

## A *Chionochloa* / *Sphagnum* / Cushion Valley Bog in East Otago, New Zealand

Susan Walker<sup>1</sup>, John B. Steel<sup>1</sup>, G. L. Rapson<sup>2</sup>, Stephen H. Roxburgh<sup>3</sup>, Warren McG. King<sup>4</sup>, Anni J. Watkins<sup>1</sup>, Tom E. Myers<sup>5</sup>, Jonathan A. Keogh<sup>6</sup>, Amelia A. M. McQueen<sup>1</sup> and J. Bastow Wilson<sup>1,\*</sup>

<sup>1</sup>Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand

<sup>2</sup>Ecology Group, Institute of Natural Resources, Massey University, Private Bag, Palmerston North, New Zealand

<sup>3</sup>Ecosystem Dynamics Group, RSBS, Institute of Advanced Studies, Australian National University, Canberra, ACT 0200, Australia

<sup>4</sup>NSW Agriculture, Agricultural Research and Veterinary Centre, Forest Road, Orange, NSW 2800, Australia

<sup>5</sup>Dunedin Botanic Garden, Dunedin City Council, P.O. Box 5045, Dunedin, New Zealand

<sup>6</sup>Portobello Marine Laboratory, University of Otago, P.O. Box 8, Portobello, New Zealand

\*Corresponding author (E-mail: bastow@otago.ac.nz)

**Abstract:** A valley mire was sampled on the flanks of Swampy Hill, east Otago, New Zealand. It formed in a narrow valley, apparently originally comprising two basins. The end of the mire nearest the outlet contained species typical of fens (*i.e.*, rheotrophic mires). At the head of the valley there was a section of the mire with mixed vegetation cover comprising the tussock grass *Chionochloa rubra*, *Sphagnum* species, and cushion/herb/shrub cover. Ombrotrophic status of this section was indicated by a slightly raised profile, greater acidity, lower exchangeable Na and K, and lower substrate cation exchange capacity, identifying it as a bog. Total Ca:Mg molar ratios were generally above 1.0, but this rule-of-thumb for ombrotrophic status may be inapplicable here. It is not known whether New Zealand *Sphagnum* species are as efficient at lowering the pH as those investigated elsewhere. Macrofossil evidence indicates that some components of the bog, such as *Sphagnum* and epacridaceous subshrubs, have remained constant, almost since the inception of the bog. However, *Empodisma minus*, currently absent from the bog and rare in the region, was present at one stage. The change from cover with *Empodisma* and *Dracophyllum* as significant components, to the present *Chionochloa/Sphagnum*/cushion composition, occurred a few hundred years ago, probably initiated by fire. Comparison with preliminary information for other bogs suggests that those in the eastern part of the South Island vary considerably in species composition, with individualistic assemblages of species. The site is seen as having high conservation values. To protect these values the bog needs protection from invasive exotic weeds, and from damage by wild pigs.

**Keywords:** Bog; conservation; fen; mire; ombrotrophic; rheotrophic; *Sphagnum*.

## Introduction

Peatlands (*i.e.*, mires) are estimated to cover almost 1% of New Zealand's land surface (166 000 ha: Moore and Bellamy, 1974). These areas include a wide variety of vegetation types (Dobson, 1979). Mire types such as the pākihi of Westland have been described (Williams *et al.*, 1990; Agnew *et al.*, 1993), as have the *Empodisma* bogs of Southland (Agnew *et al.*, 1993). Yet, many New Zealand mire types remain undescribed. There has been no detailed description of the much more varied *Chionochloa rubra* / *Sphagnum* mires, of which several examples exist in eastern South Island, and

which were probably even more common before European settlement.

Rheotrophic mires, or 'fens', receive inflow of water from surrounding land, bringing with it a supply of mineral nutrients (Sykes *et al.*, 1991). In contrast, mires which have a domed topography are dependent on rain for both water and mineral input, *i.e.*, they are ombrotrophic, or 'bogs' (Moore, 1989). Thus, a bog is a specific type of mire. Since rain is low in nutrients, ombrotrophic bogs are nutrient-deficient (Damman, 1990; Holdsworth and Mark, 1990). Values of pH are usually low (*i.e.*, below 4.0) - because of leaching by rainwater and often also the acidifying effect of

*Sphagnum* species (Wilson and Agnew, 1992). The peat in an ombrotrophic bog is anaerobic due to the high water table. The high acidity and the lack of oxygen inhibit the microbial decomposition of organic matter, resulting in a buildup of peat, eventually to a depth of many metres. Because these conditions increase the growth of *Sphagnum* species, peat builds up especially in the centre of the bog, giving the raised dome. This topography increases the independence of the bog surface from inflow of water from surrounding areas. The result is a positive-feedback switch, in which the *Sphagnum* increases the acidity, leaching and waterlogging, conditions which in turn encourage the growth of *Sphagnum* (Wilson and Agnew, 1992).

A raised bog comprises the bog centre, the marginal slopes, and a sluggish perimeter stream, or lagg, which contains more nutrient-rich water (Heathwaite *et al.*, 1993). In New Zealand, raised bogs are common in the south, and occur on poorly drained soils, as interfluvies within swamps, on terraces with podzolised soils, or on plateaux (Wardle, 1991).

Our aim is to describe a particular mire dominated by *Chionochloa rubra*, *Sphagnum* and cushion/herb/shrub species, as an example of this type and as a step towards understanding the range of variation between mires of the region. We particularly seek evidence on the ombrotrophic/rheotrophic status of the mire.

### Study site

Swampy-spur Mire is at 620 m a.s.l., in a small valley on the flanks of Swampy, a hill some 10 km north of Dunedin, Otago, New Zealand. The site is at 170° 30' E 45° 48' 30"S, map reference NZMS260 I24 151868, 1.5 km east of Swampy summit, about 200 m to the northwest of the knoll at the end of Swampy Spur. Mean annual temperature, interpolating between sea level and the summit is c. 6°C. Fogs are frequent. Total annual precipitation by interpolation is 1280 mm yr<sup>-1</sup> (1991-1996 summit values: D.L. Murray, University of Otago, Dunedin, N.Z., *pers. comm.*). Surrounding soils are of the category Acid Brown Soil (Hewitt, 1993). The pre-Polynesian vegetation of the area surrounding the mire was probably originally mixed podocarp forest (Wardle and Mark, 1956) but it presently comprises montane scrub with interspersed tussock grasses. The mire is elongated from east to west (Figure 1). A slow stream runs along the lagg on the southern side, and exits through a narrow neck at the western end.

## Methods

### Vegetation

The mire and its immediate surrounds (2.3 ha) were sampled using 462 1 m diameter circular quadrats,

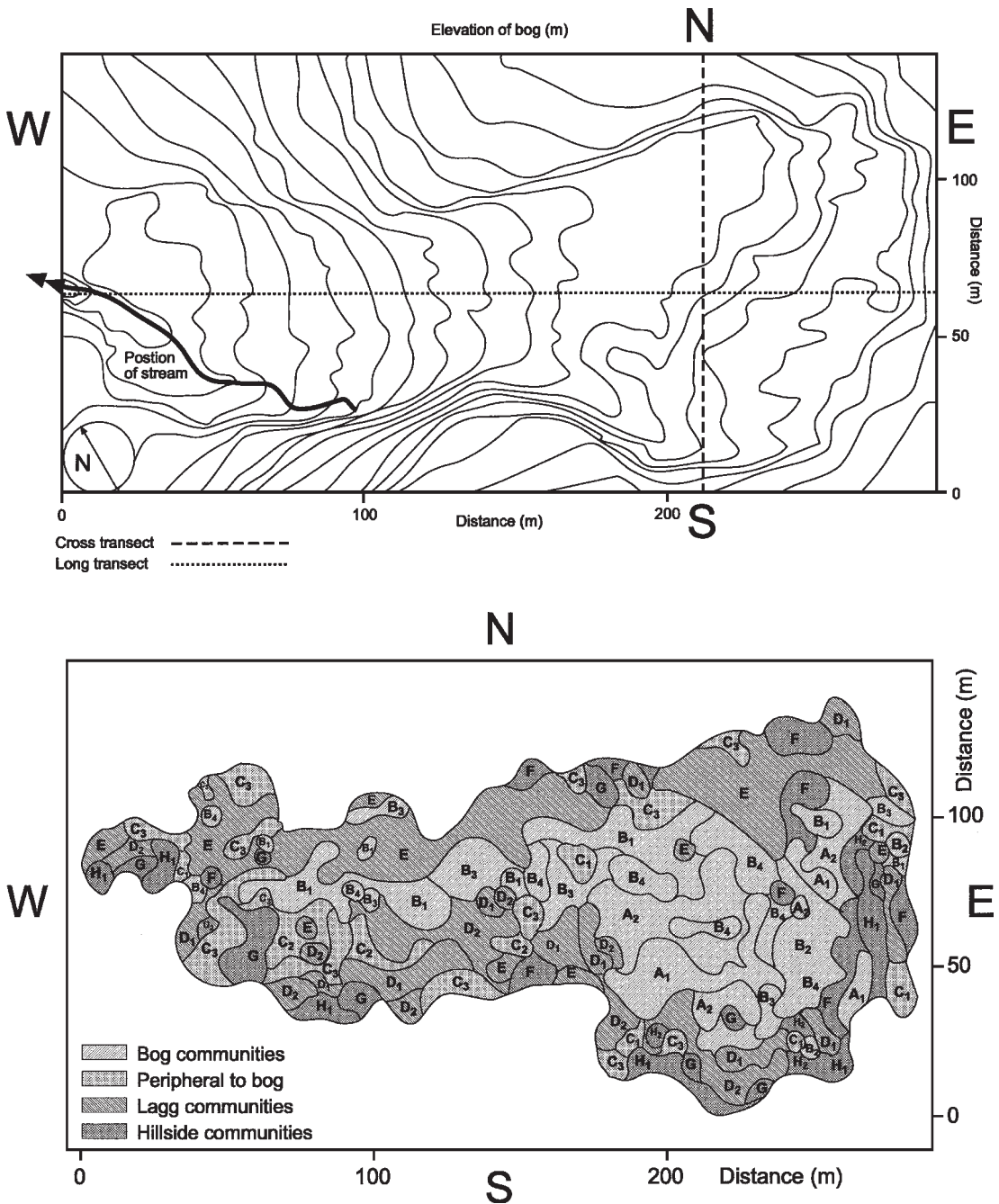
placed over the entire area by restricted randomisation (Greig-Smith, 1983). The sampling area included the vegetation immediately surrounding the mire, in conformance with the Sykes Principle (Roxburgh *et al.*, 1994). The shoot presence of all macroscopic plant species was recorded within each quadrat, excluding liverworts (many of which were minute and would have been impossible to detect in the field). Cluster analysis was performed on the species data, using the Jaccard measure of similarity and the Flexible sorting strategy with beta = -0.25 (Clifford and Stephenson, 1975).

Nomenclature follows Connor and Edgar (1987) and references therein except where indicated in Table 1, Stace (1997) for naturalised species, Brownsey and Smith-Dodsworth (1989) for pteridophytes, Beever *et al.* (1992) for mosses and Galloway (1985) for lichens. We follow Heads (1987) for *Veronica sensu lato*, since it is generally recognised that *Hebe* as used by Allan (1961) is inappropriate. We do not follow alternative names of Wagstaff and Garnock-Jones (1998), if only because they did not give any. We use the spelling '*Hypochaeris*' because we are following Stace (1997) as the most recent source. We use a broad circumscription for *Coprosma* because of the unrefuted logic of Heads (1996) that: (a) there is no character that distinguishes *Nertera* from *Coprosma sensu stricto*, and (b) *Nertera* is no more different from *Coprosma s.s.* than the sections of *Coprosma s.s.* are from each other.

### Topography and peat analysis

The elevation of the vegetation surface was surveyed over the mire, and also along lines across the widest part of the short axis (the cross transect), and on long axis (the long transect). At each of the levelling points, the position of the water table was recorded (by digging pits where necessary), and a peat probe was used to determine the depth of the peat.

Peat or soil samples were collected from 0 to 15 cm depth, at 5 m intervals along the cross transect and 15 m intervals along the long transect. Moisture (in summer, and additionally in winter on the cross transect) was estimated by drying at 80°C, organic matter by loss-on-ignition at 500°C, and total Ca and Mg by atomic absorption spectroscopy after wet digestion with nitric acid. On the cross transect, pH was measured on a water extract, exchangeable K and Na by atomic absorption spectrophotometer after semi-micro leaching with 1M ammonium acetate at pH 7 (Blakemore *et al.*, 1987), and CEC by pH change of extractions with 1M ammonium acetate and acetic acid.



**Figure 1.** Swampy-spur bog, east Otago. Above: Contours (m) of the surface of the bog and the surrounding hill slopes, and below: Distribution of communities, formed by interpolating between the 462 quadrats. For explanation of community abbreviations see Table 1 and text.

**Table 1.** Species frequencies in the sub-communities on the bog.

Species	Sub-community															
	A1	A2	B1	B2	B3	B4	C1	C2	C3	D1	D2	E	F	G	H1	H2
<b>Vascular plants</b>																
<i>Acaena caesiiglauca</i>												1				
<i>Aciphylla scott-thomsonii</i>	5		8	12	5		17	20				19	9	14	5	71
<i>Agrostis capillaris</i> <sup>1</sup>		8	83	35	50		83	54	76			88	72	62	20	
<i>Anaphaloides bellidioides</i> <sup>2</sup>			6	18			83	41		54	72	8	17	3	52	10
<i>Anemone tenuicaulis</i>								12				6	3			5
<i>Anthoxanthum odoratum</i> <sup>1</sup>	5		31	65	15	13	83	77	20	69	81	37	38	5	5	
<i>Aporostylis bifolia</i>	19	36	28	24	20	83		12				24	3	5		
<i>Astelia nervosa</i>	5	19		6	15	4			2		3	1	9	38	15	
<i>Blechnum penna-marina</i>	76	87	81	94	100	96	17	54	46	35	28	83	94	52	20	
<i>Blechnum novae-zelandiae</i> <sup>3</sup>																
<i>Blechnum montanum</i> <sup>3</sup>							17	10					3	33	55	71
<i>Brachyglottis bellidioides</i>												1				
<i>Bulbinella angustifolia</i>			14					23	15		8	29	3	10	15	
<i>Caladenia lyalli</i>									2					5		
<i>Callitriche stagnalis</i> <sup>1</sup>										4	3					
<i>Cardamine debilis</i>			11	12				8	7	8	3	4	56			
<i>Carex coriacea</i>	90	79	86	94	95	75	100	92	71	92	89	84	66	38	20	
<i>Carex ovalis</i>									2							
<i>Celmisia gracilentia</i>	48	91	56	71	40	96		23	34	19	3	62	22	57	10	
<i>Centrolepis pallida</i>		2														
<i>Cerastium fontanum</i> <sup>1</sup>											14					
<i>Chionochloa rigida</i>									5		3			24	35	
<i>Chionochloa rubra</i>	95	100	97	82	90	96	17	54	78	19	19	84	53	71	25	
<i>Coprosma acerosa</i>		6	69		50	8		62	15	8		30	3			
<i>Coprosma cheesmanii</i>	5	34	19		5	17	17	17		4	8	17	28	29	15	
<i>Coprosma ciliata</i>		4											6		5	
<i>Coprosma nertera</i>	5	4	44		10	21		46	15		3	13	6			
<i>Coprosma propinqua</i>	43	30	19	24	20	38		31	49	14		48	13	52	90	71
<i>Coprosma rugosa</i>	14	8	8	6	5	21	17	8	5		6	24	25	10	15	
<i>Cortaderia richardii</i>									2	4	3				5	
<i>Corybas orbiculatus</i>		8			5							4				
<i>Crepis capillaris</i> <sup>1</sup>								23		4	22	1	3		5	
<i>Cyathodes pumila</i>	90	89		12		17							6	10		
<i>Dracophyllum longifolium</i>	19	6	3	24		4			2			1	3	10	20	
<i>Drosera arcturi</i>	5	40			5	8										
<i>Epilobium alsinoides</i>								46			6					
<i>Erica vagans</i> <sup>1</sup>							17									
<i>Euphrasia zelandica</i>												2		10		
<i>Festuca rubra</i> <sup>1</sup>	5	32	3			13						1	9			
<i>Forstera tenella</i>	10	11	22		5	21			5			2		5		
<i>Galium propinquum</i>								8								
<i>Gaultheria macrostigma</i> <sup>4</sup>	95	85	50	100	65	96		15	10	4		41	59	86	10	29
<i>Gentiana grisebachii</i>												1		5		
<i>Geranium microphyllum</i>			69	59		21		46	63	15		80	3	43	20	29
<i>Gonocarpus micranthus</i>		2														
<i>Grammitis billiardierii</i>														5		
<i>Griselinia littoralis</i>														10		
<i>Hierochloa novae-zelandiae</i>		15	61	47	20	38	33	15	27	81	39	31	63			
<i>Holcus lanatus</i> <sup>1</sup>	5		11		15			85	29	77	94	6	6			
<i>Hydrocotyle heteromeria</i>								15	4		14			5	5	
<i>Hypochaeris radicata</i> <sup>1</sup>	5	19	56	65	10	4	100	69	68		6	48	3	71	10	
<i>Isolepis aucklandicus</i>		2	3		25			15	2			3		14		
<i>Juncus articulatus</i> <sup>1</sup>	29		3							4	14					
<i>Juncus gregiflorus</i>	10	8	72	53	20	38	33	38	32	81	39	66	59		5	
<i>Juncus pallidus</i>			6		25		17		17	4	3	22	28			
<i>Leonohebe odora</i> <sup>5</sup>	5	21	81	65	65	71	33	31	78	65	3	92	56	48	35	
<i>Leucopogon fraseri</i>									2			4		24	15	
<i>Luzula banksii</i>		2									3					
<i>Luzula picta</i>		9	8	12		8			5			8	9	10		
<i>Luzula rufo</i>	19	30	3	24	10	8			10	4		13	9	5		
<i>Lycopodium fastigiatum</i>	5	58	25	59	10	29			12			14	3	33	10	5
<i>Lycopodium scariosum</i>	24													10	5	
<i>Meliclytus alpinus</i>							17						3	10	25	
<i>Muehlenbeckia australis</i>														5	5	
<i>Microtis unifolia</i>	62	6	8	24	5	8					3			5	5	
<i>Mimulus moschatus</i> <sup>1</sup>											3					
<i>Olearia bullata</i> <sup>6</sup>					6											
<i>Oreobolus strictus</i>	86	77		6		13		15								
<i>Oreomyrrhis colensoi</i>			3							7		23	3	14		

Table 1. Continued

Species	Sub-community															
	A1	A2	B1	B2	B3	B4	C1	C2	C3	D1	D2	E	F	G	H1	H2
<i>Oreomyrhis ramosa</i>	5								10	8	8	6				
<i>Ozothamnus leptophyllus</i> <sup>7</sup>	19	30	22	82	10	21	33	8	32		3	11	13	33	20	
<i>Pentachondra pumila</i>	19	49				13						1				
<i>Phormium cookianum</i>	5	21	6	41	5		50		2	4	8	2	19	62	85	100
<i>Poa colensoi</i>						25				4			3			
<i>Poa pratensis</i> <sup>1</sup>										4	3					
<i>Poa trivialis</i> <sup>1</sup>											3					
<i>Podocarpus totara</i>														5		
<i>Polystichum vestitum</i>									5							10
<i>Pratia angulata</i>									2			3				
<i>Pterostylis australis</i>	10	30	44		35				10			27	22	43	5	
<i>Ranunculus acris</i> <sup>1</sup>			3													
<i>Ranunculus foliosus</i>											11					
<i>Ranunculus glabrifolius</i>			3				69	7		15	67	1				
<i>Ranunculus reflexus</i>							8				17			5		
<i>Ranunculus repens</i> <sup>1</sup>							23			8	17					
<i>Rubus schmideliioides</i>																10
<i>Rumex acetosella</i> <sup>1</sup>										8		4	6			
<i>Rumex crispus</i> <sup>1</sup>											3					
<i>Rytidosperma nigricans</i>	5	2	6		10		50		2			6	6	38	5	
<i>Senecio jacobaea</i> <sup>1</sup>																
<i>Stellaria alsine</i> <sup>1</sup>								38		4	8	1	3			
<i>Taraxacum officinalis</i> <sup>1</sup>											3					
<i>Thelymitra longifolia</i>	10	6			5								6	5		
<i>Trifolium repens</i> <sup>1</sup>								23	2	4	39					
<i>Ulex europaeus</i> <sup>1</sup>										4						15
<i>Uncinia banksii</i>			3									3				
<i>Uncinia filiformis</i>		13			5											
<i>Uncinia rubra</i>		2			10		17	38	2			3	3	24		
<i>Uncinia species</i>		2	17	6		4	17	8	2	4	3	24	13	43	5	
<i>Viola cunninghamii</i>										4	6	2	6			
<i>Wahlenbergia albomarginata</i>									2							
<b>Mosses</b>																
<i>Acrocladium cuspidatum</i>					5				2							
<i>Bryum billiardieri</i> <sup>8</sup>				12				8	7			20	9	5		
<i>Campylopus vesticaulis</i>													3	5		
<i>Cyatophorum bulbosum</i>																5
<i>Dicranaloma billardieri</i>		21			5							1	3	5		
<i>Distichophyllum pulchellum</i>	19	19	72	76	25	38		15	41	4		43	53	95	40	
<i>Drepanocladus fluitans</i>	5	4												5		
<i>Hypnum cupressiforme</i>	52	75	11	82	25	38	17	15	22	8	11	78	56	48	25	
<i>Leptotheca gaudichaudii</i>			14					8	5			8			5	
<i>Neckera pennata</i>									5			2		10		
<i>Polytrichum juniperinum</i>	29	45	86	12	20	17		8	32			62	19	52	5	
<i>Ptychomnion aciculare</i>														19	10	
<i>Pyrrhobryum bifarium</i>	10	8		6					5			1	25	38	5	
<i>Rhytidelphus squarrosus</i>												1		5		
<i>Sphagnum cristatum</i>	48	55	92	59	80	96		8	12			16	41			
<i>Sphagnum falciculatum</i>			14	6	5	4						7				
<i>Thuidium furfurulosum</i>								23	2			6		14		
<b>Lichens</b>																
<i>Candelaria concolor</i>		6	6	6	5		17						13	19	5	
<i>Catillaria species</i>													3			
<i>Cladia retipora</i>		2												5		
<i>Cladina mitis</i>	33	17										1		14		
<i>Cladonia calycantha</i>												1				
<i>Cladonia carassensis</i>									2			1		5	10	
<i>Cladonia pyxidata</i>		6										3		19	5	
<i>Cladonia scabriuscula</i>												7	3	14	10	
<i>Peltigera dolichorhiza</i>		4	8	24	5	4		31	32			58	3	43		
<i>Sticta subcaperata</i>														5		
<i>Thamnolia vermicularis</i>	14	2														
<i>Usnea arida</i>									2							
<i>Usnea contexta</i>		4	11	24	10	4	17	15	54		3	21	28	14	20	14
<i>Usnea pusilla</i>			6			4						8		5		

<sup>1</sup>Exotic species<sup>2</sup>(G.Forst.) Glenny = *Helichrysum bellidioides*<sup>3</sup>T.C. Chambers et P.A. Farrant<sup>4</sup>(Colenso) Middleton = *Pernettya macrostigma*<sup>5</sup>(Hook. f.) Heads = *Hebe odora*<sup>6</sup>H.D.Wilson et Garn.-Jones cf. *Olearia virgata*<sup>7</sup>(G. Forst.) Breitwieser et J.M. Ward = *Cassinia leptophylla*<sup>8</sup>var. *platyloma*

## Macrofossil analysis

A peat core was taken from the centre of the widest (raised) part of the mire, currently bearing Community A2 (see below). The peat was divided into 5 cm vertical intervals. Each sample was washed free of fine material with a 1mm sieve, and then examined under the dissecting microscope. All leaf cuticle material was examined with the optical transmission microscope, and compared to reference slides of known plant leaf cuticles.

## Results

### Vegetation

Altogether, 157 species were recorded, *i.e.*, 16 lichens, 14 liverworts [recorded when seen], 21 mosses, 2 lycophytes, 5 ferns, 38 monocots and 61 dicots. Of the 143 non-liverwort species, 134 occurred in quadrats, though 18 only once. Species richness in quadrats

ranged from 2 to 28 species, with a mean of 12.8 species per quadrat.

The most abundant physiognomic dominant was the tussock grass *Chionochloa rubra* (Figure 2). Other species in the same stratum included the shrubs *Coprosma propinqua*, *Leonohebe odora* and *Ozothamnus leptophyllus* and the megaherb *Phormium cookianum*. Below them was a herb layer with species such as *Astelia nervosa*, *Carex coriacea*, *Celmisia gracilentia*, *Juncus gregiflorus*, and the subshrub *Gaultheria macrostigma*. Against the peat was a cushion layer with *Blechnum penna-marina*, *Cyathodes pumila*, *Oreobolus strictus* and the mosses *Sphagnum cristatum*, *Hypnum cupressiforme* and *Polystichum juniperinum*.

The vegetation classification is described at the arbitrary level of 8 communities (A to H; Figure 1b; Table 1). These communities are named for convenience, generally after the most characteristic species. Communities A and B are the bog communities in the centre of the mire, including the raised ombrotrophic portion, and community C tends to be peripheral to the bog communities. D is the lagg

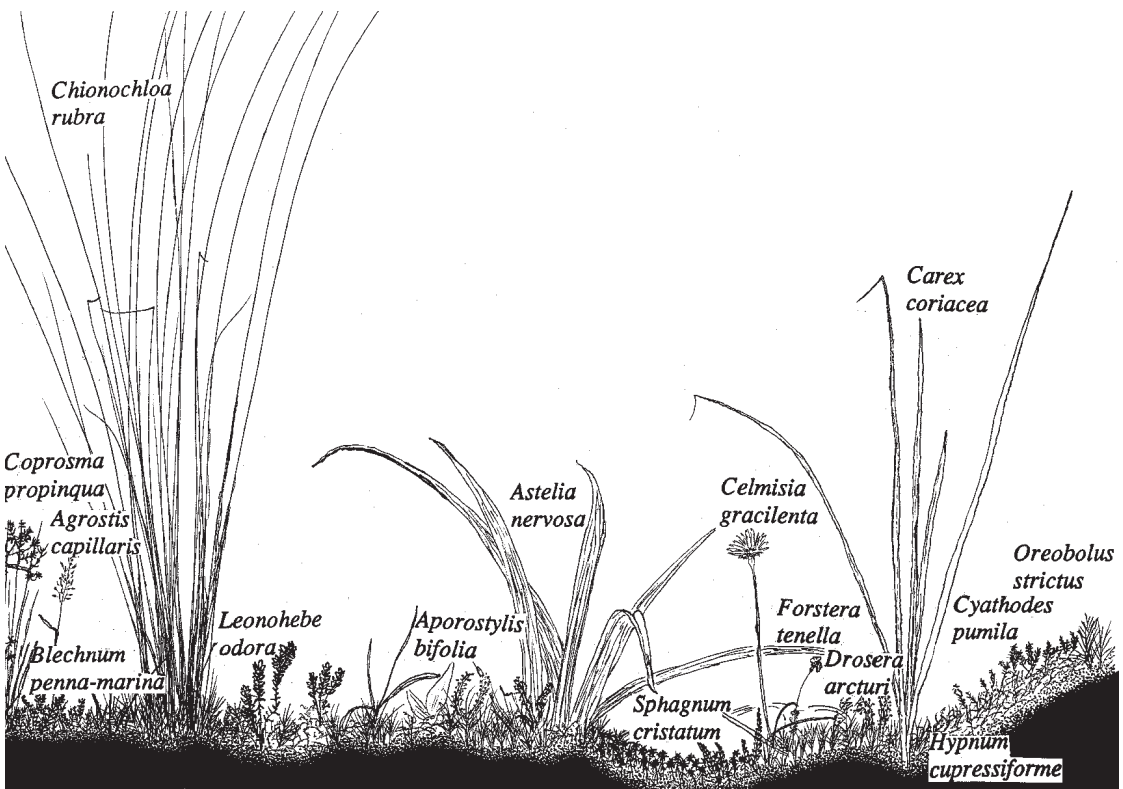


Figure 2. Vegetation profile through Community A.

community on the southern side; because the lag forms a stream at one end it is termed the 'Lagg Stream' community. At the northern edge, no stream is formed, and the community, E, is therefore called the 'Lagg Fen' community. F, G and H are communities generally of the surrounding hill slopes. Further subdivisions into two or more sub-communities are made within five of these communities, generally named after a species that reaches its greatest frequency in that sub-community, the one most diagnostic of the sub-community, at least within its community.

### A. Cushion Bog community

The Cushion Bog community occurs only in the raised portion of the mire (Figs. 1, 3a), and occupies 14% of the area sampled (as % of quadrats). The community is distinguished by the presence of *Oreobolus strictus* and the sub-shrub *Cyathodes pumila* (Table 1; Figure 2), though *Chionochloa rubra* tussocks are common. Species richness is relatively high (c. 14 species per 1 m diameter quadrat). Two distinct variants are recognised:

A1: *Microtis unifolia* sub-community. This vegetation type is found towards the south of the raised portion of the bog, and was recorded in only 4% of the area sampled. Small shrubs of *Coprosma propinqua* are present.

A2: *Pentachondra pumila* sub-community. Occupying some 10% of the area sampled, this sub-community is richer in species than sub-community A1, with an average of 15 species per quadrat. Several shrubs are present, including *Coprosma cheesemaniai*, *C. propinqua* and *Ozothamnus leptophyllus*.

### B. Sphagnum community

The *Sphagnum* community is extensive, occupying 21% of the area sampled. It is found from east to west along the length of the bog, and borders on the Lagg Fen community to the north. Species richness is as high as in Community A, with an average of 14 per quadrat. Four distinct sub-communities may be recognised within this community. In all of these, the tussock grass *Chionochloa rubra*, shrubs (especially *Leonohebe odora*), *Blechnum penna-marina*, *Carex coriacea*, and *Sphagnum* spp. (mainly *S. cristatum*) are frequent.

B1: *Juncus gregiflorus* sub-community. This *Sphagnum* sub-community is found at the northern margin of the raised bog area (A), between it and the Lagg Fen (E), and also down-valley in the centre of the mire. It occupies a substantial 8% of the area sampled.

B2: *Hypnum cupressiforme* sub-community. This localised sub-community is confined to the up-valley (eastern) end of the bog, adjacent to the hill slopes, and occupies some 4% of the area sampled.

B3: *Blechnum penna-marina* sub-community. Also occupying 4% of the area, this sub-community is the most species-poor of the *Sphagnum* vegetation types, with an average of 11 species per quadrat.

B4: *Aporostylis bifolia* sub-community. Slightly, but not significantly, richer in species than sub-community B3, this sub-community similarly occupies some 5% of the area sampled, in patches around the edges of the raised portion of the bog.

### C. Carex - exotic grasses community

The community occurs in peripheral areas just beyond the bog proper, including the eastern and western extremes, with some occurrences in the centre of the bog. It occupies 13% of the sampled area. *Carex coriacea* is common throughout this predominantly graminoid community, in which the native *Leonohebe odora* is the only frequent shrub species. Exotic grasses, particularly *Agrostis capillaris* and *Anthoxanthum odoratum*, are usually present, while *Hierochloa novae-zelandiae* and *Juncus gregiflorus* are somewhat less common. The exotic forb *Hypochoeris radicata* is frequently present in the sward. Community C is moderately rich in species, and may be divided into three sub-communities.

C1: *Phormium* sub-community. This sub-community occurs in small, localised patches at south and east margins of the mire. It is significantly less rich ( $P < 0.05$ , by *t*-test) than subcommunities C2 and C3, with an average of only 9 species per quadrat. This may be due to the presence of clumps of native flax (*Phormium cookianum*), and the shrub *Ozothamnus leptophyllus*.

C2: *Coprosma acerosa* sub-community. This sub-community occupies a small area of the western (lower) end of mire.

C3: Shrub - mixed herbs sub-community. Patches of Community C3 are scattered, generally around the periphery, both among scrub and also adjacent to the Lagg Fen (E). The sub-community occupies some 9% of the sampled area. The vegetation comprises the relatively tall species *Chionochloa rubra*, *Coprosma propinqua* and *Leonohebe odora*, with a diverse understorey.

### D: Lagg Stream community

This vegetation is mainly confined to the lag on the southern side, which runs the length of the mire, from east to west. The stream originates in it, and then flows to the outlet (Figure 1a). Community D is found only in the downstream portion, where the stream is more commonly flowing. Patches of this type of vegetation are also found on the northern margin, in the Lagg Fen area. The community occupies some 13% of the area

sampled. In contrast to the Lagg Fen community (Community E), it is relatively species-poor, having an average of only 8 species per quadrat. Herbaceous species predominate, and the vegetation comprises a sward of *Carex coriacea*, *Hierochloa novae-zelandiae* and *Holcus lanatus*, while *Agrostis capillaris* and *Anthoxanthum odoratum* are also common. *Viola cunninghamii* and *Oreomyrrhis ramosa* are characteristic species of this community, and the moss *Hypnum cupressiforme* is frequently present. Two sub-communities are recognised.

D1: *Leonohebe odora* sub-community. This sub-community occurs in patches both within the Lagg Stream area, and amongst the Lagg Fen area to the north of the mire.

D2: *Ranunculus glabrifolius* sub-community. D2 is confined to the area around the lagg stream, and covers a larger area than the *Leonohebe* sub-community (D1). There are few shrubs or other tall species. Not very common, but characteristic of the community, are three *Ranunculus* species: *R. glabrifolius*, *R. acris* and *R. repens*.

### E: Lagg Fen community

Twenty one percent of the area sampled falls into this community, which is restricted to the wide lagg area on the northern side of the mire. It is relatively rich in species, with an average of 16 species per quadrat. Taller species, including *Leonohebe odora* and *Chionochloa rubra* and occasionally *Coprosma propinqua*, are scattered in a short, graminoid/forb sward which includes *Agrostis capillaris*, *Carex coriacea*, *Celmisia gracilentia*, *Geranium microphyllum*, *Blechnum penna-marina*, and the mosses *Hypnum cupressiforme* and *Polytrichum juniperinum*. The lichen *Peltigera dolichorhiza* is common. Species less frequently present include the sub-shrub *Gaultheria macrostigma*, the rush *Juncus gregiflorus*, and the exotic forb *Hypochaeris radicata*.

### F: *Blechnum penna-marina* community

Recorded in 7% of the sampled area, this community is found mainly in areas towards the eastern (up-valley) end of the mire. The community is moderately rich in species. *Leonohebe odora* and *Chionochloa rubra* are the only common taller species.

### G: *Distichophyllum pulchellum* – *Gaultheria macrostigma* community

This community is found scattered on higher ground on the hill slopes, and comprises some 5% of the area sampled. It is the richest in species of all communities, containing an average of 17 species per

quadrat. The vegetation comprises an open canopy of *Chionochloa rubra*, *Coprosma propinqua*, *Leonohebe odora* and *Phormium cookianum*, with an understorey which includes the large herb *Astelia nervosa*, the orchid *Pterostylis australis*, the small fern *Blechnum penna-marina*, and sub-shrubs as well as several low-growing herbs. Many mosses are present.

### H: *Phormium* - *Coprosma scrub* community

This montane scrub community is found on the slopes surrounding the mire on the southern and eastern margins. Species richness is the lowest of all communities, with an average of only 7 species present per quadrat. The canopy comprises a mixture of tall *Coprosma propinqua*, *Phormium cookianum* and occasional tussocks of *Chionochloa rigida* and *C. rubra*. Two sub-communities may be distinguished:

H1: Mixed shrub sub-community. Found from the eastern to the western extreme along hill slopes on the southern margin of the mire, this sub-community is richer in species than sub-community H2. *Chionochloa* spp. are common.

H2: *Aciphylla scott-thomsonii* sub-community. This is the most species-poor vegetation sampled, with only 4 species per quadrat. It was found on the slopes on the eastern margins of the mire. *Phormium cookianum* is constant, while *Aciphylla scott-thomsonii* is usually present. We noted that *A. scott-thomsonii* had been abundant on the mire itself some months earlier, but by the time of sampling most plants had been destroyed, apparently by rooting pigs.

### Topography

The profile of the mineral substrate below the mire confirms that the site was originally a steep-sided valley (Figure 3). The topography is thus that of a

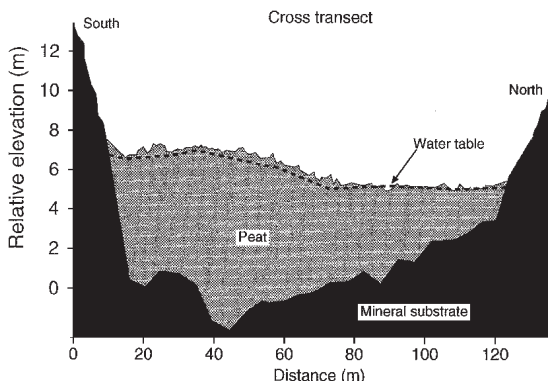


Figure 3. Physical profile across the bog (cross transect).



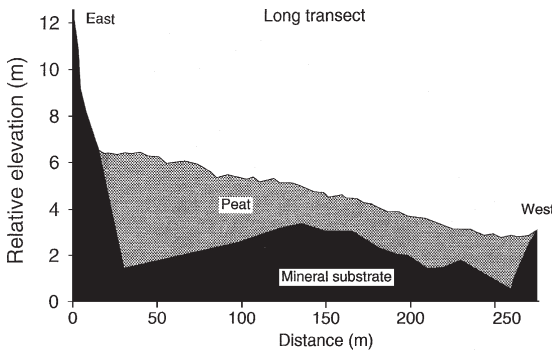


Figure 4. Physical profile along the bog (long transect).

typical valley mire, the slope of the underlying mineral soil being congruent with the slope of the surrounding hillsides. The down-valley basin is closed by a lip in the mineral substrate that also marks the present down-valley limit of the mire. The lengthwise profile indicates that the mire originated in a double basin (Figure 4), the up-valley basin separated from the down-valley basin by a gentle rise. The tendency for community C to occur across the centre of the mire (Figure 1b) may be a relict of this central rise.

The surface of Swampy-spur Mire is close to being horizontal across the valley, but the mire slopes gently towards the outlet. Towards the up-valley end, the mire is convex in cross-section, suggesting that this part of the mire is a raised ombrotrophic bog, but it is raised

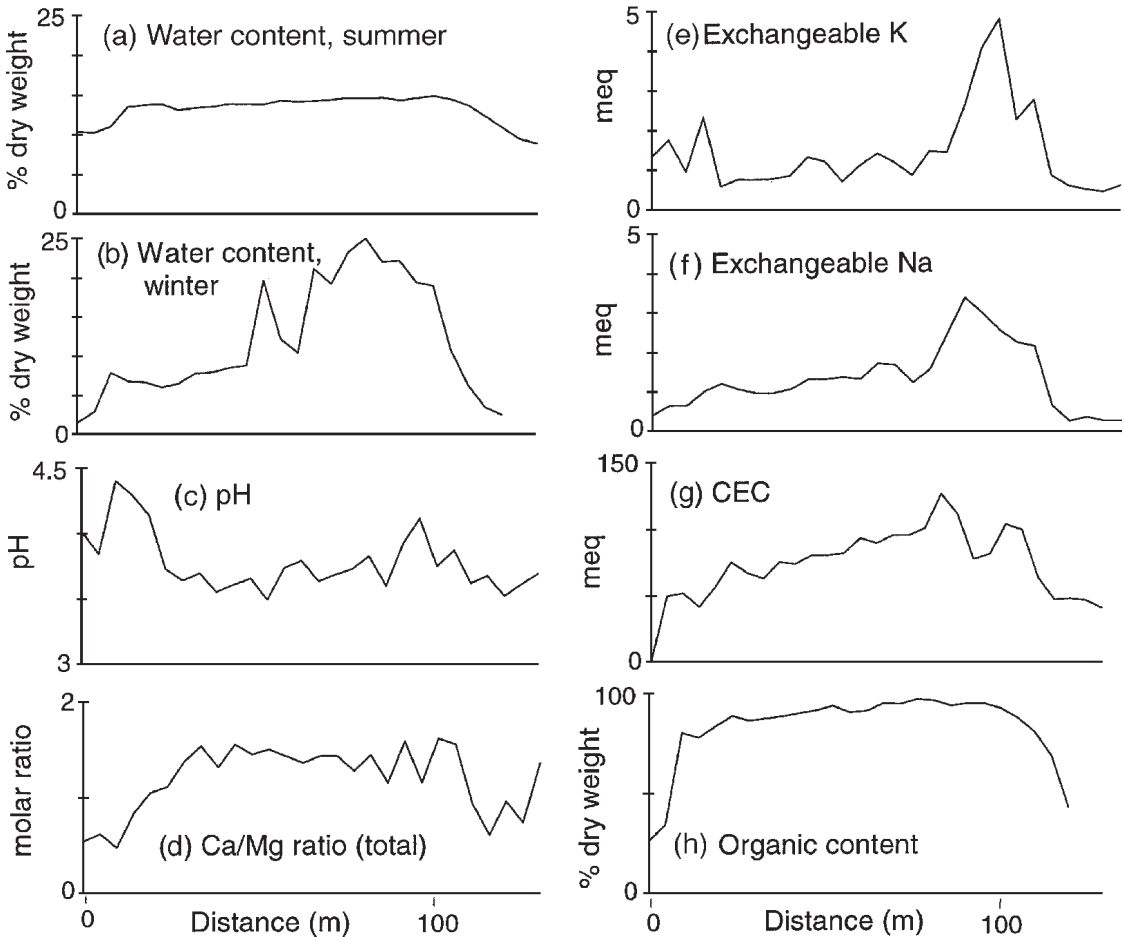


Figure 5. Trends in environmental factors (in summer unless indicated otherwise) across the bog (cross transect).

only slightly and locally (Figure 1). The asymmetry of the mire in terms of the position of the raised portion, and the more definite lagg stream on the southern side, mirrors an asymmetry in the underlying valley (Figure 3). The detailed mire profile (Figure 3) indicates an irregular surface, especially on the raised portion, with a hollow-and-hummock physiognomy, but with no pools. The water table follows the surface closely across the mire (Figure 3), breaking above the surface in the lagg stream (Figure 1), and intermittently in the Lagg Fen.

### Peat analyses

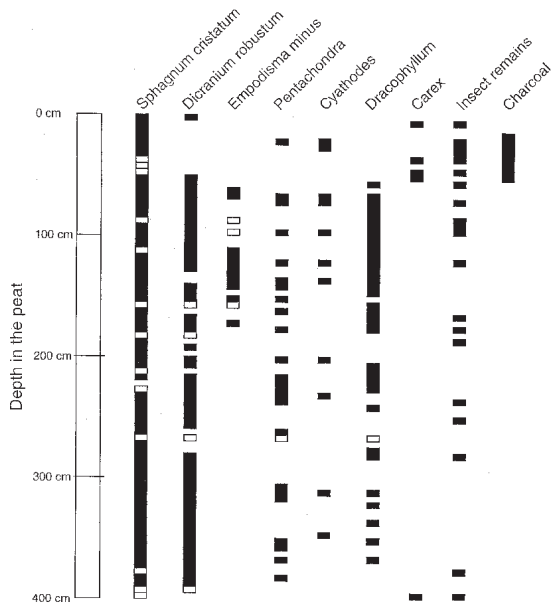
Organic content shows the expected trend across the mire, being low (< 50%) on the mineral soil of the banks, and in the 90-95% loss-on-ignition range across the bog itself (Figure 5h). The gradient from the raised ombrotrophic part of the mire to the rheotrophic western end is not reflected in any change in organic content, which is rather constant along and across the mire (Figure 5). Only at the very edges of the mire does there seem to be a significant component of mineral sediment washed in.

Water content was lower on the mineral soil than on the mire. It was highest in the Lagg Fen, only slightly higher than in the raised portion in summer (Figure 5a), but markedly so when the mire was charged with water in winter (Figure 5b). On both dates, it was, as expected, slightly higher in the southern lagg stream than on the adjacent slightly-raised part of the mire. Water content was rather constant along the long transect (results not shown), except in the mineral soil of the eastern slopes and the western lip.

Values of pH for the raised portion of the mire were 3.5-3.7 (Figure 5c). In both Lagg Stream and Lagg Fen areas, pH rose to > 4.0. Potassium and sodium are clearly highest in the Lagg Fen community (Figure 5e, f), as would be expected in a fen. Potassium was particularly low in the raised bog portion. The index that has been most used for distinguishing between ombrotrophic and rheotrophic conditions is the Ca/Mg molar quotient. Here, in spite of a flora characteristic of raised ombrotrophic bogs in the region (*e.g. Drosera arcturi, Oreobolus strictus, Centrolepis pallida*), it is not particularly low (>1.0; Figure 5d). Cation exchange capacity (CEC) is highest in the Lagg Fen (Figure 5g), and within the mire itself is lowest in the raised bog section.

### Macrofossil analysis

The macrofossil record (Figure 6) shows that *Sphagnum* has been a consistent component of the vegetation almost since the inception of the mire. *Dicranum robustum*, *Cyathodes*, *Dracophyllum* and *Pentachondra*



**Figure 6.** Macrofossil occurrences in a core from the Swampy-spur bog. Solid bars represent a major presence, open bars represent minor presence (< 1%).

have been present for most of that time, but intermittently in our peat core, suggesting that they formed smaller amounts of the vegetation. At least the first three of these have been much less prominent in the period represented by the top 60 cm, although all are at least present today. *Empodisma minus* was fairly consistently present from the time represented by 180 cm depth, up until 60 cm. Charcoal is present only the 20-60 cm layer.

## Discussion

### Ombrotrophy

Mires forming in valleys are normally rheotrophic at the beginning of their development, i.e. they start their succession as fens and may later become domed and ombrotrophic (Orme, 1990). The Eastern end of Swampy-spur Mire is close to being horizontal across the valley, but with slight doming. Towards the outlet at the western end, the mire has topography typical of a sloping fen (Sjörs, 1983), though it has fewer pools than the sloping mires that Sjörs describes.

Ombrotrophic status can be indicated by three substrate factors: low pH (Moore and Bellamy, 1974), low nutrient status (Gore, 1983) and calcium/

magnesium molar quotients less than or approaching unity (Malmer, 1962; Schneider, 1968; Agnew *et al.*, 1993; Heathwaite *et al.*, 1993). Five lines of evidence, comparing the raised part to areas such as the Lagg Fen, suggest an ombrotrophic status for the raised part of the mire. (1) The surface is raised above the surrounding mire, which is the feature giving raised bogs their name, also implying that the topography makes it difficult for this part of the mire to receive mineral nutrients from groundwater. (2) The raised part is more acidic (*i.e.*, pH is lower than 4.0, as expected in ombrotrophic conditions, and the values of 3.5–3.7 are within the range suggested by Moore and Bellamy (1974) for ombrotrophic bogs). (3) Exchangeable K is lower. (4) Cation exchange capacity is lower. (5) The substrate is purely organic (Figure 5). Exchangeable Na and CEC are even lower on the mineral soil of the surrounding slopes, but these are not particular indicators of ombrotrophy.

In the raised section, Ca:Mg molar ratios are slightly above the value of 1.0 that has been seen as an upper-limit indicator of ombrotrophy, but some workers have seen this as only a rough guide to ombrotrophy (Clymo, 1983), not applicable in some regions (Waughman, 1980). Some differences from other bogs might be explained by the influence of the sea, *c.* 10 km away. It was suggested by Heathwaite *et al.* (1993) that the potassium content of mires is generally one fifth of their sodium content, but amounts here were comparable, and this cannot be explained by the sea's influence, since the ratio of K:Na input via rain is normally lower near the sea (Holdsworth & Mark, 1990). The lack of pools in the raised section, which occur in many raised bogs (Moore, 1990), may imply that the ombrotrophy is only marginal.

Ombrotrophic bogs often start in fens, especially in valleys, and presumably this was how the Swampy-spur Bog originated. Ombrotrophic growth normally starts in a small area (or areas), and spreads (Bellamy and Rieley, 1967; Almqvist-Jacobson and Foster, 1995). Since in Swampy-spur Mire only one area is slightly raised, and it is on the margin of ombrotrophy, this part of the mire may have become ombrotrophic only recently. This is confirmed by the juxtaposition of species typical of ombrotrophic bog, such as *Sphagnum cristatum* and *Oreobolus strictus* (Dobson, 1979), with species that are normally found not in ombrotrophic bogs but rather in fens and carrs, such as *Carex coriacea*, *Coprosma propinqua* and *Astelia nervosa* (Cockayne, 1928; Sykes *et al.*, 1991). The vegetation is clearly at the boundary between the *Chionochloa rubra* and *Sphagnum* mires of Dobson (1979), and probably adjacent to the Cushion mire type. His chart suggests that a site with such vegetation would have a mean annual temperature *c.* 8 °C, and it is actually *c.* 6 °C. The chart also suggests that such a community would

occur in slightly oligotrophic conditions, which seems to be correct. Ombrotrophication may have been slowed by the relatively low cover of *Sphagnum*. Moreover, there is a general assumption in the literature that all *Sphagnum* species are equal in their ability to acidify the substrate and retain water, but this is not the case (Clymo and Hayward, 1982). The acidifying ability of the New Zealand *Sphagnum* species is unknown. The other species in southern New Zealand with an ability to produce ombrotrophic growth, *Empodisma minus* (Agnew *et al.*, 1993), is absent in Swampy-spur Mire, as it is from most mires on the east coast.

### History of the mire

We have no date for the origin of the mire; the safest working hypothesis is that it commenced growth at about the same time as the mire at nearby Swampy summit (McIntyre and McKellar, 1970), *i.e.*, *c.* 12,000 yr BP. We have to be cautious in interpreting macrofossil data, since peat conditions at the time can affect preservation, and of course the rate of peat accumulation. Even so, the vegetation of the mire has remained remarkably constant in some ways. At least, there is no indication of progression through a long fen stage to a quite different mire vegetation, as is common (Gore, 1983; Bellamy and Rieley, 1967). The only sign of such a trend is the occurrence of *Carex* (probably *Carex coriacea*) at the very commencement of the mire, and then its absence at this point for the next several thousand years.

A major change occurs at a depth of 180 cm, when *Empodisma* appeared, and when the presence of *Dracophyllum* became almost constant. This indicates a vegetation rather similar to that presently existing under higher rainfall at Borland Bog (McQueen & Wilson, 2000). We do not have a definite date for this change. However, if we use the very approximate technique of linear interpolation (*i.e.* making the assumption of a constant rate of peat accumulation) from an origin of *c.* 12,000 yr BP, we get an age of 5500 yr BP. Since *Empodisma minus* tends to occur in higher-rainfall areas, this vegetation change corresponds well to McGlone *et al.*'s (1995) conclusion of higher precipitation after 7500 yr BP, within the error inherent in linear interpolation and allowing for a migration lag in the arrival of *E. minus*. The change also matches the time at which Burrows (1979) suggested the climate of South Island became cooler.

Another marked change occurs at 60 cm depth, for which linear interpolation gives an estimate of 1800 yr BP. Most remarkable is the appearance of charcoal, which suggests that the true time was *c.* 800 yr BP, the time Polynesian fire appeared in this area (McGlone *et al.*, 1995). At this time, *Empodisma* disappeared and several epacridaceous shrubs became more intermittent,

as did *Dicranum robustum*. *Carex* reappeared, for the first time at this point for many thousand years, which might suggest less ombrotrophic conditions. It seems clear that the shrubs were decreased by fire. Rogers and McGlone (1989) suggested that fire could lead to a community of *Chionochloa rubra*, sedges, rushes and *Sphagnum*. This cannot explain the disappearance of *Empodisma*, since it is able to recover well from fire in areas climatically optimal for it, such as the higher-rainfall West Coast (Norton, 1989). Restiads are typical of wetter periods (Campbell *et al.*, 1973). However, the species is rare in east Otago, being present only in the Glendhu catchment and at Black Swamp. This suggests that the climate of the area, including Swampy, is marginal for it. Fire may have tipped the balance against its ability to persist on the site. However, a failure to recover from fire can be seen in other species at the same time. For example, *Nothofagus* forest on the Lammermoor and Lammerlaw range in east Otago was reduced to small remnants, *e.g.*, in gullies, by Polynesian fire, but then failed to re-invade except very slowly. This failure, and the failure of *Empodisma* on the Swampy-spur Mire to recover after fire, may also reflect a change to a somewhat drier climate at that time suggested by Holloway (1954). Others have explained some of Holloway's evidence in other ways (Wardle, 1985), but McGlone *et al.* (1995) have supported Holloway's theory in suggesting a greater frequency of warm drying winds in the region at this time, especially in early summer.

### Relation to the vegetation of other bogs

We have described here only one bog. Brief descriptions of other ombrotrophic bogs in the area (Johnson and Lee, 1988; Carter, 1994; Johnson, 1994, 1995) suggest that they bear quite different species assemblages. The vegetation of the ombrotrophic section of Swampy-spur Bog (Table 1, Figures. 1, 2) comprises a combination of hard mats (*Oreobolus strictus*), mosses (*Sphagnum cristatum*), shrubs (*Coprosma propinqua*), creeping subshrubs (*Cyathodes pumila*), and taller species, notably the tussock grass *Chionochloa rubra* (Figure 2). This combination of *Chionochloa rubra*, *Sphagnum* spp. and cushion/herb/shrub species in Swampy-spur Bog seems not to have been recorded before in the region, though there are similarities to bogs elsewhere, *e.g.* Ahukawakawa Swamp on Mt Egmont (Clarkson, 1986). Pending detailed sampling of other bogs, we hypothesise that bog communities in the region are individualistic. This throws light on the continuing argument in community ecology on whether repeated assemblages of species recur at separate sites (Wilson *et al.*, 1996), *i.e.*, whether there are distinct and repeated plant communities. In some habitats, very similar assemblages of species can be found in many

sites over a wide geographic range, for example carr vegetation within New Zealand (Sykes *et al.*, 1991). In other habitats, such as saltmarshes (Partridge and Wilson, 1988) and apparently bogs in the Otago region, each site seems to bear an individualistic assemblage of species.

### Conservation implications

The area of New Zealand now occupied by mires is only a fraction of that existing before European settlement (Stephenson *et al.*, 1983). Among the various types, the literature is strangely silent on the bogs of eastern South Island, which has led to a lack of recognition of the importance of those that remain. Davoren (1978), listing mire types in New Zealand, did not even mention raised *Sphagnum* and/or *Chionochloa* bogs. There are few current pressures on the Swampy-spur Bog. Nutrient inflow needs to be kept low, but as the bog is in a water catchment reserve this seems not to be a problem. There are no immediate threats of invasion by exotic species; in the long term *Erica lusitanica*, which is in the area, could be a problem at least in the rheotrophic parts of the site. *Erica vagans*, another potential weed, occurs quite near the bog, but does not normally occur in the bog habitat. *Calluna vulgaris*, originally planted on some bogs in Southland, is now dominant on them (Chapman and Bannister, 1994), and should be eradicated immediately if it appears. The main current threat seems to be from wild pigs, with an observed selective grazing of *Aciphylla scott-thomsonii*, and perhaps unobserved effects on other species. Pig numbers in the area need greater control.

### Acknowledgements

We thank David Murray for climate data, Andrea Wallace for help in the field, and Lance Currie, Kate McNutt and Christine MacArthur for the soil nutrient and water analyses. SW, SHR and WMCGK thank the Hellaby Indigenous Grasslands Research Trust for support.

### References

- Allan, H.H. 1961. *Flora of New Zealand*, Volume 1. Government Printer, Wellington, N.Z.
- Agnew, A.D.Q.; Rapson, G.L.; Sykes, M.T.; Wilson, J.B. 1993. The functional ecology of *Empodisma minus* (Hook. f.) Johnson & Cutler in New Zealand ombrotrophic mires. *New Phytologist* 124: 703-710.

- Almquist-Jacobson, H.; Foster, D.R. 1995. Toward an integrated model for raised-bog development: theory and field evidence. *Ecology* 76: 2503-2516.
- Beever, J.E.; Allison, K.W.; Child, J. 1992. *The mosses of New Zealand*. Second Edition. University of Otago Press, Dunedin, N.Z.
- Bellamy, D.J.; Rieley, J. 1967. Some ecological statistics of a "miniature bog". *Oikos* 18: 33-40.
- Blakemore, L.C.; Searle, P.L.; Daly, B.K. 1987. *Methods for chemical analysis of soil*. New Zealand Soil Bureau Scientific Report 80. Department of Scientific and Industrial Research, Lower Hutt, N.Z.
- Brownsey, P.J.; Smith-Dodsworth, J.C. 1989. *New Zealand ferns and allied plants*. Bateman, Auckland, N.Z.
- Burrows, C.J. 1979. A chronology for cool-climate episodes in the Southern Hemisphere, 12 000 - 1000 yr B.P. *Palaeogeography, Palaeoclimatology, Palaeoecology* 27: 287-347.
- Campbell, E.O.; Heine, J.C.; Pullar, W.A. 1973. Identification of plant fragments and pollen from peat deposits in Rangitaiki plains and Maketu basins. *New Zealand Journal of Botany* 11: 317-330.
- Carter, J. 1994. *Waipori Ecological District: a survey report for the protected natural areas programme*. Department of Conservation, Dunedin, N.Z.
- Chapman, H.M.; Bannister, P. 1994. Vegetative production and performance of *Calluna vulgaris* in New Zealand, with particular reference to Tongariro National Park. *New Zealand Journal of Ecology* 18: 109-121.
- Clarkson, B. 1986. *Vegetation of Egmont National Park, New Zealand*. Science Information Publishing Centre, Department of Scientific and Industrial Research, Wellington, N.Z.
- Clifford, H.T.; Stephenson, W. 1975. *An introduction to numerical classification*. Academic Press, New York, U.S.A.
- Clymo, R.S. 1983. Peat. In: Gore, A.J.P (Editor), *Mires: swamp, bog, fen and moor; General studies*, pp. 159-224. Elsevier, Amsterdam, The Netherlands.
- Clymo, R.S.; Hayward, P.M. 1982. The ecology of *Sphagnum*. In: Smith, A.J.E. (Editor), *Bryophyte ecology*, pp. 229-289. Chapman and Hall, London, U.K.
- Cockayne, L. 1928. *The Vegetation of New Zealand*. Second Edition. Englemann Press, Leipzig, Germany.
- Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand Flora, 1960-1986 and Nomina Nova IV, 1983-1986. *New Zealand Journal of Botany* 25: 115-170.
- Damman, A.W.H. 1990. Nutrient status of ombrotrophic peat bogs. *Aquilo Series Botanica* 28: 5-14.
- Davoren, A. 1978. *A survey of New Zealand peat resources*. Water and Soil Technical Publication No. 14. Ministry of Works and Development, Hamilton, N.Z.
- Dobson, A.T. 1979. Mire types of New Zealand. *Proceedings of the International Symposium on Classification of Peat and Peatlands, Hyytlälä, Finland*: 82-95.
- Galloway, D.J. 1985. *Flora of New Zealand: lichens*. Government Printer, Wellington, N.Z.
- Gore, A.J.P. 1983. Introduction. In: Gore, A.J.P. (Editor). *Mires: swamp, bog, fen and moor: General studies*, pp. 1-34. Elsevier, Amsterdam, The Netherlands.
- Greig-Smith, P. 1983. *Quantitative plant ecology*. Third Edition. Blackwell, Oxford, U.K.
- Heads, M.J. 1987. New names in the New Zealand Scrophulariaceae. *Botanical Society of Otago Newsletter* 5: 4-11.
- Heads, M.J. 1996. Biogeography, taxonomy and evolution in the Pacific genus *Coprosma* (Rubiaceae). *Candollea* 51: 381-405.
- Heathwaite, A.L.; Göttlich, Kh.; Burmeister, E.G.; Kaule, G.; Grospietsch, Th. 1993. Mires: Definitions and Form. In: Heathwaite, A.L.; Göttlich, Kh. (Editors), *Mires. Process, exploitation and conservation*, pp. 1-75. Wiley, Chichester, UK.
- Hewitt, A.E. 1993. New Zealand soil classification. Landcare Research, Lincoln, N.Z.
- Holdsworth, D.K.; Mark, A.F. 1990. Water and nutrient input:output budgets: effects of plant cover at seven sites in upland snow tussock grasslands of Eastern and Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 20: 1-24.
- Holloway, J.T. 1954. Forests and climates in the South Island of New Zealand. *Transactions of the Royal Society of New Zealand* 82: 329-410.
- Johnson, P.N. 1994. *Little Valley - Greenland RAP: vegetation assessment*. Department of Conservation, Dunedin, N.Z.
- Johnson, P.N. 1995. *Manorburn Conservation Area: vegetation assessment*. Department of Conservation, Dunedin, N.Z.
- Johnson, P.N.; Lee, W.G. 1988. *Lammerlaw Range uplands: botanical report*. Botany Division, Department of Scientific and Industrial Research, Dunedin, N.Z.
- Malmer, N. 1962. Studies on the mire vegetation in the archaean area of southwestern Gotland (S. Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. *Opera Botanica* 7: 1-67.

- McQueen, A.A.M. & Wilson, J.B. 2000. Vegetation and environment of a New Zealand raised bog. *Journal of Vegetation Science* 11: 547-554.
- McIntyre, D.J.; McKellar, I.C. 1970. A radiocarbon dated post glacial pollen profile from Swampy Hill, Dunedin, New Zealand. *New Zealand Journal of Geology and Geophysics* 13: 346-349.
- McGlone, M.S.; Mark, A.F.; Bell, D. 1995. Late Pleistocene and Holocene vegetation history, Central Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 25: 1-22.
- Moore, P.D. 1989. The ecology of peat-forming processes: a review. *International Journal of Coal Geology* 12: 89-103.
- Moore, P.D. 1990. Soils and ecology: temperate wetlands. In: Williams, M. (Editor), *Wetlands: a threatened landscape*, pp. 95-114. Blackwell, Oxford, U.K.
- Moore, P.D.; Bellamy, D.J. 1974. *Peatlands*. Elek Science, London, U.K.
- Norton, D.A. 1989. Floristics and structure of mire-forest ecotones, west coast South Island, New Zealand. *Journal of the Royal Society of New Zealand* 19: 31-42.
- Orme, A.R. 1990. Wetland morphology, hydrodynamic and sedimentation. In: Williams, M. (Editor), *Wetlands: a threatened landscape*, pp. 26-94. Blackwell, Oxford, U.K.
- Partridge, T.R.; Wilson, J.B. 1988. Vegetation patterns in salt marshes of Otago, New Zealand. *New Zealand Journal of Botany* 26: 497-510.
- Rogers, G.M.; McGlone, M.S. 1989. A postglacial vegetation history of the southern-central uplands of North Island, New Zealand. *Journal of the Royal Society of New Zealand* 19: 229-248.
- Roxburgh, S.H.; Wilson, J.B.; Gitay, H.; King, W. McG. 1994. Dune slack vegetation in southern New Zealand. *New Zealand Journal of Ecology* 18: 51-64.
- Schneider, S. 1968. Chemical and stratigraphical investigations of high-moor profiles in north-west Germany. *Transactions of the Second International Peatlands Congress, Leningrad* 1: 75-90.
- Sjörs, H. 1983. Mires of Sweden. In: Gore, A.J.P. (Editor), *Mires: swamp, bog, fen and moor; Regional studies*, pp. 69-94. Elsevier, Amsterdam, The Netherlands.
- Stace, C.A. 1997. *New flora of the British Isles*. Second Edition. Cambridge University Press, Cambridge, U.K.
- Stephenson, G.K.; Card, B.; Mark, A.F.; McLean, R.; Thompson, K.; Priest, R.M. 1983. *Wetlands: a diminishing resource*. Water and Soil Miscellaneous Publication No. 58. New Zealand Environmental Council, Wellington, N.Z.
- Sykes, M.T.; Wilson, J.B.; Lee, W.G.; Allen, R.B. 1991. A remnant New Zealand carr. *Journal of Vegetation Science* 2: 209-216.
- Wagstaff, S.J.; Garnock-Jones, P.J. 1998. Evolution and biogeography of the *Hebe* complex (Schophulariaceae) inferred from ITS sequences. *New Zealand Journal of Botany* 36: 425-437.
- Wardle, P. 1985. Environmental influences on the vegetation of New Zealand. *New Zealand Journal of Botany* 23: 773-788.
- Wardle, P. 1991. *The vegetation of New Zealand*. Cambridge University Press, Cambridge, U.K.
- Wardle, P.; Mark, A.F. 1956. Vegetation and climate in the Dunedin District. *Transactions and Proceedings of the Royal Society of New Zealand* 84: 33-44.
- Waughman, G.J. 1980. Chemical aspects of the ecology of some south German peatlands. *Journal of Ecology* 68: 1025-1046.
- Williams, P.A.; Courtney, S.; Glenny, D.; Hall, G.; Mew, G. 1990. Pakihi and surrounding vegetation in North Westland, South Island. *Journal of the Royal Society of New Zealand* 20: 179-203.
- Wilson, J.B.; Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23: 263-336.
- Wilson, J.B.; Ullmann, I.; Bannister, P. 1996. Do species assemblages ever recur? *Journal of Ecology* 84: 471-474.