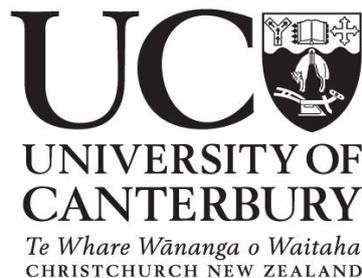


**Reconstructing Historical Vegetation Cover in Otago,
New Zealand, Using Multi-proxy Analysis of
Peat Cores**

A thesis submitted in partial fulfilment of the
requirements for the degree of
Master of Science in Environmental Science
in the University of Canterbury

by

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Abstract

This research has examined the historical vegetation of two Eastern Otago sites below the regional treeline, with the aim of addressing questions about the distribution and spread of native tussock grasslands prior to human arrival in New Zealand c. 800 yr BP. Pollen and phytolith (plant opaline silicate) proxies have been extracted from peat cores at Swampy Summit and Clarks Junction to provide a record of vegetation spanning the Holocene. Using multiple proxies and two sample sites has allowed for comparisons of the record of vegetation from within sites and between sites. A record of the modern pollen rain was also gathered from localised moss polsters at Swampy Summit in order to reconcile modern pollen assemblages and transport patterns with historical findings. It became clear from the research that the record of vegetation inferred from phytoliths was not analogous to the pollen-based records, which supported the hypothesis that vegetation reconstructions based solely on pollen may be unreliable. Good pollen preservation in the sediments allowed for the identification of over 50 taxa, although only *Chionochloid* forms were identifiable to a family level in the phytolith records. *Poaceae* pollen was abundant throughout the Clarks Junction record, suggesting grassland had persisted at this site during the Holocene, while *Poaceae* pollen at Swampy Summit was minimal and sporadic. Phytoliths at Swampy Summit show grasses have persisted at the site throughout the Holocene, at times in much greater proportions than the pollen record would suggest, while *Chionochloid* phytoliths only become common near the top of the record, possibly reflecting increasing dominance of this taxa after human disturbance. In contrast to Swampy Summit, the Clarks Junction phytolith record reflects a more stable presence of grasses throughout the Holocene, with *Chionochloid* forms present throughout. Phytoliths appear to be a more reliable proxy for local vegetation, with both sites indicating a Holocene presence of grasses below the regional treeline prior to human arrival in New Zealand. In comparison, the pollen record appears to indicate a more regional pattern of vegetation, with the grassland pollen record complicated by pollen dispersal and deposition factors.

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1. Introduction

The spread of tussock-grassland plant communities post human arrival in New Zealand has been the subject of contention (Mark and Dickinson, 2003; Walker et al., 2004). It is widely postulated that native tussock grasslands have radiated from high altitude vestiges above the treeline (e.g. in the South Island high country) to occupy large tracts of lowland, cleared of forest by human induced disturbance (McGlone and Moar, 1998; Wardle, 1964). The rate and extent of deforestation occurring as a result of human activities subsequent to Polynesian settlement and later European development in New Zealand has been dramatic, however the rate of dispersal of open tussock grasslands to their current range leaves questions remaining about their distribution and extent prior to human arrival in New Zealand.

Throughout the Holocene, there has been ongoing modification of the pattern of vegetation in the New Zealand landscape, initially as a result of climatic fluctuations in precipitation and temperature which have directly affected the development and spread of the New Zealand flora (e.g. Alloway et al., 2007). Secondary to this, there has been widespread disturbance to natural vegetation by fire, predominantly in the drier eastern regions where conditions have favoured ignition by lightning strikes (McGlone, 2001), while natural fires in the North Island have also been triggered by volcanism (McGlone, 1989).

In conjunction with natural disturbance, human induced disturbance has vastly changed the natural landscape of New Zealand. Direct disturbance by uncontrolled and deliberate anthropogenic burning has completely removed natural vegetation communities from large areas of New Zealand during the late Holocene period, beginning approximately 800 years ago with the arrival of Polynesian colonisers and continuing through European settlement until the present day (McGlone, 2001; McGlone and Moar, 1998; Walker et al., 2004). Logging of indigenous hardwood and softwood forests throughout the country has also contributed to forest clearance. The magnitude of human induced clearance of native vegetation in New Zealand has been massive, with repeated disturbance suppressing successional communities, resulting in a 70 % reduction of forest cover in the last 1000 years (Ogden et al., 1998). Further complicating the re-generation of indigenous flora has been the introduction

of exotic plant species. The spread of these non-native competitors has been uncontrolled and rapid, vastly altering the composition of modern grassland communities from their original structure. Other indirect effects on native vegetation resulting from human activities include the introduction of a variety of herbivorous mammalian pests which have spread throughout the country to occupy a range of forest and grassland areas.

More recent changes to the pattern of vegetation in New Zealand are obvious; however the distribution and structure of indigenous flora and the mechanisms affecting vegetation under historical conditions need to be identified in order to fully understand ecosystem processes. The role of climate influencing the distribution and composition of vegetation can be inferred from palynological records gathered from sediments pre-dating human induced disturbance in New Zealand. Significant changes in the New Zealand climate during the early Holocene have been identified and mirrored in the vegetation record prior to human arrival, as interpreted from dominant palynomorph types in pollen diagrams. Further, radiocarbon dating of macrofossils preserved in these records has enabled important climate events to be constrained and related to changes in the structure of vegetation.

Post-human arrival, the palynological record of vegetation shows evidence of widespread anthropogenic disturbance, signalled by a spike in charcoal concentrations and seral pollen types in many sediment records (McGlone, 2001; McGlone et al., 1997; McGlone and Wilmshurst, 1999b). According to these pollen records, frequent anthropogenic fires began to significantly alter the structure of native vegetation beginning about 750-800 years ago (McGlone, 1989, 2001; Walker et al., 2004) and repeated burning has been the main driver of vegetation change through Polynesian and European settlement phases. Since then there has been a transition to open grassland and scrubland across much of the country, especially in drier East Coast regions (McGlone, 1989, 2001), with forest remnants persisting on rocky outcrops and isolated damp sites in the montane zone (Hall and McGlone, 2001; Ogden et al., 1998). Widespread forest persists in the rugged western South Island.

Extensive grassland is thought to have been restricted to high alpine and dry intermontane areas with only patches of grassland possibly surviving in wooded areas

by colonising sites unfavourable to woody vegetation such as wetlands (McGlone, 2001). An examination of the ecological characteristics of many of the high altitude native grass species indicates that their life histories do not account for such a rapid spread to lowland areas, solely from high alpine communities (K Dickinson, pers. comm., 2008; Scott, 1970). This study will test the hypothesis that the modern pattern of native tussock-grassland vegetation in New Zealand has most likely expanded to its current range from numerous isolated areas of grassland, interspersed throughout a much larger expanse of woody forest and shrubland communities (Mark and Dickinson, 2003). This radiation of tussock-grassland to occupy lowland areas after disturbance below the natural treeline is more likely to have occurred from a combination of high alpine and lowland sites where source taxa have already been present locally in the landscape. It is hypothesised that grassland communities survived below the natural treeline as a mosaic with woody vegetation types on areas where disturbance regimes have prevented succession to woody vegetation (Mark and Dickinson, 2003). McGlone (2001) suggests that areas with low precipitation or poor soils such as inter-montane basins formed a key source of colonising grass species after forest clearance.

This study of palynological profiles preserved in peat from two Otago sites in the South Island - Swampy Summit and Clarks Junction- seeks to add to the pool of palynological records forming the basis of Holocene vegetation reconstructions in New Zealand. Selection of these sites was based on their favourable pollen preservation which ensured good pollen records could be obtained and compared with phytolith records. Both pollen and phytolith proxies will be used to analyse Holocene vegetation change, with emphasis on the distribution of grasslands at these below-treeline sites. It is hoped that an improved picture of vegetation communities and their distribution during the last 10,000 years can be gained from these sites, while also testing the compatibility between pollen and phytolith records preserved in peat for interpretation of historical vegetation cover at a regional scale.

By developing a more detailed picture of natural vegetation cover at these sites prior to human arrival in New Zealand, there is potential for improving our knowledge of the historical structure of native vegetation communities in these areas. This has implications for reconstructing past climate and environmental change as well as

assessing current land management strategies in many high country tussock-grassland areas within the crown conservation estate, and may lead to re-assessment of natural values and restoration aims in these areas.

This research will use the comparison of pollen and phytolith records from two Otago sites to examine patterns of vegetation and critique the representativeness of these proxies as tools for understanding and quantifying the pattern of vegetation throughout the Holocene. This research also aims to test the hypothesis that tussock grassland may have persisted at sites below the treeline prior to widespread human clearance of lowland forests.

2. Literature Study

There are a number of important natural and human-induced drivers of vegetation change which have been attributed to developing the present structure of New Zealand's vegetation communities. These mechanisms have resulted in the modification of large parts of New Zealand's vegetated landscape during the Holocene and evidence for these drivers comes from a broad spectrum of quaternary research. Modern observations of remaining indigenous vegetation in its natural setting have provided insight into the environmental requirements and tolerances of some species. This has aided our understanding of the pattern of historical vegetation in order to correlate changes with natural or anthropogenic disturbance. After isolating a chronological sequence of vegetation cover, it can be difficult to link observed patterns in the proxy record with causal mechanisms of vegetation change. Alloway et al. (2007) have attempted to link climate and vegetation patterns by comparing vegetation composition from the Okarito wetland pollen record with proxies for climate events, such as fluctuations in temperature and precipitation from speleothem isotope records (Williams et al., 2005). Other evidence used to interpret vegetation changes in the landscape include charcoal counts for fire histories (Clark, 1982; McGlone, 2001), and macrofossils such as wood fragments suitable for radio carbon dating, while beetle remains have been used as a proxy to test vegetative associations indicating the presence of associated woodland taxa (Burge and Shulmeister, 2007). Other invertebrate studies have examined beetle genetics to date

the exclusion of Beech forest from the Westland Beech Gap by glacial ice during the Pleistocene (Leschen et al., 2008).

Besides these *in-situ* proxies for interpreting vegetation change, it is also useful for paleoecologists to look at much broader drivers of vegetation change such as climate cycles, associated glaciations and other natural processes including fire history. These will be discussed below.

2.1 Regional Climate Dynamics

The most significant influence on the pattern of native vegetation in New Zealand is climate, which is still evident in regions where natural vegetation has been protected from modification by human activity such as in remote areas and National Parks and reserves in the conservation estate. By examining differences in the environmental requirements and tolerances of vegetation communities that existed throughout the Holocene and earlier, it is possible to gain an understanding of localised climatic conditions that existed at that time and place. In sites with well-preserved, stratified sediments such as peat bogs, a continual record of vegetation can be inferred from palynological records throughout the Holocene, with observed succession of vegetation in many places reflecting the amelioration of the post-glacial climate (McGlone, 1995).

New Zealand's position in the South Pacific is directly in the path of mid-latitude westerlies, which control the pattern of regional precipitation and produce the dominant west-east precipitation gradient across the country (Lorrey et al., 2007; Sturman and Tapper, 1996). Regional precipitation differences are compounded by the effect of having the Southwest-northeast orientated mountains in both main islands blocking the westerly flow of moisture-laden air (Wratt et al., 1996).

The topographic barrier of the Southern Alps has the effect of accentuating the differences in climate between the west and east coasts by initiating orographic precipitation west of the Alps. As predominant westerly weather systems are forced higher in altitude, moist air condenses, forming clouds and generating precipitation (Gray and Seed, 2000). Triggered convection can further enhance precipitation west

of the main divide as windflow over the ranges causes instability of the rising air column, increasing convection and leading to increased precipitation (Gray and Seed, 2000). Eastern regions are generally drier as they receive less precipitation under foehn conditions, while the west coast can receive up to 12,000mm precipitation annually (Griffiths and McSaveney, 1983). Salinger (1980a) attributed most variation in New Zealand precipitation patterns to the strength and position of westerly flow of weather. It was noted by Salinger (1980b), that the orography of New Zealand has an effect on local and regional temperatures, influencing the pattern of warming and cooling as maritime air masses pass over New Zealand.

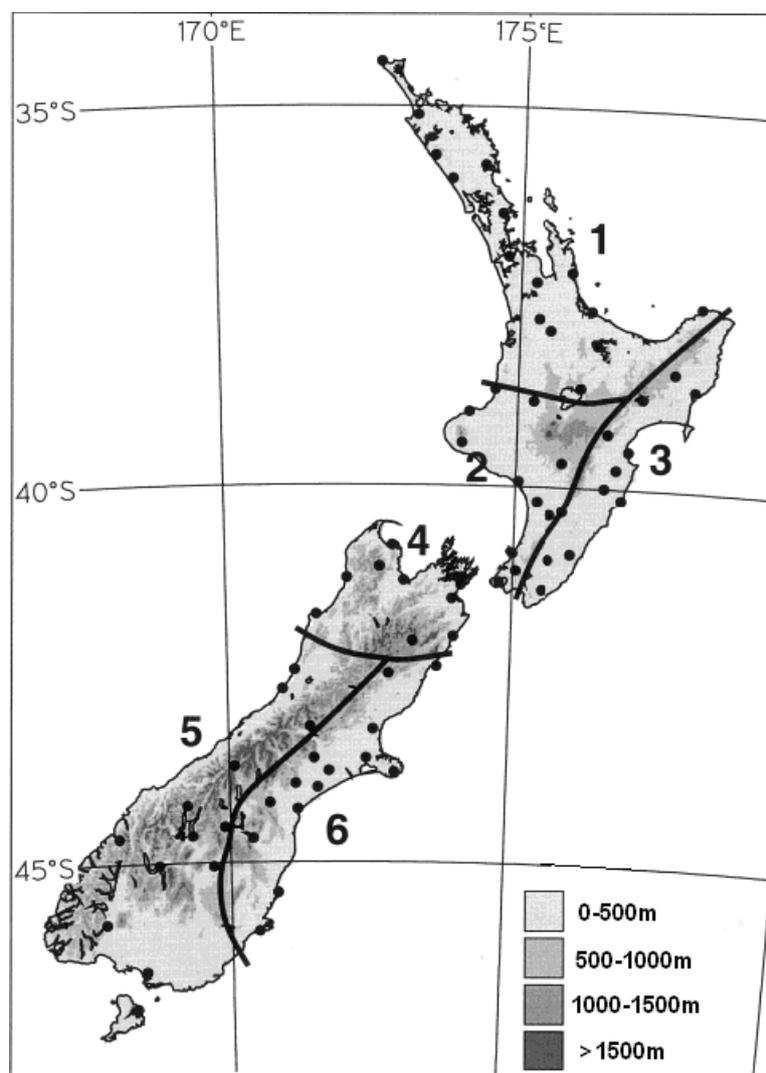


Figure 1. Six Regional Climate Zones based on precipitation, showing point locations of rainfall stations (black dots), with mountainous topography indicated by shaded 500m contours (Source: Kidson, 2000, p.302).

Figure 1 shows six regional climate zones for New Zealand proposed by Kidson (2000), based on precipitation. These zones have been defined using rainfall data gathered from weather stations, with zone boundaries generally determined by the interaction of mountain ranges with westerly weather flow (Kidson, 2000). These regional climate zones are useful indications of regional precipitation influences on vegetation, and illustrate the Eastern South Island region (zone 6) that encompasses the two field sites used in this study. Evapotranspiration is also greater in the eastern South Island due to the occurrence of westerly Foehn winds, which flow east from the Southern Alps as hot, dry air, desiccating vegetation and influencing the pattern of vegetation growing in eastern regions (McGowan and Sturman, 1996).

Coupled with climatic contrasts between east and west, there are differences in the localised climate with elevation, which have led to distinct patterns of vegetation from the temperate coastal lowlands to the high altitude alpine zone. This altitudinal zonation is reflected most obviously in the formation of a 'bushline' or 'treeline', where forest reaches its altitudinal limit and vegetation becomes a mixture of cold-tolerant alpine herbs and *Chionochloa* tussock grasses (Wardle, 1964). The regional altitude of the treeline in New Zealand also varies with latitude, and Wardle (1965) has described the position of 'timber lines' to be between 1200-1300m at 41°S and only 900-1000m at 45°S. The altitudinal extent of forest vegetation also differs between east and west of the South Island, with Mountain Beech (*Nothofagus solandri* var. *cliffortioides*) able to grow 150-300m higher in the east of the South Island than at sites west of the Southern Alps at equal latitude (Wardle, 1965). This contrast in altitudinal tree limits is most likely controlled by summer temperatures (Wardle, 1964), and Zotov (1938) first suggested the link between vegetation distribution and mean temperature during the warmest summer month (January). Wardle (1971) has since demonstrated the importance of growing season warmth on seedling success, regardless of winter extremes, with experiments in the Craigieburn Range involving seedling survival and growth comparisons, showing growing season length affecting treeline altitude.

Regional patterns of vegetation are also influenced by latitudinal climatic differences between the northern and southern areas of the New Zealand landmass. This is a result of differences in average temperatures between sites at opposing ends of the

country, resulting in a temperature gradient from warm temperate northern areas to the Sub-Antarctic climate of the far south of New Zealand, and a reduction in maximum treeline altitudes mirroring the transition to cooler mean annual temperatures (Wardle, 1985). These latitudinal effects on vegetation are reduced by the maritime nature of New Zealand's climate, even at sites inland from the coast.

Additionally, coastal margins are thought to offer some protection from the extreme cold temperatures and frosts associated with sites further inland, allowing some species to thrive on warmer coastal sites at latitudes where they would not survive in colder inland regions (Wardle, 1964). Conversely, cold katabatic winds flowing from icefields and glaciers on the West Coast to the coastal lowlands are likely to have some localised influence on vegetation by reducing the coastal lowland air temperature and inducing winter frosts (Moar and McKellar, 2001) directly in front of valley mouths. This effect is similar to cold air drainage in sub-alpine valleys, which can suppress locally dominant woody vegetation in favour of high alpine species, able to tolerate these nocturnal cold air sinks to the valley floor (Wardle, 1964).

It has also been noted by Wardle (1964), that western coastal margins support the most diverse forest vegetation communities, including a mix of warm-temperate species restricted to the coastal belt and cold tolerant species that extend from the coast, inland to the cool-temperate zone.

2.2 Glacial Influence on Vegetation

New Zealand experienced significant glaciations during the Last Glacial Maximum (LGM), especially in the South Island where the presence of glacial ice had an influence on the distribution of historical across a range of altitudes. One of the most enduring features of glacial vegetation still evident today is the Westland beech gap on the West Coast of the South Island where beech (*Nothofagus*) remains absent from the high alpine zone to the coast (Leschen et al., 2008). Pleistocene glaciation was the driver behind this exclusion of beech forest from Westland as glacial ice advanced during the LGM and earlier (Hall and McGlone, 2006; Leschen et al., 2008). During the LGM, annual temperatures in New Zealand averaged 4-5° C cooler than today

(Soons, 1979), which combined with other climate factors led to the dominance of extensive scrub and grasslands leading into the Holocene (Alloway et al., 2007; McGlone et al., 1995). A lack of beech refugia and competitive exclusion by Podocarp forest are likely factors sustaining the beech gap as the post-LGM climate warmed (Leschen et al., 2008).

Besides topographic affects on regional and local microclimates, New Zealand's maritime climate has undergone numerous large-scale fluctuations over the last 30,000 years as compiled in a Climate Event Stratigraphy by Alloway et al. (2007). A speleothem record from northwest Nelson in the South Island has provided the basis of recorded climatic events in New Zealand and reflects a general warming of the New Zealand climate after a late-glacial reversal 11,600 cal. yr B.P. (Alloway et al., 2007; Williams et al., 2005). Between 11,600 and 10,800 cal. yr B.P. there was an Early-Holocene warming represented by deviations in $\delta^{18}\text{O}$ isotope values of speleothems, and a synchronous North Island pollen record from Otamangakau Wetland reflects a change from shrubland-grassland to lowland forest species by 11,000 cal. yr B.P. as the climate ameliorated (McGlone and Topping, 1977). Several pollen records also indicate a closely-timed Early-Holocene warm period between 9,000-7,000 yr B.P., however this is not reflected in the speleothem record (McGlone, 1988; Newnham, 1992).

A pollen record taken from Okarito Wetland in the South Island shows an increase in Dacrydium-based Podocarp forest coinciding with Early-Holocene Warming, as modern interglacial vegetation became established on the West Coast of the South Island (Alloway et al., 2007, Vandergoes et al., 2005). A Mid-Holocene Warming also occurred between 6,500 and 6,800 cal. yr B.P., and is reflected in the speleothem record of Williams et al. (2005), although there is contention over the interpretation of oxygen isotope signals, with Hellstrom et al. (1998) suggesting an inverse relationship between $\delta^{18}\text{O}$ and temperature in New Zealand speleothems. The isotope record from speleothems also reflect a more variable climate from 6,500 cal. yr B.P., with several brief cooling events, possibly complicated in the speleothem record by increases in precipitation (Alloway et al., 2007).

These recognised Holocene climate changes (Figure 2) are likely to have influenced the Holocene pattern of vegetation at my two Otago core sites, enabling the identification of regional differences in the timing of these events.

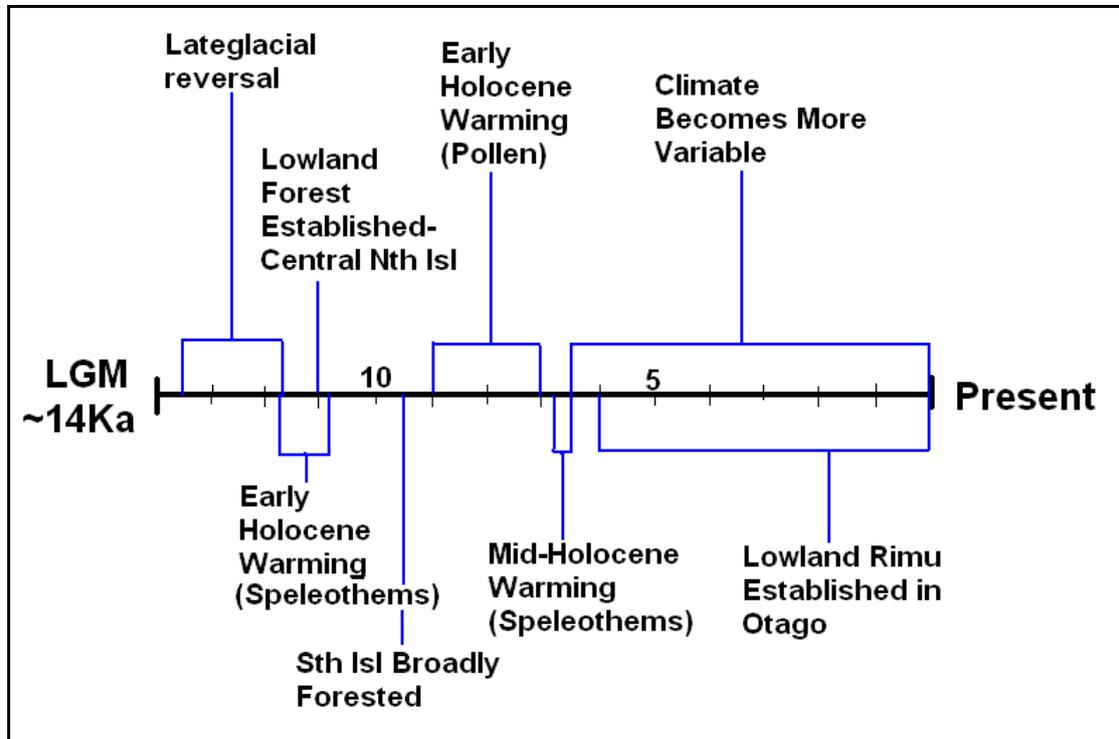


Figure 2. Timeline of Holocene Climate Events and Forest Arrival.

2.3 El Niño Southern Oscillation and Other Climatic Fluctuations

The direction of the prevailing weather systems reaching New Zealand largely control the precipitation regime experienced by the country. Present day climatic conditions and precipitation varies on an inter-annual basis with the ENSO (El Niño Southern Oscillation) which typically occurs every 18 months-7 years (Wratt et al., 2007). ENSO is a climatic phenomenon driven by sea surface temperatures in the Pacific Ocean, which affect the strength of the Walker Circulation, oscillating between *El Niño* and *La Niña* phases (Philander, 1990). This is the 'Southern Oscillation' and occurs when the trade winds weaken and the Walker Circulation pattern becomes disturbed, affecting the strength and location of moist rising air in the Pacific (Philander, 1990).

Under 'normal' conditions, easterly tradewinds force warm surface water to the western pacific, where rising moist air brings precipitation to Indonesia and Australia

(Wratt et al, 2007). The El Niño phase of the Southern Oscillation reflects a weakening of tradewinds and a strong contrast between low pressure in the eastern Pacific and high pressure in the western tropical Pacific (Philander, 1990).

La Niña occurs in an opposing manner, whereby central and eastern sea surface temperatures are colder than usual and the easterly trade winds intensify (Philander, 1990).

In New Zealand, summer El Niño conditions tend to heighten the west-east precipitation gradient, bringing increased rainfall to the west coast while increasing the likelihood of drought in the east, while winter El Niño conditions increase the frequency of Southerly winds, causing a general decrease in sea temperatures and a cooling of the climate on land (Wratt et al., 2007). La Niña events are not as severe on the NZ climate, and La Niña has been described as an intensification of 'normal' conditions in the Pacific (Wratt et al., 2007). A general warming of New Zealand's climate is common during La Niña, due to increased northeasterly winds, which in turn bring more rain to the northeastern North Island, reversing the precipitation gradient and reducing rainfall in the southwestern South Island (Wratt et al., 2007).

Regional climate conditions associated with the El Niño Southern Oscillation include increased west-to-southwest flow of weather systems, bringing cooler and wetter temperatures to west and southwest regions, but with all other areas experiencing dry conditions and cooler temperatures, especially in the east where drought often occurs in extreme cases (Gordon, 1985).

The New Zealand climate has undergone several significant changes during the Holocene, with a key shift to an increasingly drought-prone, frosty environment thought to have occurred about 5,000 yr B.P. (McGlone and Moar, 1998; Shulmeister, 1999). This corresponds with an increase in glacial activity from 5,000 yr B.P., also supporting a mid-Holocene change in climate (Gellatly et al., 1988). This climatic instability has been linked with an intensification of ENSO (El Niño Southern Oscillation), increasing westerly and southwesterly flow over the country beginning about the mid-Holocene (McGlone and Moar, 1998; Shulmeister, 1999). This change in atmospheric circulation has been linked to a synchronous glacial advance at this time (Fitzharris et al., 1992). Further support for the strengthened ENSO conditions

comes from Shulmeister and Lees (1995), who note a peak in effective precipitation between 5,000-4,000 yr B.P. in Northern Australia before the modern ENSO-dominated cycle became established, as recorded in the pollen record c. 4,000 yr B.P.

The increased precipitation required for glacial advance does not discount the rise in frequency of drought during the mid-holocene, although it does suggest that the source of precipitation was regular winter southerlies and more flow from the southwest of New Zealand (McGlone and Moar, 1998).

A summary of climatic changes affecting the distribution of Holocene vegetation in New Zealand has been proposed by Shulmeister (1999), who identifies four major climatic shifts. These are outlined below:

10,000-7,000 BP: Reduced westerly flow with regular incursions of warm northerly air masses. Reduced frosts and drought as a result of the stable climate led to expansion of frost and drought prone species.

7,000 BP onwards: Summer northerlies gradually eliminated from Northern New Zealand with regional droughts becoming common. Minimal westerly flow, while drought intolerant species are replaced by drought tolerant taxa in the North Island. Expansion of drought tolerant species in northern South Island also.

5,000 BP: Intensification of westerly airflow and an increase in the strength of winter southerlies/southwesterlies associated with ENSO lead to glacial advance. Frosts become more common, reducing the range of frost prone species in the south of the North Island.

3,000 BP: Further increase in westerly flow, coinciding with the continued expansion of Rimu and Silver Beech into South Island coastal regions.

Overall, the effect of ENSO on climate led to increased drought and fires associated with dry summers (McGlone and Moar, 1998). This climate variability is likely to have favoured the persistence of grasslands in dry areas and in fire disturbed areas, especially in the east of the South Island. As ENSO was a significant feature of the New Zealand climate prior to the arrival of humans, there were already likely to be areas of lowland grasses in the east, before human disturbance triggered further grassland expansion. The effect of climate on life history traits of some species is also significant, with La Niña climate phases linked to simultaneous fruiting by some species, brought-on by exceptionally high summer temperatures (Schauber et al., 2002).

Other Pacific climatic fluctuations have also undoubtedly had an effect on the New Zealand climate, although the full effect of these climate forcing mechanisms is still to be determined. The Southern Annular Mode (SAM) is a phenomenon centred at the South Pole but reaching north to 40-50° S, causing alternating storm patterns between the mid-latitudes and the coast of Antarctica (The Southern Annular Mode and New Zealand Climate, 2006). In its positive phase, it causes significant warming in southern New Zealand and a significantly drier climate, due to storms travelling closer to Antarctica and less frequently in the mid-latitudes, resulting in less precipitation (Gillett et al., 2006) This positive phase resulting in more settled weather and light winds in New Zealand and negative phase increasing storm frequency and westerly circulation (The Southern Annular Mode and New Zealand Climate, 2006) is also likely to have affected the Holocene climate at Otago sites examined in this study.

The Interdecadal Pacific Oscillation (IPO) is another Climatic Fluctuation affecting climate in New Zealand. It has been linked with decadal climate variations over parts of the Pacific, and with alterations to ENSO affecting Australia (Salinger et al., 2001). The relationship between IPO and ENSO is complex; however there is a consistent trend towards strengthening of the ENSO for the positive IPO period (Salinger et al., 2001).

2.4 Fire History

In New Zealand, fires have been a naturally occurring phenomenon in the landscape throughout the Holocene (Burrows, 1996; McGlone, 2001), probably as a result of lightning strikes and volcanic activity, although it is generally accepted that natural fires would have been rare and localised (Ogden et al., 1998; Wardle, 2002). Major natural fires in New Zealand have been found to occur mostly on the dryer East Coasts of the North Island and South Island (McGlone et al., 1997), burning areas of continuous open forest and lowland scrub where rainfall was generally below $1,000\text{mm yr}^{-1}$ (McGlone and Wilmshurst, 1999b).

Repeated human generated fires have had a sustained impact on vegetation structure, and are responsible for clearing about 70% of the New Zealand forest area (Ogden et al., 1998). Non-natural fires are thought to have begun ~800 yr B.P. (McGlone, 2001), often attributed to human sources by their occurrence in areas of moist dense forest that are rarely burnt naturally, and also by their relative frequency (McGlone and Wilmshurst, 1999b). It is likely there have been occasionally severe fires in these forested areas before human arrival, triggered by drought in eastern regions and sustained by a high fuel load.

Fire frequency is difficult to determine although the prolonged appearance of short-living vegetation species in the pollen records gives an indication of the regularity of fire disturbance, which if frequent enough can allow bracken and grassland species to dominate secondary succession over long periods (McGlone and Wilmshurst, 1999b).

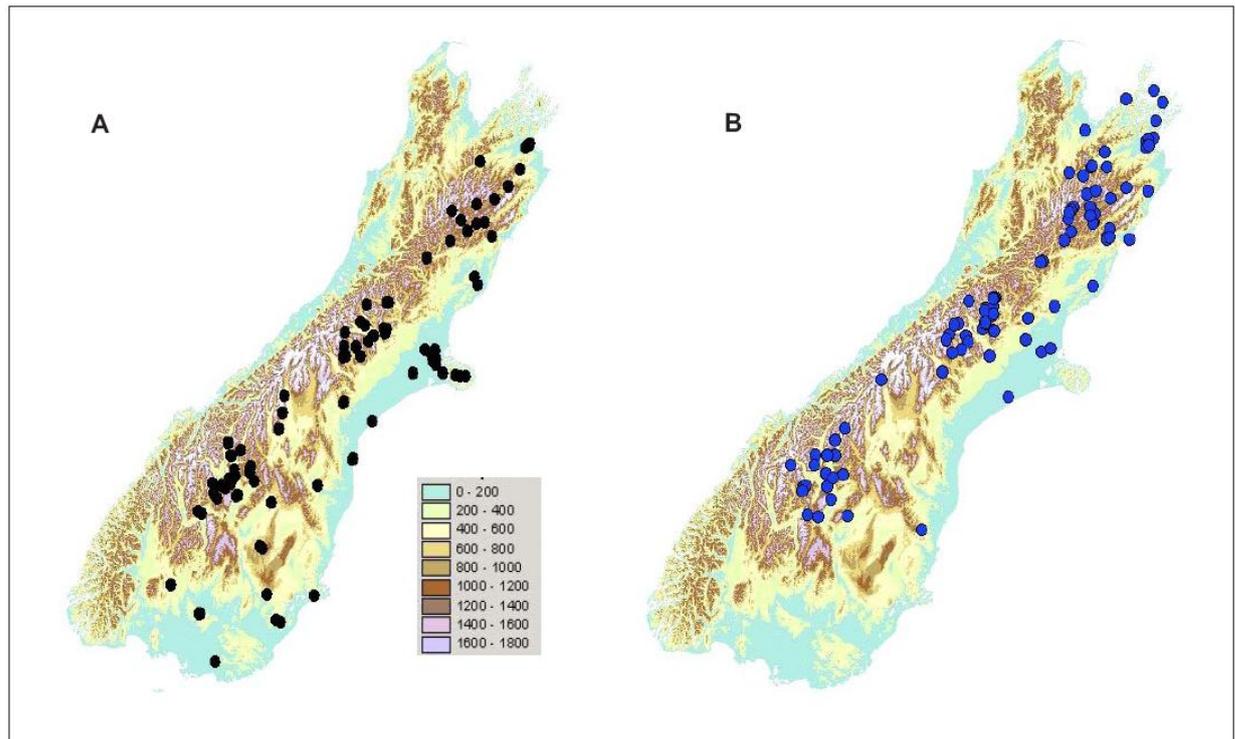


Figure 3. Distribution of radiocarbon dated charcoal sources east of the Main Divide in the South Island. Pre-human charcoal deposits indicated by A. >1,000 yr B.P.; Post-human charcoal deposits by B. <1,000 yr B.P. (Source: Rogers et al., 2005: p28).

Frequent burning has only been common subsequent to human arrival in New Zealand, beginning with Polynesian settlement and widespread fires in the eastern South Island about 750 yr B.P. (McGlone 1989, 2001). The distribution of fire in the Holocene has changed little, and the drier eastern districts of both main islands have had numerous fires throughout the pre-human and post-human settlement period (Figure 3). One view is that the removal of this woody vegetation allowed *Chionochloa* tussock grasslands to spread into dry and high altitude sites such as Central Otago (Wardle, 2002). Where there was cleared land in mild areas of high precipitation, bracken fern (*Pteridium esculentum*) was the early colonising species, and repeated fire disturbance at some sites has maintained these tussock-grasslands/fern communities (Wardle, 2002).

McGlone (2001), suggests that bracken and *Poaceae* species (excluding *Chionochloa*) were the primary colonisers after fire, and only after repeated burning did *Chionochloa* tussock grasslands become common. Tussock grasslands by nature are slow spreading and extremely fire prone, due to the large amount of fuel they provide

from their dead leaves and stems; however, fires also benefit these communities by stimulating growth and reproduction (Mark, 1969; Ogden et al., 1998).

The current structure of vegetation in the drier eastern districts is dominated by fire-induced grasses (McGlone, 2001), with forest remnants confined primarily to high altitude sites with high precipitation and poor soils (Hall and McGlone, 2001). The drought-tolerant woody vegetation has now almost totally been cleared from these areas due to the fire susceptibility of these native species (McGlone, 2001). With such widespread fire-prone grasslands and continued suppression of woody vegetation by farming practices, it is unlikely regeneration of woody forest will occur any time soon

Fire Chronology of the Otago Region, South Island

Natural fires have occurred intermittently nearly every century throughout the Holocene (Ogden et al., 1998). Although there is consensus among plant ecologists that natural forest experienced relatively infrequent fires until after human arrival (Burrows, 1990; Wardle, 2001), McGlone (1988) argues that fire 2,500 yr B.P. cleared large parts of the Central Otago forest cover, which never fully recovered. The long-lasting effects of fire on New Zealand's native forests are due to comprehensive fire-mortality of many forest species and the long successional sequence required for recovery in the absence of further disturbance (Ogden et al., 1998).

Mean South Island fire intervals for most of the Holocene were approximately 200 years, before burning frequency increased to about 50 years around 3,000 yr B.P., possibly a reflection of a strengthened ENSO cycle (Ogden et al., 1998). The anthropogenic influence became apparent about 1,000 yr B.P. as fire intervals reduced by a further 70%, before the most regular period of burning took place from 700-500 yr B.P. when mean fire intervals were only 7 years (Ogden et al., 1998).

By this stage, fire-induced vegetation communities were extensive in the eastern South Island, although continued European burning sustained the low mean fire interval from 240-60 yr B.P. (Ogden et al., 1998).

Table 1. Regional Holocene fire history of Otago based on charcoal encountered in sediment cores. (* Radiocarbon dating directly from charcoal).

Site	Altitude	Depth	Age C ¹⁴ yr B.P.	Laboratory Number	Reference
Clarks Junction	520m	50 cm	442 ± 67	Unknown	McGlone, unpublished data, 1972
Islands 1, Garvie Mtns	1460m	50-55 cm	553 ± 82	NZA 541	McGlone et al., 1995
Swampy Spur Mire	620m	60 cm	800 (estimated)		Walker et al., 2001
Manorburn	670m (mean)	unknown	1400 (approx)	unknown	Molloy in McGlone, 2001
Clarks Junction	520m	Unknown	1680	NZ 9139A	McGlone, 2001
Glendhu Bog	600m	110cm	2104 ± 71	NZA 6918	McGlone and Wilmshurst, 1999a
Kawarau Gorge	800m	90-95 cm	2260 ± 260	NZ 7702	McGlone et al., 1995
Duncan Stream	900m	48 cm	2929 ± 82*	NZA 2497	McGlone and Moar, 1998
Glendhu Bog	600m	165 cm	3722 ± 73*	NZA 6919	McGlone and Wilmshurst, 1999a
Pleasant River	5m	145 cm	3840	Unknown	McGlone, 2001
Glendhu Bog	600m	186 cm	4338 ± 62	NZA 8721	McGlone and Wilmshurst, 1999a
Duncan Stream	900m	95 cm	4825 ± 84*	NZ 7937	McGlone and Moar, 1998
Kawarau Gorge	800m	160-165 cm	5055 ± 97	NZA 842	McGlone et al., 1995
Duncan Stream	900m	120-125 cm	5068 ± 130*	NZ 7936	McGlone and Moar, 1998
Spring Bog, Idaburn Valley	420m	135cm	5083 ± 76	NZA 5832	McGlone and Moar, 1998
Campbell Creek	1200m	131-139 cm	7740 ± 160	NZ 3910	McGlone et al. 1997
Manorburn	670m (mean)	unknown	7500 (approx)	unknown	Molloy in McGlone, 2001
Duncan Stream	900m	166 cm	7996 ± 93*	NZA 2496	McGlone and Moar, 1998
Islands 1, Garvie Mtns	1460m	120 cm	9080 ± 110	NZA 1557	McGlone et al., 1995
Kawarau Gorge	800m	320-325 cm	9500 (estimated)		McGlone et al., 1995
Islands 1, Garvie Mtns	1460m	130-135 cm	9610 ± 120	NZA 539	McGlone et al., 1995
Kawarau Gorge	800m	356-358 cm	11300 ± 3200	NZ 7703	McGlone et al., 1995

Table 1 illustrates the repeated occurrence of fire in Otago throughout the Holocene, with the majority of identified fire profiles occurring at inland sites. It was noted by McGlone (2001), that wetter sites near the coast record less charcoal than drier inland sites, while charcoal size also varies between sites and within sites.

Charcoal fragments $>50\mu\text{m}$ are thought to be from locally occurring fires, while charcoal peaks of predominantly $<50\mu$ size gives a more regional fire record (Clark and Royall, 1995). Table 1 outlines the large number of recorded Holocene fires in Otago based on all charcoal size classes, and fits with the general trend of extensive fire evidence from the eastern South Island (Burrows, 1996).

At Kawarau Gorge, there is a charcoal record of five fires during the last 12,000 years, although charcoal is found throughout the 3.5m core from the site (McGlone et al., 1995). All radiocarbon dates obtained from this site were from peat or peaty silt with the exception of one wood fragment (McGlone et al., 1995). Molloy et al. (1963) notes the need to be careful when interpreting radiocarbon dates implying forest destruction, as charcoal can be produced from old or young trees that were either alive or dead at the time of the fire. This coupled with variable burning characteristics of old and young wood can bias radiocarbon ages obtained from charcoal (Molloy et al., 1963). Laboratory confidence intervals are also variable for radiocarbon dates, rendering charcoal ages useful for approximations only (Molloy et al., 1963).

The significance of lightning as a source of ignition in the South Island varies with regional climate regimes and existing vegetation type. Lightning associated with low-pressure systems usually coincides with rain and is more common on the wetter west coast of the South Island (Ogden et al., 1998). As a result, lightning induced fires are thought to be rare and more likely to occur in localised eastern areas (McGlone, 2001). The extent of these fires was probably limited to some extent by vegetation type, and of twelve lightning triggered fires recorded by the Department of Conservation between 1987 and 2002, the mean burn area was only 2.9ha, supporting the localised nature of natural fire (Flenley in Butler, 2008). However, a tussock fire caused by lightning at Red Hills burnt across 15ha (Flenley in Butler, 2008) so perhaps in situations where previously burned vegetation had not fully recovered to climax forest communities, early tussock and scrub promoted larger fires.

It is interesting to note that radiocarbon dates from the Islands 1 site in the Garvie Mountains and a site in Kawarau Gorge (Table 1) both record a fire about 9,500 yr B.P. (McGlone et al., 1995). These sites are 54 km apart, which would seem to suggest either significant transport of charcoal, a large fire reached both sites or two fires occurred at about the same time. A summary of the evidence for uncommon, localised fires caused by lightning would suggest charcoal transport is the most likely scenario; however this conflicts with the quantity of charcoal at both sites, suggesting local fires at both sites at this time.

Fires have had a selective effect on the pattern of vegetation in the South Island, causing widespread destruction of forests on flat and rolling hill country, in areas of minimal soil moisture and in the drier eastern districts (Hall and McGlone, 2001). Beginning about 7,500 yr B.P., Manorburn in Central Otago experienced several major fires, which were evident as layers of *Phyllocladus* charcoal (McGlone, 2001). From 6,000 yr B.P. there were a number of localised fires, which reduced *Phyllocladus* scrub at Duncan Stream and Kawarau Gorge and cleared conifer scrub and beech forest from Glendhu Bog (McGlone, 2001).

In the Idaburn Valley and at Duncan Stream, fire did not completely devastate the vegetation, although about 5,000 yr B.P. both these sites exhibited a thinning of the scrub vegetation and a transition to grass-herbland communities (McGlone and Moar, 1998). This was initiated at Duncan Stream by several fires close to 5,100 yr B.P. (McGlone and Moar, 1998).

Three sites-Kawarau Gorge, Duncan Stream and Spring Bog- share a similar record of fire about 5,100 yr B.P. (Table 1). Duncan Stream produced macroscopic charcoal used directly for dating so was likely to have had a local fire around this time. The Kawarau Gorge and Idaburn Valley Sites are 130km south of Duncan Stream; however, the Kawarau Gorge charcoal also supports a significant fire at this time. Spring Bog in the Idaburn Valley is 50km east of Kawarau Gorge and contained only small quantities of microscopic charcoal, suggesting it was transported to the site by wind. West to east transport of charcoal from Kawarau Gorge to Idaburn Valley seems likely, while the 130km gap between fires at Duncan Stream and Kawarau

Gorge would indicate two separate fires occurred at about 5,100 yr B.P., possibly indicating climatic conditions promoted fire at this time.

McGlone and Wilmshurst (1999a) noted at least three major fires in Otago between 4,000-3,700 yr B.P. that significantly reduced local conifer scrub and gave the opportunity for *Nothofagus menziesii* to expand, which continued until 1,300 yr B.P. It is likely that drought stalled the spread of *N. menziesii* at this time, contributing to a major fire at 1,100 yr B.P. that destroyed most of the silver beech forest which subsequent fires then removed permanently (McGlone and Wilmshurst, 1999a).

Infrequent but repeated fires have been inferred from charcoal at central and eastern Otago sites; however, significant charcoal was not encountered in the Swampy Spur Mire until 60 cm from the bog surface, inferred to be about 800 yr B.P. (Table 1). The charcoal count from Pleasant River possibly indicates a local fire at 3,840 yr B.P. but otherwise it suggests an absence of local fire until the Polynesian settlement period (McGlone, 2001). The record of burning at these two coastal Otago sites suggests that fire was an unlikely event prior to human arrival, and less frequent than at drier inland sites. This coastal fire regime is likely shared by our nearby core site at Swampy Summit, and is in keeping with observations by McGlone (2001) of reduced fire frequency in coastal areas.

At Idaburn and Duncan Stream, a succession to *Halocarpus* (Bog Pine) and tussock grassland-scrubland occurred after 3,000 yr B.P. in competition with *Phyllocladus*, before an intense fire allowed *Dracophyllum*-based shrubland to colonise amidst the persistent *Halocarpus* and tussock grasses (McGlone and Moar, 1998).

Leading up to the first human arrivals in New Zealand, the east of the South Island experienced a climate-related increase in fire frequency beginning about 3,000 yr B.P. (Ogden et al., 1998), with sporadic fires continuing to occur up until the Polynesian burning period ca. 800 yr B.P. (McGlone, 2001).

2.5 Anthropogenic Induced Disturbance

Before humans inhabited New Zealand, it was estimated that forests covered at least 75% of the mainland (Newsome, 1987). An even higher estimate of forest cover was given by McGlone (1989), who suggested as much as 85-90% of New Zealand was forested at 3,000 yr B.P., with only 15% of the South Island and 1.5% of the North Island above the treeline. Fitting this hypothesis is the belief that prior to widespread anthropogenic disturbance around 1200 -1400 AD, there was near complete forest cover in the East of New Zealand (Hall and McGlone, 2001). Since then, deforestation has occurred at an astonishing rate and today, only approximately a third of pre-human forest cover remains (Figure 4), with the rest of New Zealand's native forest having been cleared in less than 1,000 years (Ogden et al., 1998). Initial human settlement by Polynesians resulted in the loss of at least half the lowland forest cover through burning, and severely depleted the herbivorous vertebrates that browsed on the native vegetation (McGlone, 1989). As these avian residents were hunted to scarcity or driven to extinction including at least 30 bird species (McGlone, 1989), it is likely that some plant species lost an important means of distributing seeds, while some understorey vegetation species possibly benefitted from a reduction in predatory herbivores such as moa.

Fire severity increased between 750 and 500 years ago (McGlone, 1989) and by the time Europeans arrived in the mid-1800's, large-scale forest clearance and habitat destruction had already occurred (McGlone, 1989). However, the Europeans engaged in further forest clearance, by burning to clear land for farming and through their intensive logging of the native hardwood timber. In 1886, there were 22 million acres of forest; this had been reduced to 17 million acres by 1909, although by 1907 nearly 3 million acres had been designated as scenic reserve under the 1892 Land Act, to preserve significant areas of indigenous vegetation for recreational purposes and amenity value (Star and Lochhead, 2002, p.119).

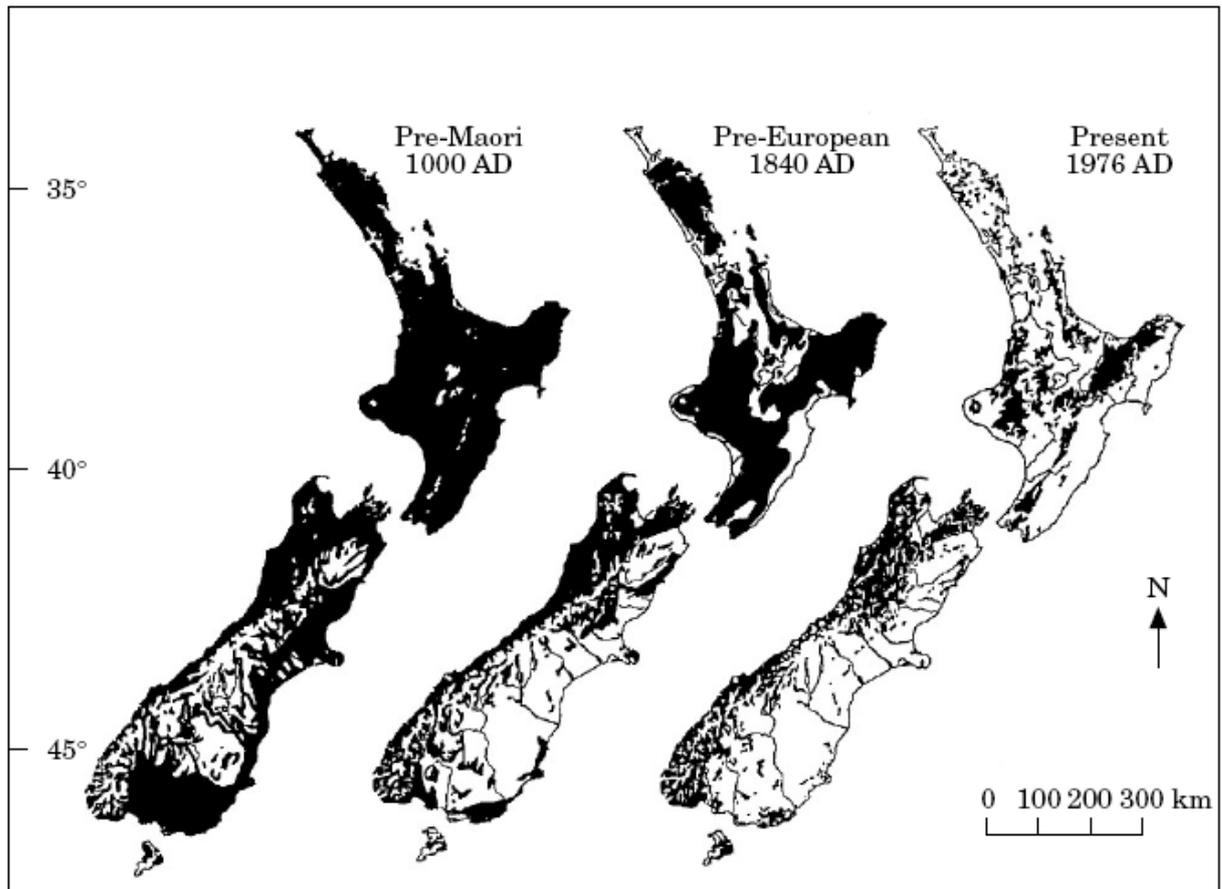


Figure 4. Forest cover (shown in black) from 1000 AD to the present (Source: Wendelken cited in Ogden et al., 1998, p.688).

New Zealand has a unique suite of native flora, evolved during its long isolation, resulting in over 80% of native plant species being endemic to the country (McGlone et al., 2001) rising to 93% endemism of vascular alpine flora (Halloy and Mark, 2003). Unfortunately, human modification of the landscape has adversely affected huge areas of native forest and grassland communities, and now only 10-15% of the New Zealand land area is covered with native vegetation (Department of Conservation, n.d). Because of this widespread destruction of native vegetation, over 4.8 million hectares of land has been classified for protection under the Conservation Act, including 14 National Parks (Department of Conservation, n.d.).

3. Proxies for Reconstructing Historical Vegetation Cover

Proxies for reconstructing historical vegetation are wide ranging, and can provide information on local and regional vegetation surrounding a site. The representativeness of inferred vegetation records depends on preservation conditions at the site and the proxy used. Peat bogs are ideally suited to pollen preservation due to their acidity, although wide dispersal of some pollen can mask the local vegetation signal in some samples. Preserved macrofossil proxies such as wood fragments and leaves can also yield valuable clues from bog and swamp environments, and are generally taken to be a direct record of vegetation at a site. Phytoliths are a very resilient proxy for vegetation that can be extracted from a range of sedimentary deposits, and are especially useful in loess sediments where pollen preservation is poor.

3.1 Palynological Records

Sporopollenin is a highly resilient structural component of pollen and spores that resists decay, assisting the preservation of palynomorphs and underpinning their use as proxy for vegetation (Faegri in Jacobson and Bradshaw, 1981).

Palynology has been used extensively in the reconstruction of historical vegetation, and is the study of pollen from seed producing angiosperms and gymnosperms; palynology also includes the study of spores from pteridophytes, bryophytes, algae and fungi (Moore et al., 1991). Pollen and spores are prolific in waterlogged sediments (e.g. peat) where anoxic conditions and acidity assist preservation, although low pH soils and humus can also retain a record of palynomorphs, while being more prone to differential rates of decay between pollen and spore types, introducing a potential source of bias to the sample (Jacobson and Bradshaw, 1981).

Pollen Representation

New Zealand is fortunate to have a large number of sites containing well-preserved pollen and macrofossils from late Quaternary peats. The analysis of pollen records for reconstructions of historical vegetation raises important questions about the representativeness of pollen in palynological records. The main issues with using proportionate pollen counts to infer vegetation relate to the life history traits governing pollen production of different taxa, while the dispersive nature of pollen

and spores also affect the amount and type of pollen appearing in core samples (Macphail and McQueen, 1983). Pollen dispersal varies greatly between species according to the method of pollination (wind or insect), pollen morphology, and climatic factors including prevailing winds and precipitation patterns (Macphail and McQueen, 1983). It was noted by Moar (1970), that small amounts of Australian-derived *Casuarina* pollen were present in modern pollen spectra from the Fox Range in Westland, New Zealand. This reinforces the need to consider the pollen dispersal ability of taxa before drawing conclusions about local and regional vegetation composition.

Regional dispersal of pollen also affects pollen counts, and Randall (1990) noted high levels of *Podocarpaceae* pollen in pollen traps above the treeline in the Southern Alps, inconsistent with local vegetation and therefore transported from outside sources on the West Coast. Shallow peat cores taken from the main divide also contain anomalous *Podocarpaceae* pollen spanning a record of the last 500 years (Randall, 1990). There appears to be minimal transport of *Nothofagus fusca*-type pollen, which rapidly declines from dominating forest sourced pollen records to comprising just 10% of the pollen sum near the edge of beech forest (Randall, 1990). This conflicts with work by Macphail and McQueen (1983) and McKellar (1973), which strongly supports the dispersive nature of *N. fusca*-type pollen. A study of *Nothofagus* pollen dispersal found *N. fusca* made up 4% of the modern pollen rain at Swampy Summit, despite the nearest source being 80km away (McKellar, 1973). *Nothofagus* pollen was also found to be present in a core from Banks Peninsula constrained to MIS Stage 7, and similarly low frequencies suggest the pollen was sourced from elsewhere (Soons et al., 2002). In contrast, Moar (1970) and McKellar (1973) found pollen from *N. menziesii* (a species native to east Otago) to be under-represented in pollen records. This has implications for our understanding of Silver Beech distribution in post-glacial forests (McKellar, 1973).

Modern Rimu (*Dacrydium cupressinum*) pollen rain was found to be generally representative of the local vegetation in Westland, with the exception of several samples taken where forest density affected airflow and pollen deposition (Pocknall, 1978). Macphail and McQueen (1983) list Rimu as one of the few native pollen taxa

with naturally large pollen dispersal, along with Punga (*Cyathea smithii*-type), Beech (*Nothofagus fuscasporea*-type), *Coprosma* and Grass (*Poaceae*) pollen.

Overall, it would appear that despite being widely dispersed, the proportion of Rimu and Beech pollen in the sedimentary record is largely affected by vegetation structure of the site and relative dispersal of other pollen taxa in the record (Pocknall, 1978).

The location of the sample site relative to prevailing winds and pollen sources is also likely to play a role in pollen representation, especially as coastal forests expanded inland as the climate ameliorated.

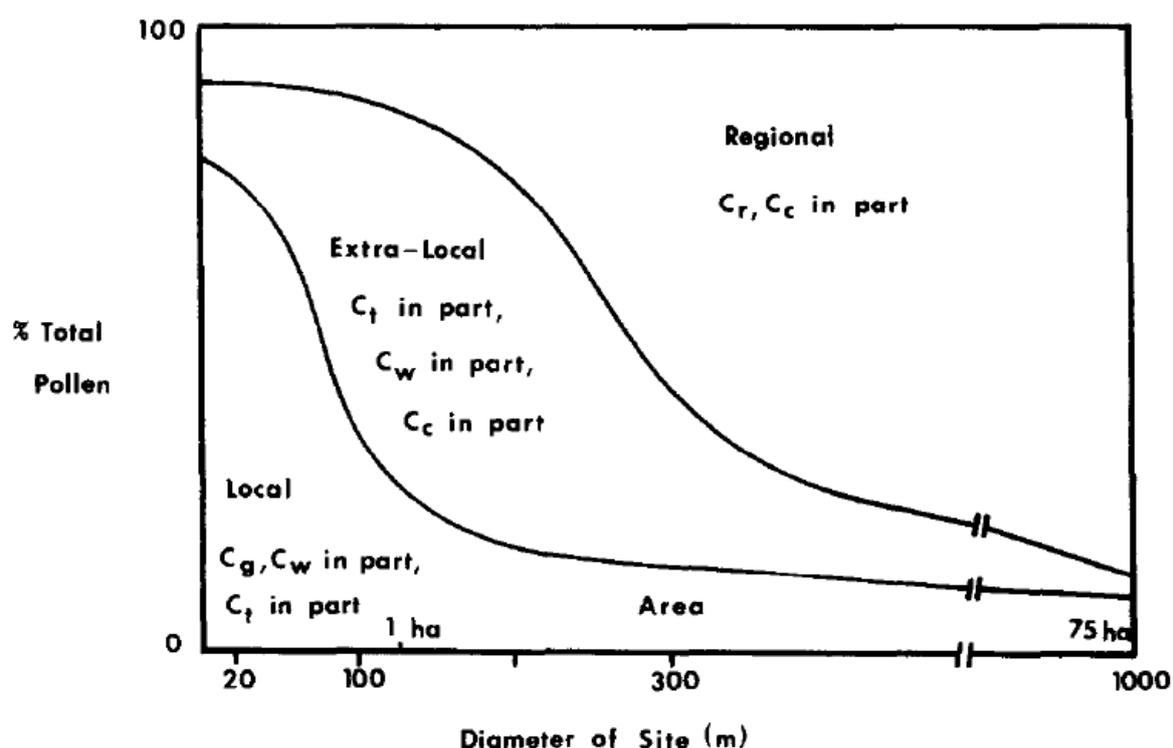


Figure 5. Relative significance of pollen sources in sites of varying size with no in-flowing stream. Modes of pollen transport include C_w -surface runoff; C_t -space between trees; C_c -above canopy wind transport; C_r -raindrops; C_g - settling down from overhanging vegetation. (Source: Jacobson and Bradshaw, 1981, p.82).

Kahikatea (*Dacrycarpus dacrydioides*) has been identified as an underrepresented species in the local pollen rain (Pocknall, 1978) but has been grouped with 25 other poorly dispersed palynomorph types that commonly occur in New Zealand pollen records due to widely distributed source vegetation (Macphail and McQueen, 1983).

These species gives a good indication of localised vegetation in the pollen record, and include: *Asteraceae*, *Phyllocladus*, *Podocarpus* types, *Halocarpus*, *Quintinia*, *Ascarina*, *Metrosideros*, *Weinmannia*, *Elaeocarpus*, *Griselinia*, *Pseudopanax*, *Myrsine*, *Leptospermum*, *Dicksonia*, *Cyathea*, Monolete Fern Spores, *Lycopodium*, and *Dacrycarpus dacrydioides* (Macphail and McQueen, 1983).

In contrast to Macphail and McQueen (1983) who listed grass pollen as widely dispersed, *Poaceae* pollen was found to be abundant at grassland sites but not in forested areas, suggesting that grass pollen remains close to the source and doesn't penetrate forested areas well (Pocknall, 1978; Randall, 1990).

The swampy nature of sites with the best accumulation of pollen in sediments also gives rise to the issue of wetland taxa dominating the pollen record, which is why vegetative reconstructions generally focus on dryland plant taxa represented in the pollen sum, resulting in reconstructions that may be influenced by deposition of regional palynomorphs at the site. Jacobsen and Bradshaw (1981) note the relationship between site size and the proportion of local to non-locally derived pollen in the sample (Figure 5).

Moar (1970) found there is significant transport of lowland and montane forest pollen to sites in subalpine scrub and open alpine vegetation. Regional transport of pollen also has a significant role in pollen representations therefore limiting the exclusive use of pollen spectra when trying to identifying the local composition of historical vegetation communities. Many of these issues will never be fully resolved for pollen-based reconstructions, including the discrepancy between pollen production of wind and insect pollinated species, although wind pollinators are not necessarily well represented e.g. Kahikatea (Macphail and McQueen, 1983; Moar, 1970). The effect of a heavy pollen rain from a small number of specimens near the sample site remains indistinguishable from regional abundance of the same taxa (Macphail and McQueen, 1983).

3.2 Phytoliths

Phytoliths are plant microfossils formed when plants deposit solid silica in and between their cell structures (Piperno, 2006). This silica is assimilated into plant cells from groundwater in the form of monosilic acid and forms distinct shapes as it is deposited within the plant (J Carter, pers. comm., 2008). Phytoliths form mostly in the stems and leaves of plants, and are released into the sedimentary record when a plant dies and decays (Kondo et al., 1994; Piperno, 2006). It is thought that phytoliths give a more accurate record of local vegetation growing on a site as they remain close to the site where the plant grew, whereas pollen is released to the air and potentially dispersed over long distances (Thorn, 2004). Another advantage of phytoliths over pollen as proxy for vegetation is that phytoliths are resistant to the types of decay and damage that affect pollen and spores, notably oxidation, due to their robust inorganic nature (Piperno, 2006). However, extreme pH promotes the dissolution of phytolithic silica, with solubility increasing above pH9 and below pH3 (Piperno, 2006).

Phytolith research in New Zealand is still in its infancy compared to pollen studies, it was first initiated by Raeside who looked at loess deposit phytolith assemblages in 1964 (Kondo et al., 1994). Carter (2002) has been able to construct a continuous phytolith-based record of vegetation at Lake Poukawa in the North Island reaching as far back as MIS Stage 5 using a dozen basic forms. Additional work by Kondo et al. (1994), Thorn (2004) and Marx et al. (2004) looking at phytolith morphologies of New Zealand native plants has increased knowledge of phytolith forms and representations in New Zealand. A phytolith key was also developed for this project, examining a variety of species growing naturally at Swampy Summit in Otago (Appendix 1), although forms identified were of little diagnostic value except for *Chionochloa* tussock phytoliths which were easily identifiable in the assemblage. Overall, phytoliths provide a useful comparison to pollen and spore based reconstructions, while also presenting a valuable alternative in areas where preservation of palynomorphs is poor.

Prebble and Shulmeister (2002) have previously used phytolith based reconstructions to interpret the paleoenvironment of the lower Taieri Plain in East Otago. These environmental reconstructions were conducted using transfer functions developed by Prebble et al. (2002), who found that sites yielding predominantly Chloridoid

phytoliths were common between 450-800m altitudes, reflecting the presence of *Chionochloa* tussock grasslands at some point in time. Conversely, lowland areas up to 400m altitude were dominated by spherical phytoliths sourced largely from forest species. Altitude was found to explain the most variance in phytolith assemblages, accounting for 0.2% ($P=0.001$), while sites under forest had the highest variability in contrast to wetland and grassland sites which were generally less species diverse with lower phytolith variability (Prebble et al., 2002).

4. Location and Methods

The purpose of the study is to test the possibility of grassland persistence below the treeline. This was achieved by choosing sites that were located within the montane environment, but remained below the natural treeline (Figure 6), where the microclimate would not prohibit the growth of woody vegetation in favour of non-woody species.

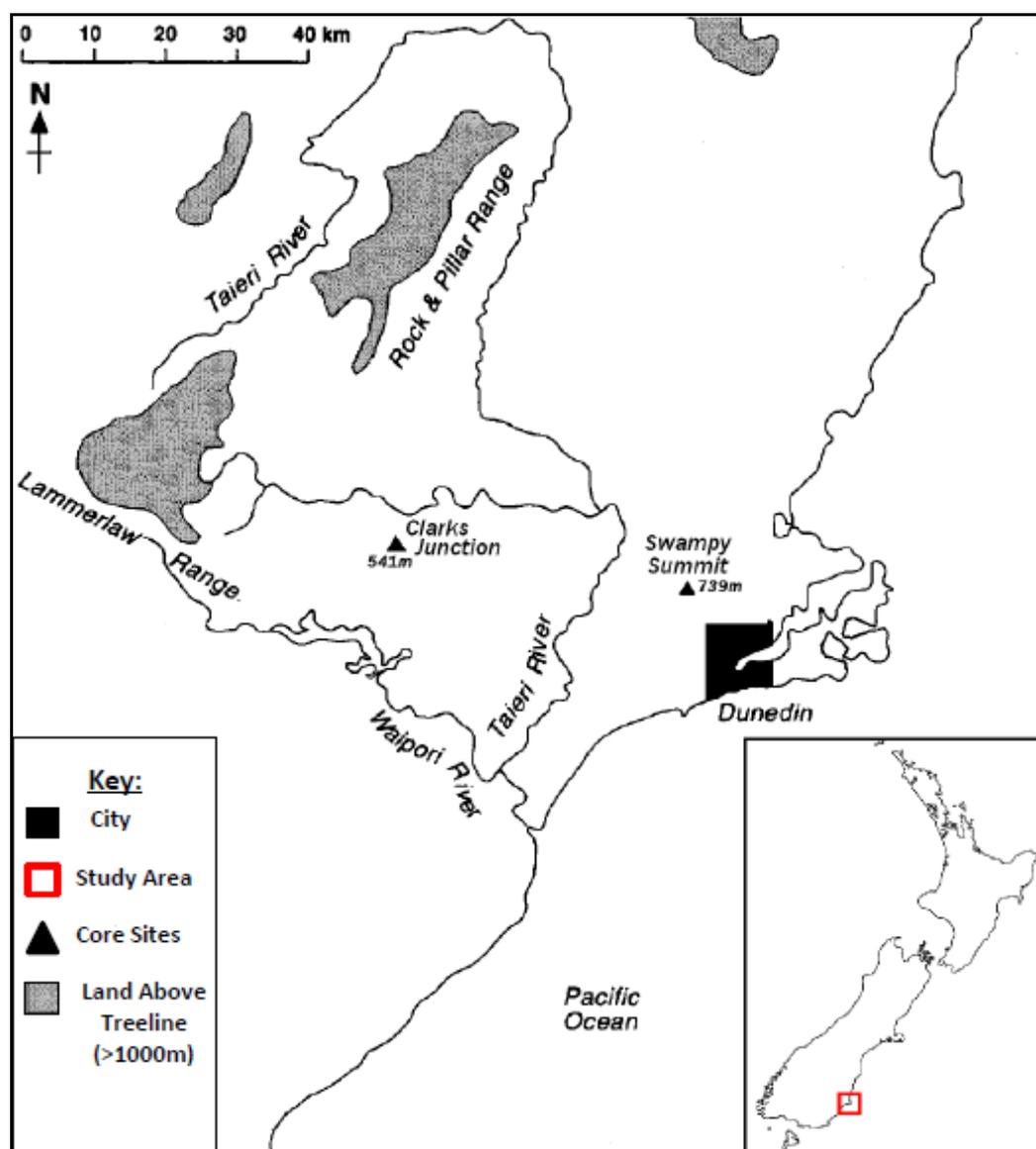


Figure 6. Location of Swamy Summit and Clarks Junction Core Sites in relation to land above the 1000m regional treeline (Modified from Cameron et al. 1997).

Although altitudinal factors played a part in site selection, as did accessibility, the main criteria was the presence of peat-forming mires, which would ensure

preservation of pollen and hopefully phytolith proxies and provide a continuous record of vegetation cover.

4.1 Swampy Summit

Swampy Summit is a bog which has developed at the summit of a hill, only about 7km north of Dunedin. The site (E2314076/N5487210, NZMG Sheet I44 2002) sits at an average elevation of 740m above sea level, with minor topographic changes across the bog surface, including several raised peat scarps, which sit almost a metre above the present water table. The current vegetation of Swampy Summit is mixed tussock-shrubland, composed primarily of *Chionochloa rubra* (Red Tussock) and *Coprosma cheesmanii*, with sporadic patches of *Phormium cookianum* (flax), and *Dracophyllum longifolium* (Figure 7). Areas of the bog above the water table commonly had *Griselinia littoralis* (Broadleaf) shrubs growing on them while sedges are abundant around waterlogged areas within the bog where the water table is at ground level.

The aim for this research was to extract cores where there would be the thickest accumulation of peat in the bog, providing the best record of vegetation at the site. The location of the first core site was chosen as it was close to the middle of the peat bog, yet it was raised above the water table on a high peat mound. This site was specifically chosen for comparison with an earlier core from Swampy Summit, taken by McIntyre and McKellar (1970). Their core seemed to lack any obvious evidence of human disturbance in the pollen record (McIntyre and McKellar, 1970), suggesting the most recent deposition of peat had been eroded from their core site, thus by coring from the highest point it was hoped I could minimise any loss of the peat record.



Figure 7. Vegetation at Swampy Summit (E2313720/N5487380, NZMG Sheet I44 2002) consisting primarily of *Chionochloa rubra* tussocks and *Coprosma cheesmanii*, with sporadic patches of *Phormium cookianum* (flax) and *Leptospermum scoparium* (teatree). A variety of sedge species border the area of open water while *Dracophyllum longifolium* and *Griselinia littoralis* (Broadleaf) shrubs are common on areas above the water table surrounding the core site.

After several unsuccessful attempts to drive the D-corer through a thick matrix of *Griselinia* roots it was decided to move the core site to an adjacent area with less woody vegetation. We were eventually able to extract peat core to a depth of 3.7m before the corer was damaged. The sample depth we achieved compares favourably with previous cores taken from the bog by Cranwell (1953) and McIntyre and McKellar (1970) to depths of 3.8m and 3.6m respectively. The base of the core at 3.6m depth was radiocarbon dated by McIntyre and McKellar (1970) at $11,850 \pm 110$ B.P. which demonstrates that peat growth started on the underlying basalt boulders of Swampy Summit prior to the Holocene, and continued at an average rate of 31cm per thousand years.

4.2 Clarks Junction

The second Otago site used for this study was situated further inland, 35km north-west of Dunedin. The coring site was situated between 520-540 m.a.s.l, in a small gully adjacent to State Highway 87 at Clarks Junction (E2280154/N5493441, NZMG Sheet H44 2006). One reason this site was chosen was to build on the pollen work of McGlone (1995), which demonstrated the persistence of grasses at the site throughout the Holocene.

The topography of the area was gently sloping, which resulted in a well drained core site and the water table was not evident, as it was at Swampy Summit. The peat base at Clarks Junction had accumulated at the head of a drainage catchment, which linked into a much larger swamp further down the valley. As this site was located on pastoral farmland, the surrounding vegetation had been extensively modified.

At the time of sampling the paddock contained a *Brassica* crop and a variety of pasture grasses (*Poaceae*) with shelter-belts of *Cupressus macrocarpa* nearby. Despite this, the gully itself was vegetated with large (1m tall) Red Tussocks (*Chionochloa rubra*), interspersed with introduced pasture grasses and several gorse (*Ulex europaeus*) plants (Figure 7).

The size of the *Chionochloa* tussock specimens at Clarks Junction could imply that they are at least 50-100 years old (K Dickinson, pers. comm., 2008), although dating tussock specimens is problematic due to their ability to replace stems. It was noted by Mark (1969) that there is no means to accurately date tussock plants, however stems age can be roughly estimated from leaf scars, and suggests it is possible for mature tussocks to live for over 200 years. Moore (1955) states that size is not an accurate guide when ageing small tussocks, however tussocks classed as 'mature' by Williams (1977) had a mean height of 73 ± 3 cm, which would suggest the gully vegetation at Clarks Junction is mature and has not been drastically modified in recent times.

The precise coring site at Clarks Junction was chosen by observing the firmness and rebound of the ground surface when stood on, as indicators of sub-surface peat, then by examining the consistency of sediment extracted with a makeshift wooden probe which was pushed into the top metre of the bog surface. This method proved adequate for identifying core sites with a suitable depth of peat. Again, a D-corer was used to extract the peat core, reaching a depth of 1.7m where we encountered a stiff sediment plug as the corer hit a layer of blue-grey silty clay.



Figure 8. Vegetation at Clarks Junction (E2280154/N5493441, NZMG Sheet H44 2006) showing cultivated *Brassica* crop in the foreground and dense *Chionochloa rubra* (Red Tussock) occupying the gully area where the core was taken.

5. Sample Collection

At each sample site, two cores were extracted within 50cm of each other. This was to create a 10cm ‘overlap’ between each section of peat core, by alternating between holes e.g. 0-50cm (Hole 1), 40-90cm (Hole 2), 80-130cm (Hole 1). This method avoided any loss of sample material or contamination in the transition between each section of peat core. To gauge the depth of the D-corer (Figure 9), depths were measured from the top of the corer barrel up the connecting rods to the handle, marking each respective interval with a band of tape and a permanent marker.

5.1 D-Corer (Russian Corer)

Achieving the required depth was simply a matter of pushing the corer head into the peat surface, then attaching the connecting rods 1m at a time and pushing the corer down to the required depth before cutting the sample. The samples were cut by turning the corer handle clockwise, which then ‘locked’ the peat section in the barrel of the D-Corer, ready for extraction (Figure 9).

All sections of peat core were photographed and described prior to being sealed in plastic wrap. Samples were encased in sections of PVC pipe for added protection during transport and labels were added indicating depth, date, location and orientation of the peat sections.

5.2 Vegetation Survey

A vegetation survey was conducted at Swampy Summit to estimate percentage cover of plant species and to develop a record of species diversity at the site. I was aided by plant ecologists Kath Dickinson (University of Otago) and Alan Mark (University of Otago), to locate and identify as many species as were present on and adjacent to the bog. The result was a species abundance list of thirty-seven plant taxa (Table 2). After identification, a small sample was taken for each species and brought back to the lab, where they were dried in an oven at 50°C overnight to preserve the samples for later processing to extract phytoliths.

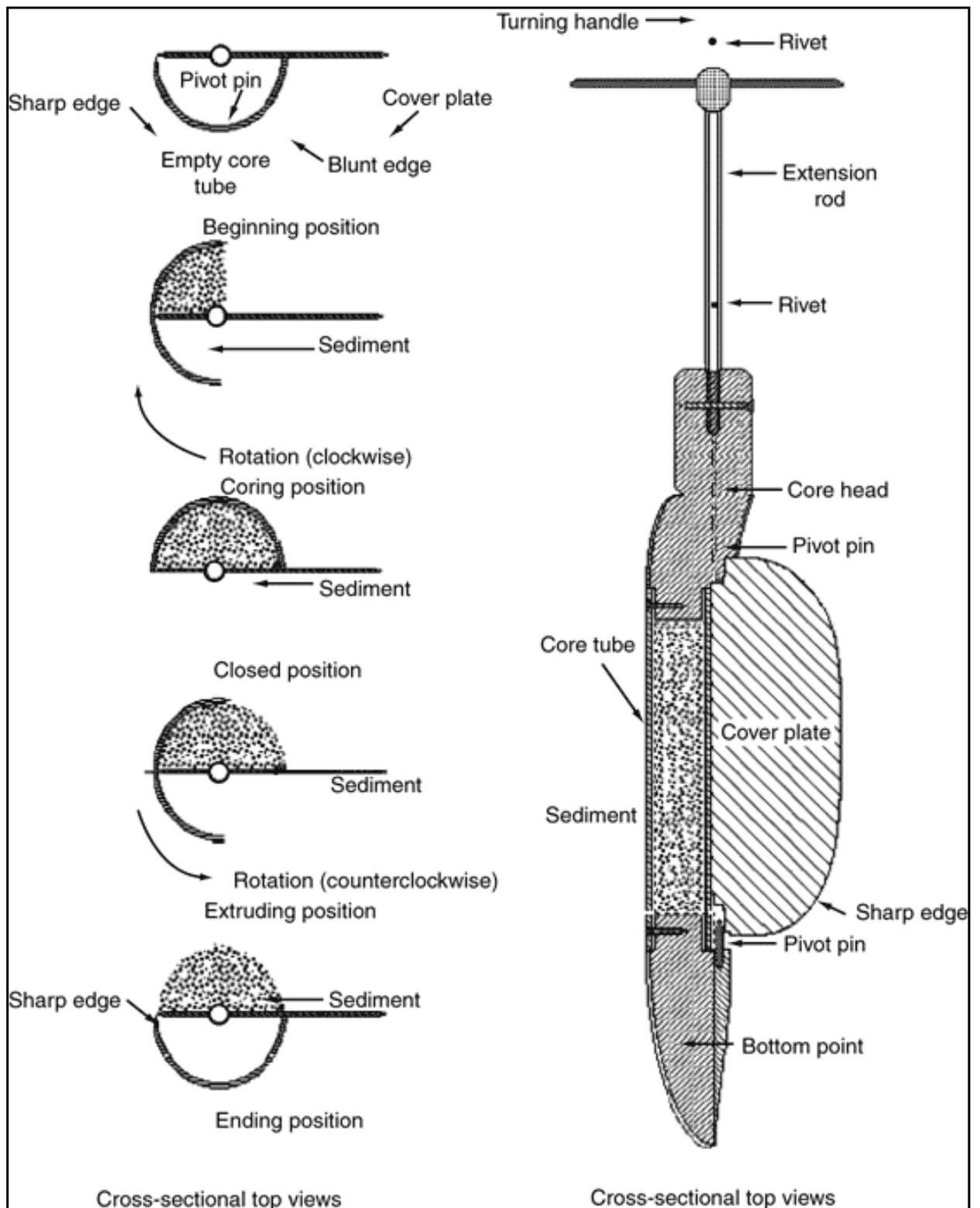


Figure 9. Schematic of D-Corer as used at Swampy Summit and Clarks Junction (Source: USEPA, 1999: Pg 6).

6. Laboratory Methods

Sub-samples for pollen and phytolith processing were taken at 10cm depth intervals down each peat core. Palynological processing followed the techniques outlined in Moore et al. (1991). Pollen identification was conducted with the help of a guide by Moar (1993). Pollen and Phytolith assemblage diagrams were prepared using the Psimpoll programme and vegetative zoning of the assemblage was created using constrained cluster analysis by sum-of-squares (CONISS) (Bennett, 2005).

6.1 Extracting Pollen from Peat

Pollen extraction from core samples followed the methods outlined in Moore et al. (1991). Peat samples approximately 1cm³ were cut from the cores every 10cm, put in beakers with 10% KOH and transferred to a hot water bath for 1 hour. Samples were spiked with *Lycopodium* tablets during this process to assist with statistical processing of pollen counts. Each sample was sieved through an 80µm mesh to remove larger detritus and wood fragments. Test tubes were labelled and topped-up with distilled water before being centrifuged at 2000rpm for 3 minutes. After centrifuging, the supernatant was poured off and distilled water added to samples. An agitator was used to re-suspend the samples following addition of water. This process was repeated three times. Initial mounts showed a large volume of undigested organic material remained, so each sample was short centrifuged by increasing the revolution speed steadily up to a maximum of 2000rpm over 30 seconds. This was repeated three times, replacing the supernatant with distilled water as above. To clean-up any remaining organic material, household bleach (sodium hyperchlorite) was added to the samples and left to stand for 3 minutes. All samples were then diluted with distilled water and centrifuged a further three times (2000 rpm for 3 minutes) as described previously. Slides were produced by combining a small amount of each pollen sample with a drop of gelatine/ethanol based mounting solution, and then warmed gently to evaporate excess water before adding a coverslip. Slides were counted at 25x magnification and a minimum of 300 palynomorphs were counted for each slide.

6.2 Extracting Phytoliths from Peat

Phytolith extraction was conducted based on methods provided by Vanessa Thorn and John Carter in Thorn (2004). Sample sizes were increased to 2cm³ however sample intervals remained unchanged at 10cm. Samples were initially digested to remove organics by heating in 27% hydrogen peroxide until visible reactions had finished. Acid removal was conducted by centrifuging samples at 3000rpm for 10 minutes, pouring off the supernatant and re-agitating the sample with distilled water. This process was repeated three times. Each sample was poured through a 250µm sieve to separate the < 250µm fraction. Remaining organics were removed by digestion with highly corrosive Schulzes Solution (50ml potassium chlorate added to 250ml nitric acid) in a water bath in a fume cupboard. Distilled water was then added to the samples before they were centrifuged at 3000rpm for 5 minutes and the supernatant poured off. This process was again repeated three times to remove any Schulzes Solution.

Phytoliths were isolated from the sediment in the samples by using a heavy liquid (sodium polytungstate) to take advantage of the density contrast between phytoliths (<2.3) and clastic material (>2.3). Distilled water was added to sodium polytungstate (2.85 ± 0.02g/ml) until a liquid with a specific density of 2.3 was achieved. The heavy liquid was then added to test tubes containing each sample and agitated. Samples were centrifuged at 2000 rpm for 15 minutes to separate the light fraction containing the phytoliths, which was then pipetted off into clean test tubes and diluted with distilled water to reduce the density of the liquid. Test tubes containing the liquid were then centrifuged a further three times at 3000rpm for 5 minutes, pouring off the supernatant and diluting with distilled water after each cycle. Phytoliths were mounted on slides using the same process outlined for pollen extraction.

6.3 Phytolith Key

It became apparent from initial observation of phytolith slides that there were many phytolith forms that did not fit with the 10 basic forms described by Carter and Lian (2000) and Kondo et al. (1994). In order to produce a more detailed identification of phytolith morphologies encountered, it was necessary to produce a phytolith key by

extracting phytoliths from the 37 vegetation species obtained from the field. Ray Marx from the University of Otago (pers. comm., 2008) assisted with this goal by providing a digital catalogue of *Chionochloa* phytolith forms, and several other bracken fern phytolith structures were identified using Kondo et al. (1994). Vegetation samples were oven dried and weighed after returning from the field to assist preservation. Phytolith extraction consisted of washing vegetation samples in distilled water then 10% HCl (Marx et al., 2004), then digesting all organic material associated with the vegetative tissue using a wet ashing technique (Parr et al., 2001). Residual phytoliths were photographed under a light microscope and classified according to their source taxa.

6.4 Modern Pollen Rain

An estimate of the relative proportions of source taxa represented in the modern pollen rain was achieved using moss polsters and one lichen polster collected during the vegetation survey at Swampy Summit. Six variations of bryophyte were chosen to provide the polsters based on their perceived ability to trap pollen. Species chosen were *Cladonia* lichen, *Sphagnum falcatum*, *Dicranoloma menziesii*, *Sphagnum cristatum*, *Thuidium furfuraceum* and *Oreobolus strictus*. Samples from each were washed vigorously in distilled water and poured through a 250µm sieve, then concentrated using a centrifuge and mounted on slides as described in section 7.1 above. A pollen catalogue by Moore et al. (1991) was used to identify individual pollen grains.

7. Results

7.1 Vegetation of Swampy Summit- Past and Present

Table 2. Species abundance at Swampy Summit as percentage of ground cover.

Swampy Summit Vegetation Survey		
Taxa	General Area	Core Site
Grassland Community		
<i>Aciphylla aurea</i>	<1	
<i>Anaphalioides bellidioides</i>	<1	
<i>Astelia nervosa</i>	1	2
<i>Blechnum minus</i>	<1	
<i>Blechnum penna-marina</i>	<1	
<i>Blechnum procerum</i>	<1	<1
<i>Carex coriacea</i>	15	<1
<i>Chionochloa rubra</i>	60	10
<i>Coprosma cheesemanii</i>	20	20
<i>Coprosma ciliata</i>	<1	<1
<i>Forstera tenella</i>	<1	
<i>Gaultheria macrostigma</i>	<1	
<i>Hierochloa redolens</i>	1	
<i>Lycopodium fastigiatum</i>	<1	<1
<i>Oreobolus strictus</i>	<1	3
<i>Poa colensoi</i>	<1	
<i>Viola cunninghamii</i>	<1	
Shrub Community		
<i>Dracophyllum longifolium</i>	10	60
<i>Cyathodes empetrifolia</i>	3	1
<i>Griselinia littoralis</i>	<1	2
<i>Hebe odora</i>	2	1
<i>Leptospermum scoparium</i>	<1	<1
<i>Ozothamnus leptophyllus</i>	1	
<i>Pentachondra pumila</i>	<1	<1
<i>Phormium cookianum</i>	5	5
<i>Pseudopanax simplex</i>	<1	1
Mosses and Lichens		
<i>Cladia retipora</i>	<1	<1
<i>Cladia</i> sp.	<1	<1
<i>Cladonia</i> sp.	<1	
<i>Dicranoloma menziesii</i>	<1	

Table 2. *Continued*

<i>Hypogymnia lugubris</i>	<1	
<i>Polystichum vestitum</i>	<1	
<i>Sphagnum cristatum</i>	5	<1
<i>Sphagnum falciculatum</i>	<1	
<i>Thuidium fufurosum</i>	<1	
Unidentified lichen (fine)	<1	<1
Unidentified Moss (bright green)	1	

Description of Modern Vegetation

The present vegetation at Swampy Summit can be described as a shrubland-grassland community, with 60% of the general area covered by *Chionochloa rubra*, and *Coprosma cheesemanii* forming 20% of ground cover (Table 2). Other common taxa found at Swampy Summit were *Dracophyllum longifolium* (10% cover), and *Phormium cookianum* (5% cover). Overall there were 37 taxa encountered during a vegetation survey of Swampy Summit, although most were only present as sporadic patches, interspersed among the dominant taxa of the site. Although lichen is not strictly a plant, lichens have been included in the taxa described in the Vegetation Survey due to their prevalence as ground cover and potential contribution to the sedimentary record at the site.

The vegetation immediately surrounding the core site had less diversity than the general bog area, and had developed a dominant woody assemblage of taxa. This site was selected for this reason as there was a potential loss of peat from lower sites. For this area *Chionochloa rubra* abundance was ~10%, while the shrub *Dracophyllum* was dominant with 60% cover (Table 2).

Coprosma cheesemanii abundance was consistent with the rest of Swampy Summit at 20% cover, while *Phormium cookianum* was the other main species forming 5% of ground cover.

Modern Pollen Rain from Moss Polsters

The modern dryland taxa pollen rain at Swampy Summit was dominated by *Prymnopterys/Podocarpus* pollen, ranging between 11.11% of the assemblage from

Thuidium furfurosum Polster to 51.41% from the *Sphagnum falcatulum* Polster (Table 3). *Dacrydium cupressinum* and *Prymnopterys/Podocarpus* were present in all moss polsters, as were Monolete fern spores, Trilete fern spores and *Cyperaceae* pollen grains.

Table 3. Composition of Modern Pollen Rain extracted from Moss\Lichen Polsters at Swamy Summit (expressed as percentage of pollen sum).

Pollen Sum	Polster Taxa						
	<i>Cladoma</i> lichen	<i>Oreobolus</i> <i>strictus</i>	<i>Sphagnum</i> <i>cristatum</i>	<i>Sphagnum</i> <i>falcatulum</i>	<i>Thuidium</i> <i>furfurosum</i>	Undiff. Moss	<i>Dichranoloma</i> <i>menziesii</i>
<i>Dacrydium cupressinum</i>	0.56	3.06	0.95	0.85	0.56	0.28	0.28
<i>Prymnopterys/Podocarpus</i>	20.62	33.98	30.79	51.41	11.11	14.29	25.41
<i>Dacrycarpus dacrydioides</i>	0.00	0.28	0.00	0.28	0.00	0.00	0.83
<i>Nothofagus- Fuscasporea</i> type	4.24	0.84	0.95	0.00	1.11	0.56	1.38
<i>Nothofagus menziesii</i>	1.41	0.56	0.00	0.00	0.00	0.56	0.28
<i>Halocarpus bidwillii</i>	0.28	0.00	0.00	0.00	0.56	0.56	0.00
<i>Phyllocladus</i>	0.00	1.39	0.63	0.00	0.28	0.84	0.00
<i>Libocedrus</i>	0.00	0.00	0.00	0.00	0.00	0.28	0.00
<i>Pinus</i>	1.41	0.00	0.00	23.16	5.00	6.44	11.33
<i>Coprosma</i>	0.85	0.28	0.00	0.28	0.56	0.84	0.55
<i>Myrsine</i>	0.28	0.28	0.00	0.00	0.00	0.28	0.00
<i>Pseudopanax arboreus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.28
<i>Pseudowintera</i>	0.00	0.00	0.00	0.28	0.00	0.00	0.00
<i>Griselinia</i>	0.00	0.00	0.32	0.00	0.00	0.00	0.00
<i>Nertera</i>	0.00	0.00	0.00	0.00	0.00	1.40	0.00
<i>Malvaceae</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.28
<i>Ericaceae</i>	0.00	0.00	0.00	0.00	0.00	1.40	0.83
<i>Brassicaceae</i>	0.00	0.00	0.00	0.00	0.00	0.28	0.00
Monolete Fern Spores	5.08	3.90	8.25	2.82	7.22	2.80	5.25
Trilete Fern Spores	9.60	34.54	25.40	20.34	2.50	7.56	12.71
<i>Apiaceae</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.28
<i>Poaceae</i>	0.85	0.84	4.44	0.00	5.56	30.81	15.47
<i>Asteraceae</i>	0.28	0.28	0.63	0.00	1.39	0.00	0.00
<i>Liliaceae</i>	0.85	0.00	0.63	0.00	0.00	0.84	0.00
<i>Forstera spp.</i>	0.00	1.11	0.00	0.00	0.00	0.00	0.00
<i>Ranunculaceae</i>	0.00	0.00	0.00	0.00	0.00	0.56	0.00
<i>Cyperaceae</i>	47.74	18.66	26.98	0.56	56.11	9.52	3.31
<i>Chenopodiaceae</i>	0.00	0.00	0.00	0.00	0.28	1.40	0.00
<i>Phormium</i>	0.28	0.00	0.00	0.00	0.00	0.00	0.00
<i>Triglochin</i>	0.00	0.00	0.00	0.00	0.83	0.00	0.00
<i>Lycopodium</i> spike	5.65	0.00	0.00	0.00	6.94	18.49	21.55

There were less than 5% *Nothofagus fuscasporea*-type palynomorphs in all moss polsters with the exception of *Sphagnum falcatulum*, which had none. Exotic *Pinus*

pollen was present in most polsters, peaking at 23.16% in *Sphagnum falcatulum* and comprising 11.33% of the pollen rain recorded from *Dichranoloma menziesii*. Pinus pollen also featured in smaller amounts in *Cladoma* lichen, *Thuidium furfurosum* and undifferentiated moss recording 1.41%, 5% and 6.44% respectively. Poaceae pollen recorded from moss polsters was less than 1% for *Cladoma* lichen and *Oreobolus strictus*, but made up 4.44% of the pollen rain from *Sphagnum cristatum* and 5.56% from *Thuidium furfurosum* (Table 3). Poaceae pollen spiked in undifferentiated moss at 30.81%, and also made up 15.47% of pollen recorded in the sedge *Dichranoloma menziesii*. Overall there were 30 taxa recorded in the modern pollen rain.

Oreobolus strictus had the highest concentration of *Dacrydium cupressinum* pollen at 3.06% with all other moss polsters recording between 0.28 % and 0.95%. *Cyperaceae* pollen was abundant in most polsters (Table 3), except *Sphagnum falcatulum* with 0.56% and *Dichranoloma menziesii*, which had 3.31%. *Thuidium furfurosum* recorded the highest percentage of *Cyperaceae* spores at 56.11 %, while *Cladoma* lichen also recorded abundant *Cyperaceae* spores with 47.74%. *Oreobolus strictus* and *Sphagnum cristatum* recorded 18.66% and 26.98% *Cyperaceae* spores respectively.

The percentage of *Lycopodium* spores from the spike added during processing varied greatly between polster taxa, with *Dichranoloma menziesii* yielding the largest ratio during analysis at 21.55%. Undifferentiated Moss retained a similar amount of spores from the *Lycopodium* Spike with 18.49%. Samples from *Thuidium furfurosum* and *Cladoma* lichen contained 6.94% and 5.65% *Lycopodium* spike respectively, while polsters from *Sphagnum sp.* and *Oreobolus strictus* recorded none. This demonstrated there were large differences in the pollen concentration obtained from Polster Taxa used to gauge the modern pollen rain.

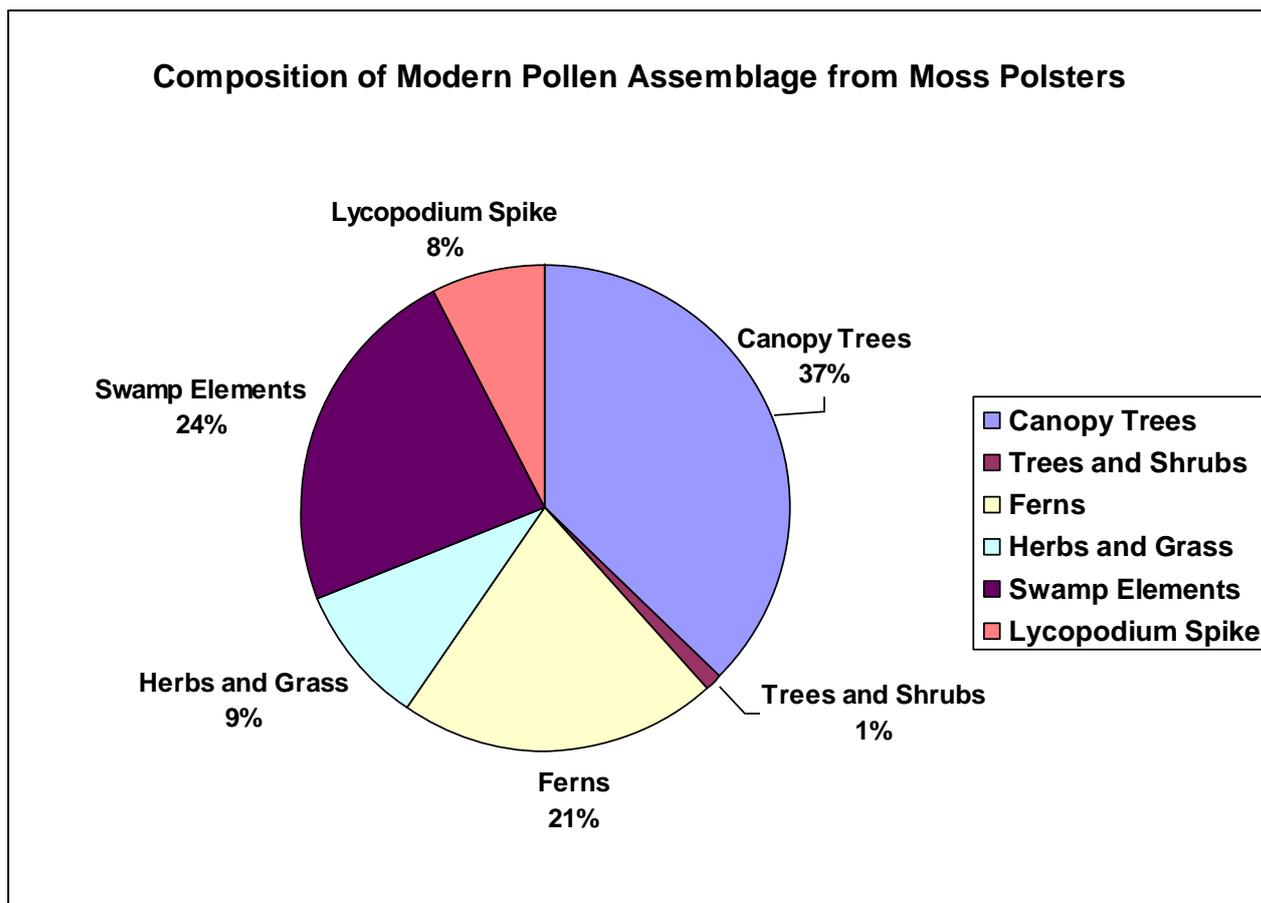


Figure 10. Composition of modern pollen rain at Swampy Summit from all moss polsters combined. Pollen was classified by vegetation type and includes exotic conifers in the canopy tree pollen sum. This assemblage from the modern pollen rain shows some remarkable contrasts with the resident species at the site, with 37% Canopy Trees represented yet none growing at the sample location. Ferns are also overrepresented, comprising 21% of the pollen rain yet less <3% in reality.

It is worth noting that the modern pollen rain from these polsters shows variation between the abundance of different pollen types, depending on the taxa used as a pollen trap (Table 3). This discrepancy in the modern pollen rain from different polsters was apparent for several dryland species including *Prumnopitys/Podocarpus* and *Nothofagus- Fuscaspora* type, and major differences were also apparent for Trilete Fern Spores, *Poaceae* and *Cyperaceae* pollen. The most variable modern pollen counts occurred for *Cyperaceae*, which differed by two orders of magnitude between highest and lowest counts.

Figure 10 illustrates the composition of modern pollen at Swampy Summit, based on vegetation type. Overall, 38% of the modern pollen is dominated by woody dryland

taxa, and canopy trees dominate the pollen assemblage, accounting for 37% of all pollen grains identified. For this analysis, canopy trees include *Dacrydium cupressinum*, *Prumnopitys/Podocarpus*, *Dacrycarpus dacrydioides*, *Nothofagus-Fuscaspora* type, *Nothofagus menziesii*, *Halocarpus bidwillii*, *Phyllocladus*, *Libocedrus* and exotic *Pinus*.

Other Trees and Shrubs are classified according to descriptions given by the Plant Conservation Network (2010). Trees and shrubs are largely under-represented at the site, providing over 60% ground cover directly surrounding the core site (Table 2), yet forming only 1% of the pollen rain (Figure 10).

Swamp elements and ferns formed the other major groupings of plants represented in the pollen rain, accounting for 24% and 21% respectively. Ferns were overrepresented at the site, and commonly formed <1% of ground cover in the general area. Herbs and grass comprised 9% of the pollen sum, marginally more than the *lycopodium* spike, which was 8%. Surprisingly, swamp elements accounted for only about a quarter of palynomorphs in the modern assemblage, despite the collection site being located in the centre of a bog wetland. The high proportion of canopy tree pollen collected in modern samples was not representative of the site vegetation, and was more representative of regional vestiges of vegetation, with *Nothofagus* and *D. cupressinum* pollen demonstrating long distance transport to the site. The prevalence of *Pinus* species in a nearby plantation added to the canopy tree pollen sum, although these exotic conifers were outnumbered by native conifers in all pollen samples (Table 3).

Pollen Zones:

Using CONISS within Psimpol (Bennett, 2005) three pollen zones are recognised from Figure 11, which are described below.

Zone 1: 3.7-3.35m *Coprosma* sp., *Myrsine* sp., *Griselinia* sp and *Malvaceae* Zone. *Coprosma* sp. dominate, peaking at 25% before reducing to 15% at the top of the zone. *Myrsine*, *Griselinia* and *Malvaceae* all peak at 5% in parallel with *Coprosma*. Monolete fern spores peak at the beginning of the zone with over 25% while in the swamp elements *Cyperaceae* are common, attaining values of >20% throughout the zone.

Zone 2: 3.35-1.85m *Prumnopitys/Podocarpus* type, *D. dacrydioides*, *H. bidwillii* Zone.

Prumnopitys/Podocarpus pollen is abundant throughout the zone, peaking at 50% but remaining above 20% throughout the zone. *D. dacrydioides* increases from 0% to 10% early in the zone, then remains stable at between 7-10%. *H. bidwillii* peaks early in the zone at 20% before declining to <5% and recovering to above 10% in the second half of the zone. *Phyllocladus* appears throughout (5% or less), while *Coprosma* steadily declines to <1% by the end of the zone. *Poaceae* pollen is virtually absent from the zone while *Myriophyllum* peaks at over 5% near the start of the zone before disappearing as *Restionaceae* becomes common (>20%).

Zone 3: 1.85-0m *D. cupressinum*, *Prumnopitys/Podocarpus* type Zone.

D. cupressinum exhibits a steady increase from 10% to 30%.

Prumnopitys/Podocarpus is stable at between 17% and 45% throughout, while *D. dacrydioides* becomes absent by the end of the zone. *N. fuscaspora*-type is present at <5% throughout, and *Poaceae* becomes more frequent but still remains below 5%.

Swampy Summit Phytolith Diagram 3.7m

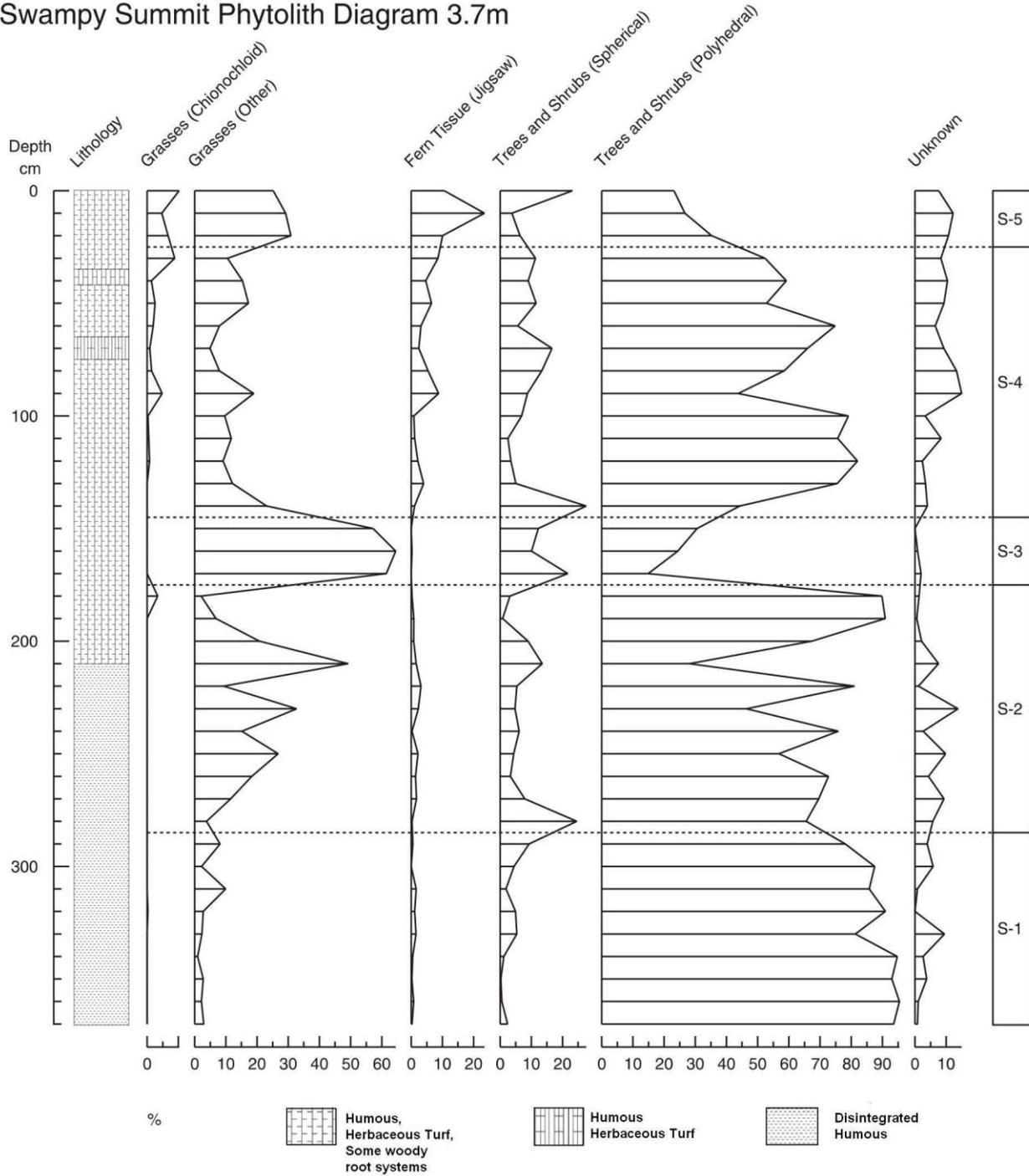


Figure 12. Core Phytolith Diagram from Swampy Summit, Otago, alt. 733m.

Phytolith Zones:

Using the CONISS function within Psimpoll (Bennett, 2005) five phytolith zones are recognised from Figure 12.

Zone 1: 3.7-2.85 m Tree and Shrub Zone.

Polyhedral Tree and Shrub phytoliths are abundant between 70-95% throughout the zone. Ferns makeup <1% while Grasses (elongates) are present but below 10%.

Zone 2: 2.85-1.75 m Mixed Tree, Shrub and Grassland Zone.

Polyhedral Tree and Shrub forms become more variable but remain between 30-90%. Grasses (elongates) increase to 50% before declining to <5%.

Zone 3: 1.75-1.45m Grassland Zone.

Grasses (elongates) spike to over 60% while Polyhedral Tree and Shrub phytoliths decline to a low of 15%.

Zone 4: 1.45-0.25m Mixed Tree, Shrub and Grassland Zone.

Polyhedral Tree and Shrub phytoliths vary between 35-85%. Elongates are present between 5-40% while Chionochloid Tussock phytoliths (spools and dumbbells) increases to a maximum of 10% near the end of the zone, as does Fern Tissue.

Zone 5: 0.25-0m Mixed Tree, Shrub and Grassland with Ferns Zone.

Polyhedral Tree and Shrub phytoliths decline from 45-25% by the end of the zone, while elongate grass phytoliths are present between 25-30%. Fern tissue peaks at 20%, with Chionochloid Tussock Grasses present between 5-10%.

7.2 Vegetation of Clarks Junction-Past and Present

In contrast to Swampy Summit, the vegetation of Clarks Junction was highly modified and contained a variety of introduced species. Natural vegetation (predominantly *Chionochloa rubra*, interspersed with *Cyperaceae* species and *Poa* and *Festuca* grasses) was limited to the gully area adjacent to the core site and extended down valley where drainage was poor.

Clarks Junction Pollen Diagram 1.7m

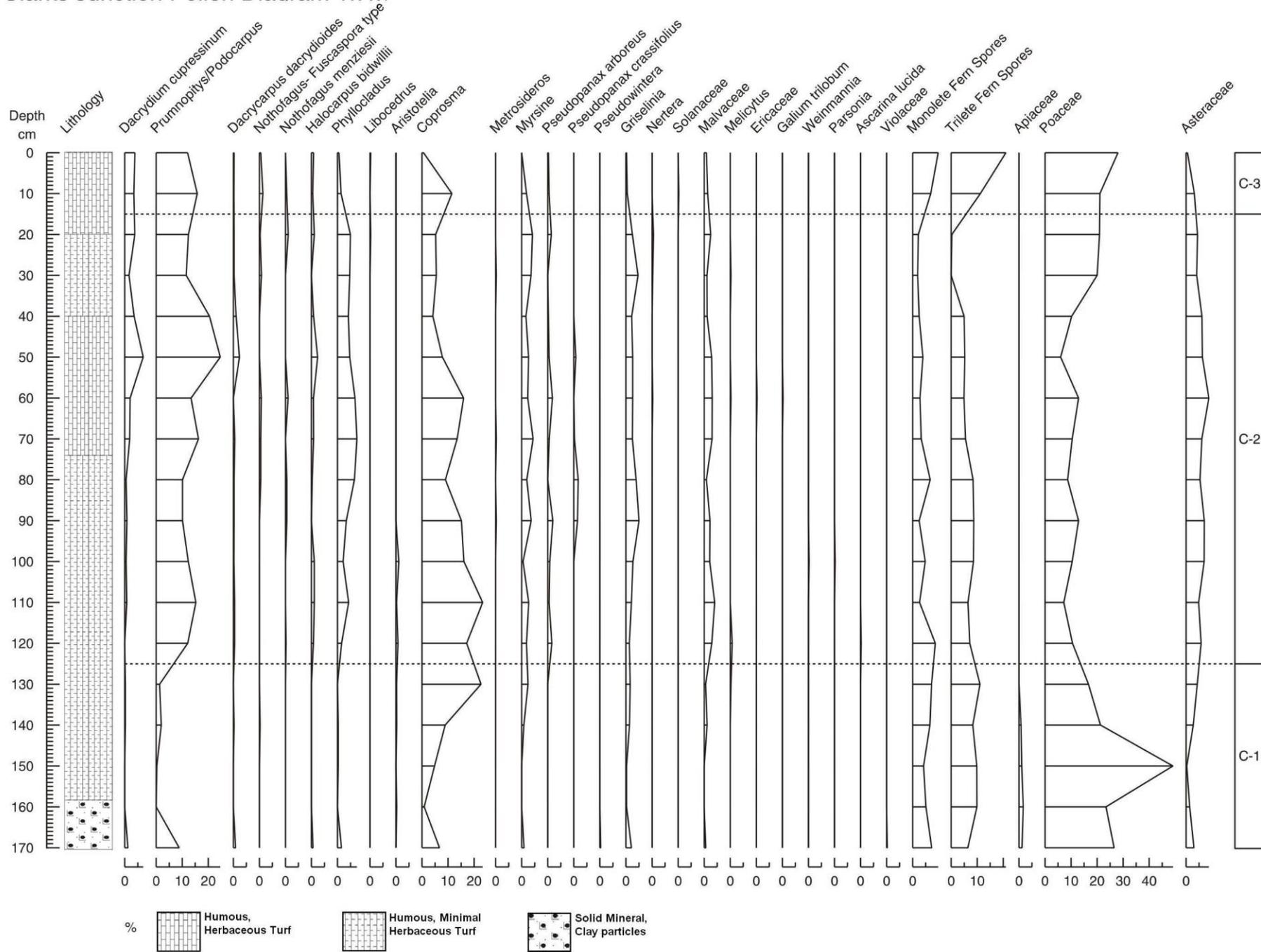


Figure 13. Core Pollen Diagram from Clarks Junction, Otago, alt. 541m.

Clarks Junction Pollen Diagram 1.7m

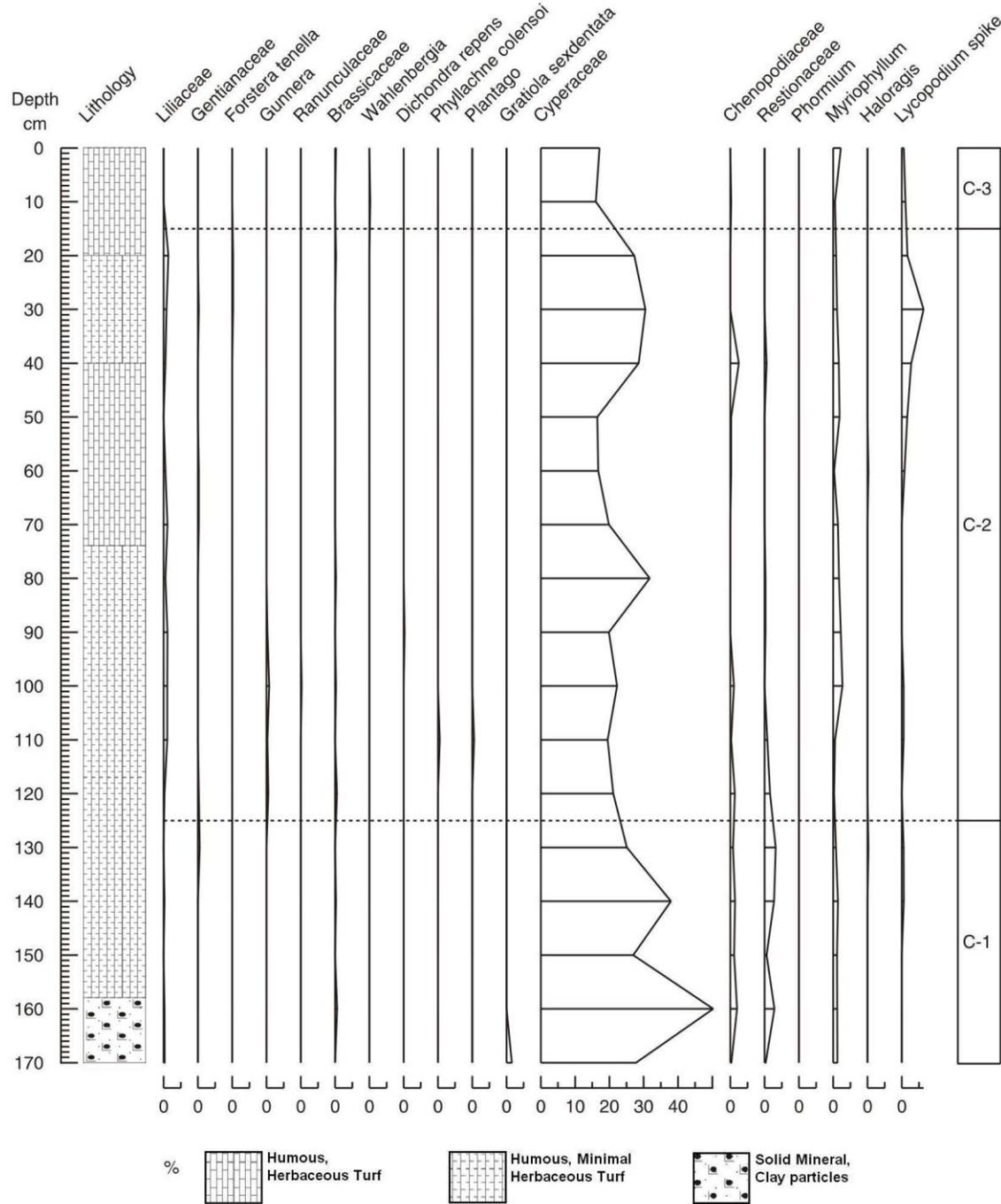


Figure 13 Continued. Core Pollen Diagram from from Clarks Junction, Otago, alt. 541m.

Pollen Zones:

Using CONISS within Psimpol (Bennett, 2005) three pollen zones were identified in the Clarks Junction core (Figure 13). These are described below.

Zone 1: 1.7-1.25 m *Poaceae*, *Coprosma* sp, Monolete and Trilete Fern Zone.

Poaceae peaks at nearly 50% near the middle of the zone and is consistently above 15% throughout. *Coprosma* sp. increase from 7% at the base of the core to nearly 20% by the top of the zone, while *Myrsine* sp, *Griselinia* sp. and *Malvaceae* sp. all begin to increase from about 140cm. Monolete and trilete ferns are common at between 5-10% of the pollen sum throughout the zone. *Cyperaceae* dominate the initial period at >50%.

Zone 2: 1.25-0.15 m *Prumnopitys/Podocarpus*, *Phyllocladus*, *Coprosma* sp. Zone.

There is a steady increase in *Prumnopitys/Podocarpus* from 7% at the base of the zone to a maximum of 24%, before stabilizing at 14%. *Phyllocladus* becomes common, increasing from virtually nothing to consistently above 5% of the assemblage. *Coprosma* steadily declines from a maximum of 23% near the base of the zone to a minimum of 4% but is present throughout, as are *Myrsine* sp., *Griselinia* sp. and *Malvaceae* sp. at values <5%. Grasses decrease, with *Poaceae* dropping to 6% before recovering to 20%. *Asteraceae* are persistent at approximately 5% throughout the zone.

Zone 3: 0.15-0m *Prumnopitys/Podocarpus*, *Coprosma* sp., Monolete and Trilete Fern Zone.

Prumnopitys/Podocarpus are stable at about 15%, while *Coprosma* increase slightly to 11%. *Phyllocladus*, *Myrsine*, *Griselinia* and *Malvaceae* all but disappear from the record, while Monolete and Trilete ferns increase dramatically to 10% and 20% respectively. *Poaceae* increase marginally to 28%, while *Cyperaceae* stabilize at about 15%.

Clarks Junction Phytolith Diagram 1.7m

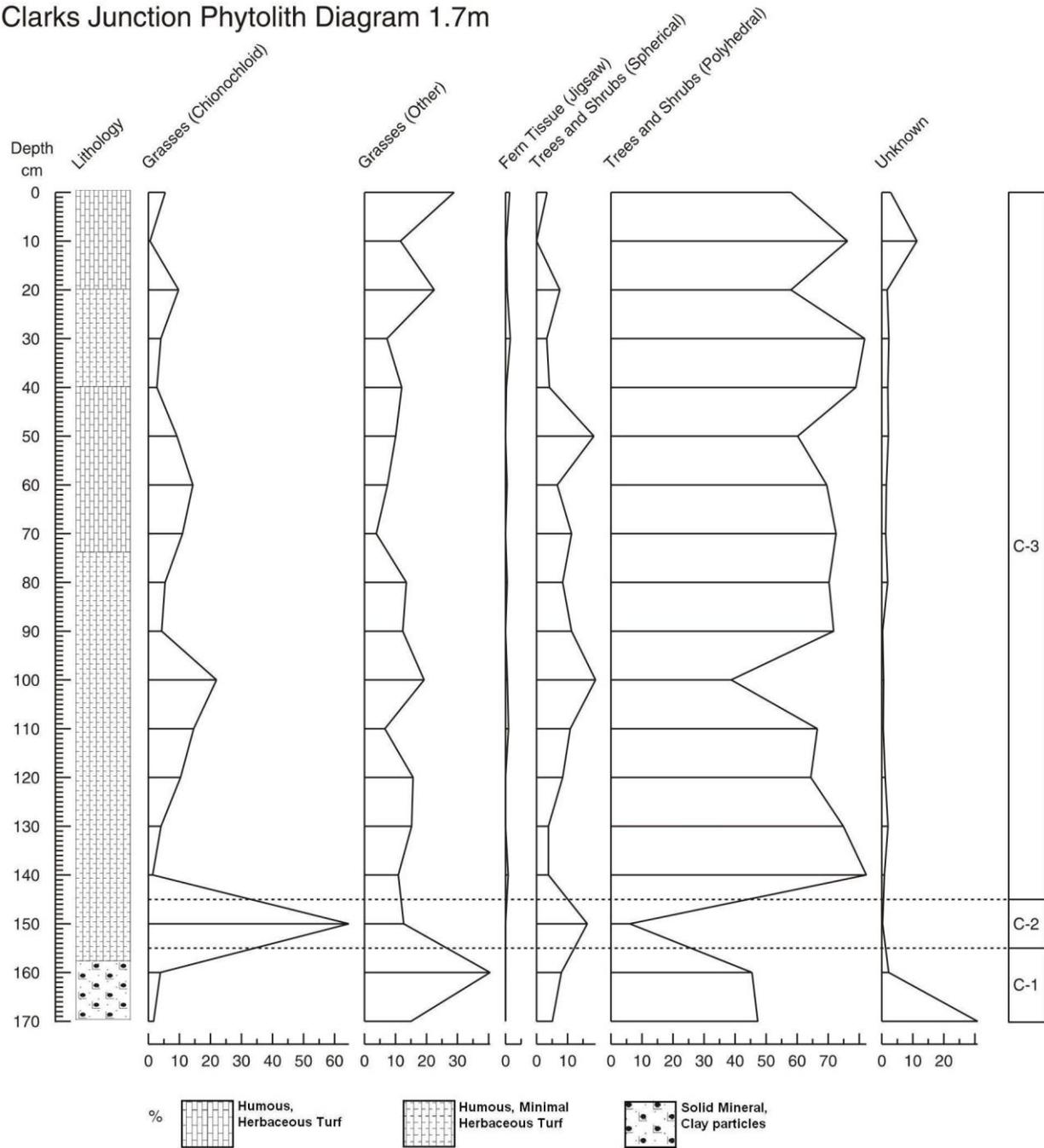


Figure 14. Core Phytolith Diagram from Clarks Junction, Otago, alt. 541m.

Phytolith Zones:

Three phytolith zones were identified using CONISS within Psimpol (Bennett, 2005) in the Clarks Junction core (Figure 14), described below. The CONISS feature of the programme program requires the user to designate the required number of zones for analysis; in this case, three zones were designated as this produced the best fit with the phytolith diagram.

Zone 1: 1.70-1.55m Mixed Grassland, Tree and Shrub Zone

Tree and shrub polyhedral phytoliths dominate the assemblage with nearly 50%, in comparison to spherical tree and shrubs, which remain close to 10%. Other grass phytoliths peak at 40%, while there are few (<5%) Chionochloid phytoliths at the base of this zone where the lithology is silty-clay and mineral quartz. This zone was identified based on one core sample which is not common practice, however various other zoning schemes were trialled which produced questionable demarcations so I decided to accept the 3 zone CONISS analysis.

Zone 2: 1.55-1.45m Grassland Zone

Chionochloid phytoliths peak at 65% in the middle of this zone, while other woody species phytoliths decline. Other grasses initially decline but stabilize near the top of the zone at about 10%. Trees and Shrubs (polyhedral) decline most significantly, to just 6% from their maximum of 47% in Zone 1. Spherical tree and shrubs show a slight increase to 15% in the middle of this zone before declining slightly to 10%.

Zone 3: 1.45-0m Tree and Shrub Zone

There are numerous small-scale fluctuations throughout zone 3, however tree and shrub (spherical) phytoliths are consistently above 38% of the assemblage. Two increases in Chionochloid grasses appear to coincide with slight reductions in trees and shrubs (polyhedral) to about 40% at 1m depth, and later, near the top of the core, to about 60%. Trees and shrubs (polyhedral) peak early in the zone at 82%, the highest proportion of any vegetation type throughout the core. A later, secondary polyhedral tree and shrub peak of 81% occurs towards the top of the zone, when fern tissue is at its maximum- a modest 1.5%. Other grasses remain above 5% throughout the zone, while Chionochloid grasses display three progressively smaller increases during the zone, with none as significant as in zone 2.

8. Phytolith Production from Swampy Summit Taxa

Samples from taxa encountered during the vegetation survey at Swampy Summit (Table 2) were used to develop a table of leaf-bound silica proportions inferring phytolith production.

Table 4. Comparison of residual silica from Swampy Summit vegetation specimens digested using a wet ashing technique.

Species	Dry Leaf Weight (g)	Phytolithic Silica (g)	Phytolith/Leaf (%)
<i>Aciphylla aurea</i>	0.945	0.081	8.571
<i>Anaphaloides bellidioides</i>	0.961	0.14	14.568
<i>Astelia nervosa</i>	1.095	0.187	17.078
<i>Blechnum minus</i>	1.021	0.074	7.248
<i>Blechnum penna-marina</i>	0.379	0.024	6.332
<i>Blechnum procerum</i>	1.088	0.08	7.353
Bright Green Moss (Unidentified)	1.004	0.12	11.952
<i>Carex coriacea</i>	0.981	0.168	17.125
<i>Chionochloa rubra</i>	0.993	0.084	8.459
<i>Cladia</i> sp.	1.016	0.02	1.969
<i>Cladia retipora</i>	1.018	0.074	7.269
<i>Cladonia</i> lichen (Dark)	1.014	0.023	2.268
<i>Coprosma cheesemani</i>	0.935	0.032	3.422
<i>Coprosma ciliata</i>	0.992	0.04	4.032
<i>Cyathodes empetrifolia</i>	1.051	0.049	4.662
<i>Dicranoloma menziesii</i>	0.983	0.15	15.259
<i>Dracophyllum longifolium</i>	1.028	0.026	2.529
<i>Forstera tenella</i>	0.206	0.008	3.883
<i>Gaultheria macrostigma</i>	0.884	0.041	4.638
<i>Griselinia littoralis</i>	1.023	0.035	3.421
<i>Hebe odora</i>	1.055	0.019	1.801
<i>Hierochloa redolens</i>	1.025	0.044	4.293
<i>Hypogymnia lugubris</i>	0.982	0.025	2.546
Lichen (fine)	1.037	0.019	1.832
<i>Leptospermum scoparium</i>	0.271	0.01	3.690
<i>Lycopodium fastigiatum</i>	1.004	0.076	7.570
<i>Oreobolus strictus</i>	1.014	0.149	14.694
<i>Ozothamnus leptophyllus</i>	1.036	0.072	6.950
<i>Pentachondra pumila</i>	1.039	0.069	6.641
<i>Phormium cookianum</i>	1.015	0.033	3.251
<i>Poa colensoi</i>	1.025	0.159	15.512
<i>Polystichum vestitum</i>	0.998	0.063	6.313
<i>Pseudopanax simplex</i> (juvenile)	1.026	0.033	3.216
<i>Sphagnum cristatum</i>	0.891	0.317	35.578
<i>Sphagnum falcatulum</i>	0.343	0.028	8.163
<i>Thuidium furfuraceum</i>	1.034	0.243	23.501
<i>Viola cuninhamii</i>	0.565	0.025	4.425

Leaves from individual specimens were analysed to determine percentage weights of biogenic silica for each taxon (Table 4). Phytolith extraction from the vegetation samples followed a wet ashing technique (Parr et al., 2001). There were large variations in the amount of biogenic silica extracted from Swampy Summit vegetation samples (Table 4), with few, if any diagnostic phytolith forms. *Sphagnum cristatum* had the highest concentration of phytoliths, totalling 35.578% of the dry sample weight, while the lichen *Thuidium furfuraceum* had 23%. Seven species contained between 11% and 18% phytoliths by weight. These included *Anaphaloides bellidioides*, *Astelia nervosa*, Bright Green Moss (Unidentified), *Carex coriacea*, *Dicranoloma menziesii*, *Oreobolus strictus* and *Poa colensoi*. The majority of taxa sampled contained 1%-10% phytoliths by leaf weight, while the shrub *Hebe odora* had the lowest proportion of leaf phytoliths at 1.801%, closely followed by the unidentified fine lichen, which had 1.832 %.

Species of the *Sphagnum* genus showed considerable variation between them, with *S. falcatulum* containing only 8.163% phytoliths in comparison to the 35.578% extracted from *S. cristatum*. Both *Coprosma* species contained a similar amount of phytoliths and there was <1% difference between them. *C. cheesemani* and *C. ciliata* had 3.422% and 4.032% respectively.

The three *Cladia* lichen samples yielded between 1.969 and 7.269 % phytoliths, while three *Blechnum* fern specimens exhibited much less variation. *B. penna-marina* produced 6.332% while *B. minus* had 7.248% and *B. procerum* 7.353% phytoliths from leaf samples.

9. Discussion: Inferred Vegetation Histories

9.1 Reliability of Proxies

Phytolith records formed a key comparison proxy for vegetation in this study, and although there is a substantial amount of overseas research based on these plant silicates, phytolith research in New Zealand is still developing.

In order to infer vegetation types from phytoliths found in the sedimentary records at Clarks Junction and Swampy Summit it was necessary to classify the phytoliths according to several morphological types. Little is known about species-specific phytoliths of native New Zealand plants so a more generalised classification scheme was used. For the purposes of this study the generalised scheme was resolute enough to infer key vegetation types and also reduced the risk of human error during microscopic analysis as this scheme required less technical ability for classification. There were however, several potential sources of variation which may have reduced the reliability of using phytoliths as a proxy. Previous phytolith work has focused on extracting phytoliths from sediments low in organics, in sediments where pollen preservation is poor or the age of the sediments has excluded pollen due to degradation. Phytoliths obtained here were extracted from peat, which was predominantly composed of organic material and required repeated acid digestion in order to obtain enough concentrated phytoliths for analysis. Although phytolithic silica is championed as being resilient and readily preserved in a range of sediments, it is unknown what the effect of long-term exposure to acidic conditions may have had on the phytoliths obtained from these acidic peat bogs. As a result, we are uncertain if prolonged exposure to acidic water could cause some part of the assemblage to go into solution or if degradation of phytoliths could have occurred while in situ, rendering them difficult to according to the key used.

Advice by John Carter suggested that although a heavy liquid separation was used to separate biogenic silica from mineral silica, the high counts of polyhedral morphs in these samples may have been wind-deposited mineral silica. Another potential source of bias in the phytolith assemblage is the documented lack of phytoliths from *Podocarpaceae* genera (Kondo et al., 1994). This highlights a common issue which is a lack of knowledge about the production and form of phytoliths in New Zealand

plant species. Grass phytoliths however, are well documented and detailed phytolith keys have been produced for native New Zealand grasses (Kondo et al., 1994; Marx et al., 2004). Grasses are recognised worldwide as a major source of phytoliths (Piperno, 2006) so phytoliths provide the ideal proxy for this project focussing on grassland history in Otago.

Pollen as a proxy is more widely developed, and as a consequence there are fewer unknowns and more confidence can be placed on the specific identification of taxa. The key considerations for interpreting pollen-based vegetation reconstructions are where the pollen was sourced from and how productive the source taxa are. Pollen transport can vary greatly but there have been examples of wind-blown *Casuarina* pollen from Australia reaching New Zealand via the prevailing westerly winds (Close et al., 1978; Moar, 1969).

Differences in pollen deposition were also evident between closely adjacent areas in this study, reinforcing the need to evaluate factors affecting pollen deposition in these peat bogs and as a consequence, the representation of taxa in the assemblage. Similarly, the apparent variation in modern pollen ‘trapping’ ability between mosses and lichens (Table 5) emphasises the need for consistency during sampling, in order to accurately gauge pollen assemblages from the modern pollen rain. Consistency was achieved in this study by adding pollen counts from all polster samples in order to reduce the potential for any bias associated with trapping efficiency of polster taxa. There was huge variation between pollen assemblages collected from Swampy Summit moss polsters, despite the polsters being collected from a very small area surrounding the core site. During collection of moss polsters for pollen rain analysis, polsters were only selected from exposed areas of the peat bog in order to exclude the effects of nearby shrubs on windflow and pollen settling rates. Turbulence within the windflow resulting from sporadic woody vegetation is likely to increase pollen deposition downwind of any obstruction. Conversely, Jacobson and Bradshaw (1981) discuss the relative importance of different modes of pollen deposition, including the role of above-canopy wind transport influencing the regional and extra-local pollen rain present in the assemblage.

Table 5. Chi-Square Test of Independence for vegetation type as recorded in the modern pollen rain from moss polsters and lichen at Swampy Summit. Data are observed pollen counts (expected values in brackets).

	Moss Polsters/ Lichen used for Pollen Rain Collection						
	<i>Cladoma lichen</i>	<i>Oreobolus strictus</i>	<i>Sphagnum cristatum</i>	<i>Sphagnum falciculatum</i>	<i>Thuidium furfuraceum</i>	Undiff. Bright Green Moss	<i>Dicranoloma menziesii</i>
Trees and Shrubs	105 (151.1)	146 (117.9)	106 (111)	270 (144.8)	69 (159.6)	100 (142.2)	150 (119.4)
Ferns	4 (5.3)	2 (4.1)	1 (3.9)	2 (5.1)	2 (5.6)	15 (5)	7 (4.2)
Herbs and Grass	7 (36.7)	8 (28.7)	18 (27)	0 (35.2)	25 (38.8)	115 (34.6)	57 (29)
Swamp Elements	170 (92.8)	67 (72.4)	85 (68.2)	2 (88.9)	206 (98)	39 (87.3)	12 (73.4)
X²=789.8, P=<0.01, 18 d.f.							

There was significant variation in the pollen rain captured from the moss polsters. The null hypothesis is rejected ($P < 0.01$) therefore the relative proportions of modern pollen captured from the modern pollen rain is dependent on the species of Moss Polster/Lichen used to obtain the sample. This is most likely explained by the morphology of moss/lichen species used as pollen traps, with dense mats likely to trap more spores and have less likelihood of spore removal by wind and heavy rain. The amount of pollen deposited at the bog site may also be affected by small-scale differences in topography and shelter provided by nearby vegetation. This has implications for future studies of the modern pollen rain as using only a few, selected moss polster species to obtain pollen samples may bias the results. For this research, this has been overcome by combining all moss polster pollen rain results (Figure 10), which minimises the effect of small-scale variations in pollen deposition and differences in trapping ability of moss polsters.

Pollen proxies remain a useful tool for vegetation reconstructions as they can be high resolution in terms of identifying source taxa to a species level, depending on the ability of the pollen palynologist and the quality of pollen in the sample, while being complicated by pollen, transport and depositional factors. Table 3 reflects the remarkable variation in pollen rain recorded from multiple moss sources within the same local site, indicating there is still a lot of unknown factors influencing pollen deposition and moss polster yields. Conversely, phytoliths as a proxy for vegetation

give a more generalised picture of the type of vegetation, while also giving a more accurate representation of localised vegetation at a site due to their limited dispersal and tendency to be deposited in sediments adjacent to the source.

The relatively low taxon resolution phytolith records presented here are due to the inherent difficulty identifying phytoliths to a species level in the absence of previous phytolith research for many New Zealand native species. Grasses were grouped as either Chionochloid or 'other' for this reason, and for the purposes of most studies this method is accurate enough to satisfy the research aims. The advantage of researching tussock grasslands is that their Chionochloid phytoliths are easier than any other grasses to identify and give a more accurate proxy for the type of grasses growing at the site.

9.2 Swampy Summit Vegetation Record

The first core analysed in this study was taken from a peat deposit at Swampy Summit, where two previous studies by Cranwell and von Post (1936), and later McIntyre and McKellar (1970), also examined the sedimentary pollen record. The later study by McIntyre and McKellar (1970) has provided a useful comparison with the pollen diagram from this research in order to get an age control on key features within the pollen record. It is apparent that the two pollen records share a strong similarity (Figure 15) and there are two obvious tie points between the diagrams. The first occurs at 11-10 ka with the arrival of *Podocarpus*, *Dacrycarpus* and *Phyllocladus* pollen. The second tie point is more recent, at about 6 ka when Rimu (*Dacrydium cupressinum*) pollen becomes prevalent (Figure 15).

The two Swampy Summit diagrams mirror the analogous arrival of several key taxa, however the McIntyre and McKellar diagram (1970) marks the onset of Rimu 6ka with a simultaneous increase in *Dacrydioid* (*Halocarpus*) species. This contrasts with the *Halocarpus bidwillii* sum from my research which shows the reverse. My core exhibits an initial peak in *Halocarpus* shortly after 11ka, then a short decline until about 7ka before *Halocarpus* recovers to early Holocene levels, continuing until 6ka when there is a steady decline until the present. *Halocarpus* is consistently low until 6ka in the core of McIntyre and McKellar (1970) and is most abundant from 6ka to the present- the period of decline in my core. The exact co-ordinates of the Swampy Summit core taken by McIntyre and McKellar (1970) are unknown; however there is

limited scope for such a significant contrast in the abundance of *Halocarpus* at this locale, especially considering the frost tolerant nature of *Halocarpus bidwillii* (Wardle and Campbell, 1976). An alternative explanation for the contrast in *Halocarpus* between these two Swampy Summit peat cores is that deposition of *Halocarpus* pollen has been affected in some way, perhaps by the presence of standing water or lack thereof. Pollen is well preserved in water-logged peat but the presence of streams or surface runoff can significantly affect the transport of local pollen to a site. Likewise, variable drainage or vegetation characteristics of a site can also be reflected in changes to deposition rates and pollen yield so this apparent variability in *Halocarpus* abundance needs to be viewed with caution, as *Halocarpus* is generally underrepresented in the pollen sum also (Macphail and McQueen, 1983). *Halocarpus* is likely to have been present at Swampy Summit for the last 11,000 yrs although perhaps in localised outcrops for the first half of the Holocene, before increasing after 6000 yr B.P. The highly variable pollen sum from *Halocarpus bidwillii* in my core is likely to be the result of one or several localised drainage factors discussed above, coupled with poor pollen representation of this genus (Macphail and McQueen, 1983). I was unable to identify any *Halocarpus biformis* (formerly *Dacrydium biforme*) which was presumably included in the *Dacrydioid* sum of McIntyre and McKellar (1970), although the environmental preferences of this species suggest it would be uncommon at this site. The apparent lack of *Halocarpus* pollen after 6ka in my core does not exclude *Halocarpus* from the local vegetation community at the site, as pollen production from this genus is sparse and commonly underrepresented (Macphail and McQueen, 1983), however it suggests that pollen deposition can vary greatly across relatively small spatial scales.

In Figure 15, Kahikatea (*Dacrycarpus dacrydioides*, formerly *P.dacrydioides*) is noteworthy as the two pollen diagrams illustrate a near identical trend with Kahikatea becoming common shortly after the onset of *Podocarpus* and remaining consistently around 10% of the total pollen sum, before tailing off after 6 ka. This demonstrates a close link between both pollen records and reinforces the decline in Kahikatea over the last 6ka.

Prior to the arrival of *Podocarpus* and other key forest taxa, both diagrams start with a zone of shrubland dominated by *Coprosma* pollen. *Coprosma* remains throughout the pollen record in both diagrams but does not reach the levels recorded before 11-10ka.

Poaceae (*Gramineae*) is present sporadically throughout both diagrams but generally <10% of the pollen sum. At no time does grassland dominate the record in either diagram, indicating that grass was present in localised pockets but was unlikely to have formed a true grassland at these sites, instead remaining interspersed with mixed woody vegetation. Grass pollen is generally well represented in pollen records (Macphail and McQueen, 1983), so low levels recorded in the cores could be attributed to low abundance of grassland sources or factors affecting pollen deposition at these study sites such as a canopy of vegetation influencing wind deposition. The role of above-canopy wind transport is signified by the symbol C_c in Figure 5. It is also important to note that the large size of *Chionochloa* pollen grains mean they are less likely to be transported long distances (McGlone, 2001), instead depositing close to their source which gives us confidence that the *Poaceae* sum represents a localised source of grasses dominated by *Chionochloa*.

From the comparison of Swampy Summit pollen records, we can conclude that the core sampled in this research covers most of the Holocene, with the lowland forest taxon Rimu (*Dacrydium cupressinum*) appearing at about 6,000 years B.P. which is at a depth of 1.85 m in the core presented here (Figure 15-B). The spread of Rimu has been linked with the climate becoming warmer and wetter (McGlone, 1995; Ogden et al., 1998), coinciding with the expansion of Celery Pine (*Phyllocladus*). There is also a more recent increase in *Phyllocladus* from 20cm depth in both cores, which may indicate increased Late-Holocene disturbance as Macphail and McQueen (1983) have indicated an increase in localised *Phyllocladus* is common after fire. McGlone et al. (1997) has also suggested that increased abundance of *Phyllocladus* at the expense of sub-alpine scrub is a function of warmer summers and rising timberlines, inferring a drier environment and potentially more susceptibility to fire. All taxa represented in Figure 15 match closely between the cores, with the exception of *Halocarpus*. The decline of frost-tolerant *Halocarpus* after 6ka in this core (Figure 15-B) is in contrast to the increased *Halocarpus* (*Dacrydioid*) sum seen in the earlier core from Swampy Summit (Figure 15-A). This variance between cores taken from the same bog cannot

be explained by climatic changes and is more likely due to localised variation in pollen deposition of this hardy but underrepresented taxon, although the absence of frost and bog tolerant *Halocarpus* from the species abundance survey (Table 2) also supports the decline of this taxon in the pollen record from Swampy Summit. The decline of *Halocarpus* from my core in the last 6,000 yrs (Figure 15-B) culminates with a late Holocene peak in *Phyllocladus*-also evident in the earlier core. This may indicate a shift to drier conditions at the site as *Phyllocladus* is less tolerant of waterlogged roots than *Halocarpus*.

McIntyre and McKellar (1970) inferred that they were missing the top 2,000 years or so from their core record and the pollen record presented here remains similar to theirs from the base to the surface, but as will be noted below there is good evidence from the phytoliths that most or all of this Late-Holocene period is actually present. In short, the core record (Figure 11) covers most of the Holocene and the very end of the last glacial termination. The pattern is mirrored from other sites in the southern South Island, as outlined below.

Pollen diagrams from the Longwood Range in Southland (McGlone and Bathgate, 1983) reflect a similar pattern of vegetation to Swampy Summit in the early Holocene-Late Glacial Period. In Southland, a grassland-shrubland existed prior to 12,000 B.P. before a successional shrubland became established leading to the expansion of *Dacrydium cupressinum* (Rimu) beginning around 7,000 yr B.P. (McGlone and Bathgate, 1983). A similar progression was recorded by McGlone and Wilmshurst (1999a) at Glendhu Bog in Eastern Otago, where a *Coprosma*-based shrubland-grassland existed between 12,000-9,580 yr B.P. About 7,000 yr B.P. conifer forest became established, marked by an increase in Rimu and other *Podocarpus* pollen in the record (McGlone and Wilmshurst, 1999a).

The record of vegetation in Southern New Zealand during this Late-Glacial period suggests that a tundra-like grassland-shrubland existed between 12,000- 7,000 yr B.P. across much of the South (McGlone and Wilmshurst, 1999a). In the eastern South Island, an increase in *Prumnopitys-Podocarpus* pollen between 11,600-9,700 yr B.P. marks the expansion of conifer forest in at least some coastal areas (McGlone, 1995). In Central Otago, low altitude sites had a mixed-conifer forest by 7,500 yr B.P., about

2,000 years after the coastal expansion of *Podocarpus* species due to a drier early-Holocene Climate (McGlone, 1995). In summary, the patterns in this core are consistent with the core covering the whole Holocene.

Persistence of grass in the pollen and phytolith records

What is immediately clear is that grass plays a minor role in the pollen record at this site at any stage. In the summary of the Swampy Summit core (Figure 15), grass is virtually absent until c. 6,000 years ago and then forms a minor component of the pollen rain in the top part of the diagram. The core of McIntyre and McKellar (1970) has somewhat higher grass values in the pre-Holocene section in Zone 1 but they are still low (<5%). Grass pollen is virtually absent from their record in the early Holocene and re-establishes as a trace at about the time of Rimu appearance, as per Figure 15-A. In contrast, elongate phytoliths that are attributed to grasses (Kondo et al., 1994) occur throughout the core and in relatively high values above 3.2m depth in the core (start of the Holocene). The lowest frequency of grass phytoliths is in the pre-Holocene section in Zone S-1 of the core where we might expect them to dominate!

The first appearance of distinctive *Chionochoild* phytoliths is at 1.8 m and they are continuously present from 1.2 m. This is undated but clearly significantly precedes the latest expansion of general grass and fern types at the site in the top 20 cm. We have no direct age control but by comparison with McIntyre and McKellar (1970), there is tussock grass at the core site for about 3,800 years. Prior to this, there was a peak in other grass types coinciding with a reduction in polyhedral Tree and Shrub phytoliths as reflected Zone S-3 in the Swampy Summit phytolith diagram (Figure 12). This precedes human arrival by several thousand years so can likely be attributed to some natural disturbance mechanism. This apparent discrepancy with the pollen record is most likely due to the local origin of phytoliths in contrast to the widely dispersed nature of pollen, which gives a regional vegetation signal (Carter, 2002). McGlone (2001) has noted the low pollen representation of alpine grasslands, and attributes it to limited source area of upland grasses in relation to expansive areas of lowland, dominated by prolific pollen sources. This ‘dilution’ effect of grass pollen by lowland taxa offers an alternative explanation to the low representation of grass pollen in the Swampy Summit record. Another factor influencing pollen representation of tussock

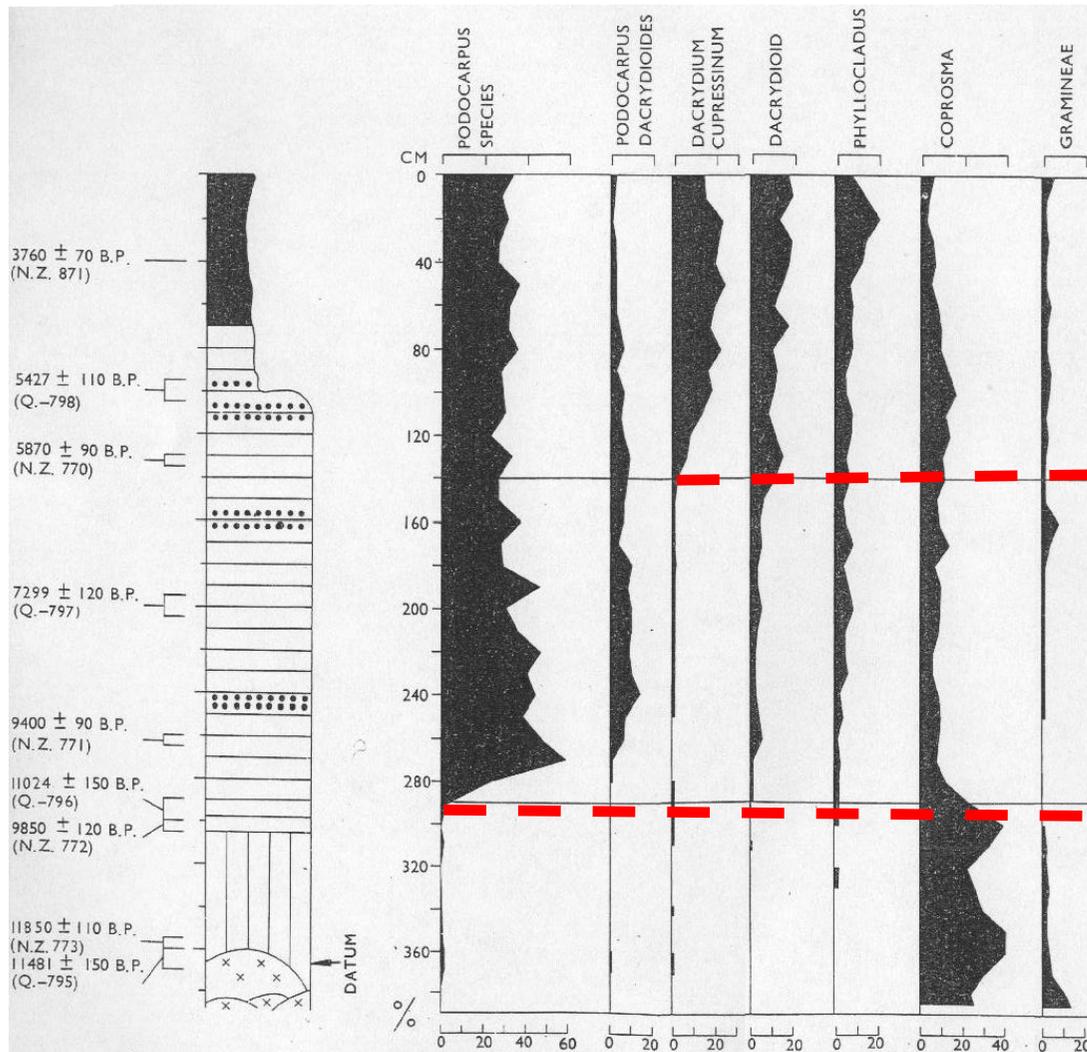
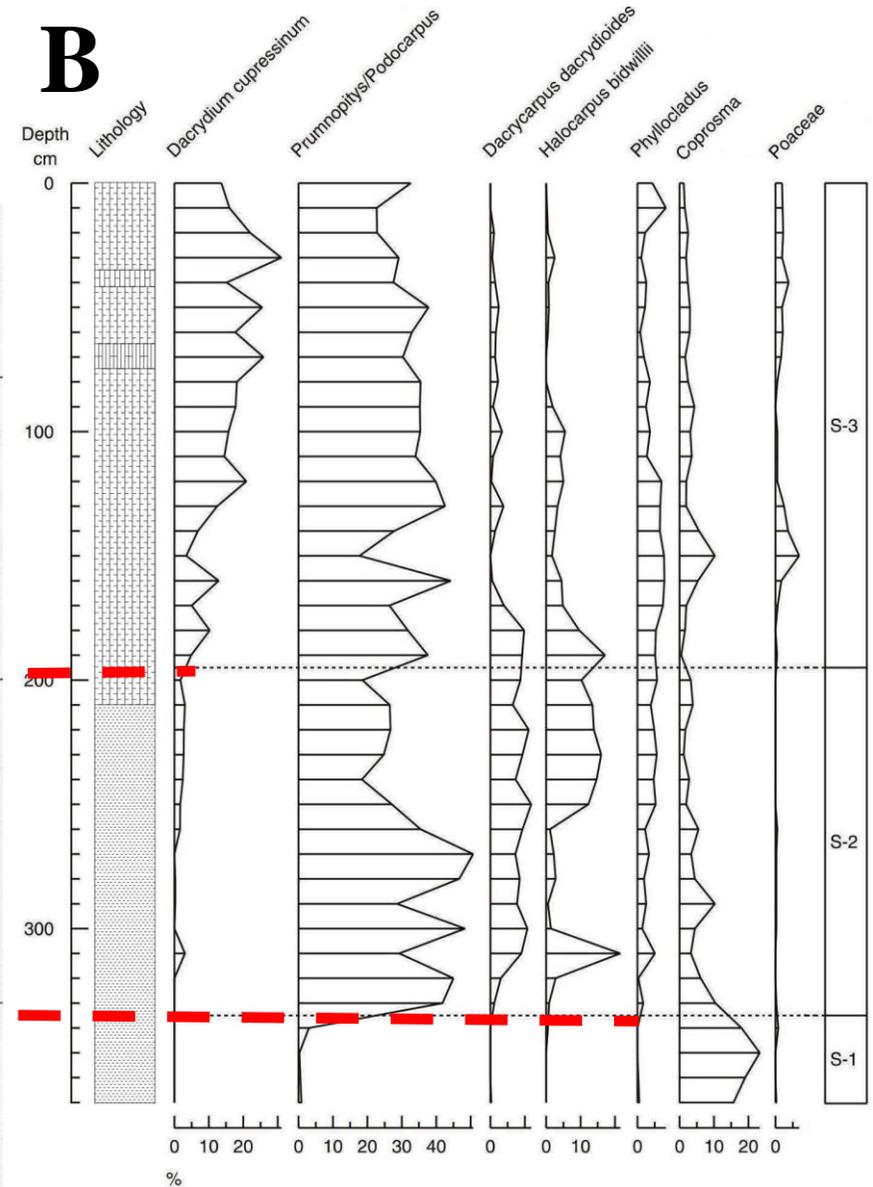
A**B**

Figure 15. Comparison of Swampy Summit Pollen Diagrams. A-McIntyre and McKellar Pear Core (1970); B-Recent Peat Core (2008). Note that *Podocarpus dacrydioides* has undergone a name change to become *Dacrycarpus dacrydioides* and *Dacrydioid* pollen is now referred to as *Halocarpus bidwillii* type. *Gramineae* grasses have become *Poaceae*. From this comparison we are able to correlate the two cores and transfer radiocarbon ages from the earlier core of McIntyre and McKellar (1970) to date the analogous arrival of key taxa in the latter core.

grasses is the intensity and frequency of flowering. *Chionochloa* in particular, flowers sporadically during masting events up to 5 years apart (McKone et al., 1998), triggered by warm temperatures during the previous summer (Mark, 1969). Additionally, flowering intensity has been shown by Hay et al. (2008) to be related to resource availability, therefore grasses in less favourable places are likely to pollenate less. The reproductive strategy of *Chionochloa*, coupled with large pollen grains which are not well dispersed, therefore mean that dominance of *Chionochloa* at a particular site is not necessarily reflected in the core pollen record (McGlone, 2001).

The sensitivity of the pollen record to the recording environment is highlighted by moss polster pollen trap results where adjacent moss polsters of different species yielded dramatically different floras. The use of a *Sphagnum* polster to provide a representative sample of pollen rain, which is a taxon widely used for this purpose, yielded the best representation of regional vegetation, but conversely a poor indication of local vegetation. It is not at all clear why adjacent polsters should yield such dramatically different results but it does highlight the potential problem of interpreting local vegetation from the pollen record.

Human disturbance in the Swampy Summit record

The pollen record also fails to pick up human disturbance at the top of the core, as does the pollen record of McIntyre and McKellar (1970), but the phytoliths definitely do. There is an opening up of the swamp in the top 20 cm (Zone S-5) with ferns and grasses becoming more important. This challenges the interpretation of McIntyre and McKellar (1970) that they are missing the top 2,000 year of their core; however, the presence of raised peat scarps above the water table at Swampy Summit indicates that some erosion may have taken place.

There is little published in the scientific literature about human disturbance of Swampy Summit but its history is relatively well known. Post human settlement in Dunedin there has been widespread land clearance and disturbance adjacent to the 40 ha area of Swampy Summit, with large areas to the south now dominated by exotic conifer forest (Mason, 1989).

The extent of fire disturbance on vegetation at Swampy Summit is unknown, although microscopic charcoal was present in some of the pollen slides analysed. There were, however, several known fires in the area immediately surrounding Swampy Summit such as one on Mt Cargill in the early 1900's when large areas of Mountain Cedar (*Libocedrus bidwillii*) were burnt (Mason, 1989). The adjacent Flagstaff scenic reserve was also subjected to periodic fires between 1868 and 1904 when it was grazed and burnt under private farm ownership (Mason, 1989). It is not unlikely that these pastoral fires got out of control from time to time and burnt along the ridge to Swampy Summit. There was also an extensive uncontrolled fire on Flagstaff in 1976, which was followed by an experimental burn to test tussock recovery (Mason, 1989). Stock grazing continued to have a significant impact on local vegetation until adjoining land was fully fenced in 1916, and even now, there are still feral pigs, sheep and goats in the area around Swampy Summit (Mason, 1989).

It is worth noting that in 1984 it was predicted that if there were no further fires, then by 2026 Flagstaff Scenic Reserve adjacent to Swampy Summit would revert to snow-tussock-scrubland with manuka (*Leptospermum*) forming the dominant woody species. It later became apparent that exotic conifers from neighbouring plantations would succeed the native shrubland/grassland if left to colonise unchecked (Mason, 1989).

What this study clearly shows is that both woody and grassland vegetation co-existed on swampy summit throughout the Holocene. The pollen diagram is flooded by lowland pollen types (Rimu, Totara and Kahikatea in particular) during the Holocene which minimises the local pollen signal. In the swamp, the grass pollen is out-recorded by *Cyperaceae*, and *Restionaceae*. This probably reflects the dominance of these taxa in the wetter areas of the swamp where the peat is forming, contrasting with the wider drier areas which have tussock and woody vegetation cover.

In summary, Swampy Summit demonstrates that grassland in general and tussock, in particular, arrived at this site many thousands of years before anthropogenic burning or clearance opened the site up. It provides strong support for the hypothesis of long-term survival of tussock and other grasslands below the treeline in New Zealand. It is

interesting that tussock does not appear at this site until about 6,000 years ago. It suggests that tussock colonisation and local extinction is a dynamic process through the Holocene.

9.3 Clarks Junction Vegetation Record

The Clarks Junction pollen record shows less overall diversity than the Swampy Summit pollen record; however, they both contain pollen from the same major canopy species. Previous palynological work at Clarks Junction (Leslie and McGlone, 1973; McGlone, unpublished data, 1972; McGlone, 1995) has aided interpretation of this core, and an earlier pollen diagram by McGlone (unpublished data, 1972) has been used for comparison to time the arrival of several key taxa (Figure 16).

The two pollen diagrams presented in Figure 16 reflect a similar pattern of vegetation during the Holocene, beginning with an increase in *Coprosma* beginning ~12,400 yr B.P.

Halocarpus and *Phyllocladus* were present at Clarks Junction as a mixed conifer shrubland throughout much of the Holocene. *Phyllocladus* forms a major component of the conifer shrubland in the early Holocene at Clarks Junction, and is present in trace amounts from 11,600 yr B.P. Equally tolerant of the extreme frosts and poor soils; *Halocarpus* was established by 9,700 yr B.P. (Figure 16). The early establishment of *Phyllocladus* and *Halocarpus* during the transition to Podocarp forest at Clarks Junction is likely a reflection of the resilience of these taxa to frosts and infertile soils (McGlone and Moar, 1998). Both these taxa commonly inhabit gley podzol soils and bogs (Macphail and McQueen, 1983).

Coprosma peaked approximately 9,000 yr B.P. as reflected in both diagrams, which marks the first major tie point at about 9,000 yr B.P. It is interesting to note that despite being an under-represented taxon in pollen records, *Halocarpus* is noticeably more abundant in the McGlone diagram (16-B), again illustrating the variability between two pollen diagrams from the same locale. This variability is the result of localised influences on the pollen rain, possibly reflecting differences between water transport of pollen at the core sites. Byrami et al. (2002) have previously described similar variability in records from a single swamp. We also need to take into account that although cores used for comparisons with this study were from the same local

areas; their exact source locations are unknown. Unlike Swampy Summit, at Clarks Junction there is a large area of suitable peat accumulation where cores could be obtained, leading to the possibility that my core may not have been taken from a site close to that of McGlone's (unpublished data, 1972) used in this comparison.

Another possible tie point between the two diagrams is a layer of silty mineral clay, which marked the base of the core at 160cm depth, and similarly was encountered at 270cm depth in the McGlone core (unpublished data, 1972). Assuming that peat development on this clay surface began at the same time at both core sites, this would infer a basal age of approximately 9,700 years for the peat core extracted in this reconstruction of Clarks Junction vegetation (Figure 16-A). This was also the conclusion of McGlone (1995) who noted 9,700 yr B.P. as the beginning of continual peat growth at the site.

The second obvious tie-point illustrated in Figure 16 occurs soon after the first, and is dated at approximately 8,600 yr B.P., marked by the appearance of Rimu (*Dacrydium cupressinum*), *Podocarpus* and Kahikatea (*Dacrycarpus dacrydioides*) pollen in the records. The onset of these canopy tree species comes on the heels of a significant decline in grasses prior to 8,600 yr B.P. and is followed by a period of reduced grass (*Poaceae*) abundance reflected in both core diagrams. Although *Phyllocladus* was present at the site throughout the Holocene, it was not widely established until after 8,600 yr B.P. in parallel with *Podocarpus* and other canopy species recorded in both pollen diagrams (Figure 16).

Podocarpaceae did not become established at the site until after 8,600 yr B.P. as Rimu, Kahikatea and *Prymnopterys/Podocarpus* forest began to colonise the area. The expansion of Podocarp species into eastern Otago at this time fits with the generalised pattern of Podocarp spread, coinciding with early Holocene warming 9,000-7,000 yr B.P. (McGlone, 1988).

In Figure 16-B, *Coprosma* is persistent until approximately 800 yr B.P. when it drops from the record, however it remains a significant taxa throughout the most recent Clarks Junction core (Figure 16-A).

The McGlone diagram from Clarks Junction possibly contains a more complete record of vegetation from the late Holocene period of human settlement. This assumption is based on the comparison of pollen diagrams illustrated in Figure 16. It shows a period of about 600 years of almost no *Coprosma* pollen in the McGlone core, which is unusual given that *Coprosma* pollen is well represented to over-represented in most samples (Macphail and McQueen, 1983). This would indicate almost complete removal of *Coprosma* from Clarks Junction and the surrounding area during this time, creating a vegetation assemblage similar to what is currently present at the site. In contrast, *Coprosma* pollen was abundant throughout the core in Figure 16-A, and only diminished to <1% at the core surface. This seems to indicate that either peat accumulation at the core site has virtually stalled in the last 800 years or, increased erosion as a result of deforestation and changing land-use has removed the surface peat from the core site spanning the last 600 years. The absence of a late-Holocene decline in *Podocarpaceae* pollen from the top of Figure 16-A supports the erosional theory. This erosion of the peat surface is also likely to have been exacerbated by modern farming methods and it was apparent during fieldwork that land adjacent to core site had been recently cultivated.

A rapid deforestation is recorded about 800 yr B.P., coinciding with the expansion of human settlement in New Zealand (McGlone, 1989). From 600 yr B.P. Podocarp species are virtually eliminated from the record, although *Dacrydium cupressinum* continues to appear in the record at <5%, a feature most likely resulting from the abundant pollen production and long distance dispersal of this species.

In summary, the Clarks Junction pollen diagram produced here illustrates a period of grassland dominance in the early Holocene, which continued from the end of the last glacial period until about 9000 yr B.P. (Figure 16). Peat accumulation at this time was most rapid between 12,400 and 11,600 yr B.P. (McGlone, unpublished data, 1972) which suggests the climate was wet enough to encourage peat growth but cold enough to limit the development of forest.

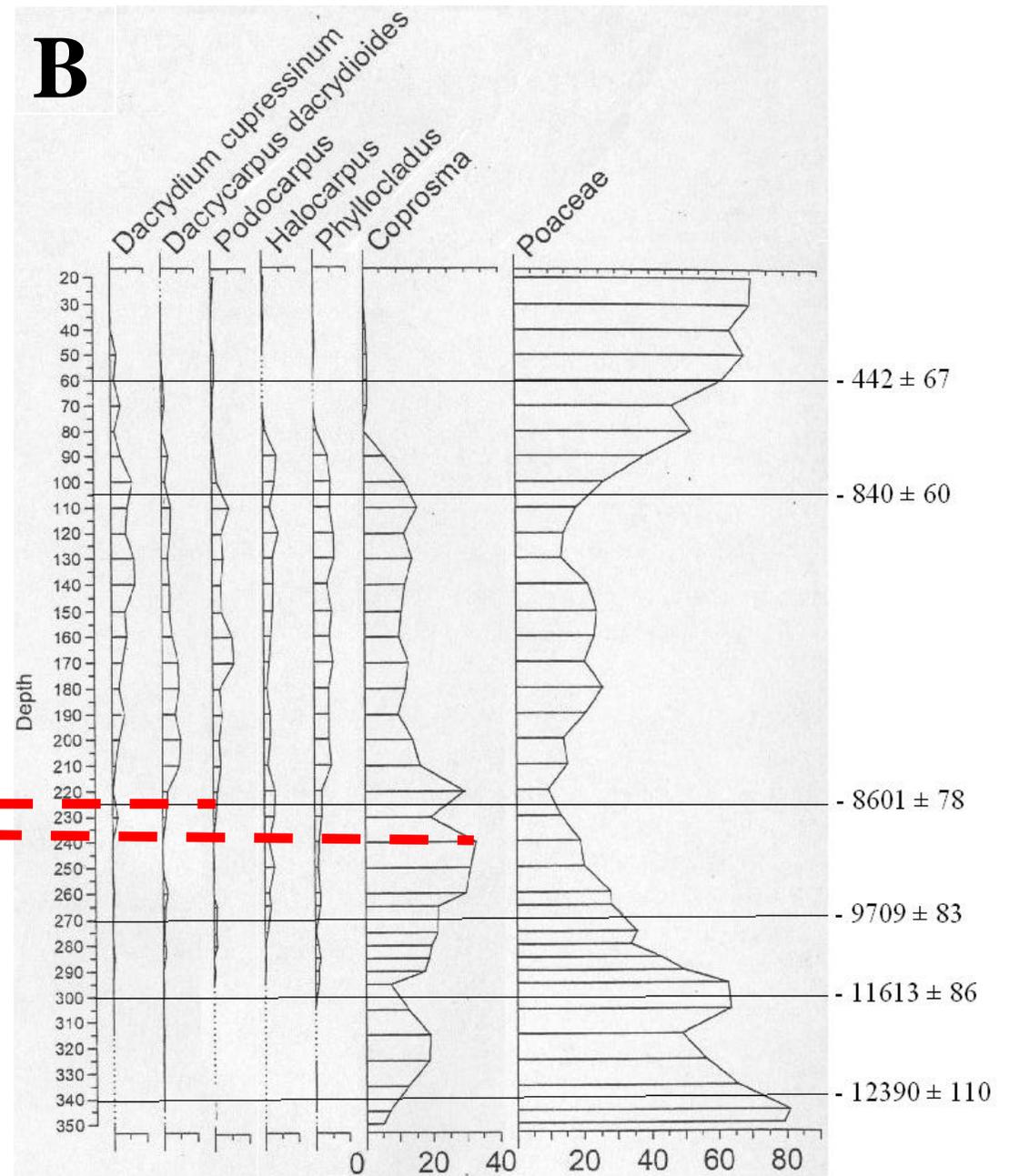
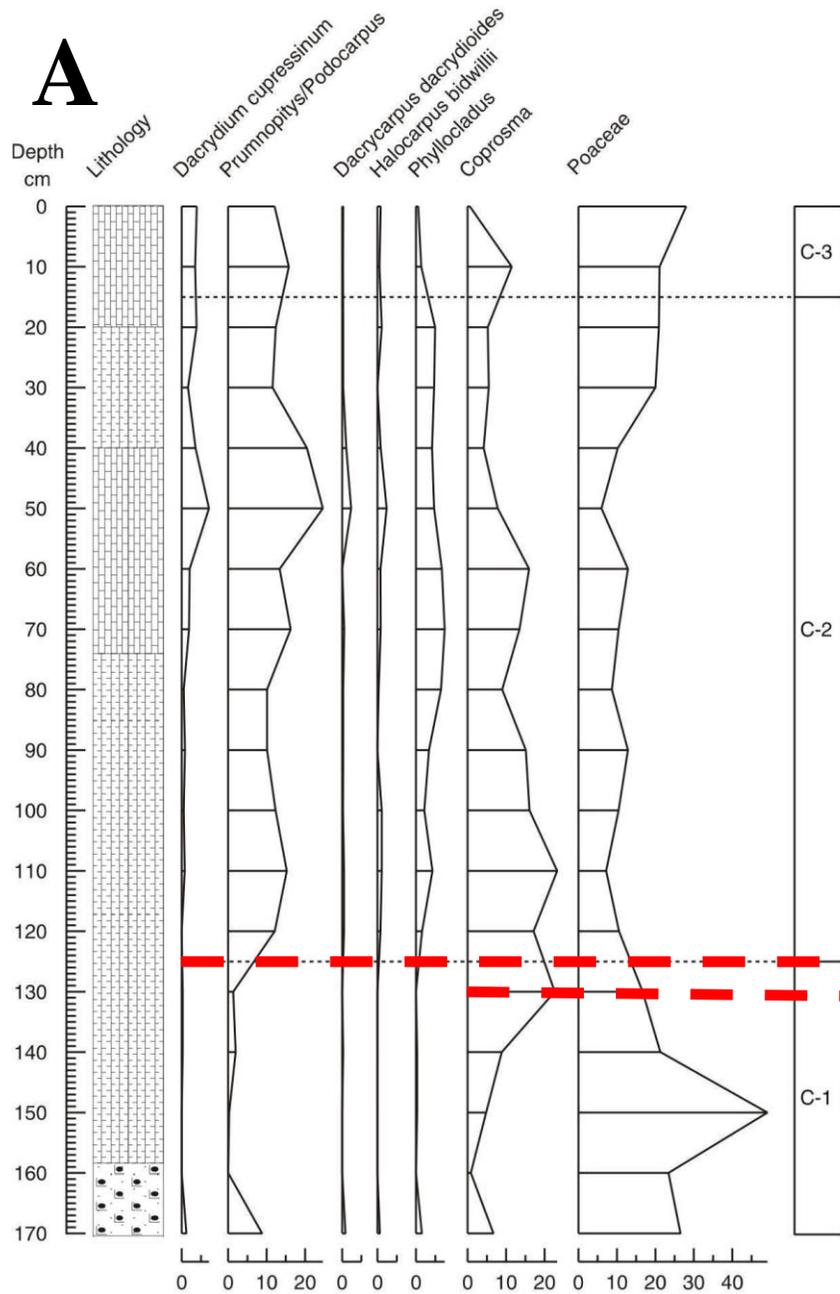


Figure 16. Comparison of Clarks Junction Pollen Diagrams showing analogous arrival of key taxa. A- From this study (2008); B-McGlone, unpublished data (1972).

As the climate warmed, conditions favoured the spread of small, hardy trees such as *Halocarpus* and *Phyllocladus* into the Clarks Junction area, beginning about 11,600 yr B.P. Gradual succession to a grassland–shrubland ecosystem occurred up until 8,800 yr B.P., with *Coprosma* dominating the shrubland community and reaching peak abundance at 8,800 yr B.P. Around this time larger canopy trees such as Rimu, *Podocarpus* sp. and Kahikatea became common in the record as the climate became more favourable for forest development, while *Coprosma* was still significant in the assemblage but grasses declined rapidly. From 8,600 to 600 yr B.P. forest-shrubland was common at the site while grasses remained low, although wind distribution of grass pollen may also have been reduced at the site due to shelter from a closed forest canopy.

The most recent changes since 600 yr B.P. have been human induced, leading to the clearance of local woody vegetation and a subsequent expansion of grasses once more. The absence of the last 200-400 years of my core reflects increased erosional processes at the site, caused by the clearance of vegetation and conversion to agricultural landuse.

Persistence of grass in the pollen and phytolith records

The pollen record at Clarks Junction reflects a transition from a *Coprosma*-based open grassland-shrubland community to Podocarp forest-shrubland and back to grassland in the space of 12,000 years (Figure 16). Grassland according to pollen records has dominated the late glacial to early Holocene phase at Clarks Junction, and has persisted at the site throughout the Holocene. Grassland was abundant at this time as it tolerates drought-prone and wetland areas equally, while also surviving in infertile soils (McGlone, 2001). Coupled with this, grasses are able to rapidly re-colonise areas of disturbance due to their lifecycle traits (Lloyd et al., 2003). The core by McGlone (unpublished data, 1972), was considerably deeper than the one presented in this study, and dated an initial peak in *Poaceae* pollen at the base of the core to 12,390 ± 110 yr B.P., reflecting a Holocene maximum for grassland at the site (Figure 16-B). A small increase in grassland is evident about 11,600 yr B.P. before *Poaceae* species taper off as *Coprosma*-shrubland increases. Grassland pollen is at its minimum about

8,600 yr B.P. before stabilising as forest colonised the site. Grassland remains a significant component of the vegetation at Clarks Junction throughout the mid-Holocene, with *Poaceae* pollen consistently present in the pollen record at levels of 10-30%. In this research grass pollen was undifferentiated and classified merely as *Poaceae*, however McGlone (2001) has described how *Chionochloa* grasses often account for only 10-15% of the pollen sum, despite dominance at a site. As deforestation accelerated beginning about 800 yr B.P., grass pollen dominates the record once more, almost reaching early-Holocene levels in the assemblage.

In contrast to Swampy Summit, grass pollen is present at Clarks Junction throughout the Holocene, and the phytolith record supports the long-term presence of *Chionochloa* tussock grassland at this site. Figure 14 illustrates an early peak in elongate grass phytolith forms in the mineral clay at the base of the Clarks Junction core (Zone C-1). This is closely followed by a large spike in Chionochloid grass phytoliths coinciding with the initial period of peat growth (Zone C-2). This period of rapid *Chionochloa* tussock expansion at the site is mirrored by a sharp decline in polyhedral tree and shrub phytolith forms, while other grass phytolith forms decline by two-thirds before stabilising at about 10-20% for the majority of Zone C-3.

Chionochloid grasses then follow a saw-tooth pattern of expansion and decline, which cycles nearly every 50cm along the core. Other grass phytoliths remain more or less stable at around 10-20% throughout the core and do not exhibit the same apparent cyclicity. The most significant increase in Chionochloid tussock grass phytoliths in Zone C-3 occurs at 100cm depth in the core and there is also a slight increase in other grass phytoliths at this time. This coincides with a decline in *Phyllocladus* and *Myrsine* in the pollen record, possibly indicating drier conditions favouring grasses over bog colonising trees and shrubs. There is also a reduction in polyhedral tree and shrub phytoliths at this time, although spherical tree and shrub phytoliths gain slightly. Overall, the grass phytolith record seems to match the pollen record fairly well for Clarks Junction, with the *Chionochloa* tussock maximum evident in both the phytolith record and the pollen record at 150cm.

The persistence of grassland in Clarks Junction pollen and phytolith records reflects the view shared by McGlone (2001), that forest cover never completely dominated the

site. The mixed forest community had previously been interpreted as a result of extensive deforestation in Otago 3,000-800 yr B.P. (McGlone, 2001). However, there is evidence of deforestation at the site as a macroscopic charcoal horizon in a core taken by Leslie and McGlone (1973). This has since been dated by McGlone (2001) to 1,680 yr B.P. (NZ9139A), which may coincide with the decline in *Coprosma* and increase in *Poaceae* pollen from about 50cm depth in the core. Chionochloid phytoliths decline from 60-40cm in the core before making a short recovery, which is curtailed at 10cm depth, likely signalling the start of human burning and the near complete denudation of *Chionochloa* tussock from the site.

Human disturbance in the Clarks Junction record

The phytolith record looks as though it may reflect some part of the human disturbance period, as spherical tree and shrub phytoliths, fern tissue and Chionochloid phytoliths all but disappear from the record at 10cm depth in the core, before recovering slightly as polyhedral tree and shrub phytoliths decline toward the surface. Throughout the core there appears to be an inverse relationship between Chionochloid phytoliths and tree and shrub phytoliths. Firstly, there is a reduction in polyhedral tree and shrub phytoliths at depths down the core coinciding with peaks in Chionochloid grass phytoliths. This is true for all peaks in Chionochloid phytoliths with the exception of a peak at 60cm depth. Inverse to this polyhedral phytolith trend there is also a response reflected in proportions of spherical tree and shrub phytoliths, which peak in parallel with Chionochloid grass phytoliths throughout the core. This would suggest that prior to Chionochloid grass peaks, some form of disturbance has occurred at the site which has resulted in the destruction of woody vegetation inclined to produce polyhedral phytoliths. The exact source of polyhedral phytoliths is unknown; however this broad morphological group has been attributed to tree and shrub sources based on work by Kondo et al. (1994) and Piperno (2006).

Peaks in spherical woody phytoliths are possibly from shrub species which are able to flourish in the absence of a forest canopy, while peaks in *Chionochloa* grass phytoliths are likely due to the initial recolonisation of these disturbed areas by Tussock grasslands, which decline with time as woody vegetation returns to the site. This study does not identify the nature of disturbance at Clarks Junction resulting in

the short-term expansion of *Chionochloa* at these intervals; however the *Phyllocladus* pollen sum could be expected to reflect disturbance by fire as the trees are susceptible to fire and slow to re-colonise after burning (Wardle, 1969). McGlone and Moar (1998) emphasise the vulnerability of this taxon at Duncan Stream in Central Otago, where burning has virtually eliminated *Phyllocladus* from the site. The Clarks Junction pollen diagram presented here shows no similar impact on the *Phyllocladus* pollen sum until 600 yr B.P., although the impact of less frequent natural fires on the pollen sum may be masked by the long distance transport of *Phyllocladus* pollen (Macphail and McQueen, 1983).

The pollen record from Clarks Junction may also reflect some human disturbance, though arguably not the most intense period spanning the last 600 years. Zone C-3 in Figure 13 shows the near-elimination of *Phyllocladus* from the vegetation record, although *Prymnopterys/Podocarpus* pollen remains a significant component at >10%. Shulmeister et al. (2003) noted that pollen records from the Cobb Valley were not significantly affected by clearing for pastoralism. This suggests that a large component of the pollen assemblage was not locally sourced, and is probably the case for *Prymnopterys/Podocarpus* pollen at Clarks Junction, with dispersal of *Podocarpus* pollen highly variable from well to under-represented in pollen records (Macphail and McQueen, 1983).

Coprosma displays an initial flourish in Zone S-3 before declining rapidly, while *Myrsine*, *Griselinia* and *Malvaceae* shrubs all virtually drop from the record in the top 15cm of the core. In contrast to this, there is an increase in fern and grass palynomorphs over this period. Trilete fern spores are especially noticeable, and reach their highest levels of the Holocene at the surface of the core, despite there currently being no fern community in the vicinity of the core site. This supports the initial succession of fern species after fire, and subsequent removal of ferns with repeated burning (McGlone, 2001). The rapid increase in fern spores in the most recent period of the core is in marked contrast to phytolith representation of the fern record at Clarks Junction. Jigsaw fern tissue phytoliths were present throughout the record beginning at 140cm depth but only at trace amounts (<2%) of the phytolith assemblage, while monolet and trilete fern spores were consistently between 5-10% and peaked at 20% of the pollen assemblage, despite monolet and trilete ferns being

generally underrepresented in the pollen rain. Both records in this comparison suggest that ferns persisted at Clarks Junction throughout the Holocene, although the scarcity of fern phytoliths prevents their use as an indicator of disturbance at the site and is reflected by a lack of fern phytoliths during the most recent period of human disturbance which is evident in the fern spore record in Zone C-3. *Poaceae* pollen also increases during Zone C-3 to levels similar to those of the early Holocene, supporting a record of at least some anthropogenic disturbance in the pollen assemblage.

At this point it is pertinent to discuss the reliability of the phytolith record at Clarks Junction. Phytoliths were classified according to ten morphological types outlined in Carter and Lian (2000). These ten classifications were further summarised into six groups, broadly identifying phytoliths by vegetation type with the exception of Chionochloid grasses which were morphologically distinct and easy to differentiate. We can place a high degree of confidence on Chionochloid phytolith counts; however resolution is low for all other phytolith classes used here, due to a lack of species specific knowledge on phytolith forms and production. John Carter (pers. comm., 2009) has questioned the authenticity of the same polyhedral tree and shrub phytoliths from the core, suggesting that many of the polyhedral phytoliths may in fact be grains of mineral silica. The prevalence of schist in the Otago region (Leslie and McGlone, 1973) could provide a source of wind-blown mineral silica, however heavy liquid separation was used in processing which should have separated biogenic phytolith silicates (SG=2.3) from residual mineral silicates (SG=2.65), producing uncontaminated slides for phytolith counts. Despite some difficulties with phytolith classification, it is obvious from the Chionochloid record at Clarks Junction that tussock grasses have persisted at the site throughout the Holocene, reaching their lowest abundance at 10cm depth in the core which would seem to coincide with some period of increased disturbance, likely to be human induced burning of this grassland area leading to the proliferation of other, faster colonising grasses such as *Poa* and *Festuca*.

It is apparent from the summary of fire histories (Figure 3) that the spatial distribution of fires in the South Island has been consistent across a range of temporal scales. This concentration of fire disturbance in the Eastern Ranges of the South Island during pre-human and post-human settlement of New Zealand supports ongoing disturbance to

vegetation in localised areas such as Clarks Junction, ultimately leading to changes in vegetation structure and composition. Fires that occurred pre-human arrival in New Zealand would have encouraged the development of mixed vegetation mosaics (McGlone, 2001; Ogden et al., 1998), supporting the persistence of early-colonising species such as grasses in areas of disturbance below the natural treeline. The radiation of these pockets of grasses from vestiges below the treeline seems to be a more likely source of genetic material supporting the spread of lowland grass communities than grasses seeding solely from above the treeline. Many more sites are needed, however, to demonstrate that a mosaic of grasslands existed below the natural treeline throughout New Zealand during the Holocene. This study of Holocene vegetation at Clarks Junction indicates that they did at least this one site.

9.4 General Discussion

The cores presented here from Swampy Summit and Clarks Junction cover most of the Holocene and in the case of Swampy Summit, the very end of the last glacial termination. The pattern of grassland-shrubland succession to mixed shrubland-low forest and later canopy forming Podocarp/Beech forest has been consistent throughout a number of sites in the southern South Island, albeit occurring at different temporal scales due to regional climatic differences and topographical barriers.

During the early-Holocene-Late Glacial period in Southland, a grassland-shrubland community existed which was succeeded by more continuous shrubland leading to the expansion of *Dacrydium cupressinum* (Rimu) beginning around 7000 yr BP (McGlone and Bathgate, 1983). Eastern Otago, mirrored this trend where a *Coprosma*-based shrubland-grassland paved the way for conifer broadleaf forest, marked by an increase in Rimu and other *Podocarpus* pollen in the record (McGlone and Wilmshurst, 1999a).

A common feature of South Island pollen cores is the prevalence of resilient, frost tolerant species forming a grassland-shrubland at the end of the Late-Glacial leading into the Holocene 12,000- 7,000 yr BP (McGlone and Wilmshurst, 1999a). During this Late-Glacial period grasslands were becoming established in many areas and it is notable from a Kawarau Gorge pollen diagrams produced by McGlone et al. (1995),

that daisy (*Asteraceae*) pollen featured significantly in the pollen sum at the beginning of the Holocene. At Clarks Junction, McGlone (1995) also recorded up to 15% *Asteraceae* pollen present in the pollen record between 12,400 yr B.P and 11,600 yr B.P.

The subsequent expansion of Podocarp/conifer forests in the eastern South Island does not appear to be continuous but had begun as early as 11,600 yr BP in some coastal areas (McGlone, 1995). The drier more extreme climate of the Central Otago region had excluded mixed-conifer type forest until ~7,500 yr BP, when a variety of conifer species replaced lowland areas of grassland as the climate ameliorated (McGlone, 1995). This forest expansion occurred about 2000 years after the coastal expansion of *Podocarpus* species (McGlone, 1995).

It appears that grass has never dominated the coastal sub-alpine environment of Swampy Summit yet it has maintained a continual presence at the site throughout the Holocene. According to the phytolith record, grasses were present at Swampy Summit for the duration of the core, a marked contrast to the pollen record which only illustrates sporadic periods of grass at low abundances. This underestimation from the pollen record is possibly a function of the intermittent mast-seeding nature of New Zealand's native tussock grasses, coupled with barriers to consistent pollen deposition such as flowing surface water or closed canopy forest-scrubland affecting settling of pollen. Historically, local patches of tussock grassland at the bog were likely to have been sporadic as they are today, with the wettest areas of the bog close to the water table inhabited by other non-tussock species.

From this study we can conclude that phytoliths provide a more accurate proxy for investigating the localised presence of grasses at a site as they generally remain in-situ after the plant decays.

One interesting note is that at Swampy Summit, the lowest frequency of grass phytoliths is in the pre-Holocene section in Zone S-1 of the core where we might expect them to dominate. Instead, polyhedral tree and shrub phytoliths make up 70-95% of the phytolith assemblage at this time. This apparent abundance of woody vegetation at the expense of grasses may be a function of unfavourable conditions

limiting localised grass growth and tussock stem production, or high precipitation during this early peat-forming period may have washed significant amounts of phytolithic silica away from the bog surface. Either way, subsequent zones show much greater variation in the phytolith record coinciding with an increase in abundance of grasses.

Natural disturbance is a likely trigger of variation in the phytolith record and is also a key driver of the composition of vegetation communities prior to human arrival in New Zealand, especially in the drier regions of Central Otago which already had larger areas of fire-prone grass biomass colonising the most unfavourable growing areas. One example of this is a rapid drop in the polyhedral tree and shrub phytoliths in Zone S-3 at Swampy Summit which precedes human arrival by several thousand years so can likely be attributed to some natural disturbance mechanism. This apparent discrepancy with the pollen record is most likely due to the local origin of phytoliths in contrast to the widely dispersed nature of pollen which gives a regional vegetation signal (Carter, 2002). Other forms of disturbance with the potential to alter the local vegetation assemblage include wind throw, heavy snow, landslides and slumps, inflows of silt and biological attack by invertebrates such as Pinhole Borer, which usually inhabits dead Beech logs but in some cases will attack and kill live trees. In the North Island volcanism has also directly affecting the structure and distribution of vegetation communities (Ogden et al., 1998).

The most recent period of vegetation change in the cores has been complicated in the records by the erosion that has occurred in bogs/wetlands which are now actively farmed or have been heavily modified by other forms of human disturbance such as scrub fires. Both Swampy Summit and Clarks Junction cores appear to have at least some Late-Holocene record of human disturbance which is evident in both phytolith records but is difficult to constrain in the Swampy Summit pollen assemblage. At this site the bog reverts toward open scrubby vegetation in the top 20 cm (Zone S-5) with ferns and grasses becoming more important. What this study clearly shows is that both woody and grassland vegetation formed a mixed assemblage on Swampy Summit throughout the Holocene, as a mosaic in the largely forested lowland areas of coastal Otago.

For the Holocene, the apparent late emergence of low-altitude tussock grasslands is inconsistent with the physiology and reproductive strategy of tall tussock grasses. The life history traits of these species adapted them for longevity rather than rapid expansion, and Mark (1969) has proposed that some mature tussock specimens could be centuries old. Seed production occurs during intermittent masting events which utilize nutrients stored during previous summers and favourable growing conditions. With up to 5 years between flowering and only slow vegetative reproduction in some species of tussock, it is unlikely that rapid expansion of these native tussock grasslands has occurred post-human arrival in New Zealand. In contrast to the belief that tussocks are able to rapidly colonize a disturbed site, Gradwell (1960) notes that in the absence of a microclimate provided by the mature tussock canopy, seedlings are rare and suffer losses due to freezing of the soil surface. It also was illustrated by Prebble et al. (2002) that tussock is widespread in Otago at undisturbed sites. Their study collected surface phytolith samples at 28 east-Otago locations, with *Chionochloa* phytoliths accounting for up to 80% of the phytolith sum in many samples, indicating the long-term establishment of *Chionochloa* grasses at many of these sites (Prebble et al., 2002).

The Late-Holocene spread of tussocks into the lowlands is also inconsistent with the relatively high frequency of fire in some inland South island basins during the Holocene (Burrows, 1996; Clark et al., 1996; McGlone, 2001; McGlone and Wilmshurst, 1999a) and casts doubt on the inferred non-adaptation of New Zealand flora to fire. The evidence presented here from two Otago sites is that low-elevation high tussock grasslands have persisted throughout the Holocene.

Cranwell and von Post (1936) concluded the distribution and type of tussock grasslands at South Island sites are temperature and moisture dependent, describing the prevalence of the short-tussock *Festuca novae-zealandiae* in the more arid areas of the central South Island below the treeline and into the valley floors. Above the treeline they described a transition to a tall-tussock grassland zone, dominated by *Danthonia raoulii* interspersed with subalpine scrub species (Cranwell and von Post, 1936). Much of the distribution of tall-tussock in the South Island has been attributed to its greater affinity for wetter sites, while acknowledging that other factors are responsible for the spread of tall-tussock into moist lowlands where soil moisture is

not limiting and forest should naturally prevail. At the time of this early work of Cranwell and von Post (1936), *Chionochloa* tussocks were included in the *Danthonia* genus but they have since been recognized as a genus in their own right (Mark, 1969).

The dominance of *Chionochloa* among native grasses currently found at the core sites can be explained from observations of earlier work (Cranwell and von Post, 1936; Mark, 1969). Both sites are below the natural treeline, and receive significant precipitation, despite their easterly location. Climate data from the last 60 years at Whare Flat near the Swampy Summit core site and Lee Flat near the Clarks Junction core site confirms this, with mean annual precipitation approximately 1000mm in the vicinity of Swampy Summit and 700mm in the vicinity of Clarks Junction (NIWA CliFlo Database, 2007). The mean annual precipitation of these sites therefore is not limiting the growth of woody vegetation, but the poorly draining nature of these peat bogs have provided the ideal conditions for tussock grasses to prevail. Mark (1969) noted that *Chionochloa rubra* in particular dominates mid-altitude areas where drainage is poor, which would explain the dominance of this species at both these core sites. The presence of *Chionochloid* phytoliths throughout the Clarks Junction peat core and after approximately 6000 yr B.P in the Swampy Summit core suggests that both these sites have provided a vestige for tussock grasslands during the Holocene, and perhaps the presence of *Chionochloa* species at Clarks Junction before 6000 yr B.P was partly due to the frost tolerant nature of *Chionochloa* grasses at this frost-prone inland site.

It is likely that a variety of no-modern analogue vegetation communities existed during both glacial and interglacial times, while the reproductive strategies of many New Zealand taxa lend themselves to a multimodal response to environmental forcing, most notably through vegetative reproduction. I postulate that the R-factors used in New Zealand pollen analyses over-represent the local forest taxa signal during interglacial times, but instead give a more accurate regional representation of forest cover and structure.

The implications of these observations are important to conservation management regimes in New Zealand and to the understanding of the resilience of New Zealand flora to climate change.

Conclusions

The pollen records presented from both sites in this study are taxonomically diverse, and in general have shown a similar record of Holocene vegetation to previous work from the sites (Figure 15 & Figure 16). Key changes in vegetation abundance have been identified at Swampy Summit and Clarks Junction and have been dated from comparisons with synchronous events in previous pollen diagrams from these sites (McGlone, unpublished data, 1972; McIntyre and McKellar, 1970).

The core from Swampy Summit spans from the Late-Glacial to present, and the pollen record identified an early-Holocene grassland-shrubland with *Coprosma* dominating the assemblage. The arrival of key forest taxa dominated by *Podocarpus/Prymnoptis* began about 11,000 yr B.P and the record matches findings from other East Otago sites. A regional expansion of Rimu occurred in East-Otago approximately 6,000 yr B.P marked by the arrival of Rimu pollen which steadily increases in the pollen record throughout the mid-to-late-Holocene period. The expansion of Rimu coincides with a decline in Kahikatea and *Halocarpus bidwillii* in the pollen record, beginning shortly after 6,000 yr B.P. which are suggestive of a drying local climate. Prior to this, *Restionaceae* was abundant at the site, indicating the presence of a high water table in the bog during this time.

Grass pollen is mostly absent in the Swampy Summit record and occurs only sporadically, reaching a maximum abundance of <5% after 6ka. This contrasts with the phytolith record which indicates grasses persisted at Swampy Summit throughout the Holocene, reaching maximum abundance (~60%) for a short period after 6,000 yr B.P before stabilizing at approximately 10-20% of the phytolith total. Tree and shrub phytolith forms dominate the record at Swampy Summit except for the period of maximum abundance of grass phytoliths. A more recent peak in grass phytoliths occurs in the top 30cm of the core, most likely indicating the arrival of people in New Zealand and subsequent increased disturbance favouring grassland. *Chionochloa* grasses appear briefly around 6000 yr B.P before disappearing from the record and reappearing after 3,000 yr B.P. reaching maximum abundance at the top of the core in the period coinciding with human disturbance.

Overall, the pollen record from Swampy Summit produced a high resolution record of vegetation throughout the Holocene, although interpretation is complicated due to pollen dispersal and deposition factors. A large part of the forest pollen represented is explained by long distance transport to the site from elsewhere in the region as reflected by lowland types such as Rimu, which would not grow to this elevation. Likewise the proportion of forest species at the site is equally hard to distinguish from the phytolith record of woody vegetation, with shrubs potentially accounting for the high proportions of polyhedral tree and shrub phytoliths in the record.

The Clarks Junction record of vegetation is equally comprehensive, spanning the period 12,000 yr B.P to the present. Pollen from Clarks Junction indicates a grassland-shrubland existed in the early Holocene, with *Poaceae* dominating the assemblage until approximately 9,000 yr B.P.

The main arrival of forest taxa from the pollen record at Clarks Junction occurred about 1.5ka after the arrival of dominant forest taxa in the pollen record at Swampy Summit. There is an initial trace of *Podocarpus/Prymnopterys* pollen around 1,000 years earlier than the main expansion at 9,500 yr B.P which coincides with the deposition of a blue-grey clay layer in the peat bog. A core taken from Campbell Creek in Central Otago by McGlone et al. (1997) attributes a similar blue-grey mineral silt layer to a period of shallow ponding and inwash of silt from within the catchment. This suggests the earliest *Podocarpus/Prymnopterys* pollen signal at Clarks Junction is very likely sourced from elsewhere in the region, as the deposition of a silt layer at this time is probably due to erosion of mineral material from upslope of the peat bog in areas that lacked the stabilizing influence of forest.

Coprosma is present in moderate amounts throughout the core peaking about 9,000 yr B.P. but remaining common until the surface where it drops from the record-providing further evidence for human disturbance as *Coprosma* has persisted in the pollen record throughout the Holocene, therefore its disappearance near the surface is most likely due to recent anthropogenic disturbance and not related to natural disturbance which should have had a similar effect on the pollen record during disturbance events prior to human arrival.

Podocarpus/Prymnopterys pollen does not become common until 8,600 yr B.P. which also marks the arrival of *Phyllocladus*. In contrast to the coastal site at Swampy Summit, Rimu makes up only a small proportion (<5%) of the assemblage at Clarks Junction as a result of the drier inland conditions. The arrival of Rimu is also delayed in the Clarks Junction pollen record, becoming apparent about 8,600 yr B.P. in contrast to Swampy Summit where it was evident from 6,000 yr B.P.

Notable at Clarks Junction is the long-term presence of monolete and trilete fern spores in the record. Ferns remain at stable levels throughout the record until the most recent period of human disturbance when both types increase dramatically. At the surface of the core trilete fern spores (most likely bracken) reach proportions second only to grass. This expansion is also linked to human disturbance but was ultimately short-lived as there are currently no ferns in the vicinity of the site, although the recovery of ferns is possible in the future. This fern expansion is attributed to anthropogenic burning, which also explains the increase in grass pollen at this time. Subsequent burning has removed ferns from the site but fire tolerant *Chionochloa* tussocks remain. Increased drainage of the adjacent farmland via ditches was also a likely factor in the decline of ferns at the site, leading to a drying of the peat surface more suited to *Chionochloa* grasses.

A surprising feature of the Clarks Junction pollen record is the importance of grassland pollen types such as *Poaceae* and *Asteraceae*. Grass pollen is persistent in the pollen record throughout the Holocene, consistently at levels >10% of the assemblage and more recently reaching levels in the surface of the core similar to those of the early-Holocene maximum. This is in stark contrast to Swampy Summit where grass pollen was sparse. *Asteraceae* is similarly persistent throughout the Holocene at Clarks Junction, which supports the long-term presence of grassland at this site.

The record of grasses from phytoliths at Clarks Junction mirror the pollen record, illustrating an early Holocene grass maximum, followed by a sustained presence of 10-20% throughout the core before a late-Holocene peak in the period of human occupation of New Zealand. Chionochloid grasses are also present at the site throughout the Holocene, which is likely a contributing factor to the increased

representation of grasses in the pollen record of this site. Interestingly there is a pattern of alternating increases and decreases in the *Chionochloa* phytoliths at this site, with phytolith abundance dropping to a minimum for this genus near the surface of the core.

Chionochloid grasses reach their maximum abundance shortly after peat accumulation begins at the site following the deposition of a clay layer around 9,700 yr B.P. This peak in *Chionochloa* tussock coincides with a decline in tree and shrub phytoliths to their Holocene minimum. After this minimum, tree and shrub phytoliths rapidly increase to dominate the phytolith record of vegetation at Clarks Junction; however there are minor decreases in the tree and shrub phytolith sum which mirror later peaks in Chionochloid grass phytoliths.

Overall the pollen record is less species-diverse at Clarks Junction than Swampy Summit. A key feature at Clarks Junction is the identification of the zone near the surface most likely marking the recent period of human disturbance after about ~700 yr (Figure 16). Both sites demonstrate an early Holocene grassland maximum, followed by a marked increase in pollen signifying the regional arrival of key forest taxa. Rimu arrives later than *Podocarpus* species at both sites, and is less abundant in the pollen record inland at Clarks Junction than it is at the coastal site of Swampy Summit where precipitation is higher.

Although phytoliths provide a lower resolution record of vegetation types at the site in terms of taxa identified, they illustrate a more local assemblage due to their limited dispersal. They are invaluable for determining the presence of Chionochloid grasses due to the intermittent pollen production of *Chionochloa*, the localised nature of phytoliths in contrast to the pollen rain and the morphologically distinct nature of Chionochloid phytolith forms which makes them easy to identify.

Recommendations for future work

Future work to improve the catalogue of phytolith forms from New Zealand's native plants would aid reconstructions of vegetation immensely. Increasing the knowledge

of phytolith production and morphology is necessary in order to improve the vegetation community resolution of phytolith records like the ones presented here. Extracting phytoliths from peat is also a relatively uncommon practice as peat bogs like these core sites are known for their pollen preserving qualities and hence have been used to produce pollen records of vegetation, rarely in combination with phytoliths. This study has shown the merit of phytolith analysis of acidic peats and future vegetation reconstructions could gain more detail by examining phytoliths and other siliceous fossils in conjunction with pollen. The multi-proxy approach in this study has provided valuable comparisons between the records and helped to identify local components of the pollen rain in relation to regional components.

The effect of high acidity on phytoliths has been little investigated, but is almost certainly deleterious, and it would be useful to investigate the preservation of phytoliths and potential for their degradation in simulated peat bog environments using lab experiments of a similar pH. Until there is a more species specific understanding of phytolith forms for New Zealand's native plants it is unknown whether any taxa are excluded from the phytolith record due to producing fragile or easily degraded phytoliths.

Further apparent from this research was the remarkable differences occurring between pollen deposition recorded by different types of moss polsters. All polsters obtained for this research were taken from a very small localised area, yet there were significant differences in proportions of taxa represented in the assemblage between polster types. Further research into the cause of this variability would potentially improve knowledge of local-scale pollen transport and deposition while demonstrating the suitability of using selected mosses for studies of modern pollen rain. Pinpointing the cause(s) of this variability would also increase the confidence of palynologists in modern pollen rain studies with respect to the interpretation of historical pollen records.

Summary

In summary, Swampy Summit and Clarks Junction demonstrate that grassland in general and tussock in particular, arrived at these sites many thousands of years before anthropogenic burning or clearance opened these sites up. This research provides strong support for the hypothesis of long-term survival of tussock and other grasslands below the natural treeline in New Zealand. It is interesting that tussock does not appear at Swampy Summit until about 6000 years ago; while at Clarks Junction there have been *Chionochloa* present at the site for at least 10,000 years. It suggests that tussock colonisation and extirpation is a dynamic process through the Holocene. Clearly these east coast montane sites are the most likely places for tussock grassland to persist, while more sites are needed to demonstrate that a mosaic of grasslands existed below the natural treeline throughout New Zealand during the Holocene. This study of Holocene vegetation at Swampy Summit and Clarks Junction indicates that the idea of tussock naturally occurring below the treeline must be considered, and this may be important for future tussock-grassland management and vegetation restoration strategies.

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12. Appendices

-See CD inside back cover of thesis.

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