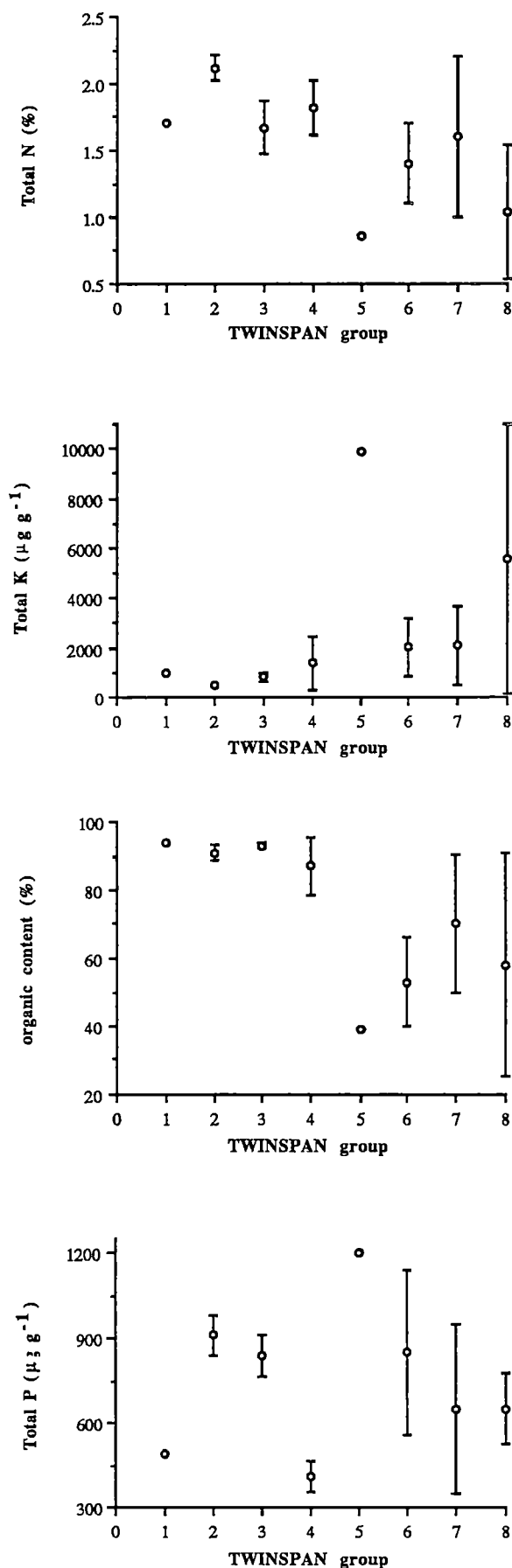


Fig. 3.7 Nutrient analysis of the peat samples from a subset of 26 quadrats (with S.E.M.). TWINSpan group 1=snowpatch-*Sphagnum* mires, 2=sub-alpine coniferous mires, 3=buttongrass-*Sphagnum* bogs, 4=*Richea-Sphagnum* bogs, 5=*Richea pandanifolia-Sphagnum* mires, 6=tussock grassland-*Sphagnum* mires, 7=rainforest-*Sphagnum* mires and 8=aquatic *Sphagnum* bogs.

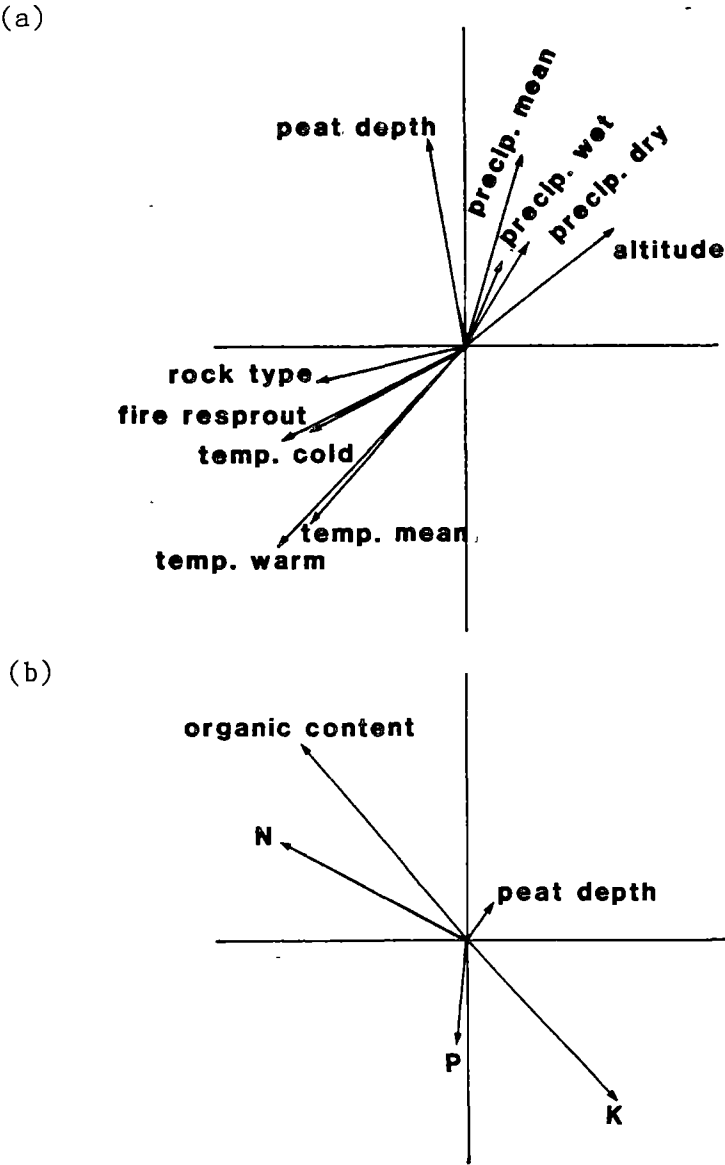


Fig. 3.8 Vectors of environmental and vegetational variables in the normalised space of the two-dimensional non-metric multidimensional scaling solution for (a) the subsample of 47 quadrats and (b) the subsample of 26 quadrats for which nutrient data were available. The arrows indicate the line of best fit in the ordination space, and point towards the direction with highest values. The maximum correlations between the properties and their projections on the fitted vectors are indicated by their proportionate length (1mm : $r=0.1$). Precip. wet = mean precipitation of the wettest month; precip. mean = mean annual precipitation; precip. dry = mean precipitation of the driest month; temp. cold = mean minimum temperature of the coldest month; temp. warm = mean maximum temperature of the warmest month; temp. mean = mean annual temperature.

3.5 Discussion and conclusions

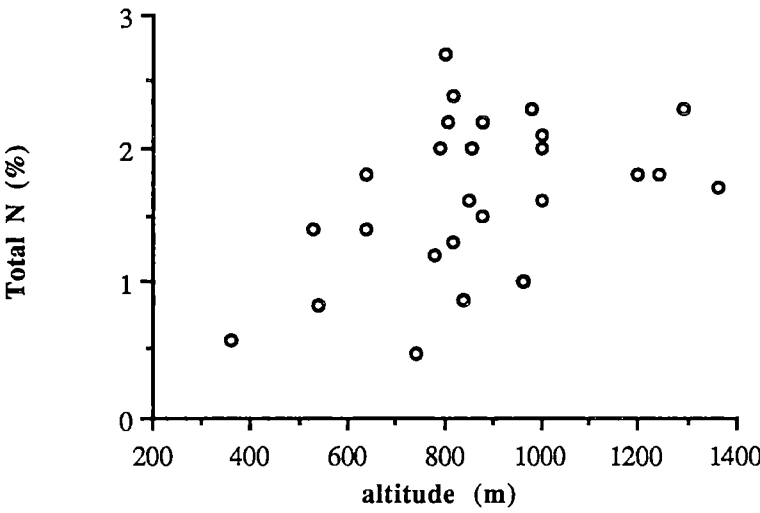
Overall variation in vegetation of Tasmanian *Sphagnum* peatlands appears to be determined by the effects of temperature and precipitation. The composite nature of the vegetation of Tasmanian *Sphagnum* peatlands means that the vegetation of these peatlands reflects variation in the regional flora. Temperature and precipitation, combined with topography and drainage patterns, are likely to determine regional moisture availability. The effects of altitude on temperature and precipitation have been found to be important in distinguishing between floristic groups in other Tasmanian studies (Kirkpatrick 1984, Pemberton 1986, Kirkpatrick and Whinam 1988). It appears that mean maximum temperature of the warmest month and mean precipitation in the wettest month have a strong influence on mire floristics in Tasmania.

Nutrients and fire also appear to affect variation in vegetation between sites. It has been suggested that nitrogen, phosphorus and potassium are of overriding importance insofar as nutrient deficiency is concerned (Brock and Bregman 1989). The results suggest that the elements N and K are the most important in influencing the floristics of Tasmanian *Sphagnum* mires. Both total N and percentage organic matter increase with altitude in Tasmanian *Sphagnum* mires (fig. 3.9). Similar results have been found in organic soils in Tasmanian forests (R.C. Ellis, personal communication). The apparent lack of effect of P in influencing the Tasmanian mire floristics may be because phosphorus is present in sufficient quantity not to be a major limiting factor, as suggested by comparisons with the European data (fig. 2.9).

The correlation of percentage organic matter with the projections of vectors fitted to KYST may be due to circularity, as the vegetation affects the organic content of the peat, which in turn affects vegetation. However, the percentage organic matter may imply a relationship between breakdown/accumulation of plant matter and fertility. The rate of peat humification and accumulation is likely to have implications for nutrient availability (Moore and Bellamy 1974). The correlation between rock type with the projections of vectors fitted to NMDS may reflect differences in nutrient status, while the correlation with peat depth may reflect differences in drainage and fire history.

Variation in the vegetation between Tasmanian *Sphagnum* mires reflects the effects of fire. The vegetation at some sites in the generally more fire-prone buttongrass-*Sphagnum* peatlands (Jarman *et al.* 1988) and *Richea-Sphagnum* bogs is comprised of species that all can regenerate after fire, while some of the rainforest-*Sphagnum* mires consist of species that can re-establish after fire only by seed, or for some species, not easily re-establish at all.

(a)



(b)

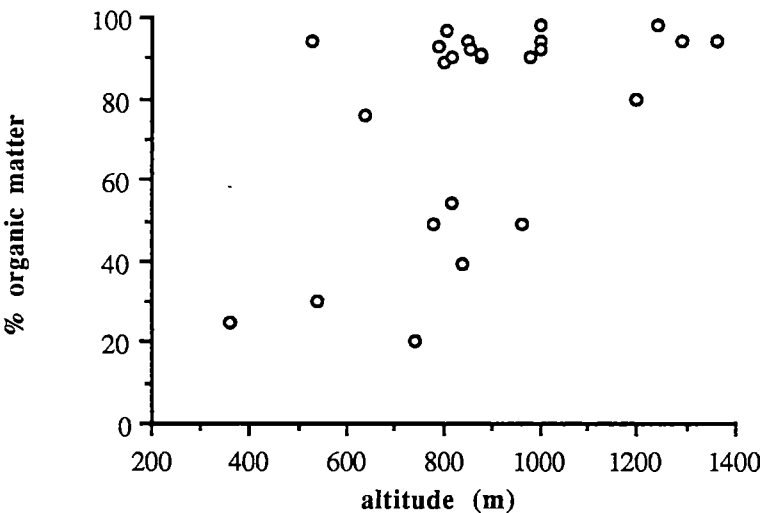


Fig. 3.9 (a) Total Nitrogen (%) and (b) organic matter (%) from Tasmanian *Sphagnum* peatlands at different altitudes.

It appears likely that the topographic setting of the peatlands may influence the exposure of the peatland vegetation to fire. For example, the pillow form of the rainforest-*Sphagnum* mire is located in a fire-protected valley. The buttongrass-*Sphagnum* bogs, which largely consist of species able to regenerate after fire, tend to be located in broad valleys susceptible to fire. It also seems reasonable to assume that the general trend would be for a decrease in fire frequency and/or intensity with increasing altitude (e.g. snowpatch and sub-alpine coniferous *Sphagnum* mires), given protection provided by mist, lakes, cliffs and screes (Kirkpatrick 1984), and lesser fuel loads. The effects of weather on fire characteristics, along with topography, geology and fire history, are thought to be important in determining the floristics of the major peatland type in Tasmania - buttongrass moorland (Jarman *et al.* 1988).

In the northern hemisphere, the main gradient is from fen to bog (Sims *et al.* 1982, Rybníček 1985). In Tasmania, however, there does not appear to be a clear fen-bog gradient. Classification and ordination resulted in buttongrass-*Sphagnum* bogs and the more common *Richea-Sphagnum* bogs being positioned centrally. The extreme ends of the classification and ordination contained the two most infrequent and habitat specialised *Sphagnum* peatland types - the snowpatch *Sphagnum* community at one end and aquatic *Sphagnum* bogs at the other.

Snow cover and duration may be factors distinguishing the snowpatch *Sphagnum* community, as these factors are thought to play a role in determining vegetation differences within Canadian peatlands (Gignac and Vitt 1990). However, the lower temperatures associated with altitude may be more important. This community occurs in sheltered locations below ridges, reducing the potential effects of wind dessication. A similar situation is recorded on the Bennison High Plains in Victoria, where there is a small isolated patch of *S. cristatum* around a clump of *Epacris* in an area subjected to snowlie (Farrell and Ashton 1973).

The distinct vegetation of the aquatic *Sphagnum* bogs reflect habitat conditions. The sinkhole/seepage environment of this mire type results in nutrient, moisture and hydrologic conditions different from those of other types of Tasmanian *Sphagnum* mire. These differences are reflected by an absence of the usually dominant *S. cristatum*, and the presence of *S. falcatulum*.

CHAPTER 4 - THE EFFECTS OF DROUGHT, SHADE AND NUTRIENTS ON *SPHAGNUM CRISTATUM* AND ASSOCIATED SPECIES

4.1 Introduction

Moisture, topography and nutrients, and their interactions are thought to be some of the major influences on the distribution of *Sphagnum* peatlands on a global scale (Moore and Bellamy 1974). On a meso scale, moisture availability, the type and quantity of available nutrients and degree of exposure to dessication are thought to be crucial in determining the distribution of *Sphagnum* moss across a peatland (Vitt and Slack 1975, Godley 1978). On a micro scale, in the northern hemisphere, the differential ability of particular *Sphagnum* species, and *Sphagnum*-associated species, to survive the unusual moisture regimes imposed by the hummock/hollow pattern of peatlands is thought to be a major factor in determining their distribution in relation to microtopography (Vitt and Slack 1984, Andrus 1986).

Accurate measurements of productivity of *Sphagnum* have proved difficult (Clymo and Hayward 1982). The various methods employed measure either growth in length or growth in weight (Clymo 1970, 1973; Clymo and Hayward 1982). The methods considered to cause least disturbance to the intact mossbed make use of the innate pattern of branch density of *Sphagnum* or utilize some sort of external marker such as vertical wires, or the modified cranked vertical wires, which all measure growth in length (Clymo 1970). The use of vertical or cranked wires may introduce the possibility of the moss using the wire as a form of structural support, as the moss has been observed using shrubs in this way (Kenkel 1988).

A method commonly used, which causes more disturbance than the cranked wire method, is to cut plants to a known length, pot them and then measure changes in length. Another method is to mark individual plants with a thread, but this again causes disturbance to the *Sphagnum* carpet. There is also the capitulum correction method which measures growth in weight, which has been described in detail by Clymo (1973).

Problems are likely to arise when measuring the length of *Sphagnum* growth in shade experiments, as dense shade has been found to result in plants becoming more etiolated (Clymo 1973). *Sphagnum* also shows a laxer growth-form in wetter conditions, as indicated by variation in weight per unit length of stem (Clymo and Reddaway 1971).

Shading experiments have inherent problems, illustrated by the difficulties encountered by Clymo (1973). Clymo reduced the incident radiation flux on *Sphagnum* plants in a glasshouse experiment by using either two or six layers of black nylon gauze. While nylon gauze is a relatively simple and effective means of shading, Clymo (1973) points out that shading in natural conditions may be selective for wavelength.

Furthermore, shade differences were confounded with temperature differences of up to 4°C. Other possible effects of such shading techniques are reduced ventilation, increased humidity and mechanical restrictions (Hayward 1980). Although such differences exist in natural conditions, the relationship between natural and experimental shade is not known (Clymo 1973). Sophisticated equipment to create shade, and instruments for measuring light flux in a *Sphagnum* canopy were developed for use in detailed growth experiments on *Sphagnum* (Hayward 1980, Clymo and Hayward 1982, Hayward and Clymo 1983) in an attempt to overcome some of these problems.

Several field and glasshouse experiments have been carried out on the effects of additional nutrients on *Sphagnum* productivity and growth. After examining the effects on growth of different *Sphagnum* species, Clymo (1973) found that there was a positive correlation between growth and supply of inorganic ions (varied concentration and flow rate). Boch and Kuz'mina (1983) found that *S. papillosum* and *S. fimbriatum* died within a month in a radius of up to 2 metres from an area fertilised with liquid swine manure, which contained a very high nitrogen content (154 g/m²). The greater concentration of minerals in the soil caused water stress. Conversely when subjected to much lower rates of nutrient addition, such as moose dung buried in *S. fuscum* hummocks in bogs in south Finland, a locally brighter green colour and increased vigour were recorded (Pakarinen 1978a). On the basis of glasshouse experimentation, Clymo and Hayward (1982) suggested that the growth rate of adult plants of *Sphagnum* may be limited by the supply of phosphate.

Several field studies have shown that shade influences the growth of *Sphagnum*, albeit with differing results. Increased light caused by removal of the forest canopy allowed the reinvasion of *Sphagnum magellanicum* over an area from which it had been eliminated by shade (Pisano 1983). However, Gignac and Vitt (1990) found that tree-shade did not limit the habitat of any of the *Sphagnum* species studied. A strong negative correlation was found between the growth rate of *Sphagnum* species and solar irradiance in a shady environment beneath a canopy (Murray *et al.* 1989).

In shade and watertable experiments conducted by Clymo (1973) and detailed experiments of these parameters conducted by Hayward and Clymo (1983) on northern hemisphere species, differential responses were recorded. Clymo (1973) found that in general, if the *Sphagnum* moss was shaded and/or the watertable was high, growth in weight was less. However, growth in length was reduced only when the watertable was low and shade was dense. The combined effect was that the plants became more etiolated in shade and/or with high watertable (Clymo 1973).

The literature suggests that nutrients, moisture and shade influence the growth rate of *Sphagnum*, although the results vary depending on the intensity of the treatment, species used and methods of measurement (length vs. biomass). A glasshouse experiment was designed to examine the effects of nutrients, shading and drought on the relative growth rates of *S. cristatum* and its associated peatland species. These results are then compared with northern hemisphere studies that have used various methods of experimentation and measurement (Clymo 1973, Hayward 1980, Clymo and Hayward 1982) to examine the effects of environmental variables on *Sphagnum* species.

4.2 Methods

One hundred and twenty pots of *Sphagnum* and with embedded herbs, grasses and were collected from a *Sphagnum* bog in the Mersey River valley in 1987.

The *Sphagnum* was gathered into 7 cm diameter, straight-sided black pots. These pots were left to acclimitise for one month in a glasshouse. The *Sphagnum* was then repotted into 8 cm diameter pots in March 1987. Prior to the commencement of the experiment the pots contained only live stems (i.e. no highly humified moss or peat). Cranked wires were inserted into two pots of each treatment following the methods of Clymo (1970). The experiment commenced in June and ran for seven weeks.

Twelve combinations of treatments, each with 10 self-draining pots, were used. The treatments are summarised in fig. 4.1. Those pots being subjected to drought were watered once a fortnight, as after two weeks without watering the *Sphagnum* showed signs of wilt. "Aquasol" was made up to a strength of 2 grams per 5 litres of water for nutrients 1 (low nutrients) and 4 grams per 5 litres of water for nutrients 2 (high nutrients). The nitrogen:phosphorus:potassium ratio of "Aquasol" is 23:4:18 (see Appendix 5 for chemical composition). Individual shade caps were made for those pots subjected to shading. A commercial shade cloth ("Sardex") with 70% shade was used.

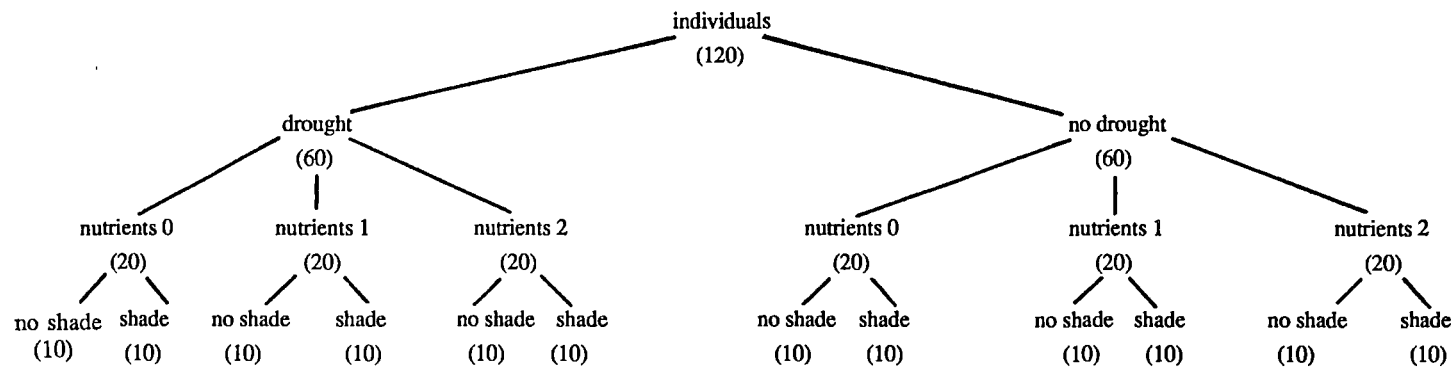


Figure 4.1 Summary of different treatments for glasshouse experiment, with number of pots for each treatment indicated (in brackets). Drought pots were watered once every two weeks; no drought pots were watered daily. Nutrients 0 = no nutrients, nutrients 1 = one-quarter dose of 'Aquasol' fertiliser, nutrients 2 = one-half dose of Aquasol. No shade = no shade, shade = 70% shade.

As the vascular plants were embedded in the *Sphagnum* moss, it was not possible to weigh these species separately. Therefore, the total weight of *Sphagnum* and the small amount of vascular plants present were recorded together prior to the commencement of the experiment.

The pots were placed in randomised blocks in the glasshouse. The pots not subjected to droughting were watered daily. The pots subjected to droughting were watered once a fortnight, by which time *Sphagnum* showed signs of wilting. All pots were weighed fortnightly on a Sartorius analytical balance, after the pots had drained naturally after watering. Water was poured from above until the moss was saturated and free draining from the pots. The glasshouse had a normal (non-assisted) photoperiod. The range of temperatures over the period of the experiment were minimum range between 8^o and 13^oC and maximum range between 16^o and 23^oC. Humidity ranged between 48% and 89%.

It became obvious during the course of the experiment that measurement of growth using the cranked wires was not possible, due to the etiolated nature of *Sphagnum* under all treatments. The etiolation could be due to a combination of the relatively high temperatures and humidity in the glasshouse compared to conditions at the site. The minimum temperature of the coldest month for the Mersey River site is 0.3^oC, while the maximum temperature of the warmest month is 18.3^oC (BIOCLIM). In some cases the moss had used the wires as a trellis (cf. Kenkel 1988).

At the end of seven weeks, the pots were all weighed and the plants from each pot were sorted into species. Whilst acknowledging the considerable problems of differentiation (Clymo 1970), *Sphagnum* was separated into "live" and "humified", in an attempt to determine whether any particular treatment resulted in a greater degree of humification. All green and white *Sphagnum* moss was treated as "live" *Sphagnum*, with the generally less distinct brown moss being treated as "humified". There was no humified moss in the pots at the start of the experiment. The sorted plants were oven-dried at 105^oC for 24 hours, and weighed.

The failure of the cranked wire technique meant it was not possible to use increase in weight vs increase in length as a measure of productivity (Clymo 1970). The total dry weights at the end of the experiment were used as a measure of productivity. The starting weights of the 10 pots for each treatment were subjected to one way analysis of variance, which confirmed that there were no significant differences in starting weights of the different treatments ($p > 0.1$). The results presented can only be taken as a relative indication of the effects of different experimental treatments on *S. cristatum* and its associated species.

In calculating the increase in biomass, the recorded weights of both the humified and live *Sphagnum* were grouped together as a measure of *Sphagnum* productivity. The total weights of all remaining species were grouped together to calculate growth rates of *Sphagnum*-associates.

The dry weight of *Sphagnum* and the amount of humified *Sphagnum* as a fraction of total *Sphagnum*, were square root transformed, and the dry weight of the combined coinhabitant species was log transformed, as the data were not normally distributed, before three way analysis of variance (Sokal and Rohlf 1969).

4.3 Results and discussion

4.3.1 *Sphagnum*

The *Sphagnum* biomass index showed no statistically significant response to any of the experimental treatments (table 4.1, appendix 5). However, the interactive effects of drought and nutrients appear to have been the most significant influence on *Sphagnum* biomass ($p=0.05$). No drought with low nutrients resulted in a significantly reduced biomass compared with drought with low nutrients (backtransformed means of 6.66 gms cf. 8.25 gms). While an increase in biomass with the addition of low dose nutrients is not surprising given previous results (Clymo 1973, Pakarinen 1978a), the greater productivity when interactively subjected to drought was not expected. The interactive effects of drought and fertilisation might have been expected to cause dry conditions, as fertilisation can cause moisture stress in peatlands (Boch and Kuz'mina 1983). The level of droughting and/or fertilisation in the current experiment may not have been so severe as to cause moisture stress.

In measurements on *S. fuscum*, *S. balticum* and *S. majus* on Finnish mires, Pakarinen (1978a) found no relationship between nutrient content and variation in growth rate of the three species. Pakarinen (1978a) concluded that the extent to which higher nutrient concentrations are linked with a higher rate of production or growth remains uncertain. The results from the current experiment appear to be in accordance with the literature, which suggests that results vary according to concentration of added nutrients, the species subjected to fertilisation, moisture availability and methods of measurement (productivity vs length).

Shade produced no significant effects on productivity of *S. cristatum* in this experiment. This is perhaps surprising given that in field conditions some shade is thought to give protection from dessication, but dense shade normally excludes *Sphagnum* (Godwin and Turner 1933, Clapham 1940). Shade can result in

Table 4.1 Analysis of variance of biomass index for different experimental treatments for *S. cristatum*. For details of treatments see text. * $p=0.05$

Sources of variation	DF	Mean Sq.	F
MAIN EFFECTS			
Drought-0/1	1	0.19	1.44
Nutrients-0/1/2	2	0.15	0.12
Shade-0/1	1	0.39	3.02
2-WAY INTERACTIONS			
Drought x Nutri	2	0.39	3.04*
Drought x Shade	1	0.01	0.05
Nutri x Shade	2	0.27	2.13
3-WAY INTERACTIONS			
Drought x Nutri x Shade	2	0.02	0.13

Sphagnum becoming more etiolated (Clymo 1973). In the current experiment, *S. cristatum* became etiolated in the glasshouse, regardless of experimental treatment.

The absence of variation in dry matter in response to the effects of droughting is perhaps surprising, given that *Sphagnum* requires moist conditions for survival (Clymo and Hayward 1982, Backeus 1988). Unlike in a stand of vascular plants, there is no sustained supply of water to the surface of a *Sphagnum* cushion under strongly evaporative conditions (Ingram 1983). Several experiments have found that hummock species tend to have greater productivity when the watertable is lower (Moore 1989, Rydin and McDonald 1985), perhaps by an ability to withstand greater rates of dessication than hollow species (Andrus 1986). *S. cristatum* was observed in both hummock and hollow situations in Tasmanian peatlands, with no apparent preference. However in Victoria it has been suggested that this species shows a preference for hummock micro-topography (Ashton and Hargreaves 1983). The absence of any effect on biomass when *Sphagnum* is subjected to drought, in this and other experiments (Clymo and Hayward 1982), appears to run counter to the moisture conditions considered crucial for *Sphagnum* survival. It may be that the level of droughting imposed in these experiments was not severe enough to have a significant effect.

The lack of a significant response in dry weight to most of the experimental treatments by *S. cristatum* is not surprising, given the results of other experimental studies on other *Sphagnum* species. In glasshouse experiments Hayward (1980) and Clymo and Hayward (1982) found there were no significant interactions for dry matter increase, although there were highly significant interactions for growth in length, with individual species behaving differently in response to shade, and to a lesser extent, in response to water level. The response of different species to different experimental treatments is likely to produce variable results. For example, Vitt and Slack (1984) looked at 13

species of *Sphagnum* in terms of habitat occupation and niche breadth. They examined gradients of pH, conductivity, minerotrophy, shade and watertable levels and found that individual species of *Sphagnum* had different responses to different factor gradients.

4.3.2 *Sphagnum*-associated species

Poa labillardieri accounted for 60% of the total coinhabitant biomass in this experiment. Other species recorded in the pots were: *Empodisma minus*, *Epilobium* sp., *Erigeron stellatus*, *Holcus lanatus*, *Hydrocotyle* sp., *Hypericum japonicum*, *Montia australasica*, *Polytrichum* sp. and liverworts. All these species were recorded in both sunny and shady situations during the vegetation survey (chapter 3). The small numbers of coinhabitant species in this experiment meant it was not possible to assess interspecific differences.

The major experimental treatment to affect biomass productivity of *Sphagnum*-associated species is shade (table 4.2, $p<0.004$), with shade resulting in less biomass (mean backtransformed 0.13 cf. 0.15 g, appendix 5). There were no statistically significant interactive effects. Shading resulted in a higher ratio of *Sphagnum* vs *Sphagnum*-associated species than no shade (table 4.3).

Table 4.2 Analysis of variance of biomass index for different experimental treatments for *Sphagnum*-associated species. For details of treatments see text. **=significant $p<0.01$.

Source of variation	DF	Mean Sq.	F
MAIN EFFECTS			
Drought-0/1	1	0.01	0.17
Nutri-0/1/2	2	0.03	2.96
Shade-0/2	1	0.09	8.83**
2-WAY INTERACTIONS			
Drought x Nutri	2	0.02	1.85
Drought x Shade	1	0.01	1.23
Nutri x Shade	2	0.01	0.72
3-WAY INTERACTIONS			
Drought x Nutri x Shade	2	0.01	0.88

Table 4.3 Ratios of *Sphagnum* to *Sphagnum*-associated species for different shade treatments, based on final dry weights.

No Shade	14:1
Shade (70% shade)	21:1

The results of this experiment can be compared to field observations. Changes in cover of individual species on a Danish mire were found to be generally correlated with light conditions and/or the water content (Hansen and Madsen 1984). In New Zealand Cockayne (1958) observed that there was a "struggle for the mastery" between *Sphagnum* and its occupants, as the moss tends to bury any plant whose growth is too slow. Similar observations have been made in Tasmania (Jarman *et al.* 1988). The results of this experiment suggest that there may be some competition between *Sphagnum* and its coinhabitants for light. No shade tends to favour the coinhabitant species. In the absence of shade, other species may be able to outgrow *Sphagnum* and thereby outcompete the moss.

No statistically significant differences in biomass of *Sphagnum*-associates were found between the different fertilisation treatments. This is surprising given that Sanville (1988) found that nutrient addition stimulated production of all plants on an Alaskan peatland, and that nitrogen and phosphorus in combination were more effective than either added singly. Although no quantitative measurements of *Sphagnum* productivity were made, Sanville (1988) speculated that *Sphagnum* productivity would be equal to or greater than that of the herbs, because of its immediate proximity to the nutrients. Other experiments have shown that mire plants generally grow faster when fertilised with P (Tamm, cited in Malmer 1986). The fertiliser used in the current experiment has a relatively low P content.

4.3.3 Humified *Sphagnum*

Two separate interactive effects were found to influence the rate of humification of *S. cristatum*. These were the combined effects of drought and nutrients ($f=3.569$, $p<0.05$), and nutrients combined with shade ($f=4.488$, $p<0.05$, table 4.4). Droughting without nutrients resulted in a significantly lower proportion of humified *Sphagnum* moss than either no droughting combined with no nutrients, or no droughting combined with high nutrients, (fig. 4.2, appendix 5). In addition, the experimental treatment of no shade combined with high nutrients resulted in a significantly greater proportion of humified moss than either no nutrients combined with no shade, or low nutrients combined with shade (fig. 4.2).

Table 4.4 Analysis of variance of the effects of the different experimental treatments on the fraction of live:humified *S. cristatum* (dry weight). Significance levels are *p<0.05, **p<0.01.

Source of variation	DF	Mean Sq.	F
MAIN EFFECTS			
Drought-0/1	1	0.019	8.045**
Nutri-0/1/2	2	0.005	1.960
Shade-0/2	1	0.001	0.031
2-WAY INTERACTIONS			
Drought x Nutri	2	0.008	3.569*
Drought x Shade	1	0.001	0.596
Nutri x Shade	2	0.011	4.488*
3-WAY INTERACTIONS			
Drought x Nutri x Shade	2	0.005	2.211

Little experimental work on the humification of *Sphagnum* appears in the literature. Clymo and Hayward (1982) found a positive correlation between the decay rate of *Sphagnum* moss and nitrogen concentration. They also found that increasing the nitrogen concentration of the plants by fertilising the live plants increased the rate of decay when the plants died, but that this did not occur when the plants were enriched with phosphorus. The results of the current experiment, where two different nutrient concentrations were used, are less clear.

The lowest proportion of humified moss occurred when *Sphagnum* was subjected to droughting with no nutrients. The effects of droughting on inhibiting humification are confirmed by the main effects analysis (table 4.4). It seems surprising that droughting had no significant impact on *Sphagnum* growth but resulted in decreased humification. The drier conditions inhibit the breakdown of *Sphagnum* moss.

The highest proportion of humified moss occurred under several experimental conditions - no drought, no nutrients; no drought, high nutrients; and no shade, high nutrients. It would appear that the addition of nutrients at the higher rate did result in increased humification, when subjected to neither shading nor droughting. This is in line with the results of Clymo and Hayward (1982), except the fertilisation treatments used here included both nitrogen and phosphorus (N:P ratio 23:4). It is, however, more difficult to explain why the experimental treatment of no drought and no nutrients should result in an increased decay rate.

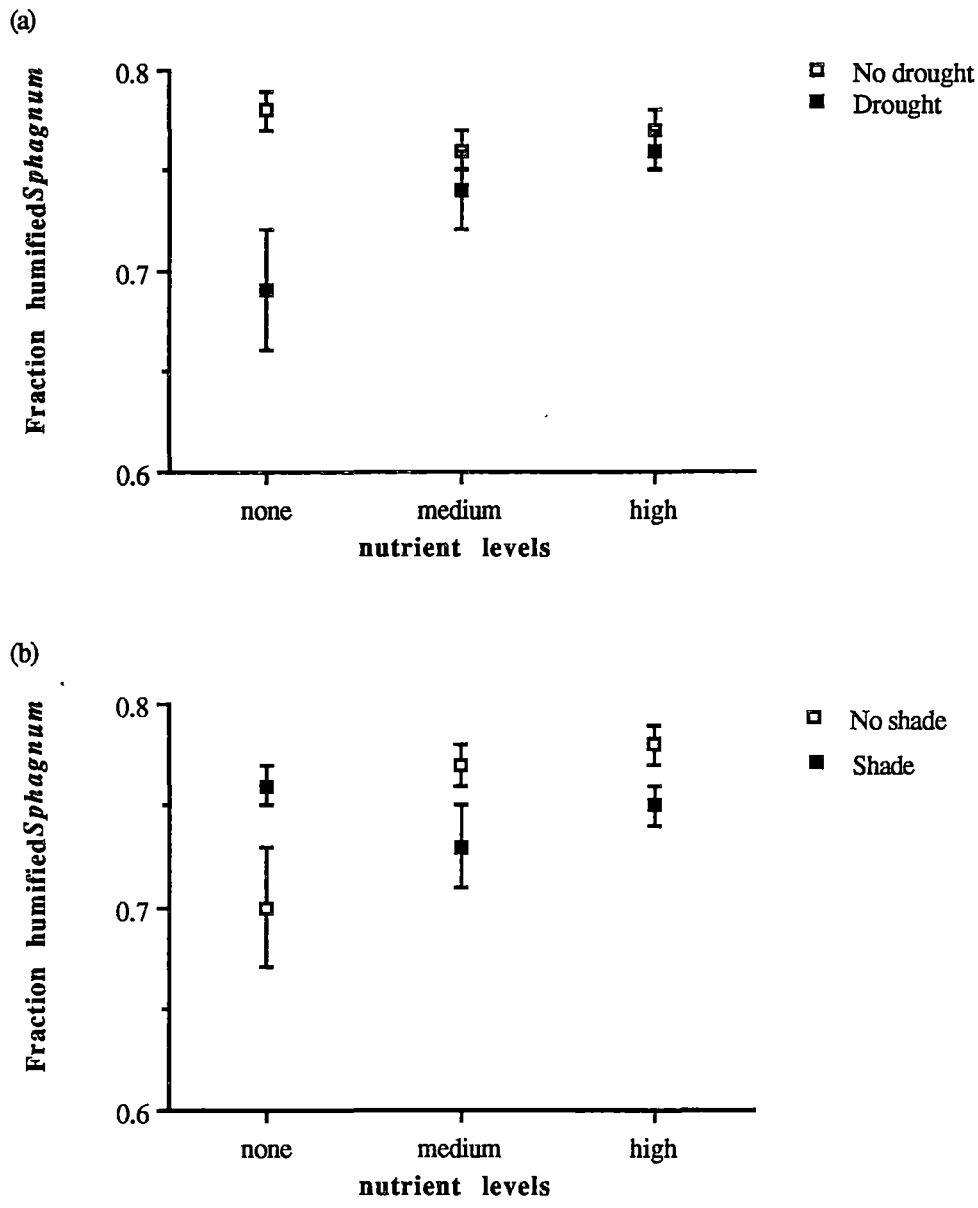


Fig. 4.2 Mean values (and S.E.M.) of humified *Sphagnum* moss as a fraction of total moss weight under different experimental treatments (a) Nutrients combined with droughting treatments; (b) Nutrients combined with shading treatments. For details of treatments see fig. 4.1. Mean values have been retransformed from square roots.

4.4 Conclusions

While problems with measurements of *Sphagnum* in the current experiment, largely due to the degree of etiolation, meant that only comparisons between the dry weights of *S. cristatum* and its associated species could be made, the results suggest how the environmental parameters of drought, shade and added nutrients may affect dry matter productivity of *S. cristatum* and its associated species.

It appears that while there is no statistically significant effect on the dry matter biomass of *S. cristatum* the interactive effects of drought and fertiliser produced the greatest effect. However, interpretation of the results of the glasshouse experiment must be tempered by the apparent contradictions of some of the findings when compared to field observations.

No shade resulted in an increased biomass of *Sphagnum*-associates when compared with *S. cristatum*. It may be that the degree of shade affects the moisture regime and the competitive ability of *Sphagnum*-associates. All vascular species recorded in the glasshouse experiment were observed in both shady and sunny positions in the field. While the results from other shade field experiments and observations vary, the results of this experiment support the contention that some shade generally favours *Sphagnum* over associated species.

The addition of nutrients (N, P and K) at the higher rate resulted in increased humification, when subjected to neither shading nor droughting. Similar findings have been made when N only was added to *Sphagnum* (Clymo and Hayward 1982). The lowest proportion of humified moss occurred when *Sphagnum* was subjected only to droughting. A combination of warmer temperatures and drier conditions may result in conditions less suitable for the breakdown of *Sphagnum* moss.

CHAPTER 5 - THE EFFECTS OF MARSUPIAL GRAZING ON TASMANIAN *SPHAGNUM* PEATLANDS

5.1 Introduction

None of the literature contains any suggestion that vertebrates eat *Sphagnum* (Clymo and Hayward 1982), although *S. cristatum* mires provide habitat for a large number of invertebrates (Whinam *et al.* 1989). However, marsupials graze the palatable herbs, grasses and shrubs that occur in Tasmanian *Sphagnum* peatlands (Gibson and Kirkpatrick 1989). The evidence for marsupial grazing is supported by the number of scats observed on *Sphagnum* peatlands.

Accurate measurement of *Sphagnum* for monitoring purposes is difficult (Clymo and Hayward 1982, chapter 4). In addition to time constraints, problems with accuracy and disturbance were encountered in monitoring the effects of grazing on a *Sphagnum* mossbed on the Bogong High Plains, Victoria (McDougall 1989). Over a long period estimates of average net annual growth based on height may be reduced by the decay of the *Sphagnum* carpet (Clymo and Reddaway 1974). A major stress on the surface layers of *Sphagnum* peatlands is the weight of snow; this is likely to have a marked compressive effect if the surface layer of peat is not frozen (Clymo and Reddaway 1974), as is usually the case in Tasmania (Gibson 1988).

Some studies have been carried out on the effects of grazing in the subalpine and alpine zones in Australia, although these have mostly been in relation to cattle (Wimbush and Costin 1979a, 1979b, 1979c; Williams and Ashton 1987), fire and cattle (Bryant 1973) and cattle and insects (Carr and Turner 1959a, 1959b). The evidence available from *Sphagnum* mires in Australia (Rowe 1970, Bryant 1973, Wimbush and Costin 1979a, 1979b 1979c; Williams and Ashton 1987), suggests that while palatable species are likely to be affected by cattle grazing, with a reduced percentage cover of vegetation, the trampling of cattle may have more detrimental effects on the mires than the actual browsing. However, the effects of trampling are difficult to separate from the other effects that a grazing animal has on the ecosystem (Harper 1977).

Over a 20 year period, exclusion of cattle grazing in the subalpine zone at Kosciusko saw the replacement of small rhizomatous, grazing-resistant herbs by taller sedges, then rushes and hygrophilous shrubs, with some hummocks of *Sphagnum* moss observed spreading from protected *Sphagnum* relicts under shrubs (Wimbush and Costin 1979b). Wimbush and Costin (1979b) forecast that the continued absence of fire and cattle trampling would result in *Sphagnum* eventually occupying most areas of

peat that are not too deeply eroded or humified. However, they postulated that the full recovery of *Sphagnum* with its associated peat may take several hundred years, as the response of *Sphagnum* bogs to protection from fires and grazing is slower than that of the tall alpine herbfield vegetation (Wimbush and Costin 1979c). After hygrophilous sedges recovered from the effects of grazing and grew rapidly, they began to block the small streams, resulting in an increase in shrubs, and a spread and increase in depth of *Sphagnum* (Wimbush and Costin 1979c).

Most Australian studies have involved monitoring changes in percentage cover of plant species. However, McDougall (1989) noted that the most obvious difference between grazed and ungrazed *Sphagnum* mires on the Bogong High Plains was the height of shrubs, with observed changes in species cover being negligible.

Some data are available on the effects of rabbits and native mammals on the subalpine vegetation at Kosciusko using a series of exclosures (Leigh *et al.* 1987). The results suggest there is no significant difference in plant cover or biomass between plots grazed by wombats, rabbits and other mammals and those grazed only by rabbits. It was concluded that when compared to the marked effects on the vegetation by rabbits, the effect of selective grazing by wombats was slight and that of macropods even less (Leigh *et al.* 1987).

In this chapter investigations are reported on the possible effects of mammal grazing, mainly wallabies [*Macropus rufogriseus* (Desmarest)] and wombats [*Vombatus ursinus* (Shaw)] on the vegetation of Tasmanian *Sphagnum* peatlands. In particular, it attempts to answer the question of whether preferential grazing of some species may alter the interspecific balance of *Sphagnum* peatlands.

5.2 Methods

Two grazing exclosures and two control plots (all 4 m²) were established in November 1987 at two *Sphagnum* bogs in Tasmania, at Mt Field National Park and at the Walls of Jerusalem National Park (see fig. 1.2). The size of the plots was felt to be sufficient for comparison, as the vegetation at both sites showed a high degree of homogeneity and there were no noticeable edge effects. Larger plots were not feasible, as the fencing material had to be carried for some distance. The exclosures were constructed with four steel star pickets and rabbit-proof mesh. The corners of the control plots were marked by small wooden stakes.

The two study areas were chosen to represent *Sphagnum* peatlands at different altitudes (1020 m and 1200 m respectively) and geographic locations (south-east and north-west respectively). The *Sphagnum* bog located in a valley at the Walls of Jerusalem National Park (the 'Walls') is probably the largest ombrotrophic *Sphagnum* bog in Tasmania (plate 2). At Mt Field National Park the exclosures and control plots were established in two kettleholes (plate 2). The exclosures and control plots (i.e. ungrazed and grazed plots) were subjectively located at the study areas by choosing sites that :

1. were away from the margin of the bog, to minimise edge effects (Godwin and Conway 1939);
2. were not affected by animal pads through the bog;
3. had no obvious signs of mechanical disturbance; and
4. appeared to be representative of the vegetation present.

A vertical wooden stake was driven through the peat to rock at either end of the grazed and ungrazed plots. A horizontal rod was then placed across the top of the stake, with plant heights recorded from this fixed datum point in summer 1987/88. Random sampling was used to locate points along the rod until at least 10 individual plants of each common species in each plot (where possible) were located. Species localities were both marked on the rod and recorded. The tallest individual was measured where there were rhizomatous species, such as *Empodisma minus*. Where there were rosettes, such as *Astelia alpina*, the tallest leaf was measured. All plants at each marked sample point were remeasured and plots re-photographed in the autumn and spring seasons of 1988 and 1989. Observed natalities and mortalities of all species at these points were also recorded. Natalities and mortalities were counted as the appearance/death of any new plant, or shoots, in the case of the rhizomatous *Empodisma minus* and *Gleichenia alpina*. Natalities and mortalities of small cushions of *Oreobolus pumilio* were recorded.

Measurements made from the horizontal rod to a patch of bare peat suggest there has been no episodic period of peat collapse (Clymo 1984) during the time of monitoring. However, heavy snowfalls resulted in some compaction of plants and moss, as has been noted by researchers in Kosciuszko National Park (Wimbush and Costin 1979a), where snowlie tends to be deeper and more persistent than in Tasmania. As the growth measurements were not normally distributed, they were subjected to analyses by Kruskal-Wallis one way analysis of variance (Sokal and Rohlf 1969).

(a)



(b)



Plate 2. Grazing exclosures at (a) the Walls of Jerusalem,
(b) Mt Field.

Six cranked wires (Clymo 1970) marked with coloured masking tape, were inserted in each grazed and ungrazed plot at the Walls of Jerusalem to measure *Sphagnum* growth. Also, in February 1988 mesh was fixed to the surface of the *Sphagnum* moss adjacent to the two grazed plots at Mt Field National Park. These mesh plots were photographed, in an attempt to measure vertical *Sphagnum* growth.

The number of wallabies was greater at the Walls of Jerusalem than Mt Field, as evidenced by the number of sightings and random scat counts. The number of wallaby scats was counted in ten 4 m² plots along a transect at both the Walls of Jerusalem and Mt Field in April 1990, when cooler conditions were likely to give greater accuracy in scat counts (Johnson and Jarman 1987).

5.3 Results and discussion

The galvanised wire mesh placed on the surface of the *Sphagnum* moss gave interesting, if unexpected, results. Where the wire mesh was in contact with the *Sphagnum* moss, the moss at first turned a bright yellow colour mirroring the hexagonal pattern of the mesh, and by the end of 1989 much of the moss in contact with the mesh had died. Similarly the same mesh used for the exclosures resulted in the death of much of the moss and some of the vascular plants outside the exclosures where the mesh was in contact with the vegetation. It is suggested that the zinc coating on the wire gradually leached out in quantities sufficient to kill plants, as this phenomenon has been reported previously (Good 1987). However, growth measurements are unlikely to have been affected as measurements were not made near the edges of the exclosure.

The cranked wires did not provide meaningful results. Both the mean growth rates of the 12 grazed *Sphagnum* plants (0.60 cm) and the 12 ungrazed *Sphagnum* plants (0.49 cm) at the Walls of Jerusalem over almost two years are very low when compared to the fixed vertical rod method at the same site over the same time period (2.41 cm ungrazed and 2.53 cm grazed plots). It is likely that as the cranked wires were zinc-coated, there may also have been some phytotoxic effect inhibiting *Sphagnum* growth. Also, two pegs were bent at one of the grazed plots, numerous scats suggesting wallaby activity as the cause.

The growth in length measured by the fixed vertical rod technique is comparable with data from two other Australian sites. It is estimated from productivity figures that *Sphagnum* grows approximately 2 cm per year on the Bogong Plains in Victoria (Carr *et. al* 1980). Using a number of methods, direct measurements of *Sphagnum cristatum* at the Brindabella Range in the Australian Capital Territory recorded growth of between 1.18 and 3 cm per year (Carr *et. al* 1980).

Wallaby faecal pellets were more numerous at both sites than wombat faecal pellets. Occasional rabbit dung pellets were also observed at the Walls of Jerusalem. The number of faecal pellets was extremely variable and they tended to be concentrated in small areas. Scat density has been shown to be correlated to grazing density for native mammals (Johnson and Jarman 1987). The difference in the number of fresh (i.e. moist) wallaby scats between the Walls (mean 35.7) and Mt Field (mean 18.9) suggests that there is a greater marsupial grazing intensity at the Walls of Jerusalem.

The results are presented by species where sufficient individuals were monitored to make statistical analyses valid (tables 5.1, 5.2).

All species measured, other than *S. cristatum*, showed relatively greater growth at Mt Field than at the Walls of Jerusalem (table 5.1). Similar results have been found in grassy vegetation in Tasmania when comparing the effects of grazing on high productivity sites at low altitude with low productivity sites at high altitude (Gibson and Kirkpatrick 1989).

Sphagnum cristatum showed no statistical differences between the grazed and ungrazed plots at the Walls of Jerusalem ($H=0.39$, $p<0.534$). *Sphagnum cristatum* showed relatively greater growth over the same timespan at both grazed and ungrazed plots at the Walls of Jerusalem (mean 2.53 cm and 2.41 cm respectively) than at Mt Field (mean 0.79 cm and 1.45 cm respectively). This apparent disparity may be explained by the different climatic regimes at the sites. The Walls of Jerusalem tend to be wetter and colder than Mt Field (table 5.3), resulting in conditions less suited for most vascular plant growth, but perhaps more suited to the moisture and temperature requirements of *Sphagnum*.

Table 5.1 Mean growth in height over 22 months (with standard error of the means, S.E.M.) for grazed and ungrazed plots (2 plots each) at Mt Field and the Walls of Jerusalem.

Species	Location	Mean growth (cm)	S.E.M.
<i>Astelia alpina</i>	Mt Field (ungrazed)	5.71	1.05
	Mt Field (grazed)	5.15	0.91
<i>Empodisma minus</i>	Walls (ungrazed)	3.59	0.34
	Walls (grazed)	1.58	0.36
	Mt Field (ungrazed)	5.95	0.67
	Mt Field (grazed)	1.93	0.44
<i>Epacris serpyllifolia</i>	Walls (ungrazed)	4.19	1.41
	Walls (grazed)	1.34	0.56
	Mt Field (ungrazed)	3.82	0.88
	Mt Field (grazed)	1.10	1.28
<i>Gleichenia alpina</i>	Mt Field (ungrazed)	3.22	0.84
	Mt Field (grazed)	1.83	0.88
<i>Richea acerosa</i>	Walls (ungrazed)	3.82	0.58
	Walls (grazed)	1.17	0.60
<i>Richea scoparia</i>	Walls (ungrazed)	4.21	1.07
	Walls (grazed)	2.57	0.52
	Mt Field (ungrazed)	3.14	0.84
	Mt Field (grazed)	2.72	0.74
<i>Sphagnum cristatum</i>	Walls (ungrazed)	2.41	0.34
	Walls (grazed)	2.53	0.43
	Mt Field (ungrazed)	1.45	0.20
	Mt Field (grazed)	0.79	0.13

Table 5.2 Results of Kruskal-Wallis analysis of variance tests for total growth rates over 22 months of species for grazed and ungrazed plots at the Walls of Jerusalem and Mt Field. Statistically significant results are marked: *= $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species	No.	H
<i>Astelia alpina</i>		
Mt Field	37	0.49
<i>Empodisma minus</i>		
Walls of Jerusalem	53	16.28***
Mt Field	59	13.05***
<i>Epacris serpyllifolia</i>		
Walls of Jerusalem	38	3.70
Mt Field	20	3.87*
<i>Gleichenia alpina</i>		
Mt Field	22	0.69
<i>Richea acerosa</i>		
Walls of Jerusalem	18	5.82*
<i>Richea scoparia</i>		
Walls of Jerusalem	34	1.46
Mt Field	27	0.05
<i>Sphagnum cristatum</i>		
Walls of Jerusalem	82	0.39
Mt Field	73	7.31**

Table 5.3 BIOCLIM data (climatic values interpolated from known stations as functions of latitude, longitude and elevation, Busby 1986) for Mt Field and the Walls of Jerusalem.

	Mean Annual Temperature (°C)	Mean Annual Precipitation (mm)
Mt Field	6.2	1478
Walls of Jerusalem	5.9	1942

There was a difference in growth of *R. acerosa* between the grazed and ungrazed plots at the Walls of Jerusalem ($H=5.82$, $p>0.1$). There were no statistical differences in growth rates of *R. scoparia* between the grazed and ungrazed plots at the Walls ($H=1.46$, $p>0.2$) or Mt Field ($H=0.05$, $p>0.8$). Nor was there any difference between the growth rates of *G. alpina* between the grazed and ungrazed plots at Mt Field. However, whilst there were no statistical differences for *E. serpyllifolia* for the complete data set, there was a difference between the growth rates of *E. serpyllifolia* at the grazed and ungrazed plots at Mt Field ($H=3.87$, $p<0.05$).

There was no statistically significant difference in the growth rates of *A. alpina* in the grazed and ungrazed plots at Mt Field ($H=0.49$). The absence of any statistical difference in growth rates between the grazed and ungrazed plots may be due to differences in grazing pressure between the sites. Clumps of *A. alpina* showed obvious signs of grazing at the Walls of Jerusalem, particularly after heavy snowfalls. When little else protrudes from the snow cover, the erect leaves of *A. alpina* may be subject to greater grazing pressure. *A. alpina* was found to be preferentially grazed by cattle on the Bogong High Plains (van Rees 1984). There was only one clump of *A. alpina* in the grazed plot at the Walls of Jerusalem (not measured). This clump showed obvious signs of grazing, especially after the winter of 1989, with half the clump being chewed back to the basal sheaths. As evidenced by the greater number of wallaby scats, the Walls of Jerusalem site appears to offer greater food resources, being surrounding by grasslands and herbfields. In comparison, the site at Mt Field is surrounded by eucalypt forest with a dense shrub understorey.

Overall, the most palatable of the species recorded appears to be *E. serpyllifolia* (table 5.4). Growth in the grazed plots for this species at both Mt Field and the Walls amounted to only 30.7% of growth in the ungrazed plots. *R. acerosa* also appears to be quite palatable, with growth in the grazed plots at the Walls of Jerusalem accounting for only 30.6% of the growth recorded in the ungrazed plots (table 5.4). *E. minus* showed the greatest impact of grazing at Mt Field, where growth in the grazed plot accounted for only 28.7% of growth in the ungrazed plot (table 5.4). *E. minus* has

been described as palatable, showing a small (0-2%) increasing trend in cover on ungrazed plots at Kosciusko (Wimbush and Costin 1979a).

Table 5.4 Growth in grazed plots as a percentage of ungrazed plots for vascular plants at Mt Field and the Walls of Jerusalem, both separately and combined.

Species	Location	Growth - grazed/ ungrazed (%)		
<i>Astelia alpina</i>	Mt Field	90.2		
<i>Empodisma minus</i>	Walls	44.0)	
	Mt Field	28.7)	34.5
<i>Epacris serpyllifolia</i>	Walls	32.0)	
	Mt Field	29.3)	30.7
<i>Gleichenia alpina</i>	Mt Field	56.8		
<i>Richea acerosa</i>	Walls	30.6		
<i>Richea scoparia</i>	Walls	61.0)	
	Mt Field	86.6)	72.0

Analyses of data to determine how the plant species responded at different locations during different seasons produced variable results (fig. 5.1). There were no statistical differences between plant growth at the sites over time for *R. scoparia* ($H=1.55$, $p>0.6$), *G. alpina* ($H=0.69$, $p>0.4$), or *A. alpina* ($H=0.49$, $p>0.4$). However, there were differences for *S. cristatum*, *E. minus* and *E. serpyllifolia* (table 5.5). Productivity of all species declined at all sites over winter (fig. 5.1).

There is no consistent trend between grazed and ungrazed plots in the *S. cristatum* results at Mt Field (fig. 5.1). Over the first and third growth periods there is less growth in the grazed plots; during growth period 2 there is no significant difference between the grazed and ungrazed plots ($H=0.07$); while during growth period 3 there is less growth in the ungrazed plot. There is no significant difference between the grazed and ungrazed plots at the Walls of Jerusalem ($H=2.14$, $p>0.1$).

Table 5.5 Results of Kruskal-Wallis analysis of variance tests for variation in growth of *S. cristatum*, *E. minus* and *E. serpyllifolia* at all locations during different seasons. Significant differences are marked : * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Growth period	H values		
	<i>S. cristatum</i>	<i>E. minus</i>	<i>E. serpyllifolia</i>
1/88 - 4/88	15.68***	15.03**	1.51
4/88 - 11/88	22.91**	5.65	3.95
11/88 - 4/89	15.20**	6.29	7.82*
4/89 - 9/89	6.61	7.38	3.79

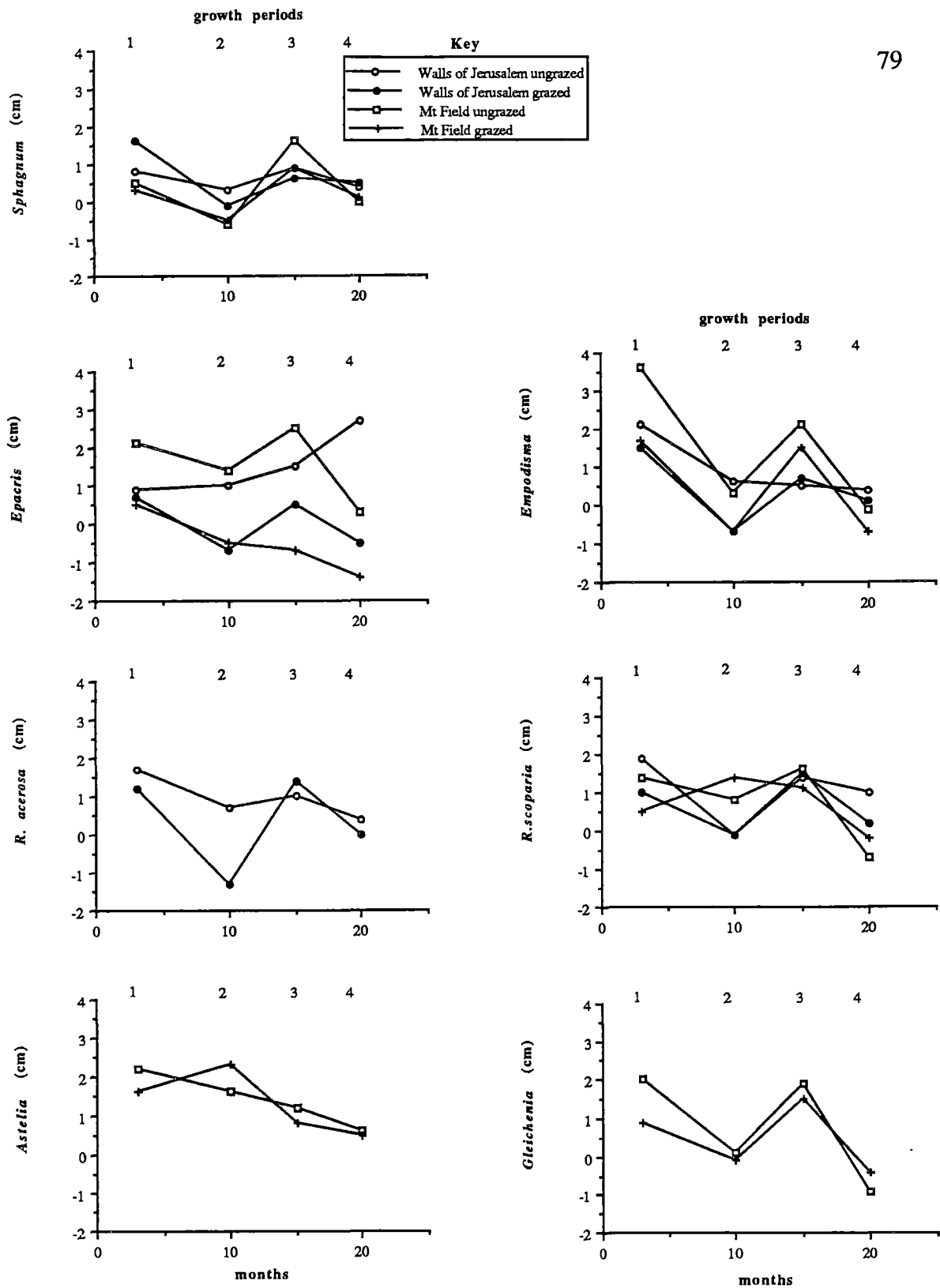


Fig. 5.1 Growth in height of species at different locations over time. Growth period 1 is from 1/88 to 4/88, growth period 2 is from 4/88 to 11/88, growth period 3 is from 11/88 to 4/89 and growth period 4 is from 4/89 to 9/89.

Over growth period one, the trend for *E. minus* is greater growth in the ungrazed plots at both the Walls of Jerusalem and Mt Field (fig. 5.1). Whilst the growth rates overall of *E. minus* were not statistically different over growth period two, the growth difference at the Walls of Jerusalem grazed and ungrazed plots was significant ($H=4.63$, $p<0.05$). However, no other statistically significant differences occurred between grazed and ungrazed plots at the same location for other growth periods.

The only growth period for which there were statistical differences in the growth rate of *E. serpyllifolia* was over growth period 3 (fig. 5.1). During this period there were smaller rates of growth at the grazed plots at both sites compared with the ungrazed plots.

There were no statistical differences in either the total number of natalities ($H=0.99$, $p>0.8$) or mortalities ($H=3.87$, $p>0.2$) of species recorded at Mt Field and the Walls. However, the total number of natalities declined significantly over time ($H=11.36$, $p<0.01$, table 5.6). The total number of mortalities showed no statistical differences over time ($H=6.41$, $p>0.09$). There were no statistical differences between grazed and ungrazed sites for either the number of natalities ($H=0.18$, $p>0.6$) or mortalities ($H=0.77$, $p>0.3$).

Table 5.6 Mean number of natalities and mortalities for all species at grazed and ungrazed sites at the Walls of Jerusalem and Mt Field at different measurement times (with S.E.M. in brackets).

Time of re-measurement	Natalities		Mortalities	
	Walls	Field	Walls	Field
April 1988	18.5 (4.5)	9.5 (1.5)	0.0 (0.0)	0.0 (0.0)
November 1988	7.0 (2.0)	16.5 (1.5)	0.0 (0.0)	3.5 (1.5)
April 1989	1.0 (1.0)	5.0 (3.0)	2.0 (0.0)	4.0 (3.0)
September 1989	0.0 (0.0)	0.5 (0.5)	1.5 (1.5)	8.0 (4.0)

5.4 Conclusions

Whilst there are differences between the grazed and ungrazed sites at *Sphagnum* mires at the Walls of Jerusalem and Mt Field, it does not appear that the effects of marsupial grazing on *Sphagnum* peatlands are as severe as the documented effects of cattle grazing. This may be because the marsupials do not subject the sensitive moss cover to the same degree of trampling. The combination of a history free from cattle grazing, infrequent fires, and 100% vegetation cover may also explain the minimal variation between the grazed and ungrazed plots (e.g. Bryant 1973).

Epacris serpyllifolia, *Empodisma minus* and *Richea acerosa* show the greatest impact of grazing. The growth in height of *Sphagnum cristatum* in the grazed plots was significantly greater than in the ungrazed plots at Mt Field, but not at the Walls of Jerusalem. No signs of grazing of the *Sphagnum* layer were observed. The difference in height of *Sphagnum* may be due to the effects of marsupial trampling. Grazing does not appear to significantly affect either the number of natalities or mortalities.

The major effect of marsupial grazing at both Mt Field and the Walls of Jerusalem appears to be to reduce the growth of vascular mire species. This may result in a dynamic equilibrium between vascular mire species and *Sphagnum*. Grazing reduces light competition from the vascular species and enables *Sphagnum* to grow. However, wallaby scats deposited during grazing provide extra nutrients for the moss, resulting in localised patches of green *Sphagnum*, with new growing tips. The impact of marsupial grazing on the vascular mire species is more noticeable at the lower altitude, high productivity site.

CHAPTER 6 - EFFECTS OF FIRE ON A *SPHAGNUM* PEATLAND

6.1 Introduction

The effects of fire on peatlands vary depending on the moisture content and depth of peat, and also the frequency and severity of the fire (Hofstetter 1983, Tallis 1983). The impact of fire on peatland vegetation is likely to be related to topographic and edaphic conditions, with the effects seldom being uniform (Tallis 1983, Jarman *et al.* 1988). A peatland fire is likely to promote the subsequent growth of some species while deterring others, and thereby affect the vegetation of the mire (Hofstetter 1983). Fires that occur during dry conditions or fierce fires at any time can cause loss of surface peat (Tallis 1983). While some information is available on the general effects of fire on peatlands, the influence of fire on *Sphagnum* peatlands is poorly understood (Andrus 1986).

Few data are available on the effects of fire on peatland ecosystems in Australia. Detailed long term vegetation trends in response to variation in grazing and fire are available for the subalpine and alpine vegetation of the Snowy Mountains (Wimbush and Costin 1979a, 1979b, 1979c). In these studies it was concluded that, in the absence of further fires and trampling, *Sphagnum* will eventually reoccupy most areas of peat that have not been deeply eroded. However, they suggest that the full recovery of *Sphagnum* mires may take several hundred years, with the response of *Sphagnum* bogs when freed from disturbance being slower than that of the tall alpine herbfield vegetation (Wimbush and Costin 1979c).

Generalisations have been made on the fire ecology of Tasmanian buttongrass (*Gymnoschoenus sphaerocephalus*) moorlands (Bowman and Jackson 1981, Bowman *et al.* 1986, Jarman *et al.* 1988). It has been suggested that buttongrass moorlands and *Sphagnum* peatlands may be climax communities at opposite ends of the fire regime (Jarman *et al.* 1988). However, whilst a decline in *Sphagnum* cover after fire in Tasmania has been observed (Jarman *et al.* 1988, Whinam *et al.* 1989), there is no quantitative data on the effects of fire on the relative abundance of *Sphagnum* mire species. The question addressed in this chapter is what short-term effects fire has had on the relative abundance of species of a sub-alpine *Sphagnum* mire on the Central Plateau.

6.2 Methods

6.2.1 Field methods

Ten quadrats were established in each of burnt and unburnt vegetation near Kenneth Lagoon on the Central Plateau (980 m altitude, fig 1.2). The plots were established after a low-intensity, slow moving fire on 11 April 1988 (A. Blanks pers. comm.). Conditions at the time of the fire were quite dry, as indicated by the Soil Dryness Index (SDI) (Mount 1972). The SDI is a water budget model incorporating precipitation, evapotranspiration, interception, runoff and storage, and is expressed as a precipitation deficit in millimetres. The SDI is zero when the soil is at field capacity and rises with evapotranspiration and falls with effective precipitation. At the time of the fire, the SDI in the area was approximately 50 - 60 mm (Tasmanian Forestry Commission unpubl. data). Records from nearby Lake St. Clair (750 m) suggest that temperature was near average while precipitation was below average over the monitoring period (Bureau of Meteorology, unpubl. data).

Pairs of plots (all 0.16 m²) were randomly located on the fire boundary (fig. 6.1). A single 0.25 m² plot was established on an area where a mature *Richea scoparia* bush had been killed by the fire. All surface vegetation on this plot was killed in the fire and the surface mantle was exposed.

Plots were established on 9/10/88, (six months after a wildfire), with measurements and photographs retaken on 18/12/88, 29/9/89 and 13/2/90. This meant that changes in the plots were monitored shortly after the fire, after the first winter, and at the end of the second summer.

Cover abundance for all species in all plots was recorded, with numbers of individuals (or shoots of individuals in the case of rhizomatous species, such as *Empodisma minus*) also being recorded. Where individuals were monitored, the numbers of new appearances (natalities) and disappearances (mortalities) were counted.

Although almost all the above ground vegetation was dead on most burnt plots at the beginning of monitoring, most plots had no exposed bare ground, but were covered by dead *Astelia alpina* and *Gleichenia alpina* fronds, and dead mats of *Sphagnum cristatum* and *Empodisma minus*. Only two burnt plots had exposed bare ground (2% and 75% bare ground respectively).

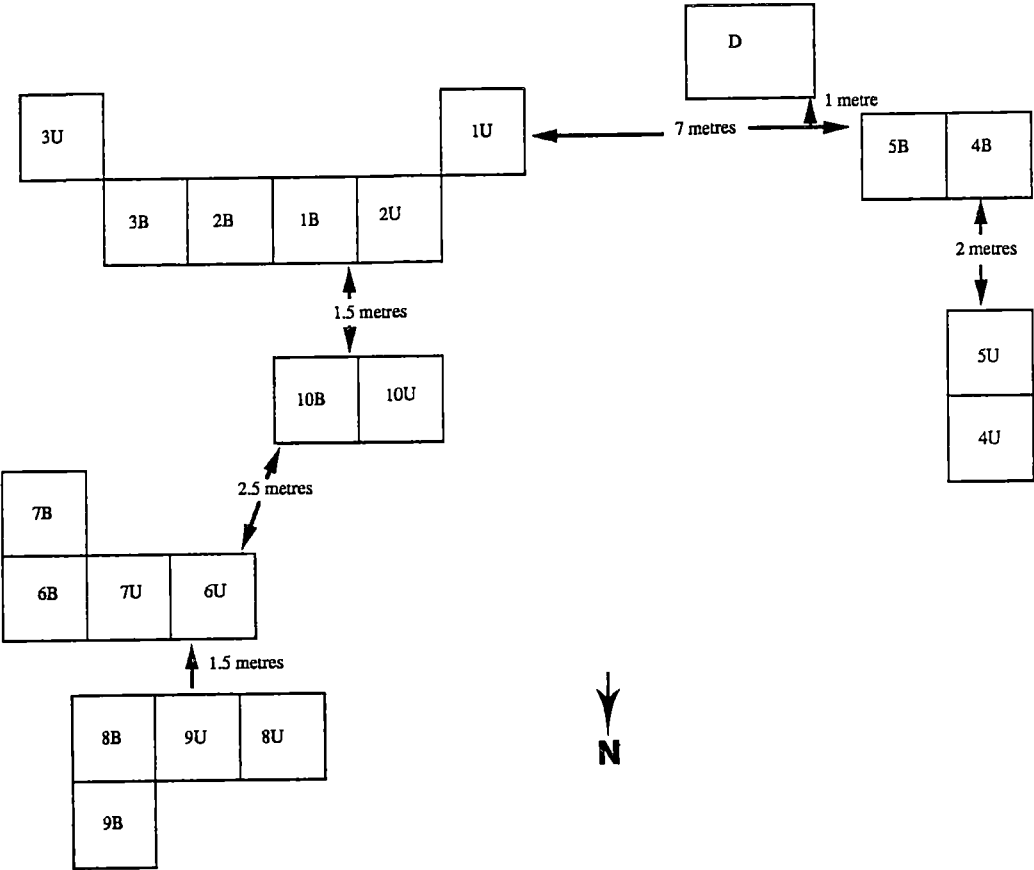


Fig. 6.1 Layout of burnt (B) and unburnt (U) plots at Kenneth Lagoon. Plots are all 0.16m², except for one fire-devastated 0.25m² plot (D).

6.2.2 Data Analyses

The underlying assumption of the data analyses is that the floristics of the burnt and unburnt plots prior to the fire was the same. This assumption is supported by the remains of the burnt vegetation. The total data set consists of all species recorded both individually and aggregated into lifeforms. The Kruskal-Wallis analysis of variance test was used for analyses, as the data were not normally distributed (Sokal and Rohlf 1969). Results presented have been adjusted for ties. The data set was analysed both for cover differences between the burnt and unburnt plots and changes in cover 8, 17 and 22 months post-fire. Mean changes in cover abundance are presented.

When the data set was explored for differences in changes in cover over time post-fire, one large increase/decrease in cover was found to swamp the more numerous small increases/decreases. The amount of change (i.e. % cover at time.b - % cover at time.a) most commonly encountered on both burnt and unburnt plots was an increase/decrease in the range of 0.5-1%. One large change tended to skew the data and analysis (McPherson 1990). For example, a 25% decline in *Sphagnum* growth in one unburnt plot overwhelmed all other changes. Therefore, in order to assess differences between burnt and unburnt plots the rate of change was calculated. The rate of change was calculated by summing the number of positive and negative growth records compared to the median value for each lifeform and then aggregated for each quadrat (McPherson, pers. comm.). The median value for all lifeforms at all times, except ferns, was zero. Chi-square tests were used to test for differences in the rate of change (Sokal and Rohlf 1969).

From the total number of 26 species, sufficient data were available for eight species (*Empodisma minus*, *Sphagnum cristatum*, *Restio australis*, *Rubus gunnianus*, *Poa* sp., *Gleichenia alpina*, *Asperula gunnii* and *Celmisia asteliifolia*) to compare differences between burnt and unburnt plots. These data were also tested for rates of change by chi-square tests. However, two of these species (*A. gunnii* and *C. asteliifolia*), did not attain more than 1% total cover, and therefore were not subjected to the same statistical analyses. For these two species the numbers of individuals or individual rosettes were recorded and analysed. The data from the 0.25 m² plot are presented separately.

6.3 Results

The mean cover of live *Sphagnum* six months after the fire was 0.85% on the burnt plots and 33.5% on the unburnt plots. A total of 26 species were recorded over the monitoring period (table 6.1). Of these, the moss *Polytrichum juniperinum* occurred only on the burnt plots, while the herb *Plantago glabrata* occurred only on the unburnt plots.

Table 6.1 Species and lifeforms recorded from Kenneth Lagoon plots.

SPECIES	LIFEFORM
<i>Asperula gunnii</i>	herb
<i>Astelia alpina</i>	graminoid
<i>Carex</i> sp.	graminoid
<i>Carpha alpina</i>	graminoid
<i>Celmisia asteliifolia</i>	herb
<i>Deyeuxia carinata</i>	grass
<i>Empodisma minus</i>	graminoid
<i>Erigeron stellatus</i>	herb
<i>Gleichenia alpina</i>	fern
<i>Gnaphalium</i> sp.	herb
<i>Hydrocotyle</i> sp.	herb
<i>Luzula</i> sp.	graminoid
<i>Lycopodium fastigiatum</i>	fern
<i>Olearia algida</i>	shrub
<i>Olearia erubescens</i>	shrub
<i>Oreomyrrhis eriopoda</i>	herb
<i>Plantago glabrata</i>	herb
<i>Poa</i> sp.	grass
<i>Polytrichum juniperinum</i>	moss
<i>Ranunculus</i> sp.	herb
<i>Restio australis</i>	graminoid
<i>Richea scoparia</i>	shrub
<i>Rubus gunnianus</i>	herb
<i>Senecio</i> sp.	herb
<i>Sphagnum cristatum</i>	moss
<i>Velleia montana</i>	herb
<i>Viola hederacea</i>	herb

6.3.1 Comparison of burnt and unburnt plots

The vegetation cover differed significantly between burnt and unburnt plots at all measurements ($p < 0.001$ at all times, fig. 6.2). Both the burnt and unburnt plots showed an increase in cover eight months post-fire. The increase in cover on the unburnt plots may be due an initial response to post-fire nutrient accession and altered moisture regime. Only three species - *Gleichenia*, *Sphagnum* and *Rubus* - showed significant differences between burnt and unburnt plots post-fire. *Gleichenia* and *Sphagnum*, which are major components of the biomass, both had significantly greater

cover on unburnt compared to burnt plots (fig. 6.3, tables 6.2, 6.3). Conversely, *Rubus* had significantly greater cover on burnt than on unburnt plots (fig. 6.3, table 6.2).

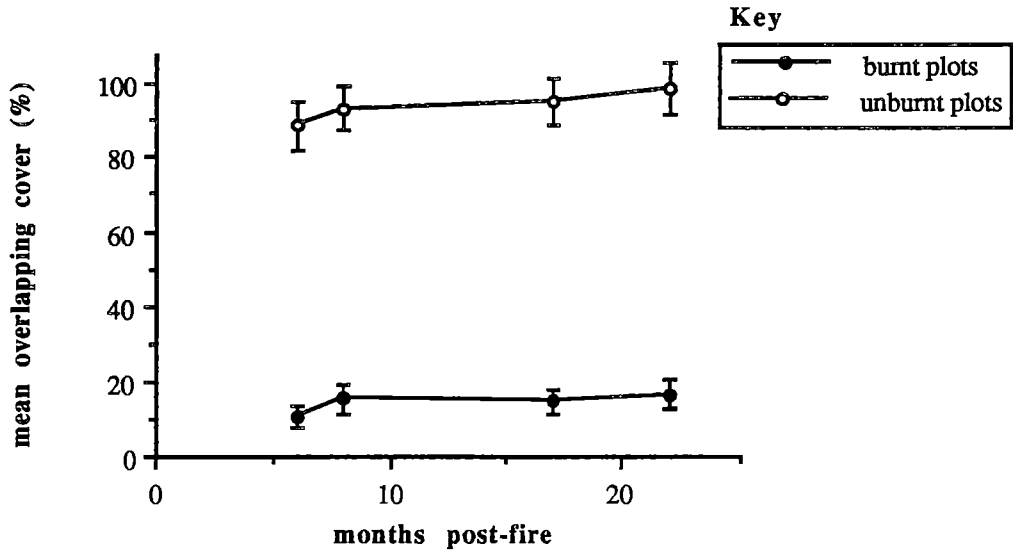


Fig. 6.2 Mean total overlapping cover (with standard error of the means S.E.M.) on burnt and unburnt plots at different times post-fire.

Both *Gleichenia* and *Sphagnum* maintain statistically significant differences between burnt and unburnt plots over time (fig 6.3, table 6.2). However, *Rubus* shows increasing cover on burnt plots compared to unburnt plots.

Table 6.2 Mean percentage cover of species with significantly different cover on burnt and unburnt plots at different times post-fire. ** $p < 0.01$, * $p < 0.05$, n.s.=not significant.

Species & Date of Measurement	Mean % cover		H value	Significance
	Burnt plots	Unburnt plots		
<i>Gleichenia</i>				
9/10/88	4.4	31.6	6.30	*
18/12/88	7.5	37.6	4.51	*
29/9/89	6.9	38.5	5.18	*
13/2/90	8.6	40.0	4.20	*
<i>Sphagnum</i>				
9/10/88	0.8	33.5	8.37	**
18/12/88	1.0	30.0	8.17	**
29/9/89	0.8	30.5	8.38	**
13/2/90	0.6	32.0	8.62	**
<i>Rubus</i>				
9/10/88	0.7	0.5	1.68	n.s.
18/12/88	1.3	0.6	4.94	*
29/9/89	1.3	0.6	7.40	**
13/2/90	1.7	0.6	7.41	**

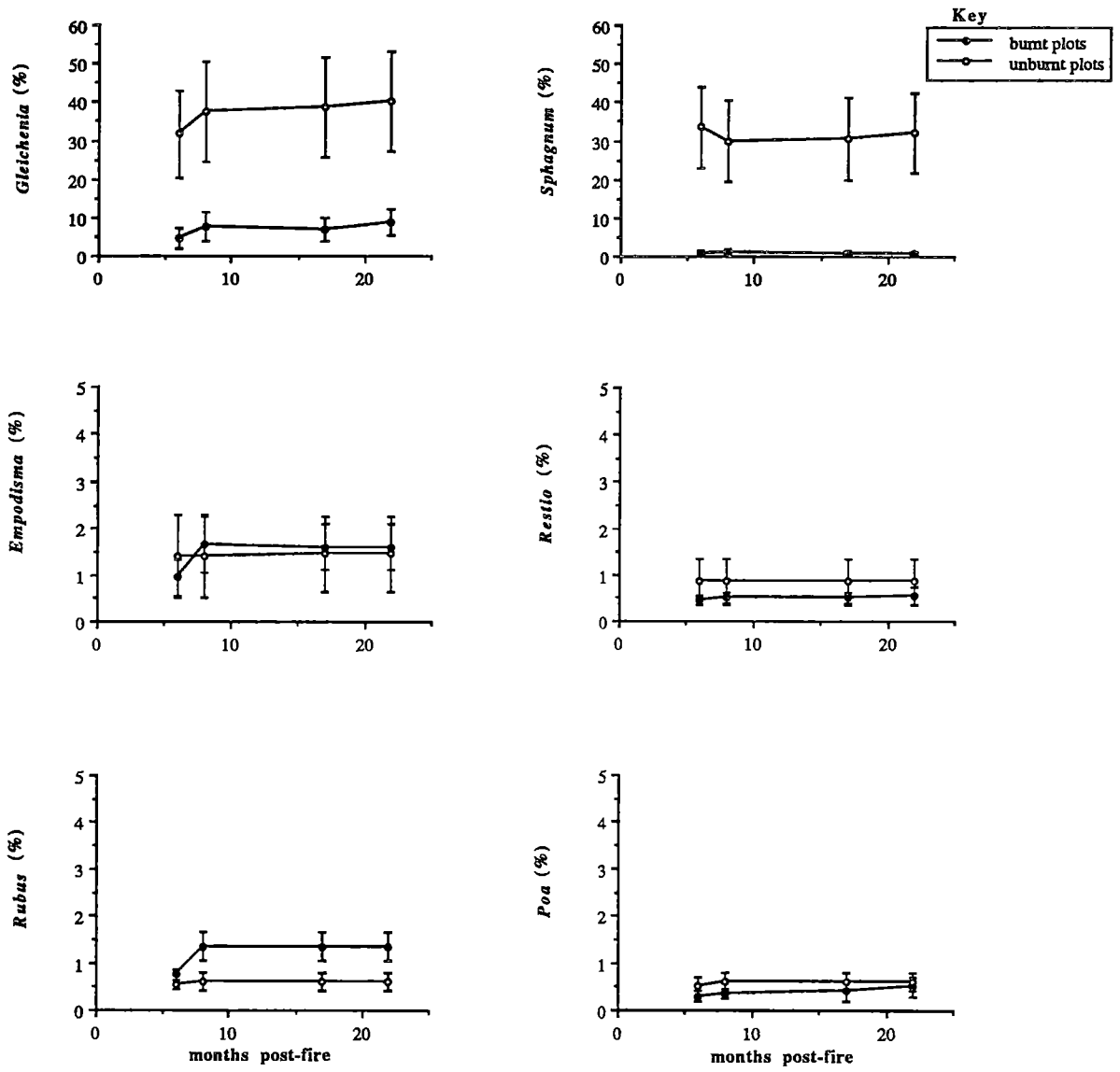


Fig. 6.3 Mean percentage cover (with S.E.M.) on burnt and unburnt plots at different times post-fire (note different vertical scales).

Table 6.3 Changes in cover abundance in the lifeform (l/f) categories occurring on burnt and unburnt plots, 22 months post-fire, with H values. * $p < 0.05$

Lifeform	<u>BURNT PLOTS</u>			<u>UNBURNT PLOTS</u>			H value
	No. in	Mean % increase/	S.E.M.	No. in	Mean % increase/	S.E.M.	
	l/f	decrease		l/f	decrease		
Herb	18	0.61	0.16	22	0.14	0.05	5.27*
Graminoid	24	0.38	0.26	25	0.60	0.41	0.21
Fern	10	4.20	1.63	10	8.40	2.29	2.22
Moss	10	-0.20	0.20	11	-1.36	1.92	0.01
Grass	11	0.09	0.06	10	0.20	0.11	0.51
Shrub	12	0.00	0.00	12	0.83	0.47	3.27

6.3.2 Rate of change post-fire

Between the time of the fire and eight months post-fire there has been a greater rate of change on the burnt plots compared with the unburnt plots (chi-square=6.0, $p < 0.001$, table 6.4), if shrubs are excluded from the analyses. This exclusion is justified as shrubs show a different trend in their rates of change than other lifeforms (table 6.5). However, there is no significant difference in the overall rate of change of species as a whole on the burnt compared to unburnt plots 8, 17 and 22 months post-fire, whether shrubs are excluded or not (table 6.4).

Table 6.4 Number of instances where species were recorded in quadrats occurring above the median, equal to the median and below the median growth rate, in periods since the fire.

	9/10/88- 18/12/88	19/12/88- 29/9/89	30/9/89- 13/2/90
Burnt plots			
above	25	6	14
equal	59	72	67
below	0	6	3
Unburnt plots			
above	16	11	11
equal	70	75	77
below	2	2	0

Herbs were the only lifeform class to show significant differences between burnt and unburnt plots. In the periods 6 to 8 months post-fire and 17-22 months post-fire herbs show a greater rate of change on burnt compared to unburnt plots (chi-square=7.2, $p < 0.05$, table 6.5). The only species to show significant differences in the rates of change between burnt and unburnt plots were *Rubus*, *Empodisma* and *Gleichenia*. *Rubus* had a greater increase in the rate of change on the burnt than in the unburnt plots in both the first and third growth period (5:1 above median both instances, chi-

Table 6.5 Numbers of quadrats in which lifeform classes are above, equal to (=) and below the median on burnt and unburnt plots.

	9/10/88- 18/12/88			19/12/88- 29/9/89			30/9/89- 13/2/90		
	Above	=	Below	Above	=	Below	Above	=	Below
<u>Herb</u>									
burnt	6	0	12	3	1	14	6	0	12
unburnt	3	0	19	2	0	20	1	0	21
<u>Graminoid</u>									
burnt	8	0	15	1	2	20	3	2	18
unburnt	3	0	20	3	1	19	2	0	21
<u>Fern</u>									
burnt	7	0	3	2	1	7	5	0	5
unburnt	6	0	4	4	1	5	3	0	7
<u>Moss</u>									
burnt	2	0	8	0	2	8	0	1	9
unburnt	0	2	9	1	0	10	2	0	9
<u>Grass</u>									
burnt	2	0	9	0	0	11	0	0	11
unburnt	1	0	9	1	0	9	2	0	8
<u>Shrub</u>									
burnt	0	0	12	0	0	12	0	0	12
unburnt	3	0	9	0	0	12	1	0	11

square=3.8, $p<0.05$). *Empodisma* showed a greater rate of change on the burnt plots compared to the unburnt plots in the first growth period (5:0 above median, chi-square=6.7, $p<0.01$), but the rate of change then declined.

The rate of change on burnt plots did change significantly between growth periods 1 and 2 for both *Rubus* (5:2 above median, chi-square=6.0, $p<0.05$) and *Empodisma* (4:1 above median, chi-square=10.0, $p<0.05$). The time difference in the two growth periods (2 months compared with 9 months) highlights the increased rate of growth in the first growth period, although seasonality may also be a factor.

6.3.3 Natalities/Mortalities

There were no significant differences between the burnt and unburnt plots for either the number of natalities or mortalities recorded. The number of natalities rose in the period 8-17 months post-fire, but subsequently declined (table 6.6). *Sphagnum* (counted as individual clumps of moss) showed the highest mortality rate, accounting for 27.3% of the total mortalities. *Erigeron stellatus*, *Viola hederacea* and *Polytrichum juniperinum* showed the highest natality rates, each of these accounting for 8.7% of the total natalities. Thirteen percent of natalities had died by the last measurement, with *Sphagnum* on the burnt plots accounting for half this number.

Table 6.6 Numbers of natalities and mortalities on burnt and unburnt plots over the periods of measurement.

No.	9/10/88- 18/12/88	19/12/88- 29/9/89	30/9/89- 13/2/90
Natalities - burnt plots	5	12	5
Natalities - unburnt plots	6	11	2
Mortalities - burnt plots	1	3	7
Mortalities - unburnt plots	1	1	5

6.3.4 *Asperula gunnii* and *Celmisia asteliifolia*

Asperula gunnii and *Celmisia asteliifolia* occurred on both the burnt (9 and 5 plots respectively) and unburnt (8 and 6 plots respectively) sites. However, neither species attained total values of greater than 1% cover on any plot. The trends for individuals (individual rosettes for *Celmisia*) are shown in fig. 6.4. *Asperula* is preferentially located on the burnt plots (chi square=4.84, $p<0.05$). There are no statistical differences in numbers between the burnt and unburnt plots for *Celmisia*.

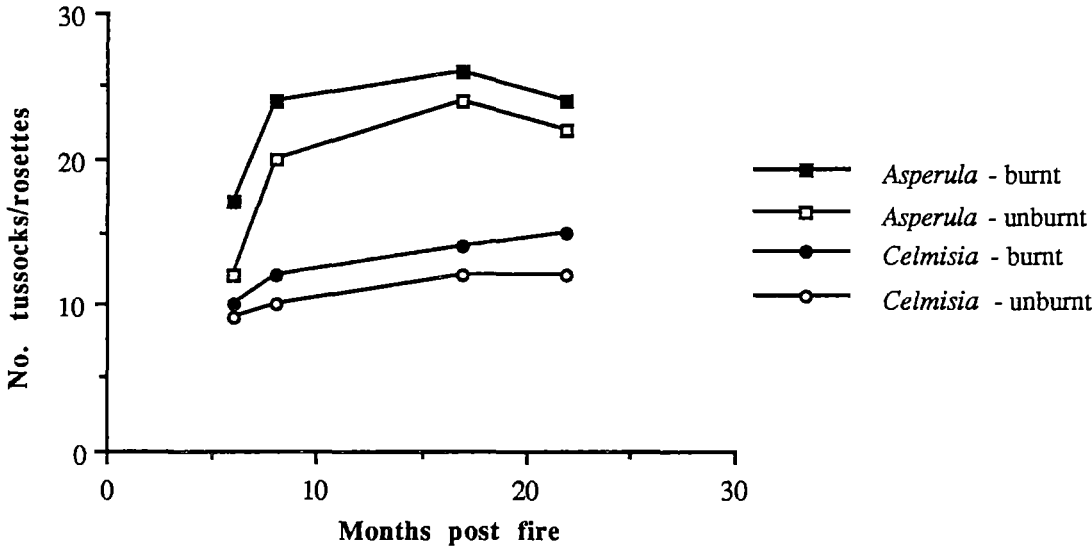


Fig. 6.4 Total number of individual tussocks/rosettes of *Asperula gunnii* and *Celmisia asteliifolia* on burnt and unburnt plots.

6.3.5 0.25 m² plot with bare peat

The percentage cover of species on a 0.25m² plot where all vegetation cover and the peat surface were burnt is shown on fig. 6.5. Taxa not shown include *Restio australis*, *Empodisma minus*, and *Epilobium* spp., all of which maintained a constant cover value of <1%. Liverworts maintained a constant cover value of 1%.

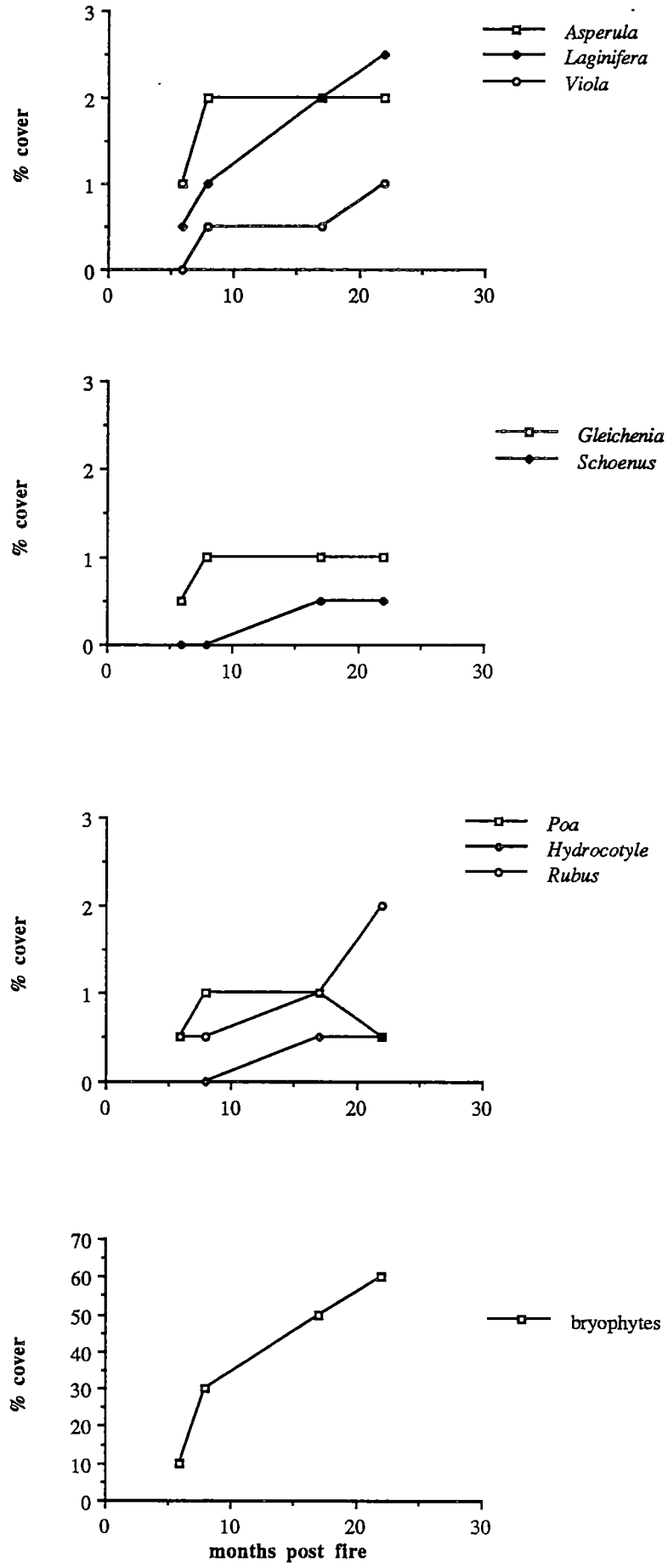


Fig. 6.5 Total overlapping cover of species on a 0.25m² plot, where both vegetation cover and peat were burned (note different scale on bryophyte graph).

Gnaphalium sp., *Ranunculus* sp. and *Viola* sp. all appeared on the plot in small quantities (<1%) 17-22 months after the fire. The total projected cover on this plot reached over 11%, 22 months post-fire.

The only species to attain values of greater than 3% cover on the razed plot are the bryophytes, composed predominantly of *Polytrichum* spp. (fig. 6.5). The bryophytes show a rapid recruitment rate which has been maintained since the fire. *Gleichenia*, *Schoenus* spp. and *Asperula* all show an initial rise in percentage cover after the fire, followed by the maintenance of this cover. *Lagenifera* and *Rubus* show a continuing rise in abundance (fig. 6.5).

6.4 Discussion and conclusions

The results of this study suggest that even when subjected to a cool burn with little destruction of the peat surface, there were marked effects on *Sphagnum* and its associated plant species in a subalpine mire. The most significant change caused by the fire at Kenneth Lagoon has been the almost complete elimination of *Sphagnum* from the burnt plots. There has been no apparent recovery in moss cover two years post-fire. Hummocks of *Sphagnum* on the unburnt plots showed declining cover and vigour after the fire, as did several species on the hummocks, such as the shrub *Richea scoparia*. Wimbush and Costin (1979b) observed that *Sphagnum* hummocks remaining after fire in the Snowy Mountains were rapidly drying out and forecast probable replacement by disclimax heath and/or sod tussock grassland.

Gleichenia also appears to have been adversely affected by the fire, having significantly greater cover on unburnt than on burnt plots. However, there has been an increase in cover post-fire of *G. alpina* on both the burnt and unburnt plots. It is likely that this peatland may change, at least in the short-term, from a moss-dominant community to one dominated by sedges and ferns (Jarman *et al.* 1988) if the current trend of an increase in *G. alpina* and decline of *Sphagnum* at Kenneth Lagoon continues. However, it is possible that in the longer-term, and in the absence of fire and trampling, *Sphagnum* may recover, as forecast for the Snowy Mountains (Wimbush and Costin 1979c).

Conversely, *Rubus* and *Asperula* have significantly greater cover on burnt compared to unburnt plots. *Rubus* has shown similar trends in alpine vegetation (Kirkpatrick and Dickinson 1984). *Asperula* prefers an intertussock habitat with some bare ground, where it is considered both an early-season and an early-stage coloniser (Wimbush and Costin 1979a), which establishes on burnt ground (Williams and Ashton 1987).

Richea scoparia is considered to be very fire sensitive (Kirkpatrick and Dickinson 1984, Jarman *et al.* 1988). *R. scoparia* is capable of seed regeneration, but only very low numbers of seedlings are produced after fire (Jarman *et al.* 1988). Whilst this species occurs on five unburnt plots, it is present on only one burnt plot and was not burnt in the fire. No *Richea* germinates were observed. The only increase in cover abundance of this generally mire-dominant shrub occurred on the unburnt plots. *Olearia erubescens* was the only shrub germinate observed on the burnt plots, appearing on three plots, but never totalling more than four individuals. After initial recruitment, several individuals disappeared from the plots, suggesting that they may have been grazed. This is supported by chewed leaves and wallaby scats observed on the plots.

Poa sp. showed a small but consistent increase on the unburnt plots, while the burnt plots have maintained the cover values of 8 months post-fire. On both the burnt and unburnt plots, *Poa* tussocks showed evidence of grazing, were pallid and appeared to be senescing. *Celmisia* showed no difference between burnt and unburnt plots. The strong, persistent rhizome system of *Celmisia* at and just below the soil surface (Wimbush and Costin 1979c) may make it relatively fire resistant.

There are significant differences between the rate of change on the burnt plots 6 to 8 months post-fire and 8 to 17 months post-fire. Whilst the time between each measuring period differed, the initial, smaller time period showed the greatest change. The rate of change of both *E. minus* and *G. alpina* declined from the first period to the second period. This may in part reflect seasonality. However, it may also reflect an initial increase in productivity on the burnt sites with reduced competition, followed by a subsequent decline, probably due to a combination of drier conditions and loss of nutrients (Moore and Bellamy 1974, Raison 1979).

The rate of growth of herbs was greater on the burnt plots compared with the unburnt plots 6 to 8 months and 8 to 17 months post-fire. This increased rate of growth of herbs on the burnt plots is consistent with alpine data from the Snowy Mountains and Tasmania. Bryant (1973) found that fire stimulated herb development in a subalpine tussock grassland, and suggested this was due to increased light penetration and decreased competition. Leigh *et al.* (1987) found that herb cover recovered completely one year after fire, except where delayed by drought and/or rabbits. Kirkpatrick and Dickinson (1984) found that most herbaceous species on areas burnt 11-40 years

previously had cover equal to or greater than unburnt areas. *Empodisma* also showed a greater rate of growth on the burnt than the unburnt plots between 6 and 8 months post-fire.

The greater number of natalities on the unburnt plot compared to the burnt plot appears contrary to expectations (Leigh *et al.* 1987, Williams and Ashton 1987), as a pulse of recruitment or regrowth is common immediately after a disturbance, due to little competition for space or other resources (Noble and Slatyer 1980). However, the establishment of new individuals at Kenneth Lagoon may be only short-lived, as 13% of all natalities had died two years post fire.

The rate of colonisation of the 0.25 m² plot, where all surface vegetation was destroyed in the fire, appeared to be much slower than in the paired plots. The absence of peat around the base of the dead *R. scoparia* bush suggests that the fire burnt down into the peat. The fire may have been locally hot enough to destroy the underground rhizomes of some species common in the paired plots, such as *Restio australis* (Jarman *et al.* 1988). The dominance of *Polytrichum* on this site is consistent with the preference of this genus for damp, semi-bare sites (Wimbush and Costin 1979c) subjected to fire (Duncan and Dalton 1982), but such dominance is not always the case (Brasell and Mattay 1984).

Whilst the data from Kenneth Lagoon support observations that have been made on the detrimental effects of fire on *Sphagnum* peatlands (Jarman *et al.* 1988, Whinam *et al.* 1989), the initial effects may vary. A fire of moderate intensity during 1988 at a *Sphagnum* peatland in north-eastern Tasmania resulted in the destruction of the dominant *Lepidosperma filiforme* and an increase in the cover of *Sphagnum* (I. Thomas, pers. comm.). However, in a northern hemisphere peatland the initial growth spurt of *Sphagnum* spp. was followed by a very considerable reduction over 15 years, due to development of a dense, low canopy of *Calluna vulgaris* (Rawes 1983). In Minnesota fire scars are typically covered by a nearly continuous carpet of *Sphagnum*, indicating that *Sphagnum* may recover quickly, at least initially, after fire in midcontinental sites (Glaser and Janssens 1986).

It does seem likely that *Sphagnum* peatlands develop under a different fire regime from that of the buttongrass moorlands, as suggested by Jarman *et al.* (1988). Attempts were made to quantify changes in species abundance in an area containing both *Gymnoschoenus* and *Sphagnum* subjected to frequent but irregular low intensity burns beside the Lyell Highway in south-west Tasmania, but were thwarted by several fires which destroyed plot markers. However, observations made at this site suggest that

Sphagnum is in decline, with *Gymnoschoenus* and *Ehrharta tasmanica* var. *subalpina* increasing. The area also contains several exotic species, such as *Holcus lanatus* and *Poa annua*, uncommon in other *Sphagnum* peatlands. Whilst little peat appears to have been removed during the fires, the exposed peat surface is extremely dry, forming a 'crust' in several places. It may be that the frequency and intensity of fire are important in determining the long-term survival of *Sphagnum*.

It appears that at Kenneth Lagoon, in the short-term at least, rhizomatous species, such as *Gleichenia* and *Empodisma* will become dominant, with *Celmisia*, *Asperula*, *Rubus* and other herbs present. As the peat mantle was not disturbed by fire, the presence of plants able to recover vegetatively has resulted in short-term changes being simply changes in dominance rather than a dramatic alteration of the vegetation (Brown and Podger 1982, Bowman *et al.* 1986).

CHAPTER 7 - MEDIUM TERM SUCCESSIONAL PROCESSES IN TASMANIAN *SPHAGNUM* PEATLANDS

7.1 Introduction

Statements about succession are conditional, limited in their validity to the timespan and spatial scale within which changes are observed (Orloci 1981). More specific patterns may emerge within broader general trends (Tilman 1986). Much of the literature related to successional change in *Sphagnum* peatlands has addressed the question of whether such change is either cyclic, a theory usually attributed to Osvald 1923 (Clymo 1983), or 'persistent', i.e. repeatable (Sjors 1980) and unidirectional (Katz 1926, Cockayne 1958).

An understanding of present-day patterns and processes often provides a key to the past (van Leeuwen 1966, Orloci 1981). Several studies have shown that individual species of *Sphagnum*, in association with peatland vascular species, are preferentially located on either hummocks or hollows (Vitt and Slack 1984, Luken 1985, Rydin and McDonald 1985, Vitt *et al.* 1975, Slack *et al.* 1980, Kenkel 1988). This present-day partitioning of species has then been used to analyse whether successional sequences inferred from stratigraphic evidence relate to development to and from hummocks and hollows (Walker and Walker 1961, Ashton and Hargreaves 1983, Svensson 1988).

Cockayne (1958) claimed that there was a distinct succession of vegetation in mires in North Island, New Zealand. He suggested that the initial *Sphagnum* bog was succeeded by various related combinations of species in which Cyperaceae and *Gleichenia* are dominant, with this stage being followed by shrubland or low forest, which may later be replaced by high forest. Contrary to this suggested unidirectional change, Katz (1926) proposed that the 'transition bogs' of Russia formed a continuous developmental series, with the *Sphagnum* bog complex tending to be the natural climax. Katz (1926) recognised that changes may involve retrogression.

Examples from boreal peatlands appear to show both differences in origin and divergence in local development (Sjors 1980). Similarly, vegetational changes and evolution in some peatlands have shown no consistent trend toward either mesophytism or terrestrialsation, or even uniformity (Heinselman 1970). Various parts of the mire vegetation pattern have been found to follow one another in a cyclic microsuccession (Ratcliffe and Walker 1958). Heinselman (1970) concluded that the overriding impression is one of ceaseless and almost random change, initiated by innumerable local or regional events.

The conflicting suggestions of cyclic change versus multi-directional change led Walker and Walker (1961) to claim that only an examination of the most recently formed peats can establish the status of the present bog communities. The question addressed in this chapter is whether there is supporting evidence for the concept of cyclic change in Tasmanian *Sphagnum* peatlands.

7.2 Description of the sites

The two sites selected for testing the possible successional phases in *Sphagnum* peatlands were Pine Valley and the Little Fisher River (fig. 1.2). These sites were chosen because there is a mosaic of *Sphagnum* with other species and they are situated at different altitudes, in different parts of Tasmania.

Pine Valley is a glacial valley north of Lake St. Clair at 760 m elevation, approximately 2 km long and 0.5 km wide. The vegetation is largely swampy heathland and sedgeland, with areas of *Sphagnum* peatland, *E. coccifera* woodland and *Athrotaxis cupressoides* forest. The vegetation is situated on glacial outwash deposits.

The headwaters of the Little Fisher River are set in a small glacial valley at 870 m, within the Great Western Tiers. The vegetation is a mosaic dominated variously by *Gleichenia alpina*, *Astelia alpina*, *Abrotanella forsteroides*, *Sphagnum cristatum* and herbs.

Two sites were selected for determining whether species can be separated into hummock and hollow species on mires. These sites were located at Paradise Plains (800 m) and the Walls of Jerusalem (1200 m, fig. 1.2). The site at the Walls of Jerusalem is an ombrotrophic *Richea-Sphagnum* bog. The site at Paradise Plains is a tussock-grassland *Sphagnum* mire.

7.3 Methods

Species presence/absence data, peat depth and surface topography were recorded on a contiguous transect at both sites, which ran across the mire. The transect at Paradise Plains was 130 m and at the Walls of Jerusalem was 270 m.

Eight cores, 50 cm in depth, were extracted from each of Pine Valley and the Little Fisher River using a D-section corer. At Pine Valley the cores were extracted at 50 m intervals on a transect running across the valley. One core 1.5 m in depth was also extracted from Pine Valley. At the Little Fisher River the *Sphagnum* is confined to one side of the valley, so cores were extracted from the centre of each of the major plant communities on that side of the valley. The cores were described in the field and placed in poly-pipe for transporting. Species presence/absence and projected foliage cover were recorded in a 0.16 m² quadrat centred on each extraction hole. The cores were searched for macro-fossils in the laboratory using a binocular microscope.

Excavation of the moss and/or peat around several shrubs enabled the root zone of the shrubs to be described. Details were recorded in the field. Peat depths were measured with a peat probe and surface topography was determined with a tape measure and clinometer.

Species and lifeform presence/absence on hummocks/hollows for transect data were subjected to chi-square tests and to polythetic divisive classification by TWINSpan (Hill 1979).

7.4 Results

Radiocarbon dates are not available for any of the cores discussed in this chapter. Peat depths cannot be directly correlated with the age of peatlands, due to factors such as peat compression, fire and other erosional events (Simmons and Cundill 1974). An indication of the age of Tasmanian *Sphagnum* mires is given by dates from a core extracted from a *Sphagnum* mire covering an area of approximately 10 ha at the Walls of Jerusalem. The fibrous peat of this core is underlain by clays, probably lacustrine sediments. The basal radiocarbon date of the peat at 2.0 metres is 8270 \pm 270 years BP (ANU 5794). Dates from the same core at 1.6 m are 7350 \pm 300 years BP (ANU 5792) and at 0.7 m 5240 \pm 140 years BP (ANU 5793). One radiocarbon date is available from a core dominated by *Sphagnum* and sedge peats at Brown Marsh (750 m, fig. 1.2) on the southern Central Plateau. A sample from 30-50 cm of detritus mud underlying 100 cm of *Sphagnum* peat and 70 cm of sedge peat has been radiocarbon dated at 8575 \pm 125 years BP (I-9558, Macphail 1979). This indicates a possible peat accumulation rate in Tasmania of 1-2 cm per century.

7.4.1 Pine Valley cores

There was significant variation in the amount of *Sphagnum*, the degree of humification and the number and type of plant remains (fig. 7.1).

Core 1 was extracted from a site with no surface *Sphagnum* (fig. 7.2). The core revealed no evidence of *Sphagnum* (fig. 7.3). The remainder of the core contained reddish-black fibrous peat with macrofossils of the Restionaceae species, *Restio australis* and *Empodisma minus*. These species occur on the surface.

The surface vegetation of core 2 was dominated by *S. cristatum* to 10 cm depth. The core contained reddish-black fibrous peat, with *Sphagnum* visible throughout the core. Occasional fragments of *Restio australis* and *Empodisma minus* occurred from 15 to 50 cm. At 40 cm there was a large (8 mm diameter) unidentified woody fragment.

The surface vegetation of core 3 was dominated by *Sphagnum*, with *E. minus* and *R. australis* and occasional *Rubus gunnianus*, *Lycopodium fastigiatum* and *Blechnum penna-marina*. The full length of core 3 was dominated by *Sphagnum*, with the degree of humification increasing from 12 cm. *Restio australis* fragments occurred from 8 to 33 cm. The surface of core 4 was dominated by *Leptospermum lanigerum* and *Richea scoparia*, with *Sphagnum*, *Gleichenia* and *Empodisma*. Core 4 was dominated by *Sphagnum* to 30 cm, where there was a change to brownish-black peat with clay and few identifiable macrofossils. There were large woody fragments (possibly *Leptospermum lanigerum*) scattered from 22 to 30 cm.

The surface of core 5 had no surface *Sphagnum*, but was dominated by shrubs - *Richea scoparia* (50% cover), *Richea gunnii* (10% cover) and *Baeckea gunniana* (10% cover). However, the core largely consisted of *Sphagnum*, humifying at 30 cm into a very dark reddish-brown *Sphagnum* peat. There were *R. australis* remains scattered from 10 to 40 cm.

The surface vegetation of core 6 was dominated by *Sphagnum* with *E. minus* and *R. australis*. Core 6 was dominated by *Sphagnum* peat, with *E. minus* remains scattered throughout the length of the core. There was a small amount of clay in the peat from 22 to 50 cm.

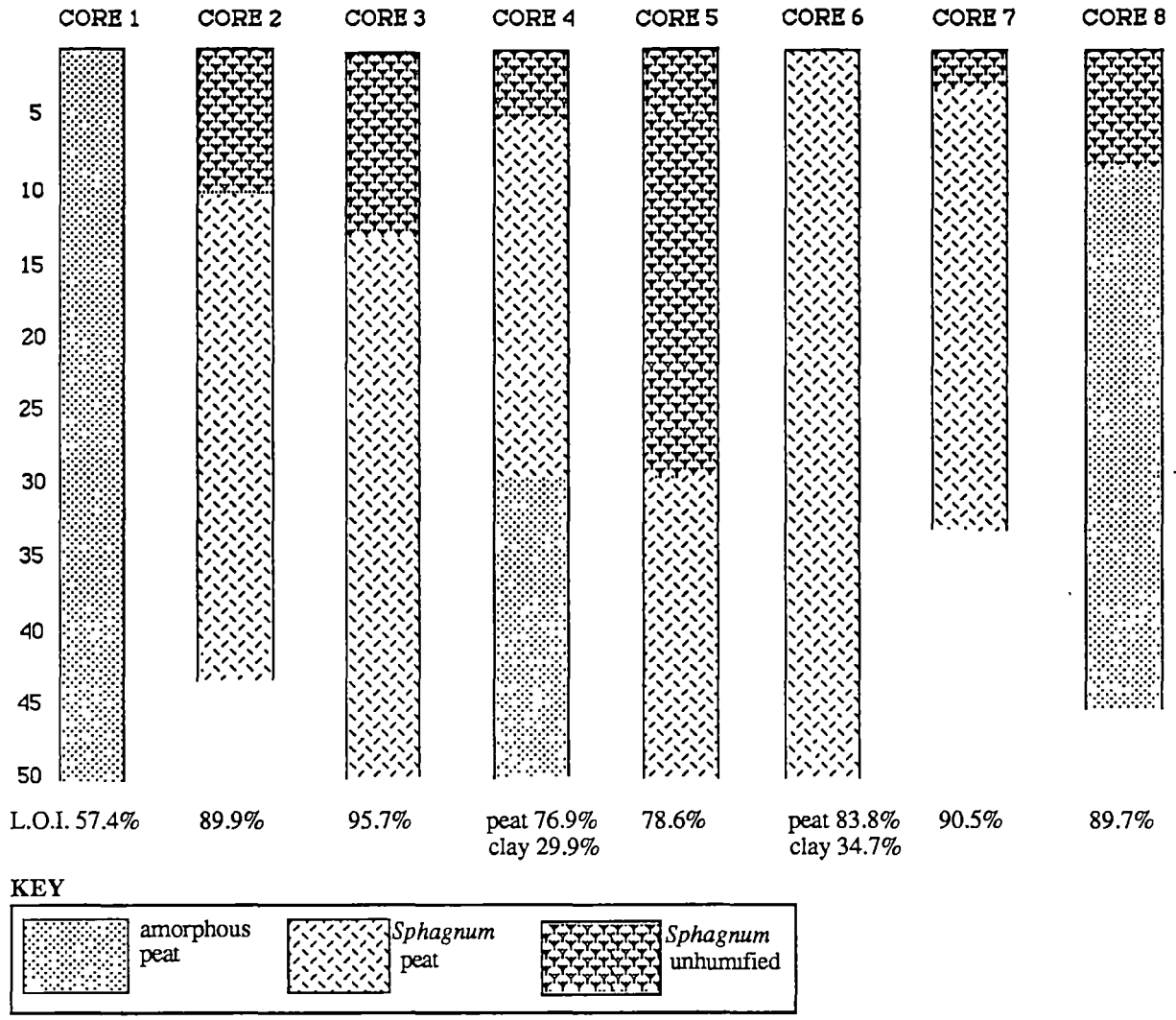


Fig. 7.1 Cross-section of cores taken at 50 metre intervals across Pine Valley. Loss-on-ignition (L.O.I.) values are bulked organic values (except where otherwise indicated) at 550°C. All core depths are in cm.

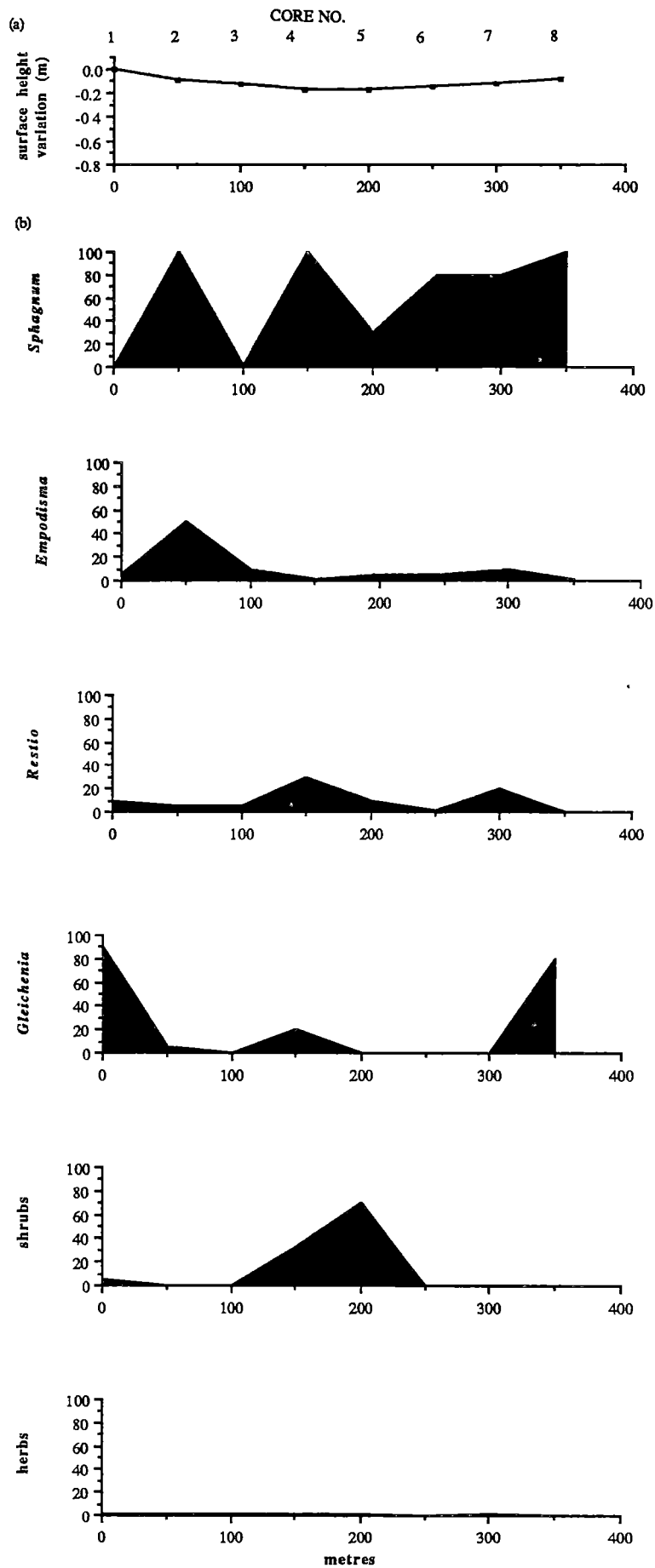
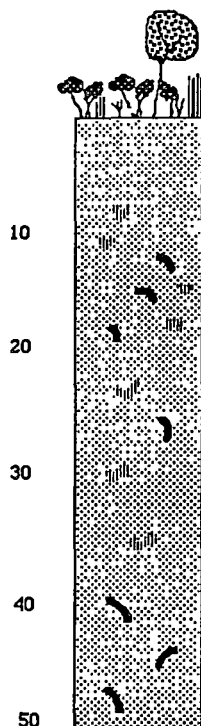
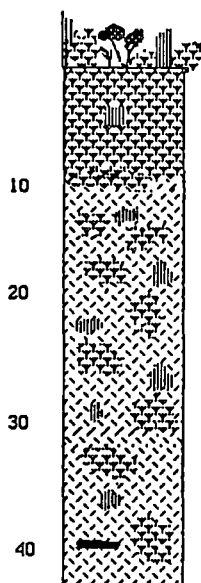


Fig. 7.2 Pine Valley (a) surface cross-section and (b) % cover of species and lifeforms on surface of core sites (50 m intervals).



CORE 1

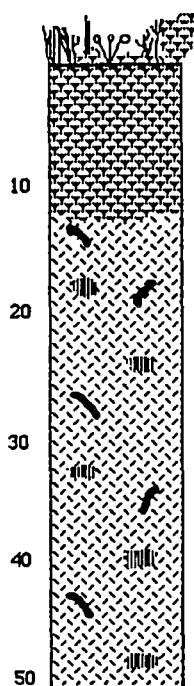
0-50 7.5R 1.7/1; reddish-black peat, fibrous.



CORE 2

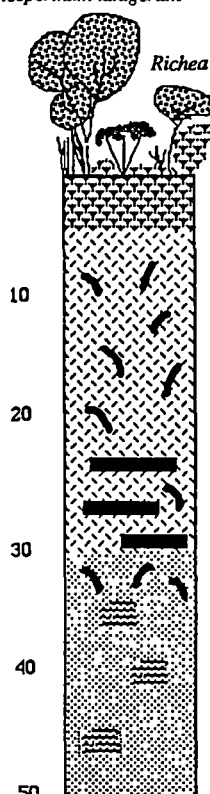
0-42 7.5R 1.7/1; reddish-black peat; very fibrous. *Sphagnum* visible throughout core.

Leptospermum lanigerum



CORE 3

0-12 *Sphagnum* humifying
13-50 2.5YR 2/1; very dark reddish-black peat



CORE 4

0-5 *Sphagnum* humifying
6-39 2.5YR 2/1; reddish-black peat
31-50 5YR 2/2; brownish-black peat with clay

KEY - peats

<i>Sphagnum</i>	
<i>Sphagnum</i> peat	
<i>Empodisma minus</i>	
<i>Restio australis</i>	
<i>Gleichenia alpina</i>	
Charcoal bands	
Peaty clay	
Sandy clay with peat	
Peat	
Clay	
Unidentified woody fragment	

KEY - vegetation

<i>Sphagnum</i>	
<i>Empodisma minus</i>	
<i>Restio australis</i>	
<i>Gleichenia alpina</i>	
herbs	

Fig. 7.3 Details of eight cores extracted at 50 metre intervals across Pine Valley. Vertical measurements are depths (cm) below the surface.

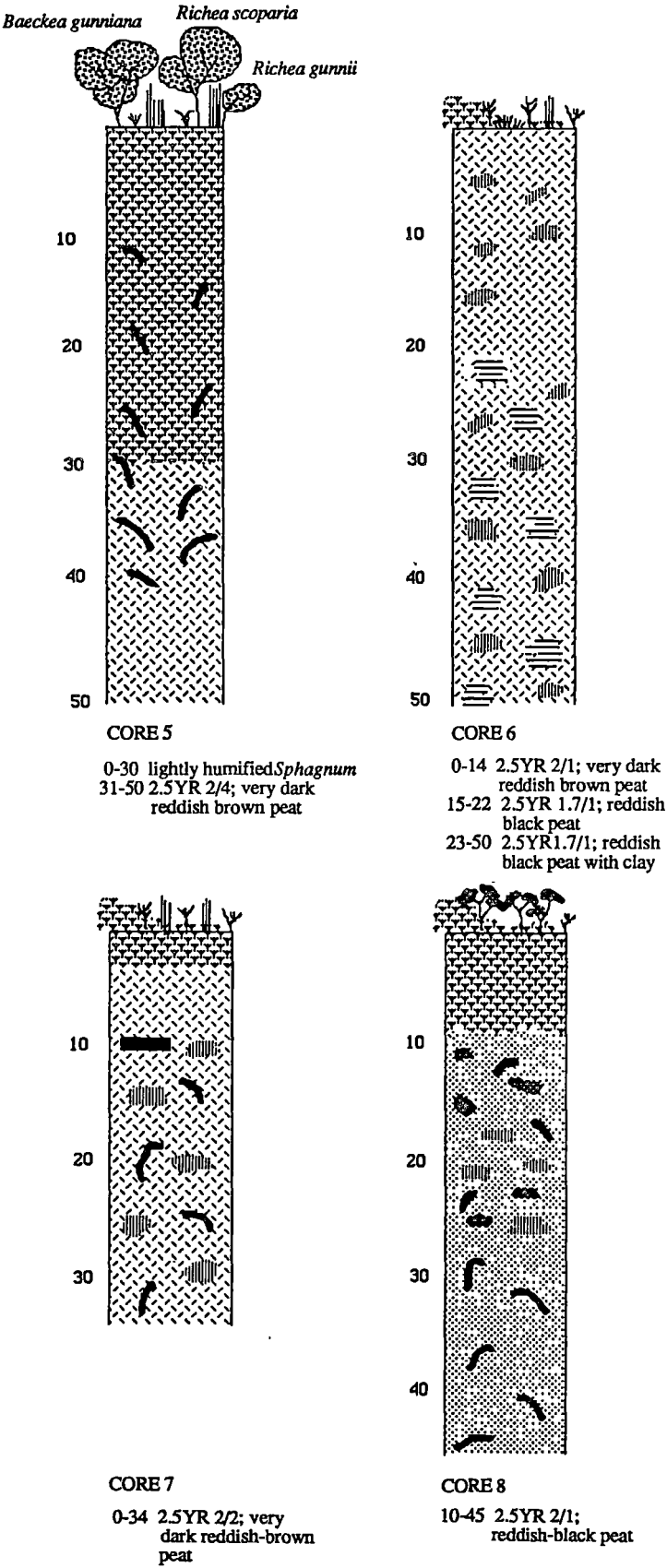


Fig. 7.3 (continued)

The surface vegetation of core 7 was similar to core 6. Core 7 was also dominated by *Sphagnum*, with humification increasing at 3 cm. There were remains of both *E. minus* and *R. australis* scattered through the core from 10 to 34 cm. At 10 cm there was an unidentified woody fragment.

The surface vegetation of core 8 was dominated by *Sphagnum* and *Gleichenia*. Core 8 consisted entirely of *Sphagnum* to 9 cm. There was then a change to reddish-black peat, with *Gleichenia alpina* remains to 25 cm. *E. minus* fragments appeared between 18 and 25 cm, and intermittent *R. australis* appeared throughout the core.

The 1.5 m long core was located near the edge of the mire, close to core 8. The surface vegetation of the core was dominated by *Sphagnum*, *R. australis* and *E. minus*. The core consisted of *Sphagnum*, which is only lightly humified to 35 cm, with more humified *Sphagnum* peat to 65 cm (fig. 7.4). The core changes to a greyish brown peat from 65 to 82 cm, with bands of charcoal to 97 cm. The core contains fragments of *Empodisma* and *Restio* from 0 - 90 cm, with occasional fragments of *Gleichenia* between 10 - 40 cm. From 98 to 130 cm the core changes to a greyish yellow brown peat, with a high clay content. The macrofossils from 100 to 150 cm are dominated by a species not recorded in any other cores or quadrats from this site. This macrofossil may be a *Juncus* species, but insufficient material remained for positive identification, with oxidation occurring after exposure to the atmosphere. At 130 to 150 cm the core has a similar colour, but the peaty clay has a high sand content.

7.4.2 Little Fisher River

The surface vegetation of core 1 was dominated by *Sphagnum* and *Baeckea gunniana* (fig. 7.5). Core 1 was dominated by *Sphagnum*, which became humified at 12 cm, with fragments of *R. australis* occurring from 12 to 42 cm (fig. 7.6). Core 2 had no surface *Sphagnum*, but was dominated by herbs such as *Rubus gunnianus* (20% cover), *Gnaphalium collinum* var. *monocephalum* (20% cover), *Plantago paradoxa* (10% cover) and *Hydrocotyle sibthorpioides* (10% cover). However the peat was dominated by *Sphagnum* to 20 cm, where there was a change to restiad peat (sensu Campbell 1964). The only observable *Sphagnum* in the restiad peat occurred at 28 cm. *E. minus* occurred between 1 and 15 cm. There was a small amount of clay in the *Sphagnum* peat between 15 and 20 cm.

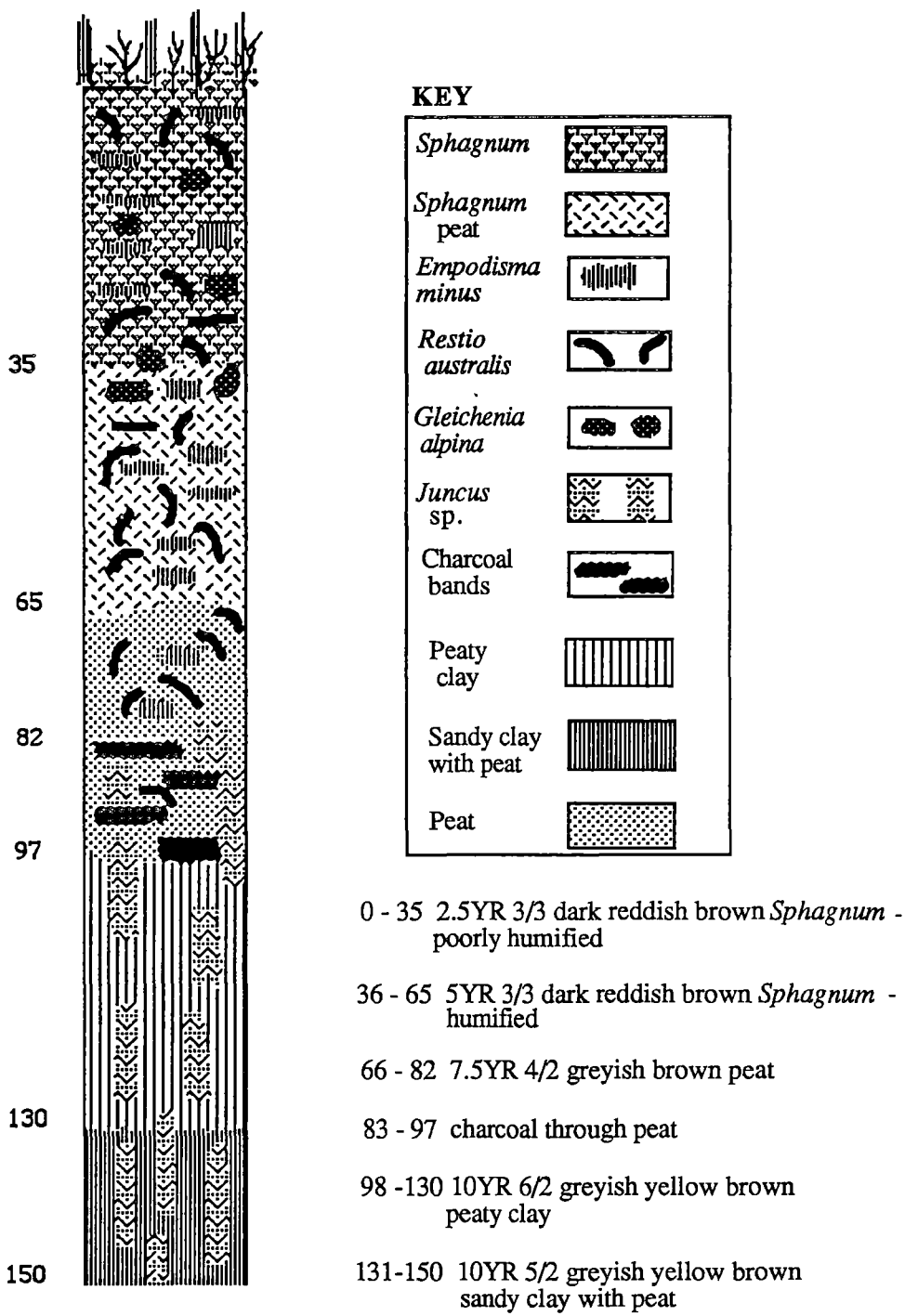


Fig. 7.4 1.5 m core extracted from Pine Valley.

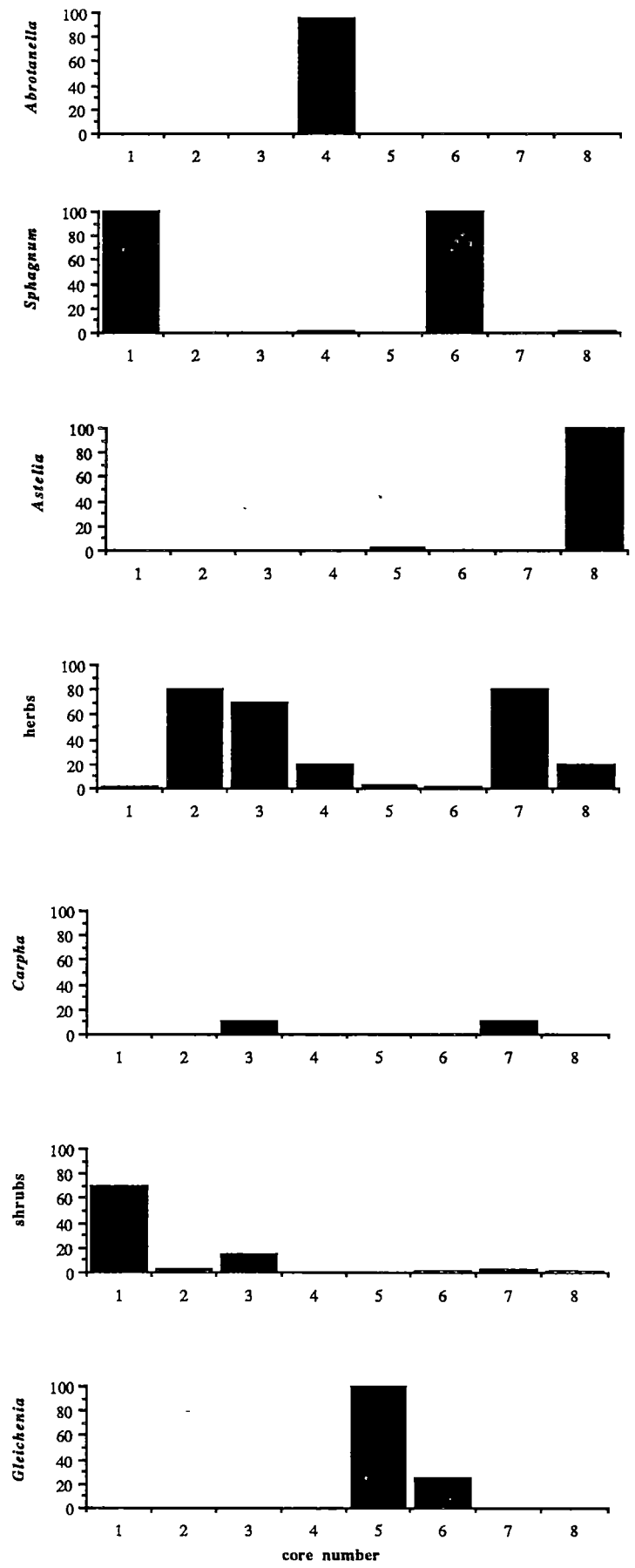


Fig. 7.5 Percentage cover of species and lifeforms on surface of core sites at the Little Fisher River.

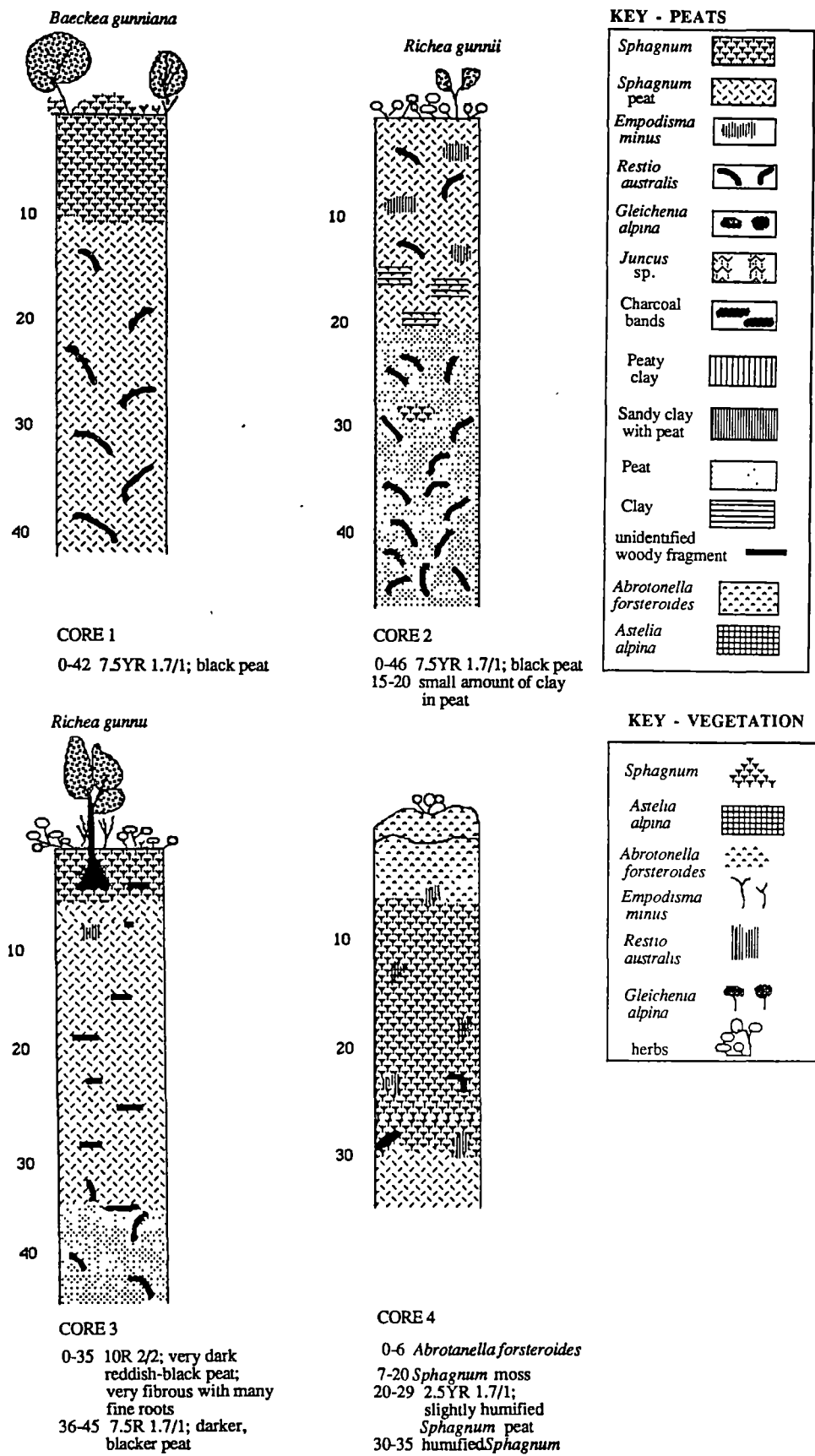
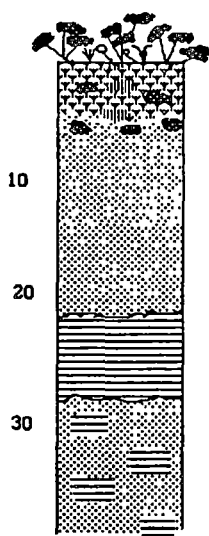
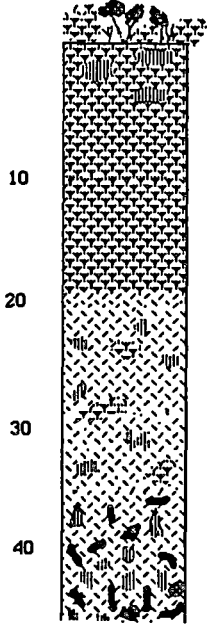


Fig. 7.6 Details of eight cores extracted from the Little Fisher River. Vertical measurements are depths (cm) below the surface.



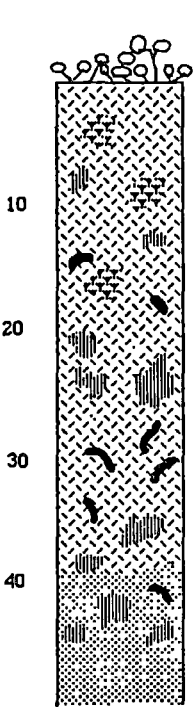
CORE 5

0-5 *Sphagnum* moss
 5-21 7.5YR 1.7/1;
 black peat
 22-27 5YR 2/1;
 brownish-black
 clay band
 28-37 7.5YR 1.7/1;
 black peat with
 occasional clay fragments



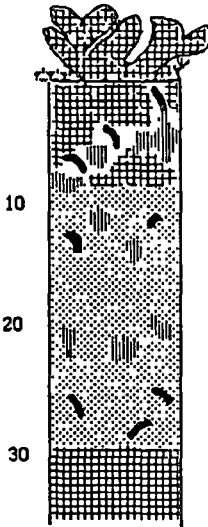
CORE 6

0-19 *Sphagnum* moss
 20-43 7.5R 1.7/1;
 black peat



CORE 7

0-40 10R 2/1; reddish-black
 peat
 41-50 10R 1.7/1



CORE 8

9-30 7.5YR 2/2; brownish-black
 peat; highly humified, very
 fibrous, many fine rootlets

Fig. 7.6 (continued)

There was no surface *Sphagnum* in core 3, with the surface being dominated by *Richea gunnii* (15% cover) and the herbs *Gnaphalium collinum* var. *monocephalum* (25% cover) and *Plantago paradoxa* (20% cover). The core is dominated by *Richea gunnii* roots and *Sphagnum* moss to 5 cm. From 6 to 36 cm the core is dominated by humified *Sphagnum* with many fine rootlets to 10 cm. There are occasional *R. australis* remains from 31 to 43 cm. There were unidentified woody fragments scattered from 3 to 35 cm.

The surface vegetation of core 4 is dominated by the cushion forming *Abrotanella forsteroides*, with no *S. cristatum*. The core is dominated by *A. forsteroides* to 6 cm, where there is a change of dominance to *S. cristatum*, which becomes slightly humified at 20 cm, with occasional *E. minus* and *R. australis* fragments. From 30 cm the core is dominated by humified *Sphagnum*.

The surface vegetation of core 5 is dominated by *Gleichenia alpina* (100% cover). The core is composed of *Sphagnum*, *G. alpina* and *E. minus* to 5 cm, where there is a change to a less fibrous black peat. This peat is more compact than previous cores, with few identifiable remains. There is a clay band mixed with peat between 22 and 27 cm, then a reversion to black peat with occasional clay fragments.

The surface vegetation of core 6 is dominated by *Sphagnum* and *Gleichenia*. Core 6 is dominated by *Sphagnum* moss to 20 cm, where there is an increase in humification, but *Sphagnum* is identifiable for the entire length of the core. There are occasional *E. minus* fragments to 5 cm, then no identifiable remains to 20 cm. From 20 cm there are occasional *E. minus* and *R. australis* remains from 20 to 35 cm. From 35 to 45 cm there is an increased number of *R. australis* and *E. minus* remains, and the appearance of *Gleichenia* fronds.

The surface vegetation of core 7 consists of herbfield, with a similar species composition to core 3 from this site. *Sphagnum* is absent from the surface. The core is dominated by humified *Sphagnum* peat to 40 cm, where there is a change to a darker, less fibrous, more compact reddish black peat. There are patches of non-humified *Sphagnum* to 20 cm and *E. minus* fragments throughout the core, with occasional *R. australis* fragments.

The surface of core 8 is dominated by *Astelia alpina* (100% cover), with herbs such as *Acaena novae-zelandiae* and *Hydrocotyle sibthorpioides*, and a small amount of *S. cristatum* (<1% cover). The core is dominated by the remains of *A. alpina* to 8 cm.

From there to 30 cm, there is a highly humified, very fibrous brownish-black peat. *E. minus* and *R. australis* remains occur from 0 to 29 cm. From 30 to 35 cm the core consists entirely of *A. alpina* remains.

The sole clay band in core 5 from the Little Fisher River does not appear to signify a change in vegetation at this site. Core 3 is the only example of a restiad peat both preceding and succeeding *Sphagnum* peat (fig. 7.7).

As well as the cores presented, several cores were taken beneath sites dominated by *Gleichenia* at the Little Fisher River and examined on site to determine if any *Sphagnum* was present in the core. It seemed possible that the hummocky appearance typical of many Tasmanian *Gleichenia* mires may have been the result of succession from *Sphagnum* mires. *Sphagnum* was not, however, present in any of these cores.

7.4.3 Excavations

The results of excavations around and below plants to elucidate the root zone are shown in fig. 7.8. An 80 cm tall *Eucalyptus coccifera* seedling (no visible lignotuber) had its thickest roots commencing 10 cm below the surface in *Sphagnum* peat. A *Helichrysum hookeri* shrub, 1 m tall, had its thickest roots located approximately 70 cm beneath the surface, with finer rootlets continuing to 102 cm beneath the surface, in humified *Sphagnum*. A *Richea scoparia* bush, 1 m tall, had its thickest roots at 10 cm beneath the surface, with adventitious roots continuing to 15 cm below the surface in *Sphagnum* peat. *Empodisma minus* had its main zone of rhizomes and roots 10 cm beneath the surface in *Sphagnum*.

7.4.4 Surface trends

No meaningful results were obtained by the TWINSpan classification. Surface topography and vegetation cover for a transect at Paradise Plains (fig. 7.9) and the Walls of Jerusalem (fig. 7.10) show no significant partitioning of species between hummocks and hollows. At the Walls of Jerusalem, *Pentachondra pumila* occurs only on hummocks (3 records), with *Oreobolus pumilio*, *Coprosma pumilio* and *Celmisia asteliifolia* also occurring only on hummocks (2 records each), but the small numbers prevent meaningful analysis. Only *Oreobolus pumilio* is restricted to hummocks at Paradise Plains (2 records).

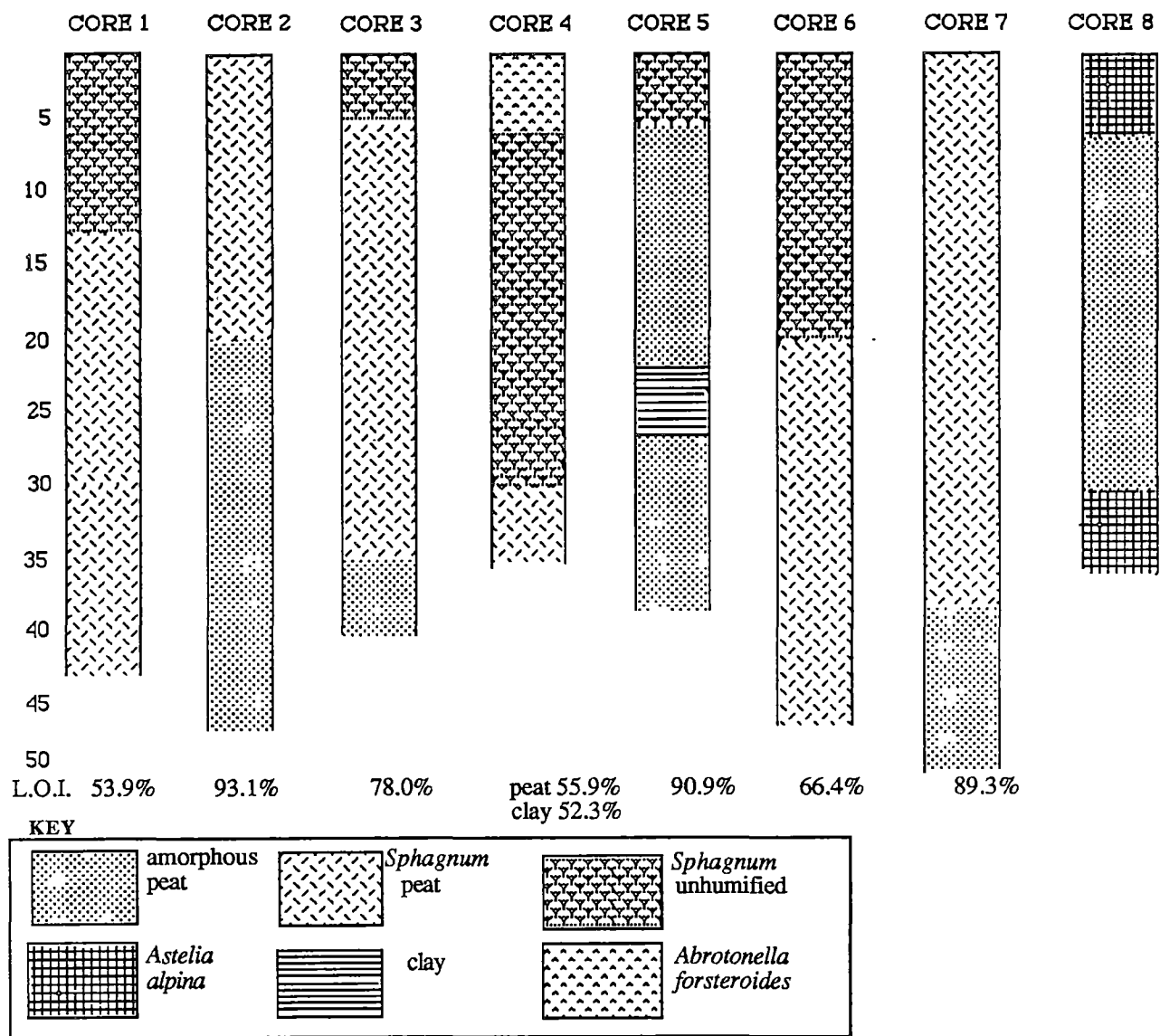
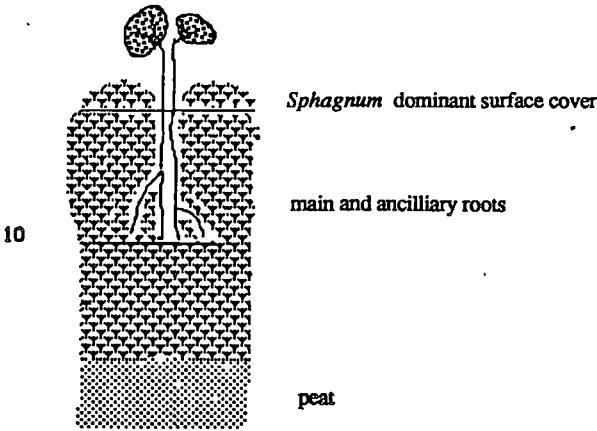
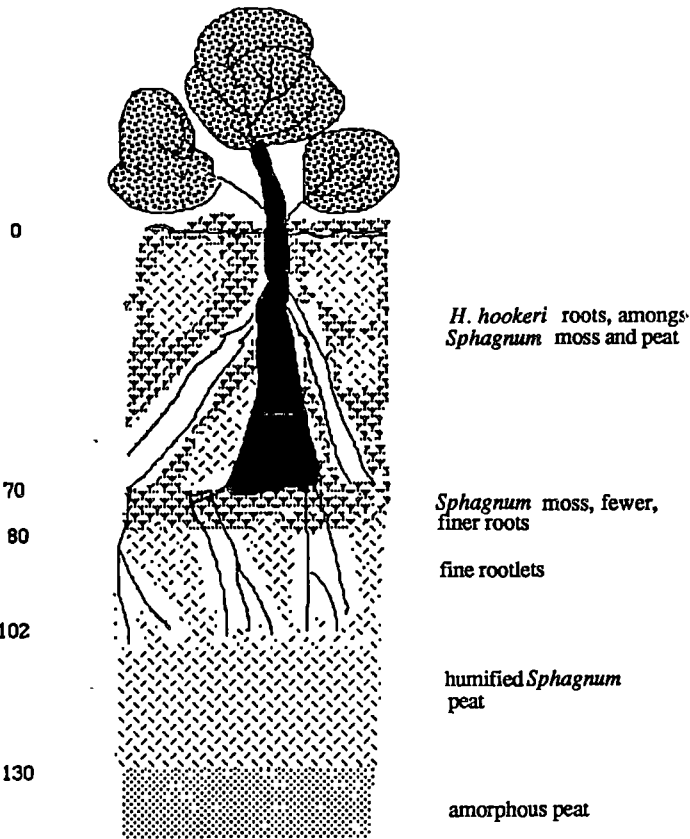


Fig. 7.7 Peat cores from a heterogeneous *Sphagnum* mire at the Little Fisher River. Loss-on-ignition (L.O.I.) values are bulked organic values (except where otherwise indicated) at 550°C.

(a) *Eucalyptus coccifera* seedling - 80 cm tall



(b) *Helichrysum hookerii*



(c) *Richea scoparia*

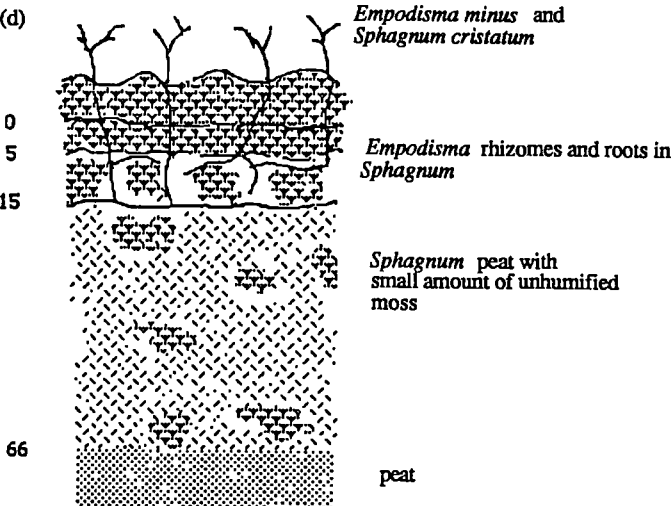
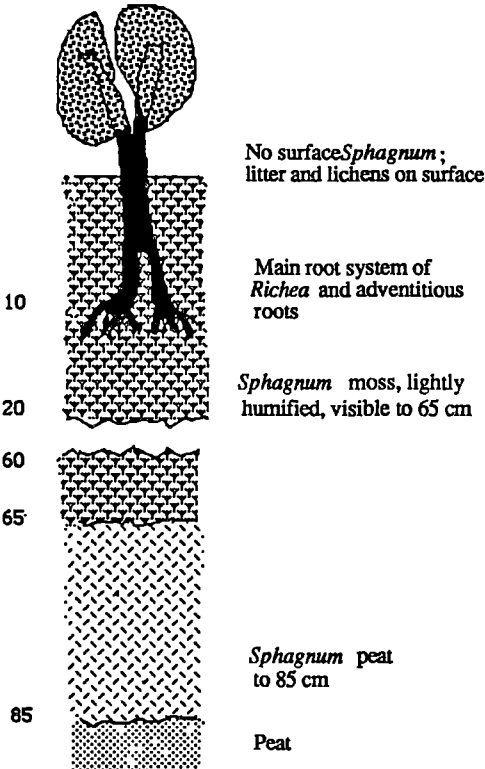


Fig. 7.8 Details of four excavations made at Pine Valley. For key to core and vegetation, see fig. 7.3. Vegetation above the surface is not to scale.

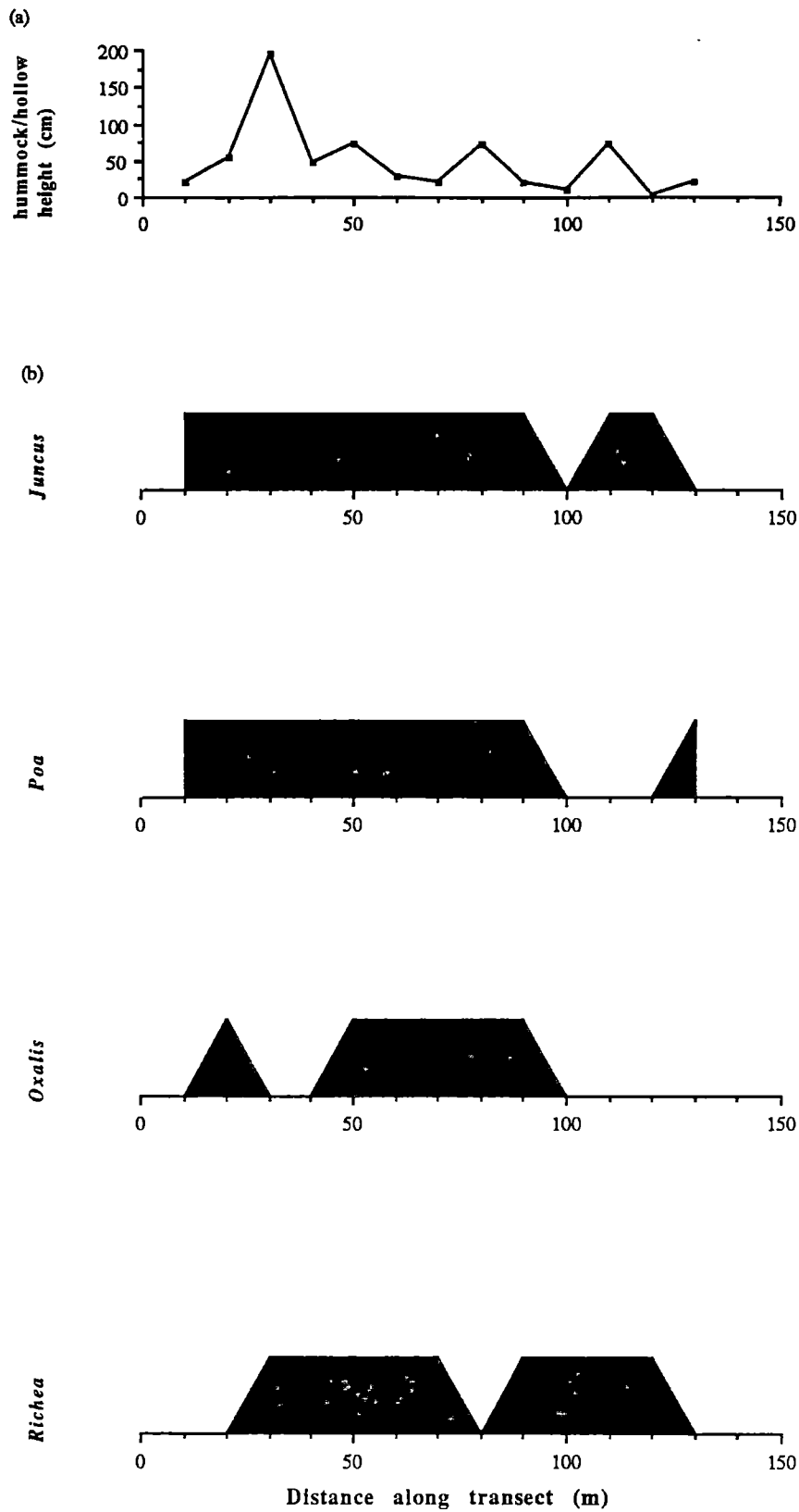


Fig. 7.9 (a) surface transect and (b) species presence/absence on hummocks and hollows along a 130 m transect at Paradise Plains. Species that occurred less than twice along the transect are not depicted. *Sphagnum* (not depicted) occurred on all hummocks and hollows.

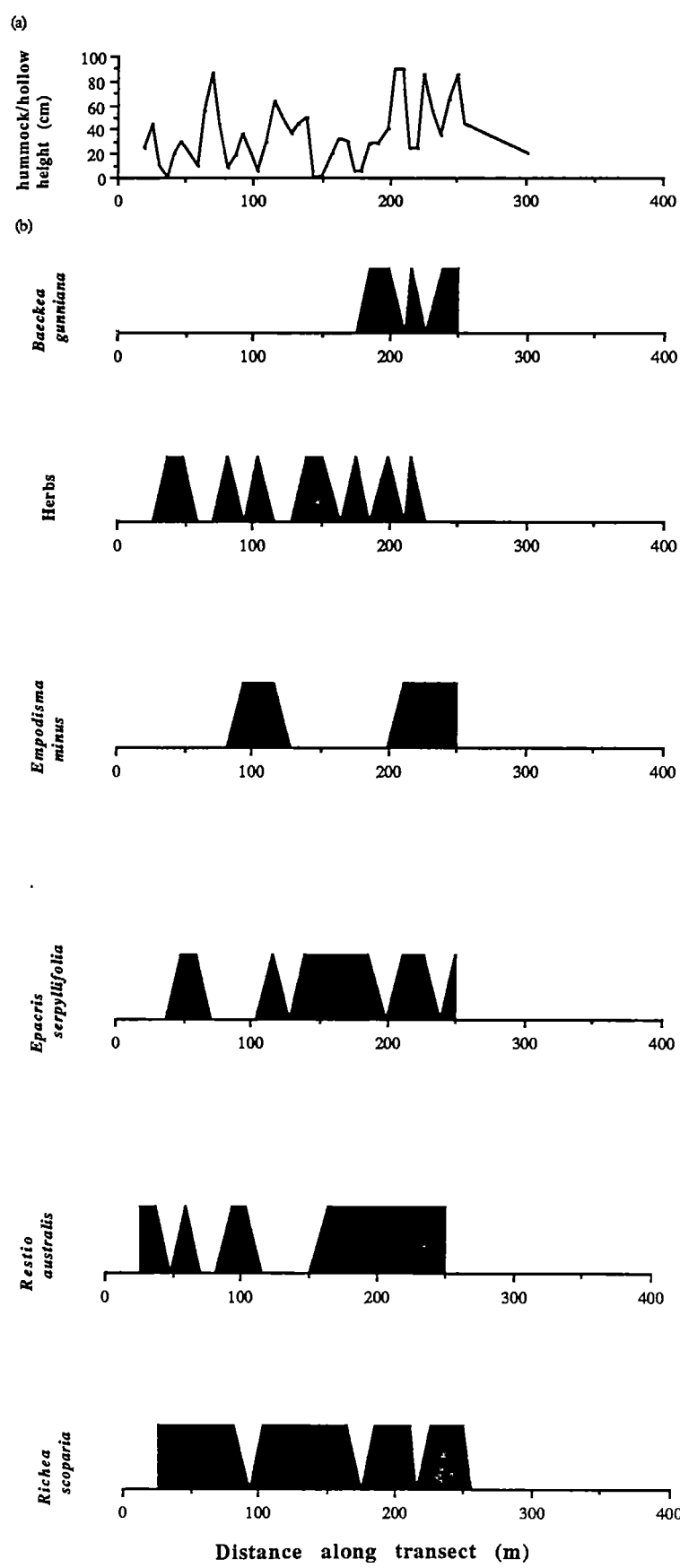


Fig. 7.10 (a) surface transect and (b) species presence/absence on hummocks and hollows along a 270 m transect at the Walls of Jerusalem. Only species that occurred more than twice along the transect are depicted. *Sphagnum* (not depicted) occurred on all hummocks and hollows.

While there was no significant partitioning by species, herbs are preferentially located in hollows at the Walls of Jerusalem (chi-square=5.5, $p<0.05$). No other lifeforms are preferentially located on either hummocks or hollows at either Paradise Plains or the Walls of Jerusalem (table 7.1).

Table 7.1 Numbers of instances each lifeform recorded on hummocks and hollows.

Site and Lifeform	No. times recorded on		Total. no. of
	hummocks	hollows	hummocks/hollows
<u>Walls of Jerusalem</u>			13/8
Graminoid	12	9	
Herb	8	17	
Shrub	23	12	
<u>Paradise Plains</u>			5/5
Graminoid	7	12	
Herb	5	5	
Shrub	7	12	

7.5 Discussion

The identified presence of all the major species that comprise the contemporary vegetation throughout the cores suggests that differential decay rates (Clymo 1987) have not biased macrofossil representation in these cores.

Neither the cores from the transect across Pine Valley (fig. 7.1) nor the cores from the mosaic of vegetation types at the Little Fisher River mire (fig. 7.7) show any consistency in peat types at different depths. The amorphous peat of cores 1 and 8 is of interest, as these cores are at either edge of the flat-bottomed valley floor at Pine Valley. One possible interpretation is that these cores define the past margins of *Sphagnum* at this site. However, the presence of amorphous peat at the base of core 4 (in the centre of the valley basin) is evidence for localised vegetation patterning and succession rather than an indication of marginal : central differences.

The site at the Little Fisher River where *Sphagnum* preceded present-day herbfield is a wet site (core 7), on a slope at the edge of the mire. This area appears to be undergoing some contemporary change, as suggested by the presence of a dead *Richea scoparia* shrub, the presence of eucalypt seedlings in the moss and the absence of *Sphagnum*. It may be that moisture conditions at the edge of the mire have been altered, favouring succession away from *Sphagnum*.

Cushion bogs and *Sphagnum* bogs form mosaics in Tasmania (Campbell 1983). The change from *Sphagnum* peat to *Abrotanella* at the Little Fisher River suggests a possible successional sequence of these two morphologically different (Gibson 1988) cushion forming species.

The cores from both sites suggest that succession in Tasmanian *Sphagnum* mires is multidirectional. Change appears to be localised, with 'microsuccessions' occurring across mires (e.g. Ratcliffe and Walker 1958). Core 8 from the Little Fisher River provides support for the concept of repeatable change (Sjors 1980) during succession. The surface and upper 8 cm of the core are dominated by *A. alpina*. The core then changes to an amorphous peat with Restionaceae fragments, but no visible remains of *A. alpina*. The base of the core is dominated by *Astelia alpina*. Fig. 7.11 summarises the recent successional changes suggested by 16 cores from two sites.

There is only one example from the cores of a transitional change from *Sphagnum* to another peat type (amorphous peat with restiad fragments, core 3, Little Fisher). However, the change from *Sphagnum*-dominated cores to present-day vegetation, dominated by herbs, cushion plants or shrubs, does not support the concept of a *Sphagnum* climax (Katz 1926). Conversely, it may be that succession away from *Sphagnum* is in response to an altered fire regime. Current fire frequency in many locations is thought to be different from that imposed by the aborigines (Bowman and Brown 1986). Past firing practices may have prevented fire-sensitive shrubs, such as *Richea scoparia* (chapter 6), from becoming dominant.

The model of recent successional change suggested by cores from these two sites may be similar for other mires with present-day vegetation which categorises them as 'central' type Tasmanian *Sphagnum* peatlands (chapter 3). However, 'fringe' peatlands, such as rainforest, aquatic and snowpatch *Sphagnum* mires, are likely to have quite different successional histories which reflect the specialised habitats of these types (chapter 3). For example, the successional sequence of aquatic *Sphagnum* bogs may follow that suggested by the traditional hydrosere (Sjors 1980, Moore and Bellamy 1974).

Five of the cores and excavated sites are currently dominated by shrubs, such as *Richea scoparia* and *Baeckea gunniana*, with no surface *Sphagnum*, even though *Sphagnum* occurs immediately below the surface in all cases. The data from these cores supports the proposal that over time a shrub layer develops. In the northern hemisphere this most commonly occurs on *Sphagnum* hummocks (Luken *et al.* 1985). The data from Tasmania are more equivocal.

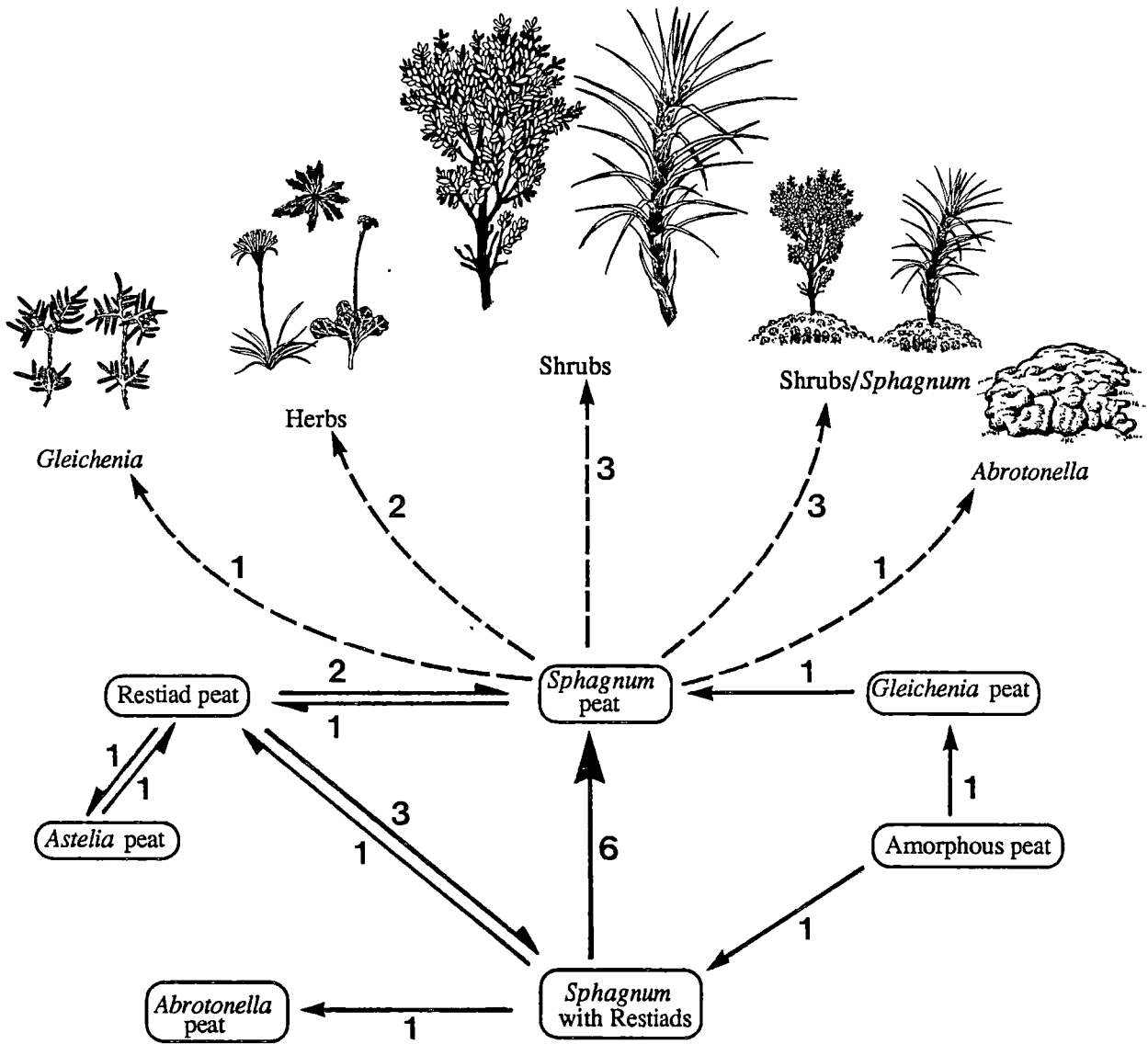


Fig. 7.11 Model of successional changes from 50 cm cores from Pine Valley and the Little Fisher River. The number against each arrow gives the number of recorded instances of that particular transition. Solid lines indicate changes in peat type. Dotted lines indicate change from cores to present-day vegetation.

The rooting of shrubs in the *Sphagnum* moss is evidence that plants can germinate and grow amongst *Sphagnum*, with the possibility that shrubs will become dominant. The relatively unhumified *Sphagnum* moss that forms the substratum for these shrubs forms a peat with large pore spaces. This peat holds large quantities of water and has a high hydraulic conductivity (Andrus 1986), conditions which might favour woody growth. It has been found in the northern hemisphere that if a *Sphagnum* mat is established and continues to grow (Glaser and Janssens 1986), the acidifying properties of the *Sphagnum* can allow domination by *Sphagnum* (Andrus 1986), thereby limiting the potential co-existing plants to those that can survive acid conditions. However, in Tasmania alpine vegetation occupies sites which are more acid than sites dominated by *Sphagnum* (Kirkpatrick 1984).

The preferential location of herbs in hollows at one site was the only discernible patterning of species between hummocks and hollows along transects. This is surprising given the descriptions of such partitioning from the northern hemisphere (Vitt and Slack 1984, Luken 1985, Rydin and McDonald 1985, Kenkel 1988). However, species presence/absence may not be the best indicator of hummock/hollow patterning (Greig-Smith 1983), which could be better expressed in abundance rather than expressed in exclusion. Sampling in a greater number of geomorphic types may also give different results. Observations of some linear peatlands [chapter 2, plate 2(a)] suggest a greater density of shrubs on the hummocks compared to the hollows.

Conversely, the relative absence of species partitioning may be because species do not need to specialise to such an extent as in northern hemisphere peatlands. The habitat conditions on Tasmanian mires do not appear to be as extreme as northern hemisphere mires, with hollows rarely containing permanent water. The vegetation on Tasmanian mires does not contain *Sphagnum*-obligate species, with almost all species recorded on *Sphagnum* peatlands occurring in other vegetation types (chapter 2). Changes in species abundance across Tasmanian *Sphagnum* mires (Kirkpatrick and Whinam 1988) may largely be a response to environmental changes across the peatland, rather than to moisture regimes imposed by hummock-hollow topography. Not all northern hemisphere *Sphagnum* peatlands exhibit hummock-hollow development (Hofstetter 1983), with small-scale distribution of species better explained for ombrotrophic sites than for minerotrophic sites (Andrus 1986).

7.6 Conclusion

The most common pathway observed in cores from two Tasmanian *Sphagnum* peatlands is restiad peat to *Sphagnum*/restiad peat to *Sphagnum* peat to present-day shrubs. The presence of herbs and shrubs on sites currently without *Sphagnum* but with *Sphagnum*-dominated cores suggests that *Sphagnum* may be succeeded by either herbs or shrubs.

Herbs appear to be preferentially located in hollows in one Tasmanian *Sphagnum* peatland. Shrubs appear to be preferentially located on hummocks in some peatlands, but not others. The absence of the environmental extremes present in northern hemisphere hummocks/hollows may have resulted in less rigorous partitioning of species.

The evidence from the peat cores suggests multi-directional succession of these Tasmanian *Sphagnum* peatlands, with recurring change occasionally bringing back earlier phases of development. This proposal is contrary to earlier descriptions of *Sphagnum* bog succession in North Island, New Zealand (Cockayne 1958), but in line with more recent studies (Walker and Walker 1961, Casparie 1969, Sjors 1980, Barber 1981, Glaser and Janssens 1986). The many temporal and spatial changes exhibited in these Tasmanian examples are likely to be the result of innumerable local and regional events (Heinselman 1970, Sjors 1980).

CHAPTER 8 - CONCLUSIONS

8.1 Summary of findings

The scenario that emerges from the preceding discussion is that there appears to be a variety of endogenous and exogenous factors influencing the past, present and future distribution, geomorphic type and floristic composition of *Sphagnum* peatlands. Many of these factors interact to result in both central types and unique mires. Some of these factors will result in both changes towards and away from *Sphagnum*-dominated mires.

To what extent do Tasmanian *Sphagnum* peatlands conform in their location and variability to the patterns described for the northern hemisphere?

Topographic and successional expression is limited in Tasmanian *Sphagnum* peatlands, due to relatively low effective precipitation. The most common topographic settings for Tasmanian *Sphagnum* peatlands are river valleys, beside lakes and streams or on sandstone shelves, settings which lend themselves to the impediment of drainage.

The various geomorphic types of *Sphagnum* peatland found in Tasmania are located in habitats with distinctly different environmental characteristics. *Sphagnum* mires occur in all parts of Tasmania except the south-west. Despite topographic and climatic suitability, the absence of *Sphagnum* peatlands on the siliceous substrate in south-western Tasmania suggests this area to be too nutrient-poor for the widespread growth of *Sphagnum*, and these peatlands are dominated by buttongrass (*Gymnoschoenus sphaerocephalus*). This is in contrast with northern hemisphere data which suggests *Sphagnum* occupies nutrient-poor habitats.

The Tasmanian *Sphagnum* mires have floristic and structural affinities with *Sphagnum* mires in New South Wales, Victoria and New Zealand. Tasmanian *Sphagnum* mires have no obligate vascular plant species, with the possible exception of *Richea gunnii*.

What phytosociological communities can be distinguished within Tasmanian *Sphagnum* peatlands and how do they relate to environmental conditions?

Eight ecologically distinct groups span a largely continuous gradation, from high altitude to low altitude sites, reflecting changes in temperature and precipitation. Floristic variation between sites can largely be explained by the climatic gradient, location along a nutrient gradient (reflected by rock type, peat depth, peat fertility) and a fire gradient. There is a correlation between some geomorphic and floristic types of *Sphagnum* mires.

The most common floristic type is the *Richea-Sphagnum* bog. Less frequent types, such as the snowpatch-*Sphagnum* community, rainforest-*Sphagnum* mires and aquatic *Sphagnum* bogs, tend to occur in specialised habitats.

Do shading, nutrient status and moisture availability affect the growth rate of *Sphagnum cristatum*? Do these environmental factors affect the growth rate of *Sphagnum* by altering its competitive relationships with other Tasmanian peatland species?

The combined experimental treatment of no drought with low nutrients resulted in relatively lower biomass of *S. cristatum* than drought combined with low nutrients. The only experimental treatment to affect the dry matter biomass of *Sphagnum*-associates significantly was shade, with shade resulting in relatively less biomass. However, in the absence of shade, *Sphagnum*-associates showed an increase in biomass when compared with *Sphagnum*, indicating a change in the competitive balance.

The degree of humification of *Sphagnum* varied with experimental treatments. A significantly higher proportion of humified moss occurred under several experimental treatments. It appears that nutrients can increase the rate of humification, a finding reported elsewhere. Droughting with no nutrients resulted in a significantly lower proportion of humified moss, suggesting that dry conditions inhibit humification.

Does marsupial grazing significantly alter the competition and productivity of plants in a *Sphagnum* peatland?

The results of monitoring at Mt Field and the Walls of Jerusalem suggest that the effects of grazing are more noticeable at lower altitude, higher productivity sites than higher altitudes, a phenomenon recorded for Tasmanian sub-alpine grasslands and grassy woodlands. Irrespective of grazing, all vascular species grew at a faster rate at the lower altitude site at Mt Field. *S. cristatum* grew at a faster rate under the cooler, moister conditions at the Walls.

There is no evidence that *Sphagnum* moss is grazed. *Epacris serpyllifolia*, *Empodisma minus* and *Richea acerosa* show the greatest impact of grazing check. Marsupials may affect the flora of *Sphagnum* mires by a combination of trampling and grazing, with the effects of grazing on species such as *Astelia alpina*, *Empodisma minus* and *Poa* spp. readily observed.

Marsupial grazing of palatable mire species suggests that grazing may assist in maintaining conditions suitable for *Sphagnum*. The grazing of herbs, shrubs, grasses and graminoids may alter competition between these species and *Sphagnum* for light.

What effect does fire have on the species composition and survival in a Tasmanian *Sphagnum* peatland?

Fire appears to have a dramatic short-term effect on the vegetation of a *Sphagnum* peatland on the Central Plateau of Tasmania. The most significant change caused by the fire at Kenneth Lagoon has been a massive decline in *Sphagnum* cover and vitality. This may be in part a response to dessication, due to altered runoff and transpiration rates. There has been an increase, at least in the short-term, in cover of restiads and *Gleichenia alpina*.

The initial effects of the fire varied according to the vegetation present, which in turn influenced the local severity of the fire. Some peatland species, such as *Richea scoparia*, appear to be fire sensitive, while the survival of other species suggests an ability to withstand fire.

These findings from Kenneth Lagoon are consistent with observations made in southern and western Tasmania, which suggest that in some situations, frequent fire may lead to the replacement of *Sphagnum* by *Gymnoschoenus sphaerocephalus*.

Is spatial variation a reflection of temporal trends in Tasmanian *Sphagnum* peatlands? Are temporal trends uniform and unidirectional?

Insufficient evidence was collected to suggest whether certain species are preferentially distributed on either hummocks or hollows in Tasmanian *Sphagnum* peatlands. However, at the Walls of Jerusalem herbs appear to be preferentially located in hollows. Shrubs appear to be preferentially located on hummocks in linear mires (string bogs).

Localised micro-succession appears to occur in Tasmanian *Sphagnum* peatlands, probably in response to innumerable local and regional events. However, evidence from peat cores and excavations suggests that there is a major successional pathway for Tasmanian *Sphagnum* mires. While exceptions do occur, the most common trend is from *Sphagnum*/restiad to *Sphagnum* mires, with possible progression to domination by shrubs or herbs.

What are the major factors influencing the distribution and types of Tasmanian *Sphagnum* mires?

This thesis has added to our knowledge of many of the pathways of *Sphagnum* mire development, and a model of causation of distribution of *Sphagnum* mires in Tasmania has been developed (fig. 8.1). *Sphagnum* mires in Tasmania occur in topographic situations where drainage is impeded and sediments can accumulate. They are restricted to these topographic situations due to potential moisture stress imposed by higher evapotranspiration rates in Tasmania than are usual in those parts of the northern hemisphere dominated by *Sphagnum*. The maximum temperature of the warmest month in areas where Tasmanian *Sphagnum* mires occur is below 20°C; mean annual precipitation is greater than 1540 mm, with precipitation not less than 68 mm in the driest month. *Sphagnum* mires occur in Tasmania when values of N are greater than 0.5%, values of P are greater than 70 $\mu\text{g g}^{-1}$ and values of K, although extremely variable, are greater than 91 $\mu\text{g g}^{-1}$. Although climatic limitations restrict morphologic expression in Tasmania, the results of this thesis suggest that the ecology of Tasmanian *Sphagnum* mires is largely congruent with global data, except for phosphorus levels, which are higher than northern hemisphere data. Unlike the situation in the northern hemisphere, *Sphagnum* mires do not occupy the poorer edaphic sites. This is because the nutrient-poor peats of western Tasmania appear to have no analogue in the northern hemisphere.

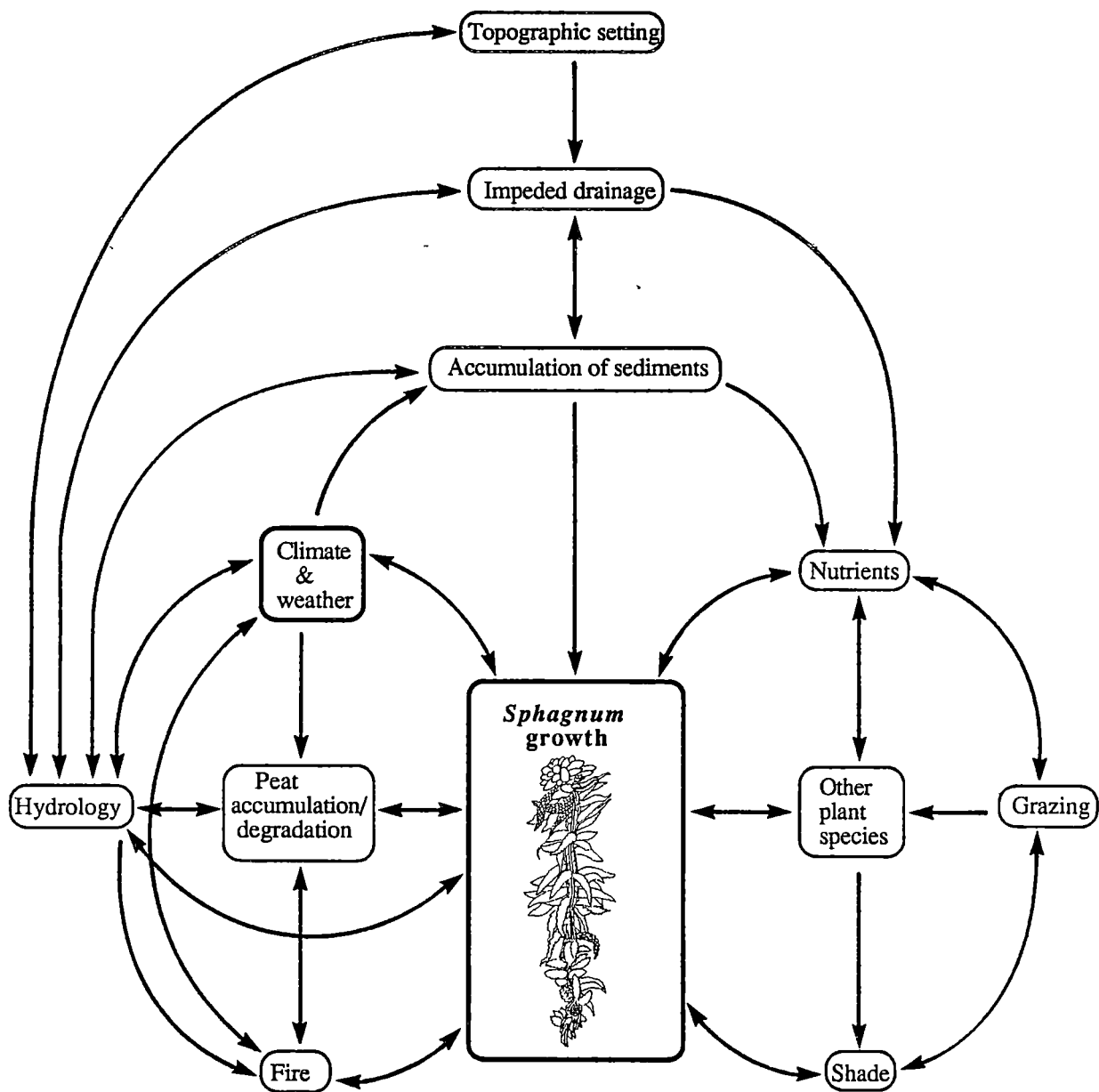


Fig. 8.1 Model of the possible development and regulating mechanisms of Tasmanian *Sphagnum* peatlands. Arrows indicate direction of influence.

The results of glasshouse and grazing experiments, and the analyses of cores, show potential competitive exclusion of *Sphagnum* by other species, commonly shrubs and, less frequently, herbs and cushion plants. Marsupial grazing may be beneficial for *Sphagnum* by inhibiting competition from other plant species. Although the results of monitoring suggest that the effects of fire on *Sphagnum* moss in the short-term are potentially devastating, occasional fire may, in the longer term, inhibit succession away from *Sphagnum* mires to shrubs. Thus, within its topographic/climatic/edaphic envelope the occurrence of *Sphagnum* is apparently contingent upon appropriate disturbance and grazing regimes.

REFERENCES

- Anderson J.A.R. (1983) The tropical peat swamps of western Malaysia. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World. Vol 4B.* (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 181-99.
- Andrus R.E. (1986) Some aspects of *Sphagnum* ecology. *Can. J. Bot.* **64**, 416-26.
- Ashton D.H. & Hargreaves G.R. (1983) Dynamics of subalpine vegetation at Echo Flat, Lake Mountain, Victoria. *Proc. Ecol. Soc. Aust.* **12**, 35-60.
- Austin M.P. (1987) Models for the analysis of species' response to environmental gradients. *Vegetatio* **69**, 35-45.
- Backeus I. (1988) Weather variables as predictors of *Sphagnum* growth on a bog. *Holarctic Ecol.* **11**, 146-150.
- Barber K.E. (1981) *Peat stratigraphy and climatic change: a paleoecological test of the theory of cyclic bog regeneration.* Balkema, Rotterdam.
- Blain J., Caron M. & Joyal P. (1987) The use of *Sphagnum* peat moss for tree seedling production. *Proceedings of Symposium '87 Wetlands/Peatlands.* Alberta, Canada, 209-11.
- Boatman D.J., Goode D.A. & Hulme P.D. (1981) The Silver Flowe. III. Pattern development of Long Loch B and Craigeazle Mires. *J. Ecol.* **69**, 897-918.
- Boatman D.J. & Tomlinson R.W. (1977) The Silver Flowe. II. Features of the vegetation and stratigraphy of Brishie Bog, and their bearing on pool formation. *J. Ecol.* **65**, 531-46.
- Boch M.S. & Kuz'mina E.O. (1983) Morphological structure of *Sphagnum* mosses in various habitats and its alteration under the effect of organic fertilizers. *Soviet J. Ecol.* **14**, 141-49.
- Bowman D.M.J.S. & Brown M.J. (1986) Bushfires in Tasmania: a botanical approach to anthropological questions. *Archaeol. Oceania* **21**, 166-71.
- Bowman D.M.J.S. & Jackson W.D. (1981) Vegetation succession in South West Tasmania. *Search* **12**, 358-62.
- Bowman D.M.J.S., Maclean A.R. & Crowden R.K. (1986) Vegetation-soil relations in the lowlands of south-west Tasmania. *Aust. J. Ecol.* **11**, 141-53.
- Bowman D.M.J.S. & Minchin P.R. (1987) Environmental relationships of woody vegetation patterns in the Australian monsoon tropics. *Aust. J. Bot.* **35**, 151-69.
- Billings W.D. & Mooney H.A. (1968) The ecology of alpine and arctic plants. *Biol. Review* **43**, 481-529.
- Brasell H.M. & Mattay J.P. (1984) Colonization by bryophytes of burned *Eucalyptus* forest in Tasmania, Australia: changes in biomass and element content. *The Bryol.* **87**, 302-07.
- Brock T.C.M. & Bregman R. (1989) Periodicity in growth, productivity, nutrient content and decomposition of *Sphagnum recurvum* var. *mucronetum* in a fen woodland. *Oecologia* **80**, 44-52.

- Brown M.J., Crowden R.K. & Jarman S.J. (1982) Vegetation of an alkaline pan - acidic peat mosaic in the Hardwood River Valley, Tasmania. *Aust. J. Ecol.* **7**, 3-12.
- Brown M.J. & Podger F.D. (1982) Floristics and fire regimes of a vegetation sequence from sedgeland-heath to rainforest at Bathurst Harbour, Tasmania. *Aust. J. Bot.* **30**, 659-76.
- Bryant W.G. (1973) The effect of grazing and burning on a mountain grassland, Snowy Mountains, New South Wales. *Soil Conservation Journal* **29**, 29-44.
- Buchanan A.M., McGeary-Brown A. & Orchard A.E. (1989) *A Census of the Vascular Plants of Tasmania*. Tasmanian Herbarium Occasional Publication No. 2.
- Budyko M.I. (1958) *The Heat Balance of the Earth's Surface*, translated by Nina Stepanova. U.S. Weather Bureau, Department of Commerce, first published Leningrad, 1956.
- Bureau of Meteorology (1986) in *Tasmanian Year Book*. Australian Bureau of Statistics, Hobart.
- Bureau of Flora and Fauna (1981) *Flora of Australia. Vol. 1 Introduction*. Australian Government Publishing Service, Canberra.
- Busby J.R. (1986) A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in southeastern Australia. *Aust. J. Ecol.* **11**, 1-7.
- Campbell E.O. (1964) The Restiad peat bogs at Motumaoho and Moanatuatua. *Trans. Roy. Soc. N.Z. Bot.* **2**, 219-27.
- Campbell E.O. (1983) Mires of Australasia. *Mires: Swamp, Bog, Fen and Moor*. In: *Ecosystems of the World. Vol 4B*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 153-80.
- Caron M. & Joyal P. (1987) The use of *Sphagnum* peat moss for tree seedling production. *Proceedings of Symposium '87 Wetlands/Peatlands*. Alberta, Canada, 209-211.
- Carr D.J., Carr S.G.M. & Papst W.R. (1980) Field studies of nitrogen fixation of Australian alpine plants and soils. *Aust. J. Ecol.* **5**, 211-20.
- Carr S.G.M. & Turner J.S. (1959a) The ecology of the Bogong High Plains. I The environmental factors and the grassland communities. *Aust. J. Bot.* **7**, 12-33.
- Carr S.G.M. & Turner J.S. (1959b) The ecology of the Bogong High Plains. II Fencing experiments in grassland C. *Aust. J. Bot.* **7**, 34-63.
- Casparie W.A. (1969) Bult- und Schlenkenbildung in Hochmoortorf. *Vegetatio* **19**, 146-80.
- Clapham A.R. (1940) The role of bryophytes in the calcareous fens of the Oxford District. *J. Ecol.* **28**, 71-80.
- Clarkson B.R. (1984) Vegetation of three mountain mires, west Taupo, New Zealand. *N.Z. J. Bot.* **22**, 361-75.
- Clymo R.S. (1970) The growth of *Sphagnum* : methods of measurement. *J. Ecol.* **58**, 13-49.
- Clymo R.S. (1973) The growth of *Sphagnum* : some effects of environment. *J. Ecol.* **61**, 849-69.

- Clymo R.S. (1980) Preliminary survey of the peat-bog Hummell Knowe Moss using various numerical methods. *Vegetatio* **42**, 129-48.
- Clymo R.S. (1983) Peat. *Mires: Swamp, Bog, Fen and Moor*. In: *Ecosystems of the World*. Vol. 4A. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 159-224.
- Clymo R.S. (1984) The limits to peat growth. *Phil. Trans. Roy. Soc. London. B.* **303**, 605-54.
- Clymo R.S. (1987) Interactions of *Sphagnum* with water and air. In: *Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems*. (eds. T.C. Hutchinson & K.M. Meema) Springer-Verlag, Berlin, pp. 513-29.
- Clymo R.S. & Duckett J.G. (1986) Regeneration of *Sphagnum*. *New Phytol.* **102**, 589-614.
- Clymo R.S. & Hayward P.M. (1982) The ecology of *Sphagnum*. In: *Bryophyte Ecology*. (ed. A.J.E. Smith) Chapman & Hall, London, pp. 229-89.
- Clymo R.S. & Reddaway E.J.F. (1971) Productivity of *Sphagnum* (bog-moss) and peat accumulation. *Hydrobiologia* **12**, 181-92.
- Clymo R.S. & Reddaway E.J.F. (1974) Growth rate of *Sphagnum rubellum* Wils. on Pennine blanket bog. *J. Ecol.* **62**, 191-96.
- Cockayne L. (1958) *The Vegetation of New Zealand* (3rd edn). Engelmann, London.
- Cody M.L. (1986) Structural niches in plant communities. In: *Community Ecology* (eds. J. Diamond & T.J. Case) Harper & Row, N.Y., pp. 145-153.
- Costin A.B. (1954) *A study of the ecosystems of the Monaro Region of New South Wales*. Government Printer, Sydney.
- Crane W.J.B. (1978) Phosphorus tability in eucalypt forests. *Aust. For.* **41**, 118-26.
- Crawford R.M.M. (1983) Root survival in flooded soils. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World*. Vol 4A. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 257-83.
- Crocker R.L. & Eardley C.M. (1939) A South Australian *Sphagnum* bog. *Trans. Roy. Soc. S.A.* **63**, 210-14.
- Damman A.W.H. (1977) Geographical changes in the vegetation pattern of raised bogs in the Bay of Fundy Region of Maine and New Brunswick. *Vegetatio* **35**, 137-51.
- Damman A.W.H. (1986) Hydrology, development and biogeochemistry of ombrogenous peat bogs with special reference to nutrient relocation in a western Newfoundland bog. *Can. J. Bot.* **64**, 384-94.
- Davoren A. (1978) *A Survey of New Zealand Peat Resources*. Water and Soil Technical Publication No. 14, University of Waikato, N.Z.
- Diamond J. (1986) Overview: laboratory experiments, field experiments, and natural experiments. In: *Community Ecology*. (eds. J. Diamond & T.J. Case). Harper & Row, New York, pp. 3-22.

- Dierssen K. (1979) A classification of community complexes in mires by phytosociological methods. *International Peat Society Classification of Peat and Peatlands, Proceedings of the International Symposium, Hyytiak, Finland, Sept. 17-21, 1979*. University of Helsinki, pp. 33-41.
- Dobson A.T. (1979) Mire types of New Zealand. *International Peat Society Classification of Peat and Peatlands, Proceedings of the International Symposium, Hyytiak, Finland, Sept. 17-21, 1979*. University of Helsinki, pp. 82-95.
- Duncan D. & Dalton P.J. (1982) Recolonisation by bryophytes following fire. *J. Bryol.* **12**, 53-63.
- Elling A.E. & Knighton M.D. (1984) *Sphagnum* moss recovery after harvest in a Minnesota bog. *J. Soil & Water Cons.* **39**, 209-11.
- Faith D.P., Minchin P.R. and Belbin L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57-68.
- Farrell T.P. & Ashton D.H. (1973) Ecological studies on the Bennison High Plains. *Vic. Naturalist* **90**, 286-98.
- Foster D.R. & Fritz (1987) Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. *J. Ecol.* **75**, 409-37.
- Foster D.R. & Glaser P.H. (1985) The raised bogs of south-eastern Labrador Canada: classification, distribution, vegetation and recent dynamics. *J. Ecol.* **74**, 47-71.
- Foster D.R., Wright H.E. (Jr.), Thelaus M. & King G.A. (1988) Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. *J. Ecol.* **76**, 1186-203.
- Frenzel B. (1983) Mires - repositories of climatic information or self-perpetuating ecosystems. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4A.* (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 35-65.
- Gentilli J. (1972) *Australian Climate Patterns*. Nelson, Melbourne.
- Gibson N. (1988) *A study on the biology of four Tasmanian cushion species*. PhD thesis, University of Tasmania.
- Gibson N. & Hope G.S. (1986) On the origin and evolution of Australasian alpine cushion plants. In: *Flora and Fauna of Alpine Australasia* (ed. B.A. Barlow) CSIRO, Melbourne, pp. 63-81.
- Gibson N. & Kirkpatrick J.B. (1989) Effects of the cessation of grazing on the grasslands and grassy woodlands of the Central Plateau, Tasmania. *Aust. J. Bot.* **37**, 55-63.
- Gignac L.D. & Vitt D.H. (1990) Habitat limitations of *Sphagnum* along climatic, chemical and physical gradients in mires of western Canada. *The Bryologist* **93**, 7-22.
- Gigon A. (1983) Ecology and principles of ecological stability and instability. *Mountain Research and Development* **3**, 95-102.
- Glaser P.H. & Janssens J.A. (1986) Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. *Can. J. Bot.* **64**, 395-415.
- Glaser P.H., Wheeler G.A., Gorham E. & Wright H.E. (Jr.) (1981) The patterned mires of the Red Lake peatland, northern Minnesota: vegetation, water chemistry and landforms. *J. Ecol.* **69**, 575-99.

- Godley E.J. (1978) Cushion bogs. In: *Geoeological relations between the southern temperate zone and the tropical mountains* (eds. C. Troll & W. Lauer) Franz Steiner Verlag GMBH, Wiesbaden, pp. 141-58.
- Godwin H. & Conway V.M. (1939) The ecology of a raised bog near Tregaron, Cardiganshire. *J. Ecol.* **27**, 313-59.
- Godwin H. & Turner J.S. (1933) Soil acidity in relation to vegetational succession in Calthorpe Broad, Norfolk. *J. Ecol.* **21**, 231-62.
- Good R. (1987) Repairing the roof of Australia. *Snowy River Country* **6**, 14-17.
- Gore A.J.P. (1983) Introduction. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World. Vol 4A.* (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 1-34.
- Gorham E., Janssens J.A., Wheeler G.A. & Glaser P.H. (1987) The natural and anthropogenic acidification of peatlands. In: *Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems* (eds. T.C. Hutchinson & K.M. Meema) Springer-Verlag, Berlin, 493-512.
- Greig-Smith P. (1983) *Quantitative Plant Ecology*. Blackwell Scientific, Oxford.
- Grime J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley & Sons, Chichester.
- Hansen K. & Madsen K.J. (1984) Vegetation changes of a Danish mire 1957-1981. *Nordic J. Bot.* **4**, 481-90.
- Harper J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Hayward P.M. (1980) *Effects of environment on the growth of Sphagnum*. PhD thesis, University of London.
- Hayward P.M. & Clymo R.S. (1983) The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. *J. Ecol.* **71**, 845-63.
- Heathwaite A.L. & Ross S.M. (1987) Evaluation of qualitative and quantitative classifications for fen peat in the Somerset Levels, England. *J. Biogeog.* **14**, 129-43.
- Heinselman M.L. (1970) Landscape evolution, peatland types and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecol. Mono.* **40**, 235-260.
- Hill A.R. (1975) Ecosystem stability in relation to stresses caused by human activities. *Can. Geogr.* **19**, 206-220.
- Hill M.O. (1979) *TWINSPAN - A FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Table by Classification of the Individuals and Attributes*. Cornell Uni., New York.
- Hill M.O. & Gauch H.G. (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* **42**, 47-58
- Hobbs R.J. & Hobbs V.J. (1987) Gophers and grassland: a model of vegetation response to patchy soil disturbance. *Vegetatio* **69**, 141-46.
- Hofstetter R.H. (1983) Wetlands in the United States. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World. Vol 4B.* (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 201-44.

- Ingram H.A.P. (1983) Hydrology. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World. Vol 4A.* (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 67-158.
- International Peat Society (1979) *Classification of peat and peatlands. Proceedings of the International Symposium, Hyytiak, Finland, Sept. 17-21, 1979.* University of Helsinki.
- Ivanov K.E. (1981) *Water Movement in Mirelands.* Academic Press, London.
- Jackson M.L. (1958) *Soil Chemical Analysis.* Prentice-Hall, New Jersey.
- Jarman S.J., Kantvilas G. & Brown M.J. (1984) *Rainforest in Tasmania.* National Parks & Wildlife Service, Tasmania.
- Jarman S.J., Kantvilas G. & Brown M.J. (1988) *Buttongrass moorland in Tasmania.* Tasmanian Forest Research Council Inc. Research Report No. 2.
- Jeglum J.K. (1987) The use of TWINSpan, tabular analysis and Finnish/Swedish concepts in classifying wooded peatlands in Ontario. *Proceedings of Symposium '87 Wetlands/Peatlands.* Alberta, Canada, pp. 383-91.
- Johnson C.N. & Jarman P.J. (1987) Macropod studies at Wallaby Creek. VI. A validation of the use of dung-pellet counts for measuring absolute densities of populations of Macropodids. *Aust. Wildl. Res.* **14**, 139-45.
- Jones R. (1969) Fire stick farming. *Aust. Natural History* **16**, 224-28.
- Jongman R.H.G. ter Braak C.J.F. & van Tongeren O.F.R. (1987) *Data analysis in community and landscape ecology.* Pudoc, Wageningen.
- Jurkovskaja T.K. (1979) Botanical-geographic classification of mire complexes of the European part of the U.S.S.R. *International Peat Society Classification of Peat and Peatlands, Proceedings of the International Symposium, Hyytiak, Finland, Sept. 17-21, 1979.* University of Helsinki, pp. 12-19.
- Katz N.J. (1926) *Sphagnum* bogs of Central Russia: phytosociology, ecology and succession. *J. Ecol.* **14**, 177-202.
- Kenkel N.C. (1988) Spectral analysis of hummock-hollow patter in a weakly minerotrophic mire. *Vegetatio* **78**, 45-52.
- Kiernan K. (1985) *Late Cainozoic glaciation and mountain geomorphology of the central highlands of Tasmania.* PhD thesis, University of Tasmania.
- Kirkpatrick J.B. (1983) Treeless plant communities of the Tasmanian high country. *Proc. Ecol. Soc. Aust.* **12**, 61-77.
- Kirkpatrick J.B. (1984) Altitudinal and successional variation in the vegetation of the northern part of the West Coast Range, Tasmania. *Aust. J. Ecol.* **9**, 81-91.
- Kirkpatrick J.B. & Dickinson K.J.M. (1984) The impact of fire on Tasmanian alpine vegetation and soils. *Aust. J. Bot.* **32**, 613-29.
- Kirkpatrick, J.B., Fensham R.J., Nunez M. & Bowman D.M.J.S. (1988) Vegetation-radiation relationships in the wet-dry tropics: granite hills in northern Australia. *Vegetatio* **76**, 103-12.

- Kirkpatrick J.B. & Gibson N. (1984) Dynamics of a Tasmanian bolster heath string fen. *Vegetatio* **58**, 71-78.
- Kirkpatrick J.B. & Harwood (1983) Plant communities of Tasmanian wetlands. *Aust. J. Bot.* **31**, 437-51.
- Kirkpatrick J.B. & Whinam J. (1988) Tasmanian high mountain vegetation III - Lake Ewart, Dome Hill and Eldon Bluff. *Pap. Proc. R. Soc. Tasm.* **118**, 5-20.
- Knox G.A. (1969) *The Natural History of Canterbury*. Reed, Wellington.
- Lee J.A., Press M.C., Woodin S. & Ferguson, P. (1987) Responses to acidic deposition in ombrotrophic mires in the U.K. In: *Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems*. (eds. T.C. Hutchinson & K.M. Meema) Springer-Verlag, Berlin, pp. 549-60.
- Leigh J.H., Wimbush D.J., Wood D.H., Holgate M.D., Slee A.V., Stranger M.G. & Forrester R.I. (1987) Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Aust. J. Bot.* **35**, 433-64.
- Lewis Smith R.I. (1979) Peat forming vegetation in the Antarctic. *International Peat Society Classification of Peat and Peatlands, Proceedings of the International Symposium, Hyytiak, Finland, Sept. 17-21, 1979*. University of Helsinki, pp. 58-67.
- Lockwood J.G. (1974) *World Climatology. An Environmental Approach*. Edward Arnold, London.
- Luken J.O. (1985) Zonation of *Sphagnum* mosses. Interaction among shoot growth, growth form and water balance. *Bryologist* **88**, 374-79.
- Luken J.O., Billings W.D. & Peterson K.M. (1985) Succession and biomass allocation as controlled by *Sphagnum* in an Alaskan peatland. *Can. J. Bot.* **63**, 1500-07.
- Macphail M.K. (1979) Vegetation and climates in southern Tasmania since the last glaciation. *Quat. Research* **11**, 306-41.
- Malmer N. (1986) Vegetational gradients in relation to environmental conditions in northwestern European mires. *Can. J. Bot.* **64**, 375-383.
- McDougall K.L. (1989) *The effect of excluding cattle from a mossbed on the Bogong High Plains, Victoria*. Arthur Rylah Institute for Environmental Research Technical Report Series No. 95. Department of Conservation, Forests and Lands, East Melbourne.
- McPherson G. (1990) *Statistics in Scientific Investigation*. Springer-Verlag, New York.
- Miles J. (1979) *Vegetation Dynamics*. Chapman & Hall, London.
- Millington R.J. (1954) *Sphagnum* bogs of the New England Plateau, N.S.W. *J. Ecol.* **42**, 328-44.
- Minchin P. R. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89-107.
- Moore P.D. (1973) The influence of prehistoric cultures upon the initiation and spread of blanket bog in upland Wales. *Nature* **241**, 350-53.

- Moore P.D. (1975) Origin of blanket mires. *Nature* **256**, 267-69.
- Moore P.D. (1977) Stratigraphy and pollen analysis of Claish Moss, north-west Scotland: significance for the origin of surface-pools and forest history. *J. Ecol.* **65**, 375-97.
- Moore P.D. & Bellamy D.J. (1974) *Peatlands*. Elek Science, London.
- Moore T.R. (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. *Can. J. Bot.* **67**, 1203-07.
- Mount A.B. (1972) Derivation and testing of a soil dryness index using run-off data. *Tas. For. Comm. Bull.* **4**.
- Mueller-Dombois D. & Ellenberg H. (1974) *Aims and Methods of Vegetation Ecology*. Wiley International, New York.
- Murray K.J., Tenhunen J.D. & Kummerow J. (1989) Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith Mountains, Alaska. *Oecologia* **80**, 256-62.
- Nicholson B.J. (1989) Peat chemistry of a continental mire complex in western Canada. *Can. J. Bot.* **67**, 763-75.
- Noble I.R. & Slatyer R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5-21.
- Noy-Meir I. & van der Maarel E. (1987) Relations between community theory and community analysis in vegetation science: some historical perspectives. *Vegetatio* **69**, 5-15.
- Nunez M. (1978) The radiation index of dryness in Tasmania. *Aust. Geogr. Stud.* **16**, 126-35.
- Orloci L. (1981) Probing time series vegetation data for evidence of succession. *Vegetatio* **46**, 31-35.
- Ovenden L. & Brassard G.R. (1989) Wetland vegetation near Old Crow, northern Yukon. *Can. J. Bot.* **67**, 954-60.
- Pakarinen P. (1978a) Production and ecology of three *Sphagnum* species in South Finnish raised bogs. *Ann. Bot. Fennici* **15**, 15-26.
- Pakarinen P. (1978b) Distribution of heavy metals in the *Sphagnum* layer of bog hummocks and hollows. *Ann. Bot. Fennici* **15**, 287-92.
- Pemberton M. (1986) *Land Systems of Tasmania, Region 5 - Central Plateau*. Dept. Agriculture, Hobart.
- Pemberton M. (1989) *Land Systems of Tasmania, Region 7 - South West*. Dept. Agriculture, Hobart.
- Pisano E. (1983) The magellanic tundra complex. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4A*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 295-329.

- Raison R.J. (1979) Modification of the soil environment by vegetation fires, with particular reference to N transformations. *Plant & Soil* **51**, 73-108.
- Ratcliffe D.A. & Walker D. (1958) The Silver Flowe, Galloway, Scotland. *J. Ecol.* **46**, 407-45.
- Rawes M. (1983) Changes in two high altitude blanket bogs after the cessation of sheep grazing. *J. Ecol.* **71**, 219-35.
- Ritchie J.C. (1986) Climate change and vegetation response. *Vegetatio* **67**, 65-74.
- Rodway L. (1914) *Tasmanian Bryophyta. Vol. 1. Mosses*. Roy. Soc. Tasmania, Hobart.
- Roughgarden J. & Diamond J. (1986) Overview: the role of species interaction in community ecology. In: *Community Ecology*. (eds. J. Diamond & T.J. Case). Harper & Row, New York, pp. 333-43.
- Rowe, R.K. (1970) *A Study of the Land in Mt Buffalo National Park*. Soil Conservation Authority, Melbourne.
- Ruuhijarvi R. (1983) The Finnish mire types and their regional distribution. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4B*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 47-67.
- Rybnicek K. (1985) A Central European approach to the classification of mire vegetation. *Aquilo Ser. Botanica* **21**, 19-31.
- Rydin H. & McDonald A.J.S. (1985) Tolerance of *Sphagnum* to water level. *J. Bryol.* **13**, 571-78.
- Sanville W. (1988) Response of an Alaskan wetland to nutrient enrichment. *Aquatic Bot.* **30**, 231-43.
- Scott G.A.M. (1971) Some problems in the quantitative ecology of bryophytes. *N.Z. J. Bot.* **9**, 744-49.
- Scott G.A.M., Stone I.G. & Rosser C. (1976) *The Mosses of Southern Australia*. Academic Press, Sydney.
- Simmons I.G. & Cundill P.R. (1974) Late Quaternary vegetation of North York Moors. I. Pollen analyses of blanket peats. *J. Biogeog.* **1**, 159-69.
- Sims R.A., Cowell D.W. & Wickware G.M. (1982) Classification of fens near southern James Bay, Ontario, using vegetational physiognomy. *Can. J. Bot.* **60**, 2608-23.
- Sjors H. (1980) An arrangement of changes along gradients, with examples from successions in boreal peatland. *Vegetatio* **43**, 1-4.
- Sjors H. (1983) Mires of Sweden. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4B*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 69-94.

- Slack N.G., Vitt D.H. & Horton D.G. (1980) Vegetation gradients of minerotrophically rich fens in western Alberta. *Can. J. Bot.* **58**, 330-50.
- Smith G.G. (1969) *Sphagnum subsecundum* in Western Australia. *W.A. Naturalist* **11**, 56-59.
- Sokal R.R. & Rohlf F.J. (1969) *Biometry*. Freeman & Co., San Francisco.
- Streimann H. & Curnow J. (1989) Catalogue of Mosses of Australia and Its External Territories. *Australian Flora and Fauna Series No. 10*. Australian Government Publishing Service, Canberra.
- Svensson G. (1986) Recognition of peat-forming plant communities from their peat deposits in two south Swedish bog complexes. *Vegetatio* **66**, 95-108.
- Svensson G. (1988) Fossil plant communities and regeneration patterns on a raised bog in south Sweden. *J. Ecol.* **76**, 41-59.
- Tallis J.H. (1983) Changes in wetland communities. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4A*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 331-73.
- Tasmanian Year Book (1986) Australian Bureau of Statistics, Hobart.
- Taylor J.A. (1983) The peatlands of Great Britain and Ireland. In: *Mires: swamp, bog, fen and moor. Ecosystems of the World. Vol 4A*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 1-46.
- ter Braak C.J.F. (1987) The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* **69**, 69-77.
- Thompson D. (1987) Battle of the bog. *New Scientist* **Jan. 8**, 41-48.
- Thompson K. (1987) Annotated bibliography of New Zealand peat and peatlands. *Water & Soil Miscellaneous Publication No. 114*. National Water & Soil Conservation Authority, Wellington.
- Thompson K. & Hamilton A.C. (1983) Peatlands and swamps of the African continent. In: *Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World. Vol 4B*. (ed. A.J.P. Gore) Elsevier Scientific, Amsterdam, pp. 331-73.
- Tilman D. (1986) Evolution and differentiation in terrestrial plant communities: the importance of the soil resource: light gradient. In: *Community Ecology* (eds. J. Diamond & T.J. Case). Harper & Row, New York, pp. 359-80.
- van Baaren M., During H. and Leltz G. (1988) Bryophyte communities in mesotrophic fens in the Netherlands. *Holarctic Ecol.*, **11**, 32-40.
- van Hulst R. (1987) Invasion models of vegetation dynamics. *Vegetatio* **69**, 123-131.
- van Leeuwen C.G. (1966) A relation theoretical approach to pattern and process in vegetation. *Wentia* **15**, 25-46.
- van Rees H. (1984) *Behaviour and Diet of Free-ranging Cattle on the Bogong High Plains Victoria*. Department of Conservation, Forests & Lands, E.S.P. No. 409.
- Vitt D.H., Achuff P. & Andrus R.E. (1975) The vegetation and chemical properties of patterned fens in the Swan Hills, north central Alberta. *Can. J. Bot.* **53**, 2776-95.

- Vitt D.H. & Bayley S. (1984) The vegetation and water chemistry of four oligotrophic basin mires in northwestern Ontario. *Can. J. Bot.* **62**, 1485-1500.
- Vitt D.H. & Slack N.G. (1975) An analysis of the vegetation of *Sphagnum*-dominated kettle hole bogs in relation to environmental gradients. *Can. J. Bot.* **53**, 332-59.
- Vitt D.H. & Slack N.G. (1984) Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. *Can. J. Bot.* **62**, 1409-30.
- Walker D. & Walker P.M. (1961) Stratigraphic evidence of regeneration in some Irish bogs. *J. Ecol.* **49**, 169-85.
- Watts, W.W. (1912) The *Sphagnum* of Australia and Tasmania. *Proc. Linn. Soc. N.S.W.* **37**, 383-89.
- Waughman G.J. (1980) Chemical aspects of the ecology of some German peatlands. *J. Ecol.* **68**, 1025-46.
- Wells E.D. (1981) Peatlands of eastern Newfoundland: distribution, morphology, vegetation and nutrient status. *Can. J. Bot.* **59**, 1978-97.
- Whinam J. (1985) *The characteristics and origin of the string bogs on Mt Wellington, Tasmania*. Hons. thesis, University of Tasmania.
- Whinam J., Eberhard S., Kirkpatrick J., Moscal A. (1989) *Ecology and Conservation of Tasmanian Sphagnum Peatlands*. Tasmanian Conservation Trust Inc., Hobart.
- Williams R.J. & Ashton D.H. (1987) Cyclical patterns of regeneration in subalpine heathland communities on the Bogong High Plains, Victoria. *Aust. J. Bot.* **36**, 605-19.
- Wimbush D.J. & Costin A.B. (1979a) Trends in vegetation at Kosciusko. I Grazing trials in the subalpine zone, 1957-1971. *Aust. J. Bot.* **27**, 741-87.
- Wimbush D.J. & Costin A.B. (1979b) Trends in vegetation at Kosciusko. II Subalpine range transects, 1959-1978. *Aust. J. Bot.* **27**, 789-831.
- Wimbush D.J. & Costin A.B. (1979c) Trends in vegetation at Kosciusko. III Alpine range transects, 1959-1978. *Aust. J. Bot.* **27**, 833-71.
- Young A.R.M. (1983) Upland swamps (dells) of the Woronora Plateau, New South Wales. PhD thesis, University of Wollongong.
- Zimmerman R.C. and Thom B.G. (1982) Physiographic plant geography. *Prog. Phys. Geog.* **6**, 45-59.

APPENDIX 1

Species codes, family, status and lifeform. Ability of species to regenerate after fire is shown in brackets. (R)=resprout, (S)=obligate seed, (U)=unable to easily regenerate.

abro	fost	<i>Abrotanella forsteroides</i>	Taxodiaceae	Endemic	Cushion (R)
acae	nova	<i>Acaena novae-zelandiae</i>	Rosaceae	Trailing herb	
acti	suff	<i>Actinotus suffocata</i>	Apiaceae	Rosette herb	
acti	moor	<i>Actinotus moorei</i>	Apiaceae	Endemic	Rosette herb
agro	spp	<i>Agrostis</i> spp.	Poaceae	Grass	
aspe	gunn	<i>Asperula gunnii</i>	Rubiaceae	Herb	
aste	alpi	<i>Astelia alpina</i>	Liliaceae	Mat	graminoid (R)
athe	mosc	<i>Atherosperma moschatum</i>	Monimiaceae	Tree (R, S)	
athr	cupp	<i>Athrotaxis cupressoides</i>	Taxodiaceae	Endemic	Tree (U)
athr	sela	<i>Athrotaxis selaginoides</i>	Taxodiaceae	Endemic	Tree (U)
baec	gunn	<i>Baeckea gunniana</i>	Myrtaceae	Shrub (S)	
baue	rubi	<i>Bauera rubioides</i>	Cunoniaceae	Trailing shrub (R)	
baum	spp.	<i>Baumea</i> spp.	Cyperaceae	Graminoid (R)	
bell	mont	<i>Bellenden montana</i>	Proteaceae	Endemic	Shrub (S)
bill	long	<i>Billardiera longiflora</i>	Pittosporaceae	Trailing shrub (R)	
blec	penn	<i>Blechnum penna-marina</i>	Blechnaceae	Fern	
blec	wats	<i>Blechnum watsii</i>	Blechnaceae	Fern	
boro	citr	<i>Boronia citriodora</i>	Rutaceae	Shrub (S)	
brac	spp	<i>Brachyscome</i> spp.	Asteraceae	Rosette herb	
call	viri	<i>Callistemon viridiflorus</i>	Myrtaceae	Endemic	Shrub (R)
card	spp	<i>Cardamine</i> spp.	Brassicaceae	Herb	
care	unde	<i>Carex</i> sp. nov.	Cyperaceae	Graminoid	
care	spp	<i>Carex</i> spp.	Cyperaceae	Graminoid	
carp	alpi	<i>Carpha alpina</i>	Cyperaceae	Graminoid	
carp	curv	<i>Carpha curvata</i>	Cyperaceae	Endemic	Graminoid
celm	long	<i>Celmisia asteliifolia</i>	Asteraceae	Rosette herb (R)	
celm	saxi	<i>Celmisia saxifraga</i>	Asteraceae	Endemic	Rosette herb (R)
cent	musc	<i>Centrolepis muscoides</i>	Centrolepidaceae	Endemic	Cushion graminoid
cent	mono	<i>Centrolepis monogyna</i>	Centrolepidaceae	Endemic	Cushion graminoid
cent	cord	<i>Centella cordifolia</i>	Apiaceae	Aquatic herb	
cera	glom	<i>Cerastium glomeratum</i>	Caryophyllaceae	Introduced	Herb
colo	apet	<i>Colobanthus apetalus</i>	Caryophyllaceae	Tufted herb	
come	retu	<i>Comesperma retusum</i>	Polygalaceae	Shrub (R)	
copr	nit	<i>Coprosma nitida</i>	Rubiaceae	Shrub (S)	
copr	moor	<i>Coprosma moorei</i>	Rubiaceae	Mat shrub	
copr	pumi	<i>Coprosma pumila</i>	Rubiaceae	Mat shrub	
cotu	alpi	<i>Cotula alpina</i>	Asteraceae	Rosette herb	
cras	spp	<i>Craspedia</i> spp.	Asteraceae	Herb	
cyat	deal	<i>Cyathodes dealbata</i>	Epacridaceae	Endemic	Mat shrub (S)
cyat	juni	<i>Cyathodes juniperina</i>	Epacridaceae	Shrub (S)	
cyat	parv	<i>Cyathodes parvifolia</i>	Epacridaceae	Endemic	Shrub (S)
dant	spp	<i>Danthonia</i> spp.	Poaceae	Grass (R)	
deye	mont	<i>Deyeuxia monticola</i>	Poaceae	Grass (R)	
deye	gunn	<i>Deyeuxia gunniana</i>	Poaceae	Grass (R)	
deye	spp	<i>Deyeuxia</i> spp.	Poaceae	Grass (R)	
deye	acce	<i>Deyeuxia accedens</i>	Poaceae	Endemic	Grass
deye	quad	<i>Deyeuxia quadriseta</i>	Poaceae	Grass (R)	
dich	rara	<i>Dichelachne rara</i>	Poaceae	Grass (R)	
dipl	cord	<i>Diplaspis cordifolia</i>	Apiaceae	Endemic	Rosette herb
dipl	mora	<i>Diplarrena moraea</i>	Iridaceae	Graminoid (R)	

Species codes (continued)

dipl	lati	<i>Diplarrena latifolia</i> Iridaceae Endemic Graminoid (R)
dros	arct	<i>Drosera arcturi</i> Droseraceae Carniverous geophyte (R)
drym	cyan	<i>Drymophila cyanocarpa</i> Liliaceae Graminoid
emp	minu	<i>Empodisma minus</i> Restionaceae Graminoid (R)
epac	gunn	<i>Epacris gunnii</i> Epacridaceae Endemic Shrub (R)
epac	lanu	<i>Epacris lanuginosa</i> Epacridaceae Shrub (R)
epac	serp	<i>Epacris serpyllifolia</i> Epacridaceae Shrub (S)
epil	spp	<i>Epilobium</i> spp. Onagraceae Herb
erig	stel	<i>Erigeron stellatus</i> Asteraceae Endemic Rosette herb (R)
euca	cocc	<i>Eucalyptus coccifera</i> Myrtaceae Endemic Tree (R)
euca	gunn	<i>Eucalyptus gunnii</i> Myrtaceae Endemic Tree (R)
euca	rubi	<i>Eucalyptus rubida</i> Myrtaceae Tree (R)
euca	rodw	<i>Eucalyptus rodwayi</i> Myrtaceae Endemic Tree (R)
euca	dela	<i>Eucalyptus delegatensis</i> Myrtaceae Tree (R)
euca	subc	<i>Eucalyptus subcrenulata</i> Myrtaceae Tree (R)
euph	spp.	<i>Euphrasia</i> spp. Scrophulariaceae Herb
gahn	gran	<i>Gahnia grandis</i> Cyperaceae Tussock graminoid (R)
gaul	hisp	<i>Gaultheria hispida</i> Ericaceae Endemic Shrub (S)
gent	diem	<i>Gentianella diemensis</i> Gentianaceae Herb
gera	pote	<i>Geranium potentilloides</i> Geraniaceae Herb
glei	spp.	<i>Gleichenia</i> spp. Gleicheniaceae Fern (R)
gnap	spp	<i>Gnaphalium</i> spp. Asteraceae Herb
gnap	coli	<i>Gnaphalium collinum</i> var. <i>monocephalum</i> Asteraceae Herb
gono	micr	<i>Gonocarpus micranthus</i> Haloragaceae Herb (R)
gono	mont	<i>Gonocarpus montanus</i> Haloragaceae Herb (R)
gono	serp	<i>Gonocarpus serpyllifolius</i> Haloragaceae Herb (R)
gono	teuc	<i>Gonocarpus teucroides</i> Haloragaceae Herb (R)
grev	aust	<i>Grevillea australis</i> Proteaceae Shrub (S)
gunn	cord	<i>Gunnera cordifolia</i> Gunneraceae Endemic Rosette herb
gymn	spha	<i>Gymnoschoenus sphaerocephalus</i> Cyperaceae Tussock graminoid (R)
heli	back	<i>Helichrysum backhousii</i> Asteraceae Endemic Shrub (S)
heli	hook	<i>Helichrysum hookeri</i> Asteraceae Shrub (S)
heli	scor	<i>Helichrysum rutidolepis</i> Asteraceae Herb
herp	nova	<i>Herpolirion novae-zelandiae</i> Liliaceae Mat graminoid (R)
hibb	proc	<i>Hibbertia procumbens</i> Dilleniaceae mat shrub (R)
hier	fras	<i>Hierochloe fraseri</i> Poaceae Grass
hier	redo	<i>Hierochloe redolens</i> Poaceae Grass
hist	inci	<i>Histiopteris incisa</i> Dennstaedtiaceae Fern
holc	lana	<i>Holcus lanatus</i> Poaceae Introduced Grass
hydr	spp	<i>Hydrocotyle</i> spp. Apiaceae Mat herb
hype	japo	<i>Hypericum japonicum</i> Hypericaceae Herb
hypo	ruغو	<i>Hypolepis rugosula</i> Dennstaedtiaceae Fern
junc	spp	<i>Juncus</i> spp. Juncaceae graminoid
lage	stip	<i>Lagenifera stipitata</i> Asteraceae Rosette herb
lepi	fili	<i>Lepidosperma filiforme</i> Cyperaceae Tussock graminoid (R)
lept	lani	<i>Leptospermum lanigerum</i> Myrtaceae Tree (R)
lept	rupe	<i>Leptospermum rupestre</i> Myrtaceae Endemic Shrub (S)
lept	scop	<i>Leptospermum scoparium</i> Myrtaceae Shrub (R)
lept	squa	<i>Leptorhynchus squamatus</i> Asteraceae Rosette Herb
lepy	tasm	<i>Lepyrodia tasmanica</i> Restionaceae Graminoid (R)
leuc	coll	<i>Leucopogon collinus</i> Epacridaceae Shrub (R)

Species codes (continued)

libe	pulc	<i>Libertia pulchella</i> Liliaceae Graminoid
lila	brow	<i>Lilaeopsis polyantha</i> Apiaceae Herb
liss	mont	<i>Lissanthe montana</i> Epacridaceae Shrub (R)
luzu	spp.	<i>Luzula</i> spp. Juncaceae Graminoid
lyco	fast	<i>Lycopodium fastigiatum</i> Lycopodiaceae Clubmoss
lyco	late	<i>Lycopodium laterale</i> Lycopodiaceae Clubmoss
mela	squa	<i>Melaleuca squamea</i> Myrtaceae Shrub (R)
micr	niph	<i>Microstrobos niphophilus</i> Podocarpaceae Endemic Coniferous shrub (U)
micr	tasm	<i>Ehrharta tasmanica</i> var. <i>subalpina</i> Poaceae Grass (R)
micr	tetr	<i>Microcachrys tetragona</i> Podocarpaceae Endemic Coniferous shrub (U)
mill	dens	<i>Milligania densiflora</i> Liliaceae Endemic Mat graminoid (R)
mitr	arch	<i>Mitrasacme archeri</i> Loganiaceae Endemic Cushion herb (R)
mitr	mont	<i>Mitrasacme montana</i> Loganiaceae Herb
mono	subm	<i>Monotoca submutica</i> Epacridaceae Endemic Shrub (S)
mono	glau	<i>Monotoca glauca</i> Epacridaceae Endemic Shrub (S)
mono	aff.	<i>Monotoca</i> sp. aff. <i>linifolia</i> Epacridaceae Endemic Shrub (S)
myri	pedu	<i>Myriophyllum pedunculatum</i> Haloragaceae Aquatic herb
nert	depr	<i>Nertera depressa</i> Rubiaceae Mat herb
noth	cunn	<i>Nothofagus cunninghamii</i> Fagaceae Tree (S)
olea	obco	<i>Olearia obcordata</i> Asteraceae Endemic Shrub (S)
olea	pini	<i>Olearia pinifolia</i> Asteraceae Endemic Shrub (S)
olea	myrs	<i>Olearia myrsinoides</i> Asteraceae Shrub (S)
olea	pers	<i>Olearia persoonioides</i> Asteraceae Endemic Shrub (S)
oreo	pumi	<i>Oreobolus pumilio</i> Cyperaceae Cushion graminoid (R)
oreo	dist	<i>Oreobolus distichus</i> Cyperaceae Mat graminoid (R)
oreo	cili	<i>Oreomyrrhis ciliata</i> Apiaceae Rosette herb
oreo	oxyc	<i>Oreobolus oxycarpus</i> Cyperaceae Cushion graminoid (R)
orit	acic	<i>Orites acicularis</i> Proteaceae Endemic shrub (S)
orit	revo	<i>Orites revoluta</i> Proteaceae Endemic shrub (R)
ouri	inte	<i>Ourisia integrifolia</i> Scrophulariaceae Herb
oxal	mage	<i>Oxalis magellanica</i> Oxalidaceae Rosette herb
oxal	corn	<i>Oxalis corniculata</i> Oxalidaceae Rosette herb
oxyl	elli	<i>Oxylobium ellipticum</i> Fabaceae Shrub (R)
pent	pumi	<i>Pentachondra pumila</i> Epacridaceae Mat shrub (R)
pern	tasm	<i>Pernettya tasmanica</i> Ericaceae Endemic Mat shrub
pers	sp	<i>Persoonia</i> sp. Proteaceae Endemic Shrub (S)
phyl	aspl	<i>Phyllocladus aspleniifolius</i> Podocarpaceae Endemic Tree (U)
picr	hier	<i>Picris hieracioides</i> Asteraceae Introduced Herb
pime	drup	<i>Pimelea drupacea</i> Thymelaceae Shrub (S)
pitt	bico	<i>Pittosporum bicolor</i> Pittosporaceae Tree (R)
plan	glab	<i>Plantago glabrata</i> Plantaginaceae Endemic Rosette herb
plan	spp	<i>Plantago</i> spp. Plantaginaceae Rosette herb
plan	dalt	<i>Plantago daltonii</i> Plantaginaceae Endemic Rosette herb
poa	labi	<i>Poa labillardieri</i> Poaceae Tussock grass (R)
poa	spp	<i>Poa</i> spp. Poaceae Tussock grass (R)
poa	annu	<i>Poa annua</i> Poaceae Introduced Grass
podo	lawr	<i>Podocarpus lawrencei</i> Podocarpaceae Coniferous shrub (U)
poly	juni	<i>Polytrichum juniperinum</i> Polytrichaceae Moss
pult	subu	<i>Pultenaea subumbellata</i> Fabaceae Shrub (R)
pult	dent	<i>Pultenaea dentata</i> Fabaceae Shrub (R)

Species codes (continued)

ranu	spp	<i>Ranunculus</i> spp. Ranunculaceae Herb
rest	aust	<i>Restio australis</i> Restionaceae Graminoid (R)
rest	tetr	<i>Restio tetraphyllus</i> Restionaceae Graminoid (R)
rest	comp	<i>Restio complanatus</i> Restionaceae Graminoid (R)
rich	acer	<i>Richea acerosa</i> Epacridaceae Endemic Shrub (R)
rich	gunn	<i>Richea gunnii</i> Epacridaceae Endemic Shrub (S)
rich	scop	<i>Richea scoparia</i> Epacridaceae Endemic Shrub (S)
rich	spre	<i>Richea sprengelioides</i> Epacridaceae Endemic Shrub (R)
rich	pand	<i>Richea pandanifolia</i> Epacridaceae Endemic Tree (S)
rubu	gunn	<i>Rubus gunnianus</i> Rosaceae Endemic Rosette herb
rume	spp	<i>Rumex</i> spp. Polygonaceae Introduced Herb
scho	spp.	<i>Schoenus</i> spp. Cyperaceae Graminoid
scir	spp.	<i>Isolepis</i> spp. Cyperaceae Graminoid
scle	sp.	<i>Scleranthus</i> sp. Caryophyllaceae Cushion herb
sene	spp.	<i>Senecio</i> spp. Asteraceae Herb
spha	cris	<i>Sphagnum cristatum</i> Sphagnaceae Moss
spha	falc	<i>Sphagnum falciculatum</i> Sphagnaceae Moss
spha	aust	<i>Sphagnum australe</i> Sphagnaceae Moss
spha	subs	<i>Sphagnum subsecundum</i> Sphagnaceae Moss
spre	inca	<i>Sprengelia incarnata</i> Epacridaceae Shrub (R)
styl	gram	<i>Stylidium graminifolium</i> Stylidiaceae Tussock herb
tasm	lanc	<i>Tasmannia lanceolata</i> Winteraceae Shrub (S)
telo	trun	<i>Telopea truncata</i> Proteaceae Endemic Shrub (S)
tetr	dist	<i>Ehrharta distichophylla</i> Poaceae Grass
tetr	tasm	<i>Tetracarpaea tasmanica</i> Escalloniaceae Endemic Shrub
tetr	acum	<i>Ehrharta acuminata</i> Poaceae Grass
troc	cunn	<i>Trochocarpa cunninghamii</i> Epacridaceae Endemic Shrub (S)
unci	spp.	<i>Uncinia</i> spp. Cyperaceae Graminoid
vell	mont	<i>Velleia montana</i> Goodeniaceae Rosette herb
vero	grac	<i>Veronica gracilis</i> Scrophulariaceae Herb
viol	hede	<i>Viola hederacea</i> Violaceae Herb
wahl	cera	<i>Wahlenbergia ceracea</i> Campanulaceae Herb
zier	arbo	<i>Zieria arborescens</i> Rutaceae Shrub (S)

Descriptions of the locations and general details of surveyed Sphagnum sites

The grid square references are in fig. 2.1. The TWINSPAN groups are described on p. 43. Geomorphic types correlate with fig. 2.5 (p. 24). Dominant species is the dominant species in the upper stratum, full species names are shown in Appendix 1. Dominant lifeform: 1-fern & fern allies, 2- moss, 3-herb, 4- gramineae, 5 - shrub, 6-orchid, 7-tree, 8-graminoid, 9-prostrate, 10-cushion/mat. Asterisk denotes missing value.

10km	TWINSPAN	GEOMORPHIC	SPP.	DOM.	DOM.	PEAT	HUMMOCK		
GRID	GROUP	TYPE	RICHNESS	SP.	L/FORM	DEPTH	HEIGHT	ALT.	COUNTRY ROCK
						(m)	(m)	(m)	
4233	1	9	19	heli back	5	0.20	*	1360	till
4233	1	9	8	heli back	5	0.22	*	1360	till
4628	2	1	23	micr niph	5	1.80	*	820	till
4627	2	8	19	lept lani	5	1.50	*	980	dolerite
4436	2	1	20	rich scop	5	2.50	*	1240	dolerite
4436	2	7	19	athr cupp	7	1.00	*	1290	till
4437	2	7	22	rich scop	5	0.75	*	1000	till
4337	2	7	16	rich scop	5	1.10	*	1200	till
4737	2	4	17	athr cupp	7	*	*	1200	dolerite
4627	2	4	21	micr niph	5	0.99	0.35	960	dolerite
4436	2	7	18	rich scop	5	1.76	0.47	1200	dolerite
4436	2	4	16	rich scop	1	0.56	0.52	1200	dolerite
4436	2	5	13	rich scop	5	0.17	0.33	1200	dolerite
4436	2	4	19	athr cupp	7	0.47	0.24	1180	dolerite
4436	2	5	13	rich scop	5	1.18	0.56	1200	dolerite
4436	2	5	13	rich scop	5	0.74	0.49	1190	dolerite
4035	2	4	20	rich scop	5	0.93	0.20	980	sandstone,siltstone
4536	2	4	22	rich scop	5	1.67	0.52	1200	dolerite
4536	2	7	12	rich scop	5	1.35	0.62	1170	dolerite
4536	2	4	16	micr niph	5	2.37	0.45	1180	dolerite
4436	2	4	16	athr cupp	7	1.10	0.40	1080	dolerite
4436	2	4	23	athr cupp	7	0.97	0.44	1080	dolerite
4233	2	5	14	glei spp	1	0.94	0.19	1040	dolerite
4434	2	5	19	rich scop	5	0.80	0.53	1040	dolerite
4434	2	3	18	rich scop	5	0.60	0.48	1080	dolerite
4434	2	3	16	athr cupp	7	0.88	0.55	1080	dolerite
4434	2	5	15	rich scop	5	0.66	0.59	980	dolerite
4434	2	3	17	rich scop	5	0.70	0.48	980	dolerite

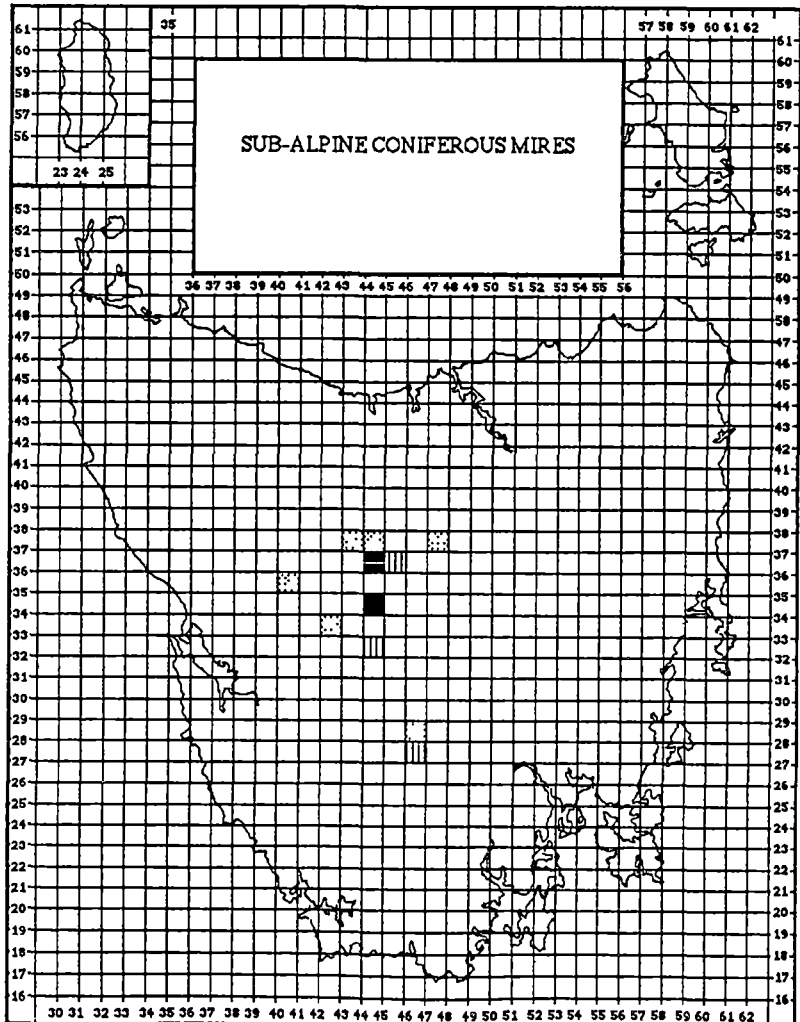
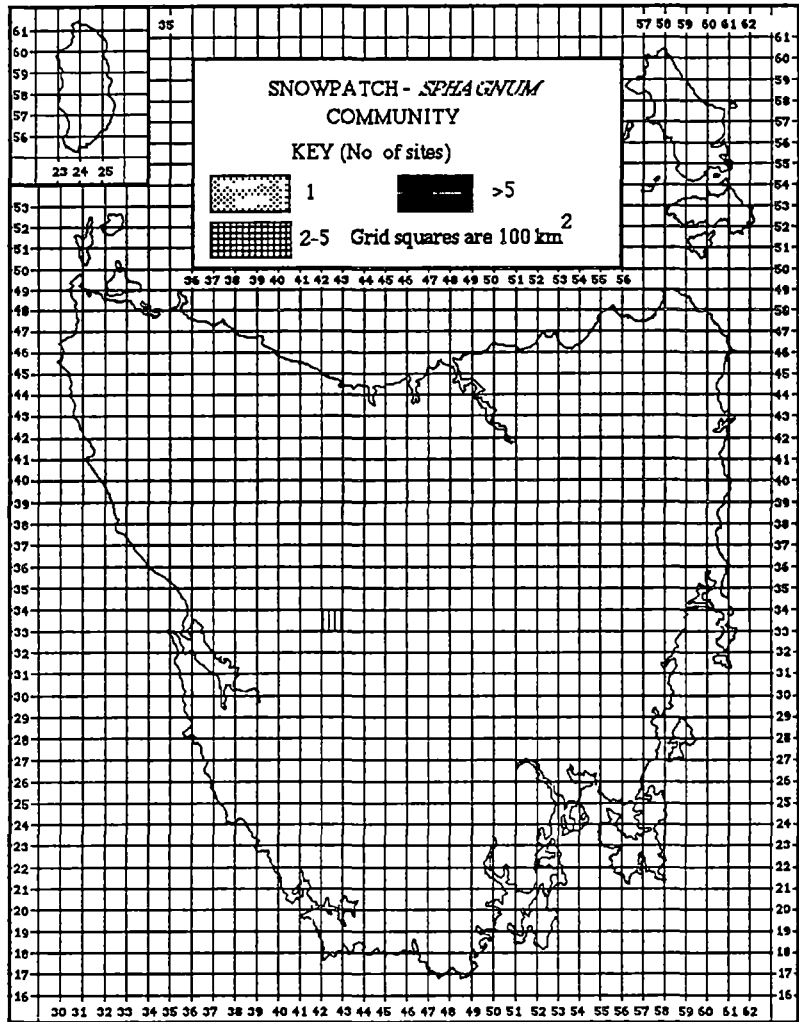
10km	TWINSPAN	GEOMORPHIC	SPP.	DOM.	DOM.	PEAT	HUMMOCK		
GRID	GROUP	TYPE	RICHNESS	SP.	L/FORM	DEPTH	HEIGHT	ALT.	COUNTRY ROCK
						(m)	(m)	(m)	
4434	2	4	15	gymn spha	8	0.50	0.54	980	sandstone/mudstone
4432	2	7	18	athr cupp	7	1.42	0.34	960	dolerite
4432	2	7	19	athr cupp	7	1.41	0.47	1000	dolerite
4432	2	4	15	rich scop	5	0.83	0.33	1000	dolerite
4432	2	7	19	glei spp	1	0.46	0.36	1080	dolerite
4432	2	7	13	athr cupp	7	1.65	0.69	1040	dolerite
4724	3	1	9	rich gunn	5	*	*	740	sandstone/mudstone
4338	3	7	13	rest aust	8	1.30	*	850	marsh deposits
4338	3	7	16	rest aust	8	1.30	*	850	marsh deposits
4631	3	5	7	gahn gran	8	1.70	*	530	marsh deposits
4233	3	7	22	rich acer	5	0.65	*	960	siltstone with sandstone
4236	3	4	15	empo minu	8	0.79	*	860	marsh deposits
4035	3	4	15	rich gunn	5	0.72	0.52	860	sandstone,siltstone
4035	3	4	16	gymn spha	8	0.69	0.25	860	sandstone,siltstone
4035	3	4	17	rest aust	8	1.20	0.40	860	sandstone,siltstone
4035	3	4	11	rich gunn	5	0.92	0.39	860	sandstone,siltstone
4035	3	4	20	rich gunn	5	1.12	0.62	850	sandstone,siltstone
4035	3	4	15	rich gunn	5	0.90	0.38	850	sandstone,siltstone
4035	3	4	12	rich gunn	5	0.80	0.48	860	sandstone,siltstone
4035	3	4	22	gymn spha	5	0.83	0.00	860	sandstone,siltstone
4233	3	5	11	baec gunn	5	1.57	0.27	720	Quat. till & fluvioglacial dep.
4235	3	4	19	gymn spha	8	1.13	0.30	880	sandstone/mudstone
4235	3	5	20	lept rupe	8	2.10	0.38	820	marsh deposits
4235	3	5	16	gymn spha	8	0.87	0.46	845	siltstone with sandstone
4235	3	5	5	glei spp	1	1.05	0.22	900	siltstone with sandstone
4235	3	5	13	athr cupp	7	1.54	0.25	900	sedimentary
4432	3	7	23	gymn spha	8	0.48	0.39	960	dolerite
4732	3	7	12	euca gunn	7	1.60	0.24	840	basalt

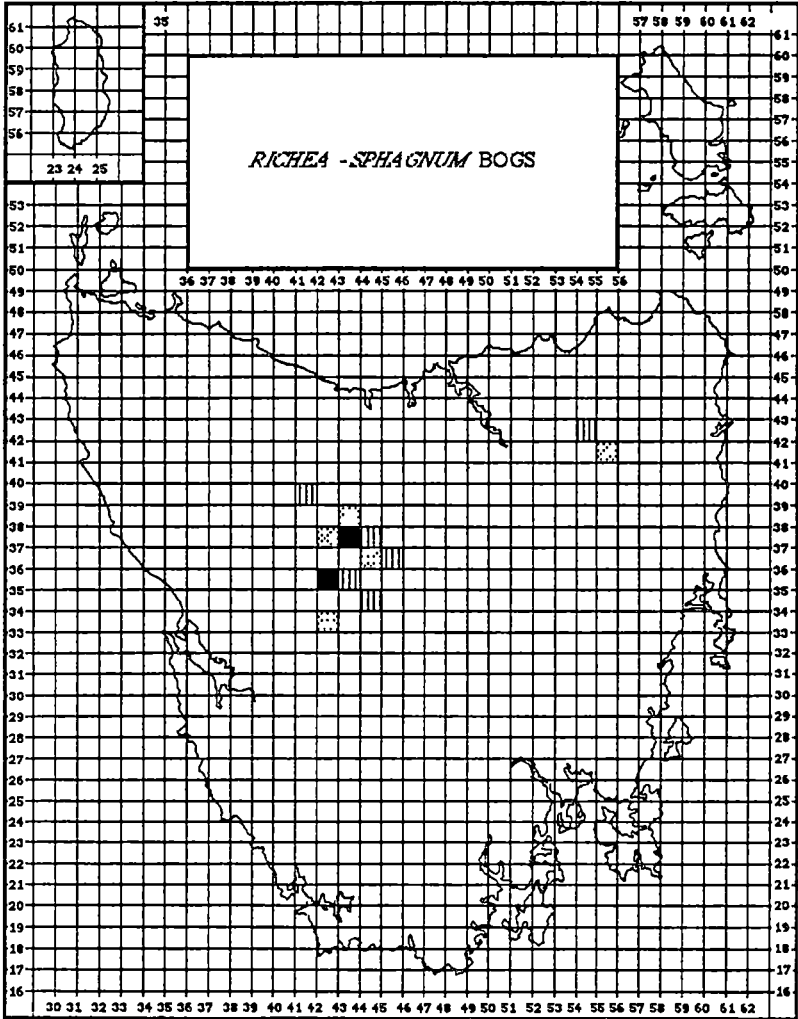
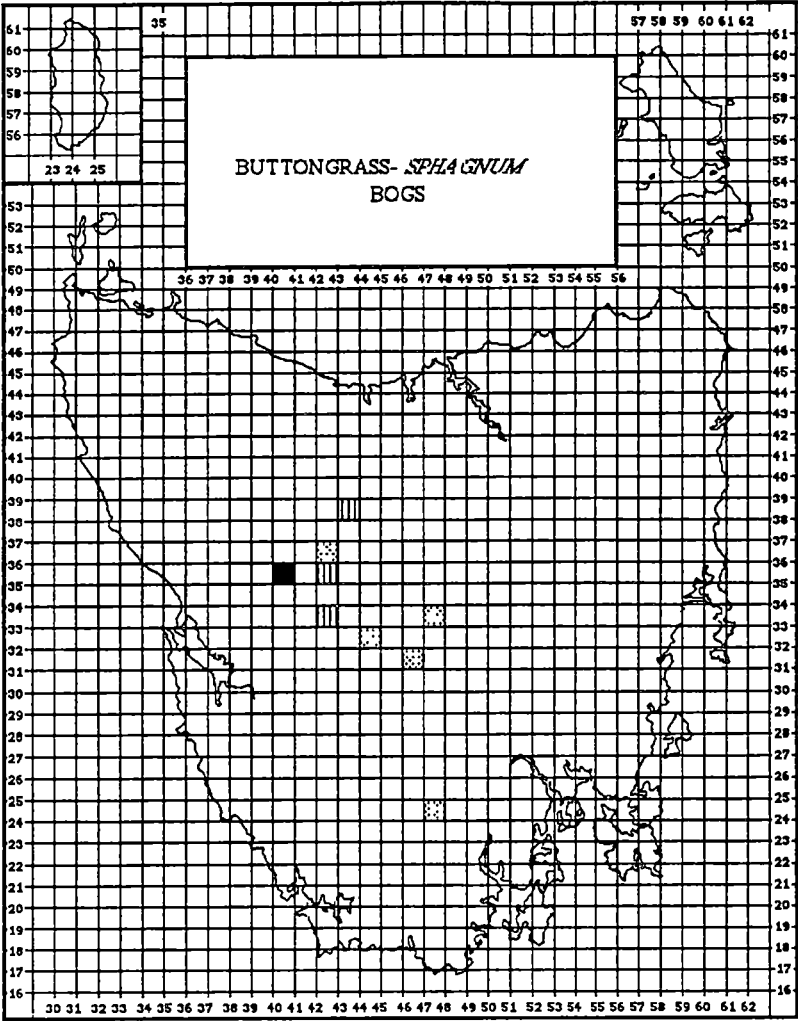
GRID	GROUP	GEOMORPHIC	RICHNESS	SP.	L/FORM	DEPTH	HEIGHT	ALT.	COUNTRY ROCK
10km	TWINSpan	TYPE	SPP.	DOM.	DOM.	PEAT	HUMMOCK		
						(m)	(m)	(m)	
5541	4	7	22	rich gunn	5	0.60	*	870	granodiorite
5442	4	4	18	lept lani	5	*	*	620	granodiorite
4337	4	7	14	rich gunn	5	0.97	*	790	marsh deposits
4337	4	7	14	rich gunn	5	1.50	1.00	810	marsh deposits
4338	4	7	13	rest aust	8	0.80	*	600	alluvium
4437	4	5	15	rich scop	5	2.60	*	1000	till
4237	4	1	13	rich scop	5	0.51	*	1000	dolerite colluvium
4139	4	4	13	gahn gran	8	0.66	0.36	820	alluvium
4139	4	4	21	rich gunn	5	0.49	0.70	800	alluvium & tallus
4139	4	7	10	rich scop	5	0.69	0.46	880	basalt
4337	4	7	15	rich scop	5	1.54	0.53	790	marsh deposits
4337	4	7	16	rich scop	5	1.66	0.59	790	marsh deposits
4337	4	7	14	rich scop	5	1.34	0.61	790	marsh deposits
4436	4	5	19	baec gunn	5	0.37	0.43	1160	dolerite
5442	4	4	28	rich scop	5	0.48	0.19	1120	granodiorite
4536	4	7	24	rich scop	5	0.50	0.70	1190	dolerite
4536	4	4	27	rich scop	5	0.86	0.61	1170	dolerite
4536	4	4	26	rich scop	5	1.07	0.62	1170	dolerite
4233	4	4	13	rest aust	8	1.67	0.30	680	Quat. till & fluvioglacial dep.
4434	4	4	24	rich scop	5	1.95	0.40	960	dolerite
4434	4	5	13	rich scop	5	0.49	0.57	980	dolerite
4434	4	4	13	rich scop	5	0.50	0.55	980	dolerite
4235	4	5	15	athr cupp	7	3.10	0.47	820	marsh deposits
4235	4	5	17	rich gunn	5	1.90	0.54	780	marsh deposits
4434	4	5	17	rich scop	5	0.93	0.59	980	Quat. till & fluvioglacial dep.
4235	4	5	16	rich scop	5	2.65	0.44	910	siltstone with sandstone
4235	4	6	14	glei spp	1	0.98	0.33	900	sedimentary
4235	4	5	14	rich scop	5	0.95	0.43	890	sedimentary

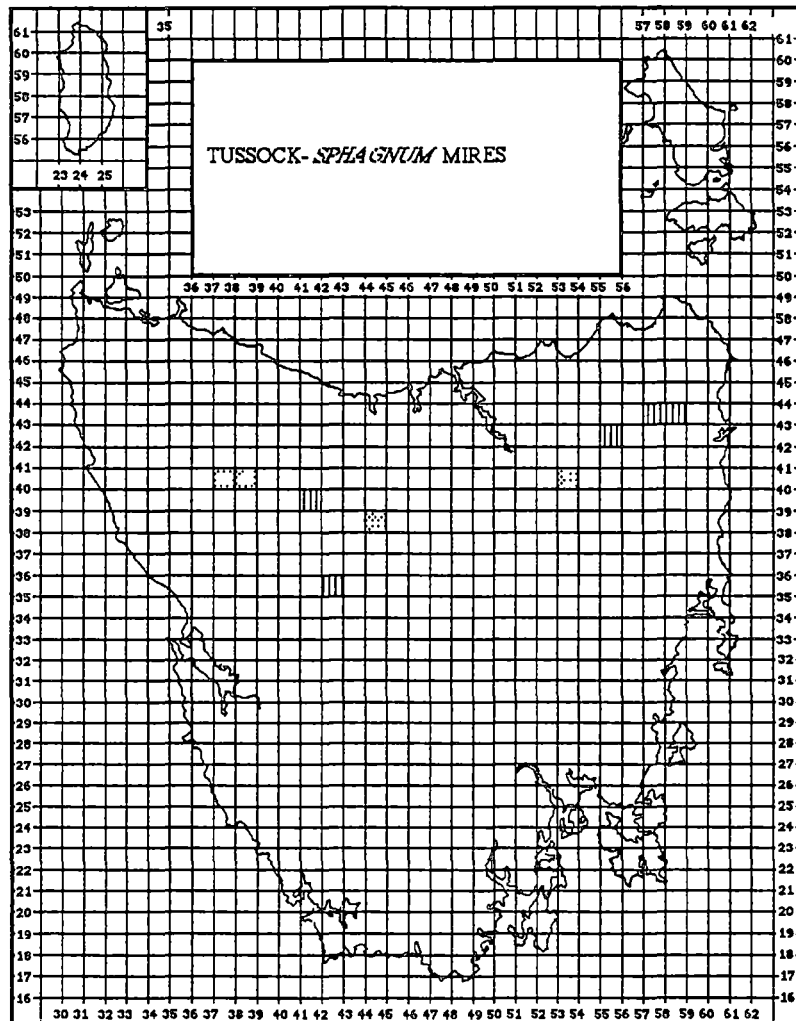
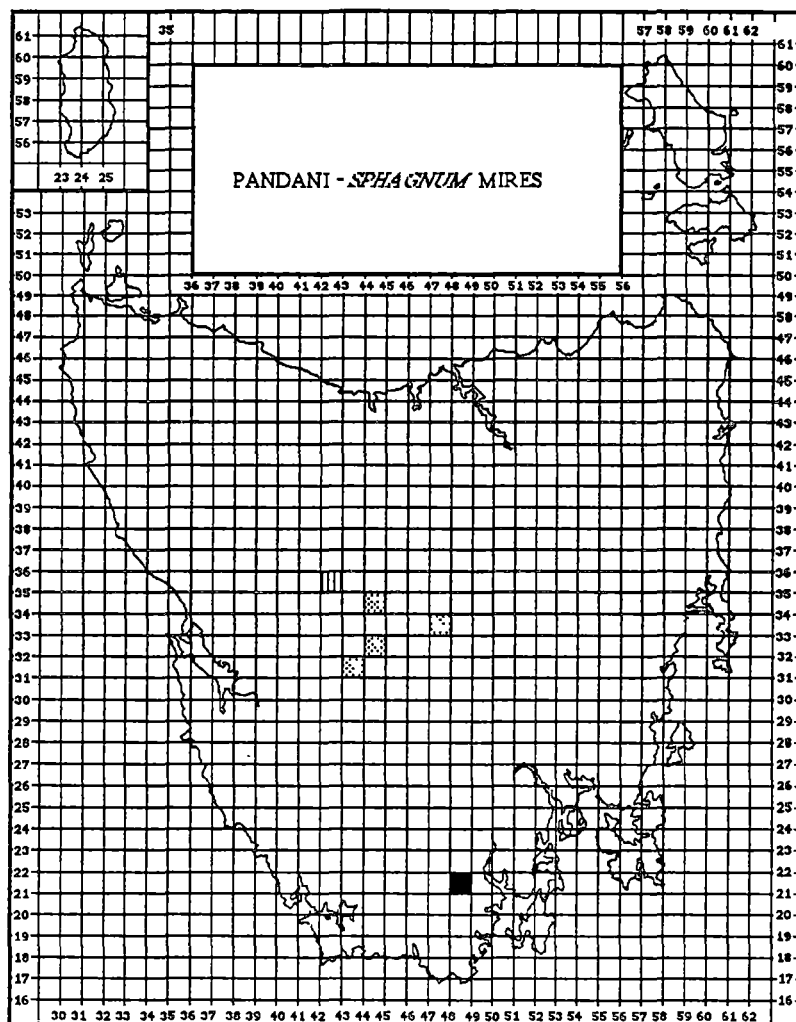
10km	TWINS	SPAN	GEOMORPHIC	SPP.	DOM.	DOM.	PEAT	HUMMOCK		
GRID	GROUP	TYPE	RICHNESS	SP.	L/FORM	DEPTH	HEIGHT	ALT.	COUNTRY	ROCK
						(m)	(m)	(m)		
4235	4	5	17	baec gunn	5	1.51	0.48	870	sedimentary	
4235	4	7	20	olea pini	5	0.62	0.48	880	sedimentary	
4335	4	7	15	rich scop	5	0.79	0.30	880	sedimentary	
4335	4	7	16	euca gunn	7	2.00	0.25	880	sedimentary	
4335	4	4	11	rest aust	8	1.38	0.47	940	marsh deposits	
4335	4	4	15	glei spp	1	2.40	0.43	960	marsh deposits	
4335	4	7	14	rich scop	5	0.87	0.60	1030	marsh deposits	
4235	4	5	14	noth cunn	7	1.43	0.48	800	marsh deposits	
4437	4	5	28	euca cocc	7	1.11	0.89	1150	marsh deposits	
4432	5	7	22	rich gunn	5	0.70	*	1100	dolerite	
4235	5	5	16	gymn spha	8	1.05	0.29	820	marsh deposits	
4434	5	5	16	emp minu	8	0.73	0.30	980	siltstone with sandstone	
4335	5	4	10	empo minu	8	2.37	0.23	880	sedimentary	
4820	5	5	25	lept lani	5	1.10	0.37	500	alluvium	
4820	5	1	22	rich pand	7	1.43	0.32	510	alluvium	
4820	5	5	19	rich pand	7	1.23	0.38	500	alluvium	
4820	5	5	16	rich pand	7	1.38	0.27	510	alluvium	
4331	5	5	20	come retu	5	*	0.18	750	marsh deposits	
4732	5	7	20	rest aust	8	0.66	0.26	840	basalt	
5743	6	4	19	heli hook	5	0.47	*	740	granite	
5743	6	4	14	lept lani	5	0.24	*	540	granite	
5743	6	4	17	tasm lanc	5	0.35	*	780	granite	
5542	6	4	19	poa labi	4	0.55	*	800	granodiorite	
3840	6	4	21	lept lani	5	0.42	0.47	600	Basalt	
3840	6	4	24	lept lani	5	0.52	0.28	660	Basalt	
4139	6	4	18	noth cunn	7	0.61	0.60	840	alluvium & tallus	
4139	6	7	21	rich gunn	5	0.58	0.55	800	basalt	
4438	6	5	14	junc spp.	5	0.49	1.33	785	marsh deposits	

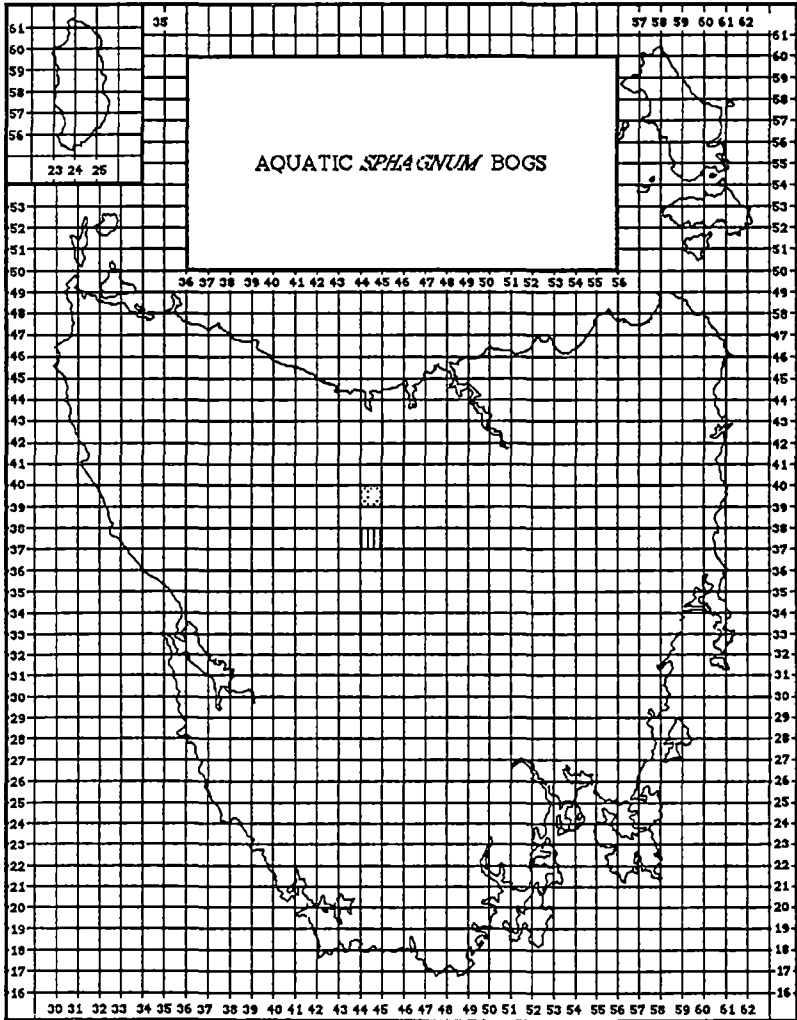
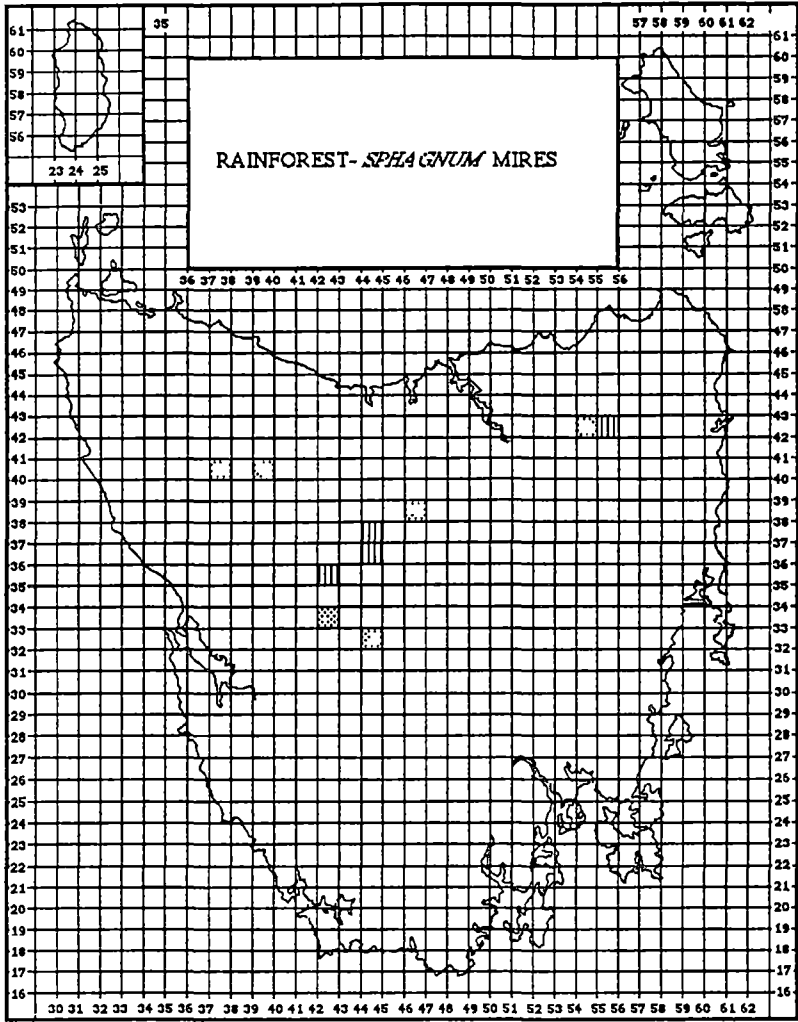
GRID	GROUP	GEOMORPHIC	RICHNESS	SP.	L/FORM	DEPTH	HEIGHT	ALT.	COUNTRY ROCK
10km	TWINSpan	TYPE	SPP.	DOM.	DOM.	PEAT	HUMMOCK		
						(m)	(m)	(m)	
5542	6	4	19	lept lani	5	0.69	0.19	640	granodiorite
5542	6	4	11	junc spp	8	0.45	*	780	granodiorite
5743	6	4	9	rich gunn	5	0.30	*	720	granite
5542	6	4	21	rich scop	5	0.90	*	790	Quat. till & fluvioglacial dep.
4235	6	5	13	heli hook	5	1.08	0.34	840	siltstone with sandstone
4235	6	5	15	rich gunn	5	1.48	0.45	870	sedimentary
5542	6	4	21	rich scop	5	0.90	*	790	granodiorite
5743	6	4	13	junc spp	8	0.46	*	720	granite
4233	7	6	17	euca cocc	7	0.92	*	960	siltstone with sandstone
4236	7	4	12	noth cunn	7	0.90	*	880	marsh deposits
4638	7	7	15	noth cunn	7	*	*	850	sandstone
4432	7	7	15	noth cunn	7	0.60	*	1100	dolerite
3840	7	4	17	lept lani	5	1.34	0.32	640	Basalt
3940	7	4	19	copr niti	5	0.61	0.35	680	Basalt
5442	7	4	18	lept lani	5	0.58	0.00	980	granodiorite
5542	7	5	19	lept lani	5	0.26	0.23	800	granodiorite
4235	7	5	14	noth cunn	7	1.23	0.20	810	marsh deposits
5542	7	4	18	lept lani	5	0.33	*	800	granodiorite
4235	7	5	14	olea obco	5	1.52	0.10	850	siltstone with sandstone
4235	7	4	17	noth cunn	7	0.67	0.00	860	sedimentary
4437	7	5	19	olea obco	7	0.81	0.33	1120	marsh deposits
4437	7	5	11	olea obco	7	0.60	0.49	900	marsh deposits
4439	8	8	5	lept scop	5	2.70	0.00	360	limestone
4437	8	6	11	noth cunn	7	0.85	0.32	880	marsh deposits
4437	8	6	5	noth cunn	7	0.73	0.53	900	marsh deposits

Distribution of each of the eight TWINSpan groups. Grid squares are 100 km²









The frequency of taxa in communities.

1=1-10%, 2=11-20%, 3=21-30%, 4=31-40%, 5=41-50%, 6=51-60%, 7=61-70%,
8=71-80%, 9=91-100%

15623478

15623478

abro fost -1---1--
acae nova -222113-
acti suff ---1----
acti moor -1--21--
agro spp 5221-12-
aspe gunn --21-21-
aste alpi -628732-
athe mosc -----27
athr cupp ---4111-
athr sela -----1-
baec gunn -513783-
baue rubi ---1-11-
baum spp. -----1--
bill long -----1-
blec penn -491279-
blec wats -----2-
boro citr ---1----
brac spp -1-----
call viri -1--111-
card spp --11--1-
care unde -8-312--
care spp --57761-
carp alpi 5--512--
carp curv -1-1----
celm long ---646--
celm saxi 9--1----
cent musc ---1----
cent mono ---11---
cent cord -1-----
cera glom -----1--
colo apet -----1-
come retu -12-----
copr niti -331125-
copr moor --22-2--
copr pumi -1--1---
cotu alpi -2---1--
cras spp ---11---
cyat deal ---1----
cyat juni -----12-
cyat parv --11-124
dant spp 5-31-2--
deye mont --11-1--
deye gunn --1--1--
deye spp ----1---

deye acce -----1--
deye quad -1-----
dich rara ---1-1--
dipl cord 5112-1--
dipl mora -1-1-1--
dipl lati ---131--
drim lanc --31-154
drym cyan -----1-
dros arct 5--5----
empo minu 5959994-
epac gunn --51221-
epac lanu ---141--
epac serp -3172---
epil spp -521-1-4
erig stel -35552--
euca cocc ---1112-
euca gunn --11432-
euca rodw -----1--
euca dela 1----1--
euca subc -----11-
euph spp. 5--2----
gahn gran --3-1274
gaul hisp -----1-
gent diem --1121--
gera pote --31-12-
glei spp. -728763-
gnap spp -322-21-
gnap coli ---111--
gono micr -131121-
gono mont --1-----
gono serp -1-1-1--
gono teuc -----1-
grev aust -----1--
gunn cord --2--12-
gymn spha -1-15---
heli back 9---1---
heli hook -15-2---
heli scor -31--1--
herp nova ----1-1-
hibb proc ----11--
hier fras 5--1-11-
hier redo --21131-
hist inci -----13-
holc lana -13-----

hydr	spp	5451343-	phyl	aspl	-----4-
hype	japo	-131-1--	picr	hier	-----4
hypo	ruco	-----1-	pime	drup	-----3-
junc	spp	-1711134	pitt	bico	-----124
lage	stip	-533256-	plan	glab	----11--
lepi	fili	----1---	plan	spp	-42112--
lept	lani	-361-15-	plan	dalt	-51-11--
lept	rupe	9-11311-	poa	labi	-151-31-
lept	scop	-----4	poa	spp	5-15452-
lept	squa	---1----	poa	annu	-----1-
lepy	tasm	----1---	podo	lawr	5-----
leuc	coll	-----1-	poly	juni	-374-33-
libe	pulc	-----24	pult	subu	-1-132--
lila	brow	--11-1--	pult	dent	-1-----
liss	mont	--21-12-	ranu	spp	-24--3--
luzu	spp.	--22121-	rest	aust	-117882-
lyco	fast	-556169-	rest	tetr	--1-1---
lyco	late	----1---	rest	comp	-1-11---
mela	squa	----11--	rich	acer	-2-313--
micr	niph	---2----	rich	gunn	-354861-
micr	tasm	522151--	rich	scop	--29162-
micr	tetr	---2----	rich	spre	5--111--
mill	dens	----111-	rich	pand	-5-1-1--
mitr	arch	---1-1--	rubu	gunn	5949893-
mitr	mont	-1-1----	rume	spp	--1-----
mono	subm	-12-112-	scho	spp.	-411-1--
mono	glau	--1-----	scir	spp.	-251213-
mono	aff.	---11---	scle	sp.	-1-----
myri	pedu	--11-1--	sene	spp.	-1-4-1--
nert	depr	-12-----	spha	cris	1999999-
noth	cunn	-12-1197	spha	falc	---1-119
olea	obco	---1-11-	spha	aust	---1-1-4
olea	pini	--1--21-	spha	subs	---1-114
olea	myrs	-----1--	spre	inca	-3-231--
olea	pers	-----1-	styl	gram	--2-----
oreo	pumi	543723--	telo	trun	-----17
oreo	dist	-111-11-	tetr	dist	----1---
oreo	cili	-31222--	tetr	tasm	-----1-
oreo	oxyc	----1---	tetr	acum	-1-----
orit	revo	-----11-	troc	cunn	-----2-
orit	acic	5-----	unci	spp.	-1-1-13-
ouri	inte	---1----	vell	mont	-----1--
oxal	lact	-85-438-	vero	grac	--1-----
oxal	corn	--2-----	viol	hede	-2-----
oxyl	elli	----1---	wahl	cera	--1-11--
pent	pumi	---111--	zier	arbo	-----1-
pern	tasm	-----1--			
pers	sp	-----1-			

APPENDIX 5

Chemical composition of 'Aquasol'

Manufactured by Hortico Ltd.

	%	%
N as mono ammonium phosphate	1.8	
N as potassium nitrate	2.6	
N as urea	18.6	
Total N		23.0
Total P water soluble as mono ammonium phosphate		4.0
K as potassium nitrate	7.8	
K as potassium chloride	10.2	
Total K		18.0
Zn as zinc sulphate	0.05	
Cu as copper sulphate	0.06	
Molybdenum as sodium molybdate	0.0013	
Manganese as manganese sulphate	0.15	
Iron as sodium ferris EDTA	0.06	
Boron as sodium borate	0.011	
Maximum biuret	0.40	

APPENDIX 6

Mean dry weights (with number of pots and standard deviations) for different experimental treatments. Mean values of humified *Sphagnum* have been back-transformed from square roots.

	<i>Sphagnum cristatum</i>			Associated species		Humified	<i>Sphagnum</i>
	No.	Mean Wt. (g)	St.Dev.	Mean Wt. (g)	St.Dev.	Proportion humified	St. Dev.
Experimental treatment	120	3.41	0.47	0.20	0.16	0.75	0.08
						0.00	0.00
No drought	60	3.32	0.47	0.22	0.19	0.77	0.06
Drought	60	3.50	0.46	0.19	0.13	0.73	0.10
						0.00	0.00
Nutrients-none	40	3.39	0.38	0.17	0.10	0.73	0.11
Nutrients-1	40	3.39	0.54	0.24	0.17	0.75	0.08
Nutrients-2	40	3.45	0.49	0.19	0.19	0.77	0.06
						0.00	0.00
Shade-none	60	3.48	0.50	0.24	0.17	0.75	0.10
Shade	60	3.33	0.43	0.16	0.14	0.75	0.07
						0.00	0.00
Drought x no shade	30	3.60	0.50	0.21	0.14	0.73	0.12
No drought x no shade	30	3.36	0.49	0.27	0.19	0.78	0.05
Drought x shade	30	3.40	0.40	0.16	0.10	0.73	0.08
No drought x shade	30	3.26	0.49	0.16	0.17	0.76	0.07
						0.00	0.00
Drought x no nutrients	20	3.50	0.46	0.16	0.11	0.69	0.13
No drought x no nutrients	20	3.27	0.25	0.18	0.10	0.78	0.06
Drought x nutrients-1	20	3.63	0.47	0.24	0.12	0.74	0.09
No drought x nutrients-1	20	3.14	0.51	0.25	0.21	0.76	0.06
Drought x nutrients-2	20	3.38	0.43	0.14	0.14	0.76	0.06
No drought x nutrients-2	20	3.52	0.54	0.24	0.21	0.77	0.06
						0.00	0.00
No shade x no nutrients	20	3.51	0.43	0.17	0.11	0.71	0.14
No shade x nutrients-1	20	3.34	0.55	0.29	0.16	0.77	0.06
No shade x nutrients-2	20	3.59	0.52	0.26	0.21	0.78	0.05
Shade x no nutrients	20	3.27	0.28	0.16	0.11	0.76	0.07
Shade x nutrients-1	20	3.43	0.55	0.20	0.18	0.73	0.09
Shade x nutrients-2	20	3.30	0.42	0.12	0.13	0.75	0.06
						0.00	0.00
No shade x no nutrients x no drought	10	3.41	0.28	0.18	0.12	0.78	0.06
No shade x no nutrients x drought	10	3.61	0.54	0.17	0.11	0.63	0.16
No shade x nutrients 1 x no drought	10	3.01	0.27	0.28	0.19	0.77	0.05
No shade x nutrients 1 x drought	10	3.68	0.56	0.30	0.12	0.77	0.06
No shade x nutrients 2 x no drought	10	3.68	0.62	0.35	0.22	0.78	0.05
No shade x nutrients 2 x drought	10	3.51	0.40	0.16	0.16	0.77	0.06
						0.00	0.00
Shade x no nutrients x no drought	10	3.14	0.11	0.13	0.10	0.78	0.06
Shade x no nutrients x drought	10	3.39	0.34	0.20	0.08	0.74	0.07
Shade x nutrients 1 x no drought	10	3.28	0.66	0.21	0.23	0.75	0.07
Shade x nutrients 1 x drought	10	3.58	0.38	0.18	0.11	0.71	0.10
Shade x nutrients 2 x no drought	10	3.60	0.41	0.13	0.15	0.76	0.07
Shade x nutrients 2 x drought	10	3.30	0.44	0.11	0.11	0.75	0.06