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# Palynological Evidence of Vegetation Dynamics in Relatively Undisturbed and Disturbed Sites in New Zealand

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A thesis presented in partial fulfilment of the requirements for the degree of
Doctor of Philosophy at Massey University
Palmerston North, New Zealand

2004

# Abstract

New Zealand forest has been affected by both natural and anthropogenic disturbances. Protecting and restoring indigenous forest is one of the focal issues in conservation of New Zealand, and understanding vegetation dynamics is a key part of management strategies. The longevity of most of New Zealand trees impedes short-term vegetation dynamic studies. Instead fossil pollen records provide one of the most valuable sources of long term data to trace vegetation development. In this study, pollen records are used as proxies of vegetation population to test the roles of long-term climate change and transient environmental disturbances in vegetation dynamics. Two sediment cores, from Sponge Swamp, Haast, and Tiniroto Lakes, Gisborne, were collected as representatives of undisturbed and disturbed sites, the former being used as a reference site to separate out the effects of climate and evaluate the impact of disturbance on the vegetation.

Pollen data were inspected using Tilia, and zones defined. Principal component analysis (PCA) was performed on pollen data to summarise the change in species composition over time, and the sample scores of the first PCA axis were exploited as an index of vegetation dynamics for further comparison. Redundancy analysis (RDA) is also applied to help interpretation of the vegetation change with respect to environmental factors.

The result of this study indicates that the vegetation development in both sites is characterized by non-equilibrium dynamics, in which vegetation composition is changing continually through time. In Sponge Swamp, this change is steady and consistent over the whole time span, with a consistent decline of *Ascarina lucida* and a progressive increase of cold tolerant or moisture-stressed taxa, like *Gleichenia* and *Lycopodium australianum*. Subsequently there is a partial replacement of swamp forest taxa such as *Dacrycarps dacrydioides* and tree ferns by *Prumnopitys taxifolia*, and further expansion of *Nothofagus* and *Phyllocladus* is distinguished. A climate gradient, from mild and wet to cooler and/or drier is suggested from the pollen evidence, and appears the driving force for the vegetation dynamics at that undisturbed site. At Tiniroto, however, the vegetation development is divided into two stages. Before c. 2300 yr BP, the vegetation change is steady and consistent which is comparable to that from Sponge Swamp. A forest invasion, a process of gradually replacing open land and light-adapted taxa, such as *Dodonaea viscosa, Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the family Fabaceae and Asteraceae, by increasing proportions of forest taxa, characterise this change. Climate amelioration with increased rainfall is responsible. After c. 2300 yr BP, this trend was frequently punctuated by disturbances, in which sudden changes of vegetation occur, generating substantial fluctuations about the trend.

From RDA, sample age explains more than 20% of the variance of species data at both sites. The long-term directional climate change derived from pollen evidence of Sponge Swamp and at least partly at the Tiniroto site, may be represented by the explanatory variable age. At Tiniroto, additional variance is also explained by the explanatory variables charcoal and pollen taxonomic richness, suggesting the impact of disturbance on vegetation dynamics. The impact of disturbance on vegetation dynamics becomes clearer after the climate gradient is removed. Autocorrelation analysis on detrended sample scores of the first PCA axis suggests further differences between the two sites, in response to local disturbances. There is little dependence of the present state of vegetation composition on its past state in the Sponge Swamp site; instead, the vegetation composition is affected by various "random" events, implying small disturbances such as floods, or landslides caused by earthquakes etc. At Tiniroto, the change of vegetation composition is more "successional", and the present state of vegetation depends only on the immediate past state, due to the impact of catastrophic disturbance.

Despite the Tiniroto site having been subjected to a long history of disturbance, the climate gradient, which is distinct at the earlier stage, becomes less identifiable and partially masked by outbreaks of disturbances only since c. 2300 yr BP. This implies that the relative role of disturbance on vegetation dynamics with respect to climate is depended on different types or different levels of disturbances and different responses by the vegetation.

Short-term vegetation responses to different types of disturbance were examined by fine resolution pollen analyses around five disturbance episodes, including the Taupo (1850±10 yr BP), Waimihia (3280±20 yr BP), Whakatane (4830±20 yr BP) eruptions, and two charcoal peaks (c. 1100 yr BP and c. 2300 yr BP). Almost no vegetation change occurred relative to the eruption within the Whakatane and Waimihia episodes, except that a temporary rise of shrubs and ferns corresponded with intermittent occurrence of charcoal particles. Substantial vegetation change relative to disturbance was found within both the Taupo episode and the fire episode around c. 2300 yr BP, in which establishment of ensuing semi-open vegetation was encouraged for decades. The fire c. 2300 yr BP transformed part of the forest into fernland, while the Taupo eruption turned part of the shrubs and tree ferns into bracken field. Although it is difficult to judge the effect of the fire around 1100 yr BP as the result was unreliable due to contamination, the vegetation at Tiniroto is suggested to be more vulnerable to fire than tephra.

Non-equilibrium dynamics are common in New Zealand forests, even at stable sites such as Sponge Swamp, due to climate change. Locally these non-equilibrium dynamics appear highly responsive to disturbances, esp. at Tiniroto. Even disturbances at Tiniroto are dynamic and a change of disturbance regime is suggested around the later disturbance episodes. This change is possibly due to climate increasing the fire frequency, but an alternative explanation is the presence of humans earlier than currently accepted. Forests and forest ecological studies in New Zealand are very dynamic, and forest management needs to improve to incorporate these dynamics.

# ACKNOWLEDGEMENTS

First of all, I would like to express my sincere gratitude to those esteemed people who do science with pure, unselfish and honest passion, as they are the people who made me grow and appreciate the world in the way I see it.

I would like to give my sincere gratitude to my chief supervisor, Prof. John Flenley, for his expert supervision, constant source of encouragement, and considerable caring throughout this study. It was a great pleasure to me to conduct this thesis under his supervision, as he made the process of study full of a motivating, enthusiastic and caring atmosphere.

I would also like to acknowledge with much appreciation the help from my co-supervisor, Prof. Robert McLachlan, for showing me the wonderful world of mathematical models. I especially appreciated his sagacious thinking in exploring problems and valuable suggestions to the work.

I am deeply indebted to my co-supervisor Dr. Jill Rapson whose inspiring advices, stimulating suggestions, critical comments and ever-ready helping were the constant motivating factors pushing me to complete this thesis, without which this work could not have materialized in the present form. I should say that every word in my thesis was built by Jill's effort.

I would like to make special thanks to David Feek for his crucial role in the field trip. His talent promised all the beautiful coring which made this study possible.

I would also thank Michael Shepherd for the valuable suggestions on choosing the core site, and Geoff Jones for discussion on time series analysis.

For those who created a friendly working environment in the pollen laboratory, I am specially obliged to Kevin Butler, Bernd Striewski, Dynpa Crase for generous help and valuable hints in discussion; to Leighanne Empson for her assistance in the lab and Tim O'Dea for his assistance on my computer whenever I got trouble.

Many thanks to Olive Harris, Karen Puklowski and Elaine Bristol for their support and ensuring everything ran perfectly in the department. My thanks also extended to Tarnia Hodges for sharing the office and benefit of talking; Rosemary van Essen for typing; and Dean Richards for all his assistance on solving computer problems.

I gratefuly acknowledge the financial support from Massey doctoral scholarship, School of People, Environment and Planning; MURF for providing fund for AMS dating; and the New Zealand Ecological Society and Ecology Group, Institute of Natural Resources for kindly offering conference expenses.

My acknowledgement goes to the Geography Programme, School of People, Environment & Planning, Massey University who provided the equipment and facilities to allow me to carry out the research for this thesis. I would like to make special mention about the Department of Conservation for permission to core Sponge Swamp; and Syd Kent for his kindly acquiescence for access to coring at Tiniroto.

I give my specially thanks to my parents in-law, Tieji Wang, Kangjian Chen and sister Fanghua for their support and understanding all the time. Thanks to all my close friends, especially Bin and Ling for listening and sharing the experiences. I appreciate their friendship which always a great part of my life.

Most of all, I would like to give my deepest gratitude to my parents, Xianwan Zhang and Zhongming Li, who have been consistently standing behind me, giving me their dedicated support and never asking for any return. They are my source of strength and example for my life. I love you.

Finally, I would like to give my most devoted thanks to my husband, Huoguang, for his patient love, his dedicated effort to our family, which enable me to complete this study. Thank you for being my companion, for sharing both my pleasure and depression, for bring me the joy of life. I would also like to give my special thanks to my dear daughter, Lucy, for excusing my absence always, for her incredible understanding at her age, and for all the beautiful dream she brought to me.

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# Chapter One

# General Introduction

## 1.1 Equilibrium and Non-equilibrium Vegetation Dynamics

Understanding vegetation dynamics is a key part of theoretical ecology and offers evidence for resource management. Forestry practices, for example, from clearcutting to selective logging, represent an attempt to manage or imitate natural vegetation dynamic processes. Simplistic ideas about ecological change can result in ineffective management practices and environmental policies.

This issue is a recurring dilemma in conservation management. Until the middle of last century, it was assumed that the forests would replace themselves in an orderly, immutable sequence once clear-cut. However, the actual responses of the forests to clearcutting are much more open-ended and unpredictable. Moreover, past land management techniques, when applied to contemporary communities, no longer render the same effects as before. This dilemma has led researchers to suggest that attempting to preserve current stand structure may not be appropriate or practical (Sykes & van der Maarel, 1992; Motzin et al., 1993). This problem is probably due to a change in composition and structure of vegetation over time. Thus discerning the relationships of nonequilibrium dynamics in vegetation is crucial to understanding the strategy of conservation management, and the vegetation history may thus serve as a useful analogue for current change (Carcaillet et al., 2001).

Equilibrium has been considered as the classic and fundamental theory for community dynamics during the last few centuries (DeAngelis & Waterhouse, 1987). A biological community is at equilibrium when the abundances for all species at each spatial location remain constant over time, though there is variation in space in the densities of species in the community (Chesson & Case, 1986). All the allogenic factors, like historical effects and environment perturbations play a small role in an equilibrium ecosystem; e.g. all the species return to their equilibrium abundance following such perturbations.

A shift away from equilibrium to non-equilibrium thinking has occurred since the mid-1970's (Ritchie, 1995), which recognizes that communities are seldom at equilibrium and they are constantly subject to environmental disturbances. The non-equilibrium situation also indicates a lack of autogenic forces to stabilize ecosystems in terms of weak competition, density-independence and abiotic limitation rather than resource limitation.

Recent research in community ecology has recognized the prevalence of non-equilibrium conditions in vegetation (DeAngelis & Waterhouse 1987; Reice, 1994). Besides stochastic effects from the environment, which could result in non-equilibrium, mathematical models revealed the potential biotic feedback instability inherent in complex natural systems (May & Oster, 1976; Gilpin, 1979).

## 1.2 Importance of Palynology in Studying Vegetation Dynamics

Most of the theories attempting to explain changes in community composition over time are empirical, and based on short time studies, simulation modelling, or chronosequences (Franklin & Tolonen, 2000). However, the dynamics of vegetation are long-term processes and the data currently available from permanent plots are not enough to understand vegetation dynamics. Vegetation should be monitored for at least the length of time taken for one complete turnover of individuals of all species in the community, which could be more than several centuries, to demonstrate the vegetation dynamics (Connell & Sousa, 1983). In short-term observations, transient cyclical or extreme weather phenomena can temporarily mask other underlying long-term trends in vegetation, or they may drive short-term responses, which misleadingly suggest directional changes where there are no long-term trends (Walker & Wilson, 2002).

Pollen data, though limited by the uncertainties about source area, limited taxonomic precision and poor chronological control in many sediments (Birks & Birks, 1980), have been successfully used to examine the vegetation history. With the development of either theoretical models of pollen dispersal (Prentice, 1985, 1988) or of the relationships between pollen and vegetation (Andersen, 1973; Bradshaw, 1981, Prentice, et al., 1987), the understanding of the origin of fossil pollen has been improved, and allowed the better interpretation of pollen data. Pollen records thus provide one of the most valuable sources of long-term data for a more complete understanding of vegetation dynamics, and have been shown to be better indicators of vegetation dynamics over longer periods than chronosequence studies (Jackson et al., 1988).

Investigation of long-term vegetation dynamics by pollen analysis rapidly increased during the 1960's, and promoted interests in the links between palaeobotany and ecology (West, 1964; Huntley, 1996). Although most pollen records have been successfully used to examine the vegetation history, the very limited extent to which they can be translated into floristically and structurally comparable plant communities is one of the major challenges of palaeoecology (Ritchie, 1995). Nevertheless, promising applications to studies of plant invasion, immigration and competition were indicated by Bennett (1990) and MacDonald (1993).

The existence of non-equilibrium dynamics, which at $10^3$ yr timescales were controlled by climate change, has been validated by numerous pollen studies (Davis, 1986; Webb, 1988; Prentice et al., 1991; Ritchie 1995). As suggested by Davis (1986), no matter what time scale is considered, climatic parameters change in a directional way through time, varying about a trajectory of values rather than around a constant mean. The directional changes of climate have profound effects on the structure of biological communities, in which plant communities may frequently be in non-equilibrium situations. Due to the time lags involved in the response of forest communities to climate change (many decades at the community level), climatic changes that persist for decades will not change most forest communities, and century-long directional temperature trends will not result in noticeable changes among canopy trees until more than a century after the event. However, dynamics at shorter scales, 10 or $10^2$ yr, may be system dependent and controlled by their local disturbance regimes (Clark, 1996). The importance of disturbance risk to a plant depends on age, its survivorship to that age, risk of mortality to that age class from the disturbance, and seed production at that age. Thus the impact of disturbance with changing regimes on vegetation dynamics at shorter scales is validated via timescales that describe plants' life histories.

## 1.3 Discriminating Equilibrium and Non-Equilibrium Dynamics from Pollen Data

To distinguish between equilibrium and non-equilibrium dynamics, directional change in vegetation composition is the most important criterion. If a forest is at an equilibrium state, the abundances for all species at one location remain basically constant, so that the vegetation composition tends to fluctuate around some average state, which is relatively invariant over time (Silvertown, 1987). Since the community structure is determined by biotic interactions, when subject to perturbations, all the species will rapidly return to their previous equilibrium abundances, a stable and self-sustaining state of "climax", along a well-defined successional pathway (Chesson & Case, 1986; Sprugel, 1991; Walker & Wilson, 2002).

On the other hand, non-equilibrium behaviour is characterised by unstable, transient behaviours as the system moves from one state to another. In the non-equilibrium view of community organization, community structure is determined by the interactions of environmental heterogeneity, disturbance and recruitment (Reice, 1994). Community composition is always changing and never in balance (Cole, 1996), and the past vegetation behaviour cannot be used to predict vegetation in the future. These principles are known as the essence of non-equilibrium dynamics (Franklin & Tolonen, 2000).

Generally, non-equilibrium dynamics could be detected in the mathematical sense by equations, which simulate the processes of the natural ecosystem (DeAngelis & Waterhouse, 1987; Cole, 1996). However, the natural system appears too complex, and it will never be possible for ecologists to write down the complete governing equations for any particular system (Schaffer, 1985; Bennet, 1993). Another approach in the geometrical sense is to probe the trajectory of an ecosystem in some open m-dimensional Euclidean space (assuming m taxa in an ecosystem), which has been summarised in 2 or 3 dimensional space by PCA or some other ordination technique (Anand, 2000; Franklin & Tolonen, 2000). Directional change in vegetation composition could be detected by the trajectory of sample sites projected on this space.

## 1.4 Characteristics of Vegetation Dynamics in New Zealand

New Zealand forests are frequently affected by disturbances characterised by either small-scale gap formation, such as windstorms (Foster & Boose, 1995; Turner et al., 1997), soil erosion and deposition (Roche, 1997), floods (Duncan, 1993), or large-scale disturbances including earthquakes (Wells et al., 2001), catastrophic fires (Johnson, 2001; Ogden, 1998) and volcanic eruptions (Clarkson, 1990; Wilmshurst & McGlone, 1996). Although most disturbances are infrequent and with brief occurrence, they have effects on plant communities which are out of proportion to their short duration. As a result, understanding the role of disturbance on the plant community is essential to understand vegetation dynamics. However, the relative influence of disturbance and climatic factors on forest development in New Zealand has not been very clear yet.

One of the major problems of native lowland forest of New Zealand is the apparently inadequate regeneration of most canopy trees, such as *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Podocarpus totara, Libocedrus bidwillii* and *Agathis australis* (Cockayne, 1928; Holloway, 1954; Wardle, 1963; June, 1982). The early research tended to attribute this phenomenon to a succession process from a seral stage towards a climax of broadleaved trees (Cockayne, 1928; Robbins, 1962), or the increasing aridity and decreasing temperature within the last millennium (Holloway, 1948; Mckelvey, 1963; Grant, 1963; Wardle, 1963, 1978). Only recently has it been realized that disturbance might be responsible for these forest structures, since successful conifer regeneration is largely dependent on the extensive disturbed surfaces formed by large disturbances (Morton, et al., 1984; Wells, 2001). Due to the great longevity of many trees in New Zealand forests, many of the present forest structures are probably a consequence of the impact of previous, large disturbances

(Foster et al., 1998), and the direct evidence of their impact has been obscured by forest regrowth (Wells, 2001). Nevertheless, it is impossible to deny the effect of climate change on vegetation development, and in fact climate and disturbance are compounded together, with either one being the overriding issue at any specific time. In order to clarify the role of both climate and disturbance in vegetation development, it is necessary to understand vegetation dynamics in a historical view.

## 1.5 Aim and Outline of This Study

Since the vegetation history reconstructed from pollen records and the associated independent sediments provides evidence of both climate change and outbreaks of disturbance, it also gives an opportunity to trace the vegetation development by means of vegetation composition change. The aim of this study is to use pollen records as proxies of vegetation populations to understand the long-term vegetation dynamics under the impacts of disturbance and climate change. In order to test the role of climate and disturbance in vegetation dynamics, an accepted "undisturbed site" is used as a reference site or baseline for a more disturbed one, so that effects of climate can be separated out, and the impact of disturbance can thus be evaluated.

In this study, for a relatively stable reference point, the Sponge Swamp site in south Westland was selected for two reasons. Geographically, it is within a continuously forested area both in space and in time, which is one of the rare relicts free from anthropogenic burning, due to its special locality, high rainfall in excess of 3,500 mm and mild year-round temperatures (Ogden, 1998). Historically, as mentioned by McGlone (1988) and Vandergoes (2000), podocarp/hardwood forest started to be present in Westland from the beginning of the Holocene, and such forests have survived, apparently little changed, to the present day. Although this site is in an area susceptible to earthquake-induced disturbances, e.g. landslides, because the Alpine Fault Zone runs through to the south, the very luxuriant vegetation cover resulting from the optimal climate appears to play a significant role in maintaining slope stability, even on steep valley sides (Soons, 1991). Also, this kind of disturbance tends to be patchy, with the affected area usually rapidly recolonised.

In contrast, another site, selected as the disturbed one, was from the Tiniroto district, Gisborne, which is currently a predominantly adventive pasture. In addition to recent human clearing, forest around Tiniroto was subjected to at least three major volcanic eruptions in pre-human times (Kohn et al., 1980). Thus the forests of these two sites can respectively be considered to be characterised by stable and unstable features, and therefore can be expected to be dominated by equilibrium and non-equilibrium dynamics.

The general structure of this thesis is outlined as follows: palynological results from both sites and comparison with other palynological studies of New Zealand are presented, and overall patterns of vegetation change of both sites are indicated separately in Chapters 2 and 3. In Chapter 4, vegetation dynamics of both sites are summarized from principal component analysis and time series analysis, and possible environmental gradients associated with vegetation development were explored by redundancy analysis. From comparison of both sites, the role of climate change and disturbance in vegetation dynamics are discussed. Detailed short-term vegetation response to different types of disturbances are analysed and compared, in order to further evaluate the impact of disturbance on vegetation in Chapter 5. The thesis concludes with a general integration of these issues in the content of vegetation dynamics in Chapter 6.

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# Chapter Two

## Pollen Evidence of Vegetation Changes since 7600 yr BP from Sponge Swamp, Haast, New Zealand

### Abstract

Westland is one of the largest areas to be continuously forested since the start of the Holocene in New Zealand. The high rainfall and relatively mild year-round temperatures result in luxuriant vegetation cover which makes Westland a much more continuous forest cover than elsewhere in New Zealand. In spite of the frequency of tectonic activity in this area, the strong resilience of the present vegetation to tectonically induced disturbances may allow vegetation change over time to be interpreted as a response to climate change. In order to trace any climate change during the Holocene, a pollen diagram with good age control was derived from Sponge Swamp in South Westland.

Pollen evidence records the changing pattern of vegetation through much of the Holocene since c.7600 yr BP. The lowland forest is dominated by *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Podocarpus* spp., *Prumnopitys taxifolia*, *Dacrycarpus dacrydioides, Nothofagus menziesii* and *Weinmannia*. There is no substantial change in vegetation composition of the lowland forest over the duration of the core. However, regional climate change and local environment conditions could be derived from interpretation of the responses of individual taxa. The climate before c. 7200 yr BP is cool but wet, and a high water level is indicated by the extent of mire and aquatic taxa. From c.7200 yr BP, the climate became warmer with diminishing of shrubland and invasion of forest. Increasing peat humification at this time corresponds to a drier mire surface which might suggest a slight drop in precipitation. A harsh climate condition is suggested by the drop of *Ascarina lucida* from c. 6800 yr BP (though other explanations are possible), and expansion of cold tolerant or moisture

stressed taxa, e.g. *Plantago, Gleichenia, Lycopodium australianum* and Ericaceae occurred soon after. Decreasing temperature is more likely to be responsible for these changes. From c. 3700 yr BP, water level dropped and the exposed damp surface was occupied by dense stands of *Leptospermum* and restiads. A slow replacement of swamp forest taxa *Dacrycarpus dacrydioides* and tree ferns by less flood tolerant *Prumnopitys taxifolia* occurred at the fringe of the mire. *Nothofagus menziesii* trees increased, probably by expansion into the former lowland or higher altitude vegetation around c. 1200 yr BP which might indicate a cooler and drier episode, or might be a consequence of edaphic change in terms of soil leaching and deterioration.

Though this area is relatively free from human disturbances, the slight decrease of several tree taxa probably reflects some sort of forest destruction occurring elsewhere. Most of the charcoal fragments scattered throughout the profile, do not coincide with the pollen evidence, so were probably blown in from Australia.

Although this site is located in the stable area and there is no obvious change with the forest composition, small variations of environmental index such as temperature, water level, and precipitation could be traced from changes in levels of individual taxa. These phenomena probably equate to oscillations in the mire/forest margin, as a subtle indicator of the vegetation's response to climate change.

## 2.1 Introduction

Pollen analytical studies of the Holocene in New Zealand have established a broad regional framework of terrestrial changes and wetland development (McGlone, 1988). By 9500 yr BP, nearly all the lowland was reforested following the climate amelioration, and the early Holocene climate is characterised by a generally mild, drought-free, weakly seasonal climate.

In the later Holocene (from 7500 yr BP), however, patterns of change for vegetation and climate on a New Zealand-wide scale are less clear because of the few data available. A known defined character for the later Holocene is the spread of *Nothofagus* forest, though there is no precise country-wide synchrony. Edaphic changes were probably part of the driving force behind these changes; however, their more abrupt nature and relative synchronicity suggests climate change, reflecting shifts to cooler climate.

Though lots of pollen analyses have been done in the South Island, most of the evidence so far obtained was from relatively drier regions and thus sensitive to precipitation, such as Marlborough (McGlone & Basher, 1995), Nelson (McLea, 1996), Canterbury (Burrows et al., 1990, 1993) Southland (McGlone & Bathgate, 1983; Vandergoes et al., 1997) and Otago (McGlone et al., 1995, 1997; McGlone & Moar, 1998; McGlone & Wilmshurst, 1999). Most of these sites are relatively vulnerable to fire and were seriously damaged by human activities. Unlike these sites, Westland, characterised by a mild and perhumid climate which is very favourable to forest plants and least vulnerable to fire, is one of the largest areas in New Zealand continuously forested since 11700 yr BP (Ogden et al., 1998). Westland is regarded as being very stable during the whole Holocene, as depicted by very few and brief records from its north and central parts (Harris, 1968; Moar & Suggate, 1973; Pocknall, 1980). However, only a few sites have been studied from Westland, and the work done mostly focused on either interglacial or early postglacial vegetation change (Moar & Suggate, 1973, 1996; Moar & McKellar, 2001).

Due to the high rainfall and relatively mild year-round temperatures, the vigorous vegetative growth in this area makes South Westland an ideal area to study vegetative change. Compared to most other places in New Zealand, this area is relatively free from anthropogenic disturbances. The effects of disturbances induced by tectonic movements due to the proximity of the Alpine Fault Zone, are likely to be limited to steeper slopes and adjacent lowlands, generating vegetation mosaics of different ages in the podocarp forest of Central and South Westland (Soons, 1991). As a result, any regional vegetation change during the Holocene is likely to be more indicative of climate change. However, this information is sketchy from previous work due to the small sample size and poor age control. More detailed information of vegetation or climate change through the Holocene is desirable from Westland because a more complete vegetation history is likely to be achieved here, and a regional pattern of climate change could be obtained from comparison with sites from other parts of New Zealand.

South Westland is characterized by the occurrence of openings in otherwise tall lowland forests on poorly drained sites, known as pakihi, which are peat-accumulating and provide suitable pollen sites. Moreover, most of the large pakihi contain buried timbers (Rigg, 1962), which might suggest shifts between forests and pakihi resulting from either change of climate or edaphic conditions. Conflicting suggestions have been made as to whether the forest-wetland boundary is static or not in Westland (Wardle et al., 1973; Mark & Smith, 1975; Mew, 1983; Norton, 1989; OUSSA, 1989; Williams et al., 1990; Agnew et al., 1993; Dickinson & Mark, 1994). Although it is hard to find any major change of forest composition in this most stable area, the boundary between forest and wetland is possibly the vegetation system most sensitive to climate changes. This could be examined by studying the vegetation history of both terrestrial vegetation and wetland plants at suitable core sites.

Taking a sediment core in inland southern Westland provides an opportunity to examine these questions. A detailed study of a small pakihi swamp was made in order to record the local vegetation change for comparison with the regional pattern of climate change. In addition, due to the frequency of anthropogenic forest destruction in most other sites in New Zealand, it is difficult to evaluate the climate influence on vegetation especially during the last 1000 yr. The studied area however, has been entirely forested till the present, and will provide pollen records assumed to be free from human disturbances to give more clear evidence of climate change during the Late Holocene.

## 2.2 Methods

### 2.2.1 Site Description

The study site, Sponge Swamp, is located at Burmeister Morass, the southern end of the Haast costal plain in South Westland (Fig. 2.1). The coastal plain is characterized by extensive fluvio-glacial outwash plains up to 10 km wide, interrupted only by some isolated, ice-smoothed domes, like Mt. McLean, protruding over 600 m in the centre of the plain (Dickinson & Mark, 1994). Geologically, this plain is composed of gravel, sand, silt, and scattered peat and swamp deposits. The isolated dome-shaped reliefs consist of Paleozoic greywacke intruded by granite.

Running across the south-eastern border of this coastal plain is the main Alpine Fault Zone (AFZ), which bounds the Indo-Australian and Pacific Plates, and has a known lateral displacement of surface rocks of over 500 km affecting this region. In contrast to the coastal plain, rugged Haast Ranges rising up to 1000-1500 m lie on the eastern side of the faultline, and are composed of relatively young, weak schist rocks of the Paleozoic era (Mutch & McKellar, 1964).

Sponge Swamp is actually a bog, situated between the braided Arawhata River and the meandering Waiatoto River. Both rivers carry sediments derived from fluvio-glacial processes. The swamp is only 5 km distant from the Tasman Sea, at 12 m a.s.l. altitude, and only slightly elevated above the surrounding stream levels by about 0.5 m, but nearly 9 m above the stream levels of Arawhata River. The water table in Sponge Swamp frequently fluctuates from 14 cm above the surface of the peat, as a result of intense rainfall, to 43 cm below during periods without rain (Moore & Shearer, 2003). The core site is selected from a strip-like swamp stretched along the Haast - Jackson Bay Road, about 1 km long and 0.23 km wide. Being at the piedmont of Mt McLean, the swamp is to some extent protected against the effect of flooding from the two rivers.

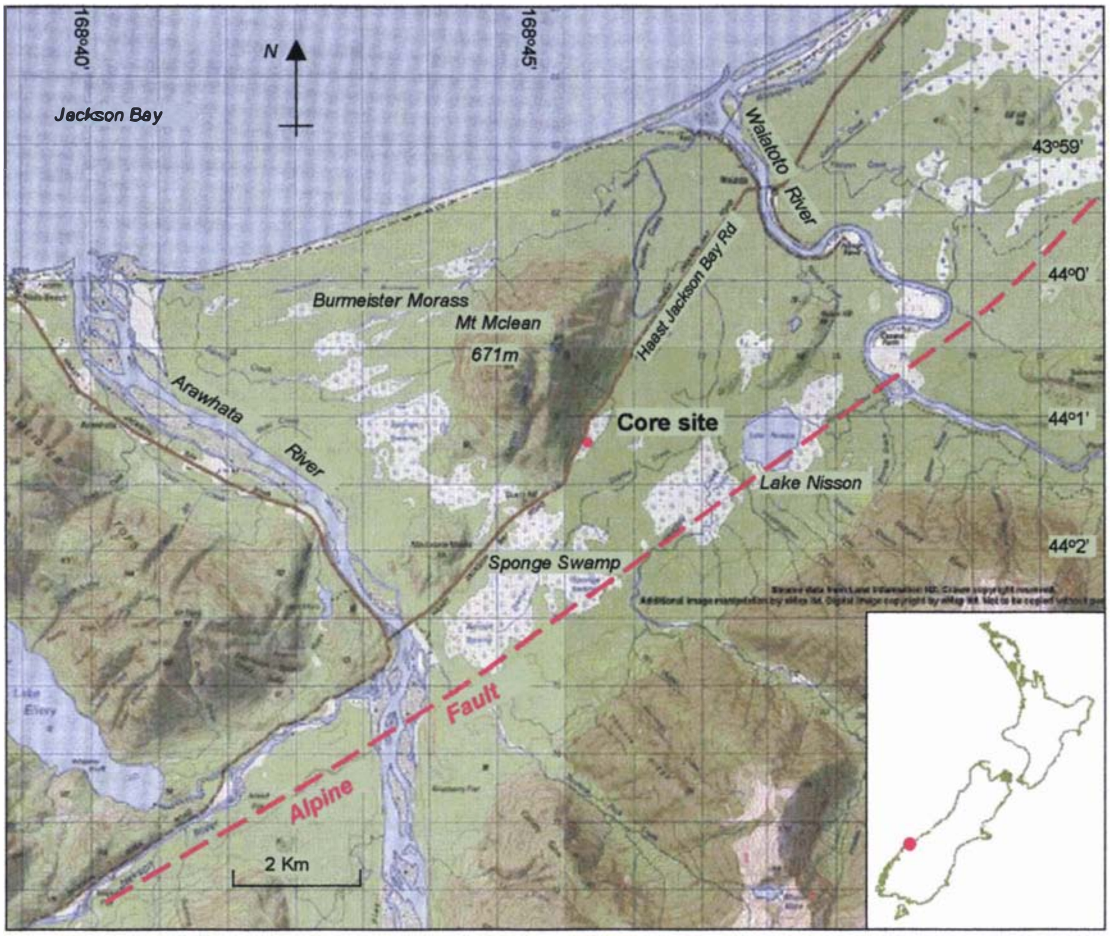

**Fig. 2.1** Location of the Sponge Swamp core site; source data from Land Information NZ Ltd, with additional image manipulation by e-map Ltd.

### Climate

This area is characterized by a strongly perhumid and mesothermal climate. The average annual precipitation recorded from the nearby station, Jackson's Bay, is in excess of 4,600 mm, and is spread over 180 days per year with relatively more frequent occurrence in spring and summer (New Zealand Meteorological Service, 1983). Most of the rain is associated with the predominant westerly or northwesterly airflows. Generally such air streams tend to be humid and often bring overcast skies with scattered drizzle, and also heavy and persistent rainfall when the air is blocked and uplifted by the Southern Alps. Westerly or southwesterly air flow usually brings showers but with bright intervals. Winds from the south and east are usually associated with dry and clear weather (Hessell, 1982).

Temperatures are relatively mild with a mean annual temperature of 10.9°C. The difference between the average of the warmest and the coldest months is 6.9°C. The mean maximum temperature of the warmest month (Jan) is 22.3°C, and the mean minimum temperature of the coldest month in mid-winter (July) is –0.1°C (New Zealand Meteorological Service, 1983). Air frosts are infrequent, occurring on only 3.3 days per year between May and October, while ground frosts occur on 56.2 days throughout the year. Fog and snow are both uncommon, occurring 6.6 and 0.8 days per year, respectively (Hessell, 1982).

### Vegetation

The indigenous vegetation around Sponge Swamp comprises extensive stands of podocarp-broadleaved and mixed podocarp-*Nothofagus*-broadleaved forest, interspersed by swamps and mires (Wardle, 1991). A clear vegetation transition from pakihi to lowland forest in the studied site is given by Mark and Smith (1975).

The mire surface is composed of depressions and peaty mounds. Most depressions are colonized by the mosses *Dicranoloma billardieri* and *Campylopus introflexus*, with other species present including *Lycopodium* spp. *Drosera* spp. and *Euphrasia* spp. etc. On peaty mounds, *Empodisma minor*, *Gleichenia circinata*, and *Baumea teretifolia* are generally common (Mark and Smith, 1975). Dense shrublands of *Leptospermum scoparium* and *Monoao colensoi* form at the fringe of the mire, leading to establishment of forest species such as *Phyllocladus alpinus*, *Dacrycarpus* *dacrydioides*, *Dacrydium cupressinum* and *Weinmannia racemosa*. The lowland forests are dominated by *Dacrydium cupressinum*, *Dacrycarpus dacrydioides,* and *Prumnopitys ferruginea*, which form an emergent stratum above a canopy of *Nothofagus menziesii* and *Weinmannia racemosa*. An undergrowth of small trees and shrubs includes *Ascarina lucida*, *Griselinia littoralis*, *Coprosma* spp., *Pseudopanax arboreus* and *P. crassifolius*. Tree ferns *Cyathea smithii* and *Dicksonia squarrosa* are also frequent.

At c. 400 m a.s.l., lowland forest is replaced by montane forest with predominant components of *Weinmannia racemosa*, *Metrosideros umbellata* and *Phyllocladus alpinus*. *Libocedrus bidwillii*, co-dominant with *Metrosideros umbellata* and *Phyllocladus alpinus,* occurs in subalpine forests. For further details see Wardle (1991) and Mark and Smith (1975).

### 2.2.2 Coring Method and Core Stratigraphy

A 7.3 m deep core was taken from near the centre of the Sponge Swamp using a D-section sampler. Sections of the core were placed in plastic cases, sealed with plastic film, labelled and transported to the laboratory for sub-sampling and analysis.

The stratigraphy of the core from Sponge Swamp is simple. The sediments above 4.72 m comprise mostly homogeneous peat. Below 4.72 m the sediments are characterised by frequent appearances of clay layers embedded in peat materials. The description of the stratigraphy of this core follows:

| | |
|---|---|
| 0.00-4.72 m | dark brown softly fibrous peat composed of mostly herbaceous detritus and fine detritus fragments. |
| 4.73-6.07 m | brown humified peat comprised of fine detritus and humus with very scarce herb detritus. Green-grey clay layers less than 1 cm are embedded in peat materials. |
| 6.08-6.50 m | more frequent clay layers embedded in brown humified peat comprised of fine detritus and humus. |
| 6.51-7.25 m | frequent clay layers embedded in brown fibrous peat composed of mostly plant detritus and fine detritus. |

### 2.2.3 Laboratory Procedures

Various chemical processes developed for the treatment of pollen samples relate to the different materials in which pollen may be embedded. The following laboratory procedures were based on those of Faegri & Iversen (1989). The order in which the various procedures are undertaken should be considered according to the nature of sediments bearing pollen grains. General processes are described as follows (Fig. 2.2).

Sub-sampling

73 samples were taken from the 7.3 m core with an interval of 0.1 m. The volume of each sample was accurately measured. About 0.5 $cm^3$ of sample was needed although the higher the organic level in the sample, the smaller the amount of sample needed. Before preparation, one exotic *Lycopodium* tablet was added to each sample for estimation of pollen concentration (Stockmarr, 1971).

Acid and alkaline wash

In order to remove any possible presence of calcium carbonate, 7 $cm^3$ of 10% hydrochloric acid (HCl) was added to each sample, which was then centrifuged and the decant discarded. Then, a mixture of 3 $cm^3$ of 10% potassium hydroxide (KOH) and 3 $cm^3$ of 0.1M sodium pyrophosphate ($Na_4P_2O_7$) was added, to break up the sediment materials, and to dissolve humic acid; after that the sample was gently heated for 5 minutes. Then after washing the sample with distilled water until the liquid was clear, it was finally passed through a terylene gauze for further treatment. Big plant fragments were retained as these could provide valuable additional information.

Acetolysis

Each sample was washed with glacial acetic acid ($CH_3COOH$) until it was dehydrated in order to avoid undesired chemical reactions that would occur during acetolysis. Acetolysis is a special method to remove plant cellulose. Samples are boiled in a mixture of acetic anhydride ($(CH_3CO)_2O$) and concentrated sulphuric acid ($H_2SO_4$) at a ratio of 9:1. Generally samples were placed on a hot plate and heated for 4-5 minutes in a fume cupboard, then centrifuged and the decant discarded.

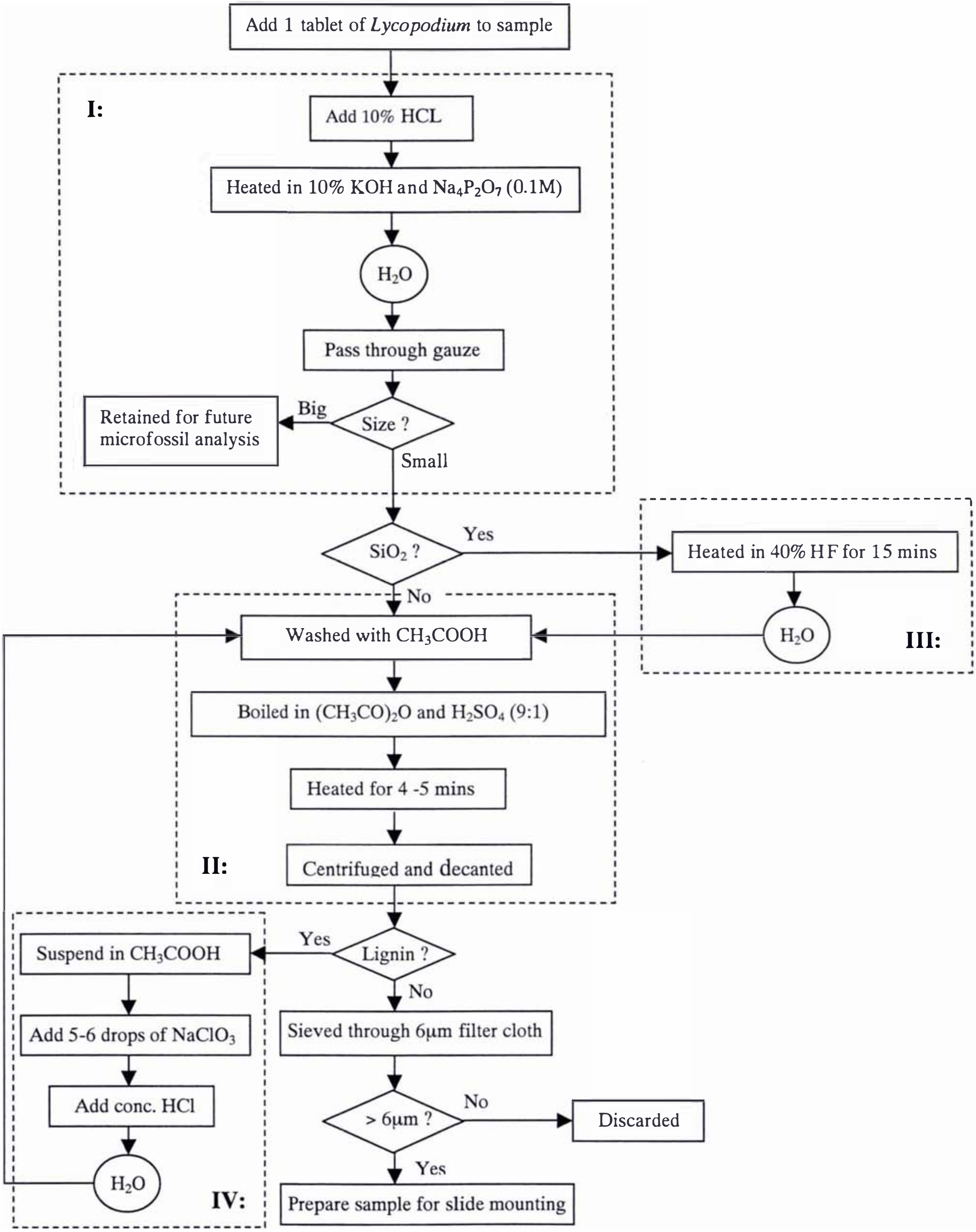

**Fig.2.2** Flow chart of the laboratory procedures. I: Acid and alkaline wash; II: Acetolysis; III: Hydrofluoric acid treatment; IV: Oxidation

Hydrofluoric acid treatment

When there is an abundance of silica present in the sample, a hydrofluoric acid treatment was applied. Concentrated (40%) hydrofluoric acid (HF) (4 $cm^3$) was added to each sample, which was then heated for 15 minutes or longer until the sample was reduced in volume which means that most siliceous matter was dissolved. Samples were washed thoroughly to remove any residual acid before the next step was taken.

Oxidation

In some cases oxidation of deposits is necessary to break down lignin which resists acetolysis. The sample was suspended in glacial acetic acid, and 5-6 drops of saturated sodium chlorate ($NaClO_3$) solution, and then 1 $cm^3$ of concentrated hydrochloric acid (HCl) were added. A violent reaction occurs and results in bleaching of the material. Usually acetolysis should follow this in order to darken the pollen grains and make them easy to identify.

Sieving

Sieving was always the last step, to wash through the fine clay, and concentrate the pollen. A sieving cloth with aperture of 6 μm was appropriate as this allows all clay particles to pass through, but retains pollen grains.

### 2.2.4 Radiocarbon Dating

Instead of dating bulk sediments (e.g. peat, organic mud or clay), concentrated pollen samples were submitted to the Rafter Radiocarbon Laboratory of the Institute of Geological and Nuclear Sciences Ltd. for Accelerated Mass Spectrometry (AMS) dating. The advantage of dating pollen rather than sediments is outlined by Brown et al. (1989), Regnell (1992) and Regnell & Everitt (1996). The most important advantage is that pollen is free of reservoir effects, regardless whether lacustrine or marine deposits are used. Most pollen is of terrestrial origin, and is resistant to the impregnation of humic acids, unlike other macro or microfossils including wood, leaves and other organic matter, so these acids do not contaminate the radiocarbon dates based on pollen. Thus the chance of contamination from inwashed younger or older carbon within bulk sediments was also avoided. As a result, dating pollen provides the most direct evidence of the time when pollen was shed.

Pollen-bearing sediment samples for age determination were taken from the core at zones where major changes occurred in the pollen stratigraphy. If a sample is pollen rich, generally sediments with dry weight of 5-6 g are enough for pollen extraction. All samples were prepared generally with ordinary pollen preparation processes as indicated by Fig 2.2 but without acetolysis. Hygienic procedures must be carefully followed to avoid any carbon contamination either in chemicals or from lab processes. All glassware was soaked in distilled water with pyroneg detergent overnight, and rinsed thoroughly with distilled water at least four times before use. The sample preparation procedure is basically the same as described previously for pollen extraction including acid and alkali wash, hydrofluoric acid treatment, oxidation and sieving. The only different process is oxidation. Nitric acid (10%) was used instead of sodium chlorate solution, after which the sample was heated for several minutes, and then neutralized by 5 % alkali solution.

Materials sized between 6 -150 µm, in which pollen is included, were obtained by two separate sieving steps. Density separation is the key procedure for extracting pollen from other organic materials. The technique works on the principle that the density of pollen is slightly different from other organic fractions (Forster & Flenley, 1993). The optimum range for pollen density is between 1.2-1.3, which largely depends on the pollen flora. A heavy liquid, sodium polytungstate (SPT), is used to provide media of different densities. Concentrated liquid SPT was diluted with distilled water to a specific gravity of 1.7 (C. Prior, pers. comm.). Samples were combined with 6 $cm^3$ of SPT, mixed thoroughly using a vortex mixer, and centrifuged for five minutes at 3500 rpm. The precipitate is the large fraction of organic material other than pollen. The supernatant was collected for repeated use in the process with SPT solutions of specific gravity reducing from 1.7, in 0.1 and 0.01 intervals as necessary. At every step, pollen abundance was checked in both the precipitate and the supernatant, until a relatively pollen-rich fraction was found, which was then used for AMS dating. If the target sample is close to pure pollen, the percentage carbon yield from sample combustion during the AMS dating would be close to the range of 65%-75%, which is the percentage of carbon contained in pollen material. This allows a check on the purity of the sample tested.

### 2.2.5 Analysis of Pollen Data

For each sample, at least 300 grains of terrestrial pollen were counted. Pollen counts were calculated and presented in the form of relative frequency, and pollen percentage was calculated upon a pollen sum including all the terrestrial pollen and spores, i.e. tall trees, small trees and shrubs, herb taxa, and fern spores. Pollen of mire taxa were excluded from the pollen sum and their percentage is calculated based on their own total plus pollen sum. TILIA and TILIA Graph (Grimm, 1991) were used for the analysis and presentation of pollen data. The pollen percentage diagram displays the relative composition of vegetation, and thus the vegetation change through time. The terrestrial percentage pollen data have been zoned using the agglomerative cluster analysis CONISS available within the TILIA program. The sample clustering was constrained by the depth. On the base of the cluster analysis, pollen zones displayed in the pollen diagram are finally defined with consideration of species that have palaeoecological significance, but regardless of the level of charcoal fragments.

## 2.3 Results

### 2.3.1 AMS Dating of this Core

Seven samples were taken from this core at various depths for AMS dating and the result is summarized in Table 2.1. Because the level of $^{14}C$ absorbted by living plants may be affected directly or indirectly by many factors, such as changes in the Earth's magnetic field or in background cosmic radiation, or changing climate and human activities etc, radiocarbon dates are calibrated to give calendar dates. The calibrated age is based on comparison of radiocarbon dates with other methods, such as examination of tree rings, ice cores, lake sediment varves etc. The calibrated ages for these samples were provided by the Rafter Radiocarbon Laboratory of the Institute of Geological and Nuclear Sciences Ltd. according to Stuiver et al. (1993).

The percentage carbon yield from the sample combustion averages around 75%, which indicates the AMS dates were estimated from very concentrated pollen samples. A date to depth diagram is derived from the data obtained (Fig. 2.3), which suggests that this core is dated back to c.7500 yr BP by extrapolation. The deposition rates of the sediments at Sponge Swamp have been generally very consistent throughout the profile.

**Table 2.1** Result of pollen AMS radiocarbon dating from the Sponge Swamp site. Calibrated ages are shown with an analytical error of one standard deviation

| Depth (m) | Carbon yielded (%) | Conventional $^{14}$C age (yr BP) | Calibrated age range (yr BP) | NZA reference No. |
|---|---|---|---|---|
| 0.47 – 0.475 | 22.3 | 599 ± 75 | 656-533 | NZA 12595 |
| 0.895 – 0.90 | NA | 1194 ± 55 | 1178-1055 | NZA 12374 |
| 2.230 | 72.1 | 3129 ± 80 | 3445-3257 | NZA 12596 |
| 3.230 | 76.0 | 4139 ± 75 | 4827-4527 | NZA 12597 |
| 4.326 – 4.33 | 48.2 | 5330 ± 120 | 6278-5937 | NZA 12598 |
| 5.295 – 5.30 | 76.5 | 5953 ± 65 | 6802-6678 | NZA 12375 |
| 6.395 – 6.40 | 74.8 | 6322 ± 55 | 7295-7210 | NZA 12376 |

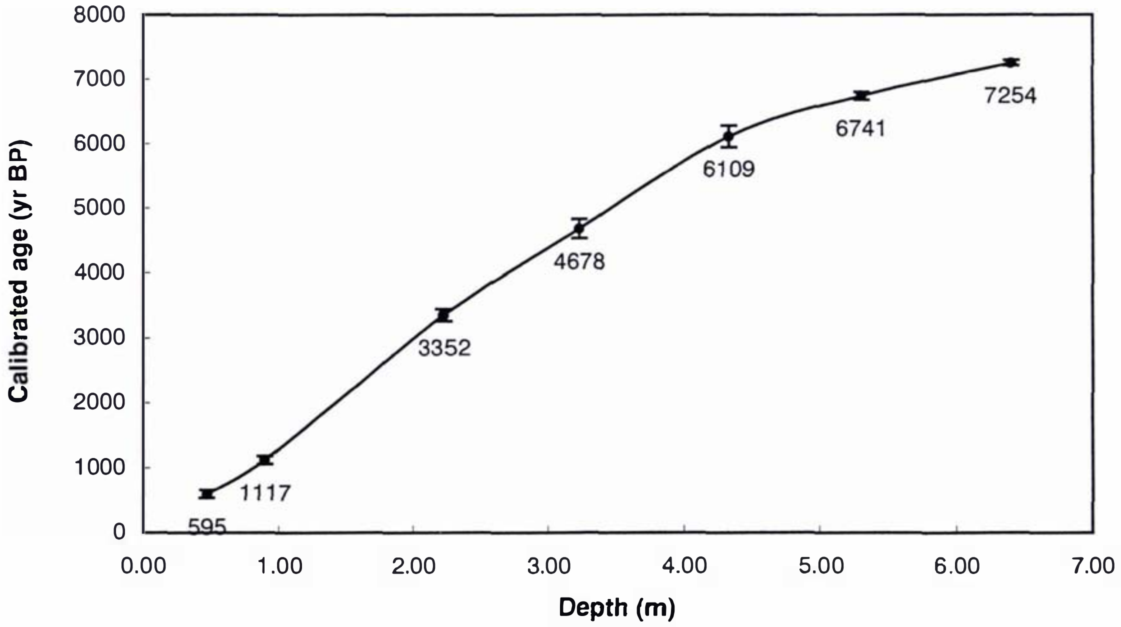

**Fig. 2.3** Sedimentation rate for the core from the Sponge Swamp site. The displayed calibrated dates are the mid-point of the calibrated range measured at that level.

**Fig. 2.4** Summary pollen percentage diagram from Sponge Swamp, Haast, New Zealand

### 2.3.2 Pollen Zones of this Core

The result of pollen percentage calculations from Sponge Swamp is summarized in Fig. 2.4 by TILIA and TILIA Graph (Grimm, 1991).

As the most predominant type of tree pollen, *Dacrydium cupressinum* remains constantly high throughout the profile, though sometimes varying by 10% between adjacent samples. There is a slight increasing trend of *Dacrydium cupressinum* over time. *Nothofagus menziesii*, as the second commonest taxon in tree pollen, generally increases through time as well. Such a trend also exists in other tree taxa, such as *Prumnopitys taxifolia, Phyllocladus* and *Nothofagus* fuscospora type, though on a much smaller scale. *Ascarina lucida* and *Coprosma* decrease substantially early in this profile. Especially for *Ascarina lucida*, there is a nearly exponential decline throughout the profile (Fig. 2.5). Values of *Cyathea* spores are high (c. 30%) but highly variable until the top third of the profile, when a consistent decline begins. Spores of monoletes generally decrease over time. Exotic pollen grains of *Casuarina* are present throughout the profile.

The pollen totals (Fig. 2.4) show a general trend across time of increasing tree pollen, and decreasing fern spores, with variable but consistently low values of small trees and shrubs and herbs. Pollen of mire taxa peaks at an early stage of the profile, and drops and keeps constant levels in the following period.

Five pollen zones labelled SSI-SSV are derived from the pollen diagram.

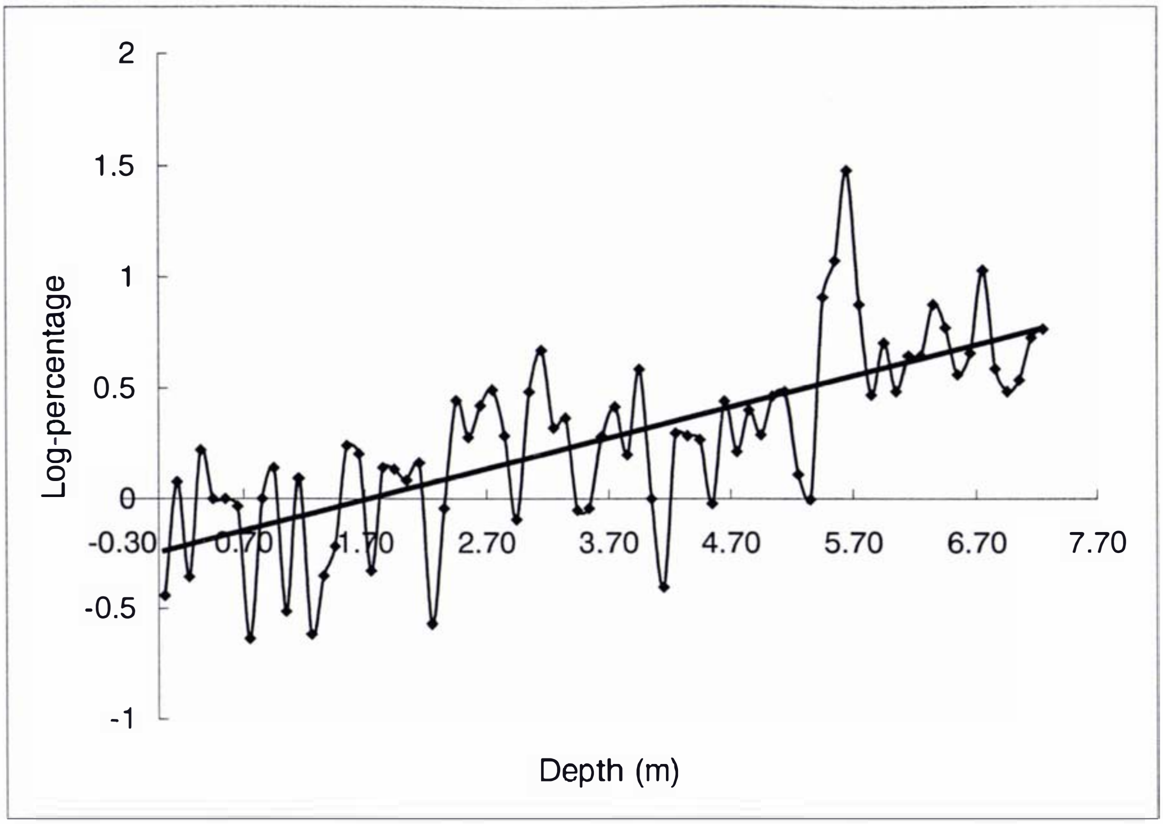

**Fig. 2.5** Pollen percentage of *Ascarina lucida* throughout the profile. Pollen percentage data are log-transformed, and the formulated linear trend is $\log y = 0.1403 \log x - 0.2437$, suggesting an exponential decline of percentage of *Ascarina lucida* over time.

Zone SSI (7.25-5.45 m, c.7600 yr BP-6800 yr BP)

Zone SSI is characterised by high values of both arboreal pollen (between 35% and 70%) and fern spores (between 30% and 67%). Tree taxa are predominant in the arboreal pollen, and shrub taxa only take about 6% to 16% throughout most of this zone but increase to c.35% close to the top. Herb pollen is at low levels, at less than 2%. Pollen of mire taxa is at very high levels from the beginning to the middle of this zone, with 37% of samples above 15% and reaching a peak of 87% at 6.85 m. After 6.45 m, there is a substantial drop in mire taxa to less than 5%, with only one sample reaching 9%.

Arboreal pollen in this zone is dominated by *Dacrydium cupressinum* which averages 24%, but shows a steady but slow decline throughout this zone. *Ascarina lucida, Coprosma, Nothofagus menziesii, Prumnopitys ferruginea,* and *Podocarpus* spp. are less important, but reach levels above 5% in average. *Ascarina lucida* is approximately constant around 5% until it peaks at 30% near the top of this zone. *Coprosma,* however, is very prominent at an early stage, but suddenly drops to trace amount at 6.15 m. Such a trend is also shown by *Podocarpus* spp. Both *Nothofagus menziesii* and *Prumnopitys ferruginea* slightly rise in the middle of this zone. Other taxa present are either lower than 5% or appear as trace amounts.

Spores of tree ferns, *Cyathea* and *Dicksonia,* are dominant amongst the ferns and fern allies. Among mire taxa, *Empodisma minus* and Cyperaceae are the commonest types which remain high from early to mid zone and decline around 6.45 m, approximately in phase with *Coprosma*. A relatively high level of *Myriophyllum* is recorded at 3% in the early stage.

Charcoal fragments are scattered sporadically throughout this zone. Most are small sized particles ranging from 5 to 50 µm. Particles above 50 µm are recorded mostly as trace amounts.

### Zone SSII (5.45-2.55 m, c. 6800 yr BP - 3700 yr BP)

This zone is distinguished from Zone SSI by a decreased abundance of pollen of small tree and shrub taxa to less than 9%. There is an increase in mire taxa, but the range is much lower than that of early zone SSI.

This zone is continuously dominated by *Dacrydium cupressinum.* It remains at a moderate but variable level, at an average of 29%, and 80% of the samples are greater than the mean for zone SSI. Coincident are small increases in *Nothofagus menziesii,* and *Dacrycarpus dacrydioides* which become subdominants in this zone. The other important podocarp taxa keep constant levels as in zone SSI. The most obvious feature in this zone is the low value of *Ascarina lucida* (at average of 2%) compared to an average of 6.9% in zone SSI. *Phyllocladus* and *Halocarpus* persist at a low level at the beginning, but become less important or even absent from the record towards the end of this zone. Other taxa, such as Ericaceae and *Plantago*, absent for most of zone SSI, are consistently present in this zone. Similarly for fern spores of *Gleichenia* and *Lycopodium australianum* which enter the record from near the base of this zone. *Gleichenia* peaks briefly at 6.7% at 4.55 m and *Lycopodium australianum* expands much later, achieving its maximum at 20.3% towards the top of this zone. Mire taxa, dominated by *Empodisma minus*, *Carex* and Cyperaceae, peak at several levels but not simultaneously.

Charcoal particles appear fairly constantly early in this zone. After a big gap from 3.85 m to 3.45 m, they become more frequent again in the late part of this zone.

### Zone SSIII (2.55-0.95 m, c. 3700 yr BP- 1200 yr BP)

This zone is represented by a progressive increase in pollen of small trees and shrubs, and a steady decrease of fern spores. Herb pollen also becomes more common near the top of this zone.

This zone is distinguished from the previous zone by a decrease of *Dacrycarpus dacrydioides* and *Prumnopitys ferruginea,* although *Prumnopitys taxifolia* shows a slight increase. *Ascarina lucida* and *Coprosma* show a further decrease relative to zone SSI as well. Instead, there is a large increase of *Leptospermum* type from 1.65 m towards the upper zone boundary, with a maximum value of 16.4% at 1.45 m. After a period of absence, *Halocarpus* is recorded consistently from 1.45 m. Tree ferns, *Cyathea* and *Dicksonia,* show a substantial decline from 2.05 m towards the top of this zone. Other important taxa include *Plantago* and *Histiopteris incisa.* Mire taxa remain with little change within this zone, except that *Haloragis* peaks at 6% at 1.85 m.

Charcoal particles remain high until 1.85 m, and thereafter they are totally absent from this zone except in the uppermost sample.

### Zone SSIV (0.95-0.25 m, c. 1200 yr BP- 300 yr BP)

This zone is characterised by a steady increase of big tree pollen and a continuous decrease of fern spores.

There is a substantial increase of *Nothofagus menziesii* from averaging 10.4% in the previous zone to about 21.6% in this zone. This is later followed by increases of *Prumnopitys ferruginea, Phyllocladus* and *Nothofagus* fuscospora type. *Leptospermum* type, however, drops to trace amounts at the beginning of this zone. Tree ferns, *Cyathea* and *Dicksonia,* decrease consistently. Mire taxa, *Carex,* present in trace levels in the early stages, rise suddenly to 9.2% from mid-zone. *Drosera* occurs once at the level of 2.2%, together with the rise of *Carex.*

Charcoal particles are continuously absent from the entire zone except in the uppermost sample.

Zone SSV (0.25-0.00 m, c. 300 yr BP- present)

This zone is represented by only two samples. Tree pollen levels remain high although *Nothofagus menziesii* drops substantially from an average of 21.6% to 4.3% in this zone, and so do *Phyllocladus* and *Prumnopitys taxifolia. Elaeocarpus, Metrosideros* and *Leptospermum* type, though present consistently before, totally disappear from the record. Mire taxa are only represented by *Empodisma minus* and trace amounts of Cyperaceae.

There is a sudden increase in charcoal with total charcoal particles rising from trace amounts in Zone IV to 12 in this zone. These particles are of small size, as occurs throughout the profile.

## 2.4 Discussion

The 7.3 m core from Sponge Swamp extends back as far as c. 7500 yr BP, and thus a long history of vegetation and environment change is recorded by the pollen and spores embedded in the sediments. The almost linear relationship between calibrated age and sample depth makes the reconstructed time sequence reliable for interpretation and for comparison with other sites.

Although it has been suggested by pollen evidence from other Westland sites (Harris, 1968; Moar & Suggate, 1973, 1996; Pocknall, 1980; Vandergoes, 2000; Moar & McKellar, 2001), that there is little evidence of major changes of forest composition in terms of climate variations, changes within both the dryland floras and wetland taxa from this site are still informative for climate reconstructions. In spite of the fact that the stable lowland podocarp-broadleaved forest which has been established for nearly 10000 yr might be more resistant to climate change, the boundary between forest and wetland is possibly sensitive to climate conditions, though the possibility of successional influences needs also to be considered.

The high levels of *Dacrydium cupressinum* and other trees from the beginning of the profile (zone SSI) suggests that the area around Sponge Swamp was already entirely surrounded by forest dominated by podocarp trees when the sediments of the core started to form. Within the lowland forest, *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Podocarpus* spp., formed an overstory and occupied lowland terraces. As under-represented species in pollen rain (Pocknall, 1980), *Weinmannia racemosa*, though represented by very low levels of pollen grains, was probably also very common in the subcanopy together with *Nothofagus menziesii*. *Ascarina lucida* was most conspicuous at the forest margins or gaps. The high levels of *Cyathea* and *Dicksonia* indicate that tree ferns persisted among the tall forest and remained as an important component of the “small tree” tier.

However, the relatively high levels of *Coprosma* before c. 7200 yr BP, suggest that a large area of shrubland was also nearby. As indicated by Moar (1970) from modern pollen studies from south Westland, pollen for shrubland taxa are generally poorly represented in the pollen rain, unless they comprise a significant component in the local vegetation or form a regionally dominant shrub cover. Therefore, patches of *Coprosma* stands in the penalpine belt, similar to that currently found in south Westland above 600 m, probably expanded downward to places near the swamp, or may have colonized the alluvium deposited along river beds (Wardle, 1991), in response to tectonic events. On the poorly drained sites, *Empodisma minus* and Cyperaceae became most abundant. The relatively high frequency of the submerged aquatic plant *Myriophyllum* indicates a high water table before c. 7200 yr BP. This situation was maintained until c. 7200 yr BP, when the mire size was apparently reduced and all the mire taxa receded. *Ascarina lucida* probably expanded much closer to the sampling site (shown by nearly 30% around 6800 yr BP.), indicating a possible shift of the forest/wetland boundary outwards from the existing forest. This interpretation is substantiated by surface samples taken from within the *Ascarina* zone on Mt. Moehau (Coromandel) which recorded c. 20% *Ascarina* pollen only if mature trees were quite close by (McGlone & Moar, 1977).

The climate through this zone (SSI) was probably characterised by a shift from cool wet to warm wet climates. The cool, wet climate in the early stage (before c. 7200 yr BP) is indicated by existence of large openings of shrubland and wetland. The predominance of Cyperaceae among mire taxa at this time supports this suggestion, as it is widespread in temperate and colder regions, especially in open damp habitats, at present (Johnson & Brooke, 1989). The climate became slightly warmer after c. 7200 yr BP, with diminishing *Coprosma* stands or reducing mire size as a result of forest invasion. The increase of *Ascarina lucida* provides further evidence for this interpretation. The present distribution of *Ascarina lucida,* which is currently found in places where precipitation is close to or above 1500 mm/yr, and which is intolerant of frost below –4°C, suggests that it is a frost and drought sensitive taxon (McGlone & Moar, 1977). Recent research also found that it shares many common features in germination strategies with species that often colonise disturbed sites (Burrows, 1996; Martin & Ogden, 2002). As a pioneer species, the large colonization of *Ascarina lucida* might indicate directly a result of revegetation on open land with the improvement of climate conditions. Evidence from elsewhere in New Zealand also supports the idea that mean annual temperatures between 8000 yr BP and 6000 yr BP were either similar to or higher than at present and this was responsible for the rapid spread of forest in New Zealand (McGlone et al., 1993; McGlone, 2002). Marine and ice cores from Antarctica provide further evidence for this climate scenario as well (Masson et al., 2000; Domack et al., 2001). The lowering of the water table after c. 7200 yr BP might be directly due to the increased transpiration of the expanding forest area, or a result from gradual processes of hydroseral succession. Under stable climate conditions, this process could take a long time. However, climate change could affect the rate of succession (Charman, 2002). It is also possible that there is a slight decrease of precipitation after c. 7200 yr BP, but this did not affect the expansion of forest under the prehumid site. Usually the survival of a forest is more determined by winter minimum (Leathwick, 1995). Moreover, the high content of humus in peat after c. 7200 yr BP contrasts with the large content of organic fragments characterising peat deposits before that time and suggests an increasing humification of peat, closely corresponding to a drying mire surface (McGlone & Wilmshurst, 1999).

A remarkable change around c. 6800 yr BP (start of SSII) is initiated by the sudden decline in stands of *Ascarina lucida.* At the same time, expanding or establishing of taxa such as *Nothofagus menziesii*, ericaceous shrubs, *Lycopodium australianum* and *Gleichenia*, coincide with this change. Like *Nothofagus menziesii,* a common feature of the other three taxa is that they are all cold tolerant or withstand stress of moisture extremes (Wilmshurst et al., 2002). *Gleichenia* species are robust ferns with extensive buried rhizomes, and they usually occur in canopy gaps in high altitude mixed forest, or in the early stages of secondary succession (Wardle, 1991). Shrubs of Ericaceae and the small tufted fern ally *Lycopodium australianum*, are both common in the subalpine and lower alpine herb fields above the temporal forest (Wardle, 1991). The peak of *Lycopodium australianum* at c. 4000 yr BP and persistence of Ericaceae from c. 6800 yr BP suggest that they spread out on the neighbouring highland close to the core site at that time.

The substantial decline of *Ascarina lucida* is widely recorded elsewhere in New Zealand from Northland to West Coast, although it occurred asynchronously (Mildenhall, 1994; Newnham et al., 1995; Elliot at al., 1997; Elliot, 1998). This has been interpreted as changing to episodes of severe climatic conditions, with much more frequent frosts and droughts through New Zealand (McGlone & Moar, 1977). Although harsh climate conditions, especially as a result of temperature drops, is supported by frequent appearance of cold tolerant or moisture stressed taxa in this site and also by the advance of glaciers north of this area since 5000 yr BP, and drop of Sea Surface Temperature in southern New Zealand waters (Nelson et al., 2000; Porter, 2000), the decline of *Ascarina* could not be totally attributed to climate change. Since *Ascarina* tends to grow in opening sites, such as forest gaps, forest margins and in early successional vegetation (Burrows, 1996), a natural forest invasion could easily suppress the growth of *Ascarina*. One has to be very careful when interpreting the change of *Ascarina*, and both climatic variability and disturbance regime should be considered (Martin, 2003).

From c. 3700 yr BP (start of SSIII), a less obvious change within the lowland forest is indicated by the slow replacement of tree ferns and swamp forest taxa such as *Dacrycarpus dacrydioides*, by the less flood tolerant *Prumnopitys taxifolia,* which suggests a decrease of water table. As the mire in the study site is principally fed by rainfall, and the water table in the Sponge swamp could drop to 43 cm below the peat surface during periods without rain (Moore & Shearer, 2003). So the substantial drop of water level is likely a result of decrease of precipitation. Mire plants fringed by thick shrubland of *Leptospermum*, quickly occupied the subsequent large exposure of damp surfaces, indicating another shifting of the forest/wetland boundary. At the same time, aquatic plants almost disappeared from this site and gave way to mire taxa such as *Haloragis, Empodisma minus*, *Carex* and Cyperaceae, which grow on moist open places. The absence of charcoal after c. 3400 yr BP in this site suggests that, although decreased, the precipitation in this region was still too high to encourage any wild fires.

As indicated by a number of pollen works, the eastern part of the South Island at the same time was experiencing drought episodes. Natural fires were then common in central and eastern Otago (McGlone et al., 1995; McGlone & Moar, 1998; McGlone & Wilmshurst, 1999; Wilmshurst et al., 2002), the upper Clutha district (Wardle, 2001), and other eastern parts (Burrows & Randall, 1993). Both the terrestrial pollen combination and the water table estimation from Eweburn Bog, Otago, also indicate a shift to drier conditions after c. 3400 yr BP (Wilmshurst et al., 2002). If this climate condition was caused by the continuously increasing westerly flow, it is then hard to explain the lower precipitation in Westland, which should show the opposite change to the eastern sites.

The probable cause might be the more variable and stronger seasonality of the climate. As suggested by McGlone (2002), by the time around 3000-4000 yr BP, the climate switched to a regime characterised by cooler but clearer southwesterly airflows, with a reduction in humid, cloudy, northerly airflows, and consequently a rise in summer solar radiation levels. This could be interpreted as reflecting a change from warm winters with moist summers in the early to middle Holocene, to cooler winters and drier summers over the past 3000 yr BP. The montane peat growth within the drier districts and the change from podocarp to *Nothofagus* dominated forest at Eweburn Bog around c. 3400 yr BP correspond with this change (Wilmshurst et al., 2002). Also, the reduction of humid northerly airflows is likely to be responsible for the precipitation drop in Westland.

A large invasion of *Nothofagus menziesii* trees in lowland forest started after c. 1200 yr BP in the Spange Swamp region. A change to a cooler climatic episode is one explanation for the further expansion of *Nothofagus menziesii.* However, this is much delayed compared with the regional spread of *Nothofagus menziesii* in New Zealand (c. 6000 – 7000 yr BP in northern Ruahine Range, southern Westland and coastal Southland, and after c. 4000 yr BP in the Urewera Range, and c. 2500 yr BP in the south-eastern South Island and north central Westland; McGlone, 1988). This is probably because of the moist climate conditions, which were better suited to the conifer-broadleaved forests. Another explanation for the expansion of *Nothofagus menziesii* is edaphic change. Due to very high precipitation in this area, leaching, loss of fertility in soils, and development of large, poorly drained areas as soil structure degenerated over time, created conditions less favourable for podocarp trees, but probably encouraged the establishment of *Nothofagus menziesii* (McGlone, 1988). The common presence of the semi-aquatic plant *Drosera,* and the expansion of *Carex* which dominates oligotrophic lowland mires, provides more evidence for this interpretation.

The most recent period, from c. 300 yr BP (zone V) or earlier, is characterised by the large decrease of *Nothofagus menziesii, Prumnopitys taxifolia* and *Phyllocladus,* accompanied by a sudden increase of charcoal particles. However, all the other lowland forest taxa were almost intact. It is thus reasonable to assume that, although anthropogenic burning may not have been affected Westland as in other places, this vegetation change might reflect sort of forest destruction occurred somewhere else (Pocknall, 1980).

Despite the differences in climate, the poor comparability of the charcoal record at this site with other sites from the South Island, except for zone V, might also suggest that the source area for most charcoal is not local. Since the potential for substantial transport of suspended material in the air from Australia to New Zealand is corroborated by Sturman et al. (1997) and McGowan et al. (2000), these charcoals could be brought from south-eastern Australia by strong westerly winds (Flenley, 2004). There is evidence of burning throughout the Holocene in south-eastern Australia (Singh & Luly, 1991). This interpretation is supported by the presence of pollen grains of *Casuarina* throughout the profile, which could only be windblown in across the Tasman Sea. Moreover, the absence of charcoal particles from c. 3400 yr BP is probably also related to the reduction of the northerly airflow from 4000-3000 yr BP, which has lasted to the present (McGlone & Wilmshurst, 2000).

## 2.5 Conclusions

The pollen diagram from Sponge Swamp records the subtly changing pattern of vegetation through much of the Holocene. Though lowland forest, which occupied the site consistently from the beginning of the sedimentation, shows little change throughout the Holocene, and is even similar to present vegetation, subtler environmental changes such as in temperature, water level, and precipitation can be traced from changes in levels of some terrestrial individuals, the presence of mire taxa, and by and comparison with other sites nearby. The changes between the terrestrial and mire taxa probably equate to oscillations in the mire/forest margin, as a subtle indicator of the vegetation's response to climate change. The presence of charcoal particles does not coincide with the evidence of a drier climate regime as derived from pollen, suggesting that most of the charcoal particles were not local, and were probably blown in from Australia.

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# Chapter Three

## Pollen Evidence of Vegetation Changes since 5300 yr BP from Tiniroto Lakes, Gisborne, New Zealand

### Abstract

The Tiniroto Lakes area, near Gisborne, which is substantially influenced by human activities, and has well documented tephra layers, provides an opportunity to trace impacts on vegetation from both natural and anthropogenic disturbances under the changing climate conditions of the Holocene. The vegetation history and associated environment change of the catchment during mid-late Holocene has been reconstructed via pollen analysis from a sediment core.

From c. 5300 yr BP, the catchment was almost completely covered with lowland podocarp-broadleaved forests, dominated by *Dacrydium cupressinum, Prumnopitys taxifolia, Podocarpus* spp. and *Dacrycarpus dacrydioides,* and the forest was similar to that of the forest remnants present in adjacent areas today.

Changes occurring within the forest composition over time are not big enough to indicate any significant climate change. However, forest invasions took place since c. 4900 yr BP with the diminishing of *Dodonaea viscosa* and other open and light-adapted taxa, such as *Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the families Fabaceae and Asteraceae. This coincides well with pollen records from other places in central and eastern North Island. This might suggest an improving of climate conditions, especially with increasing precipitation during middle Holocene in the wider area. At the same time, a succession happened within mire vegetation from *Typha* to Cyperaceae to *Phormium* in this site, and probably resulted from the hydroseral infilling of the lake under these favourable

climatic conditions. The intensified La Niñas with enhanced ENSO commenced from 5 000 yr BP could lead to increasing rainfalls.

A fire occurring around 2300 yr BP was responsible for the first relatively obvious destruction of forest seen in this core, which is indicated by relative decline of canopy trees such as *Dacrydium cupressinum, Podocarpus* spp., *Prumnopitys taxifolia*, *Nothofagus fuscospora* type, and *Prumnopitys ferruginea*. This fire episode is also observed on a regional scale, as indicated by a body of palynological evidence from vast areas of the North Island.

The Taupo eruption of 1850 yr BP had a much bigger impact on the vegetation than both the earlier Waimihia and Whakatane eruptions. Tree ferns and fern allies with monolete spores were extensively destroyed by the Taupo eruption, while *Nothofagus* trees, *Pteridium* and *Typha* were actually encouraged. Comparing Taupo with the Waimihia and Whakatane eruptions in which little vegetation changes were inferred, it appears that the destruction of forest is not necessarily dependent on the thickness of tephra layers deposited. However, fire is more important, resulting in significant destruction of forests.

There is no doubt that fires that occurred at c. 800 yr BP and 290 yr BP, which resulted in the second and third forest destructions, are human activated (inferred as Maori and European fires). The fires set at c. 2300 yr BP and subsequent to the Taupo eruption, could either be due to lightning fires under variable climate conditions and eruption phenomena, or alternatively be interpreted as caused by early human interference, at a date for which there is debate about Maori presence.

## 3.1 Introduction

The North Island is characterised by the distribution of the volcanic centres in the central part (Froggatt & Lowe, 1990). During the Holocene, active volcanoes deposited at least 13 distinctive tephras over the whole central North Island, and have affected the vegetation in the central North Island to various degrees. Besides the volcanic disturbances, human interference is the other major reason for the loss of indigenous forest there. The forest cover in the North Island has been reduced by more than 90% after the Maori and European arrivals (Ogden et al., 1998). In addition, other disturbances such as fires, droughts, and cyclonic storms also threaten the vegetation in this area (Wilmshurst et al., 1997). These disturbances make the driving forces for vegetation change more complex in terms of their integration with climate change.

As suggested by many evidence from the North Island, the climate in the middle and late Holocene apparently became more variable and is associated with more climate extremes (Horrocks & Ogden, 1998a, 1998b; McGlone, 1983; Rogers & McGlone, 1989). The climatic conditions derived from pollen evidence vary a lot in different localities. As for a period a millennium prior to the Taupo eruption of 1850 yr BP, the climate either became cooler and stormier (as shown by evidence from Mt Taranaki, Gibson Swamp and Gisborne area; McGlone et al., 1988; Horrocks & Ogden, 1998b; Eden & Page, 1998), drier at Lake Rotorua, Ohinewai, Hawke's Bay and Lake Waiatarua (McGlone, 1983; McGlone et al., 1984; Wilmshurst et al., 1997; Horrocks et al., 2002), or wetter (from Lake Taumatawhana, Papamoa and Waihi beach, Wharau Road Swamp and Repongaere Swamp; Elliot, 1995; Newnham et al., 1995; Elliot, 1997; Wilmshurst et al., 1999). These more variable climate conditions make it more complicated when interpreting the impact of disturbances in the North Island.

The Taupo eruption (1850±10 yr BP) is the most catastrophic disturbance which caused vegetation destruction during the Holocene besides anthropogenic deforestation. The airborne volcanic ash was deposited over an area of c. 30 000 km$^2$ east of the vent, and the pyroclastic flow surged over a roughly circular area around 70-90 km away from the vent (Wilson & Walker, 1985; Wilson & Houghton, 1993). The effects of this eruption have been widely recorded in pollen data from a number of sites, which lie at various distances and directions from the eruptive centre in the central North Island (Leathwick & Mitchell, 1992; Wilmshurst & McGlone, 1996; Horrocks & Ogden, 1998a). These analyses suggested that the impacts of tephra on vegetation differ a lot and are not necessarily related to either the thickness of tephra layers in each site or the distance from the volcanic centre. Some sites, which are further away from the volcanic centre, like Tunapahore in the Bay of Plenty, show severe forest destruction after the Taupo tephra (Wilmshurst & McGlone, 1996). At some sites, though very close to the volcanic centre, like the Three Kings Range and Mt. Hauhungatahi (Rogers and McGlone, 1989; Horrocks & Ogden, 1998a), the vegetation was little changed compared with the distinctive vegetation destruction preceding the Taupo eruption. Because of the rapid revegetation even at sites overwhelmed by the Taupo ignimbrite, one simple explanation for this discrepancy on the impact of the Taupo eruption might be due to the transient events un-recorded by large sampling intervals. Otherwise, the extent of vegetation damage above the Taupo tephra is also affected by other factors, like climatic conditions, vegetation types, and angle of slope. Volcanic disturbances might be weakened by climatic variation alone, or emphasised by triggering an incipient change due to climate and make the vegetation change rapid and long-lasting (Horrocks & Ogden, 2000. The relative influences of climate change and volcanism on vegetation of central North Island have not yet been satisfactorily resolved (Leathwick & Mitchell, 1992).

The core from Tiniroto, which dated back to c. 5000 yr BP and well documents several tephra layers, provides an opportunity to examine the relative impacts on vegetation of long-term climate change and of short-term volcanic eruptions and other disturbances, such as fires. Moreover, this result could be compared with other pollen work from the central North Island and thus improve understanding of the regional patterns of climate change and disturbance history.

## 3.2 Methods

### 3.2.1 Site Description

Location and setting

The Tiniroto lakes (Fig. 3.1) lie 2.5 km to the northwest of Tiniroto township, which is 30 km distant to the west of Poverty Bay. This region is characterised by gently rolling hills and isolated plateaux. Hill summits are generally 300-500 m high through most of this area, rising up to 600-900 m to the southeast, with Whakapunake reaching over 961 m (Whaley et al., 2001).

Geologically, Pliocene limestone form the localised plateau, but the predominant lithologies are young sedimentary rocks mainly of late Tertiary age, especially sandstone, siltstone, and mudstone, which result in a large area of moderate relief. The geological structure in this area is simple, with the Wairoa syncline running through Tiniroto northeastwards, along which runs the Hangaroa River. In the catchment of Hangaroa River, erosion is exceptionally rapid and has created a very unstable topography (Kingma, 1964). Tiniroro lakes were formed by mass movements blocking the former drainage pattern of the Hangaroa River (Kohn et al., 1980).

Since the whole Gisborne region is situated on an actively rising fold of the Earth's crust, which has been forced upwards as the Indo-Australian and Pacific plates meet, the high rates of geological uplift and erodible soft rocks make the landscape in this region most unstable.

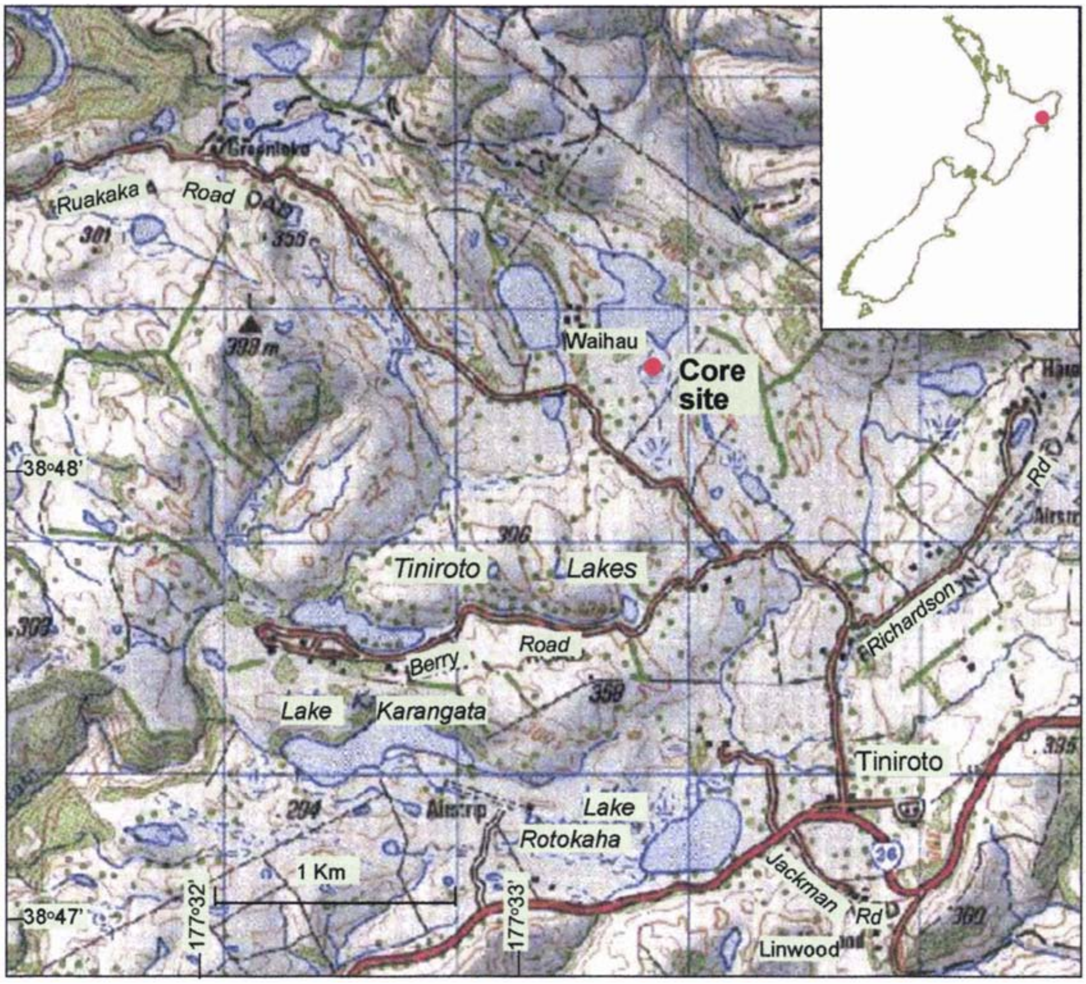

**Fig. 3.1** Location of the Tiniroto core site; source data from Land Information NZ Crown, with additional image manipulation by e-map Ltd.

## Climate

The weather of the Gisborne area is greatly influenced by the orography of this region. East of the Main Divide, the Raukumara Ranges, the prevailing northwesterly winds are commonly associated with warm, low humidity weather. South and south-east winds bring cold, wet weather. Heavy rains over the whole region are usually brought about by southeasterlies. Rainfall increases inland, with average annual rainfall ranging from 1200 mm near the coast to more than 4000 mm in the Raukumara Ranges. The Tiniroto Lakes and surrounding area are lowland hill-country, with elevated annual rainfalls ranging from 1600-2200 mm. Rainfall levels vary widely from year to year. Periods of low rainfall are comparatively common from October to February, while periods of high rainfall generally occur mostly in winter from June to September when easterly winds prevail. Generally wind flow over the Gisborne region is mild; however, winds from north-west and southerly directions can be very strong and damage tree crops when accompanied by heavy rain (Hessell, 1980; Ministry of Forestry, 1996).

Due to the modifying effect of the sea, temperatures in most of the region are mild throughout the year, except for higher altitude inland areas, where heavy frost and snow fall occur during winter months. The mean monthly temperature for the whole Gisborne region below 500 metres ranges between 7°C and 20°C. According to data from the station nearest Tiniroto, Waerenga-O-Kuri, the mean maximum temperature in the warmest month January is about 28 °C, and the mean minimum temperature in the coldest month, July, is about –1 °C. Air frosts are infrequent, occurring about 5.5 days per year. Ground frosts are more common, occurring 40.7 days per year, mostly between June and August (Hessell, 1980).

Cyclones are another extreme feature of the climate in the Gisborne region, which is in the path of occasional cyclonic storms originating in the Pacific Ocean to the north of New Zealand, and moving further south than usual. Though major cyclones are rare events (one in one hundred years), they can cause intense widespread rainfall and have significant effects on forests.

## Vegetation

Little is known of the original vegetation of the Tiniroto district. Most of the forest in this area was cleared by Maori. Nearby, tracts of original vegetation at the time of European arrival remained only to the north around the upper Hangaroa River, to the west around the foothills of the southern Urewera, to the south around Putere, and in the wet upland in the east (Whaley et al., 2001). The broad vegetation pattern of this region is thus extrapolated from the existing forest remnants, and ecology of the major species (Grant, 1996; Whaley et al., 2001).

Lowland forests were dominated by *Beilschmiedia tawa,* with emergent *Dacrydium cupressinum, Prumnopitys taxifolia, Podocarpus totara, Knightia excelsa, Metrosideros robusta* and *Dacrycarpus dacrydioides. Nothofagus solandri* var. *solandri* was prevalent on the drier and less fertile ridges.

With increasing altitude the lowland forests merged into *Dacrydium cupressinum / Beilschmiedia tawa - Nothofagus* forest, *Dacrydium cupressinum / Nothofagus* forest, and finally to pure *Nothofagus fusca - Nothofagus menziesii* forest in the cooler, wetter areas. Other species associated with this higher altitude forest included *Prumnopitys ferruginea, Weinmannia racemosa, Podocarpus totara, Podocarpus cunninghamii,* and *Phyllocladus trichomanoides* etc.

Freshwater swamp and wetland vegetation occurred around numerous small lakes. Vegetation within and around the wetlands included sedgeland, rushland and raupo reedland. Around Tiniroto lakes, the common taxa included *Myriophyllum, Ranunculus flammula, Ranunculus repens, Carex secta, Carex* spp., Cyperaceae, *Juncus effusus, J. articulatus, Rumex crispus, Polygonum hydropiper,* Poaceae and Asteraceae. Many other wetlands also include *Typha* and *Leptospermum/Sphagnum* scrub around their margins.

*Kunzea ericoides* and *Leptospermum scoparium* are both dominant species in the secondary vegetation.

### 3.2.2 Coring Method and Core Stratigraphy

Cores were taken from a small strip swamp (500 m × 150 m) adjacent to the lake east of Waihau. Cores 1 and Core 2 were collected within the swamp about 33 m from the edge of the lake, by D-section corer. These two cores were taken at 0.5 m apart, from levels differing by 0.5 m, to depths of 5.5 m and 5.42 m. In order to prevent end-contamination from the core taken each time by the piston corer, the whole profile used for pollen study was reconstructed from sections except for both ends of each core, with each sample being taken at about 10 cm intervals, except those at 5 cm immediately above tephra layers. The comparisons of levels from these two cores are chiefly based on core stratigraphy and X-ray photography as well. Due to slight displacement at several levels between Core 1 and Core 2, revised depths of these levels are used in producing pollen diagram to keep the sequence consistent (see Appendix 2).

The stratigraphies of Core 1 and Core 2 are very similar. As in Core 1, the sediments above 2.38 m comprise mostly homogeneous peat. Below 2.38 m, the sediments are characterised by yellow/brown homogeneous organic nekron mud, though with darker layers in some levels. Clay occurs below 4.94 m. Four tephra layers are embedded in sediments at different levels. The description of the stratigraphy of Core 1 follows:

| | |
|---|---|
| 0.25-2.38 m | Dark fibrous peat composed of mostly herb detritus and fine detritus. Two grey-white tephra layers are embedded in peat deposits at 0.19-0.21 m and 1.35-1.55 m. The latter is composed of fine to coarse pumice. |
| 2.38-2.58 m | Transition from dark fibrous peat to brown-yellow organic nekron mud. |
| 2.58-3.14 m | Brown-yellow organic nekron mud with semi-laminated layers and abundant fresh-water mollusc shells around 2.72 m and 2.8 m. |
| 3.14-3.34 m | Grey volcanic pumice underlain by dark grey fine volcanic ash. |
| 3.34-4.60 m | Yellow-brown organic nekron mud with abundant fresh-water mollusc shells, frequently embedded in layers of dark nekron mud. |
| 4.60-4.66 m | Grey volcanic ash underlain by volcanic pumice. |

| | |
|---|---|
| 4.66-4.94 m | Organic nekron mud with sections of brown, dark brown and dark colour. Fresh-water mollusc shells are distributed throughout. |
| 4.94-5.50 m | Dark greenish grey clay. |

### 3.2.3 Laboratory Procedures

Please refer to Chapter 2.

### 3.2.4 Tephrochronology and Radiocarbon Dating

Four distinct tephra layers from this core were identified as Whakatane tephra (4.60-4.66 m from core 1, 4830±20 yr BP), Waimihia tephra (3.14-3.36 m from core 1, 3280±20 yr BP), Taupo tephra (1.63-1.85 m from core 2, 1850±10 yr BP) and Kaharoa tephra (0.37-0.41 m from core 2, 770±20 yr BP) by A. Palmer in Soil & Earth Sciences, INR of Massey University, using stratigraphy and glass chemistry of glass shards. As supplements, four concentrated pollen samples from levels of 0.20 m, 0.74 m, 1.57 m and 2.24 m, were submitted to the Rafter Radiocarbon Laboratory of the Institute of Geological and Nuclear Sciences Ltd. for Accelerated Mass Spectrometry (AMS) dating (Table 3.1). Two radiocarbon dates at levels of 0.74 m and 1.57 m are not consistent with the age of the adjacent tephra layers; instead both of them are much older than associated tephra layers. From Table 3.1, the percentage of carbon yield from sample combustion during the AMS dating of these two levels are 15% and 3%, which are much lower than pollen (65%-75%) and plant cellulose (44%). The low combustion yields suggest that the samples from these two levels contained a significant amount of inorganic material, suggesting inwash of soil from the catchment of the lake. Thus the dating errors are probably caused by "old carbon" existing in these samples (C. Prior, pers. comm.). Although the radiocarbon dates at level of 2.24 m were consistent with the tephrochronology, the low percentage of carbon yield (20.8%) suggests the presence of inorganic dating materials as well. As a result, the core chronology was mainly based on the ages of tephra layers and AMS radiocarbon dates from levels of 0.20 m.

**Table 3.1** Result of pollen AMS radiocarbon dating from the Tiniroto site. Calibrated ages are shown with an analytical error of one standard deviation

| Depth (m) | Carbon yielded (%) | Conventional $^{14}$C age (yr BP) | Calibrated age range (yr BP) | NZA reference No. |
|---|---|---|---|---|
| 0.20 | 71.8 | 224 ± 55 | 306-274 | NZA 15647 |
| 0.74 | 15.0 | 2564 ± 70 | 2641-2493 | NZA 15648 |
| 1.57 | 3.0 | 3124 ± 90 | 3448-3246 | NZA 15649 |
| 2.24 | 20.8 | 2291 ± 60 | 2348-2306 | NZA 15650 |

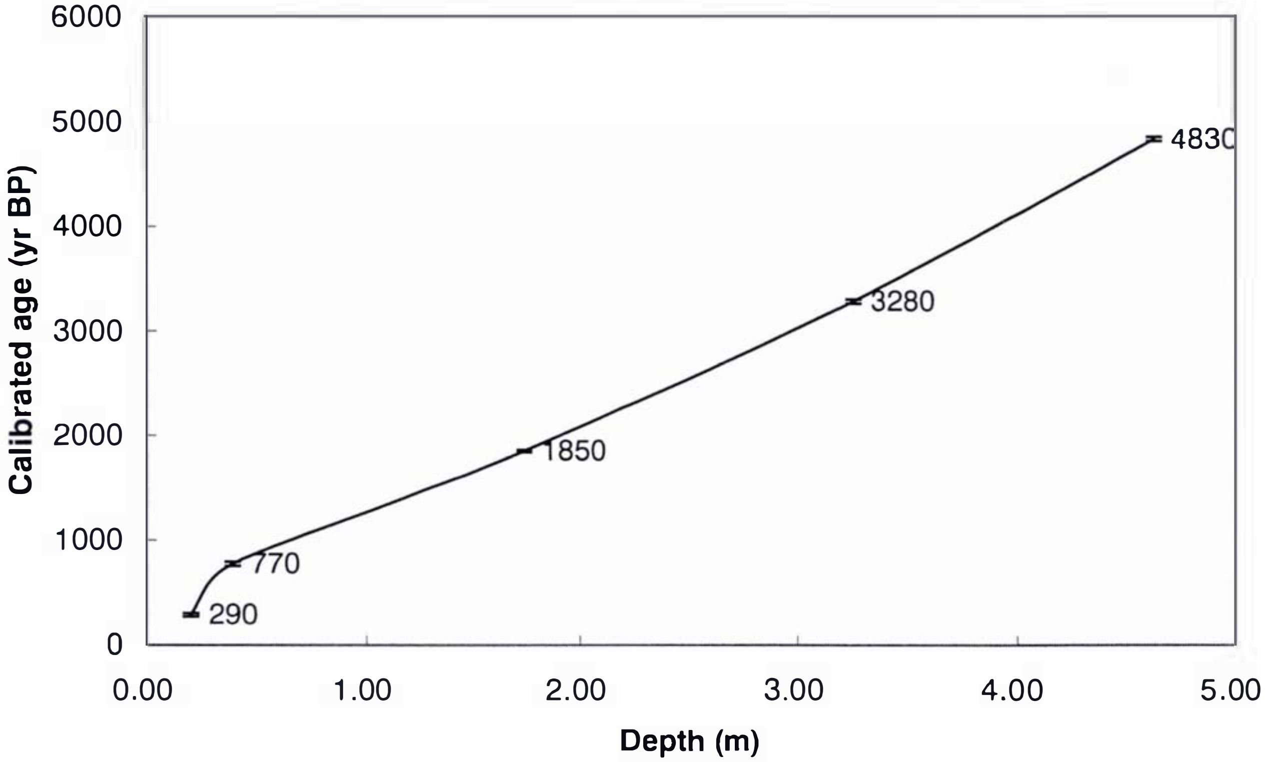

**Fig. 3.2** Sedimentation rate for the core from the Tiniroto site. The displayed calibrated dates are the mid-point of the calibrated range measured at that level. The date of 290 yr BP is an AMS date, but the other four dates are all estimated from tephra layers.

### 3.2.5 Analysis of Pollen Data

Pollen samples were analysed from the base of the Tiniroto core at 5.42 m, at 10 cm intervals for this whole profile, but at 2-3 cm intervals when close to the boundary of tephra layers and clay. Samples from 5.42 m to 5.12 m yielded very little pollen but contained more than 90% of spores of ferns and fern allies, and are not included in the pollen diagram.

75 samples were analysed, in which more than 300 terrestrial pollen grains were identified for each sample. Pollen percentage was calculated with respect to the pollen sum including all the terrestrial pollen and spores, e.g. tall trees, small trees and shrubs, herb taxa, and fern spores. Pollen of mire taxa were excluded from the pollen sum and their percentage is calculated based on the terrestrial plus aquatics pollen sum. Only a small percentage of pollen grains were unidentified. The result is summarized in Fig. 3.3 using the programs TILIA and TILIA GRAPH (Grimm, 1991), and four pollen zones labelled TN1-TN4 are derived from the pollen diagram (Fig. 3.3).

## 3.3 Results

From an overall view, there has been little change in composition of pollen taxa through most of the profile. *Dacrydium cupressinum* is consistently at high levels and dominates the pollen taxa, averaging above 30%. *Prumnopitys taxifolia* and *Nothofagus fuscospora* type are also major components of the tree taxa, averaging around 10%, though fluctuating through most of the profile. Similar fluctuations occur with pollen of *Dacrycarpus dacrydioides* and *Podocarpus* spp. though these are present in much smaller amounts (c. 5%). Pollen of small trees and shrubs are all at trace levels except that *Coprosma, Dodonaea viscosa* and *Leptospermum* peak briefly in the profile.

Besides the sudden drop close to the top, all the main taxa of tree pollen show a synchronous decline at 0.75 m. This sudden change is also associated with tree ferns though this occurs slightly later. At the same time, there is an expansion of *Leptospermum,* followed by colonization of *Pteridium* and herbs such as *Taraxacum officinale* and Poaceae from 0.25 m.

**Fig. 3.3** Summary pollen percentage diagram from the Tiniroto Lakes, Gisborne, New Zealand

Another decline of tree pollen takes place at c. 2.25 m, but on a much smaller scale. *Dodonaea viscosa*, together with some herb taxa, are consistently present at the early stage before 4.70 m, but at trace levels after that. *Cyathea* spores are at relatively high levels (c. 30%) in the first half of the profile, but steadily decline towards the top. Pollen of mire taxa becomes more prominent from the middle of the profile.

Four pollen zones labelled TN1-TN4 are derived from the pollen diagram based on the change of pollen totals, especially tree pollen.

### Zone TN1 (5.11 m-4.76 m, c. 5300 yr BP-4900 yr BP)

Pollen of big trees rise early to c. 75.5% before beginning a steady decline to lower levels at the upper zone boundary (c. 50%). Tree ferns change in the opposite way. Pollen of small trees and shrubs, along with herbaceous pollen, though at low levels, are consistently present in this zone. Mire taxa are rare.

The changing pattern with big trees is most associated with *Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Nothofagus fuscospora* type, *Podocarpus* spp. and *Prumnopitys ferruginea*. *Dodonaea viscosa,* although having relatively low representation, achieves its highest value (3.3%) for this zone at the top. *Pteridium* also achieves high percentages at c. 10% in the middle of this zone. Other relatively important taxa include *Coprosma,* Fabaceae, *Schefflera digitata*, and herbs like Asteraceae.

Very small amounts of charcoal particles ranging from 25-100 μm are scattered within this zone.

### Zone TN-2 (4.76-2.25 m, c. 4900 yr BP-2300 yr BP)

This zone is characterised by the relatively stable amounts of big tree pollen, and also of fern spores. However, pollen of small trees and shrubs decrease continuously to the top. Herb pollen, which persists in the previous zone, almost disappear in this zone. Pollen of mire taxa become consistently represented from the middle of this zone and peak above 5.9% near the top.

This zone is distinguished from the previous zone by a sudden decline of *Dodonaea viscosa* which remains at trace levels from the beginning. *Pteridium* disappears completely after the first two samples. *Coprosma,* though continuously present throughout, decreases slightly at the beginning of this zone but peaks again when close to the top. Other taxa which are relatively common or consistently occur in the previous zone, e.g., Fabaceae, *Schefflera digitata,* Asteraceae, *Pseudopanax, Alectryon,* and *Hebe*, become less important or almost disappear from the record. *Passiflora,* however, starts to enter the record from this zone onwards. *Typha* starts to be constantly present at trace levels from the middle of this zone, then becomes more frequent, and achieves 2.4% on average near the top, when Cyperaceae and *Phormium* come into consistent presence.

Charcoal particles become more frequent near the top, especially with large particles ranging from 50-200 μm. Although this zone contains two tephra layers, Whakatane and Waimihia, there is no substantial change in most of the pollen taxa around these layers.

Zone TN-3 (2.25-0.75 m, c. 2300 yr BP-800 yr BP)

This zone is characterised by a substantial decrease of tree pollen from the beginning by more than 28% compared with the previous zone, and followed by a gradual but steady rise towards the top. Pollen of small trees and shrubs show a continuous decline but recover from 1.95 m and peak at c. 11.6% close to the upper boundary. Pollen of mire taxa also decrease to a certain degree, but increases suddenly from 1.6 m (upper Taupo boundary) and peaks at c. 22.7% later.

From the beginning of this zone, a slight but synchronous decrease of pollen occurs among tree taxa of *Dacrydium cupressinum, Podocarpus* spp., *Prumnopitys taxifolia, Nothofagus fuscospora* type, and *Prumnopitys ferruginea,* along with an increase of tree ferns like *Cyathea, Dicksonia* and monolete spores. Most of the tree taxa regain their previous level shortly thereafter and stay invariant after the Taupo tephra (1.65 m - 1.84 m). There is a sharp but transient expansion in *Nothofagus menziesii, Nothofagus fuscospora* type and *Pteridium* immediately after the Taupo tephra, and so with *Prumnopitys ferruginea*. *Prumnopitys taxifolia, Podocarpus* spp., and *Dacrycarpus dacrydioides* slowly increase from c. 1.25 m and peak at the top of this zone. *Leptospermum* experiences a large increase in the upper two samples. Some mire taxa, such as *Typha*, Cyperaceae and *Phormium,* display a successive expansion after the Taupo tephra.

Charcoal particles, especially those of small size, become constantly present within this zone. Larger particles (>50 μm) appear associated with the Taupo tephra. However, almost all sized particles peak near the top in phase with the expansion of *Leptospermum.*

Zone TN-4 (0.75-0.20 m, c. 800 yr BP-290 yr BP)

This zone is represented by a constant decrease of big tree pollen. Herbaceous pollen rise from trace amounts to 22.7% above 0.35 m. Pollen of mire taxa also rise from the trace level to c. 7% near the top. Fern spores are less variable.

Almost all big tree taxa show a consistent decline from the beginning of this zone except *Nothofagus menziesii* and *Nothofagus fuscospora* type. This sudden change also occurs with tree ferns, though slightly later. *Leptospermum* stays important until 0.35 m when a large rise occurs for many taxa, including *Pinus, Pteridium, Taraxacum officinale,* Poaceae, Cyperaceae, *Gleichenia, Lycopodium deuterodensum* and other monoletes.

There is a huge increase of charcoal particles of all sizes from 0.35 m onwards to the top of this zone.

## 3.4 Discussion

The peat and lake sediments from Tiniroto Lakes extend back as far as c. 5300 yr BP which is extrapolated using a sedimentation rate of 0.1 cm/yr, and this seems likely to be the time when the Tiniroto Lakes formed. According to Kohn et al. (1980), the lakes were formed by mass earth movements blocking the former drainage pattern of the Hangaroa River. This is reflected in the pollen diagram by almost pure fern spores in the bottom clay samples. The bed of Tiniroto Lakes is possibly composed of paleosols characterised by strong oxidation conditions, in which the more oxidation-resistant fern spores could be preserved better than pollen grains (Dimbleby, 1962).

From pollen evidence at c. 5300 yr BP, lowland podocarp-broadleaved forests were present around the lakes, and were dominated by *Dacrydium cupressinum, Prumnopitys taxifolia, Podocarpus* spp. and *Dacrycarpus dacrydioides.* Though represented in much smaller pollen amounts, *Knightia excelsa* and *Nestegis* might also occupy a certain amount of the canopy tree layer. Tree ferns and other broad-leaved trees formed a small tree tier around the lake. *Nothofagus* might have dominated higher altitudes, together with other trees including *Prumnopitys ferruginea, Weinmannia racemosa* and *Phyllocladus* as they occur today. This forest seems similar to those remnants still existing in the Tiniroto district.

However, the decline of *Dodonaea viscosa* since c. 4900 yr BP is of particular interest. *Dodonaea viscosa* used to be relatively common in the early Holocene, as shown in numbers of pollen diagrams from the North Island (McGlone, 1983, 2001, 2002a; Kershaw & Strickland, 1988; Mildenhall, 1994). Since *Dodonaea* is a frost-sensitive small tree (Wardle, 1991) and its decline is often accompanied by the decline of *Ascarina lucida,* and even mangroves, the change of *Dodonaea* has been interpreted as a result of climate deterioration (McGlone & Topping, 1977; McGlone, 1983, 2002a; McGlone & Neall, 1994; Elliot, 1998; Mildenhall, 1994, 2001). However, this interpretation seems to be not singular as the decline of *Dodonaea* was sometimes followed by the expanding of forest taxa. It has been noticed that in this core, the decline of *Dodonaea* is simultaneously accompanied by decline in many open land and light-adapted taxa, such as *Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the family Fabaceae and Asteraceae. As pointed out by Wardle (1991), *Dodonaea viscosa* also prefers open and drier sites, and usually appears on cliff faces or forest margins. Due to these being common features with *Ascarina*, which also tends to grow in forest gaps, forest margins and early successional vegetation as a pioneer species (Burrows, 1996; Martin & Ogden, 2002), the simultaneous change of *Dodonaea* and *Ascarina* could also reinforce *Ascarina*'s adaptability to disturbance rather than be due to climate. Thus the forest in the early stage at Tiniroto, though floristically similar to the present remnants, was probably more open than today. The decline of *Dodonaea* is subsequent to forest invasion. The later occurrence of the climber, *Passiflora*, might suggest the increasing of forestland.

It seems reasonable to assume that the forest invasion might represent a successional process of recovery from the mass movement, by which the Tiniroto Lakes were formed. Nevertheless, evidence from pollen records of other places in central North Island, manifests that such forest invasion is not only restricted to Tiniroto. Pollen records (McGlone, 2002a) from Lake Poukawa, Hawke's Bay, show beech trees and angiosperm trees superseded *Dodonaea* and other open site taxa, such as *Coprosma*, *Leptospermum* and *Elaeocarpus* around the lake *c.* 5000 yr BP. At Lake Rototua (McGlone, 1983), *Dodonaea viscosa*, together with other open land taxa, was eliminated by the growth of tall forest c. 3500 yr BP. The rather regional behaviour of *Dodonaea* argues that the forest invasion in the central North Island during the middle Holocene might suggest an improvement of climate conditions, especially with increasing precipitation.

As mentioned by McGlone (1988, 2002b), the enhanced easterly to southeasterly weather patterns in the middle to late Holocene might have brought increased rainfall to the east side of New Zealand. Water levels rose from 6500-4500 yr BP in Lake Poukawa (McGlone, 2002a). Evidence for a relatively wet period is also supported in the Repongaere Swamp near Tiniroto, by the consistent existence of aquatic and mire taxa, e.g. *Myriophyllum*, *Microsorum* and *Urtica linearifolia*, from *c.* 3500 yr BP (Wilmshurst, 1999). Such climatic improvement was also reflected in the Far North at Wharau Road Swamp and Lake Taumatawhana at about 3500-4000 yr BP as well (Elliot et al., 1995; Elliot, 1997). A decreasing influx of terrestrial sediment supply from 3500-1000 yr BP in deep-sea core off eastern New Zealand, though explained as retention of the sediments on the coastal shelf by wind-strengthened along-shelf currents (Carter et al., 2002), might also be related to reducing erosion as a result of forest invasion.

This state of the forest persisted until c. 2300 yr BP when responses to several disturbances began. During the long period from 4900 yr BP to 2300 yr BP, a succession occurred with mire vegetation. *Typha* started to develop at the edge of the lakes from c. 3280 yr BP, and was gradually replaced by Cyperaceae, and finally both gave way to *Phormium* which became most conspicuous at c. 2000 yr BP. *Typha* grows in a wide variety of wetland habitats with annual inundation, and without this it will be restricted by other mire vegetation (Wardle, 1991; McGlone, 2002a). Beyond the *Typha* band, Cyperaceae, and perhaps *Phormium*, were likely to have been more dominant (McGlone, 2002a). Although the successive change from *Typha,* to *Phormium* could be argued to result from lowering of the water table, this could also have resulted from the hydroseral infilling of the lake under the favourable climatic conditions. Similar patterns appear in the Auckland Isthmus as a result of hydroseral infillings instead of drying climate (Horrocks, 2002). Disturbances could accelerate this process. Similar succession of *Typha* to Cyperaceae to *Phormium* appeared immediately after the deposition of Taupo tephra in this core, but the changes within mire taxa are substantially larger in magnitude and more rapid.

A fire occurred around 2300 yr BP, and is responsible for the first relatively obvious destruction of forest in this core. This destruction of forest is characterised by the relative decline of big trees, such as *Dacrydium cupressinum, Podocarpus* spp., *Prumnopitys taxifolia*, *Nothofagus fuscospora* type and *Prumnopitys ferruginea*, as well as *Coprosma*. As a result, tree ferns and other fern allies quickly took over the forest gap until later destroyed by the Taupo eruption.

Two volcanic eruptions from the Taupo Volcanic Centre are recorded around that period, i.e. the Mapara Eruption occurred at 2160±25 yr BP and the Whakaipo eruption at 2685±20 yr BP, and it could be suggested that the charcoal particles around 2300 yr BP in the Tiniroto site could have been carried from a near-to-source area ignited by pyroclastic flows. However, the larger size of the charcoal fragments (>200 μm) is a good indicator of local fires, and the vegetation change corresponding to this charcoal level also confirms the presence of fire close to the study site. Moreover, a body of palynological evidence supports this regional fire episode around 2000-3000 yr BP prevailing in vast areas of the North Island, in which most of the forests underwent severe disturbance during the millennium prior to the Taupo eruption (Newnham et al., 1995; Horrocks & Ogden, 1998b; Wilmshurst et al., 1999; Empson et al., 2002; McGlone, 2002a). Frequent fires not associated with tephra were recorded in the Three Kings Range, Reporoa, southern Kaimanawa Mountains

(Rogers & McGlone, 1989), and at Mayor Island (Empson et al., 2002), and caused different damage to the forest, leading to the decline of *Nothofagus* forest, or even replacing the local podocarp forest by grassland. Considering that almost no vegetation change occurred in this site during the Whakatane and Waimihia eruptions, which were much bigger than the Mapara and Whakaipo eruptions in terms of volume of airfall tephra (Froggatt & Lowe, 1990), it is hard to imagine these small eruptions could have such a regional-scale effect.

The onset of the fire disturbances around 3000-2000 yr BP is regarded as a result of more frequent and intense El Niño/La Niña events commencing in New Zealand after 3000 yr BP (McGlone, 1992; Wilmshurst, 1999). This scenario is also used to explain other environmental changes around New Zealand at this time, such as the increased storminess on the east coast of the North Island around 2090-1855 yr BP, based on erosion pulses in lake sediments (Eden & Page, 1998), and the expansion of *Libocedrus* prior to the Taupo eruption (Horrocks & Ogden, 1998a).

Some other evidence supporting the onset of ENSO has been traced back even earlier in New Zealand. Shulmeister (1999) pointed out that increasing seasonality is closely associated with the enhanced Walker Circulation, driven by the temperature contrast between the west and east Pacific, after 5000 yr BP, and the onset of ENSO appears to be a response to that increased seasonality. Sediment records from floodplain, continental-shelf, and continental-slope settings of the eastern North Island of New Zealand underwent a synchronous textural variation, a transition from fluvial deposition to landsliding, providing evidence of increasing storminess after c. 4000 yr BP. This signal indicates a regional response to intensified ENSO (Gomez et al., 2004). If this is the case, the rising rainfall since c. 4900 yr BP reflected at this site might well be correlated with the increasing storminess in the eastern North Island, which should be associated with the enhanced La Niñas. However, a substantial decline in the temperature amplitude of the warm seasons is noted from 1900 yr BP from a tree ring study in Tasmania; fluctuations reduced by 35% after 1900 yr BP, and this indicates a decrease of El Niño frequencies (Cook, et al., 2000). The El Niño frequencies also decrease at 2600-2800 yr BP in Venezuela and Ecuador and other widely scattered sites (Haug et al., 2001; Rodbell et al., 1999). Therefore it is hard to ascribe the start of the intensified disturbances after c. 2300 yr BP at Tiniroto to any ENSO related climate events.

An alternative explanation for this change is early Polynesian impact (Holdaway, 1996), although this is argued against by some palynologists (Ogden, 1998; McGlone & Wilmshurst, 1999). The early dates of human settlements were rejected by them because of the possible contamination of "old carbon" in-washed into the lake and swamp. Instead, the sudden decrease of tree pollen and increase of charcoals and spores of *Pteridium esculentum* about 700 yr BP have been taken as indications of first colonization by people. Since there is no comparable rise of spores of *Pteridium esculentum* in the earlier stage, the destructions of vegetation before Taupo eruption are assumed to be caused by natural disturbances (Wilmshurst et al., 1997). As in Waiatarua wetland, the Auckland Isthmus, after c. 2500 yr BP, Cyperaceae is substantially decreased and replaced by a sudden and large increase of *Leptospermum*, *Gleichenia* and *Sphagnum* (Horrocks et al., 2002). The possibility of human interference to this substantial vegetation change is rejected simply because of the absences of charcoal (which occurred relatively later), and of *Pteridium*. However, as indicated in this site, the presence of *Pteridium* is not necessarily associated with forest destruction. At Tiniroto *Pteridium* did not occur until the European time, when it became abundant along with the introduced taxa such as *Pinus*, *Taraxacum officinale* , and Poaceae. Charcoal particles occurred extremely frequently at that time, the most likely consequences being disappearance of shrublands and development of grassland rather than forest. The loss of forest occurred at the same rate as prior to the deposition of the Kaharoa tephra at 0.95 m in this core, which is referred to as the time of Maori arrival, and *Pteridium* is totally absent at that time too.

As suggested by the experimental results of Wassilieff (1986), *Pteridium* vegetation will revert to manuka-kanuka scrub within 10 years, and to five finger-mahoe forest within 40-45 years. So, it is possible that, either the sampling scale did not record the existence of *Pteridium*, or that fire in this region was not frequent enough to maintain the fernland. A similar absence of *Pteridium* in the Maori era is also noticed in pollen diagrams from the Tiniroto region, very close to the Tiniroto Lakes (K. Butler, unpubl.). On Great Barrier Island, at Northern Awana and Cureens' Paddock adjacent to Awana Bay, tall trees decreased by nearly 40%, and *Pteridium* increased up to 70-

80 % and charcoal to 30-50% during Polynesian settlement (c. 600 yr BP; Horrocks et al., 2001). Consequently at the site of Cureens' Gate, less than 1 km from both the above sites, tall trees dominate the pollen sum in all samples and charcoal and bracken spores are absent from all samples before and after the Kaharoa tephra, which ranged from at least 800 yr BP to less than 500 yr BP, as estimated from the diagram of Horrocks et al. (2001). This disagreement probably resulted from the local transportation of the bracken spores. It seems that it is difficult to detect any rise of *Pteridium* spores in pollen records when the coring site is away from the bracken fernland, or when human activity close to the coring site is limited by small population size. Also, the susceptibility of forest to fire depends on its type. As mentioned by Steel (1989), in Mt. Hauhungatahi, areas outside the forest were repeatedly burned, while the forest itself was not affected. Accordingly, the possibility that the onset of the fire disturbances before the Taupo eruption resulted from the continuous presence of people cannot be ignored (Flenley, 2004).

As for the volcanic eruptions, the Taupo eruption was the most violent volcanic eruption in the world for the past 5000 years (Wilson & Walker, 1985). Considering the vegetation damage from the eruptions in New Zealand during historical times (Clarkson, 1990), the impact of the Taupo eruption on vegetation should be catastrophic. Within the vast area subjected to the pyroclastic flow, about 70-90 km from the vent, vegetation that lay in the path of the Taupo Ignimbrite was completely destroyed. In the area affected by the deposition of airfall tephra, vegetation damage is also obvious but highly variable (Wilmshurst & McGlone, 1996). In spite of the considerable change, patches of vegetation could have survived due to the protection of local topographic barriers. Since the source area of pollen deposition is regional, the pollen records to some extent average out the impact of disturbance on a regional scale. Thus pollen evidence is relatively unlikely to depict the impacts of the Taupo eruption to local vegetation far from the eruption centre. Nevertheless, in the Tiniroto site, it is obvious that the Taupo eruption exerted a much bigger impact on the vegetation than both the Waimihia and Whakatane eruptions. Although the destruction of trees by the Taupo tephra is not obvious, tree ferns and fern allies with monolete spores were seriously reduced. On the other hand, the deposition of the Taupo tephra actually encouraged the expansion of *Nothofagus* trees, *Pteridium* and *Typha.* It seems that the tephra deposit might block streams, increase the fire chances, and also provide suitable environment for *Nothofagus* trees which are reliant on disturbances for regeneration (Horrocks & Ogden, 2000). Another explanation for the expansion of *Nothofagus* trees could be long-distance transport of Fuscospora pollen mainly derived from the beech forests on the wetter upland areas of the axial ranges of the North Island, which were probably less affected by the fires (Wilmshurst, 1997).

Though depositing a similar thickness of tephra to Taupo, c. 20 cm, the Waimihia eruption has not affected the vegetation at all. As indicated by Wilmshurst & McGlone (1996), the destruction of forest is not necessarily dependent on the thickness of tephra layers. Although the airfall tephra could destroy the vegetation to some extent, the vegetation could survive where protected from tephra fall on the leeward side of mountain ranges, or on steeper slopes, where ash is quickly removed by erosion (V. Neall, pers. comm). The recent volcanic eruption of Mt St. Helens, shows that the direct impact on the vegetation outside the actual blast zone was not severe and consisted mainly of mechanical damage to herbs by ashfall, the ash-coating of trees being largely washed off after the first rainfall (Mack, 1981). In fact, the most significant difference between the Taupo sequence and the other Waimihia and Whakatane sequences is the large amount of charcoal fragments which appeared with the Taupo eruption. Of course, the large pyroclastic flow-affected area is a possible source for these charcoal fragments. However, the existence of bigger charcoal particles (>50 μm), less likely to be wind dispersed, and the persistence of *Pteridium*, an early successional species, inevitably suggest long-lasting outbreaks of local fires. Thus the vegetation damage here is more likely to be related to fire outbreaks rather than tephra itself, and possibly due to climate conditions as well. If the fires and forest destruction around c. 2300 yr BP were human induced, as suggested above, people could also have played a role in forest destruction after the Taupo eruption.

To further explore these questions, detailed analysis on additional samples around both tephra and charcoal peaks is needed to get insight into the vegetation pattern in response to these disturbances, and to further understand the disturbance regime in this area.

## 3.5 Conclusions

Pollen analysis from the Tiniroto site indicated that directional change of forest composition over time is not apparent. However, the impact of both climate and volcanic disturbances could still be detected from the pollen diagram. The decline of *Dodonaea viscosa* and the subsequent forest invasion, which occurred in other places of the central North Island since c.4900 yr BP, might suggest an improvement of climate conditions with increasing precipitation. The forest around this site experienced significant destruction around 2300 yr BP due to a fire episode which was responsible for vegetation changing widely throughout the North Island. The intensified ENSO signals might indicate responsibility for these changes. The Taupo eruption has a much bigger impact on the vegetation than both the Waimihia and Whakatane eruptions, and the vegetation is more vulnerable to fire than deposition of tephra. However, an earlier than accepted arrival date for humans cannot be excluded.

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# Chapter Four

## Comparison of Vegetation Dynamics from Pollen Data of Sponge Swamp and Tiniroto Lakes

### Abstract

Many present vegetation peculiarities suggest a non-equilibrium situation in New Zealand, whether due to climate or disturbance. As a supplement to these short-time ecological observations, pollen records provide one of the most valuable sources of long-term data for a more complete understanding of vegetation dynamics in response to either climate or disturbance.

In order to test for equilibrium or non-equilibrium features of vegetation dynamics, and examine the impact of climate and disturbance on these vegetation dynamics in New Zealand, two sites were chosen: Sponge Swamp from Haast and Tiniroto Lakes from Gisborne, with different backgrounds of disturbance history. The role of climate in vegetation dynamics will be examined for each site; the pollen records from the stable site could provide a baseline for understanding pollen records in which changes occur, and could test the role of disturbance on vegetation dynamics from the other core.

Ordination analyses (PCA and RDA) were performed on pollen data to examine pattern change within each data set and to try to interpret this change with respect to environment variables. The sample scores of the first PCA axis of each data set were examined for stationarity with autocorrelation analysis.

The result of this study indicated that non-equilibrium characterized the vegetation dynamics in both sites, in which vegetation composition is changing continually

through time. However, the different pattern of change suggests that the underlying forcing mechanisms for non-equilibrium vegetation dynamics at each site are different.

In Sponge Swamp, change is steady and consistent over the whole time span. A consistent decline of *Ascarina lucida*, and subsequent expansion of *Gleichenia*, *Lycopodium australianum*, *Nothofagus*, *Phyllocladus*, *Halocarpus,* and *Prumnopitys taxifolia*, characterise this change. A climate gradient, from mild and wet to cooler and/or drier is responsible.

At Tiniroto, comparably steady and consistent vegetation change only occurred before c. 2300 yr BP, which is indicated by a forest invasion, a process of gradually replacing open land and light-adapted taxa, such as *Dodonaea viscosa*, *Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the family Fabaceae and Asteraceae, by increasing forest taxa. Climate amelioration with increased rainfall is suggested as the driving force for this vegetation change. After c. 2300 yr BP, this trend was frequently punctuated by disturbances like tephra layers and/or fires, in which sudden changes of vegetation occur, making substantial fluctuations about the trend. The climate gradient was thus partially masked by the outbreaks of disturbances.

Sample age explains more than 20% of the variance of species data from a RDA at both sites, associated with long-term forcing mechanisms such as directional climate change. In the Tiniroto site, additional variance is explained by charcoal and pollen taxonomic richness as well, suggesting the contribution of disturbance to vegetation dynamics.

After removing the climate gradient, comparison of vegetation behaviours between both sites indicates differences in response to disturbances. In Sponge Swamp, the vegetation composition is affected by various “random” events, such as floods or landslides caused by earthquakes etc., and there is little dependence of the present state of vegetation composition on its past state. This is due to the nature of these disturbances which are independent of vegetation structure and stage of development. In the Tiniroto site, the impact of catastrophic disturbances, such as fires and volcanic eruptions, on the vegetation is substantial and often influenced by its structure; thus the vegetation composition is expressed in a more successional way, i.e. the present state of vegetation depends only on the immediate past state.

Consequently, in places free from catastrophic disturbances in New Zealand, like southern Westland, the present vegetation structure is generally determined by the current climate conditions. In places subjected to big disturbances, such as the central North Island, the forest structure is basically determined by the most recent disturbances in spite of climate. This explains the dominance of podocarp forest in the central North Island.

## 4.1 Introduction

Forest cover in New Zealand has been greatly reduced due to human activities. Nearly 50% of New Zealand forest has been converted to pasture, compared with a world average of only 25% (Taylor, 1997). Protecting and restoring indigenous forest has become a big conservation issue in New Zealand. The study of vegetation dynamics is one of the keys giving solutions to these problems, and offers evidence for conservation management.

Over time, endogenous biotic interactions have been suggested to stabilise ecosystems leading to equilibrium dynamics, though these can be disrupted by environmental perturbations. Many vegetation peculiarities suggest a non-equilibrium situation in New Zealand, in which climate and disturbance are two major factors. However, whether climate or disturbance is directly responsible for the present forest structure has not yet been satisfactorily resolved. One of the major problems in the native forest of New Zealand is the apparently inadequate regeneration of most canopy trees, such as *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Podocarpus totara, Libocedrus bidwillii* and *Agathis australis.* This is known as a “regeneration gap” (Cockayne, 1928; Holloway, 1954; Wardle, 1963; June, 1982). Early research in forest dynamics ascribes this “regeneration gap” either to a feature of the subterminal stage in a succession towards a climax of broadleaved trees

(Cockayne, 1928; Robbins, 1962), or to disequilibrium with the climate (Holloway, 1954; Wardle, 1963). Thus a recent climate change with increasing aridity and decreasing temperature was suggested from this peculiarity (Grant, 1963; Wardle, 1963, 1978). Only recently has it been realized that disturbance might be responsible for these forest structures, and that the "regeneration gap" may be a response to disturbance of the particular regeneration ecology of the species involved (Veblen & Stewart, 1982; Morton et al., 1984; Wells, 2001).

Because of the longevity (centuries to millennia) of the trees in New Zealand forest (Ogden, 1985), the current forest structure could either be regarded as a fusion of remnants of vegetation in equilibrium with the previous climate (Holloway, 1954; Wardle, 1963), or be interpreted as a consequence of the impact of previous, large disturbances that have no counterpart in the recent past (Foster et al., 1998). Most of the interpretations are based on short-time studies, like age structure of forest tree cohorts. Such time scales are too short to gain a holistic understanding of forest dynamics. Vegetation should be monitored for at least the length of time taken for one complete turnover of individuals of all species in the community, to demonstrate the vegetation dynamics (Connell & Sousa, 1983).

Palynology offers a powerful tool, with the capacity to investigate both small and large time scales. With the additional information of proxies for disturbances from the sediments, like tephra for volcanic eruptions and charcoal for fires, and climate evidence from comparisons with regional pollen records or other independent evidence, pollen records could provide one of the most valuable sources of long-term data for a more complete understanding of vegetation dynamics in response to either climate or disturbances.

In order to test the impact of climate and disturbance on vegetation dynamics in New Zealand, two different sites were chosen to reconstruct vegetation dynamics over several thousand years. One site from Sponge Swamp, near Haast, is recognized as a stable site without any catastrophic disturbance in the recorded history since c. 7300 yr BP (refer to Chapter 2). The other one is selected from Tiniroto district, Gisbrone, an area which has been subjected to many big disturbances, including three volcanic eruptions, and fires throughout the core. The pollen records from the more stable site will be used to provide a baseline for understanding changes in pollen records from the other core which might be attributed to disturbance.

## 4.2 Methods

### 4.2.1 Pollen Analysis

73 pollen samples were analysed at 10cm intervals from a sediment core taken from Sponge Swamp, near Haast in southern Westland, and another 53 samples at the same interval were taken from a core collected from a small swamp east of Lake Waihau, one of the Tiniroto Lakes, in the Gisborne region. The two cores dated back to c. 7600 yr BP and c. 5300 yr BP respectively. The treatment for pollen followed the standard procedures (refer to Chapter 2). A minimum of 300 terrestrial pollen grains were counted for each sample, and pollen counts were calculated and presented in the form of relative frequencies based on the pollen sum of all terrestrial pollen and spores. Percentages of aquatic and mire taxa were calculated upon pollen sum and their own pollen totals. Charcoal fragments were recorded in categories according to their size measurements.

### 4.2.2 Ordination Analysis

Ordination is the term for multivariate analyses that arrange sites along axes on the basis of data on species composition, in which points that are close together correspond to sites that are similar in species composition. Detrended Correspondence Analysis, Principal Component Analysis and Redundancy Analysis were performed on pollen data from both sites for species with three or more occurrences in the sequence. The data sets are all compositional data, which have the constraint that the components must sum to unity. A curvature is usually displayed by such compositional data in ordination analyses, which makes them inappropriate to linear techniques (Aitchison, 1983). So, a log-ratio centering transformation suggested by Aitchison (1982, 1983) was applied to the data sets prior to ordination analysis, in order to decrease the curvature.

As the study of vegetation dynamics focuses on terrestrial taxa, all aquatic and mire taxa were made supplementary in all analyses. Samples with extremely high percentage values of individual taxa, i.e. 6.85 m in the Sponge Swamp data set, 1.35 m and 3.03 m in the Tiniroto data set are also used supplementarily in the analyses, since they were probably local effects when individual plants with poorly dispersed pollen occurred very close to the core sites. Two samples at the top of the Tiniroto site, at 0.25 m and 0.35 m, were also used supplementarily, because of the extremely high percentages of *Pteridium* spores and other exotic taxa, which will dominate the analyses and mask important aspects of other samples. Supplementary samples or species do not influence the ordination axes, but are added afterwards so that their relation to the other samples or species can still be judged from the ordination diagram. All ordination analyses were conducted by the program CANOCO 4.5 (ter Braak & Smilauer, 2002)

### 1. Detrended Correspondence Analysis (DCA)

DCA is an ordination technique developed by Hill and Gauch (1980), and is a modification of Correspondence Analysis. It is a technique that constructs the theoretical variable that best explains the species data. The detailed mechanics and algorithm of DCA can be found in Jongman et al. (1995) and in ter Braak (1996).

Each axis produced by DCA is scaled in standard deviation (SD) units, and reflects the amount of biological turnover within that axis (gradient length). DCA assumes species display a unimodal response curve to environmental gradients, with a bell shaped curve of abundance over 4 SD units. Samples which differ by more than 4 SD have few taxa in common, while a change of 1 SD units or more (up to 1.39 SD for data entirely free of noise) reflects a 50% change in sample composition (Hill & Gauch, 1980). Gradient length is fundamental to the choice of ordination technique because, over short gradients, taxa respond in a linear fashion, while over longer gradients taxa rise and fall in a unimodal manner (ter Braak & Prentice, 1988).

Accordingly, DCA was used initially to estimate the length (SD) of the floristic gradient in each data set with detrending by segments, which is a guide to whether linear or unimodal-based ordination methods are appropriate. If the data set has a relatively short gradient length, a linear ordination method, Principal Component Analysis (PCA) would be used.

## 2. Principal Component Analysis (PCA)

PCA is a linear response model. It is the ordination technique that constructs a theoretical variable that minimizes the total residual sum of squares after fitting straight lines to the species data. In other words, PCA finds a linear combination of the species data, that has as large a variance as possible, and this combination is used to depict the sample scores. Thus PCA searches for the direction of maximum variance for the sample scores. The variances of sample scores are measured by the eigenvalues of the axes, and the eigenvalue of each axis is related to the amount of variation explained by the axis. The detailed mechanics and algorithm of PCA can be found in Jongman et al. (1995).

The scores obtained from a PCA for species and sites can be used to prepare a biplot. Sites are marked by points, and species are marked by arrows (arrows are hidden in the species plots presented in the following results). The direction of the arrow indicates the direction of maximum variation in species abundance, and its length is proportional to its maximum rate of change.

PCA was performed on pollen data sets for each site separately, and on a pollen data set with both sites combined as well, in order to compare the vegetation composition and change of vegetation pattern over time for the two sites. Distances (number of standard deviations) between the adjacent samples (≈c. 100 yr), calculated from the scores of the first four axes of the individual PCA, were plotted against the sample depth, generating the rate of change in pollen spectra over time.

If the theoretical variable constructed from the PCA is further correlated with environmental variables, Redundancy Analysis will be used.

## 3. Redundancy Analysis (RDA)

### *Modelling and evaluating environmental variables in RDA*

RDA is the constrained form of PCA. It is the technique selecting the linear combination of environmental variables that gives the smallest total residuals, sum of squares after fitting it to the data of each species. The site scores are restricted to a linear combination of environmental variables, so the RDA is simply PCA with a restriction on the site scores. The species-environment correlation is calculated by the correlation between the site scores that are weighted sums of the species scores and the site scores that are a linear combination of the environmental variables. If the correlations are high, the environmental variables account for the main variation in the species composition.

Canonical coefficients define the ordination axes as linear combinations of the environmental variables, and the intra-set correlations are the correlation coefficients between the environmental variables and the ordination axes. Both canonical coefficients and intra-set correlations are used to interpret the RDA axes.

RDA enables the effect of environmental variables on a multivariate data set to be modelled and evaluated statistically (ter Braak, 1994). Through the use of Monte Carlo permutation tests, RDA could assess whether the pollen composition changes associated with environmental phenomena are no more likely than what would be expected by chance. Further more, the importance of environmental variables could be ranked by their marginal and conditional effects on the pollen data set (ter Braak & Verdonschot, 1995). The marginal effects are on the basis of the fit for each separate environmental variable, and the measure of fit is the first eigenvalue of the RDA with each one variable as the only environmental variable. The conditional effects are based on the fit that each separate environmental variable gives in conjunction with the variables already selected, and the measure of fit is the sum of all eigenvalues of the RDA with each variable as the only additional environmental variable. The statistical significances of the effects of environmental variables are tested by the Monte Carlo permutation tests.

*Measurements of environmental variables in this study*

The environmental variables used for RDA were charcoal fragments, loss-on-ignition, sample age, pollen richness, tephra effect and aquatic conditions. All environmental variables were standardized before being applied in RDA. Each variable is explained below.

*(1) Charcoal fragments*

Number of total charcoal particles was used here as representative of the effect of each fire episode.

*(2) Loss-on-ignition (LOI)*

The organic matter of the sediments has been estimated using LOI (Dean, 1974). It is a measure of the extent of erosion processes bringing non-organic matter into the sediments. However, the frequent occurrence of molluscs below 2.6 m in the Tiniroto core probably indicates the presence of autogenic carbonate in the lake. Thus the LOI value from the Tiniroto site could, to some extent bias the interpretation of LOI, as a measure of erosion processes.

*(3) Sample age*

The calibrated AMS $^{14}C$ ages were used in the analysis. Variance explained by sample age therefore is associated with long-term forcing mechanisms such as unidirectional climate change.

*(4) Pollen richness (E(Tn))*

*E(Tn)*, known as partial floristic richness of the past vegetation, was estimated at each sample time by rarefaction analysis (Hurlbert, 1971; Birks & Line, 1992;). An estimate of *E(Tn)* is given by

$$E(Tn) = \sum_{i=1}^{T} 1 - \left[ \frac{\binom{N-Ni}{n}}{\binom{N}{n}} \right] = \sum_{i=1}^{T} \left[ \frac{(N-Ni)!(N-n)!}{(N-Ni-n)!N!} \right] \qquad \text{(eqn. 4.1)}$$

where

$N$ is the total number of grains counted in the sample;

$n$ is the number of individual grains (count size) chosen for standardisation ($n \leq N$) in the rarefied sample, usually the smallest total count in the samples to be compared;

$T$ is the number of pollen types in the original pollen count;

$E(Tn)$ is the expected number of pollen types in a sample of n individual grains selected at random without replacement from a count of $N$ grains containing $T$ taxa;

$Ni$ is the number of individual grains assigned to pollen type $i$ in the original pollen count;

$\binom{N}{n}$ is the number of combinations of $n$ grains which can be drawn from a count of $N$ grains;

$\binom{N-Ni}{n}$ is the number of combinations of $n$ grains that can be drawn randomly from the count of $N$ grains without drawing any grains of taxon $i$.

(5) *Tephra effect*

The likely effects of tephra ($Te$) with time were modelled as a simple exponential decay process in the vegetation subsequent to the tephra deposition, based on Lotter & Birks (1993) by

$$Te = \begin{cases} 0 & \text{prior to deposition of tephra} \\ Dx^{-\alpha t} & \text{after deposition of tephra} \end{cases} \qquad \text{(eqn. 4.2)}$$

where

$Te$ is the tephra effect;

$D$ is the thickness of tephra;

$x$ is the assigned value for tephra, which is given a value of 4 at the time of tephra deposition (in order to be consistent with the change of aquatics, which are possibly sensitive to tephra deposition), and after deposition it decreases exponentially;

$\alpha$ is the decay coefficient, which is given a value of 0.5 as suggested by Lotter and Birks (1993);

$t$ is the depth above the tephra layer (as a surrogate for sample age) .

(6) Water level

All aquatic and mire taxa are analysed by PCA separately and the sample scores of the first axis are indicative of aquatic conditions in terms of changing with water level or nutrient level. For the Sponge Swamp site, the first PCA axis explains nearly 50% of the total variance of the mire taxa, and the first axis mainly represents a change of composition from relatively more *Carex* (left) to more components of *Empodisma minus* and Cyperaceae (right). Possibly a gradient towards lower nutrient level is also suggested. For the Tiniroto site, the first PCA axis which explains 66% of the total variance chiefly indicates an aquatic complex with increasing components of Cyperaceae and Typha, possibly a change to lower water level.

### 4.2.3 Time Series Analysis

Since the correlation of sample age is almost linear with sample depth in both sites, samples with the same interval in depth are assumed to have the same time intervals, which is a prerequisite for time series analysis. However, this assumption is violated for samples from Sponge Swamp site, since the sedimentation rate before c. 6000 yr BP is slightly lower than that after this time. Due to this, time series analyses are only used for qualitative comparisons of vegetation behaviours from both sites. For the Tiniroto site, only samples taken at 10 cm intervals are applied in this analysis. Since the sample scores of the first PCA axis recapitulate the major changes of vegetation composition, the ways they change were used as indications of vegetation dynamics (Franklin & Tolonen, 2000). The sample scores of the first PCA axis from both sites were examined for stationarity with autocorrelation analysis. The autocorrelation function (ACF) is estimated by calculating the correlation coefficients between pairs of observations Lt-τ and Lt separated by lag τ (τ=1,2,...). These correlation coefficients are then plotted as a function of lag τ in an autocorrelogram (Chatfield, 1996). The shape of the estimated ACF provides insights regarding two aspects of vegetation dynamics: stationarity and nonstationarity. A process is stationary if its dynamic properties do not change during the period of study. A stationary process is indicated by a fluctuation around its constant mean level, with constant variances. The ACF of a stationary process is characterized by an exponential decay of autocorrelation coefficients to zero, either monotonically or oscillatorily (Box and Jenkins, 1994). The autocorrelogram of a nonstationary community is characterized by a nonexponential, but continual decrease in autocorrelation with increasing lags.

## 4.3 Results

The results of DCA from both sites (Table 4.1) indicate that the gradient lengths of two data sets are relatively short (<1.4SD), which means that there is not too much difference between the samples at opposite ends of the first DCA axis. Thus the linear ordination method (PCA) was appropriate to use for further analysis.

**Table 4.1** Summary results of DCA and PCA for data sets from the Sponge Swamp and Tiniroto sites. Value * indicates the result from that part of the data set from Sponge Swamp which is relevant to that of the Tiniroto site, with same time span. Value$^{se}$ indicates the species-environment correlation (r) of the associated axis.

| | Sponge Swamp | Tiniroto Lakes |
|---|---|---|
| Number of samples | 73 | 50 |
| Number of taxa | 54 | 55 |
| Gradient length (SD) | 1.171 (1.051*) | 1.377 |
| Total inertia in DCA | 0.672 (0.551*) | 0.778 |
| Eigenvalue of PCA axis 1 | 0.270 | 0.265 |
| Eigenvalue of PCA axis 2 | 0.147 | 0.153 |
| Eigenvalue of RDA axis 1 | 0.221 (0.91$^{se}$) | 0.233 (0.95$^{se}$) |
| Eigenvalue of RDA axis 2 | 0.04 (0.74$^{se}$) | 0.065 (0.75$^{se}$) |

### 4.3.1 Pollen Data from the Sponge Swamp

General description of groups from PCA

Brief descriptions of the groups based on PCA are presented here to help give the detailed frame of vegetation composition change over time. Five pollen zones classified in the pollen percentage diagram (see Chapter 3), were identified as temporal associations in the PCA scatter plot, denoted as SS1 (5.45-7.25 m), SS2 (2.55-5.35 m), SS3 (0.95-2.45 m), SS4 (0.25-0.85 m) and SS5 (0.05-0.15 m), within a continually changing pollen sequence (Fig. 4.1). Among these groups, SS1 was subdivided by SS1a (6.35-7.25 m) and SS1b (5.45-6.25 m), and SS3 by SS3a (1.75-2.45 m) and SS3b (0.95-1.65 m). Approximately 42% of the variance in the species data was explained by the two PCA axes (Table 4.1).

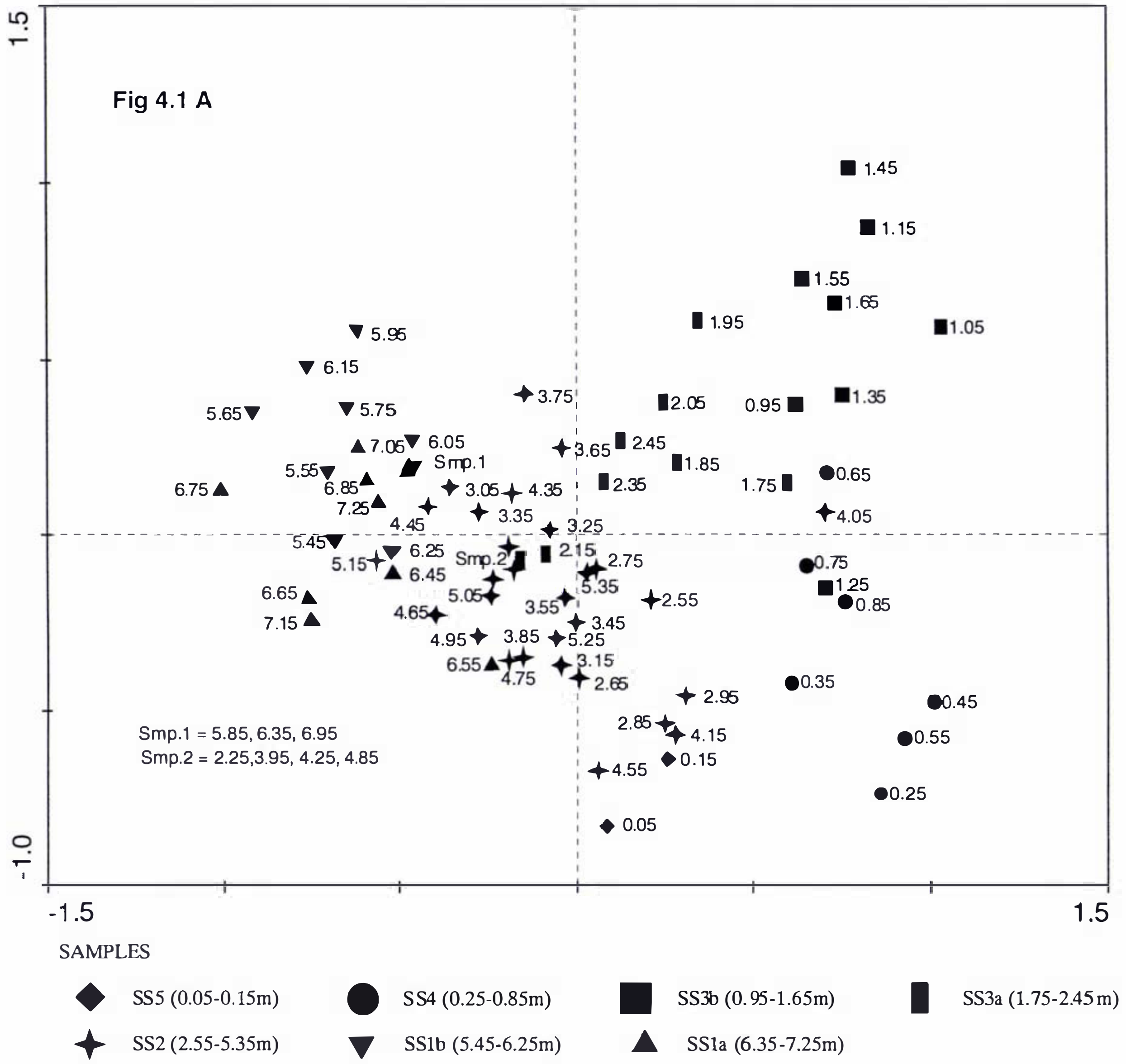


Fig 4.1 A

1.5
-1.0
-1.5
1.5
1.45
1.15
1.55
1.65
1.05
1.95
5.95
6.15
3.75
2.05
0.95
1.35
5.65
5.75
7.05
6.05
3.65
2.45
Smp.1
1.85
5.55
6.85
3.05
4.35
2.35
1.75
0.65
6.75
7.25
3.35
4.05
4.45
3.25
5.45
6.25
2.15
2.75
0.75
5.15
Smp.2
6.45
5.35
1.25
6.65
5.05
3.55
2.55
0.85
4.65
7.15
3.45
4.95
3.85
5.25
3.15
6.55
4.75
2.65
0.35
2.95
0.45
2.85
4.15
0.55
0.15
4.55
0.25
0.05
Smp.1 = 5.85, 6.35, 6.95
Smp.2 = 2.25,3.95, 4.25, 4.85
SAMPLES
◆ SS5 (0.05-0.15m)
● SS4 (0.25-0.85m)
■ SS3b (0.95-1.65m)
▮ SS3a (1.75-2.45m)
✦ SS2 (2.55-5.35m)
▼ SS1b (5.45-6.25m)
▲ SS1a (6.35-7.25m)

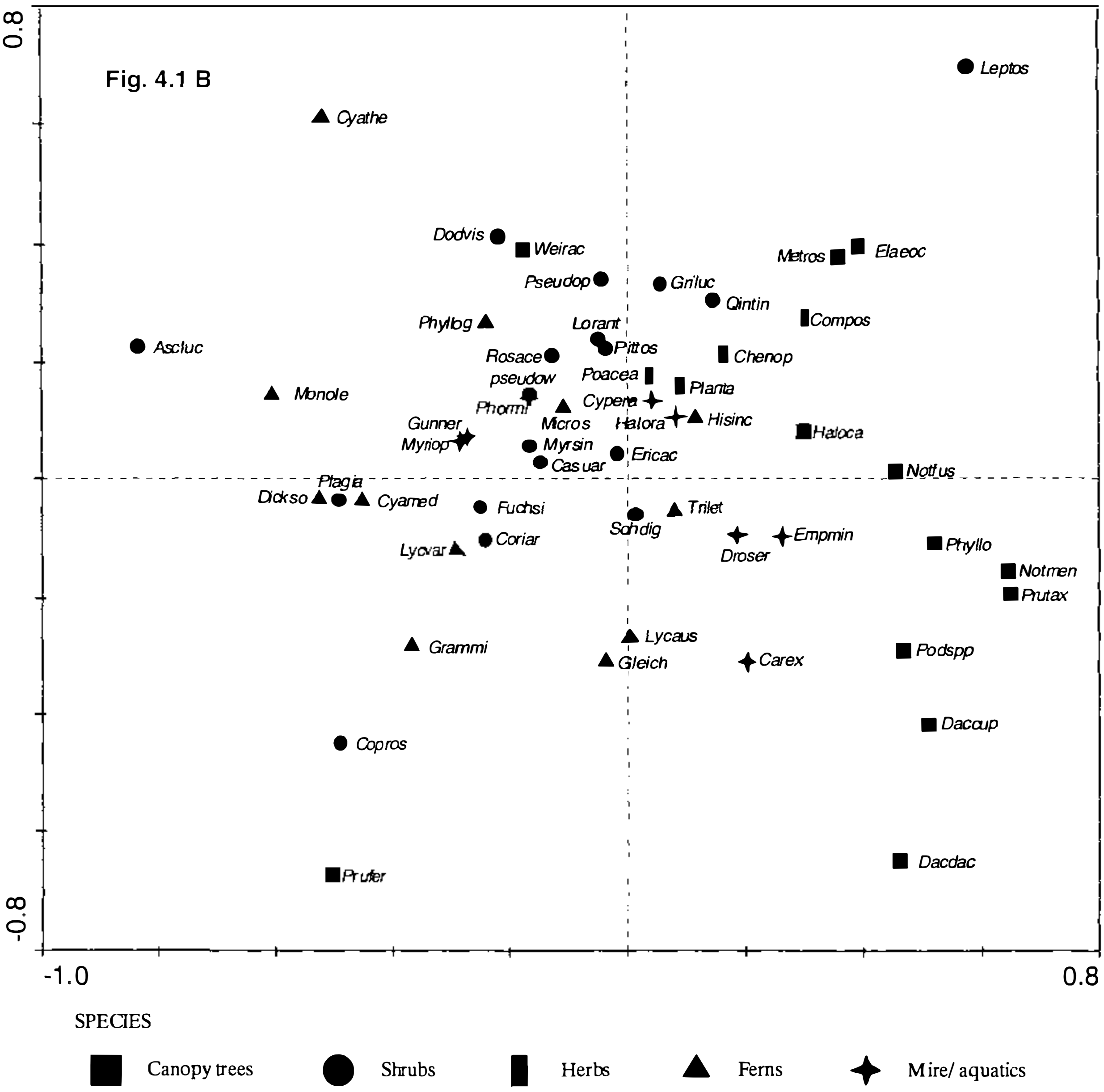


**Fig. 4.1** Scatter plot of the sample (A) and taxon (B) scores for the first two PCA axes of pollen data from Sponge Swamp. (A) The sample names represent sample depth, and some samples with positions near the centre are coded to avoid crowding. (B) For the full names of the taxa see Appendix 1.

SS1 is substantially dominated by *Ascarina lucida* with relatively common occurrences of ferns, such as *Cyathea, Cyathea medullaris, Dicksonia* and monolete fern allies. SS1a is separated from SS1 by relatively its high frequency of *Coprosma* in addition to those features. SS2 is scattered a little wide, and generally comprises relatively high frequencies of *Dacrycarpus dacrydioides, Lycopodium australianum* and *Gleichenia*. Generally speaking, SS1 and SS2 have more common taxa in their composition. Subsequent to SS3, vegetation composition started to change by a further decline of *Ascarina lucida*, *Coprosma* and fern allies, and *Dacrycarpus dacrydioides* and *Prumnopitys ferruginea* as well. SS3b is specially characterized by predominance of *Leptospermum* with relative importance of *Elaeocarpus* and *Metrosideros*. A progressive increase of beech trees and other big trees, e.g. *Phyllocladus*, *Prumnopitys taxifolia*, and *Halocarpus* occurred with SS4. However, these big trees decrease again in SS5 and make the composition of SS5 more close to SS2.

### Environmental gradients derived from RDA

As RDA restricts the axes to linear combinations of the submitted environment variables, the first two RDA axes explain less variance than the PCA axes do, namely only 26.8% (Table 4.1). Since the first two species-environment correlations are 0.91 and 0.74 from the analysis, it seems that the environmental variables account for the main variation in species composition (Fig. 4.2). From Table 4.2, the first axis is mainly an age or LOI gradient; the second axis is more related to a change of aquatic condition and pollen diversity. The rank of the importance of environment variables is summarized in Table 4.3. The impact of charcoal on vegetation composition is not statistically significant.

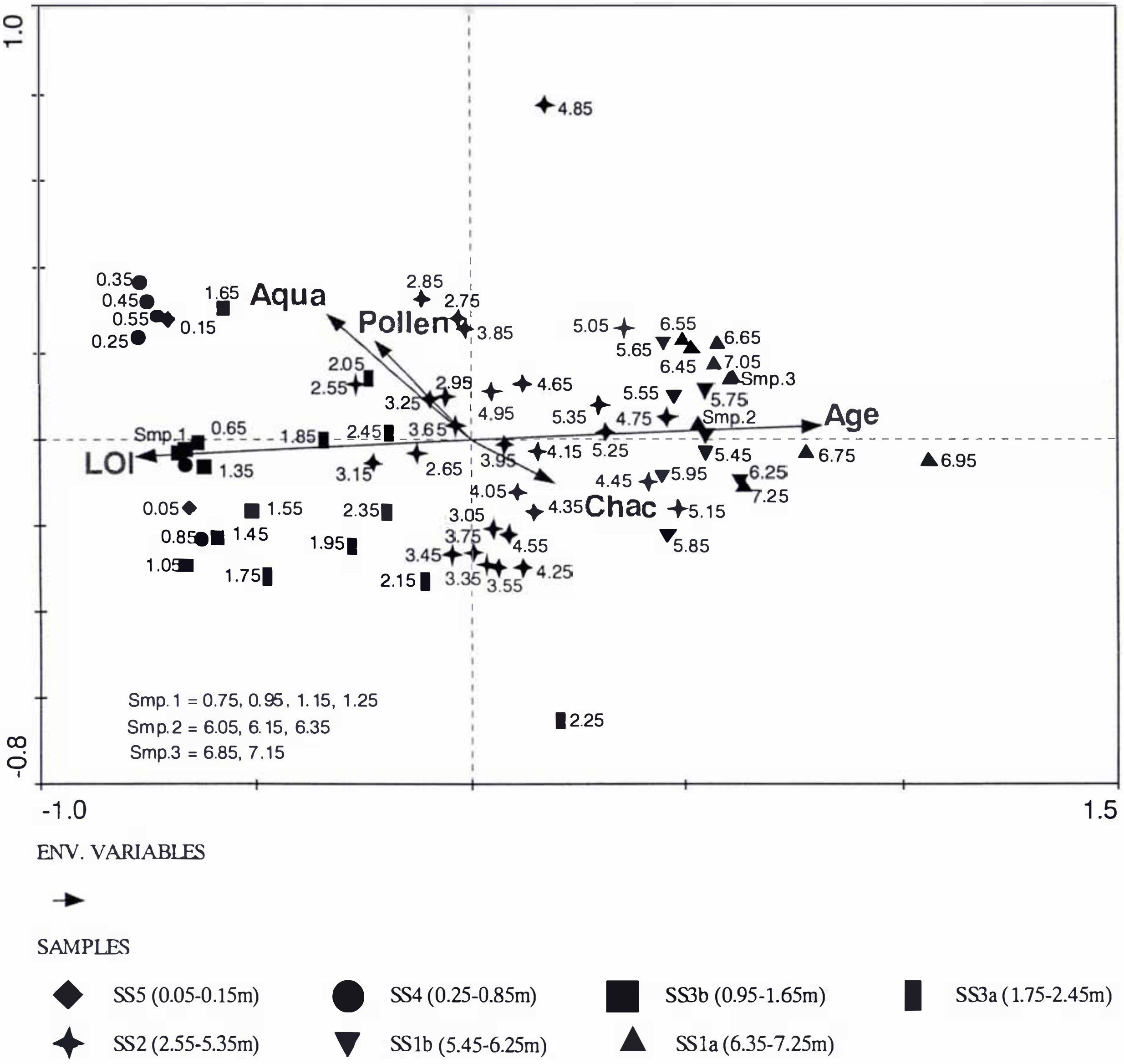


**Fig. 4.2** Scatter plot of the sample scores for the first two RDA axes of pollen data from Sponge Swamp. The sample names represent sample depth, and some samples with positions close together and coded to avoid crowding. The environmental variables are: Age = calibrated sample age, LOI = loss on ignition, Pollen = pollen richness, Chac = charcoal fragment, Aqua = aquatic conditions.

**Table 4.2** RDA: canonical coefficients and intra-set correlations of standardized environmental variables with the first two axes of the RDA for the pollen data from Sponge Swamp.

| Variable | Coefficients (100×c) | | Correlations (100×r) | |
|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Charcoal | 9 | -5 | 21 | 18 |
| LOI | -15 | -2 | -84 | 8 |
| Pollen richness | -3 | 11 | -24 | 43 |
| Sample age | 32 | 9 | 87 | 6 |
| Aquatic condition | 0.2 | 18 | -35 | 54 |

**Table 4.3** Environmental variables ranked in importance by their marginal and conditional effects on the pollen data from Sponge Swamp. $\lambda_1$ = eigenvalue with variable j only; $\lambda_a$ = increase in eigenvalue; cum ($\lambda_a$) = cumulative total of eigenvalues $\lambda_a$; P = significance level of the effect, as obtained with a Monte Carlo permutation test under the null model with 499 random permutations.

| Marginal effects | | | | Conditional effects | | | | |
|---|---|---|---|---|---|---|---|---|
| j | Variable | $\lambda_1$ | P | j | Variable | $\lambda_a$ | P | cum($\lambda_a$) |
| 1 | Sample age | 0.21 | 0.002 | 1 | LOI | 0.19 | 0.002 | 0.19 |
| 2 | LOI | 0.19 | 0.002 | 2 | Aquatic condition | 0.04 | 0.002 | 0.23 |
| 3 | Aquatic condition | 0.07 | 0.002 | 3 | Sample age | 0.03 | 0.002 | 0.26 |
| 4 | Pollen richness | 0.04 | 0.006 | 4 | Pollen richness | 0.02 | 0.006 | 0.28 |
| 5 | Charcoal | 0.02 | 0.082 | 5 | Charcoal | 0.02 | 0.080 | 0.30 |

## Vegetation dynamics at Sponge Swamp site

Since the first PCA axis explains the greatest variance of the species data, the sample scores of the first PCA axis are thus the best summary of the community dynamics as a means of tracing the change of species composition. Autocorrelation of the PCA ordination scores (i.e., community dynamics) for the entire pollen profile was typically nonstationary (Fig. 4.3a), so that there was no greater correlation between adjacent time periods than expected. A gradual trend was suggested and indicated that the pollen community continuously changes over time. This result indicates either "random walk" dynamics, or environmental changes occurring throughout the pollen profile. However, the autocorrelation on the detrended sample scores shows a significant correlation with time lag 1 (Fig. 4.3b). A first-order moving average (MA1) process is suggested by this feature (Cryer, 1986). Thus besides the continuous change over time, the community behaviour is suggested as:

$$x_t = a_t - \theta a_{t-1} \qquad \text{(eqn. 4.3)}$$

where

$x_t$ is the sample score of PCA axis 1 at time $t$;

$a_t$ is the white noise at time $t$, which is a purely random process with constant mean and variance;

$\theta$ is the parameter.

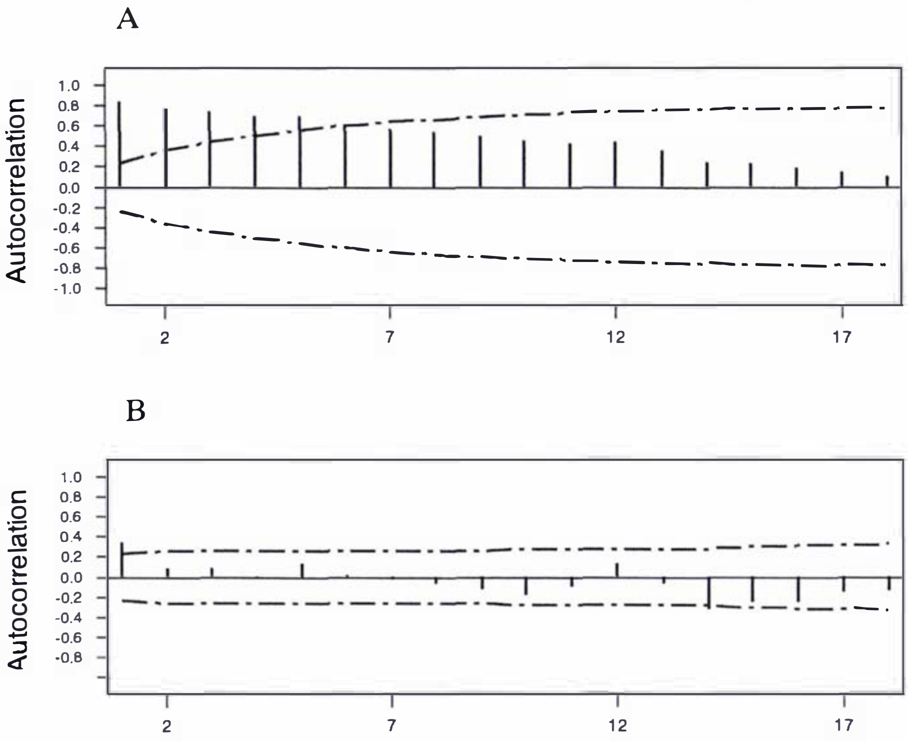


**Fig. 4.3** Autocorrelation analysis of sample scores of the first PCA axis from the data set of the Sponge Swamp site. (A) Autocorrelation on sample scores; (B) autocorrelation on detrended sample scores. The x axis is in unit time-lags, and y axis is the autocorrelation coefficient at different time-lags.

### 4.3.2 Pollen Data from the Tiniroto Lakes

General description of groups from the PCA

About 40% of the total variance of species data is explained by the first two PCA axes (Table 4.1). The four pollen zones identified in the pollen percentage diagram (see Chapter 3) are not clearly grouped in the PCA scatter plot. However, six groups divided by the onset of disturbances, i.e. Whakatane tephra (Wh), Waimihia tephra (Wa), big charcoal occurrence at 2.25 m (C2), Taupo tephra (TP), and charcoal peak at 0.95 m (C1), are clearly shown on the Fig. 4.4. Generally, the lowest zone, TN1 (pre-Wh, 4.66-5.11 m) mainly consists of *Dodonaea viscosa, Pteridium,* Fabaceae, and unidentified Podocapaceae. Within TN2 (post-Wh → pre-Wa, 3.36-4.60 m), all these taxa drop obviously while more shrub taxa occur. The distribution of samples within TN3 (post-Wa → pre-C2, 2.25-3.14 m) is scattered rather widely. Although the species composition seems to deviate from the previous groups, there is not much indication of taxa specific to this group except for increasing levels of broadleaved trees. TN4 (post-C2 → pre-TP, 1.85-2.15 m), however, is typified by a large increase of fern allies with monolete spores and *Dicksonia* compared with TN3.

The composition of TN5 (post-TP~pre-C1, 0.95-1.60 m) starts differently from the previous groups, by gradually increasing components of *Prumnopitys ferruginea, Prumnopitys taxifolia* and *Nothofagus menziesii*, though in small magnitude. TN6 (post-C1, above 0.95 m) is dominated by *Leptospermum* and *Dicksonia*.

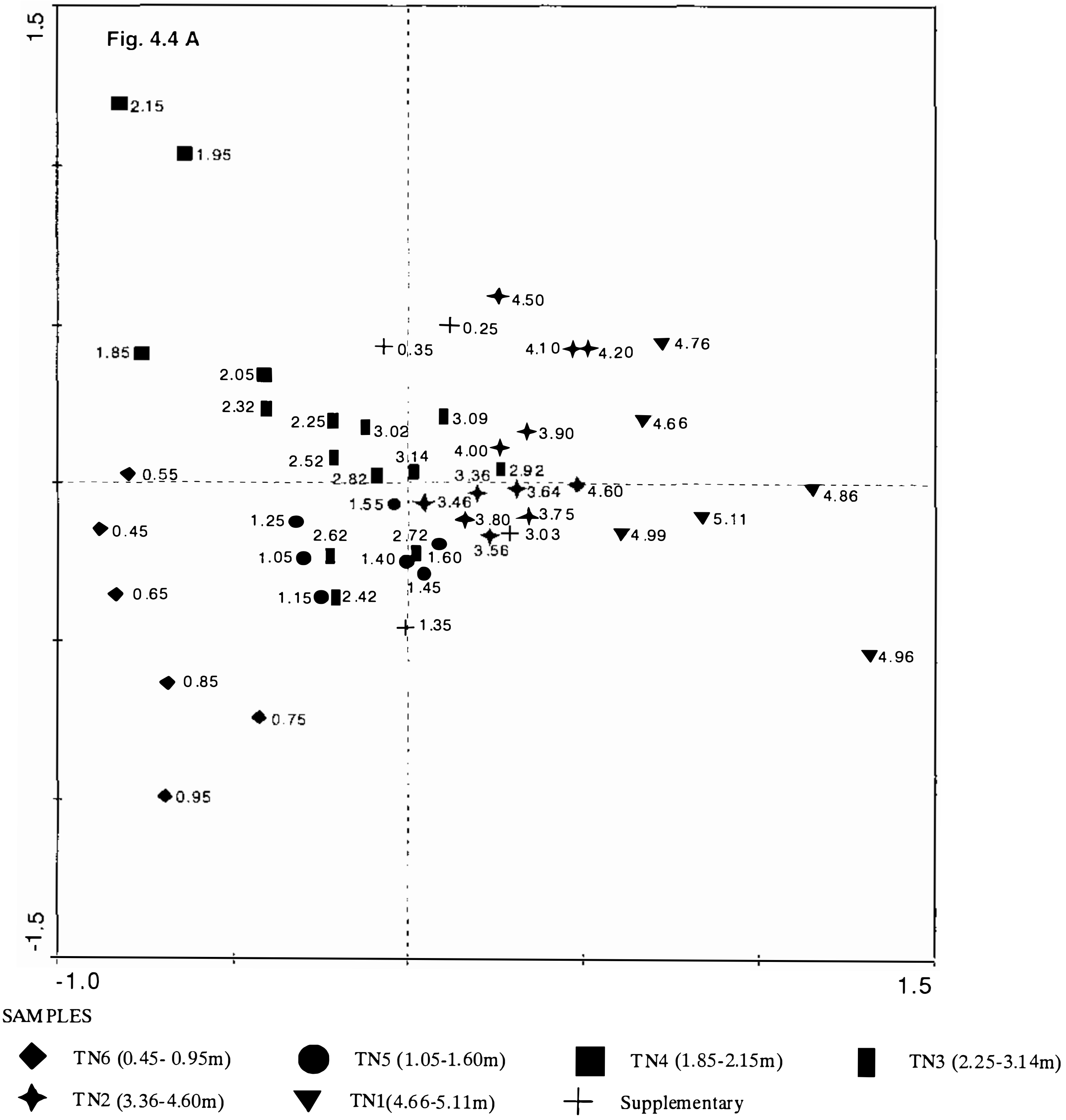


Fig. 4.4 A

1.5
-1.5
-1.0
1.5
2.15
1.95
4.50
0.25
0.35
4.10
4.20
4.76
1.85
2.05
2.32
2.25
3.02
3.09
3.90
4.66
4.00
2.52
3.14
0.55
2.82
3.36
2.92
3.64
4.60
4.86
1.55
3.46
1.25
3.80
3.75
5.11
0.45
2.62
2.72
3.03
4.99
1.05
1.40
1.60
3.56
1.45
0.65
1.15
2.42
1.35
4.96
0.85
0.75
0.95
SAMPLES
TN6 (0.45- 0.95m)
TN5 (1.05-1.60m)
TN4 (1.85-2.15m)
TN3 (2.25-3.14m)
TN2 (3.36-4.60m)
TN1(4.66-5.11m)
Supplementary

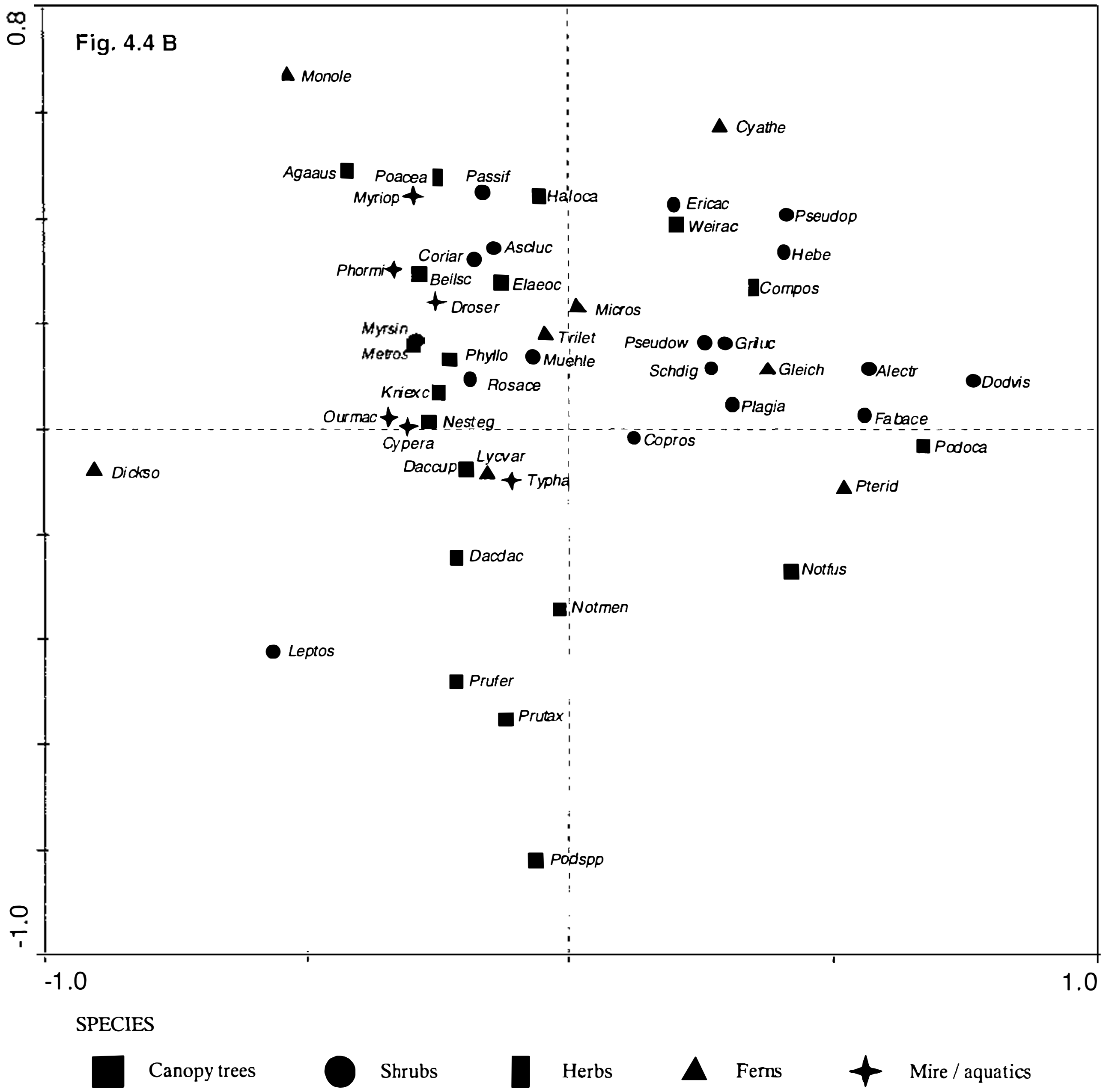


**Fig. 4.4** Scatter plot of the sample (A) and taxon (B) scores for the first two PCA axes of pollen data from the Tiniroto site. (A) The sample names represent sample depth; (B) For the full names of the taxa see Appendix 1.

### Environmental gradients derived from RDA

Almost 30% of the variance in species data was explained by the first two RDA axes (Table 4.1). Since the first two species-environment correlations are 0.95 and 0.75 from the analysis, it seems that the environmental variables account for the main variation in species composition (Fig. 4.5). According to the intra-set correlation (from Table 4.4), the first axis of RDA is indicated as a LOI or age gradient, and the second axis displays a gradient of charcoal and pollen richness (Fig. 4.5). The effects of tephra, and the aquatic condition are not statistically significant on vegetation in this site. The importance rank of environment variables is listed in Table 4.4.

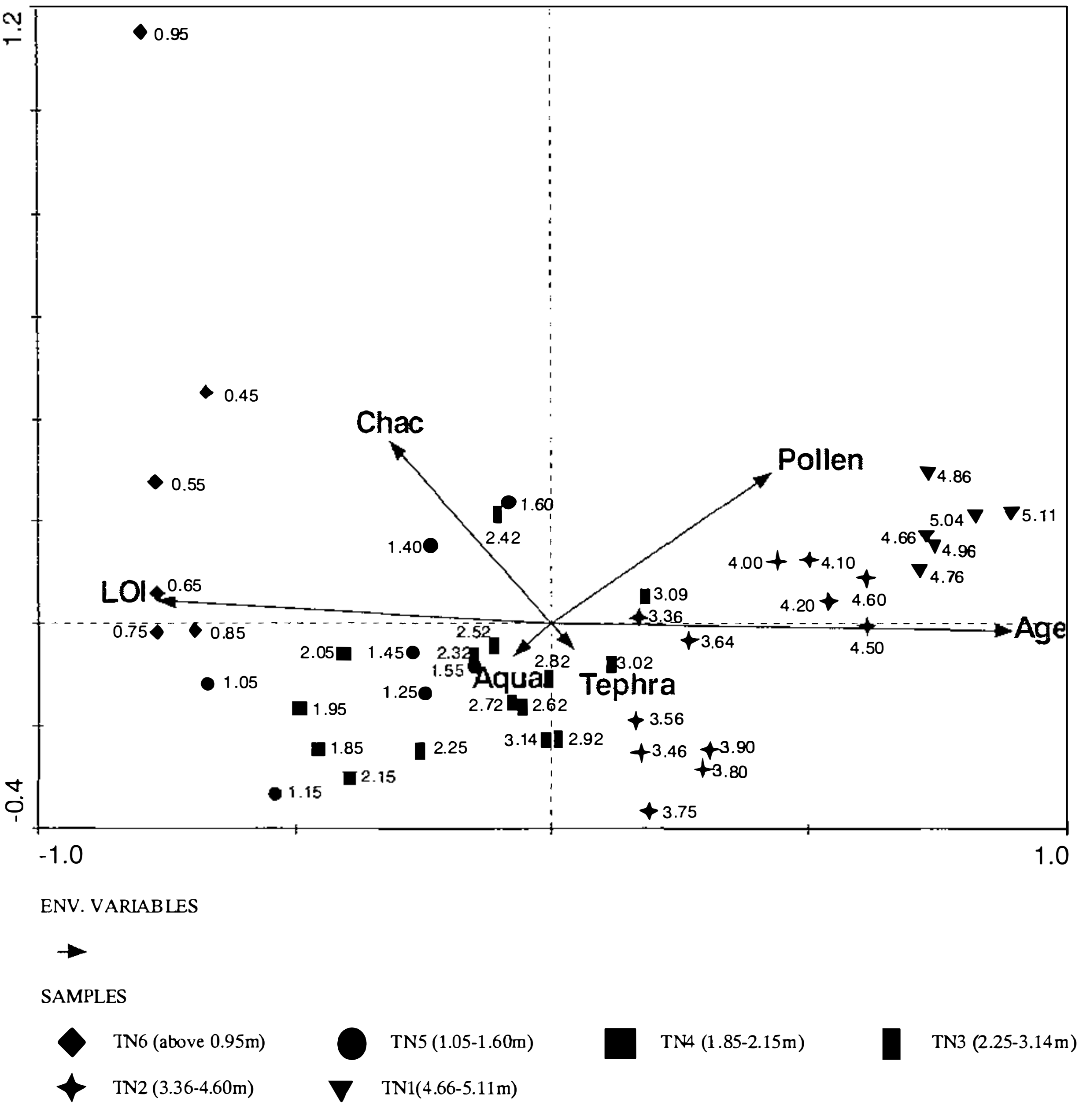


**Fig. 4.5** Scatter plot of the sample scores for the first two RDA axes of pollen data from the Tiniroto site. The sample names represent sample depth. The environmental variables are: Age = calibrated sample age, LOI = loss on ignition, Pollen = pollen richness, Chac = charcoal fragment, Aqua = aquatic conditions.

**Table 4.4** RDA: canonical coefficients and intra-set correlations of standardized environmental variables with the first two axes of the RDA for the pollen data from the Tiniroto site.

| Variable | Coefficients (100×c) | | Correlations (100×r) | |
|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Charcoal | -1 | 19 | -33 | 56 |
| LOI | -10 | -3 | -80 | 7 |
| Pollen richness | 5 | 17 | 44 | 46 |
| Sample age | 39 | -4 | 93 | -2 |
| Tephra | -3 | -2 | 4 | -7 |
| Aquatic condition | 3 | 5 | -8 | -9 |

**Table 4.5** Environmental variables ranked in importance by their marginal and conditional effects on the pollen data from the Tiniroto site. $\lambda_1$ = eigenvalue with variable j only; $\lambda_a$ = increase in eigenvalue; cum ($\lambda_a$) = cumulative total of eigenvalues $\lambda_a$; P = significance level of the effect, as obtained with a Monte Carlo permutation test under the null model with 499 random permutations

| Marginal effects | | | | Conditional effects | | | | |
|---|---|---|---|---|---|---|---|---|
| j | Variable | $\lambda_1$ | P | j | Variable | $\lambda_a$ | P | cum($\lambda_a$) |
| 1 | Sample age | 0.23 | 0.002 | 1 | LOI | 0.18 | 0.002 | 0.18 |
| 2 | LOI | 0.18 | 0.002 | 2 | Sample age | 0.10 | 0.002 | 0.27 |
| 3 | Pollen richness | 0.08 | 0.03 | 3 | Charcoal | 0.05 | 0.036 | 0.32 |
| 4 | Charcoal | 0.07 | 0.04 | 4 | Pollen richness | 0.04 | 0.002 | 0.36 |
| 5 | Aquatic condition | 0.04 | 0.08 | 5 | Tephra | 0.01 | 0.93 | 0.37 |
| 6 | Tephra | 0.01 | 0.93 | 6 | Aquatic condition | 0.03 | 0.07 | 0.39 |

Vegetation dynamics at Tiniroto Lakes site

Autocorrelation of the PCA ordination scores for the entire pollen profile was typically nonstationary (Fig. 4.6a), strongly suggesting a trend with time. However, the autocorrelation on the detrended sample scores shows a significant correlation with time lag 1, and gradual decline of correlation with time lag 2 and 3 (Fig. 4.6b). A first-order autoregressive process AR(1) is suggested by this feature. Thus besides the long-term trend, the community behaviour is expressed as:

$$x_t = \phi x_{t-1} + a_t \qquad \text{(eqn. 4.4)}$$

where

$x_t$ is the sample score of PCA axis 1 at time $t$;

$x_{t-1}$ is the sample score of PCA axis at time $t-1$;

$a_t$ is the white noise at time $t$, which is a purely random process with constant mean and variance;

$\phi$ is a parameter.

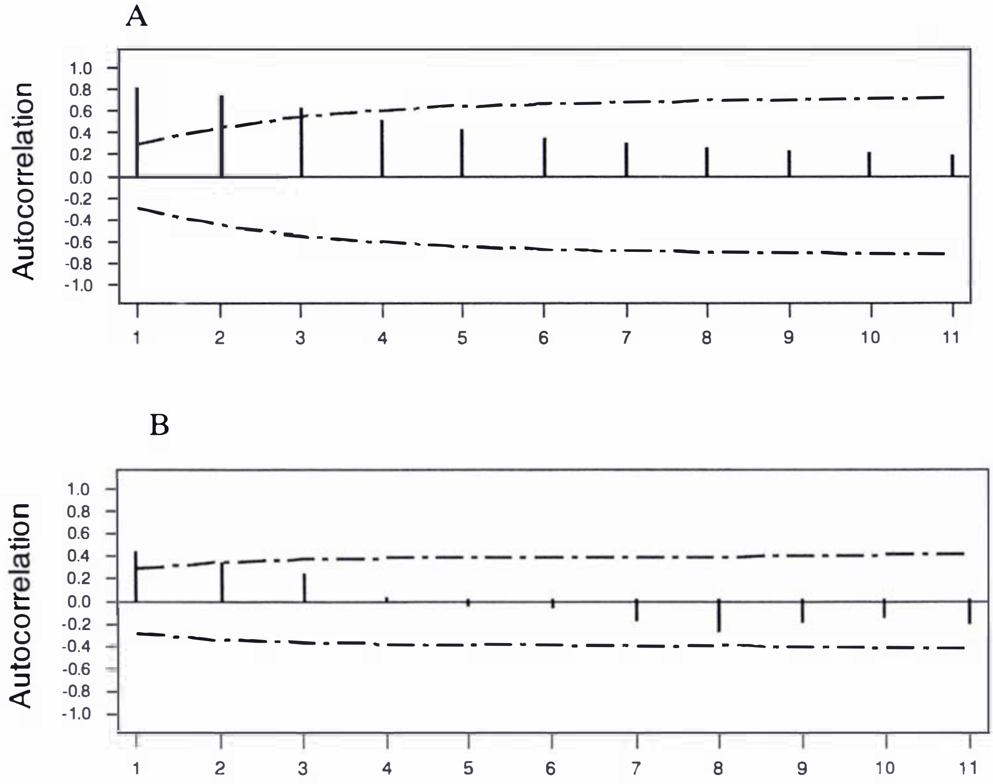


**Fig. 4.6** Autocorrelation analysis of sample scores of the first PCA axis from the data set of the Tiniroto site. (A) Autocorrelation on sample scores; (B) autocorrelation on detrended sample scores. The x axis is in unit time-lags, and y axis is the autocorrelation coefficient at different time-lags.

### 4.3.3 Comparing Vegetation Dynamics between the Sponge Swamp and the Tiniroto Lakes

From the combined PCA analysis on pollen data including sites from Sponge Swamp and Tiniroto Lakes over the same period (Fig. 4.7), it is quite clear that the first axis of PCA separates the two sites, despite that only the species presented in both sites are involved in this analysis. The second axis of the combined PCA displays a strong time sequence within the data set from Sponge Swamp. For the data set from Tiniroto, there is no trend comparable with that of Sponge Swamp, which means great dissimilarities exist both between and within the two sites.

If the sample scores of the first axis of individual PCAs from both sites are plotted against the calibrated age (Fig. 4.8), it is feasible to compare directly the vegetation dynamics between the two sites. The change of vegetation composition in terms of the fluctuation of sample scores is characterized by two stages in Sponge Swamp. From the overall view, vegetation continuously changes throughout the sequence, but with a different amplitude of fluctuations. Before 5600 yr BP, change in vegetation composition was relatively frequent, while ever since then, vegetation stabilized somewhat, to become fairly stable after c. 3400 yr BP, this situation lasting till recently. Vegetation dynamics at the Tiniroto site, though also suggestive of continuous change, indicate more variable fluctuations. Compared with Sponge Swamp, similar strong fluctuations in vegetation composition occurred from c. 5400 to c. 4300 yr BP. For a period from c. 4300 yr BP to c. 2300 yr BP, vegetation change was quite steady. After 2300 yr BP, vegetation started to break away from the long term trend of gradually changing, and fluctuated again, indicated a different regime of vegetation dynamics.

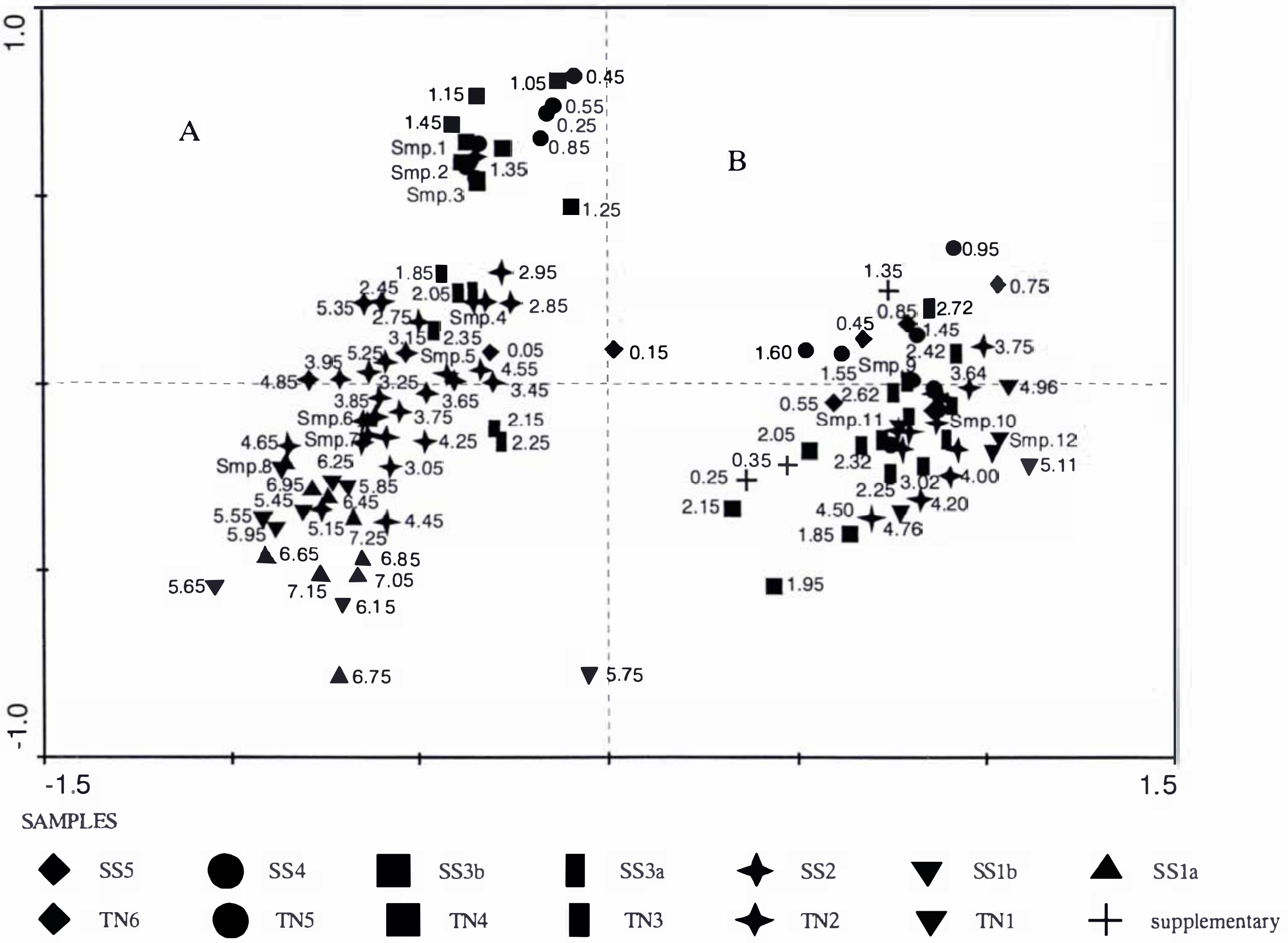


**Fig. 4.7** Scatter plot of the sample scores for the first two PCA axes of combined pollen data from Sponge Swamp (A) and Tiniroto Lakes (B). The sample names represent sample depth (m) for each core, and some samples with positions close together are coded as: Smp.1 = 0.65, 1.65; Smp.2 = 0.75, 0.95, 4.05; Smp.3 = 0.35, 1.55, 1.75; Smp.4 = 1.95, 2.55, 4.15; Smp.5 = 2.65, 3.55; Smp.6 = 4.75, 5.05, 6.55; Smp.7 = 3.35, 4.35, 4.95; Smp.8 = 6.05, 6.35; Smp.9 = 1.40, 2.82; Smp.10 = 0.65, 1.05, 1.15, 2.92, 3.03, 3.14, 3.36, 3.56, 3.80, 4.60; Smp.11 = 1.25, 2.52, 3.09, 3.46, 3.90, 4.10, 4.66; Smp.12 = 4.86, 5.04.

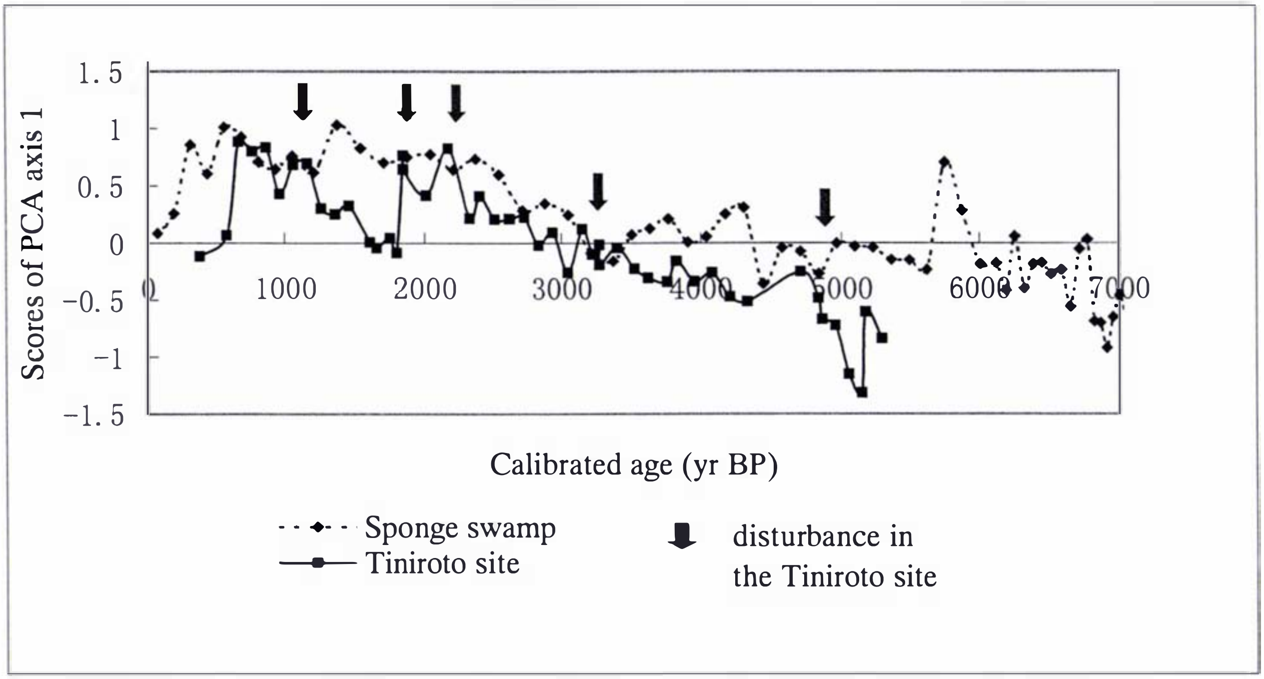
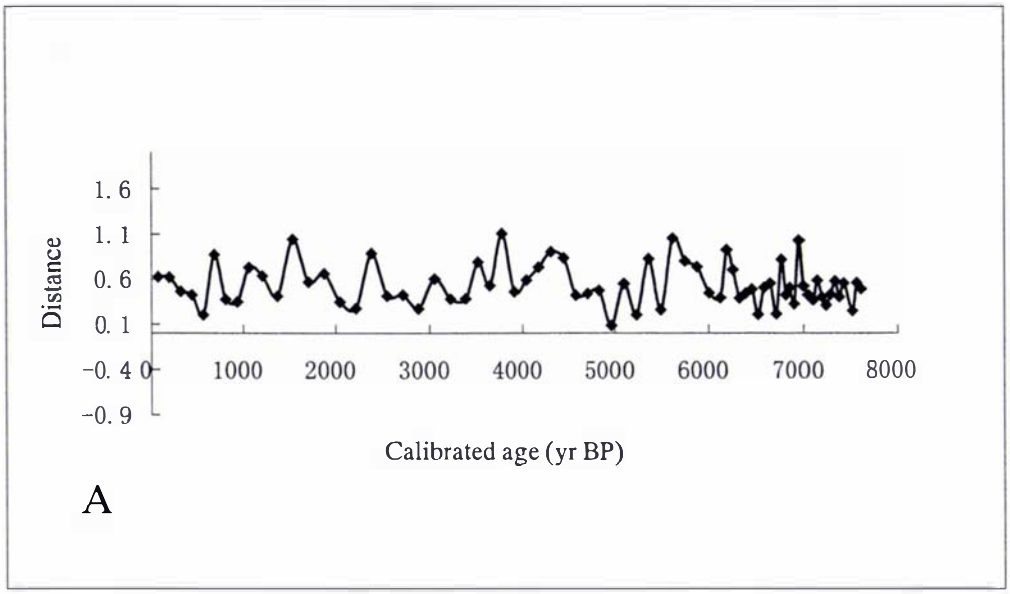


**Fig. 4.8** Sample scores of PCA axis 1 against sample age to pollen data from the Sponge Swamp and Tiniroto sites. PCA was on the data sets of the two sites individually.

Since the first PCA axis on both pollen data sets explains only 27% (Fig. 4.1, 4.4) of the variance in species data, the sample scores of axis 1 only contributes part of the information from the taxon data. Another way to help to understand vegetation dynamics is to measure the distance between the adjacent sample points (averaging c. 100 yr apart) in multi-dimensional space. As the first four PCA axes of the Sponge Swamp data explain about 58% of the variance of the species data, and Tiniroto a comparable value of about 61%, the distance between adjacent samples, measured from the sample scores of the four axes, gives a better depiction of the rate of vegetation change. The distance between adjacent samples from Sponge Swamp (Fig. 4.9a), generated a series like white noise, with constant mean and constant variance, which suggests that the rate of change of the vegetation composition over nearly 7000 yr BP keeps constant. The distance between adjacent samples from the Tiniroto site, however, reflects the general pattern in the plot of sample scores of the first PCA axis (Fig. 4.9b). A higher rate of vegetation change is clearly indicated by depths below 4.2m (c. 4900 yr BP) and above 2.25m (c.2300 yr BP), and seems to have been triggered by occurrences of charcoal particles.



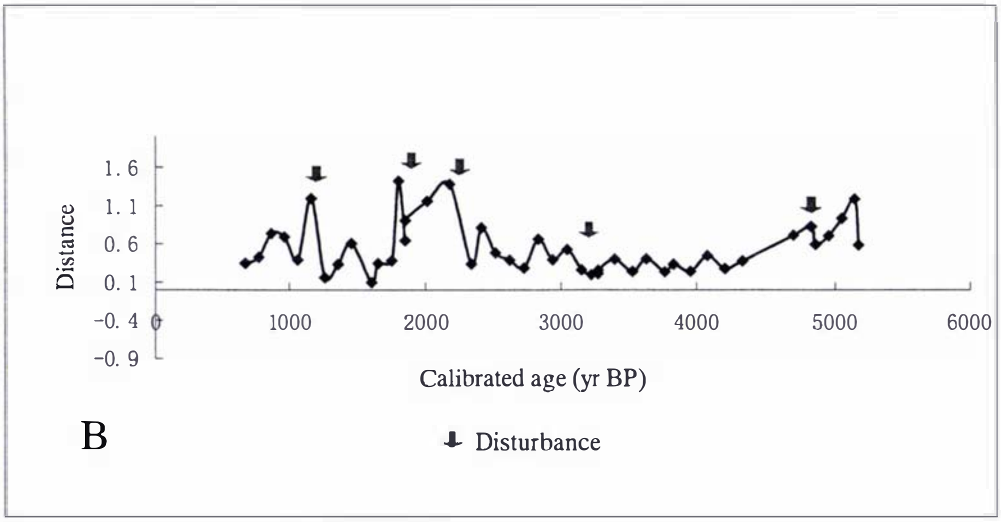


**Fig. 4.9** Distance between samples (c. 100 yr apart) measured from the first four PCA axes of data sets vs. sample age. (A) Sponge Swamp, (B) Tiniroto Lakes; greater distance indicates great change in pollen spectra in c. 100 yrs.

## 4.4 Discussion

The PCA analysis on pollen data from both sites reveals that vegetation compositions are continually changing through time. Autocorrelation of sample scores of the first PCA axis further confirmed that non-equilibrium characterized the vegetation dynamics found at both sites. However, different vegetation behaviours could still be elucidated by detailed analysis.

### 4.4.1 Vegetation Dynamics in the Sponge Swamp Site

The PCA analysis of Sponge Swamp revealed two main points regarding vegetation dynamics: (1) Vegetation composition is continually changing through time, and different stages characterized by certain pollen taxa are identifiable within the PCA plot as clearly as in the percentage pollen diagram. (2) Under the general frame of continuous vegetation change, a relatively big change in vegetation composition occurred at the time represented by 2.45 m (c. 3500 yr BP), and ever since then, vegetation composition seems to have been stabilized so that the overall change is more directional and characterised by movements from one vegetation association to another. These features are indicated in Fig. 4.8 by a general trend of sample scores of the first PCA axis, with relatively obvious fluctuation before c. 3500 yr BP.

The directional change of vegetation composition depicted in the PCA plot is further confirmed by the autocorrelation analysis. A general trend in the sample scores of the first PCA axis was reflected by the autocorrelation diagram. Generally, lack of directional change may be informal evidence that vegetation tends to fluctuate around some average equilibrium state (Silvertown, 1987). On the other hand, the directional change, in terms of nonstationarity, in which the past vegetation behaviour cannot be used to predict vegetation in the future, is regarded as the essence of nonequilibrium dynamics (Franklin & Tolonen, 2000). This directional change is shown in many other pollen data sets (Delcourt, 1979; Whitehead, 1981; Wilkins et al., 1991; Turchin & Taylor, 1992). As indicated by Turchin and Taylor (1992), the nonstationarity of the community represents the 'continual' change in the environment and thus the vegetation, during the time scale of the pollen profile. Similarly, the continuous change in vegetation composition at time scales of $10^4$ years elucidated from pollen records (Delcourt, 1979; Whitehead, 1981; Wilkins et al, 1991) is suggested to have been driven by climate change. However recurrent anthropogenic activities caused the transitions from one domain to another during the forest history of Lake Ahvenainen, southern Finland (Franklin & Tolonen, 2000).

As suggested from this PCA plot and from the detailed pollen analysis from Chapter 2, climate change is likely involved with the transition within five pollen zones, from SS1 to SS5, in Sponge Swamp. The exponential decline of *Ascarina*, could be a product of harsh climate conditions commencing during the middle Holocene, but other reasons, like forest closure, could not be ruled out. This climate deterioration is further indicated by the change of dominant pollen taxa. The loss of tree ferns and other fern allies from SS1 onward, and the expansion of the robust fern *Gleichenia* and fern ally *Lycopodium australianum* in SS2, which usually occur either in swamp areas or in the early stages of secondary succession, and in canopy gaps in high altitude mixed forest (Wardle, 1991), might indicate an open vegetation and a severe and drier climate in the middle Holocene. The dense seral scrublands of *Leptospermum* which fringed around the mire in SS3, together with other evidence of drier conditions, is nevertheless an example of how quickly the occupation of a large expanse of damp surface is produced by a further lowering of water level. The progressive increase of cool-tolerant trees, such as *Nothofagus menziesii*, *Nothofagus fusca* type, *Phyllocladus*, and *Halocarpus*, or drought-tolerant trees, like *Prumnopitys taxifolia* (Wardle, 1991), within SS4, is again representative of a cooler and/or a drier episode. The comparison of pollen evidence of this site to regional patterns is discussed in detail in Chapter 2. From this site, the severe climate conditions started at the beginning of SS2 (c. 6800 yr BP), and have been getting worse since SS3a (c. 3500 yr BP), if the presence of *Ascarina lucida* is taken as a proxy for climate.

However, the ecology of *Ascarina lucida* is controversial. The germination pattern of *A. lucida* is found to have similarities with species that often colonise disturbed sites; the maintenance of a seed bank and long germination period indicate that this species is adapted to disturbed environments (Martin & Ogden, 2002). Thus the peaks of *A. lucida* need to be interpreted with regard to both climate variability and disturbance regime (Martin, 2003). Consequently, the large presence of *A. lucida* in the early deposits of this core might be coincident with the large openings in forest which existed in south Westland at that time. The decline of this species in the pollen record of this site is thus probably related to either climate change or reduced levels of disturbance. The latter explanation is more relevant to the change to more stable vegetation dynamics after c. 3500 yr BP when *Ascarina lucida* dropped to a trace amount.

As suggested by either the change of *Ascarina lucida* or the transition of other pollen taxa, the environmental change is almost linear with the time. This could explain why sample age alone explains c. 20% of the variance in species data. Highly negatively correlated with sample age, LOI increases substantially over time, which indicates increasing amounts of organic material in the sediments. This could have resulted from the decrease in the proportion of clay materials due to the development of hydroseral infilling generating a more organic-rich deposit over time.

Although frequently present throughout the profile, the occurrence of charcoal particles explains little of the pollen composition change, according to the RDA. As suggested in Chapter 2, the charcoal occurrence in this core does not correspond with the charcoal from drier episodes in central and eastern Otago and other eastern parts (Burrows & Randall, 1993; McGlone & Moar, 1998; McGlone & Wilmshurst, 1999; Wilmshurst et al., 2002). It is possible that these charcoals could be brought from south-eastern Australia by strong westerly winds (Singh & Luly, 1991; McGowan et al. 2000, Flenley, 2004).

### 4.4.2 Vegetation Dynamics in the Tiniroto Lakes Site

Just as with Sponge Swamp, the non-equilibrium vegetation dynamics at Tiniroto are depicted from both PCA sample scores and the pattern of the autocorrelation diagram. Although vegetation composition at Tiniroto is also continually changing through time, this process is always interrupted by disturbances like tephra layers and/or fires, in which sudden changes of vegetation occur and make big fluctuations about the trend. Thus the underlying forcing mechanisms for Tiniroto forest are different from those in Sponge Swamp.

It seems that the major controlling mechanism of the vegetation processes at this site is disturbance. The climate gradient, which produces the steady and smooth vegetation transition in Sponge Swamp, is not so clear here. Only the vegetation dynamics in the period between c. 4300 yr BP and c. 2300 yr BP (TN2-TN3) are comparable to Sponge Swamp, suggesting a climatic driving mechanism. From pollen evidence of this core and the comparison of this evidence to pollen records of other sites from the North Island (refer to Chapter 3), a climate amelioration with increased rainfall dominates this period, causing the long process of forest invasion in Tiniroto and other places in the central North Island, such as Lake Poukawa (McGlone, 2002) and Lake Rototua (McGlone, 1983). This process at Tiniroto is indicated by a gradual replacing of many open land and light-adapted taxa, such as *Dodonaea viscosa*, *Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the family Fabaceae and Asteraceae, by increasing forest taxa in pollen diagrams. This forest invasion is even more clearly outlined by PCA. Transition from TN1 to TN3 manifests a process similar to a vegetation succession, in which a gradual loss of open site and light-adapted taxa happened first, subsequent to colonization by shrub communities, and finally ending by an invasion of broadleaved species. Podocarps, however, dominate in the later stages of this pollen sequence, of TN5 and TN6. The development of vegetation from the open-sited taxa to hardwood combinations in the early process of forest invasion emphases that the hardwoods are the products of vegetation succession under stable and ameliorated climate conditions. The presence of podocarps, however, is closely related to the outbreaks of disturbance. This vegetation process will help to understand the temporal vegetation pattern of the central North Island.

In the central North Island, both dense podocarp forests and podocarp-hardwood forests are scattered. According to the survey of McKelvey (1963), the dense podocarp forets are distributed around the old eruption centre (Lake Taupo), while further from the lake, hardwood components came into existence. Thus he concluded that podocarps would finally give way to hardwoods. This idea is supported by the common "regeneration gaps" in the podocarp forest. However, in the most recent clearings, abundant saplings of all species of podocarps occur (Morton, et al., 1984), and in the old burn areas the vegetation almost certainly reverted to podocarp forest (Cameron, 1955; Beveridge, 1973). Accordingly, it is hard to simply attribute the structure of the podocarp forest to dis-equilibrium with the present climate or to succession to hardwood forest. On the other hand, disturbance has been acting as a driving force for the establishment and development of such podocarp forests. The linear succession theory from McKelvey (1963) was revised by Ogden (Morton, et al., 1984) by including catastrophe and gap regeneration cycles which maintain the importance of both dense podocarp forest and podocarp-hardwood forest. In the catastrophe cycle, dense podocarp stands arise and are maintained by fire, though they shift in composition over time. In the gap regeneration cycle, hardwoods replace podocarps and vice versa. The catastrophe cycle is reinforced by the evidence from Tiniroto, in which there is increasing importance of podocarps after the Taupo eruption (TN5 and TN6) in this pollen sequence due to frequent fire outbreaks since then. The gap regeneration cycle is representated by the early process of forest invasion (especially in TN3), but implies that under favourable climate conditions hardwoods would succeed podocarps.

Besides the increasing occurrence of podocarps, the predominance of disturbances in the later stage of the pollen sequence at Tiniroto is also reflected by the different pattern of vegetation dynamics compared with the early stage, a change from a steady trend to a trend with big fluctuations. It seems that disturbances could intervene and reset the trend of vegetation change under a climate gradient, and control the forest dynamics. Although the trend was reset by disturbances, non-equilibrium still characterised the vegetation process. Since the dominant taxa in each episode of disturbance are different, e.g. increasing tree ferns and fern allies in TN4, more components such as *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Nothofagus menziesii* in TN5, and the predominance of *Leptospermum* in TN6, vegetation composition divergence is continuous. There is no tendency for the vegetation system to return to its previous equilibrium state if one existed. This is probably because either the intervals between disturbances are too short, thus preventing a system from ever reaching a stable state (Sprugel, 1991), or climate change was running through the whole sequence, causing the different forest states prior to different disturbance episodes and changing the trajectory of the succession path as well (Prentice, 1986).

Thus it is reasonable to assume that the non-equilibrium vegetation dynamics in Tiniroto are caused by both successions under improving climate conditions in their early stage and disturbances in their later stage. Since the forest invasion is probably accompanied by a loss of pollen richness, and the increasing chances of disturbances are indicated by rising charcoal fragments, such dynamics could explain why both charcoal and pollen richness account for much more variance in species data than at Sponge Swamp. Although there is an increasing magnitude of disturbance and thus more open vegetation at this site, the LOI increases over time. This contradictory finding raises the problems of LOI measurements, which fail here to take the existence of molluscs below 2.6 m into account. This could easily lead to the lower value of LOI which is caused by the autogenic carbonate coming from the molluscs reducing the LOI values.

### 4.4.3 Comparison of the Vegetation Dynamics of the Sponge Swamp and the Tiniroto Sites

Although non-equilibrium characterises the forest dynamics at both sites, the detailed vegetation dynamics for each site are different due to the differing importance of disturbance.

The great dissimilarities in the vegetation composition of both sites, due to their disparate geographic localities within different climate regions, makes it hard to directly compare their vegetation behaviours through pollen diagrams. However, numerical analysis made the comparison feasible.

When PCA was performed on the combined data set from both sites, the vegetation change over time within the Sponge Swamp set is distributed along a strong time sequence, while that within the Tiniroto set turned out to be less directional. Since vegetation in south Westland is more sensitive to temperature, and vegetation in the

Gisborne area is more affected by drought, it is hard to compare vegetation change under these different reactions to climate conditions, especially with the interruptions of disturbance at Tiniroto. The only explanation provided here for these different vegetation behaviours in both sites is the different driving forces under the vegetation dynamics. The strong time sequence indicative of vegetation change within Sponge Swamp, supports climate shifting as the prime cause for non-equilibrium at this site. Also, the relatively constant rate of palynological change over c. 7600 yrs (Fig. 4.9a) suggests that the climate change over this period is gradual and steady. Although such a gradient might also exist in Tiniroto, disturbances reset such long-term trends and mask the gradient. This point has been addressed by Clarkson (1990) in that "the patchy and asynchronous nature of disturbances would result in a continuously changing mosaic of vegetation patches of different sizes and ages, which average and disguise the directional change of vegetation when one considers the mean dynamics of an area".

If the general trend of vegetation change was removed, i. e. the main impact of climate on vegetation from Sponge Swamp and Tiniroto was separated, the impact of disturbances on vegetations from both sites becomes easier to compare. The MA(1) model ( $x_t = a_t - \theta a_{t-1}$ ), which came from the autocorrelation function of the detrended data from Sponge Swamp, suggests that vegetation composition in Sponge Swamp is affected by various "random" events, with the impacts lasting about 100 yr. This model is quite relevant to the constant rate of change in vegetation composition in Sponge Swamp. These "random" events could represent small and frequent disturbances in Westland. Although it is hard to detect any evidence of disturbance from either the pollen record or the PCA analysis from this site, this does not imply no disturbances existed in this area. As mentioned by Wells et al. (2001), many of the forests in Westland are frequently subject to disturbances such as earthquake-triggered landslides and floods due to high rainfall, steep topography, and an active fault which runs across the whole region. Unlike large disturbances such as fires, the damage caused by small-scale landslides and floods will be largely independent of vegetation structure and the stage of development, and thus independent of the time since the last major disturbance (Wells et al., 2001). Although the impacts of these kinds of disturbances on this region were rather small and have generated almost no significant effect on the dense forests today, it is possible that the relatively strong fluctuations of vegetation before c. 3500 yr BP in this core indicate more substantial impacts on forest with relatively more or larger openings caused by such disturbances.

The different nature of disturbances in Tiniroto, such as fires, determines that the vegetation dynamics should be characterised by different processes. For disturbances like fire, the pattern of damage is often influenced by the structure of the vegetation (Hemstrom & Franklin, 1982). The AR(1) model ($x_t = \phi x_{t-1} + a_t$), derived from Tiniroto, reflects the nature of disturbance and also suggests a more successional process, i.e. the present state of vegetation depends on the vegetation of the immediate past state, say 100 yr, and this process is also punctuated by unexpected exogenous disturbances. This short-term temporal autocorrelation of vegetation is typically a feature of vegetation recovery after disturbance.

## 4.5 Conclusions

As a whole, despite appearances, non-equilibrium characterises vegetation dynamics in both the undisturbed site and the disturbed site. However, the processes of vegetation dynamics in Tiniroto site differ from those in Sponge Swamp, due to the existence of catastrophic disturbances. A long-term climate change, from warm and wet to cooler and drier, is probably the main reason for the non-equilibrium dynamics of vegetation in Sponge Swamp. By contrast, in Tiniroto, apart from the climate trend in vegetation change, disturbances, especially those catastrophic ones which occurred in relatively recent times, play an important role in the vegetation dynamics.

Consequently, in southern Westland, the present vegetation structure is generally determined by the current climate conditions, and the change within the forests is slow but continuous. The impact on vegetation of disturbances with small scale is rather small and would be easily disguised by climate effects. In the central North Island, however, the predominance of podocarp forest is probably determined by the most recent disturbances, although, giving enough time free of disturbances, in places where we have plenty of rainfall, podocarp forests might be replaced by hardwoods. However, this seems unlikely because of the susceptibility to disturbances in this area.

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# Chapter Five

## Short-term Vegetation Responses to Different Types of Disturbance at Tiniroto, Gisborne, New Zealand

### Abstract

Disturbances are prevalent in New Zealand. Understanding the vegetation responses to disturbances is essential for sustainable resource management. Also, comparing vegetation responses to different types of disturbance will help to find out whether they have different effects.

Fine resolution pollen analyses around five disturbance episodes, including Taupo (1850±10 yr BP), Waimihia (3280±20 yr BP), and Whakatane (4830±20 yr BP) eruptions and two charcoal peaks (c. 1100 yr BP and c. 2300 yr BP), were done from a sediment core taken from the Tiniroto site. In combination with PCA analyses, vegetation responses to different disturbance types was examined, to reconstruct the disturbance history in this region.

No vegetation change relative to disturbance was found around the Whakatane and Waimihia episodes. However, charcoal particles intermittently occurred in samples which contain more shrubs and ferns, indicating that the forest was undergoing various degrees of fire related perturbations throughout the two episodes, but the gaps generated by these fires were to be invaded by forest taxa.

The Taupo eruption shows the most substantial modification of vegetation composition, but even then there was no major damage to the forest and the destruction is mainly restricted to the shrubs and fernland. The PCA vegetation group before the eruption mainly consists of *Prumnopitys taxifolia*, *Dacrycarpus*

*dacrydioides, Coprosma* and fern allies. Just after the eruption, *Dacrydium cupressinum* and *Pteridium* become more important. Subsequently the vegetation was characterised by increases in beech trees, *Prumnopitys ferruginea* and tree ferns. Taxa characterising the vegetation after the eruption are either fire prone or reliant on disturbances for regeneration. The period following the Taupo eruption is also accompanied by an upsurge of charcoal particles, low values of LOI, relatively high pollen richness, and gradually increasing water levels as determined by changes in macrophytic swamp plants. All these changes are strongly suggestive of disturbance subsequent to, rather than caused by the eruption.

There is no obvious pattern of vegetation change around the charcoal level at c. 1100 yr BP, due to either contamination of the samples taken from the top of the corer or the whole section being at a highly-disturbed time. However, there is vegetation perturbation around the other charcoal level at c. 2300 yr BP. Samples prior to this level consist of relatively more forest canopy trees, such as *Dacrydium cupressinum, Prumnopitys ferruginea*, *Prumnopitys taxifolia, Nothofagus fuscospora* type, and tree ferns, while samples above this level differ by the high frequency of fern allies with monolete spores, indicating a semi-open vegetation state.

After comparing vegetation change within the Taupo episode with that in the Waimihia episode which received the same thickness of tephra as Taupo, fire is suggested to have more impact on vegetation around Tiniroto Lakes than tephra.

A change of disturbance regime is suggested for the later disturbance episodes. Comparing with the early episodes, this change is characterised by increasing fire impact intensity, with a substantial change in vegetation composition, towards more seral plants in the post disturbance stage, and relative longer persistence of semi-open forest state. This could be due to increasing variability in climate conditions, or to early human impact.

## 5.1 Introduction

New Zealand forests are commonly affected by large, infrequent disturbances, like catastrophic fires (Johnson, 2001; Ogden, 1998), volcanic eruptions (Clarkson, 1990; Wilmshurst & McGlone, 1996), floods (Duncan, 1993), windstorms (Foster & Boose, 1995; Turner et al., 1997), and earthquakes (Wells et al., 2001). Some disturbances, like volcanic eruptions and fires, could be most severe, causing significant destruction of the forests, impacting over large areas and over long periods, and exerting a dominating influence on the pattern and function of the forest. The evidence of impact of disturbance on New Zealand forest on intermediate time scales is much stronger than the evidence for significant climate changes on similar time scales (Ogden, 1985).

It has been estimated that one fourth of the world's biggest eruptions in historical or prehistoric time were from the central North Island, and moreover, this region contains the world's strongest concentration of youthful rhyolite volcanoes (Simkin & Siebert, 1994). The potential for disturbance from volcanic eruption in New Zealand is high. Also, because of the low fire adaptation of most of the New Zealand tree species, forest in New Zealand is especially vulnerable to fire disturbances (Ogden & McGlone, 1998). Thus understanding the vegetation responses to these kinds of disturbances is very important, and provides evidence for making management strategies for ecosystems, and in the long term, for planning sustainable resource management.

Since forests will usually take decades, or even centuries, to recover after these catastrophic disturbances (Turner et al., 1997), studying contemporary vegetation responses to the most recent disturbance is not sufficient to get insight into the impact of such large scale disturbances, especially considering the present forest is still undergoing responses to previous and current anthropogenic influences. Moreover, there is no relevant substitute for the past catastrophic disturbance in recent history, like the Taupo eruption, and the vegetation response to this kind of disturbance would be rather different from that to the recent ones. Palynological records with fine resolution make it possible to study the impacts of past disturbances and associated vegetation response to disturbances, and permit the evaluation of contemporary disturbances and the estimation of the recovery of vegetation in a longer-term perspective (Wilshurst et al., 1997).

A body of palynological analyses have examined the vegetation responses to volcanic eruptions (mostly the Taupo eruption) and human disturbances (Rogers & McGlone, 1989; Clarkson et al., 1992, 1995; Lees & Neall, 1993; Wilmshurst & McGlone, 1996; Wilmshurst, 1997; Horrocks & Ogden, 1998). As for the Taupo eruption, its impact on vegetation is variable, which is not related to either the thickness of the tephra or the distance from the vent (Wilmshurst & McGlone, 1996). This makes the impact of disturbance on vegetation much more complicated, since climate and other factors were integrated. There is a need for documentation of vegetation response to disturbances on the spatial scale in New Zealand (Wilson, 1990), and possibly on the time scale as well.

Comparing vegetation responses to different types of disturbance is important, as those may have different effects (Collins & Glenn, 1988), but there is insufficient documentation to know to what extent this is true for New Zealand (Wilson, 1990). If the disturbance episodes compared are in a time order, a history of disturbance regime is set up for a region on the basis of vegetation responses, which is informative of climate changes or even human activities.

The Tiniroto site, as for many areas in the central North Island in historical time, is frequently disturbed by volcanic eruptions and fires. A sediment core taken from the Tiniroto Lakes comprises three tephra layers, identified as Whakatane, Waimihia, and Taupo, and other charcoal peaks. Detailed analyses of these disturbance episodes, using continuous sampling around each disturbance event, are expected to record any transient events of vegetation development and are used to examine and compare the impacts of these disturbances on vegetation.

## 5.2 Methods

### 5.2.1 Pollen Analysis

A sediment core was taken from a small swamp adjacent to the east of Lake Waihau, one of the Tiniroto lakes, located in the Gisborne region, which is frequently subjected to both natural and anthropogenic disturbances (see Chapter 3). Five disturbance episodes were chosen from this core for detailed pollen analysis, including three tephras: Whakatane, Waimihia, and Taupo, and two charcoal peaks at levels of 0.95 m and 2.25 m, chosen via the information contained in Chapter 3. About 15-30 samples were taken for each episode, among which more than two third of the samples were collected above the tephra or charcoal peak, and the other one third or less were obtained from below that level contiguously. All these samples were collected continuously every 1 cm (≈ 10 yr), approximately covering a time span of c. 150-300 years.

The pollen preparation followed standard procedures described in Chapter 2. A minimum of 300 terrestrial pollen grains were counted for each sample, and pollen counts were calculated and presented in the form of relative frequencies based on the pollen sum including terrestrial pollen and spores. Percentages of aquatic taxa were calculated upon terrestrial pollen sum plus aquatic pollen totals. Charcoal fragments were recorded in categories according to size measurements. Pollen data were initially analysed and presented by TILIA and TILIA Graph (Grimm, 1991). The results of the agglomerative cluster analysis CONISS on the terrestrial percentage pollen data are presented in the pollen diagrams as references for the manual grouping of pollen samples into zones; the sample clustering was constrained by the sample depth.

### 5.2.2 Principal Component Analysis (PCA)

PCA was performed on pollen data from each episode separately, and only species with three or more occurrences in each data set were used in the analyses. All compositional pollen data were transformed by log-ratio centering prior to the analysis (Aitchinson, 1982, 1983), and all aquatic taxa were made supplementary.

The output from each tephra episode is then categorised into three separate groups, those samples taken prior to the tephra layer (called “Pre” or “Pre-disturbance”), and those post-eruption. The latter group was subdivided into two categories of roughly equal size, the one immediately adjacent to the tephra layer (called “Adj” or “Adjacent”), and a group subsequent thereto (called “Sub” or “Subsequent”). For the two episodes of intense sampling which occurred around the two charcoal events, there are no clear groupings as charcoal is widely distributed in the profile. So the outputs are categorised as "before" and "after" these event foci.

For comparison, a PCA analysis was also applied to samples from all episodes together. In order to compare the impact of each disturbance episode on vegetation to that of the Taupo episode, which was the most recognised vegetation disturbance event in New Zealand in the last 5 000 years, samples from each episode were made supplementary in the PCA analysis on the Taupo episode only.

### 5.2.3 Correlation between Sample Scores and Environment Variables

Several environment variables were also measured from pollen samples or from sediments collected from the level of this core, i.e. charcoal fragments, loss-on-ignition (LOI), calibrated AMS sample age, and pollen richness (for details, see Chapter 4). The effects of tephra on vegetation, which are likely to have been decreasing with time since the eruption, were modelled as a simple exponential decay process subsequent to the tephra (see eqn. 4.2). All mire and aquatic taxa from each episode were analysed separately by PCA, except for Waimihia and Whakatane episodes in which the mire or aquatic taxa are almost absent. The result for the three episodes, including the Taupo and two charcoal levels, shows that the first PCA axis explain more than 60% of the total variances of mire taxa, suggesting a change in composition with relatively more components of taxa distributed outside the swamp to taxa live at the edge of the water, from right to left. Pearson correlation coefficients were calculated for each of these variables with the sample scores of the first, and then the second PCA axes, for species in each episode, for further interpretation of the changing vegetation structure.

## 5.3 Results

The general vegetation change response to each disturbance event is indicated by both the pollen percentage diagrams and the PCA plots. Pollen diagrams provide more information on the change of individual taxa over time, and PCA plots display more of the vegetation patterns associated with disturbances. The samples with similar vegetation compositions will be grouped together, especially on the first and second axes. If the samples in an episode subsection ("Pre", "Adj" or "Sub") are well grouped through ordination space, a clear vegetation change response to the associated disturbance event is indicated. Eigenvalues of the first two PCA axes for each disturbance episode are listed in Table 5.1.

**Table 5.1** Eigenvalues of the first and second axes from a PCA on pollen samples around each of the five disturbance episodes.

| Disturbance events | Eigenvalue of first axis | Eigenvalue of second axis | Culmulative variance (%) | Number of samples |
|---|---|---|---|---|
| Whakatane | 0.321 | 0.229 | 55.0 | 15 |
| Waimihia | 0.433 | 0.159 | 59.2 | 20 |
| Taupo | 0.471 | 0.178 | 64.9 | 24 |
| Charcoal-0.95m | 0.375 | 0.180 | 55.5 | 25 |
| Charcoal-2.25m | 0.554 | 0.170 | 72.4 | 25 |

### 5.3.1 Detailed Analysis on Individual Disturbances Episodes

#### 5.3.1.1 Whakatane tephra (4.60-4.66 m, 4830±20 yr BP)

Whakatane tephra, accumulating up to 6 cm of ash at Tiniroto, is the oldest of the tephra layers in this core. It was formed by an explosion of the Haroharo complex in the north of the Okataina Volcanic Centre, about 4830±20 yr BP (Froggatt and Lowe, 1990). The approximate location of the eruptive vents indicated by the isopach patterns is in the Matahina district, about 95 km to the northwest of Tiniroto (Vucetich & Pullar, 1964).

From the pollen diagram (Fig. 5.1), the changes across (before and after) the tephra in pollen taxa are very small. *Prumnopitys taxifolia* increases somewhat but is quite variable. *Nothofagus fuscospora* type, though declining above the tephra, shows a steady increase later on. Both *Dodonaea viscosa* and *Pteridium* peak below the tephra and either reduce to trace amounts or are sporadically present after it. *Cyathea* drops abruptly both previous to and some time after the tephra.

The presence of charcoal particles does not correspond to the tephra layer, but peaks at levels below and after it. Both peaks coincide well with the declines of *Cyathea.*

From the PCA analysis, more than half of the variation is explained by the first two axes (Table 5.1), so the plot depicts the vegetation composition changes well. There is no obvious grouping associated with the three vegetation stages of the Whakatane eruption (Fig. 5.2). Samples frequently vary in time, irrespective of the eruption, between vegetation with relatively more *Dacrydium cupressinum,* Ericaceae and components of seral shrubland, such as *Pteridium*, and *Coprosma* in the right half of the PCA, and vegetation with more forest taxa, e.g. *Prumnopitys taxifolia, Podocarpus* spp., and tree ferns on the left half of the first axis. Samples with relatively higher values of seral shrubland components usually coincide with high occurrences of charcoal particles, as charcoal fragments are positively correlated with sample scores of the first PCA axis (Table 5.2).

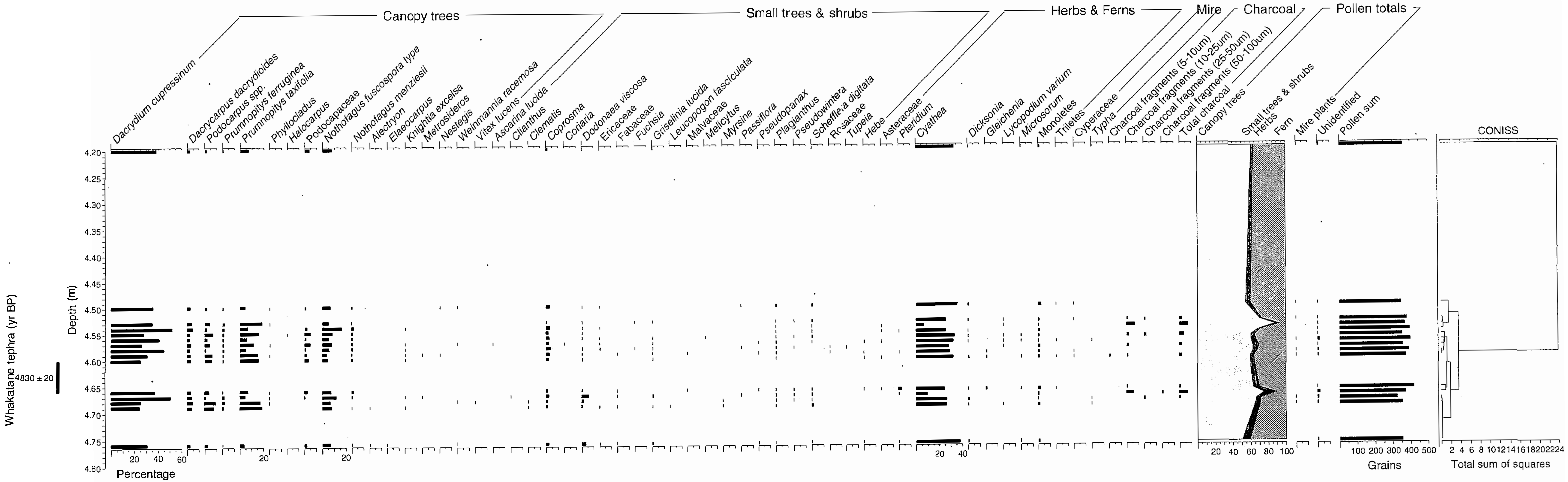


**Fig. 5.1** Pollen percentage diagram of the Whakatane episode

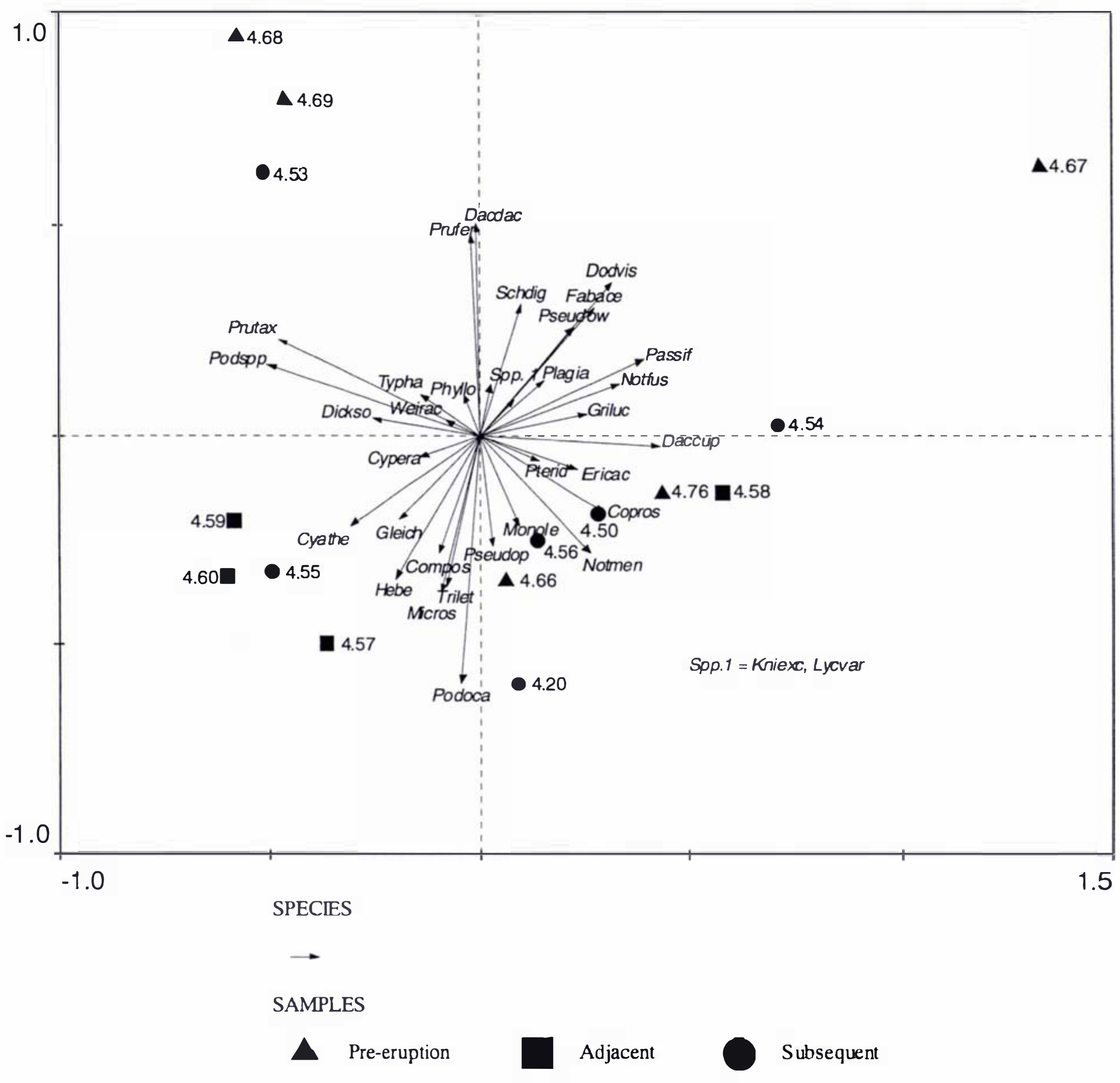


**Fig. 5.2** PCA biplot of the Whakatane episode. Some species arrows which are too close are coded to avoid crowding. For the full name of the taxa see Appendix 1. The sample names represent sample depth. Samples with charcoal fragments are: 4.53, 4.54, 4.56, 4.58, 4.60, 4.66, 4.67, 4.68; samples without charcoal fragments are: 4.20, 4.50, 4.55, 4.57, 4.59, 4.69, 4.76.

**Table 5.2** Pearson correlation coefficients of sample scores of the first and second PCA axes against environmental measurements. Correlations are given when they are significant at P<0.05.

| Disturbance event | Sample scores etc | Charcoal particles | Loss-on-ignition | Pollen richness | Sample age | Aquatic condition |
|---|---|---|---|---|---|---|
| Whakatane eruption | First axis | 0.661 | - | - | - | - |
| | Second axis | - | - | - | - | - |
| Waimihia eruption | First axis | -0.691 | - | 0.512 | - | - |
| | Second axis | - | - | - | - | - |
| | Ash effect | - | -0.617 | - | - | - |
| Taupo eruption | First axis | -0.604 | 0.868 | -0.536 | - | 0.624 |
| | Second axis | - | - | - | - | - |
| | LOI | -0.588 | - | -0.615 | - | 0.736 |
| | Ash effect | 0.762 | - | - | - | - |
| | Aquatic condition | - | - | -0.629 | - | - |
| Charcoal-0.95 m | First axis | - | 0.396 | - | - | - |
| | Second axis | 0.405 | - | - | - | - |
| | Pollen richness | 0.551 | - | - | - | - |
| | Aquatic condition | - | -0.814 | - | 0.700 | - |
| Charcoal-2.25 m | First axis | - | -0.400 | - | - | 0.661 |
| | Second axis | - | - | - | - | - |
| | Sample age | - | -0.836 | - | - | - |
| | Aquatic condition | - | 0.528 | - | - | -0.532 |

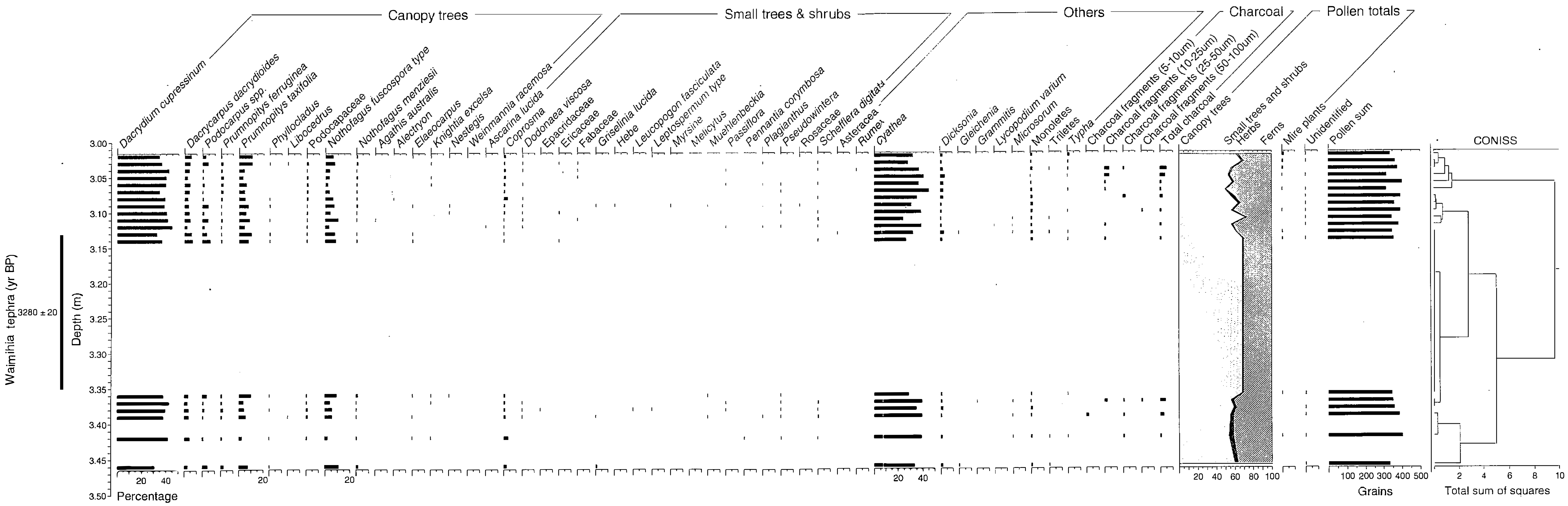


**Fig. 5.3** Pollen percentage diagram of the Waimihia episode

### 5.3.1.2 Waimihia tephra (3.14-3.36 m, 3280±20 yr BP)

The Waimihia tephra, which deposited 22 cm of ash in this core, was spread by another violent eruption from a crater south of Iwitahi in the Taupo Volcanic Centre about 3280±20 yr BP (Vucetich & Pullar, 1964; Froggatt & Lowe, 1990).

The change across the tephra in pollen taxa is very small as for the Whakatane event. Both *Prumnopitys ferruginea* and *Coprosma* show a further decline above the tephra, which was initiated prior to it, and increase again further above. *Dacrycarpus dacrydioides* and *Podocarpus* spp. exhibit little increase after the tephra and drop subsequently. Aquatic taxa are rare except that *Typha* occurs in trace levels.

Charcoal particles are present throughout the section, with a peak of small sized ones (10-25 μm) at 3.03 m, far above the tephra. This peak corresponds with the decline of *Podocarpus* spp., *Prumnopitys taxifolia* and *Nothofagus fuscospora* type, and the increase of *Coprosma*, *Dicksonia* and *Cyathea* (Fig. 5.3).

Nearly 60 percent of the total variation is explained by the first and second axes of the PCA of the 27 samples taken around this tephra (Table 5.1). Samples are divided into two groups along the first axis (Fig. 5.4). One group, with higher sample scores (ie. to the right of the PCA), is mainly composed of higher frequencies of tree pollen, including *Podocarpus* spp., *Prumnopitys taxifolia, Nothofagus fuscospora* type, and *Phyllocladus*. The other group (to the left of PCA), with low sample scores, is more associated with tree ferns and shrubs, such as *Cyathea*, *Dicksonia, Pseudowintera*, and Fabaceae.

However, these two clear groupings are not a result of consistent vegetation changes before and after the tephra deposition. The right hand group contains samples before, adjacent to and subsequent to the tephra deposition, as does the left hand group (Fig. 5.4, Table 5.2). In other words, there is no trend of change around the tephra. Instead the groups are a response to another disturbance type. Since all samples from the left group except the sample at 3.38 m are those containing charcoal fragments, and none of the samples from the right group contain charcoal, the first PCA axis represents two extremes dependent on whether the vegetation was consistently subjected to pyric disturbances (Table 5.2). Obviously, oscillation between these two groups occurred long before the eruption, as well as after, which suggests that the fires are probably independent of the eruption. The substantial decline of mineral materials in the sediments subsequent to the eruption reflects that the mineral materials are mostly from ash fall (Table 5.2).

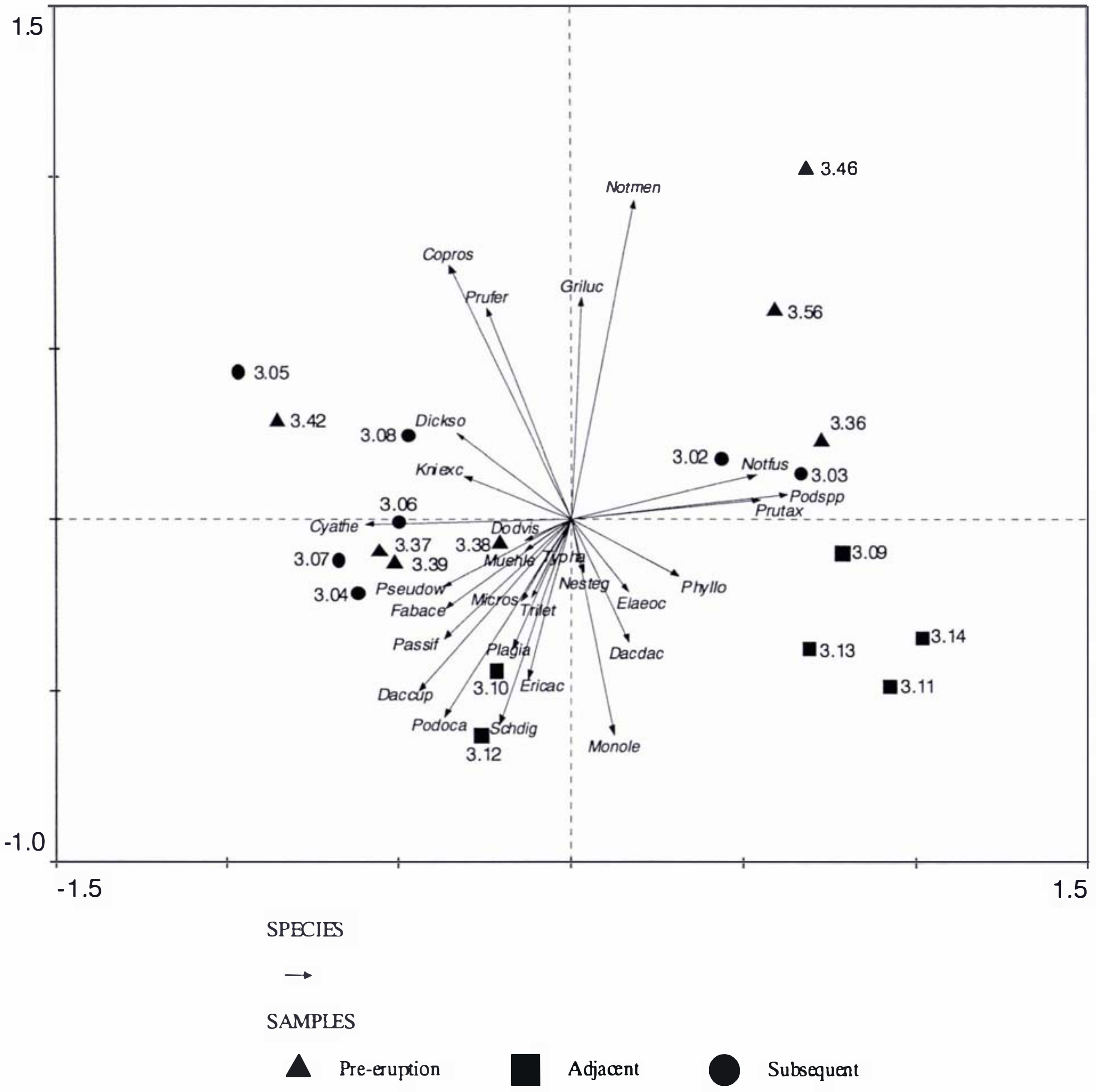


**Fig. 5.4** PCA biplot of the Waimihia episode. The sample names represent sample depth. For the full name of the taxa see Appendix 1. Samples with charcoal fragments are: 3.04, 3.05, 3.06, 3.07, 3.08, 3.10, 3.12, 3.37, 3.39, 3.42; samples without charcoal fragments are: 3.02, 3.03, 3.09, 3.11, 3.13, 3.14, 3.36, 3.38, 3.46, 3.56.

### 5.3.1.3 Taupo tephra (1.63-1.85 m, 1850±10 yr BP)

The Taupo eruption, which took place at about 1850±10 yr BP, was the most violent eruption during the Holocene. The total volume of rhyolitic material erupted from this event is 3.4 times as great as that of Whakatane, and 5 times that of Waimihia (Froggatt and Lowe, 1990). The eruption was characterised by a series of huge explosions, with their eruptive vents around Lake Taupo and Hatepe. Taupo tephra was spread over the entire middle part of the North Island, reaching to the coast on the east side (Vucetich and Pullar, 1964). About 22 cm of tephra was deposited in the Tiniroto core sampled here.

It seems that changes of pollen taxa around the Taupo event are individualistic (Fig. 5.5). Some taxa slightly decrease after the tephra by around 5%. These taxa include *Dacrycarpus dacrydioides, Podocarpus* spp., *Prumnopitys taxifolia, Coprosma* and monolete fern spores. Tree ferns, such as *Cyathea* and *Dicksonia,* decrease substantially after the tephra, by up to 30%, although peaking occasionally. In contrast, *Nothofagus fuscospora* type undergoes a substantial and consistent rise by 5% immediately above the tephra and to 25% further above it. *Dacrydium cupressinum* also shows a little rise post Taupo tephra. *Typha,* though it suddenly achieves 23%, from a trace level shortly after the tephra, decreases steadily to 7% later. *Pteridium* comes into existence in the record right above the tephra and peaks at 20% shortly thereafter, before a substantial decline to trace level. Many taxa of small trees and shrubs, though almost absent below the tephra, become consistently well represented above it. Table 5.3 summarises the pollen diagram of this episode, which makes the differences between subsequent stages quite clear.

There is a large increase in charcoal particles, with different sizes, associated with the tephra. In a very short time, they decrease synchronously, but keep a constant presence, which is very well correlated with changes in *Pteridium.*

About 65% of the total variation in the data is explained by the first two axes of the PCA, which is the highest variation explained in PCAs of all tephra episodes (Table 5.1). This effect is not due to the slightly more intensive sampling around the Taupo tephra than around other episodes, since the correlation of variance explained by the first two axes of PCA and the number of sample analyses for each disturbance episode is very low ($R^2$=0.3199, n=5). Axis 1 separates the samples taken around the Taupo tephra into the three defined groups: prior to the eruption, adjacent to the eruption and subsequent to the eruption, while axis 2 primarily differentiates samples subsequent to the eruption from those prior to and adjacent to the eruption (Fig. 5.6). The group prior to the eruption mainly consists of *Prumnopitys taxifolia*, *Dacrycarpus dacrydioides*, *Coprosma,* fern allies and *Phormium*. Just after the eruption, the vegetation is characterised by relatively high frequencies of *Dacrydium cupressinum* and *Pteridium*, together with increasing components of *Myrsine* and *Pseudowintera*. The only taxa reduced in abundance by the eruption are fern allies, including tree ferns and ferns with monolete spores, and *Coprosma*. Subsequently, tree ferns started to flourish again and the vegetation in this group is featured by increasing components of beech trees and *Prumnopitys ferruginea*. In addition, there is a big change with the macrophytic swamp plants. *Phormium*, which used to be very important previous to the eruption, dropped substantially right after the eruption and was replaced by a sudden flourishing of *Typha*, with Cyperaceae establishing shortly thereafter.

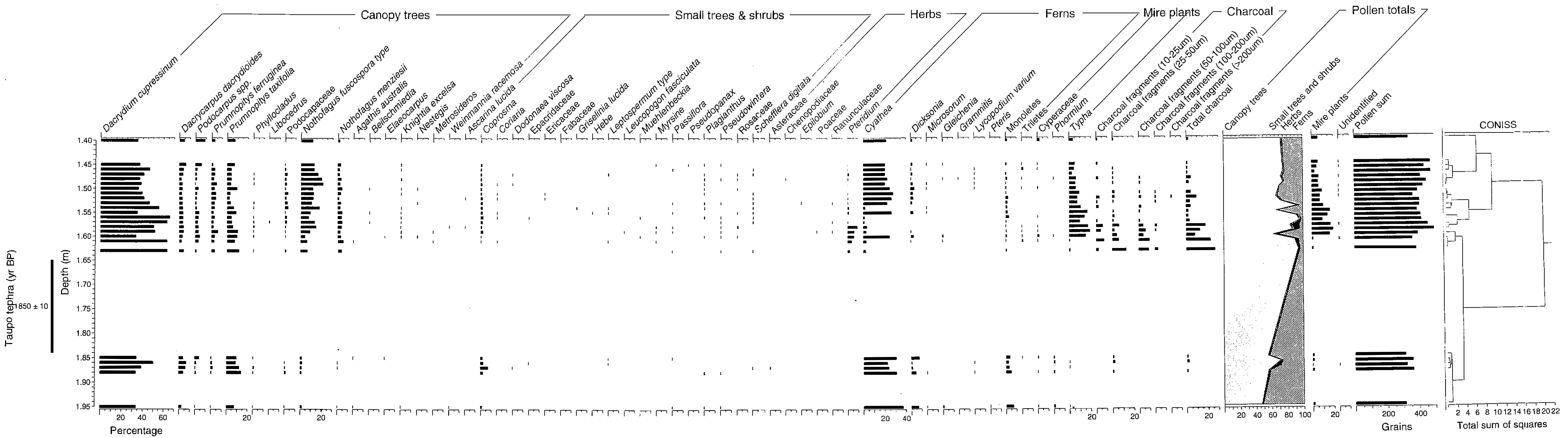


**Fig. 5.5** Pollen percentage diagram of the Taupo episode

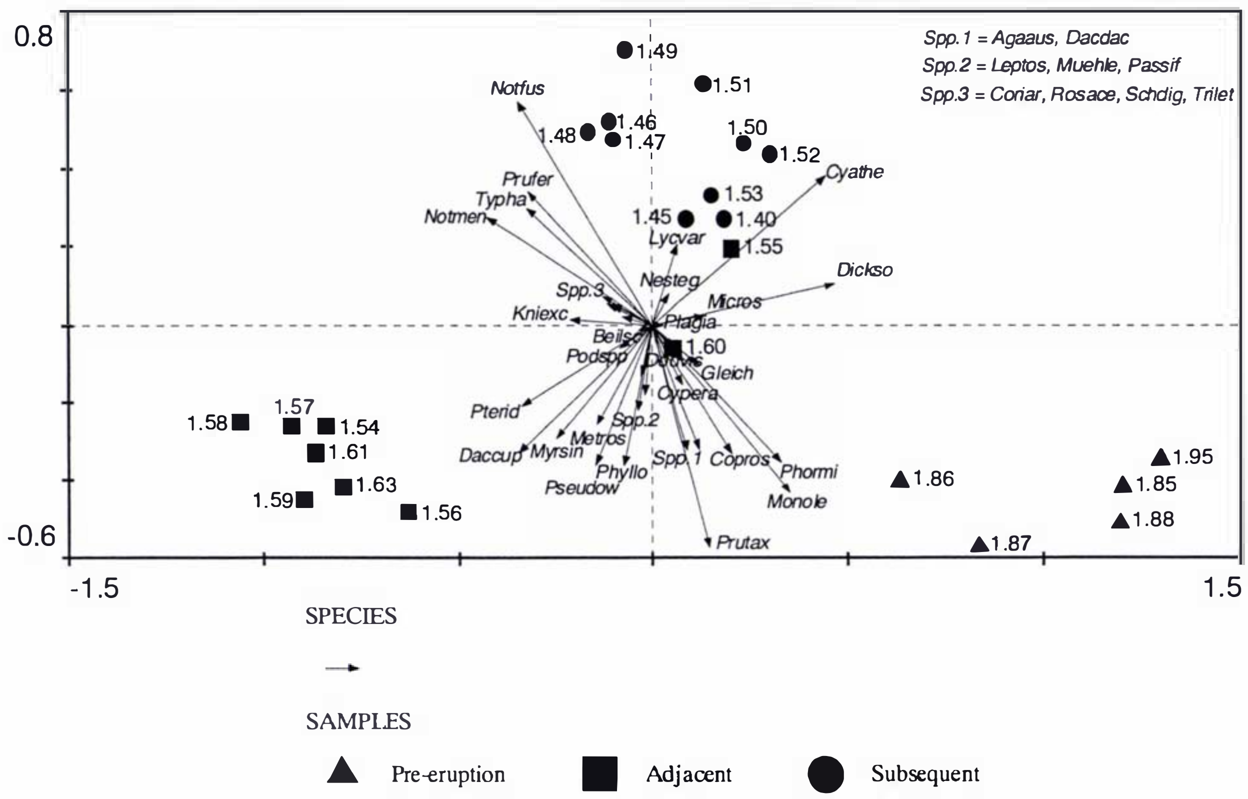


**Fig. 5.6** PCA biplot of the Taupo episode. Some species arrows which are too close are coded to avoid crowding. For the full name of the taxa see Appendix 1. The sample names represent sample depth.

**Table 5.3** Average percentages of the main taxa in vegetation at different stages around the Taupo eruption. Dominant taxa for each stage are indicated by bold values.

| Taxa | Pre-Taupo (1.95m-1.85m) | Adj-Taupo (1.63m-1.54m) | Sub-Taupo (1.53m-1.40m) |
|---|---|---|---|
| *Cyathea* | **29.10** | 7.53 | **22.82** |
| *Dicksonia* | **4.26** | 0.62 | **1.62** |
| Monoletes | **4.17** | 1.13 | 0.99 |
| *Coprosma* | **3.03** | 1.11 | 0.99 |
| *Prumnopitys taxifolia* | **10.3** | 7.47 | 4.92 |
| *Dacrycarpus dacrydioides* | **4.69** | 3.49 | 3.46 |
| *Phormium* | **0.72** | 0.02 | 0.02 |
| *Typha* | 0.12 | **11.58** | 5.72 |
| Cyperaceae | 0.27 | **0.31** | 0.29 |
| *Pteridium* type | 0.00 | **3.39** | 0.31 |
| *Dacrydium cupressinum* | 38.3 | **53.42** | 39.76 |
| *Nothofagus menziesii* | 0.2 | **3.35** | **2.38** |
| *Nothofagus fuscospora* | 1.5 | **9.62** | **13.74** |
| *Prumnopitys ferruginea* | 0.99 | 2.85 | **3.08** |

Taking environmental factors into account, the occurrence of the Taupo eruption is accompanied by an increase of charcoal particles, and changes in LOI, water levels, and pollen richness. Samples right after the eruption, in contrast to those before the eruption, closely coincided with high values of charcoal appearances, low values of LOI, relatively high pollen richness, and gradually increasing water levels as determined by changes in levels of macrophytic swamp plants (Table 5.2). As a result, the first PCA axis probably represents a gradient of disturbances, and the increasing disturbance level is clearly represented by the replacing of tree ferns and fern allies by brackens. The slight increase of *Dacrydium cupressinum* is probably also due to its adaptability to disturbance (Fig. 5.6)

### 5.3.1.4 Charcoal peak at 2.25 m (c. 2300 yr BP)

This episode is the one of the two charcoal peaks present in the main pollen profile, which is characterised by the occurrence of big charcoal particles (>200 μm).

Although from the overall pollen profile of this core (see Chapter 3), the charcoal peak is found at 2.25 m, analyses of additional samples indicate that total charcoal particles, especially those ranging from 25-50 μm, continue to increase in the later stage of this section. So the "peak" is really a series of fires. Pollen spectra are divided into two subzones at 2.25 m. After the level of 2.25 m, most of the tree pollen starts to decline, such as *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Nothofagus fuscospora* type, and so do spores of tree ferns. *Coprosma* drops much later, at about 2.19 m, but more abruptly. In contrast, monolete spores increase substantially from c. 5.8% to 25.2% across the level 2.24 m.

More than 70 percent of the total variation is explained by the first two axes of PCA (Table 5.1). Axis 1 primarily separates the samples into two groups, with most of the samples before this level (2.25 m), placed to the right side of axis, and samples above this level to the left. The right-side group consists of relatively more canopy trees, such as *Dacrydium cupressinum, Prumnopitys ferruginea*, *Prumnopitys taxifolia,* and *Nothofagus fuscospora* type, as well as tree ferns. The left-side group differs by the high frequency of fern allies with monolete spores (Fig. 5.8). Additionally, the value of LOI obviously rises through time (Table. 5.2), which indicates the increasing organic materials in the sediments.

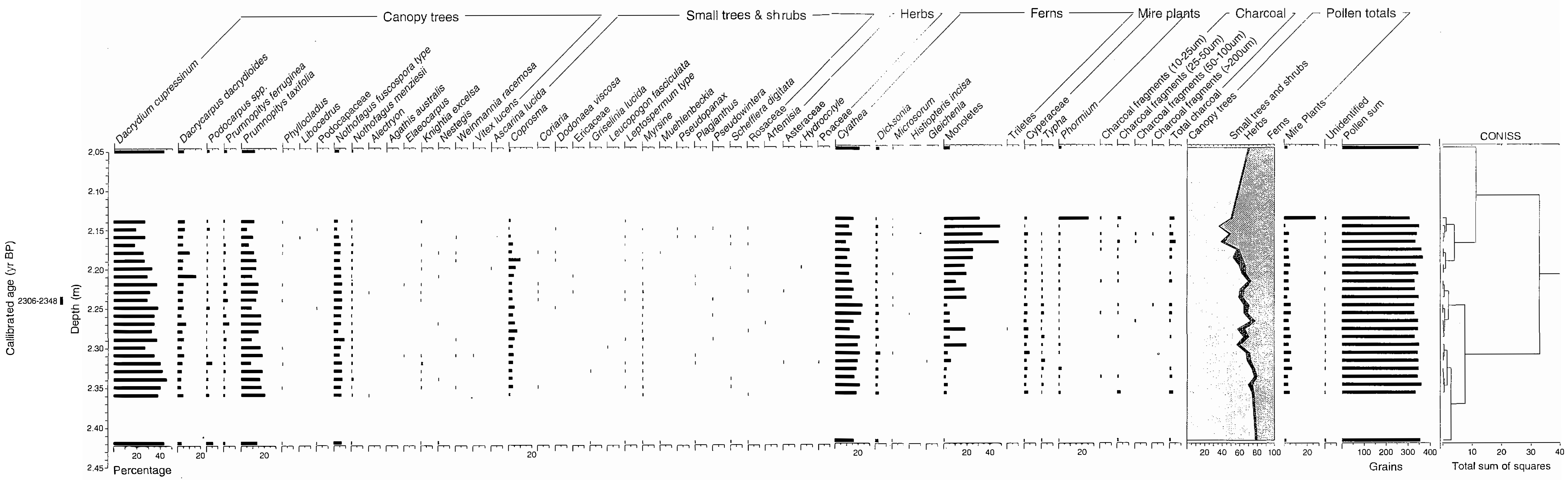


Fig. 5.7 Pollen percentage diagram of the charcoal episode at 2.25m

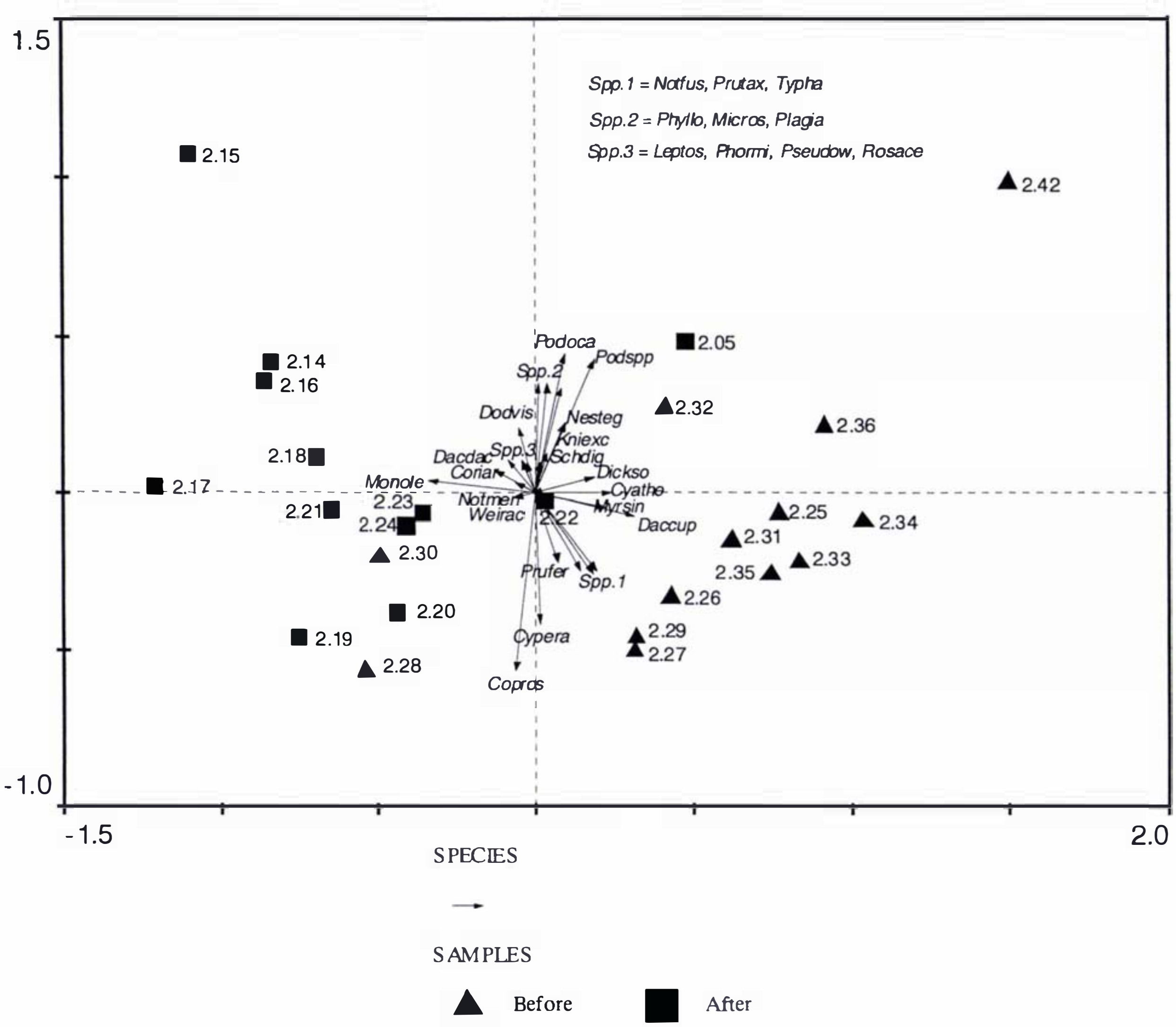


**Fig. 5.8** PCA biplot of the charcoal episode at 2.25 m. The sample names represent sample depth. Some species arrows which are too close are coded to avoid crowding. For the full name of the taxa see Appendix 1.

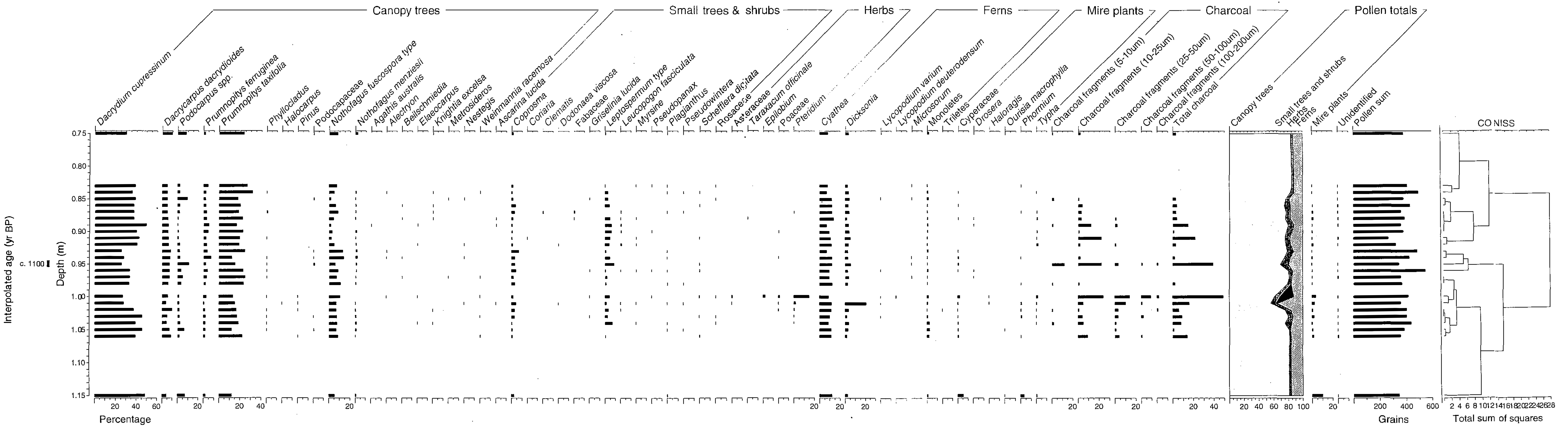


**Fig. 5.9** Pollen percentage diagram of the charcoal episode at 0.95m

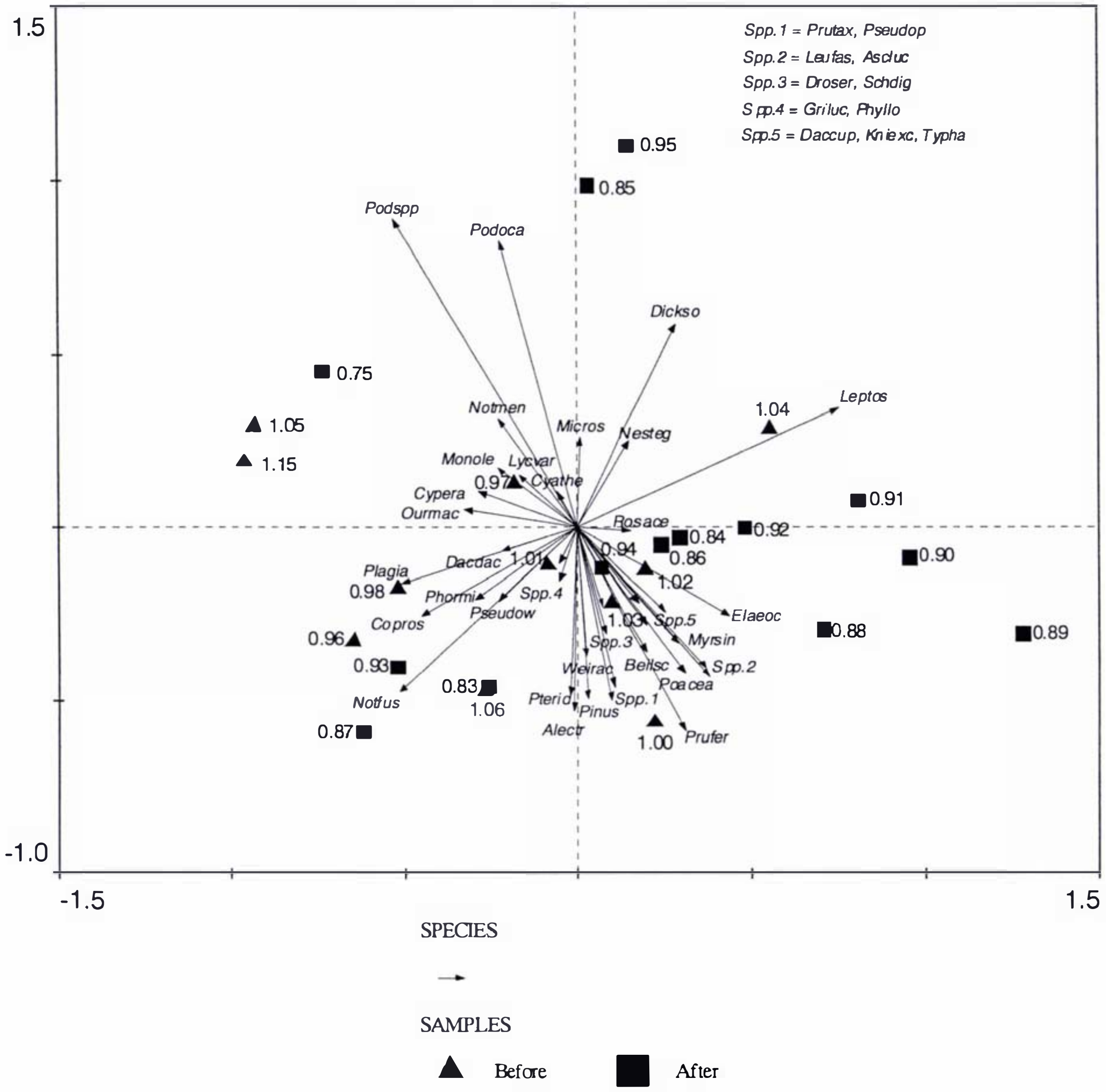


**Fig. 5.10** PCA biplot of the charcoal episode at 0.95 m; the sample names represent sample depth. Some species arrows which are too close are coded to avoid crowding. For the full name of the taxa see Appendix 1.

#### 5.3.1.5 Charcoal peak at 0.95 m (c. 1100 yr BP)

This episode is one of the two charcoal peaks present in the main pollen profile (see Chapter 3). It had been noticed during the process of subsampling that at least 4 samples at levels of 1.00 m, 1.01 m, 1.02 m and 1.06 m might be contaminated by the top sediments of this core. This is indicated by the occurrence of pine pollen at these levels; pine is exotic and was introduced by European settlers some 200 yr BP. Also, the huge charcoal peak at 1.00 m associated with high values of *Pteridium* and Poaceae is probably due to contamination from the top as well. Thus the data from samples at these levels are unreliable. Generally there is a temporary decline in taxa of *Podocarpus* spp., *Nothofagus fuscospora* type, *Nothofagus menziesii* and *Coprosma* subsequent to the charcoal peak at 0.95 m. However, *Leptospermum* tends to increase at the same time (Fig. 5.9).

Although nearly half of the variation between the samples is explained by the first two axes of the PCA, the vegetation composition at the different stages associated with the charcoal peak is not distinguishable. An increasing of LOI over time is accompanied by a gradual replacement of *Typha* by Cyperaceae and *Phormium* (Table 5.2, Fig. 5.10).

### 5.3.2 Combined PCA Analysis on all Disturbance Episodes

If PCA analysis is performed on the samples from all the disturbance episodes, the differences within and among each episode are apparent (Fig. 5.11). In general, there is little change in vegetation composition within the episodes of Whakatane and Waimihia tephras and the Charcoal peak at 0.95 m, where the episodes are not able to be subdivided into groups prior, adjacent and subsequent to the disturbance event, which suggests that the impacts of these disturbances on vegetation are not big enough to change the vegetation structure. However, more variable vegetation structures are identified within the episodes of the Taupo tephra and the charcoal peak at 2.25 m, implying that vegetation has deviated from its previous state, in association with the forces of those disturbances.

The vegetation combination characterising each episode is different, except those around Whakatane and Waimihia. Vegetation composition in these latter two episodes is relatively similar, and consists of higher frequencies of *Dodonaea viscosa, Cyathea* and shrubs. Vegetation associated with the later charcoal episode (0.95 m) is typified by increasing conifers, e.g. *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Dacrycarpus dacrydioides*, and large amounts of *Leptospermum*. As for the other two episodes, vegetation that followed the Taupo eruption is represented by increasing abundance of *Pteridium, Nothofagus* and *Dacrydium cupressinum,* while vegetation modified by the early charcoal episode (2.25 m) exhibits *Coprosma* and ferns with monolete spores.

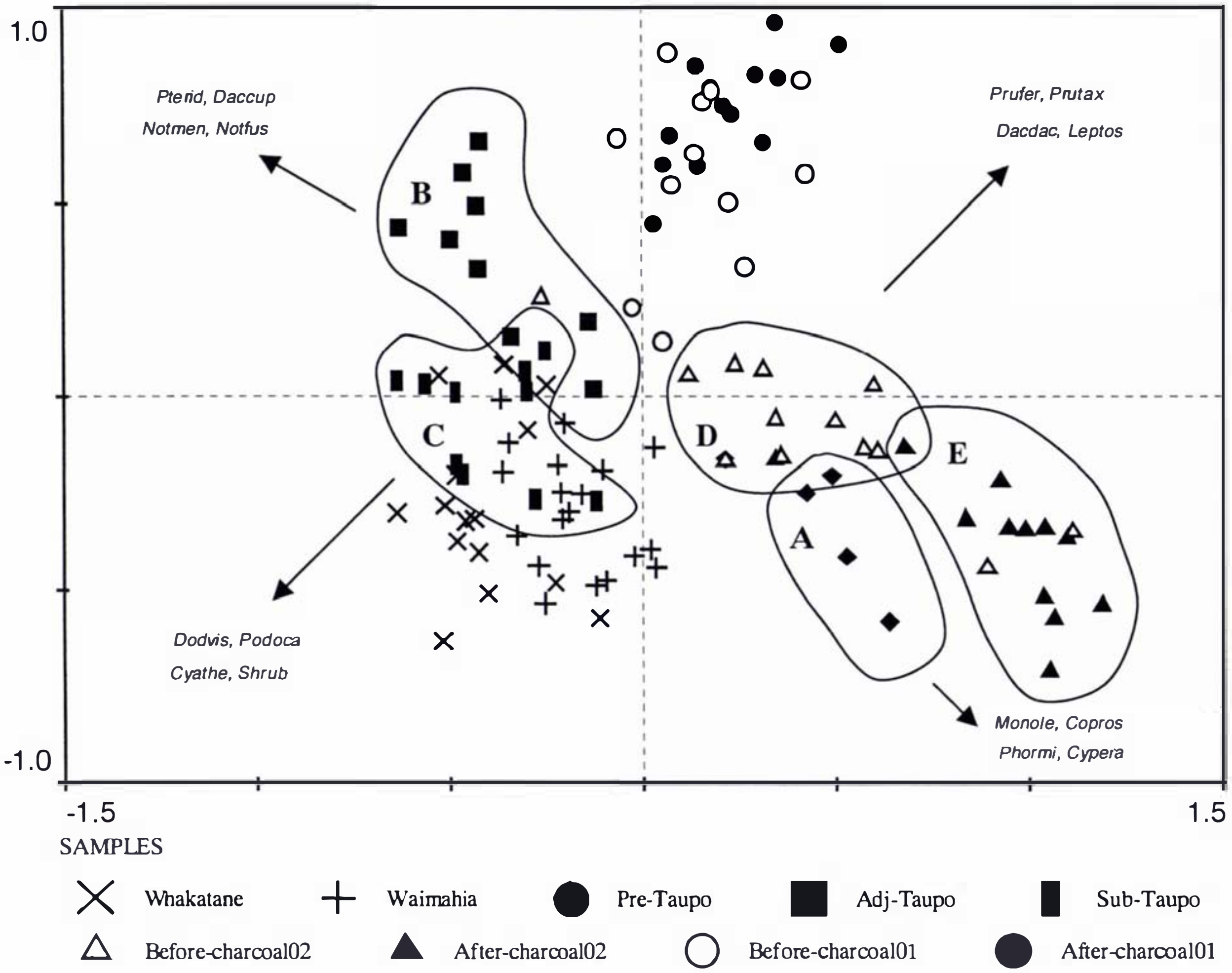


**Fig. 5.11** Combined PCA plot on samples from all five disturbance episodes using both pre and post disturbance samples. Only five groups of samples sort by the type of disturbance and by the time the sample was taken around the disturbance. These are: (A) Pre-Taupo, (B) Adj-Taupo, (C) Sub-Taupo, (D) Before-charcoal02 (i.e. before the second charcoal event), (E) After-charcoal02. The highest loading taxa from the PCA of the species are superimposed on this plot. For the full name of the taxa see Appendix 1.

### 5.3.3 Disturbances Relative to the Taupo Episode

Compared with all those episodes of disturbance, the Taupo episode displayed the most variable pattern, and the best groupings related to vegetation recovery after disturbance, which indicates that three relatively stable vegetation stages existed in response to this eruption. It would be interesting to know whether other disturbance episodes also contain stages equivalent to any of these three subsections, and so help to assess the impact of these disturbances on vegetation compared with the Taupo episode. This can be done by making each disturbance episode supplementary in the PCA of the Taupo episode.

Comparing the vegetation composition with the three groups from the Taupo episode (Pre-Taupo, Adj-Taupo and Sub-Taupo), samples from the Waimihia episode are similar to the sub-eruption group of Taupo. The Whakatane episode, however, is rather more variable, with most of the samples similar to the group subsequent to the Taupo eruption, but a few close to groups prior or post to the Taupo eruption. Episodes around both charcoal peaks, on the other hand, are more similar to the vegetation group found previous to the Taupo eruption, with the samples above 2.25 m (the early charcoal peak) closer to the group prior to the Taupo eruption, while samples below 2.25 m are further away in ordination space, towards the group subsequent to the eruption (Fig. 5.12).

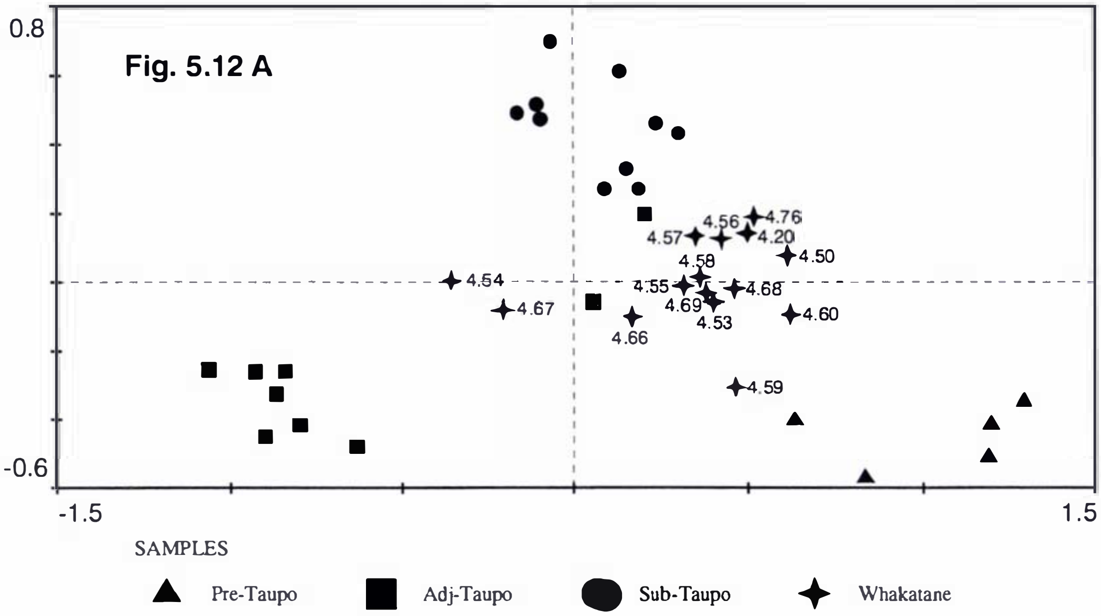


Fig. 5.12 A
0.8
-0.6
-1.5
1.5
4.56
4.76
4.57
4.20
4.58
4.50
4.54
4.55
4.68
4.67
4.69
4.53
4.60
4.66
4.59
SAMPLES
Pre-Taupo
Adj-Taupo
Sub-Taupo
Whakatane

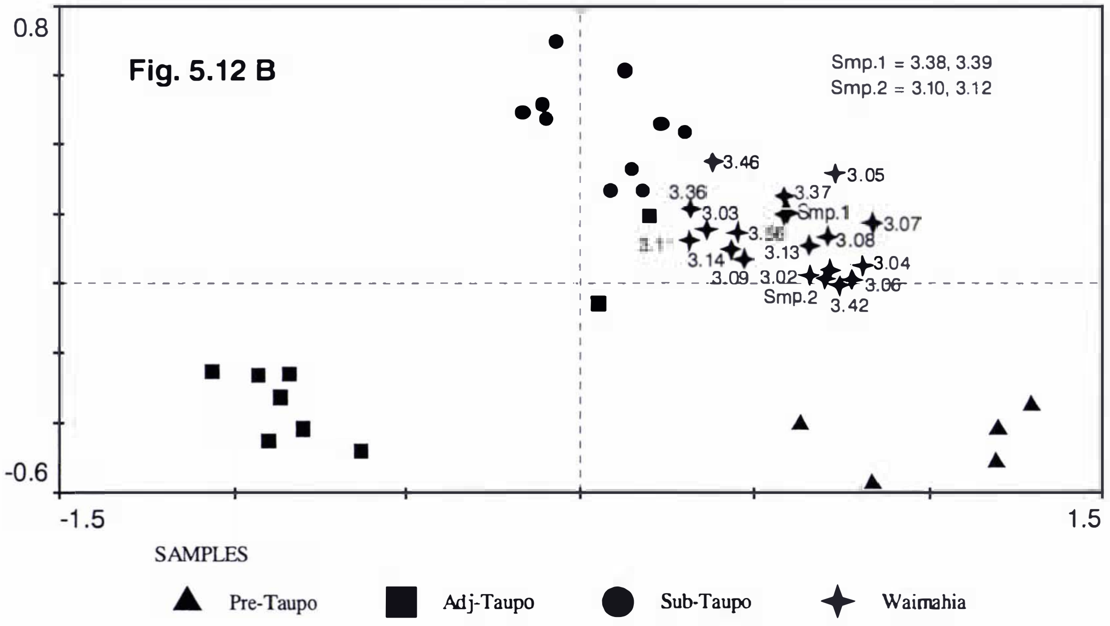
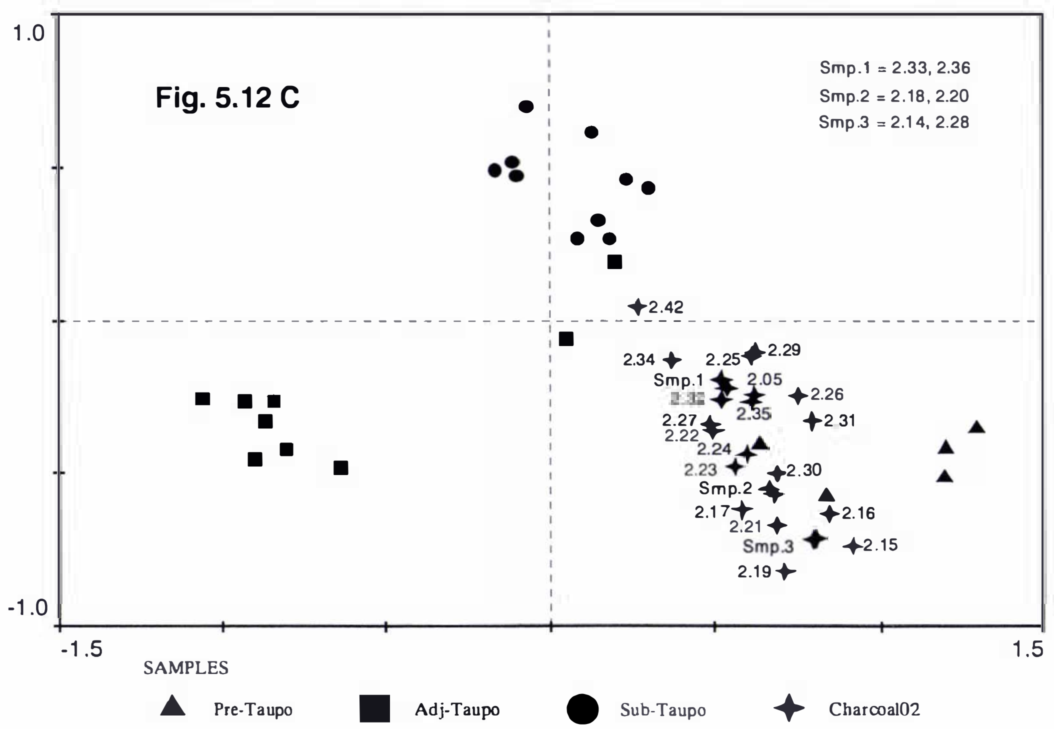


Fig. 5.12 B
0.8
-0.6
-1.5
1.5
Smp.1 = 3.38, 3.39
Smp.2 = 3.10, 3.12
3.46
3.05
3.36
3.37
3.03
Smp.1
3.07
3.08
3.1
3.13
3.14
3.04
3.09
3.02
3.06
Smp.2
3.42
SAMPLES
Pre-Taupo
Adj-Taupo
Sub-Taupo
Waimahia



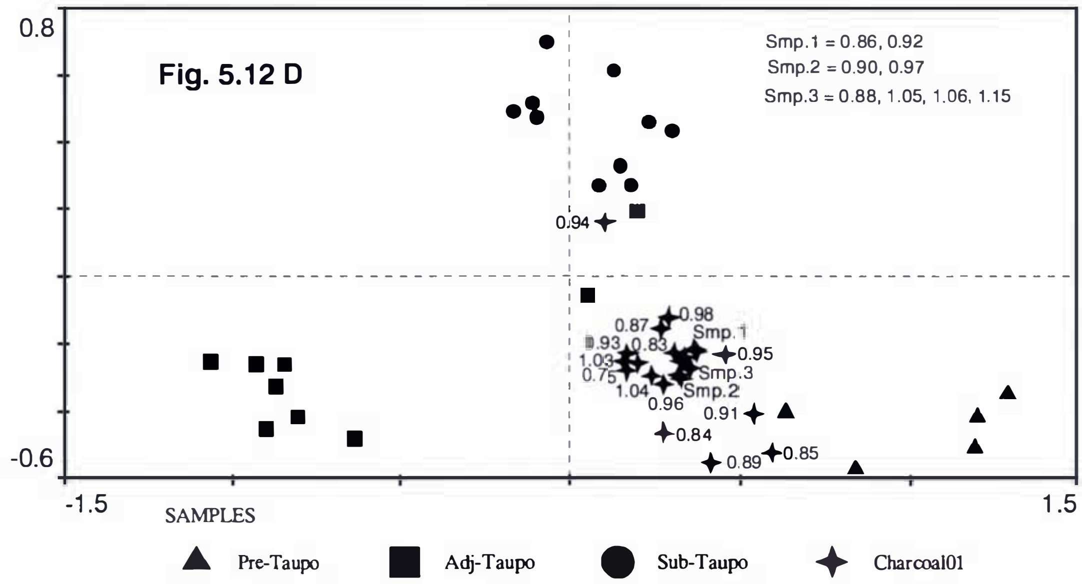


**Fig. 5.12** PCA of the disturbance episodes relative to the Taupo eruption for the four other main disturbances: (A) Whakatane, (B) Waimihia, (C) charcoal at 2.25 m, (D) charcoal at 0.95 m. Only depths for each disturbance episode are labelled. Some samples with positions close together are coded to avoid crowding.

## 5.4 Discussion

The detailed analyses with the additional samples around each disturbance event provide much more information about the vegetation change associated with disturbances than the general pollen diagram. The large intervals between sub-sampling in the general pollen diagram probably make it difficult to record any transient changes caused by these disturbances.

From the analysis of both pollen diagrams and PCAs on detailed sampling, the level of vegetation damage following disturbances varies a lot, despite the thickness of the tephra layers and the number of charcoal fragments found in the pollen records. Though it deposited the same thickness of tephra layer, the impact of the Waimihia eruption on the vegetation at Tiniroto is far less than that of the Taupo eruption. However, the vegetation composition in the Waimihia episode indicates more sensitivity to fire presence. The apparent change in vegetation response following fire disturbance did not occur until c. 2300 yr BP. In general, the later disturbance episodes, including fires and the Taupo eruption, affected the vegetation more substantially than the early disturbance episodes, i.e. the Waimihia and Whakatane eruptions.

### 5.4.1 Fire Disturbances

Although charcoal particles were present throughout the Whakatane and Waimihia episodes, vegetation damage caused by these fires is very small. Forest gaps were generated after fires and quickly occupied by seral scrub such as *Pteridium* and *Coprosma* in the Whakatane, and *Cyathea*, *Dicksonia, Pseudowintera*, and members of Fabaceae in the Waimihia episode. However, all these gaps were transient and quickly invaded by forest trees.

The fire episode indicated by the charcoal level at 2.25 m is different from the previous ones. The huge charcoal fragments (>200 μm) found at this level suggest that the fire was very local, as larger charcoal particles tend not to be dispersed very far (Clark & Royall, 1995). Many of the canopy trees including *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Nothofagus fuscospora* type and tree ferns were affected by the fire, and decrease almost synchronously after the big fire. Fern allies with monolete spores prevailed on the semi-open land, and these fernlands were maintained and enlarged by the subsequent outbreaks of fires. Despite the increasing openness of the land, there is no evidence of acceleration of erosion. This is probably due to the vegetation cover left or the lack of extreme climate events. The increase of LOI is a result of infilling of the hydroseral process, since necron mud was gradually replaced by peat around this level (see Chapter 3).

Although vegetation response to the fire disturbance, indicated by the charcoal peak at 0.95 m, is insignificant in PCA, significant forest damage after the charcoal peak was observed in the pollen diagram, indicated by the loss of some canopy trees and expansion of seral scrub of *Leptospermum*. The contamination in samples from 1.00 to 1.06 m in depth is part of the reason for the patternless structure of vegetation in the PCA plot. Another interpretation is probably that the whole section is at a highly-disturbed time, as high frequencies of charcoal particles are encountered. Thus it is almost impossible to distinguish any vegetation groups relevant to this disturbance. Nevertheless, there is a strong indication of a change in aquatic conditions over time, possibly lowering of the water level, or a change in nutrient conditions.

### 5.4.2 Tephra Disturbances

In Tiniroto, vegetation responses to the early volcanic eruptions, Waimihia and Whakatane, are quite similar. Despite the different depths of ashfall deposited by each eruption in this area, i.e. 6 cm for Whakatane and 22 cm for Waimihia, no associated vegetation change directly results from these eruptions, at least such as can be detected by pollen analysis. For the Waimihia eruption, typical broadleaved-podocarp forest, including *Podocarpus* spp., *Prumnopitys taxifolia, Phyllocladus, Dacrycarpus dacrydioides* and *Elaeocarpus,* characterise the vegetation composition before and again right after the eruption, and so no deforestation was indicated in this episode. Although increasing mineral materials appeared in the sediments following the eruption, the subsequent in-wash of ignimbrite materials deposited nearby is more likely to be responsible for this change, rather than it representing the change in levels of open ground created by the eruption.

However, the intermittent occurrences of charcoal particles throughout the whole Waimihia episode, which are not associated with volcanic eruptions, are more related to the subtle changes of vegetation composition, which encourage the growth of tree ferns, shrubs such as *Pseudowintera*, and Fabaceae. It is likely that the forest was undergoing various degrees of perturbation, like natural fires caused by lightning, even before these eruptions, and such perturbations continue after the eruptions. These sorts of disturbances are very small in scale and the newly created openings were soon filled up by forest taxa; thus they only generated small temporary influences on pollen records.

Unlike the Whakatane and Waimihia eruptions, the Taupo eruption shows the most significant impact on vegetation composition. However, even this was not accompanied by major damage to the forest, as there is no obvious evidence of diminishing abundance of canopy trees. The destruction directly caused by this eruption is largely confined to the shrubs and ferns common along forest margins or in openings within the forest, including tree ferns, *Coprosma* and other fern allies. This is probably due to the widespread fires associated with the eruption. Charcoal peaks occur immediately above the Taupo tephra in this core and many other pollen diagrams from central North Island as well (Wilmshurst & McGlone, 1996). As a result, bracken rapidly colonised the clearings created by the fire after the eruption, with other shrubs including *Myrsine* and *Pseudowintera.* As reported by Levy (1923) and Druce (1957), *Pteridium* can be shaded out by regenerating forest trees and shrubs within 20 to 60 years in an undisturbed environment. The persistence of *Pteridium* after the tephra shows that frequent fires lasted for several decades after the eruption, which coincides with the evidence of continuous fires for at least 100 yr in the central North Island (Wilmshurst & McGlone, 1996). *Dacrydium cupressinum* is the only big tree favoured by the eruption. As suggested by McKelvey (1963), *Dacrydium cupressinum* has many fire-promoting and fire-tolerating characteristics, and frequently develops on old Maori burn sites.

Another apparent change caused by the eruption is the sudden flourishing of raupo over Cyperaceae and *Phormium* at the edge of the lake, indicating the spread of swampland. This is more likely due to the increase of erosion after forest damage, so that the edge of the swamp was built up by the inwash of soil and litter from the catchment. In the subsequent stage, the rapid loss of *Pteridium,* and reoccupation by tree ferns, indicates forest recovery. However, the persistence of charcoal in all sizes, though in much smaller amounts, suggests that the forest was continuously subjected to fire disturbances, but far less intensively. This change of disturbance regime probably caused the expansion of beech trees. Since there is no synchronous decline of lowland forest taxa in the diagram, the increase of beech trees in higher altitude areas nearby is unlikely to be just a consequence of converting the pollen data to percents. Unlike conifers, beech trees are more prone to disturbances which are small in scale and low in intensity (Leathwick, 1995), and also, beeches are light demanding, and their recruitment probably requires a disturbance-related canopy opening (Cullen et al., 2001). In West Ruapehu, Steel (1989) found that *Nothofagus solandri* could compete successfully with podocarp/hardwood associations following the Taupo eruption, and quickly recover its former composition. Similar situations occurred at Gibson's Swamp as well (Horrocks & Ogden, 1998b). Beech forest there not only suffered less damage from the Taupo eruption but also had been expanding towards the core site since the eruption. Nevertheless, there is no direct evidence of expansion of beech trees after the Taupo eruption. Among the 18 sites summarised by Wilmshurst & McGlone (1996) on forest disturbance in the central North island following the Taupo eruption, *Nothofagus* pollen seems to decline in sites which are relatively close to the vent, but either stays the same or increases in sites that are generally further away. Whether *Nothofagus* favours intermediate disturbances needs further consideration.

From the evidence above, it seems that the thickness of tephra does not correspond with the extent of vegetation destruction. With more or less the same thickness of tephra layer (~20 cm) and also almost the same grain-size of ash deposits, response of vegetation to the Taupo eruption is much stronger than to the Waimihia eruption. This conclusion agrees with the fact that forest damage is not related to the thickness of tephra, which is drawn from reviewing vegetation responses to the Taupo eruption from 18 sites in central North Island (Wilmshurst & McGlone, 1996), despite the fact that impacts of tephra on herbs and soils will change with increasing thickness (Blong, 1984). This does not mean that all ash falls will damage forests, e.g. forest trees unaffected from tephra deposition are recorded in the recent eruption of Mount St. Helens, USA, in 1980. On Mts Tarawera, Egmont and Ruapehu following recent eruptions, plant roots after tephra fall appear able to nourish new growth from buried soils (Clarkson & Clarkson, 1995; Lees, 1993; Clarkson, 1990). However, fine-grained tephra particles can easily concentrate toxic fluorine compounds which is a great hazard to forest trees. Also, the fine-grained moist tephra, which tends to form surface crusts that encourage runoff, can inhibit plant penetration (Blong, 1984), and probably impede photosynthesis if coating leaves. Furthermore, the extent of impact of tephra on trees is also affected by other factors such as local topographical conditions. This is probably why vegetation around the Tiniroto site could survive 20 cm of tephra deposited during the Waimihia eruption. The vegetation reconstructed from pollen evidence actually represents the regional scale, including patches protected by local topography. At Tiniroto, the impact of the actual ashfall is probably only apparent in mire taxa, whose distributions are affected by the varying water levels and nutrient conditions caused by deposition of tephra.

Chemical damage from volcanic eruptions is another cause of vegetation destruction especially at distant localities. Volcanic gases and fluids from volcanic hydrothermal systems can be important sources of chemical compounds which can have severe effects on plants (Froggatt, 1997; Neild, 1998). Acid rain from an eruption plume is the most common factor that attacks foliage over a wide area (Newnham, 1999; Froggatt, 1997). Acid rain has been reported as causing a number of effects on plants, such as blossom drop and poor fruit set (Neild, 1998). By changing soil pH conditions, nutrient availability might be altered, so that nitrogen and magnesium deficiency might occur, which affects the vegetation development (Neild, 1998). The hazardous effects by acid rain and gases will decrease with the dilution or dispersal of gases and tephra clouds away from the vent. Fluorine and sulphur are other dangerous components that impact vegetation growth. They are usually concentrated on finer tephra grains and thus may be a hazard at distances quite remote from the eruption source. This is also the way many other toxic substances can be transported. The difference in chemical component from different volcanic eruptions could also lead to different impacts on vegetation. However, geochemical studies of the Waimihia and

Taupo eruptives have demonstrated that the mineralogical composition of the tephras is uniform, suggesting that they were derived from a common magma chamber (Ewart, 1963; Froggatt, 1982; Wilson, 1993). Although different in size, it is difficult to assertain whether these comparable eruptions would result in such substantially different degrees of vegetation destruction by chemical damage as occurred at Tiniroto.

The most significant difference in this sedimentation record between the Taupo and Waimihia eruptions is the occurrence of large amounts of charcoal fragments above the Taupo tephra. The size classes of charcoal from 10 μm to 200 μm suggest that apart from small charcoal particles carried from the fire ignited by pyroclastic flows, local fires were widespread following the Taupo eruption, and lasted for a long period. These fires seem to be the most likely cause of the different impacts of these eruptions. Since Plinian ash cools rapidly in the air, with a temperature on landing of 10-30°C (Froggatt, 1982), there is little difference in the deposited ash temperature from these two eruptions, and the fires following the Taupo eruption seem not directly ignited by the tephra. Lightning activity related to the large volume of ash in the atmosphere and fires generated by pyroclastic flows are the most likely causes of the fires immediately after the eruption, and the fuel from the killed trees increased the later fire potential (Wilmshurst & McGlone, 1996). Since the total volume of rhyolitic material erupted from the Taupo eruption is 3.4 times as great as that at Whakatane, and 5 times that of Waimihia (Froggatt & Lowe, 1990), the probability for lightning fire associated with the Waimihia and Whakatane eruptions is much lower.

### 5.4.3 Comparing Disturbance Events

Since New Zealand forest is characterised by non-equilibrium dynamics, vegetation punctuated by catastrophic perturbation is unlikely to be able to return to the previous state. PCA analysis on these combined episodes from this core indicates that each disturbance is characterised by certain dominant taxa depending on both the nature of the disturbance and the state of forest on which the disturbance takes effect, and in addition, the forest composition is continuously changing as a result of changing climate. The development of the forest is driven by both disturbance and climate.

In this core, there is no major change between and within the Waimihia and Whakatane sections, i. e. no vegetation response was observed to the massive disturbances of these tephra depositions. Disturbances within this period are relatively small in scale which suggests that their impacts on vegetation are not big enough to change the vegetation structure, even temporarily. Disturbances after the Waimihia eruption, however, differ from the early disturbances in modifying the vegetation structure, especially the Taupo eruption (c. 1850 yr BP) and the fire disturbance around 2300 yr BP. This can be illustrated in three aspects. First, charcoal particles larger than 100 μm, which were never encountered in the Whakatane and Waimihia episodes, are frequently encountered in the episodes thereafter. Secondly, the commonest taxa characterising the episodes after Waimihia are those conifers, beech trees and seral plants, which are more competitive species and are indicative of higher degrees of disturbance. This is mainly because both conifers and beech trees usually endure moderate to severe edaphic limitations and thus are prone to various disturbances (Leathwick, 1995). Most important, vegetation responses to these disturbances, in terms of structure change, were identified within episodes of the Taupo tephra and the charcoal peak c.2300 yr BP, implying that vegetation has deviated from its previous state by the force of those disturbances. Openings occupied by seral plants tended to be maintained for several hundred years in these episodes. This change of disturbance regime seems not restricted to Tiniroto. An increase in the fire regime since c. 3000 yr BP is also found, in the South Island from evidence of carbon-dated charcoal preserved in soils, and in the North Island from charcoal records in the pollen diagram from Kopuatai Bog, Waikato lowlands (Ogden, 1998). Ogden found that in the South Island, fires occurred with an interval measured at about 200 years for much of the Holocene, while after c. 3000 yr BP there was an almost four-fold increase in fire frequency. In the North Island, though the increase of fire frequency started a bit earlier, approx. 7000 yr BP, the major rise did not occur until approx. 3000 yr BP.

If the Taupo episode is used as an example of vegetation response to an intensive disturbance, it provides another way to judge the other disturbance episodes, i.e. by comparing the vegetation composition of each disturbance episode to the three groups of the Taupo episode (Pre-Taupo, Adj-Taupo and Sub-Taupo). Since the Whakatane and Waimihia episodes indicate minimal vegetation change to disturbance, we can refer to the Waimihia and Whakatane episodes as showing the vegetation state closest to a forest state (see Chapter 3 & Chapter 4). The responses of vegetation to fires are similar and most comparable. Both the fire episodes around 2.25 m and 0.95 m show a similar deviation from the forest state. The Taupo episode displays a completely different path of vegetation change, but subsequently returns to that forest state. This difference is largely because of the different type of vegetation prior to the disturbance. The vegetation prior to the Taupo eruption is much more open (a result of previous disturbance) and more vulnerable to disturbance than vegetation prior to the other disturbances. In Ongarue, about 20 km to the northwest of Lake Taupo, the forest damage is largely restricted to the shrub *Phyllocladus* c.f. *alpinus*; more than 85% of its pollen declined after the Taupo eruption, while other canopy trees only decreased slightly. This shrubland was actually formed prior to the Taupo eruption following forest destruction by a previous fire (Wilmshurst & McGlone, 1996). Similar situations also occur on Mayor Island, in which forest was more severely damaged by a fire episode c. 2200 yr BP, and the shrub and grass land created was then further destroyed by the Taupo eruption (Empson et al., 2002). The likely impact of the Taupo eruption on vegetation in a locality is thus determined by the possibility of fire occurrences due to climate conditions. This could partly explain why the impact of the Taupo eruption on vegetation is so variable and not necessarily related to the distance from the vent.

### 5.4.4 Explanations for the Change in Vegetation Vulnerability to Disturbance

The significant vegetation vulnerability to disturbance around 2000-3000 yr BP is supported by a body of palynological evidence from Southland to Northland (McGlone & Moar, 1977; McGlone & Bathgate, 1983; Dodson et al., 1988; Rogers & McGlone, 1989; Horrocks & Ogden, 1998a, 1998b; Empson et al., 2002). Forest destruction caused by fires within that period is widely recorded in the North Island. The decline of *Agathis australis* in Northland might be related to burning, since charcoal input increased between 2620 and 2150 yr BP in Te Werahi (Dodson et al., 1988; Kershaw & Strickland, 1988). In Reporoa around 2500 yr BP, fires temporarily replaced the local *Libocedrus, Prumnopitys taxifolia* and *Podocarpus* spp. with *Coprosma, Pteridium* and grass. Such deforestation initiated by fires was also found in the southern Kaimanawa Mountains and Three Kings Range about 3000 yr ago

(Rogers & McGlone, 1989). Forest destruction at Mayor Island is even more significant. An outbreak of fire disturbance dates back to c. 2200 yr BP, and the landscape of Mayor Island became more open and bare. The establishment of seral plants such as *Pteridium,* Poaceae, and *Leptospermum* has persisted on the open lands for more than 300 yr (Empson et al., 2002). In some places, this disturbance-prone period is indicated by expansion of species favourable to extreme climate events. In Fiordland and inland Otago, *Nothofagus fusca* type forest spread vigorously after 2500 yr BP, and this was attributed to a higher level of disturbance, e.g. increased strom frequency, to the forests (McGlone & Bathgate, 1983). Similar stormier and cooler climate conditions were also responsible for the expansion of *Libocedrus bidwillii* at Gibson's Swamp prior to the Taupo eruption (Horrocks & Ogden, 1998b). The increased storminess from 2090 to 1855 yr BP is further supported by the erosion pulse in lake sediments from the North Island (Eden & Page, 1998).

Generally, a long-term climate trend towards a more seasonal climate is believed to have caused these changes. The intense climate variations associated with increased amplitude of the El Niño/Southern Oscillation (ENSO) could lead to more climate extremes, triggering more frequent disturbances. Severe droughts are probably more common during strong El Niño years (Ogden et al., 1998), which increase the fire probability.

However, the onset of ENSO in New Zealand is about 2000 years earlier than the time when fire outbreaks started at the Tiniroto site and many other places in the North Island (Shulmeister, 1999), and the vegetation at Tiniroto during that time was experiencing a forest invasion. There is hardly any sign of dry climatic conditions for this area. Moreover, the time when the severe disturbance started to affect vegetation cover which has no proximity before, around 2000-2500 yr BP, is the time when the frequencies of ENSO began to decrease at many sites around the world, such as Venezuela and Ecuador around 2600 yr BP (Haug et al., 2001; Rodbell et al., 1999), and Tasmania around 1900 yr BP (Cook, et al., 2000). As a result, the increase in fire probability could not simply be ascribed to enhanced ENSO signals.

There is a problem when using pollen data to interpret environmental change, since they are evidence for both climate and disturbance. The existence of disturbance would hide and mask the climate trend, if it is not directly caused by climate (see Chapter 4). *Ascarina lucida* used to be considered a critical climatic indicator since it is intolerant of drought and frost (McGlone & Moar, 1977). Recent research by Martin (2002, 2003) suggested that the germination pattern of *Ascarina lucida* is adaptive to disturbance. It could be a pioneer species that regenerates following forest disturbances. Thus the decrease of *Ascarina lucida* during Mid to Late Holocene needs to be interpreted with regard to both climatic variability and disturbance regime. In this case, the interpretation of the intensified disturbance between 2000 to 2500 yr BP as a climate shift needs more careful consideration.

Accordingly, without proper climate conditions, it is hard to establish natural fires in this area. According to the data from Department of Conservation, only 12 lightning fires have occurred in New Zealand from April, 1987 to January, 2002, and in the most cases the area burnt was only 0.01 ha. In Hawke's Bay, no natural fires were recorded from 1994 to 1999 (Flenley, 2004). Actually, the charcoal presences and the associated transient vegetation responses in the Waimihia and Whakatane episodes are more likely to be associated with natural fires.

Another possibility is that the change of fire regime since c. 2300 yr BP resulted from interference by people rather than climate, although this time is much earlier than the accepted 600-800 yr BP for the arrival of humans in New Zealand (Flenley, 2004). Despite the lack of direct evidence to support the presence of people from this study, a body of evidence is gathering to suggest a much earlier date of initial human colonization in New Zealand by 2200-1500 yr BP (Sutton, 1994; Holdaway, 1996). Although there has long been debate on the reliability of the dates obtained from rat bone gelatine (McGlone & Wilmshurst, 1999), tests against established chronological markers (like the Taupo tephra) and other dating materials, and the dating method (optical dating technique) indicate that these dates are quite robust (Holdaway & Beavan, 1999). Also, research from the study of moa DNA claimed that moa numbers had already largely declined before human arrival as accepted 600-800 yr BP (Gemmell et al., 2004). Since there is no compelling evidence for climate change during these last two thousand years, which is considered to be minor compared with past events, early human predation could not be excluded, though diseases might be one reason. Apart from moa extinction, the extinction of Finsch's duck, and the decline by 69% in the number of breeding bird species after 2000 yr BP is of particular interest. For at least the past 100 000 years, until 2000 years ago, the fauna appears to have been very stable in composition, and no extinctions are known to have occurred from before the LGM to 2000 yr BP (Holdaway et al., 2002; Holdaway et al., 2001). Bird disease is excluded as a cause of these recent losses, since there is no evidence for a pandemic disease affecting birds in New Zealand at any time in the recent past. So predation by humans and rats remains the most likely causes (Holdaway et al., 2002). So, as Holdway (1999) suggested,

> "if people had the technology and motivation to reach New Zealand nearly 2000 yr ago, then it is plausible they could have visited at other times before permanent settlement. It seems unlikely that during the period when some of the remotest parts of Polynesia were settled (Hawaii 1400 BP) including islands very close to New Zealand (New Caledonia 3000-2900 BP), people did not move south as well, whether by accident or intent."

Humans ought not to be excluded as a cause of the different response of the Tiniroto vegetation to the Taupo erution.

## 5.5 Conclusions

According to the detailed analysis on sections around three volcanic eruptions and two fire disturbances in this core, there is no associated vegetation change directly resulting from the eruptions known as Whakatane and Waimihia. Instead, the forest was undergoing various degrees of perturbations throughout and around these episodes, caused by fires at small scales.

The Taupo eruption shows the most significant effect in modifying the vegetation composition. Three vegetation groups are subdivided around the tephra, indicating different vegetation stages relevant to the eruption. The major vegetation destruction is mostly restricted to forest margins and patches of tree ferns and shrubs, without any major damage to the forest itself. The impact of ashfall is limited to responsibility for the change of mire composition.

The changes around the charcoal levels are indicative of typical responses of vegetation to fire disturbances. The relatively long state of semi-open vegetation after fire since c. 2300 yr BP implies a change of fire regime.

Increasing intensity of disturbances from c. 2300 yr BP is suggested by the more variable vegetation response to the disturbance. The reasons responsible for the changing disturbance regimes might be either much more variable climate conditions since c. 3000 yr BP or might involve early human activities.

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# Chapter Six

## General Discussion

### 6.1 Introduction

As one of the last places on Earth to be settled by humans (Anderson, 1991; Taylor, 1997), New Zealand's biodiversity is considered internationally important. Yet 50% of New Zealand forest has been converted to pasture compared with a world average of only 25% (Taylor, 1997). New Zealand has one of the worst records of biodiversity loss. Protection and restoration of indigenous forest has become a focus issue in conservation in New Zealand, and investigations in New Zealand vegetation dynamics provide solid references for these conservation managements.

Early research in forest dynamics in New Zealand was strongly influenced by the ideas of equilibrium theory (Ogden, 1985a), and emphasizes the succession to a stable climax community. Thus the usual apparently inadequate regeneration in New Zealand lowland podocarp forest is regarded as a stage in a succession towards a climax of broadleaved trees (Cockayne, 1928; Robbins, 1962), since in climax communities all-aged populations are expected to be present which indicate demographic stability in equilibrium with the regional climate. A concentric successional pattern of forest types, with podocarp stands close to the Taupo explosive centre and forest with more abundant hardwoods further away, found by McKelvey (1963) provides evidence for this hypothesis. However, evidence of the plant macrofossils from the buried forest of the Benneydale-Pureora district supported dominance of dense podocarp forest in the central North Island prior to the Taupo eruption, and pointed out that hardwood forest is not the endpoint of forest succession (Clarkson et al., 1992).

Only recently has it been realized that disturbance might be responsible for these podocarp forest structures, and the “regeneration gap” may be a response to disturbance of the particular regeneration ecology of the species involved (Veblen & Stewart, 1982; Morton et al., 1984; Wells et al., 2001). New Zealand forests are frequently affected by various disturbances, especially volcanism, earthquake and anthropogenic fires (Wardle, 1985). Because of the prevalence of disturbance, Ogden (1985) recommended that equilibrium models be seen as inappropriate for New Zealand forests. Most of the forests in New Zealand are not stable in composition or in the demographic characteristics of their constituent species; rather they are in various stages of recovery from past disturbances (Ogden, 1985b)

Despite the impact of disturbance, Leathwick & John (1995) address the importance of climatic relationships for the distribution of New Zealand tree species. It was found that the distribution of forest in central North Island was closely related to the topography and climate data, such as temperature and solar radiation (Leathwick & Mitchell, 1992). Edaphic conditions played an important role in the forest distribution as well (Clarkson et al., 1992). Consequently, the present forest system is complicated, and is determined by more than one factor.

Since vegetation history provides evidence of both climate and disturbance, pollen records thus provide one of the most valuable sources of long-term data for understanding vegetation dynamics from both angles.

An approach which allows disturbance to be studied in the presence of climate change is to use an accepted "undisturbed site" as a reference pointer or baseline for a more disturbed one, so that effects of climate can be separated out, and the impact of disturbance can be evaluated. As suggested in Chapter 1, two sites, from Sponge Swamp, Haast and from the Tiniroto Lakes, Gisborne, were chosen as an "undisturbed site" and a "disturbed site" in this thesis, according to their background and history, and pollen records from both sites were used to compare the vegetation dynamics in a climate and disturbance view.

## 6.2 Discriminating Vegetation Dynamics at Sponge Swamp and Tiniroto

Such techniques as outlined above have been applied to the two pollen records from Sponge Swamp and Tiniroto in order to discriminate different vegetation dynamics due to different environment backgrounds. Payette et al. (1989) claimed that disturbance events could frequently trigger ecosystem shifts, but that in sites which escape such disturbances, vegetation can remain largely unchanged through major climatic changes. The hypothesis here is that the former case (i.e. disturbance driven dynamics) apply at Tiniroto, while Sponge Swamp is driven only by climate change. The conclusions of such analyses are outlined below, while in later sections the detailed evidence of the nature of these vegetation dynamics is presented.

From both the pollen diagrams (Fig. 2.4, Fig. 3.4) and the scores of PCA axis 1 from an ordination of the samples and their pollen contents (Fig. 4.8), the vegetation reconstructed from the Sponge Swamp pollen data showed continuous, slow, smooth divergence away from its initial composition over time. This kind of smooth trend is also depicted from the autocorrelation analysis performed on the sample scores of PCA axis 1 (Chapter 4), by the gradual decline of the autocorrelation coefficients of current vegetation vs. previous vegetation with increasing time lags (Fig. 4.3a). Nonstationarity is indicated by the change of vegetation composition, which means that the past vegetation could not be used to predict vegetation in the future. All these analyses demonstrate non-equilibrium dynamics even in this undisturbed site. This contradicts the initial assumption, i.e. that Sponge Swamp is a stable reference site, but it is hard to envisage how a site could be more stable. Perhaps no site is ever at equilibrium, as the non-equilibrium dynamics are responding to subtle, but ongoing changes over time. However, this site is still useful as a reference to compare with the very different non-equilibra of Tiniroto. Consequently, there must be some factors other than disturbance, which cause these non-equilibrium dynamics at this site.

As indicated by other autocorrelation analyses on pollen data sets (Franklin & Tolonen, 2000; Turchin & Taylor, 1992), a possible cause for these nonstationary dynamics could be either environmental change or long-term succession, which could both make the current vegetation state shift away from its previous state. Succession can be ruled out at both sites simply because of the length of time studied, which is an order of magnitude greater than the longevity of the longest lived-trees in the forest. Climate change is another factor to result in non-equilibrium dynamics (Davis, 1984). Although it will take many years for ecosystems to respond to climate change (Starfield & Chapin, III, 1996), given enough time even small climate variations can lead to large vegetation changes (Davis, 1984). Since there is direct or indirect evidence for climate fluctuation on all time scales in a directional way rather than around a constant mean, this pattern of climate change has profound effects on the structure of biological communities (Davis, 1984; Wilson, 1990). Also, climate shifts are already taking place within the lifespan of forest trees, and the time over which climate change has an impact is shorter than that required by communities to reach equilibrium (Delcourt et al., 1982; Davis, 1984). This is confirmed by continuous change in vegetation composition at time scales of $10^4$ years (Delcourt, 1979; Whitehead, 1981; Davis, 1984; Wilkins et al., 1991; Ritchie, 1995). The mechanism underlying this non-equilibrium hypothesis is that, with the changing climate, the community will comprise a mixture of species that are favoured by the current environment, with remnants of species favoured by the previous environments, due to the "storage effect", either because of the longevity of individuals, or by storage in seed banks (Wilson, 1990).

Thus climate shifting in time scales of $10^3$-$10^2$ years, could possibly be responsible for the non-equilibrium of vegetation dynamics around Sponge Swamp, although further evidence of climate change needs to be derived from pollen records.

Though not quite as clearly indicated by changes in individual pollen percentages (Fig. 3.3), vegetation composition at Tiniroto was continually changing through time as well. The trend of sample scores of PCA axis 1 within the data set from the Tiniroto site (Fig. 4.8) is comparable with that from Sponge Swamp. However, in contrast with the change in Sponge Swamp which is more steady and consistent over the whole time span, the trend of change at Tiniroto is always inhibited. Thus the non-equilibrium dynamics revealed here differ from the trend at Sponge Swamp. At Tiniroto, the sudden floristic changes seem to be stimulated by disturbances. This phenomenon is especially obvious for the last c. 2300 yr BP. Nonstationarity is also manifested by the gradual decline of autocorrelation coefficients of current vegetation vs. previous vegetation with increasing time lags (Fig. 4.6a). The vegetation dynamics around Tiniroto are characterised by non-equilibrium, but it is of a stochastic nature, compared with the continual change of Sponge Swamp.

There are good reasons to expect the non-equilibrium dynamics which were found at Tiniroto, with its history of the occurrence of disturbance. It is because of the recognition of the importance of disturbance in the 20th century, that non-equilibrium theory started to be invoked. Over the last few years it has become apparent that natural disturbance is so common that it keeps a system from ever reaching a stable state (Sprugel, 1991). Most of the current vegetation communities, including those in New Zealand, are actually composed of continuously changing mosaics or patches of different ages, created by recent or past, anthropogenic or natural disturbances (Ogden, 1985a; Sprugel, 1991; Reice, 1994). Of course, scale is critical for understanding the mechanisms and consequences of a disturbance (Rykiel, 1985). When the disturbance events are large enough to affect a relatively large proportion of the landscape, the achievement of an equilibrium state is unlikely (Franklin & Hemstrom, 1981; Shugart & West, 1981; Shugart, 1984). This situation seems to apply in the Tiniroto site (refer to Chapter 3). However, beside disturbance, are there any other factors involved in producing such non-equilibrium dynamics?

Both Tiniroto and Sponge Swamp exhibit non-equilibrium dynamics. Although vegetation at Sponge Swamp is characterised by non-equilibrium dynamics, which violated previously held assumptions, the mechanisms underlying vegetation dynamics of both Sponge Swamp and Tiniroto are different due to the existence of disturbances. Below the evidence of climate change and of disturbance is explored in detail.

## 6.3 Role of Climate Change in Vegetation Dynamics

As mentioned above, climate change might play an important role in the vegetation dynamics of both sites, although the effects might be interrupted and modified by disturbance. Evidence of climate change derived from pollen data of both sites will be discussed below separately.

### 6.3.1 Evidence of Climate Change from Pollen Data of Sponge Swamp

From an over-view of the pollen diagram and the PCA plot, the continuous change in the vegetation composition in Sponge Swamp is likely to be climate-related.

The most significant change in vegetation composition in this site is the consistent decline of *Ascarina lucida,* and gradual increasing of *Nothofagus menziesii* and *Prumnopitys taxifolia*, which might indicate climate change. The relative higher frequency of *Ascarina* in the early Holocene found in the body of pollen records throughout New Zealand, has been interpreted as indicating periods of mild and moist climatic conditions. This is largely based on its present distribution, which suggests that high rainfall and absence of heavy frosts are important factors in its distribution (McGlone & Moar, 1977). However, recent research also suggests the adaptability for *Ascarina* to disturbance, and points out that *Ascarina* tends to grow in forest gaps, forest margins, and in early sucession vegetation (Burrows, 1996; Martin & Ogden, 2002). Thus the peak abundance of *Ascarina* needs to be interpreted with regard to both climatic variability and disturbance regime (Martin, 2003). Despite the controversly over *Ascarina*, a warmer climate episode in the early Holocene is supported by evidence from elsewhere New Zealand, which suggests that the mean annual temperatures between 8000 yr BP and 6000 yr BP were either similar to or higher than at present (McGlone, 1993). The marine and ice cores from Antarctica provide good evidence for this climate scenario as well (McGlone, 2002b).

A nearly exponential decline (up to 80%) of *Ascarina lucida* from c. 6800 yr BP might indicate a harsh climate condition which surpassed its ecological threshold, though can be partly attributed to the natural successional process. The subsequent expanding or establishing of cold tolerant or moisture stressed taxa in this site, e.g. *Nothofagus menziesii*, ericaceous shrubs, *Lycopodium australianum* and *Gleichenia* (Wardle, 1991; Wilmshurst, 2002), coincides with this change. This is also supported by the drop of Sea Surface Temperature in southern New Zealand waters by 1-2 °C from the early Holocene (Nelson et al., 2000).

Precipitation seems to have decreased from c. 3700 yr BP in this core as shown by the gradual replacement of aquatic taxa with mire taxa. Swamp forest taxa such as *Dacrycarpus dacrydioides*, also gave way to *Prumnopitys taxifolia,* which is a flood-intolerant species in New Zealand (Wardle, 1991). At the same time, natural fire was also common in central and eastern Otago (McGlone et al., 1995; McGlone & Moar, 1998; McGlone & Wilmshurst, 1999; Wilmshurst et al., 2002), the upper Clutha district (Wardle, 2001), and other eastern parts of the South Island (Burrows & Russell, 1990; Burrows & Randall, 1993), coincident with the drought episode experienced at Eweburn Bog, Otago, after c. 3400 yr BP (Wilmshurst et al., 2002). The rather similar tendency to drier conditions on the opposite coast of the country indicates increasing climate variability and seasonality. This is due to the humid northerly airflow gradually giving way to the cooler but clearer southwesterly airflow, which lowered the winter temperature and decreased the summer humidity (McGlone, 2002). This change of climate regime is also confirmed by the high El Niño frequencies occurring in Venezuela and Ecuador between 3500-2600 yr BP (Haug et al. 2001; Rodbell et al., 1999).

In RDA analysis, about 20% of the total variance in vegetation composition is explained by the explanatory variable "sample age", and this variance may therefore be associated with long-term forcing mechanisms such as unidirectional climate change.

### 6.3.2 Evidence of Climate Change from Pollen Data of the Tiniroto Site

Evidence for climate change at Tiniroto is not as distinctive as in Sponge Swamp.

Percentages of most tree pollen taxa fluctuated frequently without any long-term trend. The only obvious change over time in the pollen diagram is the gradual decline of *Dodonaea viscosa* since c. 4900 yr BP, together with some components of shrubs and herbs. One implication for this decline of *Dodonaea viscosa* is climate related, since it is a frost-sensitive small tree (Wardle, 1991), and its decline is usually accompanied by the decline of *Ascarina lucida,* and even mangroves (McGlone and Topping, 1977; McGlone, 1983, 2002a; Mildenhall, 1994, 2001), implying deterioration from warmer climates. According to Wardle (1991), *Dodonaea viscosa* also prefers open and drier sites, and usually appears on cliff faces or forest margins. At Tiniroto, simultaneously with a drop of *Dodonaea*, there is also a decline of many open land and light-adapted taxa, such as *Coprosma, Pseudopanax, Schefflera digitata, Pteridium, Hebe* and members of the families Fabaceae and Asteraceae. Thus the decline of *Dodonaea* within this site is more likely a result of forest invasion. Forest taxa increase substantially after *c.* 3280 yr BP as shown in the PCA plot (Fig. 5.4).

There are at least two possible explanations for the observed forest invasion. Forest invasion could be either regarded as a successional process in recovery from disturbances, or a result of climate ameliorations. If it is disturbance-related, it might be caused by a local event, although disturbances like volcanic eruption could have relatively widespread effects. If it is climate-driven, it will be a regional effect. The evidence at Tiniroto would first exclude disturbances like volcanism, due to a lack of tephra at those levels. Earthquakes is another possible disturbance, since the Tiniroto Lakes were formed by large mass movements. However, as shown by evidence from other places in the central North Island, such forest invasion is not only restricted to Tiniroto.

Pollen records (McGlone, 2002a) from Lake Poukawa, Hawke's Bay, manifest the same situation at the same time. Beech trees and angiosperm trees superseded *Dodonaea* and other open site taxa, such as *Coprosma*, *Leptospermum* and *Elaeocarpus* around the lake *c.* 5000 yr BP. At Lake Rotorua (McGlone, 1983), *Dodonaea viscosa*, together with other open land taxa, has subsequently been eliminated by the growth of tall forest at *c.* 3500 yr BP. Since the same transitions happened in several sites, ubiquitous climate amelioration is more likely responsible for this change.

According to McGlone (1988), in contrast to western districts, where climates are linked to more drought-prone and frostier conditions, in the eastern South Island and eastern North Island, climates became wetter during the middle to late Holocene. Evidence for a relatively wet period is also supported in the Repongaere Swamp near Tiniroto, by the consistent existence of aquatic taxa from *c.* 3500 yr BP (Wilmshurst, 1999). Increased rainfall in the mid to late Holocene might have been brought about by the enhanced easterly to southeasterly weather patterns, compared to the more westerly or north-westerly flow in the early Holocene (McGlone, 2002b). A decreasing influx of terrestrial sediment supply from 3500 yr BP in the deep-sea core off eastern New Zealand, is possibly due to the change of this weather pattern which retained the sediments on the shelf by the wind-strengthened along-shelf currents (Carter et al., 2002). Moreover, this might also be related to the reduction in erosion as a result of forest invasion.

This situation was interrupted around 2300 yr BP when forest composition is largely changed by a series of disturbances (Fig. 4.8). The strong directional change of vegetation, e.g. the gradual invasion of forest taxa, is interrupted and gives way to predominantly stochastic processes.

Thus in the middle Holocene, climate amelioration with increased rainfall is responsible for the long process of forest invasion, as shown by LOI, which increases steadily, accompanied by a decrease in pollen richness (Fig. 4.5).

In the late Holocene, the impact of climate is largely masked by the frequent disturbances encountered. Consequently, both climate change and later disturbance events play an important role in the non-equilibrium forest dynamics at Tiniroto.

### 6.3.3 Vegetation Dynamics under Climate Change at both Sites

Although non-equilibrium characterises the forest dynamics at both sites, vegetation dynamics for each site are different due to the existence of disturbance. In the undisturbed Sponge Swamp site, the strong underlying climate gradient is the main factor that controls its vegetation dynamics, while in the disturbed Tiniroto site, disturbance intervenes and makes this climate gradient less distinctive.

Comparing data sets from both sites, great dissimilarities exist in the vegetation composition despite comparable floristic change over time (Fig. 4.7). The vegetation change over time within the Sponge Swamp set is distributed along a strong time sequence, while within the Tiniroto set, it turned out to be less directional. Two explanations might be involved. Firstly, these two regions lie within different climate gradients, and the associated pollen records from which the climate trend is derived are not comparable. The vegetational dissimilarity between sites is beyond all doubt a result of the geographic and climatic differences in plant taxa involved. The strong time sequence indicative of vegetation change over time within Sponge Swamp, supports climate shifting as the prime cause for non-equilibrium at this site. Also, the relatively constant rate of palynological change over 7000 years (Fig. 4.9a) suggests gradual climate change over this period. Secondly, disturbance at Tiniroto might reset any long-term sequence and thus mask the gradient. In the former case, at least it could be argued that the climate trend, if it exists at Tiniroto, is much weaker than that at Sponge Swamp. However it seems unlikely that the vegetation in Gisborne is less sensitive than that in Westland; at the least, it should be more sensitive to change of precipitation. The second explanation is more feasible. As indicated by Clarkson (1990), the patchy and asynchronous nature of disturbances would result in a continuously changing mosaic of vegetation patches of different sizes and ages, which average and disguise the directional change of vegetation when one considers the mean dynamics of an area.

## 6.4 Role of Disturbance in Vegetation Dynamics

It has been already noticed that disturbance makes a big difference to vegetation dynamics at Tiniroto. The disturbance events, especially after *c.* 2300 yr BP, significantly drive short-term responses in the vegetation, and thus mask the underlying long-term climate trend, which totally controls the vegetation processes in sites free from the interference of disturbances, such as at Sponge Swamp. Here the impacts of different kinds of disturbances on vegetation will be addressed in detail for both sites, but especially for Tiniroto, and the implications of disturbance for non-equilibrium dynamics will be discussed later.

### 6.4.1 Impact of Disturbances on Vegetation Dynamics at Tiniroto

Both the pollen data and the PCA analysis show that the floristic change at the Tiniroto site is largely controlled by catastrophic disturbances. Compared with consistent and steady vegetation change in the Sponge Swamp site, abrupt and substantial vegetation changes correspond well with independently identifiable disturbances, especially since 2300 yr BP. This is even clearer when looking at the rate of vegetation change at Tiniroto (Fig. 4.9b).

Although it has been suggested that disturbance could largely alter and control the vegetation processes which are presumably regulated by long-term climate trend, this does not apply equally to all sorts of disturbances. In Tiniroto, the Taupo eruption and the fire episode around *c.* 2300 yr BP seem much more significant in terms of vegetation change than the Whakatane and Waimihia eruptions.

The significant differences in vegetation responses to the Taupo and Waimihia eruptions imply that the thickness of tephra does not correspond with the extent of vegetation destruction. The deposition of tephra layer could affect the vegetation in many ways. The thick ash deposits could break small tree branches, suffocate plant roots, and inhibit plant photosynthesis (Wilmshurst & McGlone, 1996). The fine-grained tephra could be even more hazardous to plants since it tends to concentrate toxic compounds e.g. fluorine and sulphate, and form ground crusts which impede infiltration of water, seedling root penetration, and emergence of shoots of surviving plants (Blong, 1984). In spite of these hazardous effects, damage to plants varies locally in intensity as a result of topography, slope angle, subsequent erosion of ashfall , and vegetation types. Protection on the leeward side of mountain ranges allows patches of vegetation to survive, and erosion of ashfall deposits always facilitates plant recovery on slopes, especially in deep tephra. In the 1980 eruption of Mount St. Helens, although all forest was destroyed within an area of 61000 ha, over a much larger area the forest canopy remained intact but the understory was buried by tephra; tephra 15 cm deep killed most understory plants (Zobel & Antos, 1997). Also, recovery of vegetation from tephra is fast and vigorous. At Mount St. Helens, most plants recovered after several years, and plants may emerge from tephra as long as 10 yr after burial (Zobel & Antos, 1997). Regrowth of plants roots in buried soils is also observed on Mt. Egmont and Ruapehu following recent eruptions (Lees, 1993; Clarkson, 1990). In the Tiniroto site, the vegetation survival from the Waimihia tephra layer 20 cm deep might be a result of all these factors.

The vegetation damage after the Taupo eruption must have resulted from other disturbances regardless of tephra deposition. The most significant difference between the Taupo and Waimihia eruptions is the existence of the large amount of charcoal particles following the Taupo eruption. Some of the particles might be blown from an area nearer to the source affected by huge pyroclastic flows. The occurrence of big charcoal particles and persistence of fire-prone bracken *Pteridium* above the Taupo tephra indicate outbreaks of long-lasting local fires at this site. This led to the loss of shrubland, presumably at the margin of the forest, mainly composed of *Coprosma,* tree ferns and fern allies. Although some charcoal particles were also scattered through the Waimihia episode, the occurrence of fires is intermittent and independent of the eruption, only causing short-term vegetation changes. It seems likely that fire is the main reason for most vegetation change at Tiniroto. The fires c. 2300 yr BP, also brought about big changes in the vegetation, during which some tree taxa and

*Coprosma* were destroyed, which encouraged the establishment of enduring semi-open vegetation chiefly of fern and fern allies.

Despite the presence of fire in every disturbance episode, increasing fire frequency and intensity is obviously characteristic of the disturbances later than *c.* 2300 yr BP. This change of fire regime is probably the main cause of the big vegetation damage caused by the later disturbances, and thus largely controls the vegetation dynamics of the Tiniroto site. Most of the short-term vegetation changes in response to the earlier disturbances, e.g. Whakatane and Waimihia eruptions, however, are very small in scale and only generate small temporary influences on the pollen records, thus hardly affecting the vegetation dynamics under the changing climate.

### 6.4.2 Possible Impact of Disturbances on Vegetation Dynamics at Sponge Swamp and Comparison with that from Tiniroto

Although Sponge Swamp is assumed to be relatively "undisturbed" compared with the Tiniroto site, this is only valid when taking the scales and effects of disturbances into account.

As a matter of fact, many of the forests in Westland are frequently subject to disturbances such as earthquakes, landslides and floods, due to high rainfall, steep topography, and an active fault which runs across the whole region. However, the floristic change in Sponge Swamp is generally characterised by a gradual, consistent and steady change over time (Fig. 4.7), and it is hard to detect any evidence of disturbance from either the pollen record or the PCA analysis. Therefore the properties of any disturbances and associated impacts on vegetation must differ from those at Tiniroto. Also, the vegetation dynamics in Sponge Swamp share some common features with those from the portion of the Tiniroto core containing the Whakatane and Waimihia sections. This suggests that the effects of disturbances around Sponge Swamp are small, like those around the Whakatane and Waimihia eruptions at Tiniroto, and suggests that the vegetation dynamics is apparently driven by a climate trend rather than disturbance.

In Westland, the luxuriant vegetation cover stabilizes the slopes from further erosion, and any slips are usually rapidly recolonised under natural conditions (Soons, 1991). The previous landslide activity is indicated by mosaics of vegetation of different ages. Thus the overall vegetation state in the Sponge Swamp site would be different from that in the Tiniroto site where the area of affected vegetation would be much larger under the most severe disturbances, like Taupo and the 2300 yr BP fire episodes.

Sugita (1994) suggested that small lakes with a 50 m radius could receive pollen grains from a source area 300-400 m away, while medium lakes with a 250 m radius could receive pollen grains from a source area 600-800m away. Vegetation may appear homogeneous even when the actual pattern of vegetation is heterogeneous and patchy, depending on the size of lake relative to the size of patches. Sponge Swamp and Tiniroto are both less than 150 m in radius, so are likely to catch pollen grains from up to 400-600 m away. If disturbances in these areas are patchy and transient, like disturbances in Sponge Swamp and like the Whakatane and Waimihia eruptions at Tiniroto, it might be difficult to pick up evidence of their impacts from vegetation composition change. Then vegetation dynamics would be more governed by changing climate than by local disturbances.

Due to the different nature of disturbances in both sites, the vegetation dynamics affected by these disturbances should be characterised by different processes. The impact of disturbance is clearer when the general trend of vegetation change is taken away. The MA(1) model (equation 4.1), derived from the autocorrelation function of the de-trended data from Sponge Swamp, suggests that vegetation composition in Sponge Swamp is affected by various "random" events, like tectonic-induced disturbances, with their impacts lasting about 100 yr. This model is quite compatible with the constant rate of change in vegetation composition which appears in the PCA analysis. Not surprisingly, the vegetation dynamics at Tiniroto indicated by the AR(1) model (equation 4.2), suggest a more successional process, i.e. the present state of vegetation depends on the vegetation of the immediate past state, say 100 yr, and this process is also punctuated by unexpected exogenous disturbances.

Thus, in the relatively stable site, Sponge Swamp, as the climate change is gradual and slow, in the long term the vegetation composition at each stage closely follows the climate, and any change within the vegetation in the short term, is rather "random" and dependent on transient local disturbance events. In the disturbed site, Tiniroto, the vegetation is frequently reset by the disturbances, and thus is much more reliant on the previous state, unless a big disturbance event is experienced.

### 6.4.3 Disturbance as a Causal Mechanism for Non-Equilibrium Dynamics

As stated above, disturbance is ubiquitous, and has different impacts on vegetation. It could nest within the climate regime, so it hardly affects the climatic-driven vegetation processes, as in Sponge Swamp. Or it could intervene in vegetation processes under climate control, as in Tiniroto. This poses two questions. What is responsible for disturbance having different impacts on vegetation? To what extent is disturbance driving the vegetation process, and so accounting for the non-equilibrium dynamics?

Of course, different types of disturbances have different impacts on vegetation. The vegetation compositional change, the extent of vegetation damage and response of vegetation varies significantly from disturbances cause by volcanic eruption, fire, earthquake, flooding, windstorm, insect attack, drought and frost etc. Due to the lack of direct indices of other disturbances in sediment records and probably their less intensive significances, only volcanic eruptions and fire episodes are addressed in the Tiniroto site. Despite the different nature of disturbance, in a general way, disturbances with different scales, intensities, and frequencies have different impacts on vegetation dynamics, and these parameters are explored below.

#### 6.4.3.1 Disturbances with different scales

Disturbance is scale dependent (Reice, 1994). In Westland, the age structures of the current forests are characterised by extensive, similar-aged cohorts, and the earthquakes occurring in 1826 AD are proposed to be the prime cause for the present vegetation pattern (Wells et al., 2001). Although in-washed clay which is probably brought by flooding or earthquake, is frequently embedded over the profile, pollen evidence from Sponge Swamp, which was sampled at time scales of about 100 yr, is unlikely to capture the signal of such extensive cohort regenerations. This situation also applies to disturbances like landslides, windstorms and floods, which are quite common nowadays but much smaller in scale than earthquakes in Westland. As mentioned by Sprugel (1991), "when natural disturbances are frequent and small compared with natural landscape units, the creation of new patches is balanced by the regrowth and maturation of old ones and the vegetation process appears fairly constant over the whole area." This is probably why evidence of disturbance is insignificant in the Sponge Swamp site.

When disturbance events are large, i.e. approach or exceed the landscape unit, even if infrequent, these occasional events could have long-lasting disruptive effects on vegetation (Sprugel, 1991). This is the case with the Taupo eruption and the fire episode around *c.* 2300 yr BP at Tiniroto. Evidence from the distribution of Taupo pumice and from a number of pollen records indicate that the impact of the Taupo eruption on vegetation was severe, overwhelming most of the central North Island (Wilmshurst & McGlone, 1996). The regional fire episode around 2300 yr BP is also supported by a body of palynological evidence, in which forests in vast areas of the North Island underwent severe disturbance during the millennium prior to the Taupo eruption i.e, c. 3000-2000 yr BP (Newnham et al., 1995; Horrocks & Ogden, 1998; Wilmshurst et al., 1999; McGlone, 2002a; Empson et al., 2002). When disturbances of this kind occur, the system will diverge from its initial state, leading to non-equilibrium dynamics. Moreover, these kinds of disturbances are always high in intensity as well.

#### 6.4.3.2 Disturbances with different intensities

Systems have thresholds, past which the feedback mechanisms change. Prior to and following the threshold, periods of relative stability exist within systems (With & Crist, 1995). Resistance and resilience are features of communities within the threshold zone (Franklin & Tolonen, 2002). Non-equilibrium is a result from the threshold being past, which is chiefly determined by intensities of disturbances. In the case of Tiniroto, though types of disturbance and available vegetation are important, the intensities of disturbance determine the extent of vegetation destruction. The existence of large charcoal particles (>100 μm) in the episodes of the Taupo eruption and the fire around 2300 yr BP, which are never recorded in the Whakatane and Waimihia episodes, implies increasing fire proximity to the site, possibly due to enlarging of affected area. The Taupo eruption and the 2300 yr BP fire episode made the forest cross its threshold, while the intensities of the Whakatane and Waimihia eruptions are not high enough to cause any divergences in vegetation composition. Similarly the insignificant impact of disturbances in the vegetation dynamics in the Sponge Swamp site suggest no threshold was crossed.

#### 6.4.3.3 Disturbances with different frequencies

It has been proposed that if the interval between disturbances is long relative to the generation time of the dominant species, biotic interactions may have an important role, and approaches to equilibrium would be attained (Reice, 1994). However, natural systems are so frequently disturbed that this almost never happens. According to Reice (1994), the return interval of disturbance is roughly proportional to the life span of the dominant species, since the return interval of disturbance may be a critical determinant of life-history characteristics. The “fire interval” measured from New Zealand suggested that fires occurred with an interval measured in centuries to decades (Ogden, 1998). Comparing this with the life span of dominant New Zealand tree species, which can exceed several centuries or even longer than a millennium (Ogden, 1985), the disturbance interval is short enough to encourage non-equilibrium dynamics. However, as stated above, not all kinds of non-equilibrium dynamics are detectable in pollen records of 100 yr sampling intervals.

Besides the issue of disturbance scales and intensities, disturbances with relatively high frequencies might still change the structure of the vegetation and be traceable in pollen records. Although it is hard to detect any change of fire frequencies using charcoal fragments, even through 1cm sampling intervals, it might be traced by the post-fire vegetation complex, which is largely determined by the fire frequencies. For example, the persistence of *Pteridium* after the Taupo eruption, indicates an increasing intensity and frequency of fires, since it can be shaded out by forest trees and shrubs within 20 to 60 years in an undisturbed, moist environment (Levy, 1923; Druce, 1957). Similarly, around the 2300 yr BP fire episode, the semi-open vegetation produced after the fire would also need to be frequently disturbed to prevent the invasion of forest taxa.

### 6.4.3.4 Disturbances with unpredictable responses by the vegetation

Some apparently unpredictable responses of vegetation after disturbance complicate the process of vegetation recovery and always lead to non-equilibrium dynamics, so that it is hard to get restoration of the previous vegetation after disturbances. At Tiniroto, different disturbance recovery episodes occupy different domains in the PCA plot (Fig. 5.11). In other words, each episode is characterised by certain dominant plant taxa. Although the vegetation damage in each episode of disturbance is mainly caused by fire, the response of vegetation in each episode is quite different, as shown by both the pollen records and the PCA analysis (Fig. 5.1-5.10). Climate change could be part of the reason, either responsible for the different forest states prior to different disturbance episodes, or by changing the trajectory of the successional path (Prentice, 1986).

The property of disturbance is another factor causing unpredictable responses of vegetation. Different disturbances remove different species to different degrees, and also create different habitats, release different seed banks, or change the edaphic conditions by altering nutrient levels. All these changes also provide new recruitment opportunities for the establishment of new colonizers (Reice, 1994). Therefore the recovery process of the community is likely to include different taxa, creating a unique successional sequence. This is especially applicable to disturbance at a medium level of intensity. In an agent-based model of forest development, at low levels of disturbance, the simulated forest resembles a deterministic climax forest; at high levels of disturbance, vegetation assemblages are dominated by early successional species; at intermediate levels of disturbance, forest assemblages are highly sensitive to probabilistic events and diverse developmental pathways occur (Savage et al., 2000). In the natural ecosystem, recovery of vegetation after perturbation is always hard to achieve, due to these unpredictable factors. In a study in southern Wisconsin, sedge meadows were monitored at two sites, with or excluding cattle grazing, in order to examine the effects of disturbance by cattle grazing on long term structural characteristics. The results suggested that, since cattle grazing encouraged the invasion of woody species, the successional trajectory in these sedge meadows may never resemble the reference ungrazed site (Middleton, 2002). Similar situations also exist in New Zealand. When testing for equilibrium in grazed semiarid grassland in central Otago, Walker and Wilson (2002) found that recovery from herbicide treatments, relative to untreated controls, always failed due to the rapid invasion of exotic species which excluded the native species. Also, vegetation change accompanied by a loss of desirable soil properties, which was caused by grazing, is another piece of evidence for vegetation divergence due to grazing in central Otago (Gibson et al., 2000)

## 6.5 Beyond Vegetation Dynamics — Possible Interpretations for the Changing Disturbance Regime at Tiniroto

It has been pointed out above that in the Tiniroto site, the later disturbance episodes (including the Taupo eruption and the fire around 2300 yr BP) differ from the early disturbance episodes (including the Whakatane and Waimihia eruption) in scale, intensity and frequency. This suggests a change of disturbance regime, actually a fire regime, is responsible for the vegetation damage characterised by compositional change within forest during the late Holocene. Although the relatively severe damage could be solely attributed to pre-disturbance vegetation if it is more combustible, the increase of forest taxa in the vegetation complex from the early disturbance episode does not support this idea.

As pointed by Ogden et al. (1998), the change in the fire regime since 3000 yr BP is a nation-wide event in New Zealand. For much of the Holocene in the eastern South Island fires occurred with an interval measured at about 200 years, while after approx. 3000 yr BP there was an almost four-fold increase in fire frequency. Though the increase of fire frequency in the North Island started earlier, approx. 7000 yr. BP, the most obvious rise did not occur until approx. 3000 yr BP. This coincides well with the change of fire regime at Tiniroto.

This change of fire frequencies could be interpreted as a climate response to intensified ENSO frequencies. The onset of ENSO from c. 5000 yr BP in New Zealand and many other places in the world is supported by Shulmeister (1999), as a response to increasing seasonality which is closely associated with the enhanced Walker Circulation in the Pacific. Furthermore, this scenario is confirmed by the sediment records from floodplain, continental-shelf, and continental-slope settings of the eastern North Island of New Zealand, by a transition from fluvial deposition to landsliding, as a result of increasing storminess after c. 4000 yr BP (Gomez et al., 2004). The great climate variations associated with increased amplititude of the El Niño/Southern Oscillation (ENSO) could lead to more climate extremes, triggering more frequent disturbances. Severe droughts are probably more common during strong El Niño years (Ogden et al., 1998), which raises the fire probability.

However, evidence from pollen records of this core does not support the occurrence of drier climate conditions from the middle Holocene (~c. 5000 yr BP) . An onset of forest invasion is strongly suggested from *c.* 4900 yr BP by the decline of *Dodonaea viscosa*, which prefers open and drier sites, and other open land and light-adapted taxa. Pollen evidence from other places in the central North Island (McGlone, 1983, 2002a), shows such forest invasion is not only restricted to Tiniroto. This regional phenomenon suggests climate amelioration, especially increasing rainfall, from the middle Holocene. Evidence for a relatively wet period is also supported in the Repongaere Swamp near Tiniroto, by the consistent existence of aquatic taxa from *c.* 3500 yr BP (Wilmshurst, 1999). This conflict might suggested that the Tiniroto area is more affected by the La Niña signals which are associated with the arrival of late summer storms from the SW Pacific convergence.

The later change of disturbance regime around c. 2300 yr BP rises another problem for interpretation. As suggested by evidence from Venezuela and Ecuador (Haug et al., 2001; Rodbell et al., 1999), the El Niño frequencies started to drop after c. 2600 yr BP. In Tasmania, this happed even later, at c. 1900 yr BP (Cook, et al., 2000). It is hard to ascribe the intensified disturbances after c 2300 yr BP at Tiniroto to any ENSO related climates.

Thus, if the climate condition, under which the outbreaks of fires prevailed, is assumed to be similar with that in the earlier stage when forest invasion took place, it is unlikely to encourage any lightning fire. The opportunity for setting lightning fire is extremely low, e.g. only 0.03% of lightning discharges that strike vegetation result in forest fires (Taylor, 1974), and ignition by lightning is of very small probability and probably occurred only every few centuries in the east of the North Island of New Zealand (Ogden et al., 1998; Flenley, 2004). This time span is far longer than the time for forest species to regenerate after a burn. Since the post-Taupo fires and the 2300 yr BP fires kept the vegetation in a semi-open stage, mostly fernland for more than

100 years, there are probably other factors which delayed the return of the forest at the Tiniroto site.

Human activity is another possible reason for increased fire frequency and the change in the fire regime, though this would imply human arrival in New Zealand at c. 2300 yr BP, which is a much earlier date than the accepted 600-800 yr BP (McGlone & Wilmshurst, 1999b). Despite the wide acceptance of the later date (800 yr BP), a body of evidence is gathering to suggest a much earlier date of initial human colonization, by 2200-1500 yr BP (Sutton, 1994; Holdaway, 1996). However, the reliability of most of these carbon dates is seriously debated, and chiefly ascribed to contamination by inwash of old carbon and hard water effects in sample sites mostly from lakes and swamps (McGlone & Wilmshurst, 1999b). Reassessment of these early dates found that these tend to be seaside and in climatically favourable areas, which are supposed to be the sites visited by people earliest (Flenley & Todd, 2000). Thus it is inappropriate to simply reject these early dates.

In New Zealand, human colonization is usually indicated by a sustained rise of *Pteridium* in most pollen diagrams, about 600-800 yr BP. The persistence of *Pteridium* is an important indicator of regularly and frequently repeated fire which is most likely due to human intervention (McGlone & Wilmshurst, 1999b). However, in the Tiniroto site, although the coring site is next to a Maori pa, this change in *Pteridium* did not happen until the European era. The lack of or delay in the *Pleridium* rise is also reflected in pollen diagrams from Gibson's Swamp (Horrocks, 1998) and Mt. Ruapehu (Steel, 1989) and Currents'Gate in Great Barrier Island (Horrocks et al., 2001). This disagreement probably resulted from the local transportation of the bracken spores (Wilmshurst, 1995). It seems that it is difficult to detect any rise of *Pteridium* spores in pollen records when the coring site is away from the bracken fernland, or when human activity close to the coring site is limited by a small population size. Consequently, even a low level of *Pteridium* occurrence might indicate human presence though in smaller numbers. The significant rise of *Pteridium* around 1300 yr BP and even the persistence of *Pteridium* prior to the Taupo eruption, shown from a marine core off the eastern North Island (Carter et al., 2000), though much smaller in magnitude compared with the rise from 800 yr BP, are probably formed by adding up all the intermittent occurrences of *Pteridium* from large source areas. These intermittent occurrences of *Pteridium* might indicate a high fire frequency regime as indicated in the Tiniroto site, which is probably encouraged by early establishment of slash and burn agriculture restricted to small numbers of people (Flenley & Todd, 2000).

## 6.6 Recognition of Vegetation Dynamics in New Zealand

As a whole, finding irrefutable equilibrium dynamics within vegetation processes in natural systems is unlikely. Even in sites free from disturbance effects, equilibrium is hard to achieve because of the changing climatic conditions, which drive the vegetation to diverge from its previous state. This process goes smoothly but continuously, resulting in this special kind of non-equilibrium dynamics. Equilibrium dynamics may be an ecological fiction, and instead all dynamics are characterised by non-equilibrium.

In places subjected to catastrophic disturbances, non-equilibrium dynamics are caused by both gradual climate change and by abrupt disturbance outbreaks. The prominence of these two factors in vegetation dynamics depends on the properties of the disturbances. When disturbance is large and intensive, vegetation dynamics will be more affected by it despite the climate change; when disturbance is small and less severe, the impact of climate change will predominate vegetation dynamics.

In central North Island, the lowland podocarp forests are encouraged by the recent disturbances. It is possible that under favourable climate conditions and free of catastrophic disturbances, hardwoods would replace podocarps. In Westland, less subject to catastrophic disturbances, forest structure is mainly determined by the current climate. The change within the forests is slow and continuous; although impacts of disturbances with small scales can be identified from the forest structure, these only last a short time.

## 6.7 Suggestions for the Future Work

Although the equilibrium/non-equilibrium vegetation dynamics could be detected from PCA plot by visualization, it would be more convincing to apply some statistical techniques, such as tests of rank consistency and tests of directional change, to examine equilibrium dynamics.

An independent climate index, such as temperature indices from oxygen isotopes, proxies of peat humification or percentage of testate amoebae from the same core, should be obtained to confirm the role of climate in vegetation dynamics.

When assessing the impact of disturbance on vegetation, surface samples of vegetation under various degrees of disturbance would act as better indicators to compare the impact of different disturbance on vegetation, and correlate this information with vegetation stability. As a result, quantitative estimations of disturbance responsible for non-equilibrium would be made.

To make tests more comparable, it would be ideal to choose a reference site from a more similar climate region, to ensure similar climate trends occur at each site. Similarity calculated from these two sites over time would provide more information to estimate the impact of disturbance on vegetation, and also to examine whether vegetation would recover from disturbance.

## 6.8 Conclusions

Non-equilibrium dynamics characterize the vegetation in both undisturbed and disturbed sites, as vegetation composition continually changes through time. In the Sponge Swamp site, the change of vegetation is characterised by a steady and consistent process over the whole time span. In contrast, in the Tiniroto site, the comparable trend of vegetation change over time is more inhibited, and instead imposed on it are some sudden floristic changes stimulated by disturbances, especially apparent for the last c. 2300 yr BP.

Evidence from pollen records suggests that long-term climate change, from warm and wet to cooler and drier conditions, is probably responsible for the non-equilibrium vegetation dynamics around Sponge Swamp. In the Tiniroto site, a comparable long-term climate trend, which is represented by the climate amelioration with increaseing rainfall, plays an important role in the vegetation process before c. 2300 yr BP. However, after c. 2300 yr BP, this process is largely changed by a series of disturbances. The strong directional vegetation change gives way to predominantly stochastic processes.

Two categories of disturbance regimes are recognized in the Tiniroto site according to the extent of vegetation damage caused by these disturbances. Most of the short-term vegetation changes in response to the earlier disturbances, e.g. Whakatane and Waimihia eruptions, are very small in scale and only generate small temporary influences on vegetation. Thus the early disturbance episodes, including the Whakatane and Waimihia eruptions, are at relatively low intensities and hardly affect the vegetation dynamics under climate control. However, after the Taupo eruption and outbreak of the fire around 2300 yr BP, enduring semi-open vegetation characterised by fernland was established for more than 100 yr. So the later episodes, composed of the Taupo eruption and the fire around 2300 yr BP, are of relatively high intensities, and highly modify the vegetation processes driven by climate change.

The change in vegetation responses to the disturbance regime of the early and late episodes at Tiniroto probably resulted from either more variable climate conditions from the mid-Holocene onwards or from human activities at an earlier date than currently accepted.

Despite appearance, non-equilibrium dynamics are common in New Zealand. In places subjected to catastrophic disturbances, such as the central North Island, forest structures are highly determined by prior disturbances. In places with relatively stable environments, like Westland, forest structure is mainly responsive to current climate, and changing consistently.

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**Appendix 1**: Full name of the species code used in the principal component analysis and redundancy analysis.

| Species code | Name of species |
|---|---|
| Aciphy | *Aciphylla* |
| Agaaus | *Agathis australis* |
| Alectr | *Alectryon* |
| Artemi | *Artemisia* |
| Ascluc | *Ascarina lucida* |
| Astera | Asteraceae |
| Beilsc | *Beilschmiedia* |
| Carex | *Carex* |
| Casuar | *Casuarina* |
| Chenop | Chenopodiaceae |
| Clemat | *Clematis* |
| Client | *Clianthus* |
| Copros | *Coprosma* |
| Coriar | *Coriaria* |
| Cyamed | *Cyathea medullaris* |
| Cyathe | *Cyathea* |
| Cypera | Cyperaceae |
| Daccup | *Dacrydium cupressinum* |
| Dacdac | *Dacrycarpus dacrydioides* |
| Dickso | *Dicksonia* |
| Dodvis | *Dodonaea viscosa* |
| Droser | *Drosera* |
| Elaeoc | *Elaeocarpus* |
| Empmin | *Empodisma minus* |
| Epacri | Epacridaceae |
| Epilob | *Epilobium* |
| Ericac | Ericaceae |
| Euprev | *Euphrasia revoluta* |
| Fabace | Fabaceae |

Continued:

| | |
|---|---|
| Fuchsi | *Fuchsia* |
| Gleich | *Gleichenia* |
| Grammi | *Grammitis* |
| Griluc | *Griselinia lucida* |
| Gunner | *Gunnera* |
| Haloca | *Halocarpus* |
| Halora | *Haloragis* |
| Hebe | *Hebe* |
| Hisinc | *Histiopteris incisa* |
| Hydroc | *Hydrocotyle* |
| Kniexc | *Knightia excelsa* |
| Leptos | *Leptospermum* type |
| Leufas | *Leucopogon fasciculata* |
| Liboce | *Libocedrus* |
| Lipgun | *Liparophyllum gunnii* |
| Lorant | Loranthaceae |
| Lycaus | *Lycopodium australianum* |
| Lycdeu | *Lycopodium deuterodensum* |
| Lycser | *Lycopodium serpentinum* |
| Lycvar | *Lycopodium varium* |
| Malvac | Malvaceae |
| Melicy | *Melicytus* |
| Metros | *Metrosideros* |
| Micros | *Microsorum* |
| Monole | Monoletes |
| Morace | *Moraceae* |
| Muehle | *Muehlenbeckia* |
| Myriop | *Myriophyllum* |
| Myrsin | *Myrsine* |
| Nesteg | *Nestegis* |
| Notfus | *Nothofagus fuscospora* type |
| Notmen | *Nothofagus menziesii* |
| Ourmac | *Ourisia macrophylla* |

Continued:

| | |
|---|---|
| Passif | *Passiflora* |
| Pencor | *Pennantia corymbosa* |
| Phormi | *Phormium* |
| Phydru | *Phylloglossum drummondii* |
| Phyllo | *Phyllocladus* |
| Pinus | *Pinus* |
| Pittos | *Pittosporum* |
| Plagia | *Plagianthus* |
| Planta | *Plantago* |
| Poacea | Poaceae |
| Podoca | Podocapaceae |
| Podspp | *Podocarpus* spp. |
| Prufer | *Prumnopitys ferruginea* |
| Prutax | *Prumnopitys taxifolia* |
| Pseudop | *Pseudopanax* |
| Pseudow | *Pseudowintera* |
| Pterid | *Pteridium* |
| Pteris | *Pteris* |
| Qintin | *Quintinia* |
| Ranunc | Ranunculaceae |
| Rosace | Rosaceae |
| Rumex | *Rumex* |
| Schdig | *Schefflera digitata* |
| Taroff | *Taraxacum officinale* |
| Trilet | Triletes |
| Tupeia | *Tupeia* |
| Typha | *Typha* |
| Uniden | Unidentified |
| Vitluc | *Vitex lucens* |
| Weirac | *Weinmannia racemosa* |

**Appendix 2**: Source of samples used for summary pollen percentage diagram from Tiniroto Lakes. Sample depths in ranges were used unrevised.

| Sample depth (m) as used in pollen diagram | Core depth (m) | Core number |
|---|---|---|
| 0.25 | 0.05 | 2 |
| 0.35 | 0.15 | 2 |
| 0.45 | 0.25 | 2 |
| 0.55 | 0.35 | 2 |
| 0.65 | 0.45 | 2 |
| 0.75 | 0.55 | 2 |
| 0.85 | 0.65 | 2 |
| 0.95 | 0.75 | 2 |
| 1.05-2.32 | 1.05-2.32 | 2 |
| 2.42 | 2.22 | 1 |
| 2.52 | 2.32 | 1 |
| 2.62 | 2.42 | 1 |
| 2.72 | 2.52 | 1 |
| 2.82 | 2.62 | 1 |
| 2.92 | 2.72 | 1 |
| 3.02 | 2.82 | 1 |
| 3.09-3.14 | 3.09-3.14 | 2 |
| 3.36-3.64 | 3.36-3.64 | 1 |
| 3.75-4.20 | 3.75-4.20 | 2 |
| 4.50-4.96 | 4.50-4.96 | 1 |
| 4.99-5.11 | 4.99-5.11 | 2 |