The role of *Empodisma minus* as the ecosystem engineer of the fen-bog transition (FBT) in New Zealand mires.

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Abstract

Mire ecosystem engineers create an acidic, nutrient poor and slowly permeable peat due to specific morphological, physiological and organo-chemical properties, changing the ecology of fens (high-nutrient, wet mires) so that they become bogs (low nutrient mires with drier surfaces), the so-called fen-bog transition. Observations on the development of raised restiad bogs in New Zealand support the concept of ecosystem engineering in forming raised mires, but involving the species *Empodisma minus* and *Empodisma robustum*, of the family Restionaceae.

The aim of this thesis is to examine the facility with which *Empodisma minus* fits the model of the ecosystem engineer of the fen-bog transition in New Zealand, and the techniques used to achieve that transition. A model for identifying mire engineers is proposed, based on the collated literature. Species best able to compete in the low nutrient raised mire environment possess morphological adaptations to increase nutrient capture, or traits which minimise nutrient losses (low tissue nutrient levels, high leaf longevity, high nutrient resorption prior to abscission). Whilst both *Empodisma minus* and *Chionochloa rubra* appear to possess nutrient retention and capture traits, Empodisma minus appears to out-compete *Chionochloa rubra* in low nutrient mires, implying superior nutrient capture or retention strategies.

In a survey of 70 mire communities in New Zealand – taking canopy biomass, soil physico-chemistry and the existence of capillaroid root growth and hummock-hollow topography into account - it is clearly shown that *Empodidma minus* is tolerant of a wide range of environmental conditions, thus enabling it to establish in minerotrophic fens, and persist after the fen-bog transition. In contrast to its widespread occurrence in wetland vegetation communities, extensive capillaroid root growth and the associated hummock-hollow topography occur less frequently. Despite P-limited growth being indicated, capillaroid root growth is infrequent or absent in coal pavement and pakihi communities, or where *Empodisma minus* is not the dominant canopy species. *Empodisma minus* appears to form capillaroid roots to maximise nutrient capture in the surface litter layer under a dense *Empodisma* canopy, and a complex relationship between capillaroid root formation, climate, canopy biomass and nutrients is indicated.

Lower tissue nutrient levels where the species co-exist in mires suggest *Empodisma minus* is a more frugal user of limiting nutrients than *Chionochloa rubra*, of importance as the growing surface of the mire becomes increasingly dependent on ombrotrophic (rainfall) nutrient sources as a result of peat accumulation. I studied the competitive relations between *Empodisma minus* and *Chionochloa rubra* in a 26 month long, de Wit replacement competition experiment. *Empodisma minus* is the superior competitor long-term in the oligotrophic conditions of the fen-bog transition and raised mire environments, providing a high water table is maintained; otherwise species co-existence will likely occur. These results suggest a dense *Empodisma* canopy is required to maintain the wet environment needed for apogeotropic root weft growth, which displayed plasticity in proliferation and placement.

To further examine nutrient retention and loss traits in *Empodisma minus* and *Chionochloa rubra*, I evaluated their production and decomposition characteristics in a 12 month Litter Decomposition Experiment in a montane transitional mire. *Empodisma minus* culms comprise much of the canopy biomass in wet, oligotrophic conditions of the mire environment, while *Chionochloa rubra* tussocks are reduced in density and biomass. Mass losses after 12 months were lowest from *Empodisma minus* capillaroid roots, which contain high fibre, and less P, K, and celluose than *Chionochloa rubra* below-ground biomass. Both *Empodisma minus* and *Chionochloa rubra* produce low nutrient, slowly decomposing foliar litters, with *Empodisma minus* withdrawing much of the nutrient content from its senescing culms. While a large component of total litter inputs in transitional restiad fens may be comprised of senesced *Empodisma minus* culms, the slower decay of *Empodisma minus* capillaroid roots suggest these contribute an increasing proportion of the accumulating organic matter after 12 months.

There is a significant relationship between short-term decay rates and location within the mire, however, this appears to be unrelated to the nutrient content or geochemistry of the substrate, and may reflect the influence of hummock-hollow topography and/or hydrology on decomposition.

Empodisma minus possesses both mechanisms employed in engineering the fen-bog transition - superior nutrient capture and nutrient retention - which results in increased production of slowly decaying capillaroid roots and foliage in oligotrophic mires, and hence increased peat accumulation. The mechanisms enable *Empodisma minus* to engineer the fen-bog transition in New Zealand mires.

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List of Abbreviations

BD	Bulk density
C:N	Carbon:Nitrogen ratio
CEC	Cation exchange capacity
Cond	Conductivity
EE	Ecosystem Engineer
FBT	Fen-Bog Transition
ICP-MS	Inductively coupled plasma mass spectrometer
k	Decay rate constant
LOI	Loss on Ignition
M_0	Initial mass
Moist	Moisture content
M_t	Final mass
N:P	Nitrogen:Phosphorus ratio
PCA	Principal components analysis
PVC	Polyvinyl chloride
REI	Relative Efficiency Index
RYT	Relative Yield Total
TC	Total carbon
TN	Total nitrogen
TK	Total potassium
TP	Total phosphorus
TY	Total Yield
VP	Von Post decomposition index
WCI	Wetland condition index
X_0	Initial nutrient content
X_1	Final nutrient content
Y	Yield

Chapter 1: General Introduction

Empodisma species are a common component of New Zealand and Australian wetland communities, including mires (peat accumulating wetlands). They are widely distributed, being found throughout New Zealand, eastern and southern Australia and Tasmania, from sub-alpine to sea-level, in a wide variety of wetland habitats. As a member of the Restionaceae, they have many characteristics typical of species adapted to dry, mediterranean habitats, and it is due to their eco-hydrological characteristics that raised mires can form in the summer dry regions of New Zealand (McGlone, 2009). While not as commercially important as a source of peat as *Sphagnum*, *Empodisma* peat still represents a large carbon sink and reservoir, and the peat based soils of New Zealand's agricultural heartland owe much to its previous abundance.

Although *Empodisma* dominated raised mires and pakihi are still relatively common within some regions of New Zealand (Southland, Westland, Waikato), most accounts of this vegetation type throughout New Zealand were confined to descriptive studies, with experimental investigation of mire functioning being a recent development (e.g. (Campbell & Williamson, 1997); Clarkson *et al.*, 2005; 2009; Fritz *et al.*, 2008) confined largely to sites dominated by the recently described northern species *Empodisma robustum* above latitudes of 38°S (Wagstaff & Clarkson, 2012).

Empodisma minus peatlands, or wire rush rushland communities as they were previously known, comprise dense swards of *Empodisma minus* forming a large component of the canopy layer, interspersed with a characteristic suite of erect and sprawling epacrid shrubs and large tussock grasses (e.g. *Dracophyllum*, *Leptospermum*, *Chionochloa*). These mires are also characterised by hummock-hollow topography scattered with small tarns, rather than the extensive lawns often associated with New Zealand *Sphagnum* communities. In addition to supporting a distinctive vegetation community, these sites are acidic, often overlying extensive peat deposits, and provide habitat for rare fauna such as the NZ fernbird (*Megalurus punctatus*).

1.1 Investigating the formation of raised mires

Traditional views of raised mire development utilise a model incorporating the effects of allogenic (factors external to the mire, e.g. climate) and autogenic (internal mire) processes, without clearly identifying the role that mire plant species might play in the process. For example, Hughes & Barber (2003), when commenting on the transition of a fen to a raised bog (also termed the FBT), initially state that "All that is required for ombrotrophic conditions to develop is the separation of the mire growing surface from the supply of surface and sub-surface waters". While the contribution of plant species to the fen-bog transition (FBT) is acknowledged later, and in preceding papers (Hughes 2000; Hughes *et al*., 2000; Hughes & Dumayne-Peaty 2002), the oversimplification of the process in the literature may have historically led to the dismissal of the important part that individual plant species contribute to the mire development process.

Mire ecosystems are not the result of a single successional process, nor can the various New Zealand mires be viewed as merely stages in an orderly development of plant communities towards a single, fixed mire community. Rather, each mire is the net result of of the interplay of numerous ecological processes during the development of the mire. Topography, bedrock geology and catchment hydrology are clearly related to individual mire initiation, however, the general direction of mire development is primarily influenced by autogenic processes such as peat accumulation, oligotrophication and acidification, which are mediated by the mire ecosystem (Rydin & Jeglum, 2006). Mire succession can be studied by exploring changes in paleoecology or geological evidence using macrofossils or pollen records (Horrocks & Ogden 1998a), by examining chronosequences of mires within a region (Clarkson *et al.*, 2004), or using a modelling approach (Frolking *et al.*, 2010). Due to the slow rate of successional change in mires, experimental studies are required to determine the mechanisms behind succession, utilising the manipulation of light, water and nutrient resources (Hajek *et al.*, 2008).

Species dominance during the various stages of mire development is determined by aspects of plant ecology (e.g. relative growth rate, seed dispersal), as affected by edaphic and hydrological factors. In addition, the plant community can itself bring about change in the environment, for example, by changing nutrient availability via litter production (Berendse, 1998). Change in the mire environment may affect ecosystem processes, leading to species replacement, directly influencing rates of peat accumulation, and therefore mire development (Kuhry *et al.* , 1993). The degree of autonomy of a mire increases as mire development proceeds (Korhola, 1992). Although external disturbances such as fire can alter mire developmental pathways, these changes are usually temporary in nature (Zobel & Masing, 1987; Robichaud & Begin, 2009).

While several paradigms have sprung up in recent times to describe the interaction of species and environment, such as the Extended Phenotype (Dawkins 1982), Positive Feedback Switches (Wilson & Agnew, 1992), Ecosystem Engineering (Jones *et al.*, 1994), and Niche

Construction (OdlingSmee, 1988), ecosystem engineering has been by far the most utilized concept (1653 Citations of Jones *et al.*, 1994 in Web of Science). The concept has been extensively applied to a variety of life forms including beavers (Wright *et al.*, 2002) and caterpillars (Lill & Marquis, 2003). The ecosystem engineering concept addresses two linked biotic processes: (i) the way certain species alter the physical environment; and (ii) how these changes then alter the biota (Jones & Gutierrez, 2007). Such species are called Ecosystem Engineers; engineers are "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials" (Jones *et al.*, 1994). More specifically, autogenic engineers "change the environment via their own physical structures, i.e. their living and dead tissue" (Jones *et al.*, 1994). The impacts of engineers may be small or large, positive or negative, resulting in competition or facilitation with other species for altered resource flows (e.g. carbon, nutrients), and result in increased or decreased species richness in the engineered environment (Wright & Jones, 2004).

The literature supports the view that some mire species may increase peat deposition, altering the physical and chemical environment of the mire, bringing about the FBT (Van Breeman, 1997). *Sphagnum fuscum* is known as an ecosystem engineer in Northern Hemisphere mires, but although New Zealand contains several species of *Sphagnum*, the literature suggests they do not appear to play an engineering role here (Wilmshurst *et al.,* 2003). Instead, *Empodisma* species have been proposed as the ecosystem engineers (Van Breeman, 1997; Charman, 2002). While a superficial examination of the literature might suggest *Empodisma* and *Sphagnum* share similar engineering properties, unlike *Sphagnum*, *Empodisma'*s role as a mire engineer has not been closely examined.

The importance of the ecosystem engineering concept has been highlighted recently in the literature due to its application to invasive engineering species (Crooks, 2002), and the amelioration of harsh environments by engineers leading to invasion by exotic species (Badano *et al.*, 2007). The application of mire engineering principles to a wider range of species is also demonstrating the ubiquity of engineering in the mire environment (Dommain *et al.*, 2010).

In general, the field of mire development, or succession, has become a timely issue in mire ecology. Further knowledge of mire ecosystem function is essential, given the declining state of New Zealand wetlands, especially with the expansion of intensive agriculture in Southland, and changing climate conditions. While Clarkson *et al.*'s (2005; 2009) research has shed considerable light on the function and ecological processes of northern lowland restiad mires, less is known of the causal mechanisms leading to changes in southern restiad mires dominated by *Empodisma minus*.

Ecosystem engineering (Jones *et al.*, 1994) offers a useful framework within which to address the autogenic driving forces behind southern restiad mire development. The purpose of this thesis is address the concept of *Empodisma minus* as an engineer. I examine existing literature that supports the concept of *Empodisma minus* as an ecosystem engineer of the New Zealand FBT, placing the information in the context of the current model for *Sphagnum* as an ecosystem engineer. I examine biotic processes such as competition in the acidic, oligotrophic environment created during the engineering process, and I examine more closely crucial traits underlying the construction of the raised mire environment, the production of decomposition resistant litter, and the growth of capillaroid roots.

1.2 Thesis structure

This thesis is organised in eight chapters.

Chapter One (Introduction) contains a brief background, general aims, and terminology used in the thesis.

Chapter Two (Literature Review) gives a brief overview of the Ecosystem Engineering concept and its application in mires, the process of mire development and the fen-bog transition, and also introduces likely engineers in New Zealand mires.

Chapter Three (Field Survey) examines a range of wire rush-tussock mires throughout New Zealand, describing community composition, physical and chemical gradients, the effect of disturbance on current community composition, examines the community types for the presence of engineering traits, and then compares these findings to those from previous studies in New Zealand restiad mires.

Chapter Four (Hodges & Rapson, 2010) outlines a model for mire engineering, surveying the literature in support of specific engineers from Northern and Southern Hemisphere mires.

Chapter Five (Competition Experiment) examines a competition experiment between two putative ecosystem engineers (*Empodisma minus* and *Chionochloa rubra*), along an artificial fen-bog gradient.

Chapter Six (Litter Experiment) compares short-term litter decomposition rates of *Empodisma minus* and *Chionochloa rubra* foliar and root litters along an internal mire gradient in a tephratrophic fen, and also discusses the an alternative nutrient source for cluster root bearing species such as *Empodisma* in the tephratrophic mires of the central North Island.

Chapter Seven contains a summary of the preceding four chapters.

Chapter Eight contains the final synthesis, conclusions and suggestions for further research

Appendices (CD in back packet) contain expanded methods, vegetation and chemistry results in support of the previous chapters.

1.3 Terminology and Nomenclature

The wetland classes of bog, fen and pakihi will be used as the basis for classification of peatlands and similar vegetation types formed on ultra-infertile, acidic peat accumulating substrates of poor drainage.

Bog, raised bog, and ombrotrophic bog/mire will be used interchangeably to refer to peatlands receiving water supply from rainfall only, and therefore unaffected by groundwater and nutrients from adjacent mineral soils. Bogs are subsequently nutrient poor, acidic (pH 3-4.8), with a water table approaching the peatland surface (Johnson & Gerbeaux, 2004).

Fen, or minerotrophic fen, refers to a peatland receiving water and nutrient inputs from adjacent mineral soils. Fens have a high water table, moderate nutrient status and a pH 4-6 (Johnson & Gerbeaux, 2004).

Pakihi will be used to describe wetlands formed on level or sloping surfaces in areas of high rainfall. As a result the substrate, which may contain little peat, is severely leached, extremely infertile, acidic (pH 4-5.1) and poorly drained, though prone to occasional drought conditions (Johnson & Gerbeaux, 2004).

Peatland is synonymous with mire, referring to all peat accumulating wetlands, and the two terms will be used interchangeably.

Tussockland will be used to refer to a vegetation community with a high (20-100%) cover of *Chionochloa* species.

Wire rush rushland will be used to refer to a vegetation community dominated by wire rush, *Empodisma* species.

Capillaroid roots, negatively geotropic roots, apogeotropic roots, and root weft will all be used to refer to *Empodisma* cluster roots.

Species nomenclature follows Allan (1982), Moore & Edgar (1976), Healy & Edgar (1980), Webb *et al*., (1988) and Edgar & Connor (2000), except where recent taxonomic changes have been suggested (www.pcn.org.nz).

Chapter 2: *Empodisma minus* as the ecosystem engineer of the New Zealand fen-bog transition: previous research.

2.1 Introduction

This literature review firstly introduces the mire or peatland habitat, and the concept of mire succession whereby a raised mire is formed. The aim is to address recent changes in New Zealand wetland classification, clarify the concept of the fen-bog transition in mire succession, presenting the opposing ideas concerning the role of autogenic and allogenic processes in mire development, and in doing so also introduce the terminology used elsewhere in the thesis.

The second section of this review introduces the concept of ecosystem engineering. The aim is to trace the introduction of the concept, reviewing definitions, initial criticism and refinement of the concept as usage increased, and then moving to highlight its application in framing evidence for the autogenic development of raised mires. This review is deemed necessary, as the ecosystem engineering concept is relatively new, attracting both criticism and application since its inception. The general concept will be introduced first, followed by its application to mire succession involving members of the *Sphagnum* genus in the literature. In doing so, I aim to demonstrate the need for a further model to identify ecosystem engineers and engineering processes within mires.

The third section of the review aims to shift the focus to New Zealand mires. I examine the fen-bog transition in local mire development, and support for *Empodisma minus* and other species as ecosystem engineers in New Zealand mires. This review is deemed necessary due to recent taxonomic revisions of the *Empodisma* genus, which have separated *Empodisma minus* from much of the evidence previously used to support the ecosystem engineering claim. In doing so, I aim to highlight the knowledge gap that exists, and those aspects to be addressed in this thesis.

2.2 From mire to peat

Approximately 50% of the world's wetlands are peatlands, or mires, covering an estimated 4 million km^2, and containing 5 x 10^{12} m^3 of peat (Lappalainen, 1996). The majority of mires are formed in the Northern Hemisphere arctic, boreal and north temperate zones, with 1.2 million km^2 in Canada, and 220,000 km^2 in Fennoscania (Gore, 1983; Mitsch & Gosselink, 2000). While major peatlands occur in the Southern Hemisphere in South America, New Zealand, the Sub-

Antarctic Islands and Tasmania, their size is small in comparison to the Northern Hemisphere peatlands. The New Zealand Land Resource Inventory estimated that in the mid 1990's New Zealand contained 3,113 km^2 of wetlands, of which 43,900 ha were pakihi, and 35,600 ha were forest-pakihi associations (Cromarty & Scott, 1996). This represents a small fraction of their original extent. Changes in nutrient budgets, hydrological regimes, vegetation community composition, fire, sediment loads and exotic species incursions have led to biodiversity losses, peat shrinkage or loss, loss of wetland functioning and ecosystem services (Horrocks *et al.*, 2002; Green & Clarkson, 2005). Many of the remaining wetlands now comprise small remnants, of eutrophic lowland wetland types, which contain a limited species pool (McGlone, 2009), and which lack buffering from surrounding land use practices. Northern lowland restiad mires formerly extended from Kaitaia to Te Awamutu (Clarkson, 2002), the mire type now largely confined to three mires in the Waikato region, comprising 3000ha of the original 100,000ha of restiad mires (de Lange *et al.*, 1999). Drained mires within this region include the Komakorau (216 km^2) Rukuhia (345 km^2), Moanatuatua (85 km^2) and Torehape mire (100 km^2), of which a small reserved area (654 ha) remains (Champion, 1997).

The mire type formed depends upon the specific combination of climate, geology and hydrology at each site (Moore & Bellamy, 1974). A minimum peat depth is required to classify a site as a mire, though the peat depth varies between countries. An early classification suggests mires contain a basal peat deposit greater than 30cm deep (Heathwaite *et al*., 1993). The International Mire Conservation Group (IMCG) also states a minimum of 30 cm peat depth (Joosten & Clarks, 2002), although Canadian definitions require a 40 cm minimum (National Wetlands Working Group, 1997). The New Zealand wetland classification system does not specify a minimum depth or percentage organic matter content in the substrate, referring instead to substrates being peat (bog) or mainly peat (fen) (Johnson & Gerbeaux, 2004).

Peat consists of the accumulated partially decomposed remains of plants and animal constituents, with a variable amount of mineral matter (Davoren, 1978; Clymo, 1983; Rydin & Jeglum, 2006). Peat forms in situ, i.e. is a sedentary material, and much of the original biomass may originate from below-ground (Rydin & Jeglum, 2006). Peat forms under dense vegetation cover, where the soil is permanently waterlogged, though not permanently inundated (McCraw, 1987). A positive water balance is also required for mire development, i.e. precipitation must exceed evapotranspiration (Mitsch & Gosselink, 2000). The seasonal distribution of rainfall is also important, as a humid climate is required year round, and mires do not generally form in regions with hot, dry summers (Mitsch & Gosselink, 2000).

Given the appropriate vegetative cover and a positive water balance, peat will then accumulate when the rate of plant primary productivity exceeds the rate of decomposition at the site (Mitsch & Gosselink, 2000). Peat decomposition rates vary with temperature (Rosswall, 1974), water table depth (Clymo, 1983), water table fluctuation (Belyea, 1996), plant litter type (Johnson & Damman, 1991; Kuder *et al*., 1998; Kuder & Kruge, 2001; Scheffer *et al*., 2001), oxygen supply (Clymo, 1983), microbial population (Sundh *et al*., 1997), and depth of burial of the decaying peat (Clymo, 1965). Peat decomposition rates also vary in space and time, the senescing plant litter initially losing soluble compounds such as cellulose rapidly, more slowly decomposing as decay resistant secondary compounds such as lignin increasingly dominate the litter content.

Definitions of peat vary among practitioners. Davoren (1978) suggests deposits with an organic content >50% be considered peat, and those with 20-50% organic matter as organic soil. Clymo (1983) suggests peat contains less than 20% of mineral or inorganic matter, though up to 35% may be allowed by definition. The New Zealand Soil Classification classifies Organic Soils [O] as those soils formed in partially decomposed plant material, containing some mineral matter. These are separated further into fibric, hemic and sapric peat, reflecting the extent of decomposition of the organic matter.

2.2.1 New Zealand mire development and classification

Mires develop as a result of complex interactions between abiotic (climate, topography, hydrology) and biotic (the vegetation community) factors. As the importance of these factors differs between geographic locations, the various classification schemes proposed utilise differing factors, such as vegetation structure and community, peat and water chemistry, or succession (Mitsch & Gosselink, 2000).

Peat accumulation within a mire may lead to the eventual isolation of the vegetation community from surface runoff and groundwater, the resulting hydrological isolation being the basis of the most generally used classification scheme for mires, based loosely upon the degree to which hydrological isolation of the mire surface has occurred, i.e. the degree to which the mire surface receives groundwater inflows as opposed to only precipitation (Mitsch & Gosselink, 2000). ***Minerotrophic mires*** (fens) receive water that has passed through mineral soil, occupy low points in the landscape and have a high water table. ***Ombrotrophic mires*** (raised bogs) have accumulated sufficient peat that the mire surface is hydrologically isolated from minerotrophic inputs, relying instead upon precipitation for nutrient inputs. ***Mesotrophic*** or ***Transitional mires*** are intermediate between these two systems, receiving some, limited, minerotrophic inputs. Within this classification, ***fen*** and ***bog*** represent the primary division between mire types (Bridgham *et al*., 1996; Wheeler & Proctor, 2000).

The Co-ordinated Monitoring of New Zealand Wetlands project, established by The Ministry for the Environment, has provided an alternative hierarchical classification framework specific to New Zealand wetlands (Ward & Lambie, 1999; Johnson & Gerbeaux, 2004). Building upon early New Zealand schemes (Cockayne, 1928; Cranwell, 1953; Burrows, 1969; Thompson, 1987), the framework utilises hydrological setting, flow regime, chemistry, landform, biotic structure and the dominant species to define wetland types (Ward & Lambie, 1999; Johnson & Gerbeaux, 2004). Nine wetland classes are recognised, including five which potentially contain peat substrates (fen, bog, swamp, pakihi/gumland & seepage), and which share many species in common (Johnson & Gerbeaux, 2004). Of the wetland types defined, only pakihi/gumland is unique to New Zealand (Johnson & Gerbeaux, 2004), although Mitsch & Gosselink (2000) suggest they bear some similarity to the bald cypress swamps of the southeastern United States. Most large mire complexes comprise different mire types, intact ombrotrophic bogs being surrounded by a minerotrophic fen community where the peat grades into the surrounding mineral soil, the same fen communities occurring in drainage channels on the mire (Davoren, 1978; Johnson & Gerbeaux, 2004).

Fens, or minerotrophic peatlands, have significant inputs of water that have been in touch with the mineral soil, resulting in higher basic cation content and pH than bogs (Bridgham *et al*., 2001). They generally have a high water table and may occupy topographical low points, or are distributed on the margins of bogs. Fens contain relatively shallow acidic peat, and are oligotrophic to mesotrophic (Davoren, 1978; Johnson & Gerbeaux, 2004). Fen vegetation is often composed of sedges, restiads, ferns, tussocks and shrubs, the higher nutrient availability reflected in higher species richness (c.f. bog).

Bogs, or ombrotrophic peatlands, are peatlands that have accumulated sufficient peat that the peatland surface is elevated, and fully isolated from "all but atmospheric inputs of water, alkalinity-generating cations and nutrients" (Bridgham *et al*., 2001 p. 343). Bog peat is acid and anoxic, with a stable and high water table. New Zealand bogs are distributed in high rainfall areas, on level or gently sloping ground such as basins, terraces and drainage divides (Johnson & Gerbeaux, 2004). Further division of bogs can be made into blanket, raised and cushion types. Raised bogs develop a distinctive 'domed' shape, and may develop from fens (Davoren, 1978; Clarkson *et al*., 2004a). The shape arises due to a high rate of peat accumulation in the mire centre, relative to the margins, due to higher relative water table levels and resulting anoxia in the mire centre (Davoren, 1978). The size and shape of the bog will depend on its ontogeny, topographic situation and the prevailing climate. Deep peat deposits are typical of raised mires such as Kopuatai (Newnham *et al*., 1995a), whereas blanket bogs typically have shallow peat deposits (Davoren, 1978). The species diversity of bog communities is low compared to fens, due to the low nutrient availability, low pH and anoxia.

High precipitation on the western side of the South Island has resulted in the formation of ***Pakihi*** bogs overlying podzolised soils. Pakihi are thought to occur both naturally, and to be induced following forest clearance. They occur on estuarine flats, on glacial outwash material, in swampy hollows behind and between dune systems, and on infilled lakes and kettleholes from Golden Bay in Nelson, south to Fiordland (Rigg, 1962; Mew, 1983; Williams *et al.*, 1990; Wardle, 2002). Pakihi are naturally infertile, have a low pH (<4.5 in upper horizons), and slow vertical or lateral water movement (Collier, 1989). Soils underlying pakihi include shallow and deep organic substrates, as well as mineral soils (Mew, 1983). Williams *et al.* (1990) suggest pakihi are widespread in North Westland, with more than 46 distinct pakihi in the Grey, Inangahua, and lower Buller valleys and west of the Paparoa Ranges. Sedges, ferns, rushes, *Empodisma minus*, *Sphagnum* spp. and variable amounts of *Leptospermum scoparium* often dominate the vegetation community (Jackson, 1987; Williams *et al.*, 1990). Woody plants are taller and more dense on better drained substrates (Wardle, 2002). Floristic differences between pakihi are due to the influence of parent material, climate, anthropogenic and natural fires (Williams *et al.*, 1990).

Swamp has a range of meanings in international usage (Gore, 1983), but has been locally defined as a palustrine wetland receiving a rich supply of nutrients from surface runoff and groundwater (Johnson & Gerbeaux, 2004). Swamps contain pools of standing water, or channels of slowing moving water with periods of inundation of the entire swamp surface (Johnson & Gerbeaux, 2004), and are typically formed from lakes, following changes in local drainage processes due to landslides, tectonic activity or changes in river course (McGlone, 2009). Peat and mineral substrates occur, with a slightly acid to neutral pH. Swamps are meso – eutrophic in nutrient status, and sedges, flax, tall herbs or shrubs and forest dominate the vegetation (Wardle, 2002; Johnson & Gerbeaux, 2004). Swamps have been especially impacted by agricultural development (Wardle, 2002), with vegetation remnants often containing a high exotic component due to altered drainage patterns and high nutrient inputs (McGlone, 2009).

Seepages are small, localised wetlands, occurring both as a distinct wetland or portion of a larger system, where a change of slope or impermeable layer raises the water table to near the ground surface. As a result, a constant flow of ground and surface water supplies the seepage, though water flows are less than those of springs or streams (Johnson & Gerbeaux, 2004). Both mineral soil and peat substrates are common, as is a variable pH and nutrient status (Johnson & Gerbeaux, 2004). Although scrub or forest may occur, smaller stature vegetation is more common, such as moss and cushion communities (Johnson & Gerbeaux, 2004).

2.2.2 Mire development

Mire development is generally attributed to either one of two pathways, terrestrialisation or paludification (Mitsch & Gosselink, 2000). In practice both of these processes may contribute to the development of any mire, the importance of each being site specific and dependent upon other factors such as climate, geology and site history.

Terrestrialisation describes the process whereupon an existing water body (e.g. an oxbow lake or kettlehole) gradually infills with sediments, both organic and mineral, a mire community ultimately replacing the original aquatic community (e.g. Waiatarua wetland, Horrocks *et al.*, 2002). Emergent plants can construct buoyant platforms of rhizomes gradually extending from the edges towards the centre of the lake, additional species colonising the floating mat, upon which organic matter (peat) has accumulated. Organic matter falling from the platforms may further accelerate the process of terrestrialisation. The older peat on the margins is colonized by woody species, which form concentric circles around the advancing edge of the floating peat mat. Terrestrialisation occurs on small water bodies, the mires often referred to as quaking bogs, in reference to the quaking surface caused by walking on the buoyant peat surface (Mitsch & Gosselink, 2000).

Embryonic mire communities can develop on floating rafts of vegetation early in the terrestrialisation process. The hydrological conditions for the communities aboard these floating rafts differ from those communities at the lake margin. As the local water table rises and falls, the buoyant rafts rise and fall, isolating the root zone from the water table fluctuations experienced by the littoral communities. This isolation allows the colonisation of the rafts by mire species such as *Sphagnum*, whose decay resistant properties may assist in the accumulation of organic matter and ultimately peat, aboard the raft. Mire successions may occur aboard the raft as *Sphagnum* species acidify the substrate and the abundance of acid-loving species increases.

McGlone (2009) suggests the terrestrialisation model of peatland development is of limited application in New Zealand, with greatest application being in the post-glacial landscapes of the South Island. Here terrestrialisation occurred in depressions formed by blocks of melting glacial ice (Newnham *et al.*, 2007). This occurred on the largest scale in the western South Island, which contained a vast series of lakes following glacial retreat, within a portion of which, terrestrialisation and mire development has occurred (Newnham *et al.*, 2007; McGlone, 2009). Examples also exist in the North Island, with restiad mires in the Waikato region forming via terrestrialisation (Campbell, 1964; Bates, 1973), most recently, Whangamarino and Opuatia fens forming in river channels dammed by Taupo pumice (Clarkson, 2002). In Auckland, the Waiatarua wetland was initiated by the infilling of a lake impounded behind a lava flow from the nearby Mt Wellington volcano (Horrocks *et al.*, 2002). Succession at Waiatarua progressed from open water→ Cyperaceae→*Gleichenia-Leptospermum scoparium* oligotrophic mire, with further succession halted by fires and conversion to pasture (Horrocks *et al.*, 2002).

During ***Paludification***, peat deposits accumulate overtop of a mineral substrate, with no preceding aquatic phase. The lower peat layers may compact under pressure, causing an increase in bulk density, and decrease in capillarity, forcing water movement upwards in the peat (de Lange, 1989; Mitsch & Gosselink, 2000). Where a perched water table forms over this less permeable peat, mire species expand, and woody species decline (Mitsch & Gosselink, 2000). Paludification can be brought about by climate change, geomorphological change or natural expansion of a body of peat (Mitsch & Gosselink, 2000). Kaipororo Clearing in the central North Island is thought to have come about due to a combination of fire and paludification (Rogers & McGlone, 1994).

Table 2.1: Definitions and distinguishing features of New Zealand mire types (adapted from Johnson & Gerbeaux, 2004).
Note: 5 mire types are acknowledged in contrast to the classification proposed by Wheeler & Proctor (2000), which would reclassify all mires receiving minerotrophic inputs (fen, swamp, seepage, pakihi) as fen.

Wetland Class	Substrate	Water origin	Water flow	Nutrient status	pH	Predominant landform	Common Vegetation
Bog	Peat	Precipitation	Almost nil	Oligotrophic	3.0 – 4.8	Level ground, including hill crests, basins and terraces	Moss, lichen, cushion, sedge, grass, restiad, fern, shrub, forest
Fen	Mainly peat	Precipitation, Groundwater, Surface water	Slow to Moderate	Oligo – Mesotrophic	4.0 – 6.0	Bog margins, swamp perimeters, hillside toeslopes, alluvial fans	Sedge, restiad, rush, fern, tall herb or scrub
Swamp	Peat and/or mineral	Predominantly Groundwater & Surface water	Moderate	Meso - Eutrophic	4.8 – 6.3	Valley floors, deltas, plains	Sedge, rush, reed, tall herb & scrub including forest
Seepage	Peat, mineral or rock	Surface water & Groundwater	Moderate to Fast	Oligo - Eutrophic	4.0 – 7.0	Moderate to steep hill slopes, scarps, heads and sides of water courses	Low stature moss, cushion or sedge. Sometimes scrub or forest
Pakihi/gumland	Peat or mineral	Mainly Precipitation	Almost nil	Oligotrophic	4.1 – 5.0	Level to rolling land with impervious soils	Heaths and small woody plants, with restiads, ferns, sedges, lichens, mosses

2.2.3 The Fen-Bog Transition (FBT)

A transition within a wetland succession occurs when a boundary separates one set of distinctive ecological or environmental records from another, as recorded within the peat record at the site (Elliott *et al.*, 2012). The Fen-Bog Transition (FBT) is a term used by Hughes (1997) to describe the stage during raised bog development, when a fen develops early bog or pioneer bog characteristics. During the transition the surface peat horizons become isolated from ground and surface waters, and become increasingly reliant upon atmospheric water sources. In modern mires the transition is largely recognised by changes in vegetation communities (Zoltai & Vitt, 1995; Elliott *et al.*, 2012), in addition to the geochemical changes that accompany increasing isolation of the surface peat from ground and surface waters (Kazda, 1995; Hughes, 2000). Decreased nitrogen, organic carbon, calcium, magnesium and pH have been observed, with an increase in phosphorus solubility resulting from the falling pH (Kazda 1995). Transitions in UK mires have occurred via a “wet-pioneer” route, whereby near surface water tables promote the development of sedge fen and raised mire communities, or “dry-pioneer” routes associated with the presence of *Eriophorum vaginatum* and deeper, fluctuating water tables (Hughes, 2000; Hughes & Dumayne-Peaty, 2002).

Knowledge of the ombrophication process in past mire successions is based largely on mire stratigraphies, including those from the United Kingdom (Hughes & Dumayne-Peaty, 2002; Hughes & Barber, 2003; 2004; Hughes *et al.*, 2000), Minnesota (Janssens, 1992), and Canadian mires (Lavoie & Richard, 2000; Muller *et al.*, 2003). Plant macrofossils may be an effective long-term indicator of environmental change, however, they are less sensitive to minor changes in mire surface wetness (Hughes *et al.*, 2006), and the use of multiple proxies of environmental change allow better characterisation of the timing and nature of mire transitions (e.g. testate amoebae communities, Loisel & Garneau, 2010).

While the FBT has not been specifically addressed during New Zealand palaeoecological studies, there is evidence that *Empodisma* species are present from early in bog development to the latter stages (Shearer, 1997; Clarkson, 2002), and *Empodisma* arrival on site has been assumed to indicate incipient ombrotrophy (Clarkson *et al.*, 2004a). *Empodisma* species occupy a wide variety of mire habitats, including both fen and bog (Johnson & Gerbeaux, 2004), and so the presence of *Empodisma* macrofossils in a peat stratigraphy may not be an accurate indicator of mire nutrient status. Ombrophication has occurred rapidly in mires elsewhere, within a period of decades or centuries (Kuhry *et al.*, 1993; Hughes & Barber, 2003; Eckstein *et al.*, 2009; Tahvanainen, 2011), however, there may be a lag, or biological inertia

(Tahvanainen, 2011), during which deep rooted fen species persist in the newly created ombrotrophic environment. Thus the rapid decline, if not complete absence of fen species (e.g. *Machaerina*), may be a better indicator that the FBT has occurred in New Zealand mires, rather than the presence of *Empodisma*.

There has been a lack of experimental studies exploring the mechanisms and rate of ombrophication within contemporary mires (*sensu* Tahvanainen, 2011). New Zealand's current mires developed after the termination of the Last Glacial Maximum, 18, 000 cal yrs BP (McGlone, 2009), and the literature contains few references to contemporary transitional mires within which the FBT might be studied. Incipient ombrotrophy was suggested at Swampy Summit in Otago (Walker *et al.*, 2001), however, McGlone (2009) argues the presence of the mire indicator species must be weighed against indicators of minerotrophic inputs to the mire. Opuatia fen in the Hauraki Plains is a promising site for further research, building upon the work of Fritz *et al.,* (2008) which proposed a mechanism promoting ombrophication in the transitional mire*. Empodisma minus* arrival in the recently formed west Taupo mires was noted by Clarkson (1984), allowing future observation of the early stages of the FBT in a montane restiad mire. Overall, however, New Zealand mire science is still in its infancy, with mire types still being described (e.g. Rapson *et al.*, 2006), and few studies examining the mechanisms underlying mire development (Clarkson *et al.*, 2005; 2009; Fritz *et al.*, 2008).

2.2.4 Allogenic and Autogenic processes during mire development

An important issue in mire development is whether mire species determine development trajectories by modifying their environment, or whether mire development occurs in response to the external environment (Mitsch & Gosselink, 2000). Raised bog development is unusual, in that autogenic processes significantly influence the process, that is, processes related to or resulting from the biotic community of the mire, and feedbacks between the plant biota and the underlying peat substrate. In contrast, allogenic succession is vegetation change brought about by abiotic forces external to the community (e.g. fire, volcanic activity, climate). A distinction between the two may be hard to make (Hughes & Dumayne-Peaty, 2002), as both autogenic and allogenic forces are likely to play a part in any succession, the relative importance of each type depending upon the environment, and vegetation community.

Allogenic factors play an important role in controlling initiation and plant succession during the early stages of mire development, with the autogenic processes gaining importance as the mire develops (Kratz & de Witt, 1986). While some may suggest it is wrong to label individual processes as auto or allogenic in origin due to the complex nature of the mire development

(Glenn-Lewin & van der Maarel 1992; Hughes & Dumayne-Peaty, 2002), the identification of autogenic processes may be vital to the restoration of ecosystem function, such as required after peatland mining. In these instances, without the identification of those species or processes without which “normal” successional processes will not occur, divergence from previous successional pathways may occur, resulting in a new vegetation community significantly different from that previously found at the site.

2.2.5 Allogenic influences on the FBT

While the autogenic processes are assumed to be of unique importance during the development of raised mires (e.g. Rydin & Jeglum, 2006), the process is very slow (Tahavainen, 2011) and mire trajectories may also be significantly influenced by allogenic factors such as landslides (Lowe *et al.*, 1999), catchment changes (Kulczynski, 1949), sea level changes (de Lange, 1989), or volcanic activity. Peat accumulation rates may also increase following climate shifts to cool, wet conditions (Winkler, 1988; Foster & Wright, 1990; McGlone *et al.*, 1997), evapotranspiration decreasing, while increasing precipitation lessens the influence of groundwater on the peat surface.

During the long time scales within which mire development occurs, mire succession may be deflected along new trajectories, or set back to an earlier stage of development, as a result of allogenic disturbances. Hughes & Dumayne-Peaty (2002) suggest occasional disturbances followed by long periods of autogenic development will re-set the existing mire trajectory, whereas larger, or more frequent disturbances might direct the succession along substantially different successional pathways. Reversals of earlier transitions may also occur, with oligotrophic mires becoming more nutrient rich as minerotrophy increases due to subsidence, increased nutrient inputs from agricultural development, volcanic activity, or hydrological changes following land clearance or erosion (e.g. Lake Poukawa, McGlone, 2009).

2.2.5.1 Climate

Climate is the most important allogenic factor in determining mire development, climate being responsible for the volume and seasonal distribution of rainfall, pivotal in mire development (Moore & Bellamy, 1974; Mitsch & Gosselink, 2000). Climate fluctuations must be taken into account when formulating models of mire development. In a survey of 190 mires initiated since the end of the last glaciation, McGlone (2009) found a steady upwards trend in wetland initiation after an initial lag of 4000 years, during which harsh climate and disturbance limited wetland initiation. The lack of deviation from this trend during the onset of Holocene climate shifts suggesting mire initiations are largely dependent upon landscape factors, rather than climate (McGlone, 2009). McGlone (2009) accepts several departures from this overall pattern, suggesting that while alpine mires developed between 18,000 and 14,000 cal yrs BP as post-glacial landscapes stabilised, large ombrogenous mires formed mid-Holocene (between 8,500 and 5000 cal yrs BP), as climate changes bought the cooler, wetter winters necessary for raised bog growth.

2.2.5.2 Natural fires and mire development

The impact of natural and human-lit fires on mire development differs between mire types. In the Northern Hemisphere, fire has been implicated in the development of blanket bog (Charman, 2002), while in New Zealand, fire has led to forest clearance, alteration of catchment hydrology, and replacement of forest with tussockland and wetland vegetation (Rogers & McGlone, 1994; Fahey & Jackson, 1997; McGlone & Wilmshurst, 1999). While fire is a disturbance common to mires elsewhere, New Zealand mires with a high tussock and restiad component contain a large volume of senesced leaf bases, tillers and culms, which may predispose them to fire (Ogden *et al.*, 1998). However, although post-fire peat mineralisation will result in a temporary spike in nutrient availability, wetland trajectories are reset, rather than altered by the disturbance (McGlone, 2009). A well documented pattern of re-vegetation in New Zealand mires sees the rapid resprouting of species with fire resistant below-ground biomass, and the rapid reseeding by herbs and grasses in the 12-24 months after the fire (Timmin, 1992; Clarkson, 1997; Johnson, 2001). A return to pre-fire vegetation may occur after approximately 20 years (Johnson, 2005).

Prior to human lit fires, fire periodicity was determined by lightning strikes and volcanic activity. North and South Island mires have differing fire histories, with many large peatlands in the North Island having a history of natural fires largely generated by lightning strikes (de Lange, 1989; McGlone, 2009), despite low lightning strike rates in New Zealand (1-2 strikes/km^2/year) (Christian *et al.* 2003; as cited by Perry *et al.*, 2012). D'Costa *et al.* (2011) found an increase in burning on the Aupouri Peninsula following the formation of a restiad-*Leptospermum* acid bog in dry summer conditions, confirming Newnham's (1992) earlier suggestions that wet winters and drier, warmer summers contributed to severe, extensive fires in Northland during the dry season, with peat accumulation occurring through the remainder of the year. Regular fires also occurred at Kopuatai, Ohinewai and in coastal Bay of Plenty mires, as evidenced by frequent charcoal remains in the peat deposits (de Lange, 1989; McGlone *et al.*, 1984; Newnham *et al.*, 1995a;b). Fire incidence at Kopuatai increased during periods coinciding with receding sea levels and warm dry climate, resulting in drier mire surfaces (Newnham *et al.*, 1995a). Fire frequency also increases after major volcanic events, fuelled initially by plant debris, with later fires reflecting changes in vegetation community composition (Wilmshurst & McGlone, 1996; Wilmshurst *et al.*, 1997). Fires in South Island mires have occurred less frequently, and as a result of fire in the surrounding landscape spreading to the mire surface (McGlone, 2009). While a cooler, wetter climate may lessen fire intensity in the South Island (Wagstaff & Clarkson, 2012), McGlone (2001) suggests fire frequency may still be high in the drier south-eastern portion of the South Island, as at Glendhu Bog in coastal Otago (McGlone & Wilmshurst, 1999).

Geographic differences in fire frequency and intensity are suggested by Wagstaff & Clarkson (2012) as a contributing factor to the distribution of New Zealand *Empodisma* species. While *Empodisma minus* is a basal herbaceous resprouter (Clarke *et al.*, 2012), and resprouts after fire, the newly described *Empodisma robustum* is a reseeder. Soil insulates below-ground resprouting organs (Clarke *et al.*, 2012), and the resprouter strategy (R+) is favoured where fires are of low intensity, and a shallow peat depth is consumed. The reseeder strategy (R-) is utilised by those species whose shallow rhizomes are likely to be consumed by fire, whether due to increased fire intensity, or more shallow rhizome depth.

2.2.5.3 The impact of recent fires on mire trajectories and peat accumulation

While natural fires potentially reset mire trajectories (McGlone, 2009), recent fires of human origin have had a greater impact on mire communities. Human-lit fires have increased fire frequency (Irving *et al.*, 1984; Ogden *et al.*, 1998), resulting in long-term changes in mire vegetation communities (Wardle, 1977; Irving *et al.*, 1984; McGlone, 2009). North Island lowland restiad mires appear to be less impacted by the increased fire frequency, possibly due to the adaptation of local mire species to a higher frequency of natural fires (McGlone, 2009; Wagstaff & Clarkson, 2012). Southern mires dominated by *Empodisma minus*, *Sphagnum* species and *Chionochloa rubra* have also tolerated fire well, though the tree and shrub component of raised mires, which increased during the mid to late Holocene, has been removed or reduced (Wallace, 1988; McGlone, 2009). The exception may be the mires of east Otago, where recent fires are thought to be the cause of *Empodisma minus* becoming locally extinct at Swampy Mire (Walker *et al*., 2001).

In contrast, *Sphagnum* cover has increased in recent times, likely due to higher light availability on mire surfaces and increased water input to mires following catchment deforestation by Polynesian-lit fires (Lintott & Burrows, 1973; McGlone *et al.,* 1995; McGlone & Wilmshurst, 1999; McGlone, 2009), compounded by further landuse changes since European settlement (Wilmshurst *et al*., 2003). Rapid *Sphagnum* proliferation and peat accumulation at the Nokomai mire illustrates the change, with the development of string bogs after deforestation from Polynesian lit fires resulted in increased catchment runoff, delivering higher nutrient inputs to the bogs, though a cold climate shift may have also played a part in their development (McGlone *et al*., 1995). Rapidly accumulating *Sphagnum* peats were also found in upland bogs in the Old Man Range and Southland following fire and resulting deforestation (McGlone & Bathgate, 1983; McGlone *et al*., 1997). Insufficient data are available from most sites to determine if the increase in modern *Sphagnum* cover indicates a reversal of the FBT, from ombrotrophic bog to minerotrophic fen, as a result of the additional nutrient inputs and higher water table.

The vegetation community of pakihi has also been altered by recent fires, with both Polynesian and European lit fires likely contributing to the development of pakihi landscapes in Westland (Wardle, 1977; Williams *et al*., 1990). In the initial post-fire period at Dismal Swamp, the deeply rooted sedge *Machaerina teretifolia* recovered most rapidly, while *Gleichenia dicarpa* and *Empodisma minus* regained their initial cover within a five year period (Mark & Smith, 1975). When burnt frequently, the herbaceous community of pakihi is replaced with species depauperate, low growing fern-rushland vegetation (Williams *et al.,* 1990), dominated by these three species. Only in the wettest parts of Westland is the current distribution of peat soils likely to reflect prior distribution of peat accumulating systems, due to the removal of peat by fire (Williams *et al.,* 1990). While burning pakihi may mineralise peat releasing a short-term increase in nutrient availability (Mg, K, PO_4-P, NH_4-N and NO_3-N; Irving *et al.*, 1984), unlike elsewhere, the high rainfall (>2200mm annually) ensures the oligotrophic status of these mires.

2.2.5.4 Volcanic activity and mire succession

Little research in New Zealand has directly addressed the impact of volcanic activity on mire development and mire species, despite an average of one widespread tephra deposited every 370 years in the last 17, 000 years in New Zealand (Lowe, 1988). Clarkson (1990) suggests the prediction of post eruptive successions requires knowledge of resource supplies, the life history attributes of the potential flora, and quantification of invasion, maintenance and species decline processes. Successions will also depend upon the scale and severity of disturbance, and the suitability of the resulting substrate to support plant establishment or continued growth (Clarkson, 1990). Thin tephra layers (<5mm tephra) will result in plant burial, with the ash incorporated into the soil within 12 months, and rapid vegetation canopy recovery (Neild *et al.*, 1998). Moderate burial (5-25mm tephra) will result in damage to grasses, with the vegetation canopy recovering by the next growing season (Neild *et al.*, 1998).

Thick burial of 25-100 mm tephra is required for vegetation to be eliminated, requiring recolonisation of the site by many species, the canopy taking decades to recover (Neild, *et al.*, 1998). Hummock-hollow topography also influences initial depth of tephra accumulation and post eruption peat forming processes. Tephra deposits are washed into hollows, in which Lees & Neall (1993) also found greater peat accumulation between eruptions.

The deposition of extensive volcanic deposits influenced wetland development in the North Island (Clarkson, 1986; McGlone, 2009). The initiation of the Waikato peatlands and peat lakes reflects the influence of volcanic activity from the Taupo Volcanic Zone on the course of the Waikato River (McCraw, 1973; McGlone *et al.*, 1984). Changes in drainage resulting from Taupo pumice deposition also favoured the establishment of herbaceous vegetation on mires on the Hauhungaroa Ranges (Clarkson, 1984; Clarkson & Clarkson, 1984; Clarkson *et al.*, 1986; Wallace, 1988). At Erua, pre-Taupo forest was replaced by a *Gleichenia dicarpa* and *Empodisma minus* dominated mire; the deteriorating drainage likely caused by increased runoff, due to the loss of forest cover (Ogden *et al*., 1998). Extensive deposits are not required, as the weathering of clay rich tephra can form impervious layers through which drainage is impeded (McGlone, 2009). Layers of fine (<20μm) tephra at least 1cm in thickness can impede the downward movement of soil water and elements, and create Fe, Ni and Zn enriched layers (De Vleeschouwer *et al.*, 2008), as seen on the western slopes of Mt Ruapehu (Gabites, 1986).

Tephra deposition may temporarily reverse successional pathways in mires. The deposition of extensive Burrell Ash deposits onto Potaema Bog on Mt Taranaki initially raised the mire surface, blocking drainage channels, and favouring the expansion of Cyperaceae in the enlarged mire (Lees & Neall, 1993). As site drainage was restored, the drying mire was rapidly re-colonised by the shrub *Leptospermum scoparium* and marginal species tolerant of wet sites (e.g. *Phormium Astelia*). Forest species later encroached onto the shrinking mire, from which the Cyperaceae were eventually eliminated (Lees & Neall, 1993). Simple mire types dominated by *Leptospermum scoparium* and *Machaerina rubiginosa* have also developed on moderately sloping portions of debris fans deposited after the Newall eruptions of 1550 AD on Mt Taranaki (Clarkson, 1986; 1990). Prior to the recent Taupo eruption, Ongarue mires supported a high shrub component dominated by *Halocarpus bidwilli* and *Phyllocladus alpinus* (Clarkson *et al.*, 1986). The Taupo eruption deposited a 45cm deep pumice layer, upon which a wetland succession of sedge → *Gleichenia* and *Sphagnum* has progressed. Wetland successional processes were similarly re-set on the Waipapa, Pureora and Hauhungaroa mires north-west of Taupo (Clarkson 1984; Clarkson & Clarkson, 1984; Wallace, 1984; 1988).

In addition to altering site drainage, the addition of tephra to mire substrates may increase the nutrient content of the substrate (Clarkson, 1990), potentially altering wetland trajectories. Nutrients additions from frequent volcanic activity, in conjunction with mild climatic conditions, were sufficient to support dense forest cover on Eltham mire (Taranaki), at the expense of oligotrophic mire species (McGlone & Neall, 1994). The succession followed a transition from *Leptospermum*-*Gleichenia*-sedge → *Empodisma minus* oligotrophic mire*,* before the replacement of the community by swamp forest dominated by *Syzigium maire* (McGlone & Neall, 1994; Newnham & Alloway, 2004). As a result of forest expansion in the Taranaki region, *Empodisma minus* is currently absent and *Gleichenia dicarpa* of limited distribution (McGlone & Neall, 1994).

Volcanic activity may also cause fires which remove woody cover from mires, allowing the spread of non-woody species and the resetting of wetland trajectories (Elder, 1965). Senesced foliage is a large fuel load in the post-eruption landscape (Wilmshurst & McGlone, 1996; McGlone, 1998), and fires occurred after the Taupo eruption in the Waikato, Bay of Plenty and Hawkes Bay regions (McGlone, 1981). Replacement of *Dacrydium biformis* by *Chionochloa rubra* on No Mans Bog was also cotemporaneous with the Taupo eruption, and Elder (1965) suggests fires spreading from the north as a possible cause of *Dacrydium* removal, which is no longer a community dominant. Buried peat deposits in Taranaki also attest to a period of widespread damage to the vegetation community caused firstly by volcanic activity, then a period of unknown length when fires were frequent (Newnham & Alloway, 2004). Approximately 460 species found elsewhere in the North Island at similar altitudes are still missing from the flora of the Taranaki region as a result of volcanic activity, fires and geographic isolation (Druce, 1974; Clarkson, 1986; Newnham & Alloway, 2004). These species include *Empodisma minus*, present in earlier mire successions (McGlone & Neall, 1994; Newnham & Alloway, 2004), but now locally extinct in Taranaki. The probability of *Empodisma minus* invasion of Ahukawakawa Swamp on Mt Taranaki is low due to site isolation, which may lengthen the period of time before the transition to raised mire is possible at the site.

Based on studies of atmospheric pollutants on mires, and the effect of tephra on other vegetation types, Payne & Blackford (2005) suggest volcanic activity may affect mires through the physical and chemical impacts of tephra and tephra leachates, and the deposition of volcanic gases as acidic precipitation or aerosols. Research from outside New Zealand suggests the application of tephra to mire surfaces causes substantial changes to pore water chemistry, with some mire species lost, though later re-establishing (Hotes *et al*., 2004). Application of both tephra and acids to UK mires showed no changes to peat humification rates or plant communities from tephra additions, only from high acid additions, from which plant communities were slow to recover (Payne & Blackford, 2005). Payne & Blackford (2008) note both these studies had deficiencies, with Hotes *et al.* (2004) utilising non-volcanic glass and Payne & Blackford (2005) criticised for the lack of realism in the study design. Following shallow burial, *Sphagnum* is able to survive by extending up through ash layers, fine tephra having a greater effect than coarse, due to the fine tephra shards adhering to the leaves (Hotes *et al*., 2010). Capillary water rise is also impacted by fine tephra, leading to *Sphagnum* desiccation and reduced performance (Hotes *et al*., 2010). In addition, Payne (2012) demonstrated changes in testate amoebae populations in mires affected by recent tephra deposits, which the author suggests reflect widespread changes in the microbial community of the mires, as a result of sulphate deposition.

2.2.6 The influence of plant species on the FBT

Given the frequency of allogenic disturbances, and its far reaching impacts on species distribution and mire development in New Zealand, experimentation is required to determine whether the FBT is also caused by the dominant mire species, i.e. as a result of autogenic development. This is because the co-occurrence of a putative mire engineer and environmental change is descriptive, rather than causal, and so in itself insufficient as an explanation for the mechanisms underlying the FBT.

The consistent presence of *Sphagnum* macrofossil remains during the transition to early bog communities in Northern Hemisphere mires suggests that autogenic factors play an important role in mire development (van Breeman, 1997; Hughes, 2000; Hughes & Barber, 2003; 2004; Tahvanainen, 2011). *Sphagnum* peat has properties thought to encourage peat deposition, namely inherent low litter decay rates (Aerts *et al*., 1999), the creation of high moisture levels whereby the internal conduction of waters re-wets hummocks (Titus & Wagner, 1984), high water holding capacity (10-25x own weight) due to capillary films between imbricate cells (Andrus, 1986), impeded drainage following ironpan formation (Andrus, 1986), and acidification of peat due to high polyuronic acid levels (Bellamy & Reiley, 1967) with a pH of 3.0 possible in theory (Clymo, 1984). Tahvanainen (2011) suggests the common occurrence of *Sphagnum* species with wide environmental tolerances at the FBT may also reflect their ability to rapidly proliferate without delays due to dispersal limitation.

Van Breeman (1995) created an enduring model of *Sphagnum* and its role in the FBT*,* suggesting its structural and biochemical attributes enable it to reduce evapotranspirative losses, acidify substrates, scavenge nutrients and accumulate as peat. Declining vascular plant growth may then result in reduced transpiration and increased light availability, which would feed back to increase *Sphagnum* growth (van Breeman, 1995). As a result of *Sphagnum* colonisation and domination of the vegetation community, a raised mire with altered trophic status (i.e. ombrophication) occurs. Raised mires appear to have stable vegetation communities, with little or no change in floristic composition over periods of several decades (Gunnarson *et al.*, 2002), the microforms constructed are also stable (Rydin & Barber, 2001), while the peatlands constructed act as important long-term carbon sinks. Because of this, *Sphagnum* has been described as the ecosystem engineer of the FBT (Jones *et al.*, 1994).

Van Breeman's (1995) model was rapidly taken up, and is generally accepted in the mire literature, however, debate has centred on the details of the mechanisms outlined. For instance, the decline in pH occurring during ombrophication was attributed to *Sphagnum*'s high rate of cation exchange capacity (Clymo, 1963; Bellamy & Reiley, 1967; Koojiman, 1992; Rydin & Jeglum, 2006), as *Sphagnum* tissues lower the pH of solutions in which they are suspended (Koojiman & Bakker, 1994). However, although increasing *Sphagnum* density and acidity co-occur during ombrophication, causality was assumed rather than proven. Soudzilovskaia *et al.* (2010) have since demonstrated that *Sphagnum*'s ecological predecessors during peatland succession also possess high rates of cation exchange capacity, and that fen alkalinity is due solely to the pH of ground and surface waters in the fen. During mire development, peat accumulation and the growth of a groundwater mound stop the upward flow of groundwater, slowing the neutralisation of acids produced by mosses, and driving the falling pH, which then assists in the invasion by *Sphagna* characteristic of fens. Minerotrophic *Sphagna* have a high rate of primary productivity, leading to faster peat accumulation and expansion of the peat deposit. Where the underlying mineral soil is highly permeable, peat water is driven into the soil by groundwater cells, or else drains via lateral flow in the upper peat (Reeve *et al.*, 2000; as cited by Soudzilovskaia *et al.*, 2010), resulting in hydrological isolation of the surface peat. In combination with acidic precipitation and humic acids derived from organic matter decomposition, an increase in acidity results (Soudzilovskaia *et al.,* 2010).

The presence of *Sphagnum* is not essential for the FBT to occur. The physical properties of the peat deposited by other early pioneer bog species may also influence peat accumulation rates, water retention and hence the maintenance of a high and stable water table. *Eriophorum vaginatum*, a common species in European mires, has properties that encourage peat accumulation, such as the presence of persistent leaf and rhizome fibres (Coulson & Butterfield, 1978), creating a peat mass efficient at retaining water during periods of desiccation (Hughes *et al*., 2000). In addition, the *Eriophorum vaginatum* tussocks provide habitat for the establishment of *Sphagnum* in the mire (Tuittila, *et al.*, 2000). Indeed, Hughes (2000) suggests that only after a *Eriophorum vaginatum/Calluna vulgaris* bog community has laid the foundations for a stable water table, does a wetter climate shift trigger a *Sphagnum*-rich raised mire. Hughes (1997) suggested four routes across the FBT in UK mires, of which three were allogenic, following changes to climate or drainage, which resulted in isolation of the peat surface from groundwater influences. Of the transitions studied, *Sphagnum* was either missing or of low abundance in four of the eight. Instead, an intermediate stage, comprising *Eriophorum vaginatum/Calluna vulgaris or Eriophorum vaginatum/Pinus sylvestris* mire occurred, apparently favoured by the drier peat surface. Hughes (1997) suggests alternative transitional pathways occur when precipitation is insufficient to support the development of *Sphagnum* dominated lawns and pool communities, whereas periods of high precipitation coincided with phases of transition to *Sphagnum*, the higher precipitation providing the impetus for the displacement of fen species.

Sphagnum species are not dominant in all mire types including tropical domed peat (Dommain *et al.*, 2010), South African sedge mires (Sieben, 2012), and restiad mires in New Zealand, where other species play the part of ecosystem engineer. In New Zealand it has been suggested the main peat forming species *Empodisma minus* and *Empodisma robustum* may possess similar properties to *Sphagnum* in terms of their ability to influence water tables (Campbell, 1964), lower evapotranspiration rates (Campbell & Williamson, 1997) and alter substrate pH (Rogers, 1984; Agnew *et al.*, 1993).

2.3 Ecosystem Engineering

Ecosystem engineers are organisms that directly or indirectly modulate the availability (quality, quantity, distribution) of resources (other than biomass), to other species, by causing physical state changes in biotic and abiotic materials, and in doing so modifying, maintaining and or creating habitats (Jones *et al*., 1994; Lawton, 1994). While the roots of the concept might arguably be found in the Darwin‘s musings on the earthworms and soil formation (Darwin, 1883), and were touched on in early papers addressing rock eating molluscs (Shachak *et al.*, 1987; Jones & Shachak, 1990), the phrase itself was not introduced to the scientific community until 1993, when Jones, Lawton & Shachack coined the phrase at a conference (Lawton & Jones, 1993; Shachak & Jones, 1993). Their seminal article in Oikos in 1994, which introduced the concept to a wider audience, is usually taken as the first outing of the term “Ecosystem Engineering”. Jones *et al.* (1994) unified disparate theory about how organisms influence the environment around them in non-trophic manners, highlighting the role some species play in creating, changing or destroying habitat, and in so doing, altering the flow of resources to other organisms in that same habitat (see Table 2.2 for definitions). In addition to drawing attention to, and naming the process, they provided an initial framework and question based research agenda (Gutierrez & Jones, 2008).

The authors introduced two types of engineering, physical ecosystem engineers, and accidental engineers (Jones *et al*., 1994). Accidental engineers are those species who bring about change, though this change does not affect them in any way, e.g. a cow leaving a footprint in muddy soil. Physical ecosystem engineers might be autogenic whereby the species utilises its own biomass to create or change the environment, e.g. *Sphagnum* or *Empodisma minus*; or allogenic engineers that alter living or non-living materials from one state to another by mechanical or other means e.g. the North American Beaver (*Castor canadensis*) (Lawton, 1994; Jones *et al*., 1994; Little *et al.*, 2012). In 1997 Jones *et al.* published a follow up to the 1994 paper, clarifying the concept, extending the initial definition to include the creation of living space (Table 2.2), and calling for greater research effort into ecosystem engineering, the so called "poor relative" of ecological research.

2.3.1 Criticisms of the concept

Early criticism of the concept occurred when Power (1997) suggested the term "engineer" implied intent; however this was disputed by the authors (Jones *et al.,* 1997), though the criticism persisted (Reichman & Seabloom, 2002a;b). Lawton (1994) suggested that there are probably no ecosystems on earth that are not engineered in some manner, by one or more engineers. The broad nature of the definition led to criticism that the concept was being "…trivialized by characterizing any influence on the environment as a form of engineering" (Reichman & Seabloom, 2002a, p. 44); since too many organisms qualified as engineers, given most interact with their environment in some way (Reichman & Seabloom, 2002a;b).

Wilby (2002) argued, that rather than trivializing the concept, the fact that most species interact with the physical environment in some manner only emphasises the ubiquity of the concept, and that our "…goal should be to elucidate how widespread and important ecosystem engineering interactions are…" (Wilby, 2002, p.307). Additional questions were raised in the literature over the scale of impacts, and whether only engineers with impacts "…large relative to the purely physical processes operating in the system" (Reichman & Seabloom, 2002a p.44) should be distinguished, and if ecosystem engineering should be restricted to keystone species (Reichman & Seabloom, 2002a; Wilby, 2002). Lawton (1994) had very early noted that species differ in their capacity to act as ecosystem engineers, few having major impacts. He suggested the term “keystone species” was already over-worked and over-extended, and usually referred to species with trophic effects, which were specifically excluded from the engineering concept. In addition, while keystone species have a large effect on a community, disproportionate to their biomass or abundance (Power *et al*., 1996, as cited in Gutiérrez & Jones, 2008), ecosystem engineering encompasses any habitat modification, irrespective of engineer abundance or effect (Gutiérrez & Jones, 2008).

Not all early discourse was critical; Brown (1995) and Alper (1998) both stressed the previous lack of a theoretical framework to describe the ways in which organisms alter their environments in addition to biotic interactions, and the welcome addition of a set of “guiding principles” to address the phenomena (Alper, 1998). Brown (1995) continued, stressing the importance of avoiding reductionist approaches in further developing the concept, encouraging rather attempts to study ecosystems directly and in their full complexity.

The concept was rapidly taken up and many examples of organisms engineering their environment, particularly in soil and marine substrates, were presented. Cautions were raised initially by Jones *et al*. (1994) that the research effort should move away from collecting “just so” stories, examples of engineers at work, and into erecting a broader framework for the concept, within which it could be more critically examined, and models for engineers created. This caution was echoed later by Berkenbusch & Rowden (2003), who suggested that despite a decade of research, most publications failed to address the issues raised by the conceptual framework, and ignored the scaling system proposed by Jones *et al*. (1997), which allowed the formal evaluation of engineering impact. Instead, the growing body of literature merely added to the rapidly expanding list of engineers and engineered habitats. The lack of studies addressing the framework and scale of impacts was seen as an impediment to any evaluation of the validity of the concept (Berkenbusch & Rowden, 2003). Berke (2010) again raised the issue, and concluded that deleting the term “ecosystem engineer” from many papers given at a Marine Ecosystem Engineers symposium would not result in the loss of any information. Berke (2010) suggests the utility in the concept lies in promotion of integrative and comparative studies, while the on-going development of ecosystem engineering models is evidence of the advancement of theoretical understanding of ecological systems.

2.3.2 Context dependency of engineering effort

The concept of physical ecosystem engineering addresses the coupled interaction between ecosystem engineering process and consequence (Table 2.2). Process addresses how engineers change the abiotic environment, encompassing the physical influence of the engineer on the abiotic environment, irrespective of whether the structure and resulting abiotic change have any biotic effect (Jones & Gutiérrez, 2007). Consequence addresses the biotic effects of the engineering activity on other organisms, and the engineer itself. Consequence is dependent on the degree of abiotic change associated with the engineering process, and the positive or negative effects experienced by the biota, including the engineer (Jones & Gutiérrez, 2007). Structural changes will lead to changes in the abiotic environment due to the interactions between the structure with both energy and resources (Jones, 2012). For example, by creating a hummock structure on a mire, the structure (hummock) will alter organic matter accretion, but also alter light availability, substrate temperature, anoxia, nutrients, O_2 availability, and water flow. The diversity of abiotic variables examined can be constrained by focussing on the habitat created by the engineering organism, i.e. the hummock-hollow topography.

As physical ecosystem engineering is an interaction between the engineer and the abiotic environment, and because the abiotic conditions in landscapes vary, context dependency should be considered (Jones & Gutiérrez, 2007; Jones, 2012), and statements of conditionality should accompany engineering accounts (Crain & Bertness, 2006; Wright & Jones, 2006). It is well recognised that even if a species is recognised as an engineer in a given habitat, it may not engage in engineering efforts in all circumstances and environments (Crain & Bertness, 2005; Boogert *et al.*, 2006), though the extent to which engineering is context dependent is being increasingly explored (e.g. Thomsen *et al.* 2011; Navel *et al.*, 2012). Like all organisms, the engineer will have habitat requirements, in addition to engineering requirements, and these requirements therefore limit that fraction of the landscape that is modified (Jones, 2012). The habitat must be both modifiable, and contain the necessary construction materials (if required) (Jones, 2012).

Whether the abiotic change brought about by the engineering activity will be detected depends upon baseline abiotic conditions, whether the structural changes differ from those bought about by other forces (e.g. abiotic or allogenic causes of mire development), the degree of abiotic change, and the sensitivity of biota to these changes (Jones & Gutiérrez, 2007; Navel *et al.*, 2012). Thus, engineering may have large, small or no effect, and the effect detected may vary from inconsequential to large (Jones *et al.*, 1994; 1997).

2.3.3 Mire Ecosystem Engineers

Wetland ecosystem engineers are responsible for the construction of micro-topography in marshlands and estuaries (Crain & Bertness, 2006; Stribling *et al.*, 2007; Bouma *et al.*, 2010), meadows (Peach & Zedler, 2006; Lawrence & Zedler, 2011), and mires (van Breeman, 1995). The morphological and biomechanical traits of the engineer result in the entrapment of sediments, creating a positive feedback between sediment accretion and plant growth (Corenblit *et al.*, 2011), creating space for seedling establishment, and new habitat types (Lawrence & Zedler, 2011). Mosses dominate mires, where the abundant peat deposits created from their partially decomposed biomass store water, alter resource pathways and favour the survival of the moss species (van Breeman, 1995; Corenblit *et al.*, 2011).

Table 2.2 Definitions of physical ecosystem engineering (Jones & Gutiérrez, 2007)

Ecosystem engineer

"*Ecosystem engineers* are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats. The direct provision of resources by an organism to other species, in the form of living or dead tissues is not engineering". (Jones *et al.*, 1994, p374)

"*Physical ecosystem engineers* are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the physical modification, maintenance or creation of habitats. The ecological effects of engineers on other species occur because the physical state changes directly or indirectly control resources used by these species." (Jones *et al.*, 1997 p. 1947)

Physical ecosystem engineering process

"Organismally caused, structurally mediated changes in the distribution, abundance, and composition of energy and materials in the abiotic environment arising independent or irrespective of changes due to assimilation and dissimilation." (Jones & Gutiérrez, 2007, p6)

Ecosystem engineering consequence

"Influence arising from engineer control on abiotic forces that occurs independent or irrespective of use of or impact of these abiotic factors on the engineer or the participation of the engineer in biotic interactions, despite the fact that these can all affect the engineer and its engineering activities." (Jones & Gutiérrez, 2007, p6)

Sphagnum mosses are widely distributed and globally important due to their ability to produce peat, a major carbon sink (Gorham 1991), storing more carbon annually than is photosynthetically captured by all terrestrial vegetation (Clymo & Hayward, 1982). *Sphagnum* was introduced by Jones *et al.* (1994) as an allogenic and autogenic engineer, responsible for the production of blanket bog in Northern Hemisphere mires. Certain *Sphagnum* species tolerate the fen environment, and modify the site, making conditions more suitable for *Sphagnum* species tolerant of the acidic, anoxic bog environment (van Breeman, 1995). In the engineered environment, *Sphagnum* strongly control nutrient availability to vascular species by efficiently harvesting nutrients from precipitation, and reducing nutrient mineralisation and decomposition rates (Malmer *et al.*, 1994; Scheffer *et al.*, 2001), the source of nutrients for vascular plants (Svensson, 1995). Vascular species are also forced to keep pace with the rapidly rising peat surface in order to avoid burial (Svensson, 1995), and may decline in response to increasing depth to the water table as peat accumulates (Bragazza, 2006). The presence of vascular species facilitates *Sphagnum* growth, providing scaffolding and protection for *Sphagnum* height growth (Rydin & Jeglum, 2006), the abundance and distribution of peatland microforms determined in part by the architecture of vascular plants (Malmer *et al.*, 1994; Pouliot *et al.*, 2011).

Van Breeman (1995) also suggested that *Empodisma minus* might fulfil the same role as ecosystem engineer in New Zealand peatbogs, though this claim was not specifically addressed. It has long been known that northern lowland restiad peat is formed mainly from the remains of *Empodisma robustum* capillaroid rootlets, which form a thick, felted, surface layer in oligotrophic mires (Campbell, 1964; 1981; Campbell *et al.,* 1995). The rootlets comprise a decomposition resistant outer cortex, which persists in the peat (Campbell, 1964; Campbell *et al.,* 1995; Kuder *et al*., 1998). Recent studies by Campbell & Williamson (1997) also highlighted the importance of the canopy, whose eco-hydrological properties assist in maintaining low evapotranspiration losses in areas with seasonal rainfall deficits. It is assumed the morphological and ecophysiological properties investigated in *Empodisma robustum* are shared by the southern species, *Empodisma minus*, although there is no experimental evidence to support this assumption at present.

2.4 New Zealand mires

New Zealand contains 1660 km^2 of mires, 0.7% of New Zealand's total land area (Moore & Bellamy, 1974; Davoren, 1978). Land clearance and development for agricultural has reduced their extent, with some regions containing only 1% of their previous wetland area. New

Zealand mires are distributed from northern New Zealand to the sub-Antarctic islands. The main peat deposits in the North Island occur in the Waikato region (Cockayne, 1928), however, many have been developed for agricultural and horticultural use (Shearer, 1997). There are also peat deposits in the central North Island (Atkinson, 1981; Clarkson, 1984; Horrocks & Ogden, 1998a;b), Taranaki (McGlone & Neall, 1994), Manawatu (Cowie & Rijske, 1977) and lower North Island regions (Moar, 1952; 1953; 1956). South Island peat deposits are largely limited to high rainfall areas in the west and south (Cockayne, 1928), and are less frequent in eastern and northern South Island, except near the main ranges (Burrows, 1969). Further significant deposits are found on Stewart Island and in the Sub-Antarctic Islands (Cockayne, 1928; McGlone, 2002).

Despite their small extent, many New Zealand mires are unique in the world (Pfadenhauer *et al.*, 1993). Although *Sphagnum* species are present in New Zealand mires, unlike elsewhere, the dominant peat-former in many New Zealand mires are members of the Restionaceae family. In addition, mires in southern New Zealand contain cushion communities dominated by *Oreobolus pectinalus*, *Donatia novae zelandiae*, *Gaimardia setacea*, *Dracophyllum prostratum* and *Centrolepis ciliata* (Mark & Bliss, 1970; Dobson, 1975; Mark *et al.*, 1995; Johnson & Gerbeaux, 2004).

2.4.1 Previous studies in New Zealand mires

In comparison with the Northern Hemisphere, New Zealand mires and mire functioning have not been intensively studied. Early studies concentrated on the composition of vegetation communities (Cockayne, 1928), or the reconstruction of past developmental history utilising palynological techniques (e.g. Cranwell & von Post, 1936; Moar, 1952). With the push to develop peat substrates for agricultural use, attention was focused on peat as a soil resource, and overcoming nutrient deficiencies in the recently reclaimed peat (Cunningham 1946; 1948; Thompson & Elliott, 1950; Hupkens van der Elst 1958; 1969; 1971; Davoren, 1978; McLay *et al.*, 1992). Of late, mire research has widened to include the topics of recovery from fire (Johnson, 2001; 2005); the effects of agricultural development on carbon storage (Schipper & McLeod, 2002); models of restiad mire development (Clarkson *et al.*, 2004a); rehabilitation and restoration (Schipper *et al.*, 2002; Watts & Didham, 2006; Watts *et al.*, 2008a;b); water and peat chemistry (McQueen & Wilson, 2000; Chague-Goff *et al.*, 2010); hydrology (Sorrell *et al.*, 2007); ecophysiology (Sorrell *et al.*, 2000; 2012); species-nutrient dynamics (Clarkson *et al.*, 2009; Sorrell *et al.,* 2011); decomposition and nutrient cycling (Pegman & Ogden 2005; 2006; Rutledge *et al.*, 2010); carbon exchange (Nieveen *et al.*, 2005); mire patterning (Mark *et al.*, 1995; Dickinson *et al.*, 2002); and invertebrate communities (Suren & Lambert, 2010; Suren *et al.*, 2007; 2010). The importance of mires as repositories of climatic information, tephra, and vegetation history has also driven the intensive investigation of mires (e.g. Kaipo Bog, Rogers, 1984; Lowe & Hogg, 1986; Lowe *et al.*, 1999; 2013). Recently McGlone (2009) summarised the history of wetland development in New Zealand, highlighting the precarious state of the remaining wetland remnants, and the need for further protection; wetland conservation and management being of continuing concern (Ausseill *et al.*, 2011; van Roon, 2012), as wetland resources continue to decline.

2.4.2 New Zealand Mire development

Large raised bogs were abundant in the Waikato-Hauraki Plains and Southland regions of New Zealand prior to agricultural development (McGlone, 2009). Lowland raised restiad bogs are restricted to latitudes above 38° S, with increasing *Sphagnum* and decreasing restiad influence in the mires moving from north to south, and with increasing altitude (Dobson, 1979). The climate of the Waikato-Hauraki Plains region, with its warm, dry summers and negative annual water balance is not well suited to the formation of raised mires, their development due to the unique morphological and physiological traits of the restiads *Empodisma robustum* and *Sporodanthus ferrugineus* (Wagstaff & Clarkson, 2012). In comparison, Southland has cooler summers and a more even annual rainfall distribution, though it too is considered marginal for raised bog development compared with Northern Hemisphere criteria (McGlone, 2009).

The successional development of northern lowland restiad mires was recently addressed by Clarkson *et al.* (2004a). Lowland restiad peatlands of the Hauraki-Waikato region were initiated in the late Pleistocene-Holocene about 15,000 B.P., the youngest initiated only 614 yr B.P. (Clarkson *et al.*, 2004a). Macrofossil analysis from the older peatlands (Moanatuatua and Kopuatai), indicate bog development began with an initial sedge dominated phase, which lasted some hundreds to thousands of years depending upon the site disturbance regime (Clarkson *et al.*, 2004a). The second developmental phase was marked by the arrival of the restiad *Empodisma robustum*, followed after a lag of 1100 years by a second restiad species *Sporodanthus ferrugineus* (Clarkson *et al.*, 2004a).

Early investigations of South Island mires by Cranwell & von Post (1936), found the peatlands studied had similar developmental histories. The mires were initiated on wet, but not water-covered loess, prior to the initiation of forest cover. Coastal peat deposits started accumulating 9-10,000 yr BP (McIntyre & McKeller, 1970; McGlone & Bathgate, 1983), while inland Otago deposits were initiated later around 7000 yr B.P. on both the Old Man Range and

Garvie Mountains (McGlone *et al*., 1995). The Borland Bog in Southland was initiated earlier, about 12,600 yr B.P., two adjoining deposits coalescing via paludification to form the present bog (McQueen, 1997). McGlone & Bathgate (1983) found the successional pathway during bog development at Merrivale in Southland was very similar to that found at Kopuatai, an FBT dominated by *Empodisma minus* occurring rapidly during the early stages of mire development. A similar sequence of wetland species also occurred during the development of west coast pakihi mires (Newnham *et al.*, 2007; Xu *et al.*, 2008).

2.4.3 Putative Ecosystem Engineers of the New Zealand fen-bog transition

Comments by Cranwell (1953) downplaying the importance of *Sphagna* in New Zealand mires may have spawned the current perception that *Empodisma* species are the major peat formers in New Zealand mires (Van Breeman, 1995; Charman, 2002; Joosten & Clarke, 2002), the presence of other mire types or various successional stages not being mentioned, giving the mistaken impression that all New Zealand mires were perhaps of a restiad type, and that *Empodisma* species are the only ecosystem engineers. Recent studies suggest this is not the case, with the literature suggesting evidence for ecosystem engineering in the mire environment by multiple species.

2.4.3.1 *Sphagnum cristatum* Hampe (1874)

Nine species of *Sphagnum* occur in New Zealand (Fife, 1996), and *Sphagna* are an important component in oligotrophic mires, especially in cooler climates (Johnson, 1988). The various species grow in mesotrophic-oligotrophic mires, on the forest floor in wetter climates, alongside roads and tracks where drainage is impeded, in seepages and springs on hillsides, and on heated ground in thermal areas (Johnson, 1988; Beever *et al*., 1992). *Sphagnum cristatum* is the most common mire species, being found throughout mainland New Zealand, the Chatham Islands, Tasmania and mainland Australia (Beever *et al.,* 1992; Fife, 1996; Whinam & Kirkpatrick, 1995; Whinam *et al.*, 2001). It has a wide edaphic range, with average rainfall at sites ranging from 1100-10,000mm, and mean temperatures varying from 3.5-13.4°C (Mark *et al*., 1995, as cited in Whinam *et al*., 2003).

Johnson (1988) describes *Sphagnum cristatum* as:

"the commonest species, and one having a wide ecological tolerance, forming sopping wet, soft but dense cushions or extensive carpets...Its water holding capacity exceeds that of other species, so its stem tips and hummocky cushions can reach 10cm or so above the level of the water table" (p.2).

Sphagnum cristatum has robust shoots up to 30cm long, and is variable in colour being pale green in the shade, but bronze or reddish in the open (Beever *et al.,* 1992; Johnson, 1988). Growth is limited by hydrology (Clarkson, 1984; Johnson & Brooke, 1998), desiccation from high winds (Johnson, 1988) and light limitation under taller canopies (Clarkson *et al*., 2004a).

Early New Zealand botanists described *Sphagnum* bog communities, with *Sphagnum*'s role in bog formation placed firmly in the context of *Sphagnum* as dominant peatland species. For example, Speight *et al*. (1910) in describing a Mt Arrowsmith tarn, start their discussion with the words "As is well known…" (p. 355), then proceed to briefly discuss the process of *Sphagnum* peat formation, the assumption being that these newly described communities would mirror their Northern Hemisphere counterparts. However, while this may have been the initial expectation, the expansion of mire research in the early part of the 20th century challenged this view. Cranwell (1953) in her overview of New Zealand peat deposits suggested New Zealand *Sphagna* might not have been major peat formers, despite their current widespread distribution, a factor she attributes to changes in climate:

"Species of *Sphagnum* are common, but there are no reliable records as to their importance as peat-formers, except, perhaps, in the Chathams" (p. 196);

"*Sphagna* may be found in any of these areas, but they appear to be of minor importance even in bogs of marked convexity" (p.197);

"Semi-aquatic *Sphagnum subcuspidatum* and a certain amount of hummocky *Sphagnum palustre* form the ground layer, but although long strands of the former can be traced in pools, it does not appear that either is peat-forming" (p.198).

"*Sphagnum* so important elsewhere in the world, is widely spread in New Zealand, but as is well known, not all species are peat-forming" (p.203).

These comments were echoed by Davoren (1978), who conceded that while many mires are dominated by *Sphagnum* species, *Empodisma minus* "is the most frequently encountered peat former" (p. 2).

The ability of *Sphagnum cristatum* to engineer the FBT under New Zealand conditions has not been specifically addressed, however, it is potentially highly productive (Gunnarsson, 2005), acidifies the substrate more than *Empodisma minus* (Clarkson *et al*., 2004a), and the peat formed from *Sphagnum* has lower hydraulic conductivity and higher water holding capacity than restiad-sedge peat (McLay *et al*., 1992).

Some early accounts also appear to describe *Sphagnum* behaving as an ecosystem engineer, Cranwell (1953) describing *Sphagnum* hummocks with sufficient elevation to allow the establishment of shrub species, and Cockayne (1967) describing *Sphagnum* suppression of vascular species:

"True *Sphagnum* bog may form an island in raupo-*Phormium* swamp, as in a virgin swamp near Levin (Wellington). There on the *Sphagnum* the *Phormium* is much more stunted than that in the swamp proper, and browner…" (Cockayne, 1967, p. 164).

Whether the change in *Phormium* stature is due to the acid, nutrient poor *Sphagnum* substrate is not clear from Cockayne's description, however, the impact of *Sphagnum* establishment appears to fit the model for *Sphagnum* as ecosystem engineer in Northern Hemisphere bogs.

While *Sphagnum cristatum* occurs throughout New Zealand, it is a larger component of mires in upland areas, and in lowland sites on the west and south of the South Island (Johnson, 1988). The peat stratigraphy from upland Otago sites indicates a mire succession comprising sedge species followed by *Sphagnum* (Davoren, 1978). Ecosystem engineering of Otago mires by *Sphagnum* is implied by Johnson (1988), who states that *Sphagnum* grows in ombrotrophic conditions, and is capable of creating a domed bog, though these systems are rare in Otago. *Sphagnum* peat accumulation is important in the formation of upland mires in Otago, where *Sphagnum* peat accumulation results in the creation of dry mire habitat colonised by cushion species (Johnson, 1988). Water redirected around growing peat deposits may then create conditions suited to *Sphagnum* colonisation, and Johnson (1988) sees the formation of the mires consisting of a partly autogenic process, in which *Sphagnum* plays a crucial role. Mark *et al.* (1995) note that peat pedestals in upland Otago mires comprise *Sphagnum* remains mixed with *Carex gaudichaudiana* rhizomes. The *Carex* likely plays a role in maintaining optimal growing conditions for *Sphagnum cristatum* and *S. squarrosum*, though contributing little itself to the accumulating peat deposits.

In contrast to upland sites, *Sphagnum* plays a lesser role during successional trajectories at lowland, raised bogs in Southland (Davoren, 1978), due to unsuitable climatic conditions (McGlone, 2009). In these mires, *Empodisma minus* is present after the initial sedge stage, with a smaller *Sphagnum* component present (Davoren, 1978). However, the contribution of *Sphagnum cristatum* to peat accumulation and mire development in southern New Zealand has increased, which may explain the disjunction between early observations of *Sphagnum* distribution and its limited contribution to many peat deposits. Wilmshurst *et al.* (2003)

suggest *Sphagnum* played only a minor part in mire development prior to anthropogenic disturbance, and that its current distribution is a response to forest clearance and changes to local hydrological regimes. Fluctuating water tables were also suggested by McGlone & Wilmshurst (1999) to explain intermittent *Sphagnum cristatum* deposits at Glendhu bog, a permanent *Sphagnum-Empodisma* community establishing around 1860, coinciding with higher, more stable water tables at the site. Deforestation and fire were also cited by McGlone (2009) as the general cause of *Sphagnum* expansion onto Otago and Southland bogs in recent times.

Despite its recent expansion, *Sphagnum*'s prior absence during raised mire development suggests it was not the ecosystem engineer of Southland restiad raised bogs, though it has played an increasingly important role in peat accumulation in recent times, and further research is warranted into its biology, autecology, and role in modern mire successional processes (Johnson, 1988). Its expansion in recent times may mean that *Sphagnum* engineered transitions in New Zealand are increasingly possible, perhaps similar to Westland sites, where *Sphagnum* species have persisted throughout mire succession in the wet climate (Mark & Smith, 1975).

2.4.3.2 *Chionochloa rubra* Zotov (1963)

Another putative ecosystem engineer of the New Zealand FBT is the red tussock *Chionochloa rubra*, which includes four subspecific taxa (Connor, 1991), see Table 2.3 below. *Chionochloa rubra* is a large 1-1.5m high red-brown tussock, common in lowland to subalpine grasslands, shrubland and mires in poorly drained, wet, organic or peaty soils (Connor & Macrae, 1969; Espie, 1999; Wardle, 2002). The species is tolerant of a wide variety of soils conditions, though its current distribution and abundance has been altered by fire (Rogers, 1994; McGlone, 2001; Mark & McLennan, 2005). Fires of both natural and anthropogenic origins transformed the post-glacial landscape, favouring the establishment of montane tall tussock grasslands (McGlone, 2001). In recent times, fire, grazing and agricultural development of former tussocklands has dramatically reduced their extent (Mark & McLennan, 2005), and altered the species composition and diversity in the modified short-tussock grasslands into which they were transformed (Connor 1964; Espie & Barratt, 2006).

Cockayne (1967) suggested a successional mire pathway via terrestrialisation, in which "tussocks" participate.

"Sedges, raupo (*Typha muelleri*), rushes and rush-like plants growing in the shallow water near the margin of a small lake may in time, through their decay, turn by slow degrees that part into dry ground, and advance farther and farther into the lake until a water surface is no longer visible, the whole having become a raupo or *Phormium* swamp. From this the transition to grassland through tussocks gaining a foothold or to rainforest by way of swamp (kahikatea) forest is in many cases only a matter of time." (p. 156).

The species of tussock is not stated by Cockayne, the process of terrestrialisation assumed to be a function of time, rather than due to the attributes of the species themselves.

Table 2.3: Taxonomy, distribution and habitat of *Chionochloa rubra* in New Zealand.
Note: N=North Island, S=South Island distribution.

Species	**Region**	**Distribution**	**Habitat**
C. rubra ssp. *rubra* var. *rubra*	Northern/Canterbury	N: Volcanic Plateau southwards S: Marlborough, North Canterbury	Tussock grasslands, mires
C. rubra ssp. *rubra* var. *inermis*	Taranaki	N: Mt Taranaki	Tussock grassland, mires
C. rubra ssp. *cuprea*	Southland	S: Okuku, Canterbury south to Stewart Is., west to Fiordland	Mires, tussock grassland
C. rubra ssp. *occulta*	Westland	S: Nelson and west Coast to Cascade Plateau	Scrubland, tussock grassland

Dobson (1979) in his model of New Zealand mire vegetation also predicts a succession to oligotrophic conditions in cooler southern climates featuring *Chionochloa rubra*. The species tends to be displaced by bog species as ombrotrophy develops, but persists in minerotrophic zones where the mire transitions into mineral soil (the "lagg") and along mire pool margins. *Chionochloa rubra* tussocks may also persist scattered across the mire surface, though much reduced in stature.

There is evidence that *Chionochloa* tussocks may contribute to raised soil water moisture levels (Mark & Dickinson, 2008), which their dense surface roots are able to capture (Crush *et al.*, 2012). *Chionochloa* grasses have relatively low transpiration losses, their stomata located in deep furrows on the concave side of the long rolled leaves. This leaf shape, and the tussock habit, results in *Chionochloa* tussocks efficiently intercepting atmospheric water sources, and playing an important role in the maintenance of soil water levels (Mark & Dickinson, 2008).

Fog interception has been long hypothesized as a mechanism to explain the high water yields of tall *Chionochloa* tussockland compared to pasture and forestry (Mark & Rowley, 1969; 1976; Holdsworth & Mark, 1990; Ingraham & Mark, 2000). The mechanism could imply ecosystem engineering, by the creation of high soil moisture conditions and its subsequent influence on decomposition and nutrient cycling processes. A wet substrate, in combination with high volumes of decay resistant *Chionochloa* litter, may increase rates of soil carbon accumulation, hastening peat accumulation and mire development.

However, there are conflicting opinions regarding the importance of fog deposition as a contributing factor to high tussock canopy water yields, with high yields attributed instead to low transpiration rates of *Chionochloa* species or measurement error (Pearce *et al*., 1984; Campbell & Murray, 1990; Fahey *et al*., 1996; 2011; Davie *et al*., 2006). Campbell (1989) found transpiration rates above a tussock canopy decreased as atmospheric demand for water vapour increased, a finding confirmed by Espie & Grau (1994). Campbell & Williamson (1997) demonstrated a similar mechanism above an *Empodisma robustum* canopy in a northern restiad mire (*Chionochloa* species are not present), the ability of the restiad to reduce evaporative losses suggested as the mechanism by which raised mires have developed in a climate unsuited to *Sphagnum* growth (McGlone, 2009). After reviewing the evidence for both fog interception and low transpiration rates Davie *et al.* (2006) concluded that reduced transpiration was “the most likely mechanism” (p. 92), though support for fog interception remains (Mark & Dickinson, 2008). Further, Ingraham *et al.* (2008) refuted many of the conclusions drawn by Davie *et al.* (2006), presenting new evidence, and re-asserting that fog interception in tall tussock communities represents a real and important ecosystem service.

The tussock habit itself has also been found to structure wetland communities, some species acting as ecosystem engineers, ameliorating waterlogged conditions by creating microhabitat for seedling establishment for other species, for whom the high water table is a limiting factor (Crain & Bertness, 2005; 2006; Peach & Zedler, 2006). Unlike *Carex stricta,* a recognised ecosystem engineer, *Chionochloa rubra* tussocks do not form tall pedestals of underground biomass, though some change in elevation is likely as a response to preferential rooting in more oxygenated surface peat layers. Martin (1960) does note, however, the growth of *Cladonia* species on the mounds created by dead tussocks, and less commonly on the bases of the largest tussocks, indicating some habitat construction. *Chionochloa rubra* tussocks largely comprise of organic matter including leaf bases, tillers, fine roots, decomposing tiller material and rhizomes, with some fine mineral material captured in the tiller bases. Detrital accumulation under the tussock contributes to peat accumulation and may also influence community composition, due to the impacts of litter accumulation on seedling establishment.

The provision of habitat, reduction of evaporative losses, and high water yield may represent mechanisms by which *Chionochloa rubra* engineers the mire environment, though unlike the tussock forming ecosystem engineer *Eriophorum vaginatum* of Northern Hemisphere mires, there is no body of macrofossil evidence to support this. As a minerotrophic species, *Chionochloa rubra* litter likely decays faster than that of co-occurring *Empodisma minus*, contributing less to peat accumulation, and the FBT. Low nutrient litter and the presence of decay-resistant compounds inhibit the decay of *Sphagnum* litter (Johnson & Damman, 1991; 1993; Hajek *et al.*, 2011), hastening the FBT. Similar multispecies decomposition studies have not been undertaken to determine the relative decay rates of putative New Zealand mire engineers, disentangling whether litter chemistry or the mire environment determines litter decay, and hence peat accumulation rates.

Chionochloa rubra dominated grasslands may represent an anthropogenically influenced community, created as a result of human-lit fires removing woody vegetation from the landscape (McGlone, 2001). *Chionochloa rubra* has a high frost tolerance, and in establishing first after disturbance, Reitsma (1984) suggests the tussocks may ameliorate the microclimate allowing the establishment of less frost tolerant species (*Dracophyllum* spp. & *Phyllocladus alpinus*). While this may suggest a role as ecosystem engineer in disturbed or frost flat communities, there is no evidence *Chionochloa rubra* tussocks influenced the FBT in Holocene fens. The species is tolerant of nutrient stress compared to exotic grass species (Craine & Lee, 2003), frost tolerance and nutrient conservation both being typical of species with stress tolerant traits (Leps *et al.* 1982; McGillivray *et al.* 1995). However, the tussocks are presumed to be less competitive in the oligotrophic transitional and engineered raised bog environments, although its competitive ability in the oligotrophic environment engendered by the FBT has yet to be examined.

Chionochloa rubra aboveground biomass does, however, appear to facilitate *Empodisma minus* growth (Figure 2.1). Vascular species in Northern Hemisphere mires facilitate *Sphagnum* growth, providing physical support for *Sphagnum* biomass (Malmer *et al.*, 1994). *Chionochloa* tussock may play an equivalent role in restiad mires, supporting the sprawling *Empodisma* foliage, its tillers directing stemflow to *Empodisma'*s capillaroid roots. Both the existence of competition and facilitation between species can be examined using de Wit competition experiments (de Wit, 1960), in which the biomass of multiple species can be compared when grown in monoculture and various biomass ratios.

Figure 2.1: *Empodisma minus* climbing *Chionochloa rubra* ssp. *cuprea* tussocks, Castle Downs Swamp, Southland, February 2007.

2.4.3.3 *Machaerina juncea* (R. Br.) Koyama

Machaerina species are erect rush-like sedges, distributed throughout mainland New Zealand and the Chatham Islands in mesotrophic mires, pakihi, swamps, lake margins and ponds (Johnson & Brooke, 1998). Their 0.3-1.5m high stout culms form extensive, almost monotypic swards arising from stout rhizomes, buried in the peaty substrate (Johnson & Brooke, 1998).

Machaerina juncea, a common component of coastal fens and salt marshes (Johnson & Brooke, 1998), plays an important part in the process of terrestrialisation in northern mire systems (Deng *et al*., 2004; 2006; Pegman & Ogden, 2006). Studies at Great Barrier Island suggest *Machaerina juncea* stems trap organic and mineral sediments, enhancing sediment accrual rates at the land-water ecotone (Deng *et al*., 2004), the stem bases and underground biomass also being slow to decompose (Pegman & Ogden, 2005). The creation of habitat less influenced by marine processes enables establishment of species such as *Gleichenia dicarpa* R. Br., typical of more oligotrophic, drier habitats (Pegman & Ogden, 2006). This physical ecosystem engineering process appears similar to that undertaken by *Spartina* species in Northern Hemisphere marshes (Jones *et al.,* 1997; Bouma *et al.,* 2010), although Deng *et al*. (2006) label *Machaerina juncea* a "pivotal species" (p. 778), rather than an ecosystem engineer. Their description of how *Machaerina juncea* triggers a "shift from a brackish system to a more raised freshwater system" (p. 778) certainly appears to describe ecosystem engineering of the mire environment, although an earlier phase of the development, culminating in fen, rather than bog development.

Farther south, the model for northern lowland restiad bog creation developed by Campbell (1964) and refined by Clarkson *et al.* (2004a), describes a fen vegetation community dominated by sedges, particularly *Machaerina* species, creating conditions suitable for later invasion and establishment by restiad species.

"The importance of *"Machaerina"* in heathlands is that it can succeed in wetter places than many other plants" (Campbell, 1981, p.109).

They establish on lake margins, building a floating platform of roots and rhizomes, which extends outwards from the lake periphery. *Sphagnum cristatum* and *Sphagnum falcatulum* may establish on the platform between *Machaerina* clumps, indicating the buoyancy of the platform may prevent inundation from rising and falling lake levels, and allow bog species to establish. The accumulation of the stringy, water retentive peat, especially that of *Machaerina,* will result in the eventual infilling of the lake, and the FBT, under the right conditions.

The presence of *Sphagnum* may be indicative of bog conditions developing on the floating mat, with *Machaerina* species engineering a change to ombrotrophy in isolated hummocks atop the vegetation raft. However, Clarkson *et al.* (2004a) state that an *Empodisma robustum* phase is a necessary pre-cursor to raised mire development, and *Machaerina* species are outcompeted by *Empodisma robustum* mid-succession. While their engineering activities may result in the development of small embryonic or pioneer mire communities, increasing habitat complexity and hence ecosystem engineering, the Clarkson *et al*. (2004a) model suggests *Machaerina* species cannot be considered the ecosystem engineers of the FBT in northern lowland restiad mires.

2.4.3.4 *Sporodanthus ferrugineus* de Lange, Heenan & B.D. Clarkson

Empodisma's only mainland New Zealand bog inhabiting relative is the giant cane rush, *Sporodanthus ferrugineus*. The species previously dominated North Island raised mire communities above 38° latitude (de Lange *et al.*, 1999), but is now diminished in extent due to widespread peatland drainage and conversion to pasture (de Lange *et al*., 1999). Cheeseman (1879) described *Sporodanthus* as abundant in central parts of the Piako, Ohaupo and Moanatuatua swamps, the thick matted roots of the species making drain excavation difficult, and its presence being a sign of "a bad part of the swamp" (p. 325). *Sporodanthus* overlie deep peat in the mire centre, the peat containing abundant creeping rhizomes and stringy roots of *Sporodanthus* (Cheeseman, 1879). Newnham *et al.* (1995a) further describe *Sporodanthus ferrugineus* rhizomes forming a scaffolding platform, upon which the remaining mire vegetation is supported, while the tall stems shelter subcanopy species from the wind, provide shade, and reduce evaporation from the mire surface. The evaporation rates from mire canopies dominated by *Sporodanthus ferrugineus* are approximately twice those reported for an *Empodisma robustum* canopy at the same site, though similar to those reported elsewhere for vascular plant canopies, the conservative evaporation regime contributing to the maintenance of wet mire conditions (Thompson *et al.,* 1999). In addition, *Sporodanthus ferrugineus* biomass also contains high proportions of phenolic acids and tannins (Kuder *et al.,* 1998), which contribute to peat accumulation, *Sporodanthus* rootlets being a component of restiad peat (Campbell, 1975). While these actions appear to describe physical ecosystem engineering of the mire habitat, *Sporodanthus* presence in the mire is indicative of full ombrotrophic conditions (Newnham *et al*., 1995a), *Empodisma robustum* preceding it by at least 1000 years (de Lange, 1989).

2.4.4 The *Empodisma* genus as ecosystem engineers

Empodisma species grow in seasonally or permanently inundated habitats, mires, wet heathlands (including pakihi) and riparian zones with peaty soils throughout South-eastern Australia, from South-east Queensland to South Australia, Tasmania and mainland New Zealand (Campbell, 1964; Keith & Benson, 1988; Campbell *et al.*, 1995; Wardle, 2002). The name *Empodisma* refers to the much-branched, dark green, cylindrical and slender culms, with leaves reduced to scales. The culms form dense, tangled masses, which are difficult to walk through, and from hence its common names (wire rush in New Zealand; spreading rope rush in Australia) are derived (Johnson & Cutler, 1973). The long-lived culms arise from erect bract-covered, glabrous, dark brown rhizomes buried up to 25cm deep in the peaty substrate (*pers. obs.*).

The genus comprises three species, two of which are found in New Zealand, *Empodisma robustum* Wagstaff & B.R. Clarkson, sp. nov., and *Empodisma minus* (Hook. f.) L.A.S. Johnson & D.F. Cutler. A third species, *Empodisma gracillimum* (F. Mueller) L.A.S. Johnson & D.F. Cutler, is confined to Western Australia. The taxonomic history of the genus is complex, with *Empodisma* species being previously described as *Calorophus* and *Hypolaena* by early *taxonomists* (e.g. Cheeseman, 1906; Moore & Edgar, 1970). While variations in the culm length and diameter in *Empodisma minus* plants were noted, the variation was assumed to reflect the effect of latitude and elevation on the canopy biomass (Moore & Edgar, 1970).

These differences in morphology between *Empodisma minus* plants from different locations have recently been clarified, and a new species described (Wagstaff & Clarkson, 2012).

Sequencing of three cpDNA genes from *Empodisma* plants throughout New Zealand and Australia supports an Australian origin for the genus, with recent dispersal and diversification within New Zealand, with the more robust plants in northern lowland restiad mires comprising a separate species (Wagstaff & Clarkson, 2012). The two New Zealand *Empodisma* species differ in morphology and ecology (Table 2.4). *Empodisma robustum* has a more restricted distribution, being confined to mires and gumland heaths north of 38° S latitude in the North Island of New Zealand. The species has a tall canopy, robust culms (Figure 2.2), and dense capillaroid root growth in the upper peat profile (Figure 2.3). Bog vegetation dominated by *Empodisma robustum* has been associated with frequent fires (Newnham *et al.*, 1995a;b), the species regenerating by seed (i.e. a reseeder strategy) (Clarkson & Stanway, 1994; Sharp, 1995; Wagstaff & Clarkson, 2012) following canopy removal by fire (Table 2.4). The more widely distributed *Empodisma minus* is found south of 38° S latitude in New Zealand, and throughout south-eastern Queensland, New South Wales, Victoria and Tasmania (Johnson & Cutler, 1973). *Empodisma minus* is of reduced stature (Figure 2.4), forms fewer capillaroid roots (Figure 2.5), and resprouts from deeply buried rhizomes after fire (Timmin, 1992; Johnson, 2001; Walsh & McDougall, 2004), *Empodisma minus* cover has likely increased as the tree and shrub component of raised mires, which increased during the mid to late Holocene, has been removed or reduced by fire (McGlone, 2009).

Further morphological differences are evident between Australian and New Zealand *Empodisma minus* plants, however, Wagstaff & Clarkson (2012) suggest these morphological differences are small, and the low genetic divergence does not justify further division of the species.

Both *Empodisma minus* and *Empodisma robustum* have a dimorphic root structure, with thin, woody roots anchoring the rhizomes in the surrounding peat, *Empodisma minus* roots containing little in the way of reserve polysaccharides (Tolsma *et al*., 2007), which are presumably stored in the rhizomes. The second root form, the capillaroid roots, are covered with "closely crowded persistent root hairs" (Campbell *et al*., 1995, p.9). These are presumed to develop in response to low soil phosphorus levels (Lambers *et al*., 2006), and are negatively geotropic, or apogeotropic, in mires (Campbell 1981; Meney *et al*., 1990a). Capillaroid roots are not unique to the New Zealand *Empodisma* species, being reported in the Australian species *Empodisma gracillimum*, and other restiads from New Zealand (*Sporodanthus ferrugineus* and *Sporodanthus traversii*; Meney & Pate, 1999; Clarkson *et al.*, 2009), Australia (*Loxocarya* spp. and *Calorophus elongatus*; Campbell *et al*., 1995) and South Africa (Lamont, 1982). Campbell *et al*. (1995) reports that the capillaroid root structures accumulate as peat in

New Zealand due to the wetter climatic conditions, with less potential for root development in the drier climate of Australia, excepting for Tasmania. However, significant depths of capillaroid root weft are present in *Empodisma minus* dominated mires in the Blue Mountains, as is the hummock-hollow topography typical of New Zealand restiad mires (*pers. obs*).

Empodisma foliage is of low palatability (Rogers, 1984; Cheal, 1987; Forsyth *et al*., 2002; Wilson *et al.*, 2006), senesced material retained in the canopy, however, it is the below-ground biomass that comprises the majority of the peat formed (Campbell, 1975; Wagstaff & Clarkson, 2012). Raised mires in New Zealand form in a warm, moderately humid climate, in contrast to the Northern Hemisphere *Sphagnum* mires, which form in climates with higher rainfall and lower mean annual temperatures. McGlone (2009) notes that although raised bog formation can occur under many vegetation types, a case can be made that without the water-retentive canopies and ground mulches of *Empodisma minus and Empodisma robustum*, raised bogs may have been excluded from the summer-dry regions of New Zealand.

Table 2.4: Taxonomic and ecological description of New Zealand *Empodisma* species.
Note: taxonomic descriptions quoted from Wagstaff & Clarkson, 2012, additional information obtained from Rydin & Jeglum, 2006.

	Empodisma minus (Hook. f.) L.A.S. Johnson & D.F. Cutler	*Empodisma robustum* Wagstaff & B.R. Clarkson, sp. nov.
Distribution	New Zealand, below 38° S latitude; Australia, all states except WA and NT	North Island, New Zealand, North Cape southwards to 38° S latitude
Habitat	Seasonally or permanently inundated heathland, mires (fen, raised bog, blanket bog) and along stream and lake margins in organic soils	Mires (fen, raised bog), gumland heaths
Succession	Mid - late successional species	Mid - late successional species
Associated species	Dense carpet of *E. minus*, with heath shrubs (*Leptospermum scoparium, Dracophyllum* spp.), sedges (*Machaerina teretifolia, B. tenax*), ferns (*Gleichenia* spp.), *Chionochloa rubra*, sundews (*Drosera* spp.) & mosses (*Sphagnum cristatum, Dicranum robustum*)	In raised mires, dense layer of *E. robustum* with *Sporodanthus ferrugineus*, heath shrubs (*L. scoparium, D. lessonium, Epacris pauciflora*), sedges (*B. teretifolia, Schoenus brevifolius*), ferns (*G. dicarpa*), groundcover herbs (*Utricularia delicatula*), liverworts (*Riccardia crassa, Goebelobryum unguiculatum*). *S. ferrugineus* missing in early successional communities.

	Empodisma minus (Hook. f.) L.A.S. Johnson & D.F. Cutler	*Empodisma robustum* Wagstaff & B.R. Clarkson, sp. nov.
Culms	Culms dark green, 12-81cm in height, 0.7-1.3 mm in diameter, branching profusely.	Culms dark green, 38-139 cm in height (reportedly >200cm when supported by associated shrubs), 0.9-2.2 mm in diameter, branching profusely.
Culm sheaths	Leaf sheaths closely appressed, 3.5-10.2 mm in length, borne at short intervals 15-48 mm, light green to light brown early in season maturing dark brown; mouth ciliate with a prominent tuft of woolly white hairs in NZ specimens. Lamina strongly reflexed from leaf sheath, 1.5-4.2 mm long, persistent light green when young, maturing dark brown.	Leaf sheaths open, closely appressed, 5.2-21.0 mm in length, borne at intervals of 20.0-70.0 mm, light green to light brown early in the season maturing dark brown; mouth ciliate with a tuft of woolly white hairs. Lamina strongly reflexed from leaf sheath, 2.2-7.5mm long, light green when young, maturing dark brown.
Spikelets and fruits	Spikelets brown, male spikelet 3.9-8mm long, anthers 1.2-2.0 mm long, female spikelet 3.5-7.0mm long; nutlets dark brown approximately 2.6mm long. 2n=24.	Spikelets brown; male spikelet 6.8-9.0 mm long, anthers 1.9-2.5 mm; female spikelet 5.8-8.9 mm; nutlets dark brown approximately 2.7mm long.
Flowering	August - April	August – October
Capillaroid roots	Present	Present, larger and more dense than *E. minus*
Regeneration	Resprouter	Reseeder
Conservation	Not threatened	Not threatened, habitat reduced

2.4.4.1 *Empodisma robustum* Wagstaff & B.R. Clarkson (2012)

Empodisma robustum is confined to wetlands north of 38° S latitude in the North Island of New Zealand. As Wagstaff & Clarkson (2012) note, this phytogeographical boundary also marks the southernmost extent of the restiad *Sporodanthus ferrugineus*, and several other bog species. While northern restiad bogs are now largely restricted to the Waikato region, due to fires and widespread land clearances for agriculture, they previously extended northwards to far northern New Zealand (Carse, 1910; Cranwell, 1953; Elliott, 1998).

The majority of research into *Empodisma* species in New Zealand has occurred on *Empodisma robustum* mires within the Waikato region, due to their close proximity to the University of

Figure 2.2: Tall *Empodisma robustum* canopy, sedgeland fen community, Lake Tomorata, Northland.

Figure 2.3: Abundant, dense *Empodisma robustum* capillaroid roots in upper 10cm hummock peat, sedgeland fen community, Lake Tomorata, Northland.

Figure 2.4: Low *Empodisma minus* canopy, lakeside fen community, Ngapehi-O-Waikareiti, Te Urewera National Park.

Figure 2.5 *Empodisma minus* capillaroid roots in upper 10cm hummock peat (infrequent white roots in upper profile), in wire rush rushland community, Te Papa Frost Flats.

Waikato, and Landcare Research in Hamilton. Consequently, most of the information presented in Hodges & Rapson (2010) outlining the evidence for *Empodisma minus* as the ecosystem engineer of the FBT in New Zealand mires refers in fact to the newly described *Empodisma robustum*.

The xeromorphic adaptations that assist *Empodisma robustum* in maintaining the mire environment are thought to have enabled raised mire development throughout the Holocene, despite a warm and variable climate (Newnham *et al*., 1995a). Palynological and macrofossil evidence from four lowland restiad mires provide support for an autogenically driven model of restiad mire succession, in which *Empodisma robustum* is a necessary pre-cursor to bog development (Clarkson *et al*., 2004a). *Empodisma robustum* establishes after an initial sedge phase, apparently outcompeting the earlier successional species, and persisting throughout mire development to the late ombrotrophic stage in the sub-canopy, underneath the late successional species *Sporodanthus ferrugineus*.

The process by which *Empodisma robustum* engineers the mire environment has been well described. In northern New Zealand, *Empodisma robustum* capillaroid roots accumulate as deep peat deposits (up to 12m deep; Campbell, 1964), due in part to their abundance, capacity for water retention, base exchange properties and decay resistance (Campbell, 1981). In favourable conditions, live and senesced capillaroid roots can intertwine into a dense, felt-like mat, or root weft, which may grow 20-50mm above the mire surface, live roots occurring up to a depth of 300mm (Clarkson *et al*., 2009). The root weft is white when grown in deep shade, but pinkish when exposed to light, and may resemble *Sphagnum* moss in appearance (Campbell *et al*., 1995). The root weft may form the sole ground cover, building up around the shoots of adjacent plants and engulfing fallen litter (Campbell *et al*., 1995; Newnham *et al*., 1995a), the remains of other plants protected against decay by the water saturated root mass (Kuder *et al.*, 1998). The water holding capacity of the capillaroid root weft is similar to that of *Sphagnum*, retaining 15 times its dry weight (Campbell 1981; Agnew *et al*., 1993). The high moisture content lowers soil surface temperature in the *Empodisma* weft compared to pasture as measured during the height of summer (Sharp, 1995), likely further decreasing decomposition rates. The capillaroid roots themselves have high hemicellulose, and low polyphenol and lignin contents, while the thicker axis of roots are higher in lignin and polyphenols, increasing decay resistance by microbial inhibition (Kuder *et al*., 1998). The phenolic compounds are also suggested by Kuder *et al.* (1998) to show allelopathic properties, which might assist in the competitive exclusion of other vascular species. The resulting peat appears to have a higher hydraulic conductivity than *Sphagnum* peat (i.e. is more permeable)

(2.21 ±0.77 *c.f.* 0.40 ±0.21 $ms^{-1}x10^{-5}$ in the plough layer; 19.95 ±0.40 *c.f.* 0.06 ±0.02 $ms^{-1}x10^{-5}$ in the underlying peat), possibly due to the horizontal alignment of stem and roots allowing more rapid transmission of water (McLay *et al.*, 1992).

As a consequence of the formation of capillaroid roots, a "vertically displaced feeding root system" (p. 378, Clarkson *et al.*, 2009) develops underneath the *Empodisma robustum* canopy. The capillaroid roots intercept incoming rainfall via stemflow (Agnew *et al.*, 1993), while other species, including the co-occurring restiad *Sporodanthus*, access nutrients from the nutrient limited peat substrate (Clarkson *et al.*, 2009). Bannister (2000) found the uronic acid levels in *Empodisma robustum* capillaroid root weft were significantly higher than in four Northern Hemisphere *Sphagna*, contributing to high nutrient capture. Unfortunately the study did not incorporate any New Zealand *Sphagnum* species.

Despite being a wetland plant, *Empodisma robustum* roots are "poorly adapted for growth in anoxic soils" (Sorrell *et al.*, 2000, p. 682). With low cortical porosity and a heavily thickened endodermis and stele, the apogeotropic habit of the capillaroid roots may be an adaptation to avoid anoxia (Sorrell *et al.*, 2000). Its rhizomes grow horizontally near the peat surface, where, despite not generating internal pressures or convective gas flows, they maintain internal O_2 concentrations at atmospheric levels (Sorrel *et al.*, 2000). Fritz *et al.* (2008) suggests the high aerenchyma content of the rhizomes, in addition to the low density capillaroid root weft, results in temporary floatation of the upper 30cm of the peat surface. This peatland surface oscillation may benefit *Empodisma robustum* by reducing surface inundation and water table levels, and may represent another potential engineering strategy (Fritz *et al.*, 2008), or positive feedback of the engineering process.

Campbell (1964) suggests the presence of *Empodisma* species (and other mire dwelling restiads) in mires is a paradox. *Empodisma* species commonly occur in water saturated mires, yet possess xeromorphic adaptations to prevent water loss, in common with the majority of the Restionaceae, largely dwellers of sandy, infertile substrates in Australia and Southern Africa. Indeed *Empodisma robustum* exerts strong control on evaporative losses from its canopy, the dense shoots acting as a mulch, restricting movement of solar energy and water vapour between the substrate and atmosphere (Campbell & Williamson, 1997). Dead stems, comprising up to 60% of the total canopy biomass (Hodges, unpublished data), are interwoven with the living canopy material, and these intercept rainfall, so the moisture content of the lower canopy remains higher for longer than that of the upper canopy (Campbell & Williamson, 1997). In addition, Sharp (1995) found maximal stomatal conductance occurred early in the day, maximising carbon assimilation while minimizing evaporative demand. *Empodisma robustum* annual above-ground productivity was estimated as 0.30-0.36 kg/m^2 at Moanatuatua, and 0.08-0.12 kg/m^2 at Kopuatai, the higher biomass at Moanatuatua reflecting nutrient additions from the surrounding farmland (Sharp, 1995).

2.4.4.2 *Empodisma minus* (Hook. F.) L.A.S. Johnson & D.F. Cutler (1974)

The recent subdivision of the *Empodisma* genus has highlighted several differences between the two New Zealand species (Wagstaff & Clarkson, 2012) (Table 2.3). While both species are mid- to late successional species, *Empodisma minus* dominates in a wider variety of oligotrophic wetland environments, and along a wide altitudinal range in New Zealand and Australia (Campbell, 1983; Keith & Benson, 1988; Kirkpatrick *et al.*, 1996; Wardle 2002; Wagstaff & Clarkson, 2012). While *Empodisma robustum* distribution along a fen-bog gradient was explained by declining resource availability as a result of mire succession (Clarkson *et al.,* 2004a), the factors determining *Empodisma minus* distribution in New Zealand wetland habitats have yet to be separately examined. An Otago regional study by de Groot (1999) found *Empodisma minus* mires occurred in lowland coastal areas, and were associated with deep peat deposits with a low mineral content, low pH and a high water table compared to *Sphagnum* and cushion bogs. Clarkson & Clarkson (2006) suggest *Empodisma minus* mires are shallower than northern lowland mires, which may reflect differences in productivity in the cooler southern climate, or differences in decomposition rates between northern and southern sites. Rogers (1984) attributes the shallow peat deposits at Kaipo Lagoon to frequent tephra inputs which destroyed the mire vegetation, and altered mire hydrology. As a result, the mire vegetation was reset to the sedge and herb communities typical of early successional mires.

Wagstaff and Clarkson (2012) suggest *Empodisma minus* forms less abundant capillaroid roots than *Empodisma robustum*, though likely of similar morphology and function. Despite their lower abundance, capillaroid roots are the major peat component in southern raised restiad mires (Wagstaff & Clarkson, 2012). The importance of *Empodisma* capillaroid roots to peat accumulation is based on the early work of Ella Campbell (Campbell, 1964; 1975), followed by more detailed studies by Kuder *et al.* (1998), all of which utilised peat and peat precursors from *Empodisma robustum* mires in the Waikato and Bay of Plenty. While the unique phenolic components in *Empodisma robustum* roots identified by Kuder *et al.* (1998) are likely common to the genus, less abundant capillaroid root growth will influence peat accumulation rates in *Empodisma minus* mires, though fewer fires and a cooler climate will also influence peat accumulation rates.

While *Empodisma robustum* regenerates from seed following fire (Wagstaff & Clarkson 2012), *Empodisma minus* is a strongly competitive clonal resprouter (McDougal, 2007) (Figure 2.6), with infrequent recruitment from seed (Meney & Pate, 1999). New shoots appear within a few weeks post-fire, and regrow vigorously to pre-fire levels in as little as 2 years after burning in Australia (Walsh & McDougal, 2004; McDougal, 2007), where mires dominated by *Empodisma minus* regenerate more rapidly than those dominated by *Sphagnum* species (Hope *et al.*, 2005). Resprouters allocate most carbon resources and nutrients towards maintenance and vegetative growth, protecting underground components from fire by deep burial (Wagstaff & Clarkson, 2012; Clarke *et al.*, 2012). In contrast, reseeders produce less extensive underground rhizomes, with shallow, fibrous root systems, and allocate more resources to producing seed, their seedlings growing faster than those of resprouters (Bell, 2001). The reseeder strategy is more useful in the northern lowland mires, where *Empodisma robustum* is potentially exposed to a greater fire frequency. Differences in below-ground productivity and fire response strategies between the two species will influence peat accumulation rates, given the various litter components will decay at different rates. The impact of this upon the timing of the FBT is unknown, as decomposition studies in restiad mires in New Zealand have yet to be published.

Figure 2.6: *Empodisma minus* hummocks and *Chionochloa rubra* tussocks on edge of Castle Downs Mire, Southland. *Empodisma* has resprouted on the hummocks despite fire and drainage resulting in the exclusion or removal of most other wetland species.

As all studies addressing above-ground and below-ground productivity, decomposition, capillaroid root abundance, distribution and role in nutrient acquisition have occurred in northern sites, the assertion that these mechanisms crucial to the ecosystem engineering of the New Zealand FBT are shared by *Empodisma minus* (Wagstaff & Clarkson, 2012) requires further testing. In addition, the main emphasis of previous research efforts was ecosystem engineering process (the “how”), leaving ecosystem engineering consequence and context dependency largely unaddressed.

Context dependency can be addressed by a field survey of *Empodisma* mires, to investigate the abiotic resources and conditions associated with *Empodisma* distribution and density, and to investigate the expression of engineering traits along the fen-bog gradient in New Zealand restiad mires.

Investigating consequence, or the biotic effects of engineering by *Empodisma minus,* will require the examination of resource competition and facilitation between *Empodisma minus* and other mire species, and positive and negative feedbacks to *Empodisms minus* from the engineering process.

2.5 Outstanding questions

The general aim of my thesis was to study various aspects of ecosystem engineering by Empodisma minus in New Zealand restiad mires. The thesis consists of four original studies:

In the first study (Chapter 3), I focused on describing Empodisma communities in New Zealand, investigating the presence of engineering traits in the various community types, the presence of underlying physical gradients, and the abiotic limitations to engineering activities.

In the second study (Chapter 4), I examined the literature around ecosystem engineering by mire species, including Sphagnum and Empodisma species, and developed a model by which further mire engineers might be identified.

In the third study (Chapter 5), I examined the competitive relations between Empodisma minus and Chionochloa rubra along an artificial mire gradient. I tested the hypothesis that an ecosystem engineer would be more competitive long-term in the engineered environent.

The fourth study (Chapter 6) presents a short-term litter decomposition study examining the decay rates of above and below ground plant tissues in an oligotrophic fen. I tested the hypothesis that Empodisma minus, as an ecosystem engineer, would decompose more slowly than a co-occurring species, more typical of minerotrophic mire environments.

Chapter 3: Vegetation and peat characteristics of *Empodisma minus* communities in New Zealand.

Surveying an *Empodisma robustum* community, Tumarau Lagoon, Bay of Plenty.

A version of this chapter will be presented at the 56th Annual Conference of the International Association for Vegetation Science (June 2013, Tartu, Estonia),

3.1 Abstract

The development of New Zealand restiad mires, including the continuum from minerotrophic fens to ombrotrophic bogs, is presumed to be strongly controlled by autogenic processes, especially following the establishment of either of the two restiad ecosystem engineers *Empodisma minus* or *Empodisma robustum*. Investigations of the relationship between *Empodisma* distribution and mire environment along a mire chronosequence is expected to provide insights into the long-term development of restiad mires, by linking plant traits with changes in mire environment. 70 wetlands were surveyed over two summers throughout New Zealand, with the vegetation community and substrate chemistry of the sites described. The survey confirmed previous descriptions of the widespread nature of *Empodisma* distribution in New Zealand. *Empodisma* species exhibit a wide edaphic tolerance, being found in both seasonally and permanently waterlogged substrates, which ranged from acidic to circum-neutral in pH (pH=3.8-6.5), and comprised a gradient from mineral soils with <10% organic matter content, to Organic Soils with <2% ash content. Eight main types of *Empodisma* communities were suggested by the analysis, including montane fens and fernlands in the central North Island, *Empodisma-Leptospermum* vegetation on the Denniston coal measures, *Empodisma-Machaerina* communities incorporating mire edge and pakihi communities, and *Empodisma* mires. The peat of the *Sphagnum* rich mires and montane fens are least similar, the *Empodisma-Sphagnum* communities having wet, acidic peat, with a low bulk density, compared to the dry substrate of sloping montane fens and fernlands which contain little organic matter. *Empodisma* capillaroid roots were common, except on the Denniston Plateau where little organic matter has accumulated, in pakihi mires, and in dry fernland communities dominated by *Gleichenia dicarpa*. Hummock-hollow topography was most prominent in the *Empodisma* communities and under dense *Empodisma minus* canopies, with little surface microtopography evident in fernland, pakihi and mire edge communities. The survey suggests the growth-limiting nutrient in most restiad communities is phosphorus, however, nutrient enrichment has occurred at some sites, especially in *Empodisma* bog remnants in Southland and Otago. The high *Sphagnum* component in these bogs has been previously attributed to anthropogenic changes in catchment hydrology, an increase in fire frequency and higher nutrient availability in the mires. As a result of these changes in mire canopy composition, a mire chronosequence incorporating the initial establishment and later consolidation of *Empodisma minus* along a fen-bog gradient was not constructed from the surveyed sites. Further study of ecosystem engineering upon mire development will rely instead on the use of an artificial fen-bog gradient.

3.2 Introduction

3.2.1 Restiad mires in New Zealand

Mires dominated by the Restionaceae (restiad mires), while occurring in both Australia and South Africa (Lamont, 1982; Campbell *et al*., 1995; Sieben *et al.*, 2004; Araya *et al.*, 2011), are extensive throughout the New Zealand mainland and the Chatham Islands (Campbell, 1983; Walls & Baird, 1997; Wardle, 2002; Clarkson *et al.*, 2004a;b). Once widespread, New Zealand restiad mires are now reduced in extent, and are often highly modified by fire, drainage, grazing and the incursion of exotic species (Clarkson *et al.*, 1999; Clarkson *et al.*, 2011; Myers *et al.*, 2013). The peat associated with restiad mires varies according to botanical origin, mire developmental stage, and recent disturbance history (Clarkson *et al.*, 2004a;b), the usually low total and available nutrients in the peat increasing with anthropogenic disturbance. Restiad mires dominated by *Empodisma minus* are characterised by a dense *Empodisma* sward, with graminoids, small shrubs (e.g. *Dracophyllum* spp.) and low-growing herbs interspersed throughout (Johnson & Gerbeaux, 2004; McGlone, 2009). Elsewhere in New Zealand, restiad mires are dominated by either *Sporodanthus* or *Empodisma* species, with *Sporodanthus ferrugineus* and *Empodisma robustum* the dominant species in northern lowland mires, and *Sporodanthus traversii* dominating mires in the Chatham Islands (de Lange *et al.*, 1999).

The variety of wetland environments in which *Empodisma* species occur indicates the species wide ecological amplitude. *Empodisma* species occur in heathlands and tussocklands, in both wet minerotrophic fens and ombrotrophic bogs. *Empodisma minus* persists from sea level to the subalpine belt, varying from tall, dense, canopies, which exclude many competitors, to sparse scattered culms <5cm tall in cushion bogs (Wardle, 2002). While the vegetation communities of wetlands in many regions have been recently inventoried (e.g. Clarkson *et al.*, 2011), the abiotic factors determining *Empodisma minus* distribution in the full range of New Zealand wetland habitats have yet to be addressed. Restiad dominated vegetation in the Waikato is associated with low nutrient, acidic peat, with a low bulk density (Clarkson *et al.*, 2004a). *Empodisma minus* dominated mires in Otago are known to occur in lowland coastal areas, and are associated with deep peat deposits with a low mineral content, low pH and a high water table (de Groot, 1999), similar to *Sporodanthus* distribution in the Chatham Islands (Clarkson *et al.*, 2004b).

Present *Empodisma* cover in New Zealand likely reflects a disturbance gradient, as it is recognised that *Empodisma* cover increased as the tree and shrub component of raised mires, which increased during the mid to late Holocene, was removed or reduced by fire (McGlone, 2009). The influence of fire (geology and climate) is especially evident in the wetland communities of the Westland region. Tussock rushlands containing *Chionochloa rubra* overtop of *Empodisma minus* grow in Organic Soils and Podzols at previously burnt sites (Williams *et al.*, 1990), with many species excluded by the dense *Empodisma* canopy in more recently burnt communities (Williams *et al.*, 1990).

3.2.2 *Empodisma minus* capillaroid roots and hummock-hollow topography

Empodisma species are described as the ecosystem engineers of the FBT in New Zealand mires (van Breeman, 1995), however, much of the literature supporting the role of *Empodisma* as engineer examines the process of ecosystem engineering in northern lowland mires where *Empodisma robustum* rather than *Empodisma minus* is the dominant species. Northern lowland restiad peat is formed mainly from the partially decomposed remains of the thick, felted, surface layer of *Empodisma robustum* capillaroid rootlets visible in oligotrophic conditions (Campbell, 1981; Campbell *et al.,* 1995; Kuder *et al*., 1998). Capillaroid roots are a form of cluster root, found only in the Restionaceae (Lamont, 1982; Campbell *et al.*, 1995; Clarkson *et al.*, 2009). The growth of carboxylate-releasing cluster roots in non-mycorrhizal species allows the plant to 'mine' the soil for P, a successful trait on substrates where P is the limiting nutrient (Lambers *et al.*, 2008; 2012). P-limitation can occur not only on older substrates, but also due to P-sorption on organic (e.g. peat) or inorganic substrates such as weathered volcanic ash (Vitousek *et al.*, 2010; Lambers *et al.*, 2012). In the latter systems, total-P in the substrate may be high, while plant-available P may be low.

The surface of restiad mires is often uneven, with *Empodisma* capillaroid roots accumulating at the mire surface to form a thick undulating root weft, or hummock-hollow topography. Mire hummock-hollow topography comprises a mosaic of hummocks, whose upper surfaces lie at least 20cm above the reach of the highest water table, and hollows that are close to the water table, and are frequently inundated (Pouilot *et al.*, 2011). Peat accumulation in mires occurs at the scale of the individual hummock, through the processes of production, litter fall, decomposition, and compression of partially decomposed organic matter (Clymo, 1984; Belyea & Clymo, 2001). Stratigraphic studies suggest the individual hummocks and hollows in mires are stable, maintaining themselves indefinitely (Tolonen, 1971; Barber, 1981), although the mechanisms behind hummock-hollow topography are still under investigation.

Hummock formation in non-*Sphagnum* dominated wetlands is often the result of shallow rooting by vascular plants, which positions the roots above the substrate (Crain & Bertness, 2005). The shallow roots subsequently entrap falling litter and sediments, which form the substrate upon which the roots continue to grow (Fogel *et al.*, 2004). Hummock height, width and spacing increase in response to increasing water depth in the wetland (Peach & Zedler, 2006). Hummock construction benefits the hummock-forming species (ecosystem engineer, *sensu* Jones *et al.*, 1994), however, the consequences for the mire community are less clear, with species diversity both increasing (Vivian-Smith, 1997) and decreasing (Werner & Zedler, 2002) with increasing surface heterogeneity. Increased topographical heterogeneity in mires allows the co-existence of species with different habitat requirements (Larkin *et al.*, 2006), with the raised hummock offering refuge from anoxic peat substrates (Bertness *et al.*, 1992).

In Northern Hemisphere mires, the role of *Sphagnum* productivity and decomposition has comprised a large part of the discussion on the development of hummock-hollow topography and peat accumulation in mires (Clymo, 1965; Heal *et al.*, 1978; Johnson *et al.*, 1990; Johnson & Damman, 1991; 1993; van Breeman, 1995). Hummock *Sphagna* (e.g. *S. fuscum*) construct (engineer) persistent hummock microforms, avoiding competition with aquatic *Sphagna* (e.g. *S. cuspidatum*), allowing niche separation and species co-existence in the mire (Hajek, 2009). Hummock *Sphagna* possess both greater productivity and lower decomposition rates, due to poor litter quality and the presence of cell-wall polysaccharides that inhibit decomposition (Johnson *et al.*, 1990; Turetsky *et al.*, 2008; Hajek, 2009; Hajek *et al.*, 2011). The ability to outcompete vascular species in the elevated hummock is due to water retention and capillary rise generated by the uniquely structured *Sphagna* capitulum (Clymo & Hayward, 1982; Waddington *et al*, 2011; Carter & Price, 2012). The accumulation of *Sphagnum* biomass and its slow decomposition reduces nutrient mineralisation, the main source of nutrients for vascular plants (Svensson, 1995; Pouliot *et al*., 2011). Peat accumulation is highest in lawns and low hummocks closer to the water table, and least in tall hummocks and in pools (Belyea & Malmer, 2004).

Less is known of the development of hummock-hollow topography in New Zealand restiad mires. *Empodisma minus* may form hummocks in excess of 1m tall (Rogers, 1984), comprised largely of apogeotropic capillaroid roots and entrapped litter (Campbell, 1964; Rogers, 1984) (Figure 3.1). The water holding capacity of the surface root weft is high (199.5%), though less than that of *Sphagnum cristatum* biomass (283.5%) (Agnew *et al.*, 1993). The pH inside the hummocks is lower than that of the surrounding substrate, and the hummock interior is moderated from diurnal temperature extremes (Rogers, 1984; Sharp, 1995). Few vascular species persist under the edge of the dense overhanging *Empodisma* canopy (e.g. *Celmisia*, *Drosera*), restricted by the low light levels under the canopy (Rogers, 1984). Liverwort and bryophyte species line both the damp substrate of the hollows (e.g. *Telaranea* spp.) and hummocks (e.g. *Riccardia* spp.) (Hodges & Rapson, 2007).

Descriptive accounts of the development of microtopography by *Empodisma* species in New Zealand mires have discussed interactions between *Empodisma* capillaroid root development and abiotic and biotic factors (Dobson, 1975; Rogers, 1984; Agnew *et al.*, 1993) (some common New Zealand mire species shown in Figure 3.2). The role of biotic and abiotic factors in hummock formation were described by Rogers (1984) at Kaipo Lagoon, in Te Urewera National Park (Figure 3.1). Where *Empodisma minus* grows in monoculture, surface microtopography is not well developed, with the root weft only slightly elevated above the water table. It is where *Empodisma minus* and *Gleichenia dicarpa* co-exist that hummock formations are formed. Rogers (1984) suggests the rhizomes and stems of *Gleichenia dicarpa* facilitate the expansion of *Empodisma minus* by providing both support and shelter for capillaroid root growth. Hummock construction allows *Gleichenia dicarpa* to position at least part of its root mass above the water table, the overhanging hummock biomass also inhibiting the growth of plants in the hollows (Rogers, 1984). The largest hummocks at Kaipo Lagoon form alongside stream banks where the water table is high following rainfall events, Rogers (1984) suggesting the substrate is dry in the intervening periods, allowing the expansion of *Gleichenia dicarpa*, and hence *Empodisma minus*. In a study of five geographically spread sites, Agnew *et al.* (1993) also attributed hummock-hollow topography to species-hydrology interaction, hummock height increasing in magnitude with higher annual rainfall. Agnew *et al.* (1993) further elaborated that hummock development was due to the accumulation of apogeotropic capillaroid roots, which clustered around *Empodisma* stems to intercept nutrients contained in stemflow, and which are slow to decay (Kuder *et al.*, 1998).

Links between ecosystem engineering by capillaroid root production and both abiotic and biotic factors appear to be supported by the literature (Agnew *et al.*, 1993; Campbell & Williamson, 1997; Fritz *et al.*, 2008), however, the context dependency of capillaroid root formation (and hence ecosystem engineering) has not been examined. For *Empodisma minus* to engineer the FBT, capillaroid root initiation and accumulation will occur prior to the transition, i.e. in minerotrophic fens. Since *Empodisma minus* dominated communities are widely distributed (Wardle, 2002), and large raised bogs are largely confined to southern New Zealand (McGlone, 2009), this suggests *Empodisma minus* may not form extensive capillaroid roots in all wetland communities due to engineering requirements not being met. For example, capillaroid roots may not accumulate because of unsuitable substrates, competition with other vascular species, low capillaroid root productivity, or high decomposition rates.

Herbarium samples are usually devoid of capillaroid roots, and their presence or absence is not usually noted in the individual herbarium records. The distribution and abundance of capillaroid roots and hummock-hollow topography in *Empodisma* dominated communities is therefore required to shed light on the context dependency of ecosystem engineering by the genus.

3.2.3 New Zealand restiad mire development

Studying the context dependency of ecosystem engineering by *Empodisma* species requires the survey of existing mires, and their classification into a fen-bog gradient within which *Empodisma* density and engineering activity might be studied. Mire development and successional processes are usually studied using palaeoecological techniques, and/or along spatial chronosequences (Glaser *et al.*, 2004). Palynological reconstructions of New Zealand mire development have been widely reported (McIntyre & McKellar, 1970; McGlone *et al.*, 1984; 1997; Walker *et al.*, 2001; Deng *et al.*, 2006; Xu *et al.*, 2008), however, spatial chronosequences have been utilised less frequently. An “ideal” mire chronosequence occurs where all the allogenic factors (parent material, climate, topography) influencing mire development in the chosen sites remain the same (Turner *et al.*, 2012). Spatial chronosequences have been used where mires have formed on land emerging from the sea through isostatic rebound (Glaser *et al.*, 2004; Leppälä *et al.*, 2011a; 2011b; Tuittila *et al.*, 2012), with the examination of species-environmental links during the purported successional sequence. Their use is recommended when measuring changes in vegetation communities (plant cover, species richness), and soil characteristics (organic matter accumulation, nutrient cycling) that alter in a predictable, linear manner with time (Walker *et al.*, 2010).

While the fen-bog transition (FBT) has not been specifically addressed in New Zealand palaeoecological studies, there is evidence that *Empodisma* species are present from early in bog development, persisting in the mire community (Rogers, 1984; Shearer 1997; Clarkson 2002), and *Empodisma robustum* arrival in northern restiad fens has been assumed to indicate incipient ombrotrophy, i.e. the FBT (Clarkson *et al.*, 2004a). An *Empodisma minus* mire chronosequence has not been studied, instead, successional sequences in individual mires have been described (Rogers, 1984; McGlone & Bathgate, 1983), with secondary successions in *Empodisma minus* mires described after fire (Johnson, 2001; 2005), and volcanic activity (e.g. Clarkson & Clarkson, 1984). In order to study *Empodisma minus* density or abundance during mire development, and the context dependency of ecosystem engineering processes, the identification of a chronosequence of *Empodisma minus* mires with similar parent material, climate and topography is required. A national survey of mires is therefore necessary to determine if the construction of a chronosequence from the remaining *Empodisma minus* mires is possible.

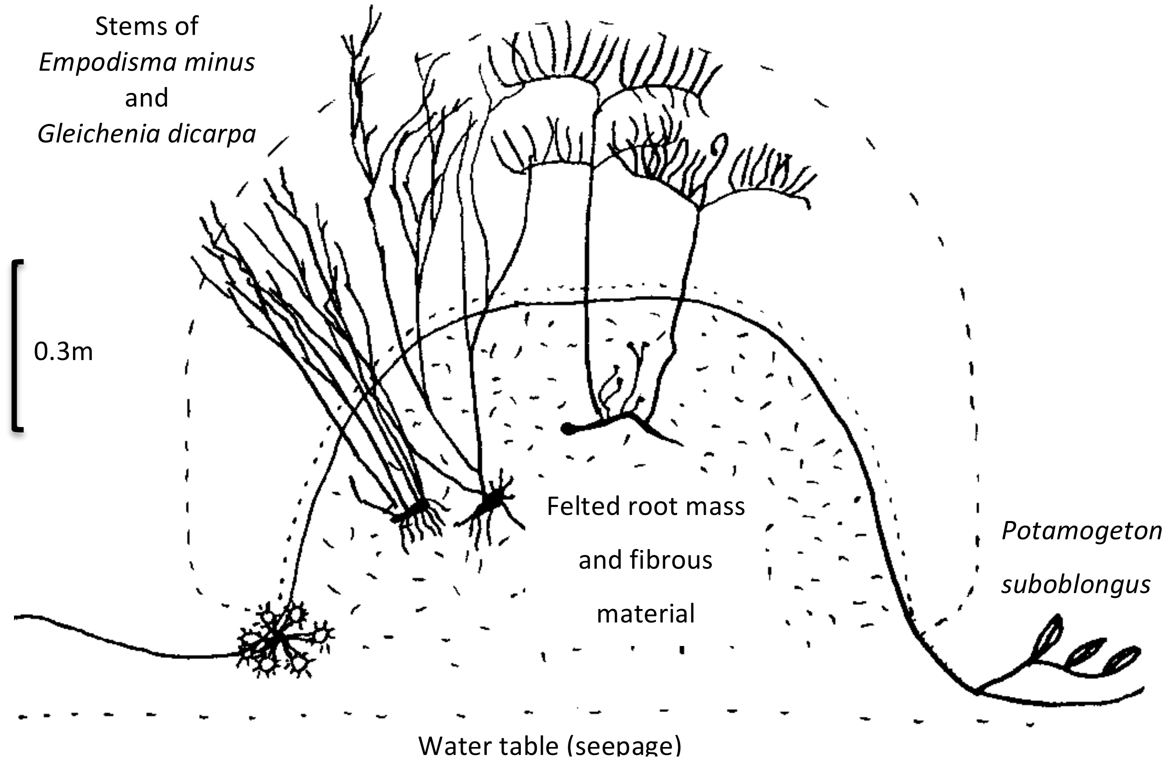


Figure 3.1: A cross section of an *Empodisma minus* hummock from Kaipo Bog, Te Urewera National Park (adapted from Rogers, 1984).
Wire rush rushland community dominated by *Empodisma minus* and *Gleichenia dicarpa* covers approximately 90% of Kaipo Bog, with hummocks 0.5m high common, increasing to 1.5m near the western margins of the mire. Hummocks comprise *Empodisma* capillaroid roots, and rhizomes/stems of both *Empodisma* and *Gleichenia*.

3.2.4 Objectives of the study:

In order to identify a mire chronosequence, and examine the part *Empodisma minus* engineering traits play in engineering the FBT, I undertook a field survey of *Empodisma* dominated vegetation communities in mainland New Zealand. I measured the floristic composition, vascular species canopy and litter biomass, biomass tissue nutrients, and peat chemistry at these sites. I also investigated *Empodisma minus* engineering attributes (capillaroid root depth) and evidence of habitat creation (hummock-hollow topography). The study objectives were:

i. To describe the variety of *Empodisma* communities in New Zealand, their floristic composition, and nutrient status; comparing these to previously described restiad communities; and
ii. To determine the canopy biomass of the engineering species, and the extent of ecosystem engineering traits in each community; and
iii. To investigate the underlying gradients (if any) of the communities, and therefore abiotic limitations to engineering activities by *Empodisma*; and
iv. To examine the suitability of the mires to construct a mire chronosequence for further study of the context dependency of ecosystem engineering by *Empodisma*.

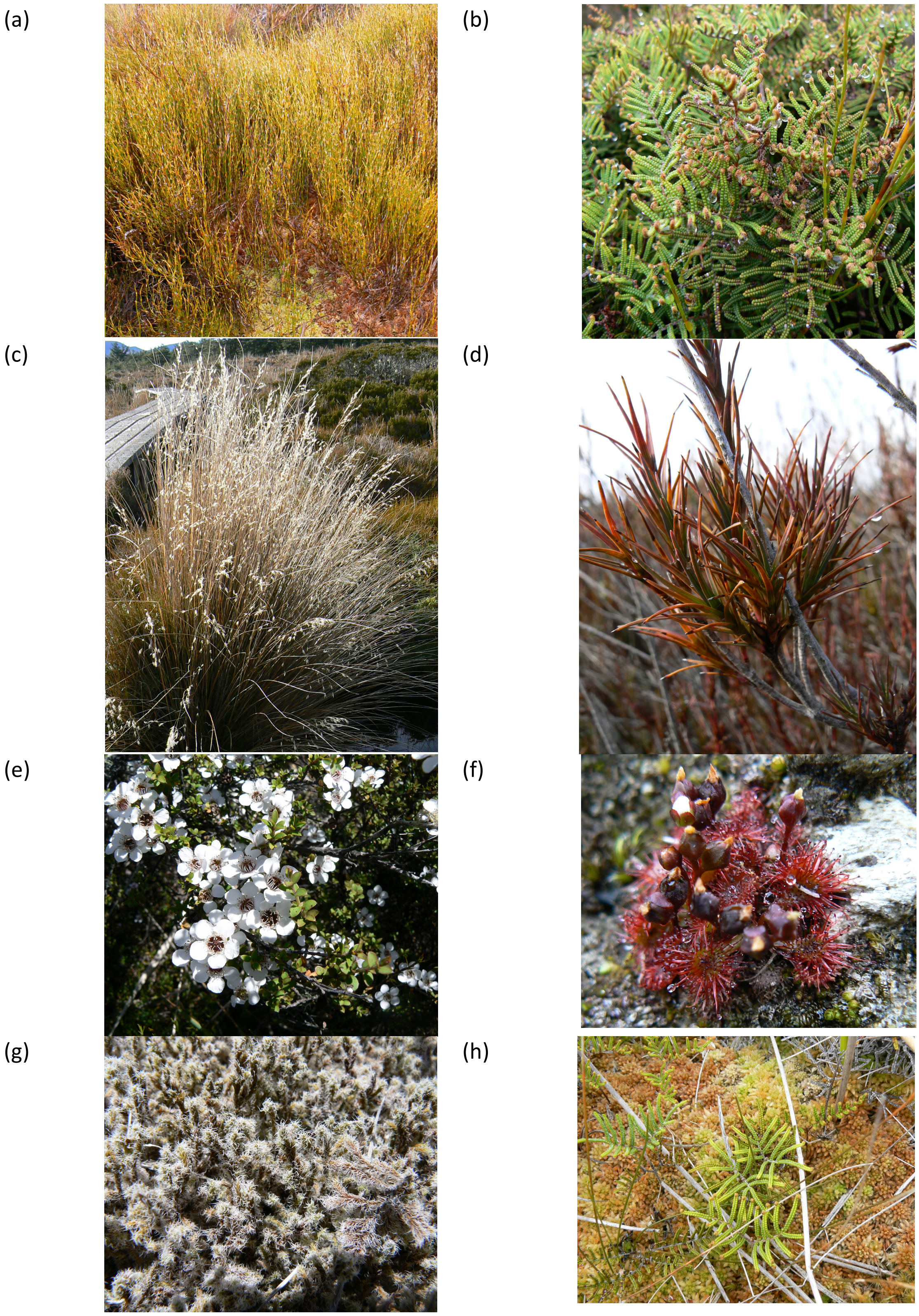


Figure 3.2: Common species of New Zealand restiad mires:.
a) *Empodisma minus*; b) *Gleichenia dicarpa*; c) *Chionochloa rubra* var. rubra *tussock*; d) *Dracophyllum oliveri*; e) *Leptospermum scoparium*; f) sundew, *Drosera pygmaea*; g) the moss *Racomitrium lanuginosum*; h) *Gleichenia* growing in carpet of *Sphagnum cristatum.*

3.3 Methods

3.3.1 Site selection

During the summers of 2002 and 2006-2007, I studied *Empodisma* dominated communities in locations around the North and South Islands of New Zealand. Sites were located using literature surveying New Zealand wetlands (e.g. Davoren, 1978; Stephenson, 1986; Cromarty & Scott, 1996), and Protected Natural Area reports (e.g. Simpson, 1998; Overmars *et al.*, 1998), with additional sites suggested by Department of Conservation staff. The locations were chosen as representative of vegetation communities in which *Empodisma minus* is a common component (Wardle, 2002; Johnson & Gerbeaux, 2004), and included oligotrophic vegetation communities on skeletal, mineral and Organic Soils. *Chionochloa rubra* dominated communities containing no *Empodisma minus* were also surveyed, in either separate mires (e.g. Swampy Summit), or in tussockland communities adjacent to restiad mires (e.g. Waipakihi Swamp).

The criteria employed in site selection were:

a) Presence of vegetation communities dominated by *Empodisma minus* and/or *Chionochloa rubra*;
b) No known fires in recent years, as the literature suggests vegetation change following fire is slow to return to previous stable states (e.g. Johnson, 2001);
c) Grazers excluded to avoid introduction of exotic species and increased nutrient levels;
d) No recent excavation for drainage, as lowering of the water table would affect peat degradation rates, nutrient availability and hence vegetation community composition. Sites with drainage channels were included, since a blanket exclusion of all sites with drainage channels on the perimeter would exclude those in many regions where mire remnants exist within an agricultural landscape (e.g. Southland).
e) Site accessible on foot.

A shortlist of sites was created and these were ranked according to site preference using the above criteria. Where a large number of suitable sites were found, such as in Southland, the final chosen sites were those recommended by local DOC staff as being most representative of local peatland types. A wide diversity of peatlands was sought, and so peatlands that were geographically close and floristically similar were avoided where possible. This was especially the case in Southland where a large number of intact peatlands exist compared to other regions. *Empodisma minus* is not present in mires in the Taranaki region, and so no sites were visited. Sites in northwest Nelson (e.g. Gouland Downs) were unable to be reached due to funding restrictions, and the difficulties of sample transportation from the isolated location.

3.3.2 Vegetation community description and biomass estimates

Vegetation descriptions were undertaken in the summers of 2002-03, and 2006. To describe the vegetation community, the cover of each species within a 0.5m x 0.5m (0.25m^2) quadrat was determined at ten random locations along a 30 m transect, laid within a representative vegetation community at each site. Three of the quadrat locations were randomly selected for further analysis. The above-ground biomass of vascular species in these 0.25m^2 quadrats was then removed at ground level, and sorted in the laboratory into the live and senesced biomass of *Empodisma minus* and *Chionochloa rubra.* The remaining biomass comprising the live and senesced biomass of other species was grouped as "other". The litter component comprised those senesced plant fragments too small to be sorted into species using the naked eye. Dominant non-vascular species were counted, but not harvested, due to the difficulty in distinguishing live versus senesced components of bryophyte capitulum in the field.

All biomass components were oven dried at 70°C for 72 hours until a constant weight was achieved, then weighed.

Vegetation height and depth of capillaroid root presence were noted, and samples of live *Empodisma minus* and *Chionochloa rubra* foliage removed for nutrient analysis. The biomass tissue samples were analyzed in the Environmental Chemistry Laboratory, Landcare Research, Palmerston North. Total-N and -P were determined using automated colorimetric methods, after Kjeldahl digestion, as described in Blakemore *et al.* (1987).

To compare hummock development between sites, the height difference between the top of the substrate on the nearest hummock and the base of the adjacent hollow was measured at the three random points used to sample substrate for chemical analysis. Pearsons correlation coefficients were also determined between hummock height, capillaroid root depth, and climate variables, since hummock height may be influenced by annual rainfall (Agnew *et al.*, 1993; de Groot, 1999).

In total 152 species were recorded during the site visits (Appendix 3.1).

Species nomenclature follows Allan (1982), Moore & Edgar 1976), Healy & Edgar (1980), Webb *et al.* (1988) and Edgar & Connor (2000), except where recent taxonomic changes have been suggested (www.pcn.org.nz). *Gleichenia* plants were grouped together as *Gleichenia* spp. for the analysis, given the current taxonomic uncertainty over the *Gleichenia* genus (Perrie *et al.*, 2007), which is yet to be resolved.

3.3.3 Substrate quality

The physical and chemical properties of the substrate were examined at the same three sample locations used for biomass and hummock measurement. Peat samples were assessed for decomposition using the Von Post Index (Von Post & Granlund, 1926), where values range from H1 (undecomposed) to H10 (highly decomposed) (Appendix 3.2). The degree of peat decomposition is linked to pore size, and hence the hydraulic conductivity of peat (Quinton *et al.*, 2008). Three peat or soil samples were retrieved from the upper 7cm of the substrate at each location using stainless steel cores (0.1 x 0.07m), after above-ground biomass had been harvested for analysis.

One core was analyzed for bulk density, the sample removed from the core, oven dried at 105°C and weighed, as described by Gradwell & Birrell (1979).

The second core was air-dried, and samples used to determine pH, conductivity and loss on ignition, following methods outlined by Blakemore *et al.* (1987). A 1:5 ratio of soil to water was used to determine pH, due to the high peat content (Blakemore *et al.*, 1987). A 1:5 soil:water slurry was shaken for 30 minutes and conductivity subsequently measured, and reported as mS/cm as described in Blakemore *et al.* (1987). Organic matter content was determined following the Loss On Ignition method (LOI) by placing weighed samples in a 500°C muffle furnace for 4 hours (Blakemore *et al.*, 1987).

In the laboratory, the remaining core from each sample was air-dried and sieved to 2mm prior to further analysis. The air-dried samples from each site were combined to form a composite sample. After wet digestion with HNO_3/H_2O_2, concentrations of K, and P were determined by a Perkin-Elmer SCIEX ELAN DRC II inductively coupled plasma mass spectrometer (ICP-MS) at the Mass Spectrometry Facility, University of Waikato. Merck XXI and Merck IV multi-element standards for ICP-MS were used for Quality Control purposes. Substrates were additionally analyzed for C and N using a Leco CNS2000 Analyzer (Leco, 2003) using the Dumas dry combustion principle, by the Waikato Stable Isotope Unit, University of Waikato. One sample for each site was analyzed, due to the high cost of analysis.

3.3.4 Biomass Nutrients

Nitrogen and phosphorus are the nutrients most likely to limit wetland productivity, and the N:P ratio is a useful predictor of nutrient limitation in New Zealand wetlands (Clarkson *et al.,* 2002). The nutrient content of *Empodisma robustum*, *Empodisma minus* and *Chionochloa rubra* live foliage was determined for each site, as the consistent use of key species decreases variation due to interspecific variation (Clarkson *et al.*, 2002). Total-N and -P were analyzed, and the N:P ratio plotted in R using the packages reshape (Wickham, 2007), car (Fox & Weisberg, 2011), gplots (Warnes *et al.*, 2011) and sciplot (Morales *et al.*, 2011).

3.3.5 Statistical analysis

Agglomerative cluster analysis of the species cover data set for the 70 samples was undertaken using the Euclidean distance matrix, and Ward's method which is based on minimizing increases in the error sums of squares, this combination being a reliable, effective clustering method (McCune & Grace, 2002).

Data transformation may affect output, and so three combinations of data transformation were utilized and compared to test the stability of the results produced. The original data set had a large number of species occurring once or twice, due in part to the geographical spread of the sites, resulting in a lot of zero values. To remove noise from these rare species, without losing too much information, those species with <3 occurrences were omitted from the data, and then a further monotonic transformation applied (McCune & Grace, 2002). The transformation is:

$b_{ij} = \log (x_{ij} + d) - c,$ where:

1. Min(x) is the smallest non-zero value in the data;
2. Int(x) is a function that truncates x to an integer by dropping digits after the decimal point;
3. c = order of magnitude constant = Int(log(Min(x)); and
4. d = decimal constant = log-1 (c) (McCune & Grace, 2002).

These actions resulted in 3 data sets:

- The raw data set (152 species);
- Rare species removed (85 species remaining); and
- Rare species removed and data transformation applied.

Visual assessment of the dendrogram produced by cluster analysis has been traditionally used to determine the point at which clusters are defined and interpreted. Because our data set is not exhaustive, inferences made from our analysis may reflect the idiosyncrasies of the communities sampled, and hence a bootstrapping technique was used to assess the strength of the clusters produced (Jackson *et al.*, 2010). The original data matrices had species arranged in columns, and sites in rows. The data were transposed, and cluster analysis undertaken using the pvclust package (Suzuki & Shimodaira, 2009) in R (R Core Development Team, 2011). Pvclust assesses the uncertainty in hierarchical cluster analysis, utilizing a bootstrapping algorithm to generate probabilities for the tree branches produced, enabling an assessment of their reliability. Two types of measures are produced, the bootstrap probability value (BP), and the alternative unbiased value (AU) (Suzuki & Shimodaira, 2006). BP values have been shown to be heavily biased (Efron *et al.*, 1996), AU values having superior characteristics (Shimodaira, 2002), and so AU values were utilized to determine the reliability of the tree branches produced. 1000 bootstraps were generated for each cluster, and since large confidence values are indicative of consistent groupings, the significance level for the clusters was set at 0.95, a commonly used cut-off to indicate a meaningful cluster, as opposed to a random assemblage of samples (Jackson *et al.*, 2010).

The cluster trees obtained for the three data matrices were examined, and AU values utilized to compare the significance of the branches produced. The best outcome (rare species removed and data transformation applied) was used to identify the vegetation communities identified for further examination.

Environmental variables were collated, and the correlation between factors examined graphically using Pearsons correlation coefficients, with the Bonferroni adjustment for multiple comparisons in the Stats module Hmisc in R (Harrell *et al.*, 2012). Significant differences between the cluster groups were identified using one-way ANOVA, with Tukey HSD and p=0.05. Boxplots of the environmental variables were created to allow visual comparisons to be made, using the R modules reshape (Wickham, 2007), car (Fox & Weisberg, 2011) and gplots (Warnes *et al.*, 2011).

A Principal Components Analysis (PCA) was performed on the substrate chemistry data collected at only those sites in the communities described by the cluster analysis using the Lattice module in R (Sarkar, 2008). PCA is a multivariate technique that captures the variation within the data set by combining physical and chemical factors into a small number of variables, or principal components. The scree plots were examined, and those components having an eigenvalue >1 were retained (n=3). Varimax rotation was undertaken to maximise the sum of the variances of the squared loadings, and the rotated and unrotated solutions compared. Biplots of the principal components were drawn using the vegan module in R (Oksanen *et al.*, 2012).

Because insufficient sites were found of some vegetation types, or in some regional locations, additional sites with a greater disturbance history had been included in the survey (e.g. Otago). As a result, the Wetland Condition Index (Clarkson *et al.,* 2002) for each site was calculated restrospectively, and included in the PCA analysis to indicate the effect of anthropogenic changes on wetland communities. The Index captures disturbance by examining five indicators of the degree of modification at the site, each of which is scored on a semi-quantitative scale from 0 (most degraded) to 5 (unmodified). The indicators highlight changes in hydrological integrity, physicochemical parameters, ecosystem intactness, changes in browsing, predation or harvesting, and changes in dominant species cover (Clarkson *et al.*, 2002). A sample Wetland Record Sheet is included in Appendix 3.3.

There were large differences in the substrate bulk density between sites, and so total nutrient pools were analysed and presented on a volumetric basis. The von Post Decomposition Index was unable to be measured at all sites due to some substrates containing little moisture, and so was eliminated from the PCA analysis, although it was used to illustrate differences between significant groupings identified by the cluster analysis.

A summary of the R code used in the analyses is contained in Appendix 3.4.

3.4 Results

3.4.1 Site location and description

70 mire communities in mainland New Zealand containing *Empodisma* species or *Chionochloa rubra* were surveyed during the summers of 2002, and 2006-07 (Figure 3.3; Table 3.1). The sites included six *Empodisma robustum* sites, 22 sites containing both *Empodisma minus* and *Chionochloa rubra*, 13 *Chionochloa rubra* wet tussockland sites, and a further 29 *Empodisma minus dominated* communities where *Chionochloa rubra* was absent. Due to the loss of biomass and peat samples en route to the laboratory, one site (Denniston Plateau 3) was removed from further analysis.

The soils at the sites comprise both Organic and mineral soils, exhibiting a wide range in soil properties (Table 3.2). The soils range from very acidic to circum-neutral (pH=3.8-6.5), and comprise a gradient from mineral soils with <10% organic matter content and a high bulk density, to Organic Soils with <2% ash content and a low bulk density. Of the Organic Soils with sufficient moisture to analyse, the von Post Index ranged from undecomposed plant material to almost completely decomposed material, within which the plant structures were unrecognisable, i.e. from fibric to sapric peat. The gravimetric moisture content of the soils was variable (81.5 ±15.9 %), influenced both by site and soil characteristics, and the period of time since rainfall occurred at the site.

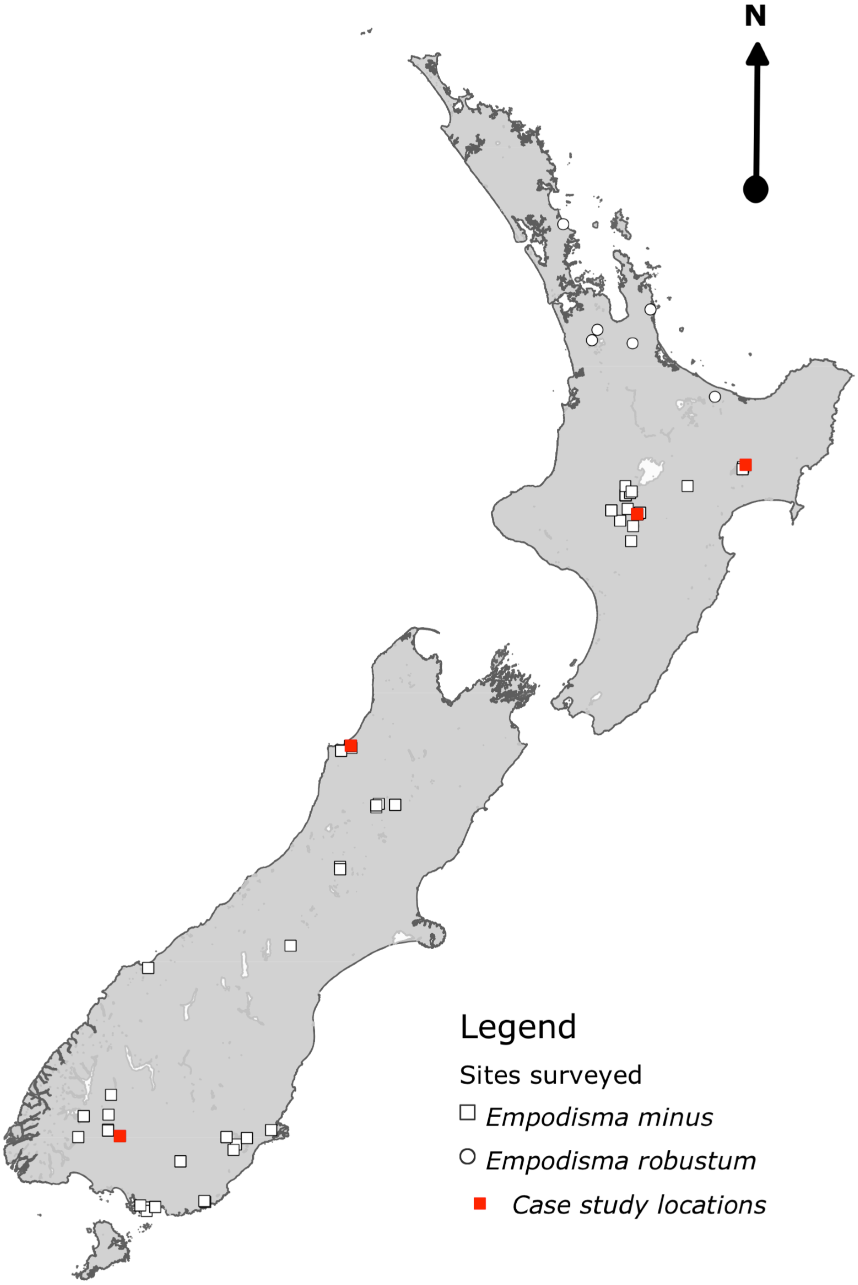


Figure 3.3 Location map of 70 sites sampled during the survey of New Zealand restiad wetlands, 2002 and 2006-07.
Sites indicated in red are, in order of increasing sourthen latitude, Ngapehi-O-Waikareiti, Waipakihi Bog, Denniston Plateau and Castle Downs Swamp. These sites are described in further detail in Section 3.4.3, to illustrate the variety of *Empodisma minus* communities and habitats in New Zealand.

Table 3.1: Sites surveyed during the 2002 and 2006 field surveys of New Zealand restiad and tussockland communities.
Site codes used in the text, Target Species present at site (Em – *Empodisma minus,* Er – *Empodisma robustum*, Cr – *Chionochloa rubra*), Location, and Elevation are presented.

Site Name	**Site code**	**Species Present**	**Longitude**	**Latitude**	**Elevation (m)**
Aparima Valley	APA1	Em	168.01	-45.73	440
Aparima Valley 2	APA2	Em/Cr	168.01	-45.71	460
Awarua	AWA	Em/Cr	168.66	-46.56	10
Bealey Spur	BEA	Em/Cr	171.59	-43.03	1208
Berwick Forest	BER	Em/Cr	169.94	-45.94	399
Black Swamp	BLK	Em	169.90	-46.00	371
Blyth Swamp	BLT	Em/Cr	175.51	-39.33	1260
Borland Bog	BOR	Em	167.56	-45.78	183
Bungtown Bog	BNG	Em/Cr	169.80	-45.86	440
Castle Downs	CAS	Em	168.19	-45.80	245
Deniston Plateau 1	DEN1	Em	171.79	-41.77	600
Denniston Plateau 2	DEN2	Em	171.78	-41.75	650
Duck Creek	DUC	Er	175.83	-37.08	
Erua Bog	ERU	Em/Cr	175.38	-39.23	744
Freestone Mire Site	FRE	Em	167.66	-45.56	192
German Terrace	GER	Em	171.64	-41.80	122
Hunters Bog	HNT	Em	172.17	-42.37	440
Kiwi Burn	KIW	Cr	168.09	-45.35	520
Kopuatai	KOP	Er	175.60	-37.45	25
Lagoon Saddle	LAG	Em/Cr	171.60	-43.05	1170
Lake Christabel	LAK	Em	172.13	-42.40	421
Lewis Pass	LEW	Cr	172.40	-42.38	823
Lilydale Station	LIL	Cr	170.85	-43.85	518
Muddy Creek	MUD	Em	168.50	-46.56	10
NZ Forest Managers	NFM	Em/Cr	175.57	-39.06	640
Ngapehi-o-Waikareiti	NGA	Em	177.19	-38.69	960
Nine Mile Rd	NMR	Em	171.63	-41.80	122
Opuatia	OPU	Er	175.07	-37.43	24
Outdoor Pursuits	OPC	Em/Cr	175.57	-39.06	776
Palmers Rd	PAL	Em	172.13	-42.38	460
Pukerau Bog	PUK	Em/Cr	169.09	-46.10	106
Puna Taeo	PUN	Em	177.15	-38.72	900
Redbank Wetland Mgt Area	RED	Cr	170.11	-45.88	500
Rotoaira	ROT	Em	175.63	-39.04	640
Ruamata	RUA	Em	175.56	-38.97	776
Silica Rapids Mire	SIL	Em/Cr	175.53	-39.21	1195
Sinclairs Bog	SIN	Em	175.66	-39.55	785
Sponge Swamp	SPO	Em	168.75	-44.03	8
St James	STJ	Cr	172.40	-42.38	863
Swampy Summit	SWA	Cr	170.48	-45.80	620
Tahakopa Peat Dome	TAH	Em/Cr	169.42	-46.53	40
Takatimu	TAK	Em/Cr	168.01	-45.73	40
Tama Lakes	TAM	Em/Cr	175.60	-39.21	1097
Te Papa Mire	TPA	Em	176.41	-38.94	730
Tiwai Pt	TIW	Cr	168.53	-46.60	12
Tomorata	TOM	Er	174.65	-36.20	4
Top Rd	TOP	Em/Cr	175.68	-39.39	806
Tumurau Lagoon	TUM	Er	176.73	37.98	8

Site Name	Site code	Species Present	Longitude	Latitude	Elevation (m)
Waipai Swamp	WAI	Em	177.15	-38.74	840
Waipakihi Swamp	WPK	Em/Cr	175.74	-39.26	1020
Wairehu Canal	WAC	Em	175.65	-39.02	600
Weydon Burn	WEY	Cr	168.03	-45.56	400
Whangamarino	WHS	Er	175.13	-37.31	24
Wharepu	WHA	Em/Cr	175.74	-39.26	1020
Wharepu East	WHE	Em/Cr	175.77	-39.24	1010

Table 3.2: Summary of substrate chemistry for New Zealand *Empodisma minus*, *Empodisma robustum* and *Chionochloa rubra* dominated communities surveyed during 2002 and 2006-07.
Soil samples collected from upper 0-7cm of substrate.

Variable	Abbrev.	Unit	Observed			
			Mean	SD	Min	Max
Substrate Chemistry						
Gravimetric Moisture Content	Moist	%	81.5	15.9	20.3	95.4
Total Carbon	TC	%	29.0	13.2	5.4	45.5
Total Nitrogen	TN	%	1.0	0.5	0.2	2.1
Total Phosphorus	TP	mg/cm^3	0.027	0.041	<0.001	0.199
Total Potassium	TK	mg/cm^3	0.064	0.132	<0.001	0.764
Carbon:Nitrogen ratio	C:N		29.7	11.1	12.7	70.6
pH	pH		5.0	0.6	3.8	6.5
Mineral content	Ash	%	33.2	29.2	1.3	91.9
Soil conductivity	Cond	mS	0.3	0.2	<0.01	1.0
Von Post Index	VP		4	2	1	9
Bulk density	BD	g/cm^{-3}	0.155	0.150	0.033	0.682

3.4.2 Nutrient limitation

Large differences in tissue nutrient content were indicated, and all tissue biomass contents suggest N-limitation, P-limitation, or NP co-limitation (Figure 3.4). The nutrient limitation inferred from *Empodisma* vegetation N:P ratios is presented in Appendix 3.5.

The results suggest the growth limiting nutrient in most restiad communities is P, however, nutrient enrichment is also suggested at some sites. Oligotrophic sites, where *Empodisma* tissue P is approximately 0.010% dry wt, are present in the Waikato (Kopuatai & Whangamarino), Central North Island (Erua, Blyth, Waipakihi mire complex), Te Urewera National Park (Waipai Swamp) and the West Coast of the South Island (Denniston Plateau sites) (see Appendix 3.5). The N:P ratios at these sites are very high (N:P=38.1 – 53.1), the highest ratios found in *Empodisma minus* foliage from the Denniston Plateau (N:P=52.0 & 53.1). Seven *Empodisma minus* sites have highly elevated tissue P contents (0.06-0.09% dry wt), which may indicate nutrient enrichment in these communities. The low N:P ratios at these sites (N:P=9.4–13.8) indicate N rather than P is currently the limiting nutrient. The sites are located in Otago and Southland (Berwick Forest, Bungtown Bog, Borland Mire, Muddy Creek, Tahakopa Peat Dome), and largely comprise mire remnants (e.g. Bungtown Bog, approximately 18ha in size), the surrounding land utilized for pastoral farming or silviculture.

N, rather than P, is suggested as the growth limiting nutrient for *Chionochloa rubra* at the majority of sites, P-limited growth being indicated at only 7 sites in the Central North Island (Erua, Waipakihi complex, NZ Forest Managers) and Otago (Tahakopa). Growth appears co-limited by both N and P at 10 sites, including wet tussockland communities in the Central North Island (Silica Rapids, Waipakihi complex, Tama Lakes), and on the St James walkway, at Bealey Spur, and the Redbank Management Reserve. *Chionochloa rubra* tissues contain a wider range of tissue N (0.27-1.08% dry wt) and P (0.02-0.13% dry wt) than *Empodisma* biomass. *Chionochloa rubra* is present at three sites where nutrient additions are indicated by elevated *Empodisma* tissue P, and *Chionochloa* tissue P is similarly elevated at the sites. In addition, *Chionochloa rubra* tissue P concentrations appear elevated at a further five sites (Swampy Summit, Weydon Burn, Tiwai Point, Lilydale Station & Kiwi Burn) where *Empodisma* species are absent. N:P ratios are low compared to those for *Empodisma* species (average N:P=12.9). The highest N:P ratio (N:P=37.1) is found in *Chionochloa rubra* growing in a mire surrounded by *Pinus radiata* forest, west of Mt Tongariro; the lowest N:P ratio (N:P = 5.5) is also found in a mire surrounded by *Pinus radiata* forest, in the Berwick Forest in Otago.

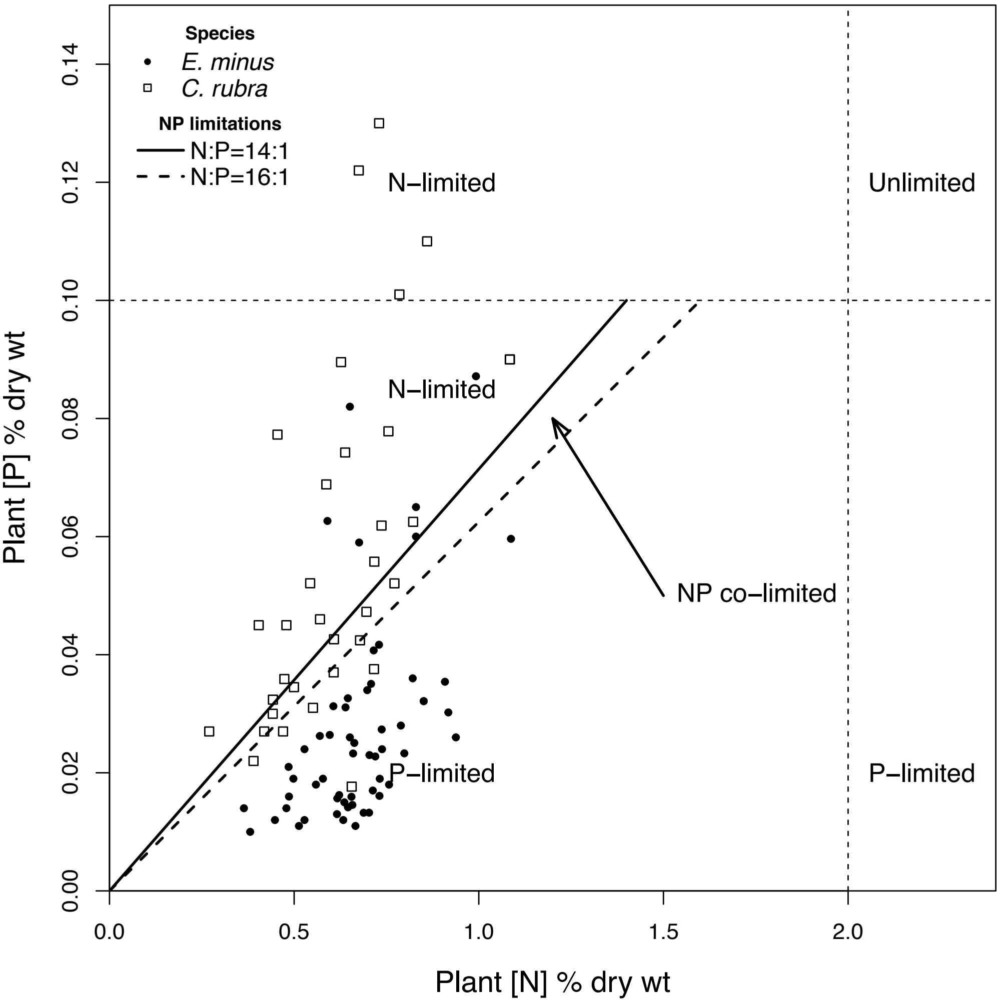


Figure 3.4: Tissue N and P concentrations for *Empodisma* species and *Chionochloa rubra* from wetland sites around New Zealand (n=70 sites, 3 species).

Where N<2% dry wt and P<0.1% dry wt, the N:P ratio can be used (Clarkon *et al*., 2004). The N:P = 14:1 and N:P = 16:1 lines demarcate N and P limitation within the range of potential limitation by both nutrients. Points falling in the upper right quadrant would indicate N and P concentrations exceed growth limiting threshold (0 sites), while points in the upper left quadrant (4 *Chionochloa rubra* sites) indicate growth is N-limited.

3.4.3 Description of four *Empodisma minus* communities

Vegetation communities and their substrates at four geographically spread locations are described to illustrate the range of New Zealand *Empodisma minus* vegetation communities in New Zealand. Community types are indicated by cluster analysis of floristic data (Section 3.4.4). Substrate chemistry are the mean values (n=3) obtained from analysis of uppermost 7cm of soil or peat at the site, except for Waipakihi, where data are the range of values obtained, as a variety of communities were sampled in the large wetland complex. Annual rainfall data are obtained from the LENZ database (Leathwicke *et al.*, 2003).

The four sites are:

(i) a tephrotrophic mire on the Rangipo Plains, Tongariro National Park, North Island;

(ii) a lakeside fen community near Lake Waikareiti in the Urewera National Park, North Island;

(iii) a pakihi community on the Denniston Coal measures above Westport, South Island; and

(iv) Castle Downs Swamp, a raised bog in Southland, South Island.

3.4.3.1 Waipakihi Swamp, Tongariro National Park

Location	Long:175.7396 Lat:-39.26032
Altitude (m)	1020
Comunity type	1a (see section 3.4.4)
Structural class	Wire rush rushland/ shrub-tussockland
Canopy height (m)	0.48 – 0.92
Distance to coast (km)	99.5
Annual rainfall (mm)	2645
Bulk density g/cm^3	0.103-0.519
Ash content (%)	32 - 86
Von Post Index	3.3 - 5
Soil pH	5.3 - 5.9
C:N	24.5 – 31.5

Waipakihi Swamp is a large mire complex located on the Rangipo Plain, on the north-eastern slopes of Mt Ruapehu, in the Tongariro National Park (Figure 3.5 & Figure 3.6). Due to the predominantly west to southwest windflow in the area, tephra deposits fall mainly to the east of the volcanoes, and the most complete record of Ruapehu's eruptive history is found on the extensive ring plain surrounding the mountain, on which the site lies. While the substrate at the lowest point in the mire has a high organic content (68%), the low organic content elsewhere (14%) reflects the high eolian tephra inputs from the mountain, while the variable water table likely contributes to fast litter decomposition rates, and the moderately high von Post score.

Waipakihi Swamp is a gently sloping fen, the eastern portion extending along Waipakihi Road. Dissected by SH1, it continues west towards Mt Ruapehu. An unnamed stream drains the eastern portion of the mire, the Te Piripiri Stream draining the western portion. The mire lies immediately north of the drainage divide between rivers flowing to the north and south of Mt Ruapehu.

The Waipakihi Road wetland comprises a mosaic of tussockland, fernland and rushland vegetation communities (Table 3.3). The eastern end of the wetland is dominated by the tussock *Chionochloa rubra* var. *rubra* over the fern *Gleichenia dicarpa*, and the shrubs *Dracophyllum subulatum, Hebe odora* and *Epacris alpina*. The drier margins, including disturbed edges alongside Waipakihi Road, are dominated by shrublands of *Dracophyllum* *subulatum*, *Leptospermum scoparium* and *Ozothamnus vauvilliersii* over a *Chionochloa rubra* sub-canopy. Wet areas support hummocks of *Empodisma minus* and *Gleichenia dicarpa*, with ephemeral pools in the wettest areas. Communities in these inundated areas feature *Lepidosperma australe* and *Hierochloe redoleus,* with occasional *Drosera* species present on the muddy pool margins, though not sampled during the survey. The bog grades upslope into a drier rushland community dominated by *Empodisma minus*, but featuring increased *Chionochloa rubra* cover, small shrubs (*Andostroma empetrifolia* & *Lepidothamnus laxifolius*), and the herb *Celmisia spectabilis*. The exotic species *Calluna vulgaris*, present in high densities in similar communities in Tongariro National Park, is present in drier portions of the wetland and along the road verge, though is absent from the surveyed area.

Figure 3.5: Wire rush rushland community at Waipakihi Swamp in Tongariro National Park. Species include *Gleichenia dicarpa*, *Empodisma minus*, *Chionochloa rubra* var. *rubra* and *Dracophyllum subulatum*, providing support for a large spider web.

Table 3.3: Species frequencies in 3 communities surveyed in Waipakihi Swamp, Tongariro National Park, Summer 2008.
Number indicates frequency (+ present in less than 10% of quadrats; 1 in 10-19%; 2 in 20-29%; 3 in 30-39%; 4 in 40-49%; 5 in 50-59%; 6 in 60-69%; 7 in 70-79%; 8 in 80-89%; 9 in 90-99%; C in 100%).

	Community		
Species	**Rushland 1**	**Rushland 2**	**Shrub-tussockland**
Aciphylla colensoi			+
Androstoma empetrifolia	+	+	+
Carpha alpina	+	+	
Celmisia gracilenta			1
Celmisia spectabilis		+	1
Chionochloa rubra var. *rubra*	+	3	5
Coprosma cheesemanii			3
Coprosma pseudocuneata	+		
Craspedia spp.			+
Dicranoloma billardierdei			+
Dracophyllum subulatum	+	2	7
Empodisma minus	C	8	
Epacris alpina			3
Gaultheria colensoi			+
Gleichenia spp.	6	7	
Hebe odora			1
Hierochloe redoleus		+	
Hypochoeris radicata			+
Lepidosperma australe	1	+	+
Lepidothamnus laxifolius	+	1	
Ozothamnus vauvilliersii		1	1
Pentachondra pumila			+
Podocarpus nivalis		+	
Ranunculus nivalis	+	+	1
Wahlenbergia pygmaea			+

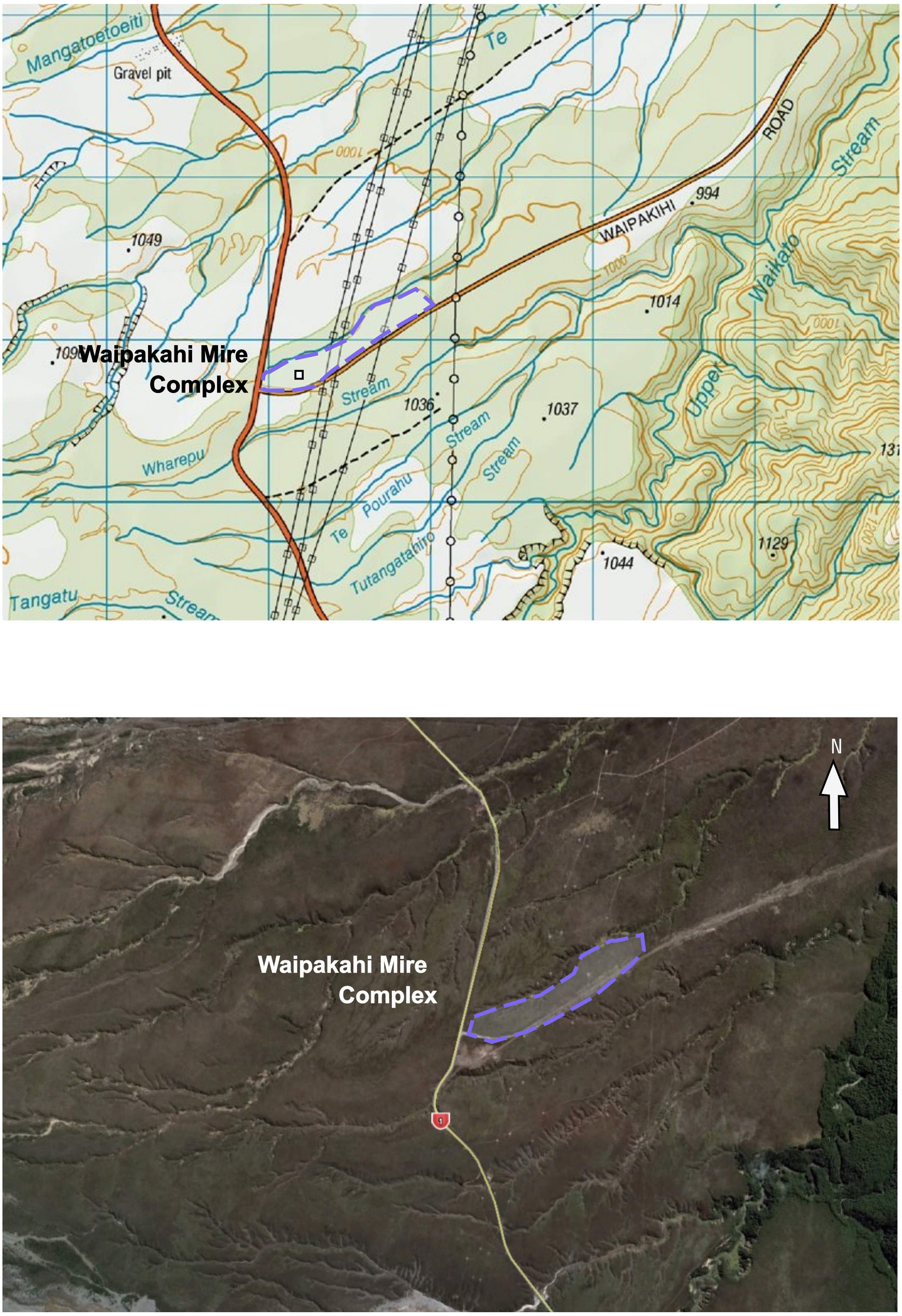


Figure 3.6: Location map and Google Earth image of the Waipakihi Mire Complex, Tongariro National Park. The area outlined on the maps indicates the eastern side of the complex which was sampled in this study. The mire continues over SH1 to the west, but less organic matter has accumulated compared to the eastern portion of the mire. Similar wire rush rushland communities are present further to the east, the communities separated by expanses of *Chionochloa* tussockland.

3.4.3.2 Ngapehi O Waikareiti, Ruapani Tarns, Urewera National Park

Location	Long:177.1871 Lat:-38.69437
Altitude (m)	960
Comunity type	4b (see section 3.4.4)
Structural class	Wire rush rushland
Canopy height (m)	0.78
Distance to coast (km)	45
Annual rainfall (mm)	2655
Bulk density g/cm^3	0.053
Ash content (%)	6
Von Post Index	2.7
Soil pH	4.44
C:N	42

Ngapehi O Waikareiti (Clay Patch) is a 5.8 ha montane peat bog lying at an altitude of 960 m in the south-eastern portion of the Urewera National Park, one of a series of small wetlands surrounding Lake Waikareiti (Figure 3.7 & Figure 3.8). The mire is situated in an extensive landslide complex, in which subsequent infilling and the formation of a series of mires has occurred (Lowe *et al.*, 1999; 2013). These include Ngapehi-o-Waikareiti, Kaipo Lagoon, Sopps Lagoon, Oranga Kohau and the Ruapani Tarns (Waipai, Ruapani, Whano-o-Ruapani, Hine Waho, Hine Rere, Puna Hokoi, Puna Taeo). The vegetation of Kaipo Lagoon was described in detail by Rogers (1984), however, only species lists and a brief description of vegetation types exists for the remaining wetlands (Druce, 1978; Jack, 2004).

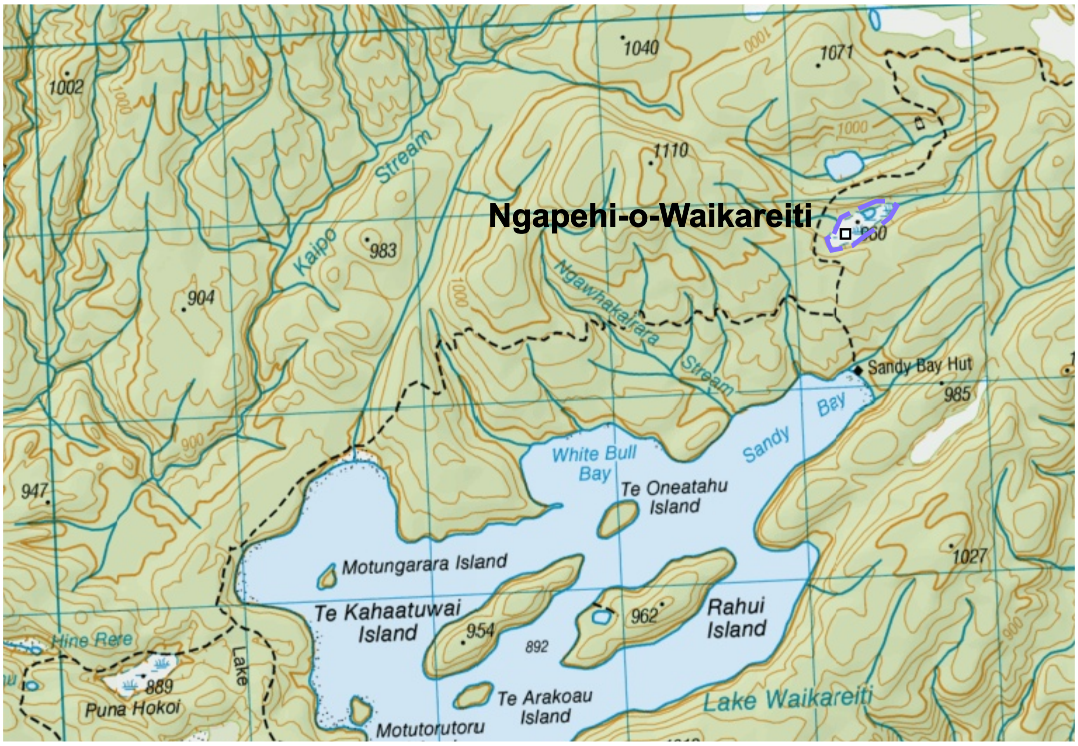
Ngapehi O Waikareiti contains seven vegetation communities including shrubland, wire rush rushland (*Empodisma minus*; *Sphagnum* species; *Dracophyllum longifolium*), *Juncus/Carex*, *Lepidosperma*, *Myriophyllum*/grass turf, open water, and *Nothofagus* forest surrounding the mire (Jack, 2004). The rushland community was surveyed and found to contain large hummocks, >50 cm high, similar to those recorded by Rogers (1984) at Kaipo Lagoon. These comprise a mass of live *Empodisma minus* capillaroid roots and litter. The community contains the grasses *Carex sinclairii* and *Carex gaudichaudiana*, with *Netera scapanioides* and *Androstoma empetrifolia* scrambling among the hummocks, interspersed with patches of short turf dominated by *Carpha alpina* (Table 3.4 & Figure 3.7). *Gleichenia dicarpa*, a common component in montane mires in the Tongariro National Park, is absent from the site, the community instead having a minor *Sphagnum* component indicative of wet conditions. Deer browse is present at the site, indicated both by deer sign and by taller vegetation within the nearby exclusion pen.

The bog substrate is acidic, and has a very high organic matter content (94%), which is reflected in the low bulk density. The average von Post Index is low (mean=2.7), which may reflect the presence of *Sphagnum cristatum* in the community.

Table 3.4: Species frequencies in wire rush rushland community surveyed in Ngapehi-o-Waikareiti, Urewera National Park, Summer 2008.
Number indicates frequency (+ present in less than 10% of quadrats; 1 in 10-19%; 2 in 20-29%; 3 in 30-39%; 4 in 40-49%; 5 in 50-59%; 6 in 60-69%; 7 in 70-79%; 8 in 80-89%; 9 in 90-99%; C in 100%).

Species	**Ngapehi-o-waikareiti**
Androstoma empetrifolia	+
Carpha alpina	+
Carex gaudichaudiana	+
Carex sinclairii	+
Celmisia gracilenta	2
Coprosma propinqua	+
Dracophyllum longifolium	2
Drosera spathulata	+
Empodisma minus	9
Halocarpus bidwillii	+
Hebe odora	+
Lachnagrostis filiformis	+
Lepidosperma australe	+
Lobelia angulata	+
Nertera scapanioides	+
Oreobolus pectinatus	+
Sphagnum cristatum	1

Figure 3.7: Ngapehi-o-Waikareiti in Urewera National Park.
Species present in the community surveyed include *Dracophyllum longifolium* and *Empodisma minus.*



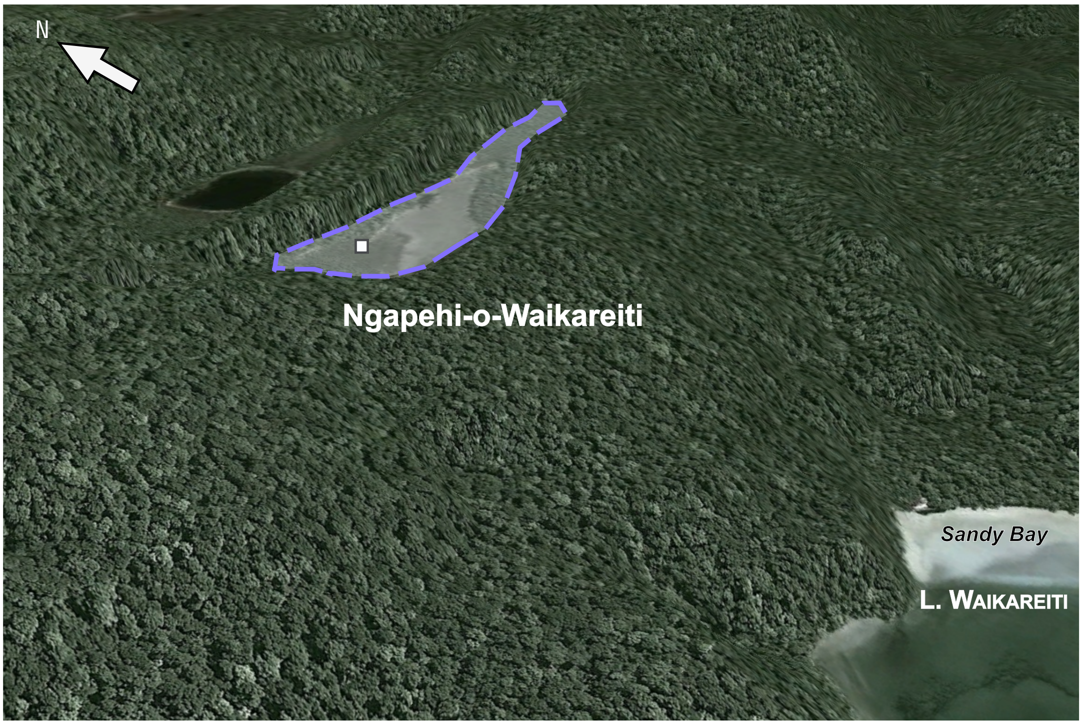


Figure 3.8: Location and Google Earth perspective view of Ngapehi-o-Waikareiti, Te Urewera National Park. The location of the community surveyed is indicated in both images. Lake Waikareiti is located to the south-east of Ngapehi-O-Waikareiti, with Lake Henrietta to the north-west. One of the Ruapani Tarns, Puna Hokoi, is visble west of Lake Waikareiti, though was not sampled as *Empodisma minus* is not present at the site.

3.4.3.3 Denniston Plateau, West Coast, South Island

Location	Long:171.7802 Lat:-41.7641
Altitude (m)	960
Comunity type	2a (see section 3.4.4)
Structural class	Manuka/wire rush rush-shrubland
Canopy height (m)	0.54
Distance to coast (km)	7.7
Annual rainfall (mm)	2200
Bulk density g/cm^3	0.682
Ash content (%)	91.9
Von Post Index	NA
Soil pH	4.97
C:N	26.6

The Denniston communities surveyed lie on the Denniston Coal Measures plateau (Overmars *et al.*, 1998), in the Ngakawau Ecological District, on the West Coast of the South Island. The plateau is located east of Westport, much of the plateau and surrounding land owned by various crown agencies. The plateau comprises a large uplifted and faulted tableland of Brunner coal measures, and includes many landforms, including fault scarps, alluvial flats, and the sandstone pavement (Overmars *et al.*, 1998), upon which the site is located. The coal pavements occur on gentle slopes, the quartzose coal measure exposed near bluff edges (Figure 3.9 & Figure 3.10). Annual rainfall is high, and fog frequently forms on the plateau as a result of moist air from the nearby coast (7km) ascending the steep plateau escarpment (Overmars *et al.*, 1998).

Attention has been focused on the area lately due to the expansion of coal mining on the plateau, and as a result, the vegetation of the plateau is now quite well described (Nichol & Overmars, 2008; Glenny & Dawson, 2011). The vegetation communities of the coal pavements consist of a mosaic of dwarf and prostrate shrubs, tussock and species typical of infertile, humid environments in New Zealand (Given & Park, 1975; Wardle, 2002). 80% of the vegetation communities on the Denniston Plateau have either a history of burning, or are highly modified by fire, road construction and encroachment of exotic species (Nichol & Overmar, 2008). The area surveyed has likely been altered by fire, and comprises low growing Mānuka/*Empodisma minus–Gleichenia microcarpa* fern rushland on gently sloping, poorly drained peat soils overtop of coal pavement (Table 3.5). The local endemic *Chionochloa juncea* grows in association with *Empodisma minus* and *Gleichenia microcarpa* in the community, largely replacing *Chionochloa rubra*, a typical part of the assemblage in mires elsewhere (Wardle, 2002).

The substrate is shallow, acidic (pH 4.97), and contains little organic matter (8.1%), and hence has a very high bulk density (0.682 g/cm^3) compared to mire vegetation elsewhere. The substrate on the rock pavement has been previously removed by fire, or erosion. No fire history is available for the site, but smoke from a persistent underground fire was observed a few hundred meters from the site.

Table 3.5 Species frequencies in a manuka/wire rush rush-shrubland community surveyed on the Denniston Plateau, South Island, NZ, March 2008.
Number indicates frequency (+ present in less than 10% of quadrats; 1 in 10-19%; 2 in 20-29%; 3 in 30-39%; 4 in 40-49%; 5 in 50-59%; 6 in 60-69%; 7 in 70-79%; 8 in 80-89%; 9 in 90-99%; C in 100%).

Species	**Denniston Plateau**
Androstoma empetrifolia	1
Carpha alpina	3
Celmisia dubia	1
Chionochloa juncea	4
Chionochloa rubra var. *rubra*	1
Donatia novae-zelandiae	+
Dracophyllum politum	+
Drosera spathulata	1
Empodisma minus	7
Gleichenia spp	1
Halocarpus bidwillii	+
Juncus squarrosus	+
Leptospermum scoparium	6
Lycopodiella laterale	1
Oreobolus strictus	+
Ourisia macrocarpa	+
Thelymitra cyanea	+

Figure 3.9: Manuka/wire rush rush-shrubland surrounded by bare pavement on coal measures, Denniston Plateau, South Island, Summer 2007

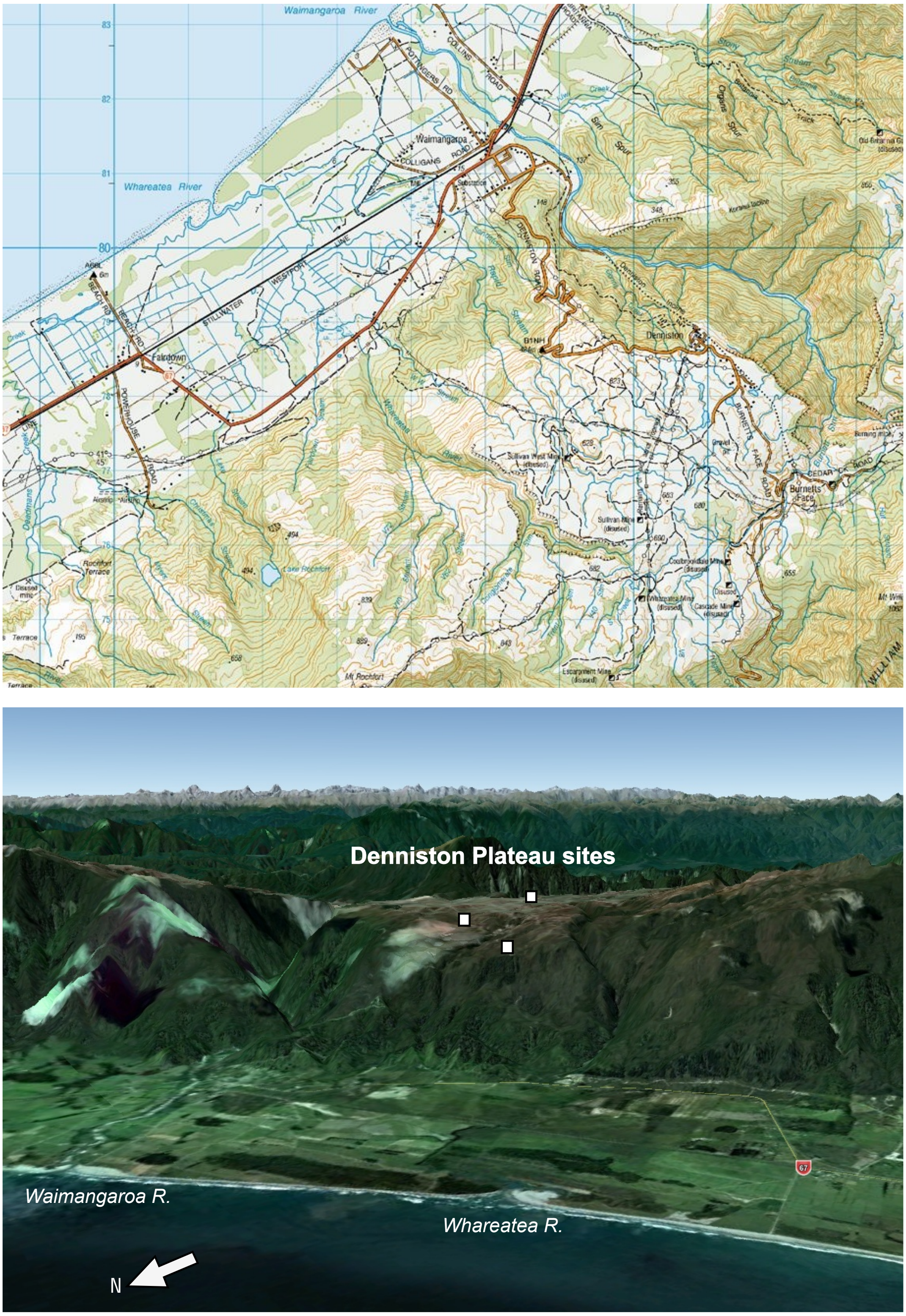


Figure 3.10: Location map and Google image of the Denniston Plateau, Westland. The location of the communities sampled is indicated on the Google image.

3.4.3.4 Castle Downs Bog, Southland, South Island

Location	Long:168.1904 Lat:-45.79589
Altitude (m)	245
Comunity type	4b (see section 3.4.4)
Structural class	Wire rush rushland
Canopy height (m)	0.2
Distance to coast (km)	61
Annual rainfall (mm)	957
Bulk density g/cm^3	0.073
Ash content (%)	6.8
Von Post	3.7
Soil pH	4.62
C:N	33.6

The Castle Downs Bog is the largest remaining peat bog in the Taringatura Ecological District, Southland (Simpson, 1998), lying in a large synclinal basin filled with Quaternary glacial outwash gravels and alluvium that extends from Centre Hill to the Castle Downs site (Simpson, 1998). A series of peat bogs with similar flora occur in fault angle depressions and depressions between valley terraces, including the Centre, Braxton, Hamilton and Waterloo Burns (Simpson, 1998). The area has a cool, temperate climate, with strong NW winds, and semi-drought conditions experienced on occasion (Simpson, 1998).

The mire consists of a 1000ha peat bog remnant, and is currently privately owned. The vegetation community consists of 5 communities, four of which are dominated by *Empodisma minus* (wire rush bog, red tussock-wire rush bog, wire rush-flax bog & wire rush-*Sphagnum* bog) (Simpson, 1998). The transect in the survey dissected the wire rush and wire rush-*Sphagnum* bog communities (Table 3.6 & Figure 3.11). The latter community contained *Sphagnum falcatulum*, indicative of open water or pools within this portion of the mire. The presence of exotic grass and herb species (*Agrostis capillaris, Ranunculus repens, Hypochoeris radicata,* & *Holcus lanatus*) in the mire centre may reflect increasing nutrient availability, or stock access to the mire. The bog margin is dominated by *Chionochloa rubra* var. *cuprea* and *Dracophyllum oliveri*, and contains a higher proportion of exotic grass species. Scattered shrubs in the community suggest no recent fires in the surveyed area, shrubs being greater than 1m in height (Rance & Edwards, 2002).

The mire is described as in relatively natural condition, compared with other raised mires in the ecological district (Simpson, 1998; Campbell *et al.*, 2003), though the mire's low nutrient status is threatened by drainage (Figure 3.12), and a historic black backed gull colony on the mire (Simson, 1998). The increased nutrient availability is reflected in the slightly elevated von Post index (3.7). The peat substrate is acidic (pH 4.62), with a low soil bulk density (0.073 Mg/m3), reflecting its low ash content (6.8%).

Empodisma minus forms extensive capillaroid roots in the peat, compared to the other communities (Figure 3.13).

Table 3.6: Species frequencies in a wire rush rushland community surveyed on the Castle Downs Bog, South Island, NZ, March 2008.
Number indicates frequency (+ present in less than 10% of quadrats; 1 in 10-19%; 2 in 20-29%; 3 in 30-39%; 4 in 40-49%; 5 in 50-59%; 6 in 60-69%; 7 in 70-79%; 8 in 80-89%; 9 in 90-99%; C in 100%).

Species	**Castle Downs**
*Agrostis capillaris**	1
Carex echinata	2
Celmisia gracilenta	1
Coprosma intertexta	+
Coprosma parviflora	1
Dracophyllum oliveri	1
Empodisma minus	C
Gaultheria depressa	+
*Holcus lanatus**	1
*Hypochoeris radicata**	1
Juncus edgariae	1
Leptospermum scoparium	1
Netera depressa	1
Ozothamnus vauvilliersii	1
*Ranunculus repens**	1
Sphagnum cristatum	3
Sphagnum falcatulum	1
Thelymitra cyanea	+

Figure 3.11: Castle Downs Bog, Southland, Summer 2008.
Scattered *Chionochloa rubra* tussocks in a dense *Empodisma minus* sward.

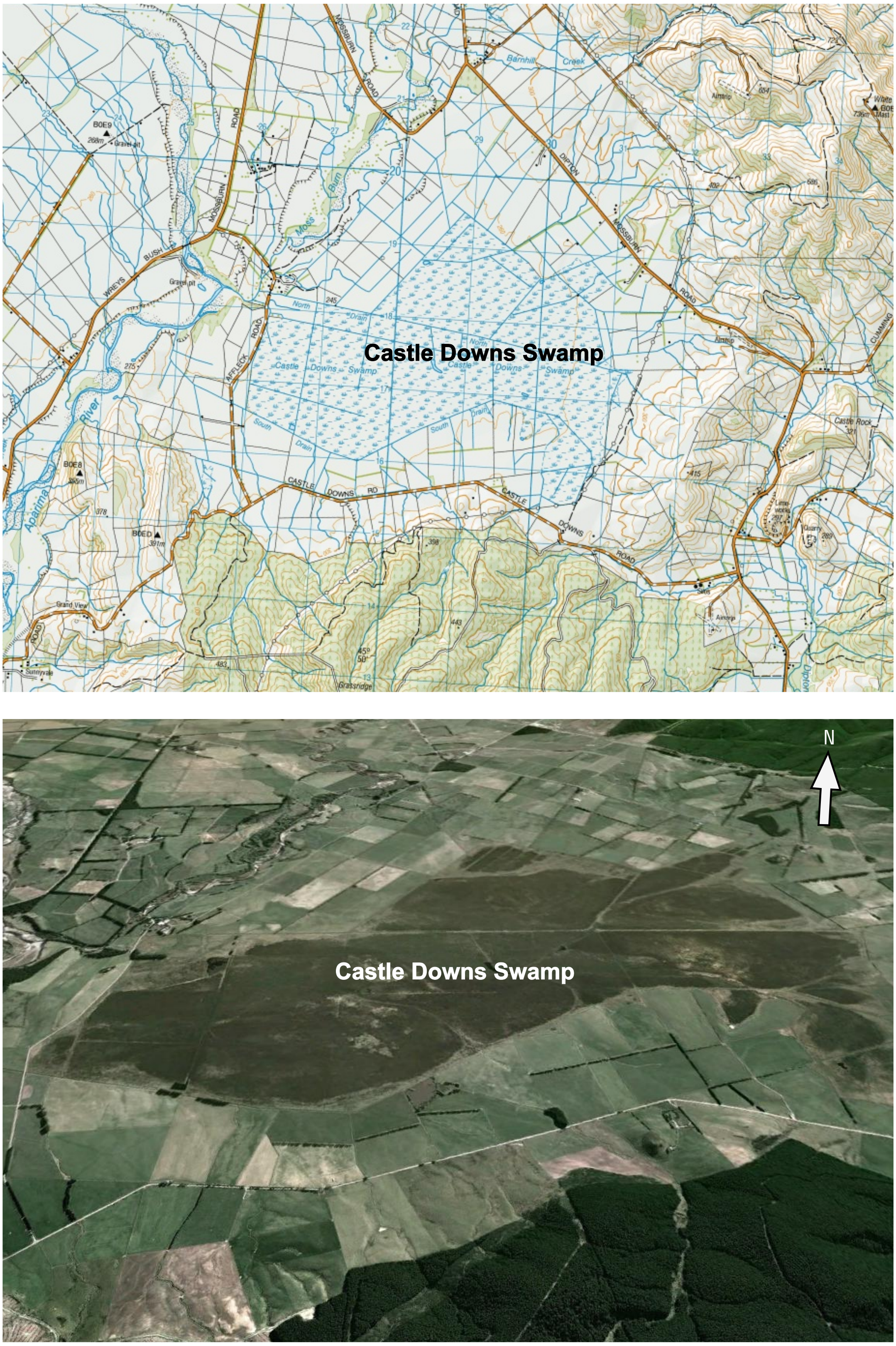


Figure 3.12: Location map and Google Earth image of Castle Downs, Southland. The large mire is ringed and dissected by drainage ditches and surrounded by agricultural land.

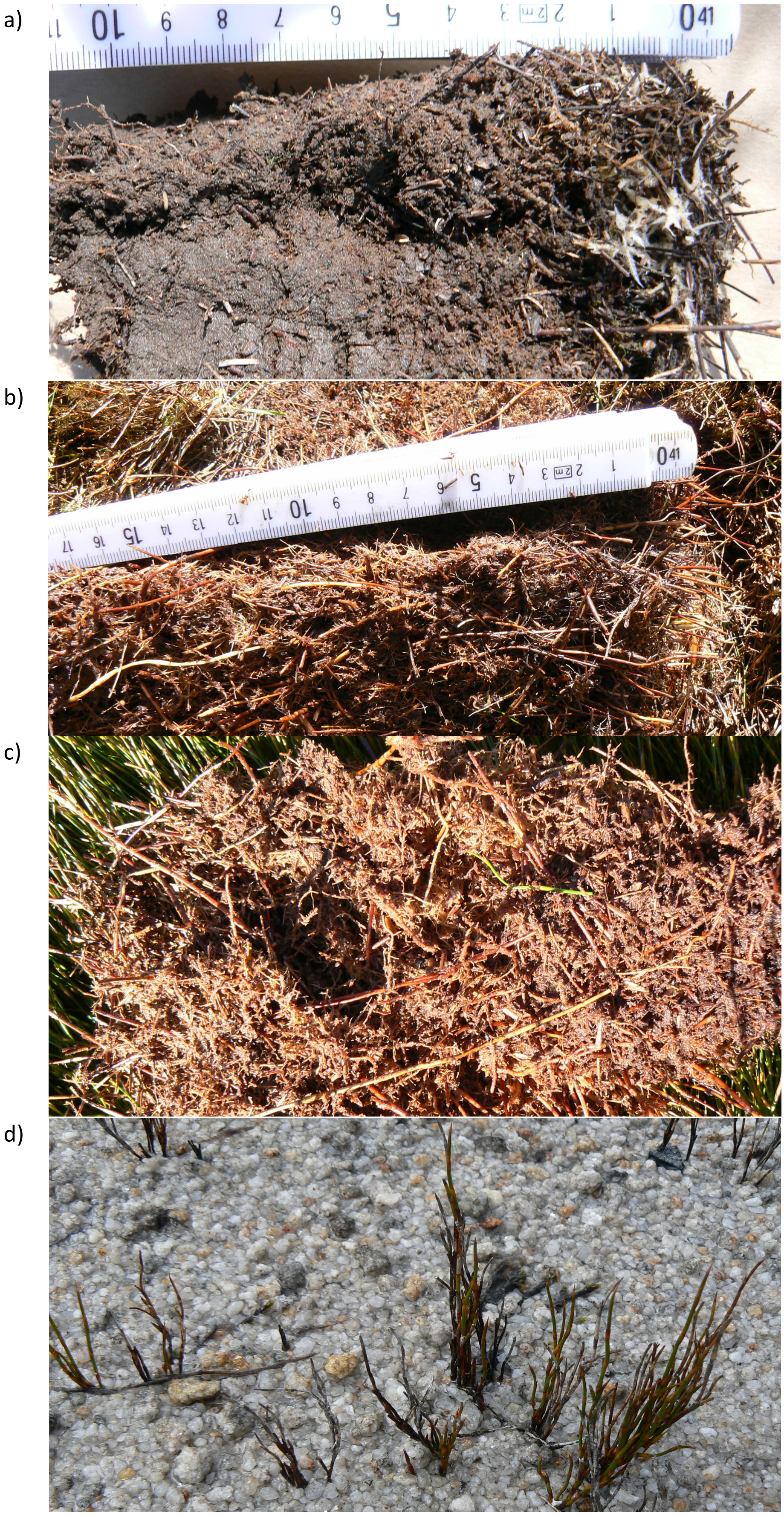


Figure 3.13: Examples of substrates underlying *Empodisma minus* communities in New Zealand.

a) Soil derived form volcanic materials, Waipakihi Road, central North Island. Note the few white capillaroid roots at top of soil; b) Ngapehi-o-Waikareiti and c) Castle Downs peat substrate, a loose, unhumified peat, with high concentrations of capillaroid roots and *Empodisma minus* culms; d) *Empodisma minus* persisting in quartzose sands, Denniston Plateau, West Coast.

3.4.4 Species associations

Species associations were determined using Wards method and the Euclidean distance matrix of the three species data matrices. The resulting dendrogram shows the series of significant or meaningful clusters identified by the analysis (Figure 3.14). The dendrogram from the log transformed data set contains fewer significant clusters, which formed at higher dissimilarity levels than the untransformed data sets (Appendix 3.6), and was therefore chosen for further investigation.

The classification of the communities suggested by pvclust, and the cover of dominant canopy species are summarised in Table 3.7. Above-ground biomass, the proportion comprised of *Empodisma* foliage, and the extent of *Empodisma* capillaroid root growth and development of hummock-hollow topography in the communities are summarised in Table 3.8. The first main branch contains two significant clusters (Group 1a, AU=0.99 & Group 1b, AU=0.96) comprising *Empodisma minus* communities surveyed in mires from the central North Island, with the addition of a site from Lagoon Saddle in Canterbury (Figure 3.14; Table 3.7). The second main branch contains four significant sub-clusters (Groups 2a-2d). The most strongly associated cluster (Group 2a; AU=1.00) comprises two *Empodisma minus* communities from the Denniston coal measures near Westport. The second cluster (Group 2b, AU=0.99) contains *Empodisma minus* communities from Southland and Otago raised and blanket bogs. The third cluster (Group 2c; AU=0.99) comprises four communities surveyed on the edge of *Empodisma robustum* mires. The fourth cluster (Group 2d; AU=0.95) largely comprises communities surveyed in Westland pakihi mires (n=4). The third main branch contains sites with no *Empodisma* component, i.e. wet tussockland sites, and contains no significant clusters. The fourth main branch contains *Empodisma minus* sites from throughout New Zealand with a large *Sphagnum* component, and is sub-divided into two significant clusters (Group 4a, AU=0.97; Group 4b, AU=0.96).

3.4.4.1 Floristic Group 1a. Montane shrubby *Empodisma* peatlands

Group 1a includes three montane communities from the central North Island and another from Lagoon Saddle in Canterbury. The highly species diverse vegetation community features a canopy of scattered *Chionochloa rubra* tussocks and *Dracophyllum* species, with a dense sub-canopy co-dominated by *Empodisma minus* and *Gleichenia dicarpa*. The presence of flush indicator species (e.g. *Carpha alpina*, *Schoenus pauciflora*) (Dobson, 1975) in hollows and pools on the sloping landforms suggest the communities are minerotrophic fens. The above-ground biomass at the sites is variable (0.94 ±0.61kgm^{-2}) due to the presence of scattered shrubs and tussocks in the canopy (Table 3.8). *Empodisma minus* comprises a smaller percentage of the total canopy biomass compared to other communities, reflecting the shrub and tussock cover, the canopy also consisting of slightly more live than senesced *Empodisma* biomass (0.16 ±0.69& 0.15±0.73 kgm^{-2} respectively). A thick litter layer covers the peat surface, the upper surface of which contains a very shallow capillaroid root zone ranging from 0-4cm thick, with maximum hummock height at the sites ranging from only 8-15cm above the hollows. The altitudinal range of the communities ranges from 1097-1260m, with mean annual precipitation ranges from 1346-2825mm.

3.4.4.2 Floristic Group 1b. *Gleichenia-Empodisma* fernlands – central North Island

Group 1b sites include a further three communities from the central North Island, which occur at a lower elevation (776-1020m) and contain a smaller species pool than the sites in Group 1a. The vegetation community features a mixed *Dracophyllum-Chionochloa rubra* canopy, over a subcanopy which contains a larger proportion of *Gleichenia dicarpa* than *Empodisma minus*. The drier substrate is reflected in the absence of flush species, and the higher shrub and *Gleichenia* component. The community also contains a thicker litter layer (0.21 ±0.30 kgm^{-2}) over the substrate, which contains only a few, scattered capillaroid roots (0-1cm). There is little evidence of the development of surface microtopography, with a maximum hummock height ranging of 8cm in the community. Mean annual precipitation ranges from 2423-2645mm, and the root zone water deficit ranges from 0.66-10.69 Mpa days.

3.4.4.3 Floristic Group 2a. Coal pavement vegetation – Denniston Plateau

The two Group 2a sites are located between 600-650m elevation on the coal measures east of Westport, and contain a unique species assemblage including *Chionochloa juncea*, which replaces *Chionochloa rubra* at many sites on the plateaus. This short-statured community (0.38 ±0.22m) contains little above-ground biomass compared to the other vegetation types (0.31 ±0.17 kgm^{-2}), few capillaroid roots in the upper peat (0-1cm), or hummock-hollow topography development (0-9cm). Despite a species assemblage very similar to that of an oligotrophic bog, these systems have accumulated little organic matter. Mean annual rainfall is 2200mm (likely an underestimation), and there is no root zone water deficit at the site.

3.4.4.4 Floristic Group 2b. *Empodisma* bog – Southland & Otago

Group 2b includes communities from seven raised and blanket bogs between 10-1208m elevation in southern New Zealand. A dense *Empodisma minus* canopy dominates the sites, with occasional *Chionochloa rubra* tussocks, and only a small *Gleichenia dicarpa* component. Despite the low shrub and tussock cover, the *Empodisma* canopy is of a similar height to communities with a large tussock or sedge component (0.71 ±0.28m). The tall, dense *Empodisma minus* canopy contains the highest volume of senesced material, which contributes to the dense litter layer (0.26 ±0.11 kgm^{-2}). Beneath the litter is the deepest live capillaroid root zone ranging from 1-20cm, with hummock-hollow topography also well developed at some sites (2-32cm). The deepest capillaroid root zone and second highest hummock-hollow topography is present at Pukerau Scientific Reserve, where live capillaroid roots extend to 20cm below the surface, in the 32cm high hummocks. Mean annual rainfall at the sites ranges from 957-1662mm, and the root zone water deficit ranged from 0.63-52.34 Mpa days.

3.4.4.5 Floristic Group 2c. *Empodisma-Machaerina* sedgelands – Waikato & BOP

Group 2c comprises four sites with a large *Empodisma robustum*, *Gleichenia* and *Machaerina rubiginosa* component, and very low species diversity. This species combination is found in the *Empodisma robustum* dominated canopies of young bogs, and the margins of older mires north of 38° S, of similarly low elevation (4-28m). This vegetation type has the tallest canopy of the communities surveyed (1.27 ±0.16m), high canopy biomass (1.10 ±0.20 kgm^{-2}), live *Empodisma* foliage biomass (0.37 ±0.16 kgm^{-2}), high litter biomass (0.17 ±0.79 kgm^{-2}), and a deep zone of capillaroid root development (0-15cm). Mean annual rainfall at the sites ranges from 1028-1730mm, and the root zone water deficit ranged from 10.1-55.73 Mpa days.

3.4.4.6 Floristic Group 2d. Pakihi – Westland

Group 2d had the largest *Machaerina teretifolia* component, and comprises three fen communities from *Empodisma minus* pakihi on the West Coast of the South Island, and a *Empodisma robustum* community from the edge of a North Island mire. Group 2d has a high average canopy biomass (1.06 ±0.62 kgm^{-2}), a more diverse species pool (27 & 7 species respectively) and deeper litter layer than Group 2c (0.18 ±0.15 kgm^{-2}). As a result of the large sedge component, the canopy contains proportionally less live *Empodisma* biomass. There is a shallow zone of capillaroid root growth ranging from 1-5cm deep, and maximum hummock height ranging from 1-14cm high. Mean annual rainfall at the sites ranges from 1204-4474mm, while the root zone water deficit ranged from 0-55.3 Mpa days, the higher water deficit occurring in the North Island site.

3.4.4.7 Floristic Group 4a. Tussock rich *Empodisma* mires - Otago

Sphagnum cristatum is a large component of Group 4a sites, which are dominated by *Empodisma minus*, and from which *Gleichenia* is absent. These communities are all located in Otago fen and bog remnants between 40-640m elevation, and differ from Group 4b by their large *Chionochloa rubra* component. Four of the five Group 4a sites are located within an agricultural or forestry setting. Live *Empodisma minus* biomass comprises almost a third of the live canopy biomass (29.4 ±20.4%), and the canopy contains a large volume of senesced *Empodisma* (40.8 ±7.9%). The mean zone of capillaroid root growth and height of hummock-hollow topography is similar in Groups 4a and 4b. Hummock height is extremely variable ranging from 0-45cm, hummocks at the wetland in the Berwick Forest site being the tallest measured during the survey (45cm), despite capillaroid root depths of 1-5cm. Mean annual rainfall at the sites ranges from 571-1258mm, while the root zone water deficit ranged from 14.24-28.66 Mpa days.

3.4.4.8 Floristic Group 4b. Shrubby *Empodisma-Sphagnum* mires

Group 4b comprises a large group of sites (n=15) with a vegetation canopy dominated by *Empodisma minus* and *Sphagnum cristatum*, with a large shrub component, and an absence of *Chionochloa rubra* and *Gleichenia dicarpa*. This vegetation type is widespread, being representative of communities at higher elevations in the Ruapani Tarns in Urewera National Park (840-960m), inland communities at 420-460m elevation at Springs Junction near Lewis Pass, and in raised and blanket bogs up to 460m altitude in Southland, Otago and Fiordland. The communities contain a high number of exotic species compared to non-*Sphagnum* communities (7 *c.f.* <2 species elsewhere). The sites also contain a high total species pool, due to the wide geographic and altitudinal spread of the sites. Capillaroid root depth at the sites ranged from 0-8cm, with maximum hummock height ranging fromm 0-38cm. Mean annual rainfall at the sites ranges from 828-2654mm, while the root zone water deficit ranged from 0.04-16.77 Mpa days.

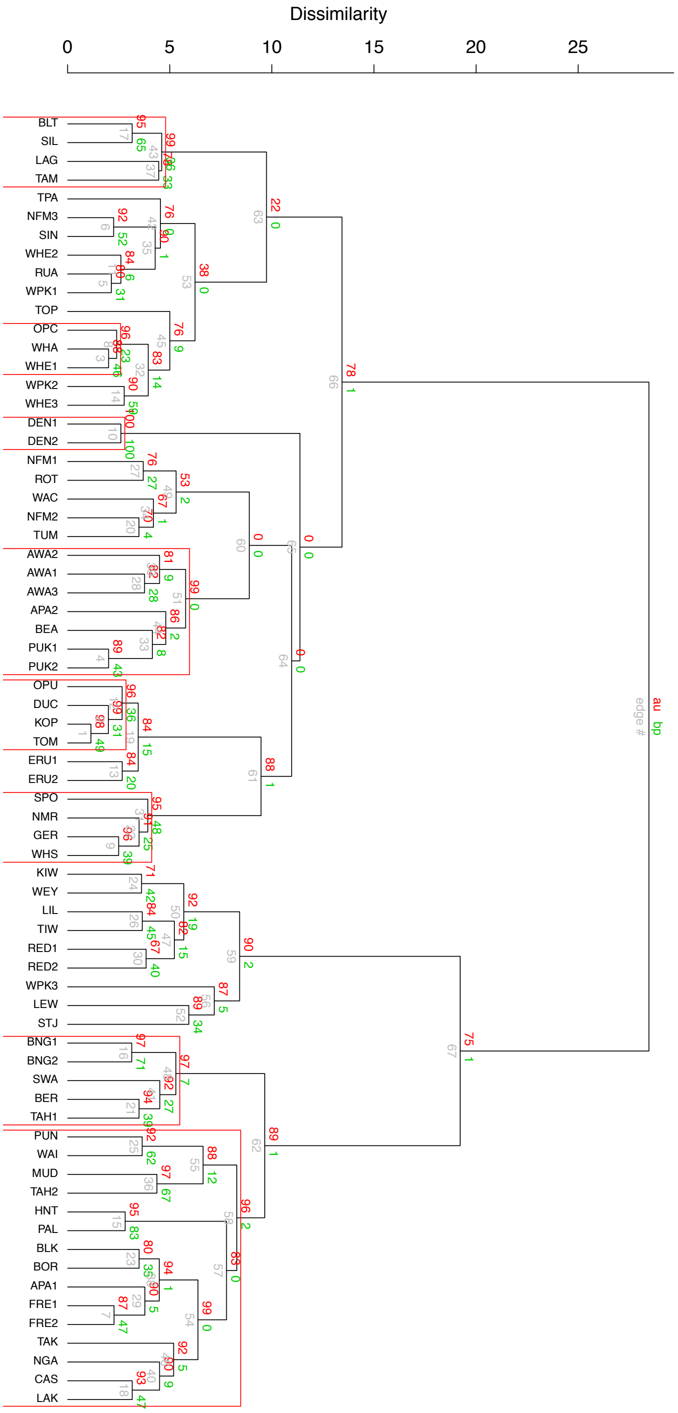


Figure 3.14: Dendrogram of the sites for the 2002 and 2006-07 field survey of New Zealand *Empodisma* and *Chionochloa rubra* wetland communities using Ward's linkage with the Euclidean distance.
Data consist of species cover, log transformed, with rare species (<3 occurrences) removed (n=85). AU probability values are indicated in red on the dendrogram, with significant clusters of sites indicated in red.

Table 3.7 Summary of wetland classification and species composition of the community types identified by cluster analysis of New Zealand mainland restiad wetlands.

Sites surveyed are identified by wetland and structural class according to Johnson & Gerbeaux (2004). A full description of vascular and most abundant non-vascular species frequencies in the 8 communities is found in Appendix 3.7.

Community ID	**Wetland class**	**Structural class**	**No. of sites**	**Species composition**
1a: *Empodisma-Gleichenia*	Fen	Wire rushland/ fernland	4	*Empodisma minus, Gleichenia dicarpa, Chionochloa rubra, Androstoma empetrifolia, Coprosma cheesemanii, Dracophyllum recurvum, Carpha alpina, Schoenus pauciflora, Oreobolus pectinatus*.
1b: *Gleichenia-Empodisma*	Fen	Wire rushland/ fernland/ tussockland	3	*Gleichenia dicarpa, Empodisma minus, Chionochloa rubra, Androstoma empetrifolia, Dracophyllum subulatum, Lepidosperma australe, Leptospermum scoparium, Celmisia spectabilis.*
2a: *Empodisma-Leptospermum*	Pakihi	Wire rushland	2	*Empodisma minus, Leptospermum scoparium, Dracophyllum politum, Chionochloa juncea, Celmisia dubia, Carpha alpina, Oreobolus stricta.*
2b: *Empodisma*	Bog	Wire rushland	7	*Empodisma minus, Gleichenia dicarpa, Chionochloa rubra, Gaultheria depressa, Coprosma intertexta, Androstoma empetrifolia, Carex coriacea, Celmisia gracilenta, Thelymitra cyanea, Phormium tenx.*
2c: *Empodisma-Gleichenia- Machaerina*	Fen	Sedgeland	4	*Machaerina rubiginosa, M. teretifolia, Empodisma minus, Gleichenia* spp., *Leptospermum scoparium, Drosera binata*.
2d: *Empodisma-Machaerina-Gleichenia*	Fen	Sedgeland	4	*Machaerina teretifolia, Empodisma* spp., *Gleichenia* spp., *Leptospermum scoparium, Drosera* spp. *Thelymitra cyanea, Campylopus introflexus*.
4a: *Empodisma-Sphagnum-Chionochloa*	Bog	Wire rushland/ mossfield/ tussockland	5	*Empodisma minus, Sphanum cristatum, Chionochloa rubra, Androstoma empetrifolia, Blechnum penna-marina, Carex* spp., *Aporostylis bifolia, Herpolirion novae-zelandiae, Hierachloe redolens, Drosera* spp., *Celmisia gracilenta*.
4b: *Empodisma-Sphagnum*	Fen/Bog	Wire rushland/ mossland	15	*Empodisma minus, Sphanum cristatum, Dracophyllum* spp., *Coprosma* spp., *Halocarpus bidwillii, Androstoma empetrifolia, Carex* spp., *Celmisia gracilenta, Drosera* spp., *Herpolirion novae-zelandiae, Thelymitra cyanea*.

Table 3.8: Summary of *Empodisma* biomass, capillaroid root growth and extent of hummock-hollow topography in the six significant vegetation communities identified by cluster analysis of *Empodisma* and *Chionochloa rubra* wetland communities.

Species richness per community and vegetation height are provided. Vegetation height and biomass data are means with standard deviations shown in brackets. Capillaroid root depth and hummock height are means with range in brackets. Note: Swampy Summit was removed from community 4a prior to calculations, as no *Empodisma minus* is present at the site

	1a	1b	2a	2b	2c	2d	4a	4b
Community	*Empodisma-Gleichenia*	*Gleichenia-Empodisma*	*Empodisma-Leptospermum*	*Empodisma*	*Empodisma-Gleichenia-Machaerina*	*Empodisma-Machaerina-Gleichenia*	*Empodisma-Sphagnum-Chionochloa*	*Empodisma-Sphagnum*
Number of sites	4	3	2	7	4	4	4*	15
Canopy height (m)	0.6(0.06)	0.72(0.07)	0.38(0.22)	0.71(0.28)	1.27(0.16)	0.72(0.25)	0.60(0.16)	0.42(0.20)
Species richness	46	13	24	44	7	27	47	61
Total above-ground biomass (gm^{-2})	939 (613)	792 (418)	312 (174)	1623 (784)	1101 (197)	1058 (621)	882 (309)	856 (624)
Live above-ground biomass (gm^{-2})	447 (354)	315 (193)	169 (98)	701 (397)	485 (143)	414 (256)	395 (43)	445 (302)
Litter (gm^{-2})	121 (136)	212 (30)	17 (12)	257 (106)	171 (79)	181 (150)	59 (29)	57 (40)
Live *Empodisma* biomass (gm^{-2})	162 (69)	131 (125)	93 (27)	589 (419)	372 (161)	246 (174)	310 (88)	348 (276)
Live *Empodisma*/total biomass (%)	20.8 (11.5)	14.8 (10.2)	32.3 (9.5)	35.9 (13.3)	32.7 (11.2)	23.4 (9.4)	29.4 (20.4)	40.8 (10.9)
Dead *Empodisma* biomass (gm^{-2})	145 (73)	205 (176)	110 (43)	695 (404)	337 (180)	257 (58)	390 (204)	394 (351)
Dead *Empodisma*/total biomass (%)	22.6 (18.4)	25.6 (23.7)	37.0 (6.9)	44.5 (16.8)	29.5 (15.3)	31.0 (16.5)	40.8 (7.9)	40.3 (14.9)
Capillaroid root depth (cm)	1.6 (1-4)	<1 (0-1)	<1 (0-1)	7.4 (1-20)	6.9 (0-15)	2.6 (1-5)	2.7 (1-5)	2.5 (0-8)
Hummock height (cm)	11 (8-15)	4 (0-8)	4 (0-9)	17 (2-32)	9 (1-23)	6 (1-14)	19 (0-45)	15 (0-38)

Extensive capillaroid root development or hummock-hollow topography are not associated with any one community type. Capillaroid roots were present in communities either side of the FBT, and absent from only 7 sites; these include three *Sphagnum*-rich communities, a coal measures community, and two recently formed *Empodisma robustum* fens where the peat substrate appears periodically inundated. Similarly, sites where capillaroid root development was extensive (>5cm deep) were not resticted to any one community type, the ten sites having a wide range of annual rainfall (922-4474mm), altitude (10-1020m), and substrate chemistry (e.g. pH 4.34-5.42; Von Post Index 1.3-5.0). Pearsons correlations suggest the height of hummock-hollow development at the sites is also uncorrelated with either annual rainfall (r^2=0.02), or water deficit (r^2=0.32).

3.4.5 Tissue nutrient levels

The tissue nutrient contents for the six communities were replotted (Figure 3.15). *Empodisma* tissue N and P contents in the *Empodisma-Sphagnum-Chionochloa* (Group 4a) and *Empodisma-Sphagnum* (Group 4b) communities are higher overall than for the other groups, suggesting nutrient enrichment of some *Sphagnum* rich communities may have occurred. The results indicate *Empodisma minus* growth in three sites in Groups 4a (Bungtown Bog sites, Berwick Forest) and 4b (Borland, Muddy Creek & Takakopa) may be currently N-limited, rather than P-limited.

Empodisma minus vegetation at Castle Downs Swamp (Group 4b) has the highest tissue N concentrations of all the sites (1.095% dry weight). The high tissue-N levels may explain the high *Empodisma minus* biomass at Castle Downs, which is crowding the tall *Chionochloa rubra* tussocks on the mire perimeter. The live foliar biomass at Castle Downs (0.97 kgm^{-2}) is second only to that of the Pukerau Tussock Reserve (1.30 & 1.05 kgm^{-2}), the vegetation at Pukerau consisting of a dense *Empodisma minus* canopy, with few other vascular species present.

Tissue P contents are consistently lowest in the *Gleichenia-Empodisma* communities from the central North island, the *Empodisma-Leptospermum* communities on the Denniston coal measures (Group 2a), and in the Westland *Empodisma-Machaerina-Glechenia* pakihi communities (Group 2d).

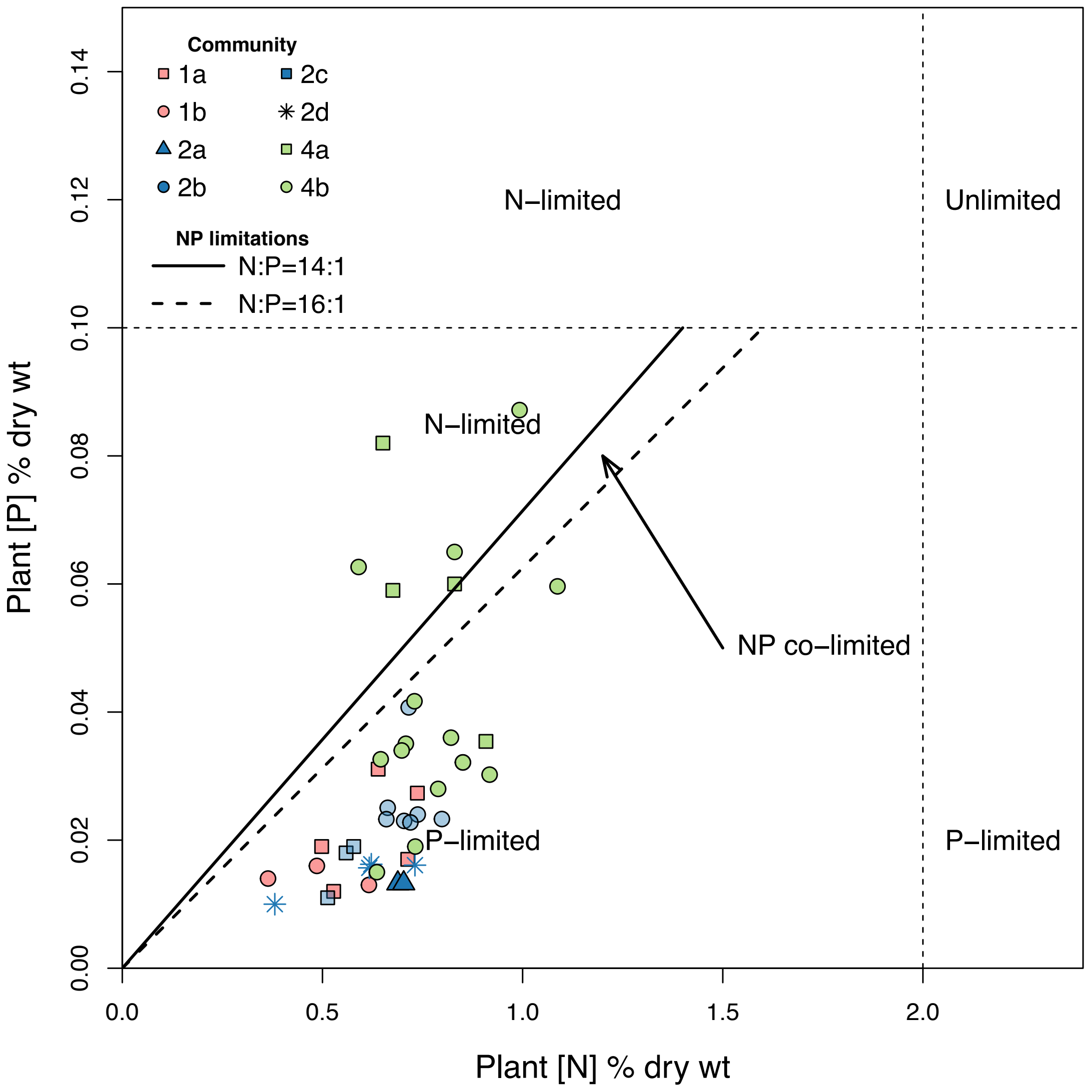


Figure 3.15: Tissue N and P concentrations for *Empodisma* species from significantly clustered communities (Groups 1a-4b) indicated by cluster analysis of wetland sites around New Zealand (n=45 sites, 2 species).
Where N<2% dry wt and P<0.1% dry wt, the N:P ratio can be used. The N:P = 14:1 and N:P = 16:1 lines demarcate N and P limitation within the range of potential limitation by both nutrients (Clarkson *et al*. (2002). Points falling in the upper right quadrant would indicate N and P conentrations exceed growth limiting threshold (0 sites), while points in the upper left quadrant would indicate growth is N-limited.

3.4.6 Wetland community and environment relationships

Pearsons Correlation co-efficients with Bonferroni adjustment suggest significant corrrelations exist between the environmental variables (Table 3.9). The environmental variables from the subset of 44 sites were analysed further using principal component analysis (PCA). Varimax rotation decreased the number of variables strongly correlated with the retained components, and so the unrotated solution was kept. The correlation of the variables with the first three principal components is presented in Figure 3.16, with the sites labelled according to the communities suggested by the cluster analysis. The PCA of substrate characteristics supports our grouping of sites into floristic types using pvclust, with some overlapping between communities (Figure 3.16).

The first principal component (PC1) explains most of the variation, and is positively correlated with moisture content, and negatively correlated with ash content and bulk density. This suggests that PC1 describes a hydrological-soil texture gradient with sites with high positive loadings being wetter peats with a low bulk density and high organic matter content, and sites with high positive loadings having drier mineral soils with a lower organic content, and a high bulk density. The second principal component (PC2) describes a nutrient gradient, with sites with high negative loadings having peat with high Total-P and -K and a low mineral content, and those with high positive loadings having peat with a high mineral content, but lower Total-P and -K. The third principal component (PC3) describes wetland condition, with sites with a high positive loading showing fewer indications of modification to hydrological processes and community composition, and also being closer to the coast, and peat with a high C:N ratio. The sites are arranged in a sequence along PC1, from drier restiad-tussockland and restiad-fernland mires with a high shrub, *Chionochloa rubra* and *Gleichenia* component (Group 1a & 1b), to wetter minerotrophic edge communities (Groups 2c & 2d) and mires with a high *Sphagnum* content (Group 4a & 4b) which partially overlap.

The environmental data for the six communities are displayed in Figure 3.17. ANOVA and Tukeys HSD suggest there are significant differences between communities for several environmental variables. The most significant differences are between communities containing *Sphagnum* (Groups 4a & 4b), and the central North Island and Denniston communities (Group 1a, 1b & 2a), which are arranged towards opposite ends of PC1. *Empodisma-Sphagnum* (Group 4b) and *Empodisma-Gleichenia* (Group 1a) peats are the least similar, *Empodisma-Sphagnum* peat having a significantly lower bulk density, pH, and ash content ($p=0.03$, $p=0.01$ & $p<0.001$ respectively). The *Empodisma-Sphagnum* peat also has a higher organic content and lower bulk density than *Empodisma-Leptospermum* (Group 2a) peat (p<0.001 & p<0.001, respectively). The peat of *Empodisma-Sphagnum-Chionochloa* (Group 4a) communities is significantly wetter and more acidic than that of *Empodisma-Gleichenia* (Group 1a) communities (p=0.008 & p=0.008 respectively), and has a lower ash content and bulk density than those of *Empodisma-Leptospermum* (Group 2a) communities (p=0.004 & p=0.009 respectively).

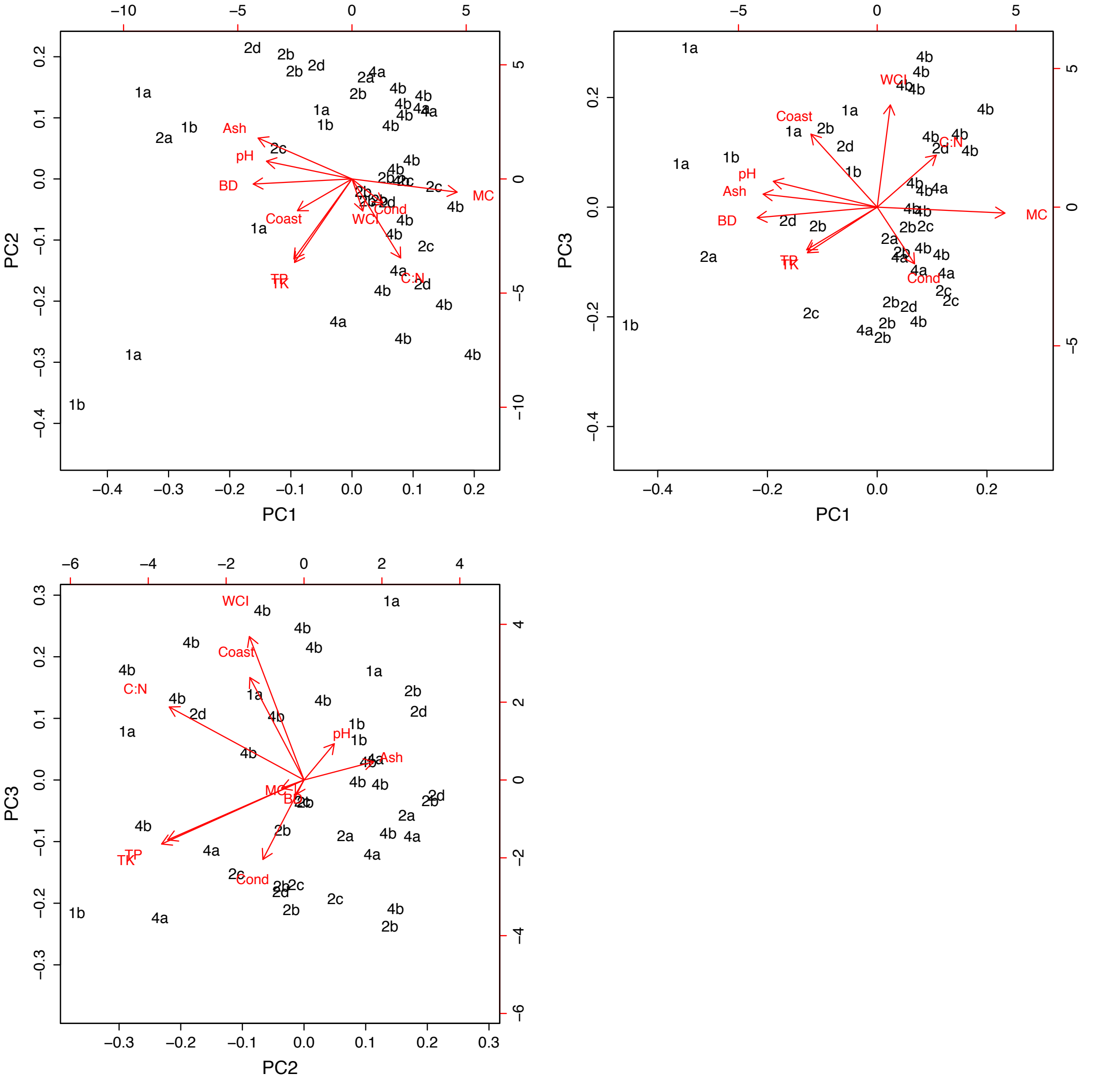


Figure 3.16: PCA ordination of 44 sites based on cover of species.
The vegetation communities identified by cluster analysis are superimposed on the ordinations.

Table 3.9: Pearsons correlation coefficients between the environmental variables used in the habitat ordination, with a Bonferroni adjustment for multiple comparisons. ***P<0.001, **P<0.01, *P<0.05.

	Distance to coast	C:N ratio	Wetland condition	Bulk density	pH	Soil conductivity	Ash%	Moisture content	Total-P	Total-K
Distance to coast	1									
C:N ratio	-0.04	1								
Wetland conditin	-0.04	0.49**	1							
Bulk density	0.11	-0.35	-0.19	1						
pH	0.55***	-0.45**	-0.24	0.31	1					
Soil Conductivity	-0.05	0.12	0.1	-0.29	-0.08	1				
Ash%	0.25*	-0.47**	-0.23	0.69***	0.55***	-0.18	1			
Moisture content	-0.14	0.37	0.24	0.80***	-0.32	0.29	-0.64***	1		
Total-P	0.11	0.03	-0.19	0.23	0.2	-0.01	0.07	-0.17	1	
Total-K	0.11	-0.14	-0.25	0.1	0.26	0.04	0.15	0-.10	0.81***	1

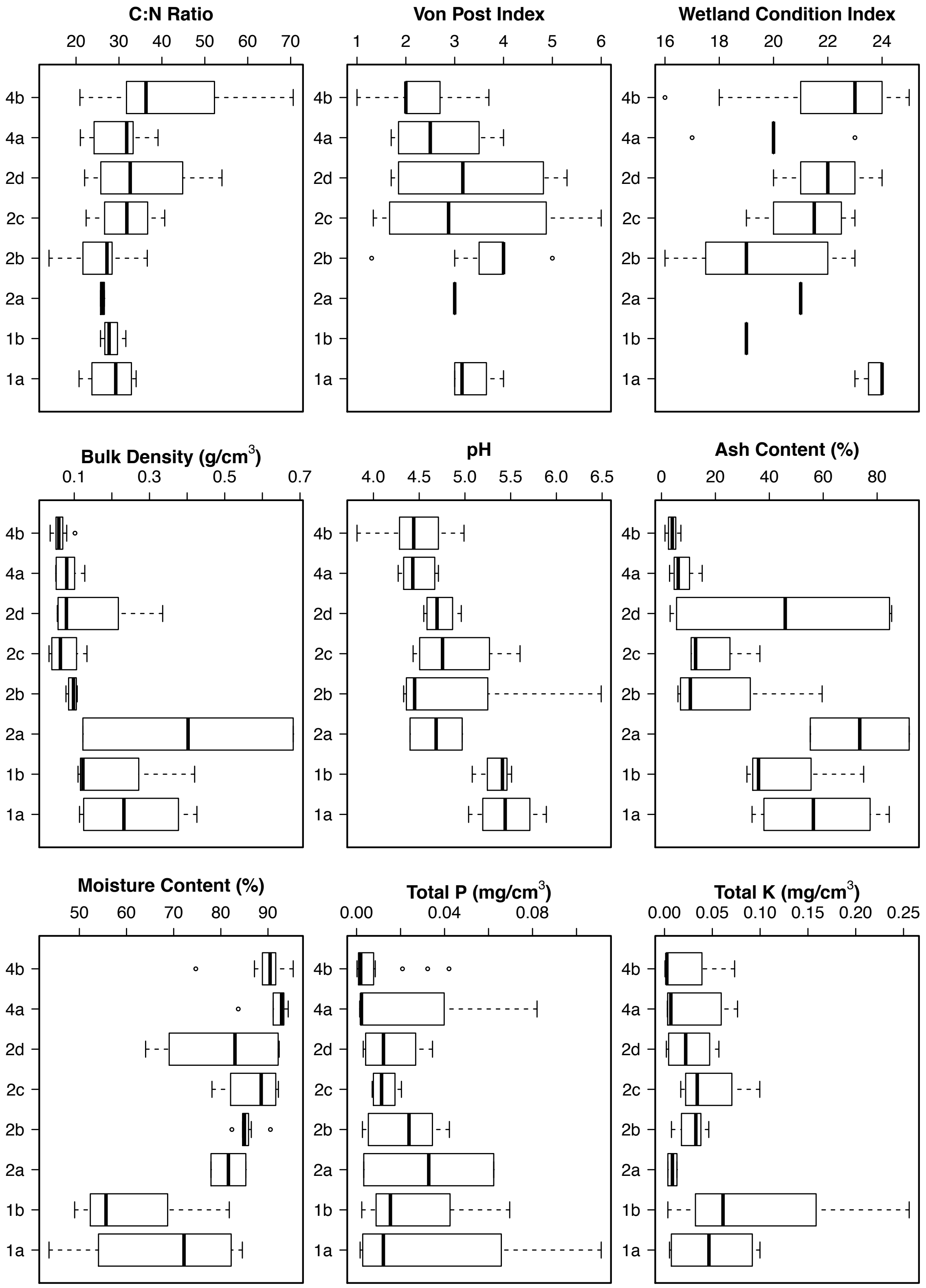


Figure 3.17: Box plot summary showing median, upper and lower quartiles for environmental variables for the six significant communities identified in the cluster analysis.
Site and variable abbreviations as in Table 3.1 and Table 3.2.

The driest substrate was found in the *Gleichenia–Empodisma* community. The peat was significantly drier and contained less Total-P and -K than that of the *Empodisma-Sphagnum* (4b) and *Empodisma* (Group 2b) communities, and was also drier than that of the *Empodisma-Gleichenia-Machaerina* (Group 2c) and *Empodisma-Sphagnum-Chionochloa* (group 4a) communities. There are no significant differences in von Post Index, Wetland condition or C:N ratio between the peat of the eight communities.

3.5 Discussion

This study describes the variety, floristic composition, nutrient status and substrate chemistry of a range of *Empodisma* dominated communities in New Zealand, and outlines the context within which it might engineer the mire environment. The survey confirms previous descriptions of the widespread nature of *Empodisma minus* distribution in New Zealand. *Empodisma* species were found in a range of sites from sea level to 1260m elevation, including both seasonally and permanently waterlogged substrates of acidic to circum-neutral pH, and comprising a gradient from mineral to Organic Soils. *Empodisma* cover was consistently high where present, and so the eight communities identified in this study were determined by the presence or absence of other species (e.g. *Gleichenia, Sphagnum, Chionochloa, Leptospermum* and *Machaerina*). *Empodisma* capillaroid roots were frequently present in the substrate, though not always abundant. Capillaroid roots were absent in shallow soils on the Denniston Plateau where little organic matter has accumulated, and in drier mineral soils in the central North Island fernland communities dominated by *Gleichenia dicarpa*. Hummock-hollow topography was highest in the *Empodisma-Sphagnum* communities and under dense *Empodisma minus* canopies, though little microtopography is evident in dry fernland, pakihi, and mire edge communities containing a high sedge component. The survey confirms that P is the growth-limiting nutrient in most *Empodisma* communities, however, nutrient enrichment appears to have occurred in some *Empodisma minus* mires, especially in the *Empodisma-Sphagnum* bog remnants of Southland and Otago. Capillaroid root abundance and P-limitation are not correlated, and it is likely the ecological factors influencing *Empodisma minus* abundance and ecosystem engineering include abiotic resources and conditions, facilitative and resource competition interactions between mire species, and positive feedbacks to the engineer from the engineering process.

3.5.1 New Zealand *Empodisma* communities

In his survey of Otago mires, De Groot (1999) found *Empodisma minus* communities to be distinctive from other types, and restricted to coastal areas. In contrast, by expanding the geographic range examined, this study found *Empodisma* communities at a range of latitudes and elevation (Table 3.1), incorporating a diverse range of mire types and species assemblages. The 8 *Empodisma* communities identified demonstrate differences in their substrate physico-chemistry, which is mirrored by floristic differences amongst the groups. *Empodisma* canopy biomass and capillaroid root depth also differed between the communities.

Oligotrophic montane fens and fernlands dominated by *Empodisma* and *Gleichenia* formed one end of the hydrological-soil texture gradient of communities. Mid-way along the gradient are the wet minerotrophic communities and West Coast pakihi, dominated by tall *Machaerina* species overtopping the shorter *Empodisma* and *Gleichenia* sub-canopy. Another closely related type is the *Empodisma-Leptospermum* community of the Denniston coal plateau. At the opposite end of the gradient to the montane fens are the *Sphagnum*-rich mires of the West Coast of the South Island, Southland, and Te Urewera National Park. These mires contain a higher *Sphagnum* component, while *Gleichenia* and *Chionochloa rubra* are both absent from the wettest sites. A similar *Sphagnum* rich community type is found in Otago mires, however, *Chionochloa rubra* is present here at low densities.

3.5.2 Comparison of peat physico-chemistry and biomass between New Zealand restiad communities

The soil physico-chemistry data from this study were compared with *Empodisma robustum* and *Sporodanthus* communities in the Waikato and Chatham Islands (Clarkson *et al.*, 2004a; 2004b). These comparisons (Table 3.11) show that while *Empodisma robustum* communities appear confined to oligotrophic peat with a consistently low P levels (0.035 ±0.003 mg/cm^3), *Empodisma minus* dominated wetland communities are associated with substrates of a more variable nutrient content. Soil N in the *Empodisma minus* communities is also higher than that of the Waikato mires, being more similar to that of Chatham Island *Sporodanthus* communities.

These differences may be partially explained by considering the criteria employed in choosing sites. Small mires are subject to greater anthropogenic pressures (e.g. altered hydrology, increased edge effects), potentially influencing decomposition and nutrient mineralisation processes within the mire. In contrast, the central bog communities of large mires are buffered against external inputs (Ausseil *et al.*, 2008). Only 9% of the historic wetland cover of the Waikato region remains, largely comprising restiad bog contained within two large Ramsar protected wetlands (Kopuatai & Whangamarino) (Ausseil *et al.*, 2008). Sampling effort by Clarkson *et al.* (2004a) was concentrated in these large mires, with only one or two plots surveyed in the smaller, more heavily modified mires (e.g. Te Mimiha). By comparison, in order to describe the variety of *Empodisma minus* dominated communities in New Zealand, many sites chosen for the current study are small, reflecting the 74% of New Zealand's remaining wetlands that are <10ha in size (Ausseil *et al.*, 2008).

The oligotrophic peat associated with *Empodisma robustum* communities will also reflect the restricted range of the northern species, as a result of extensive historical drainage of the Waikato wetlands for agriculture. While Clarkson *et al.* (2004a) surveyed *Empodisma robustum* fen communities on the edge of raised mire complexes, and in recently formed mires, the current study examined a wider range of fen communities, and hence more variable substrate chemistry. The high nutrient content of peat in an *Empodisma robustum* fen at Tumurau Lagoon (total-P=0.044 mg/cm^3, total-K=0.104 mg/cm^3 & bulk density=0.104 mg/cm^3) suggests *Empodisma robustum* has a similarly wide edaphic range as *Empodisma minus*. The analysis of peat from fens in Northland and Bay of Plenty (e.g. Matakana Island) would provide confirmation of this, as would a common garden experiment including both species.

Biomass data for New Zealand mires is not routinely reported, and so comparisons between restiad communities are limited. Due to the taller stature of the northern species, *Empodisma robustum* communities contain more live above-ground biomass (0.67 kgm^{-2}) (Sharp, 1995) than most *Empodisma minus* communities in this study. The exception was the *Empodisma-Sphagnum-Chionochloa* community, which contained a similar live *Empodisma* canopy biomass to the *Empodisma robustum* sites (0.70 ±0.40 kgm^{-2}), possibly due to nutrient enrichment at some sites. The data are within the ranges of live above-ground biomass from herbaceous bogs (0.01-0.13 kgm^{-2}), shrub bogs (0.80-1.02 kgm^{-2}), and fens (0.18-3.73 kgm^{-2}) compiled by Sorrell (2008) from the literature.

The live:dead canopy ratio for *Empodisma minus* sites appears to vary between community types (Table 3.8). *Empodisma robustum* canopies contain similar biomass volumes of live and dead material (Sharp, 1995). The senesced canopy provides a mulch-like effect, which lowers evapotranspiration rates, allowing the formation of raised bogs despite a seasonal rainfall deficit which would otherwise limit bog formation (Campbell & Williamson, 1997; McGlone, 2009). *Empodisma minus* forms a smaller component of the canopy in many fens, due to the high shrub component (Table 3.8), and the mulch-like effect of the *Empodisma robustum* canopy may not occur in shrub and tussock rich fens, potentially limiting engineering activities in these mires. In contrast, in the *Empodisma* bog community type a dense canopy of *Empodisma minus* comprises over 80% of the total above-ground biomass. Senesced material comprises >50% of the canopy, and a thick litter layer covers the peat surface (0.26 ±0.11 kgm^{-2}). The thick litter layer and high volume of standing dead material suggests that southern bogs with a high *Empodisma minus* cover may potentially utilise the same mulch effect as *Empodisma robustum* in order to reduce evapotranspirative losses, and ultimately engineer the formation of raised bogs.

3.5.3 Tissue nutrient levels in *Empodisma*

Foliar nutrient levels control the relative growth rate (RGR) and nutrient use efficiency (NUE) of plants (Aerts & Chapin, 2000). Foliar nutrient levels may vary due to species effects, or nutrient availability in the substrate (Clarkson *et al.*, 2005; Bombonato *et al.*, 2010). Long-lived leaves and the production of low nutrient litter are traits typical of species in low productivity environments, (Chapin, 1980a; Craine, 2009) such as mires, allowing species to achieve higher nutrient use efficiency (Craine, 2009), and are key components of autogenic models of bog formation (van Breeman, 1995). *Empodisma robustum* plants exhibit low mean foliar-N and P levels, which, in combination with nutrient acquiring capillaroid roots, and high nutrient use efficiency, enable the species to be competitive in the raised bog environment (Clarkson *et al.*, 2005). This study suggests *Empodisma minus* has similarly low tissue-N and P levels, confirming all New Zealand restiads are similarly well adapted to the oligotrophic conditions of the raised bog environment. Other engineering processes such as the production of low nutrient litter, the timing of capillaroid root growth along the FBT, and nutrient retention by *Empodisma minus* plants remain to be examined.

Co-occurring mire species with different growth forms may have varying foliar nutrient contents (e.g. *Empodisma robustum* & *Leptospermum scoparium,* Clarkson *et al.*, 2005), due to variations in tissue chemistry, or the different abilities of plants to exploit the soil environment (Bombonato *et al.*, 2010). While foliar-N levels in co-occurring *Empodisma minus* and *Chionochloa rubra* plants (n=22 sites) were similar (Table 3.10), *Empodisma minus* foliar-P levels were lower than those of *Chionochloa rubra*. Both species have traits associated with low resource use; *Empodisma* species having long-lived, sclerophyllous culms (Johnson & Cutler, 1973; Campbell, 1983), and *Chionochloa rubra* also producing long-lived leaves, with a low nutrient content, and high lignin and structural polysaccharides levels (Bailey & Ulyatt, 1970; Connor *et al.*, 1970; Meurk, 1978; Williams *et al.*, 1978a;b). *Empodisma's* lower tissue-P likely reflects more frugal nutrient use. These findings suggest *Empodisma minus* possesses adaptations to avoid the consequences of the engineering process (low nutrient availability), resulting in greater competitiveness in the oligotrophic raised mire conditions. Confirmation of this will require further investigation of species interactions along the FBT, utilising competition experiments which simulate the changing abiotic mire environment.

The N:P ratios found in *Empodisma minus* and *Empodisma robustum* foliage suggest *Empodisma* growth in most mires is P-limited (Table 3.10). Further work is required to test this hypothesis, including field fertilisation trials in both fen and bog communities.

Table 3.10: Comparison of foliar nutrient levels in New Zealand wire rushland and tussockland sites. Data presented are summary of all *Empodisma minus*, *Empodisma robustum* and *Chionochloa rubra* communities in the 65 New Zealand communities visited[1], and sites at which *Empodisma minus* and *Chionochloa rubra* co-occur[2].
Data are also presented from Clarkson *et al.* (2005) for *Empodisma robustum*, *Sporodanthus ferrugineus*, and *Sporodanthus traversii* for comparison[3]. Data are means with one standard deviation.

Species	**Variable**			**n**
	N **% dry wt**	**P** **% dry wt**	**N:P** **ratio**	
Empodisma minus[1]	0.69 ±0.14	0.029 ±0.018	30.17 ±12.47	53
Chionochloa rubra[1]	0.62 ±0.18	0.057 ±0.030	12.88 ±5.68	34
Empodisma robustum[1]	0.54 ±0.10	0.017 ±0.007	34.25 ±8.34	5
Empodisma minus[2]	0.66 ±0.12	0.031 ±0.019	27.27 ±11.41	22
Chionochloa rubra[2]	0.65 ±0.20	0.057 ±0.033	13.84 ±6.57	22
Previous studies				
Empodisma robustum[3]	0.90 ±0.03	0.035 ±0.003	26.57 ±1.34	20
Sporodanthus ferrugineus[3]	0.69 ±0.02	0.029 ±0.001	22.03 ±0.83	8
Sporodanthus traversii[3]	0.73 ±0.04	0.031 ±0.002	25.25 ±1.20	27

Table 3.11: Comparison of soil physico-chemistry of *Empodisma minus* communities from this study with *Empodisma robustum* and *Sporodanthus* communities from the Waikato and Chatham Islands (Clarkson *et al.*, 2004a;b).

Values presented are means with standard deviations shown in brackets for all data.

Community	**Number of sites**	**Total-N (mg/cm^3)**	**Total-P (mg/cm^3)**	**Total-K (mg/cm^3)**	**pH**	**Von Post Index**	**Bulk density (g/cm^3)**
Empodisma-Gleichenia	4	1.21 (0.52)	0.034 (0.052)	0.050 (0.049)	5.45 (0.36)	3.3 (0.5)	0.251 (0.151)
Gleichenia-Empodisma	4	0.90 (0.32)	0.029 (0.036)	0.107 (0.132)	5.33 (0.23)	NA	0.218 (0.175)
Empodisma-Leptospermum	2	2.15 (0.19)	0.033 (0.042)	0.008 (0.007)	4.69 (0.40)	3	0.403 (0.395)
Empodisma	7	1.24 (0.51)	0.021 (0.017)	0.028 (0.015)	4.93 (0.84)	3.6 (1.2)	0.095 (0.012)
Empodisma-Sphagnum-Chionochloa	4	1.22 (0.58)	0.025 (0.036)	0.030 (0.035)	4.48 (0.20)	2.7 (1.0)	0.082 (0.033)
Empodisma-Sphagnum	15	0.72 (0.29)	0.009 (0.013)	0.019 (0.027)	4.46 (0.34)	2.2 (0.8)	0.062 (0.016)
Sporodanthus traversii	18	1.20 (0.46)	0.057 (0.030)	0.083 (0.022)	4.0 (0.1)	4.0 (0.5)	0.101 (0.024)
Sporodanthus ferrugineus	9	0.53 (0.16)	0.019 (0.014)	0.013 (0.009)	4.4 (0.2)	1.8 (0.4)	0.059 (0.022)
Empodisma robustum	22	0.78 (0.46)	0.035 (0.003)	0.027 (0.023)	4.8 (0.4)	2.8 (1.4)	0.065 (0.026)

3.5.4 Abiotic interactions and ecosystem engineering in New Zealand restiad mires

Like all species, ecosystem engineers have habitat requirements which restrict their density, so that not all wetlands are suitable sites for the engineer (Jones, 2012). In addition, the species have engineering requirements (Jones, 2012), so that not all wetlands will be modifiable, and these habitat and engineering requirements will limit that portion of New Zealand wetlands in which *Empodisma minus* can engineer an FBT. Cluster root formation has been previously linked to soil pH, Fe and organic matter content, and nutrient deficiency in plants (Diem *et al.*, 2000), while being inhibited by excess soil water (Watt & Evans, 1999). The lack of capillaroid root growth in communities types associated with one end of the hydrological-soil texture gradient of communities indicates strong controls by abiotic resources and soil conditions on ecosystem engineering processes.

The central North Island fens have mineral soils with high bulk density, Total-P, Total-K and pH, compared to other *Empodisma* or *Sporodanthus* mire communities. These community types have been previously described on the Central North Island volcanoes and axial ranges, forming part of a large complex of *Chionochloa rubra* tussocklands, *Gleichenia* fernlands and wire rush rushland, which grade into dunes of volcanic sand and gravel on the eastern side of the Mt Ruapehu (Atkinson, 1981; Rogers, 1987; Wardle 2002). The substrate under these communities may contain little organic matter, and be seasonally, rather than permanently inundated (Figure 3.18). *Empodisma minus* develops no capillaroid roots in the most organic matter poor substrates, which also contain no hummock-hollow topography. On wetter sites, where more organic matter has accumulated (e.g. the eastern arm of Waipakihi Swamp & Erua Swamp), capillaroid roots are present, and hummock-hollow topography has developed.

The wide edaphic range and context dependency of ecosystem engineering by *Empodisma* is further illustrated in the wire rushland communities on the Denniston Plateau. Here *Empodisma minus* persists in shallow and skeletal soils and quartzose sands (Figure 3.13), high in Total-N and -P, but containing little Total-K compared to other restiad communities. The formerly extensive coal measures vegetation formed in the cool, wet climate of the plateau (annual rainfall 6100mm/yr), the infertile soils being at, or near saturation throughout the year (Leathwicke, *et al.* 2002; 2003; Nichol & Overmars, 2008; Wildland Consultants, 2010). Plant nutrients in the communities are supplied via mineralisation of organic matter (with additional nutrient inputs from precipitation), rather than from soil weathering (Nichol & Overmars, 2008). The resulting low fertility explains an abundance of oligotrophic mire species (e.g. *Empodisma minus, Oreobolus strictus, Donatia novae-zelandiae*), which likely possess high nutrient use efficiency (Chapin, 1980a; Craine, 2009). The high N:P ratios in the stunted *Empodisma minus* biomass suggest growth in the coal measures communities is highly P-limited, with a mean N:P ratio of 52.02 at the Denniston sites. Despite the conditions likely favouring species with superior nutrient capture and retention traits, no *Empodisma minus* capillaroid roots were observed in shallow soils (<8% organic matter) or bare pavement areas on the Plateau, with only occasional capillaroid roots found in the upper 0.5cm of deeper Organic Soils. While further investigation is required to determine the environmental factor(s) limiting capillaroid root formation at Denniston Plateau (and in other pakihi), an interaction between high rainfall, excessive soil moisture, erosion and shallow soil development appears a likely constraint.

Although often reduced in stature and shoot density, *Empodisma minus* persists in *Sphagnum* rich communities in Te Urewera National Park, Springs Junction, Otago and Southland mires. Mire communities containing *Empodisma minus* are found in two of the Ruapani Tarns, in Kaipo Lagoon and Sopps Hollow. These mires also receive high annual rainfall, however, in contrast to the central North Island fens and coal pavement communities, their acidic (pH<4.5), saturated peat substrates contain little mineral content (<6% ash).

Despite similar climatic influences on the Urewera sites, the sites differ in *Empodisma* cover, and evidence of engineering process, suggesting a correlation between high soil moisture and the limited extent of capillaroid root development. Where *Empodisma-Sphagnum* lawn dominates the mire centre at the wettest site (Waipai Swamp), the undecomposed peat (von Post Index=1.0) contains no capillaroid roots or hummock-hollow topography, the peat comprising mainly *Sphagnum* biomass. In contrast, at Ngapehi-O-Waikareiti Mire *Empodisma minus* forms the large hummocks previously described by Rogers (1984) at Kaipo Lagoon (Figure 3.1). The substrate at Ngapehi-O-Waikareiti is drier, less acidic (pH=4.44), and more decomposed (von Post Index=2.7), with extensive live capillaroid roots present throughout the hummock microforms, which provide habitat for nesting *Delomedes minor* (nursery web spider) (Figure 3.19).

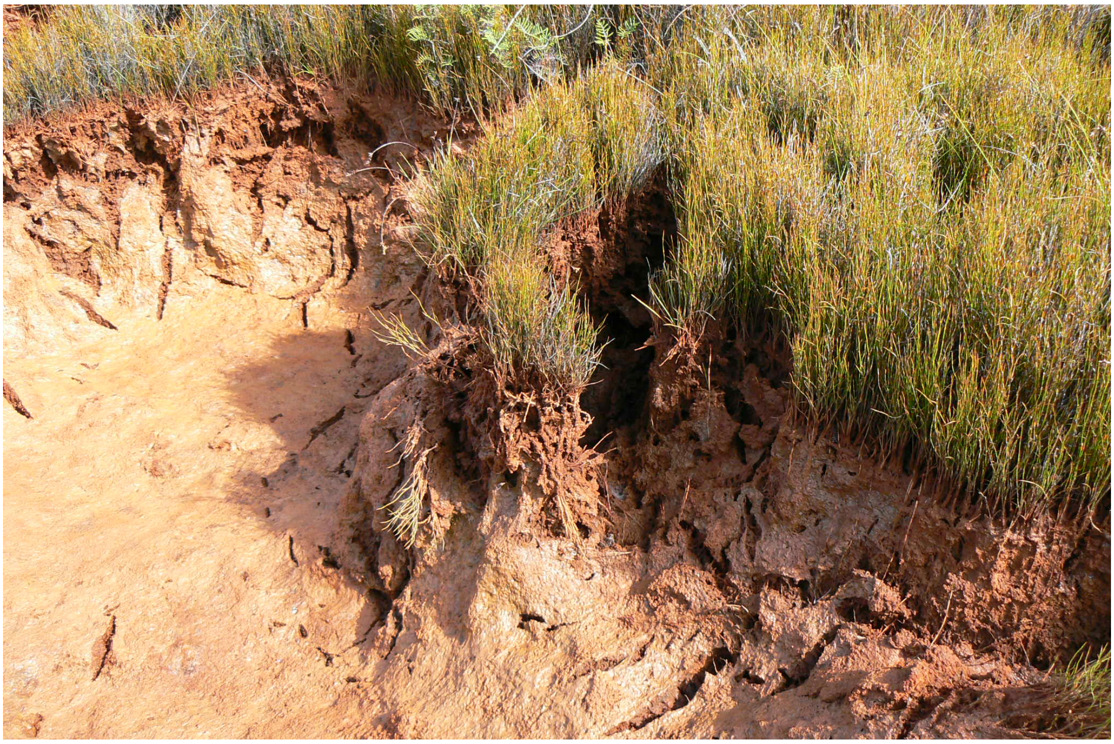


Figure 3.18: *Empodisma minus* community in the western portion of Waipakihi Mire, Tongariro National Park, March 2007. Here *Empodisma minus* persists in tephra rich soils containing little organic matter, and which are only seasonally inundated.

Figure 3.19 *Dolomedes minor* (the nursery web spider) is a large Pisaurid spider endemic to New Zealand. This 7cm long individual was found inside a hummock at Ngapehi-O-Waikareiti mire, Te Urewera National Park.

While recognising these as only preliminary findings, the low abundance of capillaroid roots and hummock-hollow topography in both very dry, and very wet substrates, and in skeletal soils, suggests strong abiotic control of the engineering process in New Zealand restiad mires.

The lack of engineering process in *Sphagnum*-rich mires (e.g. Waipai Swamp, Figure 3.20) suggests engineering is either limited further by low *Empodisma* density, linked to specific habitat requirements not being met, or by the results of biotic interactions (e.g. competition, facilitation) impacting on engineering activities (*sensu* Rogers, 1984). Extensive capillaroid root growth and hummock-hollow topography is present in mires in low rainfall regions (e.g. Pukerua, Otago), confirming both the importance of ecosystem engineering by *Empodisma minus* in those regions where climate limits *Sphagnum* distribution and abundance (McGlone, 2009), and the importance of context dependency in further discussions.

Figure 3.20: The mire community at Puna Taeo, one of the Ruapani Tarns, Te Urewera National Park (February 2007).

The community is dominated by *Dracophyllum*, *Empodisma minus* and *Sphagnum cristatum,* the latter forming large, irregular hummocks, visible to the right of the photo.

3.5.5 Biotic interactions and ecosystem engineering in New Zealand restiad mires

Biotic resources and interactions between species (e.g. disease, resource competition, mutualism) can alter the density of the engineer species (Jones, 2012), and hence influence the engineering process. Positive interactions, such as facilitation between species, are important in stressful environments such as mires (Bertness *et al.*, 1992; Bertness & Callaway, 1994). Vascular species in *Sphagnum* communities moderate diurnal temperature and humidity extremes, resulting in increased *Sphagnum* capitulum length (Pouliot *et al.*, 2011). In addition, ericaceous shrubs and Cyperaceae act as ecosystem engineers (*sensu* Jones *et al.*, 1994), providing internal structure during the early stages of hummock formation, increasing the availability of structures and habitat for other species (Wallen & Malmer, 1992; Pouliot *et al.*, 2011).

Positive and negative interactions appear to influence ecosystem engineering in New Zealand restiad mire communities. The surface of some *Sphagnum*-rich wire rushland communities contained more hummock-hollow topography than where *Sphagnum* was absent from the community, however, both abiotic and biotic factors have been previously implicated in the development of microtopography (and hence peat accumulation) in *Empodisma minus* mires (Rogers, 1984; Agnew *et al.*, 1993; de Groot, 1999). Agnew *et al.* (1993) studied five *Empodisma* dominated sites, finding *Empodisma* shoots grew densely on hummocks microforms. Hummock-hollow topography was greatest at Dismal Swamp in Westland, and Agnew *et al.* (1993) attributed the hummock development at the site to high annual rainfall. Agnew *et al.* (1993) proposed hummock development occurred as the decay resistant, apogeotropic capillaroid roots clustered around *Empodisma* stems, intercepting the nutrients contained in the stemflow. Local areas with fewer *Empodisma* stems captured less rainfall; differences in nutrient capture and root production resulting in the growth of surface microtopography. I found little capillaroid root growth in the upper peat of *Empodisma-Sphagnum* communities during the field survey, including Dismal Swamp. As the internal construction of hummocks at Dismal Swamp were not investigated by Agnew *et al.* (1993), the proportion of hummock biomass comprised of *Empodisma minus* capillaroid roots versus *Sphagnum* biomass in their study is unknown. As Dismal Swamp is a *Sphagnum* rich site, the explanation for the hummock-hollow topography most likely lies in the provision of orthotropic support by *Empodisma minus* for *Sphagnum* biomass (*sensu* de Groot, 1999), with *Sphagnum* growth promoted by the high annual rainfall and high water table at the site.

Other vascular species may also facilitate hummock construction, providing orthotropic support for *Empodisma* capillaroid root expansion (e.g. *Gleichenia dicarpa*, Rogers, 1984). *Chionochloa rubra* appears to also provide support for hummock growth by *Empodisma minus*. Live capillaroid roots at Castle Downs Swamp (annual rainfall <1000mm/yr) were extensive (15-20cm deep), in loosely packed, springy deposits (Figure 3.13), entwined between the individual tillers of *Chionochloa rubra* tussocks. Nutrient tissue contents suggest nutrient enrichment of the site (N=1.09% & P=0.06% dry wt), and the extensive capillaroid root growth around the *Chionochloa* tillers and *Empodisma* culms suggests nutrient enrichment is enhanced via wet or dry aerial deposition, low annual rainfall being possibly augmented by higher nutrient concentrations in the intercepted precipitation. *Empodisma robustum* capillaroid roots are slow to decompose (Kuder *et al.*, 1998), and a similarly slow decay rate of *Empodisma minus* capillaroid roots would contribute to the extensive hummocks developed at the site (hummock height=0.38m). By providing orthotropic support for the construction of habitat via *Empodisma minus* capillaroid root growth and hummock formation, both *Gleichenia dicarpa* and *Chionochloa rubra* also act as ecosystem engineers, supporting *Empodisma minus* in its engineering activities (Jones *et al.*, 1994; Pouliot *et al.*, 2011).

3.5.6 Can a fen-bog gradient in *Empodisma minus* mires be created?

The FBT cannot be examined in terms of temporal change, due to the length of time required for raised bog development. Alternative strategies are to substitute space for time by constructing a fen-bog gradient along a chronosequence, to examine engineering traits along an artificial fen-bog gradient, or to examine mire history using peat cores. Previous studies in restiad mires used Waikato mires of known age and a limited geographic range to construct a fen-bog gradient, allowing developmental processes to be investigated (Clarkson *et al.*, 2004a). Despite the present study incorporating both fens and bogs, a chronosequence is unable to be constructed. The sites are geographically spread, and have a variety of vegetation and disturbance histories, which restrict their usage in chronosequence construction (Walker & del Moral, 2003; Johnson & Miyanishi, 2008; Walker *et al.*, 2010; Tuittila *et al.*, 2012).

Large raised bogs with domed elements were abundant in two regions of New Zealand, the Waikato-Hauraki Plains and Southland regions (McGlone, 2009). In the Southland region, *Empodisma minus* is an important peat former (Davoren, 1978), macrofossil records suggesting the species is present after an initial sedge and rush dominated phase, its arrival signalling the transition to oligotrophic bog (McGlone & Bathgate, 1983), i.e the FBT. McGlone (2009) suggests New Zealand raised bogs contain a large shrub component, typical taxa including *Leptospermum scoparium, Coprosma* spp., *Dracophyllum* spp., *Halocarpus bidwillii* and *Epacris pauciflora*, and also contain extensive *Chionochloa rubra* tussocks and *Sphagnum* mosses. These community components were encountered during the wetland survey, indicating that raised mire communities typically present after the FBT in Southland are represented in the dataset.

Encountering sufficient sedge and rush fens representative of the early stages of mire development in Southland (McGlone, 2009), proved more problematic. The diverse range of mire communities, in addition to the restrictions placed by limited time and money, resulted in insufficient fens and transitional mire communities being surveyed. For example, Clarkson *et al.* (2011) list 11 bog, and 4 fen wire rushland communities in Southland, with an additional 13 communities where *Empodisma minus* is present, but sub-dominant to, *Chionochloa rubra*, *Dracophyllum oliveri, Gleichenia dicarpa*, or *Sphagnum cristatum*. This diverse range of communities persists despite the loss of 90% of Southlands wetlands, but was not adequately represented in the eight communities identified in the current study. While bog vegetation is still well represented in Southland (64% remaining), little remains of the more easily drained, fertile fen, marsh and swamp vegetation (13%, 4% and 1% remaining, respectively) (Clarkson *et al.*, 2011), resulting in little fen vegetation being successfully located and sampled. The under representation of pre-FBT sedge and restiad fen communities in the Southland portion of the dataset prevents the construction of a chronosequence in the region.

In the Central North Island region, only the pre-FBT stages of the peatland trajectory were surveyed, reflecting the influence of recent volcanic activity on the mires of the region. The developmental sequence in montane West Taupo mires follows a sequence similar to that of raised bogs, the arrival of *Empodisma minus* in the *Machaerina* dominated community signalling increasingly oligotrophic conditions in the mire (Clarkson, 1984). Small recently established *Empodisma minus* communities were located in a riparian zones surrounded by frost flats on the Rangitaiki Plains, and in clearings in *Pinus radiata* forest in the central North Island. These sites consisted of floating mats of vegetation alongside small rivers, within which *Empodisma minus* dominated the canopy. Hummock-hollow topography had developed, despite the very small size, and presumably young age of the communities. Sloping fens including more established *Empodisma minus* communities are widespread in the central North Island (Chapter 6), however, despite their oligotrophic nutrient status, these fens receive regular inputs of surface and ground water, i.e. are not transitional fens. While no ombrotrophic mires were found in the central North Island, the presence of newly established *Empodisma* communities in the region, alongside those earlier located by Clarkson & Clarkson

(1984), offers a unique opportunity to study the spread of *Empodisma minus*, and the effect of its engineering activities in a transitional fen.

The extent of *Empodisma minus* dominated communities surveyed by Clarkson *et al.* (2011) in Southland suggests the identification of a fen-bog gradient for future field-based studies is possible, however, Campbell *et al.* (2003) caution that the flourishing *Empodisma minus* canopy in Southland mires may reflect recent drainage changes, with former *Sphagnum* communities now being replaced by *Empodisma*. Prior to constructing a mire chronosequence to study mire development in southern raised mires, it would be advisable to undertake an analysis of site vegetation history, including peat stratigraphy and macrofossil analysis at the proposed sites, similar to the study undertaken by Hughes (1987) to investigate the FBT in British mires.

3.5.7 Conservation and management issues

A recent national survey has highlighted the incursion of exotic species in wetland communities, the small size, and low ecological integrity of remaining wetlands (Ausseil *et al.*, 2011; Myers *et al.*, in press). Most New Zealand palustrine wetlands are <10ha in size, and occur on private land (Ausseil, *et al.*, 2008; Myers *et al.*, in press), therefore relying upon voluntary management accords and covenants to protect biodiversity. Myers *et al.* (in press) recommend comprehensive monitoring of wetland condition, as currently there is no national assessment of changes in wetland condition and extent.

Tissue nutrient contents, community changes and live above-ground biomass of wetland species are useful indicators for wetland management (Clarkson *et al.*, 2002; Sorrell, 2008). Aboveground biomass data for New Zealand mires is limited, offering little opportunity for comparison with previous studies (Sorrell, 2008), however, this study allows the construction of reference ranges of live above-ground biomass for some *Empodisma* communities and sites. High above-ground biomass can be a good indicator of nutrient enrichment (Sorrell, 2008), as indicated at Pukerau Scientific Reserve, where the dense *Empodisma* canopy is engulfing the former *Chionochloa rubra* tussock canopy (Figure 2.1). In comparison, the above-ground biomass in unimpacted *Empodisma-Sphagnum-Chionochloa* sites at Waituna and Bealey Spur is <0.40 kgm^{-2}, less than half the biomass than at Pukerau (1.05 & 1.30 kgm^{-2}). While acknowledging differences in latitude and altitude between the sites, the data from Bealey and Waituna give a better representative range of biomass for the *Empodisma-Sphagnum-Chionochloa* vegetation type for future management purposes (*sensu* Sorrell, 2008).

Plant N:P ratios are used in Northern Hemisphere mires as an indicator of nutrient limitation, with N:P ratios >16 indicating P-limitation, and N:P ratios <14 indicating N-limitation (Güsewell & Koerselman, 2002). Tissue N and P are useful in detecting enrichment in oligotrophic mires, as incoming nutrients are rapidly absorbed by the nutrient limited vegetation (Sorrell, 2008). Unexpectedly, tissue nutrient contents in *Empodisma minus* oligotrophic fen communities were lower than in bogs in this study, with the lowest tissue nutrient contents in oligotrophic fens in the central North Island. The high tissue nutrients measured may not be reflected in the current vegetation cover of *Empodisma minus* bogs. The current wetland description of Bungtown Bog (Figure 3.21) as having "a high degree of naturalness" (ORC, 2011) was not borne out by the nutrient and live biomass analyses undertaken in this study. Similarly, Castle Downs Swamp is described as the largest and most diverse mire in the Taringatura District in Southland (Simpson, 1998), and yet tissue nutrient contents suggest nutrient enrichment of the central mire vegetation has occurred. While more expensive to undertake than descriptions of community composition, these analyses appear crucial to obtaining an accurate indication of the current state of mire remnants, especially those in private ownership, and those surrounded by agricultural land or exotic forests.

While the abiotic controls of capillaroid root development in *Empodisma minus* require further investigation, the proliferation of capillaroid roots (and high canopy biomass) in some Otago and Southland raised bog remnants may reflect high ammonium inputs to these bogs (Sas *et al.*, 2002). In addition to directing ombrotrophic nutrients to its capillaroid roots (Agnew *et al.*, 1993), high stemflow rates may also act to redirect leached ammonium from the culms back to the capillaroid roots (*sensu* Raubenheimer & Day, 1991), increasing nutrient retention by *Empodisma minus* in oligotrophic conditions. Since ammonia inputs to wetland communities bordering on farmland are high (Blyth *et al.*, 2013), high ammonium inputs via stemflow could initiate and maintain high capillaroid root production. This effect would be more noticeable in small bog remnants, such as Pukerua Reserve and Bungtown Bog, since Blyth *et al.* (2013) found ammonium only decreased to background levels 500m into Whangamarino Swamp. This suggests all the *Empodisma minus* biomass in small bog remnants would receive elevated ammonium inputs, the extensive capillaroid roots representing anthropogenic disturbance, rather than evidence of engineering activities in these raised mire remnants. The potential impact of excess nutrients on capillaroid root growth, decomposition and nutrient mineralisation warrants further attention, especially given the ongoing expansion of intensive agriculture in the South Island where many restiad bog remnants remain.

Figure 3.21: Bungtown Bog, Otago. A 17.6ha bog part of which is administered by the Department of Conservation as a Scientific Reserve.
An *Empodisma minus* community (olive green vegetation) is nestled among *Chionochloa* tussocks, with scattered bog pine (*Halocarpus bidwilli*). The small bog is surrounded by agricultural land, and the *Empodisma* foliar biomass has a high nitrogen and phosphorus content.

3.6 Conclusion

Empodisma species are widely distributed in wetlands and wetland remnants in New Zealand. *Empodisma* species grow in skeletal, mineral and Organic Soils, in a wide altitudinal and latitudinal range across much of New Zealand. *Empodisma minus* is tolerant of a wide range of environmental conditions, thus enabling it to establish in minerotrophic fens, and persist after the fen-bog transition, in the oligotrophic bog environment. Biomass nutrient contents are similar to those of other New Zealand restiad species, indicating the frugal use of limiting nutrients by *Empodisma minus* in the oligotrophic mire environment. Other traits of species from nutrient poor environments, such as the production of low nutrient litter, nutrient capture by cluster root production, and the nutrient efficiency of *Empodisma minus* plants remain to be examined.

A closer examination of the role that engineering processes play during the fen-bog transition was unable to be tested. A mire chronosequence requires differently aged mires with similar landscape histories within a region, which the surveyed sites did not provide. Instead, an artificial fen-bog gradient could be utilised to study changes in engineering processes across the fen-bog transition.

The dense mulch-like canopy and capillaroid root deposits which enable *Empodisma robustum* to engineer the construction of northern lowland raised mires (Campbell, 1983; Campbell & Williamson, 1997), appear to be present in *Empodisma minus*. *Empodisma minus* has formed a dense sward of senesced and live canopy material in communities in the Rangitaiki Forest Flats and central North Island, with capillaroid root growth and hummock-hollow topography evident in these small, recently established wire rushland communities. Capillaroid root growth is less extensive in pakihi and coal pavement communties, and the complex relationships between biotic and abiotic factors in promoting capillaroid root growth, hummock-hollow development and ecosystem engineering warrant further investigation; specifically the role of pH, substrate moisture and organic matter content, and tissue-N and P levels, the provision of orthotropic support, and the decay rates of both engineers and common mire species (e.g. Pegman & Ogden, 2005; 2006).

Capillaroid root growth and hummock-hollow topography appear limited by the habitat and engineering requirements of *Empodisma minus*, suggesting the context dependency of engineering should be discussed in future literature, in contrast to early, broader statements of *Empodisma's* involvement in mire formation. Although the abiotic and biotic drivers of hummock-hollow topography also require further investigation, the extensive hummock-hollow topography in *Empodisma-Sphagnum* mires may exist in part due to the provision of structure and support by *Empodisma minus*, while *Gleichenia dicarpa* and *Chionochloa rubra* appear to provide support for *Empodisma minus* hummocks in wire rush rushlands. The positive engineering feedbacks to the supporting species require further investigation, especially as regards the provision of habitat, and access to nutrients mined by the capillaroid roots.

Empodisma minus persists in New Zealand mires, despite recent and historical anthropogenic disturbances such as fire, and changes to mire hydrology. Biomass nutrient levels suggest nutrient enrichment has occurred at some sites, with growth now N-limited, rather than P-limited in some southern mires. The effect of nutrient enrichment upon capillaroid root function requires further investigation, especially given the on-going expansion of agriculture into regions with a higher number of bog remnants, and the importance of maintaining the ecological integrity of the mires.

Chapter 4: Is *Empodisma minus* the ecosystem engineer of the FBT (Fen-Bog Transition zone) in New Zealand?

Mire edge community, Waipakihi Mire Complex, Tongariro National Park.

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4.1 Abstract

The role of ecosystem engineers (EE) in the formation of ombrotrophic mires (bogs) from fens, called the fen-bog transition (FBT), can be best understood through categorisation of the autogenic and allogenic processes causing bog initiation. Here we review these pathways, discuss the drivers of change in both cases, and tabulate an approach for distinguishing between them. We then compare the engineering ability of acknowledged and putative engineers against a number of characters which plants require to cross the FBT, and to stabilise occupancy on the bog side. While some *Sphagnum* spp. are accepted as the EE of the fen-bog transition in Northern Hemisphere bogs, they appear unimportant in New Zealand. Instead its role appears to be occupied by a restiad, *Empodisma minus*, a plant with leafless, wiry stems and capillaroid roots. *Empodisma minus* appears capable of engineering autogenic transitions from fen to bog across New Zealand, even more efficiently than *Sphagnum*.

4.2 Introduction

The Ecosystem Engineer (EE; Jones *et al.*, 1994; Charman, 2002; Wright & Jones, 2006) is a concept which has proved useful in elucidating some important ecological processes. Engineers are “organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials” (p. 374, Jones *et al.*, 1994). While the ecological effects upon other species are described as ecosystem engineering (Kylafis & Loreau, 2008), the evolutionary consequences of feedbacks to the EE have more recently been addressed in the concept of niche construction (Odling-Smee *et al.*, 1996; 2003). While noting the comments of Reichman & Seabloom (2002 a,b) and Wilby (2002), that engineering can be interpreted teleologically and can be all encompassing, as Jones *et al*. (1994) previously noted, the concept has received widespread application in the mire literature, and increases our understanding of the processes involved.

Species from the bryophyte genus *Sphagnum* are widely considered to be EEs of mires in the Northern Hemisphere (Jones *et al.*, 1994; Moore, 1995; Svensson, 1995; van Breeman, 1995; Frankl & Schmeidl, 2000). Although several *Sphagnum* species occur in the Southern Hemisphere, they appear to have no engineering role here (Moore, 1995), restiad rather than *Sphagnum* bogs being the norm (Campbell, 1975; Whinam *et al.*, 2003). The only known Southern Hemispheric candidate for mire engineering is *Empodisma minus* (Hook. f.) Johnson & Cutler *s.l.*. A small member of the “jointed rush” family, the Restionaceae, a Southern Hemisphere family closely allied to the Poaceae, *Empodisma minus* is widely distributed throughout New Zealand, Tasmania and the south and east of the Australian mainland (Campbell, 1964; Moore, 1995; Charman, 2002).

The process being considered here is the fen-bog transition (FBT), where an oligotrophic fen (terminology as per Wheeler & Proctor, 2000) changes to an ombrotrophic bog. A peat accumulating system or zone is a prerequisite, but it is otherwise far from clear how the process occurs (Hughes, 2000; Hughes *et al*., 2000; 2007; Hughes & Dumayne-Peaty, 2002; Hughes & Barber, 2003; 2004).

Since pathways across the FBT have been inadequately categorised, we here review the models of the pathways involved. We use this as background to discuss the role of ecosystem engineers in crossing the FBT, review the characters EEs must possess to manipulate the environment in relevant ways, and go on to compare the abilities of *Empodisma minus* as EE of the FBT with *Sphagnum* spp., in addition to putative EEs in Northern Hemisphere and New Zealand mires, respectively the cyperad *Eriophorum vaginatum* L. and poad *Chionochloa rubra* Zotov.

4.3 Crossing the FBT

In its simplest sense, peat is the accumulated remains of undecomposed plant material. A peat deposit forms when the rate of deposition of dead plant matter produced by net primary production exceeds the rate of decomposition, i.e. Decomposition/Productivity = D/P <1 (Clymo, 1983; 1984). The rate of decomposition is the more variable determinant of peat accumulation (Damman, 1986; Charman, 2002), and it is affected by depth of burial (Clymo, 1965), temperature (Rosswall, 1974), water table depth (Clymo, 1983), water table fluctuation (Belyea, 1996), plant litter type and quality (Linkins & Neal, 1982; Johnson & Damman, 1991; Kuder *et al*., 1998; Scheffer *et al*., 2001; Trinder *et al*., 2009), oxygen supply (Clymo, 1983), and microbial populations (Linkins & Neal, 1982; Sundh *et al*., 1997; Pankratov & Dedysh, 2009). In a bog, primary productivity occurs atop the acrotelm (euphotic and aerobic decay layers; Clymo 1984; 1992), while decomposition occurs in both the acrotelm and catotelm (collapsing, anaerobic decay layers).

Accumulation of fen peat is in itself inadequate to engender a transition to a bog. Three other developments are required (Moore, 1995; Hughes & Barber, 2003):

1. Hydrological isolation of the peat surface from groundwater and surface water, so that the only nutrient source is nutrient-poor rainfall (hence inducing ombrotrophy);
2. Occurrence of mechanisms to retain water within the elevated peat mass;
3. Establishment of plant species capable of growth in the newly created oligotrophic and acidic conditions, which then perpetuate the trophic change.

The requisite developments are not achieved simply. A peat system where decomposition equals, if not exceeds, productivity (i.e. a fen) has to be replaced by one in which productivity exceeds decomposition (i.e. a bog). The transition between the two states is the crucial phase of this process, hence the name FBT. Changes in pH, nutrient status and water table are in part consequent upon those changes, and in part induced by the incoming bog species. When ombrotrophic specialist species establish and dominate the mire community, they demonstrate that its trophic status has changed to that of a bog (Moore & Bellamy, 1974). However the above developments are descriptors of events, but are not causal, and so are not in themselves sufficient as explanations for the mechanisms of transition from fen to bog.

There are two potential pathways across the FBT, based upon allogenic vs. autogenic forcing mechanisms (*sensu* Nicholson & Vitt, 1990), which we outline here. We use "allogenic" to refer to processes which are external to the system concerned (omitting those which are anthropogenic in origin, e.g. Hughes *et al.*, 2007; Hughes & Barber, 2003), and so must be of abiotic origin. This includes processes such as climate change, or physical or hydrological events. "Autogenic" processes are those resulting from inherent features of system, particularly the plants themselves, and the peat derived therefrom, and so do not occur in the absence of adapted vegetation.

4.4 Allogenic pathways across the FBT

Allogenic pathways to transit an FBT operate in two categories (Table 4.1). The first set of mechanisms isolate an existing peat outcrop by physical means, so that only meteoric water can impinge upon the incipient bog surface, increasing its hydrological isolation, and initiating ombrotrophic conditions:

(i) Physical decrease in water table, which, when occurring allogenically, can only be by changes in catchment-level hydrology such as that caused by landslides (cf. Lowe *et al.*, 1999), river channel adjustments (Kulczynski, 1949; Campbell, 1964), sea level changes (Newnham *et al*., 1995a), isostatic rebound (Glaser *et al*., 2004), and tephra deposition (de Lange, 1989; Shearer, 1997);

(ii) Climatic change in rainfall leading to groundwater flow reversals, isolating the peatland surface (Winkler, 1988; Foster & Wright, 1990; Siegel *et al*., 1995; Glaser *et al*., 1996; McGlone *et al*., 1997; Halsey *et al*., 2000; Robichaud & Begin, 2009).

The second set of mechanisms lead to an increase in height of a peat body by decreasing the peat decomposition rate (by implication, while maintaining D/P < 1):

(i) Decrease in temperature, decreasing evapotranspiration, thereby decreasing the depth of the (aerobic) acrotelm, so that litter reaches the catotelm in a less decomposed state;

(ii) Increase in precipitation, so that the ground water influence on the peat mass is lessened, and ombrotrophy is promoted.

These allogenic mechanisms result in warmer and better drained patches, which will immediately be exposed to heightened erosion and decomposition rates, reducing the projecting outcrop of peat, and tending to bring it into line with the main fen peat surface. However the patch may be stabilised by timely establishment of ombrotrophic vegetation, completing the FBT.

4.5 Autogenic pathways across the FBT

A large scale autogenic mechanism for crossing the FBT which comes into play in fens, but only over long expanses of time, is the lateral expansion of the surface outwards from its founder location, and across the landscape (Korhola, 1992; Table 4.1). Eventually such a system will become sufficiently large spatially (Heinselman, 1970) for meteoric water to become the only source of nutrients onto the inner parts of the mire (the “stagnation zones” of Vitt, 1994), as any lateral inflow of water is stripped barren of nutrients by competing organisms before reaching the centre. This creates centralised bog conditions into which ombrotrophic specialist species can invade.

At smaller scales, the role of mire vegetation in generating autogenic pathways across the FBT has received much recent attention, such pathways requiring the presence of EEs, which “change the environment via their own physical structures, i.e. their living and dead tissue” (p.

373, Jones *et al*., 1994). The physical consequences of such engineering on the growing peat body are (Zobel, 1988; Malmer *et al*., 1994; van Breeman, 1995):

- A high internal water table within the peat bog, above the groundwater level of the surrounding minerotrophic fen peat;
- Development in the peat body of an acrotelm, engendering trophic isolation from the catotelm;
- Decline in water table fluctuations within the peat body, i.e. a dampening down the effects of rainfall events and seasonal variations;
- Decreasing ash or inorganic content and increasing carbon content in peat as rheophilous inputs decline;
- Slowing of decompositional processes due to changes in soil chemistry, and to increasing anoxia and acidity, which result in a decline in decomposer (invertebrate, microbial and fungal) communities, slowing the decomposition process;
- Increasing proportion of recalcitrant material (which is slow to decompose) in the accumulating peat.

The process of engineering the FBT requires the presence of an EE, which differs from other species potentially contributing peat in its ability to grow in both the fen and bog situations, i.e., it is present before, during, and after the engineering event (visible in the peat profile; Table 4.2), and is increasingly competitive in the bog, so that it dominates. The EE alters the environment under some or all of the categories of peat accumulation, water table maintenance, and pH manipulations. We take accepted and putative EEs of the FBT from both hemispheres, and tabulate their engineering abilities under these categories (Table 4.2).

Enhanced accumulation of peat precursors from above- and below-ground tissues is due to reduced consumption and decomposition by:

- Production of herbage of low palatability to both herbivores and detritivores (Clymo & Hayward, 1982), or existence of physical barriers to herbivory such as hairs, spines or waxes (Cornelissen, 1996), increasing litter retention on site;
- Production of sclerophyllous tissues, high in lignin and in phenolics such as tannins (Cornelissen, 1996), and low in nutrients (Clarkson *et al*., 2005), rendering litter inert and so reducing consumption;
- Production of anti-microbial components (Stalheim *et al*., 2009), reducing decomposition.

These features are fairly consistently found in species of mires (Table 4.2), especially in accepted EEs, though this may reflect availability of evidence. However edibility and palatability render a species less successful as an EE.

Maintenance of a *high and stable water table* is attained by:

- Reduced evapotranspiration from the vegetation canopy (Campbell & Williamson, 1997), using a range of passive and active characters;
- Heightened water holding capacity within living and attached dead plant tissue mass due to high capillarity (Moore, 1995), and the maintenance of macropores within the decomposing litter (Clymo & Hayward, 1982; Turetsky *et al*., 2008);
- Decreased vertical drainage down the peat profile due to increasingly dense packing with depth of partially decomposed material (Moore, 1995), leading to lower hydraulic conductivity and permanent saturation (Clymo & Hayward, 1982; Clymo, 1992);
- Drainage barriers due to mineral deposition with leaching (Andrus, 1986);
- Adaptation to water table changes, allowing growth in a range of hydrological conditions (i.e., both fen and bog);
- Development of mire microforms such as hummock-hollow topography, which help inhibit the subsurface and lateral runoff (Ivanov, 1981; Ingram, 1983).

Water table manipulations appear to occur slightly less commonly in species with apparently limited engineering ability (Table 4.2) though evidence is mixed for *Eriophorum* and almost non-existent in *Chionochloa*. It appears that ability to use all of these mechanisms is important for an EE due to feedback loops. For example, the high water table imposes physical and chemical constraints (e.g., promotion of reductive geochemical pathways) on the decomposer communities in the substrate, further increasing peat accumulation, while in the wetter substrate litter decay slows due to lower temperatures and limited rates of gas diffusion.

Lowering the pH: In addition to the more global effects of carbon dioxide levels, precipitation of acidic rain and the activities of sulphur-metabolising bacteria on pH levels (Clymo, 1964), high cation exchange capacity results in acidification of the substrate (Clymo, 1963), limiting competition and decreasing decomposition (Mitsch & Gosselink, 2000). This may be a crucial characteristic for an EE (Table 4.2).

The beauty of an engineering process is that neither the species, nor the system, needs to be dominant or large, for the mechanism to apply (e.g., engineering can occur in small kettlehole bogs or even on quarry floors; Lamentowicz *et al*. (2008) and Andreas & Host (1983), respectively). Nor are long periods of time essential, providing a fen-based peat is present (Cranwell, 1953; Zobel & Masing, 1987; Shearer, 1997; Robichaud & Begin, 2009). Therefore it is possible for FBTs to occur in small, isolated patches of a larger mire system, as proposed by Vitt (1994). Indeed, spatial dispersion of successfully engineered FBTs might be the ultimate cause of the string or flark patterning in mires which has generated so much discussion in the literature (e.g. Moore, 1982; 1991; Glaser & Janssens, 1986; Foster & Fritz, 1987; Dickinson *et al.*, 2002; Rapson *et al.*, 2006; Eppinga *et al.*, 2008).

4.6 Persisting on the bog side of the FBT

A successful engineer must be dominant in the engineered environment. Thus the engineering event can be assumed to be part of the evolutionary strategy of the species for self-perpetuation (Jones *et al.*, 1994; van Breeman & Finzi, 1998). Once on a mire the EE's structures, in altering the flow of nutrient resources, create an oligotrophic environment in which it is the superior competitor (Table 4.3). All EE characters appear dedicated to this end, so that nutrient losses from tissues accumulating as peat are matched by nutrient inputs only obtainable from atmospheric sources. Thus competitive traits in the engineered environment include superior levels of nutrient access, and rates of nutrient uptake and retention.

Superior nutrient access, compared to potential competitors, is achieved by:

- Water preemption, i.e. increased opportunity to intercept meteoric water, which is the primary incoming nutrient source in ombrotrophic conditions, so that any nutrients carried in the rainfall are disproportionately available to the intercepting species (Agnew *et al.*, 1993);
- Deep root systems extending to the base of acrotelm to enhance nutrient access (Adema *et al.*, 2006).

Superior nutrient uptake is achieved by some or all of:

- Enhanced rates of cation exchange, increasing acidification (Clymo & Hayward, 1982) and nutrient supply;
- The development of root adaptations (such as cluster roots and root hairs) to low nutrient conditions (Lamont, 1982; Lambers *et al.*, 2006; 2008), which also increase below-ground productivity and hence the below-ground contribution to peat accumulation rates.

- *Superior nutrient retention* is achieved by:
- The production of foliage which is long-lived, evergreen, and of reduced size, increasing nutrient retention times and decreasing nutrient requirements (Aerts, 1999; Aerts & Berendse, 1989);
- Translocation of scarce nutrients to perennating organs prior to litter fall (Escudero *et al*., 1992; Aerts, 1993), with large and long-lived rhizome and root systems through which scarce nutrients may be relocated or stored (Chapin, 1980a);
- Enhanced rates of release of limiting nutrients from decomposing tissues for rapid resorption from within the upper peat layers (Moore & Bellamy, 1974; Smith, 1981), perhaps via capillary water flow on the exterior of the EE's tissues (Clymo & Hayward, 1982).

Another competitive advantage may be obtained by suppression of competitors at germination, e.g., where recruitment may fail due to low light availability under a dense vegetation canopy or litter layer (following Xiong & Nilsson (1997) for riparian wetlands). In addition, perennial competitors must be capable of continuous upward growth as the peat surface rises, with new roots developing annually on a higher level (Malmer *et al*., 1994).

4.7 Identifying engineered systems

The two models for crossing of the FBT are differentiable, theoretically and mechanistically, historically and spatially, via a range of environmental, historical and peat characteristics (Table 4.1), no one line of evidence being sufficient (Langdon *et al*., 2003; Pellerin & Lavoie, 2003). In physical terms, the regional climate is important in determining whether a mire can form, but, further, a change in climate can induce allogenic crossing of the FBT (Table 4.1), as can mire size increases and hydrological changes which result in more stable peat surfaces. The contribution of testate amoeboid assemblages (Charman, 1997; 2002; Charman & Warner, 1997; Woodland *et al*., 1998) as bioindicators of the FBT looks particularly promising, especially as they have no known role in creating the changes they indicate (McMullen *et al*., 2004; Payne & Pates, 2009), though their close associations with plant species admits of circularity of logic (PD Hughes, *pers. comm*.). While fruitful, and easy to obtain, macrofossil evidence is also handicapped by circularity in determining causes of the FBT (Whinam & Kirkpatrick, 1995), as is the use of level of degradation of plant polysaccharides as a proxy for bog palaeohydrology (Kuder & Kruge, 1998; 2001). Decrease in desiccation indicators (e.g., Casparie, 1993), decline in fire rates (e.g., Hughes *et al*, 2000) and declining fluctuations in the water table (e.g., Charman & Warner, 1997) are also suggestive of allogenic crossings, while stable or gradual changes in water table indicators contribute to evidence of autogenic processes. The presence of an EE on a bog can be informative, but is not necessarily conclusive evidence of an ability to engineer the FBT, unless the species is also known to have been present in the fen stage (Table 4.1), e.g., occurs in quantity in the fen peat profile.

Though FBTs have been frequently recorded (e.g. Glaser, 1992; Hughes & Barber, 2004; Muller *et al.*, 2008), most literature I am familiar with does not present the requisite information to allow us to unequivocably assign the studied mires to either autogenic or allogenic pathways across the FBT, impeding an assessment of the relative frequency of these models. Allogenic pathways are identified by Winkler (1988) and Nicholson & Vitt (1990), and autogenic ones by Lamentowicz *et al.* (2008). Kuhry *et al.* (1993) argue that even within the framework of a wetter climate shift, the FBT in Canadian boreal mires should be attributed to autogenic acidification by *Sphagnum* species, rather than to any particular climate variable. Both pathways, operating at different times, were inferred by Payette (1988) and Hughes & Dumayne-Peaty (2002). For example, climate change to increased precipitation and cooler temperatures (an allogenic process) may slow decomposition and favour ombrotrophic *Sphagnum* growth (autogenic) in poor fens, while further decreasing decomposition rates by raising regional water tables (allogenic; Langdon *et al.*, 2003). An EE is probably also common as an accelerant of allogenically-triggered pathways (Glaser *et al.*, 1997; Hughes & Dumayne-Peaty, 2002; Hughes & Barber, 2004; Robichaud & Begin, 2009), and such hybrid transition types, where “internal factors operate within the framework of external factors” (p. 1032, Winkler, 1988), may well be the norm in the development of bog complexes. Hybrid situations would greatly increase the likelihood of crossing the FBT, autogenically stabilising any allogenic crossing, while reducing the time elapsed in attaining the conditions necessary for a successful crossing.

4.8 Who is engineering the FBT?

A successful EE must have the ability to induce environmental changes under some or all of the three manipulations detailed above (i.e., enhanced accumulation of peat precursors, maintenance of high and stable water table, and substrate acidification). In the Northern Hemisphere *Sphagnum* is the classic plant engineer (Table 4.2), its abilities widely extolled in the literature (e.g. Damman, 1986; Stoneman *et al.*, 1993; van Breeman, 1995; van Breeman & Finzi, 1998; Charman, 2002; McMullen *et al.*, 2004). It is of extremely low palatability, and though of modest productivity, is very slow to decompose, so that peat accumulates. Almost all evidence re its engineering capacity is positive for an EE (11-12 of 12 possible engineering characters in Table 4.2), except for some facets of water evaporation from hummocks. Apart from the lack of storage organs, it is highly competitive, particularly for nutrients, and so demonstrates 5 out of 8 characters known to stabilise occupancy of a bog (Table 4.3). However, species within the *Sphagnum* genus differ in their engineering ability, e.g. *S. fuscum* (Heinselman, 1970; Payette, 1988; Kuhry *et al*., 1993), and *S. austinii* (Hughes & Dumayne-Peaty, 2002, Hughes *et al*., 2008) are reported as EEs. But species in New Zealand appear to have no role in engineering the FBT, despite their apparently high productivity in comparison to Northern Hemisphere species (Buxton *et al*., 1996; Gunnarsson, 2005). Though Cockayne (1967) notes *Sphagnum* "bog" islands growing in *Typha-Phormium* swamp in lowland coastal North Island, this is probably *Sphagnum falcatulum*, a well-known swamp plant, but not a bog builder. A small montane mire possibly approaching the FBT, and reported by Walker *et al*. (2001) to have a peat profile composed of *Sphagnum cristatum* (other species being apparently unable to tolerate the fire regime), is the most plausible recorded engineering instance by New Zealand *Sphagna*.

Another putative EE, a common northern hemisphere mire species, *Eriophorum vaginatum* (Table 4.2), is known as a coloniser or pioneer species (Wein & MacLean, 1973). It has a number of characters which indicate reasonable engineering ability (5-6 out of 12 positive matches; Table 4.2). However, it is fairly palatable, and has low acidification capacity and relatively evenly draining peat (which may be mistaken for *Sphagnum* peat; Barber *et al*., 2003), reducing its engineering capacity. Additionally it has few characters which are able to stabilise a bog (4/8 characters; Table 4.3). Though providing habitat for *Sphagnum* invasion (Lavoie *et al*., 2005), against which it appears less competitive, *Eriophorum* is still able to persist in the new "pseudo-raised bog" environment (p. 65, Hughes & Barber, 2004; Korhola, 1992), supporting a designation as EE. Only a temporary precursor to *Sphagnum*-dominated raised bog (Hughes & Dumayne-Peaty, 2002; Hughes & Barber, 2004; McMullen *et al*., 2004), it acts more as a facilitator (Connell & Slatyer, 1977; Callaway, 1995). However the current relative dominance of *Sphagnum* may be due to the shift to a wetter Holocene climate about 8000 yr BP, changing the balance towards less desiccation-tolerant peat builders (Hughes & Barber, 2004). In past warmer, drier climates, changes towards ombrotrophy took place by the growth of sedge rich communities raising the surface level of the peat above the groundwater table (Barber *et al*., 2003). In such climatic conditions, *Eriophorum* may have been more successful as an engineer than it is today.

In the Southern Hemisphere *Empodisma minus* is the most likely candidate for EE of the FBT (though two taxa may be involved; B. Clarkson, *pers. comm*.). A small rhizomatous perennial, *Empodisma minus* (Hook.f.) Johnson & Cutler grows in seasonally or permanently inundated habitats, mires, wet heathlands (including pakihi; Johnson & Gerbeaux, 2004), and riparian zones with peaty soils throughout South-East Australia, Queensland, Tasmania and New Zealand (Campbell, 1964; 1981; Johnson & Cutler, 1973; Wardle, 2002). The *Empodisma* genus is a part of the Winifredia group of the Australasian Restionaceae (Briggs & Johnson, 2002). The name *Empodisma* refers to the much-branched, dark green, hollow and slender stems (culms), with extremely reduced leaves in whorls, hosting minute flowers. Stems are 12-200 cm long, forming dense, tangled masses (its local name is wirerush), which arise from bract-covered, glabrous dark brown rhizomes, buried up to 25 cm deep (pers. obs.) in the substrate. *Empodisma* is a strongly competitive clonal resprouter, with infrequent recruitment from seed (Meney & Pate, 1999), except following disturbance such as fire (Clarkson, 1997). At least in southern mires, *Empodisma* is associated with deep, well-decomposed peat, low pH, and low calcium:magnesium ratios as well as high marine sodium inputs (de Groot, 1999).

Empodisma minus has a dimorphic root system, with sturdy roots anchoring the rhizomes which presumably store nutrients and/or carbohydrates. A second root form, the capillaroid root which is covered with “closely crowded persistent root hairs” (p. 9, Campbell *et al*., 1995), develops in response to low soil nutrient levels (Campbell, 1981), and is negatively geotropic in bogs (Campbell, 1981). Capillaroid roots are not unique to *Empodisma,* being reported in other members of Restionaceae from Australia (e.g., *Loxocarya* spp. and *Calarophus elongatus*; Campbell *et al*., 1995) and South Africa (*pers. obs*.), though these areas are too dry for organic matter to accumulate (Campbell *et al*., 1995). In the wetter regimes of New Zealand, *Empodisma's* capillaroid roots accumulate as peat due to their abundance, capacity for water retention, chemical inertness and resistance to decay (Campbell, 1981). In favourable conditions, the roots can intertwine into a dense, felt-like mat which may grow 20-50 mm above the mire surface, and remain live to a depth of 300 mm (Clarkson *et al*., 2009). These mats form the sole ground cover, building up around the shoots of adjacent plants and engulfing fallen litter (Campbell *et al*., 1995). The capillaroid roots have high hemicellulose, and low polyphenol and lignin contents, chemistry which in other species is associated with fine or amorphous detritus upon decomposition (following Kuder *et al*., 1998). The thicker axes of the roots and stems are high in lignin and polyphenols, which increases their resistance to decay by inhibiting microbial activity, and, with possible allelopathic properties, facilitates competitive exclusion of other mire species (Kuder *et al*., 1998). As a result of these capillaroid root mats, a “vertically displaced feeding root system” (p. 378, Clarkson *et al*., 2009) forms underneath the restiad canopy. *Empodisma* functions with low tissue nutrient contents

(Agnew *et al*., 1993; Sharp, 1995; Clarkson *et al*., 2005), and there is only limited colonization of *Empodisma* by arbuscular mycorrhizae (Clarkson *et al*., 2005). Instead nutrient uptake from the low nutrient peat substrate is by these apogeotropic capillaroid roots and fine root hairs (Campbell, 1981). The roots intercept nutrient-bearing rainfall via stemflow (Agnew *et al*., 1993), while other mire species can only access nutrients from within the substrate (Clarkson *et al*., 2009). The base-exchange capacity of the capillaroid roots is equal to that of a co-occurring New Zealand *Sphagnum* species (Agnew *et al*., 1993), suggesting efficient uptake of any intercepted nutrients. Further Bannister (2000) found significantly higher uronic acid levels in *Empodisma* than four Northern Hemisphere *Sphagnum* species, contributing to its high nutrient capture.

Empodisma has a range of characters which result in maintenance of a high and stable water table. Despite being a wetland species, its roots are "poorly adapted for growth in anoxic soils" (p. 682, Sorrell *et al*., 2000; Johnson & Brooke, 1998), though the water holding capacity of the root mats is comparable to that of *Sphagnum* on a dry weight basis (Campbell, 1964; 1981; Agnew *et al*., 1993). With low cortical porosity and a highly thickened endodermis and stele, the negatively geotropic habit of the capillaroid roots may be an adaptation to avoid anoxia (Sorrell *et al*., 2000). Further, the high volume of gas-filled *Empodisma* tissues near the surface may result in peat floatation, a further engineering trait which may permit peatland surface oscillations (Fritz *et al*., 2008), as do occur in mire zones with high *Empodisma* cover. Campbell & Williamson (1997) indicate *Empodisma* exerts strong control on evaporative losses from its canopy, the dense shoots acting as a mulch, restricting movement of solar energy and water vapour between the substrate and atmosphere. Dead stems (including suspended litter), comprising up to 60% of the total canopy biomass (Hodges, *unpublished data*), are retained within the lower canopy. These intercept rainfall, so the moisture content of the lower canopy remains higher for longer than that of the upper canopy (Campbell & Williamson, 1997).

Though much less well studied than *Sphagnum*, *Empodisma minus* has the expected characteristics of an EE of the FBT (Table 4.2; 11/12 characters), except that there is no information on its possible production of drainage barriers. It establishes early in the fen stage, and becomes dominant in later stages (Shearer, 1997; Clarkson, 2002; Clarkson *et al*., 2004). Then *Empodisma* dominates the water table and nutrient regimes of the mire, until the peat surface is hydrologically isolated, and a bog is formed, which it effectively stabilises (Table 4.3; 7/8 characters), due to its unpalatable shoot material (van Rees & Hutson, 1983), inert litter (Campbell, 1981), and high nutrient retention capabilities. Due to "an elegant interaction between its morphology, substrate and rainfall" (p. 107, Agnew *et al*., 1993), *Empodisma* is a world-class ecosystem engineer.

New Zealand's raised restiad mires form in areas with seasonal rainfall deficits, and lower annual rainfall than that required for the development of raised mires in the Northern Hemisphere (McGlone, 2009), which may be why *Empodisma* is a better engineer here than *Sphagnum* species. Pollen and macrofossil data from four North Island mires of varying age provide support for an autogenically driven model of mire succession which can operate across a range of different climates (Clarkson *et al*., 2004a). *Empodisma* may also be more versatile in terms of climate regime under which it can engineer than Northern Hemisphere *Sphagna.*

Another possible contender for Southern Hemisphere EE of the FBT is the red snow tussock, *Chionochloa rubra* (Table 4.2, Table 4.3), which includes four subspecific taxa (Connor, 1991). Up to 1.5 m tall, it has a wide edaphic range, and occurred on the often peaty soils of south-eastern and southern New Zealand over far greater areas than today due to land clearance for agriculture (Mark & McLennan, 2005). It is absent from northern lowland restiad bogs, where its position in the FBT is taken by sedges (e.g. *Baumea* spp)*. Chionochloa* tends to be replaced in raised bog communities by *Empodisma* and other bog species, but persists on the more minerotrophic bog margins. Less well studied as an EE than the other species, it has no known characters which contradict assignment as an EE (5/12 in Table 4.2, and (3-4)/8 in Table 4.3), but it is not recorded as building peat and is of low productivity in bog situations (*pers. obs*.).

Empodisma's only mainland New Zealand bog-inhabiting relative, the rare giant restiad, (*Sporadanthus ferrugineus* de Lange, Heenan *et* B.D. Clarkson, in the Lepyrodia Group of the Restionaceae: Briggs & Johnson, 2002), contributes less than *Empodisma* to peat accumulation in its only locale, the peat domes of the Waikato region (Shearer, 1997; Clarkson, 2002). It has lower stem flow than *Empodisma* (Agnew *et al*., 1993), and is not found in fens, and so cannot be an EE. A recent segregate, *Sporadanthus traversii* (F. Muell.) F. Muell. is however reported as the major peat builder on the botanically related Chatham Islands (McGlone, 2002; Clarkson *et al*., 2004b) in the absence of *Empodisma,* and its shorter, finer, droopier canes may confer some as yet unstudied engineering abilities.

4.9 Conclusion

Work by Hughes & Barber (2003; 2004) has been pioneering in consistently addressing the FBT. Practical experimentation, such as that initiated in bogs by Clymo (1965) and Bellamy &

Reiley (1967), and more recently demonstrated by Scheffer *et al.* (2001), Heijmans *et al*. (2002) and Adema *et al*. (2006), offers much needed insight into bog mechanics. Here we review the two mechanisms for crossing the FBT which are differentiatable, and encourage determination of the types of ecological, biological, palynological or stratigraphic evidence which can irrefutably distinguish between these causes of change in mire trophic status, perhaps considering the framework proposed in Table 4.1.

The importance of the EE in crossing the FBT cannot be under-estimated. EEs certainly play pivotal roles in mires of both Southern and Northern Hemisphere temperate regions, though these are not necessarily ecologically comparable to mires of other regions (Damman, 1995). In New Zealand the apparent EE of the FBT is *Empodisma minus*. We encourage the identification, following Tables 2-3, of EE species in other parts of the world, an area where local knowledge will be crucial. We are undertaking some such work, focusing on *Empodisma minus* and the other putative engineer, *Chionochloa rubra*, in the New Zealand context.

Table 4.1: Parameters which allow differentiation between allogenic and autogenic mechanisms for crossing the Fen Bog Transition (FBT), including the role of ecosystem engineers (EE), and some examples of papers which apply these parameters to mire studies.

Parameters		**Allogenic**		**Autogenic**		**Example of use in mires**
		FEN → BOG		**FEN → BOG**		
Climate	Prevailing climate	Not applicable or relevant		Moist		Winkler (1988); Foster & Wright (1990)
	Regional climate change	Norm	Cooler and / or wetter	Not applicable		Tallis (1983); Kuhry *et al.* (1991)
Catchment history	Mire expansion	Consider		Not applicable		Korhola (1992)
	Hydrological changes	Consider		Not applicable		Kulczynski (1949); Heinselman (1970)
	Tephra or sediment layers	Absent	Present (buried)	Not applicable		Lowe *et al.*, (1999)
Water table indicators	Desiccation surfaces on peat	Present	Absent	Absent		Casparie (1993)
	Charcoal fragments	Present	Absent	Absent		Hughes *et al.*, (2000) ; Barber *et al.*, (2003)
	Diatom assemblages (in recent peat)	Differences, especially in *Eunotia*		Differences		Foster & Fritz (1987); Dell'uomo (1992)
	Collembola	Differences		Differences		Slawska (2000)
	Testate amoebae assemblage	Low and/or fluctuating water table	Stable, high water table	High water table	Stable, high water table	Charman (1997; 2002); Charman & Warner (1997); Wilmshurst *et*

Parameters		**Allogenic**		**Autogenic**		**Example of use in mires**
						al., (2003); Lamentowicz & Mitchell (2005); Lamentowicz *et al.*, (2008)
	Macrofossil analysis	Low	High	Fluctuating	Stable, high	Johnson *et al.*, (1990); Nicholson & Vitt (1990); Kuhry *et al.*, (1993)
Peat characters	Humification	Sapric	Sapric/Hemic	Sapric	Hemic	Shearer (1997); Ellis & Tallis (2001)
	Carbon:Nitrogen ratio	Increasing		Stable, high		Kuhry *et al.*, (1991); Turunen & Turunen (2003)
Inferred pH		Abrupt transition from high to low		Steady decline		Nicholson & Vitt (1990); Kuhry *et al.* (1993)
Vegetation structure	Presence of EE	EE absent or at low densities	EE absent or present	EE present	EE dominant	Payette (1988); Nicholson & Vitt (1990); Kuhry *et al.*, (1993); Hughes & Dumayne-Peaty (2002); Barber *et al.*, (2003)

Table 4.2: Characters required for a species to be an ecosystem engineer (EE) across the fen-bog transition (FBT). The match to requirements of four potential EE taxa is categorised as good (√), bad (X), mixed (±), and unknown (?).

Character	**Northern Hemisphere *Sphagnum* spp.**	***Eriophorum vaginatum***	***Empodisma minus***	***Chionochloa rubra***
Ecosystem engineering ability present				
EE present both sides of the FBT	√ *S. fuscum* (Heinselman, 1970; Payette, 1988; Kuhry *et al.*, 1993) *S. fuscum* has wide edaphic range (Bragazza, 1997) *S. imbricatum* (Hughes & Dumayne-Peaty, 2002)	X Temporary precursor only to *Sphagnum*-dominated raised bog (Hughes & Dumayne-Peaty, 2002)	√ Common in mesotrophic to oligotrophic stages (Cranwell, 1953; Shearer, 1997; Clarkson, 2002; McGlone, 2009)	√ Wide edaphic range (Connor, 1991)
Persistent macrofossil occurrence of EE throughout peat core	√ Preserved remains in 52% of samples in near continuous bands (Tallis, 1994)	± Periodic peaks in leaf sheath bundles and spindles (Tuittila *et al.*, 2007) May be a major peat former (Hughes *pers. comm.*)	√ Cranwell, 1953; Campbell *et al.*, 1973, Walker *et al.*, 2001	X Not a significant peat former in a mire largely lacking *Empodisma* (Walker *et al.*, 2001)
Accumulation of peat precursors				
Low palatability to herbivores	√ Unpalatable (Clymo & Hayward, 1982)	X Palatable; grazed by sheep, cattle, lemmings, ground squirrels, geese and caribou (Chapin & Slack, 1979; Grant *et al.*, 1987; Wein & MacLean, 1973)	√ Unpalatable (van Rees & Hutson, 1983; van Rees & Holmes, 1986; McDougall, 2007)	√ Unpalatable; “worthless" character as sheep feed (p.121, Cockayne, 1967) Fertilization increases palatability (Connor *et al.*, 1970) Organic matter digestibility is low (Fenner *et al.*, 1993)
Inherent inertness of litter	√ Low rate of decomposition (Aerts *et al.*, 1999) High phenolic	√ Low rate of decomposition (Coulson & Butterfield, 1978; Cornelissen, 1996;	√ Inherently low tissue nutrients (Agnew *et al.*, 1993; Sharp, 1995; Clarkson *et al.*,	√ Lignin 6.8-10.3 % (oven dry weight) in shoot material (Connor *et al.*, 1970)

Character	**Northern Hemisphere *Sphagnum* spp.**	***Eriophorum vaginatum***	***Empodisma minus***	***Chionochloa rubra***
	content (Dickinson & Maggs, 1974) High refractory nature of peat (Scheffer *et al.*, 2001) Low N content impacts on decay (Aerts *et al.,* 2001) Presence of sphagnan may cause a form of C limitation as consequence of humification (Thomas & Pearce, 2004)	Hughes & Barber, 2004) Non-significant differences between nutrient content in rain-protected and unprotected leaves (Jonasson & Chapin, 1985) Litter of rhizomes, leaf bases and roots accumulates as peat (Hughes *pers. comm*.)	2005) Decay resistant outer cortex, central strand and endodermis in root (Campbell, 1981) High polyphenol and lignin in stems; anhydro-galactosan in root hairs (Kuder *et al*., 1998) Heavily lignified mature roots (Sorrell *et al*., 2000)	High mechanical strength (Connor & Bailey, 1972) High mean tiller weight and leaf dieback, and low mineral content in low nutrient soil (Lee & Fenner, 1989)
Inhibition of microbial activity	√ Microbial inhibition (Dickinson, 1983; Verhoeven & Toth, 1995; Borsheim *et al*., 2001; Bonnett *et al.,* 2006; Opelt *et al.,* 2007; Pankratov & Dedysh, 2009) Toxic organochemicals (Verhoeven & Liefveld, 1997) Sphagnol and sphagnan inhibit decomposition (Smidsrød & Painter, 1984; Rudolph & Samland, 1985; Painter, 1991; Stalheim *et al*., 2009)	?	√ Microbial inhibition due to allelopathic properties of tissues (Kuder *et al.*, 1998) Low microbial biomass (Schipper *et al.*, 1998) Litter and moss protected from degradation through incorporation into apogeotropic root mass, (Campbell, 1981; Agnew *et al.*, 1993)	?
Maintenance of high and stable water table				
Reduced evapotranspiration	√ In hummocks, internal conduction of waters re-wets hummocks (Titus & Wagner, 1984) In hummocks,	√ Increased relative humidity under canopy (Lavoie *et al.*, 2005)	√ Low evapotranspiration rates (<2.5 mm day^{-1}) due to thick litter and dense canopy (Campbell &	√ Low transpiration losses c.f. *Festuca novae-zelandiae* and *Chionochloa australis* (Espie, 1999)

Character	**Northern Hemisphere *Sphagnum* spp.**	***Eriophorum vaginatum***	***Empodisma minus***	***Chionochloa rubra***
	inrolled cucullate leaves and compact form reduce surface area for evaporation (Green, 1968) In hollows, dehydrated *S. cuspidatum* hyaline cells have high albedo, reflecting light and reducing temperature (van der Molen & Wijmstra, 1994)		Williamson, 1997) Stomatal conductance maximized in morning (Sharp, 1995)	Few stomata, located in deep adaxial furrows, preventing desiccation (Espie, 1999)
Water-holding capacity	√ High water holding capacity (10-25x own weight) (Andrus, 1986) High effective porosity with depth (Holden, 2009) Maintenance of macropore structure via litter quality (Turetsky *et al.*, 2008)	√ Peat mass efficient at retaining water during periods of desiccation (Hughes *et al.*, 2000)	√ High water holding capacity (15x own weight) in sponge-like root weft (Campbell, 1964) Dense canopy retains moisture at deeper canopy levels (Campbell & Williamson, 1997) Moisture retained in peat (Campbell *et al.*, 1995)	?
Decreased vertical drainage	√ Hydraulic conductivity decreases with depth (Adema *et al.*, 2006; Price *et al.*, 2008) *Sphagnum* structure collapses and bulk density increases with depth (Hayward & Clymo, 1982; Johnson *et al.*, 1990) Variable infiltration rates with depth (Holden, 2009)	X No change in infiltration rates with depth (Holden, 2009)	√ Decreasing hydraulic conductivity with depth; most water exchange in surface 1.5m of peat layer (Maggs, 1997) Acrotelm drainable porosity halved within 200 mm of surface (Miller, 1994)	?
Drainage barriers	√ Iron hardpan formation (Andrus,	√ Iron oxide deposits in soil surrounding roots (Koch *et al.*,	?	?

Character	**Northern Hemisphere *Sphagnum* spp.**	***Eriophorum vaginatum***	***Empodisma minus***	***Chionochloa rubra***
	1986) Fe-Mg hardpan formation (Klinger, 1996; Kusel *et al.,* 2008)	1991)		
Adaptations to water table fluctuation	√ Ability to grow under both wet and dry conditions of mire surface (Green, 1968; Casparie, 1972; Barber, 1981; van der Molen & Hoekstra, 1988)	√ Wide tolerance to water table depth (Gore & Urquhart, 1966; Barber, 1981)	√ Structural elements may protect chlorenchyma from collapse in dry spells (Linder, 2000) Surficial roots avoid anoxia by negatively geotropic growth habit (Campbell, 1981; Sorrell *et al.,* 2000) Surface rhizomes maintain atmospheric O_2 concentrations (Sorrell *et al*,. 2000)	√ Wide tolerances (MacIntosh *et al*., 1983)
Development of mire microforms	√ Hummocks (Green 1968; Titus & Wagner, 1984) *S. imbricatum* has two morphologically distinct ecads, allowing it to grow in both hummocks and semi-aquatic habitats (Green, 1968)	?	√ Hummock and hollow topography forms near edges of mire (Rogers, 1984)	X No microtopography known (*pers. obs*.)
Features altering pH				
Acidification	√ pH of approximately 4 (Sonesson, 1970; Braekke, 1981; Glaser *et al*., 1981) Acidification via polyuronic acids (Clymo, 1963; Bellamy & Reiley, 1967)	± Low cation exchange capacity (Hughes & Dumayne-Peaty, 2002) Acidification of substrate occurs under continental climate conditions (Hughes *pers.*	√ Acidification via polyuronic acids, at higher levels than for *Sphagnum* (Bannister, 2000)	?

Character	**Northern Hemisphere *Sphagnum* spp.**	***Eriophorum vaginatum***	***Empodisma minus***	***Chionochloa rubra***
	Polyuronic acid content 10-30% of dry weight; larger values for hummock species (Clymo, 1964; 1967; Vile *et al*., 1999) Organic acid production acidifies subsurface waters (Hemond, 1980)	*comm*.)		

Table 4.3: Characters required for a species to persist on the bog side of the fen-bog transition (FBT). The match of four potential EE taxa is categorised as good (√), bad (X), mixed (±), and unknown (?).

Character	**Northern Hemisphere *Sphagnum* spp.**	**Eriophorum vaginatum**	**Empodisma minus**	**Chionochloa rubra**
EE dominance				
Competitive?	√ Dominant (Moore & Bellamy, 1974)	X Increased relative humidity under canopy facilitates establishment of moss species (Lavoie *et al*., 2005) Only temporary on raised bogs (Hughes & Dumayne-Peaty, 2002)	√ Shrubs stunted by low P concentrations on restiad mires (Clarkson *et al*., 2005) Clonal resprouter (Meney & Pate, 1999)	± Tussocks appear stunted in restiad mires (*pers. obs*.) and string fens (Rapson *et al*., 2006)
Nutrient access				
Water pre-emption	√ Efficient capture of atmospheric water (Lee & Woodin, 1988; Aldous, 2002) External capture via capillary water flow (Clymo & Hayward, 1982) Buoyancy-driven water flow replenishes nutrients (Rappoldt *et al*., 2003; Adema *et al*., 2006)	√ Exploitation of subsurface waters via deep roots overcoming nutrient limitation (Chapin *et al*., 1988)	√ Pre-emption by high stem flow (Agnew *et al*., 1993) Accesses atmospheric nutrient sources (Clarkson *et al*., 2009)	± By fog-water interception (Ingraham & Mark, 2000)
Deep root systems	X No roots present	?	X Cluster roots retrieve N from only the top 5 cm of substrate (Clarkson *et al*., 2009)	√ Deep roots (Craine & Lee, 2002)
Nutrient uptake				
Cation exchange	√ High cation exchange capacity (Clymo, 1963; Daniels & Eddy, 1985)	√ Absorbs organic N and has preferential use of amino acids as N source (Schimel &	√ Presence of uronic acids suggest uptake capability	?

	S. rubellum takes up amino acids as N source (Kielland, 1997) Symbiotic methanotrophs oxidize methane for *Sphagnum* assimilation (Raghoebarsing *et al*., 2005) Incorporation of nitrate and phosphate rapidly from solutions of unusually low concentration (Clymo & Hayward, 1982; Bragazza *et al*., 2003)	Chapin, 1996) Methanotrophs in *Eriophorum/Sphagnum* dominant community similar to those of ombrotrophic peatlands (Chen *et al*., 2008) Very efficient in taking up nutrients in luxury nutrient conditions (Shaver *et al*., 1986) Root surface phosphatases contribute up to 69% of annual P demand (Kroehler & Linkins, 1991; Moorhead *et al*., 1993)	(Bannister, 2000) High efficiency of nutrient uptake across a range of substrate values (Clarkson *et al.*, 2005)	
Root adaptations	X None	?	√ Scavenges nutrients with negatively geotropic roots and 1 mm root hairs (Campbell, 1975; 1981; Agnew *et al*., 1993)	?
Leaf life span	√ Long leaf longevity (Chapin *et al.,* 1995)	X Short leaf longevity (Jonasson & Chapin, 1985)	√ Stems long-lived, dead shoots retained in canopy layer (*Pers. obs*.)	√ Long-lived (Greer, 1979)
Nutrient storage organs	X None	√ Seasonal variation in nutrients of tundra species' organs (Chapin, 1980b) Storage of limiting nutrients (especially P and K) in perennating organs (Goodman & Perkins, 1959; Defoliart *et al*., 1988)	√ Rhizomes to 1 cm thick (*pers. obs*.)	√ High nutrient concentrations in leaf sheaths (Williams *et al*., 1978a) High carbohydrate storage in stems and leaf bases of congeners (Payton & Brasch, 1978)
Nutrient recycling				
Nutrient resorption	√ Nutrient translocation (Rydin & Clymo, 1989; Svensson, 1995; Aldous,	√ 90% leaf P and 80% leaf N resorbed (Jonasson & Chapin,	√ Nutrient uptake occurs in upper 5 cm of root weft	?

	2002) Internal nutrient transport through perforations in stem parenchyma cells (Rydin & Clymo, 1989)	1985) High nutrient use efficiency under low nutrient conditions (Thormann and Bayley, 1997) Competitive on cold, infertile sites with other sedges (Shaver & Laundre, 2003) Vascular sclerenchyma in corm aids in nutrient recovery and redistribution (Cholewa & Griffith, 2004).	(Clarkson *et al.*, 2005), so leachates can be scavenged	

Chapter 5: Competitive relationships and Ecosystem Engineering across the New Zealand fen-bog transition

Rosemary and Yvette potting up *Chionochloa rubra* and *Empodisma minus* at the Plant Growth Unit, Massey University, December 2002.

A version of this chapter has been presented at the 54th Annual Conference of the International Association for Vegetation Science (20-24 June 2011, Lyon, France), and the New Zealand Ecological Society Conference (28 August – 1 September, 2011, Rotorua).

5.1 Abstract

An artificial wetland containing the two dominant species in New Zealand montane restiad mire communities was created to investigate the role of *Empodisma minus* as the ecosystem engineer of the fen-bog transition in New Zealand montane restiad mires. Biomass accumulation and competition between wire rush (*Empodisma minus*) and red tussock (*Chionochloa rubra*) were investigated under different water and nutrient levels using a de Wit replacement series design over a 27 month period, with species grown in monoculture and binary mixtures at a constant density. Competition indices (Relative Yield, Relative Yield Total & Relative Efficiency Index) were determined from initial and final biomass data, and suggest that *Chionochloa rubra* is the better competitor in high nutrient, and in drier conditions. However, *Empodisma minus* foliage and capillaroid roots increase in mesotrophic conditions, the starting point of the fen-bog transition. The apogeotropic roots also displayed plasticity in root proliferation and placement. *Empodisma minus* is the superior competitor long-term in the mesotrophic and oligotrophic conditions of the fen-bog transition and raised mire environments, providing a high water table is maintained; otherwise species co-existence will likely occur. These findings provide some preliminary evidence for *Empodisma minus* as an ecosystem engineer, however, they also suggest a dense *Empodisma* canopy is required to maintain the wet environment needed for apogeotropic root weft growth.

5.2 Introduction

Ecosystem engineers (EE) are “organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials” (Jones *et al.*, 1994, p.374). Since the inception of the EE concept, it has received widespread application in the mire literature, especially in application to members of the bryophyte genus, *Sphagnum*, and their ability to generate autogenic pathways across the fen-bog transition (FBT) (e.g. van Breeman, 1995; Svensson, 1995; Granath *et al.*, 2010). The FBT occurs due to the accumulation of slowly decomposing *Sphagnum* litter, the positive feedbacks between the litter and *Sphagnum* resulting in increasing isolation of the mire surface from groundwater interaction, with accompanying peat acidification and anoxia. This facilitates the expansion of the *Sphagnum* community and a decrease in vascular plant richness and productivity (van Breeman, 1995). Rather than competing for light, *Sphagnum* literally attacks vascular species “at the root” (van Breeman, 1995, p. 273), controlling nutrient availability to vascular species by efficiently harvesting nutrients from precipitation, and reducing nutrient mineralisation and decomposition rates (Malmer *et al.*, 1994; Scheffer *et al.*, 2001), the source of nutrients for vascular plants (Svensson, 1995).

While many New Zealand fen-bog complexes contain domed ombrotrophic elements, large raised bogs are less common due to the climatic constraints imposed by seasonal rainfall deficits (McGlone, 2009). The main peat-forming species in mires south of 38°S latitude is not a *Sphagnum* species, but the restiad *Empodisma minus* (Hook. f.) Johnson & Cutler s.l.*,* a small rhizomatous perennial. The northern species *Empodisma robustum* Wagstaff & B.R.Clarkson, sp. nov. inhabits mires north of 38°S (Wagstaff & Clarkson, 2012). Most of the recent ecophysiological research into *Empodisma* species has occurred in the northern lowland raised bogs of the Hauraki Plains (Campbell & Williamson 1997; Kuder *et al.*, 1998; Clarkson *et al.*, 2005; 2009; Rutledge *et al.*, 2009), i.e. on *Empodisma robustum*. In contrast, there has been little research of a similar nature undertaken with *Empodisma minus*, which is more widely spread, inhabiting a larger range of wetland habitats (Chapter 3). At present, it is assumed that the plant-environment feedbacks that lead to raised mire formation in New Zealand northern lowland bogs, as elucidated in Hodges & Rapson (2010), are also prominent during the formation of southern and montane mires (Wagstaff & Clarkson, 2012). By investigating the potential ecosystem engineering properties of *Empodisma minus*, this research will assist in determining the validity of this assumption.

The extension of the concept of ecosystem engineering to the FBT in New Zealand mires has been recently addressed, and the likely means by which *Empodisma* species engineer the FBT elucidated (Hodges & Rapson, 2010). The process of engineering the FBT requires the presence of an ecosystem engineer, which alters the mire environment by enhancing accumulation of peat precursors from above- and below-ground tissues, maintaining a high and stable water, and increasing acidity (van Breeman, 1995; Hodges & Rapson, 2010). The Ecosystem Engineer possesses superior competitive traits in the oligotrophic environment created, having better levels of nutrient access, and rates of nutrient uptake and retention (Hodges & Rapson, 2010).

Though less intensively studied than *Sphagnum* as a mire engineer, *Empodisma* species have many of the traits expected (Hodges & Rapson, 2010). While cluster roots have been the subject of much research of late (see Lamont, 2003 for a review), the capillaroid roots of the Restionaceae are less studied. *Empodisma* capillaroid roots are covered with ‘closely crowded persistent root hairs’ (Campbell *et al.*, 1995, p. 9), and assist in nutrient acquisition in oligotrophic environments (Clarkson *et al.*, 2009). The roots have high base-exchange capacity

(Bannister, 2000), and intercept nutrient-bearing rainfall via stemflow (Agnew *et al.*, 1993), proliferating in the upper soil horizons rich in litter and humus (Clarkson *et al.*, 2005; McGlone, 2009) to form a thick water-retentive root weft (Campbell *et al.*, 1995), which is resistant to decay (Kuder *et al.*, 1998). Thus *Empodisma* species dominate the water table and nutrient regimes of the developing mire, maintaining hydrological isolation of the peat surface due to their wide range of engineering properties (see Hodges & Rapson (2010) for review).

Empodisma species have a wide environmental range, being dominant in both fen and bog environments (Chapter 3). The high proportion of *Empodisma robustum* apogeotropic roots in northern lowland restiad peat (Campbell, 1975; Campbell *et al.*, 1973) suggests that for the FBT to occur via ecosystem engineering by *Empodisma minus*, the right conditions for root formation must be met. In general, cluster root formation is linked to soil pH, Fe and organic matter content, soil water levels and with nutrient deficiency in plants (Watt & Evans, 1999; Diem *et al.*, 2000; Lamont, 2003), however, the physiological requirements for capillaroid root formation in the Restionaceae have not been determined. Field studies suggest *Empodisma minus* capillaroid root growth is linked with higher soil organic matter content, is present in both fen and bog, and may be inhibited by excess soil moisture (Chapter 3).

It is not known at this time what proportion of *Empodisma minus* biomass in the vegetation canopy is required to produce the “wet desert” effect (reduced evapotranspiration) conducive to raised bog formation in northern mires (Campbell & Williamson, 1997; McGlone, 2009), nor the relationship between the canopy effects and apogeotropic root development. Small clusters of capillaroid roots have been observed growing under mixed wet fynbos canopies in the restiads *Cannamois virgata* and *Calopsis paniculata* in South Africa (*pers. obs.*), however, the dense carpets of apogeotropic roots described by Agnew *et al.* (1993) were found under a dense *Empodisma robustum* near the centre of Kopuatai Bog, in the Waikato region. Field studies suggest canopy dominance may be a pre-requisite for root formation, the dense canopy and mulch-like litter layer of *Empodisma minus* reducing evapotranspiration, and maintaining the high humidity required by the rootlets. Alternatively, apogeotropic root formation may develop independently of canopy biomass, in response to below-ground competition for scarce nutrients. Increased nutrient acquisition via their formation may then enable increased above-ground biomass accumulation, canopy dominance and increasing hydrological impacts.

In order to determine whether *Empodisma minus* benefits from the altered habitat conditions engendered during the FBT, it is necessary to examine competitive relations between

Empodisma minus and another species along the environmental gradients created. The red snow tussock *Chionochloa rubra* is another common indigenous mire species in southern New Zealand mires (McGlone, 2009; Clarkson *et al.*, 2011), having a wide geographic range and broad ecological niche. While *Chionochloa rubra* possesses some attributes in common with mire engineers (Hodges & Rapson, 2010), it does not appear to contribute significantly to peat accumulation. *Chionochloa rubra* often dominates in the minerotrophic conditions of montane fens, its productivity declining in bog conditions (Clarkson *et al.*, 2011). This suggests differences in the competitive relations of these two species, with the outcome of competition affected by the changing water and nutrient status of the mire as the FBT proceeds.

The transition from fen to bog cannot be examined directly, due to the length of time required for the process to occur, while a mire chronosequence of *Empodisma minus* mires was also unable to be constructed (Chapter 3). Therefore an artificial mire gradient was recreated, and competitive relationships along nutrient and water table gradients examined. During restiad mire development total and available nutrients decline (Clarkson *et al*., 2004a), while Northern Hemisphere models suggest water logging is maintained, due to the declining influence of surrounding groundwater tables and changes in hydraulic conductivity of the peat (Ingram, 1983; Clymo, 1983; Moore, 1995). The treatments incorporated both high and low water tables and a three nutrient levels.

The objective of the study is to investigate the importance of nutrients, water table depth and interspecific competition on the biomass allocation patterns of the two putative engineers, *Empodisma minus* and *Chionochloa rubra.* Specifically I am interested to find if it is possible to alter biomass allocation patterns relating to ecosystem engineering traits by simulating the increasingly ombrotrophic conditions typical of the FBT in an artificial wetland gradient. This experiment is a test of two hypotheses:

- That *Empodisma minus* engineers the FBT; producing nutrient scavenging capillaroid roots in response to low nutrient, high water table conditions.
- That *Empodisma minus* is more competitive than *Chionochloa rubra* in the oligotrophic environment created.

5.2.1 De Wit Replacement Series Experiments

The study comprises a De Wit replacement series with three nutrient and two water table levels chosen to simulate the conditions measured in a transitional restiad mire. In a simple replacement series design, two species are grown in various proportions for a period of time, and compared to growth in a monoculture. The most common replacement design is one in which only 2 monocultures and a binary mixture containing an equal density of both species is used. The time period must be sufficient for constant yield to be determined (Firbank & Watkinson, 1985). The ratio and replacement diagrams constructed from yield data offer graphical presentation of the results (de Wit & Van den Bergh, 1965; Harper, 1977), though other measures (e.g. root:shoot ratios) assist in illustrating the basis of the observed species interactions (Bi & Turvey, 1994). Where appropriate initial and final harvest data are available, replacement series offer valid information on the questions of which species dominates in a mixed species culture; which species gains, and how one species in a mixture affects the performance of another (Connolly *et al.*, 2001).

The duration of a microcosm study depends upon the process under investigation, and the life history of the species studied (Fraser & Keddy, 1997). The slow establishment of the species studied required a lengthy experiment, as a short-term study would have only measured initial vegetative growth. While long-term experiments may ordinarily lead to restriction of rooting volume, forcing species to utilise the same soil resources (Harper, 1977; Gibson *et al.*, 1999), some spatial separation of the two species' rooting systems was expected, with the development of capillaroid roots by *Empodisma* to access atmospheric nutrient sources. Previous studies investigating competitive relationships between South African restiads and grasses along nutrient gradients had indicated that capillaroid root development could occur in cultivation within a short time frame (Bell *et al.*, 2000).

Criticism of replacement designs is widespread (Donald, 1963; Firbank & Watkinson, 1985; Connolly, 1986; Snaydon, 1991; Connolly *et al.*, 2001). The criticisms have been focussed on the design rather than the indices used (Weigelt & Jolliffe, 2003). The outcome of a replacement experiment can be dependent on the planting density chosen (Inouye & Schaffer, 1981), however, determining which species is the better competitor may well be independent of density, and so the chosen density should simply be sufficient to "ensure strong interference among species" (Cousens, 1991, p. 667). Gibson *et al.* (1999) also maintain that despite the limitations of replacement series designs, these experiments efficiently address "questions as to the changing balance between species along gradients" (p. 12). In addition, greenhouse experiments allow a high degree of experimental control, repeatability and precision (de Wit, 1960; Harper, 1983), allowing the effects of competition to be explored with other variables (e.g. nutrient levels) held constant.

5.3 Materials and Methods

The experiment was carried out in an ambient temperature tunnelhouse, at the Plant Growth Unit, Massey University.

5.3.1 Plant Material

The two species used were *Empodisma minus* and *Chionochloa rubra* var. *rubra*, herein referred to as *Empodisma minus* and *Chionochloa rubra*.

Plant material was collected from Silica Rapids fen on the slopes of Mt Ruapehu, situated in Tongariro National Park, New Zealand. Small peat cores (approximately 10cm diameter, 20cm length) containing *Empodisma minus* rhizomes with emerging new shoots were extracted from the central portion of the mire, at random points. Three tillers of *Chionochloa rubra* were also collected from the tussock nearest each random point. Bacteria may have an inductive role in initiating cluster root formation (Malajczuk & Bowen, 1974; Lamont, 1986), and so all plant material was packed into small root trainers with local peat (Figure 5.1 & Figure 5.2), and watered with distilled water twice daily prior to transportation. Approximately 800 peat cores containing the sampled species were removed from the fen, transported to the Plant Growth Unit (PGU) at Massey University, placed in a glasshouse for 6 weeks, and watered twice daily with distilled water to maintain the inherently high water content of the peat.

All senesced shoots were removed from the plants prior to potting up, and senesced material collected after this time analysed as the litter component of each samples biomass. Multiples of two plugs of *Chionochloa rubra* and *Empodisma minus* were planted in a 20cm diameter 6L pot. A small pilot study with *Empodisma minus* prior to the main experiment found a low mortality rate in excavated plants with the use of a peat:sand substrate, compared with a pure sand or peat substrate. Hence, pots were filled with a 50:50 Hauraki peat:river sand mixture, the peat being sieved through a 10mm diameter mesh, and the sand washed to remove surface contamination. Hauraki peat has a low pH (4.3-4.5) and is comprised of mixed *Sphagnum* and *Empodisma minus* peat from the Hauraki Peat basin. The C:N ratios of the prepared media and the Silica Rapids substrate were analysed, and found to be similar (18.9 & 16.7 respectively).

5.3.2 Experimental design and set-up

A factorial design incorporating 3 nutrient levels, 2 water-table levels x 4 species was designed, and treatments replicated six times (N=144). To avoid difficulties associated with non-independence, the number of mixed species cultivation pots was doubled, and the biomass of only one species was measured within each pot (Sackville Hamilton, 1994). The 144 pots were arranged in six blocks in a factorial block design, pot assignment to the six experimental blocks being determined by the number of live shoots per *Empodisma minus* plant, which varied from 2-11 culms per plant (Table 5.1). Each *Chionochloa rubra* plant had 3 live tillers. Blocks were re-randomised monthly to reduce neighbour effects and internal glasshouse environmental gradients. Final harvest occurred in February 2004, incorporating three growing seasons.

Table 5.1: Initial size of *Empodisma minus* plants and Block assignment.

Block	**Number of *Empodisma minus* shoots/plant**
1	2
2	3
3	4
4	5-6
5	6-7
6	8-11

Figure 5.1: Gathering plant material from Silica Rapids fen, October 2002.

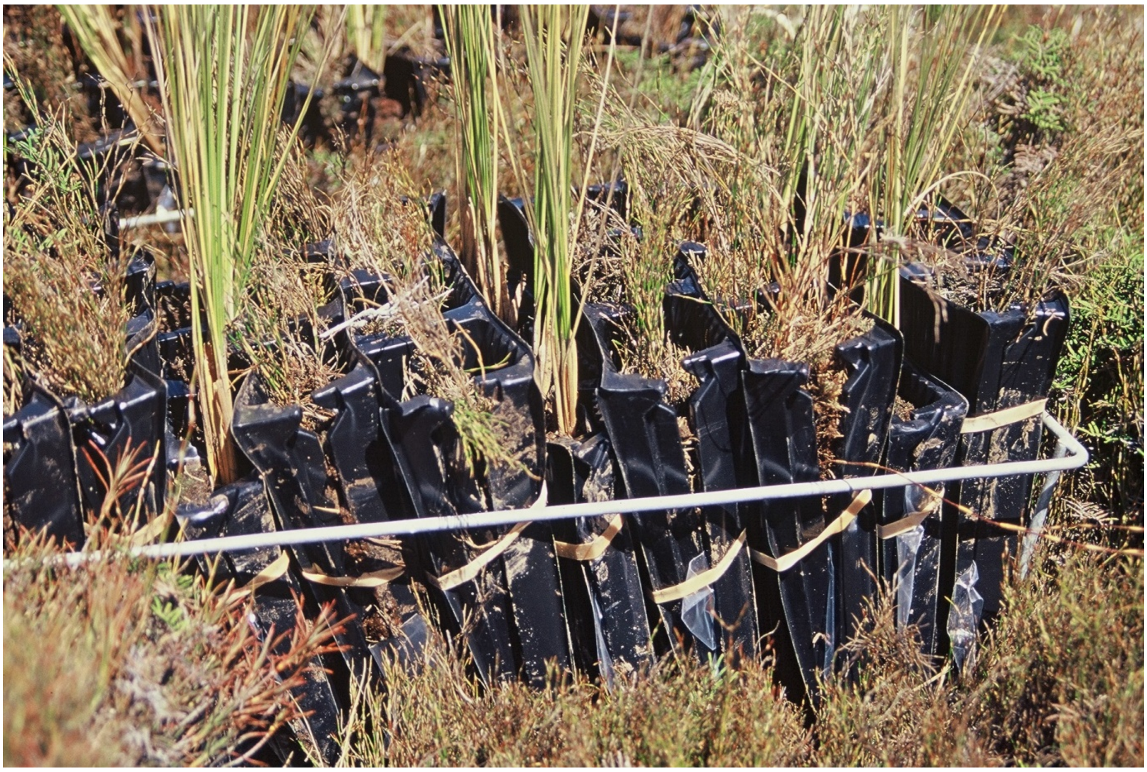


Figure 5.2: Plant material and peat cores packed in root trainers for transportation to Massey University, October 2002.

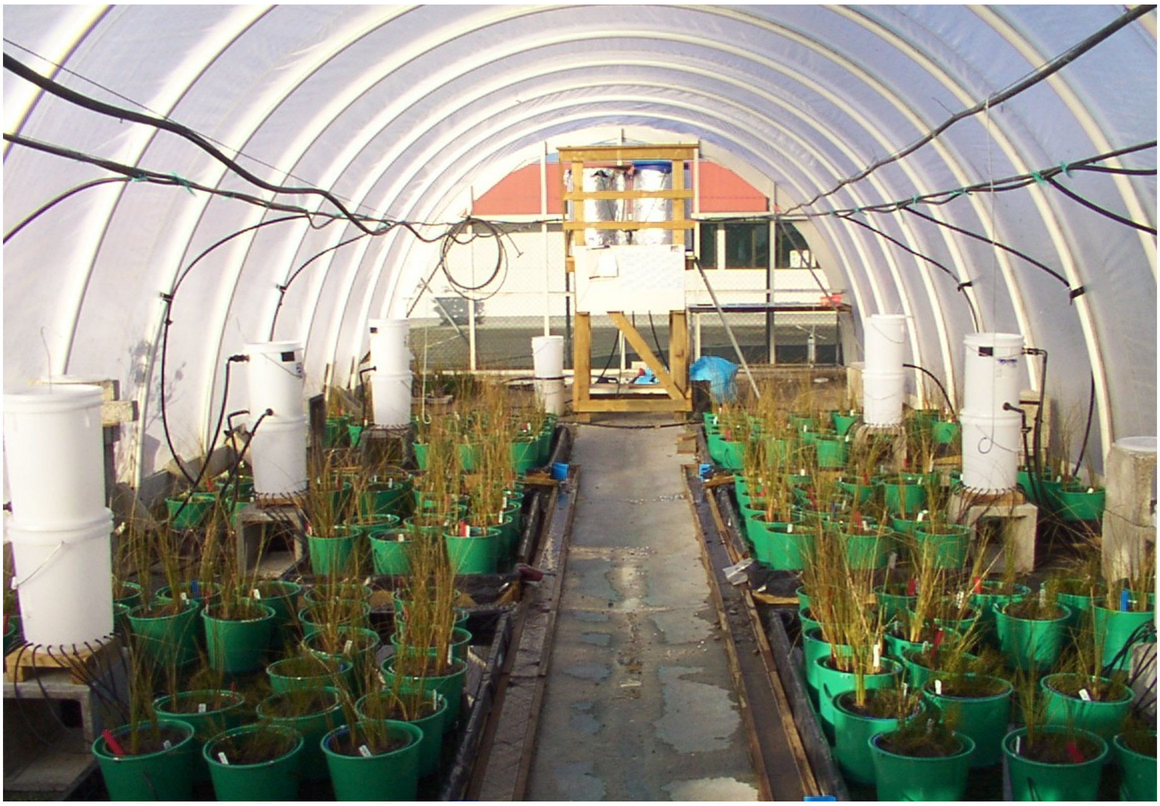


Figure 5.3: Artificial wetland in tunnelhouse at Plant Growth Unit, Massey University 2003.

Figure 5.4: *Empodisma minus* apogeotropic roots in a monoculture treatment pot, 2003.

5.3.3 Artificial wetland construction

An artificial wetland was constructed to manipulate water table levels and nutrient inputs within an experimental framework (Figure 5.3). Water table levels in a mire vary depending upon proximity to seepages, season, rainfall events, and along internal mire gradients. Water table levels were measured relative to hollows at various points in the Silica Rapids mire in Spring 2001, and water table treatments set to reflect these measurements (10 and 20cm) relative to the pot surface.

Each pot was elevated to the rim of the enclosing bucket, and placed within one of six water and gravel filled beds. Water was circulated within the gravel beds to control temperatures within the pots. 7.5mm diameter irrigation pipe connected each bucket with a 20L header tank in each bed, these in turn being connected to two 200L tanks on an elevated tank stand (Figure 5.3). Water table levels in the treatments were maintained once daily, using a gravity-fed system. Water was replenished using the local groundwater utilised by Massey University (Table 5.2). This is low in available nutrients (see Appendix 1 for a full analysis), and was used as large volumes of distilled or deionised water as used elsewhere (Bell *et al.*, 2000), were unavailable at the site for this purpose.

The water in each elevated 200L tank was adjusted to pH 5.5 using concentrated sulphuric acid to match the pH of pore water in the original fen (Hodges, *unpubl. data*), and mean pH of

New Zealand rainfall (Harvey & Clarkson, 1988). Water flowed from the elevated tanks to the 20L header tanks, which distributed water via irrigation pipes to individual buckets, with the position of drainage holes in the buckets determining the water table level.

Table 5.2: Summary of water quality data for Atawhai No. 2 bore groundwater utilised to maintain water table levels in Experiment (n=2). Analysis performed by PNCC Laboratory, Palmerston North City Council, 08/04/99. Full set of data in Appendix 5.1

Analysis	
Conductivity @ 25°	23.0 mS/m @ 25°
pH	7.7
Nitrate-Nitrogen	<0.1 g/m^3 NO_3-N
Nitrite-Nitrogen	<0.003 g/m^3 NO_2-N
Ammoniacal-Nitrogen	1.66 g/m^3 NH_3-N
Phosphate	0.08 g/m^3 PO_4-P

Monthly nutrient applications of 20ml dilute fertiliser solution were applied via a handheld spray apparatus, each pot being enclosed in a spray jacket to avoid spray drift. This method of application was chosen, as both *Chionochloa* species and *Empodisma minus* are suggested to pre-empt the nutrients contained in precipitation and fog (Ingraham & Mark, 2000; Agnew *et al.*, 1993), which in ombrotrophic mires provides an important source of nutrient input to the system. Annual nutrient inputs are indicated below (Table 5.3), and a description of the fertiliser used is included in Appendix 5.2. Monthly nutrient treatments were applied throughout the experiment, as shoot extension continued throughout the year.

Table 5.3: Nutrient and water table treatments used in the de Wit Replacement Series during the period Spring 2002- Autumn 2004.
*Nutrient additions are calculated from monthly fertiliser additions only.

Treatment	**Nutrient solution concentration**	**Depth to water table (cm)**	**N (mg/ pot/year)**	**P (mg/pot/year)**
1	50%	20	0.96	0.19
2	50%	10	0.96	0.19
3	25%	20	0.48	0.09
4	25%	10	0.48	0.09
5	Nil	20	Nil	Nil
6	Nil	10	Nil	Nil

5.3.3.1 Data Collection

An initial biomass harvest was performed at the onset of the experiment in December 2001. The relationship between approximate initial shoot length and biomass was determined from these data, to allow us to determine the approximate initial biomass of the plants in the main experiment for the calculation of the Relative Efficiency Index.

5.3.3.2 Apogeotropic Root Development

Measuring the mass of apogeotropic root development in a peat substrate is difficult and Sharp (1995) indicated large errors result from losses incurred during the washing process to separate peat and roots. Depth of apogeotropic root depth development below the pot surface and increases in surface microtopography in the pot were thus used as proxies for root weft development (Figure 5.4). The method outlined by Clymo (1970) for measuring vertical *Sphagnum* growth, was adapted to measure *Empodisma minus* apogeotropic root growth and the development of microtopography on the pot surface. S-shaped wire cranks were inserted into each pot at a random point around the pot edge in March 2003. The upper surface of each 'S' bend was level with the pot surface. Measurements were made from the top of the crank down to the substrate upon insertion, and again eleven months later, immediately prior to harvest. The difference between the two measurements was taken as an indicator of root weft development within the pot.

5.3.3.3 Final harvest

Plants were harvested in February 2004 after 26 months growth. *Empodisma minus* shoot height and surface micro-topography were measured per pot, and then shoots clipped at ground surface. The pots were cut in half and capillaroid root growth was measured at equal distances along the diameter of the pot. Soil was washed away from the roots with water, and the rhizomes, anchor and coarse feeding roots retained. *Empodisma minus* biomass was divided into live and dead above- and below-ground biomass on a pot basis, as the material belonging to the two original *Empodisma* cores was unable to be separated. All samples were dried at 70^{o}C until constant mass was obtained, and then weighed. *Empodisma minus* biomass Total Kjeldahl N and P levels (live, senesced and rhizome) were determined as described by Blakemore *et al.* (1987), since reasonable estimates of Total-P content are possible using Kjeldahl digestion (Taylor, 2000). N:P ratios were then calculated to determine if N- or P-limited growth was indicated (Koerselman & Meuleman, 1996; Clarkson *et al.*, 2002).

Chionochloa rubra maximum tiller height and tiller number was recorded per plant, and then the entire plant removed from the pot. The biomass was divided into above-ground (live and dead) and below-ground (bases and roots) portions. All samples were dried at 70°C for 72 hours, or until a constant mass was reached, then weighed.

5.3.4 Statistical treatment

Competitive effects, response and outcome were analysed using various analyses (Table 5.4):

- De Wit diagrams utilising Yield (Y) and Relative Yield Total (RYT) to contrast interspecific and intraspecific effects;
- Analysis of Relative Yield (RY), RYT, and Relative Efficiency Index (REI) competition indices to determine competitive intensity, response and outcome. The RY of the two species were plotted and overyielding calculated to further investigate the nature of the species interactions. Indices were tested for departure from unity at the 5% significance level.

Tests for differences in various biomass components such as apogeotropic root development were made using factorial analysis of variance (ANOVA) using STATISTICA v.7 (Statsoft Inc., 2004) with graphs and figures produced in R (R Development Core Team, 2011). Data were tested for normality and homogeneity of variance using Shapiro-Wilks and Levene's tests, and square root or log transformed prior to ANOVA as required. Differences in means were considered significant if $p<0.05$. Mean values are reported along with their standard errors. As initial plant size determined Block allocation, Block was included as a covariate in statistical analyses to measure for the effect of initial size on final biomass components.

As some data contained zero values (e.g. *Empodisma minus* root weft measures), rather than adding a small constant to the data prior to transformation (Wilson, 2007), the data were analysed using a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001; McArdle & Anderson, 2001). PERMANOVA makes no particular assumptions about the distribution of the data, as all p-values are obtained by permutation.

Changes in surface microtopography due to apogeotropic root growth were treated as a binomial response, as the counts were all small integers (mm), and there were many zero responses. The values were changed to either 1 for a value greater than 0, or 0, and analysed using PERMANOVA.

5.3.4.1 De Wit Replacement Diagrams

Dry matter Yields (Y) for the two species and Total Yield (TY) were plotted against the density of the species in binary mixture and monoculture using replacement diagrams (de Wit & Van den Bergh, 1965). If there is no species interaction, then species achieve their expected yield, which in the 50:50 mixtures used, is half their yield in monoculture (Hector, 1998). Means and standard deviations of yield were plotted to present some estimation of error (Cousens, 1991). While replacement diagrams may be inadequate as a sole measure of competitive interactions (Jolliffe, 2000), they are a useful descriptive tool (Harper, 1977; Wildin & Hall, 1980; Inouye & Schaffer, 1981), especially when used in conjunction with other analyses (Gurevitch *et al.*, 1990).

5.3.4.2 Competition Indices

There are many indicators developed to illustrate species interactions, and it is desirable to use several indices in a study, especially when several attributes of competition are being examined to determine the robustness and reproducibility of the patterns ascertained (Goldberg *et al.*, 1999; Weigelt & Jolliffe, 2003). RY and RYT were calculated to measure competitive effect (the ability to suppress resource levels for other species; Goldberg, 1990) and REI to measure competitive outcome, utilising yield per plant where possible to give a clearer interpretation of competitive effect (Weigelt & Jolliffe, 2003). Formulae used are presented below in Table 5.4.

RY measures the yield of a species in mixed cultivation, compared with its yield in the monoculture. RY=0.5 indicates that inter and intraspecific competition are equal, i.e. that a species grows as well in competition with another species, as with plants of its own species. If RY>0.5, the plant competes better with members of other species than its own, while a RY<0.5 indicates interspecific competition is greater (Williams & McCarthy, 2001).

RYT was introduced to measure competition in two-species mixtures in replacement series designs (de Wit, 1960; de Wit & Van den Bergh, 1965). It has been popular as a measure of the extent to which components of a mixture compete for limiting resources, i.e. a measure of complementary resource use (Snaydon & Satorre, 1989; Hector, 1998; Xu *et al.*, 2010). Values of RYT are commonly close to 1.0, and values greater than 1.5 are rare (Snaydon, 1991). Connolly (1987) described the RYT as an index to quantify the extent to which a species in mixture capture more, or uses resources more effectively than when grown in a monoculture.

RYT =1.0 indicates that the species fully share the same limiting resources, exhibiting no resource complementarity.

RYT >1.0 indicates species do not fully share common limiting resources, and partial resource complementarity may be occurring.

RYT =2.0 indicates the species share no common limiting resources, and exhibited full resource complementarity.

RYT <1.0 indicates a mutual antagonism between species (Harper 1977; Hector, 1998).

The use of RYT as a measure of resource complementarity is disputed (Loreau, 1998), the argument being that RYT merely examines the null hypothesis that observed yields are accounted for by changes in the proportional contributions of the species. Various species interactions, in addition to resource complementarity, may explain the changes in observed yields, including direct interference and facilitation. By plotting the RY of both species, these alternative interactions can be investigated (Williams & McCarthy, 2001); though the display of RYT data alongside RY to allow interpretation is still recommended (Williams & McCarthy, 2001).

Table 5.4: Summary of formulae used in the Replacement Series experiment examining competition between *Empodisma minus* and *Chionochloa rubra*; adapted from Walck et al. (1999).

Parameter	**Formula**
De Wit indices[1]	
Relative yield of species a (RYa)	Yab/Yaa
Relative yield of species b (RYb)	Yba/Ybb
Relative yield total (RYT)	RYa + RYb
Relative Efficiency Index (REI)	RGRa(ab) – RGRb(ba)
Relative growth rate (RGR)	(logW2 - logW1)/(t2 - t1)

[1] Abbreviations: Yab (or Yba) = total yield (root + rhizome + shoot) of species a (or b) when grown with species b (or a); Ya (or Yb) = mean total yield of species a (or b) in monoculture; RGR = Relative Growth Rate; RY = Relative Yield; W = total dry mass (all plant parts) of individual plant; t = time of harvest.

While yield is a summation of the effects of plant interactions over the course of the experiment, it will also partially reflect initial size differences between species (Gibson *et al.*, 1999), though if the experimental time frame is sufficiently long; this bias may be overcome (Grace *et al.*, 1992). By including a measure of initial size, the range of inference from a simple replacement series experiment is increased (Gibson *et al.*, 1999; Connolly *et al.,* 2001). REI incorporates initial size with yield by comparing the relative growth rates of the two species, and is used to address the question of competitive outcome (Connolly, 1987), i.e. the efficiency of one species over another in a mixture with time (Connolly *et al.*, 2001). REI is size independent, thus eliminating the bias that occurs in RY and RYT when interpreting results from species of asymmetrical initial biomass (Grace *et al.*, 1992).

5.4 Results

After 27 months interspecific interactions between the two species were assumed to have fully developed, as the plants had grown sufficiently to fill the pots. The biomass yield (dead and live, including above- and below-ground material) is examined first, as an indicator of overall productivity. Live foliar yield is also examined, since this biomass component appeared to explain much of the variation observed in total biomass yield.

5.4.1 De Wit Replacement Diagrams

The de Wit Replacement diagrams for total biomass (Figure 5.5) suggest *Chionochloa rubra* produced more biomass in monoculture and mixed cultivation than *Empodisma minus* in all treatments. Actual yields are greater than expected yields for *Chionochloa rubra* in all treatments, though the difference between these decreased along the nutrient gradient. In contrast, the actual yields of *Empodisma minus* are less than expected in all treatments, though actual yields in Treatments 3 and 5 appear closer to expected yield than other treatments.

The live foliar biomass of *Empodisma minus* is similar to that of *Chionochloa rubra* in monoculture in the two high nutrient treatments (Figure 5.6). Despite this, the actual yield of both species in mixed cultivation followed the pattern observed for total biomass, with *Chionochloa rubra* overyielding, and *Empodisma minus* underyielding in all treatments. The live foliar yield of both species in monoculture decreased along the nutrient gradient, with differences in water table depth showing less of an impact upon foliar productivity in monoculture than in mixed cultivation.

5.4.2 Competition Indices

Relative yields were determined for each species total and live foliar biomass in all treatments (Table 5.5). An RY value greater than 0.5 indicates a positive net effect for a given species grown in mixed cultivation, values less than 0.5 indicating the species was negatively affected, while a RY of 0.5 indicates the species grew equally well regardless of its neighbour (Rebele, 2000). The mean RY for both species ranged from 0.24 to 0.80 for total biomass and 0.25 to 1.02 for live foliar biomass.

Empodisma minus appears to be a poor competitor, with low RY values in the presence of *Chionochloa rubra* in most treatments, except Treatments 3 and 5, where expected and actual yields were similar for both live and total biomass (RY=0.48 & 0.42 respectively). The high RY's for *Chionochloa rubra* suggests that it grows better in the presence of *Empodisma minus* than alone, except in low nutrient and water conditions where neighbour identity matters less. The RY's of the two species exhibit different patterns with regard to the nutrient and water gradients. The RY of *Chionochloa rubra* decreased as nutrient additions declined, with little influence of water table depth. In contrast, the negative affect of *Chionochloa rubra* on *Empodisma minus* was greatest in low water table depths (RY=0.24-0.27). The RY of 1.02 for *Chionochloa rubra* live foliar biomass in high water table and nutrient levels suggests it grew as well in the presence of *Empodisma minus* as alone, the two *Chionochloa* plants in mixed cultivation producing as much biomass as the four plants in the monoculture treatment. This also suggests the experiment continued sufficiently long that resources, rather than starting density, determined the observed results (Zedler *et al.*, 1990).

At first glance the RYT values >1 (Table 5.5) suggests partial resource complementarity may exist between the two species (Snaydon & Satorre, 1989). However, the RYT are not significantly greater than unity, and therefore there is no evidence for partial resource complementarity in our treatments. Plotting the RY of each species highlights the growth suppression observed in each treatment, the high RYT values being due to the high *Chionochloa rubra* RY (Figure 5.7). Thus, despite the development of apogeotropic roots by *Empodisma minus*, no evidence for resource complementarity via resource partitioning in the root zone was observed.

The mean REI in Treatments 3 and 5 are significantly greater than unity, indicating the long-term outcome of competition in these treatments is in favour of *Empodisma minus.* The non-significant REI values of the remaining treatments suggested long-term co-existence of the two species will occur in conditions other than wet, oligotrophic or mesotrophic mires (Treatments 3 & 5). This finding confirms the observation that *Chionochloa rubra* tussocks persist in montane mires, the community often described as restiad-tussocklands, due to the co-dominance of the two species.

5.4.3 Biomass Analysis

Because the two species behave differently in response to the treatments, resulting in different means and variances for the two species, the species variables were analysed separately. Both total biomass and its components (live foliar biomass, standing dead, litter and rhizomes) were analysed, as was the depth of *Empodisma minus* capillaroid root depth developed. The response of both species was compared when grown in monoculture and in binary mixtures with each other.

5.4.3.1 Effect of Initial Size

In the field, *Empodisma minus* is found in small isolated plants of a few culms on mire margins, the *Empodisma* proportion of the canopy increasing towards the mire centre (*pers. obs*.). Where the two species co-exist in the mire centre, *Empodisma minus* culms may intertwine through the taller *Chionochloa* tussocks, extending higher into the canopy than on the mire margins, while *Empodisma minus* apogeotropic roots may grow between the individual *Chionochloa* tillers. Because the intensity of competition would likely vary due to size asymmetry, *Empodisma minus* plants were put into Blocks according to initial biomass (Table 5.1). Block was incorporated into the model as a co-variate and the duration of the experiment extended to overcome this factor. Unfortunately the Block effect was still found to be significant for most biomass components (ANOVA tables in Appendix 5.3), implying the initial size of the *Empodisma minus* plants may have had an effect on final biomass production of *Chionochloa rubra*. This relationship is not linear, however, with the highest *Chionochloa rubra* live and litter biomass produced in Block 2, and the least in Block 3, which contained *Empodisma minus* plants marginally larger than Block 2. The Block effect may thus reflect the impact of environmental gradients within the tunnelhouse upon treatments at key times, which monthly randomisation of the Blocks failed to overcome.

5.4.3.2 Total and Live Foliar Biomass

The biomass data showed significant effects of species mixture and nutrient addition upon most biomass components for both species (Table 5.6). Total, live and senesced biomass is significantly higher per plant for *Chionochloa rubra* when grown in a binary mixture with *Empodisma minus.* In contrast, *Empodisma minus* productivity is higher when grown in monoculture for all biomass components. Overall, the biomass of both species increased significantly with higher nutrient additions, with a significant interaction between nutrient and species mixture occurring for all components of *Chionochloa rubra* biomass except litter production and maximum tiller height.

Water table depth and species mixture interacted significantly on the total and live biomass components of *Empodisma minus,* the effect on live biomass production underlying the effect seen on total biomass. When grown in mixture *Empodisma minus* produces less biomass, especially at low water table levels, i.e. *Chionochloa rubra* having the greatest effect in reducing *Empodisma* stature on drier substrates.

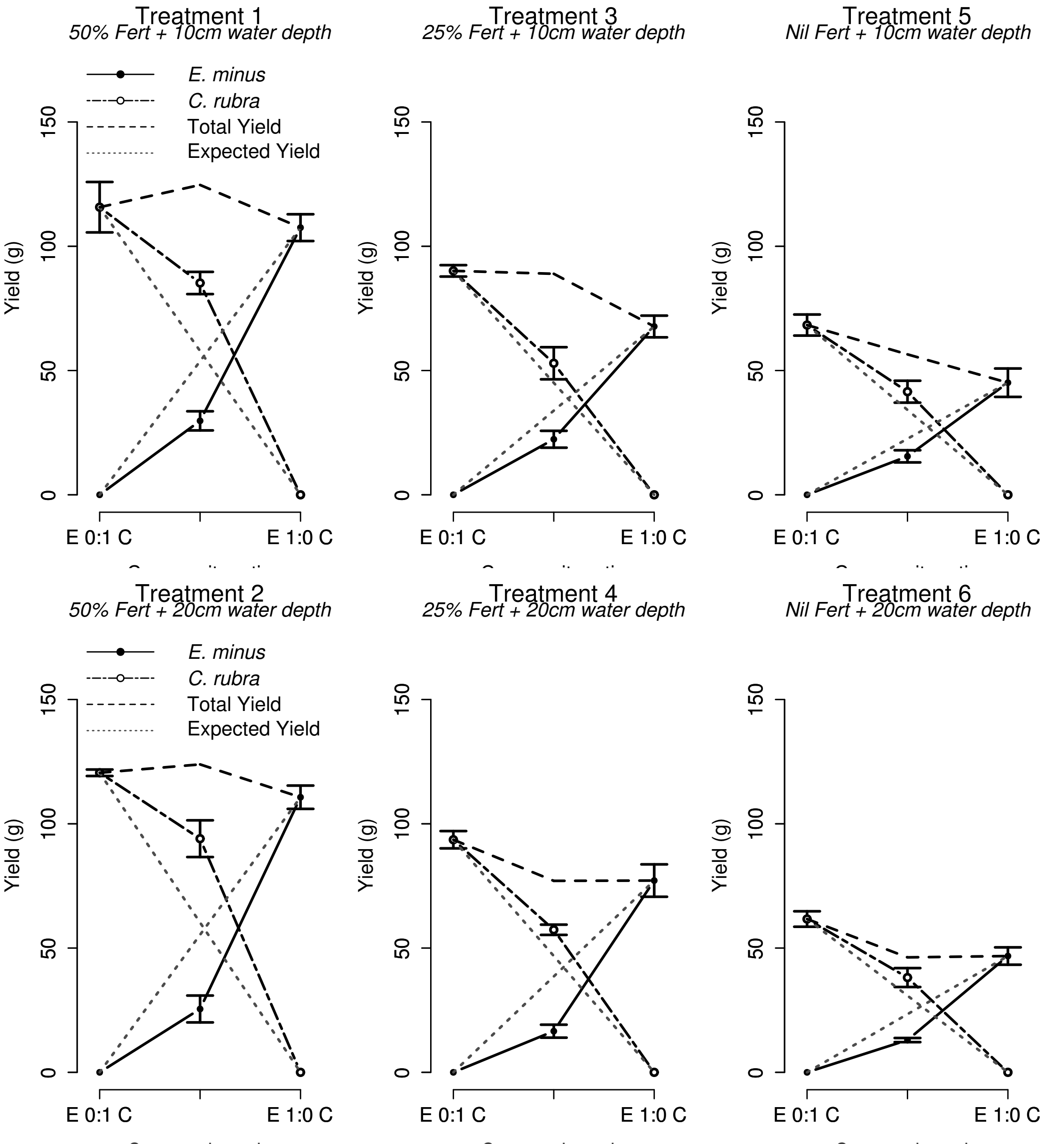


Figure 5.5: De Wit replacement series diagrams of Total Biomass Yield (dry weight per pot) for *Empodisma minus* and *Chionochloa rubra* in monoculture and binary mixtures at constant density (4 plants per pot total).

Species treatment indicated by ratio on x axis; E 0:1 C = *Chionochloa rubra* monoculture; E 0.5:0.5 C = binary mixture; E 1:0 C = *Empodisma minus* monoculture . Broken lines represent expected (theoretical) yield, dashed line represents Relative Yield Total (RYT). Means ± SE, n=5. See Table 5.3 for treatment details.

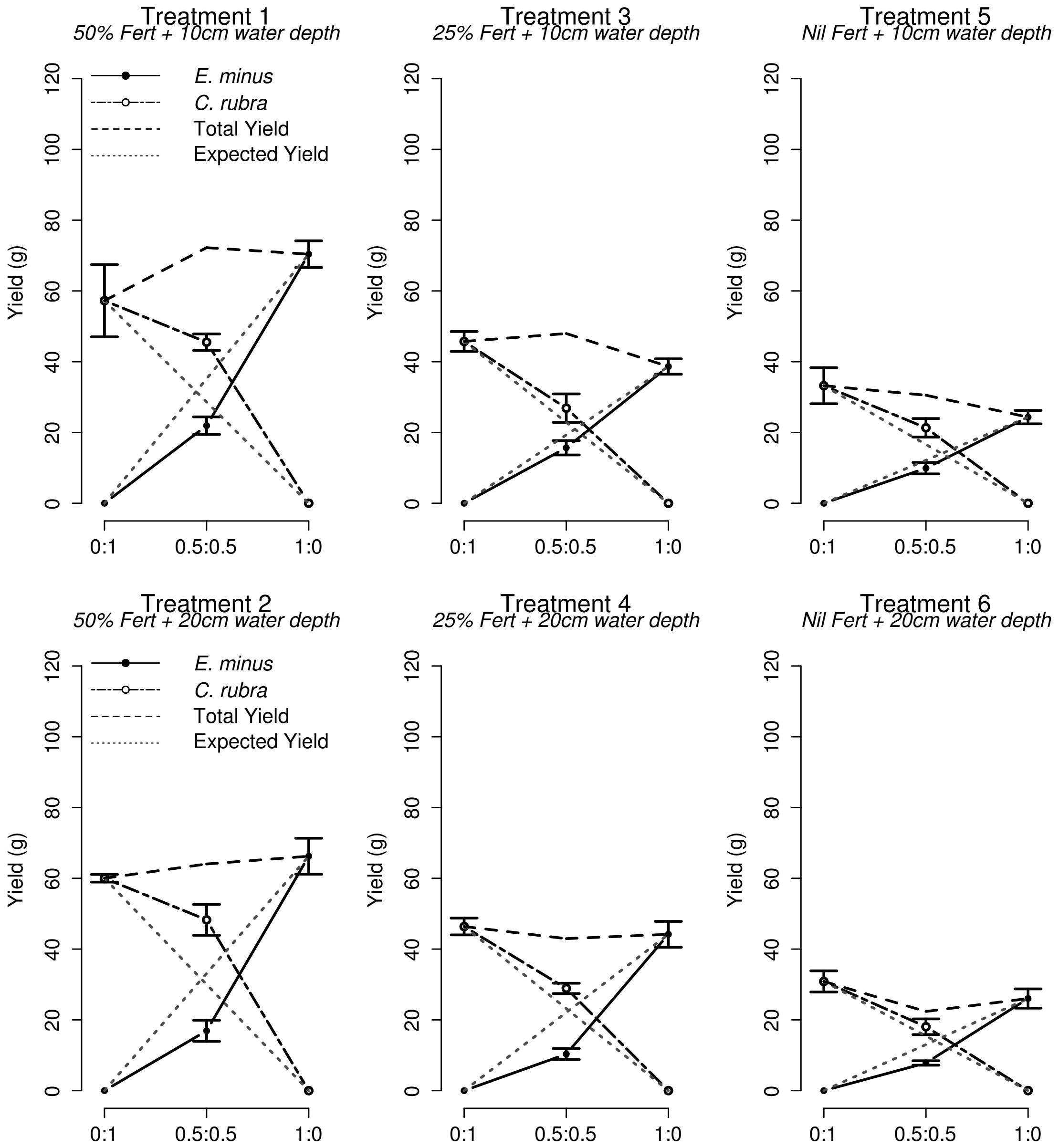


Figure 5.6: De Wit replacement series diagrams of Live Foliar Yield (dry weight per pot) for *Empodisma minus* (E) and *Chionochloa rubra* (C) in monoculture and binary mixtures at constant density (4 plants per pot total).

Species treatment indicated by ratio on x axis; E 0:1 C = *Chionochloa rubra* monoculture; E 0.5:0.5 C = binary mixture; E 1:0 C = *Empodisma minus* monoculture . Broken lines represent expected (theoretical) yield, dashed line represents Relative Yield Total (RYT). Means ± SE, n=5. See Table 5.3 for treatment details.

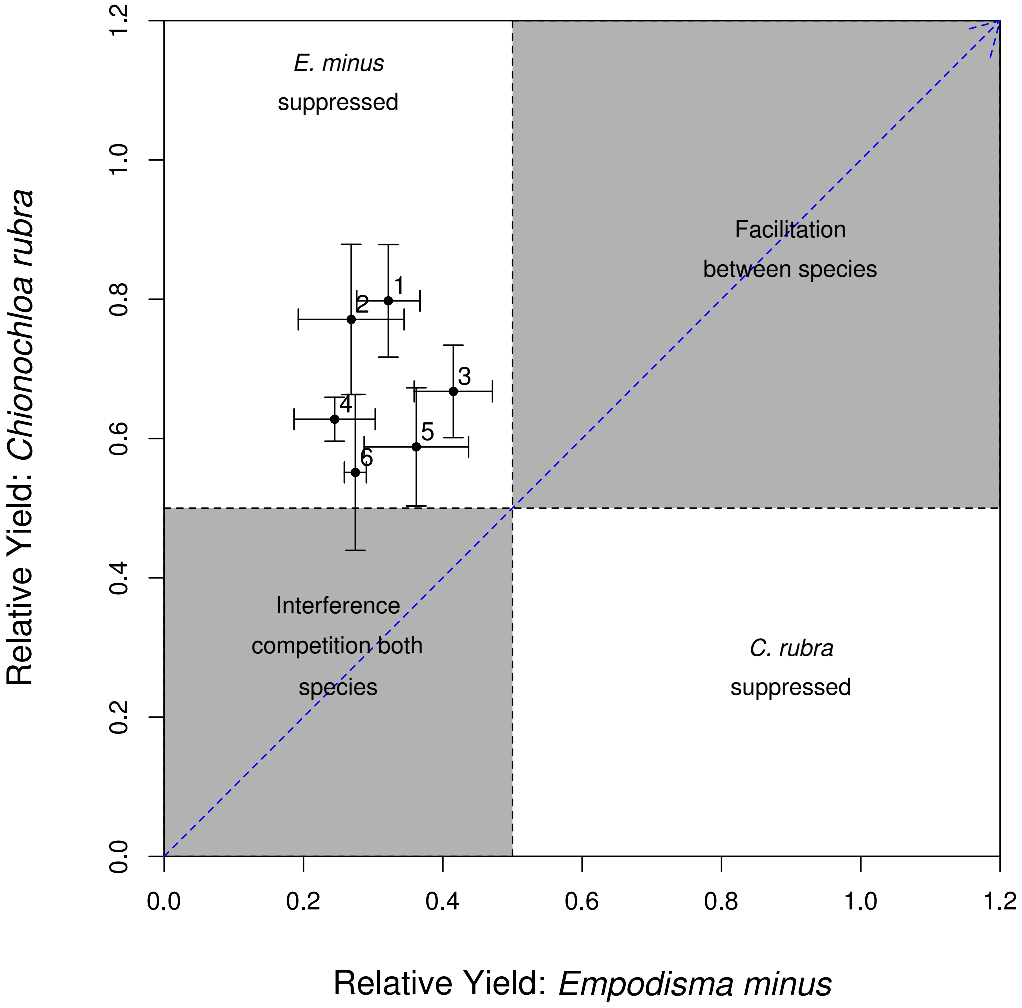


Figure 5.7: Graphic representation of Relative Yield (RY) of Total Biomass of de Wit replacement series of *Empodisma minus* and *Chionochloa rubra* in binary mixtures at equal densities (Hodges & Rapson, 2011).

Diagonal reference line denotes the areas of the graph in which *Empodisma minus* has a competitive advantage over *Chionochloa rubra* (area above line) and where *Chionochloa rubra* has a competitive advantage over *Empodisma minus* (below the line). Shaded area where RYE <0.5 and RYC <0.5 denotes where both species are suppressed in mixed cultivation. Shaded area where RYE >0.5 and RYC >0.5 denotes where both species are doing better in competition than in monoculture, indicating facilitation of both species. The area where RYE <0.5 and RYC >0.5 denotes where *Chionochloa rubra* is doing better in mixed cultivation and is suppressing *Empodisma minus*, whereas where RYE >0.5 and RYC <0.5, *Empodisma minus* is doing better in mixed cultivation and is suppressing *Chionochloa rubra*.

5.4.3.3 Capillaroid Root Growth

Empodisma capillaroid roots developed in most treatments, being absent only in the dry fen conditions of Treatment 4. Contrary to expectations, sub-surface capillaroid root weft growth peaked in Treatment 3, and was lower in the oligotrophic treatments (Treatments 5 and 6), which also contained less above-ground biomass. Water table depth had a significant effect, with greater capillaroid root weft developing at high water table levels, and greater weft development was also found in monoculture, rather than mixed species treatments. There were no significant interactions between treatments.

Apogeotropic root growth was small over the 12-month period, with a maximum height increase of 6mm, with 17% of treatments showing no height increase. As found for subsurface capillaroid root growth, water table height was found to be significant in enabling root growth and hence changes in surface microtopography, with greater height increase in high water table treatments than low water treatments. There was also a significant interaction between species composition and nutrient levels. While apogeotropic root growth significantly increased with each increasing nutrient level in monoculture treatments, this effect was less pronounced in mixed species treatments, where high and medium nutrient additions resulted in similar apogeotropic root growth to that found in medium nutrient additions in monoculture treatments.

5.4.3.4 Litter Production and Standing Dead Biomass

Fallen litter was collected from most *Chionochloa rubra* plants over the 27-month experiment, but insufficient litter was collected from *Empodisma minus* to analyse (8 litter samples only). The lack of data suggests insufficient time elapsed for litter production by *Empodisma minus* in the experiment, the senesced material being retained within the canopy. On average, each *Chionochloa* plant created 0.89g of litter over the course of the experiment. Rates of litter production by *Chionochloa rubra* appear to be constant across the treatments, being independent of nutrient availability, water table depth or species mixture.

The senesced canopy material partially reflected the initial biomass of the plants, which had senesced over the 26 months of the experiment. The amount of dead canopy material in both species was also sensitive to species mixture and nutrient additions, reflecting similar patterns in the live biomass from which the material originated. There was a significant interaction between these factors for *Chionochloa rubra,* with more senesced material produced in mixture and at higher nutrient levels, again reflecting the higher live biomass produced in these treatments.

5.4.3.5 Canopy Height

Analysis of the canopy height of each species shows differences in response to the treatments. Both species respond significantly to nutrient additions ($p<0.001$), with the tallest canopy occurring in the highest nutrient treatments. The most pronounced effect of the treatments occurs in the *Empodisma minus* canopy, where there is a significant interaction between nutrients, water table depth and species mixture upon height. In the *Chionochloa rubra* canopy there is a significant Block effect, which suggests the initial size of the *Empodisma minus* plants affected the final *Chionochloa* canopy height ($p<0.05$). However, there was no significant Block effect for *Empodisma minus*.

5.4.3.6 Biomass N:P ratios

While live foliar N contents are low (<0.74% dry wt.), tissue P levels are high (0.05-0.18% dry wt.), indicating P levels may have exceeded growth-limiting thresholds in some treatments (Treatments 1, 4 & 6 in mixed species cultivation) (Figure 5.8). Clarkson *et al.* (2002) note that these growth-limiting thresholds are indicative only, with variability caused by the nutrient requirements of different species, and by seasonal changes in tissue nutrient content. Since these data are to be used for internal comparison between treatments only, I proceeded to interpret the data, though recognising these findings should be interpreted with some caution.

The low N:P ratios for the *Empodisma minus* foliage (Table 5.7) suggest that growth in most treatments is N limited, although as noted above, P exceeded the growth limiting thresholds in Treatments 1, 4 and 6 in mixed species cultivation. The high P content (0.30-0.52% P) and low N:P ratios (range=0.75–1.60) in the rhizome biomass suggest that *Empodisma minus* rhizomes are utilised as an effective storage organ for P, a common limiting nutrient in New Zealand restiad mires (Chapter 3).

Senesced foliage contains a slightly higher P content (0.05-0.27% dry wt.) than live foliage (0.05-0.21% dry wt.), in contrast to the N content, which is lower in senesced (0.30-0.47% dry wt.) than live foliage (0.39-0.74% dry wt.). These findings may indicate that *Empodisma minus* relocates limiting nutrients from its foliage prior to senescence, or may reflect the lower nutrient content of the biomass originally relocated from Silica Rapids mire, which senesced over the course of the experiment.

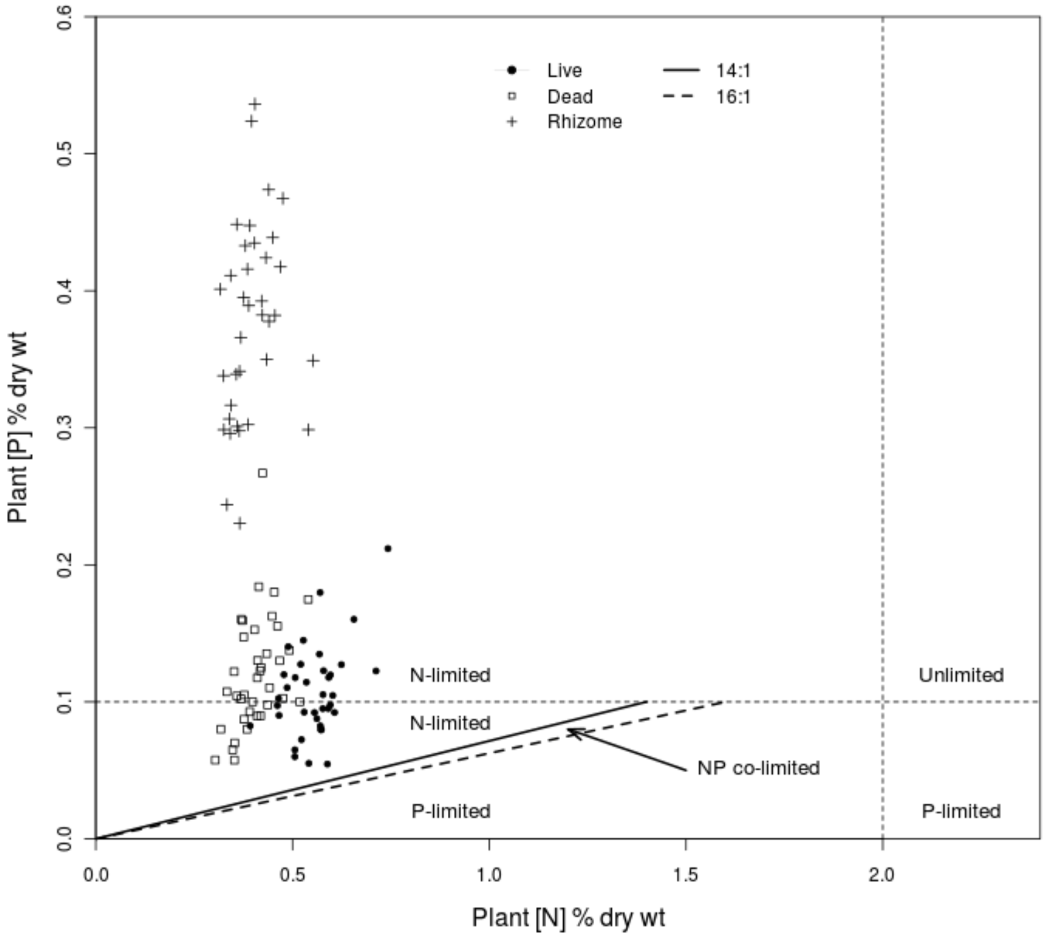


Figure 5.8: Tissue N:P ratios in live and dead foliage and rhizomes of E*mpodisma minus* in de Wit replacement experiment illustrating phosphorus enrichment in most foliage, and high phosphorus content of rhizomes.

The N:P = 14:1 and N:P = 16:1 lines demarcate nitrogen and phosphorus limitation, and can be used where N<2% and P<0.1% (Clarkson et al., 2002). Growth is nitrogen-limited if N<2% and P%>0.1%. Biomass containing P>0.1% indicate phosphorus concentrations exceeded growth limiting threshold.

Table 5.5: Relative Yield (RY), Relative Yield Total (RYT) and Relative Efficiency Index (REI) of live biomass at final harvest of de Wit replacement series of *Chionochloa rubra* and *Empodisma minus* in binary mixtures at equal densities.

Values are mean ± SE. RY values significantly different from 0.5, RYT values significantly different from 1, or REI values significantly different from 1 are indicated by * (t-test, p<0.05). See Table 5.3 for treatment details.

	Live biomass			Total biomass			REI
Treatment	$RY_{Chionochloa}$	$RY_{Empodisma}$	RYT	$RY_{Chionochloa}$	$RY_{Empodisma}$	RYT	
1	1.02 ±0.29	*0.34 ±0.05	1.36 ±0.31	*0.80 ±0.08	*0.32 ±0.05	1.12 ±0.12	0.61±0.41
2	0.76 ±0.11	*0.25 ±0.06	1.01 ±0.15	0.77 ±0.11	*0.27 ±0.08	1.04 ±0.16	-0.01±0.15
3	0.63 ±0.11	0.48 ±0.08	1.11 ±0.14	0.67 ±0.07	0.42 ±0.06	1.08 ±0.08	*0.69±0.14
4	*0.69 ±0.02	*0.25 ±0.07	0.93 ±0.07	*0.63 ±0.03	*0.24 ±0.06	0.87 ±0.05	-0.15±0.47
5	0.69 ±0.12	0.37 ±0.09	1.06 ±0.18	0.59 ±0.08	0.36 ±0.07	0.95 ±0.14	*0.47±0.15
6	0.49 ±0.09	*0.27 ±0.04	0.77 ±0.11	0.55 ±0.11	*0.27 ±0.02	0.83 ±0.12	0.84±0.46
Mean	*0.71 ±0.06	*0.33 ±0.03	1.04 ±0.07	*0.67 ±0.04	*0.31 ±0.02	0.98 ±0.05	0.41±0.30

Table 5.6: Summary of Analysis of Variance for *Empodisma minus* and *Chionochloa rubra* at final harvest. Significant effects and interactions of treatments are indicated by ***(p<0.001), ** (p<0.01) and * (p<0.05). $^{\Upsilon}$Tests for significance on *Empodisma minus* root weft measures carried out on untransformed data using multivariate analysis of variance in PERMANOVA (Anderson, 2001). See Table 5.3 for treatment details.

Source	**Total Biomass**	**Live Foliage**	**Standing Dead**	**Rhizome Biomass**	**Root Weft Depth**$^{\Upsilon}$	**Micro-topography**$^{\Upsilon}$	**Litter Production**	**Maximum Height**
Empodisma minus								
Block	***	**	***	**			N/A	ns
Monoculture vs. Mixture with *C. rubra* (M)	***	***	***	***	***	**		***
Nutrients (N)	***	***	**	***	ns	**		***
Water Table (W)	ns	*	ns	ns	*	**		ns
M x N	ns	ns	ns	ns	ns	**		ns
M x W	*	*	ns	ns	ns	ns		ns
N x W	ns	ns	ns	ns	ns	ns		ns
M*N*W	ns	ns	ns	ns	ns	ns		**
Chionochloa rubra								
Block	ns	***	*	N/A	N/A	N/A	***	*
Monoculture vs. Mixture with *E. minus* (M)	***	***	***				ns	ns
Nutrients (N)	***	***	***				ns	***
Water Table (W)	ns	ns	ns				ns	ns
M x N	*	*	*				ns	ns
Other interactions	ns	ns	ns				ns	ns

Table 5.7: Nitrogen: Phosphorus ratios for live and dead *Empodisma* biomass in monoculture and binary mixture for each water table and nutrient treatment.

Values are means with standard deviations. Different small letters indicate significant differences ($P<0.05$) among water and nutrient treatments in same species ratio (monoculture or mixture). See Table 5.3 for treatment details.

Treatment	**N:P ratio Empodisma minus Biomass**					
	Live foliage (monoculture)	Live foliage (mixture)	Dead foliage (monoculture)	Dead foliage (mixture)	Rhizomes (monoculture)	Rhizomes (mixture)
1	5.1 ±1.3ab	3.4 ±0.2a	2.8 ±0.6a	3.7 ±0.2a	1.3 ±0.5a	1.3 ±0.2a
2	6.8 ±0.9ab	5.5 ±0.4a	4.0 ±0.9ab	3.8 ±0.6a	1.0 ±0.1a	1.0 ±0.2a
3	4.3 ±0.8a	5.8 ±1.3a	3.2 ±0.3a	2.6 ±0.5a	1.0 ±0.2a	1.1 ±0.1a
4	5.4 ±0.7ab	4.9 ±0.1a	3.7 ±0.6a	3.2 ±0.9a	1.2 ±0.2a	1.0 ±0.3a
5	7.6 ±3.0ab	5.5 ±1.4a	4.9 ±0.4b	3.6 ±1.8a	1.0 ±0.2a	1.1 ±0.4a
6	8.5 ±1.3b	4.7 ±1.0a	5.5 ±0.6b	3.2 ±0.7a	1.0 ±0.2a	1.0 ±0.1a

5.5 Discussion

5.5.1 Engineering the fen-bog transition in restiad mires

Hodges & Rapson (2010) describe the expected traits of a mire engineer, and the evidence required to support the actions of an engineer above the allogenic forces at play. These traits include the ability to increase peat moisture levels, scavenge scarce nutrients, retain these within the biomass, and produce slowly decomposing litter. The mire engineer must also be present both sides of the FBT, preferably being more competitive in the engineered environment. I observed changes in *Empodisma minus* biomass production across the FBT, which provide some support for our hypothesis that *Empodisma minus* engineers the FBT in restiad bogs, and is more competitive in the engineered environment.

Results here suggest that capillaroid root growth in montane restiad transitional fens confers an advantage to *Empodisma minus*, and would likely result in greater accumulation of peat pre-cursors, leading ultimately to ombrotrophic conditions, i.e. the fen-bog transition. The presence of capillaroid roots gave a marked benefit in transitional fen conditions (Treatment 3), as seen in increased live foliar biomass, and the higher likelihood of long-term displacement of co-existing fen species. The competitive advantage gained by *Empodisma minus* is likely due to the abundant capillaroid roots enabling a greater share of limiting nutrients. Capillaroid root weft growth to 75mm deep in this treatment would allow both surface interception of nutrient additions via stem flow, and greater access to substrate nutrients. As ombrotrophy proceeds, the significant Relative Efficiency indices also suggest that *Empodisma minus* will dominate the wet oligotrophic conditions engineered during the FBT.

5.5.1.1 Why is the FBT important, and did we cross it?

The FBT represents an important step during raised mire succession, as it is the relatively rapid transition from a vascular plant dominated community with well decomposed, mineral rich peat of an intermediate pH, to an acid, nutrient poor, less decomposed peat, dominated by *Sphagnum* and vascular species tolerant of the conditions created (Granath *et al.,* 2010). After the FBT the surface peat and vegetation community are increasingly deprived of groundwater interaction, and the relative proportion of ombrotrophic mire species increases with time (van Breeman, 1995; Juttonen *et al.*, 2005). As little as 50cm of accumulated peat may result in the separation of an oligotrophic vegetation community from base rich groundwater flows (Siegel & Glaser, 1987). Changes in species composition are accompanied by an increase in surface microtopography and spatial variation (Lepällä *et al.*, 2008). In addition, the change in dominant plant community results in alterations to key ecosystem functions, such as biogeochemical cycles and species interactions (Scheffer *et al.*, 2001; Lepällä *et al.*, 2008), while declining substrate quality alters the diversity of microbial populations and resulting rates of decomposition and methanogenesis (Juttonen *et al.*, 2005; Merila *et al.*, 2006; Jassey *et al.*, 2011).

The fen-bog transition likely occurred in our experiment between our medium and low nutrient treatments. The significant Relative Efficiency indices obtained in Treatments 3 and 5 suggest that long-term replacement of *Chionochloa rubra* would occur in mesotrophic and oligotrophic conditions, where water tables remained high (REI=0.69* & 0.47** respectively, Table 5.5). These findings support the successional model of Clarkson *et al.* (2004a) for northern restiad fens, where rapid displacement of minerotrophic sedge species by *Empodisma robustum* is suggested, soon after *Empodisma robustum* establishment. Non-significant REI indices suggest that species co-existence is likely in minerotrophic or dry oligotrophic conditions elsewhere along the mire gradient.

Although the lower N:P ratios of some treatments suggests the experimental gradient incorporated the mesotrophic conditions which occur prior to the FBT (Figure 5.8), this is not to suggest that our growing conditions in any way approximated those of New Zealand montane mires. Growth in restiad species is seasonal, with growth initiating during the periods of high rainfall, and ceasing during the hot, dry summer months (Stock *et al.*, 1987; Meney *et al.,* 1990b; Meney & Pate, 1999). The current experimental design differed, in that a constant water table was maintained, with nutrients added in regular pulses, to excess in our high nutrient treatments. In contrast, many New Zealand restiad mires form in areas with summer rainfall deficits (McGlone, 2009), and experience variable water table levels (Chapter 6). The low constant water table and use of milled peat as a substrate, likely resulted in higher P-availability in the decomposing peat substrate, compared to an intact mire. In addition, nutrient inputs into upland sites are very low, as these sites are far from the coast. Holdsworth & Mark (1990) found nitrate- and ammonium-N levels in precipitation falling on Otago tussocklands were below the levels of detection, which the nutrient treatments certainly exceeded due to the use of groundwater, rather than distilled water or rainwater to irrigate the artificial wetland. Nutrient additions from both decomposing peat and pot irrigation were not quantified during the studies, and further experiments should avoid nutrient additions from these sources, utilising a sand substrate and harvested rainfall or distilled water for irrigation.

Empodisma minus biomass yields doubled in the high nutrient treatments, compared with the addition of distilled water only in the low nutrient treatments. The capacity of *Empodisma minus* to respond positively to high nutrient loads in excess of those encountered in natural systems has been previously noted (Chapter 3). When supplied with agricultural level nutrient inputs, rapid biomass accumulation appears to be a common feature of the Restionaceae (Bell *et al.*, 2000), and unlike some cluster root bearing taxa (Shane *et al.*, 2004), the Restionaceae do not appear to suffer from P-toxicity at high nutrient levels. This may be due to greater plasticity in P uptake and management, given the pulsed nutrient supply in restiad habitats, due to frequent disturbance from fires (Craine, 2009).

5.5.1.2 Capillaroid root growth as a nutrient acquisition strategy along the fen-bog gradient

Cluster roots are an important adaptation to nutrient limitation, and species with cluster roots are often common pioneers during primary or secondary successional processes (Skene, 1998), including restiad bog formation. Here, the capillaroid root weft development in *Empodisma minus* is the functional equivalent of the nutrient scavenging, slowly decomposing *Sphagnum* carpet found in Northern Hemisphere mires (Agnew *et al.*, 1993; Van Breeman, 1995; Charman, 2002; Clarkson *et al.*, 2009). Most of the current knowledge of cluster root ecophysiology has been obtained from studies on proteoid and more recently, dauciform (Shane *et al.*, 2005) and sandsheath roots (e.g. Shane *et al.*, 2009; 2010; 2011). It is assumed that the growth and functioning of capillaroid roots are similar to proteoid roots (Lambers *et al.*, 2006), producing large volumes of carboxylates which release P from organic sources, effectively “mining” the soil (Lambers *et al.*, 2011). Due to the paucity of literature on capillaroid root growth and function, the wider cluster root literature will also be included for comparison with our findings.

We observed capillaroid root growth on the pot surface within 6 months of the experiment starting. The developing root weft was most noticeable in *Empodisma minus* monocultures with high nutrient treatments, which contained greater *Empodisma minus* canopy biomass than the mixed cultivation treatments. At harvest (26 months after initiation of experiment), sub-surface capillaroid root growth was largely restricted to the peat immediately surrounding *Empodisma minus* rhizomes, and in hindsight I conclude further time was required before an extensive root weft could develop throughout the pot. Measurements of root weft depth at harvest confirmed that capillaroid roots proliferated in monocultures of *Empodisma minus*, rather than when grown in mixed cultivation. Although grasses generally possess shallow, fibrous root systems, *Chionochloa rubra* does not possess cluster roots, and likely accesses nutrients from deeper in the peat profile than *Empodisma minus*, in addition to the decomposing litter layer (Burrows, 1963). Little interspecific competition for ombrotrophic nutrients would then result in less capillaroid root formation by *Empodisma minus.*

The dense *Empodisma robustum* canopy in northern restiad mires reduces evapotranspiration (Campbell *et al.,* 1995; Campbell & Williamson, 1997), which may encourage the growth of capillaroid roots. Water is necessary for cluster root formation, and frequent watering has been found to be optimal for cluster root function (Siddiqi & Carolin, 1976). Cluster root formation in Mediterranean climates is largely confined to the wet season (Lamont, 1976; Lamont & Bergh, 1991; Shane *et al.*, 2009), though they may be induced in summer by the application of water (Lamont, 1976; 1986). Lamont (1986) also notes that proteoid root density is highest at 1-2 times field capacity in *Hakea* species, and that cluster roots readily form in pockets of wet soil. *Banksia prionotes* has been found to extend periods of cluster root growth and nutrient acquisition via hydraulic lift, deeper lateral roots accessing deep soil water sources with which the smaller roots are supplied (Burgess *et al.*, 2000; Lambers *et al.*, 2006). Campbell *et al.* (1995) noted that while the *Empodisma minus* canopy increased soil moisture retention in Queensland marshlands, dry conditions checked capillaroid root growth during the summer months. The “wet desert” effect (Campbell & Williamson, 1997) employed by *Empodisma robustum* in northern restiad mires enables the species to facilitate cluster root growth by increasing the moisture levels of surface soil horizons, in addition to the capillary effect of the root weft itself, though the mechanism appears to operate within climatic restraints (Campbell *et al.,* 1995). While soils high in organic matter can retain too much moisture during the wet season to allow cluster root initiation in some species (Donoso-Nanculao *et al.,* 2010), the apogeotropism of *Empodisma* roots offers an advantage in these conditions (Sorrell *et al.*, 2000).

Agnew *et al.* (1993) suggest capillaroid roots enable *Empodisma* species to intercept nutrients from precipitation, other species gaining nutrients from deeper rooting depths (Clarkson *et al.*, 2005; 2009). Thus, it was expected that capillaroid root formation in *Empodisma minus* would be inversely related to nutrient additions, with root density highest in oligotrophic conditions. Instead, this research suggests capillaroid growth in *Empodisma minus* may be sub-optimal in the oligotrophic conditions typical of ombrotrophic bogs, with higher capillaroid root growth in higher nutrient, transitional fens. An increase in cluster root production in response to small increases in P supply, such as observed here, has been noted in other species (Shane *et al.*, 2008; Power *et al.*, 2010), and root proliferation in response to increased nutrient supply, is a useful strategy for cluster root bearing taxa (Raghothma, 1999). This is especially important given the high cost of investment (Lambers *et al.*, 2008; 2009), which precludes high investment in leaf growth, and hence cluster root association with slow growing species in low-P environments (Lambers *et al.,* 2011).

In this experiment it was observed that *Empodisma minus* initiated apogeotropic root growth in response to a localised zone of high nutrient availability, with initial root expansion occurring on the pot surface, into which the nutrient spray was directed via stemflow. The preferential growth of proteoid roots into nutrient rich soil layers was originally observed by Purnell (1960), and the litter layer as the site of highest proteoid and dauciform root proliferation has been since confirmed (Jeffrey, 1967; Lamont, 1974; Lamont *et al.*, 1984; Watts & Evans, 1999; Playsted *et al.*, 2006), though cluster roots may also be found at depth, depending upon P availability (Lambers *et al.*, 2011). Root proliferation occurs in response to greater phosphate release from the organic matter (Li *et al.*, 2010), which cluster roots mine for P (Lambers *et al.,* 2011). *Empodisma minus* apogeotropic root volume would thus be potentially greater in fens, where litter quality is higher. The rapid proliferation and accumulation of decay resistant apogeotropic roots in *Empodisma minus* dominated fens, possibly explaining the rapid transition observed from sedge fen to pioneer restiad bog (McGlone & Bathgate, 1983).

Fewer capillaroid roots were found in mixed species treatments in our experiment, in contrast to the findings of Clarkson *et al.* (2005; 2009) in northern restiad bogs. The greater root weft development in the *Empodisma minus* monoculture treatments may have resulted from greater intra-specific competition for nutrients in the same soil volume or zone. Dense cluster roots, with abundant root hairs, effectively exploit the surrounding soil volume, depleting soil P (Marschner *et al.*, 2002). The depletion of soil resources may cause the individual plants to invest more heavily in capillaroid root growth, so that rather than capillaroid roots suggesting partial resource complementarity (Clarkson *et al.*, 2009), capillaroid root growth and accumulation may result from intraspecific competition among the long-lived *Empodisma* clones (Sharp, 1995) for ombrotrophic nutrient sources. Alternatively, monoculture communities might reduce the penalty of slower growth, and hence reduced competitiveness, which results from the high carbon cost of cluster root investment (Lambers *et al.,* 2011) allowing further investment in cluster root production.

While the possession of scarce capillaroid roots did not appear to offer *Empodisma minus* a competitive advantage over *Chionochloa rubra*, this is not to say that a competitive advantage would not have occurred, had the experiment continued for sufficient time to allow a more extensive capillaroid root weft to form. Patterns in root weft development can be confounded by the effect of plant size or maturity upon root development (Lamont *et al.*, 1984), and so "it is sometimes difficult to distinguish a size/maturity effect from the direct effect of the treatment on root cluster production" (Lamont, 2003, p. 10). By utilising rooted cuttings we attempted to avoid ontological effects, however, the significant Block effect for root weft depth suggests initial plant size influenced root weft development. In hindsight, the use of similar sized rooted cuttings or seedlings, in conjunction with a longer experimental period, might have allowed these effects to be avoided.

The relative yield indices suggest *Chionochloa rubra* growth had a negative impact upon *Empodisma minus* in all treatments, although *Empodisma minus* live biomass was close to expected yield in Treatment 3 (wet fen conditions). However, while *Chionochloa rubra* biomass in binary mixtures decreased significantly with declining nutrient additions, the decline in *Empodisma minus* biomass was less marked. In nutrient limited environments the ability to persist may determine the competitive outcome between species (Grime, 1979), and again a long-term experiment is required to assess this. This research does suggest, however, that it is not high water table levels that cause the reduced stature of *Chionochloa rubra* observed after the FBT, but rather, low nutrient availability. These findings confirm the observation that *Chionochloa rubra* appears often confined to the minerotrophic margins of restiad mires (Dobson 1975; Rapson *et al.*, 2006), where nutrient availability is higher.

Had sufficient time elapsed for a continuous *Empodisma minus* root weft to develop within the pots, further engineering mechanisms behind the FBT, (e.g. high water holding capacity of *Empodisma minus* root weft), might have been observed. *Empodisma* capillaroid root weft is the functional equivalent of *Sphagnum* stems (Agnew *et al.*, 1993), retaining 15 times its own weight in water (Campbell, 1981). Van Breeman (1995) suggests the capillary effect assists *Sphagnum* species in creating an acidic, anoxic environment, reducing the competitiveness of co-occurring vascular species. Engineering the FBT would require considerably more time than was available in a short-term greenhouse experiment, however, the use of peat monoliths including intact root weft, rhizomes and above-ground biomass, rather than initiating experiments with small plants, might enable closer study of the engineering mechanisms to be undertaken. Alternatively, long-term field experiments such as those employed to study ecosystem engineering elsewhere (Mitchell *et al.*, 2007), could be used.

5.5.1.3 Litter production and resource conservation along the fen-bog gradient

Long-lived leaves and the production of low nutrient litter are traits typical of species in low productivity environments, (Chapin, 1980; Craine, 2009) and a key component of autogenic models of bog formation (van Breeman, 1995). This experiment confirms that *Empodisma minus* retains its senesced foliage longer than *Chionochloa rubra*, with significant differences in litter production between the two species, and *Empodisma minus* creating almost no litter during the 27-month experiment. In established northern lowland restiad mires, senesced *Empodisma* foliage is retained within the canopy, reducing evapotranspiration (Campbell & Williamson, 1997) and channelling ombrotrophic nutrients to the capillaroid roots (Agnew *et al.*, 1993). Restiad species retain senesced litter (Witkowski, 1989), and undisturbed northern restiad mire canopies often contain >50% senesced material (Clarkson *et al.*, 2009). The senesced canopy litter falls to the mire surface as small fragments and dust, up through which the capillaroid roots grow. By targeting capillaroid root growth in the recently deposited litter, which is proportionately high in P in mesotrophic conditions, *Empodisma minus* is able to maximise P acquisition. Alternatively, an as yet unknown organic matter constituent may be responsible for stimulating capillaroid root growth in the litter layer (Dinkelaker *et al.*, 1995).

The N:P ratios of senesced foliage were less than those of live foliar biomass in all treatments, suggesting some nutrient resorption may have occurred. Restiad species have an asynchronous growth habit, and a high degree of N absorption from senescing foliage is essential to overcome the nutrient shortage imposed by culm extension during periods of root inactivity (Stock *et al.,* 1987). The low N:P ratios in the rhizome biomass also suggests *Empodisma minus* conserves and recycles some nutrients, utilising underground rhizomes as storage devices, as previously postulated (Hodges & Rapson, 2010). Craine (2009) suggested that species typical of low nutrient environments produce inherently low quality litters, but also suggested there is little evidence of species altering litter quality in response to changing nutrient availability. Thus, litter nutrient pools reflect the composition of the vegetation community, with changes in community composition, and hence litter quality, potentially altering successional trajectories (Berendse, 1998; Mitchell *et al.*, 2007) and other ecosystem functions (Lepällä *et al.*, 2008). Further work is required to determine the relative importance of *Empodisma minus* litter quality, quantity and decomposition rates to the FBT, including the calculation of nutrient resorption efficiency and proficiency as better measures of nutrient conservation and limitation (Sorrell *et al.*, 2011).

5.5.1.4 Was the de Wit approach useful?

The advantage of greenhouse based microcosm studies, such as this experiment, lies in the high degree of experimental control, repeatability and precision allowed (de Wit, 1960; Harper, 1983). This enables the effects of competition to be explored, with other variables held constant. While it is not possible to separate the effects of ecosystem engineering by *Empodisma minus* entirely from the effects of climate and hydrology, the de Wit experiment allowed the autogenic mechanisms suggested to underlie the FBT to be examined. Space, time and money place limits upon the size and complexity of experiment designs, and therefore the nature of the factors examined, however, the de Wit experiment allowed the key traits of the two species to be examined, providing initial evidence for ecosystem engineering, and identifying future research needs.

This experiment also highlights the importance of examining multiple traits and indices when utilising replacement series experiments. The de Wit indices used in this research are based entirely on above-ground biomass data, whereas the engineering process is assumed to occur via the capillaroid root weft, which was not directly examined by any of the indices. The use of an alternative media, allowing separation of root and media during harvest, would allow the RY of below-ground productivity to be measured, since the separation of fine capillaroid roots and peat results in large errors (Sharp, 1995). This would then spread further light on the assumption that the outcomes suggested by the above-ground foliage were linked to capillaroid root responses below-ground.

P availability in the de Wit experiment was likely raised by the use of harvested peat, groundwater rather than rainwater, a lack of water table variability, and the warmer greenhouse environment. These factors likely contributed to increase decomposition rates of the peat substrate, increasing P availability, and hence N-limited, rather than the P-limited growth typical of New Zealand restiad mires (Clarkson *et al.*, 2002). Increased P availability inhibits capillaroid root formation in *Empodisma robustum* (pers. Comm. Bev Clarkson), and may have influenced our results. A field-based experiment would allow allogenic factors to be kept intact (e.g. hydrological regime, climate), but decrease experimental control, repeatability and precision. Future de Wit experiments could control nutrient availability by utilising sand as a substrate and harvested rainwater as a water source, while reproducing the water table variability of an intact mire with periodic inundations. Seasonal variability in rainfall chemistry and nutrient inputs (Harvey & Clarkson, 1988) could also be incorporated into the design, with higher P and N inputs in summer than winter.

5.6 Conclusion

Higher *Empodisma minus* biomass productivity and capiilaroid root growth in conditions similar to the starting point of the FBT provides preliminary evidence for *Empodisma minus* as the ecosystem engineer of montane restiad mires. While *Chionochloa rubra* is a stronger competitor than *Empodisma minus* in minerotrophic and in drier conditions, where nutrient levels approximate those of a wet transitional fen, *Empodisma's* higher relative growth rate enables it to outcompete the tussock (Table 5.5).

Extensive capillaroid root growth above the peat surface (in response to nutrient additions), and at depth, occurs in greater volumes in these conditions. The accumulation of decay resistant roots as an extensive root weft may result from the wet, anoxic substrate inhibiting the decomposer population, however, it is likely that exudates from the capillaroid roots also influence decomposition processes. Regardless, it appears that the conditions necessary for engineering the fen-bog transition occur in mesotrophic restiad fens, and that *Empodisma minus* is competitive in the engineered environment.

Resorption and relocation of limiting nutrients from senescing foliage is suggested by these findings, and further research is also required to determine the degree and importance of nutrient conservation to *Empodisma minus* growth and expansion during the FBT. Given the complex relationship between the dense, moisture retentive *Empodisma minus* canopy, and the apogeotropic root growth, the relationship between the two needs to be further explored, with the relative importance of litter, leachate and stemflow directed precipitation as nutrient sources determined. In addition, the process by which *Empodisma* capillaroid roots "mine" the soil requires investigation, as does this process in other capillaroid root bearing Restionaceae, especially since, like *Sphagnum*, *Empodisma minus* appears to engineer the FBT by "attacking its competitors, literally, at the root" (van Breeman, 1995, p. 273).

Chapter 6: Litter decomposition and nutrient release in a montane wire rush-red tussock mire.

The boardwalk across Silica Rapids Mire, Tongariro National Park, June 2007.

A version of this chapter has been presented at the 36th Annual Conference of the South African Association of Botanists (11-15 January 2010, Potchefstroom).

6.1 Abstract

During succession in New Zealand restiad mires, organic matter accumulation and a decrease in nutrient mineralisation leads to fen species with fast growth rates and high biomass loss rates being replaced by bog species with low growth rates and low biomass loss rates. The nutrient content and decomposition rate of foliar and root litter from a graminoid abundant in minerotrophic fens *Chionochloa rubra*, and the restiad *Empodisma minus* was measured in a montane restiad fen over a 12 month period in Tongariro National Park, New Zealand, using the litterbag method. Both *Empodisma minus* and *Chionochloa rubra* produce low nutrient, slowly decomposing foliar litters. Mass losses were lowest from *Empodisma minus* capillaroid roots, which contain high fibre, and less P, K, and cellulose than *Chionochloa rubra* below-ground biomass. Mass loss and nutrient release of N and P differed significantly between mire communities, but there was no linear correlation between decomposition and the environmental variables measured. P-limitation in *Empodisma minus* foliar litter increased towards the mire centre, as available-P in the substrate declined. While a large component of total litter inputs in transitional restiad fens may be comprised of senesced *Empodisma minus* culms, the slower decay of *Empodisma minus* capillaroid roots suggest these contribute an increasing proportion of the accumulating organic matter after 12 months. Conversely, the majority of *Chionochloa rubra* peat additions after 12 months may originate from its senesced tillers, with greater decay rates observed for its root and tussock bases.

6.1.1 Introduction

6.1.1.1 Litter Decomposition in Mires

Mires are important ecosystems due to among other things, the role they play in accumulating carbon, in the form of peat. Peat deposits form when the rate of deposition of dead plant material produced by net primary production exceeds the rate of decomposition (Clymo 1983). While the accumulation of soil organic matter is universal in terrestrial habitats, it is the magnitude of the imbalance between productivity and decomposition that is unique to mires (Bragazza *et al.*, 2008). In ombrotrophic mires, or bogs, plant productivity depends largely upon internal nutrient cycling, as the depth of the peat deposited separates the growing surface of the mire from interaction with the underlying mineral soil.

Litter decomposition and nutrient cycling rates are variable, and affected by environmental factors such as climate (Meentmeyer, 1978; Bragazza *et al.*, 2008), soil moisture and temperature (Hobbie, 1996; Moore *et al.*, 2008), the composition of the microbial population (Lavelle *et al.*, 2006), and leaf traits such as leaf toughness, N, lignin, secondary compounds, C:N and N:lignin ratios (Meentmeyer, 1978; Cadish & Giller, 1997; Lang *et al.*, 2009; Coq *et al.*, 2010). Many of the physiological features of green leaves persist through senescence, resulting in litter and green leaf chemistry being strongly correlated (Cornwell *et al.*, 2008). The initial rate of litter decomposition is influenced by climate, water soluble nutrients and structural carbohydrate contents, while latter stages are affected more by the lignin content of the litter (Berg & McClaughtery, 2008). The floristic composition of a community can also influence decomposition rates, via interactions among litter types, or the physical structure of the community (e.g. canopy cover), which can affect the local microclimate (Berg & McClaughtery, 2008). Litter mass loss is also greater under aerobic than anaerobic conditions, and the faster the decomposing litter enters the anaerobic peat zone, the higher the rate of peat accumulation in a mire (Bragazza *et al.*, 2008).

6.1.1.2 The role of Nutrients during Litter Decomposition

Nutrient release during litter decomposition partially determines nutrient availability for plant growth, hence structuring vegetation communities (Bragazza *et al.*, 2008). Litter quality refers to the chemical and physical composition of the litter, with low-quality litter characterised by high C:N ratios, with the carbon in the form of lignin, cellulose and hemicellulose, and therefore resistant to decomposition (Berg & McClaughtery, 2008). High quality litters have a high nitrogen and low carbon content, and are more easily decomposed. It is generally accepted that plants from oligotrophic environments (e.g. mires), produce long-lived foliage with low nitrogen content and low photosynthetic rates, and produce low quality litter high in lignin and secondary compounds, leading to slow decomposition and mineralisation rates, further lowering site fertility (Grime, 1977; Aerts & Chapin, 2000). In contrast, minerotrophic species compete by producing higher nutrient, (high quality) litters, maintaining higher rates of nutrient cycling, and therefore slower peat accumulation rates (Berendse, 1993; 1994).

Nitrogen (N) and phosphorus (P) are limiting nutrients in mires, and biomass N:P ratios reflect the relative availability of the nutrients, and the degree of nutrient limitation experienced by the plant (Koerselman & Meuleman, 1996; Güsewell *et al.*, 2003). Litter N:P ratios affect the rate of decomposition (Güsewell & Freeman, 2005, Güsewell & Verhoeven, 2006), and the relative importance of bacterial or fungal decomposition processes in the early stages of decomposition (Güsewell & Gessner, 2009), fungi becoming P-limited at higher N:P ratios than bacteria (Güsewell & Gessner, 2009). Litter N:P ratios may vary widely among species, and may not always predict which nutrient will limit decomposition, although the decomposition of litter with an N:P ratio >22 will always be P-limited (Güsewell & Freeman, 2005).

Criteria have been proposed for N and P content and the N:P ratio to show where vegetation is nutrient limited, based on prior nutrient fertilisation studies. These studies suggest P concentrations are limiting to plant growth when tissue-P concentrations <0.1% dry weight, and N when tissue-N is <2.0% (Clarkson *et al.*, 2002). The N:P ratio allows further interpretation, and ratios to indicate nitrogen or phosphorus limitation have been developed (Wilby *et al.*, 2001; Güssewell & Koerselman, 2002), and applied to New Zealand wetlands (Clarkson *et al.*, 2002; Sorrell, 2008; Chapter 3). Tissue ratios of N:P>16 indicate P-limitation, N:P<14 indicate N-limitation, with N:P ratios between these values indicating N and P co-limitation (Güssewell & Koerselman, 2002; Clarkson *et al.*, 2002).

6.1.1.3 *Empodisma* species as Ecosystem Engineers of the Fen-Bog Transition (FBT) in New Zealand Restiad Mires

Restiad mires dominated by one of two *Empodisma* species are found throughout mainland New Zealand, and are characterised by a dense *Empodisma* sward, with graminoids, small shrubs and low-growing herbs interspersed (Johnson & Gerbeaux, 2004; McGlone, 2009). In regions where high altitude combines with cool, wet and cloudy conditions, montane restiad mires are a relatively common occurrence, including both bogs formed on poorly drained substrates, and fens formed on sloping sites fed by groundwater seepages or flushes (McGlone, 2009). Functionally, *Empodisma* species are the dominant species in restiad mire succession, and the development from minerotrophic fen to raised ombrotrophic bog likely requires its involvement as an Ecosystem Engineer (van Breeman, 1995; McGlone, 2009; Hodges & Rapson, 2010). A key engineering process by which *Empodisma* engineers raised bog habitats (*sensu* Jones *et al.*, 1994) is thought to be the production of apogeotropic capillaroid roots which are resistant to decay, accumulating in situ as peat (Campbell, 1983; Agnew *et al.*, 1993; Kuder *et al.*, 1998; Kuder & Kruge, 2001; Hodges & Rapson, 2010). In their recent revision of the *Empodisma* genus, Wagstaff & Clarkson (2012) suggest *Empodisma minus* produces fewer capillaroid roots than *Empodisma robustum*. If correct, the fen-bog transition (FBT) in *Empodisma minus* mires may require a longer time period prior to ombrotrophy, the peat may incorporate a larger proportion of culm or rhizome litters in addition to capillaroid root fragments, or abiotic controls (e.g. cool climate) may play a greater role in slowing decomposition.

Due to the important role played by *Empodisma robustum* capillaroid roots in northern lowland raised bogs (Campbell, 1964; 1981; Campbell *et al.*, 1995; Kuder *et al.*, 1998; Kuder & Kruge, 2001), less attention has been paid to the decomposition of, and decay products produced by, the culm and rhizome litters of *Empodisma* species. Campbell *et al.* (1995) even note, "…it is below-ground that is of greatest interest" (p.9). While leaf veins, roots and rhizomes of the co-occurring mire species *Gleichenia dicarpa* are preserved in peat deposits to a small extent, only *Empodisma robustum* "rootlet" macrofossils are noted by Campbell (1971), implying greater decay of other *Empodisma robustum* biomass components. Senesced *Empodisma* culms are initially retained in the canopy (Chapter 3; Chapter 5), forming a water retentive blanket of mulch (Campbell & Williamson, 1997). Upon reaching the peat surface, the fragmented litter is engulfed by the apogeotropic (upwards growing) capillaroid roots (Campbell *et al.*, 1995). While the litter may provide an additional nutrient source for the capillaroid roots, the high levels of uronic acid excreted by the roots during nutrient acquisition (Bannister, 2000) likely immobilise bacteria (Agnew *et al.*, 1995), slowing the decay of both culm litter, and the rhizome and root litters produced within the surface root weft.

6.1.1.4 Decomposition and the Restionaceae

While recent research into the New Zealand Restionaceae has shed new light on the role of capillaroid roots in nutrient acquisition (Clarkson *et al.*, 2005; 2009), less is known of nutrient cycling via decomposition pathways in these mires, or of the microbial biota. In general, the Restionaceae produce sclerophyllous, evergreen, photosynthetic culms that persist for several years, although producing flowers only in their first year (Linder & Caddick, 2001). The foliage is of low quality, and nutrient resorption from senescing biomass varies between species (Stock *et al.*, 1987; Meney *et al.*, 1990b). The foliar litter produced is slow to decay; initially increasing in N and P content (Mitchell *et al.*, 1986), and in arid environments will accumulate on the soil surface until removed by frequent fires (Mitchell, 1983; Mitchell *et al*, 1986; Witkowski 1991; Stock & Lewis, 1986; Bengtsson *et al*, 2012). Restiad foliar litters are high in lignin and structural carbohydrates (Mitchell *et al*, 1986; Herppich *et al*, 2002), while ammonia and soluble reactive phosphorus are potentially leached from the canopy biomass (Raubenheimer & Day, 1991). Nutrient additions to the vegetation reduce the root:shoot ratio (Witkowski, 1989), and increase the nutrient content of the foliar litter produced (Witkowski, 1989; Bell *et al.*, 2000; Chapter 5). The roots of many restiad species, including *Empodisma minus*, do not contain starch (Meney & Pate, 1999; Tolsma *et al.*, 2007), and are not considered storage organs, although there is some evidence for temporary N storage in dormant *Lyginia barbata* roots (Shane *et al.*, 2009). The capillaroid roots formed by Restionaceae are also resistant to decay (Campbell, 1981; Campbell *et al.*, 1995; Shane *et al.*, 2011). In a comprehensive study of the persistent sand sheaths formed by *Lyginia barbata* (Restionaceae), Shane *et al.* (2011) found the longevity of the sand sheaths was linked to the formation of cellulose rich walls in root hairs prior to senescence, which were high in ferrulic acid and lignin.

Fungi are the dominant agents of decomposition in aerobic environments and in standing dead wetland vegetation (Newell *et al.*, 1993), and are mildly acidophilic with optimal growth in low pH environments (Brady, 1990). Fungal decomposition of *Empodisma robustum* capillaroid roots was identified and discussed by Kuder *et al.* (1998), however, there have been no investigations of *Empodisma* culm litters. Little is known of the influence of litter and substrate chemistry on microbial decay of *Empodisma* litters, or the identity of the bacteria and fungal species involved. While Stout (1961) included organic soils in his microbial survey of New Zealand soils, none of the samples had a restiad influence, *Sphagnum* often named as the dominant vegetation cover instead. A sole smut fungi, *Restiosporum dissimile* sp. nov., has been described from seed heads of *Apodasmia similis* from the Chatham Islands (McKenzie & Vánky, 2001; Vánky & McKenzie, 2002). In contrast, a 3 year survey of restiad culm litter in South Africa found a largely undescribed, diverse fungal population, many of which were host specific (Lee & Crous 2003a; 2003b; Mel'nik *et al.*, 2004); Lee *et al.* (2006) suggesting the relatively soft restiad culms allow easy colonisation by saprobic hyphomycetic fungi, compared to the stems of sclerophyllous shrubs (Lee *et al.*, 2004; Hyde *et al.*, 2007). These findings suggest a diverse microfungal biota is likely present in *Empodisma* litter, contributing to the breakdown of the above- and below-ground litters. With so little currently known, further investigation of the microbial biota in New Zealand mires is warranted, although outside the scope of this study.

6.1.1.5 *Chionochloa rubra* as a putative mire engineer

The red tussock (*Chionochloa rubra* Zotov) is a common species in montane restiad mires (Mark & McLennan, 2005; McGlone 2009), often dominating in minerotrophic conditions (Clarkson *et al.*, 2011). While *Chionochloa rubra* possesses some attributes in common with known mire engineers (Hodges & Rapson 2010; Chapter 4), its contribution to peat accumulation has not been addressed. *Chionochloa rubra* has root and shoot traits associated with low resource use (Craine & Lee, 2003), producing small (Lee & Fenner, 1989), long-lived (Meurk, 1978), unpalatable leaves (Cockayne, 1927; Connor *et al.*, 1970), with a low nutrient content (Williams *et al.*, 1978a;b) and high lignin and structural polysaccharides levels (Bailey & Ulyatt, 1970; Connor *et al.*, 1970; Connor & Bailey, 1972). Its mechanical leaf strength is higher than co-generic species, and significantly higher than non-native grasses (Connor & Bailey, 1972). While much prior research has been undertaken in the South Island tussock grasslands, Williams *et al.* (1978a) note that red tussocks growing on volcanic central North

Island soils have similar macro-element concentrations to South Island tussocks, though less N, while soil and tissue P levels appear positively correlated. Peat substrates were not included in early investigations of tussockland microbial biota (e.g. Ross *et al.*, 1980), however, *Chionochloa rubra* litter contains a diverse array of fungal species (Dingley, 1954; McNab, 1962; Hughes, 1965; McKenzie & Latch, 1980; McKenzie, 1982).

6.1.2 Study aims

Little is known about the productivity and decomposition dynamics of montane wire-rush land communities or the tephra-trophic mires of the central North Island in general.

I was interested in investigating the role of *Empodisma minus* as ecosystem engineer of the fen-bog transition in montane restiad mires, and:

1. Whether *Empodisma minus* produces low quality shoot and root litters in transitional mires that are slower to decompose than those of a co-existing mire species, *Chionochloa rubra*; and
2. How the litter chemistry and the decomposition process in a fen may be influenced by the transition from *Chionochloa rubra* fen to *Empodisma minus* dominated transitional bog.

The species related differences in litter chemistry and decomposition were studied by comparing nutrient content, translocation prior to senescence, decomposition and nutrient mineralisation of N, P, and K in litter from *Empodisma minus* and *Chionochloa rubra*. The importance of site differences were studied by comparing the aforementioned factors and litters in two mire communities and the surrounding tussockland. The expected outcomes of the study were: (i) the litter from the fen species *Chionochloa rubra* would both decompose faster, and show faster nutrient release, than that of the bog species *Empodisma minus*; (ii) that *Empodisma minus* capillaroid root weft will decompose more slowly than other litter types; (iii) that the nutrient content of *Empodisma minus* litter would decline towards the wet, oligotrophic mire centre; and (iv) that decomposition rates would also decline along the same gradient.

I measured short-term decomposition of *Empodisma minus* and *Chionochloa rubra* litter using the "litter bag" method (Swift *et al.,* 1979; Berg & McClaugherty, 2008), where dry, pre-weighed plant material is enclosed within mesh bags and inserted into an environment for later harvest. All methods of measuring decomposition have problems associated with them, and litter bags potentially alter decomposition rates by excluding macro-invertebrates, separating the litter from the soil environment, and reducing rates of fungal colonisation and growth into the litter (Weider & Lang, 1982; Harmon *et al.*, 1999; Bragazza *et al.*, 2008). However, despite its limitations, the method is highly repeatable, inexpensive and widely used for measuring mass loss rates of different litters in situ (Harmon *et al.*, 1999; Bragazza *et al.*, 2008). *Empodisma minus* capillaroid root weft is also unlike the *Empodisma robustum* root weft found in northern restiad mires, where a thicker, more uniform root weft was able to be collected for decomposition studies (B. Clarkson, 2007, *pers. comm.).* We know little of the functioning of *Empodisma minus* capillaroid roots, including the chemistry of live and senesced roots, and we approached this aspect of the study as an opportunity to observe the principles involved in capillaroid root decomposition.

6.1.2.1 Nomenclature

Species nomenclature follows Johnson & Brooke (1998).

6.2 Methods:

6.2.1 General site description

Empodisma minus is a common component of the montane tussockland, rushland and fernland communities on the ring plain surrounding the central North Island volcanoes (Atkinson, 1981). Wire rushland dominated mires are common on the north and northwest slopes of Mt Ruapehu (Atkinson, 1981), with similar communities extending northwards towards Rotoaira, and southwards, past Waiouru (Rogers, 1987). On the eastern portion of the ring plain, *Empodisma minus* is a sub-canopy component in seral tussockland communities in wet sites (Rogers & McGlone, 1989).

6.2.1.1 Mt Ruapehu

Silica Rapids Mire (1000 m.a.s.l.) is a montane restiad mire situated on the wet, northwest slopes of Mt Ruapehu in the Tongariro National Park (TNP), New Zealand (Figure 6.1). Due to the predominantly west to southwest wind-flow in the area, tephra deposits fall mainly to the east of the volcanoes. The Silica Rapids Mires on Ruapehu's western flanks likely received some tephra in the June 1996 eruption, and small frequent tephra additions during the 1945 series of eruptions, which deposited tephra at the Chateau a small distance away (Healy *et al.*, 1978; Johnston, 1997). Additional tephra likely arrives at the mire as a result of eolian remobilization of tephra at higher altitudes by strong winds, and further remobilization by surface water after heavy rain (Manville *et al.*, 2000).

6.2.1.2 Climate

Close to the mire at the Chateau, the mean monthly temperature in summer is 12^{o}C, and 2^{o}C in winter (Atkinson 1981). Ground frosts are also recorded in all seasons with an average of 141 per annum, and snow falls on 16 days per annum (Horrocks & Ogden, 1998b), though snow does not persist at the low elevation of the Silica Rapids Mire. Droughts are rare in the region, however, summer water deficits do occur (Horrocks & Ogden, 1998b).

6.2.2 Silica Rapids Mire – Previous studies

The mire is approximately 300m wide and 600m in length downslope, of which the sampled portion comprises approximately the upper third (Figure 6.1). The surface (0-10cm) peat has a pH of 5.0-6.5, high moisture content (70-85%), and only moderate organic matter content (36-50%), suggesting minerotrophic status (Hodges & Rapson, 2007). Silica Rapids Mire contains approximately 0.5-2.6m deep peat infilling a shallow depression, and groundwater seepages at various points around the margins (Hodges & Rapson, 2007). These mires have been colloquially labeled "perched bogs" (Gabites, 1986). The "perched bogs" occur on the wet, northwest slopes of Mt. Ruapehu, the mires underlain by tephra which have weathered to form an impermeable seal, resulting in a perched water table upon which the vegetation community has developed (Horrocks & Ogden, 1998b). Moore & Clarkson (2007) noted very low dissolved organic carbon (DOC) losses from these mires, as a result of DOC immobilisation by iron associated with the tephra substrate, or groundwater inflows.

The current vegetation community is dominated by a mosaic of tussock, shrub and wetland species (Atkinson, 1981; Trenery, 1985), with a total of 102 vascular and nonvascular species present (Hodges & Rapson, 2007) (Appendix 6.1). The drier portions of the mire are dominated by *Chionochloa rubra, Dracophyllum* hybrids, *Empodisma minus, Coprosma cheesemanii, Celmisia spectabilis* and *Gleichenia dicarpa*, and the bryophyte *Racomitrium pruinosum*. The central portion of the fen contains numerous pools, and *Empodisma minus, Lepidosperma australe, Drosera arcturi* and *Schoenus fluitans* dominate the vegetation here, with the bryophyte *Sphagnum cristatum* also present on the raised ground behind the pools. The invasive heather *Calluna vulgaris* is encroaching on the *Sphagnum* community, though absent from the remainder of the mire. The mire is dissected by a boardwalk along the Silica Rapids walkway; however the upper portion of the mire examined is largely undisturbed by tourist activities due to difficult access and warnings on the boardwalk to avoid stepping directly on to the mire vegetation.

The site was part of a previous study examining bryophyte and vascular plant dynamics (Hodges & Rapson, 2007). Cluster analysis of plant and environmental data suggested 5 communities, of which three were chosen for this study to represent the gradient from *Chionochloa rubra* tussockland to transitional fen, incorporating both wet and dry fen communities. These communities resemble those described by Atkinson (1981) as red tussock/mountain inaka tussock-shrubland and red tussock/wire rush-gleichenia rushland. The latter community is found on poorly drained soils with a near surface water table on the northern slopes of Mt Ruapehu between 950-1200 m altitude (Atkinson, 1981). Small tarns are enclosed within the *Empodisma* dominated rushland community, the seasonally saturated substrate also containing a higher *Schoenus pauciflora* component indicative of a seepage or flowing surface water (Atkinson, 1981). This wet, central portion of the mire (Wet Fen) was separated from the drier outer margins that contain little *Schoenus* and a higher *Gleichenia* component (Dry Fen). Very poorly drained slopes dominated by wire rushland are also characterised by slimy, rust-like deposits on the substrate, resulting from the oxidation of iron compounds (Atkinson, 1981).

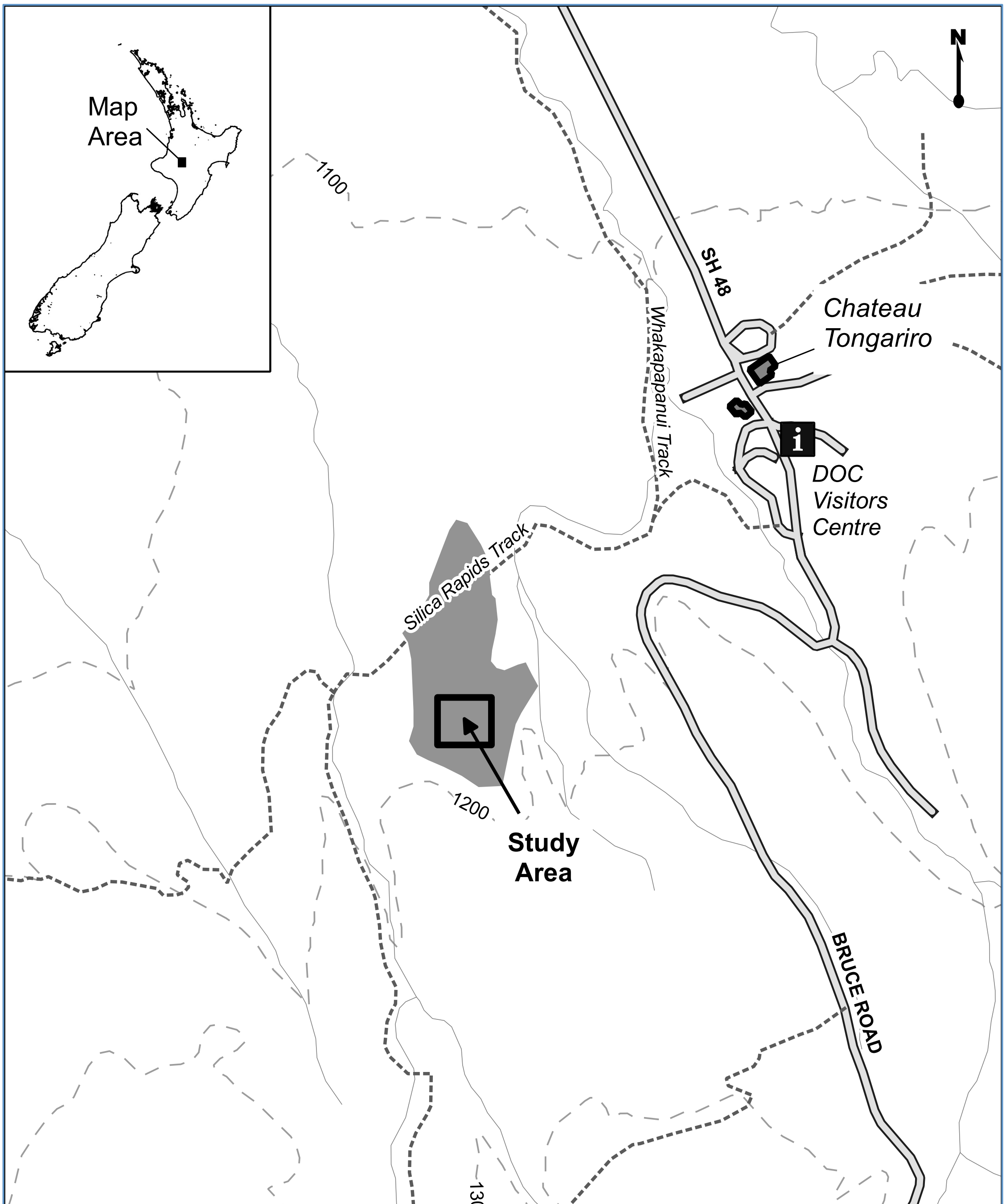


Figure 6.1: Site map of Silica Rapids Mire, Mt Ruapehu, Tongariro National Park. The mire is situated approximately 25 minutes walk along the Silica Rapids walkway.

The study site is upslope of the boardwalk crossing the site. An information plaque on the boardwalk crossing the mire contains information on the mire vegetation community.

6.2.3 Experimental methods

6.2.3.1 Experimental outline

The study comprised a 12-month litter decomposition experiment including the above- and below-ground biomass of the two species, *Chionochloa rubra* and *Empodisma minus*. The litter types were:

1. Standing dead foliage from *Chionochloa rubra;*
2. Standing dead foliage (culms) from *Empodisma minus*;
3. Stem bases of *Chionochloa rubra* with attached roots;
4. Rhizomes of *Empodisma minus* with attached coarse roots; and
5. Capillaroid root weft from *Empodisma minus*.

The design incorporated the 3 mire communities identified (Tussockland, Dry & Wet Fen), the 5 litter types, with all treatments replicated six times within each mire community (N=90). At each replicate site, aspects of substrate quality (e.g. soil geochemistry & nutrient content) and the vegetation community (e.g. cover, biomass, tissue nutrient content) were measured.

6.2.3.2 Substrate quality

The physical and chemical properties of the substrate were examined at each sample location. Peat samples were assessed for decomposition using the Von Post Index (Von Post & Granlund, 1926), where values range from H1 (undecomposed) to H10 (highly decomposed) (Appendix 3.2). Two peat or soil samples were retrieved from the upper 7cm of the substrate using stainless steel cores (0.1 x 0.07m), after above-ground biomass had been harvested for analysis. One core was analysed for bulk density, the sample removed from the core, oven dried at 105°C and weighed, as described by Gradwell & Birrell (1979). The second core was air-dried, and samples used to determine pH, conductivity and loss on ignition, following methods outlined by Blakemore *et al.* (1987). A 1:5 ratio of soil to water was used to determine pH, due to the high peat content (Blakemore *et al.*, 1987). A 1:5 soil:water slurry was shaken for 30 minutes and conductivity measured (mS/cm) (Blakemore *et al.*, 1987). Organic matter content was determined following the Loss On Ignition method (LOI) by placing weighed samples in a 500°C muffle furnace for 4 hours (Blakemore *et al.*, 1987).

The peat and soil samples were analysed further by the Environmental Laboratory, Landcare Research, Palmerston North. Exchangeable bases (K^+, Na^+, Ca^{2+} & Mg^{2+}) in peat substrates (cmol(+)/kg) were determined by flame atomic absorption spectroscopy, as described by Blakemore *et al.* (1987). KCl extractable NH_4-N and NO_3-N were measured colorimetrically (mg/kg), as an indicator of plant available nitrogen, following Blakemore *et al.* (1987). Cation exchange capacity was determined using the pH drop method, where the exchangeable hydrogen in the soil (Brown, 1943) is added to the exchangeable bases, and expressed in cmol(+)/kg. Olsen-P (mg/kg) attempts to determine the plant available phosphate fraction in soil, the method followed is based on Olsen *et al.* (1954), as described by Blakemore *et al.* (1987). Substrates were additionally analysed for Carbon (C) and N using a Leco CNS2000 Analyser (Leco, 2003) using the Dumas dry combustion principle, by the Waikato Stable Isotope Unit, University of Waikato.

6.2.3.3 Wetland hydrology

Investigations into wetland hydrology were undertaken to describe the permanent water table and the variability of water table levels within each community. At 13 of the 18 sites within the mire, shallow piezometers (<2m) were installed (Figure 6.2). A 40mm diameter PVC pipe, capped and slotted at the base, was inserted into an augured hole, which was then repacked with the original sediments in reverse order of removal. The top of the pipe had a removable cap to ensure rainfall was unable to enter. Water levels in each piezometer were measured monthly over the experimental period.

6.2.3.4 Vegetation community description and biomass estimates

To describe the vegetation community, the cover % of each species within a 50cm x 50cm (0.25m^2) quadrat was determined at each location, and the above-ground biomass harvested (live, standing dead and litter components).

Empodisma minus below-ground biomass was estimated by removing cores (8.5cm diameter) to a depth of 30cm, and sorting all live rhizome and root material from the peat. The mass of capillaroid roots was not determined during below-ground biomass estimates, due to difficulties separating live and senesced roots from organic matter (Figure 6.3).

The above-ground biomass of vascular species in each 0.25m^2 quadrat was then removed at ground level, and sorted in the laboratory into the live and senesced biomass of the species present. The litter component comprised those senesced plant fragments too small to be sorted into species using the naked eye.

Figure 6.2: Piezometers being installed in the Tussockland community on 5 June 2007 at Silica Rapids Mire, Tongariro National Park.

Figure 6.3: Capillaroid roots of Empodisma minus near surface of peat from Silica Rapids Mire, TNP. Note the 1-2mm long root hairs on the capillaroid roots in the foreground.

Since *Chionochloa rubra* tussocks were seldom represented in the quadrats, tussock biomass was examined separately by measuring tiller dynamics. The closest *Chionochloa rubra* tussock to each quadrat was chosen, and two tillers per tussock divided into leaf sheath, green leaf and senesced tip in the laboratory (Williams *et al.*, 1978a; Lee & Fenner, 1989).

All biomass components were oven dried at 70°C for 72 hours until a constant weight was achieved, then weighed. Differences in tiller weight were analysed using a one way ANOVA in Statistica (StatSoft, 2004), with community as the fixed variable.

6.2.3.5 Nutrient resorption from senescing *Empodisma minus* culms

To investigate nutrient resorption from senescing *Empodisma minus* culms, the above-ground biomass of *Empodisma* from a randomly chosen quadrat in each community was chosen for further analysis. The biomass was divided into categories on the basis of morphology and apparent age, following Stock *et al.* (1987). The classes were:

1. Newly emerged culms bearing no side shoots.
2. Recently emerged culms with side shoots extended, prior to development of inflorescences
3. Mature culms
4. Senescing culms with limited side shoot mortality
5. Fully senesced culms, still attached to the rhizome.

The culms were oven dried, ground, and culm N, P and K concentrations determined after Kjeldahl digestion, as described by Blakemore *et al.* (1987). All nutrient analyses were undertaken in the Environmental Chemistry Laboratory, Landcare Research, Palmerston North.

6.2.3.6 *Empodisma minus* litter quality

To explore the relationship between available nutrients in the three communities and the litter produced by *Empodisma minus*, litter from within each of the three communities was examined further. Fully senesced culms still attached to the rhizome (i.e. Class 6, above), were sampled from the three communities. Samples were analysed for Total-N, -P, -K, Fibre, Lignin, Cellulose and Soluble Phenolics in the Environmental Chemistry Laboratory, Landcare Research, Palmerston North. Total-N and -P were determined using automated colorimetric methods, after Kjeldahl digestion, as described in Blakemore *et al.* (1987). Phenolic and condensed tannins were determined following extraction in 50%v/v acetone, following the methods of Price & Butler (1977) and Broadhurst & Jones (1978) respectively. Condensed tannin results are expressed as catechin-equivalents, and Total Phenolics as tannic acid equivalents. Fibre, Cellulose and Lignin fractions were determined using the acid detergent fibre-sulphuric acid procedure (Rowland & Roberts, 1994). Lignin-N and N:P ratios were derived from the results generated. Plant litters were also analysed for C and N using a Leco CNS2000 Analyser (Leco, 2003) using the Dumas dry combustion principle, at the Stable Isotope Unit, the University of Waikato.

6.2.3.7 Litter Decomposition

I collected senesced material, comprising intact culms or tillers from the Dry Fen community on the mire. The *Empodisma* canopy contains a large volume of senesced material, usually equal to, or greater than the volume of live biomass (Chapter 4). As the age of the senesced material is unknown, only senesced foliage still attached to the plant was removed for inclusion in litter samples. Likewise, *Chionochloa rubra* biomass contains senesced material of varying age, and so only entire dead tillers with senesced leaf blade and sheath intact were utilised in the experiment.

Capillaroid roots were also collected. The upper peat and roots contained within it were removed from the mire, and the root layer excised from the underlying peat in the laboratory, with extraneous materials (bryophytes, litter, large roots>2mm) removed. The capillaroid root weft collected was heterogeneous in nature, and the roots collected were of varying ages and states of decomposition.

Coarse roots and rhizomes were also sampled from peat cores removed from the mire. *Empodisma minus* rhizomes were collected by cutting the peat with a pruning knife in a 20cm diameter circle around live *Empodisma* biomass in a hummock. After the peat cores were lifted, they were transported to the laboratory where adhering peat was washed free using distilled water. Only living rhizomes were used, as using senesced rhizomes would have require the acquisition of large volumes of peat. Roots and tussock bases from *Chionochloa rubra* were collected from whole extracted tussocks. The live shoot biomass was removed, and the tough woody shoot bases and attached roots were washed free of adhering peat with distilled water.

All litter materials were dried at room temperature for 48 hours, and then cut into uniform lengths of 3cm (Boulton & Boon, 1991). 1-2g samples of the individual shoot and root litters were then inserted into nylon mesh bags (7.5 x 7.5cm, 1mm mesh gauge), with 10g samples of all litter samples regularly set aside for analysis of Total-N, -P, -C, lignin, cellulose and soluble phenolics. The mesh size was chosen to allow access of small mesofauna, while preventing physical losses of the litter from the bags. Subsamples of all litters were also oven dried to a constant weight (70°C, for 72 hours) to determine the oven-dry weight of the air-dried samples (Aerts & de Caluwe, 1997). Each litterbag was sealed with nylon thread, and a numbered tag attached. Litterbags were weighed to the nearest 0.001g, then sealed inside plastic bags until insertion into the mire, after which the plastic bags were re-weighed to account for losses during transportation. In total, ninety litterbags were prepared for the 5 litter types, including six replicates within each of the three communities along the mire gradient. The root and rhizome bags were placed underground, the top of the litterbag at the mire surface. The foliar litters were placed horizontally on the mire surface, and pinned to minimise movement and bag loss. A nylon wire was used to attach all the litter bags to GPS located bamboo poles, to assist in relocation.

The litterbags were deployed in June 2007 and collected 365 days later. Adhering particles were removed in the field where possible, before transportation to the laboratory. In the laboratory intrusive live material (e.g. *Empodisma minus* capillaroid roots) and debris were removed with forceps. The samples were removed from the litter bags, oven dried (70°C, for 72 hours) until a constant mass was achieved, cooled in a desiccator and weighed again to the nearest 0.001g. Samples were then ground and stored in sealed containers for further analysis.

6.2.3.8 Decomposition and nutrient release from litters

The % mass loss (or gain) in each sample was determined by:

$$\%Mass\ Loss = \frac{W_0 - W_1}{W_0} \times 100$$

Where W_0 is the initial dry mass of the litter prior to burial, and W_1 is the weight of the same sample after 12 months burial.

Changes in litter nutrient concentrations were also calculated. Patterns in nutrient accumulation or loss during decomposition are complex, as nutrients accumulating in the litter, microbial populations and byproducts are impossible to separate (Harmon *et al.*, 1999). We therefore use the terms *net release* and *net accumulation* of nutrients, since the litterbag method does not allow us to distinguish nutrient mineralisation or immobilisation processes (Berg, 1988).

Total-N, -P and -K were determined using automated colorimetric methods, after Kjeldahl digestion, as described in Blakemore *et al.* (1987).

The % Net release (or accumulation) in each sample was determined by:

$$Net\ Release\ (accumulation)\% = \frac{X_0W_0 - X_1W_1}{X_0W_0} \times 100$$

Where X_0 is the initial nutrient concentration prior to burial, and X_1 is the nutrient concentration of the same sample after one year burial. Positive values indicate a net release of nutrients, and negative values a net nutrient accumulation.

To compare our results with recent findings in New Zealand wetlands (Pegman & Ogden 2005; 2006), we also calculated the decomposition constant *k*, assuming an exponential decomposition model (Jenny *et al.*, 1949; Olson, 1963). The constant was determined by:

$$ln\left(\frac{W_t}{W_0}\right) = -kt$$

Where W_0 is the initial mass, W_t is the final mass at time *t* (*t*=365 days), and *k* is the decay rate constant (Weider & Lang 1982; Bengtsson *et al.*, 2012).

6.2.3.9 Statistical analyses

The decomposition data were tested for homogeneity of variance with Shapiro-Wilks test, and were found not to be normally distributed. Suitable transformations of the mass loss and nutrient data could not be found, as negative values for foliar and root samples occurred in all variables analysed after the 12-month period. We therefore analysed the data using a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001; 2005). PERMANOVA makes no particular assumptions about the distribution of the data, as all p-values are obtained by permutation. Tukey post hoc tests were undertaken if community or litter type was a significant factor, and these tests were performed for separate communities if the interactions between community and litter type were significant. Exploratory graphs were produced in R (R Core Development Team, 2011).

One-way analysis of variance (ANOVA) was used to assess significant differences in environmental variables and litter quality between communities. Correlations among mass/nutrient losses and environmental variables were assessed using Spearman's rank correlation coefficients, and a Bonferroni adjustment for multiple comparisons made. Statistical analyses were performed using Statistica (StatSoft, 2004) and plots created in R (R Core Development Team, 2011). Significant differences between the cluster groups were identified using one-way ANOVA, with Tukey HSD and *p*=0.05.

6.3 Results

6.3.1 Vegetation community descriptions

26 vascular species were encountered in the three communities sampled in this study (Table 6.1; Appendix 6.1). General descriptions of the three mire communities including community composition (Table 6.1), substrate chemistry and hydrology (Table 6.2) and species biomass changes across the mire (Table 6.3).

6.3.1.1 Tussockland

These sites comprise a mixed shrub-tussock-fernland community surrounding the mire proper (Figure 6.4). *Chionochloa rubra* is the canopy dominant, with the shrubs *Coprosma cheesemanii, Dracophyllum* hybrids and *Hebe odora* a frequent component (Table 6.1). The *Chionochloa rubra* tussock biomass is greatest in the Tussockland community (Table 6.3; Appendix 6.2). A previous experiment (Chapter 5) suggests *Chionochloa rubra* tiller biomass is positively correlated with nutrient availability rather than water table depth, the large tiller size mirroring the higher available P in this community (Table 6.2).

While the community contained only minor cover of *Empodisma minus*, it contained a large mass of senesced biomass (Table 6.4), largely senesced *Chionochloa rubra* tillers.

The community has a deep, though variable water table throughout the year, which is often >1.3m below the surface (Table 6.2). As a result, piezometer readings were unable to be recorded at one site during the summer months due to the low water table. The peat has the lowest cation content (Na & K), though similar CEC to the other two communities (Table 6.2) The presence of a narrow tongue of *Sphagnum cristatum* encroaching on one side of the mire results in high organic matter content (51%), low soil bulk density (0.13 g/cm^3) and pH (4.64) at one site compared to others within this community type, however, the Tussockland peat still has a significantly higher bulk density than the Wet Fen community.

6.3.1.2 Dry Fen

Hummock-hollow topography has developed in the Dry Fen community (Figure 6.5), though absent where the bryophyte *Racomitrium pruinosum* dominates on drier, elevated sites. Despite the two fen communities containing similar *Empodisma minus* canopy cover, the elevated hummocks in the Dry Fen community contain slightly more *Empodisma* rhizome biomass than the Wet Fen community at the mire centre (Table 6.3), resulting in a higher root:shoot ratio for the plants. *Chionochloa rubra* tiller size is greatly reduced (2.65 ±0.45g), compared to tussocks growing in the Tussockland community (Table 6.3), and the surface litter component is also reduced (0.20 ±0.04kg/m^2).

The water table underlying the Dry Fen community is highly variable, being near the ground surface during the winter months, and falling considerably during the dry summer months (Table 6.2). Although the peat substrate in the Dry Fen community had a similar ash content (79-50%) as the Tussockland community, the substrate had a significantly lower bulk density (0.18-0.41 g/cm^3). The substrate also had a higher pH (5.32-5.73), higher major cation content, and lower available P than the Tussockland community, though not significantly so.

6.3.1.3 Wet Fen

The Wet Fen community closest to the mire centre contains the least number of species (6.3 ±1.4). *Empodisma minus* forms a continuous cover, with the fern *Gleichenia dicarpa* a major component (Table 6.1). While live *Empodisma* canopy and litter biomass are similar in the Wet and Dry Fen communities, the Wet Fen canopy contains more standing dead (senesced) biomass (Table 6.3). Occasional *Chionochloa rubra* tussocks are still present; although tussock frequency and stature had declined considerably compared to the other communities implying nutrient availability is low (Chapter 5). All tiller components decrease in size along the internal mire gradient, the largest decline being in the green, photosynthetic component of the *Chionochloa* tillers (-86%). While *Chionochloa rubra* tussocks persist in restiad mires (Chapter 3), tussock biomass, and hence contribution to litter biomass pools appear to decline as oligotrophic conditions develop during mire succession.

Hummock-hollow topography is not present in the wetter central mire, the topography consisting of a central lawn area, with a series of shallow tarns. The water table underlying the community is the least variable, as a seepage upslope of the mire flows through this community (Figure 6.6), giving rise to the tarns and a small stream. A previous survey of the mire suggests the greatest depth of peat occurs under this portion of the mire (>2.6m depth) (Hodges & Rapson, 2006). The peat chemistry is more similar to that of the Dry Fen, though bulk density is significantly lower (0.04-0.25 g/cm^3), due to the low ash content. The peat also contains significantly more Mg and Na, likely from the groundwater seepage upslope of the community. The higher, variable pH of the substrate (5.05-6.16) further reflects the impact of the groundwater inflows at some sites within the community (Figure 6.6).

6.3.2 Mire type and nutrient status of the site

The C:N ratios of the substrates at Silica Rapids Mire are lower than those of New Zealand bogs elsewhere (Table 6.4), reflecting the minerotrophic mire status, and likely tephra inputs from recent eruptions (1995-1996 Mt Ruapehu eruptions). The raised pH at the site suggests inputs from groundwater and surface-water runoff influence the vegetation community across the sloping site, not just in the central areas where the groundwater seepage is prominent (Table 6.2 & Figure 6.6). This has elevated cations, NO_3-N and NH_4-N in the wet, central community, through which the main seepage drains (Table 6.2). These results confirm the colloquial label “perched bog” may be discarded, instead the substrate chemistry suggests Silica Rapids Mire is better described as a sloping fen, with a seepage community at the upslope eastern margin.

Despite its minerotrophic status, the fen is oligotrophic. The substrate has very low available-P in the two central mire communities (Wet & Dry Fen), with higher available-P in the shrubby Tussockland mire margins (Table 6.2). Overall, mean available-P is lower than those of bog sites elsewhere in New Zealand (Table 6.4), and growth at the site is likely P-limited.

Table 6.1: Percentage cover of common vascular and non-vascular species, and substrate chemistry of the three communities, Silica Rapids Mire, Tongariro National Park.
* Values are means with standard deviations. Complete species list in Appendix 6.1.

	Community		
	Wet Fen	**Dry Fen**	**Tussockland**
Major vascular species			
Calluna vulgaris	0	11	4
Carex coriaceae	0	5	23
Carpha alpina	3	3	0
Celmisia spectabilis	0	2	2
Chionochloa rubra	3	35	86
Coprosma cheesemanii	0	0	27
Cyathodes empetrifolia	4	12	3
Dracophyllum recurvum	0	7	15
Empodisma minus	100	99	11
Gleichenia dicarpa	84	82	92
Hebe odora	0	3	16
Hebe venosum	0	0	8
Leptospermum scoparium	1	5	1
Ozothamnus leptophyllus	0	0	5
Schoenus fluitans	14	17	13
Major non-vascular species			
Campylopus interflexa	3	1	10
Cladia spp.	0	8	0
Dicranoloma billardii	0	4	0
Racomitrium pruinosum	27	11	0
Sphagnum cristatum	0	0	2
Total species richness/quadrat*	6 ± 1.4	8 ± 1.5	7 ± 1.9
Total vascular spp/community	16	16	15

Figure 6.4: Weather closing in at the northern end of Silica Rapids Mire, Tongariro National Park (June, 2006). Vegetation community described by Atkinson (1981) as red tussock/mountain inaka tussock-shrubland, but described as Tussockland in this study.

Figure 6.5: Looking southeast across the central mire, Silica rapids, Tongariro National Park, May 2007. Vegetation community described as red tussock/wire rush-gleichenia rushland by Atkinson (1981), but described as Dry Fen for this study. Note the hummock-hollow topography dominated by *Empodisma minus* and *Gleichenia dicarpa*, sparse *Chionochloa rubra* tussocks in the foreground, and *Nothofagus* forest at mire margin.

Figure 6.6: “Wet fen” community at Silica Rapids Mire, Tongariro National Park. *Empodisma minus* growing in seepage at eastern edge of the mire.

Table 6.2: Substrate chemistry of the three communities, Silica Rapids Mire, Tongariro National Park. Values are means with standard deviations.
Different small letters indicate significant differences.

	Community		
	Wet Fen	**Dry Fen**	**Tussockland**
Substrate chemistry			
pH	5.4 ±0.4a	5.5±0.2a	5.2±0.3a
Bulk density (g/cm^3)	0.15 ±0.07a	0.29±0.11ab	0.40±0.27b
LOI (%)	39.9 ±9.9a	35.1±10.8a	27.3±16.5a
Soil conductivity (mS/cm)	164.8 ±13.8a	204.3±106.0a	127.8±85.7a
NO_3-N (mg/kg)	1.58 ±1.50a	0.66±0.53a	0.80±0.30a
NH_4-N (mg/kg)	13.39 ±3.27a	11.2±5.7a	7.25±4.13a
Olsen-P (mg/kg)	3.77 ±1.77a	4.76±3.79a	6.13±6.13a
Ca (cmol(+)/kg)	5.42 ±5.90a	2.37±0.11a	3.95±7.08a
Mg (cmol(+)/kg)	1.83 ±1.50a	2.55±4.30a	1.22±2.03a
Na (cmol(+)/kg)	0.96 ±0.39a	0.49±0.20ab	0.16±0.15b
K (cmol(+)/kg)	1.47 ±0.72a	0.83 ±0.39ab	0.60 ±0.52b
Total-N (%)	0.51 ±0.13a	0.45 ±0.12a	0.45 ±0.13a
Total-C (%)	15.7 ±3.3a	13.6 ±5.3a	11.9 ±6.6a
C:N	30.8 ±3.3a	29.6±3.5a	25.1±5.7a
CEC (cmol(+)/kg)	28.5 ±9.2a	33.8±30.0a	20.3±17.3a
Hydrology			
Minimum water table (m)	0.05	0.01	0.10
Maximum water table (m)	0.67	1.21	>1.33

Table 6.3: Biomass and nutrient content for *Empodisma minus* and mean tiller weight of *Chionochloa rubra* at sites within three vegetation communities sampled during May 2007, Silica Rapids Mire, Tongariro National Park. 1: Data are means ±standard deviations where N>3, otherwise only means are presented. Sample numbers varied according to species presence in communities with only 3 Tussockland sites containing *Empodisma minus*. *Additional data for a northern restiad bog containing *Empodisma robustum* are presented for comparison (Sharp, 1995), n=2.

	Wet Fen	**Dry Fen**	**Tussockland**	*E. robustum* **bog***
Hummock-hollow topography	-	+	-	
Biomass Component				
Live *Empodisma* canopy (kg/m^2)	0.34 ±0.70	0.36 ±0.07	0.06	0.67
Senesced *Empodisma* canopy (kg/m^2)	0.46 ±0.10	0.34 ±0.06	0.03	1.04
Empodisma Rhizomes & Non-Capillaroid Roots (kg/m^2)	0.86 ±0.10	1.12 ±0.39	0.07	0.45
Litter (mixed species) (kg/m^2)	0.22 ±0.05	0.20 ±0.04	0.45	-
Live: Dead canopy ratio	0.76	1.12	1.92	0.64
Root: Live canopy ratio	2.53	3.11	1.17	0.67
Chionochloa tiller dry weight (g)	1.07 ±0.24	2.65 ±0.45	5.09 ±0.82	
Biomass Nutrient Content				
P (% dry wt)	0.004 ±<0.001	0.005 ±<0.001	0.017	
N:P *Empodisma* senesced culms	97.6 ±8.5	69.7 ±3.0	34.4	

Table 6.4: Initial litter quality of the above- and below-ground litters utilized in the Litter Decomposition Experiment [2]. N, P & K analyses are means (*n=3), whereas fibre, cellulose and lignin data presented are single analyses, due to high cost of analysis.[Y]

Community	**N*** **(%dry wt)**	**P*** **(% dry wt)**	**N:P**	**K*** **(% dry wt)**	**Fibre** [Y]	**Cellulose** [Y]	**Lignin**[Y]
Empodisma minus							
Foliage	0.323	0.006	51.7	0.063	46.8	28.3	16.3
Rhizome	0.324	0.008	42.1	0.526	49.6	32.2	16.6
Capillaroid root	0.463	0.017	27.4	0.166	67.3	11.4	12.6
Chionochloa rubra							
Foliage	0.208	0.008	26.3	0.095	43.5	33	7.4
Bases and roots	0.413	0.029	41.4	0.595	38.9	25.2	11.5

Table 6.5: Comparison of soil chemistry parameters (mean values with ranges shown in brackets) for Silica Rapids Mire, TNP compared to wetlands presented by Clarkson *et al* (2002)[1] for New Zealand. Note: fen and swamps sites were combined by Clarkson *et al* (2002), fen sites occupying the lower range of values presented.

Parameter	**Silica Rapids**	**Bogs[1]**	**Swamps[1]**
pH	5.38 (4.64-6.16)	4.0 (3.7-4.4)	5.2 (4.1-5.9)
C:N	25.5 (16.4-36.7)	48.5 (35.9-79.7)	18.0 (14.2-30.6)
Available P (μg cm^{-3})	4.7 (2-18)	15.9 (3.9-35.1)	87.5 (17.6-197.4)

6.3.3 Decomposition and litter quality

6.3.3.1 Nutrient content of biomass and litter

The *Empodisma minus* foliage samples suggest growth is P-limited, with tissue-P levels dropping towards the mire centre (Table 6.3). The N and P contents of fully senesced *Empodisma minus* foliage are similar to those of partially senesced foliage, the senesced culms containing 68% of the N and 42% of the P of mature culms (also see Appendix 6.2). K levels continued to decline further as the culms senesced. K is a highly mobile ion, and a greater reduction in K content was observed than for N and P, senesced culms containing only 11% of the K of mature culms.

This study suggests both species produce foliar litters with a low nutrient content, with high N:P ratios (Table 6.5). Senesced *Chionochloa rubra* foliage contained less N and lignin, similar P, fibre and cellulose, and more K than *Empodisma minus* foliage. The cellulose and lignin content of *Chionochloa rubra* tillers are similar to levels found elsewhere for the species (Connor *et al.*, 1970), suggesting lignin and cellulose content of the tillers is independent of substrate quality. *Chionochloa rubra* roots contain high nutrient concentrations, and low concentrations of fibre and lignin. *Empodisma minus* capillaroid roots contain more nutrients and fibre than the foliar litter, but less cellulose and lignin.

6.3.3.2 Mass Losses from litters

The rate of mass loss from litters vary with community and litter type, although there is no significant interaction between the two factors (Figure 6.7; Table 6.6). Decomposition rates differ significantly between the Tussockland and Dry Fen communities, but are similar in the Dry and Wet Fen communities. Mean litter mass losses range from 31.1% (*Chionochloa rubra* roots in Tussockland) to 8.4% (*Empodisma minus* capillaroid roots in Dry Fen) (Table 6.7). While the foliar litters of the two species decompose at similar rates, there are larger differences in the decay rates of below-ground litter types, the order of decreasing rate of mass loss being *C. rubra* root>*E. minus* rhizome>*E. minus* weft. *Chionochloa rubra* roots lose on average 19% more mass than *Empodisma minus* capillaroid roots in the Tussockland and Dry Fen communities, the difference being less in the Wet Fen community.

The average first year decay rates (k values) for *Empodisma minus* and *Chionochloa rubra* foliage are higher than those obtained for the New Zealand mire species *Machaerina juncea* and *Gleichenia dicarpa* in a recent study (Pegman & Ogden, 2006) (Table 6.7). Decay rates for *Empodisma minus* capillaroid root weft are lower than those of *Machaerina juncea* foliage, but still exceed the decay rate of *Gleichenia dicarpa* foliar litter.

6.3.3.3 Nutrient release from litters

N losses from above-ground litters are small, with nitrogen accumulation occurring in some samples of both species (Figure 6.7). N losses differ significantly between communities, though not litter types, and there is a significant interaction between the two factors. In the Tussockland and Wet Fen communities, N losses are similar between all litter types. However, in the Dry Fen community, differences in N release and accumulation vary significantly between litter types. Here, N release and accumulation in *Empodisma minus* weft and rhizome litters is highly variable, with N increasing in rhizome litter by >60% at one site.

Overall, P release from the various litters is greater than N release during these early stages of decomposition. The order of increasing rate of P release in litters is *C. rubra* root> *C. rubra* foliage> *E. minus* weft>*E. minus* culms>*E. minus* rhizome. P release differs significantly between litter types, and there is some evidence for a significant interaction between the litter type and community (Table 6.6). *Empodisma minus* rhizomes accumulate P in the Dry Fen community, in contrast to the other litter types, which show an overall net P release over the 12-month period.

High rates of K release occur compared to other nutrients. There is no significant difference in K release between communities or the separate litter types (Table 6.6).

Table 6.6: PERMANOVA results for %Mass Loss, P, N & K release from *Empodisma minus* and *Chionochloa rubra* litter after 12-months burial, Silica Rapids Mire, TNP.
F-values are presented for main effects (Location and litter type treatments) and their interaction with their degrees of freedom and level of significance indicated.

	Source	F	df	P-value
Mass Loss	Community	37.6879	2	0.0453
	Litter type	23.8048	4	0.0563
	Community x Litter type	-12.5723	8	0.9304
N	Community	832.8503	2	0.0022
	Litter type	-95.9359	4	0.9862
	Community x Litter type	58.2910	8	0.0192
P	Community	-231.4926	2	0.9932
	Litter type	238.9005	4	0.0042
	Community x Litter type	89.4668	8	0.0110
K	Community	5.6174	2	0.1382
	Litter type	-4.7776	4	0.9452
	Community x Litter type	2.7005	8	0.2068

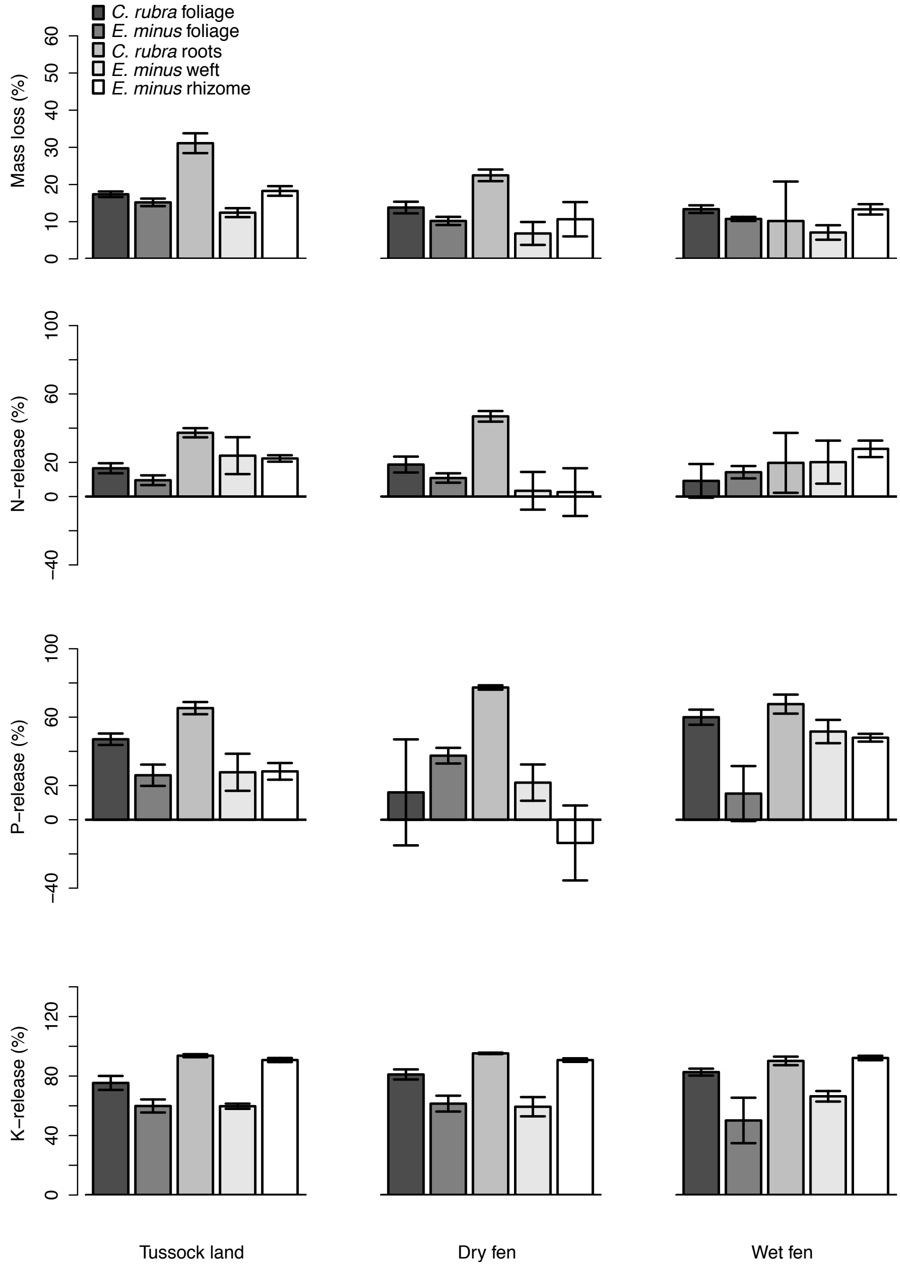


Figure 6.7: Litter decomposition and rates of N, P and K release in above- and below-ground litters of *Chionochloa rubra* and *Empodisma minus* in the three communities at Silica Rapids Mire, Tongariro National Park. Values represented as means and standard errors for each species.

Table 6.7: Mean decay parameters (% weight loss ± SE, mean k values and litter half life) for *Empodisma minus* and *Chionochloa rubra* above-ground (foliage) and below-ground (rhizome & roots) litters over a 12-month period in Silica Rapids Mire, Tongariro National Park. Note: WF = Wet Fen; DF = Dry Fen; and T = Tussockland communities. * Data obtained from Pegman & Ogden (2006), instantaneous decay rates for foliar data at peat surface, over 483 days

	% Weight Loss ± SE			**Mean k value (yr^{-1})**			**Mean half life (days)**		
	WF	**DF**	**T**	**WF**	**DF**	**T**	**WF**	**DF**	**T**
Empodisma minus									
Foliage	13.2 ± 0.7	12.6 ± 1.4	15.2 ± 1.0	0.142	0.135	0.166	1806	2010	1570
Rhizome	16.4 ± 1.7	13.1 ± 5.7	18.3 ± 1.3	0.182	0.207	0.202	1521	1278	1286
Capillaroid root	8.7 ± 2.4	8.4 ± 3.8	12.4 ± 1.2	0.127	0.134	0.15	2043	1969	1808
Chionochloa rubra									
Foliage	16.5 ± 1.3	17.0 ± 1.9	17.4 ± 0.7	0.181	0.188	0.191	1447	1446	1336
Bases and roots	12.5 ± 13.1	27.7 ± 1.9	31.1 ± 2.7	0.18	0.326	0.377	1107	801	708
*Machaerina juncea**	17.3 ± 6.4			0.142					
*Gleichenia dicarpa**	10.1 ± 1.0			0.08					

6.3.3.4 Litter decay and mire environment

A matrix of Spearman correlation coefficients with Bonferroni adjustment for multiple comparisons show mass and nutrient losses are not linearly correlated with the environmental variables measured at the study sites (Table 6.8).

Table 6.8: Nonparametric Spearman rank-correlated coefficients for litter decay and substrate quality parameters with Bonferroni adjustment for multiple comparisons. Note: No significant correlations were indicated by comparisons.

Source	**%Mass Loss**	**%N release**	**%P release**	**%K release**
pH	-0.118	-0.091	0.076	0.104
Bulk density (g/cm^3)	0.150	0.100	-0.008	0.010
LOI %	-0.041	-0.071	-0.074	-0.050
Conductivity (mS/cm)	-0.072	-0.092	0.006	0.005
Ca (cmol(+)/kg)	-0.072	-0.086	0.006	0.015
Mg (cmol(+)/kg)	-0.090	-0.052	0.016	0.003
K (cmol(+)/kg)	-0.203	-0.068	0.039	-0.028
Na (cmol(+)/kg)	-0.244	-0.062	0.147	0.018
CEC (cmol(+)/kg)	-0.134	-0.047	-0.023	-0.050
NO_3-N (mg/kg)	-0.066	-0.073	0.095	-0.018
NH_4-N (mg/kg)	-0.138	-0.096	0.013	-0.016
Olsen-P (mg/kg)	-0.020	-0.007	-0.056	-0.068
C:N	-0.113	-0.099	-0.029	-0.114

6.4 Discussion

The hypotheses raised by this study are that the litter of the ecosystem engineer *Empodisma minus* is of lower quality (i.e. lower nutrient content & higher structural carbohydrates) than that of the fen species *Chionochloa rubra*, and will therefore decompose more slowly; and that the nutrient content of the litter and the rate of decay will decline towards the mire centre. This study suggests both species produce foliar litters of low nutrient content, with high N:P ratios, which decompose at similar rates. In contrast to the foliar litters, *Chionochloa rubra* stem bases and roots contain more nutrients and lower concentrations of fibre and lignin than *Empodisma minus* capillaroid roots, and lose more mass than *Empodisma minus* capillaroid roots over the 12 month decomposition period. Olsen-P levels in the substrate decline towards the mire centre, as do *Empodisma minus* tissue-P levels, which may reflect increasing P-limitation. Percentage mass losses from below-ground litters of both species are more similar in the wet oligotrophic mire centre, than in the surrounding wet tussockland community.

6.4.1 A transitional mire

The central mire communities examined comprised two main types, a Dry Fen with a mixed *Chionochloa rubra-Empodisma minus* canopy, and a Wet Fen downstream of a groundwater seepage, with an *Empodisma minus* canopy and few, scattered tussocks. In contrast to declining *Chionochloa* tussock size, mean *Empodisma* canopy productivity was maintained in the Wet Fen, compared to the drier mire conditions elsewhere. Peat chemistry suggests that although oligotrophic, the mire might best be labeled an oligotrophic fen or transitional mire, approaching ombrotrophy. With the low summer water table, the hummock microforms are isolated from the water table for a substantial period of the year, the water table within the rooting zone during only the wettest months.

Comparisons with similar mires are difficult to make, since equivalent studies of transitional restiad mires are sparse. The peat substrate contains less carbon than Duck Creek (Coromandel), where *Empodisma robustum* has only recently arrived (Clarkson *et al.*, 2004a), though the bulk density and pH of the substrates are similar. The von Post decomposition index of surface peat at Silica Rapids was lower in both fen communities than that of Duck Creek (Von Post 7 & 3, respectively), implying a greater degree of organic matter decomposition at Duck Creek. The difference in organic matter content in the surface peat may reflect the influence of recent tephra inputs at the Silica Rapids site.

6.4.2 Nutrient content of senescing foliar litter

The foliar litter produced by *Empodisma minus* was of low nutrient content, containing low tissue-P concentrations, which declined along an internal mire gradient. While recognising the limitations of this study, these results suggest that *Empodisma minus* can potentially relocate a greater proportion of P from the senescing biomass, as oligotrophication occurs during raised mire development. In contrast to the tissue-P levels, the fibre, cellulose and lignin contents of the *Empodisma minus* litter in all communities stayed relatively constant.

Nutrients withdrawn from leaves prior to abscission are redeployed to storage or newly developing leaves, allowing nutrients to be re-used, rather than lost in the litter pool. While we did not measure nutrient resorption and proficiency *per se* in our study, our nutrient data indicate *Empodisma minus* withdraws nutrients from senescing culms in the order K (94%) >P (79%) >N (46%). This in line with findings elsewhere which demonstrate high P resorption among mire plants (Jonasson & Chapin, 1985; 1991; Sorrell *et al*, 2011), K being a highly mobile ion, rapidly depleted during senescence. The high nutrient withdrawal from *Empodisma minus* culms appears to be linked to substrate nutrient availability, senesced culms with the lowest nutrient content produced in the Wet Fen community, where P-limitation was greatest.

N and P resorption from senescing tissues in vascular species is approximately 50%, depending upon species and environmental conditions (Killingbeck, 1996; Aerts, 1996), though correcting for mass loss during senescence may increase these rates (van Heerwaarden *et al.*, 2003). Our results indicate *Empodisma minus* nutrient resorption is likely higher than the average for vascular species, reflecting the nutrient conservation strategy necessary in the oligotrophic, engineered raised mire environment (Chapter 4). Stock *et al.* (1987) demonstrated another restiad *Thamnochortus punctatus* persisted on low nutrient soil by utilising an asynchronous growth habit, enabling the plant to recycle nutrients between organs (inflorescences, culms, rhizomes and roots). 70% of N in mature culms was remobilized or lost to leaching in the senesced culms (Stock *et al.*, 1987), compared to 46% indicated in this study. *Eriophorum vaginatum*, a Northern Hemisphere mire ecosystem engineer, also utilises a sequential growth habit, exporting nutrients from mature, to subsequent leaves, and also resorbing >80% of nutrients from canopy biomass prior to senescence (Jonasson & Shaver, 1999). High nutrient resorption from fine roots has been demonstrated (Freschet *et al.*, 2010), although this is not easily demonstrated in the field, especially given the litter entrapment in the *Empodisma minus* capillaroid root weft. The nutrient efficiency and proficiency of *Empodisma minus* warrants further investigation, to confirm these preliminary findings.

The early stages of foliar litter decay in montane restiad mires occur in the canopy, as both species initially retain senesced canopy biomass. As a result, leaching may remove soluble carbohydrates and nutrients, and fungal decomposers may colonise the standing dead material (Lee *et al.*, 2004; 2006). While our results suggest only K continues to decline to any great extent in the standing dead *Empodisma minus* culms (a further 24% K reduction), we did not investigate the nutrient content of the fragmented canopy litter, or the levels of soluble carbohydrates, in order to determine how nutrient levels decline prior to litter fragments reaching the mire surface. In addition to directing ombrotrophic nutrients to its capillaroid roots via stemflow (Agnew *et al.*, 1993), the leaching of ammonium and soluble reactive P losses from Restionaceae culms (Raubenheimer & Day, 1991) suggests stemflow may also act to redirect leaching losses from the *Empodisma* canopy back to the capillaroid roots. As cluster roots production in P-limited conditions is enhanced by ammonium additions (Sas *et al.*, 2002), leaching of ammonium from *Empodisma* culms may encourage capillaroid root proliferation, explaining the proliferation of capillaroid roots around the stems (Agnew *et al.*, 1993). Conversely, removal of the ammonium "signal" by excessive precipitation may limit capillaroid root initiation, and might explain the lower abundance of *Empodisma minus* capillaroid roots in permanently saturated substrates (Chapter 3). The relevance of leached nutrients in restiad mire nutrient budgets is suggested as a future research question to be addressed.

6.4.3 Litter Decomposition and Ecosystem Engineering

The hypothesis raised in the study predicted the litter of the ecosystem engineer *Empodisma minus* would decompose more slowly that of the fen species *Chionochloa rubra*. This research demonstrates this to be true for below-ground litters only. Both species showed low initial mass losses, similar to the decay rates of the mire species *Gleichenia dicarpa* and *Machaerina juncea* (17.3 & 10.1% respectively) in a New Zealand fen (Pegman & Ogden, 2006). In contrast to the current study, Pegman & Ogden (2006) placed the litter samples below the water table at the site, further inhibiting decomposition rates, and limiting comparisons between the studies.

The Leaf Economic Spectrum (LES) (Wright *et al.*, 2004) proposes an integrated plant strategy, controlling the decomposability of all plant organs, including roots and rhizomes (Cornwell *et al.*, 2008; Freschet *et al.*, 2012; Birouste *et al.*, 2012). At an ecosystem level, this will result in a co-ordination of the impact of above- and below-ground litters on positive feedback loops between soil and plant species (Freschet *et al.*, 2012). The LES suggests that both the above and below-ground litters produced by *Empodisma* species would be similarly slow to decompose. Our results agree with those predicted by the LES, as although I found *Empodisma minus* capillaroid root litters decomposed less than culm and rhizome litters, the short-term decay rates of all litters were low. The 12-month decay rates for the capillaroid roots were within the range published for *Sphagnum* species in Northern Hemisphere bogs (5-15%) (van Breeman, 1995; Bayley *et al.*, 2005), the capillaroid roots being the functional equivalent of *Sphagnum* in restiad mires (Agnew *et al.*, 1993).

Below-ground litter from roots and rhizomes can play an important part in peat accumulation, ecosystem engineering and nutrient cycling in fens (Hughes *et al.*, 2002; Bragazza *et al.*, 2008). While roots decomposing in the acrotelm normally contribute little to long-term peat accumulation compared with *Sphagnum* biomass, or with roots growing in the catotelm (Moore *et al.*, 2007), Bragazza *et al.* (2008) suggest the roots of species adapted to waterlogging decay more slowly. The decay rates of the rhizomes and tussock bases/roots of *Chionochloa rubra* and *Empodisma minus* were higher than those of capillaroid roots (12.5 & 16.4% respectively), but less than those of a range of sedge and grass species in Northern Hemisphere fens (21-60%) (Thormann *et al.*, 2001). The accumulation of slowly decaying roots and tussock bases may also lead to the fen-bog transition, forming an impermeable layer that hastens hydrological isolation of the mire (Hughes, 1997). Biomass data suggest *Empodisma minus* may have greater below-ground biomass production than the taller *Empodisma robustum*, which suggests a greater potential contribution from rhizomes to peat accumulation in *Empodisma minus* mires. These differences reflect the resprouter versus reseeder strategies of the two species (Wagstaff & Clarkson, 2012), with resprouters investing in a greater below-ground biomass than reseeders. While there is no suggestion in the albeit limited macrofossil data available, that the roots and rhizomes of either of the two species in this study play a similar role to those of *Eriophorum vaginatum* in Northern Hemisphere mires (Hughes, 2002), litter experiments incorporating longer time periods are required to determine the ultimate fate of these litters.

Net rates of nutrient release (or accumulation) varied between both litter types, and vegetation community. *Chionochloa* foliar litters are known to accumulate nutrients during initial decomposition (Molloy *et al.*, 1977), due to a marked increase in microbial biomass, however, little is known of *Empodisma* decay processes. Bengtsson *et al.* (2012) suggests the high initial rates of nutrient accumulation in restiad litter reflect either fungal activity or passive transport into the litter from the surrounding soil, nutrient accumulation being necessary to initiate the delayed decomposition processes in the poor quality litter. While fungal activity in restiad decomposition has been extensively researched in the fynbos (e.g. Lee *et al.*, 2004; 2006), the relative importance of fungal decomposition in New Zealand restiad mire processes is unknown, though it represents a potential source of P accumulation during early decay processes. Given that P-limitation in the mire substrate was indicated, it seems unlikely that the observed P accumulation occurred as a result of passive transport processes. An additional explanation might lie in the higher *Empodisma minus* capillaroid root densities in the hummock-hollow topography of the Dry Fen community. Nutrient acquisition by the dense capillaroid roots in these hummocks may create zones of nutrient depletion, and hence higher nutrient immobilisation rates. Nutrient accumulation may also result from *Empodisma* capillaroid roots growing into litterbags, the roots being difficult to separate and remove (Bev Clarkson, *pers. comm.*). *Empodisma minus* forms capillaroid roots at lower densities than *Empodisma robustum* (Wagstaff & Clarkson, 2012), and roots penetrated only two litterbags in this study, from which they were easily removed. This suggests the explanation(s) for the increased P levels in rhizome litters lie elsewhere. Further study of the microbial and fungal biota, the function of hummock-hollow topography in restiad mires, and long-term decomposition processes is warranted.

6.4.3.1 Decomposition, environment and microtopography

Spearman correlation coefficients suggested litter decay was not linearly correlated with substrate chemistry or nutrient quality. The environmental variables measured were those chosen to highlight changes in peat chemistry with distance from mire edge, as a proxy for increasing ombrophication, however, there was no significant difference between the three communities for most of the chemistry variables measured. An incomplete set of hydrological data resulted in its exclusion from the analysis, despite large differences in water table variability being suggested by the limited piezometer data. The position of litter with regard to the water table is of importance, Johnson & Damman (1991) observing differences in *Sphagnum* decomposition rates between the anoxic and oxic zones within hummock microforms. The surface of the Wet Fen community contained negligible microtopography (lawn), while extensive hummock-hollow topography has developed in the Dry Fen, and the difference in microtopography may help explain the differences in nutrient release observed.

At Silica Rapids Mire the hummock comprises a dense collection of live and dead *Empodisma minus* capillaroid roots, rhizomes, buried stems, occasional *Gleichenia dicarpa* rhizome and stem material, and entrapped litter. *Empodisma minus* engineers the hummock environment, possessing both principle mechanisms involved in hummock construction; high below-ground productivity through apogeotropic capillaroid root and rhizome production, and a lower decomposition rate of the senesced below-ground biomass than that of co-existing mire species. These two mechanisms allow *Empodisma minus* to continuously add to the enduring geomorphological signature that is the raised peat bog (Jones, 2012), due to the continual formation of durable structures (capillaroid root filled hummocks), at a higher rate than the rate of decay. The small size, topography and recent development of the Silica Rapids mire preclude the formation of a raised bog to date, however, hydrological isolation of the hummock microforms may occur during the drier months when the water table drops considerably below the mire surface. Hydrological isolation will result in the ombrophication of the individual hummocks and increasing reliance on capillaroid root expansion for nutrient acquisition, increasing hummock size and peat accumulation rates.

Capillaroid root expansion inside hummock microforms has further consequences for decomposition processes. While some cluster root bearing taxa demonstrate the ability to reduce microbial access to phosphorus supplies by lowering pH, and release phenolics which inhibit microbial and fungal populations (Marschner *et al.,* 2002; Weisskopf *et al.*, 2006), rhizodeposition during phosphorus acquisition can also result in the proliferation of microbial populations (Lambers *et al.*, 2009). Bacteria have been implicated in the initiation of cluster roots (Malajczuk & Bowen, 1974; Lamont, 1986), and the bacterial communities in the rhizosphere surrounding cluster roots differ from those surrounding non-cluster roots, with some strains able to utilize cluster root exudates as carbon sources (Weisskopf *et al.*, 2011). Unfortunately, the microbial communities of montane restiad mires are largely undescribed, and the links between microbial populations, capillaroid root formation and decomposition processes unknown. Since capillaroid roots are a critical component of the ecosystem engineering process in montane restiad mires, the importance of rhizodeposition by *Empodisma minus* capillaroid roots as a carbon source for microbial communities, and as an inhibitory factor during plant growth and litter decomposition in restiad mire succession, warrants further investigation.

Empodisma minus rhizomes were restricted to the upper 20cm of the peat profile across the mire. I found greater underground (rhizome) biomass in the hummocks of the Dry Fen community, compared to the *Empodisma minus* lawn in the Wet Fen community, though the difference was not significant. The creation of habitat for rhizome emplacement above the water table represents a positive feedback to the species. Increased rhizome biomass further enables a greater concentration of capillaroid roots in the growing hummocks, as the capillaroid roots cluster around the stems arising from the abundant rhizomes (Campbell, 1964; Agnew *et al.*, 1995).

The capillaroid root weft relies on capillary action to maintain internal moisture levels in the hummock, and might be susceptible to desiccation, if not for the eco-hydrological effect of the dense canopy and litter layer (Campbell & Williamson, 1997). Similar findings are suggested in Northern Hemisphere bogs, where the slow decomposition of hummock *Sphagna* promotes the open structure of hummock peat that aids in water retention, despite the hummock microhabitat corresponding to higher overall decomposition rates (Turetsky *et al.*, 2008). The importance of the *Empodisma* capillaroid root weft for maintaining anoxia is well cited (Campbell, 1964; Agnew *et al.*, 1995; McGlone, 2009; Hodges & Rapson, 2010), however, Agnew *et al.* (1995) suggest anoxia does not result from root weft formation, and the interaction between capillaroid roots, hummock structure and hydrology warrants further investigation.

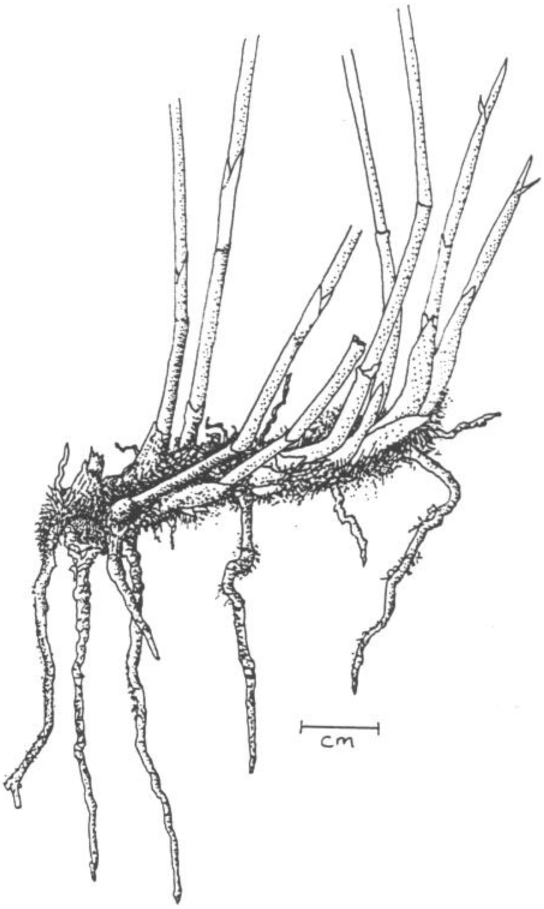
6.5 Conclusions

While the data presented represent only a snapshot of mire productivity and short-term decomposition processes in a montane restiad mire, limiting inferences about nutrient resorption and long-term decomposition processes, the preliminary results emphasize the role of *Empodisma minus* as an ecosystem engineer (*sensu* Jones *et al.*, 1994) of the FBT in New Zealand mires.

Unexpectedly, we found both *Empodisma minus* and *Chionochloa rubra* produce low quality foliar litter that decomposes slowly in the mire environment. *Empodisma minus* tissue N and P declines as its foliage senesces, with more P than N relocated prior to abscission. *Empodisma minus* capillaroid roots decay the slowest of the above- and below-ground litters, facilitating the transition from *Chionochloa* rich minerotrophic fen to restiad bog. *Empodisma minus* is a successful competitor in wet, oligotrophic conditions of the mire environment, while *Chionochloa rubra* tussocks are reduced in density and biomass. There is a significant relationship between short-term decay rates and location within the mire. However, this appears to be unrelated to the nutrient content or geochemistry of the substrate. Piezometer measurements suggest large differences in water table variability across the mire, with portions of the mire surface isolated from the water table during the summer months. Water table variability may interact with hummock microforms, dominated by *Empodisma minus* capillaroid roots and rhizomes, to alter decomposition rates across the mire.

The slow decomposition of *Empodisma minus* capillaroid roots demonstrated in this study suggest the allelopathic (Kuder *et al.*, 1998) and physiological (Campbell, 1981) processes behind *Empodisma robustum* rootlet preservation may apply equally to *Empodisma minus* capillaroid root accumulation in montane and southern restiad mires. To date, investigations into capillaroid root functioning in *Empodisma* have utilised samples now classified as *Empodisma robustum.* Given the recent taxonomic revision and the suggestion of differences in capillaroid root density between the species (Wagstaff & Clarkson, 2012), further examination of *Empodisma minus* capillaroid root morphology is warranted, especially those features which confer greater resistance to decay (Kuder *et al*, 1998).

Chapter 7: *Empodisma minus* as the ecosystem engineer of the New Zealand FBT: a summary



Empodisma minus. Drawing by Catherine Beard, reproduced with permission.

This chapter summarises the principal results of the previous four chapters in this thesis, identifying the contribution of these findings to the body of research.

The concept of ecosystem engineering received much attention following its introduction two decades ago. However, despite being identified as a likely ecosystem engineer within 12 months of the concept's introduction, the causal link between *Empodisma minus* and ecosystem engineering remained only partially examined. This situation was made more problematic by the recent taxonomic revision of the *Empodisma* genera, the existing body of literature largely examining the northern *Empodisma robustum*. I examined the mechanisms of habitat modification by *Empodisma minus*, and the implications on species interactions, with a special emphasis on the fen-bog transition (FBT). Transitional restiad mires are characterized by low nutrient availability, and the patchy distribution of *Chionochloa rubra* tussocks over a dense *Empodisma minus* sub-canopy. Research was conducted in mainland restiad mires and tussocklands, and in an artificial wetland in which the oligotrophic, anoxic wetland conditions of the FBT were approximated. I found the interactions between *Empodisma minus*, *Chionochloa rubra* and the environment to be important autogenic factors in transitional mires. While recognising the abiotic (allogenic) constraints on mire development (climate, hydrology & geology), small scale engineering activities influence peat accumulation rates and hence resource flows in the mires, having impacts at the species, community and landscape scales.

This thesis has significantly advanced the ecological understanding of New Zealand restiad mires by clarifying the role that *Empodisma minus* plays during mire development as ecosystem engineer. The thesis outlines the traits critical to the engineering process, and develops a new model by which mire engineers may be identified. The distribution and floristic composition of *Empodisma minus* wetland communities is described, and the physico-chemistry of their substrates compared. The role that slowly decaying below-ground biomass plays in carbon accumulation in southern restiad mires is confirmed, and insight into competitive relations between *Empodisma minus* and *Chionochloa rubra* during restiad mire development is provided.

Chapter 3 presents the first national survey of *Empodisma* dominated mires, and the first wetland survey to examine above-ground biomass, capillaroid root distribution, and hummock-hollow topography in New Zealand restiad mires. This survey occurred prior to the taxonomic revision of the genus, and so included both *Empodisma minus* and *Empodisma robustum* mires.

Eight *Empodisma* mire communities are described, which are underlain by a hydrological-soil texture gradient. The gradient of communities range from drier soils in central North Island sites with communities featuring a high *Gleichenia* content, to wet *Empodisma-Sphagnum* communities found in regions with high orographic rainfall, or in regions where historical anthropogenic disturbance has led to changes in catchment hydrology. The study found that hummock-hollow topography and extensive *Empodisma* capillaroid roots are not confined to any one mire type or position along the hydrological-soil texture gradient, though infrequent in dry substrates and in very wet climates, suggesting strong abiotic control of engineering processes. A mire chronosequence to examine the distribution of these engineering traits further could not be created, as insufficient sites of varying type, within any one geographic region, and with similar disturbance histories, were surveyed.

An important outcome of the study is the confirmation that *Empodisma minus* in many southern restiad mires remnants has elevated tissue nutrient levels, indicating nutrient enrichment has likely occurred.

The study described in **Chapter 4** collated the literature on mire engineering by *Sphagnum* in Northern Hemisphere mires, and *Empodisma* species in New Zealand mires. This study extends the knowledge of *Empodisma minus* mire dynamics by identifying the important attributes associated with both the FBT and the mire engineer, providing a new synthesis and interpretation of existing material.

The model proposes a mire engineer differs from other mire species in that:

1. The ecosystem engineer is present before, during and after the engineering event, and is increasingly competitive in the engineered bog environment, so that it dominates;
2. The ecosystem engineer constructs the FBT by altering the mire environment, producing unpalatable, slowly decomposing above- and below-ground tissues, maintaining a high water table in the mire, and acidifying the substrate.

The study stresses the importance of moving from descriptions of the FBT, which are not causal, to providing explanations for the mechanisms of transition from fen to bog.

The model has been taken up by researchers since publication in 2010, as it provides a neat summary of *Empodisma* traits in New Zealand (and possibly Australian) mires.

The experiment described in **Chapter 5** was undertaken primarily to examine points (a) and (b) raised in **Chapter 4**, i.e. the competitiveness of the engineer in the engineered environment, and the nutrient quality of litters produced.

This is the first experimental study utilising an artificial wetland gradient to describe the competitive relations between *Empodisma minus* and another mire species. The outcome of the competition experiment confirms the model prediction that the mire engineer will be both present after the FBT, and more competitive in the engineered environment. Long-term competition indices indicate that as a consequence of engineering activities, *Empodisma minus* will outcompete *Chionochloa rubra* as conditions approach those of a transitional bog, and telluric waters are increasingly excluded. Extensive capillaroid root growth above the peat surface and at depth, occurs in greater volumes in these conditions.

Resorption and relocation of limiting nutrients from senescing foliage is suggested by tissue nutrient analyses, suggesting nutrient conservation likely occurs during senescence of *Empodisma minus* above- and below-ground biomass.

The litter decomposition study described in **Chapter 6** was undertaken in a mire included in the earlier field survey (Chapter 3) (Group 1a: *Empodisma-Gleichenia* community type).

This is the first study to describe the decay rates or nutrient content of *Empodisma minus* above- or below-ground litters in a New Zealand mire. The study found both *Empodisma minus* and *Chionochloa rubra* produce low nutrient foliar litter that decomposes slowly in the mire environment. *Empodisma minus* tissue N and P declines as its foliage senesces, with more P than N relocated prior to abcission. The study confirms that *Empodisma minus* capillaroid roots decay the slowest of the above- and below-ground litters, and likely comprise a large component of the accumulating peat (Point b above).

Chionochloa rubra tussocks are reduced in density and biomass towards the mire centre as a consequence, providing further evidence that *Empodisma minus* dominates in the wet, oligotrophic conditions of the engineered environment (Point a).

Concluding, *Empodisma* species are a common component in wetlands across New Zealand. The genus has a wide edaphic range, occurring in wetlands with both organic and mineral substrates, variable water table levels, and occurring from sea-level to over 1260m in altitude. *Empodisma minus* dominated restiad mires form in areas with seasonal rainfall deficits, and lower annual rainfall than that required for the development of raised mires in the Northern Hemisphere (McGlone, 2009). *Empodisma minus* appears to engineer the FBT in New Zealand mires via positive feedbacks between biomass production and decomposition, peat accumulation and resource flows. This thesis illustrates that *Empodisma minus* is the functional equivalent of *Sphagnum* in Northern Hemisphere mires, the production of slowly decaying capillaroid roots resulting in small-scale habitat modification, which can result in long-term and large scale changes in the mire ecosystem.

Chapter 8: Synthesis

This chapter synthesizes the principal results of Chapters 3-7 in a model of the ecosystem engineering of restiad mires by *Empodisma minus* in New Zealand. Research gaps are identified, and suggestions for further research efforts made.

Following a literature review that suggested a role for *Empodisma minus* as the ecosystem engineer of the FBT in New Zealand mires, the research questions addressed concerning the fen-bog transition (FBT) in New Zealand mires were:

1. The literature suggests a role for *Empodisma minus* as the ecosystem engineer of the FBT in New Zealand mires. What are the processes by which *Empodisma minus* engineers the FBT?
2. What are the environmental gradients associated with *Empodisma minus* distribution in New Zealand restiad fens and bogs?
3. To what extent do purported engineering traits/processes (e.g. production of decay resistant litters, capillaroid root and hummock-hollow topography) vary in *Empodisma* wetland communities, and specifically along the fen-bog gradient, i.e. are engineering efforts context dependent?
4. What are the consequences of ecosystem engineering processes and the FBT on co-occurring mire species?
5. What insights do these strategies offer about the role of autogenic versus allogenic factors across the New Zealand FBT?

Population and community ecologists have long recognised the disproportionate impact of some species on community composition, these ‘keystone’ species impacting other organisms through biotic interactions such as competition or predation. More recently, the importance of abiotic interactions between a species and its environment have been recognised by the proposal that some species act as ecosystem engineers (Jones *et al.*, 1994; 1997). Physical ecosystem engineers physically alter their environment, impacting the supply of resources to other species, and affecting species abundance and diversity. This occurs by either impacting the habitat through their own physical structures (autogenic engineers), or by modulating resources from one physical state to another through their activities (Jones *et al.*, 1994; 1997). A number of organisms were proposed as illustrations by Jones *et al.* (1994), including *Sphagnum* mosses. A classic example of an ecosystem engineer (Jones *et al.*, 1994; van Breeman, 1995), *Sphagnum* mosses have unique organic, chemical and structural properties that contribute to autogenic processes occurring during mire development, hastening peat accumulation, and a change in trophic status in the mire (the FBT) (**Chapter 4**). *Empodisma* species are a common component of New Zealand and Australian mires, that were recognised as another putative mire engineer (van Breeman, 1995).

Mire development occurs when primary productivity in the vegetation community is greater than the rate of decay. The rate of microbial decomposition in a particular patch of mire depends upon the availability of resources to the microbial population, and the abiotic environment of the mire. Both of these factors are influenced by resource flows (e.g. nutrients, water, O_2) into and out of the mire environment, which can be directly influenced by the activities of the mire engineer. The engineer can alter the physical environment of the mire, affecting water movement across the mire and hydrologic interactions between the peat surface and atmosphere, resulting in changes to the flow of resources to the substrate, microbial and vegetation communities. Hummocks and hollows may act as barriers to water movement across the mire surface, stems of plants conduct water and nutrients to the surface via stem flow, and dense canopies act both as a barrier to atmospheric conditions, and to intercept nutrients contained in rainfall and fog.

The FBT represents an important step during raised mire development. It is the relatively rapid transition from a vascular plant dominated community with well humified, mineral rich peat of an intermediate pH, to an acidic, oligotrophic, less humified peat, with a vegetation community dominated by *Sphagna* and vascular species tolerant of the conditions created (Granath *et al*., 2010). After the FBT the surface peat and vegetation community are increasingly deprived of interactions with telluric water, and the relative proportion of ombrotrophic mire species increases with time (van Breeman, 1995; Juttonen *et al*., 2005). Key ecosystem functions such as biogeochemical cycles and species interactions are altered after the FBT (Scheffer et al., 2001; Lepällä et al., 2008), with declining substrate quality altering microbial population diversity, and resulting rates of decomposition and methanogenesis (Juttonen *et al.,* 2005; Merila *et al*., 2006; Jassey *et al*., 2011).

In Northern hemisphere mires, the *Sphagnum* species prior to and during the FBT are not those that dominate in the raised mire environment (Rydein & Jeglum, 2006), with changes in species composition also reflecting the increase in surface microtopography and spatial variation (Lepällä *et al*., 2008). Different *Sphagnum* species dominate the hummocks and hollows of the mire surface, hummock species withstanding greater dessication, due to greater capillarity and water storage abilities (Rydin, 1993). Unlike *Sphagnum* species in

Northern Hemisphere mires, *Empodisma* species tolerate a wider range of environmental conditions, being dominant in the engineered environment, the engineering event assumed to be part of the evolutionary strategy of the species for self-perpetuation (Jones *et al*. 1994; van Breeman & Finzi 1998).

In this thesis, my aims were twofold: first I generated a model of how mire engineers might operate, identifying where the literature suggested further research was required to confirm *Empodisma*'s role in New Zealand raised mire development. Second, I examined *Empodisma* traits in natural and experimental wetlands, to provide insight into how *Empodisma'*s engineering activities would influence short and long-term mire development and species interactions. The insights on the functioning of New Zealand restiad mires presented here are based largely in restiad mire communities dominated by *Empodisma minus*, and with a scattered *Chionochloa rubra* tussock component. It is assumed that similar processes occur in northern lowland and southern restiad mires, and that the results presented may be applicable in *Empodisma robustum* mires, given the morphological and physiological similarities between the species (Wagstaff & Clarkson, 2012).

8.1 Environmental gradients in New Zealand *Empodisma*-dominated mires

Empodisma species have a wide edaphic range, being found on mineral and Organic Soils, from sea-level to 1260m elevation, acidic to circum-neutral substrates, and in climates with both moderate and high annual rainfall. A hydrology-soil texture gradient explains much of the variance between the *Empodisma*-dominated communities in New Zealand (**Chapter 3**). Oligotrophic montane fens and fernlands dominated by *Empodisma minus* and *Gleichenia dicarpa* form on drier substrates on the Central North Island volcanoes and axial ranges, while at the opposite end of the hydrological gradient are the *Empodisma-Sphagnum* bogs and fens of the West Coast of the South Island, Southland, and Te Urewera National Park, which have acidic, wet peats of very low bulk density.

The increasing peat accumulation underlying the hydrology-soil texture gradient in the mires does not reflect a fen-bog gradient. *Empodisma* is very widespread in a variety of wetland types, and not all of the communities represent peat accumulating mires, notably fernland, pakihi and coal pavement communities (**Chapter 3**). In these communities capillaroid root growth is scarce or non-existent, as is the development of the hummock-hollow topography characteristic of raised mire communities (Howie & Tromp-van Meerveld, 2011). Capillaroid root growth is present in greater densities in oligotrophic fens, rand communities, and *Empodisma* dominated raised bog remnants, all of which represent communities present at various stages of the FBT in different regions of New Zealand. The presence of capillaroid roots and hummock-hollow topography in *Empodisma*-dominated mires of varying trophic status reinforces earlier literature, which suggests capillaroid roots are an important component of peat deposited during mid and later successional stages of mire development (Campbell, 1964). The absence of capillaroid roots and hummock-hollow topography in some wetlands suggests strong abiotic control of engineering process, and supports the idea that context dependency modulates the effects of mire engineering by controlling the ability of *Empodisma minus* to create peat pre-cursors, and hence modulate resources in wetland communities.

8.2 Capillaroid roots and litter production-the weapons of peat mass production

The model proposed (**Chapter 4**) suggests that once a part of the fen vegetation community, *Empodisma minus*' structures alter the flow of nutrient resources, creating an oligotrophic environment in which it is the superior competitor. Nutrient losses from tissues accumulating as peat are matched by nutrient inputs only obtainable from atmospheric sources, and thus the competitive traits in the engineered environment must include superior levels of nutrient access, and high rates of nutrient uptake and retention by *Empodisma*.

Superior nutrient access, compared to potential competitors, is achieved by pre-empting precipitation, so that any nutrients carried in the rainfall are disproportionately available to *Empodisma minus* (Agnew *et al.* 1993; Clarkson *et al.*, 2005). *Empodisma minus* has a dimorphic root system, with capillaroid roots that are apogeotropic in bogs (Campbell 1981). The roots are covered with "closely crowded persistent root hairs" (p. 9, Campbell *et al*., 1995) which allow a greater soil volume to be exploited, resulting in increased adsorption of slowly diffusing nutrients, such as P (Lambers *et al.*, 2008). In favourable conditions the roots can intertwine into a dense, felt-like mat, building up around the shoots of adjacent plants and engulfing fallen litter (Campbell *et al.*, 1995). The roots intercept nutrient-bearing rainfall via stemflow (Agnew *et al*., 1993), while other mire species can only access nutrients from within the substrate (Clarkson *et al*., 2009). Superior nutrient uptake from the low nutrient peat substrate is by these apogeotropic capillaroid roots and fine root hairs (Campbell 1981), as there is only limited colonization of *Empodisma* by arbuscular mycorrhizae (Clarkson *et al*., 2005). The roots give greater access to nutrients compared to co-ocurring species (Clarkson *et al.*, 2005; 2009).

Cluster root formation offers a competitive advantage to species in low nutrient soils (Lambers *et al.*, 2006), and has been previously linked to soil pH, Fe and organic matter content, and with nutrient deficiency in plants (Diem *et al.*, 2000). Competition and facilitation are important structuring processes within communities, and were examined in an artificial wetland where *Empodisma minus* and *Chionochloa rubra* were grown in various nutrient and water table conditions (**Chapter 5**). The competition experiment suggests capillaroid root growth in *Empodisma minus* may be high in low nutrient, transitional fens (**Chapter 5**), and in the conditions most similar to those facilitated by the actions of *Empodisma minus* as mire engineer, where *Chionochloa rubra* is excluded long-term from the community. The negative interactions revealed by the de Wit experiment are important in explaining the mosaic of communities found within and between mires, demonstrating that negative interactions can occur between ecosystem engineers and co-occurring species, and can determine long-term changes in community composition. Facililtative interactions are also thought to be important in stressful environments (Bertness & Callaway, 1994), and while not demonstrated in the de Wit study, they appear to be an important biotic influence in the construction of hummock-hollow topography in restiad and *Sphagnum* mires (**Chapter 3**).

Capillaroid root growth was first initiated in the competition experiment in response to high nutrient availability on the pot surface, into which the nutrient spray was directed via stemflow (**Chapter 5**). Root proliferation in response to increased nutrient supply is a useful strategy for cluster root bearing taxa (Raghothma, 1999), given the high cost of investment of carbon and other resources to the plant (Lambers *et al.*, 2008; 2009). The litter layer is also the site of highest proteoid and dauciform root proliferation (Jeffrey, 1967; Lamont, 1974; Playsted *et al.*, 2006), though cluster roots may also be found at depth, depending upon P availability (Lambers *et al.*, 2011). The apogeotropic root habit of *Empodisma* capillaroid roots assists in trapping the newly fallen litter, resulting in both preferential mobilisation of the P sorbed to the litter particles (Lambers *et al.*, 2008; Li *et al.*, 2010), and the formation of surface microtopography. Capillaroid root growth is extensive in *Empodisma* mires with thick litter layers under the canopy (**Chapter 3**). By targeting capillaroid root growth in the recently deposited litter, which is proportionately high in P, *Empodisma minus* is able to maximise P acquisition in an increasing P-limited mire environment. *Empodisma minus* apogeotropic root volume is thus potentially greater in transitional fens, where litter quality is higher (**Chapter 5**), or in bog remnants such as Pukerau where tissue nutrients suggest nutrient enrichment has occurred (**Chapter 3**). Rapid capillaroid root proliferation in mesotrophic fen environments would explain the rapid colonisation of mires by *Empodisma minus* following initial establishment (McGlone & Bathgate, 1983; Clarkson *et al.*, 2004a).

Where litter or organic matter is lacking, such as in the coal pavement communities of the Denniston Plateau, *Empodisma minus* forms no capillaroid roots (**Chapter 3**). Similarly, little capillaroid root development occurs in drier fernland communities in the central North Island, or in pakihi communities. The tissue nutrient levels of *Empodisma minus* are low in these communities (e.g. N:P ratio=52.03 at Denniston Plateau), indicating capillaroid root in *Empodisma minus* responds to abiotic controls in addition to tissue nutrient deficiency. Capillaroid root growth is inhibited by excess soil water (Watt & Evans, 1999), and annual rainfall at Denniston is high, resulting in high soil moisture levels. In contrast, the fernland communities are associated with drier substrates (**Chapter 3**). The paucity of capillaroid roots in both permanently wet, and drier substrates suggests *Empodisma minus* capillaroid root development is influenced by soil moisture levels (**Chapter 3**), i.e that ecosystem engineering by *Empodism minus* is limited by hydrogeomorphological controls on capillaroid root initiation and production. Annual rainfall or water deficit at the site and capillaroid root growth are not correlated (*c.f.* Agnew *et al.*, 1993), suggesting a complex relationship between engineering traits and hydrology.

The "wet desert" effect (Campbell & Williamson, 1997) employed by *Empodisma robustum* in northern restiad mires enables the species to facilitate cluster root growth by increasing the moisture levels of surface soil horizons, in addition to the capillary effect of the root weft itself. Dead stems (including suspended litter), comprise a large component of the total canopy biomass in most mire types (**Chapter 3**), and is retained within the lower *Empodisma minus* canopy (Figure 8.1). While soils high in organic matter can retain too much moisture during the wet season to allow cluster root initiation in some species (Donoso-Nanculao *et al*., 2010), the apogeotropism of *Empodisma* roots offers an advantage in these conditions (Sorrell *et al.,* 2000). Only when *Empodisma minus* canopy biomass dominates the canopy, are extensive capillaroid root produced (**Chapter 5**), suggesting an *Empodisma minus*-driven FBT will only occur in herbaceous fen communities containing less shrub and tussock canopy biomass. A high shrub or tussock component in the canopy may moderate the canopy-hydrology relationship observed by Campbell & Williamson (1997), reducing soil-moisture levels, inhibiting capillaroid root production, and hence engineering activities.

Superior nutrient retention by the engineer in the oligotrophic raised mire environment is a key component of autogenic models of bog formation (van Breeman, 1995), and is achieved by the production of long-lived evergreen foliage, and large and long-lived rhizome and root systems through which scarce nutrients may be relocated or stored (Chapin 1980). Nutrients withdrawn from leaves prior to abscission are redeployed to storage or newly developing leaves, allowing nutrients to be re-used. *Empodisma minus* produces long-lived culms, and retains its senesced foliage longer than *Chionochloa rubra* (**Chapter 5**), creating almost no litter during the 26-month experiment. The foliar litter produced by *Empodisma minus* is of low nutrient content (**Chapter 6**). While I did not measure nutrient resorption and proficiency *per se* in this study, the nutrient data indicate *Empodisma minus* withdraws nutrients in senescing culms in the order K (94%) >P (79%) >N (46%). This in line with findings elsewhere which demonstrate high P resorption among mire plants (Jonasson & Chapin, 1985; 1991; Sorrell *et al*., 2011). While the fibre, cellulose and lignin content of *Empodisma minus* litter does not alter, a greater proportion of P is relocated from the senescing culms as oligotrophication increases along internal mire gradients.

Below-ground litter from roots and rhizomes can play an important part in peat accumulation, ecosystem engineering and nutrient cycling in fens (Hughes 2002; Bragazza *et al*., 2008). *Empodisma*'s capillaroid roots accumulate as peat due to their abundance, capacity for water retention, chemical inertness and resistance to decay (Campbell, 1983; Kuder *et al.*, 1998). The capillaroid roots have high hemicellulose, and low polyphenol and lignin contents, chemistry which in other species is associated with fine or amorphous detritus upon decomposition (following Kuder *et al.*, 1998). The thicker axes of the roots and stems are high in lignin and polyphenols, which increases their resistance to decay by inhibiting microbial activity, and, with possible allelopathic properties, facilitates the competitive exclusion of other mire species (Kuder *et al.*, 1998). While roots decomposing in the acrotelm normally contribute little to long-term peat accumulation compared with *Sphagnum* biomass, or with roots growing in the catotelm (Moore *et al*., 2007), roots of species adapted to waterlogging decay more slowly (Bragazza *et al.*, 2008). The decay rates of the rhizomes and tussock bases/roots of *Chionochloa rubra* and *Empodisma minus* are higher than those of capillaroid roots (12.5 & 16.4% respectively), but less than those of a range of sedge and grass species in Northern Hemisphere fens (21-60%) (Thormann *et al*., 2001) (**Chapter 6**).

Figure 8.1 Dense senesced *Empodisma minus* culms comprise a large component of the canopy biomass of hummocks at at Waipakihi Mire, Tongariro National Park, March 2013.

Biomass data suggest *Empodisma minus* may have greater below-ground biomass production than *Empodisma robustum*, which suggests a greater potential contribution from rhizomes to peat accumulation in *Empodisma minus* sites. These differences reflect the resprouter versus reseeder strategies of the two species (Wagstaff & Clarkson, 2012), with resprouters investing in a greater below-ground biomass than reseeders.

The construction of hummock-hollow topography by *Empodisma minus* allows an intricate feedback between *Empodisma* and its environment, by creating an environment which elevates capillaroid root growth above the periodically saturated substrate. *Empodisma* hummocks comprise mainly *Empodisma* capillaroid roots, rhizomes, culms and entrapped litter (**Chapter 3**), the improved growing conditions of the hummock constituting a positive feedback to the species. The slowly decaying *Empodismsa* culms still attached to the rhizomes, and perhaps the *Gleichenia* biomass appear to provide the necessary support for hummock formation (**Chapter 3**). Where *Sphagnum* is dominant in the community, *Empodisma minus* instead appears to facilitate *Sphagnum* hummock growth by providing structural support (de Groot, 1999), the surface of the *Sphagnum*-rich *Empodisma* communities containing the most extensive hummock-hollow topography (**Chapter 3**). The FBT in these mires, which occur in regions with high annual rainfall and no seasonal water deficit, is likely engineered by *Sphagnum cristatum*.

8.3 Conclusions and recommendations for further research

All the studies in this thesis raise further questions for future research, as does the recent taxonomic revision of the genus, which occurred during the project. The revision raises several questions about the model constructed in **Chapter 4**; do engineering traits previously identified in *Empodisma robustum* as influencing northern lowland restiad fen development apply to southern restiad mires and *Empodisma minus*? Differences in fire response strategies and capillaroid root densities point to physiological differences between the species, and suggest the ready application of seminal papers in the existing body of literature to southern fens should not be assumed (e.g. Campbell & Williamson, 1997). For example, what are the compounds responsible for the low decomposition rate of *Empodisma minus* foliage and capillaroid roots? Is stem flow as important in the nutrient economy of southern mires?

New Zealand restiad wetland communities are threatened by continuing development of wetlands for agricultural purposes, fire, drainage and nutrient additions. In ideal conditions, *Empodisma minus* can invade a minerotrophic sedge fen community, rapidly forming a dense canopy and transitional bog environment (McGlone & Bathgate, 1983). However, due to the development of wetlands for agricultural purposes, there are few regions where further restiad fen development is possible (**Chapter 3**). Oligotrophication is now underway at two North-west Taupo sites (Maramataha Mire & Whenuakura Clearing), as seen by the recent arrival and rapid vegetative spread of *Empodisma minus* (Clarkson & Clarkson, 1984). These transitional mires occur at the northern-most extent of *Empodisma minus* distribution (see Appendix 8.1 for map of sites), and provide the best future opportunity for the study of *Empodisma minus* engineering processes, and accompanying mire development.

Surface patterning in mires is controlled by complex interactions between allogenic and autogenic factors (Dickinson *et al.*, 2002), and a more in depth investigation than was allowed for in this study (**Chapters 3 & 6**) is required to disentangle the relationship between *Empodisma* and hummock-hollow topography production.

Cluster roots mine the soil for scarce P resources, releasing large volumes of carboxylates (organic acids) into the soil to compete for P at binding sites, forcing the P into solution (Lambers *et al.*, 2012). *Empodisma* capillaroid roots are assumed to act similarly. However, compared to proteoid and dauciform roots, there has been little investigation of capillaroid root function, and none into the identity of the carboxylates which may be involved. With differences in capillaroid root density identified between the two *Empodisma* species (Wagstaff & Clarkson, 2012; **Chapter 3**), similar differences in carboxylate release may exist. Investigations into the relationship between capillaroid root initiation, substrate and tissue nutrent deficiency are also warranted.

Bacteria have been implicated in the initiation of cluster roots (Malajczuk & Bowen, 1974; Lamont, 1986), and the bacterial communities in the rhizosphere surrounding cluster roots differ from those surrounding non-cluster roots, with some strains able to utilize cluster root exudates as carbon sources (Weisskopf *et al*., 2011). Unfortunately, the microbial communities of montane restiad mires are largely undescribed, and the links between microbial populations, capillaroid root formation, carboxylate exudation and decomposition processes are unknown. Capillaroid roots are a critical component of the ecosystem engineering process in restiad mires. The importance of rhizodeposition by *Empodisma minus* capillaroid roots as a carbon source for microbial communities, and as an inhibitory factor during plant growth and litter decomposition in restiad mire succession, therefore warrants further investigation.

High N:P ratios in live foliar biomass from *Empodisma* species (**Chapter 3**) suggest P-limited growth in most unimpacted restiad mires, however, fertilisation experiments to confirm this have yet to be undertaken.

The Litter Decomposition and de Wit studies (**Chapters 5 & 6**) suggest nutrient relocation from senescing *Empodisma* culms occurs, while elevated nutrient concentrations in *Empodisma* rhizomes suggest the rhizomes may function as a nutrient storage organ. The part *Empodisma* rhizomes play in storing growth-limiting nutrients warrants further investigation.

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Appendices

3.1 Checklist of plant species recorded during New Zealand *Empodisma* wetland field survey.
3.2 Von Post Decomposition Index.
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Appendix 3.1

Checklist of plant species recorded during New Zealand *Empodisma* wetland field survey. Note: *= non-native species.

Acronym	*Species name*	*Family*
ACIAUR	*Aciphylla aurea* W.R.B. Oliv.	Apiaceae
AGRCAP	*Agrostis capillaris* L.*	Poaceae
AGRSTO	*Agrostis stolonifera* L.*	Poaceae
ALOGEN	*Alopecurus geniculatus* L.*	Poaceae
ANABEL	*Anaphalioides bellidioides* (G. Forst.) Glenny	Asteraceae
ANDEMP	*Androstoma empetrifolia* Hook. f.	Epacridaceae
ANIARO	*Anisotome aromatica* Hook. f.	Apiaceae
ANTODO	*Anthoxanthum odoratum* L.*	Poaceae
APOSIM	*Apodasmia similis* (Edgar) Briggs & L.A.S. Johnson	Restionaceae
APOBIF	*Aporostylis bifolia* (Hook. f.) Rupp & Hatch	Orchidaceae
ASPOBT	*Asplenium ?obtusatum* G. Forst.	Aspleniaceae
ASTNER	*Astelia nervosa* Hook. f.	Asteliaceae
BLEMIN	*Blechnum minus* (R. Br.) Ettingsh.	Blechnaceae
BLENOU	*Blechnum novae-zelandiae* T.C. Chambers & P.A. Farrant	Blechnaceae
BLEPEN	*Blechnum penna-marina* subsp. *alpina* (R. Br.) T.C. Chambers & P.A. Farrant	Blechnaceae
BULANG	*Bulbinella angustifolia* (Cockayne & Laing) L.B. Moore	Asphodelaceae
CALVUL	*Calluna vulgaris* (L.) Hull*	Ericaceae
CARALP	*Carpha alpina* R. Br.	Cyperaceae
CARCOR	*Carex coriacea* Hamlin	Cyperaceae
CARECH	*Carex echinata* Murr.	Cyperaceae
CARGAU	*Carex gaudichaudiana* Kunth	Cyperaceae
CARGER	*Carex germinata* Schkuhr	Cyperaceae
CAROVA	*Carex ovalis* Gooden.	Cyperaceae
CARSIN	*Carex sinclairii* Boott ex. Cheeseman	Cyperaceae
CARVIR	*Carex virgata* Sol. ex Boott	Cyperaceae
CELALP	*Celmisia alpina* (Kirk) Cheeseman	Asteraceae
CELDUB	*Celmisia dubia* Cheeseman	Asteraceae
CELGRA	*Celmisia gracilenta* Hook. f.	Asteraceae
CELGRM	*Celmisia graminifolia* Hook. f.	Asteraceae
CELINC	*Celmisia incana* Hook. f.	Asteraceae
CELSPE	*Celmisia spectabilis* Hook. f.	Asteraceae
CENUNI	*Centella uniflora* (Colenso) Nannf.	Apiaceae
CENCIL	*Centrolepis ciliata* (Hook. f.) Druce	Centrolepidaceae
CHIAUS	*Chionochloa australis* (Buchanan) Zotov	Poaceae
CHIJUN	*Chionochloa juncea* Zotov	Poaceae
CHIRUB	*Chionochloa rubra* Zotov	Poaceae
CIRARV	*Cirsium arvense* (L.) Scop.	Asteraceae
CLEQUA	*Clematis ?quadribracteolata* Colenso	Ranunculaceae
COPCHE	*Coprosma cheesemanii* W.R.B Oliv.	Rubiaceae
COPCOL	*Coprosma colensoi* Hook. f.	Rubiaceae
COPINT	*Coprosma intertexta* G. Simpson	Rubiaceae
COPPAR	*Coprosma parviflora* Hook. f.	Rubiaceae
COPPER	*Coprosma perpusilla* Colenso subsp. *perpusilla*	Rubiaceae
COPPRO	*Coprosma propinqua* A. Cunn.	Rubiaceae
COPPSE	*Coprosma pseudocunneata* W.R.B. Oliv. ex Garn.-Jones & Elder	Rubiaceae
COPTEN	*Coprosma tenuicaulis* Hook. f.	Rubiaceae
CRASPP	*Craspedia* "bog" unnamed	Asteraceae

DACGLO	*Dactylis glomerata* L.*	Poaceae
DONNOV	*Donatia novae-zelandiae* Hook. f.	Stylidiaceae
DRAFIL	*Dracophyllum filifolium* Hook. f.	Ericaceae
DRALON	*Dracophyllum longifolium* (J.R. Forst. & G. Forst.) R. Br. var. *longifolium*	Ericaceae
DRAOLI	*Dracophyllum oliveri* Du Rietz	Ericaceae
DRAPAL	*Dracophyllum palustre* Cockayne ex. W.R.B. Oliv.	Ericaceae
DRAPOL	*Dracophyllum politum* (Cheeseman) Cockayne	Ericaceae
DRAPRO	*Dracophyllum prostratum* Kirk	Ericaceae
DRAREC	*Dracophyllum recurvum* Hook. f.	Ericaceae
DRASUB	*Dracophyllum subulatum* Hook. f.	Ericaceae
DRAUNI	*Dracophyllum uniflorum* G. Simpson	Ericaceae
DROARC	*Drosera arcturi* Hook.	Droseraceae
DROBIN	*Drosera binata* Labill.	Droseraceae
DROSPA	*Drosera spathulata* Schult.	Droseraceae
ELEGRA	*Eleocharis gracilis* R. Br.	Cyperaceae
EMPMIN	*Empodisma minus* (Hook. f.) L.A.S. Johnson & D.F. Cutler	Restionaceae
EPAALP	*Epacris alpina* Hook. f.	Ericaceae
EPAPAU	*Epacris pauciflora* A. Rich.	Ericaceae
FESNOV	*Festuca novae-zelandiae* (Hack.) Cockayne	Poaceae
FORTEN	*Forstera tenella* Hook. f.	Stylidiaceae
GAHRIG	*Gahnia rigida* Kirk	Cyperaceae
GAISET	*Gaimardia setacea* Hook. f.	Centrolepidaceae
GAUCOL	*Gaultheria colensoi* Hook. f.	Ericaceae
GAUDEP	*Gaultheria depressa* Hook. f. var. *depressa*	Ericaceae
GAUMAC	*Gaultheria macrostigma* (Colenso) D.J. Middleton	Ericaceae
GENBEL	*Gentiana bellidifolia* Hook. f.	Gentianaceae
GERMIC	*Geranium microphyllum* Hook. f.	Geraniaceae
GLEDIC	*Gleichenia dicarpa* (R. Br.) Hook. f.	Gleicheniaceae
GLEMIC	*Gleichenia microphylla* R. Br.	Gleicheniaceae
GONMIC	*Gonocarpus micranthus* subsp. *micranthus* Thunb	Haloragaceae
HALBID	*Halocarpus bidwillii* (Hook. F. ex Kirk) Quinn	Podocarpaceae
HALBIF	*Halocarpus biformis* (Hook.) Quinn	Podocarpaceae
HEBODO	*Hebe odora* Cockayne	Plantaginaceae
HEBSTR	*Hebe stricta* var. *stricta* (Benth.) L.B. Moore	Plantaginaceae
HERNOV	*Herpolirion novae-zelandiae* Hook. f.	Anthericaceae
HIERED	*Hierachloe redolens* (Vahl.) Roem & Schult.	Poaceae
HOLLAN	*Holcus lanatus* L.	Poaceae
HYPRAD	*Hypochaeris radicata**	Asteraceae
ISOAUC	*Isolepis aucklandica* Hook. f.	Cyperaceae
JUNART	*Juncus articulatis**	Juncaceae
JUNBUF	*Juncus bufonius**	Juncaceae
JUNEDG	*Juncus edgariae* L.A.S. Johnson et K.L. Wilson	Juncaceae
JUNEFF	*Juncus effusus**	Juncaceae
JUNPLA	*Juncus planifolius* R. Br.	Juncaceae
JUNSQU	*Juncus squarrosus**	Juncaceae
LACFIL	*Lachnagrostis filiformis* (G. Forst.) Trin.	Poaceae
LEPAUS	*Lepidosperma australe* (A. Rich.) Hook. f.	Cyperaceae
LEPLAX	*Lepidothamnus laxifolius* (Hook. f.) Quinn	Podocarpaceae
LEPJUN	*Leptecophylla juniperina* (J.R. Forst. & G. Forst.) C.M. Weiller subsp. *juniperina*	Ericaceae
LEPSCO	*Leptospermum scoparium* J.R. Forst. & G. Forst.	Myrtaceae
LIPGUN	*Liparophyllum gunnii* Hook. f.	Menythaceae
LOBANG	*Lobelia angulata* G. Forst.	Campanulaceae
LOTPED	*Lotus pedunculatus**	Fabaceae
LYCDIF	*Lycopodielle diffusa* (R. Br.) B. Ollg.	Lycopoodiaceae
LYCLAT	*Lycopodiella lateralis* (R. Br.) B. Ollg.	Lycopoodiaceae
LYCFAS	*Lycopodium fastigiatum* R. Br.	Lycopoodiaceae
MACART	*Machaerina arthrophylla* (Nees) Koyama	Cyperaceae

MACRUB	*Machaerina rubiginosa* (Spreng) Koyama	Cyperaceae
MACTEN	*Machaerina tenax* (Hook. f.) Koyama	Cyperaceae
MACTER	*Machaerina teretifolia* (R. Br.) Koyama	Cyperaceae
MUHAXI	*Muehlenbeckia axillaris* (Hook. f.) Endl.	Polygonaceae
MYRNUM	*Myrsine nummularia* Hook. f.	Primulaceae
NERBAL	*Nertera balfouriana* Cockayne	Rubiaceae
NERDEP	*Nertera depressa* Banks & Sol. ex Gaertn.	Rubiaceae
NERSCA	*Nertera scapanioides* Lange	Rubiaceae
OREPEC	*Oreobolus pectinatus* Hook. f.	Cyperaceae
ORESTR	*Oreobolus strictus* Bergg.	Cyperaceae
ORESUB	*Oreostylidium subulatum* (Hook. f.) Berggr.	Stylidiaceae
OURMAC	*Ourisia macrophylla* Hook. subsp. *lactea* (L.B. Moore) Meudt	Plantaginaceae
OURVUL	*Ourisia vulcanica* L.B. Moore	Plantaginaceae
OZOLEP	*Ozothamnus leptophyllus* (G. Forst.) Breitw. & J.M. Ward	Asteraceae
PENPUM	*Pentachondra pumila* R. Br.	Epacridaceae
PHOCOO	*Phormium cookianum* Le Jol. subsp. *cookianum*	Xanthorrhoeaceae
PHOTEN	*Phormium tenax* J.R. Forst. & G. Forst	Xanthorrhoeaceae
PHYALP	*Phyllocladus alpinus* Hook. f.	Phyllocladaceae
PIMPRO	*Pimelea prostrata* (J.R. Forst. & G. Forst.) Willd. subsp. *prostrata*	Thymelaeaceae
POACOL	*Poa colensoi* Hook. f.	Poaceae
PODNIV	*Podocarpus nivalis* Hook	Podocarpaceae
POTSUB	*Potamogeton suboblongus* Hagstrom	Potamogetonaceae
PTEESC	*Pteridium esculentum* (G. Forst.) Cockayne	Dennstaedtiaceae
RACLAN	*Racomitrium lanuginosum*	Grimmiaceae
RANAMP	*Ranunculus amphitrichus* Colenso	Ranunculaceae
RANMUL	*Ranunculus multiscapus* Hook. f.	Ranunculaceae
RANREP	*Ranunculus repens* L.*	Ranunculaceae
RUBFRU	*Rubus fruticosus* agg.*	Rosaceae
RUMACE	*Rumex acetosa**	Polygonaceae
RYTGRA	*Rytidosperma gracile* (Hook. f.) Coonor & Edgar	Poaceae
SALCIN	*Salix cinerea* L.*	Salicaceae
SCHBRE	*Schoenus brevifolius* R. Br.	Cyperaceae
SCHFLU	*Schoenus fluitans* Hook. f.	Cyperaceae
SCHPAU	*Schoenus pauciflorus* (F. Muell.) F. Muell.	Cyperaceae
SPHCRI	*Sphagnum cristatum* Hampe	Sphagnaceae
SPHFAL	*Sphagnum falcatulum* Bescherelle	Sphagnaceae
STELYA	S*tegostyla lyallii* (Hook. f.) D.L. Jones & M.A. Clem	Orchidaceae
TAROFF	*Taraxacum officinale* agg.*	Asteraceae
TETCAP	*Tetraria capillaris* (F. Muell.) J.M. Black	Cyperaceae
THECYA	*Thelymitra cyanea* (Lindl.) Benth.	Orchidacea
TRIREP	*Trifolium repens**	Fabaceae
UNCRUB	*Uncinia rubra* Boott	Cyperaceae
UTRGEM	*Utricularia geminiscapa* Benj.*	Lentibulariaceae
VIOCUN	*Viola cunninghamii* Hook. f.	Violaceae
WAHALB	*Wahlenbergia albomarginata* Hook. subsp. *albomarginata*	Campanulaceae
WAHPYG	*Wahlenbergia pygmaea* Colenso subsp. *pygmaea*	Campanulaceae
ZOTTHO	*Zotovia thomsonii* (Petrie) Edgar & Connor	Poaceae

Appendix 3.2.

Von Post Decomposition Index. Adapted from Taylor & Pohlen, 1979.

Index	*Description*
D 1	Undecomposed: Plant structure unaltered. Yields only clear, colourless water.
D 2	Almost undecomposed: Plant structure distinct. Yields only clear water, coloured light yellow-brown.
D 3	Very weakly decomposed: Plant structure distinct. Yields distinctly turbid brown water; no peat substance passes between the fingers; residue not mushy.
D 4	Weakly decomposed: Plant structure distinct. Yields strongly turbid water; no peat substance escapes between the fingers, residue rather mushy.
D 5	Moderately decomposed: Plant structure still clear but becoming indistinct. Yields much turbid brown water; some peat escapes between the fingers; residue very mushy.
D 6	Strongly decomposed: Plant structure somewhat indistinct but clearer in the squeezed residue than in the undisturbed peat. About half the peat escapes between the fingers; residue strongly mushy.
D 7	Strongly decomposed: Plant structure indistinct but still recognisable. About half the peat escapes between the fingers.
D 8	Very strongly decomposed: Plant structures very indistinct. About 2/3 of the peat escapes between the fingers; residue consists almost entirely of resistant remnants such as root fibres and wood.
D 9	Almost completely decomposed: Plant structure almost unrecognisable. Almost all the peat escapes between the fingers.
D 10	Completely decomposed: Plant structure unrecognisable. All the peat escapes between the fingers.

Appendix 3.3

Wetland Condition Index worksheet. Guide to assigning degree of modification overleaf (modified from Clarkson *et al*., 2003).

Indicator	*Indicator components*	*Score 0-5*	*Mean Score*
Change in hydrological integrity	H1: Impact of manmade structure H2: Water table depth H3: Dryland plant invasion		
Changes in physico-chemical parameters	P1: Fire damage P2: Degree of sedimentation P3: Nutrient levels P4: Von Post index		
Changes in ecosystem intactness	E1: Loss in area of original wetland E2: Connectivity barriers		
Changes in browsing, predation and harvesting regimes	B1: Damage by domestic or feral animals B2: Introduced predator impacts on wildlife B3: Harvesting levels		
Changes in dominance of native plants	D1: Introduced plant canopy cover D2: Introduced plant understorey cover		
Total wetland condition index	/25		

Degree of modification:

- 5= very low/none
- 4= low
- 3= medium
- 2= high
- 1= very high
- 0= extremely high

Indicator and components	*Score and degree of modification*					
	5	4	3	2	1	0
H1: Impact of manmade structure	None/not impacting on wetland	<25% wetland affected	25-49% wetland affected	50-75% wetland affected	>75% affected	Totally dominated by structure
H2: Water table depth	No change	Lowered or raised occassionally and temporarily	Low during dry spells. Mean water table shows small decline with time	Low for long periods during dry spells. Mean water table noticeably declined with time	Very low most of year, not recharged by high rainfall events. Mean water table much lower than previous levels	Unable to be measured throughout season. "Dryland"
H3: Dryland plant invasion	No dryland plants	<25% of wetland has dryland spp.	25-49% of wetland has dryland spp.	50-75% of wetland has dryland spp.	>75% of wetland has dryland spp.	All species in wetland are dryland spp.
P1: Fire damage	No fire damage	Recent fires (<2 yr) removed vegetation in <25% of wetland; or, virtually recovered from old fires	Recent fires (<2 yr) removed vegetation in 25-49% of wetland; or, 50-75% wetland still recovering from old fires	Recent fires (<2 yr) removed vegetation in 50-75% of wetland , or >75% wetland still recovering from old fires	Recent fires (<2 yr) removed vegetation in >75% of wetland; or, fire sensitive species removed	Immediately post-fire; vegetation removed by fire
P2: Degree of sedimentation/erosion	None. Water clarity <40NTU, stable banks & soil	Water clarity 41-80 NTU; some minor spot erosion, visible sediment deposits affect <25% wetland	Water clarity 81-120 NTU; erosion spots linked and causing minor structural damage, visible sediment deposits affect 25-49% wetland	Water clarity 121-160 NTU; widespread erosion >50% wetland, visible sediment deposits affect 50-75% wetland	Water clarity >160 NTU; widespread erosion causes damage throughout wetland, visible sediment deposits affect >75% wetland	Wetland character lost, almost complete infilling by sediment, or unchecked erosion and scouring
P3: Nutrient levels	No eutrophication	<25% signs of algal blooms or change in biomass nutrient levels	25-49% signs of algal blooms, increased nutrients, or change to high nutrient species	50-75% signs of algal blooms, increased nutrients, or change to high nutrient species	>75% of wetland continuous algal blooms or monospecific stands of high nutrient plants	Dryland or pond. All wetland character lost due to eutrophication
P4: Von Post index (see Appendix)	1	2-3	4-5	6-7	8-9	10

E1: Loss in area	No loss	<25% loss	25-49% loss	50-75% loss	>75% loss	Wetland lost, or almost lost & remnants heavily modified
E2: connectivity barriers	All up- and downstream connections retained	<25% up- and downstream connections lost	25-49% up- and downstream connections lost	50-75% up- and downstream connections lost	>75% up- and downstream connections lost	All former connections to other water bodies lost
B1: Damage by domestic/feral animals	No damage	<25% wetland with light-medium damage, or light browsing throughout	25-49% wetland with medium-heavy browse/trampling	50-75% wetland with medium-heavy browse/trampling	>75% wetland heavily browsed/trampled	All wetland character lost due to severity of browsing/trampling
B2: Introduced predator impacts	No predation, or long-term effective predator control	Low levels predation: susceptible species still present; or pulsed predator control, low level predator reinvasion	Medium levels predation: decline in some species; or intermittent predator control, medium level predator reinvasion	High declines in populations &/or loss of 1-2 species; no or ineffective predator control. High predator reinvasion	Severedeclines in wildlife population & species; no predator control; high reinvasion; predator signs visible	Extreme; most native wildlife extinct in wetland; predator signs visible
B3: Harvesting levels	No harvesting activity	<25% wetland with medium-heavy damage, or light damage throughout, or recovered from earlier harvesting	25-49% wetland affected by harvesting, or 50-75% wetland recovered from earlier harvesting	50-75% wetland affected by harvesting, or >75% wetland recovered from earlier harvesting	Active harvesting affecting >75% wetland	Wetland character lost due to harvesting
D1: Introduced plant canopy cover	Entirely native species present	<25% introduced plants	25-49% introduced plants	50-75% introduced plants	>75% introduced plants	Entire canopy comprises introduced species
D2: Introduced plant undersorey cover	No (<1%) introduced species present	<25% introduced plants	25-49% introduced plants	50-75% introduced plants	>75% introduced plants	Entire canopy comprises introduced species

Appendix 3.4

R code utilised in Chapter 3.

(i) N:P graphs

```
#N:P graphs analsysis and construction
#------------------------------------------------------
# Loading data for N:P graph

library(reshape)
library(car)
library(gplots)
library(sciplot)

# Setting working directory
setwd("/Users/tarnia/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current data analysis
July 2012/Mar 2013")

#input/output values
csvFile = c("NPdata.csv")

#----------------------------------------------------------
# Loading root weft data from CSV file
my.Data <- read.table(csvFile, header=TRUE, sep=",", na.strings="NA", dec=".", strip.white=TRUE,
fill=TRUE)

# Separating out species data
E = my.Data[7:8]
E = cbind(E,my.Data[2])
E = subset(E,Community!="")

# Separating out environmental data
C = my.Data[4:5]

# Applying rownames
row.names(E) <-
  as.character(my.Data$Site)

row.names(C) <-
  as.character(my.Data$Site)

# ------------------------------------------------------
# Loading charting library for N:P graph

library(calibrate)

# ------------------------------------------------------
# Inital plot setup for N:P graph

opar <- par()                   # storing original settings
#oma=c(3,3,3,3)
#par(mar=c(3, 5, 2, 1))

plot(E$EMPMIN.N, E$EMPMIN.P,
        xlab="Plant [N] % dry wt",
        ylab="Plant [P] % dry wt",
```

```
            xlim=c(0,2.4), ylim=c(0,0.15),
            pch=20,
  col="white",
  type="p",
  xaxs="i", yaxs="i",      # suppresses 4% margin on either end of both axes
  cex.axis=0.75
)
Y=subset(E,Community=="1a")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=22, cex=1.4, col="black",bg=rgb(251,154,153,alpha=255,maxColorValue=255)
)
Y=subset(E,Community=="1b")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=21, cex=1.4, col="black",bg=rgb(251,154,153,alpha=255,maxColorValue=255)
)

Y=subset(E,Community=="2a")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=24, cex=1.5, col="black",bg=rgb(31,120,180,alpha=255,maxColorValue=255)
)

Y=subset(E,Community=="2b")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=21, cex=1.4, col="black",bg=rgb(31,120,180,alpha=100,maxColorValue=255)
)

Y=subset(E,Community=="2c")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=22, cex=1.4, col="black",bg=rgb(31,120,180,alpha=100,maxColorValue=255)
)

Y=subset(E,Community=="2d")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
      pch=8, cex=1.4, col=rgb(31,120,180,alpha=255,maxColorValue=255)
#"black",bg=rgb(31,120,180,alpha=100,maxColorValue=255)
)
Y=subset(E,Community=="4a")
points(Y$EMPMIN.N, Y$EMPMIN.P,
      xlab="",
      ylab="",
      xlim=c(0,2.4), ylim=c(0,0.15),
```

```
    pch=22, cex=1.4, col="black", bg=rgb(178,223,138,alpha=255,maxColorValue=255)
)

Y=subset(E,Community=="4b")
points(Y$EMPMIN.N, Y$EMPMIN.P,
    xlab="",
    ylab="",
    xlim=c(0,2.4), ylim=c(0,0.15),
    pch=21, cex=1.4, col="black",bg=rgb(178,223,138,alpha=255,maxColorValue=255)
)
legend(1.05,0.15,c("1a","1b","2a","2b","2c","2d","4a","4b"),ncol=2,x.intersp=0.05, y.intersp=0.55,
lwd=0, pt.lwd=1,
pch=c(22,21,24,21,22,8,22,21),cex=0.8,pt.cex=1,col=c("black"),pt.bg=c(rgb(251,154,153,maxCol
orValue=255),rgb(251,154,153,maxColorValue=255),rgb(31,120,180,maxColorValue=255),rgb(
31,120,180,maxColorValue=255),rgb(31,120,180,maxColorValue=255),rgb(31,120,180,maxColo
rValue=255),rgb(178,223,138,maxColorValue=255),rgb(178,223,138,maxColorValue=255)),bty
="n")
legend(1.55,0.15,c("14:1","16:1"),x.intersp=0.5,y.intersp=0.55, lwd=2, pt.lwd=0,
lty=c(1,2),cex=0.8,col="black",bty="n")

# ---------------------------------------------------------
# Plotting Ratio Lines on N:P graph

# Horizontal line at P % dry wt = 0.1
abline(h=0.1, lty=2, col="black")

# Vertical line at N % dry wt = 2
abline(v=2, lty=2, col="black")


# N:P = 14:1
segments(0,0, 1.4,0.1, col ="black", lty=1, lwd=2)
# N:P = 16:1
segments(0,0, 1.6,0.1, col ="black", lty=2, lwd=2)

# ---------------------------------------------------------
# Adding text annotation to N:P graph
text(0.9,0.12,"N-limited",cex=0.85)
text(0.9,0.085,"N-limited",cex=0.85)
text(0.9,0.02,"P-limited",cex=0.85)
text(2.2,0.02,"P-limited",cex=0.85)
text(2.2,0.12,"Unlimited",cex=0.85)

arrows(1.5,0.05,1.2,0.08,lwd=2,lty=1,length=0.15,angle=20)
text(1.5,0.05,"NP co-limited",cex=0.85,pos=4)

# ---------------------------------------------------------
# Over-Plotting Chio data on N:P graph
# points(Chio_NP_Ratio$CHIRUB.N, Chio_NP_Ratio$CHIRUB.P,
#           xlab="",
#           ylab="",
#           xlim=c(0,1.4), ylim=c(0,0.14),
#           pch=24, col="blue"
# )

# Labelling Chio data on N:P graph
# textxy(Chio_NP_Ratio$CHIRUB.N, Chio_NP_Ratio$CHIRUB.P,
#           Chio_NP_Ratio$Site,
#           cex = 0.5, dcol = "blue", m = c(0, 0))
```

```
par(opar)
```

(ii) Cluster analysis

```
# Cluster analsysis
#Importing master species data sheet
#Data are logged abd rare species are idicated by true/false
#Data are in transposed form, with species as rows, sites as columns, this must be transposed for
hclust

my.Data = read.csv("/Users/tarnia/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current
data analysis July 2012/Jan 2013/20130104SppDataLogTransposed.csv",header=T)

# -----------------------------------------------------------------------------
# DATA PREPARATION
# Extract common species and prepare data frame
# -----------------------------------------------------------------------------
# Extracting the Common Species only and creating a dataframe called SpeciesCommon
sppDataLogCommon <- subset(my.Data,Rare==FALSE)

SppNames <- sppDataLogCommon$Code

sppDataLogCommon$Code <- NULL
sppDataLogCommon$Count <- NULL
sppDataLogCommon$Rare <- NULL

SpeciesCommon <- t(sppDataLogCommon)
colnames(SpeciesCommon) <- SppNames
SpeciesCommonScaled<-scale(SpeciesAll)

# -----------------------------------------------------------------------------
# Transposing SpeciesCommon for bootstrapping in pvclust()
# -----------------------------------------------------------------------------
SpeciesCommonT <- t(SpeciesCommon)

# -----------------------------------------------------------------------------
# DATA ANALYSIS
# LOADING REQUIRED LIBRARY'S
# -----------------------------------------------------------------------------
# Loading pvclust() library
library (pvclust)
set.seed(79501)

 # -----------------------------------------------------------------------------
 # CLUSTER ANALYSIS - SpeciesCommon
 # Ward Hierarchical clustering with bootstrapped p values
 # -----------------------------------------------------------------------------

 fitCommon <- pvclust(SpeciesCommonT, method.hclust="ward", method.dist="euclidian")

 # -----------------------------------------------------------------------------
 #FitCommon
 plot (fitCommon,cex=c(0.6),hang=-1, main="Common species
(logged)",ylab="Dissimilarity",cex.pv=0.7) #dendrogram with p values
 #add rectangles around groups highly supported by data
 pvrect(fitCommon, alpha=.95)
```

(iii) Calculating data for Table 3.7

```
## Loading required libraries
library(reshape)
```

```
library(tables)


######################
# Source: http://www.r-statistics.com/tag/melt/
# Loading the functions
######################
# Making sure we can source code from github
source("http://www.r-statistics.com/wp-content/uploads/2012/01/source_https.r.txt")

# Reading in the function for using tabular on a cast_df object:
source_https("https://raw.github.com/talgalili/R-code-snippets/master/tabular.cast_df.r")
######################

## Tabulating Summary Statistics for Communities identified
## through pvclust()

d <- read.csv("/Users/tarnia/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current data
analysis July 2012/Mar 2013/20130310SppData.csv",header=T)

## Adjusting data to a score out of 100
## (could use dapply instead for one step, rather than for loop)
for(i in 4:length(d)) {
  d[ , i] <- d[ , i]*4
}

## Reducing dataframe columns to just those species to be tabulated
d <- d[ ,c(1:3,9,26,43,44,61,66,67,73,85,88,105,17,19,117,142,144)]

## Reshaping data in preparation to tabulate
dr <- melt(d, id=c("Sitename","Code","Community"), na.rm=TRUE)
colnames(dr)[4] <- "Species"  # because otherwise the function is having problem when relying
on the melt function of the cast object
head(dr,3)
#Sitename Code Community Species value
#1 Aparima Valley site 1 APA1       4b  ACIAUR     0
#2 Aparima Valley site 2 APA2       2b  ACIAUR     0
#3     Awarua Bog site 1 AWA1       2b  ACIAUR     0

## Removing records that have no community association
dr <- subset(dr,Community!="")

############
# Running the example:
tabular.cast_df(cast(dr, Community ~ Species, c(mean,sd)))
```

(iv) Pearsons correlations with Bonferroni adjustment

```
#-------------------------------------------------------------------
#Field Survey Chapter Envt Correlations
#Sites: NZ
#Variables: 20130102DATA
#____________________________________________________________________

#Setting working directory
setwd("~/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current data analysis July
2012/Mar 2013")

csvFile =c("20130310DATA.csv")
```

```
#______________________________________________________________________
#Loading environmental data from csv
Corr=read.csv(csvFile)

Corr<-subset(Corr,Community!="")
s=c(9,17,19,20,21,22,23,24,31,32)
Corr=Corr[ , s]

#______________________________________________________________________
#Correlations with significance levels
library(Hmisc)

a<-rcorr(as.matrix(Corr),type="pearson")

r2<-a[[1]]  # returning a 10x10 matrix or r2 values
q<-a[[3]]   # returning a 10x10 matrix of p values

write.csv(q,"rcorr-p.csv")
write.csv(r2,"rcorr-r2.csv")

q.bonf<-p.adjust(q,method="bonferroni")
q.bonf.m<-matrix(q.bonf,10,10)
write.csv(q.bonf.m,"rcorr-bonf.csv")

q.holm<-p.adjust(q,method="holm")
q.holm.m<-matrix(q.bonf,10,10)
write.csv(q.holm.m,"rcorr-holm.csv")

q.BH<-p.adjust(q,method="BH")
q.BH.m<-matrix(q.bonf,10,10)
write.csv(q.BH.m,"rcorr-BH.csv")


# Correlation diagram

panel.cor <- function(x, y, digits=2, prefix="", cex.cor)
{
 usr <- par("usr"); on.exit(par(usr))
 par(usr = c(0, 1, 0, 1))
 r <- abs(cor(x, y))
 txt <- format(c(r, 0.123456789), digits=digits)[1]
 txt <- paste(prefix, txt, sep="")
 if(missing(cex.cor)) cex <- 2/strwidth(txt)

 test <- cor.test(x,y)
 # borrowed from printCoefmat
 Signif <- symnum(test$p.value, corr = FALSE, na = FALSE,
              cutpoints = c(0, 0.001, 0.01, 0.05, 0.1, 1),
              symbols = c("***", "**", "*", ".", " "))

 text(0.5, 0.5, txt, cex = cex * r)
 text(.8, .8, Signif, cex=cex, col=2)
}
pairs(Corr,
   lower.panel=panel.smooth, upper.panel=panel.cor)
```

(v) PCA of selected environmental variables and biplot construction

```
# PRINCIPAL COMPONENTS ANALYSIS
```

```
library(lattice)

my.Data = read.csv("/Users/tarnia/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current
data analysis July 2012/Mar 2013/20130310DATA.csv",header=T)

my.Data <- subset(my.Data,Community!="")

# ===================================================================
# Separating out species data
my.SpeciesData = my.Data[33:117]
names(my.SpeciesData)
# Separating out environmental data
my.EnvData = my.Data[6:32]
names(my.EnvData)
# ====================================================================
# Dropping unneeded variables from environmental data

my.EnvData = my.EnvData[,-25]  # Ca
my.EnvData = my.EnvData[,-24]  # K
my.EnvData = my.EnvData[,-23]  # P
my.EnvData = my.EnvData[,-22]  # Al
my.EnvData = my.EnvData[,-21]  # Mg
my.EnvData = my.EnvData[,-20]  # Na
my.EnvData = my.EnvData[,-13]  # Von Post
my.EnvData = my.EnvData[,-11]  # TC
my.EnvData = my.EnvData[,-10]  # TN
my.EnvData = my.EnvData[,-9]  # PcC
my.EnvData = my.EnvData[,-8]  # PcN
my.EnvData = my.EnvData[,-7]  # Water deficit
my.EnvData = my.EnvData[,-6]  # MinTemp
my.EnvData = my.EnvData[,-5]  # SQRT Distance to coast
my.EnvData = my.EnvData[,-3]  # Altitude
my.EnvData = my.EnvData[,-2]  # Rainfall
my.EnvData = my.EnvData[,-1]  # Latitude
# ====================================================================

my.data = my.EnvData

colnames(my.data) <- c("Coast","C:N","WCI","BD","pH","Cond","Ash","MC","TP","TK")
names(my.data)
# Identifying sites
my.Sites = my.Data[1:4]


# Applying rownames
row.names(my.SpeciesData) <-
  as.character(my.Data$Code)

row.names(my.data) <-
  as.character(my.Data$Code)
#my.Sites$Sitename <- NULL


# Look at the correlations

library(gclus)
my.abs = abs(cor(my.data))
my.colors = dmat.color(my.abs)
my.ordered = order.single(cor(my.data))
```

```
cpairs(my.data,my.ordered,panel.colors=my.colors,gap=.5)

# Do the PCA

my.prc = prcomp(my.data,center=T,scale=T)

# Append the factor scores to the data.frame
my.data$x1 <- my.prc$x[,1]
my.data$x2 <- my.prc$x[,2]
my.data$x3 <- my.prc$x[,3]
my.data$x4 <- my.prc$x[,4]

# Append the cluster Id's back on onto the data.frame for
# subsequent use in plotting confidence ellipses

my.data$Community <- my.Data$Community

screeplot(my.prc,main="Scree Plot",xlab="Components")
screeplot(my.prc,type="line",main="Scree Plot")

# DotPlot PC1

load = my.prc$rotation
sorted.loadings = load[order(load[,1]),1]
Main="Loadings Plot for PC1"
xlabs="Variable Loadings"
dotplot(sorted.loadings,main=Main,xlab=xlabs,cex=1.5,col="red")

# DotPlot PC2

sorted.loadings = load[order(load[,2]),2]
Main="Loadings Plot for PC2"
xlabs="Variable Loadings"
dotplot(sorted.loadings,main=Main,xlab=xlabs,cex=1.5,col="red")

# DotPlot PC3

sorted.loadings = load[order(load[,3]),3]
Main="Loadings Plot for PC3"
xlabs="Variable Loadings"
dotplot(sorted.loadings,main=Main,xlab=xlabs,cex=1.5,col="red")

# DotPlot PC4

sorted.loadings = load[order(load[,4]),4]
Main="Loadings Plot for PC4"
xlabs="Variable Loadings"
dotplot(sorted.loadings,main=Main,xlab=xlabs,cex=1.5,col="red")

# Now draw the BiPlot

biplot(my.prc,cex=c(0.5,0.7))

my.prc

# Varimax

my.var = varimax(my.prc$rotation)
my.var
```

```
# Applying site names to data
biplot(my.prc,cex=c(0.5,0.7),xlabs=my.Data[,1])

# ==================================================================
# CHANGE 2013-01-02

# Applying site codes to data
biplot(my.prc,choices=1:2,cex=c(0.5,0.7),xlabs=my.Data[,2])
biplot(my.prc,choices=c(1,3),cex=c(0.5,0.7),xlabs=my.Data[,2])
biplot(my.prc,choices=2:3,cex=c(0.5,0.7),xlabs=my.Data[,2])

# Applying cluster codes to data
biplot(my.prc,choices=1:2,cex=c(0.5,0.7),xlabs=my.Data[,3])
#title(main="PC 1&2 All sites",cex=0.8)
biplot(my.prc,choices=c(1,3),cex=c(0.5,0.7),xlabs=my.Data[,3])
#title(main="PC 1&3 All sites",cex=0.8)
biplot(my.prc,choices=2:3,cex=c(0.5,0.7),xlabs=my.Data[,3])
#title(main="PC 2&3 All sites",cex=0.8)

# Applying significant cluster codes to data
# --------------------------------------------------

opar=par()
par(mar=c(3.8,2,3,1)+0.9,mfrow=c(2,2),cex=0.6,cex.lab=1.2)

char.size<-c(1,0.9)

biplot(my.prc,choices=1:2,cex=char.size,xlabs=my.Data[,4])
#title(main="PC 1&2 Sig sites",cex=0.8)
biplot(my.prc,choices=c(1,3),cex=char.size,xlabs=my.Data[,4])
#title(main="PC 1&3 Sig sites",cex=0.8)
biplot(my.prc,choices=2:3,cex=char.size,xlabs=my.Data[,4])
#title(main="PC 2&3 Sig sites",cex=0.8)

par(opar)
```

(vi) Boxplot construction and Tukey posthoc tests

```
#--------------------------------------------------------------------
#Field Survey Chapter
#Sites: NZ
#Variables: 20130102DATA
#____________________________________________________________

#Loading required libraries
library(reshape)
library(car)
library(gplots)

#Setting working directory
setwd("~/Documents/PhD/Draft 0/Chapter 3/Data analysis/Current data analysis July
2012/Mar 2013")

csvFile =c("20130310Data.csv")

#____________________________________________________________
#Loading environmental data from csv
BoxPlot=read.csv(csvFile)
s=c(4,17,18,19,20,21,23,24,31,32)
```

```
BoxPlot=BoxPlot[ , s]
BoxPlot.melt=melt(BoxPlot,id.vars="Community")
BoxPlot.melt<-subset(BoxPlot.melt,Community!="")

#______________________________________________________________
#Order factor variables
BoxPlot.melt$Community=ordered(BoxPlot.melt$Community,
               levels=c("1a","1b","2a","2b","2c","2d","4a","4b") )

#______________________________________________________________
plotvars=c("C_N","VonPost","Condition","Bulk.density","pH","X.Ash","Moisture.content..","TP","T
K")
plotlabels=c("C:N Ratio","Von Post Index","Wetland Condition Index","Bulk Density
(Mg/m^3)","pH","Ash Content (%)","Moisture Content (%)", "Total P (Mg/m^3)","Total K
(Mg/m^3)")
opar=par()
par(mar=c(2,2,4,1),mfrow=c(3,3),cex.main=1.1)
  for(i in 1:length(plotvars)){
   boxplot(
    value~Community,data=BoxPlot.melt,
    subset=variable==plotvars[i],
    notch=FALSE,
    horizontal=TRUE,
    axes=FALSE
    )
   axis(3)
   axis(2, 1:8, labels=c("1a","1b","2a","2b","2c","2d","4a","4b"), las=1)

   box(col="black", lwd = 1.5)

   title(
    main=plotlabels[i],
    line=3
    )
  }

par(opar)

# ---------------------
# One way anovo with Tukey's multiple correlations to look at the relationships between
Communitys
# for each plot variable

for(i in 1:length(plotvars)){

 env.variables <- subset(BoxPlot.melt,variable==plotvars[i])

 env.model <- aov(value ~ Community, data = env.variables)

 print(paste("** Environmental Variable:",plotvars[i]))
 print(summary(env.model))
 print(TukeyHSD(env.model))
 plot(TukeyHSD(env.model),sub=plotvars[i])

}
```

Appendix 3.5

Nutrient limitation at *Empodisma* sites, as inferred from live foliar tissue N:P ratios. Foliar samples were obtained during active growing season, and comprised only live foliar material, as suggested by Clarkson *et al.* (2002).

Sites are separated into four types of nutrient limitation. P-limited vegetation is divided into oligotrophic sites where tissue-P<0.015% dry weight, and P>0.015% dry weight. The division is made since Clarkson *et al.* (2002) suggest *Empodisma* from sites unimpacted by nutrient additions usually have tissue-P close to 0.010% dry weight. N-limited vegetation is divided into P<0.1% dry weight and P>0.1% dry weight, as the growth of vegetation with P>0.10% dry weight is unlimited by P (Clarkson *et al*., 2002).

Data set is obtained from single sampling event, but is indicative of nutrient enrichment at the sites.

Region	Site	P-limited vegetation		N-limited vegetation	
		P<0.015%	P>0.015%	P<0.1%	P>0.1%
Auckland	Tomorata		*E. robustum*		
Waikato-Corommandel	Duck Creek		*E. robustum*		
	Kopuatai Bog	*E. robustum*			
	Whangamarino	*E. robustum*			
Bay of Plenty	Tumurau Lagoon		*E. robustum*		
Central North Island	Blyth Swamp	*E. minus*			
	Erua site 1	*E. minus*			
	Erua site 2	*E. minus*			
	NZ Forest Managers 1		*E. minus*		
	NZ Forest Managers 2		*E. minus*		
	NZ Forest Managers 3	*E. minus*			
	Outdoor Pursuits Centre		*E. minus*		
	Rotoaira		*E. minus*		
	Ruamata		*E. minus*		
	Silica Rapids		*E. minus*		
	Sinclairs Bog		*E. minus*		
	Tama Lakes		*E. minus*		
	Te Papa Mire		*E. minus*		
	Waipakihi 1	*E. minus*			
	Waipakihi 2	*E. minus*			
	Wairehu Canal		*E. minus*		
	Wharepu 1	*E. minus*			
	Wharepu East	*E. minus*			
Te Urewera	Ngapehi-o-waikareiti		*E. minus*		
	Puna Taeo		*E. minus*		
	Waipai Swamp	*E. minus*			
Canterbury	Bealey Spur		*E. minus*		
	Lagoon Saddle		*E. minus*		
Otago	Berwick Forest			*E. minus*	
	Black Swamp, Otago		*E. minus*		
	Bungtown Bog 1			*E. minus*	
	Bungtown Bog 2			*E. minus*	
	Pukerau 1		*E. minus*		
	Pukerau 2		*E. minus*		
	Tahakopa site 1		*E. minus*		
	Tahakopa site 2			*E. minus*	
	Takitimu		*E. minus*		
Southland-Te Anau	Aparima Valley 1		*E. minus*		
	Aparima Valley 2		*E. minus*		
	Awarua Bog 1		*E. minus*		
	Awarua Bog 2		*E. minus*		
	Awarua Bog 3		*E. minus*		
	Borland Bog			*E. minus*	
	Castle Downs Bog		*E. minus*		
	Freestone Mire 1		*E. minus*		
	Freestone Mire 2		*E. minus*		
	Muddy Creek			*E. minus*	
West Coast	Denniston Plateau 1	*E. minus*			
	Denniston Plateau 2	*E. minus*			
	German Terrace		*E. minus*		
	Hunters Bog		*E. minus*		
	Lake Christabel		*E. minus*		
	Nine Mile Rd		*E. minus*		
	Palmers Road		*E. minus*		
	Sponge Swamp		*E. minus*		

Appendix 3.6

Dendrogram of the sites for the 2002 and 2006-07 field survey of New Zealand *Empodisma* and *Chionochloa rubra* wetland communities using Ward's linkage with the Euclidean distance.
The two data sets are:

1. The raw data set (152 species);
2. Rare species removed (85 species remaining).

Figure 3.11: *Dendrogram of the sites for the 2002 and 2006-07 field survey of New Zealand Empodisma and Chionochloa rubra wetland communities using Ward's linkage with the Euclidean distance. Data consist of species cover, untransformed, with all species analysed (n=152). AU probability values are indicated on the dendrogram, with dashed rectangles indicating the significant clusters. Note that not all nodes include the AU estimates, to enhance legibility.*

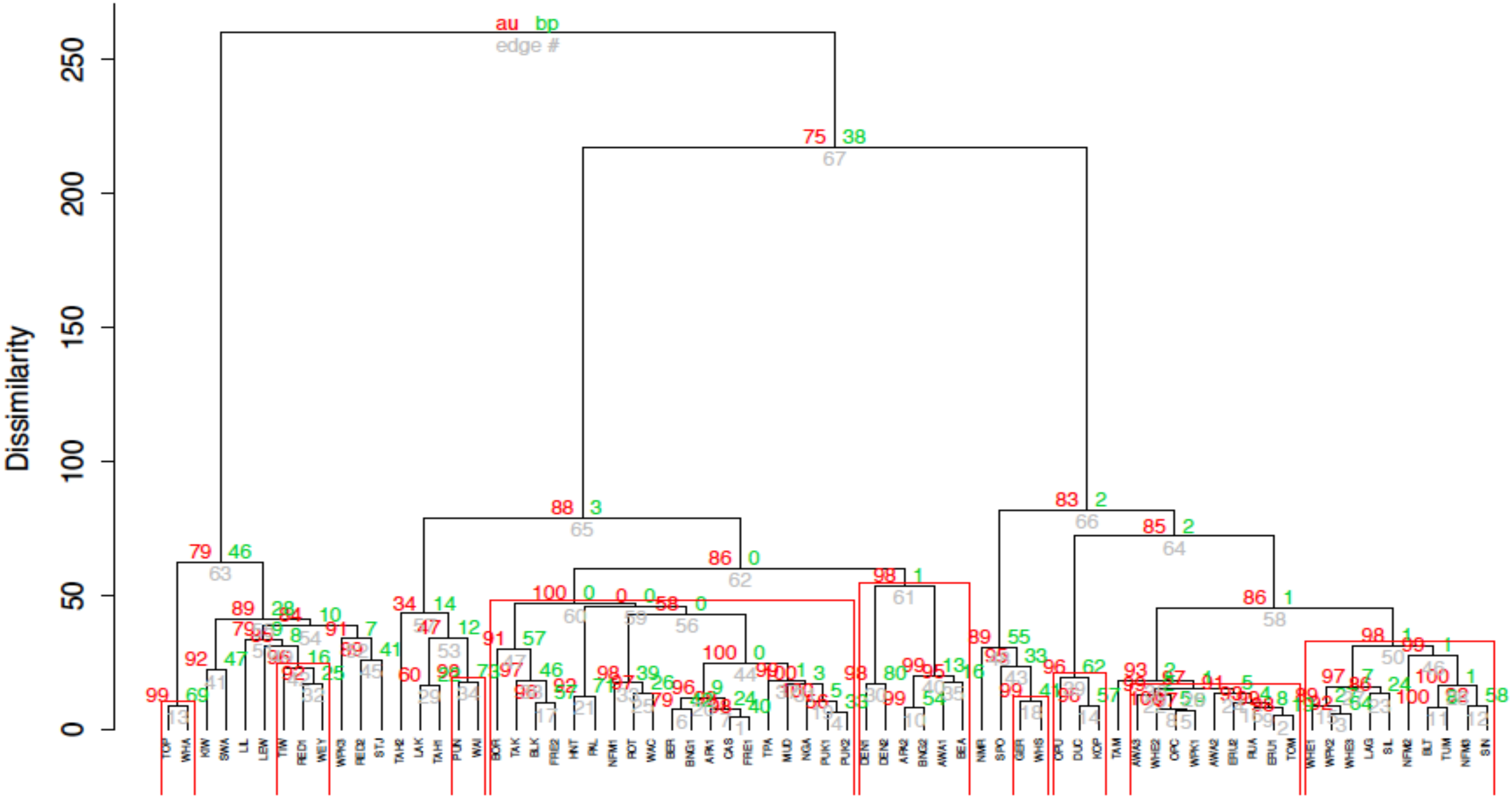
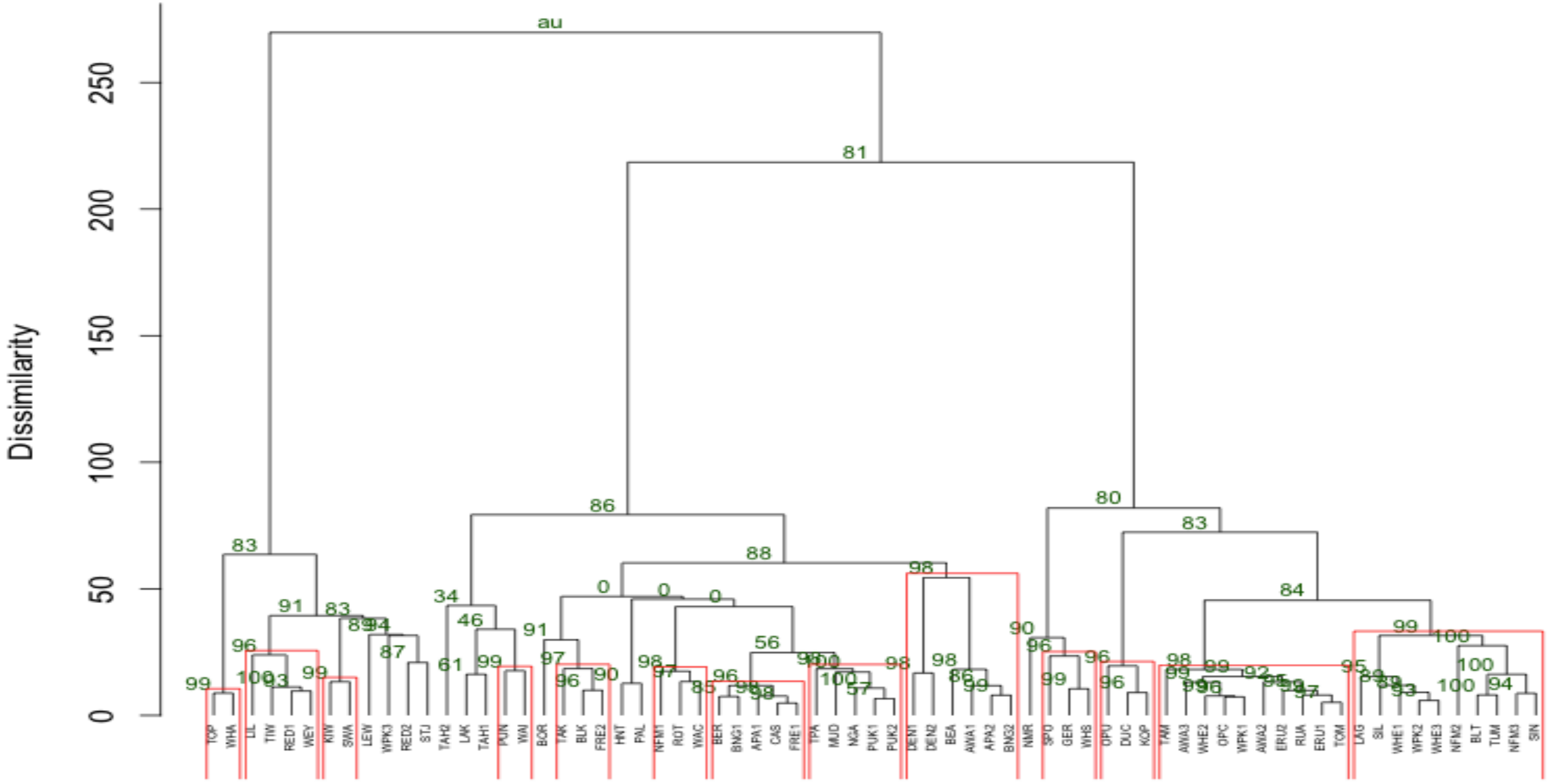


Figure 3.12*: Dendrogram of the sites for the 2002 and 2006-07 field survey of New Zealand* <u>*Empodisma*</u> *and* <u>*Chionochloa rubra*</u> *wetland communities using Ward's linkage with the Euclidean distance. Data consist of species cover, untransformed, with rare species (<3 occurrences) removed (n=85). AU probability values are indicated on the dendrogram, with dashed rectangles indicating the significant clusters. Note that not all nodes include the AU estimates, to enhance legibility.*



Appendix 3.7

Species frequencies in 8 communities predicted by combined vascular and non-vascular species in New Zealand *Empodisma* sites. Note: *= non-native species. Number indicates frquency (+ present in less than 10% of quadrats; 1 in 10-19%; 2 in 20-29%; 3 in 30-39%; 4 in 40-49%; 5 in 50-59%; 6 in 60-69%; 7 in 70-79%; 8 in 80-89%; 9 in 90-99%; C in 100%.

Species nomenclature follows Allan (1982), Moore & Edgar 1976), Healy & Edgar (1980), Webb *et al.* (1988) and Edgar & Connor (2000), except where recent taxonomic changes have been suggested (www.pcn.org.nz). *Gleichenia* plants were grouped together as *Gleichenia* spp. for the analysis, given the current taxonomic uncertainty over the *Gleichenia* genus (Perrie *et al.*, 2007), which is yet to be resolved.

Species name	*Community*							
	!a	*1b*	*2a*	*2b*	*2c*	*2d*	*4a*	*4b*
Aciphylla aurea							+	
*Agrostis capillaris**							+	+
*Agrostis stolonifera**				+				+
Anaphalioides bellidioides	+						+	
Androstoma empetrifolia	+	+	+	+		+	+	+
Anisotome aromatica.	+			+				+
*Anthoxanthum odoratum**							+	+
Apodasmia similis				+				
Aporostylis bifolia			+				+	+
Astelia nervosa							+	
Blechnum minus				+				
Blechnum novae-zelandiae						+		
Blechnum penna-marina				+			+	+
Bulbinella angustifolia								
*Calluna vulgaris**	+	+						
Carpha alpina	+		1	+	+			+
Carex coriacea				+			2	+
Carex echinata	+							+
Carex gaudichaudiana	+			+				+
Carex germinata				+				
Carex sinclairii	+							+
Carex virgata				+				
Celmisia alpina						+		
Celmisia dubia			+					
Celmisia gracilenta	+			+			+	+
Celmisia graminifolia				+				+
Celmisia incana	+							
Celmisia spectabilis	+	+						
Centella uniflora				+				
Centrolepis ciliata			+					
Chionochloa juncea			+					
Chionochloa rubra	1	1	1	3			3	+
Clematis ?quadribracteolata				+				
Coprosma cheesemanii	+	+						+
Coprosma intertexta				+				+
Coprosma parviflora							+	+
Coprosma perpusilla								
Coprosma propinqua				+			+	+
Coprosma pseudocunneata								
Coprosma tenuicaulis								
Craspedia "bog" unnamed	+							
Donatia novae-zelandiae	+		+					+
Dracophyllum filifolium	+	+						
Dracophyllum longifolium				+			+	+
Dracophyllum oliveri				+				+
Dracophyllum palustre								+
Dracophyllum politum			1					
Dracophyllum prostratum								+
Dracophyllum recurvum.	1							
Dracophyllum subulatum		3						
Dracophyllum uniflorum						+	+	+
Drosera arcturi	+						+	+

	1a	*1b*	*2a*	*2b*	*2c*	*2d*	*4a*	*4b*
Drosera binata	+			+	+	+		+
Drosera spathulata.	+		1			+		+
Eleocharis gracilis	+							
Empodisma minus	8	6	8	C	9	9	7	9
Epacris pauciflora	+		+		+	+		
Festuca novae-zelandiae							+	
Forstera tenella							+	
Gahnia rigida						+		
Gaimardia setacea						+		
Gaultheria colensoi	+							
Gaultheria depressa				+			+	+
Gaultheria macrostigma							+	+
Gentiana bellidifolia	+			+				
Geranium microphyllum				+			+	+
Gleichenia species	8	8	1	1	7	6		+
Gonocarpus micranthus				+			+	+
Halocarpus bidwillii	+		+				+	+
Halocarpus biformis			+					
Hebe odora				+			+	+
Herpolirion novae-zelandiae	+		+			+	+	+
Hierachloe redolens	+	+					+	
Holcus lanatus				+			+	+
*Hypochaeris radicata**							+	+
Isolepis aucklandica				+		+		
*Juncus articulatis**	+							
Juncus edgariae							+	+
*Juncus squarrosus**			+					
Lachnagrostis filiformis								+
Lepidosperma australe	+	+						+
Lepidothamnus laxifolius	1							+
Leptecophylla juniperina			+	+				
Leptospermum scoparium	+	+	8	+	+	+	+	+
Liparophyllum gunnii						+		
Lobelia angulata								+
*Lotus pedunculatus**							+	
Lycopodielle diffusa				+		3		+
Lycopodiella lateralis			+					+
Lycopodium fastigiatum	+						+	
Machaerina rubiginosa				+	5			+
Machaerina tenax								+
Machaerina teretifolia					+	8		
Nertera balfouriana				+				+
Nertera depressa				+		+	+	+
Nertera scapanioides				+			+	+
Oreobolus pectinatus	+						+	+
Oreobolus strictus	+		+				+	+
Oreostylidium subulatum							+	+
Ourisia macrophylla			+					
Ozothamnus leptophyllus	+			+		+	+	+
Pentachondra pumila	+			+			+	+
Phormium tenax				+		+		
Pimelea prostrata	+							
Poa colensoi.	+						+	
Pteridium esculentum				+				
Racomitrium lanuginosum	+							
Ranunculus multiscapus				+				

	1a	*1b*	*2a*	*2b*	*2c*	*2d*	*4a*	*4b*
*Ranunculus repens**								+
*Rumex acetosa**								+
Schoenus brevifolius						+		
Schoenus fluitans	+							
Schoenus pauciflorus	+	+		+		+		
Sphagnum cristatum	+				+	+	4	3
Sphagnum falcatulum							+	+
Stegostyla lyallii							+	
*Taraxacum officinale**				+				
Tetraria capillaris						+		
Thelymitra cyanea			+	+		+	+	+
*Trifolium repens**							+	
Utricularia geminiscapa						+		
Viola cunninghamii	+			+			+	+
Wahlenbergia pygmaea	+							
Zotovia thomsonii			+					

Appendix 4.1

Hodges TA, Rapson GL, 2010. Is *Empodisma minus* the ecosystem engineer of the FBT (fen-bog transition) in New Zealand. *Journal of the Royal Society of New Zealand* **40**, 181-207.

Appendix 5.1

Water Analysis: Atawhai No.2 bore. 08/04/99. Analysis performed by PNCC Laboratory, Palmerston North City Council.

Treatment	*Sample 1*	*Sample 2*
Alkalinity	107 g/m^3 CaCo$_3$	79 g/m^3 CaCo$_3$
Ammoniacal nitrogen	1.66 g/m^3 NH$_3$-N	<0.01 g/m^3 NH$_3$-N
Arsenic-acid soluble	<0.001 g/m^3	<0.001 g/m^3
Cadmium-acid soluble	<0.00005 g/m^3	<0.00005 g/m^3
Calcium hardness	51 g/m^3	53 g/m^3
Chloride	8.3 g/m^3	22.0 g/m^3
Colour	5 Hazen units	5 Hazen units
Conductivity @ 25	23.0 mS/m @ 25^o	23.9 mS/m @ 25^o
Floride	0.23 g/m^3	0.19 g/m^3
Free Carbon dioxide	1.0 g/m^3	14.0 g/m^3
Iron	<0.04 g/m^3	<0.04 g/m^3
Lead-acid soluble	0.0019 g/m^3	0.0021 g/m^3
Mercury-acid soluble	<0.0001 g/m^3	<0.0001 g/m^3
Magnesium Hardness	11 g/m^3 CaCO$_3$	10 g/ m^3 CaCO$_3$
Manganese	0.03 g/m$_3$	0.03 g/m^3
Nitrate Nitrogen	<0.1 g/m^3 NO$_2$-N	<0.1 g/m^3 NO$_2$-N
Nitrite Nitrogen	<0.003 g/m^3 NO$_2$-N	<0.003 g/m^3 NO$_2$-N
PH	8.3	7.1
Phosphate	0.08 g/m^3 PO$_4$-P	0.08 g/m^3 PO$_4$-P
Potassium	6.4 g/m^3	6.4 g/m^3
Selenium –acid soluble	<0.001 g/m^3	<0.001 g/ m^3
Silica	65.0 g/m^3 SiO$_2$	63.0 g/ m^3 SiO$_2$
Sodium	22 g/m^3	22 g/m^3
Sulphate	2 g/m^3 SO$_4$	2 g/m^3 SO4
Total hardness	62 g/m^3 CaCo$_3$	63 g/m^3 CaCo$_3$
Turbidity	0.2 NTU	0.2 NTU

Appendix 5.2

Nutrient Analysis Pete's Peat-Lite High-N Water Soluble Fertiliser.

Nutrient	*% Composition*
Nitrogen - Total	20
-Ammoniacal nitrogen	8
-Nitrate nitrogen	12
Available Phosphorus	4.4
Soluble Potash (K)	16.6
Magnesium - water soluble	0.15
Boron	0.02
Copper - chelated	0.01
Iron - chelated	0.1
Manganese - chelated	20
Molybdenum	8

Appendix 6.1

Species present in Litter Decomposition Experiment plots, Silica Rapids Mire, TNP. Community indicated (WF= Wet Fen; DF= Dry Fen; T= Tussockland communities).*=exotic/adventive species. Nomenclature follows Johnson & Brooke (1998) for vascular species, Galloway (2007) for lichen, and Beever *et al.* (1992) for mosses. Further identification of non-vascular species was provided by participants of the 19th John Child Bryophyte Workshop. A^1 = Abundance rankings qualified subjectively from 2004 site survey, using the following abundance key: p = present; o=occasional; c=common; a=abundant.

Species	*Family*	*Community*	*A*[1]
Mosses			
Amblystegium riparioides	Amblystegiaceae		p
Campylopus introflexus	Amblystegiaceae	WF, DF, T	p
Dicranoloma billardieri	Dicranaceae	DF	p
Macromitrium sp.	Orthotrichaceae		p
Racomitrium pruinosum C. Muller	Grimmiaceae	WF, DF	a
Sphagnum cristatum Hampe	Sphagnaceae	T	o
Riccia	Riccciaceae		c
Lichen			
Cladia aggregata (Sw.) Nyl.	Cladoniaceae	DF	p
Cladia retipora (Labill.) Nyl.	Cladoniaceae	DF	p
Cladonia sp.	Cladoniaceae		c
Hypogymnia sp.	Parmeliaceae		c
Menegazzia sp.	Parmeliaceae		p
Pseudocyphellaria sp.	Lobariaceae		p
Usnea sp.	Parmeliaceae		p
Vascular Species			
Androstoma empetrifolia Hook. f.	Epacridaceae	WF, DF, T	c
Calluna vulgaris (L.) Hull*	Ericaceae	DF, T	p
Carpha alpina R. Br.	Cyperaceae	WF, DF	o
Carex echinata Murray	Cyperaceae		p
Carex gaudichaudiana	Cyperaceae	WF, T	
Celmisia gracilenta Hook. f.	Asteraceae	WF	o
Celmisia incana Hook. f.	Asteraceae		o
Celmisia spectabilis Hook. f.	Astreaceae	DF, T	
Chionochloa rubra var. *rubra* Zotov	Poaceae	WF, DF, T	c
Coprosma cheesemanii W.R.B. Oliv.	Rubiaceae	T	c
Craspedia “bog” unnamed	Asteraceae		o
Dracophyllum filifolium Hook. f.	Epacridaceae	DF, T	a
Dracophyllum recurvum Hook. f.	Epacridaceae	DF, T	o
Drosera arcturi Hook.	Droseraceae		o
Drosera binata Labill.	Droseraceae		p
Drosera spathulata Schult.	Droseraceae		p
Eleocharis gracilis Nees.	Cyperaceae		p
Empodisma minus	Restionaceae	WF, DF, T	a
Festuca rubra var. commutata Gaudin	Poaceae		p
Gentiana bellidifolia Hook. f.	Gentianaceae	WF	o
Gleichenia dicarpa var. *alpina* (R. Br.) Hook. f.	Gleicheniaceae	WF, DF, T	a
Halocarpus bidwillii (Hook.f. ex Kirk) Quinn	Podocarpaceae	WF	c
Hebe odora Cockayne	Scrophulariaceae	DF, T	p
Hebe venustula Cockayne	Scrophulariaceae	T	p
Hierochloe redolens (Vahl) Roem. & Schult.	Poaceae		a
Lepidosperma australe (A. Rich.) Hook. f.	Cyperaceae	WF, DF	o
Lepidothamnus laxifolius (Hook. f.) Quinn	Podocarpaceae	WF	o
Leptospermum scoparium J.R. Forst. & G. Forst.	Myrtaceae	WF, DF, T	o
Lycopodium fastigiatum R. Br.	Lycopodiaceae	WF	

Oreobolus pectinatus Hook. f.	Cyperaceae	WF, DF	p
Ozothamnus leptophyllus (G. Forst.) Breitw. & J.M. Ward	Asteraceae	T	o
Pentachondra pumila R. Br.	Epacridaceae	WF	p
Pimelea prostrata Willd.	Thymelaeaceae		o
Potamogeton sp.	Potamogetonaceae	WF	
Schoenus fluitans Hook. f.	Cyperaceae	WF, DF, T	c
Schoenus pauciflorus (F. Muell.) F. Muell.	Cyperaceae		c
Viola cunninghamii Hook. f.	Violaceae		p

Appendix 6.2

Additional biomass and nutrient summary data for Silica Rapids Litter Experiment.

Chionochloa rubra mean dry tiller weight (g) and weight of biomass contributed by leaf sheaths, green leaves and senesced leaf tips of tussocks from the three communities utilised in the Litter Decomposition Experiment, Silica Rapids Mire, Tongariro National Park.

Community	*Tiller dry weight (g)*	*Leaf sheath (g)*	*Green leaf (g)*	*Senesced leaf tip (g)*
Tussockland (n=6)	5.09 ± 0.82	2.38 ± 0.44	1.88 ± 0.30	0.84 ± 0.20
Dry fen (n=5)	2.65 ± 0.45	1.36 ± 0.28	1.66 ±0.25	0.63 ±0.09
Wet fen (n=4)	1.07 ± 0.24	0.46 ± 0.12	0.27 ± 0.07	0.33 ± 0.06

Empodisma minus culm nutrient content, Silica Rapids Mire, TNP. Culm size classes represent a continuum from newly emerged to standing dead, based on morphological changes. Data presented are means only due to small sample number (n=3), with one sample per community analysed.

Nutrient content	***Empodisma minus* culm size class**				
	1 Unbranched shoots	*2 Side shoots developing*	*3 Mature culms*	*4 Partially senesced*	*5 Standing dead*
%N	0.740	0.653	0.563	0.421	0.403
%P	0.030	0.019	0.017	0.009	0.006
%K	0.763	0.522	0.415	0.230	0.046
N:P	25.4	38.0	39.8	48.5	65.9

Relative chemical composition (%) of Empodisma minus culm litters from the 3 communities at Silica Rapids Mire, TNP. 1: Data are means ±standard deviations where N>3, otherwise only means are presented. Sample numbers varied according to Empodisma minus presence in communities with only 3 Tussockland sites containing the species, ^{A}*n=3,* ^{B}*n=6. 2: N & P analyses are means (*n=3), whereas fibre, cellulose and lignin data presented are single analyses, due to high cost*$^{\Upsilon}$*.*

Community	*N**	*P**	*N:P*	*K**	*Fibre* $^{\Upsilon}$	*Cellulose* $^{\Upsilon}$	*Lignin*$^{\Upsilon}$
1: Litter quality of *Empodisma minus* senesced culms^{1}							
Tussockland^{A}	0.32	0.013	34.4	0.075	48.9	29.0	17.3
Dry Fen^{B}	0.36 ±0.02	0.005 ±0.000	69.7 ±3.0	0.059 ±0.007	49.3 ±0.58	30.2 ±0.7	16.9 ±0.2
Wet Fen^{B}	0.39 ±0.03	0.004 ±0.000	97.6 ±8.5	0.069 ±0.013	48.8 ±0.68	28.9 ±1.1	17.7 ±0.3

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Is *Empodisma minus* the ecosystem engineer of the FBT (fen–bog transition zone) in New Zealand?

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The role of ecosystem engineers (EE) in the formation of ombrotrophic mires (bogs) from fens, called the fen–bog transition (FBT), can be best understood through categorization of the autogenic and allogenic processes causing bog initiation. Here we review these pathways, discuss the drivers of change in both cases, and tabulate an approach for distinguishing between them. We then compare the engineering ability of acknowledged and putative engineers against a number of characters which plants require to cross the FBT, and to stabilize occupancy on the bog side. While some *Sphagnum* spp. are accepted as the EE of the fen–bog transition in northern hemisphere bogs, they appear unimportant in New Zealand. Instead their role appears to be occupied by a restiad, *Empodisma minus*, a plant with leafless, wiry stems and capillaroid roots. *Empodisma minus* appears capable of engineering autogenic transitions from fen to bog across New Zealand, even more efficiently than *Sphagnum*.

Keywords: acidification; decomposition; drainage; macrofossil; litter; microbes; nutrients; palatability; peat; peat precursors; pH; productivity; water table

Introduction

The ecosystem engineer (EE; Jones et al. 1994; Charman 2002; Wright & Jones 2006) is a concept which has proved useful in elucidating some important ecological processes. Engineers are ‘organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic and abiotic materials’ (Jones et al. 1994, p. 374). While the ecological effects upon other species are described as ecosystem engineering (Kylafis & Loreau 2008), the evolutionary consequences of feedbacks to the EE have more recently been addressed in the concept of niche construction (Odling-Smee et al. 1996, 2003). While noting the comments of Reichman & Seabloom (2002a, b) and Wilby (2002), that engineering can be interpreted teleologically and can be all-encompassing, as Jones et al. (1994) previously noted, the concept has received widespread application in the mire literature, and increases our understanding of the processes involved.

Species from the bryophyte genus *Sphagnum* are widely considered to be EEs of mires in the northern hemisphere (Jones et al. 1994; Moore 1995; Svensson 1995; van Breeman 1995; Frankl & Schmeidl 2000). Although several *Sphagnum* species occur in the southern hemisphere, they appear to have no engineering role here (Moore 1995), restiad rather than *Sphagnum* bogs being the norm (Campbell 1975; Whinam et al. 2003). The only known southern hemispheric candidate for mire engineering is *Empodisma minus*

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Dedication: We would like to dedicate this contribution to the memory of a pioneer thinker in restiad wetlands, Dame Ella Orr Campbell DSc, 28 October 1910 - 24 June 2003 (Rapson 2004).

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(Hook. f.) Johnson & Cutler *s.l.*. A small member of the 'jointed rush' family, the Restionaceae, a southern hemisphere family closely allied to the Poaceae, *Empodisma minus* is widely distributed throughout New Zealand, Tasmania and the south and east of the Australian mainland (Campbell 1964; Moore 1995; Charman, 2002).

The process being considered here is the fen–bog transition (FBT), where an oligotrophic fen (terminology as per Wheeler & Proctor 2000) changes to an ombrotrophic bog. A peat accumulating system or zone is a prerequisite, but it is otherwise far from clear how the process occurs (Hughes 2000; Hughes et al. 2000, 2007; Hughes & Dumayne-Peaty 2002; Hughes & Barber 2003, 2004).

Since pathways across the FBT have been inadequately categorized, we here review the models of the pathways involved. We use this as background to discuss the role of ecosystem engineers in crossing the FBT, and review the characters EEs must possess to manipulate the environment in relevant ways. We go on to compare the abilities of *Empodisma minus* as EE of the FBT with *Sphagnum* spp., in addition to putative EEs in northern hemisphere and New Zealand mires, respectively the cyperad *Eriophorum vaginatum* L. and poad *Chionochloa rubra* Zotov.

Crossing the FBT

In its simplest sense, peat is the accumulated remains of undecomposed plant material. A peat deposit forms when the rate of deposition of dead plant matter produced by net primary production exceeds the rate of decomposition, i.e. Decomposition/Productivity = $D/P < 1$ (Clymo 1983, 1984). The rate of decomposition is the more variable determinant of peat accumulation (Damman 1986; Charman 2002), and it is affected by depth of burial (Clymo 1965), temperature (Rosswall 1974), water table depth (Clymo 1983), water table fluctuation (Belyea 1996), plant litter type and quality (Linkins & Neal 1982; Johnson & Damman 1991; Kuder et al. 1998; Scheffer et al. 2001; Trinder et al. 2009), oxygen supply (Clymo 1983), and microbial populations (Linkins & Neal 1982; Sundh et al. 1997; Pankratov & Dedysh 2009). In a bog, primary productivity occurs atop the acrotelm (euphotic and aerobic decay layers; Clymo 1984, 1992), while decomposition occurs in both the acrotelm and catotelm (collapsing, anaerobic decay layers).

Accumulation of fen peat is in itself inadequate to engender a transition to a bog. Three other developments are required (Moore 1995; Hughes & Barber 2003):

- hydrological isolation of the peat surface from groundwater and surface water, so that the only nutrient source is nutrient-poor rainfall (hence inducing ombrotrophy);
- occurrence of mechanisms to retain water within the elevated peat mass;
- establishment of plant species capable of growth in the newly created oligotrophic and acidic conditions, which then perpetuate the trophic change.

The requisite developments are not achieved simply. A peat system where decomposition equals, if not exceeds, productivity (i.e. a fen) has to be replaced by one in which productivity exceeds decomposition (i.e. a bog). The transition between the two states is the crucial phase of this process, hence the name FBT. Changes in pH, nutrient status and water table are in part consequent upon those changes, and in part induced by the incoming bog species. When ombrotrophic specialist species establish and dominate the mire community, they demonstrate that its trophic status has changed to that of a bog (Moore & Bellamy 1974). However, the above developments are descriptors of events, but are not causal, and so are not in themselves sufficient as explanations for the mechanisms of transition from fen to bog.

There are two potential pathways across the FBT, based upon allogenic vs. autogenic forcing mechanisms (*sensu* Nicholson & Vitt 1990), which we outline here. We use 'allogenic' to refer to processes which are external to the system concerned (omitting those which are anthropogenic in origin, e.g. Hughes et al. 2000, 2007; Hughes and Barber 2003), and so must be of abiotic origin. This includes processes such as climate change, or physical or hydrological events. 'Autogenic' processes are those resulting from inherent features of systems, particularly the plants themselves, and the peat derived therefrom, and so do not occur in the absence of adapted vegetation.

Allogenic pathways across the FBT

Allogenic pathways to transit an FBT operate in two categories (Table 1). The first set of mechanisms isolate an existing peat outcrop by physical means, so that only meteoric water can impinge upon the incipient bog surface, increasing its hydrological isolation, and initiating ombrotrophic conditions:

- physical decrease in water table, which, when occurring allogenically, can only be by changes in catchment-level hydrology such as that caused by landslides (cf. Lowe et al. 1999), river channel adjustments (Kulczynski 1949; Campbell 1964), sea level changes (Newnham et al. 1995), isostatic rebound (Glaser et al. 2004), and tephra deposition (de Lange 1989; Shearer 1997);
- climatic change in rainfall leading to groundwater flow reversals, isolating the peatland surface (Winkler 1988; Foster & Wright 1990; Siegel et al. 1995; Glaser et al. 1996; McGlone et al. 1997; Halsey et al. 2000; Robichaud & Begin 2009).

The second set of mechanisms leads to an increase in height of a peat body by decreasing the peat decomposition rate (by implication, while maintaining $D/P < 1$):

- decrease in temperature, decreasing evapotranspiration, thereby decreasing the depth of the (aerobic) acrotelm, so that litter reaches the catotelm in a less decomposed state;
- increase in precipitation, so that the ground water influence on the peat mass is lessened, and ombrotrophy is promoted.

These allogenic mechanisms result in warmer and better-drained patches, which will immediately be exposed to heightened erosion and decomposition rates, reducing the projecting outcrop of peat, and tending to bring it into line with the main fen peat surface. However, the patch may be stabilized by timely establishment of ombrotrophic vegetation, completing the FBT.

Autogenic pathways across the FBT

A large-scale autogenic mechanism for crossing the FBT which comes into play in fens, but only over long expanses of time, is the lateral expansion of the mire surface outwards from its founder location, and across the landscape (Korhola 1992; Table 1). Eventually such a system will become sufficiently large spatially (Heinselman 1970) for meteoric water to become the only source of nutrients onto the inner parts of the mire (the 'stagnation zones' of Vitt 1994), as any lateral inflow of water is stripped barren of nutrients by competing organisms before reaching the centre. This creates centralized bog conditions into which ombrotrophic specialist species can invade.

At smaller scales, the role of mire vegetation in generating autogenic pathways across the FBT has received much recent attention, such pathways requiring the presence of EEs, which 'change the environment via their own physical structures, i.e. their living and dead tissue' (Jones et al. 1994, p. 373). The physical consequences of such engineering on the growing peat body are (Zobel 1988; Malmer et al. 1994; van Breeman 1995):

a. a high internal water table within the peat bog, above the groundwater level of the surrounding minerotrophic fen peat;

Table 1 Parameters which allow differentiation between allogenic and autogenic mechanisms for crossing the fen–bog transition (FBT), including the role of ecosystem engineers (EE), and some examples of papers which apply these parameters to mire studies.

		Allogenic		Autogenic		
Parameters	Tools	Fen → bog		Fen → bog		Example of use in mires
Climate	Prevailing climate	Not applicable or relevant		Moist		Winkler 1988; Foster & Wright 1990
	Regional climate change	Norm	Cooler and/or wetter	Not applicable		Tallis 1983; Kuhry et al. 1991; Langdon et al. 2003
Catchment history	Mire expansion	Consider		Not applicable		Korhola 1992
	Hydrological changes	Consider		Not applicable		Kulczynski 1949; Heinselman 1970
	Tephra or sediment layers	Absent	Present (buried)	Not applicable		Lowe et al. 1999
Water table indicators	Desiccation surfaces on peat	Present	Absent	Absent		Casparie 1993
	Charcoal fragments	Present	Absent	Absent		Hughes et al. 2000; Barber et al. 2003
	Diatom assemblages (in recent peat)	Differences, especially in *Eunotia*		Differences		Foster & Fritz 1987; Dell'uomo 1992
	Collembola	Differences		Differences		Slawska 2000
	Testate amoebae assemblage	Low and/or fluctuating water table	Stable, high water table	High water table	Stable, high water table	Charman 1997, 2002; Charman & Warner 1997; Wilmshurst et al. 2003; Lamentowicz & Mitchell 2005; Lamentowicz et al. 2008
	Macrofossil analysis	Low	High	Fluctuating	Stable, high	Johnson et al. 1990; Nicholson & Vitt 1990; Kuhry et al. 1993
Peat characters	Humification	Sapric	Sapric/Hemic	Sapric	Hemic	Shearer 1997; Ellis & Tallis 2001
	Carbon:Nitrogen ratio	Increasing		Stable, high		Kuhry et al. 1991; Turunen & Turunen 2003
Inferred pH		Abrupt transition from high to low		Steady decline		Nicholson & Vitt 1990; Kuhry et al. 1993
Vegetation structure	Presence of EE	EE absent or at low densities	EE absent or present	EE present	EE dominant	Payette 1988; Nicholson & Vitt 1990; Kuhry et al. 1993; Hughes & Dumayne-Peaty 2002; Barber et al. 2003

b. development in the peat body of an acrotelm, engendering trophic isolation from the catotelm;
c. decline in water table fluctuations within the peat body, i.e. a dampening down of the effects of rainfall events and seasonal variations;
d. decreasing ash or inorganic content and increasing carbon content in peat as rheophilous inputs decline;
e. slowing of decompositional processes due to changes in soil chemistry, and to increasing anoxia and acidity, which result in a decline in decomposer (invertebrate, microbial and fungal) communities, slowing the decomposition process;
f. increasing proportion of recalcitrant material (which is slow to decompose) in the accumulating peat.

The process of engineering the FBT requires the presence of an EE, which differs from other species potentially contributing peat in its ability to grow in both the fen and bog situations, i.e., it is present before, during, and after the engineering event (visible in the peat profile; Table 2), and is increasingly competitive in the bog, so that it dominates. The EE alters the environment under some or all of the categories of peat accumulation, water table maintenance, and pH manipulations. We take accepted and putative EEs of the FBT from both hemispheres, and tabulate their engineering abilities under these categories (Table 2).

Enhanced accumulation of peat precursors from above- and below-ground tissues is due to reduced consumption and decomposition by:

- production of herbage of low palatability to both herbivores and detritivores (Clymo & Hayward 1982), or existence of physical barriers to herbivory such as hairs, spines or waxes (Cornelissen 1996), increasing litter retention on site;
- production of sclerophyllous tissues, high in lignin and in phenolics such as tannins (Cornelissen 1996), and low in nutrients (Clarkson et al. 2005), rendering litter inert and so reducing consumption;
- production of anti-microbial components such as sphagnan (Stalheim et al. 2009), reducing decomposition.

These features are fairly consistently found in species of mires (Table 2), especially in accepted EEs, though this may reflect availability of evidence. However, edibility and palatability render a species less successful as an EE.

Maintenance of a high and stable water table is attained by:

- reduced evapotranspiration from the vegetation canopy (Campbell & Williamson 1997), using a range of passive and active characters;
- heightened water-holding capacity within living and attached dead plant tissue mass due to high capillarity (Moore 1995), and the maintenance of macropores within the decomposing litter (Clymo and Hayward 1982; Turetsky et al. 2008);
- decreased vertical drainage down the peat profile due to increasingly dense packing with depth of partially decomposed material (Moore 1995), leading to lower hydraulic conductivity and permanent saturation (Clymo & Hayward 1982; Clymo 1992);
- drainage barriers due to mineral deposition with leaching (Andrus 1986);
- adaptation to water table changes, allowing growth in a range of hydrological conditions (i.e. both fen and bog);
- development of mire microforms such as hummock-hollow topography, which help inhibit the subsurface and lateral runoff (Ivanov 1981; Ingram 1983).

Water table manipulations appear to occur slightly less commonly in species with apparently limited engineering ability (Table 2) though evidence is mixed for *Eriophorum* and almost non-existent for *Chionochloa*. It appears that ability to use all of these mechanisms is

Table 2 Characters required for a species to be an ecosystem engineer (EE) across the fen–bog transition (FBT). The match to requirements of four potential EE taxa is categorized as good (√), bad (X), mixed (±), and unknown (?).

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
Ecosystem engineering ability present				
EE present both sides of the FBT	√ *S. fuscum* (Heinselman 1970; Payette 1988; Kuhry et al. 1993) *S. fuscum* has wide edaphic range (Bragazza 1997) *S. imbricatum* (Hughes & Dumayne-Peaty 2002)	X Temporary precursor only to *Sphagnum*-dominated raised bog (Hughes & Dumayne-Peaty 2002)	√ Common in mesotrophic to oligotrophic stages (Cranwell 1953; Shearer 1997; Clarkson 2002; McGlone 2009)	√ Wide edaphic range (Connor 1991)
Persistent macrofossil occurrence of EE throughout peat core	√ Preserved remains in 52% of samples in near continuous bands (Tallis 1994)	± Periodic peaks in leaf sheath bundles and spindles (Tuittila et al. 2007) May be a major peat former (Hughes pers. comm.)	√ EE persistent (Cranwell 1953; Campbell et al. 1973; Walker et al. 2001)	X Not a significant peat former in a mire largely lacking *Empodisma* (Walker et al. 2001)
Accumulation of peat precursors				
Low palatability to herbivores	√ Unpalatable (Clymo & Hayward 1982)	X Palatable; grazed by sheep, cattle, lemmings, ground squirrels, geese and caribou (Chapin & Slack 1979; Grant et al. 1987; Wein & MacLean 1973)	√ Unpalatable (van Rees & Hutson 1983; van Rees & Holmes 1986; McDougall 2007)	√ Unpalatable; 'worthless' character as sheep feed (Cockayne 1967, p. 121) Fertilization increases palatability (Connor et al. 1970) Organic matter digestibility is low (Fenner et al. 1993)
Inherent inertness of litter	√ Low rate of decomposition (Aerts et al. 1999) High phenolic content (Dickinson & Maggs 1974)	√ Low rate of decomposition (Coulson & Butterfield 1978; Cornelissen 1996; Hughes & Barber 2004)	√ Inherently low tissue nutrients (Agnew et al. 1993; Sharp 1995; Clarkson et al. 2005)	√ Lignin 6.8–10.3% (oven dry weight) in shoot material (Connor et al. 1970)

Table 2 (*Continued*)

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
	High refractory nature of peat (Scheffer et al. 2001) Low N content impacts on decay (Aerts et al. 2001) Presence of sphagnan may cause a form of C limitation as consequence of humification (Thomas & Pearce 2004)	Non-significant differences between nutrient content in rain-protected and unprotected leaves (Jonasson & Chapin 1985) Litter of rhizomes, leaf bases and roots accumulates as peat (Hughes pers. comm.)	Decay resistant outer cortex, central strand and endodermis in root (Campbell 1981) High polyphenol and lignin in stems; anhydro-galactosan in root hairs (Kuder et al. 1998) Heavily lignified mature roots (Sorrell et al. 2000)	High mechanical strength (Connor & Bailey 1972) High mean tiller weight and leaf dieback, and low mineral content in low nutrient soil (Lee & Fenner 1989)
Inhibition of microbial activity	√ Microbial inhibition (Dickinson 1983; Verhoeven & Toth 1995; Borsheim et al. 2001; Bonnett et al. 2006; Opelt et al. 2007; Pankratov & Dedysh 2009) Toxic organochemicals (Verhoeven & Liefveld 1997) Sphagnol and sphagnan inhibit decomposition (Smidsrød & Painter 1984; Rudolph & Samland 1985; Painter 1991; Stalheim et al. 2009)	?	√ Microbial inhibition due to allelopathic properties of tissues (Kuder et al. 1998) Low microbial biomass (Schipper et al. 1998) Litter and moss protected from degradation through incorporation into negatively geotropic root mass (Campbell 1981; Agnew et al. 1993)	?
Maintenance of high and stable water table				
Reduced evapotranspiration	√ Internal conduction of water re-wets hummocks (Titus & Wagner 1984) In hummocks, inrolled cucullate leaves and compact form reduce surface area for evaporation (Green 1968) In hollows, dehydrated *S. cuspidatum* hyaline cells have high albedo, reflecting light and reducing temperature (van der Molen & Wijmstra 1994)	√ Increased relative humidity under canopy (Lavoie et al. 2005)	√ Low evapotranspiration rates ($<$2.5 mm day^{-1}) due to thick litter and dense canopy (Campbell & Williamson 1997) Stomatal conductance maximized in morning (Sharp 1995)	√ Low transpiration losses c.f. *Festuca novae-zelandiae* and *Chionochloa australis* (Espie 1999) Few stomata, located in deep adaxial furrows, preventing desiccation (Espie 1999)

Table 2 (*Continued*)

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
Water-holding capacity	√ High water holding capacity (10–25 × own weight) (Andrus 1986) High effective porosity with depth (Holden 2009) Maintenance of macropore structure via litter quality (Turetsky et al. 2008)	√ Peat mass efficient at retaining water during periods of desiccation (Hughes et al. 2000)	√ High water holding capacity (15 × own weight) in sponge-like root weft (Campbell 1964) Dense canopy retains moisture at deeper canopy levels (Campbell & Williamson 1997) Moisture retained in peat (Campbell et al. 1995)	?
Decreased vertical drainage	√ Hydraulic conductivity decreases with depth (Adema et al. 2006; Price et al. 2008) *Sphagnum* structure collapses and bulk density increases with depth (Hayward & Clymo 1982; Johnson et al. 1990) Variable infiltration rates with depth (Holden 2009)	X No change in infiltration rates with depth (Holden 2009)	√ Decreasing hydraulic conductivity with depth; most water exchange in surface 1.5 m of peat layer (Maggs 1997) Acrotelm drainable porosity halved within 200 mm of surface (Miller 1994)	?
Drainage barriers	√ Iron hardpan formation (Andrus 1986) Fe-Mg hardpan formation (Klinger 1996; Kusel et al. 2008)	√ Iron oxide deposits in soil surrounding roots (Koch et al. 1991)	?	?
Adaptations to water table fluctuation	√ Ability to grow under both wet and dry conditions of mire surface (Green 1968; Casparie 1972; Barber 1981; van der Molen & Hoekstra 1988)	√ Wide tolerance to water table depth (Gore & Urquhart 1966; Barber 1981)	√ Structural elements may protect chlorenchyma from collapse in dry spells (Linder 2000) Surficial roots avoid anoxia by negatively geotropic growth habit (Campbell 1981; Sorrell et al. 2000) Surface rhizomes maintain atmospheric O_2 concentrations (Sorrell et al. 2000)	√ Wide tolerances (MacIntosh et al. 1983)

Table 2 (*Continued*)

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
Development of mire microforms	√ Hummocks (Green 1968; Titus & Wagner 1984) *S. imbricatum* has two morphologically distinct ecads, allowing it to grow in both hummocks and semi-aquatic habitats (Green 1968)	?	√ Hummock and hollow topography forms near edges of mire (Rogers 1984)	X No microtopography known (pers. obs.)
Features altering pH				
Acidification	√ pH of approximately 4 (Sonesson 1970; Braekke 1981; Glaser et al. 1981) Acidification via polyuronic acids (Clymo 1963; Bellamy & Reiley 1967) Polyuronic acid content 10–30% of dry weight; larger values for hummock species (Clymo 1964, 1967; Vile et al. 1999) Organic acid production acidifies subsurface waters (Hemond 1980)	± Low cation exchange capacity (Hughes & Dumayne-Peaty 2002) Acidification of substrate occurs under continental climate conditions (Hughes pers. comm.)	√ Acidification via polyuronic acids, at higher levels than for *Sphagnum* (Bannister 2000)	?

important for an EE due to feedback loops. For example, the high water table imposes physical and chemical constraints (e.g. promotion of reductive geochemical pathways) on the decomposer communities in the substrate, further increasing peat accumulation, while in the wetter substrate, litter decay slows due to lower temperatures and limited rates of gas diffusion.

In addition to the more global effects of carbon dioxide levels, precipitation of acidic rain and the activities of sulphur-metabolizing bacteria on pH levels (Clymo 1964), high cation exchange capacity results in acidification of the substrate (Clymo 1963), lowering the pH, limiting competition and decreasing decomposition (Mitsch & Gosselink 2000). Thus pH manipulations may be a crucial characteristic for an EE (Table 2).

The beauty of an engineering process is that neither the species nor the system needs to be dominant or large, for the mechanism to apply (e.g. engineering can occur in small kettlehole bogs or even on quarry floors; Lamentowicz et al. 2008 and Andreas & Host 1983, respectively). Nor are long periods of time essential, providing a fen-based peat is present (Cranwell 1953; Zobel & Masing 1987; Shearer 1997; Robichaud & Begin 2009). Therefore it is possible for FBTs to occur in small, isolated patches of a larger mire system, as proposed by Vitt (1994). Indeed, spatial dispersion of successfully engineered FBTs might be the ultimate cause of the string or flark patterning in mires which has generated so much discussion in the literature (e.g. Moore 1982, 1991; Glaser & Janssens 1986; Foster & Fritz 1987; Rapson et al. 2006; Eppinga et al. 2008).

Persisting on the bog side of the FBT

A successful engineer must be dominant in the engineered environment. Thus the engineering event can be assumed to be part of the evolutionary strategy of the species for self-perpetuation (Jones et al. 1994; van Breeman & Finzi 1998). Once on a mire the EE's structures, in altering the flow of nutrient resources, create an oligotrophic environment in which it is the superior competitor (Table 3). All EE characters appear dedicated to this end, so that nutrient losses from tissues accumulating as peat are matched by nutrient inputs only obtainable from atmospheric sources. Thus competitive traits in the engineered environment include superior levels of nutrient access, and rates of nutrient uptake and retention.

Superior nutrient access, compared to potential competitors, is achieved by:

- water pre-emption, i.e. increased opportunity to intercept meteoric water, which is the primary incoming nutrient source in ombrotrophic conditions, so that any nutrients carried in the rainfall are disproportionately available to the intercepting species (Agnew et al. 1993);
- deep root systems extending to the base of acrotelm to enhance nutrient access (Adema et al. 2006).

Superior nutrient uptake is achieved by some or all of:

- enhanced rates of cation exchange, increasing acidification (Clymo & Hayward 1982) and nutrient supply;
- the development of root adaptations (such as cluster roots and root hairs) to low nutrient conditions (Lamont 1982; Lambers et al. 2006), which also increase below-ground productivity and hence the below-ground contribution to peat accumulation rates.

Superior nutrient retention is achieved by:

- the production of foliage which is long-lived, evergreen, and of reduced size, increasing nutrient retention times and decreasing nutrient requirements (Aerts 1999; Aerts & Berendse 1989);
- translocation of scarce nutrients to perennating organs prior to litter fall (Escudero et al. 1992; Aerts 1993), with large and long-lived rhizome and root systems through which scarce nutrients may be relocated or stored (Chapin 1980);

- enhanced rates of release of limiting nutrients from decomposing tissues for rapid resorption from within the upper peat layers (Moore & Bellamy 1974; Smith 1981), perhaps via capillary water flow on the exterior of the EE's tissues (Clymo & Hayward 1982).

Another competitive advantage may be obtained by suppression of competitors at germination, e.g. where recruitment may fail due to low light availability under a dense vegetation canopy or litter layer (following Xiong & Nilsson 1997 for riparian wetlands). In addition, perennial competitors must be capable of continuous upward growth as the peat surface rises, with new roots developing annually on a higher level (Malmer et al. 1994).

Identifying engineered systems

The two models for crossing of the FBT are differentiable, theoretically and mechanistically, historically and spatially, via a range of environmental, historical and peat characteristics (Table 1), no one line of evidence being sufficient (Langdon et al. 2003; Pellerin & Lavoie 2003). In physical terms, the regional climate is important in determining whether a mire can form, but, further, a change in climate can induce allogenic crossing of the FBT (Table 1), as can mire size increases and hydrological changes which result in more stable peat surfaces. The contribution of testate amoeboid assemblages (Charman 1997, 2002; Charman & Warner 1997; Woodland et al. 1998) as bioindicators of the FBT looks particularly promising, especially as they have no known role in creating the changes they indicate (McMullen et al. 2004; Payne & Pates 2009), though their close associations with plant species admits of circularity of logic (PD Hughes, pers. comm.). While fruitful, and easy to obtain, macrofossil evidence is also handicapped by circularity in determining causes of the FBT (Whinam & Kirkpatrick 1995), as is the use of level of degradation of plant polysaccharides as a proxy for bog palaeohydrology (Kuder & Kruge 1998, 2001). Decrease in desiccation indicators (e.g. Casparie 1993), decline in fire rates (e.g. Hughes et al. 2000), and declining fluctuations in the water table (e.g. Charman & Warner 1997), are also suggestive of allogenic crossings, while stable or gradual changes in water table indicators contribute to evidence of autogenic processes. The presence of a putative EE on a bog can be informative, but is not necessarily conclusive evidence of an ability to engineer the FBT, unless the species is also known to have been present in the fen stage (Table 1), e.g. occurs in quantity in the fen peat profile.

Though FBTs have been frequently recorded (e.g. Glaser 1992; Hughes & Barber 2004; Muller et al. 2008), most literature we are familiar with does not present the requisite information to allow us to unequivocally assign the studied mires to either autogenic or allogenic pathways across the FBT, impeding an assessment of the relative frequency of these models. Allogenic pathways are identified by Winkler (1988) and Nicholson & Vitt (1990), and autogenic ones by Lamentowicz et al. (2008). Kuhry et al. (1993) argue that even within the framework of a wetter climate shift, the FBT in Canadian boreal mires should be attributed to autogenic acidification by *Sphagnum* species, rather than to any particular climate variable. Both pathways, operating at different times, were inferred by Payette (1988) and Hughes & Dumayne-Peaty (2002). For example, climate change to increased precipitation and cooler temperatures (an allogenic process) may slow decomposition and favour ombrotrophic *Sphagnum* growth (autogenic) in poor fens, while further decreasing decomposition rates by raising regional water tables (allogenic; Langdon et al. 2003). An EE is probably also common as an accelerant of allogenically triggered pathways (Glaser et al. 1997; Hughes & Dumayne-Peaty 2002; Hughes & Barber 2004; Robichaud & Begin 2009), and such hybrid transition types, where 'internal factors operate within the framework of external factors' (Winkler 1988, p. 1032), may well be the norm in the development of bog complexes. Hybrid situations would greatly increase the likelihood of crossing the FBT, autogenically stabilizing any allogenic crossing, while reducing the time elapsed in attaining the conditions necessary for a successful crossing.

Who is engineering the FBT?

A successful EE must have the ability to induce environmental changes under some or all of the three manipulations detailed above (i.e. enhanced accumulation of peat precursors, maintenance of high and stable water table, and substrate acidification). In the northern hemisphere *Sphagnum* is the classic plant engineer (Table 2), its abilities widely extolled in the literature (e.g. Damman 1986; Stoneman et al. 1993; van Breeman 1995; van Breeman & Finzi 1998; Charman 2002; McMullen et al. 2004). It is of extremely low palatability, and, though of modest productivity, is very slow to decompose, so that its peat accumulates. Almost all evidence regarding its engineering capacity is positive for an EE (11–12 of 12 possible engineering characters in Table 2), except for some facets of water evaporation from hummocks. Apart from the lack of storage organs, it is highly competitive, particularly for nutrients, and so demonstrates five out of eight characters known to stabilize occupancy of a bog (Table 3). However, species within the *Sphagnum* genus differ in their engineering ability, e.g. *S. fuscum* (Heinselman 1970; Payette 1988; Kuhry et al. 1993), and *S. austinii* (Hughes & Dumayne-Peaty 2002; Hughes et al. 2008) are reported as EEs. But species in New Zealand appear to have no role in engineering the FBT, despite their apparently high productivity in comparison with northern hemisphere species (Buxton et al. 1996; Gunnarsson 2005). Though Cockayne (1967) notes *Sphagnum* 'bog' islands growing in *Typha-Phormium* swamp in lowland coastal North Island, this is probably *Sphagnum falcatulum*, a well-known swamp plant, but not a bog builder. A small montane mire possibly approaching the FBT, and reported by Walker et al. (2001) to have a peat profile composed of *Sphagnum cristatum* (other species being apparently unable to tolerate the fire regime), is the most plausible recorded engineering instance by New Zealand *Sphagna*.

Another putative EE, a common northern hemisphere mire species, *Eriophorum vaginatum* (Table 2), is known as a colonizer or pioneer species (Wein & MacLean 1973). It has a number of characters which indicate reasonable engineering ability (5–6 out of 12 positive matches; Table 2). However, it is fairly palatable, and has low acidification capacity and relatively evenly draining peat (which may be mistaken for *Sphagnum* peat; Barber et al. 2003), reducing its engineering capacity. Additionally it has few characters which are able to stabilize a bog (4/8 characters; Table 3). Though providing habitat for *Sphagnum* invasion (Lavoie et al. 2005), against which it appears less competitive, *Eriophorum* is still able to persist in the new 'pseudo-raised bog' environment (Hughes & Barber 2004, p. 65; Korhola 1992), supporting a designation as EE. Since it is only a temporary precursor to *Sphagnum*-dominated raised bog (Hughes & Dumayne-Peaty 2002; Hughes & Barber 2004; McMullen et al. 2004), it acts more as a facilitator (Connell & Slatyer 1977; Callaway 1995). However, the current relative dominance of *Sphagnum* may be due to the shift to a wetter Holocene climate about 8000 yr BP, changing the balance towards less desiccation-tolerant peat builders (Hughes & Barber 2004). In past warmer, drier climates, changes towards ombrotrophy took place by the growth of sedge-rich communities raising the surface level of the peat above the groundwater table (Barber et al. 2003). In such climatic conditions, *Eriophorum* may have been more successful as an engineer than it is today.

In the southern hemisphere *Empodisma minus* is the most likely candidate for EE of the FBT (though two taxa may be involved; B. Clarkson, pers. comm.). A small rhizomatous perennial, *Empodisma minus* (Hook.f.) Johnson

Table 3 Characters required for a species to persist on the bog side of the fen–bog transition (FBT). The match of four potential EE taxa is categorized as good (√), bad (X), mixed (±), and unknown (?).

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
EE dominance				
Competitive?	√ Dominant (Moore & Bellamy 1974)	X Increased relative humidity under canopy facilitates establishment of moss species (Lavoie et al. 2005) Only temporary on raised bogs (Hughes & Dumayne-Peaty 2002)	√ Shrubs stunted by low P concentrations on restiad mires (Clarkson et al. 2005) Clonal resprouter (Meney & Pate 1999)	± Tussocks appear stunted in restiad mires (pers. obs.) and string fens (Rapson et al. 2006)
Nutrient access				
Water pre-emption	√ Efficient capture of atmospheric water (Lee & Woodin 1988; Aldous 2002) External capture via capillary water flow (Clymo & Hayward 1982) Buoyancy-driven water flow replenishes nutrients (Rappoldt et al. 2003; Adema et al. 2006)	√ Exploitation of subsurface waters via deep roots overcoming nutrient limitation (Chapin et al. 1988)	√ Pre-emption by high stem flow (Agnew et al. 1993) Accesses atmospheric nutrient sources (Clarkson et al. 2009)	± By fog-water interception (Ingraham & Mark 2000)
Deep root systems	X No roots present	?	X Cluster roots retrieve N from only the top 5 cm of substrate (Clarkson et al. 2009)	√ Deep roots (Craine & Lee 2002)

Table 3 (*Continued*)

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
Nutrient uptake				
Cation exchange	√ High cation exchange capacity (Clymo 1963; Daniels & Eddy 1985) *S. rubellum* takes up amino acids as N source (Kielland 1997) Symbiotic methanotrophs oxidize methane for *Sphagnum* assimilation (Raghoebarsing et al. 2005) Incorporation of nitrate and phosphate rapidly from solutions of unusually low concentration (Clymo & Hayward 1982; Bragazza et al. 2003)	√ Absorbs organic N and has preferential use of amino acids as N source (Schimel & Chapin 1996) Methanotrophs in *Eriophorum*/*Sphagnum* dominant community similar to those of ombrotrophic peatlands (Chen et al. 2008) Very efficient in taking up nutrients in luxury nutrient conditions (Shaver et al. 1986) Root surface phosphatases contribute up to 69% of annual P demand (Kroehler & Linkins 1991; Moorhead et al. 1993)	√ Presence of uronic acids suggests uptake capability (Bannister 2000) High efficiency of nutrient uptake across a range of substrate values (Clarkson et al. 2005)	?
Root adaptations	X None	?	√ Scavenges nutrients with negatively geotropic roots and 1 mm root hairs (Campbell 1975, 1981; Agnew et al. 1993)	?
Leaf life span	√ Long leaf longevity (Chapin et al. 1995)	X Short leaf longevity (Jonasson & Chapin 1985)	√ Stems long-lived, dead shoots retained in canopy layer (pers. obs.)	√ Long-lived (Greer 1979)

Table 3 (*Continued*)

Character	Northern hemisphere *Sphagnum* spp.	*Eriophorum vaginatum*	*Empodisma minus*	*Chionochloa rubra*
Nutrient storage organs	X None	√ Seasonal variation in nutrients of tundra species' organs (Chapin 1980) Storage of limiting nutrients (especially P and K) in perennating organs (Goodman & Perkins 1959; Defoliart et al. 1988)	√ Rhizomes to 1 cm thick (pers. obs.)	√ High nutrient concentrations in leaf sheaths (Williams et al. 1978) High carbohydrate storage in stems and leaf bases of congeners (Payton & Brasch 1978)
Nutrient recycling				
Nutrient resorption	√ Nutrient translocation (Rydin & Clymo 1989; Svensson 1995; Aldous 2002) Internal nutrient transport through perforations in stem parenchyma cells (Rydin & Clymo 1989)	√ 90% leaf P and 80% leaf N resorbed (Jonasson & Chapin 1985) High nutrient use efficiency under low nutrient conditions (Thormann and Bayley 1997) Competitive on cold, infertile sites with other sedges (Shaver & Laundre 2003) Vascular sclerenchyma in corm aids in nutrient recovery and redistribution (Cholewa & Griffith 2004)	√ Nutrient uptake occurs in upper 5 cm of root weft (Clarkson et al. 2005), so leachates can be scavenged	?

& Cutler grows in seasonally or permanently inundated habitats, mires, wet heathlands (including pakihi; Johnson & Gerbeaux 2004), and riparian zones with peaty soils throughout South-East Australia, Queensland, Tasmania and New Zealand (Campbell 1964, 1981; Johnson & Cutler 1973; Wardle 2002). The *Empodisma* genus is a part of the Winifredia group of the Australasian Restionaceae (Briggs & Johnson 2002). The name *Empodisma* refers to the much-branched, dark green, hollow and slender stems (culms), with extremely reduced leaves in whorls, hosting minute flowers. Stems are 12–200 cm long, forming dense, tangled masses (its local name is wirerush), which arise from bract-covered, glabrous dark brown rhizomes, buried up to 25 cm deep (pers. obs.) in the substrate. *Empodisma* is a strongly competitive clonal resprouter, with infrequent recruitment from seed (Meney & Pate 1999), except following disturbance such as fire (Clarkson 1997). At least in southern mires, *Empodisma* is associated with deep, well-decomposed peat, low pH, and low Ca:Mg ratios as well as high marine sodium inputs (de Groot 1999).

Empodisma minus has a dimorphic root system, with sturdy roots anchoring the rhizomes which presumably store nutrients and/or carbohydrates. A second root form, the capillaroid root which is covered with 'closely crowded persistent root hairs' (Campbell et al. 1995, p. 9), develops in response to low soil nutrient levels, and is negatively geotropic in bogs (Campbell 1981). Capillaroid roots are not unique to *Empodisma,* being reported in other members of Restionaceae from Australia (e.g. *Loxocarya* spp. and *Calarophus elongatus*; Campbell et al. 1995) and South Africa (pers. obs.), though these areas are too dry for organic matter to accumulate (Campbell et al. 1995). In the wetter regimes of New Zealand, *Empodisma*'s capillaroid roots accumulate as peat due to their abundance, capacity for water retention, chemical inertness and resistance to decay (Campbell 1981). In favourable conditions, the roots can intertwine into a dense, felt-like mat which may grow 20–50 mm above the mire surface, and remain live to a depth of 300 mm (Clarkson et al. 2009). These mats form the sole ground cover, building up around the shoots of adjacent plants and engulfing fallen litter (Campbell et al. 1995). The capillaroid roots have high hemicellulose, and low polyphenol and lignin contents, chemistry which in other species is associated with fine or amorphous detritus upon decomposition (following Kuder et al. 1998). The thicker axes of the roots and stems are high in lignin and polyphenols, which increase their resistance to decay by inhibiting microbial activity, and, with possible allelopathic properties, facilitates competitive exclusion of other mire species (Kuder et al. 1998). As a result of these capillaroid root mats, a 'vertically displaced feeding root system' (Clarkson et al. 2009, p. 378) forms underneath the restiad canopy. *Empodisma* functions with low tissue nutrient contents (Agnew et al. 1993; Sharp 1995; Clarkson et al. 2005), and there is only limited colonization of roots by arbuscular mycorrhizae (Clarkson et al. 2005). Instead nutrient uptake from the low-nutrient peat substrate is by these negatively geotropic capillaroid roots and fine root hairs (Campbell 1981). The roots intercept nutrient-bearing rainfall via stemflow (Agnew et al. 1993), while other mire species can only access nutrients from within the substrate (Clarkson et al. 2009), or have limited stemflow (Agnew et al. 1993). The base-exchange capacity of the capillaroid roots is equal to that of a co-occurring New Zealand *Sphagnum* species (Agnew et al. 1993), suggesting efficient uptake of any intercepted nutrients. Further Bannister (2000) found significantly higher uronic acid levels in *Empodisma* than four northern hemisphere *Sphagnum* species, contributing to its high nutrient capture.

Empodisma has a range of characters which results in maintenance of a high and stable water table. Despite being a wetland species, its roots are 'poorly adapted for growth in anoxic soils' (Sorrell et al. 2000, p. 682; Johnson & Brook 1998), though the water-holding capacity of the root mat is comparable to that of *Sphagnum* on a dry weight basis (Campbell 1964, 1981; Agnew et al. 1993). With low cortical porosity and a highly thickened endodermis and stele, the negatively geotropic habit of the capillaroid roots may be an adaptation to avoid anoxia (Sorrell et al. 2000). Further, the high volume of gas-filled *Empodisma* tissues near the surface may result in peat floatation, another engineering trait which may permit peatland surface oscillations (Fritz et al. 2008), as do occur in mire zones with high *Empodisma* cover. Campbell & Williamson (1997) indicate *Empodisma* exerts strong control on evaporative losses from its canopy, the dense shoots acting as a mulch, restricting movement of solar energy and water vapour between the substrate and atmosphere. Dead stems (including suspended litter), comprising up to 60% of the total canopy biomass (Hodges, unpublished data), are retained within the lower canopy. These intercept rainfall, so the moisture content of the lower canopy remains higher for longer than that of the upper canopy (Campbell & Williamson 1997).

Though much less well studied than *Sphagnum*, *Empodisma minus* has the expected characteristics of an EE of the FBT (Table 2; 11/12 characters), except that there is no information on its possible production of drainage barriers. It establishes early in the fen stage, and becomes dominant in later stages (Shearer 1997; Clarkson 2002; Clarkson et al. 2004). Then *Empodisma* dominates the water table and nutrient regimes of the mire, until the peat surface is hydrologically isolated, and a bog is formed, which it effectively stabilizes (Table 3; 7/8 characters), due to its unpalatable shoot material (van Rees & Hutson 1983), inert litter (Campbell 1981), and high nutrient retention capabilities. Due to 'an elegant interaction between its morphology, substrate and rainfall' (p. 107, Agnew et al. 1993), *Empodisma* is a world-class ecosystem engineer.

New Zealand's raised restiad mires form in areas with seasonal rainfall deficits, and lower annual rainfall than that required for the development of raised mires in the northern hemisphere (McGlone 2009), which may be why *Empodisma* is a better engineer here than *Sphagnum* species. Pollen and macrofossil data from four North Island mires of varying age provide support for an autogenically driven model of mire succession which can operate across a range of different climates (Clarkson et al. 2004). *Empodisma* may also be more versatile in terms of climate regime under which it can engineer than northern hemisphere *Sphagna*.

Another possible contender for southern hemisphere EE of the FBT is the red snow tussock, *Chionochloa rubra* (Tables 2 and 3), which includes four subspecific taxa (Connor 1991). Up to 1.5 m tall, it has a wide edaphic range, and occurred on the often peaty soils of south-eastern and southern New Zealand over far greater areas than today before land clearance for agriculture (Mark & McLennan 2005). It is absent from northern lowland restiad bogs, where its position in the FBT is taken by sedges (e.g. *Baumea* spp). *Chionochloa* tends to be replaced in raised bog communities by *Empodisma* and other bog species, but persists on the more minerotrophic bog margins. Less well studied as an EE than the other species, it has no known characters which contradict assignment as an EE (5/12 in Table 2, and (3–4)/8 in Table 3), but it is not recorded as building peat and is of low productivity in bog situations (pers. obs.).

Empodisma's only mainland New Zealand bog-inhabiting relative, the rare giant restiad (*Sporadanthus ferrugineus* de Lange, Heenan et B.D. Clarkson, in the Lepyrodia Group of the Restionaceae: Briggs & Johnson 2002), contributes less than *Empodisma* to peat accumulation in its only locale, the peat domes of the Waikato region (Shearer 1997; Clarkson 2002). It has lower stem flow than *Empodisma* (Agnew et al. 1993), and is not found in fens, and so cannot be an EE. A recent segregate, *Sporadanthus traversii* (F. Muell.) F. Muell, is, however, reported as the major peat builder on the botanically related Chatham Islands (McGlone 2002; Clarkson et al. 2004) in the absence of *Empodisma,* and its shorter, finer, droopier canes may confer some as yet unstudied engineering abilities.

Conclusion

Work by Hughes & Barber (2003, 2004) has been pioneering in consistently addressing the FBT. Practical experimentation, such as that initiated in bogs by Clymo (1965) and Bellamy & Reiley (1967), and more recently demonstrated by Scheffer et al. (2001), Heijmans et al. (2002) and Adema et al. (2006), offers much needed insight into bog mechanics. Here we review the two mechanisms for crossing the FBT which are differentiatable, and encourage determination of the types of ecological, biological, palynological or stratigraphic evidence which can irrefutably distinguish between these causes of change in mire trophic status, perhaps considering the framework proposed in Table 1.

The importance of the EE in crossing the FBT cannot be underestimated. EEs certainly play pivotal roles in mires of both southern and northern hemisphere temperate regions, though these are not necessarily ecologically comparable to mires of other regions (Damman 1995). In New Zealand the apparent EE of the FBT is *Empodisma minus*. We encourage the identification, following Tables 2 and 3, of EE species in other parts of the world, an area where local knowledge will be crucial. We are undertaking some such work, focusing on *Empodisma minus* and the other putative engineer, *Chionochloa rubra*, in the New Zealand context.

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