RESTIAD BOG DEVELOPMENT AND NUTRIENT DYNAMICS OF THE DOMINANT SPECIES

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ABSTRACT

RESTIAD BOG DEVELOPMENT AND NUTRIENT DYNAMICS OF THE DOMINANT SPECIES

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Vegetation and peat in lowland restiad (dominated by Restionaceae) raised bogs on North Island (Waikato region) and Chatham Island, New Zealand, were sampled to investigate the main environmental controls of pattern and change. Vegetation classification based on a chronosequence of Waikato restiad bogs revealed a sequence from sedges, through *Empodisma minus*, the main peat-forming restiad, to phases dominated by a second restiad, *Sporadanthus ferrugineus*. The sequence paralleled temporal successional patterns and was used for interpreting plant-nutrient dynamics along a successional gradient. As succession proceeds, von Post (an index of peat decomposition), total P, total N and % ash in peat decrease. *Empodisma* was considered to be the key species in restiad bog development. It is tolerant of a wide environmental range, establishing early in minerotrophic wetlands to initiate restiad bog development, and persisting through to late ombrotrophic phases. On Chatham Island, the ecological role of *Sporadanthus traversii* in restiad bog development is similar to *Empodisma* in Waikato, being the main peat former and occupying a wide environmental range. Peat under *S. traversii* had significantly higher total N, total K, available P, bulk density and von Post, and lower pH than Waikato peats under *S. ferrugineus* or *Empodisma*. This was attributed to a strong oceanic influence and long history of sea-bird nutrient inputs.

Nutrient responses in the heath and restiad components of the bog were compared by measuring plant ^{15}N natural abundance across N and P gradients. Heath shrubs revealed considerable isotopic variation (–2.03 to –15.55‰ for *Leptospermum scoparium*), with foliar $\delta^{15}N$ strongly positively correlated with P concentrations in foliage and peat. In contrast, restiad species revealed little isotopic variation, with *Empodisma* and *S. traversii* having $\delta^{15}N$ levels around 0‰, and *S. ferrugineus* being significantly more depleted (mean –4.97‰). The differences in isotopic signatures between heath shrubs and restiads were linked to contrasting nutrient demands, acquisition mechanisms, and root morphology. *Leptospermum* shrubs on low nutrient peats were stunted, with low foliar %P and high N:P ratios, suggesting they were P-limited. The concurrence of $\delta^{15}N$ depletion and %P in plant tissues suggests N fractionation is promoted by P limitation. In contrast, the constancy in $\delta^{15}N$ of the restiad species through the nutrient gradients indicates these may not be P-limited.

The contrasting $\delta^{15}N$ signatures of co-habiting *Empodisma* and *S. ferrugineus* in late successional bogs suggest the species are accessing different sources of N. *Empodisma* has a thick layer of cluster roots overlying the deeper *S. ferrugineus* roots, and would be better positioned to intercept aerially derived N. The hypothesis that this root disposition allows *Empodisma* to preferentially access the primary N input from rainfall was tested using a ^{15}N-enriched tracer. At plots co-dominated by *Empodisma* and *S. ferrugineus*, 1.6 mmoles m^{-2} of 99 atom % excess ^{15}N as $(NH_4)_2SO_4$ was applied to the peat surface, followed by deionised water, simulating a rainfall event of 34 mm. After 5 hours, cores were harvested and analysed for ^{15}N. Approximately 90% of the recovered isotope was in the upper *Empodisma* root layer. Seven weeks after tracer application, young shoots of *Empodisma* were significantly enriched whereas adjacent *Sporadanthus* shoots were not. The results confirm that species acquire nutrients from different rooting zones, with *Empodisma* accessing nutrients at the surface from rainfall and *S. ferrugineus* acquiring nutrients from deeper peat layers. Niche differentiation facilitates species co-existence, which, on a successional time scale, may be a mechanism for slowing the rate of competitive displacement.

Key Words bog succession; ^{15}N natural abundance; ^{15}N-enriched tracer; nutrient gradients; New Zealand; Restionaceae; *Empodisma minus*; *Sporadanthus ferrugineus*; *S. traversii*

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1. INTRODUCTION

1.1. RESEARCH TOPIC

This research focuses on lowland raised peat bogs characterised by members of the family Restionaceae: *Sporadanthus ferrugineus* (de Lange et al. 1999), *S. traversii*, and *Empodisma minus* (for authorities see Appendices 2.1 and 3.2). Restiad bog systems are a Southern Hemisphere ecological equivalent of Northern Hemisphere *Sphagnum* moss raised bogs (Agnew et al. 1993) and are most extensively developed in New Zealand (Campbell 1983). In contrast to Northern Hemisphere bogs, very little co-ordinated research has been carried out on functioning of New Zealand systems. This study helps identify the major environmental determinants of bog succession and some of the mechanisms whereby restiad species grow and dominate in nutrient-deficient environments. The research concentrates on the extensive restiad bog systems in the Waikato region, which are co-dominated by *Sporadanthus ferrugineus* (endemic to northern North Island) and *Empodisma minus* (widespread). It also extends to a floristically different restiad bog type on geographically isolated Chatham Island, characterised by the Chatham Island endemic, *Sporadanthus traversii.*

1.2. BACKGROUND

Restiad peat bogs dominated by *Sporadanthus* represent one of New Zealand's most threatened ecosystems because of widespread drainage and conversion to pasture during the last 150 years (de Lange et al. 1999). Present day systems are now confined to the Waikato region and Chatham Island. In accordance with wetlands in general, they have multiple values, including filtering sediments, moderating the effect of floods, regulating water quality and quantity, and providing habitat for indigenous flora and fauna (Costanza et al. 1997, Cole and Patterson 1997). In addition, bogs sequester carbon through peat development and therefore are valuable in helping to offset global warming (Mitsch & Gosselink 2000). Because of their ecological and economic importance, we need an understanding of bog functioning in order to develop sound management strategies for maintenance of intact systems and restoration of those that are damaged (Zedler 2000).

Bog development is controlled by two main environmental variables: water supply and nutrient supply (Tallis 1983). In time, the system changes from a minerotrophic (= mineral-nourished) mire to an ombrotrophic mire (= precipitation-dominated) as peat accumulates and the surface rises above the influence of the groundwater (Mitsch & Gosselink 2000). For *Sphagnum* bogs worldwide, the vegetation and environmental relationships and functional processes have been widely published (e.g., Gore 1983, Vitt & Chee 1990, van Breeman 1995, Zoltai & Vitt 1995, Bridgham et al. 1998) but equivalent research in restiad bogs is limited. Existing New Zealand studies are mainly discrete and disparate, and inadequate for understanding functional processes or bog development sequences, or exploring differences and similarities with northern peatlands.

Change in nutrient availability during wetland succession is one of the key driving variables in ecosystem development. In Northern Hemisphere wetlands, fertilisation studies showed N, P, and occasionally K, to be the major limiting nutrients for plant growth (Bridgham et al. 1996), with vegetation being N-limited in early succession and P-limited in later succession (Verhoeven *et al.* 1996). Understanding the links between nutrient availability and plant response, and the mechanisms involved, are fundamental to insights into successional processes and interactions at the species, community, and ecosystem levels.

Stable isotope methodology has been used in recent years to investigate nutrient dynamics of species in natural ecosystems. As N is the nutrient that most frequently limits net primary production (Vitousek 1994), many studies are based on N isotopes. Natural abundance ^{15}N techniques give insight into N nutrition patterns and tracer ^{15}N techniques provide important information about N processes (Nadelhoffer & Fry 1994). In low nutrient environments such as wetlands, plant $\delta^{15}N$ signature has been linked with nutrient availability and changes in N demand (Fry et al. 2000). While stable isotopes have been increasingly been used to elucidate plant-nutrient relationships and processes in wetlands overseas (e.g., Michelsen et al. 1996, McKane et al. 2002, Kohzu et al.

2003, McKee et al. 2002), this approach has yet to be applied to understand bog function in New Zealand.

1.3. RESEARCH QUESTIONS

The main research questions addressed in this thesis are:

- What causes the changes in species dominance during development of restiad bogs?
- What are the limiting nutrients in restiad bog development?
- What adaptations do the dominant species have in accessing nutrients?
- What are the special characteristics of the Restionaceae that enable them to dominate in nutrient limited raised bog environments?

The research approach for the study follows that advocated by Ackoff (1968), being:

- Model and predict species/environment relationships by correlating vegetation, hydrological and biogeochemical data to assist in formulating testable hypotheses.
- Test hypotheses using field experiments to determine cause and effect relationships between nutrients and plant growth.

1.4. GOALS

The goals of this thesis are to:

- Investigate the main environmental controls of vegetation pattern and change in the development of restiad raised bogs by measuring vegetation, biogeochemical, and ecohydrological patterns and processes across a range of young-to-old restiad raised bogs in the Waikato region and on Chatham Island, and comparing these with previous studies of vegetation changes through time;
- Compare plant nutrient dynamics by analysing N, P and $\delta^{15}N$ concentrations of the dominant species across nutrient gradients in Waikato and Chatham Island bogs; and
- Examine nutrient source and dynamics in the dominant restiad species in a late-successional raised bog by using ^{15}N-enriched tracers.

The thesis comprises four main chapters (Chapters 2–5) that have been published in, or submitted to, four international journals: *Wetlands* (published in United States of America), *New Zealand Journal of Botany* (New Zealand), *Oecologia* (Germany), and *New Phytologist* (United Kingdom). Each chapter is self-contained with an introduction and background literature review, and formatted according to the relevant journal style.

Chapter 2 characterises vegetation patterns and presents a conceptual model of restiad bog development based on vegetation and environmental data from a chronosequence of restiad bogs in the Waikato region. It also includes species autecological models of the important environmental variables that direct successional changes. Dr Anthony Lehmann, Switzerland, formerly of Landcare Research, Hamilton, developed the autecological models using Generalized Regression Analysis and Spatial Prediction (GRASP), a procedure that he and colleagues designed (Lehmann et al. 2002). This research is published as: Clarkson, B.R., Schipper, L.A., Lehmann, A. 2004. Vegetation and peat characteristics in the development of lowland restiad peat bogs, North Island, New Zealand. *Wetlands 24*: 133-151.

In chapter 3 the peat physical and chemical properties of Chatham Island restiad bogs were measured and correlated with vegetation patterns, and compared with the Waikato systems outlined in Chapter 2. This research is published as: Clarkson, B.R., Schipper, L.A., Clarkson, B.D. 2004. Vegetation and peat characteristics of restiad bogs on Chatham Island (Rekohu), New Zealand. *New Zealand Journal of Botany 42*: 293–312.

Chapter 4 compares and contrasts nutrient content in the dominant woody (heath shrubs) and non-woody (restiads) species across nutrient gradients in Waikato and Chatham Island bogs and investigates the usefulness of plant $\delta^{15}N$ as an indicator of N or P limitation. The influence of mycorrhizal associations was also determined and this analysis was conducted by one of the co-authors, Dr Bernard Moyersoen, Belgium, formerly of Landcare Research, Auckland. This research has been accepted for publication in *Oecologica* as: Clarkson, B.R., Schipper, L.A., Moyersoen, B., Silvester, W.B. Foliar ^{15}N natural abundance indicates phosphorus limitation of bog species.

The final research paper, Chapter 5, builds on the Chapter 4 in which $\delta^{15}N$ isotopic signatures of co-existing restiad species suggest different N sources and/or plant N demand. The nutritional niches of *Sporadanthus ferrugineus* and *Empodisma minus* are defined using tracer stable isotope techniques to illustrate a mechanism for facilitating species co-existence in an extremely nutrient deficient environment. This research has been submitted to *New Phytologist* as: Clarkson, B.R., Schipper, L.A., Silvester, W.B. Nutritional niche separation in co-existing bog species demonstrated by enriched ^{15}N simulated rainfall.

Chapter 6 is a synthesis of the research presented in the preceeding four chapters. It summarises general trends of restiad bog development, compares functional dynamics with northern *Sphagnum* raised bogs, and considers how this research contributes to ecological theory. During the course of the study, further questions were raised on various aspects of bog functioning, and the final section develops these as directions for further research.

1.5. REFERENCES

Ackoff R. L. 1968: Scientific method: optimizing applied research decisions. John Wiley & Sons, New York.

Agnew A. D. Q.; Rapson, G. L; Sykes, M. T.; Wilson J. B. 1993: The functional ecology of *Empodisma minus* (Hook.f.) Johnson and Cutler in New Zealand ombrotrophic mires. *New Phytologist 124*: 703–710.

Bridgham, S. D.; Pastor J.; Janssens J. A.; Chapin C.; Malterer T. J. 1996: Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands 16*: 45-65.

Bridgham S. D.; Updegraff K.; Pastor J. 1998: Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology 79*: 1545–1561.

Campbell, E. O. 1983: Mires of Australasia. *In*: Gore A. J. P. *ed.* Ecosystems of the world 4A Mires: swamp, bog, fen and moor. Amsterdam, The Netherlands, Elsevier Scientific Co. Pp. 153–180.

Cole, A.O.; Patterson, M.G. 1997: The economic value of New Zealand's biodiversity. Ministry for the Environment, Wellington.

Costanza, R.; d'Arge, R.; de Groot, R.; Farber, S.; Grasso, M.; Hannon, B.; Limburg, K.; Naeem, S.; O'Neill, R.V.; Paruelo, J.; Raskin, R.G.; Sutton, P.; van den Belt, M. 1997: The value of the world's ecosystem services and natural capital. *Nature 387*: 253-260.

de Lange, P. R.; Heenan, P. B.; Clarkson, B. D.; Clarkson, B. R. 1999: *Sporadanthus* in New Zealand. *New Zealand Journal of Botany 37*: 413–431.

Fry B.; Bern A. L.; Ross M. S.; Meeder J. F 2000: ^{15}N studies of nitrogen use by the red mangrove *Rhizophora mangle* L. in South Florida. *Estuarine, Coastal and Shelf Science 50*: 723–735.

Gore A. J. P. *ed.* 1983: Mires: swamp, bog, fen and moor. Ecosystems of the world 4A. Elsevier Amsterdam.

Kohzu A.; Matsui K.; Yamada T.; Sugimoto A.; Fujita N. 2003: Significance of rooting depth in mire plants: Evidence from natural ^{15}N abundance. *Ecological Research 18*: 257–266.

Lehmann A.; Overton J. McC; Leathwick, J. R. 2002: GRASP: Generalized Regression Analysis and Spatial Prediction. *Ecological Modeling 157*: 187–205.

McKane R. B.; Johnson L. C.; Shaver G. R.; Nadelhoffer K. J.; Rastatter E. B.; Fry B.; Giblin A. E.; Kielland K.; Kwatkowski B. L ; Laundre J. A.; Murray G. 2002: Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature 425*: 68–71.

McKee K. L.; Feller I. C.; Popp M.; Wanek W. 2002: Mangrove isotopic (δ^{15}N and δ^{13}C) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology 83*: 1065–1075.

Michelsen A.; Schmidt I. K.; Jonasson S.; Quarmby C.; Sleep D. 1996: Leaf δ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia 105*: 53–63.

Mitsch, W. J.; Gosselink J. G. 2000: Wetlands, 3rd ed. John Wiley and Sons Inc New York.

Nadelhoffer K. J.; Fry B. 1994: Nitrogen isotope studies in forest ecosystems. In: K. Lajtha and R. Michener (eds.) Stable isotopes in ecology and environmental science. Blackwell Science, Oxford, UK, pp. 22–44.

Tallis J. H. 1983: Changes in wetland communities. *In:* A. J. P. Gore *ed.* Ecosystems of the world 4A Mires: swamp, bog, fen and moor. Elsevier Scientific Co., Amsterdam, The Netherlands, pp. 311–347.

van Breemen, N. 1995: How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution 10*: 270–275.

Verhoeven, J. T. A., W. Koerselmann, and A. F. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution 11*: 494-497.

Vitousek, P. M. 1994: Beyond global warming: ecology and global change. *Ecology 75*: 1861–1876.

Vitt D. H.; Chee W-L. 1990: The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio 89*: 87–106.

Zedler J. B. 2000: Progress in wetland restoration ecology. *Trends in Ecology & Evolution 15*: 402–407.

Zoltai S. C.; Vitt, D. H. 1995: Canadian wetlands: environmental gradients and classification. *Vegetatio 118*: 131-137.

2. VEGETATION AND PEAT CHARACTERISTICS IN THE DEVELOPMENT OF LOWLAND RESTIAD PEAT BOGS, NORTH ISLAND, NEW ZEALAND[1]

2.1. ABSTRACT

A chronosequence of restiad peat bogs (dominated by Restionaceae) in the lowland warm temperate zone of the Waikato region, North Island, New Zealand, was sampled to identify the major environmental determinants of vegetation pattern and dynamics. Agglomerative hierarchical classification of vegetation data from 69 plots in nine different-aged bogs, initiated from *c.* 600 to *c.* 15,000 cal yr BP, identified eight groups. Six of these groups formed a sequence from sedges through *Empodisma minus*, the main peat-forming restiad species, to phases dominated by a second restiad species, *Sporadanthus ferrugineus*. The sequence reflected bog age and paralleled patterns of temporal succession over the last 15,000 years (from early successional sedges through mid-successional *Empodisma* to late successional *Sporadanthus*) derived from previous studies of plant macrofossils and microfossils in peat cores. This indicated that different-aged bogs in the Waikato region could be used to interpret temporal succession. The remaining two classificatory groups comprised plots from sites modified by drainage, fire, or weed invasion and currently dominated by non-restiad species. The relationships between environmental variables and the six groups representing restiad bog succession indicated that, as succession proceeds, von Post decomposition index and nutrients in the top 7.5 cm peat zone decrease. The most useful indicators of successional stage were von Post, total P, total N, and % ash. Environmental response curves of the dominant plant species separated the species along nutrient and peat decompositional gradients, with early successional species having wider potential environmental ranges than late successional species. *Empodisma minus,* a mid-successional species, also had a relatively wide environmental range, which probably contributes to its key role in restiad bog development.

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[1] Published as Clarkson B. R., Schipper, L. A., Lehmann, A. 2004, *Wetlands 24*: 133–151.

Key Words: peat bog, vegetation succession, Restionaceae, *Empodisma minus, Sporadanthus ferrugineus,* nutrient gradient, von Post, environmental response curve

2.2. INTRODUCTION

Wetland development and ecosystem dynamics theory is largely based on data from the Northern Hemisphere, which may be incongruent with the development and ecosystem dynamics of certain peatlands in the Southern Hemisphere that have completely different vegetation types. The goal of this paper is to describe community- and ecosystem-level changes across a gradient of young-to-old *restiad* raised bogs in New Zealand to determine patterns of changes in vegetation and ecosystem processes through time. Restiad bogs are dominated by members of the Southern Hemisphere family, Restionaceae, a sister group to the Poaceae (Judd et al. 1999). In northern New Zealand bogs, the two main species are *Empodisma minus* (henceforth called *Empodisma*; for authorities and families see Appendix 2.1), the primary peat-former, and *Sporadanthus ferrugineus* (henceforth *Sporadanthus*). This study focuses on *Sporadanthus-Empodisma* bogs, which have been severely reduced in extent because of widespread drainage for agricultural purposes (de Lange et al. 1999) and are now confined to the Waikato region between latitudes 37° S and 38° S (Figure 2.1). In the face of ongoing anthropogenic modification, their long-term management is more likely to be successful if based on ecological theory (van der Valk 1998, Cole 1999, Keddy 2000), which is currently lacking for these peatland types.

This paper characterizes vegetation pattern and changes using two approaches: (1) vegetation survey in modern systems and (2) analysis of results from previous paleoecological studies to assess vegetation changes and rates of change through time. These approaches together will allow us to determine if peatland vegetation variation in space (corresponding from young to old wetlands) corroborate changes in time (Miles 1979, Tallis 1983, Jackson et al. 1988). To the extent they do, modern vegetation patterns most likely represent a successional gradient rather than random colonization events mediated by disturbances.

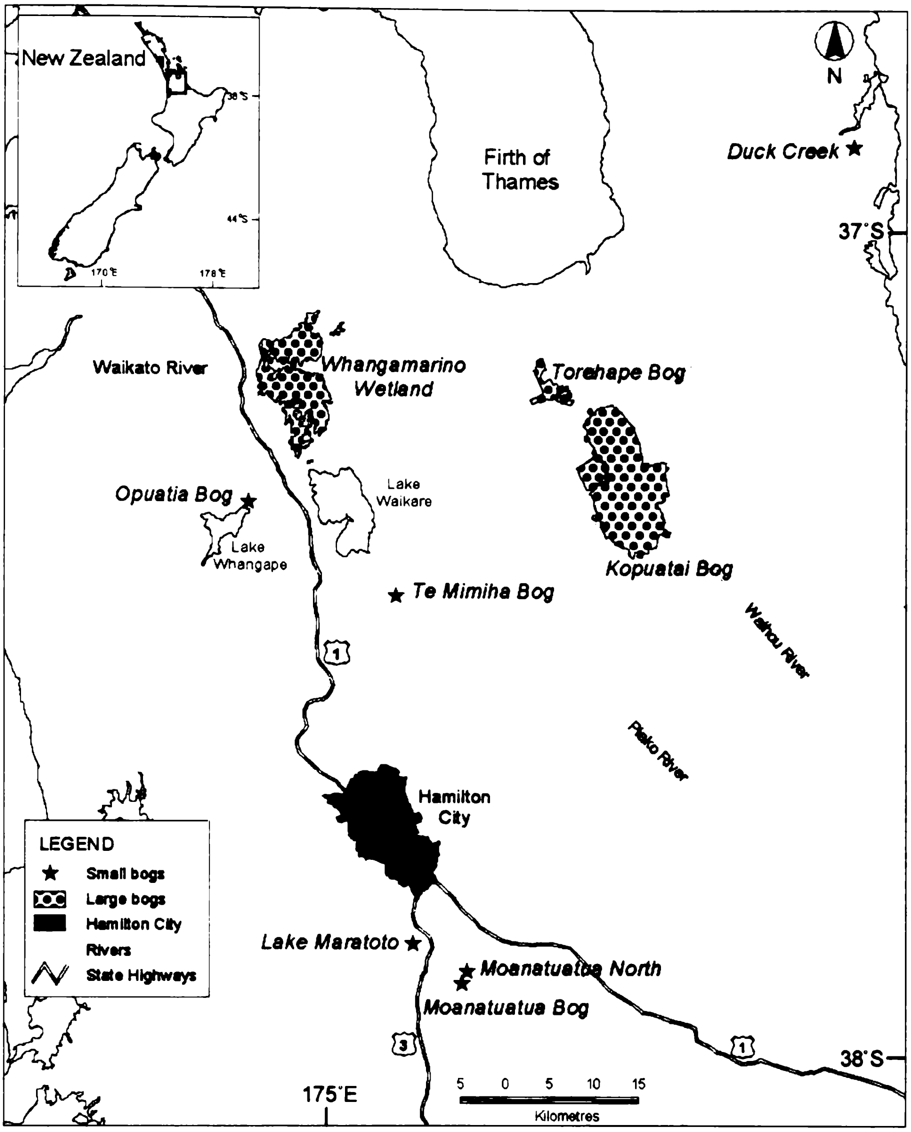

Figure 2.1 Location map of sampling bog sites (the nine known remaining restiad bogs still dominated by native vegetation) in the Waikato region, North Island, New Zealand.

Next, we explored several important environmental correlates to determine how they covary with vegetational changes across the successional gradient. This will lead to insights about changes in ecosystem function through succession, possibly identifying important variables that direct successional changes both at the vegetation type and species autecological levels. Bog succession is controlled by two main environmental variables: water supply and nutrient supply as the system changes from a minerotrophic to an ombrotrophic mire (Tallis 1983, Mitsch and Gosselink 2000). For *Sphagnum* bogs worldwide, the vegetation and environmental relationships have been widely published (e.g., Gore 1983, Vitt and Chee 1990, Zoltai and Vitt 1995, Keddy 2000, Mitsch and Gosselink 2000, Dickinson et al. 2002, Whinam et al. 2001), but little equivalent research has been done for New Zealand restiad systems. Relevant restiad studies include aspects of environment–vegetation relationships (Dobson 1979, Shearer and Clarkson 1998, Meney and Pate 1999), microbial and peat properties (Damman 1988, Schipper et al. 1998), hydrologic–physiological relationships (Campbell and Williamson 1997, Thompson et al. 1999), autecological studies (Agnew et al. 1993, Sorrell et al. 2000), and restoration (Schipper et al. 2002). However, existing work is inadequate for testing of hypotheses of function and development because studies tend to be discrete and disparate, and there is little coordinated research published on functional processes or understanding bog development sequences.

Finally, we integrate the vegetation and ecosystem-level data to present a conceptual model of succession for restiad peatlands in New Zealand and how severe anthropogenic disturbances might alter the course of successional and ecosystem dynamics. We compare these results with those developed for northen peatlands to explore differences and similarities. As New Zealand restiad bogs have been regarded as ecological equivalents of boreal *Sphagnum* bogs (Agnew et al. 1993, Kuder et al. 1998), we were interested in investigating whether functional processes were similar.

Study Area

Nine areas of restiad bog are still dominated by native vegetation in the 2.4 million ha Waikato region (Figure 2.1, Table 2.1). They are located within 110 km of each other, occur at altitudes of less than 60 m above sea level, and experience similar climatic conditions, namely mild with moderate temperatures (annual mean 13.0–14.3°C), high humidity (80–83%), and relatively few ground frosts (29–52 days per year) (New Zealand Meteorological Service 1973). Rainfall is moderate (annual mean 1112–1500 mm), and summer water deficits are common, with typical annual water deficits exceeding 60 mm. Water chemistry typically falls within the ranges of pH 3.7 to 5.0 and specific conductance 0–90 μS/cm (Shearer and Clarkson 1998, Clarkson et al. 1999, B. R. Clarkson unpub. data).

Table 2.1 Restiad bogs sampled in the Waikato Region, New Zealand.

Bog site	Current size (ha)[1]	Original size (ha)[1]	^{14}C date[2] (yr BP ± 1 SD)	Age[3] (cal yr BP)	Dominant species	Number of plots
Duck Creek	118	200	450 ±60	620-608 (mid-point 614)	*Baumea rubiginosa*, *Gleichenia*	3
Opuatia	950	1100	1850 ±10	*c.* 1750	*Empodisma*	10
Whangamarino	7000	11,000	1850 ±10	*c.* 1750	*Empodisma*	19
Torehape	700	10,000	6050 ±110	7209-7165 (7187)	*Sporadanthus*	3
Lake Maratoto	43	13,000	10,600 ±90	11,000-10,360 (10,680)	*Leptospermum*[4]	2
Kopuatai	10,500	11,000	6050[5] ±110	7209-7165 (7187)	*Sporadanthus/Empodisma*	19
Kopuatai	10,500	11,000	11,700 ±80	13,885-13,441 (13,663)	*Sporadanthus*	3
Te Mimiha	67	1100	13,000 ±55	16,082-14,630 (15,356)	*Leptospermum*[4]	1
Moanatuatua North	23	7500	13,000 ±55	16,082-14,630 (15,356)	*Leptospermum/Empodisma*[4]	2
Moanatuatua	114	7500	13,000 ±55	16,082-14,630 (15,356)	*Sporadanthus*	7

[1] sources: Grange et al. 1939, Leathwick et al. 1995

[2] sources: Green and Lowe 1985, Hogg et al. 1987, Newnham et al. 1995, Duck Creek: This study – Wk-7820; Wk = University of Waikato Radiocarbon Dating Laboratory.

[3] calibrations at two sigma based on INTCAL98: Stuiver et al. 1998. Date for Taupo eruption (Whangamarino and Opuatia) from Lowe and de Lange (2000).

[4] originally dominated by *Sporadanthus*

[5] northern part of bog is much younger

The bogs were initiated in the late Pleistocene–Holocene (i.e., since *c.* 15,000 years ago), a period of warming climate and intense volcanic activity in the Central North Island (McGlone and Topping 1977). Based on ^{14}C dates of basal sediments obtained in peat cores and known ages of marker tephras, they range in age from *c.* 614 cal yr BP to more than *c.* 15,000 cal yr BP (see Table 2.1 for ^{14}C yr BP; henceforth all dates are reported as calendar years). Around 700 years ago, Maori settlers arrived in the region but they modified little of the distinctive bog flora (Cranwell 1939, Newnham et al. 1995). Over the past 150 years, widespread settlement by Europeans has had more impact, with several extensive bogs being drained and converted to pasture. Although species compositions of remaining

Figure 2.2 Aerial photograph of Moanatuatua Bog remnant within an agricultural landscape. Maximum width of bog is 700 m. Photo: Aerial Surveys Ltd.

Figure 2.3 Clumps of brown-flowered *Sporadanthus ferrugineus* overtopping *Empodisma minus* typify original restiad bog vegetation at Moanatuatua Bog. Photo: J. Greenwood.

large systems are essentially unchanged (Cranwell 1939), some species (including restiads) have been lost from small remnants (Clarkson et al. 1999).

Three of the oldest bogs (*c.* 7187–*c.* 15,356 cal yr BP), Moanatuatua (Figure 2.2), Torehape, and Kopuatai, contain representative examples of the original restiad raised bog ecosystem (Figure 2.3). This typically comprises an upper tier of *Sporadanthus* tussocks up to 2.5 m in height, which overtops a dense lower layer of intertwining wiry-stemmed *Empodisma*. Three woody species, *Dracophyllum lessonianum* (not at Moanatuatua), *Epacris pauciflora*, and *Leptospermum scoparium*, also occur in the upper tier but are generally more common at and near the margins. Growing amongst the *Empodisma* to a height of about 1 m are the sedges *Baumea teretifolia* and *Schoenus pauciflorus* and patches of the tangle fern *Gleichenia dicarpa*. Where the understory is more open, a bryophyte-dominated ground cover is present and includes *Goebelobryum unguiculatum, Riccardia crassa, Campylopus acuminatus* var. *kirkii*, *Lycopodiella lateralis*, *Sphagnum cristatum*, and *Utricularia delicatula*. (*S. cristatum* and *U. delicatula* are recently extinct locally from Moanatuatua due to lowered water tables [Clarkson et al. 1999]).

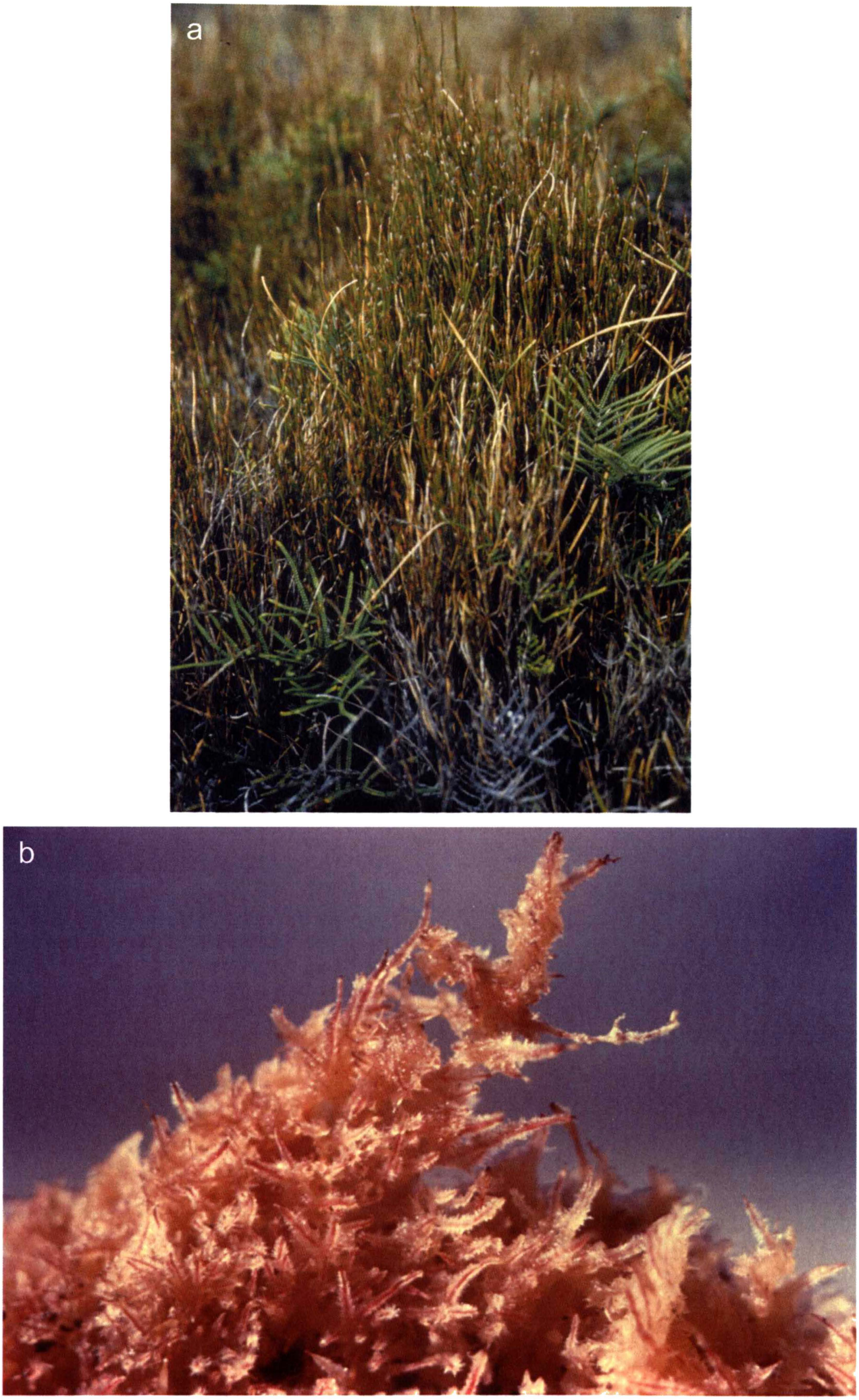

Figure 2.4 a) *Empodisma minus*, the main peat-forming species, growing with *Gleichenia dicarpa* fern. b) Profile of the *Sphagnum*-like surface layers of *Empodisma minus* peat showing the dense growth of fine cluster roots. Photo: E.W.E. Butcher.

The three remaining older bogs, Lake Maratoto, Te Mimiha, and Moanatuatua North, have been modified by fire and drainage and are dominated by *Leptospermum scoparium*. At these sites, the original *Sporadanthus/Empodisma* cover is now absent, except for patches of *Empodisma* still remaining at Moanatuatua North.

Whangamarino and Opuatia are relatively young bogs, having developed in river valleys dammed by pumice alluvium (Lowe and Green 1992) derived from the *c.* AD 200 Taupo eruption (Lowe and de Lange 2000). In these bogs, the vegetation is dominated by *Empodisma* (Figure 2.4), but *Baumea teretifolia*, *Baumea rubiginosa, Schoenus pauciflorus, Gleichenia dicarpa*, and *L. scoparium* are also common. Duck Creek (*c.* 614 cal yr BP) is the youngest bog and is dominated by sedges (*B. rubiginosa, B. teretifolia*; Figure 2.5), with *G. dicarpa* and *L. scoparium* also common. It is in the very early stages of developing into a restiad bog as *Empodisma* has only very recently colonized (probably within the last 50 years) in two small areas of the wetland. Grey willow (*Salix cinerea*), a non-native tree species, is abundant on the margins of all these young bogs.

Figure 2.5 View of *Baumea teretifolia*-dominated sedgeland at the margins of Whangamarino Wetland. Similar vegetation can be found at Duck Creek.

Paleoecological Evidence of Restiad Bog Development

Pollen and macrofossil data from bog genesis to recent time are available for *c.* 15,000-year-old Moanatuatua (Cranwell 1953), *c.* 14,000-year-old Kopuatai (northern half is *c.* 7000 years old) (de Lange 1989, Newnham et al. 1995), *c.* 1800-year-old Whangamarino (Shearer 1997), and a now-destroyed *c.* 5000-year-old bog located 115 km south-east of Kopuatai (Campbell et al. 1973). Bog development began with an initial phase dominated by sedges (e.g., *Carex* spp., *Baumea* spp.), with *Leptospermum scoparium* shrubs and *Gleichenia dicarpa* ferns being frequent associates and indicating drier conditions. The sedge phase lasted from some hundreds to several thousands of years, depending on the disturbance history (particularly flooding), and hydrologic and nutrient regimes of the site (Campbell et al. 1973, Newnham et al. 1995). The sedge phase was followed by the main restiad phase, and the evidence suggests that *Empodisma* preceded *Sporadanthus.* At three relatively young bogs at Whangamarino (*c.* 1800 years old) and two now-destroyed bogs south-east of Kopuatai (minimum age 2700 years), *Empodisma* was recorded but not *Sporadanthus* (Campbell et al. 1973, Shearer 1997, J. C. Shearer pers. comm. 1999). In older *Empodisma-Sporadanthus* bogs, interpretations of establishment patterns are necessarily based on macrofossil data because *Empodisma* and *Sporadanthus* pollen are difficult to distinguish (Newnham et al. 1995). At Kopuatai (de Lange 1989), in both the old (*c.* 13,663 cal yr BP) and young (*c.* 7187 cal yr BP) parts of the bog, the first macrofossil records of *Empodisma* and *Sporadanthus* were each separated by two marker tephras (*c.* 9500 cal yr BP and *c.* 8050 cal yr BP in the 'old' bog, and *c.* AD 200 and *c.* AD 1350 in the 'young' bog; Lowe et al. 1999). This indicated a lag of at least 1100 years for *Sporadanthus* to establish after *Empodisma* was first recorded (de Lange 1989). The interpreted vegetation sequences and rates of change were therefore equivalent despite occurring under differing climatic regimes—warm, wet and drought-free for the earlier period and warm and dry for the later period (Newnham et al. 1995).

2.3. METHODS

Vegetation Sampling

Sampling was carried out in late spring/early summer of 1997 and 1998. We selected sectors within each bog as being representative of the vegetation patterns across the bog and established transects therein from the margin to the center. Sampling plots were permanently marked using a 2-m wooden pole every 100 m (or 50 m in small bogs), and vegetation and peat were sampled. In the larger or more complex systems (e.g., Kopuatai, Whangamarino, and Opuatia), additional plots were sampled systematically at 50- or 100-m intervals in vegetation types poorly or unrepresented in the original sample. In very small, modified bogs having a single vegetation type (e.g., Te Mimiha, Lake Maratoto), only one or two plots were sampled. The total number of plots sampled was 69 (Table 2.1).

At each sampling location, a 2 m x 2 m plot was set out and canopy species cover assessed using a modified Braun-Blanquet cover scale (Mueller-Dombois and Ellenberg 1974):
1: <1%, 2: 1–5%, 3: 5–25%, 4: 25–50%, 5:50–75%, 6:75–100%.
The maximum height for each species and vascular and non-vascular plant species lists for each plot (full species list in Appendix 2.1) were also recorded.

Peat Sampling and Analysis

At each of the 69 sampling plots, we determined peat decomposition status using the qualitative von Post scale (von Post and Granlund 1926, Clymo 1983), with values ranging from 1 (least decomposed) to 10 (highly decomposed). This was assessed in the field by taking a handful of peat and squeezing; the consistency of the remaining peat and the color of squeeze water being compared against a scale of attributes. In other wetlands, simple measures of physical degree of decomposition of peat were shown to be at least as good as more complicated chemical analyses in predicting C, N, and P mineralization (Bridgham et al. 1998).

Two undisturbed cores were obtained from the surface layer of each plot by cutting steel liners (100-mm diameter by 75-mm deep) into the peat, which were then sealed in plastic bags. The peat was analyzed for pH, bulk density, ash content, total N, total P, total K, anaerobically mineralizable N, and H_2SO_4 extractable P. We chose to measure total pools of important nutrients (N, P, and K), and more available pools of N and P because fertilization studies in Northern Hemisphere wetlands revealed N, P, and occasionally K, to be the major limiting nutrients for plant growth (Bridgham et al. 1996, Verhoeven et al. 1996).

In the laboratory, one core was cut into cubes (1 cm^3) and stored at 4°C before being analyzed for pH, total N, and available N. 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. Total N was measured following Kjeldahl digestion of peat and analysis for ammonium using standard autoanalyzer 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 mineralization rate. Analysis of anaerobically mineralizable N involved placing field-moist peat (1 g dry weight equivalent) into 50-ml boiling tubes and adding 33 ml of water so that the peat was flooded with minimal head-space. The head-space was flushed with O_2-free N_2 before the tubes were sealed with rubber stoppers and incubated at 40°C for seven days. The contents were then transferred to a plastic extraction bottle (400 ml) and 50 ml of 4M KCl added. Extraction bottles were shaken for 1 h, filtered, and the extract analyzed for ammonium using standard autoanalyzer techniques (Blakemore et al. 1987). The ammonium concentration of the peat before incubation was similarly determined. Anaerobically mineralizable N was calculated as the difference between the final and initial concentration of ammonium.

The second core was analyzed for bulk density, ash content, total P, total K, and available P following Blakemore et al. (1987). Bulk density was measured gravimetrically following drying at 105°C. To measure the available pool of phosphorus, a sub-sample (0.5 g) of dried peat was extracted with 0.5M H_2SO_4 (100 ml) for 16 hours, and phosphate in the extract was determined using standard autoanalyzer techniques. We used H_2SO_4 (0.5M)-extraction, as preliminary work in this study demonstrated that less powerful extracts (e.g., Olsen P) gave very low and less consistent results (data not shown). Ash content was determined gravimetrically after dried peat was placed in a 500°C furnace. Total P and K of the ashed peat were determined following extraction with HCl (4 M) and using standard autoanalyzer and atomic adsorption techniques, respectively.

Data Analyses

Cover scores (mid-point percentages) for all 26 species recorded in the 69 plots were analyzed using classification (cluster analysis) and ordination techniques to define vegetation types and examine ecological gradients. The programs 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, 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 rather than squared input and output distances (Minchin 1987, Belbin 1995). In all analyses, we used the flexible Unweighted Pair-Group Method using Arithmetic averages (UPGMA) clustering method (with $\beta = -0.1$) 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).

The FUSE classification and SSH ordination analyses were repeated minus four plots dominated by non-native grey willow, as the species compositions of these four plots were atypical and resulted in a skewed ordination with high levels of stress. This left an essentially native species data set (= 65 plots, 25 species) in which natural bog development processes and species–environment relationships could be explored. A two-dimensional ordination with a stress value of 0.193 was considered to summarize the data adequately, as solutions of other dimensions (1D stress = 0.399, 3D stress = 0.126, 4D stress = 0.089) did not markedly change ecological interpretation.

The environmental data and plot ordination scores were then analyzed 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 of best fit for each of the environmental variables and the correlation in that direction.

Species–Environmental Models

To focus on autecology, canopy covers (midpoint percentages) of the dominant eight species were modeled as a function of five environmental variables, which were selected after screening for intervariable correlations. The species were *Baumea teretifolia*, *B. rubiginosa*, *Empodisma*, *Epacris pauciflora*, *Gleichenia dicarpa*, *Leptospermum scoparium*, *Salix cinerea*, and *Sporadanthus*, and the environmental variables were available N, pH, total K, total P, and von Post. Non-parametric regression techniques of Generalized Additive Models (GAMs: Hastie and Tibishirani 1990) were implemented in SPLUS (Venables and Ripley 1994) using a recently designed procedure and set of functions called GRASP (Lehmann et al. 2002). GAMs have the advantages over Generalized Linear Models (GLMs) of dealing better with non-linear responses and being completely data-defined (Yee and Mitchell 1991). This allows exploration of shapes of species response curves to environmental gradients and the fitting of statistical models in better agreement with ecological theory (Austin 2002).

Statistically significant environmental variables were selected for each species using a stepwise procedure and a logistic link function, as in Leathwick and Rogers (1996). Logistic models are used for modeling proportions, and the predictions are kept between 0 and 1 (then scaled from 0 to 100). Species response curves along each significant environmental gradient were then estimated by identifying the largest predicted cover (optimum combination of environmental variable values). This combination was then kept constant except for one variable incremented along a regular gradient between its minimum and its maximum observed value. Each species response curve could then be predicted from these created data sets.

2.4. RESULTS

Vegetation Classification and Peat Properties

The vegetation classification produced eight ecologically interpretable groups, whose characteristics are summarized in Table 2.2. The groups form a gradation from woody vegetation of modified bogs and bog margins (Groups 1 & 2), through sedge, fern, or *Empodisma*-dominated vegetation of young bogs and margins of older bogs (Groups 3–6), to restiad-dominated vegetation in central areas of old 'unmodified' bogs (Groups 7 & 8). Groups 3–8 therefore represent an age sequence from young to old bogs and reflect the paleoecological sequence described earlier for restiad bog succession.

The environmental data for the eight classification groups are presented in Figure 2.6 and Appendix 2.2 to show trends in peat properties along the putative successional gradient (i.e., from Group 3 through to Group 8). Many of the environmental variables were significantly (positively) correlated with each other (Table 2.3). With a few exceptions, nutrient levels and physical status of the peat decreased more or less sequentially from the early successional sedge and fern types to the late successional *Sporadanthus* restiad type (Figure 2.6). The greatest decreases were for von Post, % ash, total N, and total P. Group 1 (grey willow) and Group 2 (*Leptospermum scoparium*), which comprised plots from sites modified by fire, drainage, or weed invasion, had the highest values for most peat properties, especially available P and total N.

Plot Ordination

Figure 2.7 is a two-dimensional ordination of the 65-plot native species subset (i.e., excluding Group 1 grey willow plots), with vectors summarizing the relationships between species abundances and significant ($P<0.05$) environmental variables. The bog locations, dominant species at each plot, and the seven groups from the cluster analysis (Groups 2–8 of Figure 2.6) have been overlaid on the ordination to indicate floristic trends. The plots are in a sequence along Axis 2,

Table 2.2 Summary of vegetation characteristics of classification groups. Means with standard deviations in parentheses are given for the total species (vascular and non-vascular) number, maximum vegetation height, and cover midpoint values for the 10 most common species.

Group	1	2	3	4	5	6	7	8
Vegetation type	*Salix cinerea*	*Leptospermum scoparium*	*Baumea rubiginosa-Gleichenia dicarpa*	*Baumea teretifolia*	*Baumea teretifolia-Empodisma minus*	*Empodisma minus*	*Epacris pauciflora-Empodisma minus*	*Sporadanthus ferrugineus*
Code	Sal	Lep	Br-Gle	Bt	Bt-Emp	Emp	Epa-Emp	Spo
Number of plots	4	8	5	2	14	22	5	9
Total species number	10.25 (2.75)	6.75 (3.06)	5.40 (2.07)	6.50 (2.12)	6.93 (1.94)	8.14 (2.77)	8.40 (3.51)	5.89 (3.14)
Vascular species number	10.25 (2.75)	6.50 (2.67)	5.40 (2.07)	5.50 (0.71)	6.29 (1.07)	6.23 (1.11)	5.60 (1.67)	4.78 (1.64)
Nonvascular species number	0.0 (0.0)	0.25 (0.46)	0.0 (0.0)	1.00 (1.41)	0.64 (1.15)	1.91 (2.05)	2.8 (2.59)	1.11 (1.69)
Vegetation height (m)	8.50 (1.29)	3.72 (1.21)	1.94 (0.28)	1.45 (0.14)	1.68 (0.25)	1.57 (0.52)	1.96 (0.61)	2.48 (0.53)
Baumea rubiginosa cover	0.0 (0.0)	0.38 (1.06)	36.4 (32.56)	1.5 (2.12)	2.79 (5.32)	0.82 (3.23)	0.0 (0.0)	0.0 (0.0)
Baumea teretifolia cover	0.0 (0.0)	0.0 (0.0)	0.60 (1.34)	75.00 (18.39)	33.14 (13.48)	6.00 (7.05)	0.0 (0.0)	0.0 (0.0)
Empodisma minus cover	0.0 (0.0)	6.63 (13.72)	7.6 (16.99)	0.0 (0.0)	33.64 (11.46)	66.82 (12.81)	28.80 (12.60)	17.11 (13.17)
Epacris pauciflorus cover	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.21 (0.80)	2.68 (8.53)	30.6 (23.85)	8.89 (12.34)
Gleichenia dicarpa cover	0.0 (0.0)	0.38 (1.06)	40.00 (25.38)	7.50 (10.61)	14.93 (7.93)	10.59 (9.05)	0.60 (1.34)	2.33 (4.92)
Leptospermum scoparium cover	0.0 (0.0)	78.25 (13.46)	6.60 (7.77)	1.50 (2.12)	16.29 (13.07)	5.05 (6.370	6.60 (7.77)	1.00 (1.50)
Salix cinerea cover	81.50 (13.00)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	3.46 (11.81)	0.0 (0.0)	0.0 (0.0)
Schoenus brevifolius cover	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	26.5 (16.26)	1.71 (4.03)	2.18 (4.36)	3.00 (6.71)	0.0 (0.0)
Sporadanthus ferrugineus cover	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.36 (4.41)	10.60 (16.64)	67.78 (11.47)
Tetraria capillaris cover	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.71 (4.03)	0.68 (3.20)	0.0 (0.0)	0.0 (0.0)

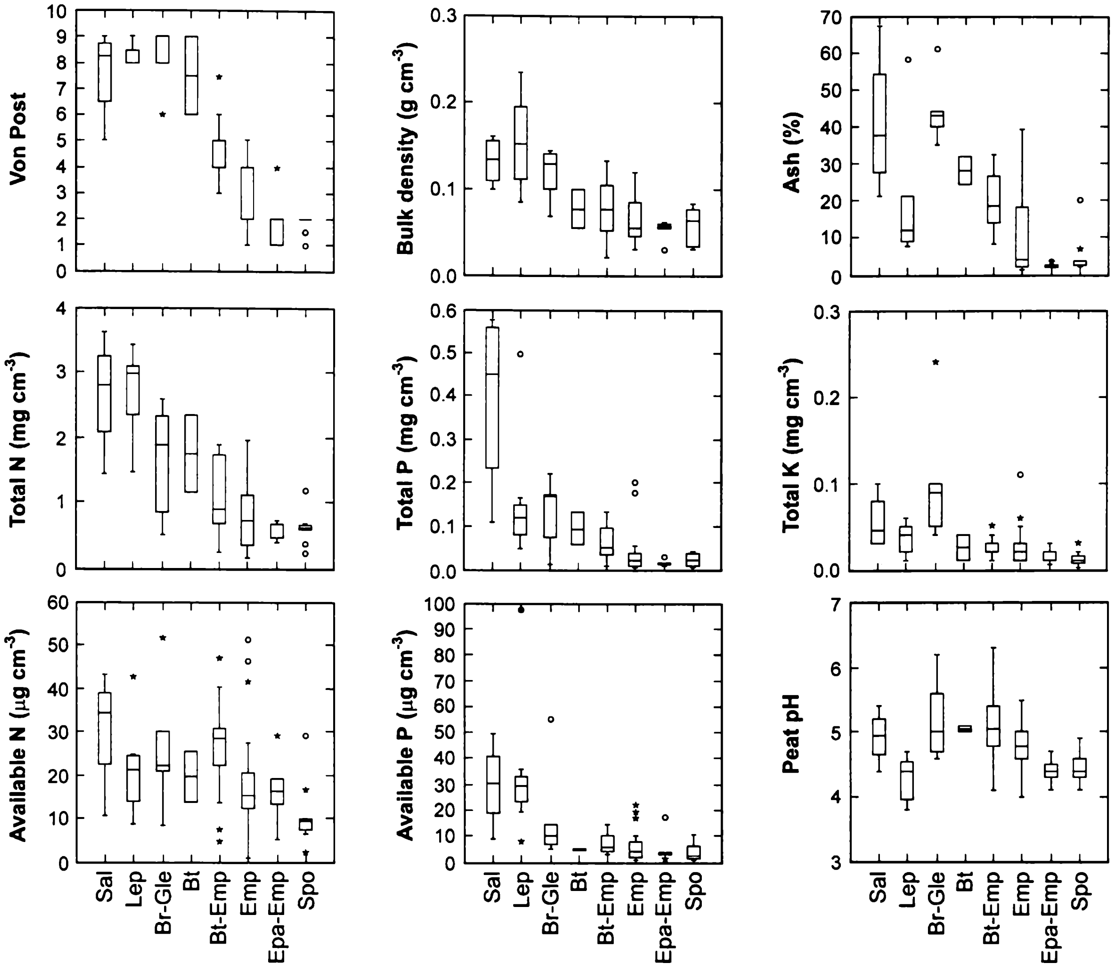

Figure 2.6 Box plot summary (using SYSTAT version7; Wilkinson 1997) showing medians, and upper and lower quartiles, for environmental data in each of eight vegetation types determined from the cluster analysis (see Table 2.2). Vegetation types: Sal = *Salix cinerea,* Lep = *Leptospermum scoparium,* Br-Gle = *Baumea rubiginosa-Gleichenia dicarpa*, Bt = *Baumea teretifolia*, Bt-Emp = *Baumea teretifolia-Empodisma minus*, Emp-Emp = *Epacris pauciflora-Empodisma minus,* Spo = *Sporadanthus ferrugineus.*

from those dominated by sedges and/or fern, through those dominated by *Empodisma*, to those in which *Sporadanthus* predominate, generally reflecting bog age. Plots dominated by *Leptospermum scoparium*, with strongly negative loadings on Axis 1, represent modified sites that either once supported the *Sporadanthus* restiad bog type (Lake Maratoto, Te Mimiha, Moanatuatua North) or occur on bog margins (Whangamarino, Kopuatai, Moanatuatua). *Leptospermum scoparium* also occurs as a co-dominant with *B. teretifolia* and *Empodisma* in the early successional sequence represented on Axis 2. *Leptospermum*-dominated plots are associated with high levels of TN, TP, available P, and high bulk density. Sedge- and/or fern-dominated plots are associated with relatively high ash content, high pH, high peat decomposition, and

Von Post	0.13	1							
Bulk density	-0.22	0.73**	1						
Ash content	0.39	0.75**	0.62**	1					
Total N	-0.21	0.81**	0.89**	0.62**	1				
Total P	-0.03	0.59**	0.71**	0.67**	0.80**	1			
Available P	-0.08	0.56**	0.74**	0.52**	0.61**	0.70**	1		
Total K	0.18	0.43*	0.46**	0.59**	0.29	0.33	0.50**	1	
Available N	0.27	0.40*	0.28	0.36	0.29	0.27	0.15	0.27	1

Table 2.3 Pearson correlations between environmental data using a Bonferroni adjustment for multiple comparisons. ** $P < 0.01$, * $P < 0.05$.

high levels of total K and available N. Conversely, restiad (*Empodisma, Sporadanthus*) and *Epacris*-dominated plots have relatively low levels of all these environmental variables.

Species–Environmental Profiles

The predicted species:environmental response curves separated the eight dominant species in relatively similar orders along nutrient and decomposition gradients (Figure 2.8). By calculating the amount of deviance explained by each environmental variable on its own and averaging across the eight species, the variables were ranked in the following order of contribution: von Post > total P > total K > pH > available N. The von Post response curve predicted that, in areas of low peat decomposition such as relatively unmodified ombrotrophic sites, *Sporadanthus, Epacris*, and *Empodisma* will dominate, and where peat is more decomposed, such as in minerotrophic and/or disturbed sites, grey willow, *Baumea rubiginosa*, and *Leptospermum* will dominate. The total P response curves indicated that most species achieve maximum cover at very low total P levels. Three exceptions were grey willow, which is predicted to dominate at high total P levels; *Leptospermum*, which had relatively high cover at all levels; and *Baumea rubiginosa*, which was most abundant at intermediate levels.

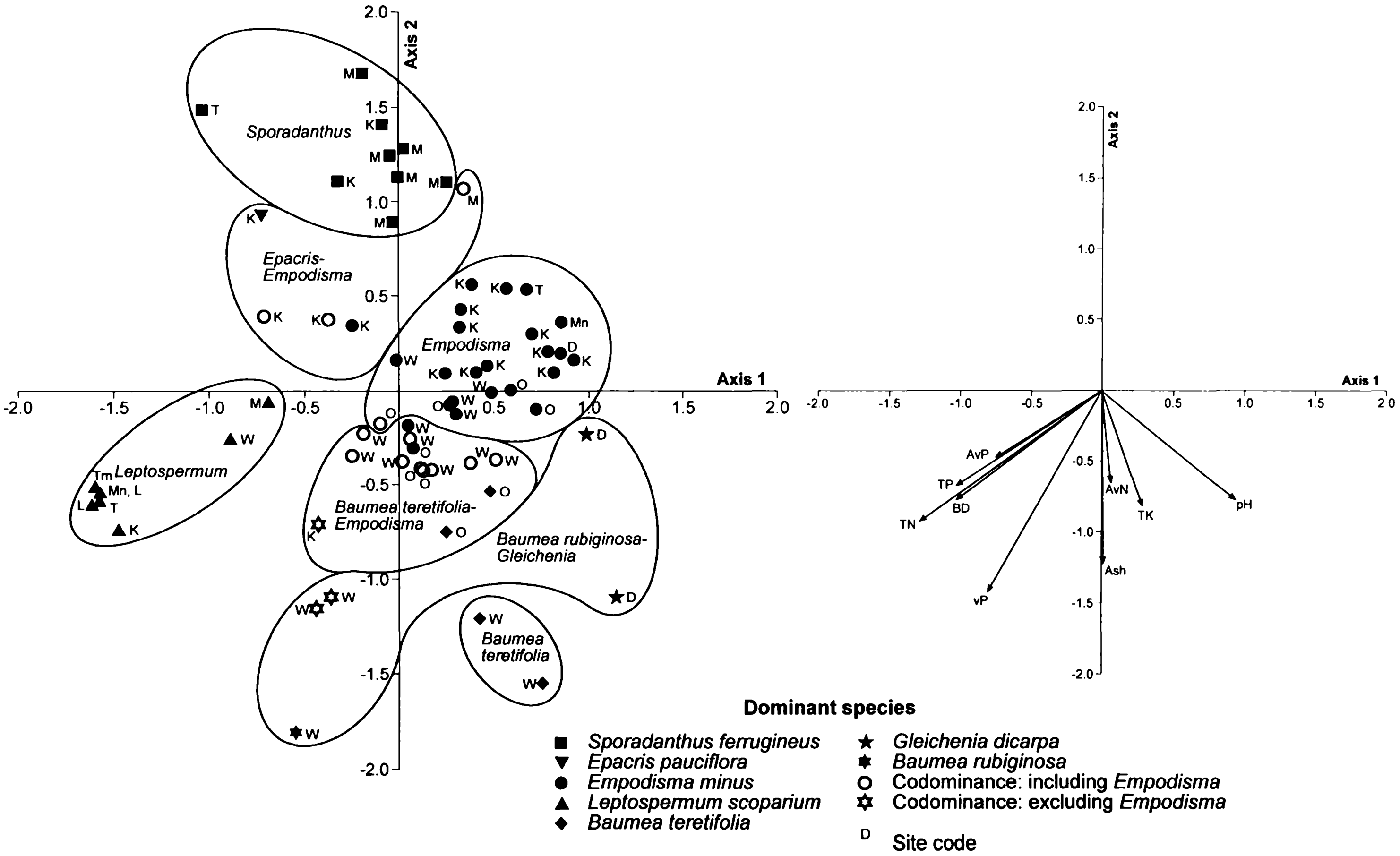

Figure 2.7 Two-dimensional ordination of 65 plots based on canopy cover of 25 species (=native plant species data set), and significant ($P<0.05$) fitted vectors for environmental variables. The vegetation types, bog locations, and dominant species for each plot have been superimposed. The length of vector indicates degree of correlation. Bog locations are: D = Duck Creek, L = Lake Maratoto, K = Kopuatai, M = Moanatuatua, Mn = Moanatuatua North, O = Opuatia, T = Torehape, Tm = Te Mimiha, W = Whangamarino. The environmental variables are: AvP = available P, AvN = available N, BD = bulk density, TK = total potassium, TN = total nitrogen, TP = total phosphorus, vP = von Post.

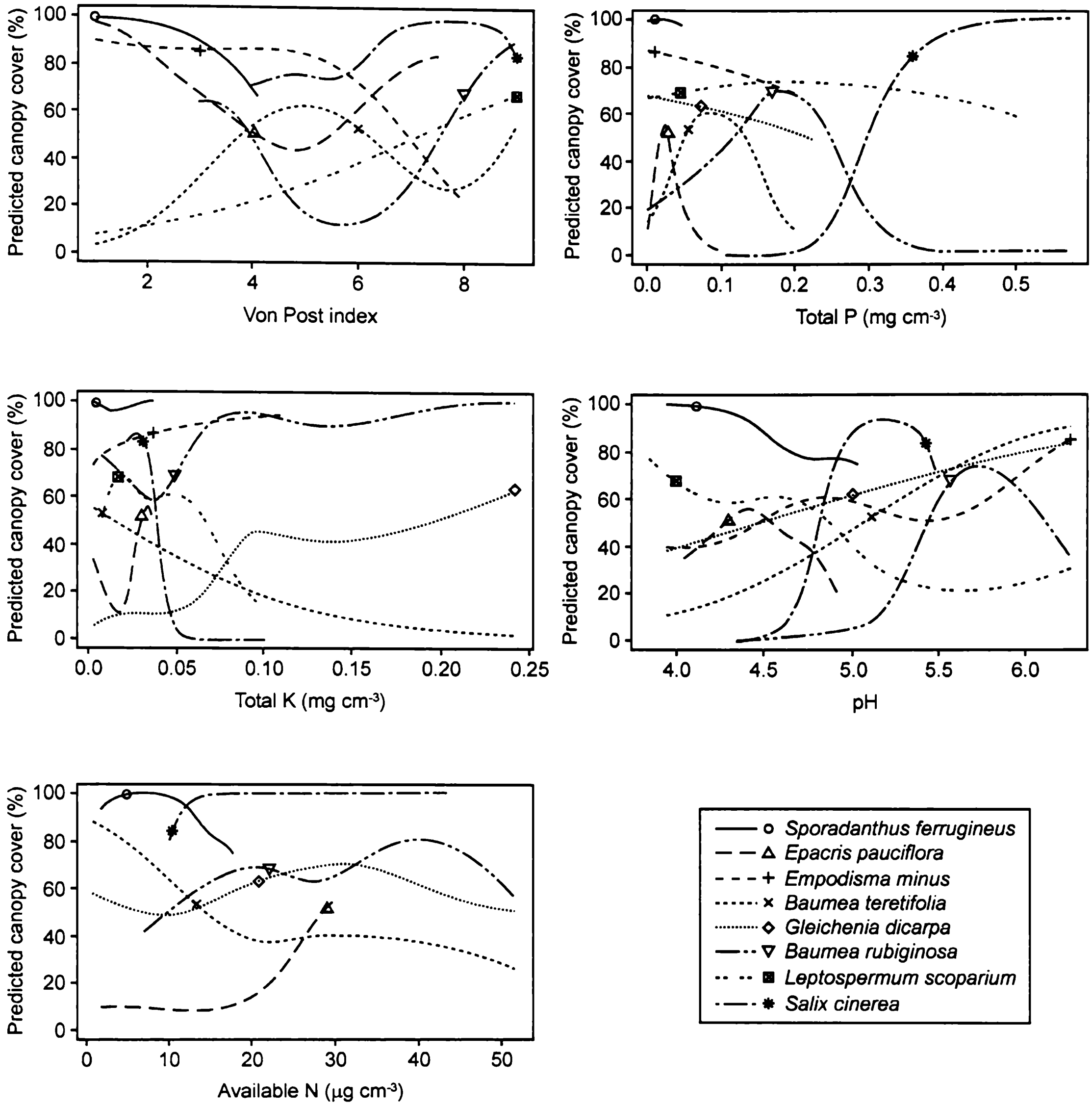

Figure 2.8 Fitted proportional covers for the dominant species in relation to von Post, Total P, Total K, pH, and Available N (based on 67 plots having no missing values). The curves were constructed for each environmental variable while setting values for remaining variables constant according to the optima at which maximum cover was predicted (symbols). The species-environment response curves are only within the distributional range of the species along each gradient. Missing species curves indicate the environmental variable was not significant in predicting cover for that species in the model.

Sporadanthus had the narrowest distributional range for all five environmental variables. It is predicted to be the cover dominant in areas of low pH, low peat decomposition, low total P, low total K, and low available N. *Epacris,* a common associate of *Sporadanthus* in ombrotrophic bogs, also had a relatively narrow environmental range, reaching maximum cover at low or relatively low pH, von Post, total P, and total K. *Empodisma* had a much wider environmental range than either *Sporadanthus* or *Epacris.* It is predicted to attain significant cover (i.e., greater than 40%) throughout the pH range at all but the very highest von

Post indices, at low and medium levels of total P, and at low and medium values of total K. The early successional native species, *Gleichenia, Baumea rubiginosa, B. teretifolia,* and *Leptospermum*, also had relatively wide environmental ranges, with maximum cover being concentrated at the medium to high portions of the decomposition, pH, and nutrient ranges.

2.5. DISCUSSION

Relationship Between Spatial Chronosequence and Temporal Succession

The results of the classifications and ordinations indicate the vegetation patterns evident in young to old bogs within the Waikato region (from early successional sedges, through mid-successional *Empodisma*, to late successional *Sporadanthus*) closely parallel the developmental sequence over time as interpreted from micro- and macrofossil records (Cranwell 1953, Campbell et al. 1973, de Lange 1989, Newnham et al. 1995, Shearer 1997). The successional sequence is also observed in adjacent concentric zones on margins of laterally expanding intact bogs where inner parts of the bog are older than the outer reaches. Although the use of spatial patterns to infer temporal sequences is problematic (Miles 1979, Tallis 1983, Jackson et al. 1988, Hughes and Barber 2003), we have demonstrated similarity with antecedent plant communities. In addition, different aged bogs underwent the successional changes at different times in their history, so common changes in vegetation pattern cannot be attributed to climatic or tectonic events alone. On this basis, we have assumed that the range of vegetation and peat characteristics inherent in Waikato extant restiad bogs is representative of major phases of bog development evident in the past.

Restiad bog succession is therefore summarized in three phases (Figure 2.9). Early successional pre-restiad states (Phase 1) are dominated by sedges (particularly *Baumea rubiginosa, B. teretifolia*), ferns (*Gleichenia dicarpa*), and occasional shrubs (particularly *Leptospermum scoparium*). The next phase (Phase 2) is establishment and dominance of the main peat-forming restiad, *Empodisma*, which is usually followed by colonization of minor amounts of the shrub, *Epacris.* Phase 3 is initiated by establishment of the much taller restiad species, *Sporadanthus*, which eventually becomes the physiognomic dominant. A

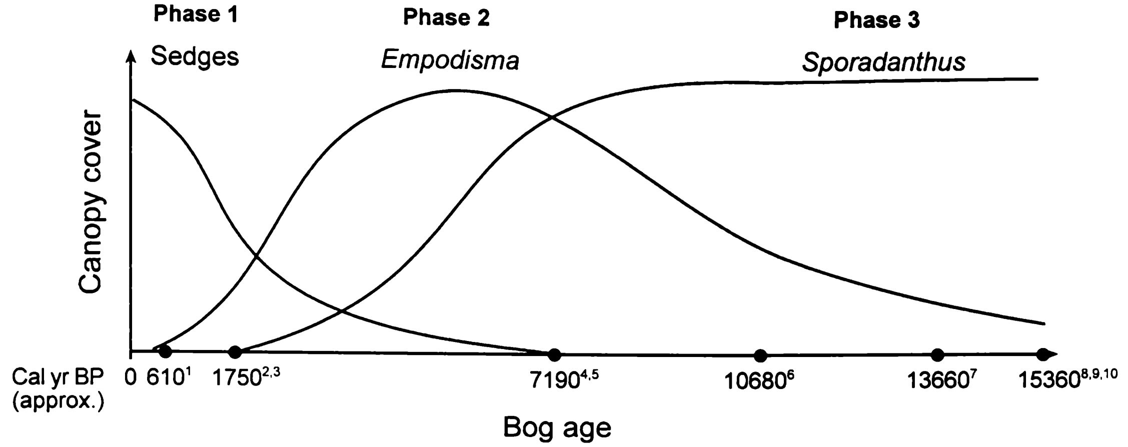

Figure 2.9 Schematic diagram showing species dominance over time during the development of restiad bogs. Ages were estimated from spatial sequence of different-aged extant bogs. 1 = Duck Creek, 2 = Whangamarino, 3 = Opuatia, 4 = Torehape, 5 = Kopuatai (northern part), 6 = Lake Maratoto, 7 = Kopuatai (southern, main part), 8 = Te Mimiha, 9 = Moanatuatua North, 10 = Moanatuatua.

time frame is estimated for rates of vegetation change based on spatial patterns of different-aged bogs (Figure 2.9). Comparing temporal and spatial rates of change is problematic because of the dearth of temporal data available; however, the historical evidence available shows they are similar. The length of time Phase 1 persists is largely dependent on disturbance events and local hydrologic and nutrient characteristics (Newnham et al. 1995). The timing of Phase 2 to Phase 3 requires some interpolation of the data available. *Sporadanthus* is not yet present at *Empodisma*-dominated Whangamarino (Shearer 1997, J. C. Shearer pers. comm. 1999). However, at similar-aged Opuatia (*c.* 1800 years old), four small *Sporadanthus* individuals were recently recorded (University of Waikato herbarium voucher: WAIK 6568, *P. J. de Lange* 1986), indicating environmental conditions there are now becoming suitable for its establishment, but it will be some time before it is dominant. Indeed, these *Sporadanthus* plants could not be subsequently relocated, and *Sporadanthus* is apparently absent from this bog at present. The estimated time taken for *Sporadanthus* to establish in *Empodisma* vegetation (Phase 3) at Opuatia therefore accords with the time period interpreted from peat cores (>1100 years). However, this model is presented only as a preliminary attempt to quantify rates of temporal change within ecosystems confined to an ecologically similar region. We currently have insufficient data available to refine the model further or reject it.

Environmental Determinants of Vegetation Patterns and Dynamics

The relationships between environmental variables and the six groups representing natural restiad bog succession (Groups 3–8) indicate that, as succession proceeds, total and available nutrient contents decrease, and peat becomes increasingly less decomposed (Figures 2.6 and 2.7). In other studies of bog development in which peat nutrient content (as opposed to water chemistry) has been measured, trends have been relatively variable (Mitsch and Gosselink 2000). For example, Bridgham et al. (1998, 2001) found that N mineralization and peat decomposition decreased along a minerotrophic-ombrotrophic gradient in Minnesota wetlands, U.S.A. The trend for P mineralization was less convincing, although P availability was generally greater in minerotrophic swamp forests and beaver meadows than *Sphagnum* bogs (Bridgham et al. 2001). In The Netherlands, Verhoeven et al. (1990) showed that minerotrophic (phanerogam) fens had greater decomposition rates than ombrotrophic (*Sphagnum*) bogs but lower N and P mineralization. There were no clear patterns for total N and total P except that both were relatively high in two fen sites and particularly low in two bog sites. Vitt and Chee (1990) found no trends in total P or total K along a gradient of poor (*Sphagnum*-dominated) to rich fens (characterized by brown mosses and sedges) in Alberta wetlands, Canada. In the Southern Hemisphere, in Whangamarino Wetland, New Zealand, total P and peat decomposition decreased with increasing bog (*Empodisma*) community development (Shearer and Clarkson 1998). In contrast to our current study, however, there was no apparent trend for total N. This might be because, being relatively young, Whangamarino is only at early *Empodisma* phase (= Phase 2), whereas in the current study, we investigated a chronosequence of bogs ranging from a few hundred to several thousand years old.

The changes in nutrient and peat decomposition status in this study coincide with the general concepts of wetland development in North America (Zoltai and Vitt 1995) except that *Empodisma* and *Sporadanthus* rather than *Sphagnum* dominate later stages. During development, peat accumulates, increasingly isolating the peat surface from local ground water, and nutrient inputs decrease. Changes in nutrient status and the state of peat decomposition through wetland development are likely to be interlinked. Plants may respond to low nutrient supply by having lower concentrations of nutrients in their tissues, withdrawing greater amounts of nutrients during senescence, and/or producing substances to inhibit herbivores and microbial activity (such as lignins, tannins and other polyphenols; Given and Dickinson 1975, Chapin et al. 1986, Pastor et al. 2002, Malmer et al. 2003). These responses are likely to slow litter decomposition and produce less degraded peat. Ombrotrophic bogs receive nutrient inputs entirely from the atmosphere, and if nutrients are entrapped during peat formation at a faster rate than replacement through atmospheric inputs, then nutrient availability will decrease. For nitrogen, denitrification can also deplete the N pool. *Empodisma*, the main peat former in restiad bogs, has been shown to contain high proportions of lignin and polyphenols, including tannins and phenolic acids (Kuder et al. 1998). The phenolic compounds show allelopathic properties, which Kuder et al. (1998) suggest may facilitate exclusion of other species. This mechanism allowing *Empodisma* to enhance its local environment is analogous to *Sphagnum* in Northern Hemisphere wetlands, which decreases competition by release of toxic organochemicals and soil acidification (van Breemen 1995, Verhoeven and Liefveld 1997).

Peat pH trends through restiad bog development were less obvious, although pH was generally lower (but not significantly) at the final two stages of succession where *Sporadanthus* was present. Studies of Northern Hemisphere peatlands have revealed changes in vegetation to be more closely linked to changes in pH (e.g., Vitt and Chee 1990, Wheeler and Proctor 2000). In these studies, however, peatlands had a much broader pH range than in our study; New Zealand lacks a high pH, rich fen equivalent (Thompson 1987) because nutrient-rich limestone formations are very limited in extent.

Highly modified peat bogs dominated by non-peat-forming grey willow and *Leptospermum* were characterized by greater peat decomposition, bulk density, and nutrients than relatively unmodified peat bogs. This indicates that anthropogenic changes such as drainage and burning probably accelerate peat degradation and nutrient release, thereby providing conditions suitable for taller, woody species that can potentially alter natural successional pathways (Clarkson 1997, Shearer and Clarkson 1998). Some disturbances may be temporary (e.g., at

Whangamarino, sedges dominated for four years after fire before *Empodisma* was able to re-assert dominance) (Clarkson 1997), but others are more permanent (e.g., removal of fire-sensitive restiad populations). The potential for restoration of a modified site may be assessed by measuring peat nutrient and decomposition status and relating this to the environmental requirements of the desired species. This will indicate how far habitat conditions have diverged from the 'original' condition and thus whether re-introduction of the extirpated species is likely to be successful. For example, peat nutrient and decomposition data (available N = 14.57 μg cm^{-3}, total K = 0.01 mg cm^{-3}, total P = 0.037 mg cm^{-3}, pH = 4.3, von Post = 2) at *Empodisma*-dominated Moanatuatua North sites indicate that conditions should still be suitable for the former dominant, *Sporadanthus*, if it were re-introduced to the area.

Species–Environmental Relationships

The results showed that the main bog species have relatively distinctive environmental profiles, which essentially separate along the proposed restiad bog developmental gradient. Three species emerged as overwhelmingly dominant (optimal canopy cover >85%) in the developmental sequence: grey willow in high nutrient early successional stages; *Empodisma* characteristic of medium nutrient, mid-successional stages; and *Sporadanthus* in low nutrient, late succession. The non-native tree, grey willow, is predicted to dominate on sites where peat decomposition, total P, and available N are relatively high, and pH is moderate. These sites are typically associated with "young" restiad bogs and on margins of older bogs. Grey willow is also widespread and a major weed problem in minerotrophic wetlands, which were not sampled in this study. The models for grey willow are therefore presented with caution, as predictions are based on limited data collected from only that part of its distributional range that overlapped with restiad bog ecosystems.

Early successional pre-restiad species (e.g., *Baumea rubiginosa, B. teretifolia*, and *Gleichenia dicarpa*) have much wider potential environmental ranges than the late successional *Sporadanthus* and *Epacris pauciflora,* whose ranges are comparatively narrow. Species interactions and competition in the field may further define or compress (or both) expression of this range. *Empodisma*, the first restiad species to establish, can potentially grow in a wide range of environmental conditions, from the relatively high nutrient, minerotrophic end of the gradient, through to late successional stages in which it is still important but subdominant to *Sporadanthus*. These results suggest that competition is important in determining species dominance during bog development. Early successional and mid-successional species can tolerate a wide range of environmental conditions, but they are outcompeted, initially by *Empodisma*, which in turn is overtopped by *Sporadanthus.* Although the latest developmental stage represented in our spatial sequence is dominated by *Sporadanthus*, *Empodisma* is still present, albeit relegated to a lower canopy layer or, more commonly, to the understory.

Empodisma can be considered as having a key role in the development of restiad bogs. It is the main peat former, having masses of upward-growing fine roots and root hairs (cluster roots) with high water-holding capacity (Campbell 1964), a similar base-exchange capacity to *Sphagnum* (Agnew et al. 1993), and has high proportions of decay-resistant lignins and allelopathic chemicals in its tissues (Kuder et al. 1998). In addition, *Empodisma* has both physiological and structural adaptations that enable it to control plant transpiration and canopy evaporation in an environment characterized by seasonal water deficits (Campbell and Williamson 1997). Stomatal control of transpiration, reduction of leaves to scale-like sheaths, and production of a dense mulch-like vegetative cover contribute to exceptionally low daily evaporation rates of *Empodisma*-dominated canopy, which are about half the evaporation rates reported for other wetlands dominated by vascular plants (Campbell and Williamson 1997, Thompson et al. 1999). In our study, we demonstrated that *Empodisma* is tolerant of a wide environmental range, is thus potentially able to establish early in relatively fertile minerotrophic wetlands to initiate restiad bog development, and can persist in significant amounts through to late developmental ombrotrophic phases. An initial *Empodisma* phase is apparently a necessary precursor to establishment of the late developmental phase bogs in which the second, taller restiad, *Sporadanthus,* becomes the physiognomic dominant.

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2.7. LITERATURE CITED

Agnew, A. D. Q., G. L. Rapson, M. T. Sykes, and J. B. Wilson. 1993. The functional ecology of *Empodisma minus* (Hook.f.) Johnson and Cutler in New Zealand ombrotrophic mires. New Phytologist 124:703-710.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological Modeling 157:101-118.

Belbin, L. 1995. PATN: Pattern analysis package. Technical reference. CSIRO Division of Wildlife and Ecology, Canberra, Australia.

Blakemore, L. C., P. L. Searle, and B. K. Daly. 1987. Methods for chemical analysis of soils. Department of Scientific and Industrial Research, Lower Hutt, New Zealand. New Zealand Soil Bureau Scientific Report 80.

Bridgham, S. D., J. Pastor, J. A. Janssens, C. Chapin, and T. J. Malterer. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. Wetlands 16:45-65.

Bridgham, S. D., K. Updegraff, and J. Pastor. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology 79:1545-1561.

Bridgham, S. D., K. Updegraff, and J. Pastor. 2001. A comparison of nutrient availability indices along an ombrotrophic-minerotrophic gradient in Minnesota wetlands. Soil Science Society of America Journal 65:259-269.

Campbell, D. I. and J. L. Williamson. 1997. Evaporation from a raised peat bog. Journal of Hydrology 193:142-160.

Campbell, E. O. 1964. The restiad peat bogs at Motumaoho and Moanatuatua. Transactions of the Royal Society of New Zealand, Botany 2:219-227.

Campbell, E. O., J. C. Heine, and W. A. Pullar. 1973. Identification of plants fragments and pollen from peat deposits in Rangitaiki Plains and Maketu Basins. New Zealand Journal of Botany 11:317-330.

Chapin, F. S. III, P. M. Vitousek, and K. van Cleve. 1986. The nature of nutrient limitation in plant communities. The American Naturalist 127:48-58.

Clarkson, B. R. 1997. Vegetation recovery following fire in two Waikato peatlands at Whangamarino and Moanatuatua. New Zealand Journal of Botany 35:167-179.

Clarkson, B. R., K. Thompson, L. A. Schipper, and M. McLeod. 1999. Moanatuatua Bog - proposed restoration of a New Zealand restiad peat bog ecosystem. p. 127-137. *In* W. Streever (ed.) An International Perspective on Wetland Rehabilitation. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Clymo, R. S. 1983. Peat. p.159-224. *In* A. J. P. Gore (ed.) Ecosystems of the World 4A Mires: Swamp, Bog, Fen and Moor. Elsevier Scientific Co., Amsterdam, The Netherlands.

Cole, C. A. 1999: Ecological theory and its role in the rehabilitation of wetlands. p. 265-275. *In* W. Streever (ed.) An International Perspective on Wetland Rehabilitation. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cranwell, L. M. 1939. Native vegetation. New Zealand Department of Scientific and Industrial Research Bulletin 76:23-30.

Cranwell, L. M. 1953. An outline of New Zealand peat deposits. Proceedings of the Seventh Pacific Science Congress 5:186-298.

Damman, A. W. H. 1988. Regulation of nitrogen removal and retention in *Sphagnum* bogs and other peatlands. Oikos 51:291-305.

de Lange, P. J. 1989. Late Quaternary development of the Kopuatai peat bog, Hauraki lowlands, and some palaeoenvironmental inferences. M.Sc. Dissertation. University of Waikato, Hamilton, New Zealand.

de Lange, P. R., P. B. Heenan, B. D. Clarkson, and B. R. Clarkson. 1999. *Sporadanthus* in New Zealand. New Zealand Journal of Botany 37:413-431.

Dickinson, K. J. M., C. Chague-Goff, A. F. Mark, and L. Cullen. 2002. Ecological processes and trophic status of two low-alpine patterned mires, south-central South Island, New Zealand. Austral Ecology 27:369-384.

Dobson, A. T. 1979. Mire types of New Zealand. p. 82-95. *In* E. Kivinen, L. Heikurainen, and P. Pakarinen (eds.) Proceedings of the International Symposium on Classification of Peat and Peatlands. International Peat Society, Hyyttala, Finland.

Faith, D. P., P. R Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57-68.

Given, P. H. and C. H Dickinson. 1975. Biochemistry and microbiology of peats. p. 123-212. *In* E. A. Paul and A. D. McLaren (eds.) Soil Biochemistry, Vol 3. Marcel Dekker, New York, NY, USA.

Gore, A. J. P. (ed.). 1983. Mires: Swamp, Bog, Fen and Moor. Ecosystems of the World 4A. Elsevier Scientific Co., Amsterdam, The Netherlands.

Grange, L. I., N. H. Taylor, C. F. Sutherland, J. K. Dixon, L. Hodgson, and F. T. Seelye. 1939. Soils. New Zealand Department of Scientific and Industrial Research Bulletin 76:30-63.

Green, J. D. and D. J. Lowe. 1985. Stratigraphy and development of *c.* 17 000 year old Lake Maratoto, North Island, New Zealand, with some inferences about postglacial climatic change. New Zealand Journal of Geology and Geophysics 28:675-699.

Hastie, T. J. and R. J. Tibishirani. 1990. Generalized Additive Models. Chapman and Hall, London, UK.

Hogg, A. G., D. J. Lowe, and C. H. Hendy. 1987. University of Waikato radiocarbon dates I. Radiocarbon 29:263-301.

Hughes, P. D. M. and K. E. Barber. 2003. Mire development across the fen-bog transition on the Teifi floodplain at Tregaron Bog, Ceredigion, Wales, and a comparison with 13 other raised bogs. Journal of Ecology 91:253-264.

Jackson, S. T., R. P. Futyma, and D. A. Wilcox. 1988. A paleoecological test of a classical hydrosere in the Lake Michigan dunes. Ecology 69:928-936.

Judd, W. S., C. S. Campbell, E. A. Kellogg, and P. F. Stevens. 1999. Plant Systematics: a Phylogenetic Approach. Sinauer Associates, Sunderland, MA, USA.

Keddy, P. A. 2000. Wetland Ecology: Principles and Conservation. University Press, Cambridge, UK.

Keeney, D. R. 1982. Nitrogen-availability indices. p. 711-735. *In* A. L. Page (ed.) Methods of Soil and Plant Analysis: Part 2. Chemical and Microbiological Properties, second edition. Soil Science Society of America, Madison, WI, USA.

Kuder, T., M. A. Kruge, J. C. Shearer, and S. L. Miller. 1998. Environmental and botanical controls on peatification-a comparative study of two New Zealand restiad peat bogs using Py-GC/MS, petrography and fungal analysis. International Journal of Coal Geology 37:3-27.

Leathwick, J. R., B. D. Clarkson, and P. T. Whaley. 1995. Vegetation of the Waikato Region: current and historical perspectives. Environment Waikato, Hamilton, New Zealand. Landcare Research Contract Report no. LC9596/022.

Leathwick, J. R. and G. M. Rogers. 1996. Modeling relationships between environment and canopy composition in secondary vegetation in Central North Island, New Zealand. New Zealand Journal of Ecology 20:147-161.

Lehmann, A., J. McC. Overton, and J. R. Leathwick. 2002. GRASP: Generalized Regression Analysis and Spatial Prediction. Ecological Modeling 157:187-205.

Lowe, D. J. and W. P. de Lange. 2000. Volcano-meteorological tsunamis, the *c.* AD 200 Taupo eruption (New Zealand) and the possibility of a global tsunami. The Holocene 10:401-407.

Lowe, D. J. and J. D. Green. 1992. Lakes. p. 107-143. *In* J. M. Soons and M. J. Selby (ed.) Landforms of New Zealand, second edition. Longman Paul, Auckland, New Zealand.

Lowe, D. J., R. M. Newnham, and C. M. Ward. 1999. Stratigraphy and chronology of a 15 ka sequence of multi-sourced silicic tephras in a montane peat bog, eastern North Island, New Zealand. New Zealand Journal of Geology and Geophysics 42:565-579.

Malmer, N., C. Albinson, B. M. Svensson, and B. Wallen. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100:469-482.

McGlone, M. S. and N. W. Topping. 1977. Aranuian (post-glacial) pollen diagrams from the Tongariro region, North Island, New Zealand. New Zealand Journal of Botany 15:749-760.

Meney, K. A. and J. S. Pate (eds.). 1999. Australian Rushes: Biology, Identification and Conservation of Restionaceae and Allied Families. University of Western Australia Press, Nedlands, Western Australia, Australia.

Miles, J. 1979. Vegetation Dynamics. Chapman and Hall, London, UK.

Minchin, P. R. 1987. An evaluation of the robustness of techniques for ecological ordination. Vegetatio 69:89-107.

Mitsch, W. J. and J. G. Gosselink. 2000. Wetlands, third edition. John Wiley & Sons, New York, NY, USA.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York, NY, USA.

New Zealand Meteorological Service 1973: Summaries of climatological observations to 1970. New Zealand Meteorological Service miscellaneous publication 143.

Newnham, R. M., P. J. de Lange, and D. J. Lowe. 1995. Holocene vegetation, climate and history of a raised bog complex, northern New Zealand based on palynology, plant macrofossils and tephrochronology. The Holocene 5:267-282.

Pastor, J., B. Peckham, S. Bridgham, J. Weltzin, and J. Chen. 2002. Plant community dynamics, nutrient cycling, and alternative stable equilibria in peatlands. The American Naturalist 160:553-568.

Schipper, L. A., B. R. Clarkson, M. Vojvodic-Vukovic, and R. Webster. 2002. Restoring cut-over peat bogs: a factorial experiment of nutrients, seeds and cultivation. Ecological Engineering 19:29-44.

Schipper, L. A., M. McLeod, B. R. Clarkson, M. Vojvodic-Vukovic, and M. Taylor. 1998. Gradients of microbial biomass, anaerobically mineralizable N and some physical properties in a restiad peat bog. International Peat Journal 8:71-75.

Shearer, J. C. 1997. Natural and anthropogenic influences on peat development in Waikato/Hauraki Plains restiad bogs. Journal of the Royal Society of New Zealand 27:295-313.

Shearer, J. C. and B. R. Clarkson. 1998: Whangamarino Wetland: effects of lowered river levels on peat and vegetation. International Peat Journal 8:52-65.

Sorrell, B. K., I. A. Mendelssohn, K. L. McKee, and R. A. Woods. 2000. Ecophysiology of wetland plant roots: a modeling comparison of aeration in relation to species distribution. Annals of Botany 86:675-685.

Stuiver, M., P. J. Reimer, E. Bard, J. W. Beck, G. S. Burr, K. A. Hughen, B. Kromer, G. McCormac, J. van der Plicht, and M. Spurk. 1998. INTCAL98 radiocarbon age calibration, 24,000-0 cal BP. Radiocarbon 40:1041-1083.

Tallis, J. H. 1983. Changes in wetland communities. p. 311-347. *In* A. J. P. Gore (ed.) Ecosystems of the World 4A Mires: Swamp, Bog, Fen and Moor. Elsevier Scientific Co., Amsterdam, The Netherlands.

Thompson, K. 1987. Annotated bibliography of New Zealand peat and peatlands. National Water and Soil Conservation Authority, Water and Soil Directorate, Ministry of Works and Development, Wellington, New Zealand. Water and Soil Miscellaneous Publications No. 114.

Thompson, M. A., D. I. Campbell, and R. A. Spronken-Smith. 1999. Evaporation from natural and modified raised peat bogs in New Zealand. Agricultural and Forest Meteorology 95:85-98.

van Breemen, N. 1995. How *Sphagnum* bogs down other plants. Trends in Ecology & Evolution 10:270-275.

van der Valk, A. G. 1998. Succession theory and restoration of wetland vegetation. p. 657-667. *In* A. J. McComb and J. A. Davis (eds.) Wetlands for the Future. Gleneagles Publishing, Adelaide, Australia.

Venables, W. N. and B. D. Ripley. 1994. Modern Applied Statistics with S-PLUS. Springer-Verlag, New York, NY, USA.

Verhoeven, J. T. A., W. Koerselmann, and A. F. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology & Evolution 11:494-497.

Verhoeven, J. T. A. and W. M. Liefveld. 1997. The ecological significance of organochemical compounds in *Sphagnum*. Acta Botanica Neerlanddica 46:117-130.

Verhoeven, J. T. A., E. Maltby, and M. B. Schmitz. 1990. Nitrogen and phosphorus mineralization in fens and bogs. Journal of Ecology 78:713-726.

Vitt, D. H. and W-L. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87-106.

von Post, L. and E. Granlund. 1926. Sodra Sveriges torvtillganger I. Sveriges geologiska undersökning. Serie C, Avhandlingar och uppsatser 335:1-127.

Wheeler, B. D. and M. C. F. Proctor. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology 88:187-203.

Whinam, J., L. A. Barmuta, and N. Chilcott. 2001. Floristic description and environmental relationships of Tasmanian Sphagnum communities and their conservation management. Australian Journal of Botany 49:673-685.

Wilkinson, L. 1997. SYSTAT 7.0. SPSS. Chicago, IL, USA.

Yee, T. W. and N. D. Mitchell. 1991. Generalized additive models in plant ecology. Journal of Vegetation Science 2:587-602.

Zoltai, S. C. and D. H. Vitt. 1995. Canadian wetlands: environmental gradients and classification. Vegetatio 118:131-137.

Appendix 2.1 Checklist of plant species recorded in vegetation plots. *=non-native species

Taxon	Family
Vascular species	
Azolla filiculoides Lam.	Salviniaceae
Baumea arthrophylla (Nees) Boeck.	Cyperaceae
B. rubiginosa (Spreng.) Boeck.	Cyperaceae
B. tenax (Hook.f.) Blake	Cyperaceae
B. teretifolia (R.Br) Palla	Cyperaceae
Bidens frondosa L. *	Asteraceae
Blechnum novae-zelandiae (swamp form "*B. minus*")	Blechnaceae
Carex geminata Schkuhr	Cyperaceae
C. virgata Boott in Hook.f.	Cyperaceae
Coprosma tenuicaulis Hook.f.	Rubiaceae
Dacrycarpus dacrydioides (A.Rich.) de Laub.	Podocarpaceae
Dianella nigra Colenso	Liliaceae
Dicksonia squarrosa (Forst.f.) Swartz	Dicksoniaceae
Dracophyllum lessonianum A.Rich.	Epacridaceae
Drosera binata Labill.	Droseraceae
D. spathulata Labill.	Droseraceae
Eleocharis sphacelata R.Br.	Cyperaceae
Empodisma minus (Hook.f.) L.A.S.Johnson & D.F.Cutler	Restionaceae
Epacris pauciflora A.Rich	Epacridaceae
Gleichenia dicarpa R.Br.	Gleicheniaceae
Histiopteris incisa (Thunb.) J.Smith	Dennstaedtiaceae
Holcus lanatus L.*	Poaceae
Hydrocotyle novae-zelandiae DC.	Umbelliferae
H. pterocarpa F. Muell.	Umbelliferae
Hypochaeris radicata L.	Asteraceae
Hypolepis distans Hook.	Dennstaedtiaceae
Juncus bulbosus L.*	Juncaceae
Lemna minor L.	Lemnaceae
Leptospermum scoparium J.R.Forst. & G.Forst.	Myrtaceae
Lobelia anceps L.f.	Lobeliaceae
Lycopodiella lateralis (R.Br.) B.Ollg.	Lycopodiaceae
L. serpentina (Kunze) B.Ollg.	Lycopodiaceae
Muehlenbeckia australis (Forst.f.) Meissn.	Polygonaceae
Nertera scapanioides Lange	Rubiaceae
Osmunda regalis L.*	Osmundaceae
Phormium tenax J.R. et G.Forst.	Agavaceae

Taxon	Family
Phymatosorus diversifolius (Willd.) Pichi Serm.	Polypodiaceae
P. scandens (Forst.f.) Pichi Serm.	Polypodiaceae
Pteridium esculentum (Forst.f.) Cockayne	Dennstaedtiaceae
Pyrrosia eleagnifolia (Bory) Hovenkamp	Polypodiaceae
Rubus cissoides A.Cunn.	Rosaceae
R. fruticosus L.*	Rosaceae
Rumex acetosella L.*	Polygonaceae
Salix cinerea L.*	Salicaceae
Schoenus brevifolius R.Br.	Cyperaceae
Sporadanthus ferrugineus de Lange Heenan et B.D.Clarkson	Restionaceae
Tetraria capillaris (F.Muell.) J.M.Black	Cyperaceae
Thelymitra cyanea (Lindl.) Benth.	Orchidaceae
Ulex europeaus L.*	Fabaceae
Utricularia delicatula Cheeseman	Lentibulariaceae
Non-vascular species	
Campylopus acuminatus var. *kirkii* (Mitt.) Frahm	Dicranaceae
C. introflexus (Hedw.) Brid.	Dicranaceae
Goebelobryum unguiculatum (Hook.f. & Taylor) Grolle	Southbyaceae
Lepidozia laevifolia (Hook.f. & Taylor) Taylor	Lepidoziaceae
Pallavicina lyellii (Hook.) Gray	Pallaviciniaceae
Riccardia crassa (Schwaegr.) C. Massal.	Aneuraceae
Sphagnum cristatum Hampe.	Sphagnaceae
S. falcatulum Besch.	Sphagnaceae
S. novo-zelandicum Mitt.	Sphagnaceae
Telaranea tetraphila (Taylor) J.J.Engel & G.L.S.Merr.	Lepidoziaceae

Appendix 2.2 Peat properties at all the sampled wetland sites. Bogs have been listed in approximate order of age. n.d.= not determined.

Bog Site	Plot ID	pH	von Post	Bulk Density g/cm^3	Ash % (w/w)	TN mg/cm^3	TP mg/cm^3	Total K mg/cm^3	Available P μg/cm^3	Available N μg/cm^3
Duckcreek	DKN1	5.4	5.0	0.120	39.0	0.94	0.031	0.11	17.16	51.34
Duckcreek	DKN2	5.0	6.0	0.144	43.0	0.85	0.073	0.24	55.27	20.79
Duckcreek	DKS	6.2	8.0	0.068	44.0	0.50	0.011	0.04	14.46	29.96
Whangamarino	WHG1	4.6	5.0	0.133	32.3	1.83	0.133	0.04	10.66	30.63
Whangamarino	WHG2	5.0	5.5	0.104	27.9	1.73	0.094	0.03	10.19	26.41
Whangamarino	WHG3	5.1	6.0	0.111	26.3	1.63	0.100	0.02	10.92	26.00
Whangamarino	WHG4	4.8	4.5	0.080	16.0	0.67	0.048	0.02	5.67	27.75
Whangamarino	WHG5	4.5	5.0	0.117	20.1	1.72	0.094	0.02	9.37	30.61
Whangamarino	WHG6	5.1	6.0	0.055	24.3	1.17	0.055	0.01	4.42	13.44
Whangamarino	WHG7	5.0	5.0	0.072	21.1	0.77	0.050	0.02	3.25	29.63
Whangamarino	WHG8	5.1	4.0	0.074	11.6	0.94	0.045	0.01	4.61	40.37
Whangamarino	WHG9	4.8	5.0	0.078	9.9	0.85	0.055	0.02	5.53	46.98
Whangamarino	WHG10	5.0	5.0	0.085	21.0	1.21	0.051	0.02	6.79	20.38
Whangamarino	WHG11	4.6	4.0	0.071	9.5	0.79	0.028	0.02	3.18	20.12
Whangamarino	WHG12	4.9	4.5	0.097	n.d.	1.26	0.029	0.03	4.36	12.31
Whangamarino	WHCS1	5.0	9.0	0.100	32.0	2.35	0.130	0.04	5.00	25.59
Whangamarino	WHCS2	4.7	9.0	0.140	40.0	2.32	0.168	0.10	9.80	8.35
Whangamarino	WHCS3	5.6	8.0	0.100	35.0	1.88	0.170	0.05	5.00	22.13
Whangamarino	WHCS4	4.6	9.0	0.130	61.0	2.59	0.221	0.09	6.50	51.69
Whangamarino	WHCS5	5.4	9.0	0.120	67.0	2.87	0.360	0.03	28.80	10.48
Whangamarino	WHIB1	4.9	4.0	0.110	25.0	1.96	0.176	0.02	5.50	41.46
Whangamarino	BW1	4.6	8.0	0.097	21.0	1.47	0.097	0.06	26.88	24.18
Opuatia	OPU1	4.7	3.0	0.079	27.2	0.89	0.024	0.06	1.42	0.86
Opuatia	OPU2	5.1	8.0	0.100	21.1	1.45	0.110	0.03	8.90	29.00
Opuatia	OPU3	5.4	5.0	0.100	37.0	1.51	0.200	0.04	10.00	27.57
Opuatia	OT1	4.9	4.0	0.087	18.0	1.20	0.052	0.05	22.19	21.25
Opuatia	OT2	5.5	4.0	0.052	17.0	0.80	0.051	0.02	14.52	22.06
Opuatia	OT3	5.4	4.0	0.027	14.0	0.27	0.009	0.02	4.05	37.96
Opuatia	OT4	5.5	4.0	0.046	14.0	0.54	0.025	0.02	7.62	46.22
Opuatia	OT5	5.6	5.0	0.075	30.0	0.94	0.034	0.05	8.75	28.69
Opuatia	OT6	5.6	4.0	0.020	16.0	0.23	0.008	0.02	3.13	7.34
Opuatia	OT7	6.3	3.0	0.035	8.0	0.25	0.010	0.04	3.44	13.69
Torehape	TORE1	4.2	2.0	0.084	7.0	1.18	0.027	0.01	5.80	9.94
Torehape	TORE2	3.9	8.0	0.125	n.d.	2.97	0.062	0.01	7.75	10.55
Torehape	TRM1	4.0	4.0	0.067	4.0	1.07	0.043	0.03	19.27	12.26
Kopuatai	KOPU0	4.5	8.0	0.085	7.7	1.80	0.12	0.05	30.5	42.7
Kopuatai	KOPU1	4.3	4.0	0.060	3.0	0.46	0.028	0.03	17.40	28.98
Kopuatai	KOPU2	4.8	2.0	0.040	1.0	0.35	0.017	0.03	5.95	14.28

Bog Site	Plot ID	pH	von Post	Bulk Density g/cm^3	Ash % (w/w)	TN mg/cm^3	TP mg/cm^3	Total K mg/cm^3	Available P µg/cm^3	Available N µg/cm^3
Kopuatai	KOPU3	4.5	1.0	0.055	2.0	0.68	0.013	0.01	3.34	16.17
Kopuatai	KOPU4	4.3	1.5	0.050	2.0	0.33	0.006	0.01	3.11	13.50
Kopuatai	KOPU5	4.4	2.0	0.061	2.0	0.72	0.014	0.01	2.98	19.3
Kopuatai	KOPU6	4.7	2.0	0.055	4.0	0.78	0.009	0.02	6.21	17.60
Kopuatai	KOPU7	5.0	1.0	0.055	2.0	0.50	0.006	0.02	3.01	15.18
Kopuatai	KOPU8	4.5	1.0	0.054	3.1	0.55	0.006	0.02	1.54	12.9
Kopuatai	KOPU9	4.8	1.0	0.055	2.0	0.35	0.004	0.02	1.68	18.70
Kopuatai	KOPU10	4.7	2.0	0.030	2.0	0.39	0.007	0.02	2.86	13.35
Kopuatai	KOPU11	4.7	2.0	0.045	2.0	0.50	0.006	0.01	2.24	18.18
Kopuatai	KOPU12	4.9	2.0	0.050	2.0	0.66	0.008	0.01	2.20	15.55
Kopuatai	KOPU13	4.7	2.0	0.030	4.0	0.22	0.002	0.03	1.23	9.63
Kopuatai	KOPU14	5.0	1.0	0.030	2.0	0.15	0.003	0.01	0.87	10.50
Kopuatai	KOPU15	4.9	1.0	0.034	2.1	0.36	0.003	0.02	0.88	6.5
Kopuatai	KOP4800	4.1	7.5	0.090	21.0	1.89	0.090	0.03	4.50	4.61
Kopuatai	KOP5600	4.4	8.5	0.160	34.0	3.61	0.576	0.06	49.60	43.28
Kopuatai	KOP5700	4.9	5.0	0.150	41.0	2.72	0.540	0.10	31.50	34.18
Lake Maratoto	MR1	4.7	9.0	0.226	58.3	3.04	0.497	0.05	97.57	8.61
Lake Maratoto	MR5	4.0	9.0	0.153	9.7	2.87	0.046	0.02	19.08	17.06
Kopuatai Teecanal	KTCANAL1	4.3	1.5	0.033	3.6	0.66	0.007	0.03	0.89	16.46
Kopuatai Teecanal	KTCANAL2	4.6	2.0	0.030	2.0	0.22	0.002	0.00	1.50	7.52
Kopuatai Teecanal	KTCANAL3	4.5	2.0	0.040	2.0	0.36	0.002	0.01	2.00	3.45
Te Mimiha	TEM1	3.9	8.0	0.234	14.4	3.41	0.164	0.04	35.54	24.80
Moanatuatua North	MNN1	4.3	2.0	0.073	7.0	1.11	0.037	0.01	8.51	14.57
Moanatuatua North	MNN2	4.4	8.0	0.165	9.0	3.16	0.132	0.02	29.52	21.13
Moanatuatua	MNB1	4.4	2.0	0.092	5.0	1.19	n.d.	n.d.	n.d.	n.d.
Moanatuatua	MNB3	4.1	2.0	0.077	2.1	0.63	0.038	0.01	2.77	2.01
Moanatuatua	MNB5	4.6	2.0	0.074	20.0	0.62	n.d.	n.d.	n.d.	n.d.
Moanatuatua	MNB7	4.4	2.0	0.083	1.9	0.60	0.033	0.01	10.43	9.23
Moanatuatua	MNB9	4.4	2.0	0.054	2.4	0.60	0.027	0.01	2.89	9.43
Moanatuatua	MNB11	4.5	2.0	0.064	3.4	0.67	0.013	0.01	2.32	10.04
Moanatuatua	MNB13	4.1	1.0	0.057	2.3	0.46	0.011	0.01	1.55	5.00

3. VEGETATION AND PEAT CHARACTERISTICS OF RESTIAD BOGS ON CHATHAM ISLAND (REKOHU), NEW ZEALAND[2]

3.1. ABSTRACT

Restiad bogs dominated by *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.

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

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3.2. 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 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:

1) 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*.

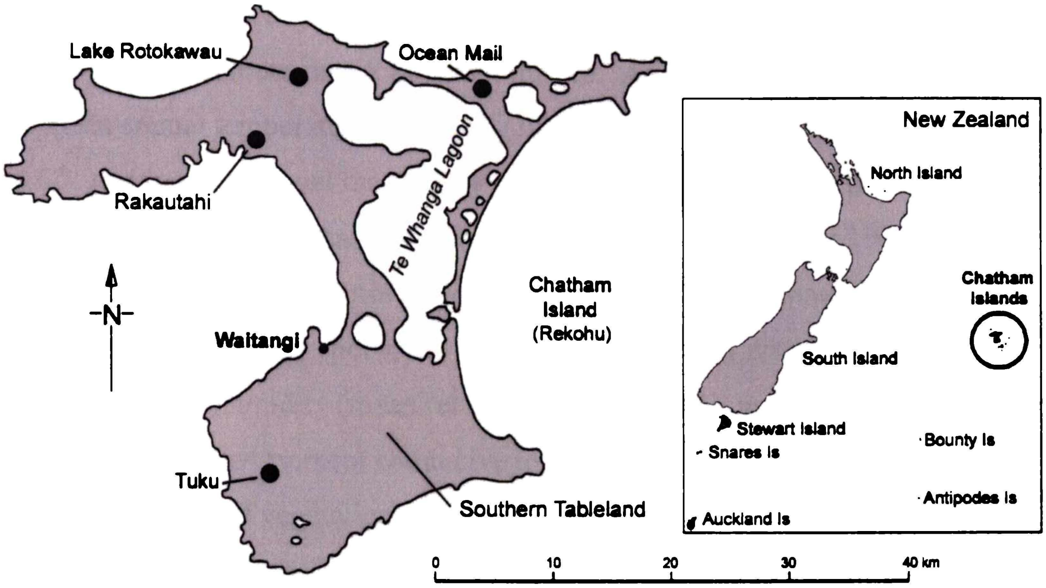

Figure 3.1 Chatham Island showing sampling locations.

3.3. 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. 3.1). 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. 3.1). 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*,

Figure 3.2 *Olearia semidentata* (in flower) is locally common at Ocean Mail and grows in association with *Sporadanthus traversii.*

Gleichenia dicarpa, and, locally, *Olearia semidentata* (Fig. 3.2). *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. 3.3). 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. 3.4) 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

Figure 3.3 *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.

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 to the 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. 3.5). 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.

Figure 3.4 Clumps of *Sporadanthus traversii* and shrubs of *Dracophyllum scoparium* typify the restiad bog vegetation at Lake Rotokawau.

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 (*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.

Figure 3.5 Charred stems of *Dracophyllum scoparium* overtop clumps of *Gleichenia dicarpa* and *Sporadanthus traversii* at recently burnt Rakautahi.

3.4. 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 × 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 3.1).

At each plot the % cover for canopy species (as defined by Atkinson 1962) was assessed, the maximum height for each species measured, and all vascular and non-vascular plant species listed (see Appendix 3.2). 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 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 N_2 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* H_2SO_4 (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, 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 $\beta = -0.1$) 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.

3.5. 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 3.1. 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. 3.6 (plot data in Appendix 3.1) 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.

Table 3.1 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 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	*Sporadanthus traversii-Apodasmia similis*	*Apodasmia similis*	*Sporadanthus traversii*	*Dracophyllum scoparium*	*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	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 (12.7)	0	0.3 (0.9)	0	0.1 (0.2)
Pteridium esculentum cover	10.5 (13.4)	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)

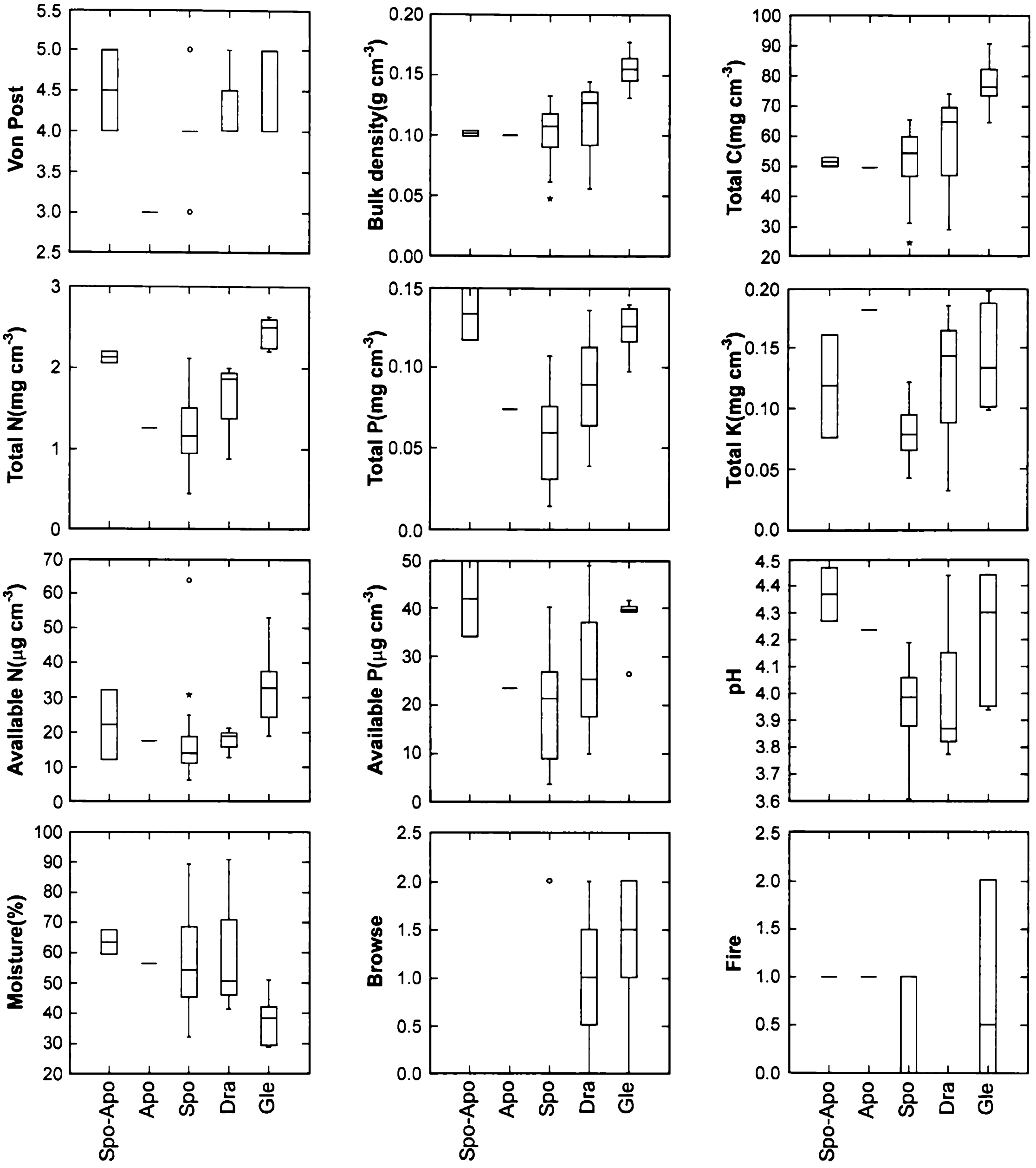

Figure 3.6 Box plot summary showing medians, and upper and lower quartiles, for environmental data in each of the vegetation types (determined from the classification). Apo, *Apodasmia similis*; Spo, *Sporadanthus traversii*; Dra, *Dracophyllum scoparium*; Gle, *Gleichenia dicarpa*.

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, nutrient and moisture contents. Peat nutrients of the second modified group (Group 4 Dra) were only marginally elevated compared with Group 3 (Spo).

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. 3.7A). 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 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. 3.8) 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).

3.6. 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.

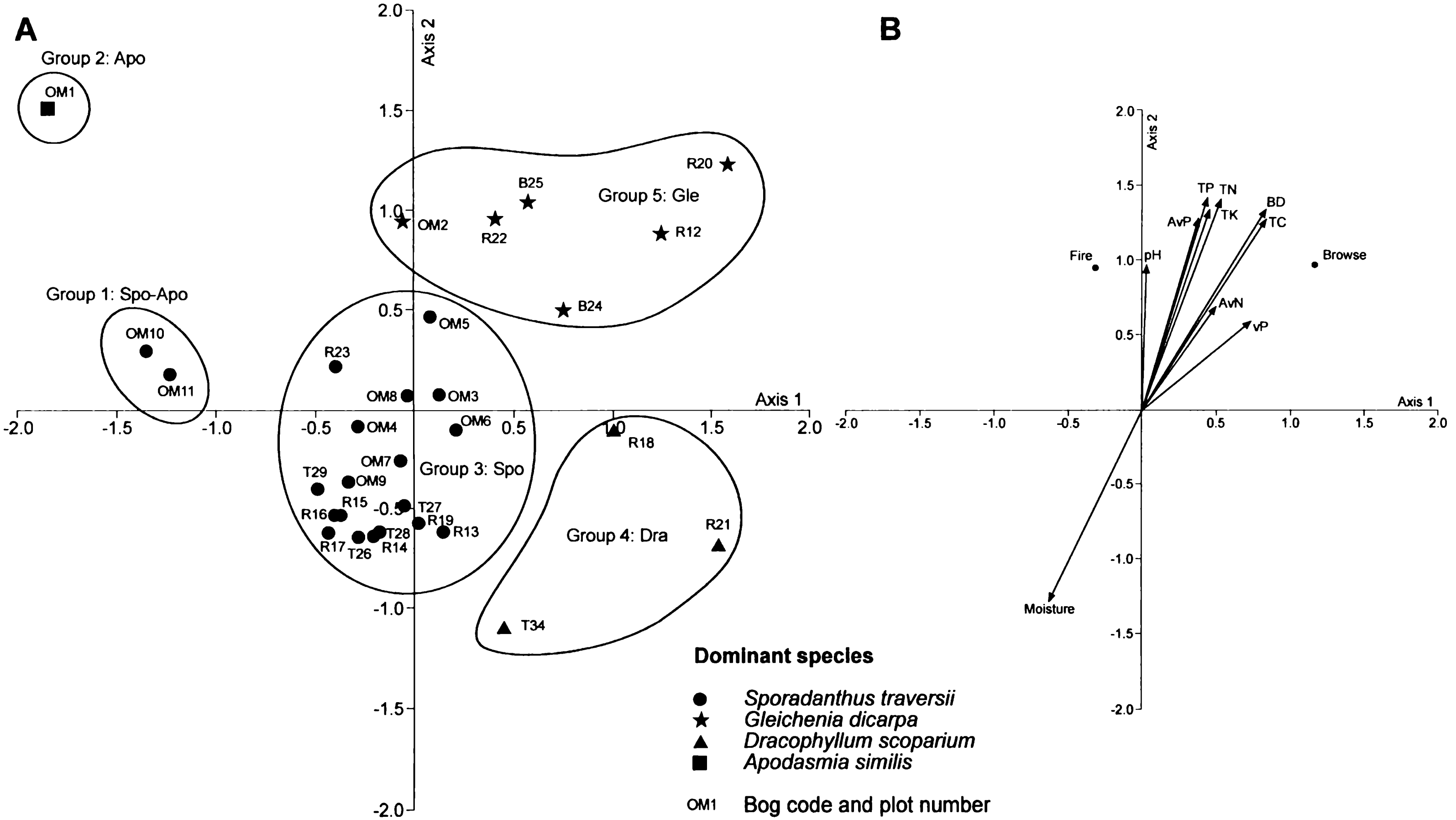

Figure 3.7 A, Two-dimensional ordination of 30 plots based on canopy cover of 38 species (= restiad bog plant species data set). The vegetation type groups have been superimposed (codes as in Fig. 3.6). Bog codes: OM, Ocean Mail; R, Lake Rotokawau; B, Rakautahi; T, Tuku; B, Species:environment biplot 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.

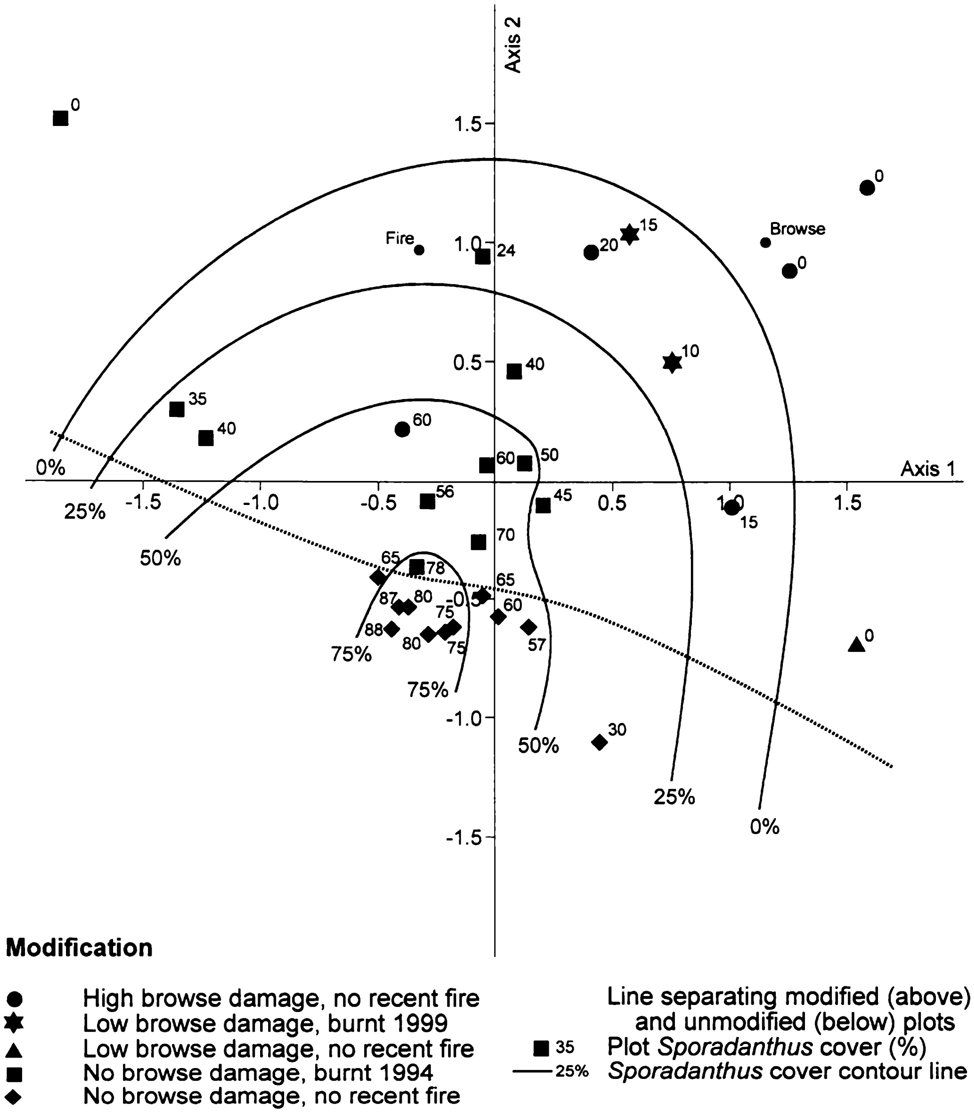

Figure 3.8 Plot ordination overlaid with *Sporadanthus traversii* cover values and type of modification at each site.

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 3.1) 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 3.2. Vegetation types were defined by cluster analyses, i.e., the "*Sporadanthus traversii*" group of Table 3.1 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*.

Table 3.2 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 $\mu g\ cm^{-3}$	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 mg cm^{-3}	0.057 (0.030) a	0.019 (0.014) a	0.035 (0.003) a
Available N $\mu g\ cm^{-3}$	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

Comparison of species richness indicated that total and vascular plant species numbers were significantly higher in the *Sporadanthus traversii* 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 non-breeding 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 ± 230 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 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 minus*, to 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. 3.6), 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 3.2), 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). *S. 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.

3.7. ACKNOWLEDGEMENTS

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3.8. REFERENCES

Atkinson, I. A. E. 1962: Semi-quantitative measurements of canopy composition as a basis for mapping vegetation. *Proceedings of the New Zealand Ecological Society 9*: 1–8.

Atkinson, I. A. E. 1996: Major habitats. *In*: Department of Conservation *ed.* The Chatham Islands heritage and conservation. Christchurch, Canterbury University Press. Pp. 49–61.

Barrow, C. J. 1983: Palynological studies in South Georgia: IV. Profiles from Barff Peninsula and Annenkov Island. *British Antarctic Survey Bulletin 58*: 61–70.

Belbin, L. 1995: PATN: Pattern analysis package. Technical reference. Canberra, CSIRO Division of Wildlife and Ecology.

Blakemore, L. C. 1958: The chemistry of organic soils. *New Zealand Soil News 2*: 46–52.

Blakemore, L. C.; Searle, P. L.; Daly, B. K. 1987: Methods for chemical analysis of soils. *New Zealand Soil Bureau Scientific Report 80.* Lower Hutt, DSIR.

Bourne, W. R. P. 1967: Subfossil petrel bones from the Chatham Islands. *The Ibis 109*: 1–7.

Bridgham, S. D.; Pastor, J.; Janssens, J. A.; Chapin, C.; Malterer, T. J. 1996: Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands 16*: 45–65.

Burger, A. E.; Lindeboom, H. J.; Williams, A. J. 1978: The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial system. *South African Journal of Antarctic Research 8*: 59–70.

Campbell, E. O. 1964: The restiad peat bogs at Motumaoho and Moanatuatua. *Transactions of the Royal Society of New Zealand, Botany 2*: 219–227.

Campbell, E. O. 1983: Mires of Australasia. *In*: Gore, A. J. P. *ed.* Ecosystems of the world 4A Mires: swamp, bog, fen and moor. Amsterdam, The Netherlands, Elsevier Scientific Co. Pp. 153–180.

Campbell, I. B. 1996: Geology. *In*: Department of Conservation *ed.* The Chatham Islands heritage and conservation. Christchurch, Canterbury University Press. Pp. 14–48.

Clarkson, B. R. 1997: Vegetation recovery following fire in two Waikato peatlands at Whangamarino and Moanatuatua. *New Zealand Journal of Botany 35*: 167–179.

Clarkson, B. R.; Schipper, L. A.; Lehmann, A. 2004: Vegetation and peat characteristics in the development of lowland restiad bogs, North Island, New Zealand, since c. 13 000 ^{14}C years BP. *Wetlands 24*: 133–151.

Clymo, R. S. 1983: Peat. *In*: Gore, A. J. P. *ed.* Ecosystems of the world 4A Mires: swamp, bog, fen and moor. Amsterdam, The Netherlands, Elsevier Scientific Co. Pp. 159–224.

Cockayne, L. 1902: A short account of the plant-covering of Chatham Island. *Transactions and Proceedings of the New Zealand Institute 34*: 243–325.

de Lange, P. R.; Sawyer, J. W. D.; Ansell, R. 1999a: Checklist of indigenous vascular plant species recorded from Chatham Islands. Wellington, Department of Conservation.

de Lange, P. R.; Heenan, P. B.; Clarkson, B. D.; Clarkson, B. R. 1999b: *Sporadanthus* in New Zealand. *New Zealand Journal of Botany 37*: 413–431.

Faith, D. P.; Minchin, P. R.; Belbin, L. 1987: Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio 69*: 57–68.

Given, D. R. 1996: Flora. *In*: Department of Conservation *ed.* The Chatham Islands heritage and conservation. Christchurch, Canterbury University Press. Pp. 80–92.

Given, D. R.; Williams, P. A. 1984: Conservation of Chatham Island flora and vegetation. Christchurch, Botany Division, DSIR.

Grange, L. I.; Taylor, N. H.; Sutherland, C. F.; Dixon, J. K.; Hodgson, L.; Seelye, F. T. 1939: Soils and agriculture of part of Waipa County: Soils. *DSIR Bulletin 76*: 30–63.

Hawke, D. J.; Holdaway, R. N.; Causer, J. E.; Ogden, S. 1999: Soil indicators of pre-European seabird breeding in New Zealand at sites identified by predator deposits. *Australian Journal of Soil Research 37*: 103–113.

Hogg, A. G.; Lowe, D. J.; Hendy, C. H. 1987: University of Waikato radiocarbon dates I. *Radiocarbon 29*: 263–301.

Keeney, D. R. 1982: Nitrogen-availability indices. *In*: Page, A. L. *ed.* Methods of soil and plant analysis: part 2 chemical and microbiological properties. 2nd ed. Madison, Wisconsin SSSA. Pp. 711–735.

Kelly, G. C. 1971: Reserves in the Chatham Islands. Unpublished Botany Division DSIR Report, held at Landcare Research, Lincoln, New Zealand.

Kelly, G. C. 1978: Proposed Chatham Island national park. Unpublished Botany Division DSIR Report, held at Landcare Research, Lincoln, New Zealand.

Kelly, G. C. 1983: Distribution and ranking of remaining areas of indigenous vegetation in the Chatham Islands. *Botany Division DSIR Vegetation Report 501*, held at Landcare Research, Lincoln, New Zealand.

Lamont, B. 1982: Mechanisms for enhancing nutrient uptake in plants, with particular reference to Mediterranean South Africa and western Australia. *The Botanical Review 48*: 597–689.

MacPherson, E. O.; Hughson, W. G. 1943: Wax from Chatham Island peat. *New Zealand Journal of Science and Technology 25*: 1–31.

McGlone, M. S. 2002: The Late Quaternary peat, vegetation and climate history of the Southern Oceanic Islands of New Zealand. *Quaternary Science Reviews 21*: 683–707.

McGlone, M. S.; Nelson, C. S.; Todd, A. J. 1984: Vegetation history and environmental significance of pre-peat and surficial peat deposits at Ohinewai, Lower Waikato lowland. *Journal of the Royal Society of New Zealand 14*: 233–244.

Meney, K. A.; Pate, J. S. 1999: Australian rushes: biology, identification and conservation of Restionaceae and allied families. Nedlands, Western Australia, University of Western Australia Press.

Meurk, C. D.; Foggo, M. N.; Thomson, B. M.; Bathurst, E. T. J. 1994: Ion-rich precipitation and vegetation pattern on subantarctic Campbell Island. *Arctic and Alpine Research 26*: 281–289.

Mildenhall, D. C. 1994: Palynological reconnaissance of early Cretaceous to Holocene sediments, Chatham Islands, New Zealand. *Institute of Geological and Nuclear Sciences Monograph 7*. 206 p.

Minchin, P. R. 1987: An evaluation of the robustness of techniques for ecological ordination. *Vegetatio 69*: 89–107.

Moore, L. B.; Edgar, E. 1976: Flora of New Zealand. Vol. II. Wellington, Government Printer.

Mueller-Dombois, D.; Ellenberg, H. 1974: Aims and methods of vegetation ecology. New York, John Wiley & Sons.

New Zealand Meteorological Service 1973: Summaries of climatological observations to 1970. *New Zealand Meteorological Service Miscellaneous Publication 143*. Wellington, Government Printer.

Neumann, G.; Martinoia, E. 2002: Cluster roots – an underground adaptation for survival in extreme environments. *Trends in Plant Science 7*: 162–167.

Newnham, R. M.; de Lange, P. J.; Lowe, D. J. 1995: Holocene vegetation, climate and history of a raised bog complex, northern New Zealand based on palynology, plant macrofossils and tephrochronology. *The Holocene 5*: 267–282.

Norton, D. A.; de Lange, P. J. 2003: Fire and vegetation in a temperate peat bog: implications for the management of threatened species. *Conservation Biology 17*: 138–148.

Smith, R. I. L.; Prince, P. A. 1985: The natural history of Beauchêne Island. *Biological Journal of the Linnean Society 24*: 233–283.

Smith, V. R. 1976: Standing crop and nutrient status of Marion Island (sub-Antarctic). *Journal of South African Botany 42*: 231–263.

Thompson, C. S. 1983: The weather and climate of the Chatham Islands. *New Zealand Meteorological Service Miscellaneous Publication 115 (13).* Wellington, Government Printer.

Verhoeven, J. T. A.; Koerselmann, W.; Meuleman, A. F. 1996: Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution 11*: 494–497.

von Post, L.; Granlund, E. 1926: Sodra Sveriges torvtillganger I. *Sveriges geologiska undersökning, Serie C, Avhandlingar och uppsatser 335*: 1–127.

Walls, G.; Baird, A. 1995: Winds of change: monitoring vegetation condition and trend in the Chatham Islands. *Conservancy Advisory Science Notes 130.* Wellington, Department of Conservation.

Walls, G.; Baird, A. 1997: Holes in the fence: The vegetation of Chatham Island reserves, 1990–1996. *Conservancy Advisory Science Notes 156.* Wellington, Department of Conservation.

Wardle, P. 1991: Vegetation of New Zealand. Cambridge, Cambridge University Press.

Wardle, P.; Atkinson, I. A. E.; Given, D. R.; Molloy, B. J. P.; Brown, C. M.; Manning, D. 1986: Botany Division visit to the Chatham Islands February–March 1985. Unpublished report to the Liquid Fuels Trust Board from Botany Division, DSIR.

Wilbur, R. B.; Christensen, N. L. 1983: Effects of fire on nutrient availability in a North Carolina coastal plain pocosin. *American Midlands Naturalist 110*: 54–61.

Wilkinson, L. 1997: SYSTAT 7.0. Chicago IL, SPSS.

Williams, A. J.; Berruti, A. 1978: Mineral and energy contributions of feathers moulted by penguins, gulls and cormorants to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research 8*: 71–74.

Williams, A. J.; Burger, A. E.; Berruti, A. 1978: Mineral and energy contributions of carcasses of selected species of seabirds to the Marion Island terrestrial ecosystem. *South African Journal of Antarctic Research 8*: 53–59.

Wills-Johnson, T. M. K. 1996: Introduction. *In*: Department of Conservation *ed.* The Chatham Islands heritage and conservation. Christchurch, Canterbury University Press. Pp. 11–20.

Wilson, C. J. N.; Switsur, V. R.; Ward, A. P. 1988: A new ^{14}C age for the Oruanui (Wairakei) eruption, New Zealand. *Geological Magazine 125*: 297–300.

Wright, A. C. S. 1959: Soils of Chatham Island (Rekohu). *Soil Bureau Bulletin 19.* Wellington, New Zealand, DSIR.

Appendix 3.1 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 *.

Wetland	Plot ID	Group	Moisture Content	pH	Available N μg cm^{-3}	Available P μg cm^{-3}	BD mg cm^{-3}	EC mS cm^{-1} g^{-1}	TC mg cm^{-3}	TN mg cm^{-3}	TP mg cm^{-3}	TK mg cm^{-3}	von Post
Ocean Mail	OM1	Apo	565.4	4.2	17.3	23.3	0.100	0.27	49.2	1.25	0.074	0.181	3
Ocean Mail	OM2	Gle	286.1	3.9	18.7	39.6	0.163	0.13	79.0	2.59	0.131	0.101	4
Ocean Mail	OM3	Spo	370.9	3.9	11.1	40.2	0.133	0.03	65.3	1.61	0.100	0.117	4
Ocean Mail	OM4	Spo	451.0	3.8	18.9	27.8	0.115	10.61	58.1	1.40	0.074	0.113	4
Ocean Mail	OM5	Spo	317.4	4.0	14.1	19.5	0.116	0.00	58.6	1.44	0.060	0.072	4
Ocean Mail	OM6	Spo	435.0	3.9	17.0	26.3	0.121	1.80	62.8	1.30	0.076	0.094	4
Ocean Mail	OM7	Spo	452.4	3.6	6.1	22.9	0.121	0.00	60.6	1.14	0.072	0.095	4
Ocean Mail	OM8	Spo	531.3	3.8	15.3	27.9	0.106	0.00	53.9	1.53	0.097	0.089	4
Ocean Mail	OM9	Spo	523.2	4.0	9.4	25.2	0.117	0.22	59.7	1.15	0.075	0.122	4
Ocean Mail	OM10	Spo-Apo	675.0	4.5	32.2	49.7	0.099	2.41	49.8	2.19	0.149	0.161	4
Ocean Mail	OM11	Spo-Apo	595.7	4.3	12.1	33.8	0.104	0.81	52.7	2.06	0.117	0.076	5
L.Rotokawau	R12	Gle	509.1	4.3	24.1	41.3	0.131	3.20	64.2	2.20	0.136	0.127	4
L.Rotokawau	R13	Spo	485.4	3.9	12.3	9.6	0.099	0.00	50.7	0.94	0.034	0.073	4
L Rotokawau	R14	Spo	707.3	4.1	12.8	5.7	0.095	0.00	46.7	0.85	0.025	0.078	4
L Rotokawau	R15	Spo	724.9	4.1	13.4	6.9	0.110	0.05	54.5	1.08	0.028	0.060	4
L.Rotokawau	R16	Spo	627.1	4.2	9.2	3.7	0.062	0.00	31.1	0.44	0.014	0.078	3
L.Rotokawau	R17	Spo	689.3	4.1	7.3	3.7	0.072	0.00	36.0	0.57	0.016	0.070	3

Appendix 3.1 (*Continued*)

Wetland	Plot ID	Group	Moisture Content	pH	Available N μg cm^{-3}	Available P μg cm^{-3}	BD mg cm^{-3}	EC mS cm^{-1} g^{-1}	TC mg cm^{-3}	TN mg cm^{-3}	TP mg cm^{-3}	TK mg cm^{-3}	von Post
L.Rotokawau	R18*	Dra	507.7	4.4	20.9	48.5	0.127	0.00	64.7	1.86	0.136	0.185	5
L.Rotokawau	R19*	Spo	718.4	3.9	10.9	10.7	0.048	0.00	24.1	0.48	0.035	0.065	4
L.Rotokawau	R20*	Gle	419.5	4.4	52.8	39.2	0.147	0.03	73.7	2.24	0.139	0.198	5
L.Rotokawau	R21*	Dra	412.2	3.9	18.6	25.1	0.144	0.00	73.8	1.99	0.089	0.143	4
L.Rotokawau	R22*	Gle	291.0	4.0	27.8	26.2	0.145	0.00	73.3	2.44	0.097	0.098	5
L.Rotokawau	R23*	Spo	527.3	4.0	18.7	26.8	0.118	0.00	58.9	2.10	0.107	0.105	5
Rakautahi	B24	Gle	363.9	4.3	37.4	39.8	0.164	2.41	82.3	2.54	0.116	0.186	5
Rakautahi	B25	Gle	400.4	4.4	32.6	40.1	0.177	1.16	90.7	2.60	0.120	0.138	5
Tuku	T26	Spo	896.0	4.0	25.1	15.8	0.068	0.18	34.6	1.04	0.104	0.042	4
Tuku	T27	Spo	648.9	4.0	14.7	9.0	0.090	0.13	46.5	1.04	0.104	0.060	4
Tuku	T28	Spo	557.3	4.1	63.6	29.6	0.121	1.00	62.2	1.96	0.104	0.087	4
Tuku	T29	Spo	660.3	4.0	30.7	23.3	0.100	1.56	51.8	1.50	0.059	0.065	5
Tuku	T30	[Sph]	3645.1	4.2	4.6	3.7	0.021	2.68	9.5	0.19	0.013	0.008	2
Tuku	T31	[Mar]	1801.3	4.3	8.8	7.5	0.039	0.00	18.8	0.49	0.029	0.074	3
Tuku	T32	[Mar]	2078.6	4.4	15.9	11.1	0.036	0.00	16.7	0.43	0.036	0.088	3
Tuku	T33	[Sph]	2524.8	4.1	8.9	5.1	0.033	0.00	15.3	0.36	0.021	0.018	2
Tuku	T34	Dra	908.9	3.8	12.5	9.7	0.056	0.00	28.7	0.87	0.039	0.032	4
Tuku	T35	[Darb]	1258.1	4.1	8.4	7.2	0.041	0.00	19.4	0.29	0.026	0.054	3
Tuku	T36	[Darb]	441.3	4.2	26.0	22.9	0.117	0.03	61.7	2.60	0.104	0.059	n.d.

Appendix 3.2 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 (swamp form "*B. minus*")	Blechnaceae
B. procerum (G.Forst.) Sw.	Blechnaceae
Carex chathamica Petrie	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

Appendix 3.2 *(Continued)*

Taxon	Family
H. multifidum[t] (G.Forst.) Sw.	Hymenophyllaceae
H. scabrum[t] A.Rich	Hymenophyllaceae
*Hypochaeris radicata** L.	Asteraceae
Hypolepis distans Hook.	Dennstaedtiaceae
Isolepis distigmatosa (C.B.Clarke) Edgar	Cyperaceae
*Juncus articulatus** L.	Juncaceae
*J. bufonius** L.	Juncaceae
*J. effusus** L.	Juncaceae
J. pallidus R.Br	Juncaceae
J. 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
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.Forst & 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.Forst. & 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

Appendix 3.2 *(Continued)*

Taxon	Family
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
Dicranum billardierei Brid.	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

4. FOLIAR ^{15}N NATURAL ABUNDANCE INDICATES PHOSPHORUS LIMITATION OF BOG SPECIES[3]

4.1. ABSTRACT

Foliar $\delta^{15}N$, %N and %P in the dominant woody and herbaceous species across nutrient gradients in New Zealand restiad (family Restionaceae) raised bogs revealed marked differences in plant $\delta^{15}N$ correlations with P. The two heath shrubs, *Leptospermum scoparium* (Myrtaceae) and *Dracophyllum scoparium* (Epacridaceae), showed considerable isotopic variation (–2.03 to –15.55‰, and –0.39 to –12.06‰ respectively) across the bogs, with foliar $\delta^{15}N$ strongly and positively correlated with P concentrations in foliage and peat, and negatively correlated with foliar N:P ratios. For *L. scoparium*, the isotopic gradient was not linked to ectomycorrhizal (ECM) fractionation as ECMs occurred only on higher nutrient marginal peats where ^{15}N depletion was least. In strong contrast, restiad species (*Empodisma minus*, *Sporadanthus ferrugineus*, *S. traversii*) showed little isotopic variation across the same nutrient gradients. *Empodisma minus* and *S. traversii* had $\delta^{15}N$ levels consistently around 0‰ (means of –0.12‰ and +0.15‰ respectively), and *S. ferrugineus*, which co-habited with *E. minus*, was more depleted (mean –4.97‰). The isotopic differences between heath shrubs and restiads were similar in floristically dissimilar bogs and may be linked to contrasting nutrient demands, acquisition mechanisms, and root morphology. *Leptospermum scoparium* shrubs on low nutrient peats were stunted, with low tissue P concentrations, and high N:P ratios, suggesting they were P-limited, which was probably exacerbated by markedly reduced mycorrhizal colonisations. The coupling of $\delta^{15}N$ depletion and %P in heath shrubs suggests that N fractionation is promoted by P limitation. In contrast, the constancy in $\delta^{15}N$ of the restiad species through the N and P gradients suggests that these are not suffering from P limitation.

Key Words Heath shrubs · Mycorrhiza · Nutrient gradients · Raised bogs · Restionaceae

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4.2. INTRODUCTION

In mangals, tundra, bogs, and other nutrient deficient environments, the nitrogen isotopic signature of plants has been linked with nutrient availability and changes in plant N demand. Studies have shown plant $\delta^{15}N$ becomes more depleted with increasing N availability and with increasing P limitation (Goerick et al. 1994; Schultze et al. 1994; Montoya and McCarthy 1995; Fry et al. 2000; McKee et al. 2002). A plant fractionation model to explain isotopic differences between source and plant across N-limitation and P-limitation gradients in mangrove communities was proposed by Fry et al. (2000) and refined by McKee et al. (2002). The model predicts that where N is in excess of demand (i.e. a P-limited system) uptake of N will show discrimination against the heavier ^{15}N isotope because not all N is assimilated.

Plant $\delta^{15}N$ depletion is also caused by mycorrhizal fractionation and varies according to mycorrhizal type. Ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) plants in tundra ecosystems showed greater $\delta^{15}N$ depletion than co-occurring non-mycorrhizal (NM) and arbuscular mycorrhizal (AM) plants (Michelsen et al. 1996, 1998).

In New Zealand, nutrient gradients occur in restiad raised bogs (dominated by Restionaceae), where minerotrophic margins have higher nutrient levels (total N, available N, total P, available P, total K) than ombrotrophic central areas (Schipper et al. 1998; Clarkson et al. 2004a, b), which, in late successional bogs, are likely to be P-limited (see Verhoeven et al. 1996). The main herbaceous and woody species occur throughout the bogs, providing opportunities to determine plant chemical composition in co-occurring species across nutrient gradients, and assess links with mycorrhizal status. This study focuses on the *Sporadanthus*-dominated restiad bog type, confined to the Waikato region of northern North Island, and Chatham Island, 850 km east of South Island, which are functionally similar but floristically different (Clarkson et al. 2004a).

We measured plant $\delta^{15}N$, N and P content in the dominant woody and herbaceous species across nutrient gradients as previous studies have shown peat total N and total P were the most important nutrients in restiad bog succession (Clarkson et al. 2004b). The aim was to determine whether different species responded similarly to N and P gradients within and between bog ecosystems at two independent field sites. We hypothesised that: (1) foliar %N and %P would decrease with decreases in peat total N and total P respectively; (2) foliar $\delta^{15}N$ would become increasingly depleted as foliar %P levels decreased, and; (3) ECM and ERM species would show greater $\delta^{15}N$ depletion than NM species.

4.3. MATERIALS AND METHODS

Study Area

The bogs sampled were Kopuatai, an extensive 9000 ha raised bog in Waikato, North Island (latitude 37° 25'S), and four smaller bogs at Ocean Mail, Lake Rotokawau, Tuku and Rakautahi on Chatham Island (1000 km southeast of Kopuatai at latitude 44°S). Kopuatai is a largely intact bog surrounded by pasture with native forest-covered hillcountry to the west and east, and much of Chatham Island retains native-dominated peatland cover. At Kopuatai, tall shrubs (c. 5 m) of *Leptospermum scoparium* (Myrtaceae; henceforth *Leptospermum*) dominated the bog margin and decreased in height (1–1.5 m) and abundance within 2–300 m into the bog, to become a minor component throughout most of the bog centre. Two herbaceous, monocotyledonous restiads, *Empodisma minus* (henceforth *Empodisma*) and *Sporadanthus ferrugineus*, 1–2 m tall, dominated the extensive central area. *Leptospermum* may have dual ECM and AM associations (Moyersoen and Fitter 1999), and *Empodisma* is classified as NM in Schmidt and Stewart (1997). *Sporadanthus ferrugineus* is probably NM on the basis that Restionaceae is generally considered to be a typical non-mycorrhizal family (Tester et al., 1987) and a preliminary study of *S. ferrugineus* roots ($n = 4$) revealed no mycorrhizal associations (BRC, unpubl. data). Peat nutrient levels decreased along a bog margin–centre transect, with total N ranging from 1.80 to 0.15 mg cm^{-3} and total P, 0.12 to 0.002 mg cm^{-3}, at the margin and centre respectively (Schipper et al. 1998, Clarkson et al. 2004b).

The Chatham Island bogs were dominated by *Sporadanthus traversii*, with the most common shrub species being *Dracophyllum scoparium* (Epacridaceae;

henceforth *Dracophyllum*). The genus *Dracophyllum* has been reported as having ERM (Reed 1987), and *S. traversii* is probably NM, similar to *S. ferrugineus*. The vegetation throughout the bogs was typically short (c. 1 m), because of occasional disturbance by fire and/or cattle browsing. Peat nutrient levels of plots with *S. traversii* and/or *Dracophyllum* ranged from 0.48 to 2.60 mg cm^{-3} for total N, and from 0.035 to 0.149 mg cm^{-3} for total P, with bog margins having higher levels than central areas (Clarkson et al. 2004a).

Methods

At Kopuatai bog, a 1500-metre long transect was established from the eastern edge towards the centre, and 2 m × 2 m plots marked out every 100 m ($n = 16$). Within the first 200 m, additional plots were established at 25 m or 50 m intervals because previous analysis of peat samples at the 16 initial plots showed the greatest decreases in N and P levels occurring between 0 m and 200 m (Schipper et al. 1998, Clarkson et al. 2004b). At each plot, plant heights were recorded, and newly matured leaf or culm samples were collected in November 2002 from *Leptospermum*, *Empodisma* (both present at all plots, $n = 20$), and *S. ferrugineus* (occurs only in bog centre, $n = 8$). On Chatham Island, similar samples were collected from *Dracophyllum* ($n = 28$) and *S. traversii* ($n = 29$, co-occurrences = 27) in plots along transects (200–800 m) at four sites sampled during a survey of restiad bogs in February 2001 (Clarkson et al. 2004a).

Foliage samples were dried for 24 hours at 60°C and ground to a fine powder in a ball mill (MM 2000, Retsch GmbH & Co, Haan, Germany). Sub-samples (10–13 mg) were analysed for $\delta^{15}N$ using an isotope ratio mass spectrometer (Europa Scientific 20-20 Stable Isotope Analyser, Europa Scientific Ltd, Crewe, U.K.). Leaf material of *Gunnera monoica* Raoul (Haloragaceae), with a $\delta^{15}N$ of −1.63 ‰ (referenced to urea: $\delta^{15}N = -0.45$ ‰ relative to air standard), was used as a running standard. The $\delta^{15}N$ abundances were calculated as follows:

$$\delta^{15}N = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000 \ (‰)$$

where R is the ratio of ^{15}N: ^{14}N. Regular referencing using IAEA standards showed the instrument achieves single sample precision and accuracy of better than ±0.2 ‰ for ^{15}N.

We tested the significance of linear regressions between δ^{15}N, total N, total P and N:P ratios in plants against peat nutrient levels (from Schipper et al. 1998, Clarkson et al. 2004a b), plant nutrient levels, and plant height to determine if there were any ecologically important correlations. In addition, paired *t*-tests were used to analyse differences between %N, %P, and δ^{15}N in foliage of co-occurring species.

We examined the mycorrhizal status of roots of species from selected plots along the transect at Kopuatai. For *Leptospermum*; two plants with intact roots were collected from each of plots 0 m, 300 m, and 1400 m ($n = 6$). Foliage samples were analysed for δ^{15}N, %N, and %P as described above, and included in the statistical analysis. Root samples of *Empodisma* and *S. ferrugineus* were obtained from plots 500 m, 1000 m, and 1400 m. Fine roots were carefully removed from the peat matrix, and prepared as outlined in Moyersoen and Fitter (1999). ECM and AM fractional colonisations were scored in 1 cm root pieces aligned on glass slides using a microscope (magnification ×200) following the intersection method described by McGonigle et al. (1990).

4.4. RESULTS

Kopuatai bog

At Kopuatai, *Leptospermum* height decreased following trends of decreasing peat P levels, and to a lesser extent, N levels in peat (Fig. 4.1). *Empodisma* did not show similar plant height gradients with decreasing nutrients, and *S. ferrugineus* was recorded only on low nutrient peats.

Correlations of foliage versus peat nutrients showed marked variation between N and P, and between species. Foliar P concentrations of *Leptospermum* and *Empodisma* were higher at the more nutrient-rich bog margin (Fig. 4.2a) and, where species co-occurred, *Leptospermum* had significantly higher P

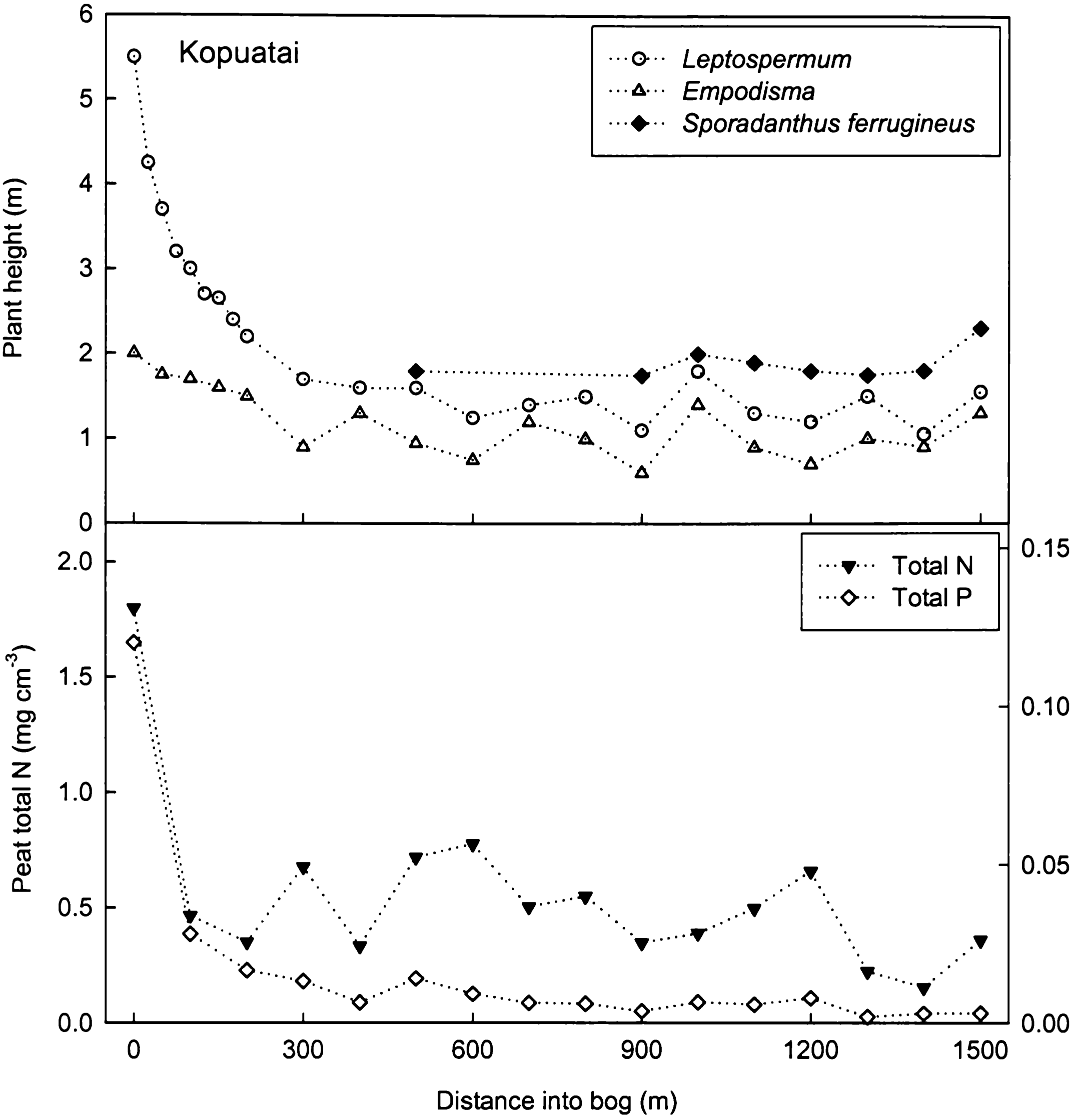

Figure 4.1 Height of dominant species (*Leptospermum scoparium, Empodisma minus, Sporadanthus ferrugineus*) from margin to 1500 m into Kopuatai Bog (above). Peat total N and total P data across the same gradient (below) are from Schipper et al. (1998), and Clarkson et al. (2004b).

concentration than *Empodisma* and *S. ferrugineus* (Table 4.1). In addition, foliage P concentration for *Leptospermum* was strongly positively correlated with P levels in the peat ($r^2 = 0.82$, $P < 0.001$, $n = 16$). Foliage P concentration for *Empodisma* was less strongly correlated with peat P ($r^2 = 0.44$, $P < 0.01$, $n = 16$) and not correlated for *S. ferrugineus* ($r^2 = 0.01$, $n = 8$). Foliar N levels were high on the more nutrient-rich peats but were not consistent on low nutrient peats (Fig. 4.2b). For co-occurring species, *Leptospermum* had significantly higher %N than both *Empodisma* and *S. ferrugineus*, and *Empodisma* had significantly higher %N than *S. ferrugineus* (Table 4.1). Foliage N concentrations and peat N levels showed

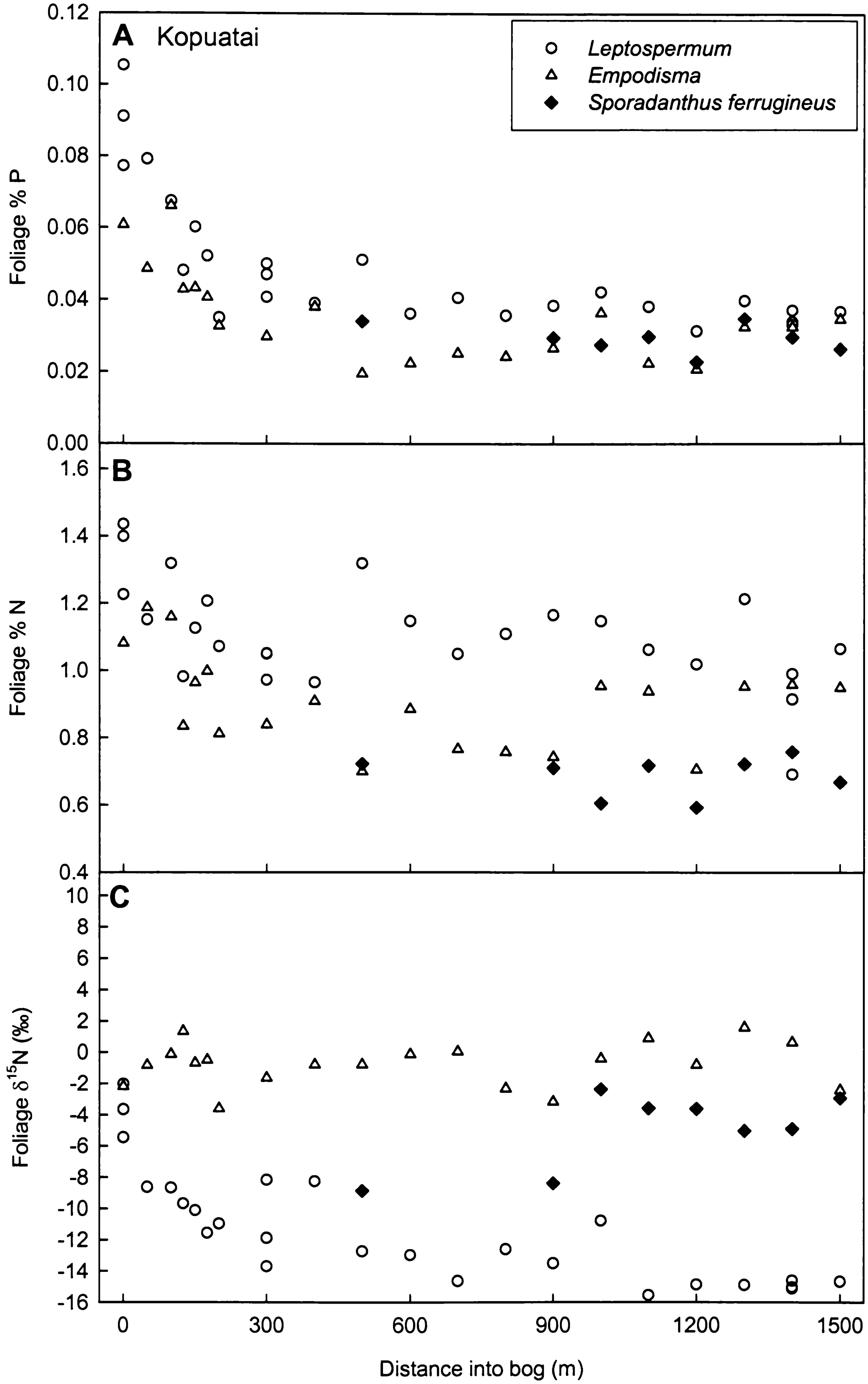

Figure 4.2 Foliage analyses of *Leptospermum scoparium*, *Empodisma minus*, and *Sporadanthus ferrugineus* from Kopuatai Bog margin to centre, A: %P, B: %N, C $\delta^{15}N$.

Table 4.1 δ^{15}N (‰), chemical composition, and paired *t*-test results, for foliage of co-occurring species at Kopuatai and Chatham Island bogs. Mean values are ± 1 SE. Significantly different means are followed by different letters in columns within blocks ($P < 0.05$).

	Variable				
Co-occurring species	%N	%P	δ^{15}N	N:P	*n*
Kopuatai					
Leptospermum scoparium	1.12 ± 0.03 a	0.047 ± 0.004 a	–11.75 ± 0.67 a	25.32 ± 1.22 a	20
Empodisma minus	0.90 ± 0.03 b	0.035 ± 0.003 b	–0.81 ± 0.32 b	26.57 ± 1.34 a	20
Leptospermum scoparium	1.11 ± 0.05 a	0.039 ± 0.002 a	–13.98 ± 0.56 a	29.23 ± 0.85 a	8
Empodisma minus	0.86 ± 0.04 b	0.028 ± 0.002 b	–0.77 ± 0.62 b	29.09 ± 1.58 a	8
Sporadanthus ferrugineus	0.69 ± 0.02 c	0.029 ± 0.001 b	–4.97 ± 0.86 c	22.03 ± 0.83 b	8
Chatham Island					
Dracophyllum scoparium	0.88 ± 0.02 a	0.065 ± 0.004 a	–6.14 ± 0.82 a	14.44 ± 0.74 a	27
Sporadanthus traversii	0.73 ± 0.04 b	0.031 ± 0.002 b	+0.20 ± 0.28 b	25.25 ± 1.20 b	27

weak correlations for *Leptospermum* ($r^2 = 0.29$, $P < 0.05$, $n = 16$) and no significant correlations for *Empodisma* ($r^2 = 0.02$, $n = 16$) or *S. ferrugineus* ($r^2 = 0.16$, $n = 8$).

Foliar δ^{15}N of *Leptospermum* ranged from –2.03‰ to –15.55‰, averaging –3.71‰ on the higher nutrient marginal peats (0 m) and –14.96‰ on the low nutrient peats of the central bog (1100–1500 m; Fig. 4.2c). This isotopic gradient along the transect was not seen in co-habiting *Empodisma* (range –3.60 to +1.58‰, mean = –0.12‰). Towards the centre of the bog, *S. ferrugineus* entered the transect and the δ^{15}N (range –2.38 to – 8.85‰, mean –4.97‰) was different from that of co-occurring *Empodisma* and *Leptospermum* (Figure 4.2c, Table 4.1).

Leptospermum scoparium foliar δ^{15}N was positively correlated with plant height ($r^2 = 0.80$, $P < 0.001$, $n = 20$), foliage %P (Fig. 4.3a, $r^2 = 0.69$, $P < 0.001$, $n = 26$), peat total P ($r^2 = 0.71$, $P < 0.001$, $n = 16$), peat total N ($r^2 = 0.47$, $P < 0.01$, $n = 16$) and foliage %N ($r^2 = 33$, $P < 0.01$ $n = 26$), and negatively correlated with foliage N:P ratio (Fig. 4.4a, $r^2 = 0.54$ $P < 0.001$, $n = 26$). Similar regressions for the restiad species showed no significant correlations. *Leptospermum scoparium* height was also positively correlated with peat total P ($r^2 = 0.93$, $P < 0.001$, $n =$

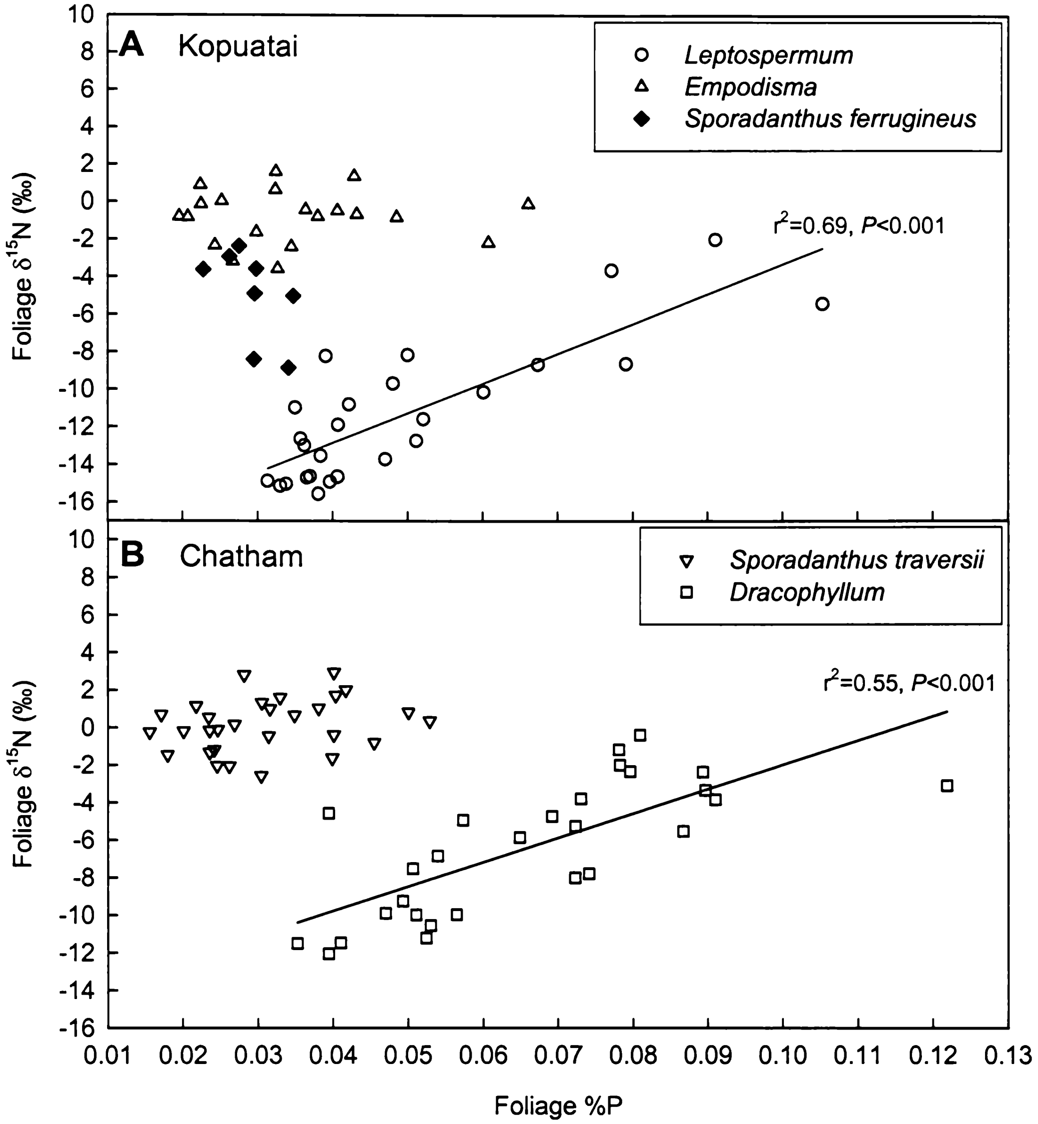

Figure 4.3 Relation between foliage $\delta^{15}N$ and foliage %P. A: *Leptospermum scoparium, Empodisma minus*, and *Sporadanthus ferrugineus* at Kopuatai Bog. B: *Dracophyllum scoparium* and *Sporadanthus traversii* at Chatham Island bogs. Significant trendlines are shown.

16), foliage %P ($r^2 = 0.88$, $P < 0.001$, $n = 20$), peat total N ($r^2 = 0.63$, $P < 0.001$, $n = 16$), and foliage %N ($r^2 = 0.31$, $P < 0.05$, n=20), and negatively correlated with foliage N:P ratio ($r^2 = 0.58$, $P < 0.001$, $n = 20$).

Chatham Island bogs

In Chatham Island bogs, foliage $\delta^{15}N$ for *Dracophyllum* (range –0.39 to –12.06‰) was positively correlated with foliage %P ($r^2 = 0.55$, $P < 0.001$, $n = 28$; Fig. 4.3b), peat total P ($r^2 = 0.40$, $P < 0.001$, $n = 28$) and peat total N ($r^2 = 0.22$, $P < 0.05$, $n = 28$), negatively correlated with foliage N:P ratio ($r^2 = 0.52$, $P < 0.001$, $n = 28$; Fig.

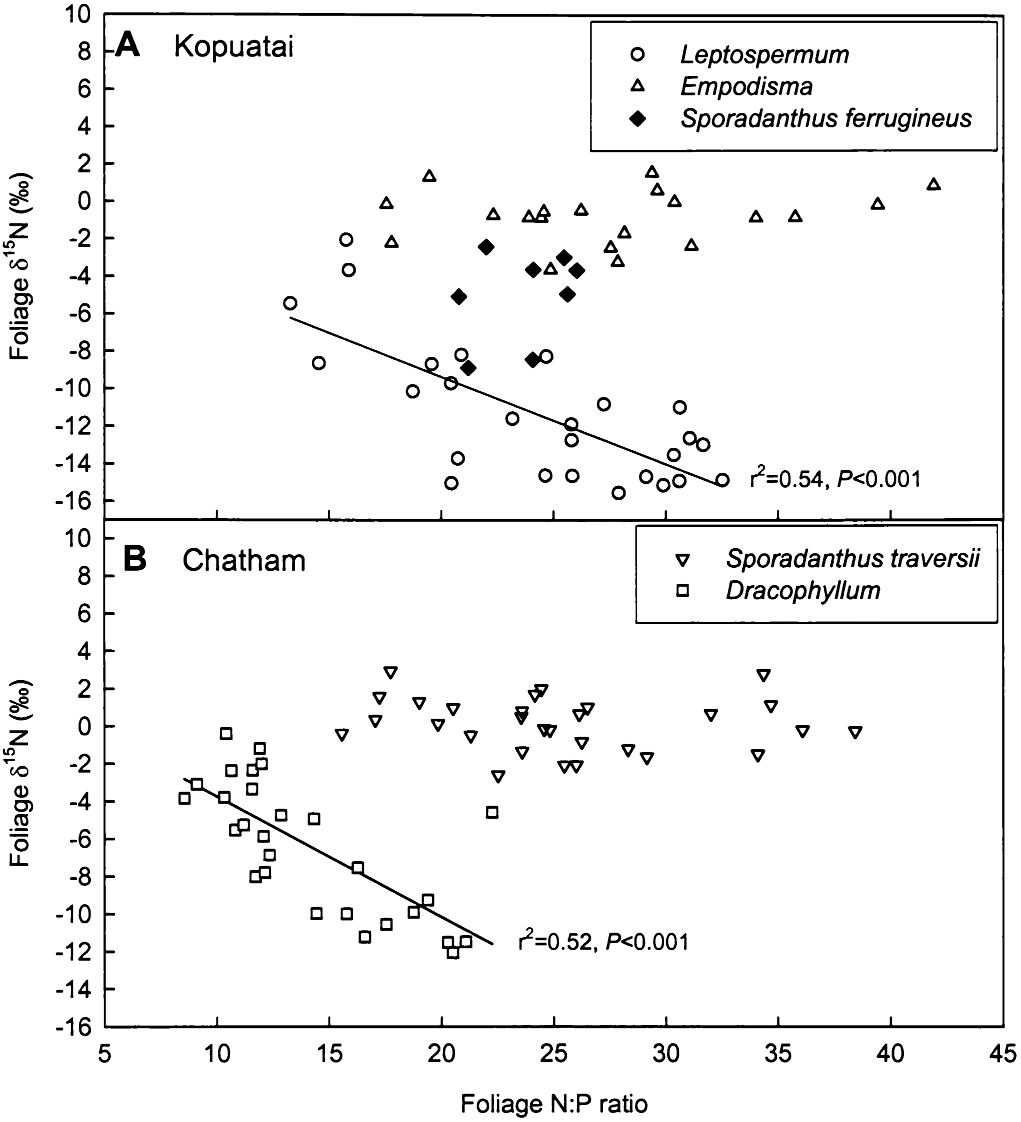

Figure 4.4 Relation between foliage $\delta^{15}N$ and foliage N:P ratio. A: *Leptospermum scoparium*, *Empodisma minus*, and *Sporadanthus ferrugineus* at Kopuatai Bog. B: *Dracophyllum scoparium* and *Sporadanthus traversii* at Chatham Island bogs. Significant trendlines are shown.

4.4b), and not significantly correlated with foliage %N. *Sporadanthus traversii* $\delta^{15}N$ ranged from –2.58 to +2.96‰, showing no significant correlations with any nutrient parameter. Foliage %N and peat %N were significantly correlated (positively) only for *S. traversii* ($r^2 = 0.32$, $P < 0.01$, $n = 29$) whereas foliage %P and peat total P were positively correlated for both species (*Dracophyllum* $r^2 = 0.27$, $P < 0.01$, $n = 28$; *S. traversii* $r^2 = 0.30$, $P < 0.01$, $n = 29$). Where the species co-occurred, *Dracophyllum* had significantly higher foliage %N and %P, more depleted $\delta^{15}N$, and lower N:P ratios than *S. traversii* (Table 1).

Mycorrhizas

The overall rate of mycorrhizal colonisation for *Leptospermum* decreased with increasing nutrient depletion (Table 4.2). Plants had both AM and ECM associations on the higher nutrient marginal peats, whereas ECM associations were absent from low nutrient peats (although fine roots were difficult to retrieve undamaged from the lowest nutrient peats). Plants having ECM associations were taller and more enriched in foliar ^{15}N than plants lacking ECM associations.

No mycorrhizal associations were detected in *S. ferrugineus*, and very limited colonisation by arbuscules, vesicles, and hyphae of AM (but no ECMs) were observed in *Empodisma*.

Table 4.2 Mycorrhizal status, and foliar δ^{15}N, %N, %P, and N:P ratio of six *Leptospermum scoparium* plants from Kopuatai

Distance in bog m	ECM % colonisation	AM % colonisation	No. of root intersects screened	Foliar δ^{15}N ‰	Foliar %N	Foliar %P	Foliar N:P ratio	Plant height m
0	62	4 c	27	−3.65	1.23	0.077	15.89	2.1[1]
0	6	57 ch	30	−5.44	1.40	0.105	13.28	2.4[1]
300	0	28 cav	36	−8.16	1.05	0.050	20.90	1.22
300	0	10 c	10	−13.70	0.97	0.047	20.74	1.16
1400	0	0	3	−14.61	0.92	0.037	24.64	0.51
1400	n.d.	n.d.	0	−15.12	0.99	0.033	29.89	0.52

c = coils, h = hyphae, a = arbuscules, v = vesicles, n.d. = not determined

[1] Small plants were selected for ease of transport and root retrieval; height of canopy plants = 5.5 m.

4.5. DISCUSSION

The restiad bogs displayed some of the largest within and between plant species δ^{15}N ranges (differences) recorded for a terrestrial ecosystem (see Nadelhoffer et al. 1996). At Kopuatai, *L. scoparium* had highly depleted δ^{15}N across all but the most nutrient-rich marginal peats (range = 13.5‰) and, on low nutrient peats, differed from co-existing *Empodisma* by an average of 13.2‰, with a maximum separation of 16.5‰. Large differences in δ^{15}N (up to 10–12‰) in co-habiting species have similarly been recorded in other nutrient-poor environments such as subarctic tundra (Michelsen et al. 1996, 1998, Nadelhoffer et al. 1996), subtropical wet heathland (Schmidt and Stewart 1997), and temperate bog-fen (Kohzu et al. 2003).

Changes in external P availability relative to internal plant demand have been shown to effect spatial changes in plant $\delta^{15}N$ across nutrient gradients in mangrove stands. For example, McKee et al. (2002) demonstrated dwarf trees with highly depleted $\delta^{15}N$ were P limited by adding P fertiliser to increase growth (Feller 1995) and plant $\delta^{15}N$ (McKee et al. 2002). The depleted $\delta^{15}N$ values associated with dwarfism were attributed to plant fractionation (following Fry et al. 2000) as a consequence of slower growth (as in Goerick et al. 1994) and reduced N demand (the lighter ^{14}N isotope being preferentially used). Fertilisation with P increased N demand and decreased fractionation because all N isotopes would be assimilated. Our results for the woody species have strong parallels with McKee et al.'s (2002) study; *Leptospermum* and *Dracophyllum* show equivalent trends of increasing $\delta^{15}N$ fractionation with decreasing P levels in foliage and peat, and with increasing plant N:P ratios (Figs. 4.3 and 4.4), despite being phylogenetically separate and growing in floristically dissimilar communities. Of the two heath shrubs, *Leptospermum* is more likely to be P-limited on low nutrient peats, having marked dwarfism, lower %P foliar concentrations (Table 4.1), more depleted $\delta^{15}N$, and higher N:P ratios (mean 25.32). Plant N:P ratio is used as an indicator of nutrient limitation in Northern Hemisphere wetlands, where N:P > 16 indicates P-limited sites and N:P < 13 indicates N-limitation (Güsewell and Koerselman 2002). Phosphorus limitation for *Leptospermum* is likely further exacerbated by the absence or reduction in mycorrhizal associations that normally enhance nutrient acquisition (particularly P). The hypothesis that *Leptospermum* is P-limited in late successional restiad bogs needs to be tested by field fertilisation experiments. Similar testing is also required for *Dracophyllum* in Chatham Island bogs.

Mycorrhizal presence and type (especially ERM and ECM) have been implicated as being major factors in N fractionation in natural habitats. In our study, normally mycorrhizal woody species at both Kopuatai (*Leptospermum*; ECM and AM) and Chatham Island (*Dracophyllum*; ERM) sites were consistently more depleted in

^{15}N on low nutrient peats, and had greater within species $\delta^{15}N$ ranges than normally NM herbaceous restiad species. Mycorrhizas (ECMs and ERMs) are known to fractionate N isotopes during the assimilation process, resulting in enriched ^{15}N in the fungal symbiont and depleted ^{15}N in the host plants (Michelsen et al. 1996, 1998, Hobbie et al. 1999, Kohzu et al. 2000). For *Leptospermum*, however, we confirmed ECM mycorrhizal associations only on the nutrient-rich marginal peat where isotopic depletion was least, indicating the $\delta^{15}N$ gradients are probably not attributable to mycorrhizal fractionation. Further work is required to test this hypothesis and to compare N fractionation in plants when acquiring N with and without mycorrhizal colonisation.

Nitrogen source and availability have also been linked with $\delta^{15}N$ depletion (Pennock et al. 1996, Erskine et al. 1998, Pearson et al. 2000, Emmerton et al. 2001,Yoneyama et al. 2001, Falkengren-Gerup et al. 2004). However, in our study, correlations between $\delta^{15}N$ and peat-N or foliage-N were not significant for restiad species, and weak ($r^2 < 0.48$) or not significant for heath shrubs, despite the presence of N gradients.

The lack of significant correlations between $\delta^{15}N$ and %N or %P for restiad species compared with woody species suggests fundamental species-specific differences in nutrient requirements and nutrient acquisition mechanism. Restiad species are known to be highly adapted to low nutrient levels and this could explain the lack of variation in $\delta^{15}N$. For example, restiad species in Australia have been shown to be extremely frugal users of mineral resources, having N and P tissue concentrations one third to one half of those of co-habiting taxa (Meney and Pate 1999). Similarly, our study showed foliage N and P levels in restiad species were significantly lower than in co-habiting shrub species. Restionaceae typically do not have mycorrhizally mediated nutrient uptake, although seasonal AM associations have been detected in some Australian species (Meney et al. 1993), and we found very low levels of AM in *Empodisma*. Instead, restiad species characteristically form cluster roots (including *Empodisma*; Lamont 1982, and *S. ferrugineus* and *S. traversii*; Clarkson et al. 2004a), consisting of a dense network of fine roots and root hairs that enhance nutrient acquisition in nutrient-poor environments (Lamont 1982, Meney et al. 1993). The combination of efficient nutrient-acquiring cluster roots, inherently low tissue nutrients, and high nutrient efficiency would contribute to restiad species being highly competitive in extremely oligotrophic raised bog environments.

4.6. ACKNOWLEDGEMENTS

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4.7. REFERENCES

Clarkson BR, Schipper LA, Clarkson BD (2004a) Vegetation and peat characteristics of restiad bogs on Chatham Island (Rekohu), New Zealand. New Zealand Journal of Botany 42:293–312

Clarkson BR, Schipper LA, Lehmann A (2004b) Vegetation and peat characteristics in the development of lowland restiad peat bogs, North Island, New Zealand. Wetlands 24:133–151

Emmerton KS, Callaghan TV, Jones HE, Leake JR, Michelsen A, Read DJ (2001) Assimilation and isotopic fractionation of nitrogen by mycorrhizal and nonmycorrhizal subarctic plants. New Phytologist 151:513–524.

Erskine PD, Bergstrom DM, Schmidt S, Stewart GR, Tweedie CE, Shaw JD (1998) Subantarctic Macquarie Island – a model ecosystem for studying animal–derived nitrogen sources using ^{15}N natural abundance. Oecologia 117:187–193.

Falkengren-Grerup U, Michelsen A, Olsson MO, Quarmby C, Sleep D (2004) Plant nitrate use in deciduous woodland: the relationship between N, ^{15}N natural abundance of forbs and soil N mineralisation. Soil Biology & Biochemistry 36:1885–1891.

Feller IC (1995) Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle* L.). Ecological Monographs 65:477–505

Fry B, Bern, AL, Ross, MS, Meeder, JF (2000) $\delta^{15}N$ studies of nitrogen use by the red mangrove *Rhizophora mangle* L. in South Florida. Estuarine, Coastal and Shelf Science 50:291–296

Goerick R, Montoya JP, Fry B (1994) Physiology of isotopic fractionation in algae and cyanobacteria. In: Lajtha K, Michener R (eds) Stable isotopes in ecology and environmental science. Blackwell Science, Oxford, UK, pp 187–221

Güsewell S, Koerselman W (2002) Variation in nitrogen and phosphorus concentrations of wetland plants. Perspectives in Plant Ecology, Evolution and Systematics 5:37–61

Hobbie EA, Macko SA, Shugart HH (1999) Interpretation of nitrogen isotope signatures using the NIFTE model. Oecologia 120:405–415

Kohzu A, Matsui K, Yamada T, Sugimoto A, Fujita N (2003) Significance of rooting depth in mire plants: evidence from natural ^{15}N abundance. Ecological Research 18:257–266

Kohzu A, Tateishi T, Yamada A, Koba K, Wada E (2000) Nitrogen isotope fractionation during nitrogen transport from ectomycorrhizal fungi, *Suillus granulatus,* to host plant, *Pinus densiflora.* Soil Science and Plant Nutrition 46:733–739

Lamont BB (1982) Mechanisms for enhancing nutrient uptake in plants, with particular reference to Mediterranean South Africa and Western Australia. The Botanical Review 48:597–689

McGonigle TP, Miller MH, Evans DG, Fairchild GL, Swan JA (1990) A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytologist 115:495–501

McKee KL, Feller IC, Popp M, Wanek W (2002) Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across a nitrogen vs. phosphorus limitation gradient. Ecology 83:1065–1075

Meney KA, Pate JS (1999) Seasonal growth and nutrition of Restionaceae. In: Meney, KA, Pate, JS (eds). Australian Rushes: biology, identification and conservation of Restionaceae and allied families. University of Western Australia Press, Nedlands, pp. 85–96

Meney KA, Dixon KW, Scheltema M, Pate JS (1993) Occurrence of vesicular mycorrhizal fungi in dryland species of Restionaceae and Cyperaceae from south-west Western Australia. Australian Journal of Botany 38:733–737

Michelsen A, Quarmby C, Sleep D, Jonasson S (1998) Vascular plant δ^{15}N natural abundance in heath and forest tundra ecosystems is closely related with presence and type of mycorrhizal fungi in roots. Oecologia 115:406–418

Michelsen A, Schmidt IK, Jonasson S, Quarmby C, Sleep D (1996) Leaf δ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53–63

Montoya JP, McCarthy JJ (1995) Isotopic fractionation during nitrate uptake by phytoplankton grown in continuous culture. Journal of Plankton Research 17:439–464

Moyersoen B, Fitter AH (1999) Presence of arbuscular mycorrhizas in typically ectomycorrhizal host species from Cameroon and New Zealand. Mycorrhiza 8:247–253

Nadelhoffer KG, Shaver G, Fry B, Giblin A, Johnson L, McKane R (1996) ^{15}N natural abundances and N use by tundra plants. Oecologia 107:386–394

Pearson J, Wells DM, Seller KJ, Bennett A, Soares A, Woodall J, Ingrouille MJ (2000) Traffic exposure increases natural ^{15}N and heavy metal concentrations in mosses. New Phytologist 147:317–326.

Pennock JR, Velinsky DJ, Ludham JM, Sharp JH (1996) Isotopic fractionation of ammonium and nitrate during uptake by *Skeletonema costatum*: implications for ^{15}N dynamics under bloom conditions. Limnology and Oceanography 41:451–459

Reed ML (1987) Ericoid mycorrhiza of Epacridaceae in Australia. In: Sylvia, DM, Hung, LL, Graham, JH (eds) Mycorrhizae in the next decade. Institute of Food and Agricultural Sciences, Gainesville, FL, USA, p 335

Schipper LA, McLeod M, Clarkson BR, Vojvodic-Vukovic M, Taylor M (1998) Gradients of microbial biomass, anaerobically mineralizable N and some physical properties in a restiad peat bog. International Peat Journal 8:71–75

Schmidt S, Stewart GR (1997) Waterlogging and fire impacts on nitrogen availability and utilization in a subtropical wet heathland (wallum). Plant Cell Environ 20:1231–1241

Schultze ED, Chapin FS III, Gebauer G (1994) Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406–412

Tester M, Smith SE, Smith FA (1987) The phenomenon of non-mycorrhizal plants. Canadian Journal of Botany 65:419–435

Verhoeven JTA, Koerselmann W, Meuleman AF (1996) Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. Trends in Ecology and Evolution 11:494–497

Yoneyama T, Matsamaru T, Usui K, Engelaar WMHG (2001) Discrimination of nitrogen isotopes during absorption of ammonium and nitrate at different nitrogen concentrations by rice (*Oryza sativa* L.) plants. Plant Cell Environ 24:133–139

5. NUTRITIONAL NICHE SEPARATION IN CO-EXISTING BOG SPECIES DEMONSTRATED BY ^{15}N-ENRICHED SIMULATED RAINFALL[4]

5.1. ABSTRACT

- *Empodisma minus* and *Sporadanthus ferrugineus* co-exist in raised bogs in New Zealand and have significantly different ^{15}N natural abundance signatures. Their root systems are spatially separated with *Empodisma* having a *c.* 50 mm thick surface layer of cluster roots overlying the deeper *Sporadanthus* roots. We hypothesized this root disposition allows *Empodisma* to preferentially access the primary N input from rainfall, thus establishing niche separation.

- We applied 1.6 mmoles m^{-2} of ^{15}N as $(NH_4)_2SO_4$ chased by 255 L m^{-2} of deionised water to simulate a rainfall event of 34 mm, then harvested cores after five hours for ^{15}N analysis.

- Ninety percent of the recovered isotope was in the upper *Empodisma* root layer. Seven weeks after application, *Empodisma* shoots were significantly enriched (mean $\delta^{15}N = +7.21‰$), whereas adjacent *Sporadanthus* shoots were not (mean $\delta^{15}N = -2.76‰$).

- The species acquire nutrients from different rooting zones, with *Empodisma* accessing nutrients at the surface from rainfall and *Sporadanthus* accessing nutrients from deeper peat layers. Niche differentiation facilitates species co-existence and may slow the rate of competitive displacement during long-term succession.

Key Words Nitrogen isotopes, tracer, raised bog, niche separation, *Empodisma minus*, *Sporadanthus ferrugineus*, Restionaceae

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[4] Submitted as Clarkson, B. R., Schipper, L. A., Silvester, W. B., *New Phytologist.*

5.2. INTRODUCTION

We have been attempting to elucidate plant-nutrient relationships in the development of New Zealand raised bogs characterised by members of the family Restionacaeae (= restiad bogs). Late successional restiad bogs in northern New Zealand are dominated by *Sporadanthus ferrugineus* and *Empodisma minus* and have exceedingly low levels of plant nutrients, particularly total and available N and P (Clarkson et al. 2004b). Earlier, we demonstrated that co-existing *Empodisma* and *Sporadanthus* have very different isotopic signatures ($\delta^{15}N$ means = –0.77‰ and –4.97‰ respectively), suggesting different N sources, acquisition, and/or plant demand (Clarkson et al. in press). Observational studies in restiad bogs have shown the two species have vertically displaced feeding root systems, with *Empodisma* forming a thick surface layer of fine roots and root hairs (= cluster roots) above *Sporadanthus* rhizomes and roots that penetrate more deeply into the peat (Campbell 1964; Meney & Pate 1999b; Clarkson et al. 2004a).

Co-existing species are predicted to occupy sufficiently different niches to ensure competitive exclusion for nutrients and other resources does not occur (Tilman 1985, 1997; Crawley 1997). In low nutrient environments, niche differentiation strategies include rooting at different depths (Sydes & Grime 1984; Kielland 1994), having inherently low nutrient demand (Meney & Pate 1999a), or utilising normally unavailable nutrient sources (Chapin et al. 1993; Tilman & Downing 1994). The sources, dynamics and methods of acquisition of nutrients of co-habiting species in natural ecosystems have been investigated in recent years using stable isotope methodology. Tracer ^{15}N techniques, in particular, have provided insights into niche differentiation in a wide range of ecosystems including tussock tundra (McKane et al. 2002), temperate forest (Nadelhoffer & Fry 1994; Currie & Nadelhoffer 1999), and old-fields (McKane & Grigal 1990).

We were interested in determining whether *Empodisma* and *Sporadanthus* were able to co-exist in an extremely oligotrophic environment by accessing different sources of nitrogen. As the main source of nutrient inputs in raised bogs is rainfall (Gore 1968; Mitsch & Gosselink 2000), we investigated whether the root disposition of *Empodisma* is better adapted to intercept atmospherically derived nutrients than that of *Sporadanthus*. Specifically, we used enriched ^{15}N to test the hypothesis that *Empodisma* accesses the primary source of incoming N in rainfall, while *Sporadanthus* accesses N from lower layers.

5.3. MATERIALS AND METHODS

Study sites

Two restiad peat bogs were used for this research, Kopuatai and Torehape. They are located on the Hauraki Plains, North Island, New Zealand, a rural area of extensive alluvial plains (mainly in pasture) and peat domes, bounded to the east, south and west by forest-covered mountain ranges, and to the north by the sea. The climate is mild, with mean air temperature 13.4°C and mean annual precipitation 1112 mm, with a winter maximum (New Zealand Meteorological Service 1973).

Most of the study was conducted 1500 m into the centre of Kopuatai Bog, a 10 000 ha largely intact restiad raised bog. At the study site (37° 25'S 175° 35'E, elevation <10 m, 15 km inland), the bog surface is raised 3 m relative to the margin and the peat is more than 7 m deep (Shearer 1997). The vegetation is dominated by erect clumps of *Sporadanthus*, up to 2.2 m tall, overtopping a dense understorey of sprawling, wiry-stemmed *Empodisma* (Fig. 5.1), with the ground virtually bare except for a dense mat of negatively geotropic *Empodisma* cluster roots. Typically, these plant communities in North Island bogs are species-poor, averaging 5 vascular and 1 non-vascular species per 4-m^2 quadrat (Clarkson et al. 2004b). The two restiad species make up the majority of the biomass, with above ground biomass for *Sporadanthus* and *Empodisma* at Kopuatai being 2100 and 1470 g m^{-2} respectively (Thompson et al. 1999).

The second study site was a peat mine progressively being restored following extraction of horticultural peat at Torehape Bog, 5 km northwest of Kopuatai Bog. Unlike Kopuatai, the Torehape mine has monotypic patches of both *Empodisma* and *Sporadanthus* in which we could be certain of root identity (Fig. 5.2).

Figure 5.1 Vegetation at the experiment location, Kopuatai Bog. The fern, *Gleichenia dicarpa*, is also present among the *Sporadanthus* and *Empodisma*.

Root profiles

For both *Sporadanthus* and *Empodisma*, we constructed profiles of root types with peat depth to define respective potential root uptake zones. Ten 2-m deep peat cores were collected under a *Sporadanthus/Empodisma* canopy at Kopuatai, and the presence of cluster roots (<0.5 mm diameter), absorbing roots (0.5–1.0 mm diameter) and anchor roots (>1.0 mm diameter) for each species determined at 50-mm intervals from the surface. These were compared with root profiles constructed from under monotypes of *Empodisma* and *Sporadanthus* at Torehape restoration site to test whether root morphology and distributional patterns were influenced by competition.

^{15}N natural abundance in peat profile

To provide reference values for the vertical distribution of ^{15}N natural abundance through the peat in the main root uptake zone at Kopuatai, two intact cores (600-

Figure 5.2 Young plants of *Empodisma* (above) and *Sporadanthus* (below) at Torehape mine restoration site.

mm depth) were collected from the experiment location. In the laboratory, peat samples were taken at 50-mm intervals down the core, oven dried at 60 °C for 24 hours, and then analysed for $\delta^{15}N$ (see below).

Tracer isotopes

Peat profile

We applied enriched ^{15}N (as ammonium sulphate) to the peat surface at sites co-dominated by *Sporadanthus* and *Empodisma*, followed by water to simulate N deposition in a typical rainfall event, and then determined the distribution of ^{15}N through the root/peat profile. Ammonium was used because it is the major inorganic form of N in rainfall in New Zealand (Wilson 1959). The experiment was carried out at Kopuatai Bog in late summer (March) 2003. Four plots, considered to be representative of the *Sporadanthus/Empodisma* late successional vegetation type, were established approximately 5 m apart. At each plot, a 100-mm diameter steel ring was placed on the cluster root surface and 100 ml of 1.9 mgL^{-1} ^{15}N (as 99 atom % excess ^{15}N ammonium sulphate dissolved in de-ionised water) was sprayed evenly within the ring using a 100-ml atomiser (equivalent to 1.6 millimoles of ^{15}N per m^2 of bog surface). Then 600 ml of de-ionised water was applied to the surface over a wider area (150-mm diameter) during the next 4 hours to distribute the ^{15}N down through the root/peat matrix. This simulated a rainfall event of 34 mm, equivalent to a typically high downpour for the area (New Zealand Meteorological Service 1973). Five hours after commencing the experiment, an intact peat core (120 mm diameter by 300 mm deep) centred on the ring, was removed using a stainless steel cylinder with a sharp cutting edge designed to slice through thick rhizomes and minimise peat compaction. Two of the four peat cores were immediately submerged in 1L 0.5*M* KCl to extract any surface adsorbed ^{15}N not taken up by the roots and then gently washed twice with de-ionised water. All cores were sealed in plastic bags and stored in ice-packed chilly bins. In the laboratory, cores were oven-dried at 60 °C for 72 hours and then sliced, using a band saw, into discs at 10, 20, 30, 50, 70, 90, 110, 200 mm from the peat surface.

Shoots

To determine whether the plants had taken up ^{15}N, newly sprouted *Empodisma* and *Sporadanthus* culms (50-mm length) growing in close proximity to the excavated cores ($n = 4$) were collected after 7 weeks. Samples for reference ^{15}N natural abundance were collected from the *Sporadanthus-Empodisma* vegetation type at least 20 m from the experiment location ($n = 9$). Shoots were dried at 60

°C for 24 hours and analysed for ^{15}N natural abundance. Co-existing *Empodisma* and *Sporadanthus* $\delta^{15}N$ values were compared using paired *t*-tests, and treatment groups were compared with two-sample *t*-tests. Data were log-transformed because of the large variation in $\delta^{15}N$ values and small sample size.

Nitrogenase activity

Nitrogenase activity was quantified for both *Empodisma* and *Sporadanthus* to assess the importance of biological nitrogen fixation as a source of N other than rainfall. This follows recent identification of N_2-fixing endophytic bacteria in some grasses (Hurek & Reinhold-Hurek 2003; Dalton et al. 2004), raising the possibility of similar endophytes occurring in restiads, which are phylogenetically closely related (Judd et al. 1999). Differential rates of N_2 fixation in *Empodisma* and *Sporadanthus* could also explain differences in their $\delta^{15}N$ signatures. The assay was conducted *in situ* using the acetylene reduction method as an indicator of nitrogenase activity (Silvester 1978, Weaver & Danso 1994). Sampling took place in spring (October 2004) at Torehape mine restoration site using three treatments: mono-dominant patches of *Empodisma* and *Sporadanthus*, and bare peat ($n = 6$). A steel cylinder of diameter 100 mm and length 300 mm with a sharp cutting edge was placed over the whole or part plant (or bare peat) after removing above ground culms, and pushed into the rhizome-root and/or peat matrix, leaving 50 mm of cylinder protruding above the surface. The top was sealed with plastic, and 60 ml of acetylene (15% of headspace) was injected through a duct tape portal. At t = 0, 3, and 27 hours, a 20-ml sample was extracted from the headspace and injected into pre-evacuated 13 ml Labco Exetainers. Subsamples (0.2 ml) from the exetainers were analysed for ethylene production from acetylene using a gas chromatograph equipped with a flame ionisation detector (Shimadzu GC-8A, Kyoto, Japan), and N_2 fixation rates calculated following Silvester (1989). Rates reported here are corrected for background traces of acetylene.

Nitrogen isotope analysis

For $\delta^{15}N$ analysis, peat and shoot samples were ground to a fine powder in a ball mill (MM 2000, Retsch GmbH & Co, Haan, Germany). Sub-samples (10–13 mg) were analysed for %N and $\delta^{15}N$ using an isotope ratio mass spectrometer (Europa

Scientific 20-20 Stable Isotope Analyser, Europa Scientific Ltd, Crewe, U.K.). The abundance of ^{15}N was expressed as $\delta^{15}N$ (‰) = (R_{sample} - R_{standard}) / R_{standard} x 1000, where R is the ratio of ^{15}N: ^{14}N. Regular referencing using IAEA standards showed the instrument achieves single sample precision and accuracy of better than ±0.2 ‰ for ^{15}N. All ^{15}N measurements ($\delta^{15}N$ and atom % excess ^{15}N) are referenced to air N_2.

To determine the mass of ^{15}N recovered in each peat sample (disc) from the isotope addition, the ^{15}N content was calculated by multiplying the atom % excess ^{15}N (atom % $^{15}N_{\text{sample}}$ – atom % $^{15}N_{\text{reference}}$) by µg N of each sample. Results were summed on a core-by-core basis to give total ^{15}N recovery.

5.4. RESULTS

Root profiles

At the mixed-species sites (Kopuatai), restiad feeder roots (cluster and absorbing) form a dense matrix confined to the upper 0–300 mm (Fig. 5.3). Within this matrix, the surface layer (0–50 mm) comprises solely *Empodisma* cluster roots, below which both *Empodisma* and *Sporadanthus* are present. Root profiles under individual plants at the monoculture sites (Torehape) showed similar vertical displacement of the two feeder root systems, with only *Empodisma* cluster roots forming extensive felt-like mats above the peat surface.

Non-feeding anchor roots originating from horizontally spreading rhizomes at both mixed and monoculture sites grew to depths of up to 1 m for *Empodisma* and more than 2 m for *Sporadanthus*.

Peat ^{15}N natural abundance

Peat $\delta^{15}N$ became less depleted with depth (Fig. 5.4), ranging from –2.59‰ at the surface to –0.94‰ at 600 mm depth. A significant depletion was observed at 300–350 mm, which coincided with a change in peat structure and consistency; from restionaceous peat to a more stringy cyperaceous peat interspersed with mainly *Sporadanthus* living anchor roots.

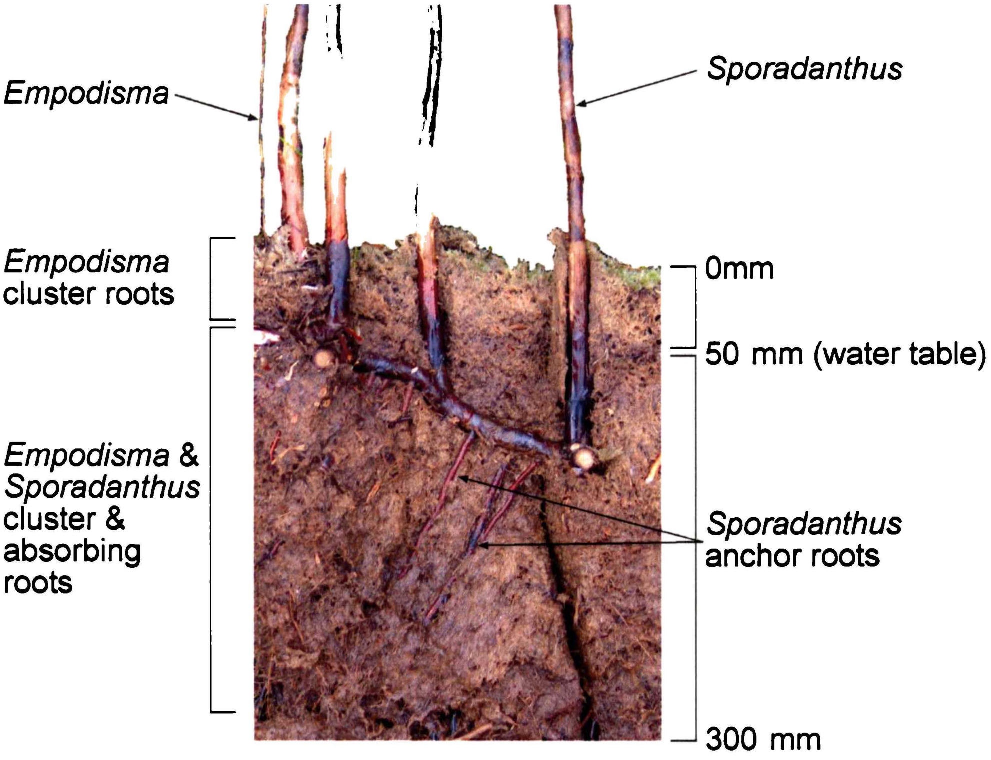

Figure 5.3 Peat sod excavated to show upper peat layers, roots and culm bases at Kopuatai. The top 300 mm of peat is shown, made up of a fine matrix of mainly *Empodisma* cluster roots. The *Sporadanthus* rhizome with anchor roots and culm bases grows at least 50 mm below the peat surface. The water table is 50 mm below the surface and can be distinguished by the light/dark peat interface.

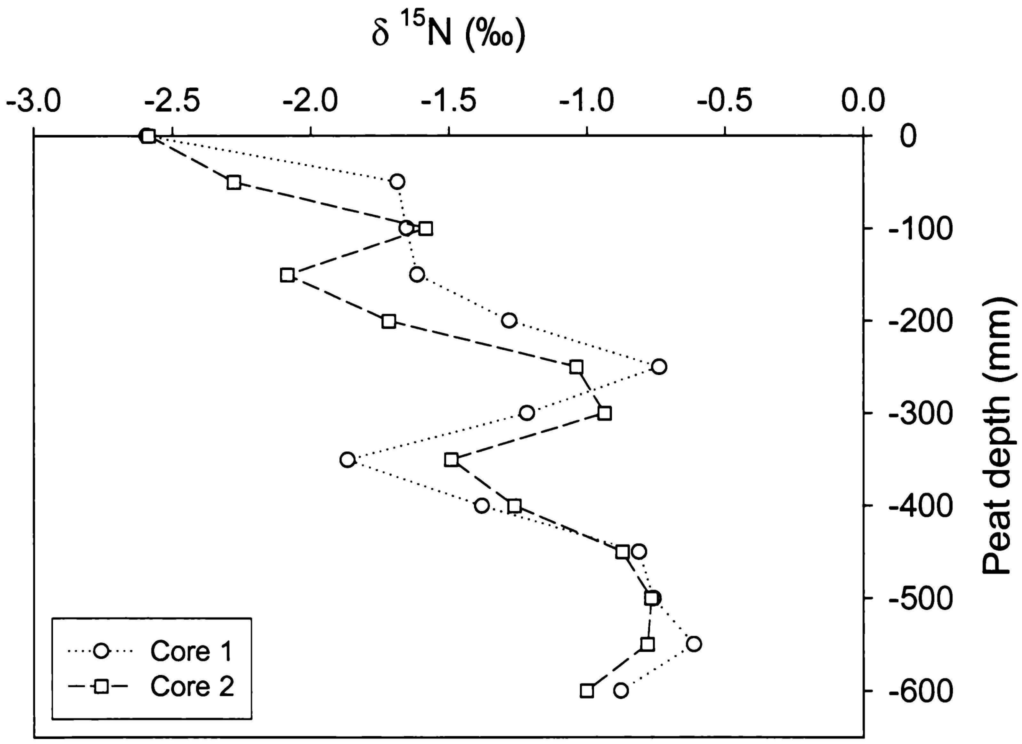

Figure 5.4 Changes in peat ^{15}N natural abundance with depth.

Tracer Experiment

Peat profile

For both KCl treated and untreated cores, $\delta^{15}N$ was extremely enriched in the uppermost 10 mm of surface roots/peat (range +687.7 to +1143.5‰) and rapidly became more depleted with increasing depth (Fig. 5.5). In total, 73–88% of the 190.23 µg of ^{15}N applied to the surface was recovered in the peat cores, and of this, 87–94% occurred in the uppermost 50 mm, with more than 50% in the top 10 mm layer (Table 5.1).

Shoots

Seven weeks after the addition of ^{15}N tracer, *Empodisma* shoots were significantly more enriched ($\delta^{15}N$ range +1.670 to +16.828) compared with both co-occurring ^{15}N-treated *Sporadanthus* shoots (range –5.087 to –0.966) and reference *Empodisma* shoots (Table 5.2). In contrast, for *Sporadanthus* there were no differences between ^{15}N-treated and reference shoots. Significant differences between reference *Empodisma* and *Sporadanthus* shoots were consistent with measurements by Clarkson et al. (in press).

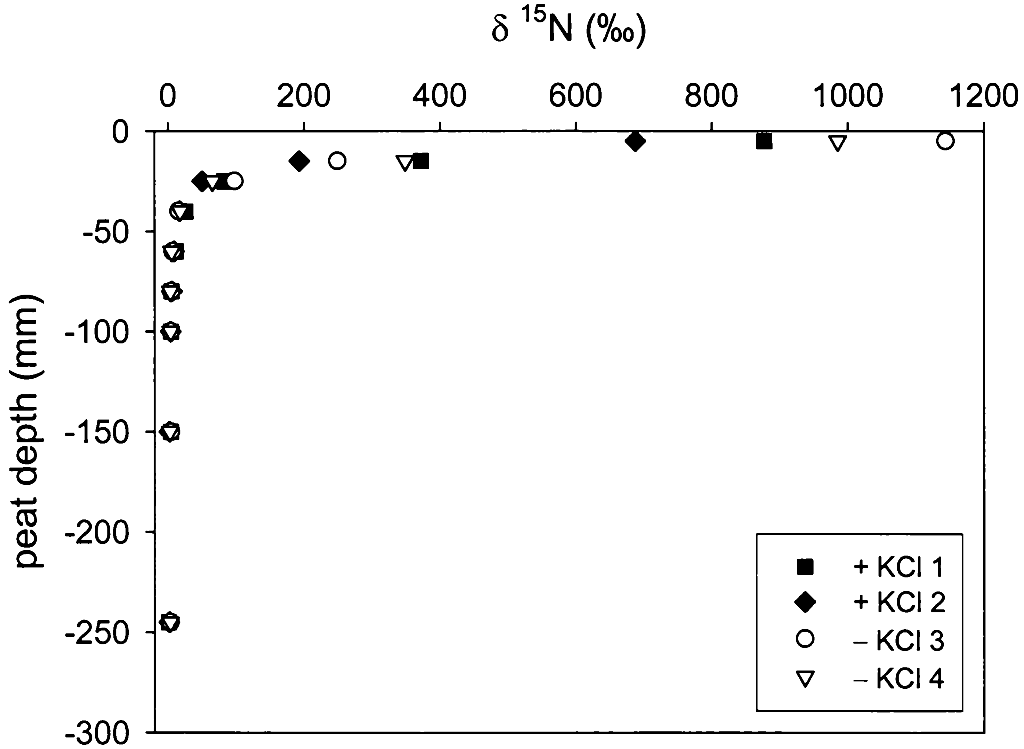

Figure 5.5 Vertical profile of $\delta^{15}N$ composition of peat cores following isotopic tracer addition. +KCl = KCl treated cores, –KCl = untreated cores.

Table 5.1 Vertical profile total ^{15}N recovered (µg ^{15}N core^{-1}) in peat cores after ^{15}N enrichment. +KCl, KCl treated cores, –KCl, untreated cores.

Depth	Core			
mm	+KCl1	+KCl2	–KCl3	–KCl4
0–10	79.87	84.97	99.40	100.32
10–20	35.06	26.58	22.02	43.77
20–30	8.95	5.53	7.56	9.79
30–50	5.38	3.65	3.52	4.50
50–70	3.27	2.13	1.86	1.49
70–90	1.84	1.33	1.44	1.48
90–110	2.03	1.70	1.29	1.26
110–200	5.75	5.20	4.63	2.33
200–300	4.50	7.82	4.08	3.36
Total ^{15}N µg	146.65	138.90	145.80	168.29
%^{15}N recovered[1]	77	73	77	88

[1] 190.23 µg ^{15}N applied per plot (1.9023 ppm N)

Table 5.2 Shoot δ^{15}N means (± SE) for *Empodisma* and *Sporadanthus* seven weeks following ^{15}N addition at Kopuatai Bog. *P* values are calculated from log data.

Treatment	Mean δ^{15}N ‰		*P* (paired *t*-test)	*n*
	Empodisma	*Sporadanthus*		
^{15}N tracer	+7.21 (±3.46)	–2.76 (±0.87)	0.037	4
Reference	–0.42 (±0.39)	–4.24 (±0.53)	0.002	9
P (two-sample t-test)	0.002	0.249		

Nitrogenase activity

Nitrogenase activity (acetylene reduction activity) was detectable in all cores except one from *Empodisma* and four from bare peat. After 3 hours, acetylene reduction activity for cores from *Sporadanthus* was significantly higher than for cores from *Empodisma* or bare peat (Table 5.3). After 27 hours, however, no significant differences between treatments were detected.

Table 5.3 Acetylene reduction activity means (± SE) after 3 and 27 hours for *Sporadanthus* and *Empodisma* at Torehape Bog restoration site, $n = 6$. Means in the same row followed by a different letter are significantly different ($P < 0.05$).

Time (h)	Mean acetylene reduction activity (μmol C_2H_2 m^{-2} h^{-1}) *Empodisma*	*Sporadanthus*	Bare peat	*n*
3	0.088 ± 0.037 a	0.207 ± 0.034 b	0.019 ± 0.012 a	6
27	0.026 ± 0.019 a	0.110 ± 0.070 a	0.002 ± 0.002 a	6

5.5. DISCUSSION

The restiad cluster root matrix is very efficient at accessing nitrogen entering the bog surface through precipitation as shown by the vertical trends of ^{15}N uptake following ^{15}N enriched simulated rainfall. Of the total ^{15}N recovered, more than half was absorbed at the surface (0–10 mm depth), and 90% was acquired within the uppermost 50 mm, which exclusively comprises dense living *Empodisma* cluster roots. *Sporadanthus* rhizomes, roots, and cluster roots were first encountered below *c.* 50 mm, indicating *Empodisma* roots would be better positioned to intercept aerially deposited N.

The dense root matrix absorbs NH_4^+-N readily, as shown by the negligible differences in total ^{15}N retrieved from cores extracted with KCl compared with controls, and the very high ^{15}N recovery rates overall (73–88%). An extensive fine-root surface area to 'soil' volume, providing abundant cellular negative charges that would attract NH_4^+ ions in an extremely nutrient-deficient environment, could explain the high uptake rates (Fitter 1997). This indicates accessible available NH_4^+-N in the oligotrophic raised bog environment would be rapidly absorbed into plant tissues rather than remaining externally adsorbed to root surfaces.

Microorganisms would also compete for N within the upper layer, but we have no data on the size of the microbial sink. However, any N assimilated by microbes would later be released in plant available form (Currie & Nadelhoffer 1999) within the *Empodisma* cluster root zone, and thus be relatively inaccessible to other plant species.

While acetylene reduction rates were near detection limits for the technique, they do indicate a low level of nitrogenase activity. Conversion of such rates to any reliable level of possible nitrogen fixation rates is fraught with difficulty (Silvester & Musgrave 1991) but an indicative N increment from this source can be calculated. The theoretical acetylene reduction/nitrogen fixation rate of 4:1 is used (Silvester 1989) and it is assumed activity occurs for 300 days per year. Using the 3-hour acetylene reduction rates, N inputs amount to 0.045 ± 0.019 and 0.104 ± 0.017 kg N ha^{-1} yr^{-1} for *Empodisma* and *Sporadanthus* respectively. As such rates are approximately 4 % of supposed rainfall N (inorganic) increments on the North Island (Wilson 1959), they must be considered ecologically insignificant in the present context.

The subsequent ^{15}N enrichment in shoots of *Empodisma* but not *Sporadanthus* further supports *Empodisma* being a better competitor for N from precipitation at or near the surface. The $\delta^{15}N$ of *Empodisma* reference shoots (mean = –0.53‰) was similar to rainfall $\delta^{15}N$ (NH_4^+) measured in temperate lowlands (100 km SE of Kopuatai; –1.23‰, WB Silvester & W Tozer unpublished data) and in the subarctic (+1.94‰; Michelsen et al. 1996). In contrast, *Sporadanthus* $\delta^{15}N$ values (mean = –2.59‰) were more similar to the more depleted values of peat than rainfall. These results suggest the vertical distribution of cluster roots by *Empodisma* denies access by *Sporadanthus* to the primary source of N to the bog by rainfall. In the absence of significant N fixation, *Sporadanthus* must obtain its N from the mineralisation of peat.

Sporadanthus may further avoid competition for resources by having an inherently low N demand, following Grime's (1977) stress tolerant strategy of plants growing on nutrient-poor soils. Green shoots of *Sporadanthus* were shown to have significantly lower N concentrations than those of co-existing *Empodisma* (means 0.69% and 0.86% respectively, Clarkson et al. in press). Very high nitrogen use efficiencies (NUEs) have been demonstrated in other species of Restionaceae. For example, Australian restiads thrive with extremely low concentrations of tissue nutrients (mean green shoot %N = 0.57, n = 4) compared with co-existing taxa, and are thus adapted to severely impoverished soils (Meney

& Pate 1999a). Further research on relative NUE of *Empodisma* and *Sporadanthus* should also include field fertilisation studies to test for N limitation.

Our tracer experiment demonstrates spatial partitioning in nutrient acquisition of two related, co-existing bog species with regard to atmospherically derived N inputs. The ecological significance of spatial partitioning for N as a limiting resource could be an effective mechanism in promoting co-existence as well as slowing the rate of competitive displacement on a successional time scale (McKane & Grigal 1990; Tilman 1997). During restiad bog succession *Empodisma* establishes before *Sporadanthus* but persists in significant amounts in late successional phases in which the taller, *Sporadanthus*, ultimately becomes the physiognomic dominant (Clarkson et al. 2004b). We have no data on whether *Sporadanthus* eventually displaces *Empodisma*, but autecological models predict *Sporadanthus* to dominate the lowest nutrient, late successional habitats (Clarkson et al. 2004b). Furthermore, anecdotal evidence (PM Bates pers. comm. to BRC 1974) suggests a depauperate vegetation type, with *Sporadanthus* the sole canopy species and *Empodisma* absent, covered several hectares of a late successional, older bog at Moanatuatua, 50 km SSW of Kopuatai, before being burnt, drained and converted to pasture. In the shorter successional time frame, at least, niche differentiation appears to be an effective mechanism for facilitating co-existence of *Empodisma* and *Sporadanthus* in nutrient deficient raised bogs.

5.6. ACKNOWLEDGEMENTS

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5.7. REFERENCES

Campbell EO. 1964. The restiad peat bogs at Motumaoho and Moanatuatua. *Transactions of the Royal Society of New Zealand, Botany* 2: 219–227.

Chapin FS III, Moilanen L, Kielland K. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* 361: 150–153.

Clarkson BR, Schipper LA, Clarkson BD. 2004a. Vegetation and peat characteristics of restiad bogs on Chatham Island (Rekohu), New Zealand. *New Zealand Journal of Botany* 42: 293–312.

Clarkson BR, Schipper LA, Lehmann A. 2004b. Vegetation and peat characteristics in the development of lowland restiad peat bogs, North Island, New Zealand. *Wetlands* 24: 133–151.

Clarkson BR, Schipper LA, Moyersoen B, Silvester WB. in press. Foliar ^{15}N natural abundance indicates phosphorus limitation of bog species. *Oecologia.*

Crawley MJ. 1997. The structure of plant communities. In: Crawley MJ, ed. *Plant ecology.* 2nd ed. London: Blackwell Science Ltd, 73–131.

Currie WS, Nadelhoffer KJ. 1999. Dynamic redistribution of isotopically labeled cohorts of nitrogen inputs in two temperate forests. *Ecosystems* 2: 4–18.

Dalton DA, Kramer S, Azios N, Fusasro S, Cahill E, Kennedy C. 2004. Endophytic nitrogen fixation in dune grasses (*Ammophila arenaria* and *Elymus mollis*) from Oregon. *FEMS Microbiology Ecology* 49: 469–479.

Fitter A. 1997. Nutrient acquisition. In: Crawley MJ, ed. *Plant ecology.* 2nd ed. London: Blackwell Science Ltd, 51–72.

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

Gore AJP. 1968. The supply of six elements by rain to an upland peat area. *Journal of Ecology* 56: 483–495.

Hurek T, Reinhold-Hurek B. 2003. *Azoarcus* sp. Strain BH72 as a model for nitrogen-fixing grass endophytes. *Journal of Biotechnology* 106: 169–178.

Judd WS, Campbell CS, Kellogg EA, Stevens PF. 1999. Plant systematics: A phylogenetic approach. Sunderland, Massachusetts, USA: Sinauer Associates.

Kielland K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* 75: 2373–2383.

Kohzu A, Matsui K, Yamada T, Sugimoto A, Fujita N. 2003. Significance of rooting depth in mire plants: Evidence from natural ^{15}N abundance. *Ecological Research* 18: 257–266.

Lima E, Boddy RM, Dobereiner J. 1987. Quantification of biological nitrogen fixation associated with sugar cane using a ^{15}N aided nitrogen balance. *Soil Biology and Biochemistry* 19: 165–170.

McKane RB, Grigal DF. 1990. Spatiotemporal differences in ^{15}N uptake and the organisation of an old-field plant community. *Ecology* 71: 1126–1132.

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastatter EB, Fry B, Giblin AE, Kielland K, Kwatkowski BL, Laundre JA, Murray G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415: 68–71.

Meney KA, Pate JS. 1999a. Seasonal growth and nutrition of Restionaceae. In: Meney, KA, Pate JS, eds. *Australian Rushes: Biology, identification and conservation of Restionaceae and allied families*. Nedlands, Australia: University of Western Australia Press, 85–96.

Meney KA, Pate JS. 1999b. Morphological and anatomical descriptions of Restionaceae and allied families and their distribution. In: Meney KA, Pate JS, eds. *Australian Rushes: Biology, identification and conservation of Restionaceae and allied families*. Nedlands, Australia: University of Western Australia Press, 161–461.

Michelsen A, Schmidt IK, Jonasson S, Quarmby C, Sleep D. 1996. Leaf $\delta^{15}N$ abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia* 105: 53–63

Mitsch WJ, Gosselink JG. 2000. *Wetlands,* 3rd ed. New York: John Wiley & Sons.

Nadelhoffer KJ, Fry B. 1994. Nitrogen isotope studies in forest ecosystems. In: Lajtha K, Michener R, eds. *Stable isotopes in ecology and environmental science*. Oxford: Blackwell Science, pp. 22–44.

New Zealand Meteorological Service. 1973. Summaries of climatological observations to 1970. *New Zealand Meteorological Service miscellaneous publication* 143. Wellington: Government Printer.

Shearer JC. 1997. Natural and anthropogenic influences on peat development in Waikato/Hauraki Plains restiad bogs. *Journal of the Royal Society of New Zealand* 27: 295–313.

Silvester WB. 1978. Nitrogen fixation and mineralisation in kauri (*Agathis australis*) forest in New Zealand. In: Loutit MW, Miles JAR, eds. *Microbial ecology*. New York/ Berlin: Springer-Verlag, 138–143.

Silvester WB. 1989. Molybdenum limitation of asymbiotic nitrogen fixation in forests of Pacific Northwest America. *Soil Biology and Biochemistry* 21: 383–289.

Silvester WB. 2000. The biology of kauri (*Agathis australis*) in New Zealand II. Nitrogen cycling in four kauri forest remnants. *New Zealand Journal of Botany* 38: 205–220.

Silvester WB, Musgrave, D. 1991. Free-living diazotrophs. In: Dilworth MJ, Glenn AR, ed. *Studies in plant science 1. Biology and biochemistry of nitrogen fixation*. The Netherlands: Elsevier, 162–186.

Sydes CL, Grime JP. 1984. A comparative study of root development using a simulated rock crevice. *Journal of Ecology* 72: 937–946.

Thompson MA, Campbell DI, Spronken-Smith RA. 1999. Evaporation from natural and modified raised peat bogs in New Zealand. *Agricultural and Forest Meteorology* 95: 85–98.

Tilman D. 1985. The resource ratio hypothesis of succession. *American Naturalist* 125: 827–852.

Tilman D. 1997. Mechanisms of plant competition. In: Crawley MJ, ed. *Plant ecology*. 2nd ed. London: Blackwell Science Ltd, 239–261.

Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363–365.

Tyler AC, Mastronicola TA, McGlathery KJ. 2003. Nitrogen fixation and nitrogen limitation of primary production along a natural marsh chronosequence. *Oecologica* 136: 431–438.

Weaver RW, Danso SKA. 1994. Dinitrogen fixation. In: Weaver RW, Angle S, Bottomley P, Bezdicek D, Smith S, Tabatabai A, Wollum A, eds. *Methods of Soil Analysis Part 2: Microbial and biochemical properties. Soil Science of America Book Series No.* 5. Wisconsin, USA: Soil Science of America Inc., 1019–1045.

Wilson AT. 1959. Surface of the ocean as a source of air-borne nitrogenous material and other plant nutrients. *Nature* 184: 99–101.

6. SYNTHESIS

6.1. DISCUSSION

This thesis research has added to our understanding of species–environment relationships in New Zealand restiad bogs and the mechanisms for species existence in low nutrient ecosystems. It has identified the major environmental determinants of vegetation patterns and dynamics and has developed a successional model of changes in species dominance over time (Chapter 2). It has compared and contrasted nutrient relationships of the dominant herbaceous (restiad) and woody (heath shrub) species within two geographically isolated, floristically dissimilar restiad bog systems, and their adaptations for nutrient acquisition (Chapters 3 and 4). Lastly, it has outlined a mechanism for niche differentiation in relation to N uptake in co-existing restiad species dominating nutrient-poor late successional bogs (Chapter 5).

Functional processes in New Zealand restiad raised bogs are similar to those in Northern Hemisphere raised bogs in which *Sphagnum* rather than restiad species dominates later, ombrotrophic phases. During restiad bog succession, the vegetation changes from early-successional sedges to mid-successional *Empodisma minus* to late-successional *Sporadanthus ferrugineus*, with concomitant decreases in nutrients (especially total N and total P), peat decomposition, and pH. The changes in environmental parameters parallel Northern Hemisphere trends of wetland development despite contrasting floristic composition (e.g., Zoltai and Vitt 1995).

Plant growth in northern herbaceous mires is commonly limited by either N or P (Bridgham et al. 1996), with wetlands being N-limited in early succession but becoming P-limited in later succession (Verhoeven et al. 1996). Similar trends are predicted in New Zealand mires based on correlational evidence of N and P concentrations, N:P ratios, degree of stuntedness of heath shrubs, and $\delta^{15}N$ depletion along the restiad bog development gradient (Chapters 2 and 4). However, the nature of the limitation on a community scale needs to be tested and refined, using techniques that have been developed for wetlands elsewhere.

Empodisma minus and *Sphagnum* are keystone species in raised bog formation in New Zealand and overseas respectively. Although phylogenetically far-related (vascular restiad versus non-vascular moss), they are the main peat formers and are considered to be functionally equivalent (Agnew et al. 1993). *Empodisma* forms a dense mass of cluster roots, which makes up the bulk of the peat, and has similar physico-chemical properties to *Sphagnum*. These include a high water-holding capacity (Campbell 1964), decay-resistant litter (Kuder et al. 1998, van Breeman 1995), and high base-exchange capacity (Agnew et al. 1993) enabling efficient absorption of nutrients from rainfall (Chapter 5). Both *Empodisma* and *Sphagnum* may be regarded as ecological engineers because they decrease competition from other plants through releasing compounds with allelopathic properties and creating acidic conditions (van Breeman 1995, Verhoeven and Liefveld 1997, Kuder et al. 1998).

The thesis results indicate that ecological dynamics in restiad bog ecosystems accord with ecological theory developed in other natural ecosystems. For example, successional changes in the bogs parallel aspects of the facilitation model of primary succession (Clements 1916, Connell & Slatyer 1977). In North Island restiad bogs, sedges and other initial wetland colonisers facilitate establishment of *Empodisma*, which, through peat accumulation and raised bog building, initiates ombrotrophic conditions suitable for establishment and eventual dominance of *Sporadanthus*. However, in the oligotrophic environments of late successional phases, competition for nutrient resources between co-habiting *Empodisma* and *Sporadanthus* is avoided by niche separation, resulting from differences in root morphology, disposition, and nutrient source. This is consistent with the theories of Hutchinson (1959), Tilman (1985) and McKane et al. (2002) on niche diversification as a mechanism for facilitating and prolonging species co-existence where resources are limiting.

6.2. DIRECTIONS FOR FURTHER RESEARCH

This thesis has identified the following areas of further research:

- In Northern Hemisphere herbaceous wetlands, plant N:P ratios have been shown to indicate N or P limitation of communities, with an N:P ratio <14 indicating N limitation, and a ratio >16 indicating P limitation (Verhoeven et al. 1996) . The correlational studies in this thesis have shown trends are similar in New Zealand wetlands but some species-specific differences (restiads versus heath shrubs) are apparent. The usefulness of N:P ratios as an indicator of N or P limitation on a community scale requires further testing in New Zealand wetlands by field fertiliser experiments. Suitable sites for future experimentation that encompass a wide range of N:P ratios have been identified in this thesis.

- The ^{15}N natural abundance studies revealed different plant functional types in restiad bogs respond differently to P gradients. Heath shrubs have significant correlations between foliar $\delta^{15}N$ and foliar %P, with ^{15}N depletion increasing as %P decreases, while the restiads show no such response to P gradients. These field data support evidence from a few recent studies in very different environments (Fry et al. 2000, McKee et al. 2002) showing that plant fractionation in some cases reflect P limitation. Further research on the applicability of using plant $\delta^{15}N$ as an indicator of P limitation is required in wetlands worldwide. Investigations should also be extended to terrestrial ecosystems in which nutrients are known to be limiting. For example, in early post-volcanic primary successions, tree-height gradients (increasing stuntedness with increasing proximity to eruptive source) may reflect similar trends in $\delta^{15}N$ and %P values. One potential site is recently erupted Mount Tarawera in central North Island, New Zealand, where strong tree height and nutrient gradients (Clarkson et al. 1995, Walker et al. 2003) and extensive ^{15}N fractionation (Tozer 2001) have been reported on the dome tops.

- The influence of mycorrhizal colonisation on plant ^{15}N depletion needs to be further investigated in wetland ecosystems. It is possible that decreasing mycorrhizal colonisation in mycorrhizal heath shrubs may cause the increasing plant ^{15}N depletion. Perhaps the mycorrhiza exerts a very small nitrogen fractionation compared with the host plant when acquiring nitrogen without colonisation. This would lead to plants being highly depleted when non-mycorrhizal and vice versa. The influence of nutrient availability and/or waterlogging on mycorrhizal colonisation of plants growing in ombrotrophic bogs also needs to be tested. For example, in extremely nutrient-deficient environments, the cost to the plant of providing C to the mycorrhizal symbiont may outweigh the benefits of enhanced nutrient, especially P, acquisition (Brundett 1991). This suggests there may be threshold nutrient (P) levels needed for mycorrhizal colonisation to occur before the plant obtains a net return in P through mycorrhizal uptake (cf. Grubb 1986).

6.3. REFERENCES

Agnew A. D. Q., Rapson G. L., Sykes M. T., Wilson, J. B. 1993: The functional ecology of *Empodisma minus* (Hook.f.) Johnson and Cutler in New Zealand ombrotrophic mires. *New Phytologist 124*: 703–710.

Bridgham S. D., Pastor J., Janssens J. A., Chapin C., Malterer T. J. 1996: Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands 16*: 45–65.

Campbell E. O. 1964: The restiad peat bogs at Motumaoho and Moanatuatua. *Transactions of the Royal Society of New Zealand, Botany 2*: 219–227.

Clarkson B. R., Clarkson B. D., 1995: Recent vegetation changes on Mount Tarawera, Rotorua, New Zealand. *New Zealand Journal of Botany 33*: 339–354.

Clements F. E. 1916: Plant succession: an analysis of the development of vegetation. *Carnegie Institution of Washington Publication 242.* Washington, DC, US.

Grubb P. J. 1986: The ecology of establishment. *Symposium of the British Ecological Society 24:* 83–97.

Hutchinson, G. E. 1959: Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist 93*: 145–159.

Fry B., Bern A. L., Ross M. S., Meeder J. F. 2000: δ^{15}N studies of nitrogen use by the red mangrove *Rhizophora mangle* L. in South Florida. *Estuarine, Coastal and Shelf Science 50*: 291–296

Kuder T., Kruge M. A., Shearer J. C., Miller S. L. 1998: Environmental and botanical controls on peatification-a comparative study of two New

Zealand restiad peat bogs using Py-GC/MS, petrography and fungal analysis. *International Journal of Coal Geology 37*: 3–27.

Malmer N., Albinson C., Svensson B. M., Wallen B. 2003: Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos 100*: 469–482.

McKee K. L., Feller I. C., Popp M., Wanek W. 2002: Mangrove isotopic ($\delta^{15}N$ and $\delta^{13}C$) fractionation across a nitrogen vs. phosphorus limitation gradient. *Ecology 83*: 1065–1075

McKane R. B, Johnson L. C., Shaver G. R., Nadelhoffer K. J., Rastetter E. B., Fry B., Giblin A. E., Kielland K., Kwiatkowski B. L., Laundre J. A., Murray G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415: 68–71.

Tilman D. 1985: The resource ratio hypothesis of succession. *American Naturalist* 125: 827–852.

Tozer, W. 2001: Nitrogen isotope ratios in nitrogen limited communities: determining origins of nitrogen. Unpublished M.Sc. Thesis. The University of Waikato, New Zealand.

van Breemen N. 1995: How *Sphagnum* bogs down other plants. *Trends in Ecology & Evolution 10*: 270–275.

Verhoeven J. T. A., Koerselmann W., Meuleman A. F. 1996: Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology and Evolution 11*: 494–497

Verhoeven, J. T. A., Liefveld W. M. 1997: The ecological significance of organochemical compounds in *Sphagnum*. *Acta Botanica Neerlanddica 46*: 117–130.

Walker, L.R., Clarkson, B. D., Silvester, W. B., Clarkson, B. R. 2003: Colonization dynamics and facilitative impacts of a nitrogen-fixing shrub in primary succession. *Journal of Vegetation Science 14*: 277–290.

Zoltai S. C., Vitt D. H. 1995: Canadian wetlands: environmental gradients and classification. *Vegetatio 118*: 131–137.