Vegetation and peat characteristics of restiad bogs on Chatham Island (Rekohu), New Zealand

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Abstract Restiad bogs dominated Sporadanthus traversii on Chatham Island, New Zealand, were sampled to correlate vegetation patterns and peat properties, and to compare with restiad systems dominated by Sporadanthus ferrugineus and Empodisma minus in the Waikato region, North Island, New Zealand. Classification and ordination resulted in five groups that reflected a disturbance gradient. The largest S. traversii group, which comprised plots from central, relatively intact bogs, had the lowest levels of total nitrogen (mean 1.20 mg cm⁻³), total phosphorus (mean 0.057 mg cm⁻³), total potassium (mean 0.083 mg cm⁻³), and available phosphorus (mean 18.6 μg cm⁻³). Modification by drainage, stock, and fires resulted in a decline of S. traversii and an increase of Gleichenia dicarpa fern cover, together with elevated peat nutrient levels and higher bulk density. Compared with peat dominated by Sporadanthus ferrugineus or Empodisma minus in relatively unmodified Waikato restiad bogs, Chatham Island peat under S. traversii has significantly higher total potassium, total nitrogen, available phosphorus, bulk density, and von Post decomposition indices, and significantly lower pH. Sporadanthus traversii and Empodisma minus have similar ecological roles in restiad bog development, occupying a relatively wide nutrient range, and regenerating readily from seed after fire. Despite differences in root morphology, S. traversii and E. minus are the major peat formers in raised restiad bogs on Chatham Island and in Waikato, respectively, and could be regarded as ecological equivalents.

Keywords peat; bog; nutrients; disturbance gradient; Restionaceae; Waikato; *Sporadanthus traversii*; *S. ferrugineus*; *Empodisma minus*

INTRODUCTION

Bogs dominated by Restionaceae (restiad bogs) on a global scale are most extensively developed on mainland New Zealand (Campbell 1983) and Chatham Island (Wardle 1991). However, there are marked differences in restiad species dominance between the two regions. *Empodisma minus* is widespread and abundant on mainland New Zealand (also found in Australia) whereas it is absent from Chatham Island (de Lange et al. 1999a). Further, *Sporadanthus ferrugineus* is endemic to northern North Island (de Lange et al. 1999b) and dominates older (>4000 years) Waikato bogs (Clarkson et al. 2004), whereas *Sporadanthus traversii* is endemic to, and widespread on, Chatham Island (de Lange et al. 1999b).

Waikato restiad bogs have been the focus of recent research on bog development and functioning (Clarkson et al. 2004) but equivalent data from Chatham Island have not been available. Following the recent revision of *Sporadanthus* (de Lange et al. 1999b), which separated the taxa on mainland New Zealand and Chatham Island as distinct species, we were particularly interested in comparing the two systems. In addition, Chatham Island peatlands are much older. Peat accumulation began there in the interglacial period about 40 000–30 000 years ago (Mildenhall 1994; Campbell 1996), while Waikato

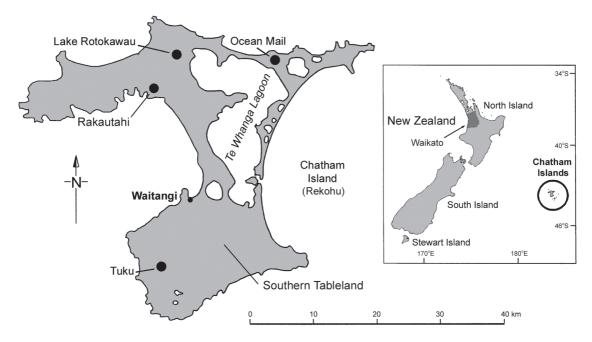


Fig. 1 Chatham Island showing sampling locations.

systems are post-glacial, ranging from a few hundred to c. 15 000 years (Hogg et al. 1987; Newnham et al. 1995). Finally, although affected by humans, the Chatham peat systems are still relatively intact compared with the much-reduced Waikato peatlands, but share similar threats of fire, drainage, and stock damage.

We therefore conducted a plot-based survey of bogs dominated by *S. traversii*, measuring both vegetation and peat characteristics, to understand basic processes of peatland functioning. Specifically, our research goals were to:

- correlate peat physical and chemical properties with vegetation patterns in Chatham Island restiad bogs; and
- 2) compare and contrast Chatham Island bogs dominated by *S. traversii* with Waikato systems dominated by *S. ferrugineus* and *Empodisma minus*.

STUDY AREA

Background

Chatham Island, c. 90 000 ha in area, lies 870 km east of the New Zealand mainland at latitude 44°S

within the New Zealand biogeographical area (Fig. 1). Its topography is mainly flat to gently rolling, with the lowland northern half dominated by a large lagoon and the southern half by a tableland averaging 260 m above sea level (a.s.l.). The highest point is Maungatere Hill, reaching 294 m a.s.l. in the centre of the Southern Tableland. Geologically the island is diverse, comprising sedimentary rocks, volcanics, and schists. Extensive areas are covered by peat, with 59% of the soils being peat or derived from peat (Wright 1959). Most of the peatlands are blanket peats, e.g., the *Dracophyllum arboreum*dominated peats on the Southern Tableland, but there are also many raised bogs, which typically occur in the middle of peat-filled basins (McGlone 2002). The raised bogs and many of the lowland blanket peats are dominated by Sporadanthus traversii, in association with Dracophyllum scoparium, Gleichenia dicarpa, and Olearia semidentata.

The island has a cool, damp, and windy climate (Wright 1959). Its first inhabitants, the Polynesian Moriori, knew it as Rekohu, Misty Skies, because of the mists that often enshroud the island for days at a time (Wills-Johnson 1996). Climatic extremes are moderated by the surrounding expanse of ocean, and no part of the land is more than 8 km from the

sea. At Waitangi, the main settlement, the mean annual temperature is 11.3°C (July average 7.8°C, January average 14.5°C) with a low annual mean daily range (5.4°C), very few air frosts (only one every 2 years), and low annual sunshine hours (1474) (Thompson 1983). Mean annual rainfall is low (895 mm at Waitangi; 715–1050 mm elsewhere on the island) with summer dry spells, but frequent cloud cover (averaging 74%), moderately high humidity (mean relative humidity 84%), and cool temperatures contribute to an environment conducive to peat accumulation (Wright 1959).

General accounts of vegetation types have been provided by Cockayne (1902), Wright (1959), Kelly (1971, 1978), Wardle et al. (1986), Given & Williams (1984), Atkinson (1996), and Given (1996). In addition, Kelly (1983) assessed significant conservation sites, Walls & Baird (1995, 1997) monitored vegetation recovery following fire, and Mildenhall (1994) and McGlone (2002) interpreted the vegetation history from palynological studies. Information on peat, including soil development processes and chemical analysis, has been published by MacPherson & Hughson (1943), Blakemore (1958), and Wright (1959).

Study sites

Four peatlands were selected (based on Kelly (1983), an extensive reconnaissance by BRC & BDC in 1996, and 1996/97 colour aerial photographs of scale 1:10 000) to encompass the range of vegetation pattern, altitude, and modification represented in the restiad ecosystems (Fig. 1). These were Ocean Mail (10 m a.s.l.), Lake Rotokawau (40 m a.s.l.), Rakautahi (60 m a.s.l.) in the northern lowlands, and Tuku (240 m a.s.l.) on the Southern Tableland. They comprise various peat types from drier blanket bogs to wetter basins to raised bogs, and are dominated by *Sporadanthus traversii*.

Ocean Mail

Ocean Mail Scenic Reserve (830 ha) on the north coast comprises a raised bog in the east and a peat basin containing several peat lakes in the west (Kelly 1971). It was burnt in November 1994 (Walls & Baird 1997), and at the time of sampling (February 2001) the raised bog was dominated by *Sporadanthus traversii* up to about 80 cm tall with common associates being *Dracophyllum scoparium*, *Gleichenia dicarpa*, and, locally, *Olearia semidentata* (Fig. 2). *Apodasmia similis* dominated the margins and was also abundant, together with *S. traversii* and *Phormium tenax*, around Lake

Kaimoumi, near the south-western margin of the peat dome (Fig. 3). The understorey was made up of a mixture of herbs, e.g., *Pratia arenaria*, *Gentiana chathamica*, sedges, e.g., *Carex chathamica*, and grasses, e.g., *Poa chathamica*.

Lake Rotokawau

This is mainly private land, although a small Conservation Area (administered by Department of Conservation) is included, and consists of a peat basin around Lake Rotokawau extending into a raised bog to the east. The vegetation (Fig. 4) is similar to Ocean Mail except it was taller (about 1 m tall), A. similis was not recorded, and non-vascular species (e.g., Sphagnum australe, Dicranum billardierei, Riccardia cochleata) were more prominent. Large areas near the bog margins and around Lake Rotokawau had been modified by cattle and drainage, having a high component of exotic herbs and grasses. In these areas S. traversii had been heavily browsed and localised patches of vegetation were dominated by D. scoparium or G. dicarpa. The vegetation condition in many parts of Lake Rotokawau had noticeably deteriorated and cattle damage was more evident than when the area was visited by BRC and BDC in 1996.

Rakautahi

Rakautahi is a large blanket bog on privately owned land, 5 km south of Lake Rotokawau, with Port Hutt Road forming its southern boundary. An extensive area was burnt in 1999, some 18 months before sampling (A. Baird pers. comm. 2001). It was still in the very early stages of recovering after the fire as much of the surface was bare peat with scattered low (<20 cm) vegetation of mainly *Gleichenia dicarpa*, *Sporadanthus traversii*, and *Dracophyllum scoparium* (Fig. 5). Several islands of vegetation (comprising *G. dicarpa*, *S. traversii*, and *D. scoparium*) up to 1 m tall had survived the fire and were prominent on the burnt landscape.

Tuku

Located on the Southern Tableland the sample site is a peat basin centred in Tuku Nature Reserve and extends north-eastward into adjacent privately owned land. Surrounded by blanket peats dominated by *Dracophyllum arboreum* forest, it was the least modified of the four peatlands sampled. In addition, an intensive control programme for introduced predators and browsing mammals is currently being undertaken within the reserve to protect populations of the rare sea bird, Chatham Island taiko



Fig. 2 Olearia semidentata (in flower) is locally common at Ocean Mail and grows in association with Sporadanthus traversii.

(Pterodroma magentae). The peat basin was dominated by S. traversii up to 1.5 m tall, with D. scoparium a frequent associate and O. semidentata and G. dicarpa locally present. Understorey species include a variety of non-vascular species (e.g., Sphagnum australe, Dicranum billardierei, Riccardia cochleata) and several herbs (e.g., Drosera binata), grasses (e.g., Hierochloe redolens), and ferns (e.g., Blechnum procerum). Mosaics of wetter areas occurred within the basin in which S. traversii was replaced by low-growing vegetation of mainly Sphagnum falcatulum, with Isolepis distigmatosa, Marchantia berteroana, and S. australe locally common.

METHODS

Vegetation and peat sampling

Sampling was carried out between 6 and 9 February 2001, when Chatham Island was experiencing

unusually dry conditions (c. 80% of normal rainfall had been experienced since mid-winter (July) 2000; National Institute of Water and Atmospheric Research unpubl. climate data). We established transects from the margin to the centre of each peatland to represent the vegetation patterns across the bogs. Sampling sites were marked every 50 m and a 2 m \times 2 m plot was set out for vegetation and peat sampling. The plot size was determined by using the species/area curve technique for calculating minimal sampling area (Mueller-Dombois & Ellenberg 1974), and was the same size used for Waikato restiad bogs (Clarkson et al. 2004). In the more modified and heterogeneous Lake Rotokawau system, additional plots were sampled in vegetation types not or poorly represented in the original sample, e.g., vegetation affected by stock. Eleven plots were sampled at Ocean Mail, 12 at Lake Rotokawau, 2 at Rakautahi, and 11 at Tuku, a total of 36 (Appendix 1).

At each plot the % cover for canopy species (as defined by Atkinson 1962) was assessed, the



Fig. 3 *Phormium tenax, Apodasmia similis*, and *Sporadanthus traversii* near Lake Kaimoumi, Ocean Mail. The rush-like restiad species are difficult to distinguish in the photo but the ratio of *Sporadanthus* to *Apodasmia* recorded at this site (plot OM10) was about 2:1.

maximum height for each species measured, and all vascular and non-vascular plant species listed (see Appendix 2). The degree of modification caused by stock access was ranked on a 3-point scale: 0 = no visible stock damage, 1 = minor foliage browsing or trampling, 2 = medium—severe foliage browsing and/or trampling damage. In addition, modification by fire was assessed as: 0 = most recent fire >8 years ago, 1 = fire 2–8 years ago (Ocean Mail fire was late 1994), and 2 = fire 0–2 years ago (Rakautahi fire was 1999).

Peat decomposition status was determined using the qualitative von Post scale (von Post & Granlund 1926; Clymo 1983) ranging from 1 (least decomposed) to 10 (highly decomposed). This was assessed in the field by taking a handful of peat from the uppermost 10 cm and squeezing; the consistency of the remaining peat and the colour of squeeze water were compared against a scale of attributes.

Two undisturbed cores were obtained from the surface layer of each plot by cutting steel liners (100 mm diam. by 75 mm deep) into the peat, and

then sealed in plastic bags. In the laboratory, one core was cut into cubes (1 cm^3) and stored at 4°C for a maximum of 7 days before analysis for pH, electrical conductivity (EC), and anaerobically mineralisable N. The other core was analysed for bulk density, moisture content, total N, total P, total K, total C, and H_2SO_4 -extractable P (see below).

Peat pH was determined the day after collection; 10 g fresh weight of peat was mixed with 25 ml of distilled water and left for 1 h before reading with a standard pH meter. Electrical conductivity was measured on a 1:5 ratio of fresh weight of peat to deionised water (Blakemore et al. 1987).

We measured total pools of N, P, and K, and more available pools of N and P because these were significantly correlated with vegetation pattern and species-environment models in Waikato restiad bogs (Clarkson et al. 2004). In addition, reviews of fertilisation studies revealed N, P, and, occasionally, K to be the major limiting nutrients for plant growth in northern hemisphere peatlands (Bridgham et al. 1996; Verhoeven et al. 1996). Total N, P, and K were



Fig. 4 Clumps of *Sporadanthus traversii* and shrubs of *Dracophyllum scoparium* typify the restiad bog vegetation at Lake Rotokawau.

measured following Kjeldahl digestion of peat using standard autoanalyser techniques (Blakemore et al. 1987). An index of available N was assessed using the anaerobic incubation method developed by Keeney (1982), which measures a pool of N rather than a mineralisation rate. The method, adapted by Clarkson et al. (2004) involved placing field moist peat (1 g dry weight equivalent) into 50-ml boiling tubes and filling them with deionised water so that the peat was flooded with minimal headspace. The headspace was flushed with N₂ before the tubes were sealed with rubber stoppers and incubated at 40°C for 7 days. After 7 days, the contents were then transferred to a 250-ml plastic extraction bottle, and 50 ml of 4 M KCl was added. Extraction bottles were shaken for 1 h, filtered, and the extract analysed for ammonium using standard autoanalyser techniques. The initial ammonium concentration of the peat was similarly determined minus the incubation period. Anaerobically mineralisable N was calculated as the difference between the final and initial concentration of ammonium.

Bulk density and moisture contents were measured gravimetrically after drying of the second peat

core at 105°C for 24 hours. To measure an available pool of phosphorus, a sub-sample (0.5 g) of the dried peat was extracted with 0.5 M H₂SO₄ (100 ml) for 16 hours; phosphate in the extract was determined using standard autoanalyser techniques (Blakemore et al. 1987). Total C was determined by dry combustion of peat at 1050°C using a LECO carbon furnace (Blakemore et al. 1987).

As there were marked differences in bulk density between sites, all results are presented on a volumetric basis.

Data analysis

Cover scores (%) for 44 species recorded in the 36 plots were subjected to classification (cluster analysis) and ordination to define vegetation types and determine ecological gradients. Rare species, defined as having less than 1% total cover, were omitted. The programmes used were FUSE (Agglomerative Hierarchical Fusion) and SSH (Semi-Strong-Hybrid Multidimensional Scaling), respectively, within the PATN multivariate analysis package (Belbin 1995). The SSH hybrid scaling ordination technique implements an improved version of the hybrid scaling,



Fig. 5 Charred stems of *Dracophyllum scoparium* overtop clumps of *Gleichenia dicarpa* and *Sporadanthus traversii* at recently burnt Rakautahi.

which combines metric and non-metric criteria, as defined by Faith et al. (1987). It is considered to be superior to other ordination techniques, such as principal components, correspondence analysis/reciprocal averaging, and other multidimensional scaling programs, for measuring ecological distance because it is more flexible and fits output distances to input distances without squaring these distances (Minchin 1987; Belbin 1995). In all analyses we used the flexible Unweighted Pair-Group Method using Arithmetic averages (UPGMA) clustering method (with β = -0.1) where equal weight is given to objects not groups, and the Bray and Curtis association measure, which consistently performed well in previous data testing (Faith et al. 1987).

In the ordination analysis, six marginal plots of non-restiad bog species were separated on Axis 3, indicating markedly dissimilar floristic composition from most of the data. As we were particularly interested in exploring species:environmental relationships in restiad bogs, the plots were omitted and the classification and ordination analyses repeated (= 30 plots, 38 species; restiad bog data set). The resulting two-dimensional ordination with a stress value

of 0.1601 was considered to summarise the data adequately (see Belbin 1995), as solutions of other dimensions (1D stress = 0.3327, 3D stress = 0.0919, 4D stress = 0.0613) did not markedly change ecological interpretability.

Five vegetation types were defined by the FUSE classification of the restiad bog data set. For each type, the environmental and modification data (pH, von Post, bulk density, moisture, conductivity, total N, P, K, C, available P, available N, browse damage, and fire) were summarised using box plots (SYSTAT version 7; Wilkinson 1997).

The environmental data and plot ordination scores were then analysed using a vector-fitting approach to examine species-environment responses. We implemented Principal Axis Correlation (PCC) within PATN, a multiple-linear regression program designed to see how well a set of environmental attributes can be fitted into an ordination space. Vectors were plotted on the two-dimensional plot ordination to indicate the direction (angle of vector) of best fit for each of the environmental variables and the strength of the correlation (length of vector) in that direction.

RESULTS

Vegetation classification and peat properties

The vegetation characteristics of the groups defined by the classification of the restiad bog data set are summarised in Table 1. Group 1 (Spo-Apo) comprised two plots dominated by the two restiad species S. traversii and Apodasmia similis, together with Phormium tenax from the lake (south-western) end of the Ocean Mail transect. Group 2 (Apo) was a single plot dominated by *Apodasmia similis* from the coastal (northern) margin of Ocean Mail, in which S. traversii was absent. Group 3 (Spo) was the largest group, being S. traversii-dominated plots of the large central areas typical of intact restiad bogs. Groups 4 (Dra) and 5 (Gle) were from sites modified by browsing or recent fire and were dominated by Dracophyllum scoparium and Gleichenia dicarpa, respectively. Of all the groups, Group 5 (Gle) was the most modified, and had the lowest vegetation height and the highest number of species in the canopy. Plots in this group were characterised by an open, usually heavily browsed and broken canopy, producing conditions favourable for establishment of small herbaceous plants (e.g., Lobelia anceps, Nertera depressa, Gentiana chathamica),

including many naturalised species, e.g., *Hypochaeris radicata*, *Leontodon taraxacoides*, *Anthoxanthum odoratum*, and *Holcus lanatus*.

The most frequent non-vascular species recorded in the restiad bog plots was *Sphagnum australe*, which occurred in the central *S. traversii*-dominated sites of the more intact bogs (Group 3). Floristically, the non-vascular component of Group 4 (Dra) plots was most similar to Group 3 (Spo), both having occasional *Riccardia cochleata*, *Dicranum billardierei*, and *Cladia retipora*.

The environmental data for the five restiad bog groups are presented in Fig. 6 (plot data in Appendix 1) to clarify vegetation:environmental patterns. Overall, the relatively unmodified Group 3 (Spo) plots had low levels of total nitrogen, total phosphorus, total potassium, available nitrogen, and available phosphorus. In contrast, the most modified Group 5 (Gle) plots typically had peat with high levels of nutrients, and low moisture content. Group 1 (Apo) and Group 2 (Spo-Apo), consisting of relatively unmodified plots from the transect margins, had relatively high pH and nutrient and moisture contents. Peat nutrients of the second modified group (Group 4 Dra) were only marginally elevated compared with Group 3 (Spo).

Table 1 Summary of vegetation characteristics of classification groups for the restiad bog data set. Means with standard deviations in parentheses are given for the total species (vascular and non-vascular) number, maximum vegetation height, and cover (%) for the nine most common species.

Group	1		2	3	4	5
Vegetation type	Sporada traver: Apodasmid	sii–	Apodasmia similis	Sporadanth traversii	1 2	Gleichenia dicarpa
Code	Spo-	Apo	Apo	Spo	Dra	Gle
Number of plots	2	•	1	18	3	6
Canopy species number	8 ((0)	5	4.6 (3.7	8.7 (6.7)	12.8 (6.8)
Total species number	12 ((2.8)	14	9.4 (3.0	9.7 (7.4)	14.7 (6.2)
Vascular species number	12 ((2.8)	14	7.6 (3.2	7.33 (5.1)	14.2 (6.4)
Non-vascular species number	0		0	1.8 (1.7	2.3 (2.3)	0.5 (1.2)
Vegetation height(m)	1.7 ((0.1)	1.0	1.0 (0.2	1.2 (0.8)	0.6 (0.3)
Apodasmia similis cover	27.5 ((3.5)	70	0	0	0
Baumea tenax cover	0	` '	0	0.5 (1.2	18.7 (20.1)	9.8 (12.6)
Cyathodes robusta cover	0		0	0	0	7.8 (8.3)
Dracophyllum scoparium cover	r 0.5 ((0.0)	1	16.1 (9.8	42.7 (21.9)	5.3 (6.1)
Gleichenia dicarpa cover	0		0	8.4 (10.1	2.3 (2.5)	33.5 (10.2)
Olearia semidentata cover	0		0	5.5 (8.1) 0	0
Phormium tenax cover	21.0 (1	2.7)	0	0.3 (0.9	ý 0	0.1 (0.2)
Pteridium esculentum cover	10.5 (1	3.4)	25	0.1 (0.2) 0	3.3 (7.7)
Sporadanthus traversii cover	37.5 ((3.5)	0	66.2 (13.9) 15 (15.0)	11.5 (10.1)

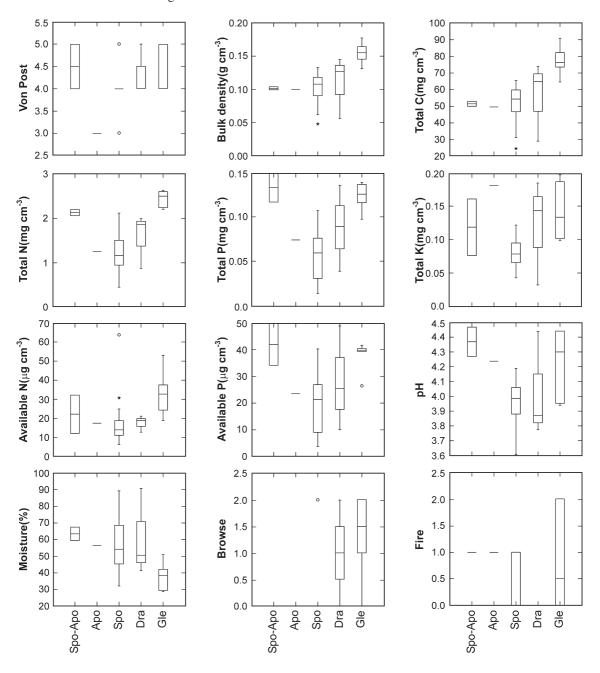


Fig. 6 Box plot summary showing medians, and upper and lower quartiles, for environmental data in each of the vegetation types (determined from the classification). Apo, *Apodasmia similis*; Spo, *Sporadanthus traversii*; Dra, *Dracophyllum scoparium*; Gle, *Gleichenia dicarpa*.

2.0

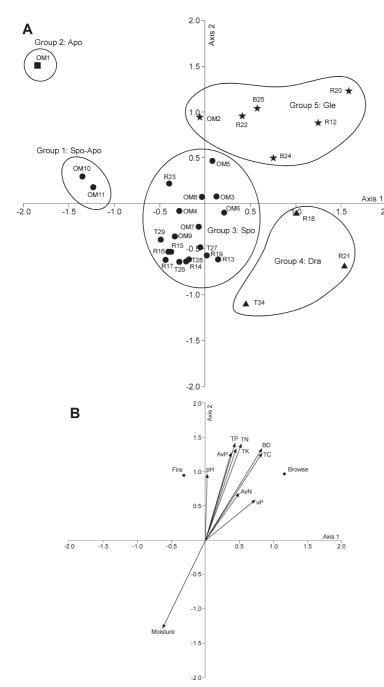


Fig. 7 A,Two-dimensional ordination of 30 plots based on canopy cover of 38 species (= restiad bog plant species data set). The vegetation type groups have been superimposed (codes as in Fig. 6). The dominant species for each plot are: Sporadanthus traversii (circles), Gleichenia dicarpa (stars), Dracophyllum scoparium triangles), *Apodasmia similis* (square). Bog codes with plot number: OM, Ocean Mail; R, Lake Rotokawau; B, Rakautahi; T, Tuku; B, Species: environment biplot analysis correlation vectors are shown for those environmental variables that are significantly correlated (P < 0.05) to the ordination axis scores. Fire and browse variables (categorical data) are shown as points.

Plot ordination and environmental correlation vectors

A two-dimensional ordination of the 30-plot restiad bog data set, overlaid with the dominant species at each plot and the cluster analysis groups, indicated floristic trends (Fig. 7A). The plots are arranged along Axis 1 from marginal plots in which *A. similis*

was a prominent component (low Axis 1 scores), through those from central intact bogs dominated by *S. traversii*, to those that have been modified by recent fire or browsing and in which *S. traversii* becomes increasingly scarce.

The species-environmental biplot analysis (Fig. 7B) based on the plot ordination summarises the

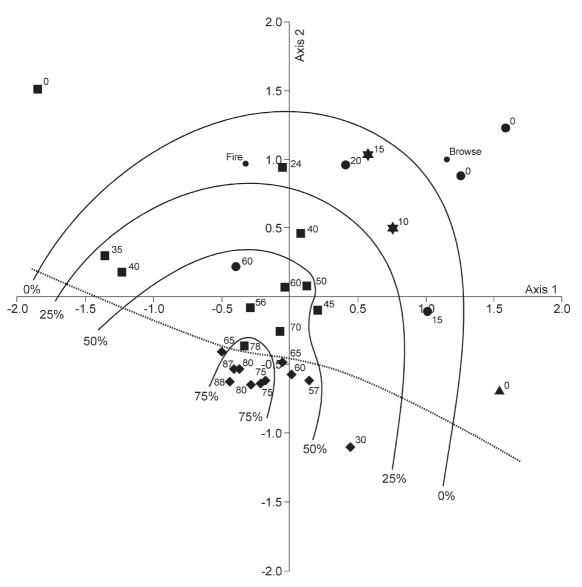


Fig. 8 Plot ordination overlaid with *Sporadanthus traversii* cover values and type of modification at each site. Contour lines are *Sporadanthus* cover. Dotted line separates modified (above) and unmodified (below) plots. Modification: high browse damage, no recent fire (circles); low browse damage, burnt 1999 (stars); low browse damage, no recent fire (triangle); no browse damage, burnt 1994 (squares); no browse damage, no recent fire (diamonds).

relationships between species abundances and those environmental variables that were significant (P < 0.05). The length of the correlation vector indicates the degree of correlation. Plots dominated by *Gleichenia dicarpa* (Group 5) are associated with high nutrient levels (total N, total P, total K, available P, available N) and high total C, pH, von Post index, and browse damage. These plots also have

typically low % moisture. Plots dominated by *S. traversii* (Group 3), in contrast, have higher % moisture.

Using the percent cover values of *S. traversii* recorded at each plot, contour lines of equal cover (25% intervals) were overlaid on the plot ordination (Fig. 8) to help interpret floristic trends. The presence and type of modification has also been included.

The figure shows that plots with the highest *S. traversii* cover occur mainly in relatively unmodified sites, and plots with lowest or zero *S. traversii* cover coincide with sites highly disturbed by stock browse (e.g., margins of Lake Rotokawau) or recent fires (Rakautahi and some Ocean Mail sites).

DISCUSSION

Species: environment relationships

The vegetation patterns in restiad bogs on Chatham Island reflect mainly a disturbance gradient. Intact bogs dominated by S. traversii, in association with D. scoparium and minor or localised G. dicarpa and O. semidentata, typically had low levels of N, P, and K, low von Post, and relatively high moisture content. Species composition and peat characteristics were similar for both lowland and higher altitude systems (the Southern Tableland is about 200 m higher elevation). Although large areas of relatively unmodified peatland vegetation still occur throughout the island, much is on land that continues to be susceptible to drainage, firing, and stocking, factors which lower water tables, remove vegetation cover, and compact the peat. In addition, cattle readily browse S. traversii and, to a lesser extent, D. scoparium (Wardle et al. 1986), and in some places, e.g., several sites at Lake Rotokawau, S. traversii has been eliminated by grazing, or trampled and broken up into individual pedestals. All these factors probably contribute to increased peat decomposition and elevated nutrient levels. Margins of less affected bogs dominated by or having large components of A. similis (S. traversii, P. tenax, and Pteridium esculentum may also be common) also had higher nutrient levels but, in contrast to modified areas, they had higher moisture, lower total C levels, and lower bulk density.

The relatively high nutrient levels at Rakautahi (Appendix 1) may have been influenced by the recent fire, 18 months before sampling. Fire in North American bogs has been shown to increase fertility but only temporarily, as nutrients return to pre-fire levels within 2 years (Wilbur & Christensen 1983). Occasional fires are a natural occurrence in New Zealand restiad bogs (e.g., Newnham et al. (1995) concluded a frequency of fire every one hundred to several hundred years in Waikato pre-human times) and the vegetation usually readily recovers to pre-fire condition within a few years (6–12 years for Waikato systems; Clarkson 1997; Norton & de

Lange 2003). At Ocean Mail, after a fire in November 1994, seedlings of all the former dominant species (S. traversii, D. scoparium, and O. semidentata) and resprouts of other important species (e.g., G. dicarpa, P. tenax) were recorded within 4 months, and a dense vegetation cover up to 20–40 cm tall had established by 17 months (Walls & Baird 1997). When we sampled at Ocean Mail, 6 years and 3 months after the fire, the canopy ranged from 0.75 to 1.5 m tall, comprising a mixture of species (mean = 7), and the understorey was also relatively diverse. Most of the bog vegetation, particularly in the lowland sites, is probably still currently recovering from fires, because the maximum heights of *D. scoparium*, S. traversii, and O. semidentata recorded during the survey were 1.99 m, 1.46 m, and 1.30 m, respectively. Relatively unburnt vegetation measured at the Lake Rotokawau peatland in 1996 was dominated by S. traversii and D. scoparium, both up to 2.2 m tall, and formed a dense thicket that excluded most other species (de Lange et al. 1999b). Although S. traversii, D. scoparium, and O. semidentata regenerate readily after fire, repeated human-induced firing can eliminate them, particularly if nearby seed sources are also destroyed (Cockayne 1902; Given & Williams 1984; Wardle et al. 1986). Replacement species include G. dicarpa in wetter areas, and bracken (Pteridium esculentum) on drier sites (Given & Williams 1984). Early European settlers, from the mid 19th century on, regularly burnt the extensive areas of open-lands or "clears" (peat domes and basins dominated by S. traversii) to improve access for travel and palatability to stock (Kelly 1983). At the beginning of the 20th century, the combination of fire and stock was considered the major cause of vegetation modification (Cockayne 1902). Fire frequency has decreased in recent years with improved roading and use of other farming practices; however, there are approximately one or two deliberately lit or accidental fires in a Chatham Island bog every 5 years (A. Baird pers. comm. 2002).

Comparison with Waikato bogs

The environmental characteristics and species richness of intact bogs dominated (>40% cover) by restiad species on Chatham Island and Waikato are summarised in Table 2. Vegetation types were defined by cluster analyses, i.e., the "Sporadanthus traversii" group of Table 1 and the Waikato "Empodisma minus" and "Sporadanthus ferrugineus" groups of Clarkson et al. (2004). The Chatham Sporadanthus traversii group had significantly higher bulk density, total N, total K, available

P, and von Post index than either Waikato group, and significantly lower pH. Between the Waikato groups, pH was significantly different, with *Sporadanthus ferrugineus* having a lower pH than *Empodisma minus*. Comparison of species richness indicated that total and vascular plant species numbers were significantly higher in the *Sporadanthus traversi* group than the *Sporadanthus ferrugineus* group.

On Chatham Island, the higher N, P, and K contents may have originated from sea birds, vast numbers of which apparently bred on Chatham Island in pre-human times (Bourne 1967). Sea birds were shown to enrich the soils (N, P) and foliage (N, K, Fe, Na) in and around breeding and roosting sites via guano, feathers, and bird carcasses on sub-antarctic Marion Island in the southern Indian Ocean (Smith 1976; Burger et al. 1978; Williams & Berruti 1978; Williams et al. 1978). Enrichment of peat and foliage (total and extractable N, extractable P, Ca, Mg) on Beauchêne Island, Falkland Islands, was also attributed to nearby sea bird colonies (Smith & Prince 1985). The remanence of bird-derived nutrients was demonstrated for pre-European sea bird nesting sites on mainland New Zealand, which still retained significantly higher N and P levels than nonbreeding sites 300–700 years after extinguishment of bird colonies (Hawke et al. 1999). The higher nutrient content of Chatham peat may also be the result of sea spray and strong winds. Meurk et al. (1994) measured high inputs of wind-transported oceanic ions on Campbell Island, another southern oceanic island of New Zealand. The maritime influence combined with the ability of tussock-forming plants to intercept and channel aerosols (including volatilised nitrogenous compounds from sea birds) to feeding roots occupying fibrous pedestals (such as in *S. traversii*) would enhance the nutrient supply to the plant (Barrow 1983). Higher bulk densities of Chatham Island peat may be partly due to its higher wax content (average crude wax yield 9.4%) compared with Waikato peat (average yield 4.7%; MacPherson & Hughson 1943).

Overall, peat depth evidence suggests that peat accumulation rates for Chatham Island and Waikato are similar. Mildenhall (1994) recorded more than 10 m of peat since the last glacial maximum on Chatham Island (marked by the Kawakawa Tephra $22\,590 \pm 230 \text{ yr BP}$; Wilson et al. 1988). This peat had begun forming on previous peat soils by c. 12 000 yr BP in response to climate amelioration (Mildenhall 1994; McGlone 2002). The oldest bogs in the Waikato were initiated post-glacially, and peat depths up to 12 m have been recorded (Grange et al. 1939), with the major peat development occurring after c. 12 000 yr BP (Hogg et al. 1987). However, there are differences in the origin and maintenance of the two peat systems. Waikato has raised bogs that were formed on poorly drained depressions on alluvial terraces associated with former river courses, and have been maintained in a relatively wet, winter rainfall and summer drought regime. The Chatham Island bogs are typically oceanic and comprise mainly blanket bogs formed on poorly drained flat, rolling, and moderately sloped terrain and, to a

Table 2 Comparison of peat properties and species richness of *Sporadanthus traversii*-dominated Chatham Island restiad bogs with *Empodisma minus- and Sporadanthus ferrugineus*-dominated Waikato restiad bogs. Means with standard deviations in parentheses are given for the vegetation types as defined by cluster analysis (Waikato data from Clarkson et al. 2004). Significantly different means are followed by different letters (P < 0.05).

Vegetation type (from cluster analysis)	Sporadanthus traversii	Sporadanthus ferrugineus	Empodisma minus			
Region	Chatham Island	Waikato	Waikato			
Number of plots	18	9	22			
Total K mg cm ⁻³	0.083 (0.022) a	0.013 (0.009) b	0.027 (0.023) b			
pH	4.0 (0.1) a	4.4 (0.2) b	4.8 (0.4) c			
Available P mg cm ⁻³	18.6 (10.7) a	3.4 (3.2) b	6.2 (6.1) b			
von Post	4.0 (0.5) a	1.8 (0.4) b	2.8 (1.4) b			
Bulk density g cm ⁻³	0.101 (0.024) a	0.059 (0.022) b	0.065 (0.026) b			
Total N mg cm ⁻³	1.20 (0.46) a	0.53 (0.16) b	0.78 (0.46) b			
Total P μg cm ⁻³	0.057 (0.030) a	0.019 (0.014) a	0.035(0.003) a			
Available N µg cm ⁻³	17.2 (13.1) a	8.9 (4.1) a	19.0 (12.6) a			
Nonvascular species number	1.8 (1.7) a	1.1 (1.7) a	1.9 (2.0) a			
Vascular species number	7.6 (3.2) a	4.8 (1.6) b	6.2 (1.1) ab			
Total species number	9.4 (3.0) a	5.9 (3.1) b	8.1 (2.8) ab			

lesser extent, raised bogs in wetter basins. These have been maintained in a relatively dry climate by low summer temperatures, moderately high humidity, and low sunshine hours (McGlone 2002). The climatic differences suggest that natural fires would be more common in Waikato bogs, and there is ample evidence of abundant charcoal remains throughout the peat profiles (e.g., McGlone et al. 1984; Newnham et al. 1995). Although charcoal has been regularly recorded in pre-human Chatham Island peats (D. H. Mildenhall pers. comm. 2003), and there is a possibility of irregular fire, it is unlikely that fire had as important a role in the long-term history of bog development. This is because Chatham Island peatlands are much older and developed mainly during long cool moist periods of the glacials (Mildenhall 1994; McGlone 2002).

In the Waikato, the vegetation patterns within a range of differently aged bogs closely paralleled the successional sequence over time as interpreted from palaeoecological fossil evidence (Clarkson et al. 2004). The sequence was from early successional sedges (particularly *Baumea rubiginosa* and *B*. teretifolia), through mid-successional Empodisma late-successional *Sporadanthus* ferrugineus. On Chatham Island the minerotrophic plots (Groups 1 and 2) may represent younger, early successional stages of S. traversii bog development (Group 3), but we have no detailed microfossil or macrofossil data of temporal vegetation changes at early stages of bog development. Broad-scale pollen analyses of peat profiles have indicated that Restionaceae (Sporadanthus) dominated the oldest peats, dating back to more than 33 500 yr BP, and have been relatively prominent ever since (Mildenhall 1994; McGlone 2002). If the Chatham Island restiad bogs were also initiated with a sedge phase, component species were likely to have been Baumea rubiginosa, B. tenax, Carex chathamica, and C. sectioides, which are common on the more minerotrophic bog margins. The restiad species, Apodasmia similis, may also have been an important species in the early successional stages, as it was once dominant in minerotrophic wetlands (Cockayne 1902). It also typically intergraded into S. traversii vegetation (Kelly 1983), and although this vegetation type is now much reduced in extent, examples were encountered at the transect extremities at Ocean Mail.

Sporadanthus traversii has been described as probably being a mid-successional to late-successional species, like *E. minus* in northern North Island (de Lange et al. 1999b). Our data further suggest that

in some respects S. traversii could be regarded as an ecological equivalent to E. minus, having an apparently comparable role in bog development on Chatham Island to E. minus in the Waikato. E. minus is the key to Waikato restiad bog development, as it occupies a wide environmental range, establishes early in fertile minerotrophic wetlands, and persists as a prominent component through to late successional ombrotrophic bogs (Clarkson et al. 2004). S. traversii also grows in relatively high fertility sites, as indicated by the peat characteristics of the S. traversii–A. similis vegetation type (Group 1 of Fig. 6), and it was still a relatively common component in most of the modified *Gleichenia* type plots (Group 5). Similarly, at the other extreme, S. traversii dominated the low-nutrient sites typical of the ombrotrophic *S. traversii* vegetation type (Group 3). In other ways S. traversii is more similar both physiognomically and ecologically to the smaller E. minus than to its closer relative, S. ferrugineus. For example, there were no significant differences in species richness between the Sporadanthus traversii and *Empodisma minus* vegetation groups (Table 2), yet differences were significant for total and vascular plant species richness between the Sporadanthus traversii and Sporadanthus ferrugineus groups. Further, S. traversii looks superficially like E. minus with its more slender culms and rhizomes (means for diameters of E. minus, S. traversii, and S. ferrugineus culms are 1.25, 6.5, and 12.5 mm, and rhizomes 5, 7.5, and 12.5 mm, respectively; Campbell 1964; Moore & Edgar 1976; de Lange et al. 1999b), and sprawling habit in the absence of supporting vegetation. Like E. minus, S. traversii regenerates readily from seed after fire and can dominate plant communities within months, in contrast to S. ferrugineus, which usually takes several years to attain pre-fire composition (Clarkson 1997; de Lange et al. 1999b).

Morphologically, however, the roots of *S. traversii* and *E. minus* have some marked differences. *S. traversii* is more similar to *S. ferrugineus* in having a hairless rhizome with deeply descending tubular roots whereas the *E. minus* rhizome is densely hairy with smaller roots mostly confined to the upper peat layers (Campbell 1964; Wardle et al. 1986). The most notable feature of *E. minus* is the mass of upward-growing fine roots and root hairs (=cluster roots; Lamont 1982; Neumann & Martinoia 2002), which grow at and above the peat surface, eventually forming the main bulk of the peat (Campbell 1964). *Sporadanthus traversii* and *S. ferrugineus* do not have the abundant surface layer of cluster roots, but the roots do develop the cluster

habit as described for the Australian species of *Sporadanthus* (Meney & Pate 1999). Young plants of *S. traversii* and *S. ferrugineus* have been observed to develop abundant fine roots that bind the upper layers of peat both in glasshouse trials and outdoor plantings in the Waikato region. However, unlike *E. minus*, these roots remain below the peat surface (BRC unpubl. data). Despite differences in root structure, *E. minus* forms the bulk of the peat in Waikato raised bogs and *S. traversii* is the main peat former in Chatham Island raised bogs, thus providing further evidence of functional equivalence between these two species.

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Appendix 1 Peat properties of 36 plots. [], additional groups, Darb, Dracophyllum arboreum; Mar, Marchantia berteroana; Sph, Sphagnum falcatulum; BD, bulk density; EC, conductivity; T, total; n.d., not determined. Plots sequentially located along transects except where indicated by *.

von Post	w 4 4 4	44	444	4 ν	44	4 4	t m	m v	, 4	w 2	t ν	S	v, v	y 4	4	4 1	n c	1 W	3	2	4	ε,	n.d.
TK mg cm ⁻³	0.181 0.101 0.117	0.072 0.094	0.095	0.161	$0.127 \\ 0.073$	0.078	0.078	0.070	0.065	0.198	0.098	0.105	0.186	0.042	090.0	0.087	0.065	0.074	0.088	0.018	0.032	0.054	0.059
TP mg cm ⁻³	0.074 0.131 0.100	0.074 0.060 0.076	0.072 0.097 0.075	0.149	0.136 0.034	0.025	0.014	0.016	0.035	0.139	0.097	0.107	0.116	0.104	0.104	0.104	0.059	0.029	0.036	0.021	0.039	0.026	0.104
TN mg cm ⁻³	1.25 2.59 1.61	1.40 1.30	1.14	2.19	2.20 0.94	0.85	0.44	0.57	0.48	2.24	2.44 2.44	2.10	2.54	1.04	1.04	1.96	0.10	0.49	0.43	0.36	0.87	0.29	2.60
TC mg cm ⁻³	49.2 79.0 65.3	58.6 62.8	60.6 53.9 59.7	49.8	64.2 50.7	46.7	31.1	36.0	24.1	73.7	73.3	58.9	82.3 90.7	34.6	46.5	62.2	51.8 0.5	18.8	16.7	15.3	28.7	19.4	61.7
EC mS cm ⁻¹ g ⁻¹	0.27 0.13 0.03	0.00 1.80	0.00	2.41	3.20	0.00	0.00	00.0	0.00	0.03	0.00	0.00	2.41	0.18	0.13	1.00	1.56 2.68	0.00	0.00	0.00	0.00	0.00	0.03
BD mg cm ⁻³	0.100 0.163 0.133	0.113 0.116 0.121	0.121 0.106	0.099	0.131	0.095	0.062	0.072	0.048	0.147	0.145	0.118	0.164	0.068	0.090	0.121	0.100	0.039	0.036	0.033	0.056	0.041	0.117
Available P µg cm ⁻³	23.3 39.6 40.2	27.8 19.5 26.3	22.9 27.9 25.2	49.7 33.8	41.3	5.7	3.7	3.7 48.5	10.7	39.2	26.2	26.8	39.8 40.1	15.8	0.6	29.6	23.3	7.5	11.1	5.1	6.7	7.2	22.9
Available N µg cm ⁻³	17.3	18.9 14.1 17.0	6.1 15.3 9.4	32.2	24.1 12.3	12.8	9.2	7.3	10.9	52.8	27.8	18.7	37.4	25.1	14.7	63.6	30.7	. «. • «.	15.9	8.9	12.5	4.8	26.0
Hd	2.8 9.8 9.9 0.6	3.9 3.9 3.9	3.6	4. 4. 7. 6.	4.3	4.1	4.2	4. 4 1. 4	3.9	4. 4.	6.6 0.4	4.0	4.4 6.4	4.0	4.0	4.1	0.4 0.4	4.3	4.4	4.1	3.8	4.1	4.2
Moisture Content	565.4 286.1 370.9	317.4 435.0	452.4 531.3 523.2			707.3	627.1	507.7	718.4	419.5	291.0	527.3	363.9	896.0	648.9	557.3	960.3	1801.3	2078.6	2524.8	6.806	1258.1	441.3
Group	Apo Gle Spo	Spo Spo	Spo Spo	Spo-Apo Spo-Apo	Gie Spo	Spo	Spo	Spo Dra	Spo	Gle	Gle Gle	Spo	Gle	Spo	$_{ m Spo}$	$_{ m Sbo}$	Spo	Mar	[Mar]	[Sph]	Dra	[Darb]	[Darb]
Plot ID	OM1 OM2 OM3	OM5 OM6 OM6	OM7 OM8 OM9	OM10 OM11	R12 R13	R14 R15	R16	R17 R18*	R19*	R20*	R22*	R23*	B24 B25	T26	T27	T28	T30	T31	T32	T33	T34	T35	T36
Wetland	Ocean Mail Ocean Mail Ocean Mail	Ocean Mail Ocean Mail Ocean Mail	Ocean Mail Ocean Mail Ocean Mail	Ocean Mail	L. Rotokawau L. Rotokawau	L. Rotokawau	Rakautahi Rakautahi	Tuku	Tuku	Tuku	Tuku	Tuku	Tuku	Tuku	Tuku	Tuku	Tuku						

Appendix 2 Plant species recorded in vegetation plots on Chatham Island. *, non-native species; ^t, confined to Tuku forest plot T36 dominated by *Dracophyllum arboreum*

Taxon	Family					
Vascular species						
Anthoxanthum odoratum* L.	Poaceae					
Apodasmia similis (Edgar) B.G.Briggs & L.A.S.Johnson	Restionaceae					
Aporostylis bifolia (Hook.f.) Rupp & Hatch	Orchidaceae					
Asplenium flaccidum ^t G.Forst.	Aspleniaceae					
A. oblongifolium ^t Colenso	Aspleniaceae					
A. polyodon ^t G.Forst.	Aspleniaceae					
Baumea rubiginosa (Spreng.) Boeck.	Cyperaceae					
B. tenax (Hook.f.) Blake	Cyperaceae					
Blechnum novae-zelandiae T.C.Chambers & P.A.Farrant	Сурстассас					
(swamp form "B. minus")	Blechnaceae					
B. procerum (G.Forst.) Sw. Carex chathamica Petrie	Blechnaceae					
	Cyperaceae					
Carex sectoides (Kuk.) Edgar	Cyperaceae					
Cerastium glomeratum* Thuill.	Caryophyllaceae					
Centella uniflora (Colenso) Nannf.	Apiaceae					
Coprosma chathamica Cockayne	Rubiaceae					
Coprosma propinqua var. martinii W.R.B.Oliv.	Rubiaceae					
Corokia macrocarpa ^t Kirk	Escalloniaceae					
Corybas sp.	Orchidaceae					
Ctenopteris heterophylla ^t (Labill.) Tindale	Grammitidaceae					
Cyathea cunninghamii ^t Hook.f.	Cyatheaceae					
Cyathodes robusta Hook.f.	Epacridaceae					
Dicksonia fibrosa ^t Colenso	Dicksoniaceae					
D. squarrosa ^t (G.Forst.) Sw.	Dicksoniaceae					
Dracophyllum arboreum Cockayne	Epacridaceae					
Dracophyllum scoparium Hook.f.	Epacridaceae					
Drosera binata Labill.	Droseraceae					
Gentiana chathamica Cheeseman	Gentianaceae					
Gleichenia dicarpa R.Br.	Gleicheniaceae					
Ficinia nodosa (Rottb.) Goetgh. Muasya & D.A.Simpson	Cyperaceae					
Hierochloe redolens (Vahl) Roem. & Schult.	Poaceae					
Holcus lanatus* L.	Poaceae					
Hydrocotyle novae-zeelandiae DC.	Apiaceae					
Hymenophyllum demissum ^t (G.Forst.) Sw.	Hymenophyllaceae					
H. dilatatum ^t (G.Forst.) Sw.	Hymenophyllaceae					
H. multifidum ^t (G.Forst.) Sw.	Hymenophyllaceae					
H. scabrum ^t A.Rich.	Hymenophyllaceae					
Hypochaeris radicata* L.	Asteraceae					
Typolepis distans Hook.	Dennstaedtiaceae					
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Isolepis distigmatosa (C.B.Clarke) Edgar Iuncus articulatus* L.	Cyperaceae Juncaceae					
	_					
I. bufonius* L.	Juncaceae					
I. effusus* L.	Juncaceae					
J. pallidus R.Br.	Juncaceae					
I. planifolius R.Br.	Juncaceae					
Leontodon taraxacoides* (Villars) Merat	Asteraceae					
Leptinella potentillina F.Muell.	Asteraceae					
Lepidosperma australe (A.Rich.) Hook.f.	Cyperaceae					
Libertia peregrinans Cockayne & Allan	Iridaceae					
Lobelia anceps L.f.	Lobeliaceae					
Luzula banksiana var. acra Edgar	Juncaceae					
Myriophyllum pedunculatum subsp. novae-zelandiae Orch.	Haloragaceae					
Myrsine chathamica ^t F.Muell.	Myrsinaceae					

(continued over page)

Appendix 2 (Continued)

Taxon	Family
M. coxii ^t Cockayne	Myrsinaceae
Nertera depressa Banks & Sol. ex Gaertn.	Rubiaceae
Olearia semidentata Decne ex Hook.f.	Asteraceae
Plantago australis* Lam.	Plantaginaceae
Phormium tenax J.R. & G.Forst.	Phormiaceae
Plantago coronopus L.	Plantaginaceae
Poa annua* L.	Poaceae
Poa chathamica Petrie	Poaceae
Pratia arenaria Hook.f.	Lobeliaceae
Peusdopanax chathamicus Kirk	Araliaceae
Pteridium esculentum (Forst.f.) Cockayne	Dennstaedtiaceae
Ripogonum scandens ^t J.R. & G.Forst.	Ripogonaceae
Rubus fruticosus* L.	Rosaceae
Rumex acetosella* L.	Polygonaceae
Sagina procumbens* L.	Caryophyllaceae
Selliera radicans Cav.	Goodeniaceae
Sporadanthus traversii (F.Muell.) F.Muell. ex Kirk	Restionaceae
Thelymitra cyanea (Lindl.) Benth.	Orchidaceae
Trichomanes reniforme ^t G.Forst.	Hymenophyllaceae
Uncinia rupestris Raoul	Cyperaceae
Utricularia delicatula Cheesem.	Lentibulariaceae
Non-vascular species	
Campylopus acuminatus var. kirkii (Mitt.) Frahm	Dicranaceae
Chiloscyphus semiteres (Lehm.) Lehm. & Lindenb.	Geocalycaceae
Cladia retipora (Labill.) Nyl.	Cladoniaceae
Cladina leptoclada (des Abb.) D.Galloway	Cladoniaceae
Dicranoloma billardieri (Brid. ex anon.) Par.	Dicranaceae
Hypnum chrysogaster C.Muell.	Hypnaceae
Kurzia compacta (Steph.) Grolle	Lepidoziaceae
Marchantia berteroana Lehm. & Lindenb.	Marchantiaceae
Pallavicinia lyellii (Hook.) S.Gray	Pallaviciniaceae
Pohlia ?nutans (Hedw.) Lindb.	Bryaceae
Ptychomnion aciculare (Brid.) Mitt.	Ptychomniaceae
Riccardia cochleata (Hook.f. & Taylor) Kuntze	Aneuraceae
R. crassa (Schwaegr.) Carrington & Pearson	Aneuraceae
Sphagnum australe Mitt.	Sphagnaceae
S. falcatulum Besch.	Sphagnaceae
Stereocaulon sp.	Stereocaulaceae