New Zealand Isopollen and Isochrone Maps: An Integrative Approach to Reconstructing the Paleoenvironment since the Last Glacial Maximum

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Abstract

A series of isopollen and isochrone maps for New Zealand since the Last Glacial Maximum (LGM) is presented; these maps suggest likely paleovegetation patterns in New Zealand since the LGM. To the best of my knowledge, they are the first constructed for any region in the Southern Hemisphere. The procedure used to construct the maps was unique in a number of ways. Contouring was predominantly acheived using kriging techniques on a computer package rather than manual contouring, which has been the norm in other regions. An integrative approach was used; marine microfossil data was utilised to derive paleo-sea surface temperatures which, when combined with faunal freezing temperatures, yielded *a priori* theoretical altitudinal limits for selected taxa to augment the fossil pollen data. Terrestrial macrofossil data was used to evaluate the resultant maps. Paleo-shorelines, also derived from macrofossil studies, are shown. Paleo-shorelines are important in that coastal areas may have served as refugia during, and migration routes after, the LGM.

The resultant maps show that an integrative approach was generally successful. The maps give a more holistic view of New Zealand's paleoenvironment than is possible from studying individual fossil pollen diagrams, and some interesting conclusions are reached. The southern limit of continual forest in the late glacial period may have been 2° south of commonly accepted limits. The existence of a Younger Dryas–synchronous cooling in New Zealand is shown to be unlikely from a palynological perspective.

Errata

page i line 9 should read "…when combined with *floral* freezing temperatures..."

page 17 caption should read "Figure 1. The Hemisphere Centred on New Zealand. Note the isolation of New Zealand, with Australia, our nearest sizeable neighbour, being 2000 km to the *west*."

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Preface

Quaternary research in the Southern Hemisphere has historically received less emphasis than research north of the equator (Partridge *et al* 1999) yet there are clear differences in the mechanisms and patterns of climate and paleovegetation change between the two hemispheres. It follows that the Southern Hemisphere's paleoclimate is not particularly well understood; typically researchers extrapolate climate reconstructions from Europe and North America to the Southern Hemisphere (eg COHMAP members 1988; Diaz & Graham 1996; Peteet *et al* 1997). Unfortunately, according to Iriondo (1999) "Such a methodological tendency is permanent and often risky," given, for example, "...both extremes of the global climate system (Antarctica and the Pacific Warm Pool) are located in the Southern Hemisphere. It is hardly probable that both regions play a passive role in climatic changes driven by North Atlantic factors."

New Zealand is rather uniquely situated in this regard as it is the only sizeable landmass in the Southern Hemisphere free from continental influences, is proximal to western boundary currents and the subtropical convergence, and is relatively well studied. Furthermore, New Zealand provides "...virtually unparalleled opportunities to examine postglacial environmental changes without the veiling effects of human influences." (Newnham & Lowe 1999) given that anthropogenic impacts on vegetation cannot be unequivocally demonstrated before 700-800 years before present.

Fossil pollen analysis provides one method of paleovegetation and paleoclimate reconstruction. Fossil pollen data has been used in New Zealand to reconstruct paleoclimate and climate change (McGlone 1973; Shulmeister *et al* 1999), and related processes such as changes in paleovegetation composition (Moar 1970); anthropogenic impact (Hume & McGlone 1986; Wilmshurst 1997; Empson *et al* 1999) including dating the first arrival of Maori in New Zealand (Ogden *et al* 1998; McGlone & Wilmshurst 1999a); the impact of cataclysmic events such as vulcanism and fire on vegetation (McGlone *et al* 1988; Bussell 1988), testing succession models (Bray 1989) and to assist with revegetation programs (Chester 1991). Palynology has also been used to reconstruct Holocene sea level change (Pocknall *et al* 1989; Mildenhall 1994).

In New Zealand, however, palynological research typically focuses at the regional level and there has been considerably less effort to systematically synthesise the results into a coherent picture of the paleoenvironment for the country as a whole. At the same time palynological researchers typically operate in isolation, to some extent under-utilising other paleoenvironment reconstruction techniques. Because palynology is fairly imprecise due to faulty representation of some taxa and complex terrain (Markgraf *et al* 1992), vegetation and climate reconstruction is best effected utilising multiple sources of evidence, including ocean cores, tephras and macrofossils to augment the pollen data. The purpose of this thesis, therefore, is to synthesise as much fossil pollen data as possible in a series of isopollen and isochrone maps for selected New Zealand taxa since the Last Glacial Maximum (*c* 22,000 years ago), at the same time integrating fossil data other than pollen. A secondary objective is to interpret these maps in terms of vegetation and climate change.

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Dedication

Dedicated to my wife Lesley, and my children Sarah, Rachel, Aimee, and Kate.

New Zealand Isopollen and Isochrone Maps:
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1. Introduction

1.1 The Need to Create Paleovegetation Maps

It is highly desirable to create paleovegetation maps for several practical and philosophical reasons. First, paleovegetation reconstruction assists us in drawing conclusions about paleoclimates, which in turn allows us to validate modern climate models by comparison against paleodata (Mullan 1994), and to place contemporary climate trends into a broader context and to identify interconnections between physical, chemical and biological interactions (IGBP 1992, cited in Soons 1994). For example, Webb (1992) suggests that the "rise in global mean temperature of 5°C ±1°C [during the past 18,000 years] closely approximates that of 4.2°C ±1.2°C predicted for the future as the result of a doubling in the effective concentration of greenhouse gases."

This is of global relevance today as scientists and policy makers contemplate the ramifications of global warming and deforestation, the threat of raised sea levels, forest conservation and reafforestation. Isopollen and isochrone maps can assist in working through the implications of climatic or catastrophic change on vegetation distribution: for example, suggesting how quickly vegetation responds to change, to establish criteria to determine whether or not reforestation programs have been successful, and to identify opportunities and constraints for agricultural and silvicultural activity in response to climate change (Huntley 1990b).

On a longer time scale, there is sound evidence to suggest that global climate responds to the various cyclical components of Milankovitch forcing (discussed below); for example Sellers (1973) claims that a decrease in the solar constant of only 0.6% would result in a temperature drop of 1.1°C in February and 1.7°C in August at 65°S. However, climate change is not globally uniform: Berger & Loutre (1994) for example found that geological time series from subpolar North Atlantic varied with a 41,000 year period, whereas further south, along the latitude of the Laurentide icesheet (*c*45°N) temperatures varied on a 23,000 year period. Over the North Pole time series of aeolian transport varied on 100,000 and 41,000 year cycles, possibly because tilt variations cause changes in the equator-to-pole temperature gradient, and therefore wind. Climatic response to orbital perturbations does not appear to be instantaneous; there may be lags of thousands of years: according to Berger (1977) "Obliquity consistently led the δO^{18} record by about 10,000 years whereas precession seemed to be in phase with the 23ka geological signal."

The corollary of this is that we cannot rely on simply applying research findings from other (predominantly northern Hemisphere) countries to accurately model possible climate change for New Zealand, but we must conduct research ourselves. Although there is abundant paleoclimate data for New Zealand for the last 25,000 years, for example, there are gaps, such as the maximum cooling during the Last Glacial Maximum, and the climate optimum during the Holocene (Salinger 1994). Fossil pollen analysis, in particular isopollen mapping, can potentially fill these gaps.

Second, present-day patterns of precipitation, temperature gradients and soils alone cannot account for the general distribution of New Zealands's subalpine forests (McGlone 1996; Leathwick 1998; Haase 1999); the distribution of contemporary flora can only be understood if historical factors such as variable migration rates from volcanic and glacial refugia are considered (Wardle 1986). Furthermore, there is good evidence that the change in vegetation distribution continues to this day (Wardle & Coleman 1992).

Third, isopollen and isochrone maps are an effective way of collating local data and enabling inferences at a regional and country-wide scale to be made about paleovegetation. Whereas Vandergoes (1999) argues that "...most of New Zealand's vegetation and climate history has been broadly characterised over large geographic areas and may not accurately represent vegetation and climate changes that have occurred at local scales," I disagree; I suggest that New Zealand's paleovegetation history in particular is understood much better at the local scale and there has been a relatively limited amount of effort applied to integrating local and regional data into a coherent, New Zealand-wide, picture.

Since pollen diagrams for a given site are the results of a sample, they tell us only about the samples; what we really want to know is what the samples can tell us about the wider area from which they are drawn: "...sample statistics are stepping stones to the final goal of understanding more about the entire population." (Isaaks & Srivastava 1989). One could argue that it is not possible to do so without systematically integrating as much data at the local level as possible utilising a graphical technique such as plotting fossil isopollen maps.

Fourth, the results of paleovegetation research in New Zealand are generally not well communicated, due in part to the lack of synthesis of palynological research and integration with other paleo-reconstruction techniques. According to du Toit *et al* (1986) "One of the most difficult tasks of a researcher is to convey findings based on statistical analysis to interested persons. Failure to communicate these findings successfully puts paid to all his [sic] data-analytical work, irrespective of its quality." Ideally, a set of isopollen maps would draw together numerous studies and successfully communicate to the reader the rate and nature of vegetation and climate change.

Fifth, according to Page (1989) "By abdicating all judgement of past continental configurations to geologists, biogeographers are effectively reduced to inventing imaginative stories to explain the history of plants and animals." Because there was an absence of geomorphological data since the LGM, in particular for the Holocene, to use in preparing the paleovegetation maps, the isopollen maps presented in this thesis vindicates biogeography to some extent by synthesising research from several disciplines within a biogeographical framework to derive Holocene shoreline and snowline maps.

Finally, philosopher Sir Karl Popper (1975) claimed that the greatest advances in science are made when hypotheses are challenged: "The game of science is, in principle, without end. He who decides that one day scientific statements do not call for any further test, and that they can be finally verified, retires from the game." Furthermore, the best scientific theory to explain a given phenomenon at a given time is transitory: "The empirical basis of objective science has thus nothing 'absolute' about it. Science does not rest upon solid bedrock. The bold structure of its theories rises, as it were, above a swamp. It is like a building erected on piles. The piles are driven down from above into the swamp, but not down to any natural or 'given' base; and if we stop driving the piles deeper, it is not because we have reached firm ground. We simply stop when we are satisfied that the piles are firm enough to carry the structure, at least for the time being."

Clearly there is a philosophical mandate to construct paleovegetation maps: by creating isopollen maps, we may be able to support or challenge various theories about New Zealand's paleovegetation and paleoclimate change.

1.2 Cartographic Representation of Paleovegetation

According to Chambers *et al* (1983) there is no single statistical tool as effective as a well chosen graph: "Our eye-brain system is the most sophisticated information processor ever developed, and through graphical displays we can put this system to good use to obtain deep insight into the structure of the data." Isopollen maps are one form of graphical display, where a map may be defined as "...a picture, diagram or analogue, usually having two dimensions, of part (or all) of the surface of the Earth (or other mappable area) and is a device for transferring selected information about the mapped area to the map user," (Loxton 1980).

Clearly, the process of creating isopollen and isochrone maps has linkages to cartography, defined as the art, science and technology of making maps, where maps may be regarded as including all types of maps, plans, charts and sections (Taylor 1988) or "The organisation, presentation, communication and utilisation of geoinformation (Taylor 1991). There are ten major types of maps utilised to describe the spatial distribution of fossil pollen assemblages; in theory, the same fossil pollen dataset could be used to derive several of the following map types.

a. Presence-absence maps – these simple maps merely indicate whether or not a given taxon is present (ie a non-zero value) or absent at a given locality and time. Davis & Webb (1975) used this technique to map common species for eastern North America, as did Davis *et al* (1991) for Michigan, Wisconsin and Minnesota. Presence-absence maps have been used to demonstrate the distribution of New Zealand's *Nothofagus* forest *c.*1840 (Wardle 1986), *Dacrydium cupressinum* (Franklin 1968) *Podocarpus totara* (Wardle 1972) and *Nothofagus truncata* (Heads 1998).

b. Dot maps display pollen percentages for an individual taxon. Dot maps have been prepared for upper Michigan and Wisconsin (Delcourt & Delcourt 1991), eastern Australia (Kershaw 1988) the former Soviet Union and Mongolia (Tarasov *et al* 1998) and for New Zealand (McGlone *et al* 1993). The area of the dots is proportional to the percentage of the pollen sum.

c. Composite maps display piecharts of frequencies of many pollen types at certain time intervals; these have been prepared for eastern Ontario (King & Kapp 1963) and the British Isles (Godwin 1975).

d. Species range maps: according to Bernabo & Webb (1977) these show "the position of the range boundaries for selected taxa and the location of ecotones at specific time intervals." Ogden *et al* (1992) prepared species range maps for *Agathis australis* to show its expansion in the Holocene, using fossil wood and charcoal.

e. Isopollen maps show the continuous distribution of individual pollen types at given time intervals. Holocene isopollen maps have been prepared for mid-western United States (Webb *et al* 1983), eastern North America (Prentice *et al* 1991), Japan (Morita 1982), Sweden (Prentice, 1983), Poland (Ralska-Jasiewiczowa 1983) Norway (Caseldine 1989) and Europe (Huntley & Birks 1983). A major motivating factor to create isopollen maps in this thesis was that they have not been constructed for New Zealand before.

f. Difference maps: by subtracting the data of an isopollen map from a predecessor map, difference maps can be established, demonstrating the advance or retreat of a given taxon between the two periods. Bernabo & Webb (1977) created difference maps for the north-eastern United States.

g. Isochrone maps indicate the progression of various pollen-defined boundaries over time thus they show when a given taxon or ecotone (by grouping several taxa) reaches or leaves the mapped area. Isochrone maps have been prepared for the British Isles (Birks 1989); mid-western United States (Webb et al 1983); and Japan (Tsukada 1982a).

h. Isophyte maps: according to Fægri & Iversen (1989) "...maps based upon data presumed to give better estimates of real abundance (corrected percentages) are called isophyte maps." Although Delcourt & Delcourt (1994) refer to their maps of eastern North America as isopollen maps, these maps are really isophyte maps since the pollen percentages have been adjusted using modern pollen rain and growing stock volumes[1].

i. Paleovegetation maps: These maps may be constructed by thorough ecological analysis of pollen diagrams and a knowledge of modern analogues. Paleovegetation maps have been constructed for the north-eastern United States (Bernabo & Webb 1977); Japan (Tsukada 1982a), British Isles (Bennett 1989); and Europe (Huntley 1990). In New Zealand paleovegetation maps were compiled for lower Northland (Beever 1981), the Wellington region (Mildenhall 1994; Dunbar, *et al* 1997), Otago-Southland at the formation level (Hall & McGlone 2001) and the entire country at a coarse, total forest cover level (Ogden *et al* 1998).

j. Isoscore maps: Contour lines in isoscore maps join geographical locations with the same score in a given principal components analysis; Prentice (1983) did this for Sweden to summarise major gradients in regional vegetation. Overpeck *et al* (1985) prepared isoscore-type maps for southern Michigan plotting both dissimilarity coefficients and squared chord distances between pollen samples and forest types.

Taylor (1991) argues that maps have "...always been a means of navigation, but can also take on fundamental importance in helping 'navigate' through an increasingly turbulent sea of raw data and information on a wide variety of topics." It is hoped that the New Zealand isopollen maps presented here will steer the way to a clearer picture of New Zealand's paleovegetation and paleoclimate change since the Last Glacial Maximum.

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[1] Although Hazel Delcourt (2001, personal communication) maintains that these *are* isopollen maps, I am not convinced.

1.3 Isopollen Maps

The function of the isopollen maps in this thesis is to complement other syntheses of NZ pollen analytical data and to provide a broad overview of the changing pollen rain and hence vegetation of NZ using an integrative approach (for example utilising foraminifera to derive sea surface temperatures and molluscs for sea level). Whereas Huntley & Birks (1983) plotted isopollen maps at the continental scale (ie Europe), claiming that "...pollen data most closely reflects vegetation at the formation level, and it is at this scale that vegetation formations are most commonly and usefully mapped." I have plotted maps at an archipelago scale to reflect vegetation at the species level which is useful to provide regional paleoclimate data.

Despite their potential usefulness, there have been surprisingly few isopollen maps constructed around the world, and to the best of my knowledge, none have been published for New Zealand or even the Southern Hemisphere. Szafer (1935 cited in Huntley & Birks 1983) proposed the term *isopoll* to describe the pollen frequency contour maps that he constructed to investigate *Fagus* and *Picea* migration across Poland. In essence, an isopoll is a line on a map joining geographical localities with the same pollen frequency for a given age. Fægri & Iversen (1989) describe isopollen lines as "...synchronous lines delimiting areas with the same [pollen] percentages of a certain species, in the same way as isotherms delimit areas having the same temperature."

Isopollen maps are an effective means of summarising large, complex pollen datasets and of displaying major patterns of spatial and temporal variation at selected times in the past. When isopoll maps for individual taxon are considered together in a time sequence they provide a means of discovering the pattern and rates of migration and of locating possible areas of glacial refuge for those taxa (Huntley & Birks 1983; Traverse 1988). Isopolls for different taxa for a given time can be treated together and use to deduce major vegetational assemblages such as formations; conversely, since vegetation formations are controlled in part by climate, past climatic conditions can be derived from the isopolls.

Although pollen diagrams showing little or no change in vegetation are as important as diagrams with large changes, when described in isolation, these 'complacent' diagrams stimulate relatively little interest. When plotted in isopollen or isochrone maps, however

"...these sites indicate nodal points in the pattern of pollen response to environmental and biogeographical change." (Bernabo & Webb 1977). Since isopolls are extrapolated from discrete pollen sites, deficiencies in the pollen record are highlighted: Webb & McAndrews (1976) constructed isopollen maps for modern pollen rain for central North America and concluded that the incompleteness of their isopolls "...provide a guide to future research by showing unsampled areas," in particular highlighting possible ecotones, "...along which steep gradients appear in the isopolls."

Another advantage of isopollen mapping is that it mitigates to some extent the effect of scale upon the apparent synchroneity of paleoecological events. Huntley & Birks (1983) give the example of trees of a given taxon migrating at the rate of 500myr^{-1}. In 500 years the taxon will migrate 250km *ceteris paribus* and could be dated at sites within a 250km circle to ±300 years with 95% confidence. However, due to the relationship between the time taken for migration and the errors involved in radiocarbon dating (discussed below) statistical testing would be almost certain to fail to reject the null hypothesis[2] that the migration event was coeval within the 250km circle of interest.

However, if a 2,500km circle was considered, trees migrating at the same rate would take 5,000 years to cross the circle and we could be more confident that statistical testing would reject the null hypothesis of synchroneity. According to Huntley & Birks (1983) "Such effects of temporal and geographical scale underlie many paleoecological problems but can easily be ignored by paleoecologists whose own investigations may cover a small fraction of the possible temporal and spatial scales that can be studied." Since isopollen mapping enables the researcher to discern trends in the pollen signature, it is a more powerful test of hypotheses regarding paleovegetation than simply identifying differences between sites or changes in individual sites over time.

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[2] In a statistical test, the researcher typically selects between two mutually exclusive hypotheses: the null and the alternate hypothesis. The null hypothesis refers to the premise that there is no statistical difference between the means of a given parameter (say, pollen frequency) for samples from two different populations. The alternative or research hypothesis is that there *is* a systematic difference between the two. It is only the null hypothesis that can be tested; data analysis indicates whether or not it can be rejected. According to Wright & Fowler (1986) "...in order to test the null hypothesis we need to assess the relative likelihood of our means having been sampled from the same population or two distinct populations. If two means are sampled from the same population then any difference between them would be simply due to sampling variation, and therefore the null hypothesis should not be rejected."

A critical limitation to pollen-stratigraphical data and therefore isopollen maps is that they are based on relative percentage counts. An excellent example of this is given by the LGM isopollen map for *Nothofagus fusca*, which shows pollen percentages of 15-20% for North Westland-Buller. The isochrone map however suggests that here were only very small pockets of this taxon present between 14,000 and 12,000 BP. Because isopollen maps reflect relative abundance, rather than absolute abundance, they can imply that the taxon was very abundant. A more likely scenario is that of the few trees present, *N.fusca* was the most common; accordingly, the isopollen maps should be interpreted with the isochrone map.

However, in New Zealand there are few absolute pollen influx diagrams available with which to construct isopollen maps that take into account differential pollen production, dispersal and preservation (discussed below). In any case, maps based on pollen influx datasets exhibit considerably more variability from site to site when compared with maps based on percentages (Huntley & Birks 1983). Furthermore, modern pollen-percentage data often reflect present day vegetation abundance as well as, or even better than, pollen influx data. Webb *et al* (1978) state that this observation "...should caution those analysts who consider influx values as correcting all the errors inherent in percentage data. Influx data merely replace one source of uncertainties in a dataset by another source [of uncertainties]."

A further potential weakness of isopollen (and isochrone) maps is that they may primarily reflect the patterns of tree expansion rather than tree arrival (Bennett 1986) since small populations of trees may go undetected in the pollen record[3]. Thus the derived maps may actually reflect rates of population increase to a critical level rather than expansion of a given taxon into a given area.

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[3] Although the reverse is also possible; for example *Nothofagus* spp values up to 20% do not necessarily indicate presence of the taxa at all.

1. 4 Isochrone Maps

A disadvantage of isopollen maps is that several maps are required to display temporal and spatial variations, since a single isopollen map represents data for a single taxon at a single point or interval in time[4]. Isochrone maps, in contrast, do show both spatial and temporal patterns simultaneously, joining sites where similar pollen-stratigraphical events occurred simultaneously, such as the first rise in values of a given pollen type which may be used to detect the direction and rate of tree migration (Birks 1989)[5].

It is essential that the first expansion of a taxon in pollen diagrams is consistently defined in order to provide comparability between isochrone maps, therefore some creativity is required to decide which values indicate presence or absence of a given taxon. Birks (1989) used a rational limit for trees with high pollen representation (ie relative to *Fagus sylvatica*[6]) where rational limit refers to the point at which the pollen curve begins to rise to sustained high levels (Smith & Pilcher 1973). For taxa with relative pollen representation approximating *Fagus sylvatica*, Birks (1989) used the empirical limit which is the point at which the pollen for a given taxon becomes consistently present in consecutive samples (Smith & Pilcher 1973).[7]

Whereas a source of error for the empirical limit can arise when different pollen sums are used, since large counts may detect rare taxa, the rational limit is not so count-dependent. In the New Zealand pollen diagrams three-quarters use a common count (200-250 grains) therefore this potential problem is minimised.

Birks (1989) maintains that despite their limitations, the use of either rational or empirical limits is superior to critical pollen percentages to determine presence or absence of taxon, since "Pollen percentages, however defined, are influenced by other taxa contributing to the pollen sum[8] and by their absolute abundance and relative pollen representation."

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[4] Webb *et al* (1983) plotted isopolls for several taxa on the same map however the maps were extremely difficult to interpret

[5] Huntley & Birks (1983) dispute this, stating isochrone maps "...show no information about the nature of the pollen stratigraphical event being mapped. They are thus a poor way of displaying spatial variations in pollen data."

[6] According to John Birks (personal communication, 2001) "I chose *Fagus* because it has a relative R-value of 1.0. All R-values are expressed relative to a standard, so-called R_rel values (Davis 1963, Andersen, 1970) and in Europe *Fagus* is set at 1 and other tree R-values are expressed relative to *Fagus*."

[7] By selecting a New Zealand taxon with an R-value close to 1.0 as a benchmark, Birks' (1989) method could theoretically be repeated, however, applying R-values has serious limitations; these are discussed below.

[8] This is known as the Fagerlind Effect, and is discussed further in Appendix 5.4.7

However, Bennett (1988) suggested that if increasing pollen frequencies represent exponentially increasing populations, then pollen curves cannot necessarily be broken down into pre-arrival and post-arrival phases, and therefore "...use cannot be made of 'sudden increases' or 'rational limits' as a basis for measuring the spread, although they may give '*terminus ante quem*' [the point before the end of] arrival times. Thus pollen curves at any one site would represent changing local abundances, and may not always be used as a measure of rate of spread to the pollen catchment of the site."

Godwin (1975) criticised the terms empirical limit and rational limit on the grounds that they "...have no generally understandable meaning...and also they lack quantitative definition." Furthermore, applying either rational or empirical limits is difficult in practice. Ascertaining when the first rise of a taxon's pollen occurred or at which point a taxon is consistently present requires some degree of subjectivity, and the process of interpolating and extrapolating ages also introduces error. The alternative to a lot of interpolation and extrapolation would be to utilise only pollen diagrams where the first rise, for example, was explicitly dated, resulting in too few data points to contour[9].

On balance, it is more sensible to use critical limits to derive isochrone maps. Several researchers have successfully used this strategy; for example Webb *et al* (1983) used critical limits to derive isochrones for the United States mid-west, and Bernabo & Webb (1977) plotted points at which *Picea* (spruce) pollen fell below 15%. Anderson & Brubaker (1994) implicitly used critical limits in plotting isochrone maps for Alaska, since their isolines "...show the locations of 'key' isopolls at each time interval. Key isopolls represent pollen percentage values that correspond to plot range limits or population centres."

Accordingly, I chose to use critical limits; the actual limit varies amongst the taxa, but broadly speaking the critical limit is higher for taxa that tend to be over-represented in the pollen rain, and lower for taxa that are under-represented.

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[9] Interestingly, Anderson & Brubaker (1994) chose to use isopollen maps rather than isochrone maps to summarise features of the Alaskan LGM because of the scarcity of LGM sites and poor dating control. Thus

1.5 New Zealand's Physical Geography

New Zealand's physical geography is characterised by strong relief, marked diversity and youthfulness (Newnham *et al* 1999) which is due to tectonic processes occurring coeval with extreme climatic fluctuation, Holocene sea-level changes of the order of 100m, high precipitation and associated weathering. New Zealand is significant from a global perspective: it is geographically isolated, the only sizeable land mass in the Southern Hemisphere where continentality is largely absent, and it is one of the few Southern Hemisphere sites where the fossil record is long enough to allow climate reconstruction right through the Quaternary, prompting Newnham *et al* (1995) to describe New Zealand as a "...virtually unrivalled 'field laboratory' for investigating environmental change in the Quaternary."

The New Zealand record of climatic events such as the Younger Dryas[10] for example is critical to understanding such phenomena at a global scale since along with Chile and Argentina, New Zealand is the only Southern Hemisphere site possessing mid-latitude glaciers (Singer *et al* 1998), and the marked sensitivity of glaciers to fluctuation in air circulation patterns permits detailed paleoclimate reconstruction (Gellatly *et al* 1988).

The archipelago of New Zealand covers an area of 265,000 km^2 and represents the emergent part of a small continental region lying across the obliquely convergent margin of the Pacific and Indo-Australian lithospheric plates (Suggate 1990). The plate boundary passes through the South Island at an oblique angle and in addition to rapid uplift is undergoing transcurrent displacement (Gellatly *et al* 1988). The major feature of compression across the intersection between these two plates is the NE-SW trending Southern Alps, a young, rapidly rising range of axial mountains formed predominantly of Paleozoic or Mesozoic greywacke and schist with several peaks over 3000m in height (Leathwick *et al* 1998). The North Island axial ranges are also being uplifted; the highest peaks are the Late Quaternary volcanoes Mt Ruapehu (2,797m) and Mt Egmont (2,518m).

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on balance, isochrone maps are best viewed as a complement to, rather than a replacement for, isopollen maps since they both suffer from some conceptual weaknesses and in any event, they display different things.

[10] An intense but short-lived climatic deterioration that occurred 11,000 to 10,000 years BP during the termination of the last glaciation.

New Zealand is seismically active; within the historical record alone earthquakes >*M* 6.5 have been recorded several times, with the Wairarapa earthquake of 1855 attaining a magnitude of between 8.0 – 8.3 (Van Dissen & Berryman 1996)[11] and as recently as 1994 an earthquake of *M* 6.5 occurred at Arthur's Pass. Van Dissen & Berryman (1996) calculated average return rates of 335 – 485 years for *M* 7.6 earthquakes in the Wellington region; Paterson (1996) estimated return periods of 9, 31, 100 and 370 years for shaking intensities of MMVI, MMVII, MMVIII and MMIX for Arthur's Pass[12].

Seismic events of these magnitudes and frequencies are of special significance for the New Zealand biota, since earthquakes and subsequent mass movement, rock fall and river obstruction have been demonstrated by several researchers to be responsible for catastrophic forest disturbance (Haase 1999; Wells *et al* 1998)[13]. Allen *et al* (1999) for example, quantified the impact of an *M* 6.7 earthquake at Basin Creek in the Southern Alps, finding 24.0 ± 5.9% mortality and 22.5 ± 4% injury to trees within *Nothofagus solandri* var *cliffortioides* forest. Since some taxon (eg *Libocedrus bidwillii*, *Phyllocladus alpinus*, *Nothofagus solandri*, *N.fusca*) are better suited than others to re-colonising an area after catastrophic disturbance (Veblen & Stewart 1982; Haase 1999), seismicity is a significant influence on the New Zealand floral assemblage.

Quaternary vulcanism has had a profound impact on New Zealand's geomorphology and biogeography; Pillans *et al* (1993) state that the Kawakawa airfall tephra amounted to 70km^3 and tephra flow material (ignimbrite) of 300 km^3. The Kawakawa tephra formation was probably a phreatomagmatic[14] eruption from the northern part of Lake Taupo; it was the largest eruption in New Zealand, and one of the biggest in the world, in the last 50,000 years. Volcanic eruptions have occurred in the North Island since the early Quaternary in a delta-shaped region known as the Central Volcanic Region (CVR) which has Mt Tongariro at the southern apex and passing (approximately) through the East Coast towns of

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[11] Eiby (1968) stated that this earthquake was destructive in Wellington, Wanganui and Marlborough and was "Felt on ships 150 miles [250 km] from the coast."

[12] *MM* refers to the Modified Mercalli scale, an index of earthquake intensity, as opposed to *M* which is a measure of magnitude or strength. The Hawkes Bay earthquake of February 2, 1931 was M 7.75, MM XI at Napier (Eiby 1968).

[13] Bull (1996) used disturbance of the biota in the form of lichenometry to derive recurrence intervals of 260 ± 15 years for earthquakes in the Southern Alps of sufficient intensity to cause "...exceptionally widespread regional rockfalls."

[14] A volcanic explosion caused by contact between magma and groundwater or shallow ocean water, in which both magmatic gases and steam are expelled (Academic Press Dictionary of Science & Technology).

Whakatane and Whitianga at its northern extremities, and then out to sea[15]. Bisecting the CVR is a second region of eruptive activity, the Taupo Volcanic Zone (TVZ) which lies in the southern half of the CVR. Vulcanism has also had a profound impact on vegetation by way of edaphic and catastrophic influences. The ultraplinian phase of the Taupo eruption 1,850 years BP deposited airfall pumice and ash > 10cm thick over an area of 30,000 km^2 (Stevens *et al* 1988); the shockwave that preceded the pyroclastic flow levelled forests in its path and coated a 20,000 km^2 area with thick ignimbrite.

The Southern Alps boast some 3,145 glaciers (Chinn & Salinger 1999) between 43 and 45°S covering 116 km^2 (Figure 3) with the largest of these, Tasman Glacier (29 km^2) sited on the flanks of the tallest peak in New Zealand, Mt Cook (3754m). The glaciation limit increases to the north so that in Fiordland the equilibrium line altitude (ELA)[16] is around 1500m in Fiordland, to 2000m at Arthurs Pass. In the North Island, glaciers are restricted to the flanks of Mt Ruapehu where the ELA is at about 2500m. Stewart Island lacks glaciers although small cirques on Mt Anglem indicate that small glaciers existed there during the Otiran glaciation (Allibone & Wilson 1997).

New Zealand lies between the high pressure belt of the subtropics and the low pressure zone of the Southern Ocean, consequently its weather is dominated by a series of alternating depressions and anticyclones approaching from the west, with an approximate weekly cycle (Sturman & Tapper 1996). A warm temperate maritime climate in the north and a cool temperate climate in the south (Markgraf *et al* 1992) is the result of the interaction of the prevailing westerly airstream with the Southern Alps so that precipitation reaches 12,000mm per year in a 'superhumid zone' (Garnier 1946; Fitzsimons 1997) to the west of the main divide. The reverse occurs when easterly winds dominate.

The mechanism used to account for the föhn phenomenon begins with the forced ascent of moist, westerly winds against the Southern Alps, causing cloud build up and precipitation on the West Coast. The rising air cools at the saturated adiabatic lapse rate (5-6°C km^{-1}) due to the release of latent heat by condensation above the cloud base, whereas on the East

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[15] For example Pillans & Wright (1992) studied tephras from the TVZ dispersed 250 km off the coast

[16] The lower margin of the snowpack overlying glacial ice, or transient snowline. The ELA rises as the summer melt progresses until it reaches a maximum altitude at the end of summer. This end of summer snowline indicates the equilibrium line where snow fall equals snow loss over the past glacial year (Chinn & Salinger 1999).

Coast (leeward) slope the descending, cloud free air warms at the dry adiabatic lapse rate of 9.8°C so that potential temperatures are warmer on the lee side.

Griffiths & McSaveney (1983) recorded rainfall along a transect bisecting the Southern Alps at the head of the Rakaia and Hokitika river catchments, and estimated that 75% of precipitation from the west falls on the west of the Main Divide (Figures 6 - 7). At the same time, the annual temperature range to the east of the Main Divide is greater due to the reduced moderating influence of the Tasman Sea, and rain shadow effects result in annual rainfall of 600-650mm. Summer droughts are frequent in these areas, and occur whenever the Southern Oscillation Index (ENSO) is either strongly positive or strongly negative (Ogden *et al* 1998).

Solar radiation shows an east-west decline which also decreases with latitude, so that the north of both islands receive >15MJ m^{-2} d^{-1}. In the far south of the South Island, radiation is as low as 12MJ m^{-2} d^{-1}. New Zealand's biologically effective UV-B irradiance (2800-3150Å) in summertime can be twice as high as countries in equivalent latitudes in the Northern Hemisphere because of lower ozone levels, differing vertical ozone distribution, less turbidity and lower industrial pollution in the atmosphere over New Zealand. Hunt *et al* (1996) suggest that the ozone concentration in the Southern Hemisphere's stratosphere is declining at around 0.4% per annum therefore adaptations and responses by New Zealand's vegetation can provide an early indicator of global vegetation response.

New Zealand has a complex soil pattern due to the wide variety of parent rocks, climate regime and the great deal of steep land, with less than one-third of the land area being flat-gently rolling (Cochrone 1973). In general, thin, immature soils predominate in the South Island due to solifluction during glaciation, whereas older soils are the norm in the North Island, particularly volcanic ash soils. Leached soils predominate throughout the country. Figure 4 shows that Northland is dominated by brown and volcanic clays; Waikato volcanic loams; central North Island pumice soils and southern North Island dense grey soils. In the South Island, podzols are common on the West Coast and coastal Southland; brown earths predominate in northern South Island; and Canterbury is characterised by stony terrace soils and recent alluvial soils. Eastern and south Otago are dominated by dense grey soils; Southland brown earths and central Otago semi-arid soils (Figure 5).

These soil groups reflect the role of topography, climate, vegetation and vulcanism in their pedogenesis.

Relative to its area, New Zealand has a disproportionately long coastline – *c*10,000 km in length (Kirk 1977); with numerous bays and the fjords of the Marlborough Sounds and Fiordland in particular enhancing this length. Because New Zealand lies adjacent to the world's major equatorward flow of circumpolar deep water, it is also in an ideal location to establish a detailed record of Quaternary paleoceanographic change for the Southern Hemisphere (Wright *et al* 1995). The Subtropical Convergence (STC) is a circum-Antarctic oceanic frontal zone that separates the subtropical waters to the north from the subantarctic waters to the south[17], marked by converging isotherms over the Chatham Rise demarcating the Southland Front[18] and the warmer waters of the East Auckland and East Cape which push south on the east coast.

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[17] The subtropical waters are characterised by average mid summer temperatures of >15°C and average winter temperatures of >10°C; the subantarctic waters have average mid summer temperatures of <14.5°C and winter temperatures of <10°C respectively (McMinn & Sun 1994).

[18] A band of relatively warm water lying adjacent to cooler subantarctic waters.

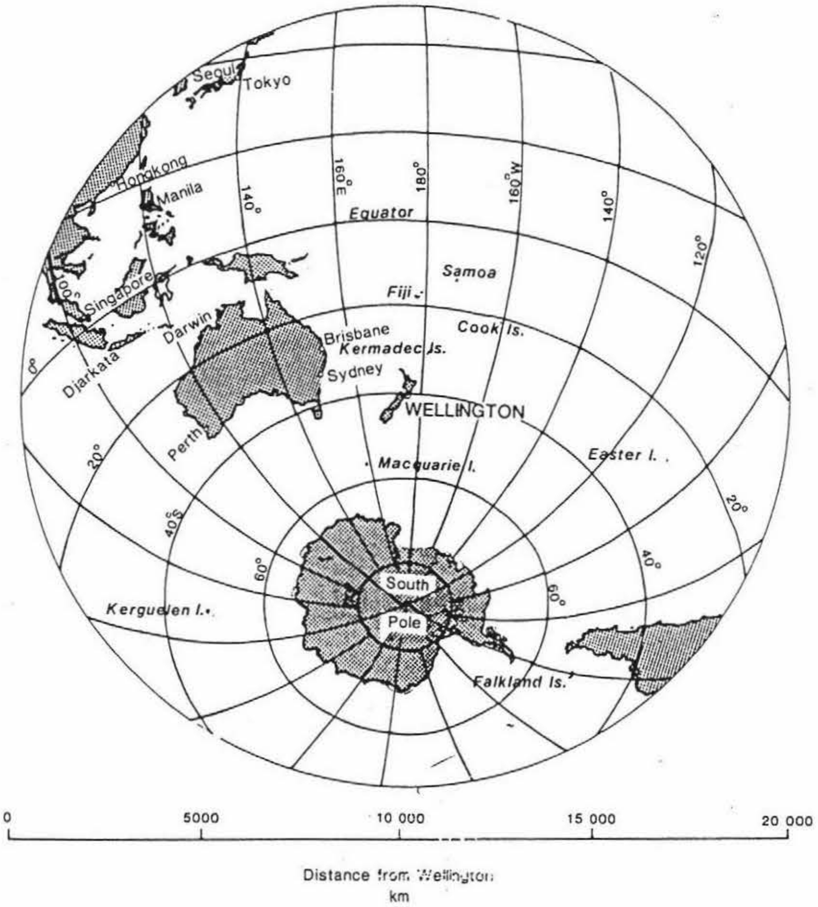


Figure 1 The Hemisphere Centred on New Zealand.

Note the isolation of New Zealand, with Australia, our nearest sizeable neighbour, being 2000km to the east.

Source: Wardle (1991)

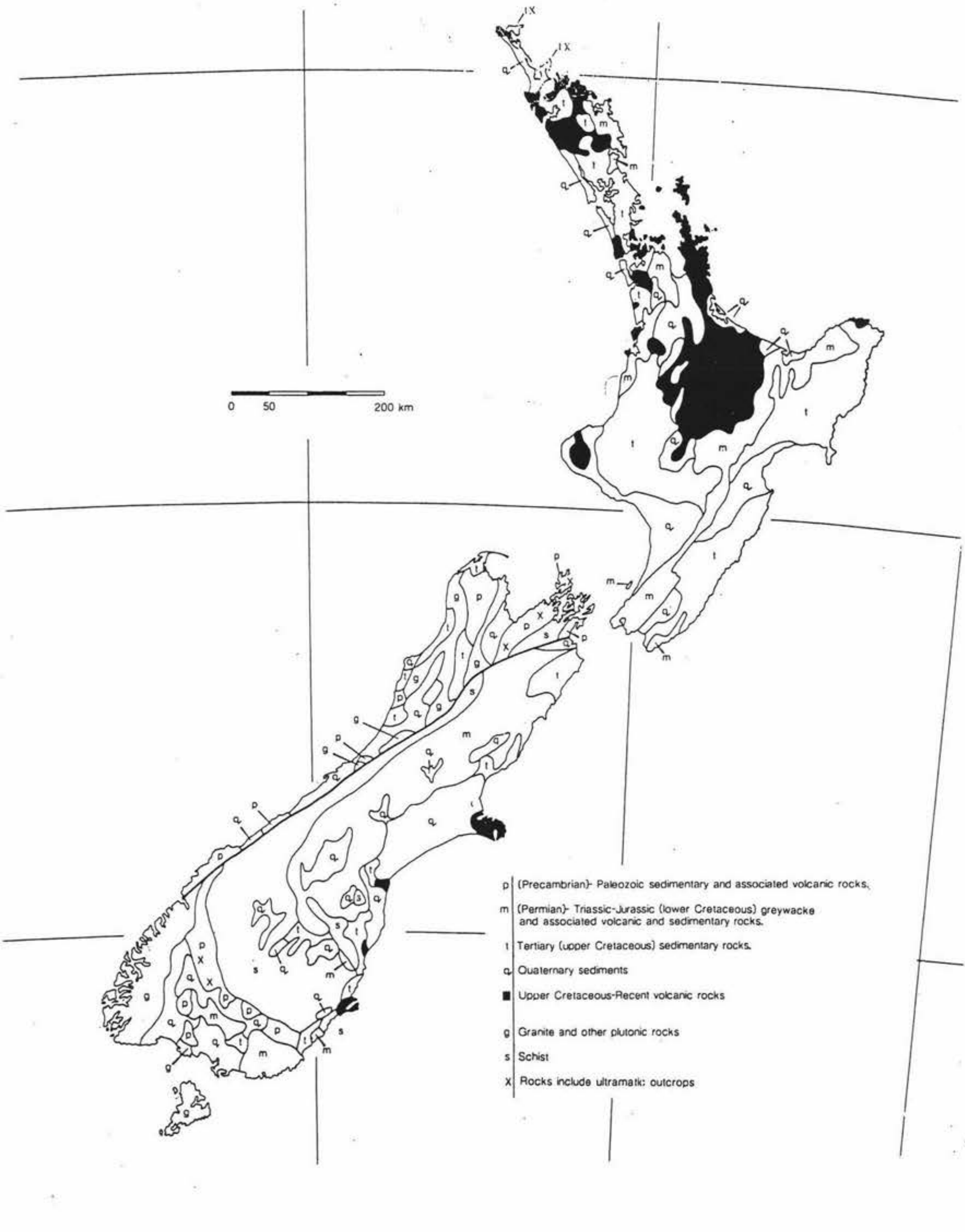


Figure 2 Geology of New Zealand

Source: Wardle (1991)

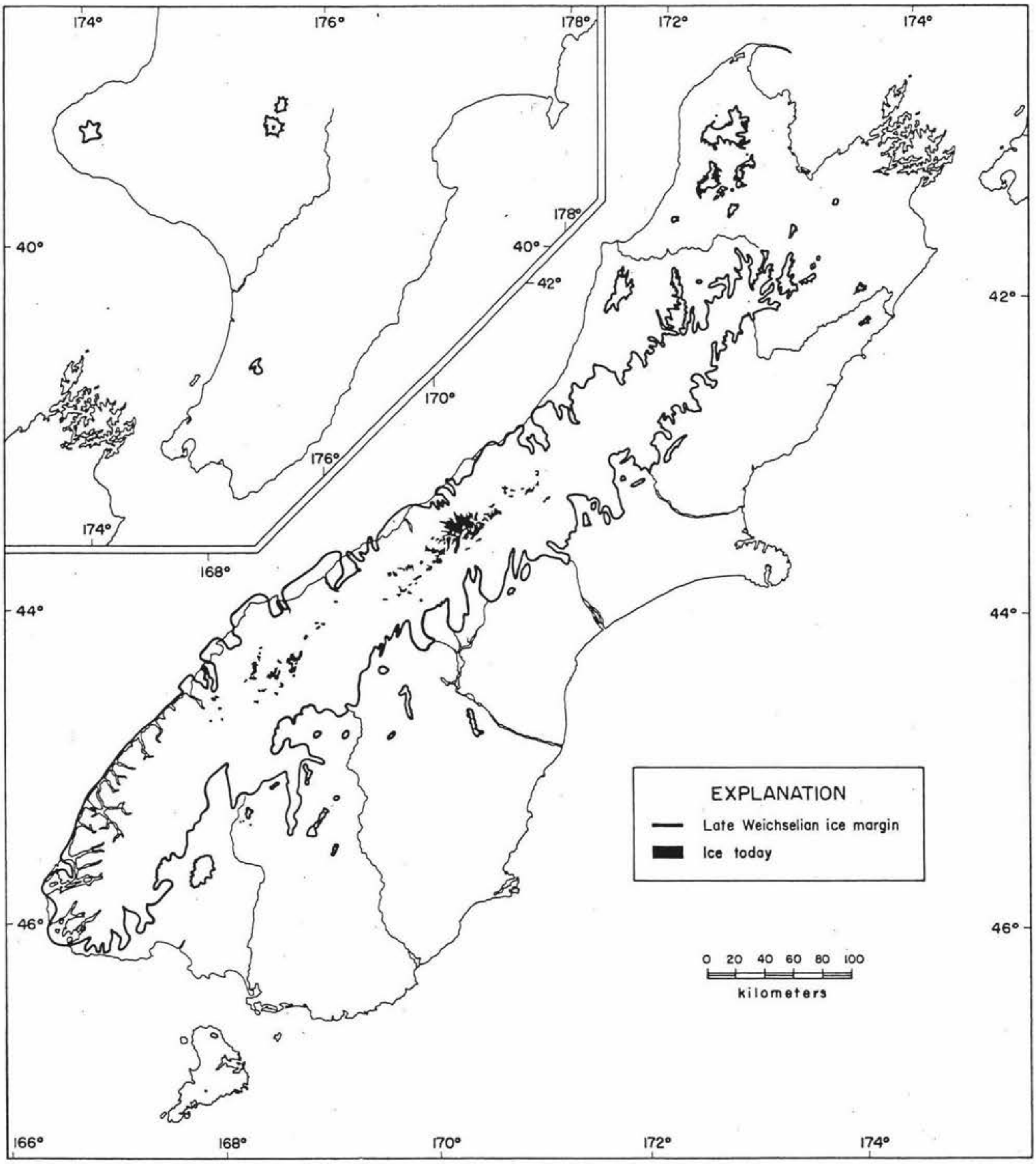
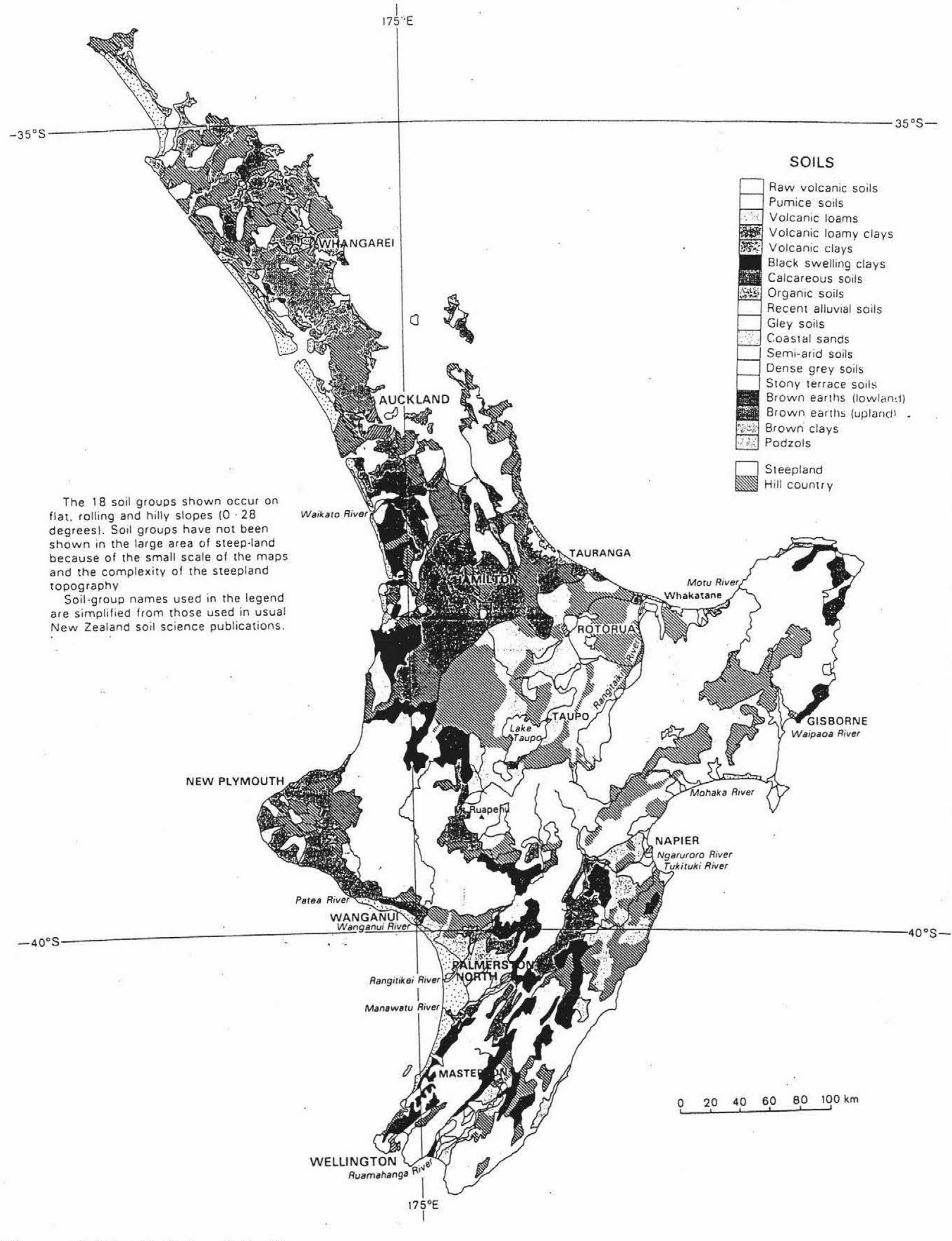


Figure 3 Modern and LGM Ice Margins in New Zealand

Source: Hollin & Schilling (1981). These researchers interpolated ice limits by applying iterative numerical calculations to geological maps of the form

$$h_{i=1} = h + \frac{\tau_{\tau av}}{c_i \; \rho \; g} \quad \frac{\Delta x}{t_i}$$

where h = ice surface elevation (m); τ = basal shear stress; g = gravitational constant; ρ = density of ice (0.91gcm $^{-3}$); x = horizontal distance of the snout (m); t = ice thickness and c = shape factor, which ranges from 1.0 for an infinitely wide glacier to 0.4 for a cirque. For the Godley and Tasman glaciers Hollin & Schilling used $c = 0.5$ and $\tau_{av} = 0.7$.



The 18 soil groups shown occur on flat, rolling and hilly slopes (0 - 28 degrees). Soil groups have not been shown in the large area of steep-land because of the small scale of the maps and the complexity of the steepland topography.

Soil-group names used in the legend are simplified from those used in usual New Zealand soil science publications.

Figure 4 North Island Soils

Source: Molloy (1993)

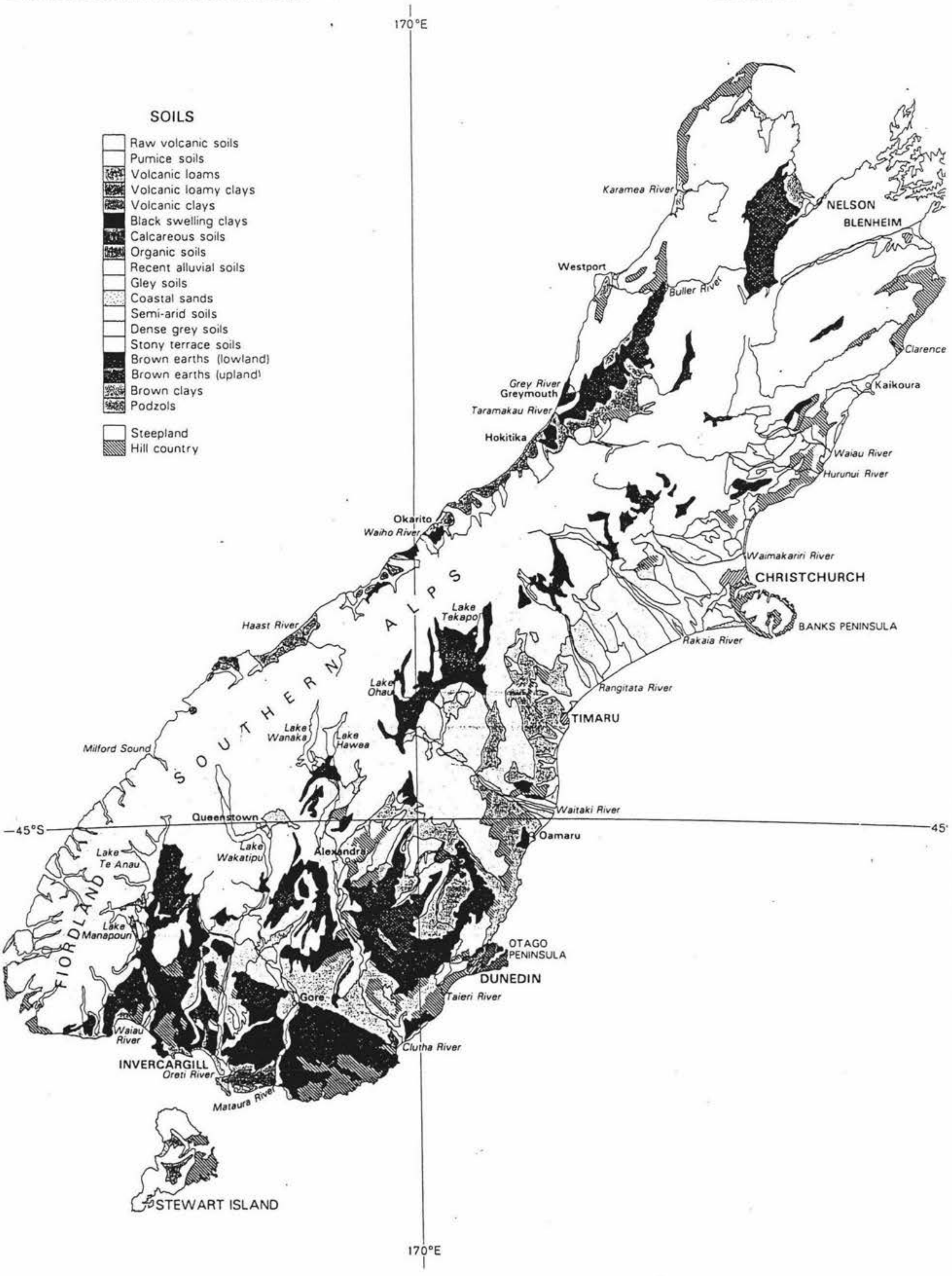


Figure 5 South Island Soils

Source: Molloy (1993)

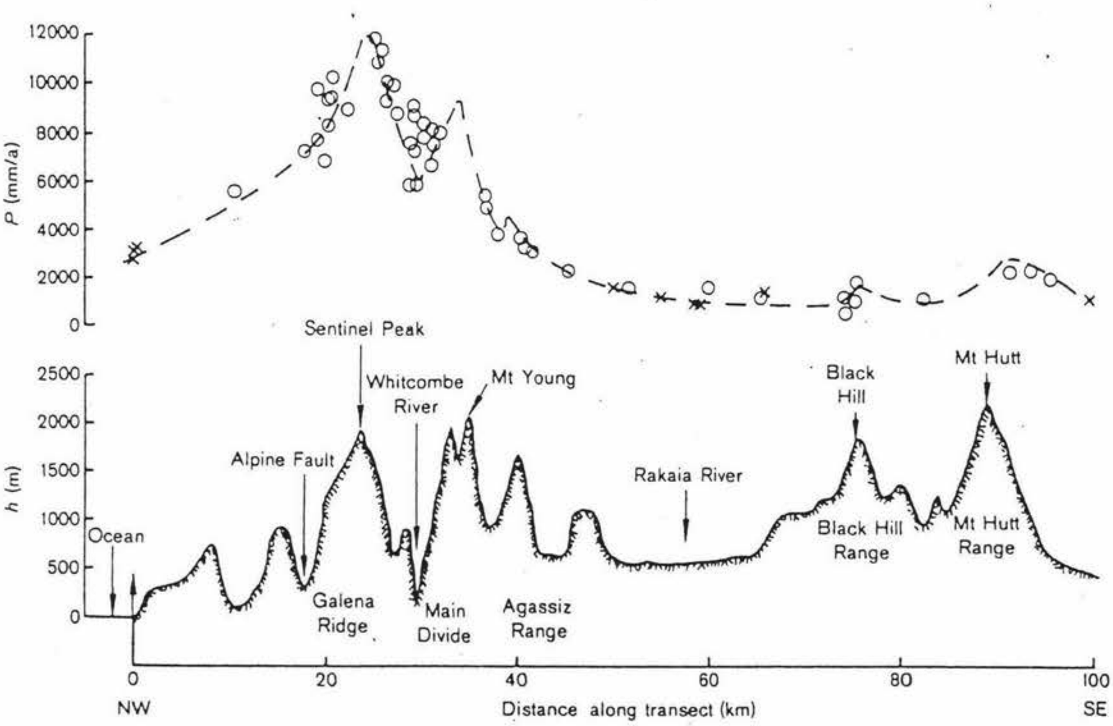


Figure 6 Southern Alps Transect: Topography and Precipitation
Transect runs through Sentinel Peak, Mt Young and Mt Hutt. Vertical exaggeration × 10
Source: Griffiths & McSaveney (1983)

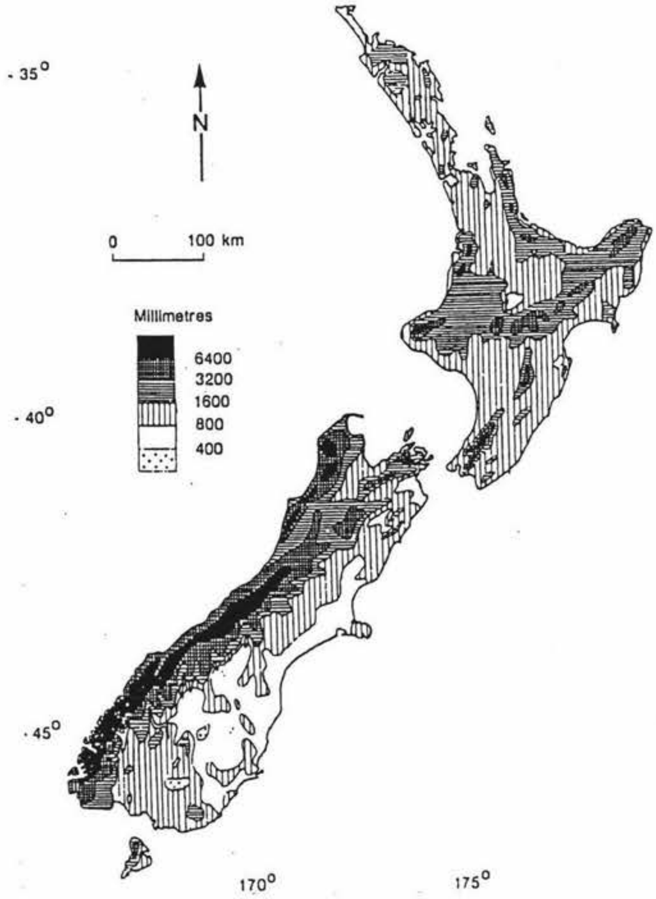


Figure 7 Major Rainfall Patterns in New Zealand
Source: Dodson (1998)

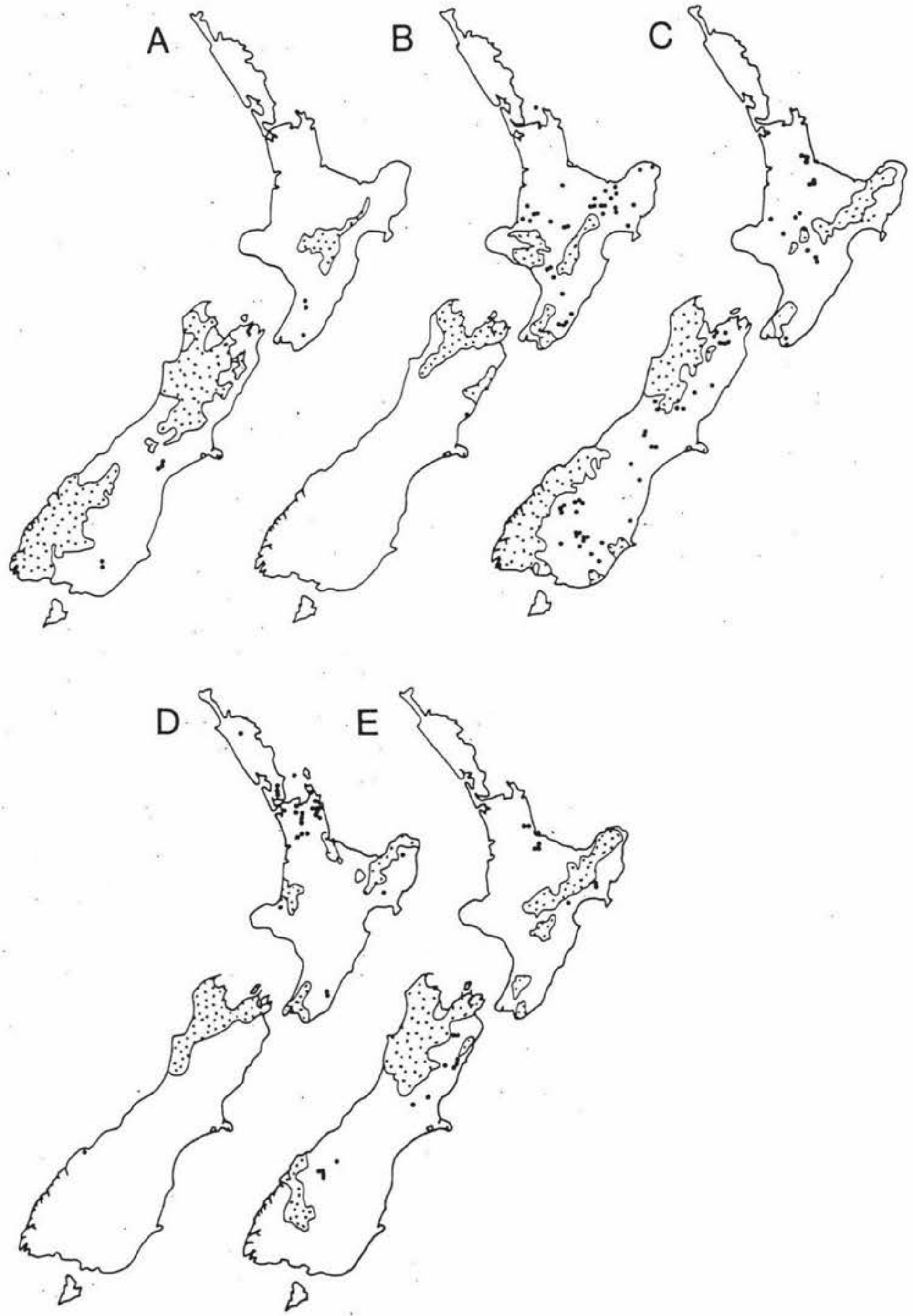


Figure 8. New Zealand Beech Gaps
(a) *Nothofagus solandri* var *cliffortioides*; (b) *N.solandri* var *solandri*; (c) *N.menziesii*; (d) *N.truncata*; (e) *N.fusca*

Source: McGlone (1985b)

1.6 New Zealand's Phytogeography

New Zealand's forests tend to be evergreen and broadleaved, a common feature in the Southern Hemisphere's temperate zone, compared with needle-leaved coniferous forests and broadleaved forests of North America and Eurasia (Sakai *et al* 1981).

The forests fall into three main formations: *Nothofagus* (beech) forests predominate in the south and montane areas; *Agathis australis* forests occur in the north of the North Island, and podocarp/hardwood forests occur elsewhere, although around 70% of New Zealand's area has been cleared of native forest first by Maori and later by Europeans following colonisation by people. In addition to being geographically isolated, New Zealand is largely floristically isolated, manifested by a high degree of endemism. Wilton & Breitwieser (2000) estimate that of the 191 families, 1,140 genera and 4,005 species in the seed plant flora of New Zealand, approximately 47% of the flora are indigenous, and some 1,566 or 82% of indigenous Gymnosperms and Angiosperms are endemic.

Maximum species alpha diversity[19] occurs in regions with relatively high temperatures, solar radiation and both atmospheric and soil moisture (Leathwick *et al* 1998) which translates to increased diversity on either side of the ranges on both islands and an increase in diversity to the north (Ohlemüller & Wilson 2000). However this trend is not unequivocal; Ogden (1995) sites examples of epiphyte diversity increasing with altitude in Waipoua forest, and herbaceous species increasing in diversity above the treeline of low-diversity *Nothofagus* forests. Heads (1997) found centres of highest biodiversity in the north-west South Island for two flowering plant families, Thymelaeaceae and Onagraceae; the mountain herb genus *Ourisia* and a group of *Olearia* species had a centre of biodiversity in Otago.

Superimposed on this general pattern of diversity is a "...much stronger pattern in which areas of high and low endemism alternate down the country," which are "...generally associated with topographically varied but geologically stable landform units," (Ogden

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[19] That is, diversity on a local scale or "...the number of species co-existing within a uniform habitat. It is an inventory of the species present within a community," (Ogden 1995), compared with beta diversity which is diversity on a regional scale or the between-community level of diversity, providing .an index of diversity across a landscape within one biogeographical region." (Ogden 1995). Gamma diversity refers to the total species inventory for a large geographical region which contains the main environmental gradients present in the area under consideration such as regions of New Zealand or the entire country (Ogden 1995).

1995). Regions demonstrating the greatest gamma diversity also tend to be those with the highest rate of endemism.

Nothofagus species form most of the timberlines in New Zealand; on drier mountains, *N.solandri* var *cliffortioides* form almost pure stands with few accompanying vascular plants whereas wetter mountains are dominated by both *N.solandri* and *N. menziesii* with a much richer accompanying flora. In areas where *Nothofagus* is absent due to deforestation in the Pleistocene glaciation and areas of Holocene vulcanism, floristically complex timberlines of Podocarpaceae (*Dacrycarpus* and *Dacrydium*), *Hoheria* and Compositae (*Senico* and *Olearia*) often form dense, interlocking scrub 100-300m above the upper limits of tall forest.

In alpine environments, plants are either absent at the most severe situations or tend to be cryptogams – mosses and lichens. Beyond the limits of the vascular plants, crustose, thallose and sometimes fruticose lichens will be found; at the limit of vascular plants graminoid, small herb cushion plants and prostrate shrubs high on rocky peaks or gipfels[20] are miniature 'snowbeds' where 'softer' plants can survive such as *Ranunculus grahami* at 2900m on Malte Brun.

New Zealand forests are 'sombre and evergreen' with annuals and geophytes being insignificant, both in numbers of species and physiognomic importance (Godley 1960). The austerity is due in part to the ubiquity of our fern taxa (Colenso 1882), a small number of very large angiosperm genera (Raven 1973)[21] and the pollination mechanisms characteristic of the New Zealand flora. Webb & Kelly (1993) point out that New Zealand trees are characterised by small, simple flowers that are inconspicuous – a high proportion (>60%) are white and there are few blue, purple and red flowers. This is particularly evident when New Zealand genera such as *Gentiana* and *Myosotis* are compared with the same genera in other countries, reflecting the relatively small role of zoophily[22] (animal pollination) compared with anemophily (wind pollination).

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[20] Sharp, pointed summits

[21] Raven (1973 suggests that these large angiosperm genera produced numerous species by way of adaptive radiation, interspecific hybridisation and recombination, and self-pollination.

Godley (1979) highlighted the unusual proportion of Diptera to Hymenoptera in New Zealand, with Diptera carrying out the role of Hymenoptera in other parts of the world. There are comparatively few native bee species (*c*40) and they are all either short-tongued Collitidae or small-tongued Halictidae. There are only 16 species of indigenous butterfly[23], but many species of moth; Godley (1979) suggests that the bulk of zoophilous pollination is carried out by beetles (cantharophily).

Examples of New Zealand taxa that are at least partly zoophilous include *Metrosideros excelsa, M.umbellata, Myoporum laetum* and *Phormium tenax*, the nectar of which is dined upon by the nocturnal gecko *Hoplodactylus duvauceli* (Whitaker 1987) and the three indigenous members of Meliphagidae (honey eating birds)[24] - tui, bellbird and stitchbird.[25] Despite producing abundant pollen, *Leptospermum scoparium* may be pollinated by the diurnal, arboreal gecko *Naultinus grayi*,[26] and *H.pacificus* has been observed feeding on the nectar of *P.tenax* and *Hebe bollonsii* (Whitaker 1987)[27]. *Metrosideros* spp are also pollinated by New Zealand's two microchiropteran bat species[28], the long- and short-tailed bat *Chalinolobus tuberculatus* and *Mystacina tuberculata* (Arkins *et al* 1999) as is the root parasite *Dactylanthus taylorii* (Eckroyd 1993; Webb & Kelly 1993). Pollen from *Knightia excelsa* and *Collospermum* spp were also found on these bats.

Sexual dimorphism, especially dioecism[29], is very frequent (*c*18%) in the New Zealand taxa (Hair 1966; Lloyd 1985; Webb & Kelly 1993). Self-incompatibility is relatively infrequent, with only around 11 species being incapable of self-fertilisation; Webb & Kelly (1993) state that this is remarkable, given the low (*c*6%) frequency of annuals where self-fertilisation is common. To promote out-crossing (ie crossing with a different genotype)

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[22] Buchanan & Nabhan (1996) list several pollinator 'syndromes' or plant-animal pollination relationships, including sapromyophily (carrion and dung flies); melittophily (bees); sphingophily (hawkmoths); and phalaenophily (small moths).

[23] *Brassaris itea*, the yellow admiral butterfly, has been observed pollinating the psychophilous (butterfly pollinated) *Pittosporum fasciculatum* (Godley 1979).

[24] Other birds affecting ornithophily include silvereye (*Zoterops lateralis*), kaka (*Nestor meridionalis*), red crowned parakeet (*Cyanoramphus novaezelandiae*), yellow-crowned parakeet (*Cyanoramphus auriceps*) and the North Island saddleback (*Philesturnus carunculatus rufusater*) (Godley 1979)

[25] *Prosthemadera novaezelandiae, Anthornis melanura*, and *Notiomystis cincta* respectively.

[26] Godley (1979) also lists tachinid and calliphorid flies and hover-flies as *Leptospermum* pollinators (myophily)

[27] According to Buchanan & Nabhan (1996) this is the only known example of reptile pollination in the world.

[28] Buchanan & Nabhan (1996) refer to this pollinator syndrome as chiropterophily.

[29] Sexual dimorphism refers to having two forms which show marked differences between male and female. Dioecious refers to having the sexes in different individuals.

the pollination mechanisms dichogamy (eg *Myosotis colensoi*) and herkogamy[30] (eg *Gentiana chathamica*) appear to be important amongst New Zealand's hermaphroditic flowers.

Although tree taxa with fleshy fruits are a conspicuous component of the New Zealand forest, particularly amongst podocarps and the genus *Coprosma*, Lord (1999) found that only 28% of taxa in New Zealand podocarp forests and 27% of taxa in *Nothofagus* forests had fleshy fruit compared with 32% in North American coniferous forests and 36% in broadleaf forests, respectively.

'Masting' is common in several New Zealand tree genera, a phenomenon whereby seed production is very high in a given year followed by several years of low production. It may transpire that only in mast years do trees leave descendants, and this may contribute to the even-agedness of *Nothofagus* forests. Harper (1977) suggests that masting may be an adaptation to predation, since the life cycle of birds is too long to adapt to the unpredictable food source. At first glance, masting may have special significance in palynology, since low pollen production precedes low seed production, and low fossil pollen counts in a core may reflect a non-mast year rather than scarcity of a given taxon. At the same time, Moar & Myers (1978) suggest that masting tends to coincide with hot dry summers.

The corollary of this is that pollen production for a given taxon may have been lower during glacial times not only because the climate precluded a taxon from living in a given habitat, but because cooler conditions meant that a smaller volume of pollen was produced for a given number of trees, *ceteris paribus*. However, according to Ogden[31] masting is unlikely to influence the pollen record since it generally occurs on a 3-7 year cycle, whereas pollen samples normally cover tens or hundreds of years.

The New Zealand floral assemblage is unique with respect to the high proportion of its plants that have a divaricating[32] habit - around 10% of the woody taxa (Wilson &

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[30] The spatial separation of anther and stigma of the same plant.

[31] Personal communication, 2002.

[32] Wilson & Galloway (1993) argue that strictly speaking, divaricating means 'branching at a wide angle' which although true of some species of 'divaricating' plants is not true of others, where the angles of the branches are more acute. The mechanism causing tangled branching is most of the branches growing at the same pace. In normal shrubs, the apical meristem of the leading shoot exerts growth regulating hormones

Galloway 1993)[33]. New Zealand divaricates such as *Coprosma propinqua* and *Aristotelia fruticosa* are characterised by small leaves, cryptic appearance of new shoots (Lowry 1980; Atkinson & Greenwood 1980) often with long distances between the internodes; tangled, twiggy forms often branching at wide angles, and occasionally a prostrate habit (eg *Sophora prostrata*). Some of these divaricates represent the juvenile forms of trees that have normal foliage and habit in adulthood, eg *Prumnopitys taxifolia*, *Plagianthus regius*, and *S.microphylla*.

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called auxins which inhibit the growth of the side shoots below it. In divaricating shrubs, the side shoots often grow as if they are not inhibited by the leading shoot (Wilson & Galloway 1993).

[33] Some 54 taxa are divaricating; in addition there are another 6 taxa that have juvenile divaricating habits.

1.7 Biogeographical Problems in New Zealand

Plotting isopollen maps may help to answer some of the biogeographical problems that characterise the New Zealand flora:

1. Placing the Otiran-Aranuian boundary: there has been some debate about the placing of the Otiran (glacial) - Aranuian (post glacial) boundary in New Zealand: Suggate & Moar (1970, 1974), Moar (1981) and Burrows (1983) propose 14,000 BP whereas Lintott & Burrows (1973) and Burrows (1974) place it at 10,000 BP. McGlone (1985a) suggests that there is sufficient pollen evidence to "...demonstrate that there was a rapid, significant warming New Zealand-wide at *c*10,000 BP. By plotting isopollen maps we should be able to either support or refute McGlone's (1985) assertion.

2. The Younger Dryas Stadial in New Zealand: there is some debate regarding the synchroneity of the Younger Dryas Stadial, and even whether there was an analogous cooling in New Zealand at all (Singer *et al* 1998). For example, a narrowing of isochrones describing the Laurentide ice cap retreat between 11,000 and 10,000 BP in Quebec, Canada may correlate with the Younger Dryas Stadial in Europe (Hillaire-Marcel & Occhietti 1980) however whether there was a synchronous cooling in the Southern Hemisphere is unclear.

3. Discontinuous Vegetation Distribution: A number of New Zealand taxa show disjunct distributions; the most well known of these are the beech gaps, however there are many other taxa that demonstrate discontinuous dispersal as shown in Table 1. Some of these species are disjunct due to the habitats they live in, for example *Elytranthe colensoi* is normally parasitic upon *Nothofagus menziesii* and therefore demonstrates the same disjunct distribution as its host. Similarly, many bog species have gaps in their distribution since cushion bogs are not generally found between the Taramakau and Waimakariri rivers in the north and Haast in the south.

More problematic from a phytogeographic perspective are the non-habitat dependent disjunctions, since there is no obvious reason for them. For example, the beech gap in the North Island commences near the head waters of the Mangatainoka River extending for about 100km north into the Ruahine Ranges. McLea (1990) suggested that the decline in the beech population began around 23,000 years BP and by 19,500 BP the beeches were gone. The South Island beech gap is twice as long as its North Island counterpart, extending from the Arnold River to Lake Paringa in the south.

Two general theories are invoked to explain the beech gaps; the glacial refugia hypothesis where beech (and other taxa) disjunction is due to the failure of the beeches to recolonise the gap following glacial retreat at the end of the last glaciation (Wardle 1986). The alternative hypothesis is that disjunction is mainly the result of climate and competition; areas lacking *Nothofagus* are characterised by high humidity, maritime climates with small annual temperature ranges and droughts occur only rarely (Haase 1990). Glacial retreat is less likely to be a satisfactory explanation for at least parts of the North Island gap since there was an absence of large glaciers; McLea (1990) concluded that the cause of the beech gap in the north was due to a lowering of the temperature possibly accompanied by a decrease in precipitation, and issues a challenge for isopollen mapping stating "Palynology does not help to explain why the beeches failed to recolonise the North Island gap once the climate ameliorated."

4. Divaricating Plants: Botanists have long recognised that the high proportion of divaricates must indicate some environmental condition unique in New Zealand; for example Cockayne (1912) suggested that divarication was an adaptation to Pleistocene conditions that were windier and drier than present. Dense branching would form a windbreak and reduce water loss by transpiration and conserve warmth by providing a microclimate in the plant's foliage. Small, widely spaced leaves on springy branches would result in reduced mechanical abrasion to the leaves further reducing transpirational losses and minimising loss of photosynthetic material (McGlone & Webb 1981).

Greenwood & Atkinson (1977) felt that climatic explanations for divaricating plants were not entirely satisfactory: climatic conditions during the Pleistocene were not unique, and divaricating plants are often a minor component of the taxa in windy areas such as the Cook Strait coast and the Chatham Islands. Furthermore, simple transpiration experiments failed to demonstrate that plants with microphyllous foliage were more drought resistant than larger-leaved plants. Instead, Greenwood & Atkinson (1977) preferred adaptation to browsing by *Dinornis* (moa) as an explanation for divarication.

Although birds of the superorder Ratites are found elsewhere[34], New Zealand is unique in that ratites were present in the absence of browsing mammals, and were sufficiently abundant to exert browsing stress on the vegetation. Since birds rely more upon their sense of sight than smell, divaricating plants with their small, widely spaced and cryptically-coloured leaves and springy, intertwined branches would be better adapted to withstand browsing stress by these large birds than tress with a normal habit. Furthermore, taxa that have divaricating juveniles tend to assume a normal, non-divaricating habit when they reach 3-4m in height, beyond the reach of the largest moa.

Burrows (1980a) examined the gizzard content of 3,600 year old *Dinornis* (moa) remains found in Pyramid Swamp, North Canterbury. Short pieces of twig made up more than 90% of the volume of plant material with >50% of the total volume of twigs from a single divaricating species, *Olearia virgata*.[35] Similar findings from moa remains found near Lake Wanaka prompted Burrows (1980a) to conclude that large moas[36] relied upon twigs as an important part of their diet. Burrows (1980b) found that the ends of the twigs in moa gizzards were generally neatly cut, indicating that they had been sheared off rather than torn off, as supposed by Greenwood & Atkinson (1977).

Unfortunately, it is difficult to demonstrate causal relationship between *Dinornis* browsing and divarication, given the mobility of moas and the lack of divaricating species in the fossil pollen record.

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[34] Australia and New Guinea: *Dromaius novaehollandiae* (emu), *Casuarius casuarius* (cassowary) and the extinct dromornithids; Africa *Struthio camelus* (ostrich); South America *Rhea americana* (rhea); Madagascar *Æpyornis maximus* (the extinct elephant bird).

[35] Other divaricating shrubs yielding macrofossils included *Coprosma rotundifolia*, *Melicope simplex* and *Myrsine divaricata*.

[36] *Dinornis*, *Emeus* and *Eurapteryx*

Species	Southern South Island	Middle South Island	Northern South Island	Southern North Island	Rest of North Island	Distance(s) (km)[37]
Habitat Dependent Disjunction: Bog Vegetation						
Drosera pygmaea	36°38'	-	-	39°39S	35°08'S	977; 543
Petriella thomsoni	N to 45°25'	-	43°31'-41°15'	-	-	318
Pseudolepyrum pallidum	N to 45°S	-	-	39°39S	-	772
Tetrachondra hamiltonii	N to 45°52'S	-	-	39°39S	-	846
Habitat Dependent Disjunction: Parasitic Plants						
Elytranthe colensoi[38]	N to 44°S	Canterbury	S to 43°20'S	-	38°-40°S	498
Non-Habitat Dependent Disjunction: Alpine Plants						
Celmisia petriei	N to 44°S	-	42°-41°15'S	-	-	276
C.traversii	46S°-45°30'S	-	41°-42°S	-	-	505
Drapetes laxus	46°16'S-45°25'S	-	42°-41°15'S	39°40'-39°S	-	498; 309
Juncus procerus	Southland	-	-	-	Auckland	1,180
Nothofagus fusca	46°-44°26'S	43°50'S	S to 43°S	N to 40°30'S	37°30'-40°S	67; 123; 56
N.solandri var *cliffortioides*	N to 44°S	Canterbury	S to 43°20'S	-	38°-40°S	557
Pimelea aridula	C.Otago	-	C.M'borough	-	-	548
Non-Habitat Dependent Disjunction: Lowland and Sub-Alpine Plants						
Dacrydium intermedium	Fiordland	Westland[39]	Nelson	-	35°-38°S	448
D.laxifolium	W.S'land	Westland	Nelson	-	39°-40°S	361
Libocedrus bidwillii	NW & E Otago	Widespread	Widespread	-	36°50'-40°S	525
L.plumosa	-	-	NW Nelson	-	S to 38°S	414
Metrosideros parkinsonii	-	-	W Nelson to 42°30'S	-	36°10'S	558
N.menziesii	N to 44°S	Canterbury	S to 43°20'S	-	38°-40°S	557
N.truncata	-	-	N&W to 42°30'S	N to 41°	35°30'S - 39°30'S	238
Phyllocladus trichomanoides	-	-	NW Nelson	-	S to 39°S	292
Quintinia acutifolia	-	Westland S to 43°30'S	W Nelson	-	S to 39°30'S	249

Table 1. Selected Disjunct and Partially Disjunct New Zealand Taxa.
Source: Wardle (1963); Burrows (1965); Allan (1982).

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[37] Estimated using the GEODESIC program (Maher 1994) utilising a Fischer spheroid first-order ellipsoidal model of the Earth (major radius = 6,378,166m; flattening = 1/298.3)

[38] *Elytranthe colensoi* is normally parasitic upon *Nothofagus menziesii.*

[39] Wardle (1963) suggests that there is possibly a gap from 43° to 43°40' for both *Dacrydium intermedium* and *D.laxifolium*, a distance of approximately 74km

2. Method Used to Construct Isopollen Maps

2.1 Data Collation

The first task was to collate fossil pollen data from as many published, well-dated pollen diagrams for New Zealand as possible. One way of ascertaining the validity of the isopollen maps presented here is to compare the procedures that I used with those of other researchers in terms of the number of sites used, the proportion of sites that were radiocarbon (or tephra) dated, the ratio of area to cores (the higher the number, the more interpolation and extrapolation is required), and so on. Whereas there was one dated site for every 9,000 km^2 for Poland for the Holocene (Ralska-Jasiewiczowa 1983) for example, the number was one for every 1,275 km^2 for New Zealand. The number of mappable sites in New Zealand compares very favourably with other countries (Table 2). Appendix 5.1 shows the pollen sites used in the New Zealand isopollen maps[40].

Huntley & Birks (1983) were very selective when constructing isopollen maps for Europe, selecting sites with the most extensive radiocarbon chronology first; where there was more than one well-dated site, lacustrine sites were chosen, and if a choice still remained, the size of the basin and the technical quality of the sequence (number of samples examined and pollen taxonomic detail) were considered. In comparison, the scarcity of published, dated pollen diagrams for New Zealand meant that very few were rejected: all pollen diagrams that had at least one carbon or tephra date attached were utilised. Where there were anachronistic carbon dates, I used my judgement to reject the anomalous carbon dates. Map and grid references as reported with pollen maps were checked against NZMS 260 series maps, since occasionally there were errors in published references[41].

Huntley & Birks (1983) also used *undated* cores by interpolating from the nearest well-dated site; a technique utilised by Webb *et al* (1983) and Ralska-Jasiewiczowa (1983)[42]. To augment her dataset, Ralska-Jasiewiczowa interpolated and extrapolated dates for

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[40] Note that not all sites are shown, since often there were several sites within a short distance of each other, and beyond the resolution of the maps in Appendix 5.1 (eg McGlone 1983a; McGlone & Bathgate 1983; Elliot 1998; Singer *et al* 1998) accordingly the number of sites in Appendix 5.1 does not tally with numbers in Tables 2 and 3.

[41] Eg Elliot *et al* 1998; Horrocks *et al* (2001).

[42] Magdalena Ralska-Jasiewiczowa (W.Szafer Institute of Botany, Polish Academy of Science, Cracow) was a pupil of Wladyslaw Szafer, who was the first person to construct isopollen maps (also of Poland), in 1935.

undated sites where palynological events were clearly recognisable within the same geographical area. In this thesis, only dated (either radiocarbon or tephra dated) sites are used; in fact, there are very few published pollen sites in New Zealand that do not have either well known tephra dates or radiocarbon dates associated with them. The corollary of this is that the dating accuracy of the New Zealand isopollen maps is likely to be greater than those prepared by Ralska-Jasiewiczowa (1983) for Poland.

Some researchers 'cleaned' the data prior to mapping; Webb *et al* (1983) for example applied corrections for ancient carbonate contamination, and Ralska-Jasiewiczowa (1983) recalculated published data to achieve a common sum for pollen percentage calculations. I did not do this since in general, published pollen sums for New Zealand are already corrected for carbon dating contamination errors and are calculated on a common basis.

	Area (km^2)[43]	Total Sites	Dated sites	Area per site (total)	Contour Interval	Contour Method
New Zealand	265,150	208	208	1,275	Various	Computer; inverse distance & kriging
British Isles (Chambers & Elliott 1989)	313,650	79	79	3,970	500 years	Manual Interpolation (?)
British Isles (Birks (1989)	313,650	135	135	2,323	250 years	Manual Interpolation
Poland (Ralska-Jasiewiczowa 1983)	312,685	64	35	4,886	0.2-2.0; 2.1-5.0; 5.1-10; 10.1-25.0; >25.1%	Manual Interpolation[44]
Japan (Tsukada 1982a)	369,700	37	<37	9,992	1,000 years	Manual: inverse distance
Europe (Huntley 1990)	7,768,000	500	500	15,536	(Vegetation map)	Manual; tricube distance function
E North America (Prentice *et al* 1991)	7,715,000	328[45]	328	23,521	>1, 5 & 10%; >0.5, 1 & 2%[46]	Manual Interpolation
Midwestern United States (Webb *et al* 1983)	1,207,000	49	47	24,633	5.0% then 10% intervals	Manual Interpolation[47]
NW Ontario (Björck 1985)	772,000	10	10	77,200	500 years	Manual Interpolation ?
NE North America (Bernabo & Webb 1977)	5,376,000	62	62?	86,710	5.0% then 10% intervals	Manual Interpolation
Southern Norway (Caseldine 1989)	1.64	38	(modern)	0.04	Various increments	Computer interpolation and plotting[48]
Central Sweden (Prentice 1983)	196,400	40	(modern)	4,910	Mainly 10% intervals	Manual Interpolation ?
Eastern North America (Davis & Webb 1975)	4,379,000	406	(modern)	10,786	5 and 10% intervals	Computer (Symap)
Central North America (Webb & McAndrews 1976)	7,353,000	606	(modern)	12,134	5.0% then 10% intervals	Computer interpolation, manual contour

Table 2. International Comparison of Isopollen & Related Maps

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[43] Land area estimated from Webster's New Geographical Dictionary (1988)

[44] According to Ralska-Jasiewiczowa (personal communication 2001) "At that time when I was compiling isopollen maps for Poland our computer equipment was still very poor, and maps were drawn by hand, without using any sophisticated methods (1981-2)."

[45] With a further 928 (modern) surface samples

[46] The interval used was determined by the taxon displayed, eg spruce, birch and oak were >1, 5 and 10% isopolls, whereas fir, hemlock and beech were plotted in >0.5, 1 and 2% isolines.

[47] According to Tom Webb (personal communication 2001) "In those days, I just hand-contoured the maps for the placement of the isopolls. But in work since 1986, we have used inverse distance algorithms of one sort or another."

[48] Chris Caseldine was unable to recall the actual estimation procedure used (personal communication 2001).

2.2 Establishing Time Intervals

Whereas Huntley & Birks (1983) extracted data for Europe at 500 radiocarbon year intervals, the small number of New Zealand pollen diagrams meant that radiocarbon dates had to be sorted via a spreadsheet package and a larger, logical time interval derived. I elected to plot 2,000 year intervals, emulating in part Ralska-Jasiewiczowa (1983) who plotted isopollen maps for Poland by interpolating and extrapolating from dated intervals within the same pollen diagram[49]. Unlike Huntley & Birks (1983) who quantified the quality of the dating of their sites, it was not necessary to rank one core over another for the New Zealand isopolls. Where there were multiple pollen diagrams for the same site for the same time period I took the average of the percentages given for each taxon.

Because there was a shortage of dated samples for certain parts of New Zealand, in particular the south and west of the South Island prior to 10,000 BP, I elected to interpolate dates for published diagrams that had at least two radiocarbon dates on either side of this time in order to juxtapose the Glacial-Postglacial adequately. This involved first, fitting cubic splines, *n*th order polynomial functions[50], linear interpolation or power functions to the fossil pollen data using the program DEP-AGE (Maher 1992) and visually inspecting the 'goodness of fit' for the resultant age versus depth curve. The second step was to enter the required depth into DEP-AGE to derive the predicted age, and finally, read the pollen percentages off the appropriate pollen diagram for that depth[51].

The basic assumptions implied in using these functions to interpolate age and depth is that first, the law of superposition[52] holds, and second, that the function applied does in fact represent the actual sedimentation rate. We cannot be certain, however, that the derived sedimentation rate is correct; increasing density with depth in a core resulting from compaction would give an age-depth curve that is concave upwards, whereas a convex[53]

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[49] Occasionally Ralska-Jasiewiczowa plotted 500 year intervals in order to understand migration history.

[50] In general, *n*th-order polynomial functions have n-1 bends, eg a first-order function is a straight line; a second-order function is either convex or concave (but does not change between the two) (Maher 1992).

[51] Other researchers to interpolate dates in this way include Wilmshurst (1997)

[52] The geological 'Law of Superposition' holds that strata that overly other strata are always younger, except in strongly folded areas. (*Chambers' Science & Technology Dictionary*)

[53] Depending on which round the age/depth relationship is plotted. Since polynomials have the form $y = a + bx + cx^2 + dx^3$ etc where x = depth (dependent variable), y = age (independent variable) and a, b, c etc are the coefficients to be estimated (Bennett 1999) depth is plotted on the x axis. Although most palynologists plot depth vertically, in reality, depth is the independent variable because sediment thickness is a function of the passage of time so should be plotted on the x axis. Depth is treated as the independent variable because it is the variable that can be controlled, and can be sampled (Bennett 1999).

depth-age curve would be the result of early, rapid sedimentation on unvegetated slopes as might occur in the early post-glacial[54].

Cubic spline functions or 3rd-order or higher polynomial functions were generally rejected where the number of terms equalled the number of 'control point' ^{14}C dates, because often, in passing through all the ^{14}C dates, the fitted spline bent back upon itself, gave infinite rates of sedimentation or negative sedimentation rates[55]. Bennett (1999) suggests that the aim of fitting curves in this type of exercise is to "...find a reasonable model of the datapoints. The curve does not necessarily have to pass through all the points because the points are only statistical estimates of the 'true' (unknown) radiocarbon age of the sample." Not only does adding more terms to the polynomial 'force' the curve to fit all the datapoints, we are unable to assess the goodness of fit using methods such as Chi-squared analysis: the χ^2 statistic will always equal zero (ie a perfect fit) when the number of terms equals the number of datapoints (Bennett 1995).

In total, around 10% of the records were interpolated in this way. The alternatives to interpolating dates for a site using information from the same core would be to either let SURFER estimate pollen percentages using neighbouring sites, or follow Isaaks & Srivastava's (1989) suggestion that extrapolating over very large distances is misleading, and "It is safer to be humble and admit our ignorance by leaving such areas blank." Most often, interpolation using DEP-AGE was used given that in some instances neighbouring sites were too distant, for example for the interval 13,000-14,000 years BP there were no dated samples south of Nelson, yet we did have some information available (best estimates of ^{14}C dates).

The divisions of time that were plotted were a compromise between selecting meaningful divisions of time, accommodating paleoshoreline maps and having sufficient sites to plot. These are given in Table 3.

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[54] Tsukada (1982) used linear interpolation and extrapolation to derive dates in Japanese cores and cautions that "...extrapolation from postglacial ^{14}C dates in progressively compacted late-glacial and full-glacial sediments may lead to relatively young estimates." In this thesis, estimated New Zealand dates were interpolated only.

[55] The slope of the line connecting two dates is a measure of the net sedimentation rate in cm/^{14}C years (Maher 1992); the inverse of which is sediment deposition time in ^{14}C years/cm (Maher 1995).

		Number of Sites
LGM	22,000 – 14,500 BP	53
Late Glacial	14,500 – 10,000 BP	68
Early Holocene	10,000 – 8,000 BP	66
Mid - Holocene	8,000 – 6,000 BP	65
	6,000 - 4,000 BP	80
Late Holocene	4,000 – 2,000 BP	113
	2,000 - 0 BP	109
	Modern	92

Table 3. Temporal Distribution of New Zealand Pollen Sites

2.3 Vegetation Assemblages Used in Pollen Sums

Pollen sums based on different taxa assemblages causes some difficulties; to be useful with regards to isopoll construction, pollen diagrams need to be comparable to each other with regards to the pollen sum. However some pollen sums are based on 'all dryland taxa excluding ferns and fern allies' (Mildenhall 1979, McGlone & Neall 1994); others based on 'all woody taxa' (Moar 1971) or 'woody taxa excluding *Leptospermum*' (Lees 1986) or woody taxa excluding some other taxa (McGlone & Moar 1977; Pocknall *et al* 1989). Clearly, the same quantity of a given taxon's pollen will yield different pollen percentages with regard to the sum of woody taxa only than it will for all terrestrial pollen and spore types.

This is not to say that one pollen sum is superior to another; Fægri & Iversen (1989) caution that the appropriate pollen sum to use depends upon the purpose of the palynological study, stating "The basic [pollen] sum for the study of regional forest development is different from the one needed to study the agricultural occupation of the inhabitants of an archaeological site, and that is again different from the one forming the basis for a study of the development of a small forest area under various influences." As discussed *supra*, the published pollen diagrams have been prepared for a variety of reasons, hence differing component species in the pollen sums[56].

The problem of different bases used for calculating pollen sums was compounded by differing or imprecise definitions of the same floral assemblage. Lees (1986) for example, excludes *Leptospermum* from 'woody taxa' for some sites, but includes *Leptospermum* in 'woody taxa' for other sites. McGlone & Bathgate (1983) treat *Astelia* as a mire herb, whereas Elliot *et al* (1997) treat it as a dryland plant. McGlone & Neall's (1994) dry land taxa excludes ferns and fern allies, whereas Elliot *et al* (1997) state that "The pollen sum includes all dryland pollen and spores," implying that ferns and fern allies are *in*cluded. Moar (1970) provided plant pollen percentages for 'dry land plant pollen,' 'woody plant pollen,' and 'total pollen counted excluding aquatics and spores,' within the same report.

Ideally, tables with absolute pollen counts would be provided with each published pollen record in order to calculate relative pollen sums of whatever assemblage of taxa was most desirable to users of the data.

Although around 85% of dated core zones exclude pteridophytes (except *Pteridium esculentum*) from the pollen sum, or simply do not enumerate spores at all, approximately 30% of pollen diagrams include *Pteridium esculentum*. Thus the inconsistent pollen sum definitions are more problematic in Late Holocene pollen diagrams when *Pteridium* is more common. Fortunately, only 3% of pollen diagrams recorded pteridophyte percentages in excess of 10%, therefore the vast majority of pollen diagrams were not significantly influenced by the fact that pteridophytes were included in the pollen sum. In other words, tree and shrub taxa percentages were not significantly under-estimated. Accordingly I resisted the temptation to simply pro-rate the percentages of ferns and fern allies across woody taxa to derive a common denominator; instead I adopted a very pragmatic approach, and assumed that the assemblages are broadly comparable on the basis that in general, they include dryland taxa and for all practical purposes, exclude aquatics and ferns.

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[56] According to Dallas Mildenhall (1998, personal communication) "The inclusion or exclusion of *Leptospermum* and *Kunzea* is difficult because in many cases inclusion makes nonsense of the pollen diagram. If it grows locally it can dominate the pollen diagram causing all other types to become under-represented. Spores and pollen are dispersed differently and spores are preserved more easily and should be excluded from the pollen sum."

2.4 Selecting Taxa to Plot

The decision as to which taxa to plot in isopollen maps is a compromise between selecting taxa that provide a useful paleoclimate and paleovegetation narrative, and those that are proportionally represented in the pollen sum, enumerated in enough sites to make it possible to plot them, and are identified to the species level.

Many New Zealand trees demonstrate clear spatial preferences (altitude and latitude), as demonstrated by Sakai & Wardle (1978). These researchers partially replicated an experiment by Leonard Cockayne (1897)[57] when they collected twigs of 42 native woody plants and tested them for freezing resistance by subjecting them to progressively colder temperatures and assessing frost injury. The measurements obtained coincided remarkably well with the geographical and ecological distribution of the taxa. Table 4 shows plant distribution by latitude and altitude of some major New Zealand trees; the numbers given refer to the maximum freezing resistance of buds after 4 hours exposure at that temperature. The terms lowland, subalpine etc in Table 4 have not been quantified since they exhibit spatial variation; Wardle (1985a) defines subalpine simply as "...vegetation belts below the tree limit." This is discussed further below.

The general, but not universal, correlation between minimum experimental freezing temperature and observed spatial preference is possibly due to factors other than temperature that vary with altitude (and less markedly, latitude) such as insolation, precipitation, wind regimes and soils. The strength of the correlation between a given taxon's latitudinal and altitudinal preferences may be ascertained by using data from modern pollen rain studies and plotting them on response surfaces (Bartlein *et al* 1986; Huntley 1990c; 1994) however the relatively small number of modern pollen rain (compared to fossil pollen) studies conducted in New Zealand and the "...general absence of quantitative accounts of species/climate relationships" (Leathwick & Mitchell 1992) precludes this.

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[57] Cockayne's experiments in the 'Lyttleton freezing-chamber' involved assessing damage to alpine plants including *Podocarpus nivalis*, *Nothofagus solandri* and *Nothofagus solandri* var *cliffortioides*. This was an innovative use of the relatively new technology of commercial refrigeration, given the first refrigerated cargo of meat to the United Kingdom did not occur until 1882 and refrigeration can hardly have been widely available at the time of Cockayne's experiment.

An exception was Norton *et al* (1986) principle components analysis of modern pollen rain, however the results were somewhat disappointing from a paleoclimate-reconstruction perspective, in that the correlations between pollen frequency and temperature were weak, with pollen frequency accounting for only 26% of the variance in mean summer temperature, and 37% of annual temperature. Norton *et al* (1996) concluded that despite the significant relationships between pollen rain and major climatic variables, "The regression equations are not robust enough to be used with any confidence in determining climatic history from fossil pollen." Herein lies a major reason for adopting an integrative approach in isopollen mapping: the use of fossil data in addition to fossil pollen is more likely to produce robust isopollen maps.

The taxa that would yield most insight into former climatic conditions and vegetation change are not necessarily the taxa most suitable for plotting on isopollen maps. For example, there is generally little enumeration of exotics such as *Pinus radiata*, and *Pteridium esculentum* is often excluded from pollen sums which results in the loss of some detail on anthropogenic impact.

Often, palynmorphs are only identified to the genus level because it is technically difficult to achieve finer discrimination. For some genera, such as *Agathis*, *Ascarina*, *Knightia*, *Syzygium*, *Ixerba* (Salmon 1996) this is not a problem since they are the sole representative of the genus in New Zealand, however this was the exception rather than the rule. Appendix 5.2 gives a brief description of species identified in Table 4 from a palynological perspective including both taxa that were plotted and those that could not be plotted which would have otherwise been suitable paleovegetation and paleoclimate indicators.

Altitude				
Lat. North of	Lowland	Lower Montane	Upper Montane	Subalpine
39°S	*Avicennia resinifera* >-3 *Metrosideros excelsa* –3 *Beilschmiedia tarairi* –4 *Planchonella novo-zelandea* -8	***Agathis australis* -7**		
41°20S	***Libocedrus plumosa* -7**	*Knightia excelsa* –8 ***Phyllocladus trichomanoides* -10**		
43°30S	*Elaeocarpus dentatus* -5	*Quintinia acutifolia* -8		
46°30S (Foveaux Strait)	***Ascarina lucida* –3** *Hedycarya arborea* -3	***Podocarpus totara* –7** *Pittosporum eugenioides* –7 ***Nothofagus menziesii***	***Nothofagus fusca* -10**	*Nothofagus solandri* –10 *Lagarostrobos colensoi* –13 ***Phyllocladus alpinus* -20**
47°20 (Stewart Is)	***Dacrycarpus dacrydioides* -7**	***Coprosma lucida* –8** ***Prumnopitys ferruginea* –7** ***Prumnopitys taxifolia*** ***Dacrydium cupressinum* -8**	*Plagianthus betulinus* –5 *Weinmannia racemosa* –8 *Podocarpus hallii* -13	*Leptospermum scoparium* –7 *Halocarpus bidwilli* -25
51°S (Auckland Is)			*Metrosideros umbellata* -8	*Dracophyllum longifolium* -10

Table 4. Modern Distribution of New Zealand Flora as a Function of Altitude, Latitude and Temperature.

The taxa[58] for which isopollen and/or isochrone maps were constructed are shown in bold. Freezing temperatures (bud) are also given.

Source: Sakai & Wardle (1978); Allan (1982).

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[58] Including four at the genus level (*Coprosma, Libocedrus, Phyllocladus* and *Poaceae*). All of the taxa highlighted correlate 'very well' with position along natural temperature gradients (Sakai & Wardle 1978) except for *P.ferruginea*, *P.totara* and *D.dacrydioides*, which correlate 'fairly well' along natural temperature gradients.

2.5 Pollen Identification

Frequent identification of pollen to only the family level and the use of different plant nomenclature was also problematic[59]. Moar (1971) and Lintott & Burrows (1973) for example, give pollen percentages for *Podocarpus* which could be made up of *Podocarpus dacrydioides* (*Dacrycarpus dacrydioides*: Connor & Edgar 1987), *Podocarpus ferrugineus* (*Prumnopitys ferruginea*: Connor & Edgar 1987), *P.spicatus* (*Prumnopitys taxifolia*: Connor & Edgar 1987), *P. nivalis*, *P.totara*, or *P.cunninghamii* (*Podocarpus hallii*: Connor & Edgar 1987). Accordingly, the only way to make the old *Podocarpus* comparable to modern taxonomical names would be to sum pollen counts for *Prumnopitys ferruginea*, *Dacrycarpus dacrydioides*, *Podocarpus nivalis*, *P.totara*, *P.cunninghamii*, and *P.lawrencei*. This would obscure vegetation history detail and render the isopolls less useful.

Dallas Mildenhall[60] offers some insight into reasons for differing resolution of pollen diagrams: "Geological palynologists often only looked at the sequences they studied as a means of determining stratigraphy and environment of [the] deposition and probably not all taxa were identified. The botanical palynologist often does detailed searches to try and identify everything on the slides, in an attempt to understand the climate inferences in more detail. These days the detail is based solely on available money which means for [I]GNS palynologists we can't even produce pollen diagrams now."

In many cases pollen grains cannot be accurately identified to the species level, and the palynologist must be content in identifying to the genus level (or often subgenus level in the case of *Fuscospora*[61]). A discussion of the pollen characteristics of the New Zealand taxa is given in Appendix 5.2.

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[59] I have used nomenclature of Edgar 1971, Edgar & Connor 1978, Edgar & Connor 1983, and Connor & Edgar 1987 for vascular plants throughout this thesis, and Brownsey, Given & Lovis (1985) for pteridophytes, and Edgar & Connor (2000) for Graminae.

[60] Personal communication 1998

[61] *Fuscospora* is a subgeneric category proposed by Hill & Read (1991) that encompasses all New Zealand *Nothofagus* species except *N.menziesii*

2.6 Recording Relative Pollen Data

Pollen taxa were read off the published tables[62]. This involved some degree of subjectivity since the resolution of most pollen diagrams is insufficient to obtain a degree of accuracy greater than one or two percent. Some authors, for example Burrows *et al* (1993) only recorded taxa whose pollen was greater than 2% of the pollen sum. However, this degree of accuracy is adequate to make reasonable inferences of past climatic conditions, and a reading error of one or two percent is probably within the sample error associated with pollen counting, use of *Lycopodium* tablets and so on in most cases.

This degree of accuracy is also adequate to construct isopoll maps which, after all, are meant to be indicative only, and is comparable to that achieved by Davis & Webb (1975) in their isopollen maps of eastern North America; interestingly, they used a dissecting microscope to read off pollen percentages from published diagrams where the small size made it difficult to read. Davis & Webb (1975) felt the percentages they obtained were accurate to the nearest percent, noting that for taxa with high pollen percentages the accuracy was reduced to perhaps two percent.

Morita (1982) inadvertently provided an example of how *not* to present fossil pollen data, by reporting relative pollen percentages from the Hakkôda Mountains, Japan to four decimal places. Not only is this degree of precision spurious – we gain no further insight into paleovegetation or paleoclimate dynamics by this level of precision than we would if the number was rounded to the nearest integer; it is also misleading, and implies a level of accuracy that is not possible, given the potential errors and inaccuracies inherent in palynology, such as differential pollen production, dispersal or preservation.

2.7 Contouring

A basic assumption in drawing contour lines is that spatial continuity exists, thus two data points close to each other are more likely to have similar values than two data points that are far apart. There is considerable variety in the choice of contour interval used in

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[62] Or, in the case of Sponge Swamp (Li 2001, personal communication) and NW Nelson sites (Bill McLea 2002, personal communication) from tables kindly provided by the authors.

isopollen maps that have been published for different regions of the world; whereas Bernabo & Webb (1977) used intervals of 10%, Prentice (1983) and Delcourt & Delcourt (1994) plotted 5% intervals. At the same time several techniques have been used to construct the pollen isolines; Prentice (1983), Tsukada (1983), Huntley & Birks (1983) and Birks (1989)[63] used 'manual interpolation' to draw contour lines; Webb & McAndrews (1976) interpolated values using a computer then hand-plotted the isolines whereas I used computer software to interpolate and plot contour lines.

Meyers (1994) claims that one should distinguish between interpolating spatial data and contouring spatial data. Contouring can be thought of as an algorithm that starts with data on a regular grid and produces graphical contour plots, whereas both interpolation and smoothing are used when the data is not available on a regular grid, "...although software packages that contour data usually provide an interpolation scheme."

In this thesis, both kriging and inverse squared distance methods were used to extrapolate and interpolate isopoll values for all isopollen maps; both methods use weighted average interpolation algorithms: the closer a pollen site is to a grid node[64] in the contouring program[65], the more weight it carries in calculating the pollen value at that node. The computer package used thus produces a regularly-spaced array of pollen values from irregularly-spaced latitude and longitude data by extrapolating and interpolating pollen values at locations where no data exists.

According to Goldenware Inc (1997) the interpolated value at any grid node (say G_j) can be computed as the weighted average of the data point values using the weighted linear combination equation:

$$G_j = \sum_{i=1}^{N} W_{ij} Z_i i$$

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[63] Huntley & Birks (1983) felt that complex topography and uneven distribution of data precluded the use of automated procedures to plot contour lines. Interestingly, John Birks (personal communication 2001) still holds this view, stating "I am not sure some automated procedure (*sic*) would be appropriate given the uneven distribution of sites," when I queried him on his methods for constructing isochrone maps for the British Isles (Birks 1989).

[64] A grid node is the intersection of *x* and *y* coordinates (ie latitude and longitude).

[65] Surfer ® (Golden Software Inc; 1997). In addition to the pollen isolines, Surfer was also used to plot theoretical vegetational altitudinal limits, sea surface temperatures and shorelines (discussed below).

where G_j is the interpolated gride node value at node j; N is the number of data points at each node; Z_i is the Z (pollen) value at the ith data point, and W_{ij} varies between 0.0 and 1.0 for each data point considered during grid interpolation. The sum of all the weighting factors used to calculate a grid node value is equal to 1.0. An improvement in giving equal weight to all samples when making point estimates is to give more weight to the closest samples and less weight to those furthest away; thus data points given more weight are assigned weighting factors closer to 1.0 while data points given less weight are assigned weighting factors closer to 0.0.

In inverse distance estimation we make the weight inversely proportional to its distance from the point being estimated according to the formula

$$V^{*} = \frac{\sum_{i=1}^{n} \frac{1}{d_i} v_i}{\sum_{i=1}^{n} \frac{1}{d_i}}$$

where $d_1,...d_n$ are the distances from each of the n sample locations to the point being estimated and $v_1,...,v_n$ are the sample values[66]. Though estimates can often be improved by incorporating more nearby samples[67], for inverse distance estimation, they can also be adversely affected if the nearby samples are strongly clustered[68].

Under certain situations inverse distance estimation produces better results than other techniques such as kriging (discussed below). Weber & Englund (1992) compared 15 different spatial estimation techniques to determine their accuracy in estimating soil contamination in waste sites by comparing the estimated results to the true values in an exhaustive dataset and using two methods to estimate quality; first, by estimating mean square error (MSE) and second, a linear loss score (LLS) function[69].

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[66] Matsuo Tsukada (personal communication 2001) used inverse distance procedures to hand contour isochrone maps for *Cryptomeria japonica* in Japan (Tsukada 1983).

[67] In kriging, all the data are used; Laslett *et al* (1987) refer to this as global estimation, *cf* local estimation which uses only neighbouring data.

[68] Clustering occurred, for example, when plotting *Agathis australis* given the numerous pollen diagrams prepared for Northland.

[69] The LLS function is not discussed further since it is a somewhat unusual test in geostatistics (it is more commonly used in econometrics eg Srivastava *et al* 1992; Christoffersen *et al* 1996, 1997), furthermore MSE is the estimation variance that kriging tries to minimise and therefore the more appropriate quality test.

Weber & Englund (1992) divided their exhaustive dataset of 19,800 records into 198 blocks of 100 records each, then drew 54 sample datasets[70] from the exhaustive dataset. The MSE equation used therefore was:

$$MSE = \frac{1}{54}\sum_{j=1}^{54}\left[\frac{1}{198}\sum_{i=1}^{198}\left(Z_{ij}^{estimate} - Z_{i}^{true}\right)^{2}\right]$$

where Z^{estimate} and Z^{true} are the estimates and true values for the blocks, and i and j represent the blocks and dataset respectively. Weber & Englund (1992) found that both inverse distance squared and inverse distance estimators had a lower mean square error than either ordinary or simple kriging, however they argued that this was due in part to serendipitous characteristics of the datasets and that at other times, kriging would give a better result[71].

Ideally, we would like an estimation method that uses all of the nearby samples but also accounts for the possibility of clustering in the sample data configuration. Kriging is one technique that achieves this. Kriging has been used in a number of physical sciences to make point estimates for geographical areas where data is sparse; for example, to estimate sulfate pollution in air across Europe (Høst 1999); conducting a forest inventory in Zürich (Mandallaz 2000), glacier mass balance equations (Hock & Jensen 1999), soil pH in France (Voltz *et al* 1997) and interpolating rainfall in southern Portugal (Goovaerts 2000).

Kriging has its origins in mining, particularly for assessing the economic viability of gold mines (Cressie 1990). Because the challenge for local estimation is to find the best estimate of the mean value of a regional variable over a limited domain, whose dimensions are small compared to the dimensions of larger, often homogeneous area (Journal & Huijbregts 1978) kriging is invaluable since not only does it provide the best linear unbiased estimator (BLUE) of the unknown characteristic (ie pollen percentage) it is also an exact interpolator, a property not always possessed by other estimation procedures.

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[70] Because it was a 3×3×2 factorial design composed of three sample sizes (104, 198 and 308 data), three sample patterns (simple random, cellular stratified and regular grid) and two levels of sample error (0% and 32%). These 18 different sample designs were repeated three times which gives a total of 54 datasets.

[71] For example where the data exhibits strong anisotropy and clustering of samples, favouring kriging (Laslett *et al* 1987; Weber & Englund 1994).

According to Isaaks & Srivastava (1989) ordinary kriging is 'linear' because its estimates are weighted linear combinations of the available data; it is 'unbiased' because it aims at have m_R, the mean residual error, equal to 0; and it is 'best' because it attempts to minimise σ^2_R, the variance of the errors. It is this last feature that differentiates ordinary kriging from most other estimation techniques.

In practice, the goals of ordinary kriging are unobtainable since m_R and σ^2_R are unknown, therefore we cannot guarantee that m_R is 0 and σ^2_R is minimised. The best we can do is to "build a model of the data and work with the average error and the error variance for the model. In [ordinary kriging] we use a probability model in which the bias and error variance can both be calculated, then choose weights for the nearby samples that ensure that the average error for the model $\tilde{m}_R$ is exactly 0 and that the modelled variance $\tilde{\sigma}^2_R$ is minimised." The contouring software SURFER applies a covariance function to the data then uses matrix multiplication to estimate the missing values according to the weighted linear combination equation above.

Exact interpolation means that the predicted value will match the data value for sites where data is available, rather than interpolate a value from the nearest grid node (Hock & Jensen 1999)[72]. This is a most desirable characteristic since given New Zealand's rugged topography, we can expect to see rapid changes within short distances with respect to floristic change with altitude. Furthermore, exact interpolation compensates in part for the fact that interpolated values are usually less variable than the original data values, and make the contoured surface appear smoother. Isaaks & Srivastava (1989) argue that although this is a benefit from an aesthetic perspective, "...a smoother surface understates the variability and may be misleading from a quantitative point of view," thus contour maps such as isopollen maps are "...helpful *qualitative* displays with questionable *quantitative* significance," (my emphasis).

Weber & Englund (1994) performed a similar experiment to their 1992 study using elevation data and elevation variance data and found that inverse distance estimators were much more sensitive to the type of data than kriging: for elevation data, the quality of the estimate increased as the number of neighbouring datapoints decreased and the power of the distance to the neighbouring sites increased. However, the reverse held for the elevation variance estimation, thus the robustness of inverse distance estimation is hard to assess.

Weber & Englund (1994) concluded "With experience, good judgement, and knowledge of the type of phenomenon being estimated, it is possible to obtain good estimates with inverse distance methods. With the same experience, judgement and knowledge, however, it is also possible to select a good ordinary kriging approach with lower sensitivity to errors in judgement." Weber & Englund (1994) hinted that in the absence of any *a priori* knowledge, it is possible that characteristics of the datasets themselves may assist in the choice of estimator: for time intervals where there are few observations, inverse distance estimation may be the best estimator. This was supported by creating isopollen maps using both inverse distance and kriging and comparing the resultant maps.

According to Polfeldt (1999) the intervals between successive contour intervals should differ from each other by several multiples of the prediction error[73]. This implies that we should aim to minimise the error in the relative pollen percentages otherwise the contour interval will be very large and the isopollen map will lose some of its usefulness because it will lack detail. Although I was not able to influence the error in the relative pollen percentages, I was able to select a contour interval that is intuitively robust: assuming that the prediction error is one or two percent, then a contour interval of five percent should suffice.

Kriging-derived isolines in this thesis were generally more acceptable than contours derived by inverse distance functions. For example, multiquadric and thin-plate spline inverse distances extrapolated values for *D.dacrydioides* distal to the grid nodes that did not look believable. On the other hand, kriging did not produce acceptable isolines for the LGM isopollen map for *Nothofagus fusca*, and inverse distance functions were used. This lends weight to Gotway *et al's* (1996) assertion "It is important to keep in mind that *all* maps constructed from interpolation are subject to some degree of uncertainty."

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[72] Laslett *et al* (1987) refer to this as 'honouring' the data.

[73] Which suggests that the precision of Ralska-Jasiewiczowa's (1983) interval of 0.2-2.0 is of doubtful validity..

2.8 Reconstructing Paleo Treelines and Timberlines

Soons (1979) suggested that the modern day snowline for the central South Island is around 2,000m whereas for the Pleistocene it was around 1,750m; Willett (1950) estimated a Pleistocene snowline of "...4,420 ft [1,347 m] above sea level which would mean that ...the three peaks of Ruapehu [2,797m], Ngaurohoe [2,291m] and Tongariro [1,968m] would have been above this snowline." The corollary of these observations is that the treeline, too, is almost certain to have changed since the Last Glacial, and that these changes need to be taken into account when plotting fossil pollen isolines.

In response to Zotov's (1938) proposition that climatic tree limit corresponded to a mean isotherm of 10°C for the warmest month, Wardle (1974) stated that "Even if the correspondence is less than complete, it suggests that a major autoecological principle is involved...in which some environmental complex abruptly exceeds the tolerance of all trees regardless of the variation among them." The abrupt floristic change with altitude appears to be primarily due to two factors. First, survival of woody taxa at high altitude is partially determined by morphological[74] and physiological[75] factors involved in ripening of shoots so that they can withstand the cold in winter, and more importantly, survive winter desiccation. Both cold and dehydration cause stress on plants, however freezing merely removes water from the protoplasts without removing it from the tissues, whereas desiccation causes more damage since water that is evapotranspired through the leaves cannot be replaced since conducting channels in the roots and stems are frozen and the tree dehydrates and dies.

The second 'autoecological principle' contributing to timberlines was elucidated by Wardle (1974) who examined the relationship between foliage temperature and the distance of foliage above the ground at the timberline. Wardle found that canopy shoots in *Nothofagus solandri* 2m above the ground were 0.5-2.0°C warmer than the ambient air

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[74] Morphological factors include completion of growth, completely lignified cells, thickening of cuticles and "...the loss of the 'soft' appearance imparted by high water content," (Wardle 1974).

[75] Physiological factors include gaining the ability to withstand low temperatures and dehydration due to increased osmotic pressure of cell sap, a decrease in free water in the cellular protoplasm, and development of protoplasts tolerant of desiccation, which will assist the plant tissues to survive when ice crystals form between the cells.

temperature, whereas the shoots of the prostrate shrub *Podocarpus nivalis* within 3cm of the ground tended to exceed air temperature by 5-11°C[76].

By creating these microclimates, low woody plants are able to survive hundreds of metres above the timberline, and tree seedlings will also become established above the timberline forming krummholz[77] to the extent that they can cope with temperature extremes.[78] *Nothofagus solandri* does not have a krummholz form[79] and at the timberline only forms in shaded areas where foliage temperatures are close to air temperatures since if the microclimate enables seedlings to develop initially, it will also allow them to reach maturity.

Wardle & Coleman (1992) tested the hypothesis that since mean air temperatures in New Zealand have risen about 0.5°C since the 1860s then the altitudinal limit of trees should have risen about 100m. However, they found that 90% of young *Nothofagus menziesii* lay within 9m of mature stands, and 90% of young *N. solandri* var *cliffortioides* lay within 7m of mature mountain beech. These researchers pointed at limited seed dispersal and lack of suitable microclimates as possible reasons why the potential altitude not reached, or alternatively, that the treeline was set during warmer intervals and persisted during the most recent cool intervals due to the favourable microclimate created by the mature stands.

A more simple explanation, not discussed by Wardle & Coleman (1992), is that there is a considerable lag between temperature amelioration and colonisation. In any event, the study does illustrate that, for whatever reason, fluctuations in treeline are neither an instantaneous nor direct response to temperature change, and that other factors are likely to be implicated.

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[76] Wilson *et al* (1987) noted a similar phenomena in the Cairngora Mountains, Scotland where meristems in krummholz were up to 15°C warmer than the atmosphere and 7°C warmer in tall vegetation.

[77] Described by Shaw (1909) as 'prostrate dwarf' plants ie plants of low stature and bent form. These forms are due in part to thigmomorphogenetic responses to wind stress ie growth response to mechanical stress that increases the ability of the plant to withstand that stress (Lawton 1982).

[78] Wardle (1964, 1974) distinguishes between tree line – the extreme upper limit of trees, krummholz and shrubs greater than 2m tall or the "...whole ecotone from the upper limit of closed forest to that of scattered stunted specimens of tree species," (Wardle (1981); and timber line which is the upper limit of tall, erect 'timber size' trees.

[79] There are two exceptions – when prevailing winds train the shoots, leading to 'flagged' krummholz, and at forest margins, when snow accumulates to >1m.

Although treelines or timberlines are difficult to assess palynologically because of upward drift of pollen from trees to higher altitudes (Moar 1971; Mildenhall 1994c), long distance dispersal (Myers 1973) and so on, deriving a treeline is most desirable since, for example, it would then be possible to use anisotropy options in the contouring package which give more weighting to points along one axis (latitude, for example) than another (longitude)[80]. By explicitly taking altitude into account (by both plotting zero values for all the taxa of interest above the tree line, and recorded pollen frequencies at varying altitudes), the contours should 'flow around' mountains, rather than having isolines curve across, say, the Southern Alps, thus giving a more accurate representation of paleovegetation.

Therefore, to derive a series of post-LGM treelines it is necessary to utilise paleoclimate data other than fossil pollen and apply environmental lapse rates to sea level temperatures (eg Axelrod & Bailey 1976). It is necessary to make several *a priori* assumptions, such as Holocene temperature-determined altitudinal vegetational limits are analogous to contemporary timberlines and treelines, the Holocene lapse rate was comparable to modern-day environmental lapse rates of 5-6.0°C/km, and complicating factors such as the Massenerhebung effect (mountain mass elevation effect)[81] and continentality[82] are absent. There are two preliminary steps; first, reconstructing the paleoshoreline, and second, derive paleotemperatures.

2.8.1 Reconstructing Paleo Shorelines

In order to plot a temporal sequence of post-LGM isopollen maps, changes to the shoreline due to isostatic and eustatic factors need to be taken into account. This is important because lower sea levels during the glacial and early Holocene periods created potential migration routes by way of land bridges between the major islands of New Zealand (Te Punga 1953, Mildenhall 1975) and coastal areas that due to their low altitude and maritime

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[80] Although there is a general north-south temperature gradient and a dominant east-west precipitation gradient in New Zealand, for example the tree limit is 1,220-1,280m in the Tararua Ranges and 915-975m in western Fiordland (Wardle 1964) the diverse topography interacts with these to give a complex spatial climate pattern (Norton *et al* 1986) hence in practice it was impractical to apply anisotropy options.

[81] The "occurrence of physiognomically and sometimes floristically similar vegetation types at higher altitudes on large mountain masses than on small isolated peaks, especially those in or near the sea," (Flenley 1993).

[82] Mountains on continental land masses have a decreased temperature lapse rate, and much larger temperature maxima and lower minima, therefore higher climatic and more biotic zones than mountains on islands (Meyer 1992). Thus timberlines of temperate zones in large land masses such as North America and Asia may be as high as they are in the tropics, despite the marked difference in air temperatures at sea level.

climates may have provided glacial refugia or coastal migration routes for floral elements (Mildenhall 1994; McGlone & Wilson 1996)[83].

Unfortunately, the few published maps available showing New Zealand's Holocene shorelines are either limited to small areas (Lewis & Mildenhall 1985; Brown & Wilson 1988; Pickrill & Fenner 1992; Moar & Suggate 1996),[84] are too simplistic to use in isopollen map construction (eg McGlone 1995a), or are not accompanied by methodologies and assumptions used to create them (McGlone & Wilson 1996)[85]. At other times, changes in late Quaternary shorelines are ignored in vegetation maps altogether (Mildenhall 1994); therefore it is necessary to derive the Holocene coastline prior to plotting the pollen isolines. Furthermore, researchers often talk of LGM treeline depression and infer a given temperature decrease without taking lowered sea levels into account, thus exaggerating the temperature decrease[86].

Eustatic rise in sea-level has been intensively studied[87] in an attempt to find a 'Holy Grail' global sea level curve (Devoy 1987). The International Geosphere-Biosphere Programme (IGCP) Project 61 (1974-1982) for example, aimed to establish a graph of the trend of mean sea level for the last 15,000 years. However, publication of IGCP Project 61 sea-level curves that differed from region to region, growing acceptance of the concept of geoidal eustasy (Mörner 1976) and other local and regional influences on sea-level, lead to the abandonment of the search for a global sea level curve and a focus on regional sea level

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[83] Mildenhall (1994a) suggested that *Avicennia marina* var *resinifera* (mangrove) may have been able to migrate around East Cape into Sponge Bay due to lower sea levels and wider tidal flats since the end of the last glaciation. McGlone & Wilson (1996) note the availability of a continuous dryland migration route across Foveux Strait during the glacial maximum followed by a series of island stepping stones between Stewart Island and the South Island as sea levels rose in the first half of the Holocene.

[84] Wellington Harbour, Banks Peninsula, Preservation Inlet and the Westport-Hokitika regions respectively

[85] Most paleovegetation researchers in other countries appear to ignore paleogeographical features such as former shorelines; exceptions include maps indicating the position of shorelines and the Laurentide continental ice sheet in isopollen (Webb 1992) and isophyte maps of eastern North America (Delcourt & Delcourt 1994).

[86] For example, at first glance an LGM treeline depression of 200m relative to contemporary treelines would imply a cooling at sealevel of 1.3°C using present lapse rates. However, if the paleosealevel was 100m lower than present, the altitude of the paleotreeline would be only 100m lower relative to present sealevel, and therefore the derived paleotemperature decrease would be exaggerated. Wardle (1988) and Bacon *et al* (2001) considered this in deriving paleoequilibrium lines.

[87] For example, the international collaborative efforts of IGCP (a branch of UNESCO) Project 200 (Late Quaternary sea-level changes: Measurement, Correlation and Future Applications) (1983-1987); CLIMAP (Climate: Long-range Investigation, Mapping and Prediction); PASH (Paleoclimate in the Southern Hemisphere), COHMAP (Co-operative Holocene Mapping Project) 1988; International Union for Quaternary Research's (INQUA) Commission for Quaternary Shorelines, and Project Cuaternario del Hemispherio Sur-Un Enfoque Geológico (Iriondo 1999).

curves (Carter 1988; Shennan 1987). Factors making estimates of the eustatic sea-level component difficult include :

(i) Geoidal humps and troughs: The geoid, or surface of a non-perturbed sea, is an equipotential surface of the combined gravitational and centrifugal force fields of the Earth expressed in gravity terms as

$$Y = c_1 + c_2 \sin^2 \phi + c_3 \cos^2 \phi + c_4 \sin^2 2\phi + c_5 \sin (\lambda - c_6) \sin \phi$$

where ϕ and λ are the latitude and longitude variables, c_1 is the mean gravity at the equator, c_2 the centrifugal acceleration at the equator, c_3 is the north-south asymmetry, c_4 is the mid-latitude correction, c_5 is the gravity difference between major and minor axes of ellipticity and c_6 is the longitude of a minor axis of ellipticity (Devoy 1987). Mörner (1980) claims that on a global scale, geoidal perturbations amount to several tens of metres, with a 180m sea level difference between the geoid hump at New Guinea and the geoidal depression at Maldave Island. In the south Pacific the geoid perturbations are up to about 120 ±3m amplitude (Gibb 1986).

(ii) Undulations in the sea-surface topography of the order of 1 to 2m: Tai & Wunsch (1983) used satellite telemetry to calculate and map the long-wavelength contribution to the zeta component of the sea surface according to the formula

$$S(\theta, \lambda, t) = N(\theta, \lambda) + \zeta(\theta, \lambda, \mathrm{t}) + r(\theta, \lambda, t)$$

where S = sea surface, N = the geoid, ζ = departure of the ocean from the geoid due to large scale movement of water; r = 'noise' (observational error and geophysical phenomena such as atmospheric load; θ, λ, t are latitude, longitude and time, respectively. Tai & Wunsch (1983) found that in the Pacific Ocean, the undulations were of the order of 1-2m, and around New Zealand approximately 60cm, ie 0cm relative to the geoid around Cape Reinga, and -60cm relative to the geoid at Stewart Island. Heath (1982) found that mean current off the west coast of New Zealand was caused by, *inter alia*, a depression in the sea surface centred at 42°30'S of the order of 0.3m using steric levelling. Although Heath (1982) cautions that offshore sea level slope cannot simply be applied inshore due to boundary effects[88] in coastal areas, "...the actual slope is at the limit of experimental error

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[88] According to Heath (1982) these boundary effects include mean flow changing from essentially on-shore in deep water to along-shore in shallow water; variation in sea surface level required to balance the change in

in the available observations," so with respect to impact on deriving sea level curves, it can be ignored.

(iii) Glacio-isostatic and hydro-isostatic effects: Common glacio-isostatic effects resulting from melting of ice sheets may be complicated if the ice load was greater in the inner part of the ice sheet, resulting in shoreline tilting (Fjeldskaar & Kanestrøm 1980); at the same time, the glacier attracts water, which acts to deform the geoid. Clark & Lingle (1979) demonstrated the difficulty in producing a Holocene sea level curve due to the assumptions that must be made regarding glacio-isostatic and hydro-isostatic effects, in particular with respect to the timing and rate of the Antarctic Ice Sheet recession. Different outcomes are predicted depending on whether ice sheet melting was assumed to be linear, logarithmic or a combination of the two; this is further compounded by conjecture that there was a re-expansion of the Antarctic Ice Sheet between 14,000 and 12,500 years BP.

(iv) Differential rates of tectonic tilting, uplift and downdrop: Data from South Island (Wellman, 1979) and North Island (Pillans, 1986) uplift maps show that the rate and sense of uplift differed between regions. According to Pillans (1986) at Mahia Peninsula a 1.5mm per year uplift rate over the last 100,000 years increased to 2.7mm per year over the last 7,000 years. In general terms, for the North Island west coast, estimated uplift rates ranged between 0.2-0.5mm per year; the Wanganui Basin –1mm per year (that is, subsidence) the east coast between 0 and 4mm per year with the Hauraki graben subsiding 1mm per year (Figure 9).

For the South Island, Wellman (1979) argues that the absence of stranded marine benches on the northern coast implies zero or negative uplift (that is, subsidence); the Kaikoura coast between 0.1 and 7mm per year uplift; for Banks Peninsula subsidence of 0.2mm per year; for the remainder of the east coast 0.1mm per year uplift; for the southern coast and Fiordland 0.1mm uplift per annum; South Westland >2.0mm per year, and for northern Westland–Buller and north-west Nelson between 0 and 0.5mm per year[89] (Figure 10).

Coriolis acceleration with latitude; and the partial balance of the sea surface elevation by an onshore momentum flux (ie wave height H increases inshore so that energy flux P, remains constant: $P = ECn$ where E = wave energy, C = wave celerity ($\sqrt{}$acceleration due to gravity, $g \times$ water depth, h) and $n = 0.5$ in deep water and 1.0 in shallow water. According to Viles & Spencer (1995) since Cn decreases inshore, E and H must increase).

[89] Although William's (1982) ^{230}Th / ^{234}U dating of speleothems (stalagmites, stalactites and flowstones) gave uplift rates of 0.27mm yr^{-1} for Metro Cave (Westport) and 0.14mm yr^{-1} for caves at Paturau (northwest Nelson).

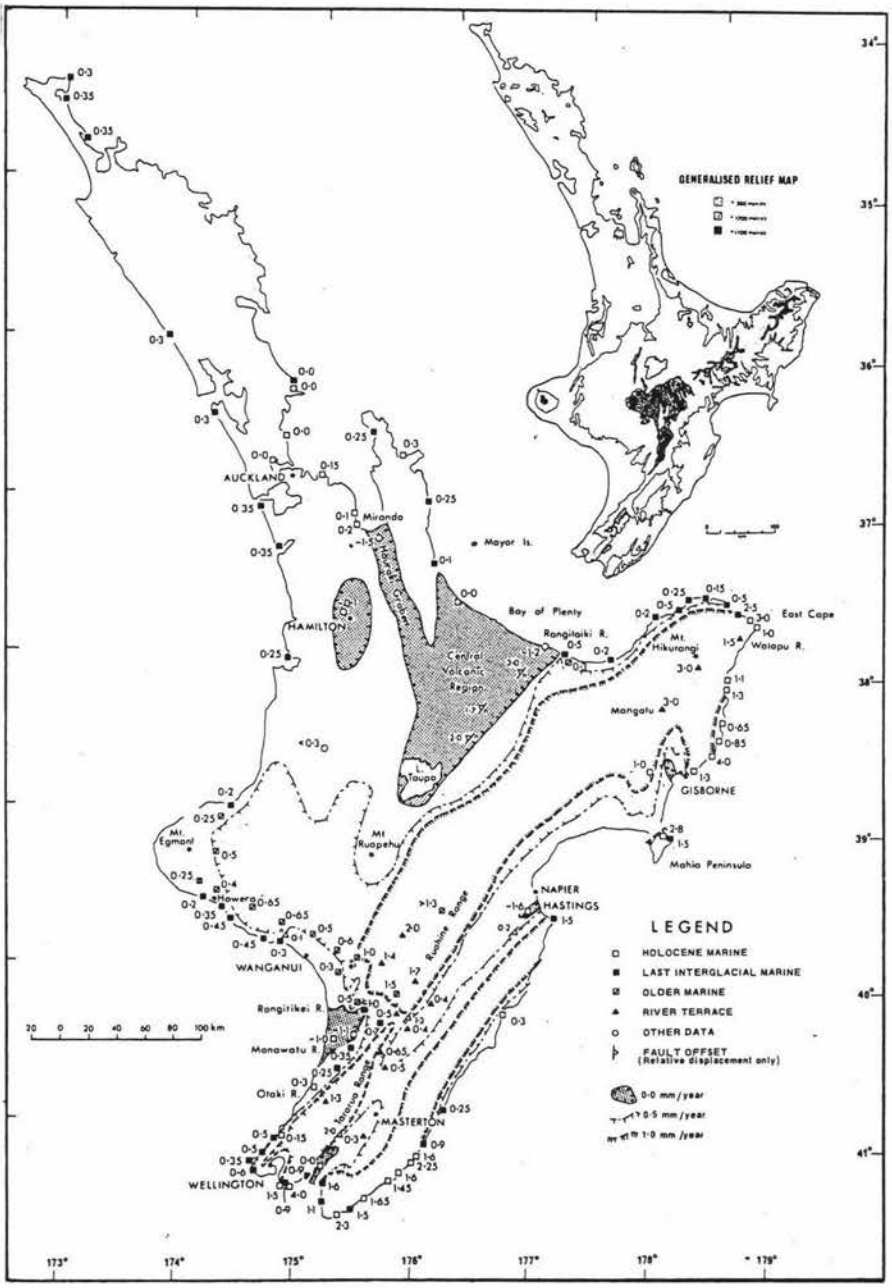

Figure 9. Late Quaternary Uplift Map, North Island.
Uplift values are in mm yr^{-1}. Areas of subsidence are stippled.

Source: Pillans (1986)

Figure 10 Late Quaternary Uplift Map, South Island.
Uplift values are in mm yr^{-1}.

Source: Wellman (1979)

(v) Thermal warming of the oceans: Wigley & Raper (1987) estimate that mean global warming of 0.6° to 1.0°C from 1985 to 2025 will induce a sea level rise of 4-8cm due to thermal expansion of the oceans[90]. By inference, thermal expansion of sea water during post glacial times would have also contributed to sea level rise. Estimated sea surface temperatures since the last glaciation using $\delta^{18}O$ changes in planktonic foraminifera (Nelson *et al* 1994; Nees *et al* 1994) imply that the offshore sea surface temperature in the Tasman Sea was <2°C cooler than present, however Wright *et al* (1995) found that cores taken inshore at Bay of Plenty had $\delta^{18}O$ values indicative of sea surface temperatures at least 2-3°C, and as much as 5°C cooler than present. Wright *et al* (1995) suggest this may be due to upwelling of cooler waters, so that the discrepant temperatures are not mutually exclusive, nevertheless, these different temperature regimes will hinder derivation of a Holocene sea level curve.

(vi) El Niño- Southern Oscillation: Sea levels across the Pacific vary in response to seasonal variations such as El Niño-Southern Oscillation (ENSO). Parnell (1994) suggests that sea level may rise 50cm in response to ENSO factors over the course of a year, although he does not specify the mechanism (eg seiching or thermal warming). The impact of ENSO on New Zealand, at least in the climatic signature, is likely to have varied throughout the Holocene (McGlone *et al* 1992) with a major influence being exerted only after 7,000 BP and a strong influence after 5,000 BP. The corollary of this is that the impact of ENSO on sea level is likely to have varied during the Holocene.

(vii) Milankovitch or Orbital Forcing: Insolation changes resulting from changing orbital parameters are thought to be a major forcing function for global climate change due to influences on the insolation budget received at the Earth's surface (Berger 1978; Jouzel *et al* 1987; Martinson *et al* 1987; Dodson & Ono 1997). There are three major orbital parameters involved; the eccentricity of the earth's orbit, e[91] with a periodicity of 96,000 years; axial tilt (obliquity), ε[92], with a periodicity of 42,000 years; and the precession of the

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[90] Peltier & Tushingham (1989) estimate that 25% of the 10-20 cm rise in sea level globally over the last century was due to thermal expansion of sea water.

[91] Whereby the Earth's orbit changes from an elliptical orbit to a circular orbit. Eccentricity is given by $e^2 = (a^2-b^2)/a^2$ where a and b are the semi-major and semi-minor axes of the elliptical orbit. Presently e is 0.016 and has ranged from 0 to 0.07 over the Quaternary with highly variable periodicity. In computation e is solved by solving the Lagrange equations of the motions of the planets around the Sun (Berger 1977).

[92] The Earth's axis of rotation is inclined at a 23.5° angle to the orbital plane at present, but this varies between 24.5° and 21.5°. When the angle of obliquity is greatest, the widest range of seasonal temperatures occur at a given latitude.

equinoxes, ω,[93] with a periodicity of 21,000 years (Hays *et al* 1976). In addition to impact on insolation, these orbital fluctuations may influence the shape of the geoid (Mörner 1980) and therefore regional sea levels. Furthermore, which orbital parameter is predominant varies with latitude (Berger & Loutre 1994). Precession in particular may have lead to increased southern Hemisphere seasonality in the mid-Holocene, causing enhanced Walker Circulation in the Pacific, in turn leading to stronger westerly winds (Shulmeister 1999).

The stronger westerly winds may have caused water on the west coast of both islands to 'pile up' in a seiche[94] leading to fluctuations in the sea level throughout the Holocene. Abraham (1997), for example, reported seiching in Wellington Harbour when wind speeds were >10ms^{-1} (although the maximum amplitude was only 8cm s-^{1}) and Stanton (1997) noted the influence of wind stress on sea level at the Chatham Islands.

(viii) Paleotidal factors: The amplitude of paleotides may have differed throughout the Holocene from contemporary tides, making sea level estimation more difficult. Tooley (1985), for example, found the tidal range in the Bristol Channel decreased from 4.3m to 1.5m with a 20m drop in sea level.

Paleotidal impacts may be especially marked in New Zealand for two reasons; first, New Zealand has a unique tidal regime whereby the semi diurnal (M_2) tide propagates around the archipelago through one complete cycle in a clockwise direction so that there is a phase change of 140° between the M_2 tides at either end of Cook Strait. Furthermore, lowered sealevels during the Pleistocene glaciation meant that Cook Strait was bridged between 18,000 and 15,000 BP (Proctor & Carter 1989) and took another 4,000 years to reach its current basin configuration. This alteration in seabed morphology resulting from sea level change may complicate sea level reconstruction due to estuary effects or flood-basin effects.[95]

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[93] The gravitational pull of the Sun and the Moon cause the time of the perihelion (ie when the Earth is closest to the Sun) to change through time.

[94] Resonant standing waves caused by wind stress on the water surface causing it to slope and pile up downwind (Carter 1988); tsunami, internal waves, pressure disturbances (Abraham 1997) and surface waves (Goring & Henry 1998) have all been reported to generate seiching.

[95] Where the tidal amplitude rises to landward in a funnel-shaped embayment due to the confinement of the tidal wave as it progresses up the estuary; for example, in the Gulf of Maine-Fundy Bay tidal system, Nova Scotia (Scott & Greenberg 1983); and the reverse, where the tidal wave passes into a flanking basin with large capacity having been confined, reducing the tidal range, respectively (Devoy 1979).

(ix) Sedimentation and erosion. Kamp & Tippett (1993) describe net surface uplift (displacement of the Earth's surface with respect to the geoid) by the function

$$U_s = U_r - \Delta E$$

where *Us* = surface uplift, *Ur* = rock uplift (displacement of rocks with respect to the geoid) and Δ *E* is denudation or exhumation (displacement of rocks with respect to the surface[96]. Thus in areas of subsidence such as coastal Canterbury, the Marlborough Sounds and the Bay of Plenty, elevation remains above sea level because of high rates of sedimentation (Newnham *et al* 1999) and a proportion of tectonic uplift is lost to erosion during mean surface uplift so that a stable equilibrium between uplift and elevation occurs to the west of the Main Divide (Tippett & Kamp 1995a).

Although sedimentation on the seabed will cause a rise in sea level, *ceteris paribus*, a major simplifying assumption is that isostatic depression of the crust beneath the sedimentary wedge and/or elevation of marine sediments above sea level in orogenic areas is likely to cancel out sea level rise due to sedimentation (Donovan & Jones 1979). Overall, the effect of sedimentation on sea level is not likely to be significant over the Holocene; Judson & Ritter (1964) estimated that if the amount of sediment removed from the United States per annum was applied globally, it would cause a sea level rise of about 1.5cm in 1,000 years[97].

(x) Incomplete data and different analytical techniques: Different analytical methodologies utilised by researchers around the world may cause 50% of the variation in estimates of contemporary sea level trends (Barnett 1984; Peltier & Tushingham 1989); therefore it seems reasonable to assume that this would apply to deriving Late Quaternary sea levels as well. An example of this is the fact that different researchers have calculated different uplift rates, so it is not clear which uplift rate to apply; for example Tippett &

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[96] Alternatively, Naish's (1997) equations for bathymetric change ($\delta\omega$) can be used: $\delta\omega = \delta\alpha - \delta\sigma$ where $\delta\alpha$ is net accommodation space ($\delta\alpha = \delta\varepsilon$ (eustatic sealevel) + $\delta\beta$ (basin subsidence) and $\delta\sigma$ is change in sediment. Thus the rate of generation and loss of accommodation produces changes in bathymetry, and the eustatic sealevel is given by $\delta\varepsilon = \delta\omega - \delta\beta + \delta\sigma$.

[97] This is despite New Zealand being a "...major supplier of terrigenous sediment," whereby "approximately 141 Mt/a of river-bourne suspended load reach the eastern seaboard south of 37°S," (Carter *et al* 2000). This is a conservative estimate, since it excludes the contribution from the West Coast that reaches the Pacific via Cook Strait: Mildenhall (1978) cites average rates of sedimentation of 8mm per year over the last 600 years for Caswell Sound and Nancy Sound; Pantin (1964) estimated sedimentation of 0.38-0.46 inches (10-12mm) per year at Milford Sound.

Kamp (1995b) gave an uplift rate for the west of, and proximal to, the Alpine Fault of 8-10mm per year, compared with Wellman's (1979) uplift rate of 0-2mm per year. At the same time, the rate of uplift is greatest proximal to the faultline, where the Australian and Pacific plates converge, so that the rate calculated for the Alpine fault is not necessarily the rate of ascent at the coast.

Lambeck & Nakiloglu (1986) argue sea level curves from different regions (eg Schofield 1960; Schofield 1964) can be aggregated into a single sea level curve for New Zealand, assuming the absence of significant tectonic movement; however the data from Wellman (1979) and Pillans (1986) described above at first glance appears to preclude such a simple strategy to construct a sea level curve for New Zealand. In contrast, Bloom (1980) and Suggate (1992) argued that when calculating the height of paleoshorelines it is necessary to make allowances for exceptionally large postglacial uplift [or subsidence]. Given the uplift rates calculated by Pillans (1986) for the North Island, and in particular Wellman (1979) for the South Island, an allowance should be made in paleoshoreline reconstruction, using Mörner's (1983) relative sea level equation[98]

$$RSL = \Delta SL\ (E^{T} + E^{Gl} + E^{Ge} + DS) - \Delta LL\ (T + I + Ge + C)$$

where SL= sea level changes (transgressions and regressions); E^{T} = tectono-eustasy (changes in basin volume); E^{Gl} = glacial eustasy (changes in ocean volume due to changes in glacier volumes); DS = dynamic sea surface (*cf* 1-2m undulations in (ii) above); T = tectonic movements, I = isostasy, Ge = geoid deformation, and C = compaction. Gibb (1986) derived a tectonically-corrected New Zealand Holocene sea-level curve (Figure 11a), using the Blueskin Bay estuary on the Otago Peninsula and Weiti River estuary, 1090 km to the north on Whangaparoa Peninsula as zero-datum points since the absence of Holocene marine terraces suggested tectonic stability[99], the sites had a range of carbon dated paleo-sea levels, and low rates of sedimentation and sedimentation compaction.

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[98] A simplified version is given by Suggate (1992) $ALT_p = R \times (A - 5000) + H_p + ALT_{pg}$ where ALT_p = present altitude (m) of shoreline; R = uplift rate (m/yr); A = age (yr) of paleosealevel; H_p = height (m) of paleosealevel with respect to present sea level; and ALT_{pg} = present altitude (m) of highest local post-glacial sea level.

[99] Tectonic stability was also inferred if the last interglacial marine benches were within six metres (to account for eustatic sea levels of the last interglacial climax being four to six metres higher than present) of its modern analogue (for example, present-day berm crests).

Gibb assumed that if "...net oceanographic influences such as changes in water density and oceanic circulation have remained fairly uniform over the last 10 ka, then an eustatic sea-level registered at any one tectonically stable coastal site should also be within a few decimetres of that level at all other stable sites around New Zealand." Next, Gibb fitted data from six sites around New Zealand[100] that were also well dated. The resultant sea level curve shows a postglacial marine transgression 10,000 years BP from around 33.5m below present sea level ending at the present sea level 6,500 years BP. The period 10,000 to 6,500 BP was punctuated by two periods of static sea level; the first, at 24m below present sea level between 9,200 and 8,400 years BP, and the second at 9m below present sea level between 7,500 and 7,200 years ago.

In showing a postglacial maximum sea level of around 2m above the present sea level, Gibb's (1986) sea level curve is consistent with inferred Holocene inundation in Fiordland (Pickrill *et al* 1992); sea level changes inferred from Banks Peninsula (Shulmeister *et al* 1999), sea levels higher than present at Kaikoura 5,000-3,500 BP (Kirk 1977) and broadly in agreement with Schofield's (1980) assertion that in Northern New Zealand the sea level maximum was about 2.1m above present sea level, 4000 years BP.

Gibbs' (1986) marine transgression is also matched by other, albeit asynchronous, south Pacific sites: ^{230}Th/^{234}U-dated coral terraces from Huon Peninsula, New Guinea (6°S) show transgression maximum ages of 9,400 years BP (Bloom *et al* 1974); New Hebrides (15°30'S -18°S) at 7,100 years BP (Bloom 1980); dated shell from Tonga (21°S) gave a Holocene sea level maximum at 5,300 years BP (Nunn & Finau 1995) and tubeworm casts at Port Hacking, Australia (34°S) 4,150 years BP (Baker & Haworth 2000). Schofield (1977) ascribed the delay in reaching sea level maxima between New Zealand and the tropical west-central Pacific to a delay in oceanic salinity mixing following ice melting.

Finally, the sea level curve matches changes in sea level height predicted by Clark & Lingle's (1979) and Clark's (1980) eustatic sea level model where *Seus*, eustatic sea level change, is given as :

$$\frac{a^{2}}{A_{o}} \iint_{ocean} s(\theta, \phi) \sin \theta \, d\theta \, d\phi$$

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[100] Kellys Beach (southern Auckland), Kaiaua (Firth of Thames), Miranda (Firth of Thames), Pauatahanui Inlet (Porirua), Kumenga (Palliser Bay) and Christchurch.

where *s* is the observed sea level change (that is, change in distance between the ocean surface and the ocean floor); A_o the ocean area, θ the colatitude[101], ϕ the east longitude, and *a* the Earth's radius. Assumptions used by Clark (1980) were that the eustatic sea level rise was 75.6m since 16,000 years BP and that ocean water volume has been constant for the last 5,000 years. Applying this formula and these assumptions, Clark's model predicts that New Zealand's sea level 5,000 BP was 2m higher than present, with a gradual lowering to the present level over the five millennia since.

Lambeck & Nakiloglu (1986) hypothesise that New Zealand Holocene sea level curves were relatively insensitive to the viscosity of the mantle (and by inference, were sensitive to the melting of glacial icesheets) if much of the meltwater was derived from Northern Hemisphere icesheets, with little addition of meltwater from the Antarctic after about 10,000 years ago. If there was a significant contribution from the Antarctic after 10,000 years BP, then New Zealand's predicted sea level change is one of gradual rise to present levels. Gibbs' (1986) findings suggest (an approximate) sea level hiatus at around 6,000 years BP[102] tentatively ruling out the likelihood of a recent Antarctic contribution[103].

Pirazzoli (1991) sounds a note of caution with regard to Gibb's (1986) sea level curve, since Gibb (1983), using the same dataset, reported two 3m sea-level drops around 9,000 and 7,500 BP and proposed even a third oscillation around 7000 yr BP, however no trace of these fluctuations remained in the 1986 publication, nor did Gibb (1986) explain the reasons for this change in interpretation[104] (Figure 11b). Pirazzoli concluded that this revised interpretation, and given that "...the zero-datum used for the estimation of tectonic rates was arbitrary," he was left with the impression that "...the effective vertical uncertainty ranges may be slightly larger than those inferred for [Gibb's 1986 sea level curve]."

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[101] The complement of the latitude.

[102] Nunn (2000) dated the Little Climatic Optimum (Medieval Warm Period) to around 1200-650 years BP and the Little Ice Age to 650-150 years BP in the Pacific islands of American Samoa, Tuamotus, Caroline Islands Guam and Rota Island. The resultant minor fluctuations in sea level that resulted in New Zealand (0.02m above, and 0.46m below, present sea level respectively) is smaller than the estimated error for each of Gibbs' (1986) data points and consequently is smoothed out in the New Zealand sea level curve.

[103] Although Wilson (1977b) suggested that calving of icebergs from the West Antarctic iceshelf following postglacial warming between 3,000 and 4,000 years BP may have lead to 3 x 10^5 km^3 of water being added to the Southern Ocean, causing it to rise 2m in only a few hundred years.

[104] It would appear that Gibbs (1986) disregarded data from the less tectonically stable sites at Christchurch for around 9,000 BP and Pauatahunui Inlet *c* 7,500 BP, smoothing the sea level curve so that it rose monotonically.

Pirazzoli's second objection - that the zero-datum sites were chosen arbitrarily – is somewhat ill-founded: several researchers have used the North Island sites in particular (eg Schofield 1960; Nunn 1998; Nunn 2000); since they meet Tooley's (1985) and Devoy's (1987) criteria[105] for assessing the suitability of a site for sea-level studies. Nevertheless, these reservations do illustrate the point that derived geomorphological features are *not* always universally accepted, nor should they be, in line with Popper's (1975) assertions discussed above.

Since Gibb's (1986) sea level curve only covers the Holocene, it was necessary to utilise another curve for the Late Glacial and the LGM. Norris & Grant-Taylor (1989) derived a sea level curve based upon shellbeds from the west coast of New Zealand from between Karamea and the Waikato River. These researchers carbon dated shells mainly from *Paphies australis*, an estuarine or intertidal species, to derive a sea level curve showing a paleoshoreline that appears to be perhaps 50m too low for the LGM.

Norris & Grant-Taylor (1989) attribute this to tectonic downwarping at a rate of between 2.3 and 2.8m per thousand years, and the use of sub-tidal species such as *Tawera spissa* and *T.bollonsi* : because these species live at depths greater than *Paphies australis*, the derived depth is exaggerated. By subtracting 2.3m per thousand years from Norris & Grant-Taylor's (1989) eustatic sea level curve, I derived a Last Glacial Maximum depth of 120m below present sea level, a level finding general acceptance amongst other Quaternary researchers in New Zealand (Carter *et al* 1986; Newnham *et al* 1999).

I used Hammer's (2001) PAST (ver 0.72) program to splice together and smooth the two curves using B-splines (Figure 12). This method involves fitting data with a least-squares criterion to a B-spline, which is "...a sequence of third order polynomials, continuous up to the second derivative," (Hammer 2001). For a B-spline, the curve does not necessarily pass through any control point, and because it is continuous at the curve segment end

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[105] In summary, (i) index points should be drawn from small, clearly .definable areas; (ii) a clear understanding of the paleogeography of the study area is required to avoid misinterpretation of isolated index points; (iii) datum points should be of the same type, representing similar paleoenvironments; (iv) radiocarbon dating should be independently verifiable; (v) a repeatable methodology should be used; and (vi) determination of the sea level indicator height should be related to a definable datum, preferably a geodetic datum.

points, it is smoother than either the Hermite or Bezier curves[106]. PAST allows the user to select a decimation factor, which essentially controls how many data points contribute to each polynomial section. For the derived curve I chose a decimation factor of five, that is, there are five bends in the curve.[107]

Norris & Grant-Taylor's (1989) sea level curve is intuitively appealing for several reasons: first, it is derived from local paleoshoreline indicators as opposed to more distal sites; it utilises a reasonably large number of well-dated fossils[108] and the curve is strongly correlated with other curves derived from fossils (eg Herzer 1981) and stratigraphic evidence (Carter *et al* 1986; Proctor & Carter 1989). The final step was to plot the resultant curve against a fine-level bathymetric map[109]. The derived shorelines are shown with the paleo-sea surface temperatures (from Table 6)[110] in Appendix 5.3 as well as the relevant isopollen maps, in Chapter 3. The scale of the paleo-sea level curve presented here belies somewhat the likely sequence of rapid rise and intervening periods of stability[111] however the overall trend appears to be acceptable.

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[106] Furthermore, B-splines can be used in the presence of incomplete boundary information (Salari & Balaji 1991) which gives the technique advantages over some other methods, such as Fourier coefficients where coefficients are affected if part of the boundary information is corrupted or missing. Interestingly, Salari & Balarji (1991) successfully used B-splines to recognise objects in a machine-vision system; this may have applications in automated pollen identification systems.

[107] Synonymous with a 5th-order polynomial function in DEP-AGE, discussed *supra.*

[108] Norris & Grant-Taylor (1989) used aragonite-depositing species such as *Paphies* and *Tawera* spp rather than calcite-depositing species such as *Zygochlamys deliculata* to counter 'younging.' This is discussed further in Appendix 5.4.12.2.

[109] I used the GTOPO30 global digital elevation model (US Geological Survey, 2000). New Zealand bathymetry data is available at 500 metre horizontal grid spacing, with 30 metre contours.

[110] Kriging was used to contour all isotherms and to smooth the isobaths to derive paleo shorelines.

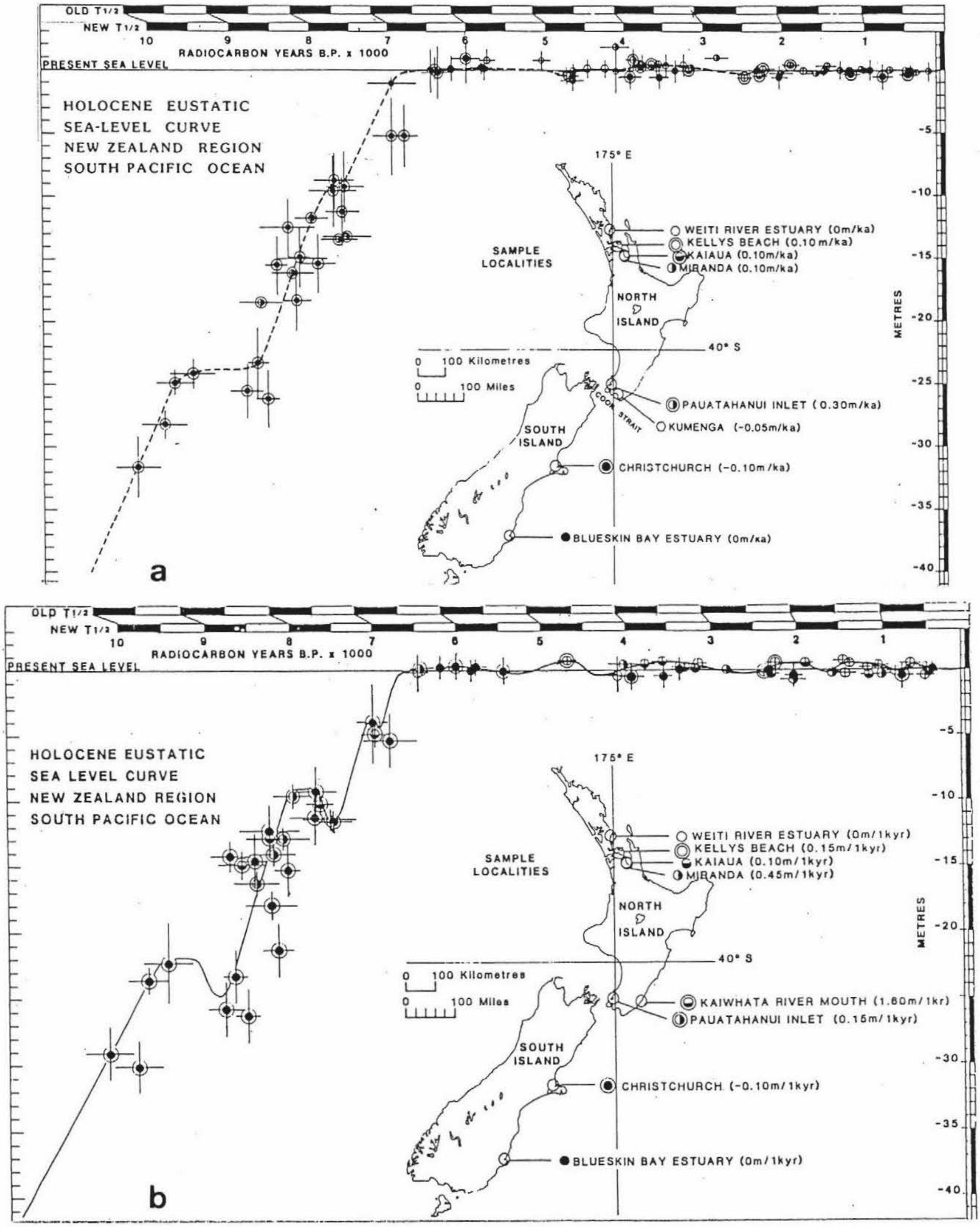

Figure 11. Post-LGM Eustatic Sea Level Curves for New Zealand, Relative to Present

Note the two reversals at 7,500 and 9,000 BP and the regression at 4,500 BP in Figure 11 (b) that have been smoothed out in Figure 11 (a).

Source: (a) Gibb (1986); (b) Gibb (1983)

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[111] Carter *et al* (1986) refer to this as 'vaulting;' a saw-tooth shaped curve is the result.

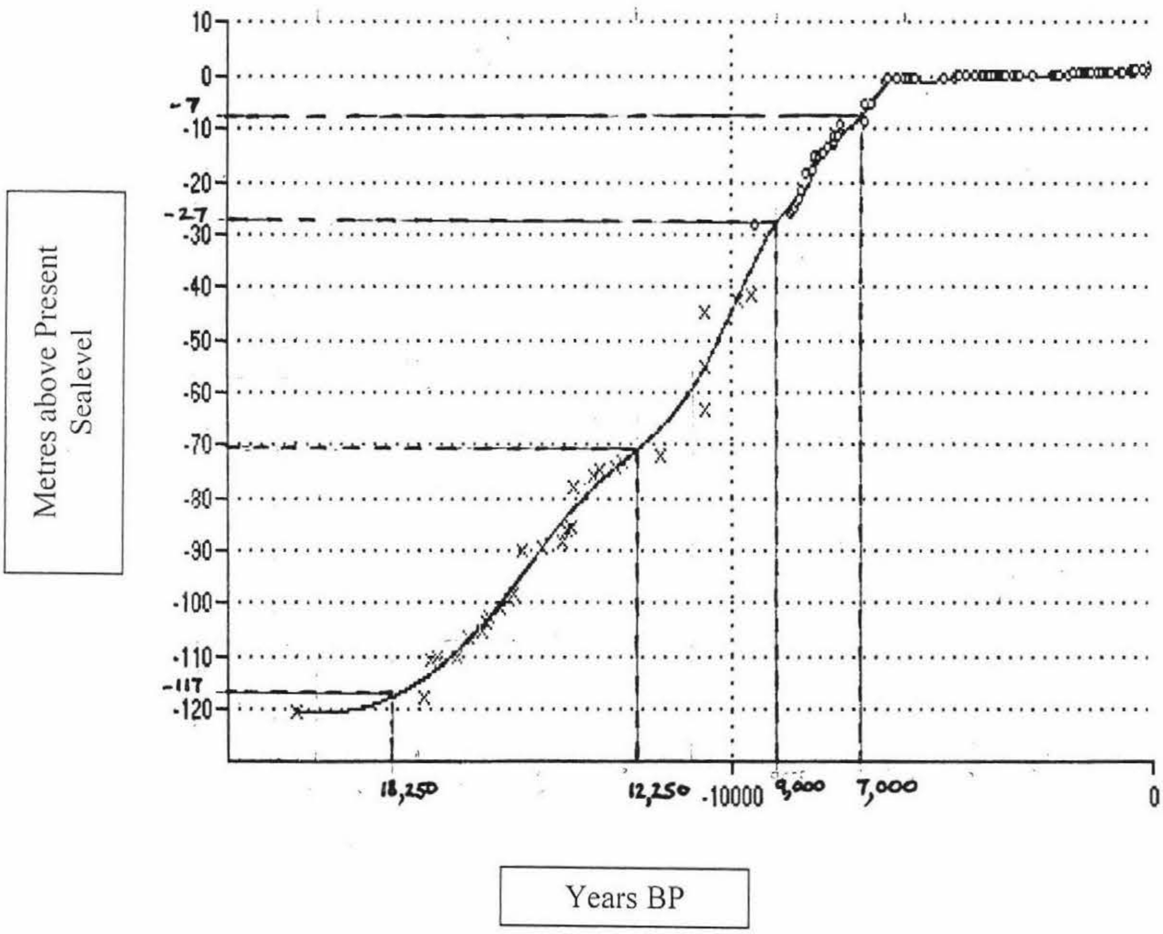

Figure 12 Eustatic Sea Level Curve for New Zealand Since the Last Glacial Maximum

Source: Sites denoted by circles Gibb (1986); crosses Norris & Grant-Taylor (1989)

2.8.2 Reconstructing Paleo Temperatures

The absence of continentality appears *prima facie* to be a reasonable assumption. Since the thermal inertia of water differs from land, coastal areas and islands such as New Zealand are modified by the influence of relatively stable maritime temperatures, whereas terrestrial temperatures in continental interiors demonstrate more extreme diurnal and seasonal temperature fluctuations. Thus Wardle (1974) reported that at a meteorological station at Fort Collins, Colorado (40°35'N, altitude 1525m) averaged +21.6°C in the warmest month and –3.3°C in the coolest month; in contrast, Mt Ruapehu (39°12'S, 1120m) has a much smaller temperature range of +11.7°C and +2.2°C respectively, despite similar altitude and distance from the equator.

Bailey (1966) gave the continentality equation

$$k = \frac{1.095 \quad Am}{0.92 + \sin(\phi - 53)} - 13.3$$

where k = the coefficient of continentality, with the limits 0 (lack of continentality) and 100 (complete continentality); Am is the mean annual range of temperature (in °F) and Φ is the latitude in decimal degrees. As expected, the estimated continentality coefficient for inland sites Alexandra and Taupo (76 and 69 respectively) are much higher than coastal sites such as Wellington and Auckland (52 and 59 respectively) however these latter sites are surprisingly close to the estimated continentality coefficient for Washington DC (k = 58) where one might expect continental influences to be less marked.

The decision to assume a lack of continentality through time is a pragmatic one, particularly since lower sea levels during the LGM led to a greater land mass and therefore almost certainly more continental conditions in New Zealand's interior than at present (McGlone *et al* 1993). However, this is compensated for by deriving treelines using the lowered shoreline as a datum, discussed below.

The assumption of absence of the Massenerhebung effect is also made for practical reasons. McGlone (1982) gives the upper limit of *Dacrydium cupressinum* on Mt Egmont as *c*. 900m, and the shrubline *c* 1200m, Horrocks & Ogden (1994) give the upper limits at Mt Hauhungatahi, 15km to the west of Mt Ruapehu as 950m and 1300m respectively, despite these mountains being within 0.7° of latitude from each other. This implies that the Massenerhebung effect *may* occur in New Zealand, despite it not being a large landmass relative to say North America or Asia.

Further evidence of the mountain mass effect was provided by Allen *et al* (1991) who analysed elevation of conifer-broadleaf forest in the South Island, stating "The lower elevation of floristically similar forest on the isolated Taramakau granite domes compared with that at nearby Camp Creek on the main axial range [that is, the Southern Alps] is a robust result, and is consistent with vegetation zones being lower on isolated peaks than on extensive mountain ranges ('Massenerhebung effect')." This highlights difficulties with regard to plotting a Massenerhebung-corrected timberline: first, identifying peaks that are sufficiently isolated to demonstrate the effect (for example, the Taramakau and Camp Creek sites are only around 5km apart), and second, plotting the lowered treelines for these isolated peaks on large scale maps such as the isopollen maps presented in this thesis. Given these difficulties and that the Massenerhebung effect in the mid-latitude mountains of New Zealand appears to be relatively weak[112], the principle of Occam's Razor is applied and the Massenerhebung effect is ignored.

Since lapse rates vary continually in time[113] and space in response to numerous meteorological and topographic factors, it is highly desirable for more extensive lapse rate research to be conducted (Flenley 1979). Pepin *et al* (1999) sought to do this in their study of environmental lapse rates in the Pennine Mountains, northern England, finding that in general, lapse rates were shallower for higher mean temperatures at ground level and for moister local air masses. However, this relationship is complicated by insolation, whereby increased daytime solar input leads to steeper lapse rates, albedo[114] and synoptic influences including wind shear, föhn winds, high cloud bases and increased specific humidity which cause the environmental lapse rate to steepen and approximate the dry adiabatic lapse rate (DALR) of 9.8°C km^{-1} rather than the saturated adiabatic lapse rate (SALR) of 5-6°C $km.^{-1}$

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[112] The Massenerhebung effect is much more pronounced in the tropics: Grubb (1971) cites the limits of lowland rain forest as 700-900m and lower montane rain forest as 1,200-1,600m on small isolated mountains, compared with 1,200-1,500m and 1,800-2,300m on main ranges, respectively; Flenley (1993) showed cloud forest on Indonesian mountains occurred at around 500m on Mt Tinggi, approximately 4.5km from the coast but not until 2,500m on Mt Pangerango, approximately 53km from the coast.

[113] Barringer (1989) found that a normal lapse rate persisted 37% of the time and a simple inversion 33% of the time at Queenstown airport in 1984–85 with intermediate temperature profiles occurring the rest of time.

(Barry 1981). Conversely, absolute and extreme temperatures, all had a 'positive' effect on lapse rates so that shallower lapse rates occurred, *ceteris paribus*.

It is clear that differing lapse rates prevail on the windward and leeward side of the same mountain; a mass of air approaching the Southern Alps from the west, for example, would rise initially at DALR until the dew point was reached whereupon it would continue to rise at the SALR. Since most of the original moisture precipitates on the west coast, the air descending on the east of the Southern Alps warms at the DALR with resulting terrestrial lapse rates and temperatures greater on the windward than the leeward slopes.

The normal lapse rate in free air differs from the thermal environment of the vegetation; Axelrod & Bailey (1976) proposed a 'terrestrial lapse rate' which accounts for modification of ground effects by the influx of air from locations well away from the ground, particularly in mountainous locations where influences such as wind speed and turbulence are caused by rough ground.

Axelrod & Bailey (1976) state that because the ground surface under the influence of sunlight becomes just as warm as the surface of the ground at lowland levels, at 3000m the ground effect adds enough heat that temperatures at instrument level height are 3°C warmer than those in free air. Therefore, failure to recognise the influence of ground effects means that "...calculation of altitudes of ancient terrains based on estimates of the temperature requirements of fossil floras will thus incorporate a systematic negative bias: they would be estimated at but 85% of their most probable [maximum] altitude."

Pepin (2000) hypothesised that a moister atmosphere (for example one associated with global warming) could enhance advection and precipitation at high altitudes (including snowfall). This would depress afternoon maxima preferentially at high elevations and strengthen daytime lapse rates, and the increased snowfall would enhance night time lapse rates. According to Pepin (2000) "In this hypothesis, it is necessary that enhanced precipitation and convection are concentrated at high elevations, as otherwise, all other things being equal, a moister atmosphere would be associated with a weaker lapse rate, at least in the free air."

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[114] α , surface albedo, of the tropical ocean is c .07 (ie 7% reflected, 93% absorbed); fresh snow α =.65-.80; subtropical land $\alpha = 0.25$; equatorial land $\alpha = 0.12$. Thus snowfields and icecaps during glacial periods would have a much higher albedo than their snow-less modern counterparts.

The corollary of this, and the implications for paleoclimate reconstruction are that at the LGM the environmental lapse rate may have been steeper than present, since the atmosphere was presumably drier than present (given cooler air can carry less water than warm air)[115]. However, this explanation is not without fault because a drier atmosphere would lead to less precipitation and a lower snowline, due to both less available moisture to condense, and because the lifting condensation level (LCL) would descend.

Axelrod & Bailey (1976) insisted that altitudes of vegetation cannot be estimated from mean annual temperature alone[116], however Meyer (1992) found that calculating lapse rates to derive altitudinal limits of trees (taken as the 10°C isotherm for WMT or warmest-month mean temperature) successfully predicted the treeline altitudes in western and mid-western states of the USA 80% of the time. Meyer suggested that despite the 20% discrepancy between calculated and actual treelines "...with so many variables, it seems noteworthy that altitude usually *can* be successfully estimated based upon thermal requirements alone." Given the much greater continentality that occurs in the United States, it would be reasonable to conclude that the discrepancy for New Zealand would be of a similar (or even smaller) size, and the simplifying assumption that Γ_E was spatially and temporally consistent throughout the Holocene appears valid.

Unfortunately, there is insufficient paleotemperature data available to estimate thermal measures other than mean annual temperature[117], so on balance, given the equivocal nature of these research findings, the simplifying assumptions that there was a constant lapse rate, Γ_E throughout the Holocene and that treeline is a linear function of temperature, are reasonable provided we remember that they are made for pragmatic reasons.

One source of sea surface temperature (SST) data is that provided by oxygen isotope analysis of deep sea cores. Because the lightest of the oxygen isotopes, $\delta^{16}O$, is preferentially evaporated, and $\delta^{18}O$, the heaviest of the isotopes is preferentially precipitated, the atmosphere in essence 'distils' the oxygen isotopic content of the moisture

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[115] This may partly account for discrepancies between derived terrestrial and marine temperatures, discussed below.

[116] Technically, the mean annual range of temperature must also be known, the warmth of the climate that defines the duration of the growing season, and the temperateness of the climate which provides an index of thermal extremes (Axelrod & Bailey 1976).

[117] Although transfer functions using marine invertebrates do give temperature maxima and minima (discussed in the text, *supra*) there is an insufficient number of published deep-sea cores to do this accurately for New Zealand.

it transports (Barron 1996) so that water locked up in the cryosphere becomes $\delta^{16}O$ enriched and the ocean correspondingly impoverished.

The oxygen isotope method of paleotemperature reconstruction utilises the temperature dependence of the fractionation of the isotopes O^{18} and O^{16} between calcite and water (Urey 1947). The equilibrium reaction between calcite and water is given as

$$CaCO_3{}^{16} + 3H_2O^{18} \leftrightarrows CaCO_3{}^{18} + 3H_2O^{16}$$

(Imbrie *et al* 1973). Microscopic oceanic fauna such as coccolithophores[118] and foraminifera take up oxygen isotopes when they form $CaCO_3$ in their tests and when diatoms and radiolarian form siliceous tests in proportion to the isotopic mix of the water in which they live so that the climate signature is recorded in the ocean sediment when they die. Like tree taxa, biomineralising protozoa such as foraminifera show marked temperature and depth preferences within the water column, so that their distribution on the ocean bed usually resembles that in the water layers above (Emiliani 1966; Herman 1972)[119]. The $\delta^{18}O$ narrative in planktonic foraminifera such as *Globigerina bulloides* reflects both ice volume - around 0.11‰ for each 10m of sea level change for the late Pleistocene; and temperature - approximately 0.24‰ per °C (Dansgaard & Tauber 1969; Broecker 1986).

Nelson *et al* (1994) compared $\delta^{18}O$ values from the Tasman Sea between isotopic stage 2 (Last Glacial) and stage 1 (Holocene) and consistently found a 1.2‰ difference. After subtracting 1.1‰ for the water composition effect, the derived temperature difference between the two stages is minimal. In contrast, for the southwest Pacific cores, the derived $\delta^{18}O$ difference between the Holocene and Late Glacial ranged from 0.3 to 0.9‰, a temperature difference of 1 to 4°C, with the high-resolution core 594 demonstrating temperature differences as high as 8°C. The isotopically derived temperature difference was supported by the predominance in southwest Pacific cores of sinistrally-coiled

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[118] Microscopic calcareous disks or rings that make up part of the covering of certain marine organisms (coccolithophorids).

[119] However, Shackleton *et al* (1973) found that "...a substantial portion of the variation in [oxygen] isotopic composition between one species and another in foraminiferal death assemblages is due to different fractionation factors rather than to different life habitats."

Neogloboquadrina pachyderma[120] and the virtual disappearance of warmer-water foraminifera including *Globorotalia inflata* and *G.truncatulinoides*.

In the absence of a simple relationship between latitude and SST, and given that most paleotemperature reconstructions focus on the Quaternary and lack fine resolution for the Holocene (eg Nees 1994; Martinez 1994), it was necessary to calculate Holocene SSTs from core information using the linear regression equation

$$\text{Temp } (^\circ\text{C}) = 16.9 - 4.38\,(\delta c - \delta w) + 0.1\,(\delta c - \delta w)^2$$

where $\delta c = \delta^{18}O$ foraminiferal carbonate ‰ (mean Holocene value); $\delta w = \delta^{18}O$ sea water, taken to be about 0.0 (SMOW[121]) but adjusted for salinity using the equation $\delta^{18}O = 0.5\ (\text{salinity} - 35.0 \times 10^{-3})$ ‰ (Nelson *et al* 1993; Nees *et al* 1994; Head & Nelson 1994; Nelson *et al* 2000)[122] and the multipliers are coefficients derived empirically from assays of carbonate-containing compounds (Epstein & Mayeda 1953 cited in Hemleben *et al* 1989).

This equation was based on Shackleton's (1974, cited in Hemleben *et al* 1989) equation that takes into account the presence of ^{17}O and instrumental inaccuracies:

$$\text{Temp } (^\circ\text{C}) = 16.5 - 4.3\,(\delta c - \delta w) + 0.14\,(\delta c - \delta w)^2.$$

Duplessy & Labeyrie (1994) claim that Shackleton's (1974) paleotemperature equation is valid over a wide temperature range (-1°C to 27°C),[123] and Erez & Luz (1982) demonstrated its robustness by growing the planktonic foraminifera *Globigerinoides*

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[120] Sinistral-coiling in response to cooler ocean water by *Globigerina pachyderma* has been demonstrated by Bandy (1960) of California, and off the New Zealand coast by Kennett (1968) and Malmgren & Kennett (1972). Other foraminifera to show this response include *Globorotalia truncatulinoides* (Herman 1972).

[121] Standard Mean Ocean Water. Hydrogen and oxygen each have two isotopes; ^2H (deuterium) and ^3H (tritium); and ^{17}O and ^{18}O respectively. Among isotopic forms of water, only ^2H_2O and $H_2{}^{18}O$ are of climatic interest. VSMOW (Vienna Standard Mean Ocean Water) has a deuterium / hydrogen R_{SMOW} (isotopic ratio) of 155.76×10^{-6} and a ^{18}O / ^{16}O ratio of 2005.2×10^{-6}. δ values are given by $R_s / R_{SMOW} - 1$ where R_s is the isotopic ratio of the sample. δ is expressed in milles. (Duplessy & Labeyrie 1994).

[122] The salinity of New Zealand's seas are between 34.3‰ (Ayress et al 1997) and 35.0‰ (Kustanowich 1963)

[123] Although their own comparison of measured summer SSTs with that derived from isotopic measurement of *G.bulloides* in both the North Atlantic and the Southern Ocean showed that $\delta^{18}O$ values of *G.bulloides* was a linear function of summer SSTs only in the range of 7°C to 22°C, the optimal temperature range for this species. Linear regression analysis showed that the isotopic temperature derived from *G.bulloides* is described by the function $T_{isotope} = \text{summer SST} - 1^\circ\text{C}$.

sacculifer under laboratory conditions, showing the correlation between isotopic and actual temperatures to be very strong ($r = 0.95$). [124]

A second method of deriving SSTs is the use of transfer functions or relative abundance studies such as that utilised by Imbrie & Kipp (1971) who used core top (modern) samples to derive the following transfer function describing summer SST:

$$T_S = 19.7A + 11.6B + 2.7C + 0.3D + 7.6$$

where T_S is estimated temperature in centigrade; A, B C, and D signify observed values for tropical, subtropical, subpolar and gyre margin planktonic assemblages, and the values preceding the planktonic assemblage factors are regression coefficients for the linear expression respectively. The constant term "...has no special significance beyond reflecting the scale of measurement," (Imbrie & Kipp 1971)[125]. Transfer functions were the standard method of SST reconstruction utilised by the CLIMAP project, and has been used by Sancetta *et al* (1972) for the North Atlantic; Hutson (1980) for the southern Indian Ocean, and Thompson (1981) for the north Pacific.

Weaver *et al* (1997) used the technique to calibrate SSTs for core H211 off the Bay of Plenty, Thunnel *et al* (1994) for the north-east Tasman, Luz (1977) for the south Pacific and Nelson *et al* (2000) to derive SSTs for core P69 to the south of Hawkes Bay. The paleotemperature equation is derived by first conducting factor analysis of the biological input data, and secondly, regression analysis of the factorial output data with modern SSTs. The order of terms in the equation reflects the order of stepwise selection such that, in Imbrie & Kipp's (1971) equation, the tropical foraminiferal assemblage (factor A) provides the best single measure of summer surface temperature.

Molfino *et al* (1982) maintain that factor analysis has three major benefits; first, it allows a large dataset to be summarised in a few components; second, the factors are

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[124] Wright *et al* (1995) used Epstein's *et al* (1951 cited in Hemleben *et al* 1989) equation; the results are similar to those obtained using Shackleton's (1974) equation, with estimated SSTs differing by between 0 and 0.4°C. Neither Ian Wright (personal communication, 2001) nor Cam Nelson could recall why Epstein's (implicitly less accurate) equation was used, although Professor Nelson doubted it would make too much difference to the calculated temperatures considering all the other assumptions that are built in to the approach (personal communication, 2001), which I verified by using both equations.

[125] Imbrie & Kipp (1971) gave the winter SST function as $T_W = 23.6A + 10.4B + 3.7D + 2.7C + 2.046$.

mathematically independent which is beneficial when the assemblage data is used as input in regression analysis; and third, the factors can be defined objectively. Nelson *et al* (2000) showed that there was a good concordance between oxygen isotope-derived SSTs and transfer function-derived SSTs.

A third technique of deriving paleotemperatures from marine sediments is provided by marine phytoplankton, especially the coccolithophorid *Emiliania huxleyi*. These algae respond to changes in water temperature by altering the molecular composition of cell membranes, so that as water temperature decreases, they increase the production of unsaturated alkenones (ketones). This type of biochemical response to temperature is known to occur in the fatty acids in phospholipids, the classical building blocks of cell membranes, in other organisms including bacteria, plants and animals. Since their cells contain a mixture of long chain alkenones with 37, 38 or 39 carbon atoms[126] which are either di- or tri-unsaturated[127], the temperature dependent unsaturation index U^K_{37} may be written as

$$U^{K}_{37} = \frac{[C_{37:2}] - [C_{37:4}]}{[C_{37:2} + C_{37:3} + C_{37:4}]}$$

(Brassell *et al* 1986). The index ranges from –1 (where all alkenones are $C_{37:4}$) to +1 (where they are all $C_{37:2}$ the diunsaturated methyl ketone, alkadienone). Because the tetra-unsaturated alkenone $C_{37:4}$ is absent from most sediments, in particular sediments in waters <12°C to the south of New Zealand (Sikes & Volkman 1993), the saturation index was re-expressed by Prahl & Wakeham (1987) as

$$U^{K'}_{37} = \frac{[C_{37:2}]}{[C_{37:2} + C_{37:3}]}$$

which also improves the linearity of the relationship between the unsaturation index and SST (Sonzogni *et al* 1997)[128]. The main advantage of these unsaturation indices is that they do not appear to degrade significantly, are not influenced by salinity or isotopic

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[126] Pelejero & Grimalt (1997) give the IUPAC names of the alkenones $C_{37:2}$, $C_{37:3}$ and $C_{37:4}$ as heptatriaconta-(15E, 22E)–dien–2-one, heptatriaconta-(8E, 15E, 22E)-trien-2-one and heptatriaconta–(8E, 15E, 22E,29E)–tetraen-2-one, respectively.

[127] That is, either two or three double bonds respectively.

[128] Although Rosell-Melé *et al* (1995) suggest the tetraunsaturated alkenone becomes more important with decreasing temperature.

composition of the seawater, are independent of calcium carbonate dissolution and require samples an order of magnitude smaller (say, 100mg) than those required for other paleoenvironmental analysis such as oxygen isotopes (Eglinton *et al* 1992).

Hiramatsu & De Dekker (1997) studied nanoplankton assemblages in the ocean surrounding New Zealand and found that *E.huxleyi* was the most ubiquitous species, making up more than 60% of the nanoplankton assemblage, its frequency having a strong, negative correlation with SST. Unlike other coccolithophorids whose percentage abundance varied markedly with environmental factors in addition to SST (nutrients[129], salinity and water density[130] and water depth) *E.huxleyi* displayed a simple linear relationship with SST; this relationship has been quantified by researchers such as Prahl & Wakeham (1987) who grew *E.huxleyi* in controlled conditions to derive the $U^{K'}_{37}$ equation

$$T\ (^\circ C) = \frac{U^{K'}_{37} - 0.039}{0.034}$$

Alkenone-derived SSTs are invariably show smaller LGM-Holocene SST differences than oxygen isotope-derived or transfer functions based on foraminifera: Bradley (1999) ascribes this to discrepancy to the fact that the various organisms achieve peak abundances at different times of the year[131] and inhabit different parts of the water column[132]. Ikehara *et al* (2000) used the alkenone unsaturation technique to derive SSTs for the Tasman Plateau to the east of New Zealand; these are also given in Table 6.

A possible shortcoming of using alkenone unsaturation indices of *E.huxleyi* to date sediments is that since it is a biologically based proxy (as are most SST proxies), its use as a temperature indicator appears in some cases to be modulated by ecological constraints. Modern sediment trap data indicates that the alkenone relationship to SST may be different in the different water masses at different seasons (Sikes & Volkman 1993); furthermore, there is another coccolithophorid that synthesises alkenones, *Geophyrocapsa oceanica*

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[129] Although researchers such as Pozzi *et al* (2000) suggest otherwise.

[130] Rosell-Melé *et al* (1995) suggest salinity and water density may affect the biosynthetic capabilities of alkenone producers so that the alkenone unsaturation index may not be strictly temperature dependent.

[131] Phytoplankton blooms usually occur rapidly in spring or early summer and last only a few weeks, whereas foraminifera reach peak abundances more slowly and throughout the year.

[132] Phytoplankton live predominantly in the photic zone (the upper 10m or so of the water column); *Globigerina bulloides*, on the other hand, has been found as deep as 1,000m (Boltovskoy, cited in Bandy 1972).

(and possibly other coccolithophorids in the *Geophyrocapsa* genus, according to Müller & Čepek 1997).

Analysis of the lipids of *G.oceanica* (strain JB02) isolated from a bloom in Jervois Bay in eastern Australia showed that this coccolithophorid, like *E.huxleyi*, synthesises C_{37}-C_{39} alkenones and esters of di- and tri-unsaturated C_{36} fatty acids (Volkman *et al* 1995). $U^{K'}_{37}$ values for *G.oceanica* plotted against temperature gave a linear relationship of the form $U^{K'}_{37} = 0.049T - 0.520$, which is statistically different from Prahl & Wakeham's (1987) equation. In other words, since the $U^{K'}_{37}$ values at any given temperature are higher for *E.huxleyi* than for *G.oceanica*; the implications of this are that dating sediments older than 85,000 years using alkenone unsaturation ratios may yield uncertain SSTs since *E.huxleyi* was not dominant at that time.[133]

In support of alkenone unsaturation dating, however, Müller & Čepek (1997) compared alkenone-derived SSTs with $\delta^{18}O$-derived SSTs for cores from Walvis Ridge off the coast of Namibia and found a good concordance, even for the Late Quaternary (before the rise of *E.huxleyi*), because *G.oceanica* responded to climate in a similar way to *E.huxleyi*; and other researchers found a good correlation between alkenone-and $\delta^{18}O$-derived SSTs at Kane Gap, off the coast of Sierra Leone (Brassell *et al* 1986).

Thus we can be reasonably confident of the alkenone-derived SSTs used in this thesis because of the relatively young sediments examined, the geographic distribution of *E.huxleyi* and *G.oceanica*, and their reproductive potential: whereas *E.huxleyi* survives within a temperature range of <0 to 29°C (optimum 15 to 25°C), *G.oceanica* is restricted to tropical and temperate waters between 13 and 26°C (optimum 20-25°C). Rhodes *et al* (1995) investigated modern day blooms around the New Zealand coast and found that the maximum growth rates were 1.9 doublings d^{-1} for *E.huxleyi* and 1.4 doublings d^{-1} for *G.oceanica*.

This finding suggests that even under optimal conditions for *G.oceanica* (ie 20-25°C) *E.huxleyi* will reproduce more quickly and dominate the assemblage, and alkenone unsaturation ratios in a given aliquot of sediment will be dominated by *E.huxleyi*.

Following extreme conditions favouring algal blooms, *G.oceanica* reached a peak concentration of 1.1×10^5 cells l^{-1} in Northland between August and December 1992 and the same concentration in Queen Charlotte Sound in March 1992. For *E.huxleyi*, on the other hand, the maximum concentration was an order of magnitude higher: 9.6×10^6 cells l^{-1} at Big Glory Bay in November 1992 (Rhodes *et al* 1995)[134]; this dominance was also observed by Hiramatsu & De Dekker (1997b) in cores in the north and mid-Tasman) where *E.huxleyi* outnumbered *G.oceanica* to the order of 15 or even 20:1. Hiramatsu & De Dekker (1997b) derived SST (summer) transfer functions of the form

$$SST = 11.443 + 17.501 \times \frac{mid - low\ latitude\ species}{mid - low\, latitude\ species + high\, latitude\ species}$$

and found a good concordance with oxygen-isotope derived temperatures; these are also given in Table 6.

The LGM snowline depression of 830m (Soons 1979, Bacon *et al* 2001) to 875m (Porter 1975) implies, *ceteris paribus*, a terrestrial cooling of 4 - 5°C relative to present, whereas CLIMAP (1986) estimates of SSTs indicate much less cooling: 1.5°C and 2.3°C cooler at 39°S and 45°S on the West Coast. The east coast had a computed SST 0.75°C warmer than present at 39°S and 0.75°C cooler at 45°S. The relatively small temperature decrease estimated by CLIMAP is also at odds with the discovery of fossil scallop *Zygochlamys deliculata* from 14,000 years BP near Three Kings Islands, 1000 km north of their modern northern-most habitat in Pegasus Canyon, implying LGM seas were 6°C cooler than present (Beu 1999). This is somewhat disturbing: either the CLIMAP estimates are flawed,[135] or SSTs do not reflect terrestrial temperatures well.[136]

Folland & Salinger (1995) claim that although *seasonal* terrestrial temperatures are less well correlated with SSTs because "...transient synoptic features will have more influence on [terrestrial temperatures] without much affecting SST," they were able to demonstrate

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[133] The timing of *E.huxleyi*'s first appearance appears to be debatable; Volkman *et al* (1980) suggest the Late Pleistocene, around 220 ky BP whereas Thierstein *et al* (1977) suggest 268 ky BP.

[134] Since these blooms are linked to increases in the sea surface reflectance (up to 25% of the light penetrating the surface water) they are easily observed from space due to the scattering of light (Westbroek *et al* 1993).

[135] A concern echoed by Rind & Peteet (1985) who made similar observations for continental land masses and masses at low latitudes, where estimated LGM SSTs were also apparently too high.

that longer term "Observed trends and shorter term variations in [terrestrial temperatures] are in excellent agreement with those of nearby SST." The correlation between SSTs and terrestrial temperatures can be determined by comparing Reynold's SSTs[137] to modern meteorological data. The agreement between the two is good, particularly for modern summer (January) temperatures: Table 5 shows the estimated correlation between Reynold's SSTs and terrestrial temperatures is 0.91 for the North Island and 0.78 for the South Island.[138] The absolute difference between the temperatures is generally small; the mean absolute difference between terrestrial and SST sites in Table 5 is 0.36°C for the North Island and 0.67°C for South Island sites.

The closeness of the relationship between marine and terrestrial paleotemperatures can also be gauged by comparing foraminiferal $\delta^{18}O$-derived SSTs to speleothem $\delta^{18}O$-derived temperatures. Oxygen isotopic fractionation between speleothem (stalactite and stalagmite) calcite and the drip water from which the speleothem forms is sensitive to temperature change; under ideal circumstances they record changes in cave temperature at the rate of –0.24‰ per °C (Hendy & Wilson 1968). Using modern temperatures for Nettlebed Caves in north-west Nelson (Hellstrom *et al* 1998), and the relationship between stalactite $\delta^{18}O$ and temperature outlined by Hendy & Wilson (1968), I derived the paleotemperature equation

$$\text{Temp} \quad (^\circ\text{C}) = 8.3 + \frac{-5.65 - \delta^{18}\text{O}}{0.24}$$

Because the Nettlebed Caves site was 400m above sea level and approximately 200m underground, the derived temperatures are quite different from SSTs, however the trend in the paleotemperature changes for core DSDP593 and the Nettlebed Caves site follow each other quite closely for the last 15,000 years [139].

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[136] For example, New Zealand may have displayed continental, rather than island, characteristics at the LGM given that its area is thought to have been around one-third bigger in area due to eustatic sea level lowering.

[137] Reynolds & Smith (1994); NOAA-CIRES Climate Diagnostics Centre (2001). Sutton & Roemmich (2001) found $r = 0.96$ between SST and air temperatures for the period 1986-2000 between Auckland and 30°S.

[138] If the west coast, South Island sites are excluded from the correlation, $r = 0.95$. Anomalously cool waters arise on the West Coast due to upwelling or tidal mixing (Chiswell 1994). July temperatures are also positively (although more weakly) correlated: $r = 0.66$ and 0.65 for the North and South Islands respectively.

[139] Temperature estimates between terrestrial and marine records is equivocal however; Williams (1996) compared cave deposits from Aurora Cave, Fiordland with the record from DSDP 594 and concluded "No convincing onshore/offshore correspondence can be seen...suggesting that the deep-sea record of planktonic $\delta^{18}O$ responds more to global oceanic than to regional events," whereas other researchers have demonstrated a strong concordance between terrestrial and marine records (Colhoun *et al* 1994; Heusser & Van de Geer

McGlone *et al* (1993) suggested that CLIMAP (1981) estimates were at fault, on the basis that small, low lying, oceanic islands such as the Chathams would "...essentially record sea-surface conditions and can directly indicate changes in oceanic temperatures in their region [44°S]." Palynological evidence suggesting there was widespread grassland in the Chathams at the LGM compared with low forest and shrubland in the Holocene, led McGlone *et al* (1993) to conclude "Such a striking change in the vegetation cover seems improbable without a lowering of SSTs of the surrounding ocean [>0.75°C]...we tentatively conclude that the CLIMAP SSTs for the New Zealand region underestimate the actual temperature depression at 18,000 yr BP by about 2°C."

The isopollen maps show the estimated altitude of the post-LGM treelines. In addition to the numerous assumptions required, there are several caveats to be considered when interpreting the derived timberlines. Often, local conditions prevent potential tree limit from being reached; for example at most timberlines, trees reach maximum limits only on a convex topography (Wardle 1985c). On concave topography and flat valley floors, alpine vegetation (defined by Wardle 1974 as low growing vegetation above forest and ecotonal krummholz) descends several hundred metres below the tree limit on convex topography[140].

1994). Furthermore, Williams *et al* (2000) suggest that because the ocean source and cave temperature effects have opposite signs, their relative influence is difficult to ascertain. The former refers to the fact that $\delta^{18}O$ is inversely related to the temperature at which calcite is deposited, around –0.24‰ per °C around 10°C, reducing to –0.22‰ per °C around 20°C, whereas the latter relates to the isotopic composition of the seepage water forming the speleothem. William *et al* (2000) concluded that for New Zealand, the net relationship between speleothem $\delta^{18}O$ and mean annual temperature at the present time is around 0.23‰ per °C.

[140] Possibly in response to katabatic winds (local downslope gravity flows caused by nocturnal radiative cooling near the surface under calm, clear skies (Barry 1981), reduced insolation, snow accumulation, avalanches, poor drainage, slope steepness and instability (Wardle 1985b) so that the valleys become frost hollows, giving an inverted timberline.

North Island				South Island			
Location	Years	Jan Mean Temp (a)	Jan SST (b)	Location	Years	Jan Mean Temp (a)	Jan SST (b)
Whangarei	1937-80	19.7	20.0	Motueka	1965-80	17.4	17.5
Thames	1946-80	19.4	19.8	Farewell Sp	1971-80	17.4	17.5
Tauranga	1970-80	19.5	19.8	Westport	1937-80	15.8	17.5
Gisborne	1937-80	18.7	19.5	Greymouth	1947-80	16.1	17.3
Wairoa	1950-63	19.4	19.2	Haast	1949-76	14.7	16.5
Hastings	1930-66	18.9	18.5	Milford Sd	1934-80	14.4	15.3
Castle Point	1972-80	18.1	18.0	Bluff	1970-80	14.1	13.5
Wanganui	1937-80	17.8	17.8	Owaka	1975-80	13.4	13.5
N. Plymouth	1974-80	17.8	18.5	Tairoa Head	1967-80	14.0	14.0
Wellington	1962-80	17.4	17.0	Oamaru	1967-80	15.1	14.5
				Timaru	1910-80	16.2	15.0
				Rangiora	1965-80	16.5	15.5
				Kaikoura	1963-80	16.2	16.2
				C Campbell	1969-80	16.6	16.5
$r = 0.91$				**$r = 0.78$**			

Table 5. Correlation of Land and Summer SSTs Peripheral to the New Zealand Coast

Source: (a) New Zealand Meteorological Service (1983); (b) NOAA-CIRES (2001)

					Years Before Present					
Core Number	Latitude	Longitude	Function	Source	0-6,0000	6,001-8,000	8,001-10,000	10,001-12,000	12,001-14,500	14,501-22,000
					Temperature °C					
RC12-109	25.88	157.87	3	5	25.0					20.8
RC12-113	24.88	163.52	4	6				26.0		25.5
DSDP590	31.17	163.36	1	1	17.5		15.5		13.5	14.8
DSDP591A	31.58	164.45	1	1			17.8	16.2	14.8	13.8
Z2108	33.37	161.61	1	1			17.0	17.8		16.5
S804	35.71	176.07	1	2						7.1
S794	36.25	175.09	1	1,2,7	17.9	12.6	16.2	11.1	10.5	10.1
DSDP 592	36.47	165.43	2	1	14.1		13.8			8.4
P69	40.39	177.99	2	3	15.0	15.1	14.2	11.9	10.5	12.7
DSDP593	40.50	167.67	1	1,4	13.5	13.5		13.3	7.7	9.3
MD3	41.25	172.66	5	10	9.0	8.1	6.3	6.8	6.7	4.4
CHAT 1K	41.58	171.50	3	6	16.8	16.6		15.5	16.0	
R 657	42.53	178.48	3	7	14.8	14.7		13.1	12.5	12.4
GC-3	44.25	149.98	4	6				14.8		12.0
U938	45.06	179.48	2	7	9.4	8.9	7.5	7.6	4.7	7.3
DSDP594	45.52	174.94	2	1,10,1		8.0	8.3	5.5	2.8	0.8
Q200	45.99	172.02	1	1,8	8.1	7.5	7.0	4.8	1.5	2.1
Q580	46.02	179.00	2	1	6.4	6.6	5.1	5.0	4.4	3.6
Q217	46.46	175.07	1	1	7.4		6.6	5.9		
TSP-2C	48.13	146.87	4	9				11.8	12.1	10.2
Q585	49.70	177.96	1	1,7	5.3		5.3		1.3	2.4

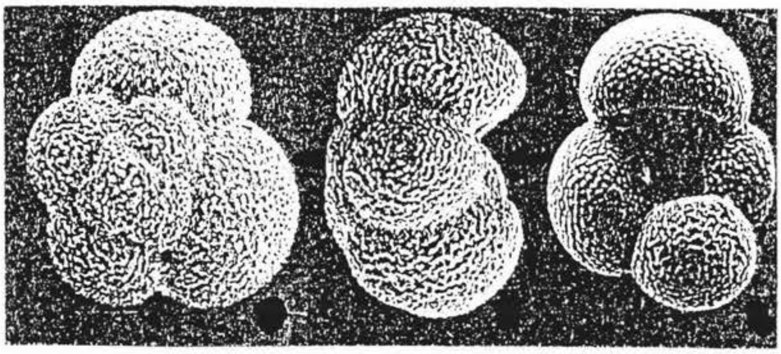
Key to function:

1. Temp (°C) = $16.9 - 4.38\,(\delta c - \delta w) + 0.10\,(\delta c - \delta w)^2$
2. Temp (°C) = $16.5 - 4.30\,(\delta c - \delta w) + 0.14\,(\delta c - \delta w)^2$
3. Modern Analogue Technique / Transfer functions (refer to text)
4. Alkenone Unsaturation.
5. Temp (°C) =$8.3 + \{(-5.65 - \delta^{18}O)/0.24\}$

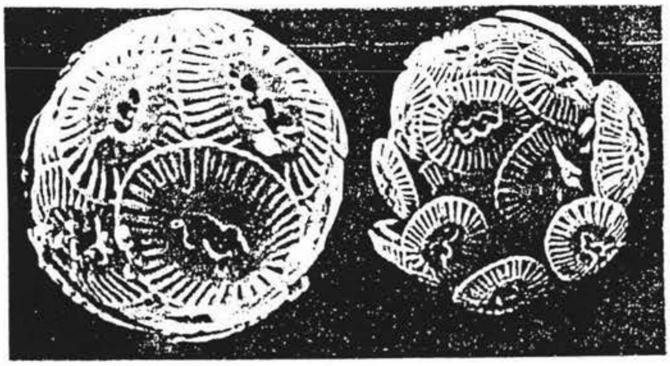
Source:

(1) Nelson *et al* (1993); (2) Nees *et al* (1994); (3) Nelson *et al* (2000); (4) Head & Nelson (1994); (5) Thunnel *et al* (1994); Hiramatsu & De Dekker (1997a) (6) McMinn & Wells (1997); (7) Hiramatsu & De Dekker (1997b); (8) Weaver *et al* (1999); (9) Ikehara *et al* (2000); (10) Hellstrom *et al* (1998); (11) Wells & Okada (1997).

Table 6. Reconstructed SSTs Peripheral to the New Zealand Coast



a



b

Figure 13. (a) Foraminifera *Globigerina bulloides* and (b) Coccolithophore *Emiliania huxleyi*

Source: Hayward (1983); Hiramatsu & De Dekker (1996)

2.8.3 Integrating Paleo Shoreline and Paleo Temperatures

When the paleo-SSTs were superimposed on the maps of New Zealand, 1°C isotherm 'zones' were obtained, and the latitude of the intersection of the isotherm with the shoreline was noted. Next, the following formula was used to derive the theoretical summer treeline for that zone:

$$\alpha = \left\{ \left(\frac{\varphi + \tau}{\Gamma} \right) \times 1000 \right\} - \Delta \ sea \ \ level$$

where α = maximum theoretical altitude, taxon A; φ = freezing temperature taxon A; τ = temperature at sea level; Γ = lapse rate of 6.5°C km^{-1} and change in sea level is relative to present. Points $\geq$ this α altitude were read off the GTOPO30 depth-altitude dataset and the coordinates for these peaks assigned a zero pollen value, and added to the fossil pollen dataset.

For species with a medium freezing temperature such as *Prumnopitys ferruginea*, *Dacrycarpus dacrydioides*, and *Podocarpus totara* (all –7°C) only one or two of these *a priori* pollen values were typically used to augment LGM and early Post-glacial pollen datasets, since the number of observed zero values was already large enough to 'overwhelm' the small number of positive values. For *Agathis australis* (freezing temperature also –7°C) none of the dummy values was used, since there was adequate delineation of presence-absence observed in the pollen diagrams; and for cold-tolerant genera such as *Phyllocladus*, there were no sites of sufficient altitude to preclude growth, at least in terms of a simple altitude-temperature relationship.

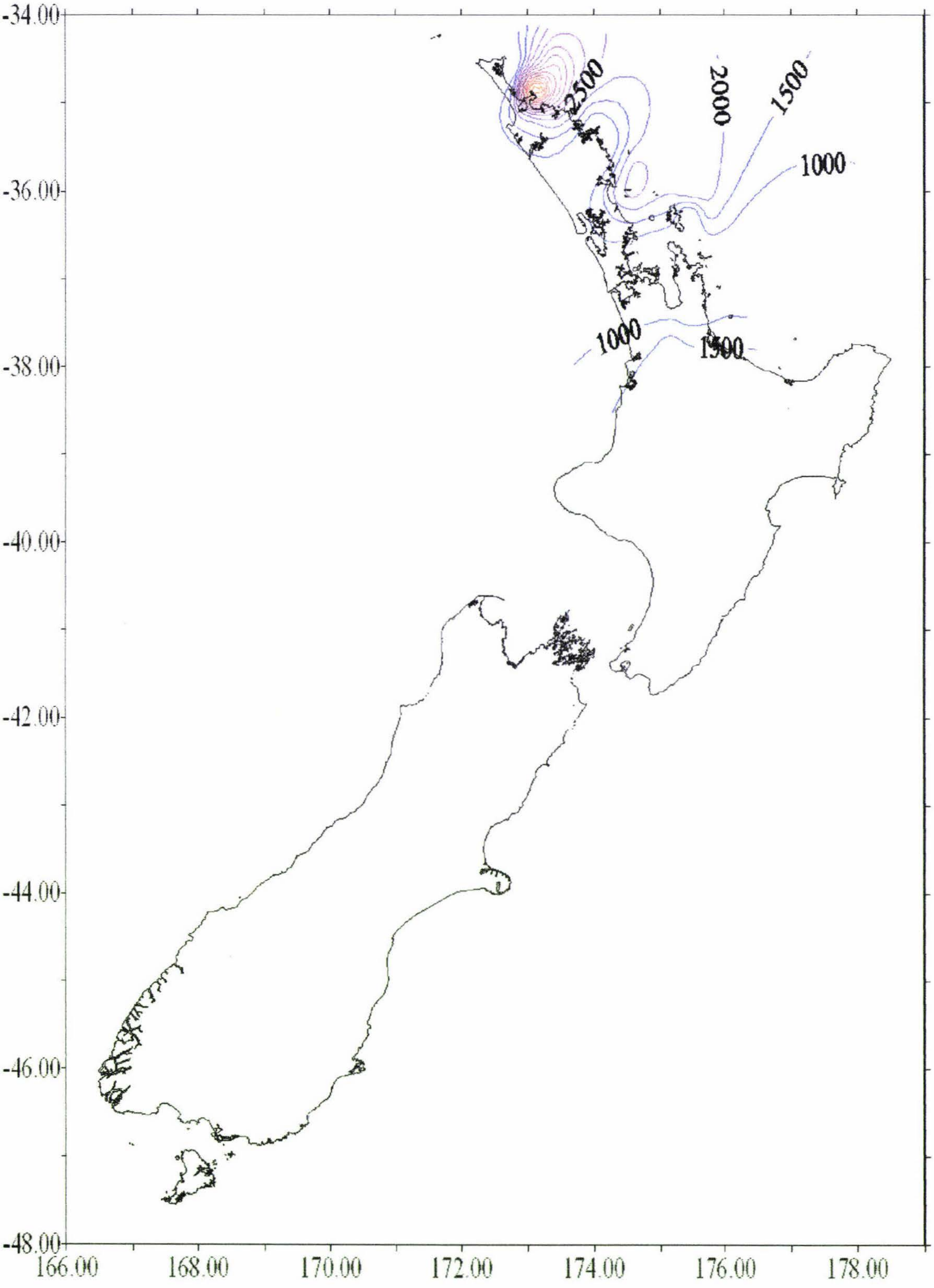
Isopollen maps are typically unaccompanied by a description of projection used (eg Tsukada 1982; Bennett 1989; Huntley 1990) or scale (eg Davis & Webb 1975; Prentice *et al* 1991) although several map projections and scales are used. The most common map projection used is a cylindrical projection (Bernabo & Webb 1977; Morita 1982) but others used include conic projections (Webb & McAndrews 1976; Hillaire-Marcel & Occhietti 1980; Huntley & Birks 1983) and azimuthal equidistant projections (Davis & Webb 1975; Webb *et al* 1983; Prentice *et al* 1991; and Tarasov *et al* 1998). The maps in this thesis use cylindrical projections; the scale of the paleo-SST and isopollen maps is approximately 1:14,000,000 and the scale for the isochrone maps is approximately 1: 8,000,000.

2.9 Isochrone Map Construction

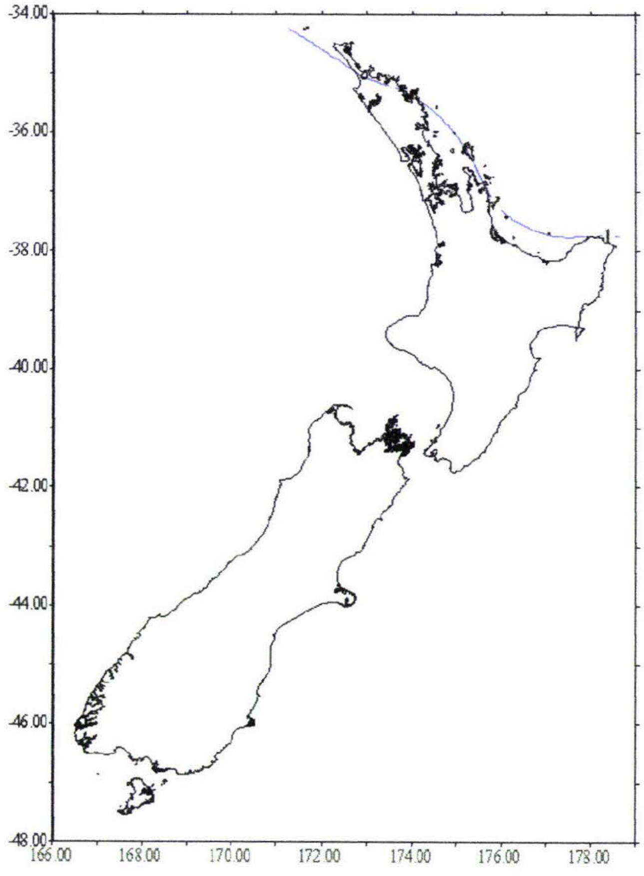
I chose to use critical limits (discussed in section 1.4) by selecting all sites having ≥ 1% pollen for taxon *A* at time *A*, with two or more subsequent samples having ≥ 1% pollen for taxon *A*. Further sorting was required to produce meaningful maps; this was typically related to whether pollen was under- or over-represented in the pollen cores.

A good example of this is provided by comparing the isochrone maps for *Nothofagus fusca* and *N.menziesii*. *Fuscospora* can dominate the pollen rain even when Fuscospora trees are absent. McGlone *et al* (1996) suggest that *Fuscospora* levels ≤ 5% in a pollen spectra cannot be easily interpreted, since "...they are as likely to be derived from long distance dispersal as they are from small local stands." Despite its description as the most aggressive species in its genus, in that isolated stands are often found in broadleaved-podocarp forests some distance from the general boundary (Haase 1989), *N.menziesii* tends to be under-represented in the pollen rain. Consistent percentages >1% of *N.menziesii* usually signify local presence and levels >5% indicate it forms a significant part of the vegetation cover. Somewhat serendipitously, I found that 5% and 1% pollen percentages were the optimal levels to plot for the *N.fusca* and *N.menziesii* isochrone maps, respectively. These points were plotted in SURFER using kriging as discussed in chapter 2.7.

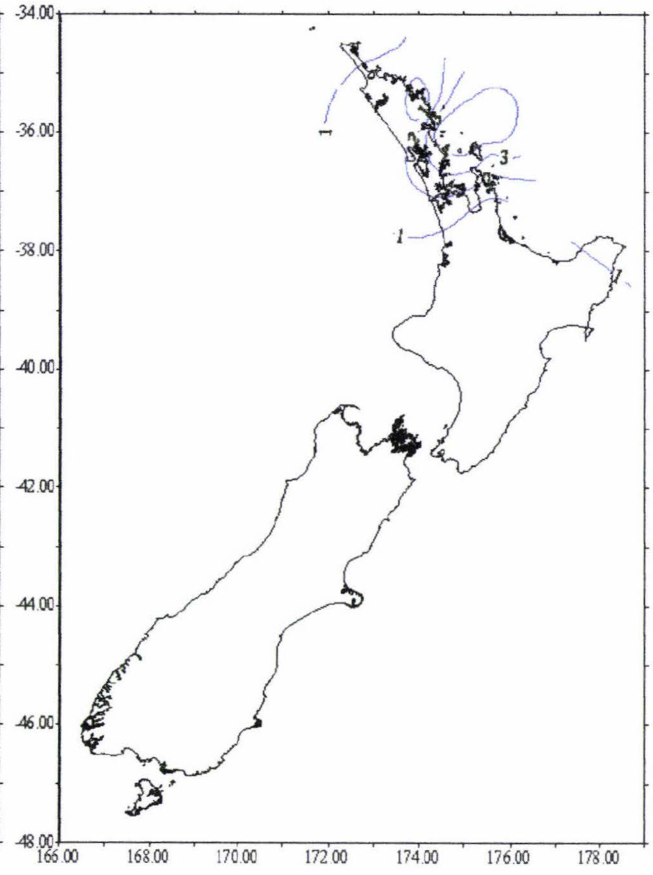
3 The Isopollen and Isochrone Maps



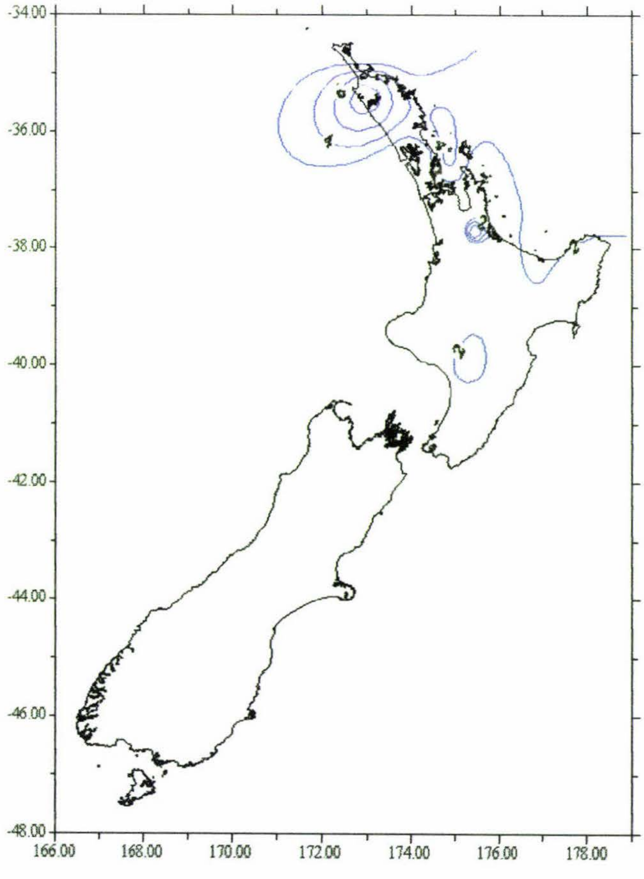
Agathis australis Isochrone Map 2% Critical Limit



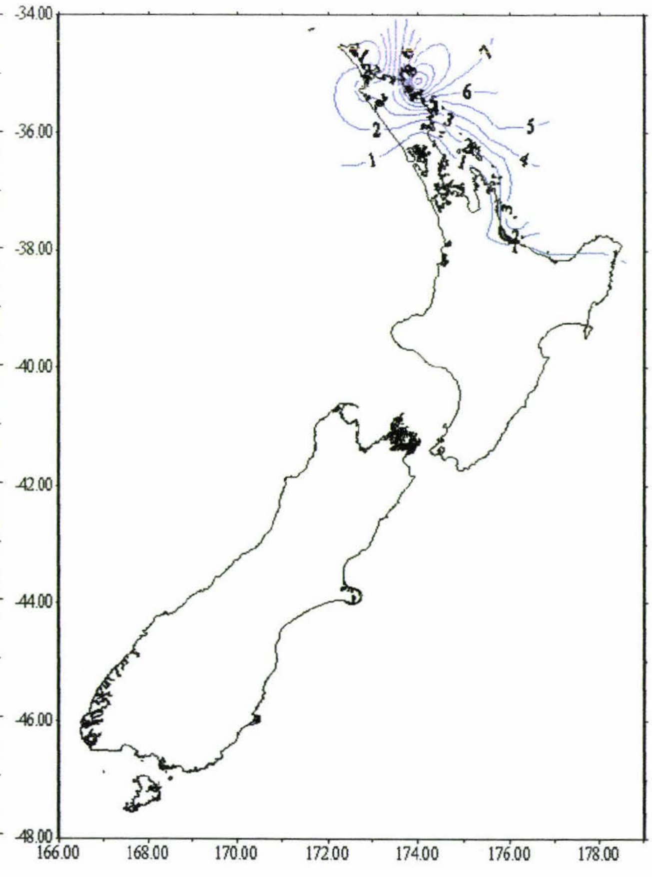
Agathis australis 10,000 - 8,000 BP



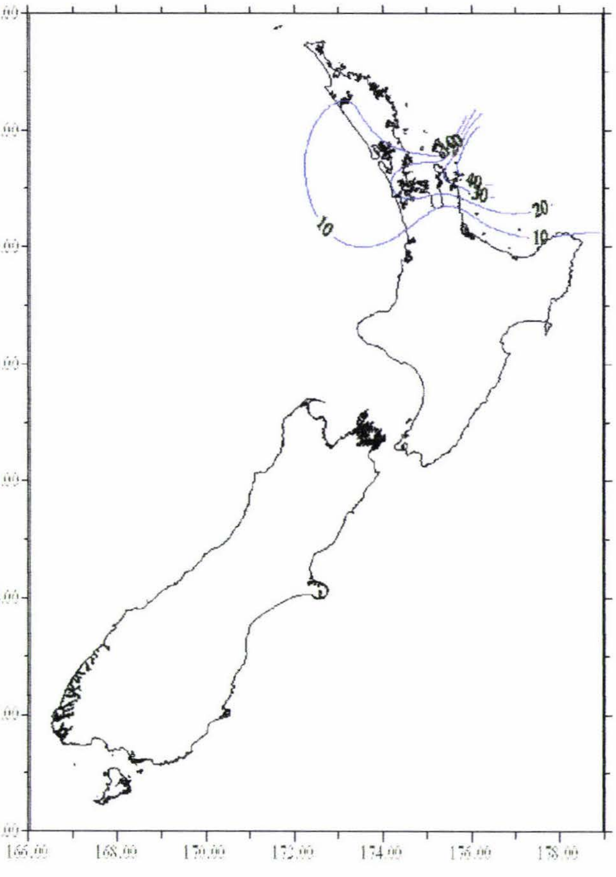
Agathis australis 8,000 - 6,000 BP



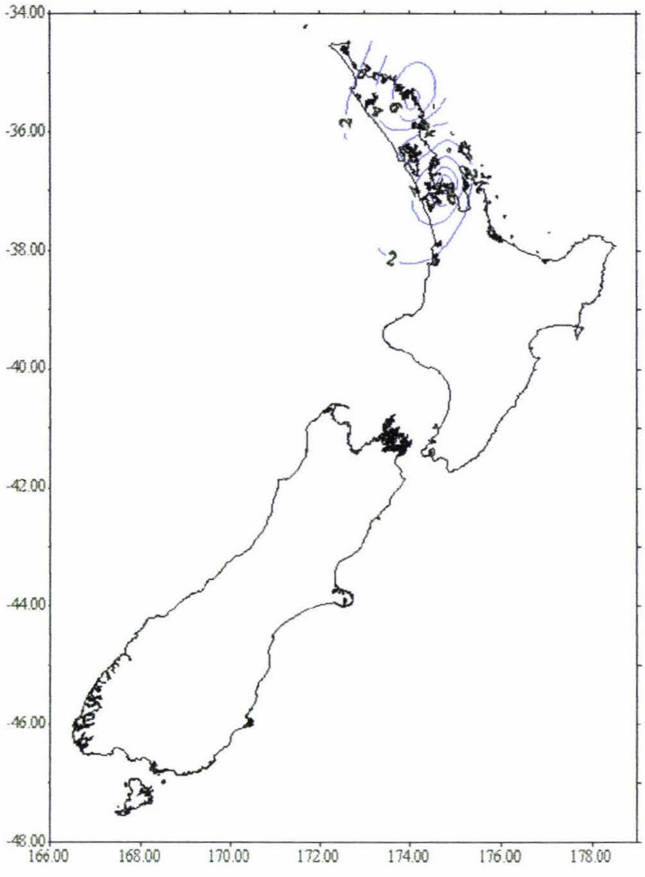
Agathis australis 6,000 - 4,000 BP



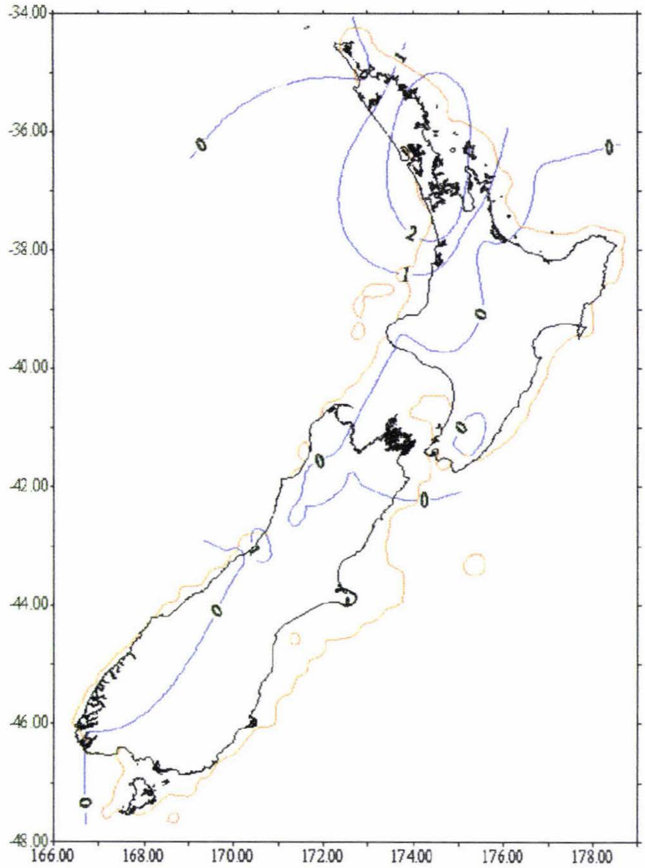
Agathis australis 4,000 - 2,000 BP



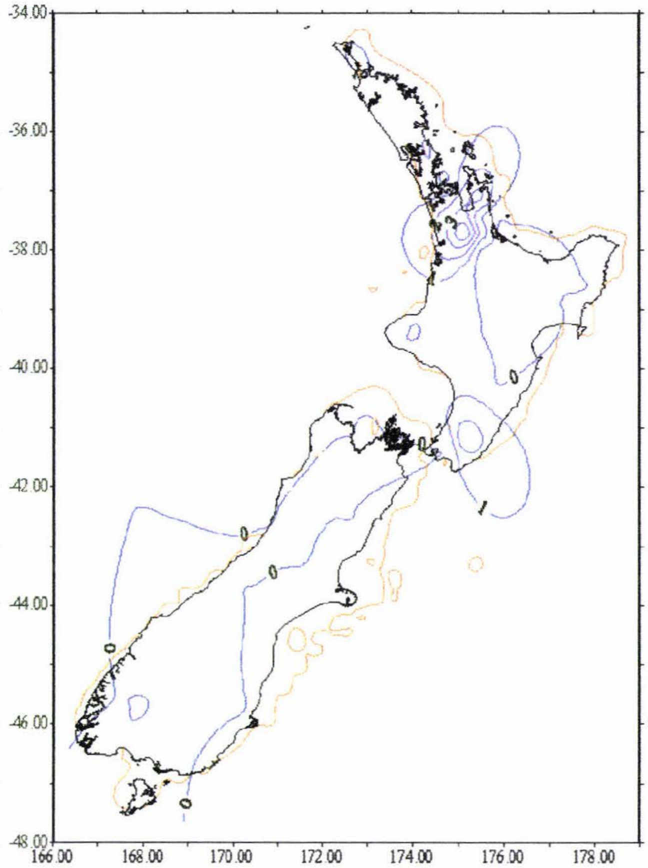
Agathis australis 2 000 - 50 BP



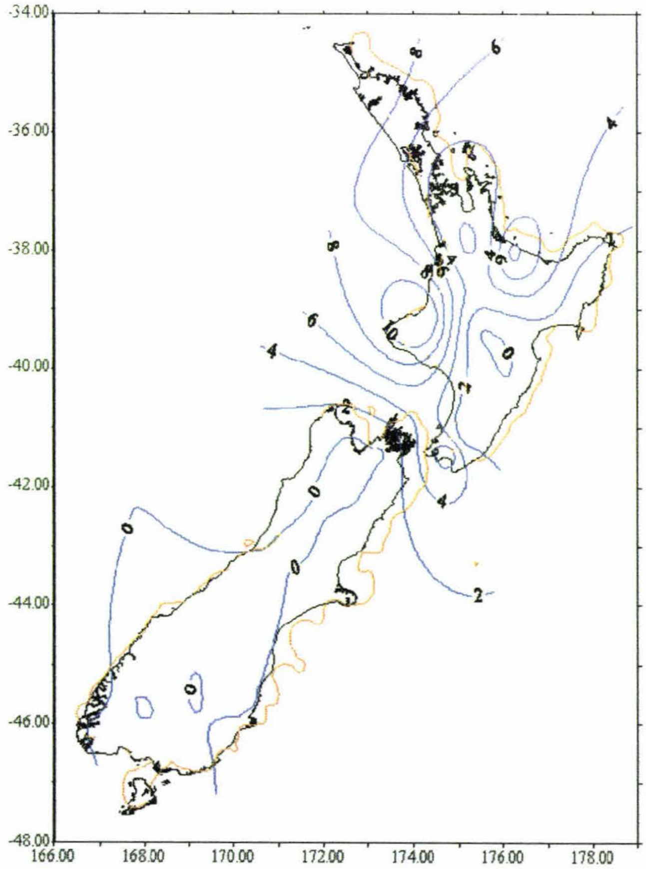
Agathis australis Modern



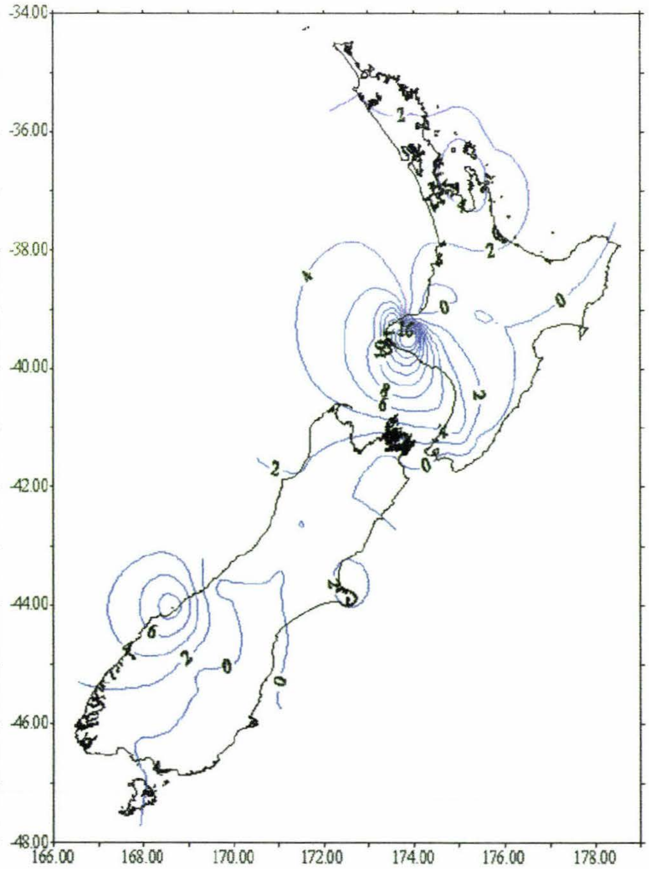
Ascarina lucida 22,000 - 14,500 BP



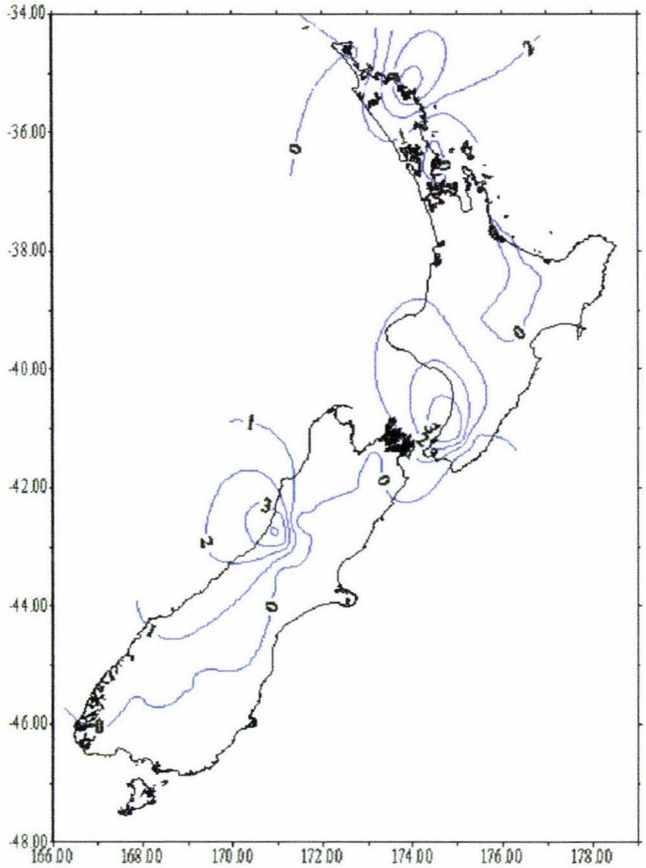
Ascarina lucida 14,500 - 10,000 BP



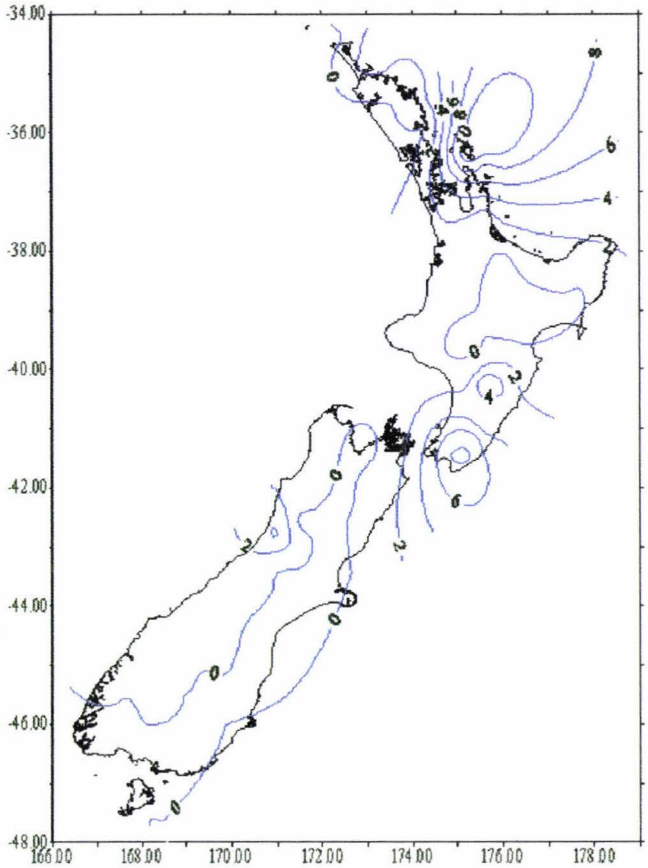
Ascarina lucida 10,000 - 8,000 BP



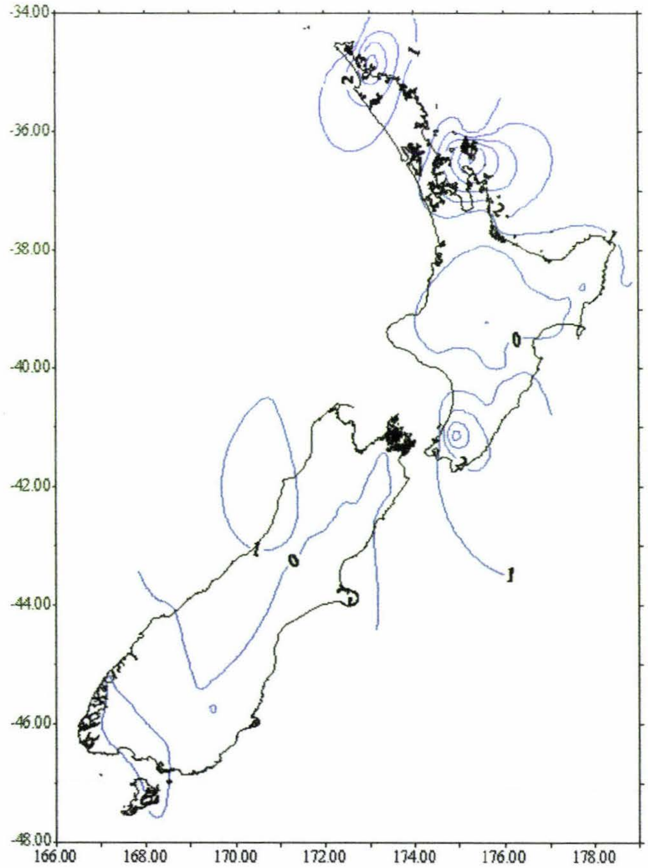
Ascarina lucida 8,000 - 6,000 BP



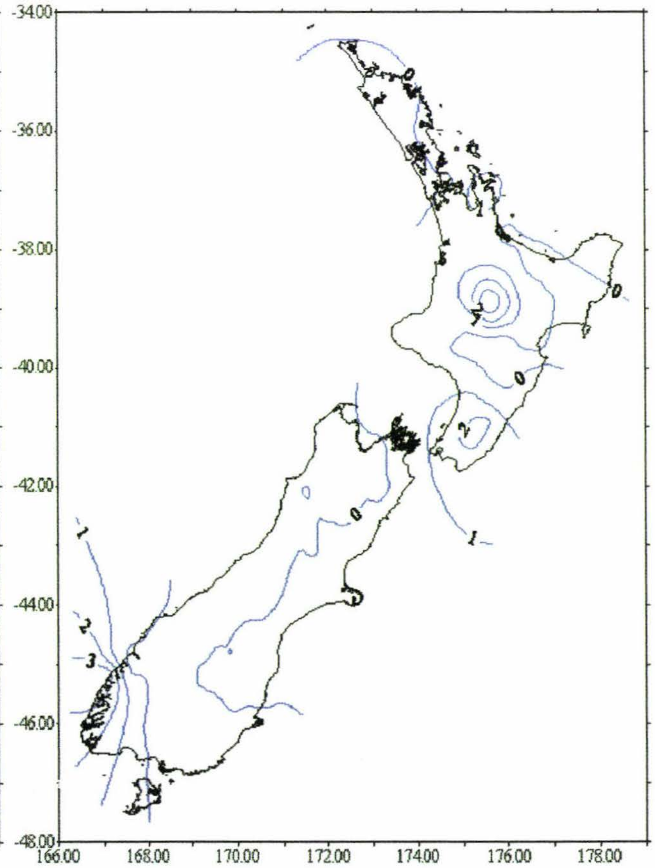
Ascarina lucida 6,000 - 4,000 BP



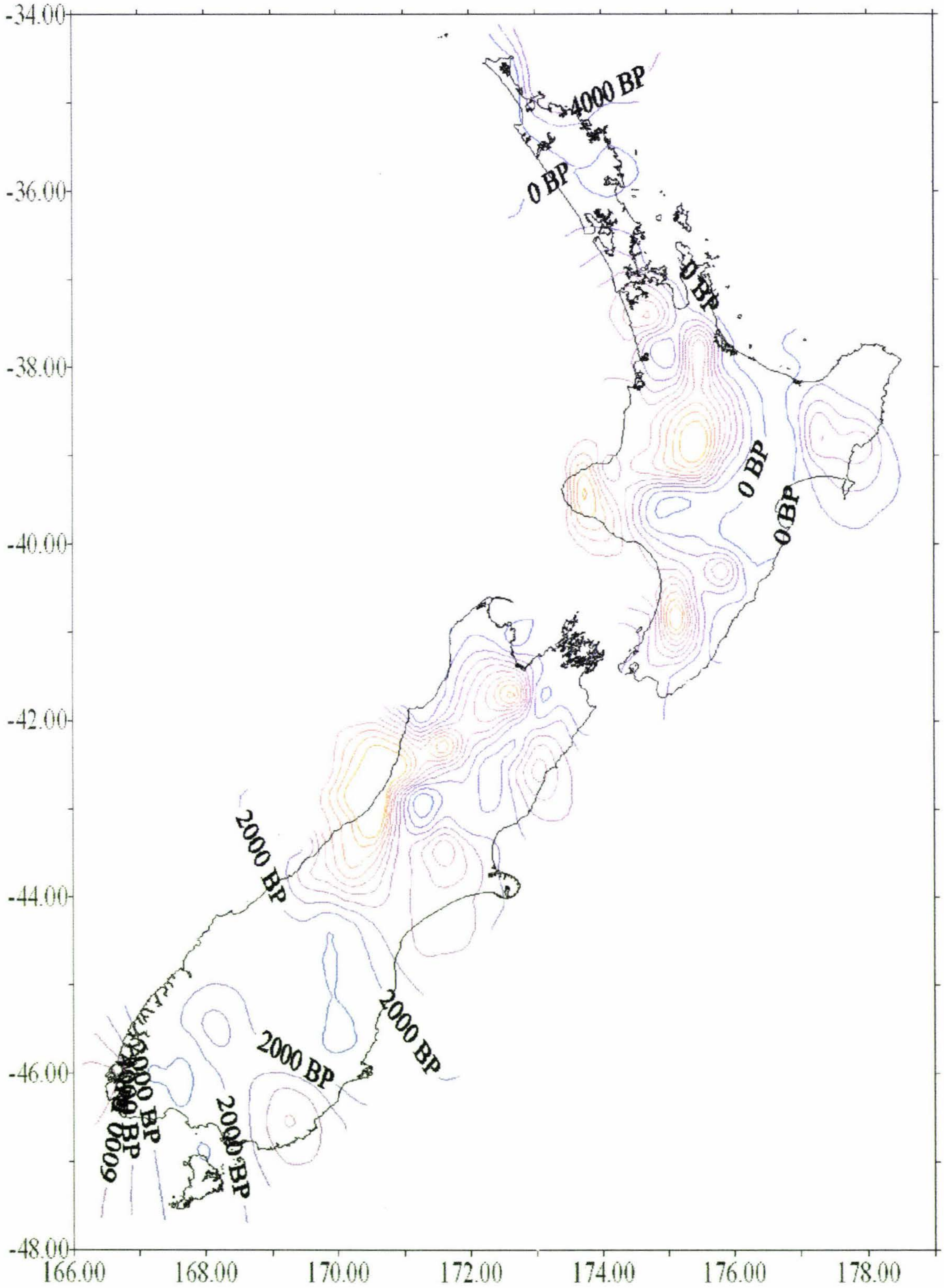
Ascarina lucida 4,000 - 2,000 BP



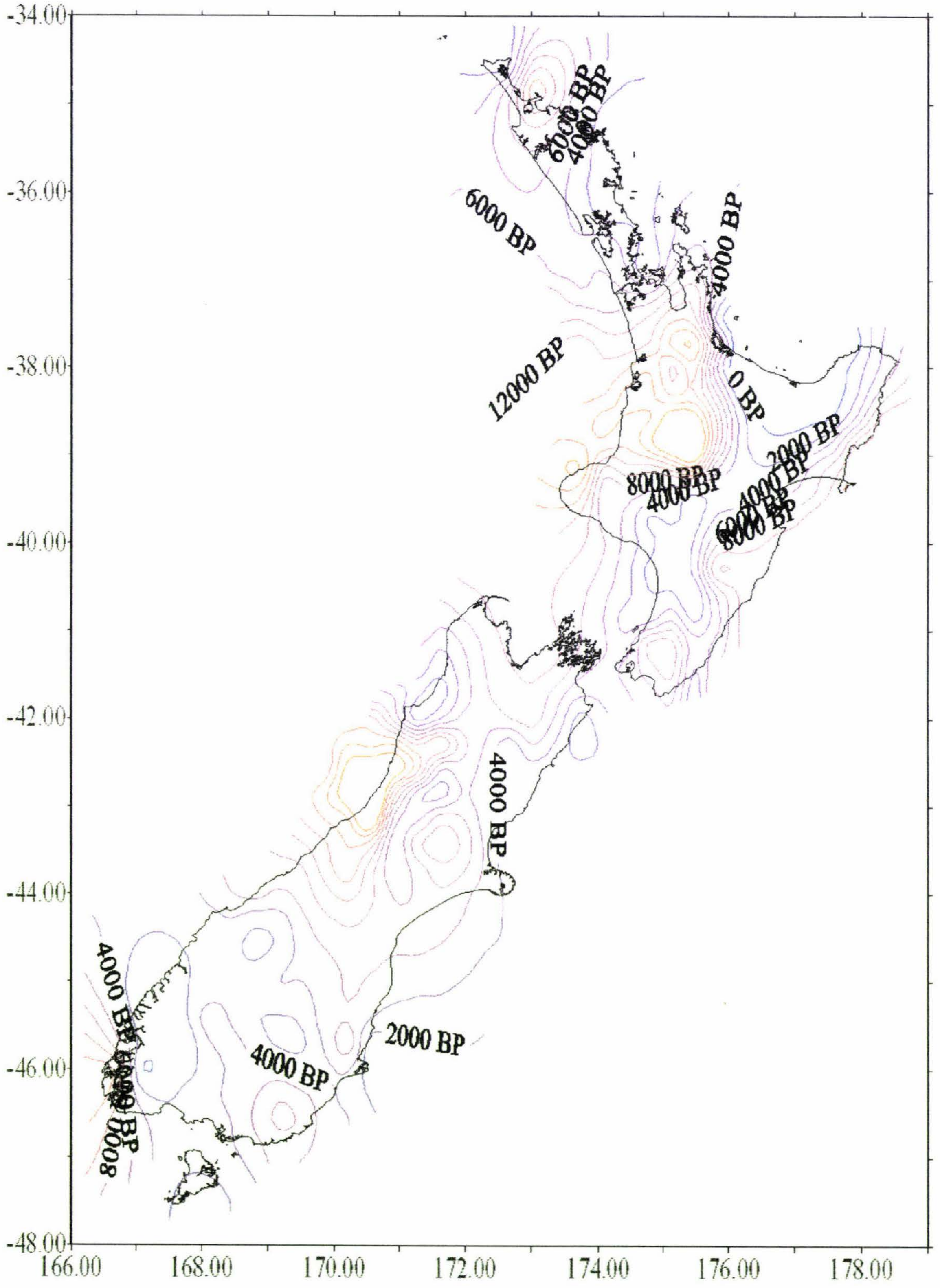
Ascarina lucida 2,000 - 0 BP



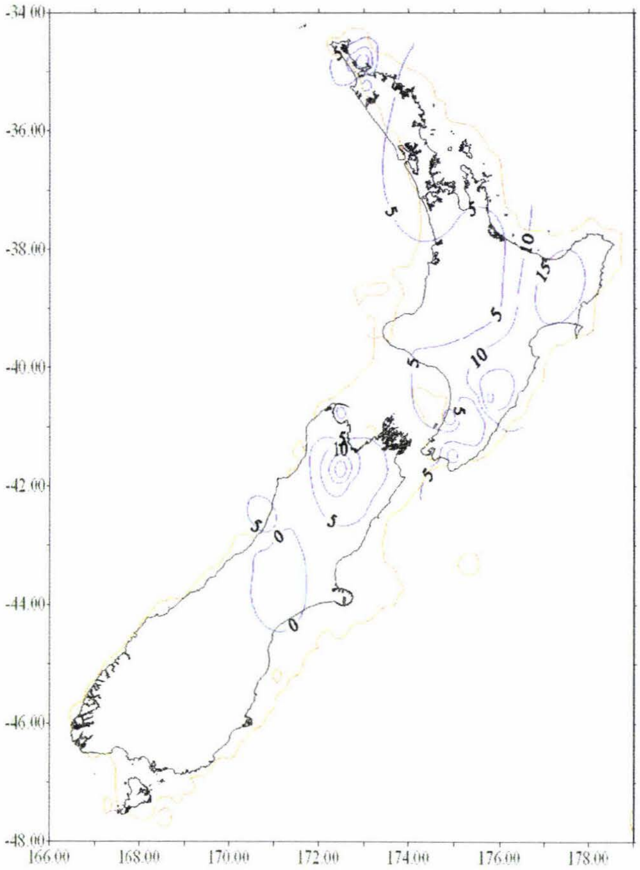
Ascarina lucida Modern



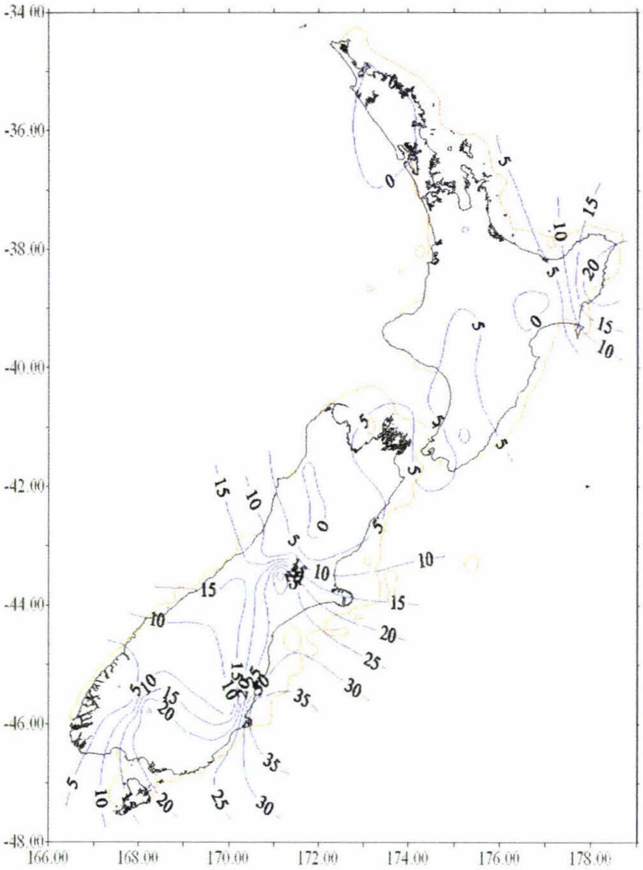
Ascarina lucida Isochrone Map 1% Critical Limit



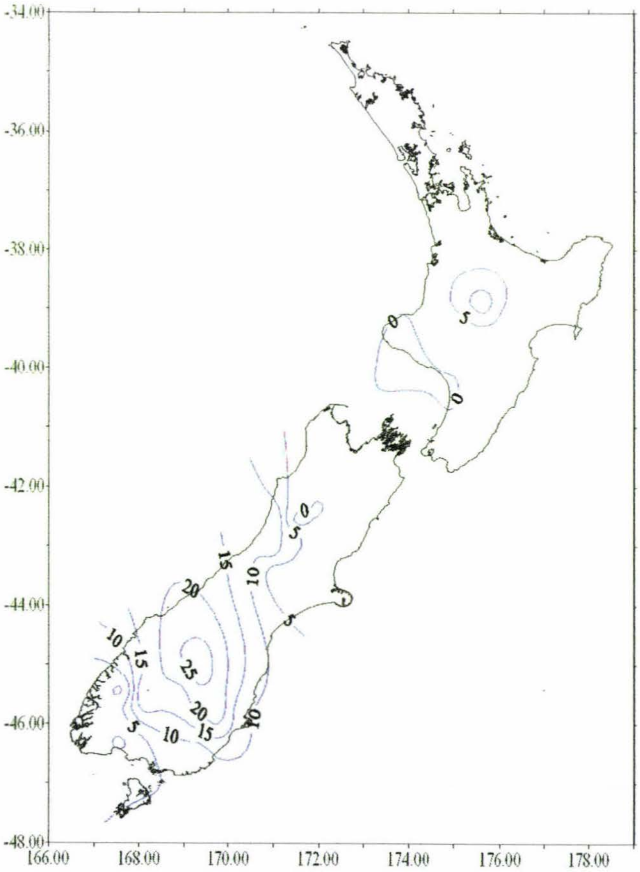
Coprosma spp Isochrone Map 3% Critical Limit



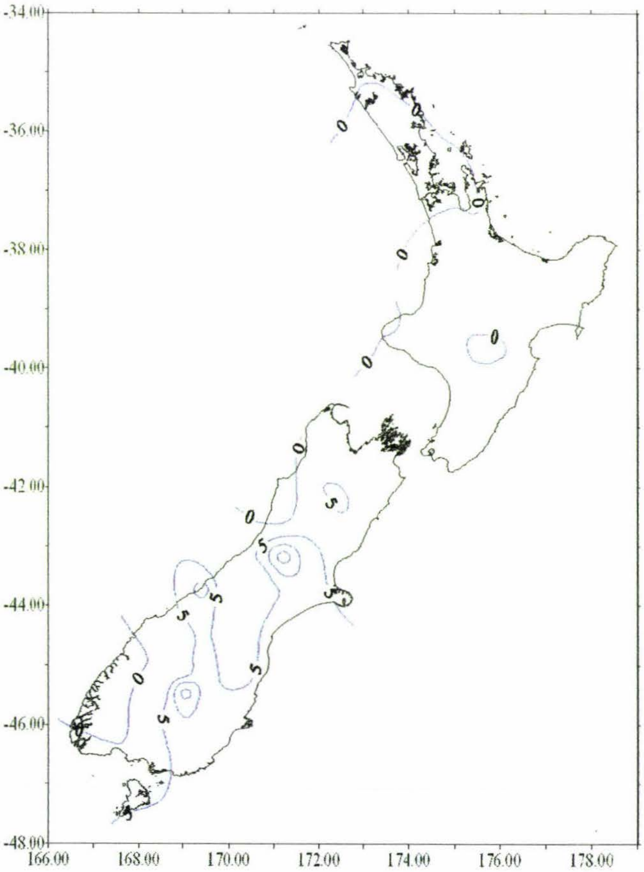
Coprosma spp 22,000 - 14,500 BP



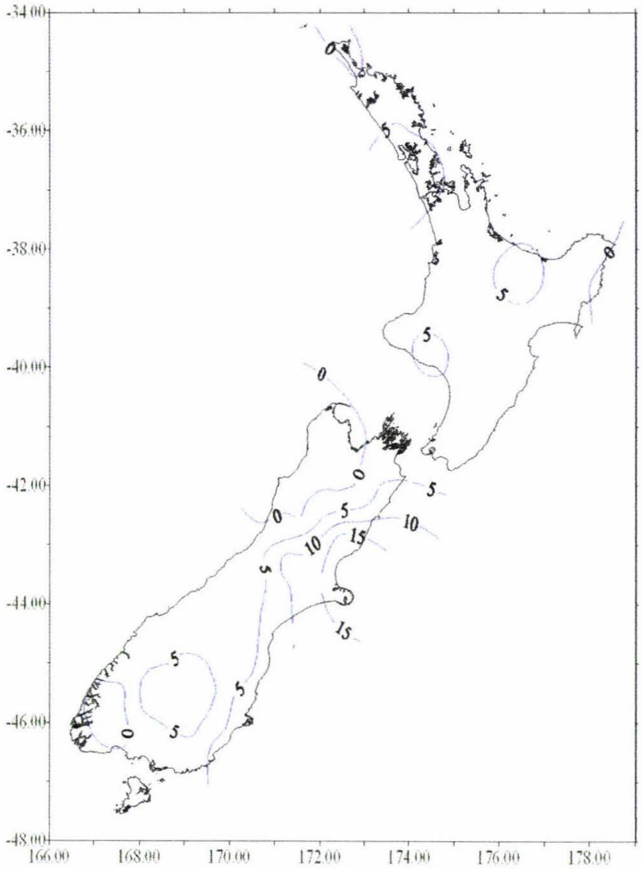
Coprosma spp 14,500 - 10,000 BP



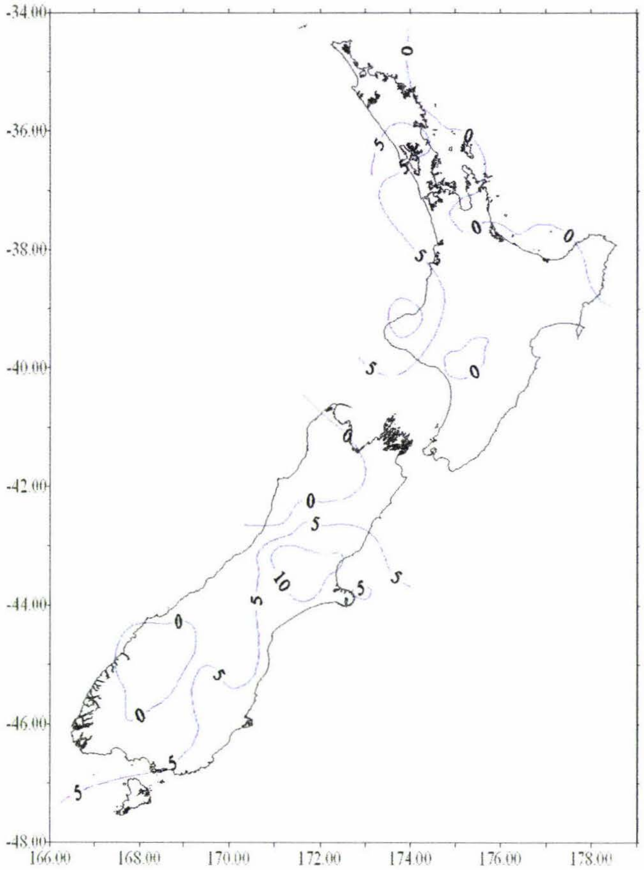
Coprosma spp 10,000 - 8,000 BP



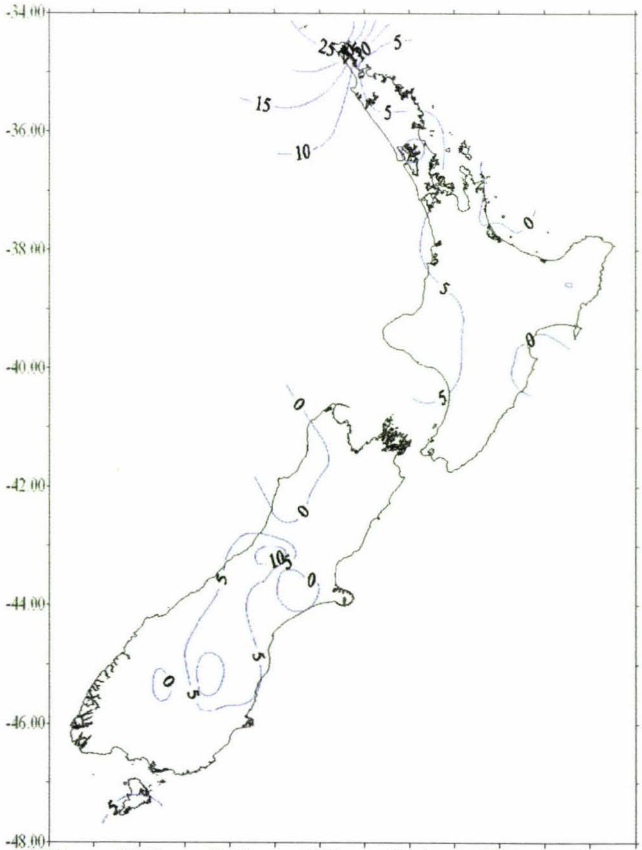
Coprosma spp 8,000 - 6,000 BP



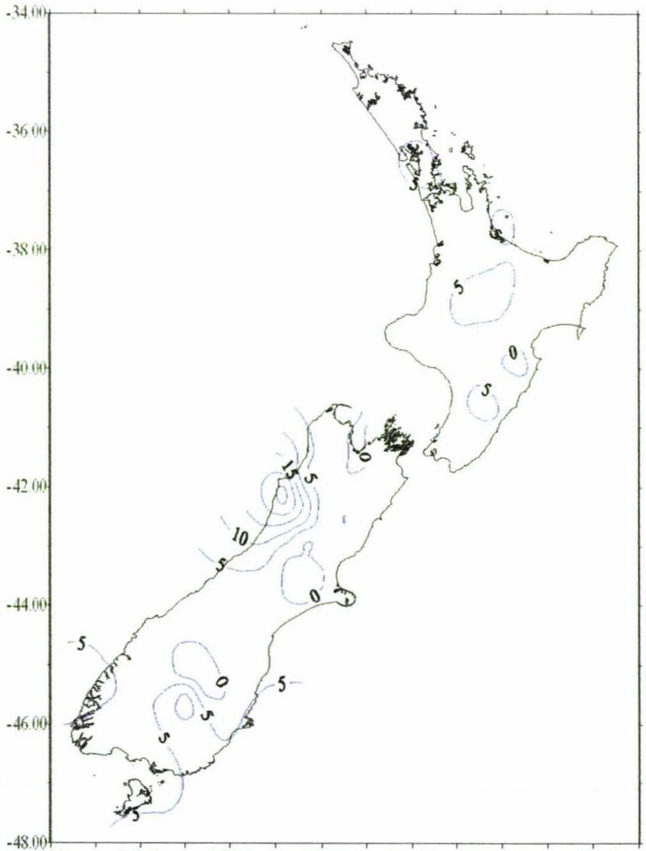
Coprosma spp 6,000 - 4,000 BP



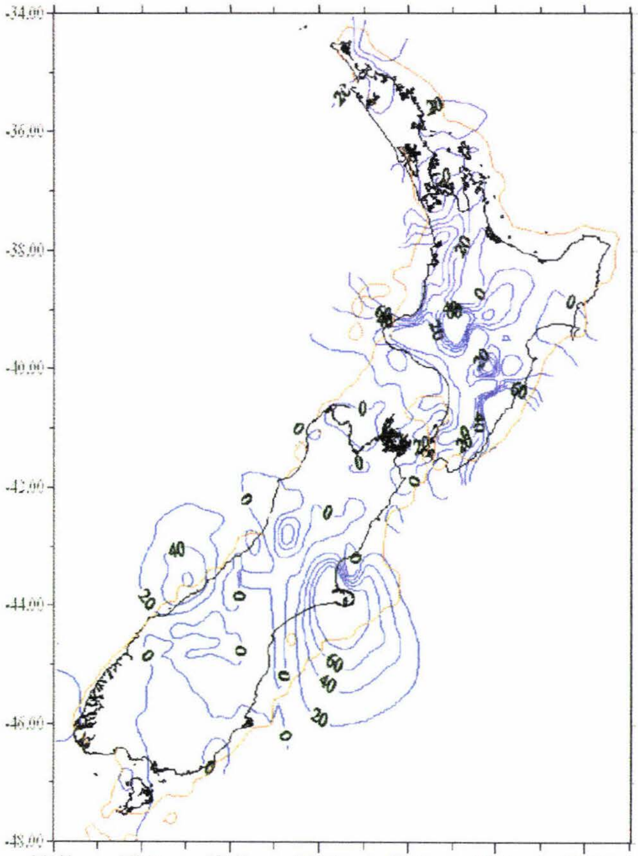
Coprosma spp 4,000 - 2,000 BP



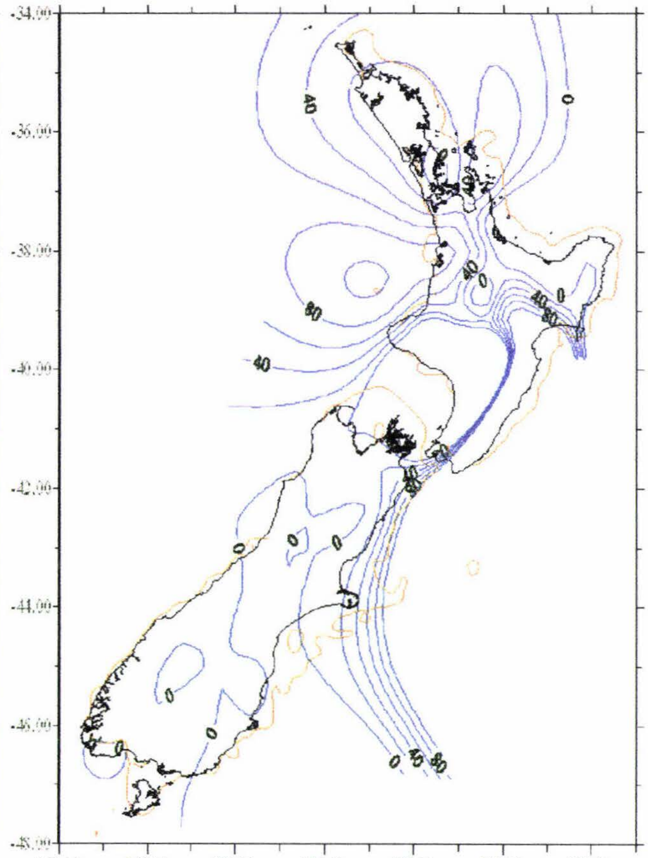
Coprosma spp 2,000 - 0 BP



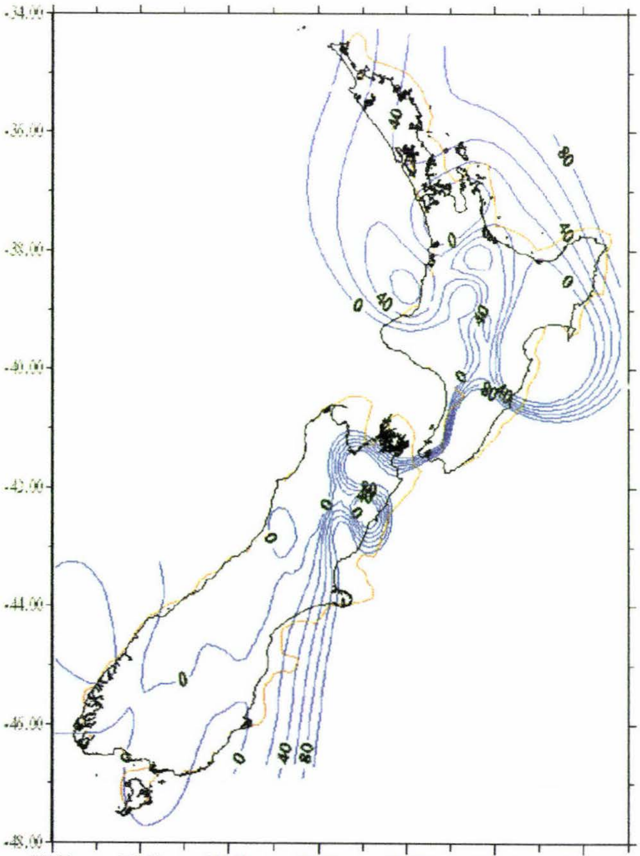
Coprosma spp Modern



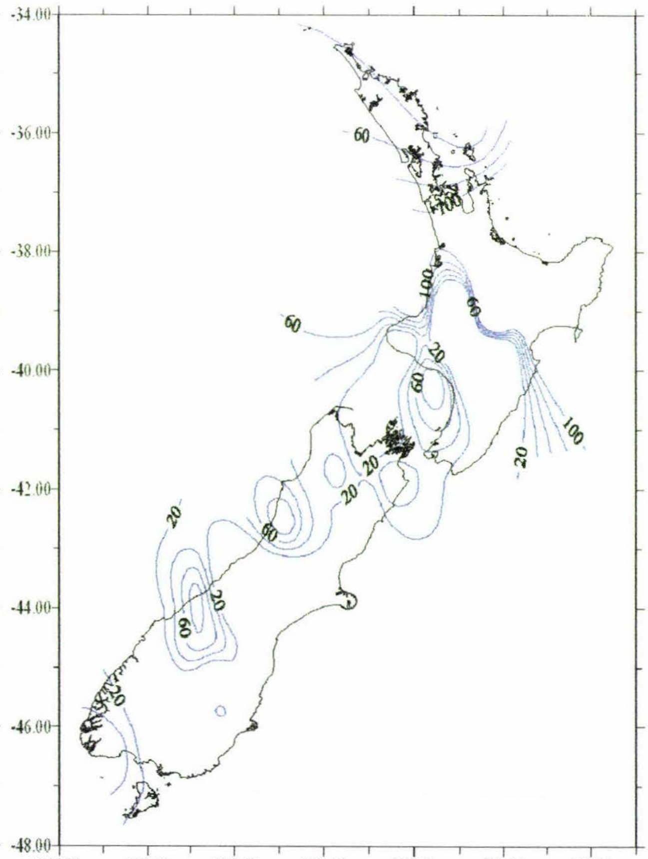
Dacrydium cupressinum 14,500-22,000 BP



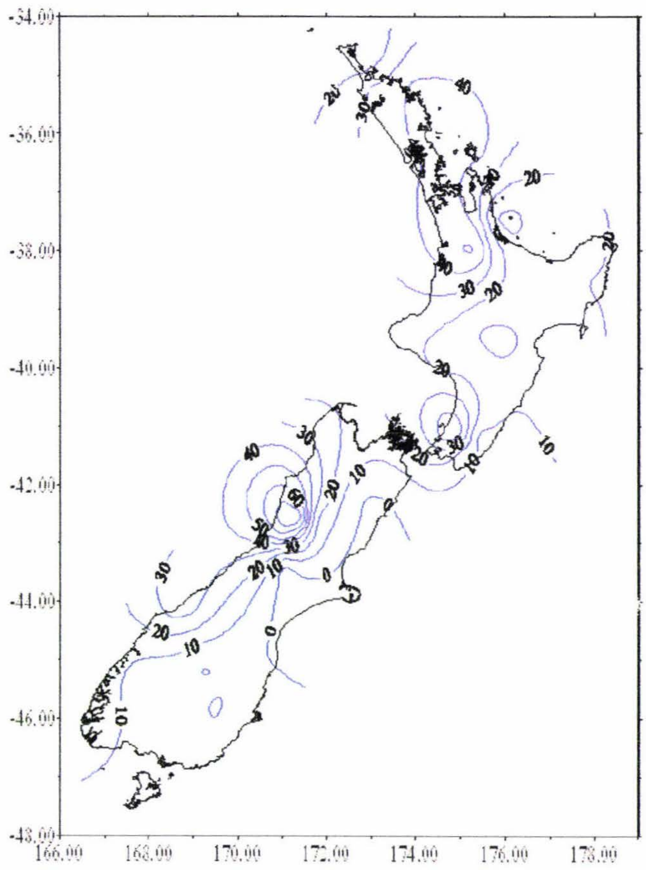
Dacrydium cupressinum 10,000-14,500 BP



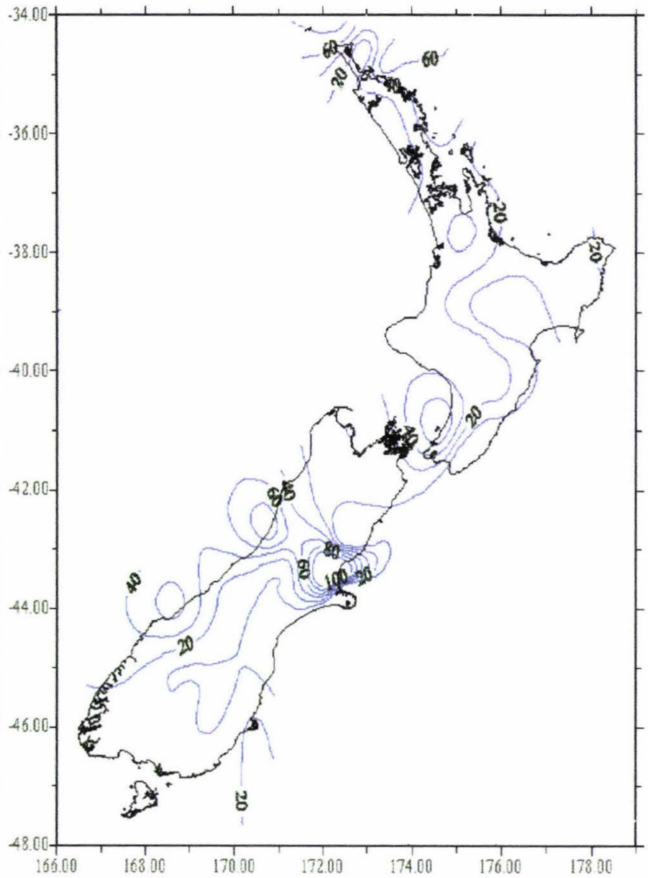
Dacrydium cupressinum 8,000-10,000 BP



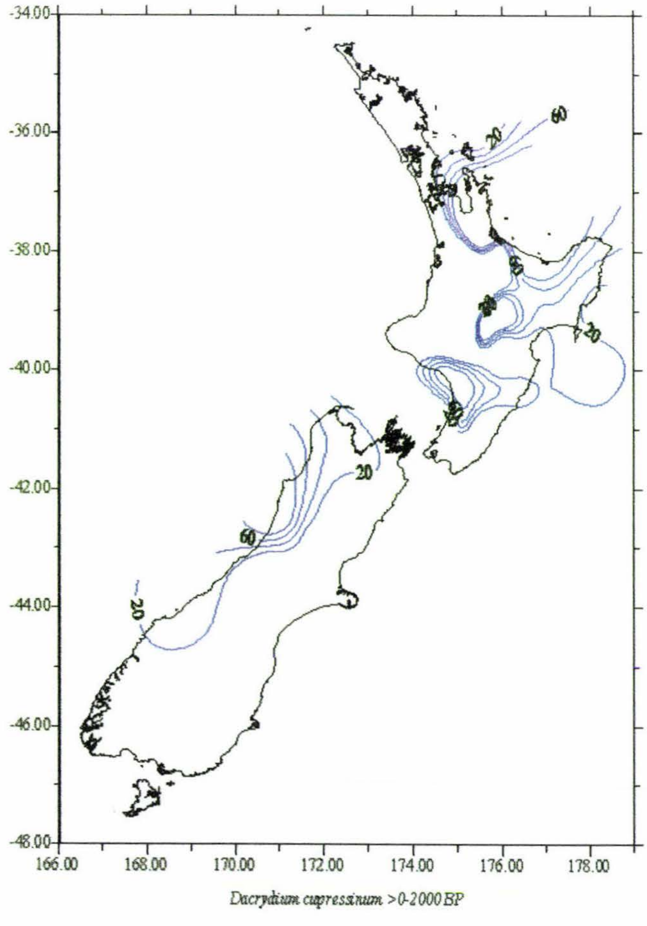
Dacrydium cupressinum 6000-8000 BP



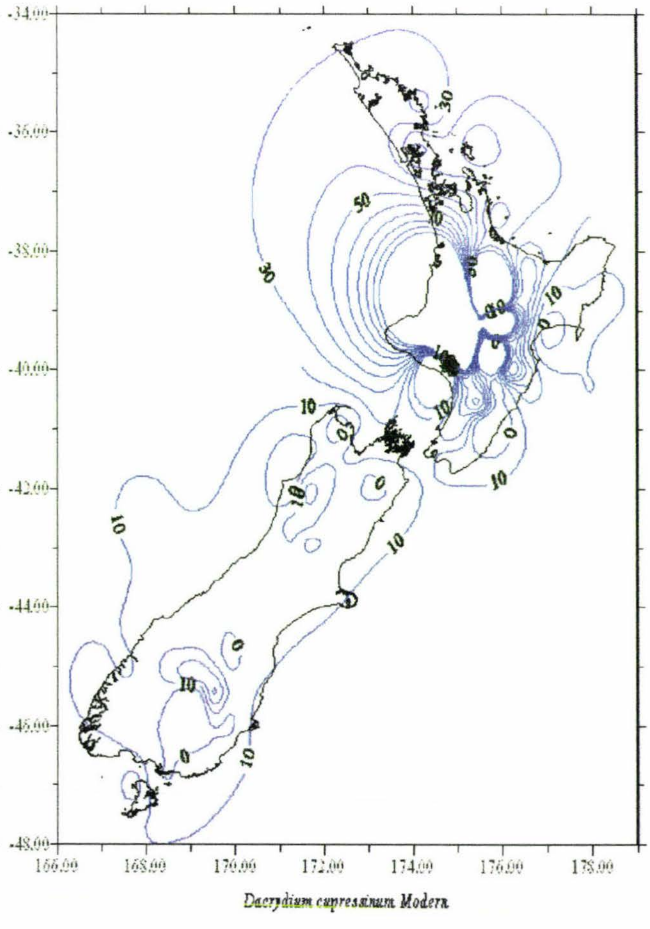
Dacrydium cupressinum 6000 - 4000 BP



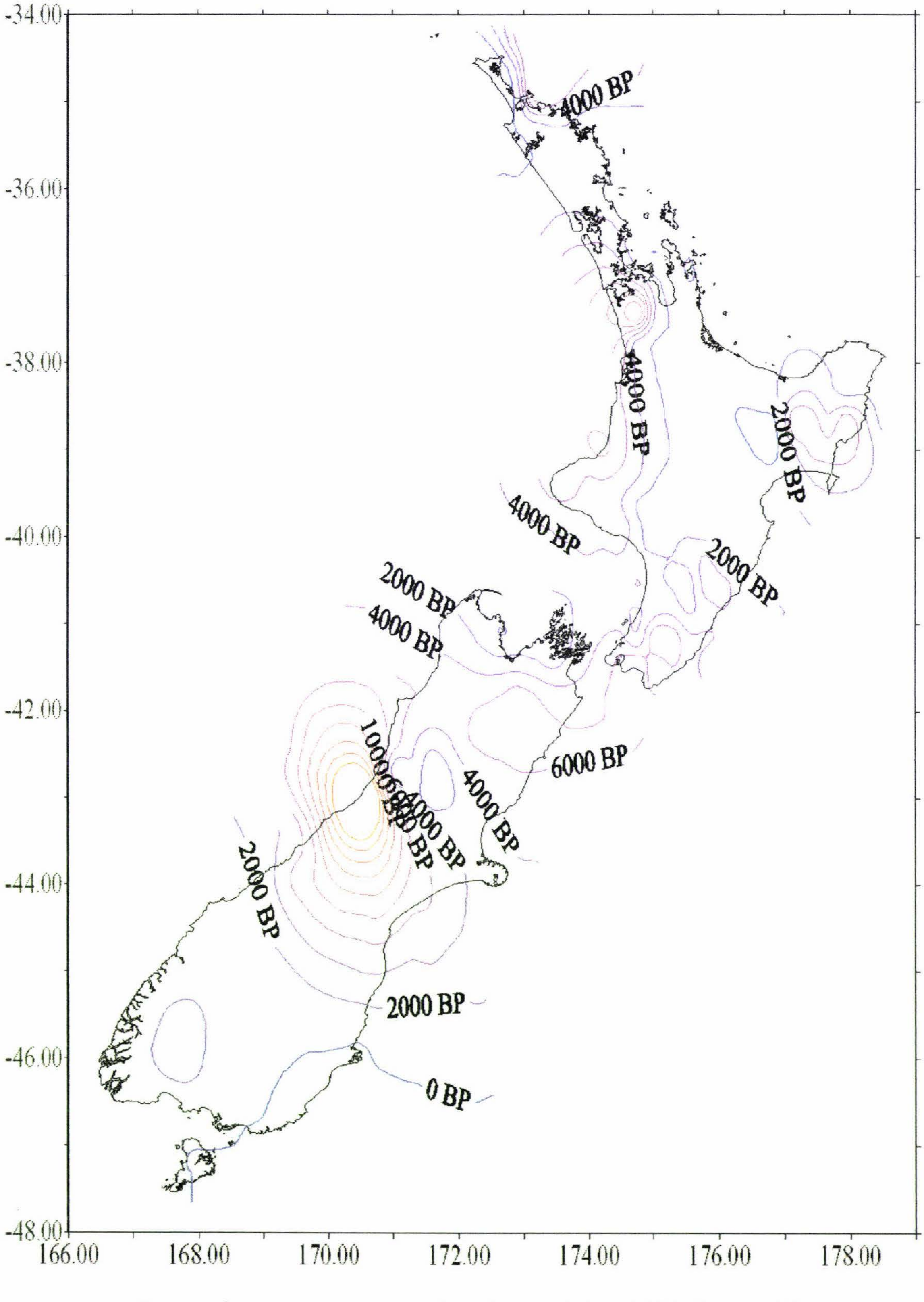
Dacrydium cupressinum 2001-4000 BP



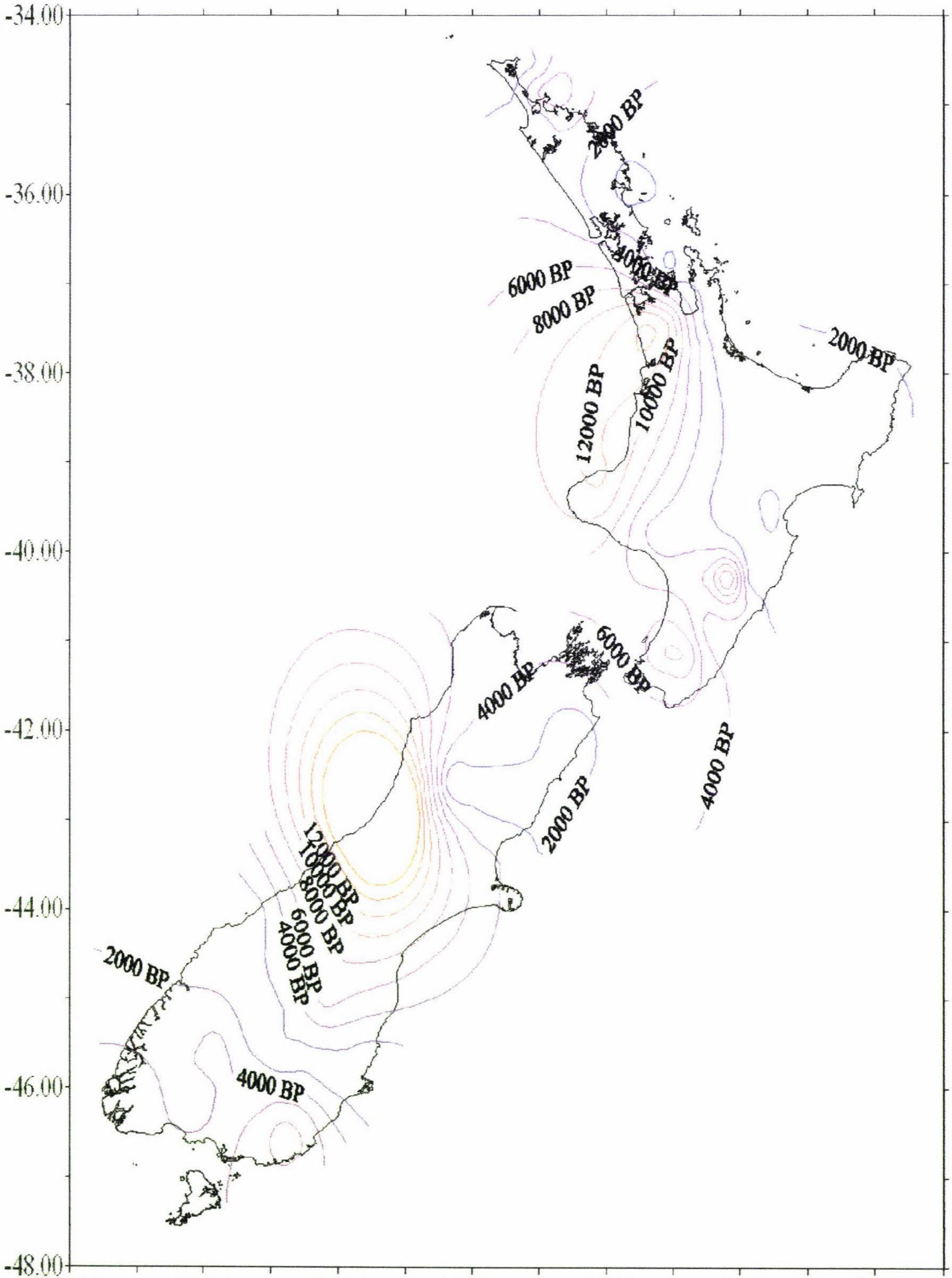
Dacrydium cupressinum >0-2000 BP



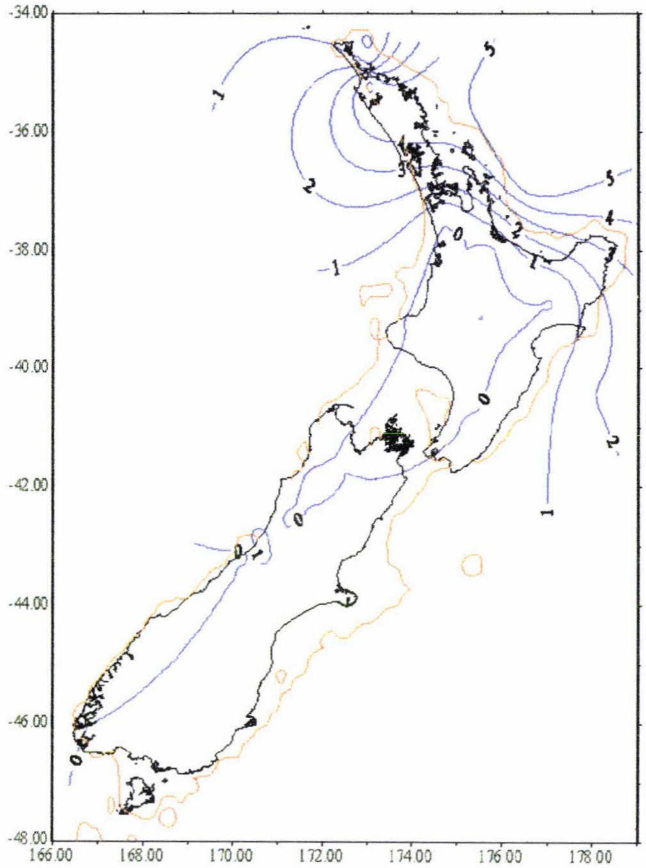
Dacrydium cupressinum Modern



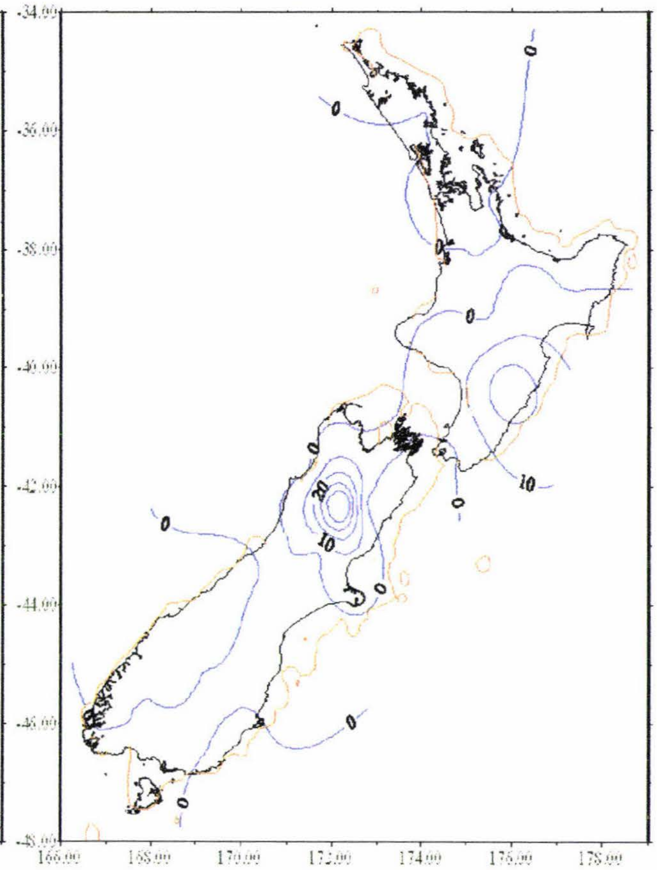
Dacrydium cupressinum Isochrone Map 10% Critical Limit



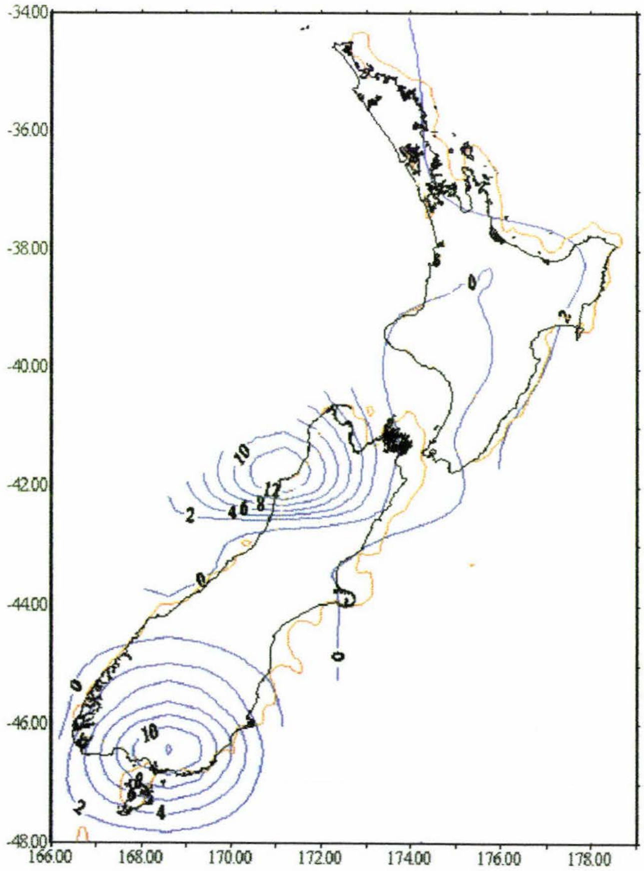
Dacrycarpus dacrydioides Isochrone Map 2% Critical Limit



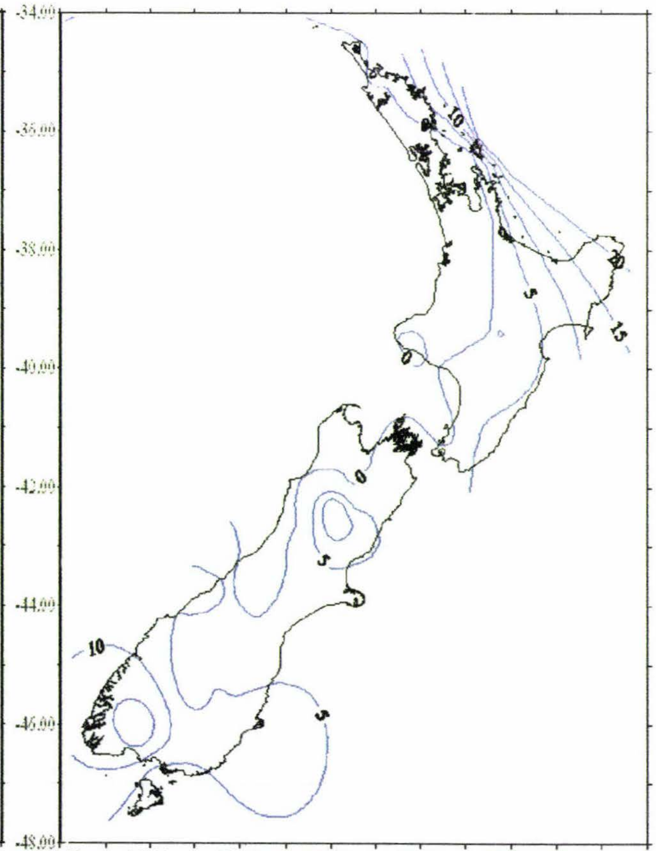
Dacrycarpus dacrydioides 22,000 - 14,500 BP



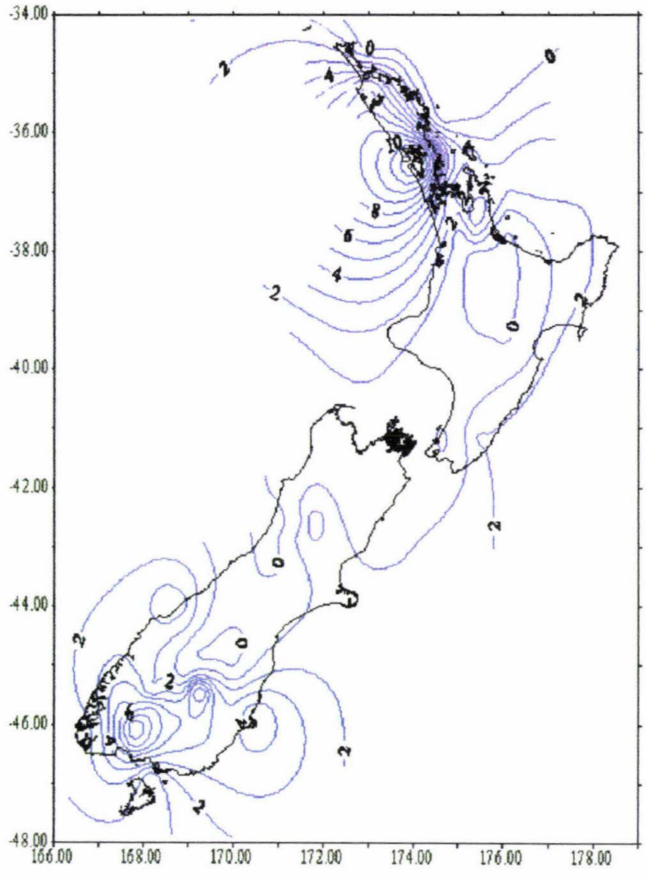
Dacrycarpus dacrydioides 14,500 - 10,000 BP



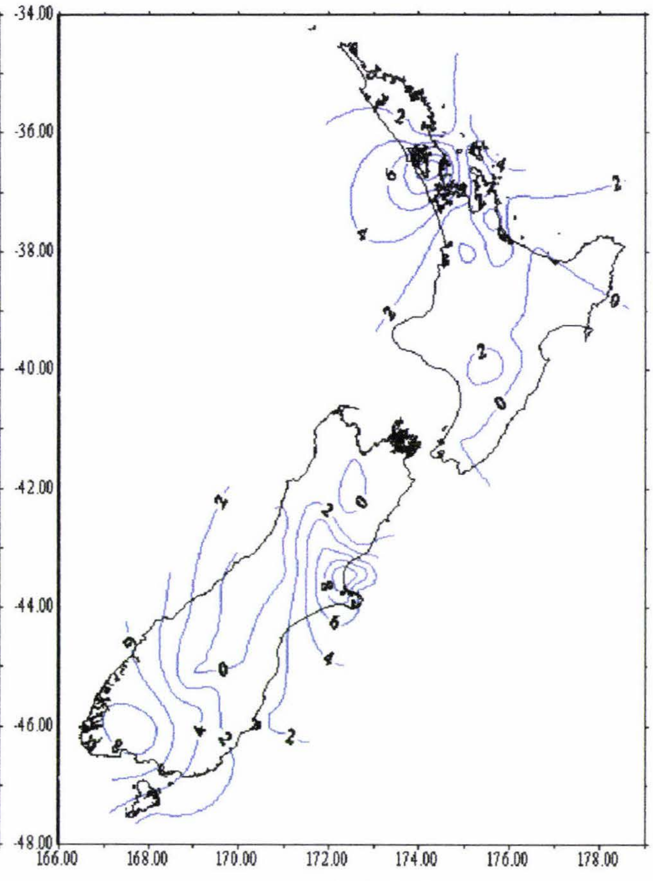
Dacrycarpus dacrydioides 10,000 - 8,000 BP



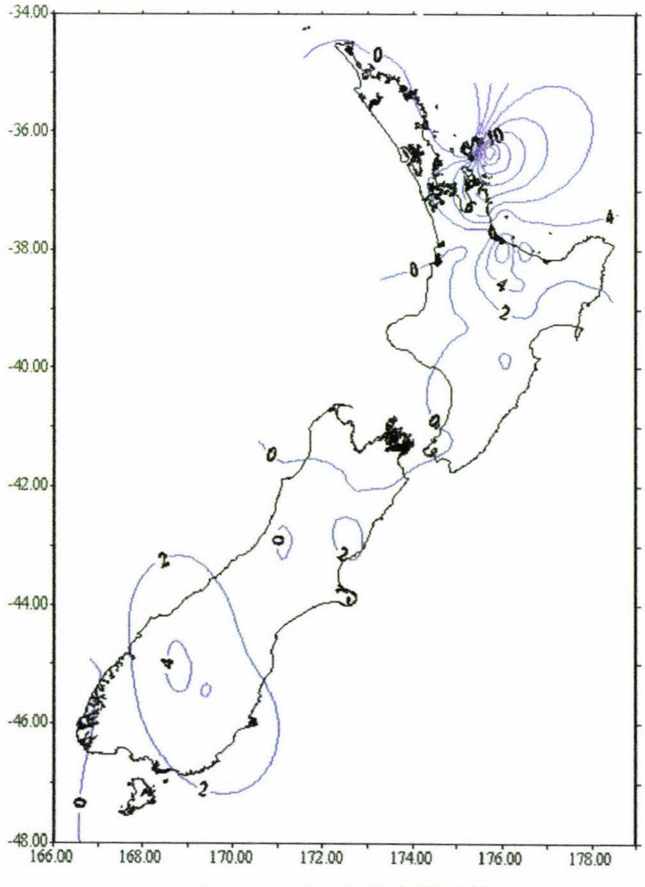
Dacrycarpus dacrydioides 8,000 - 6,000 BP



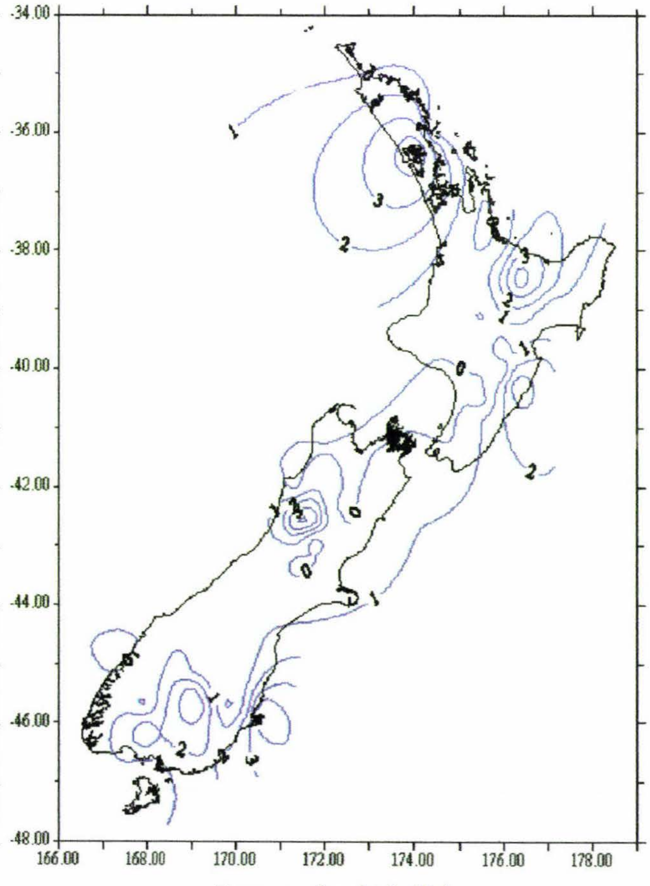
Dacrycarpus dacrydioides 4,000 - 6,000 BP



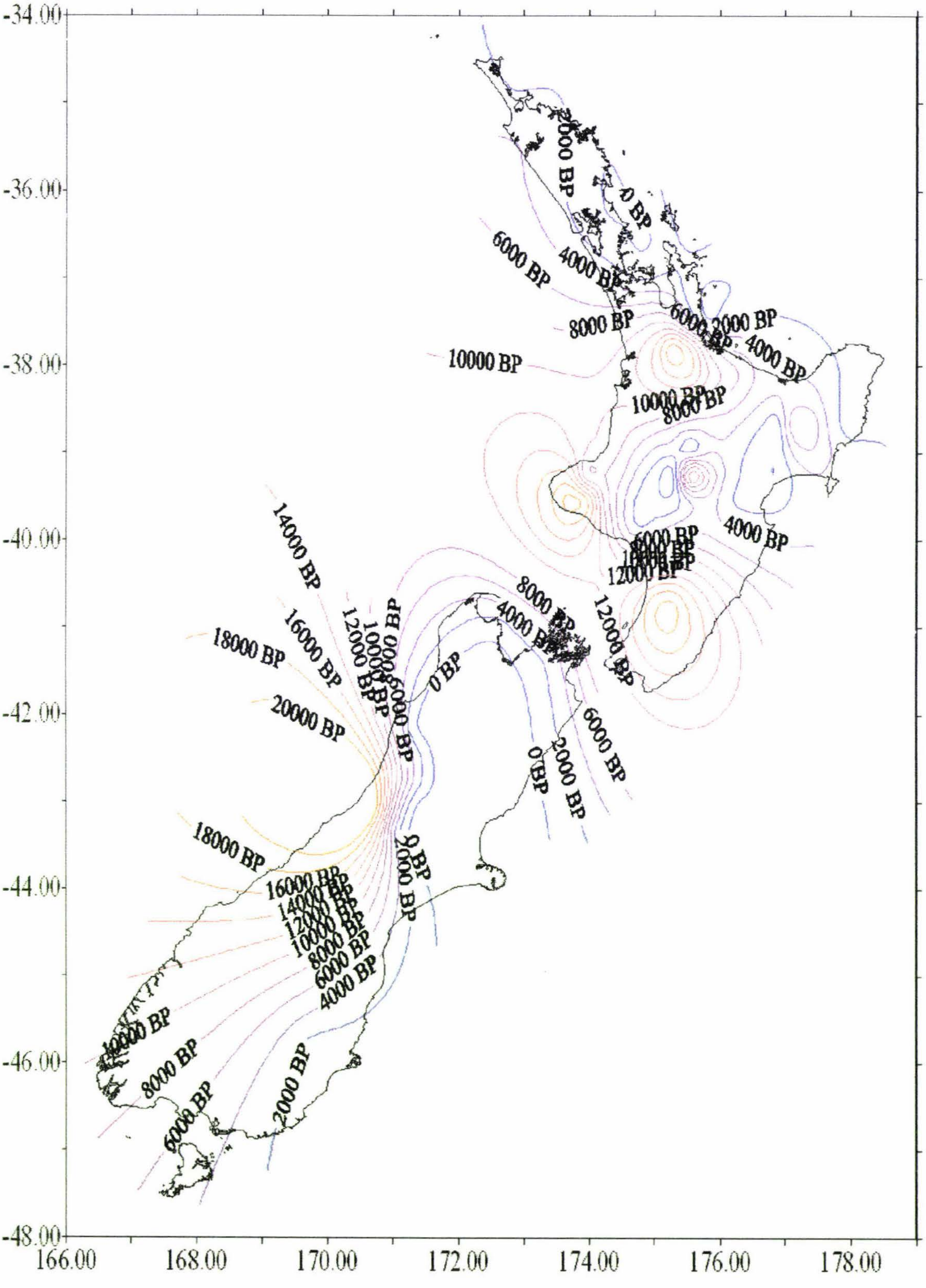
Dacrycarpus dacrydioides 4,000 - 2,000 BP



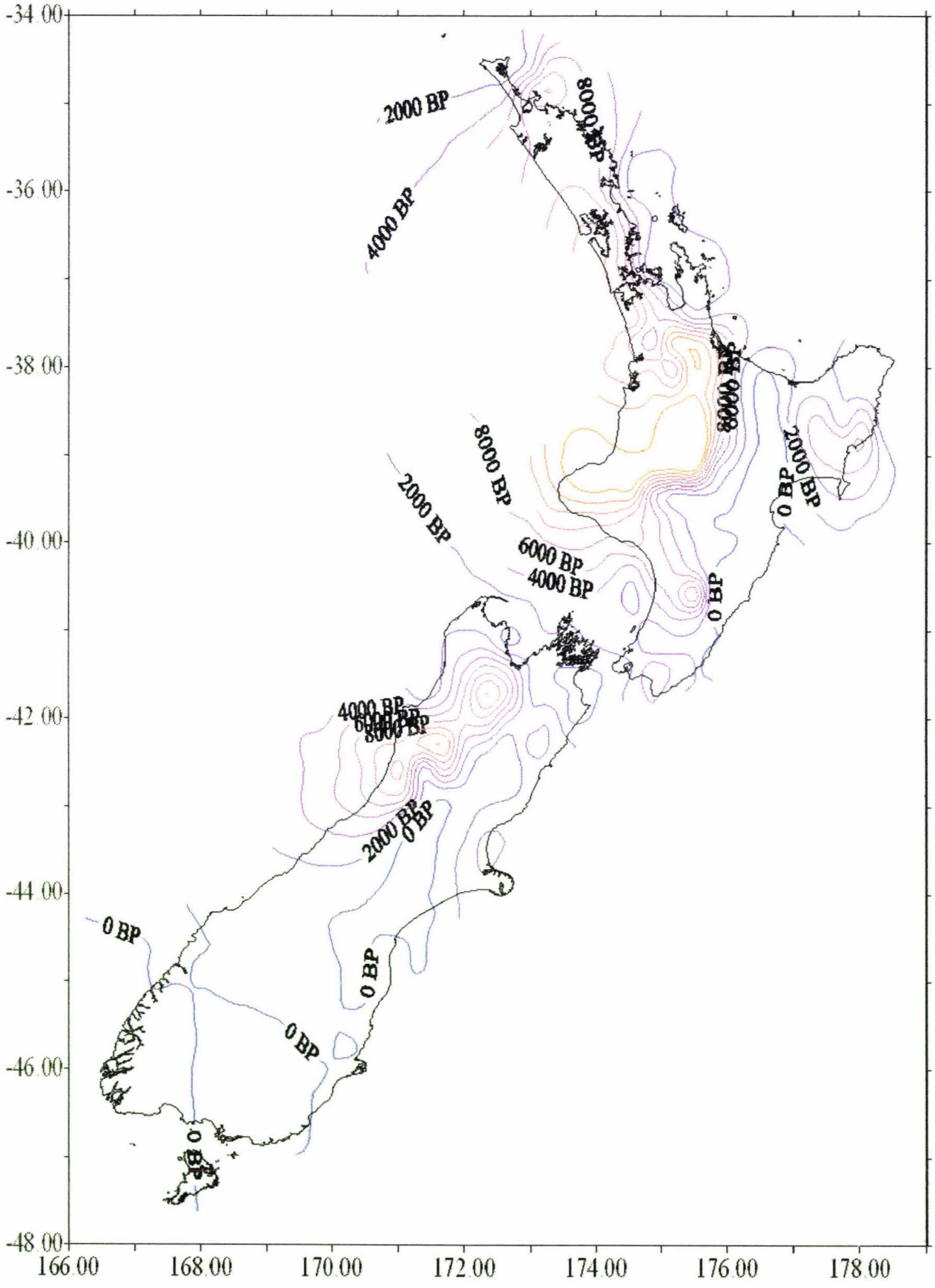
Dacrycarpus dacrydioides 2,000 - 0 BP



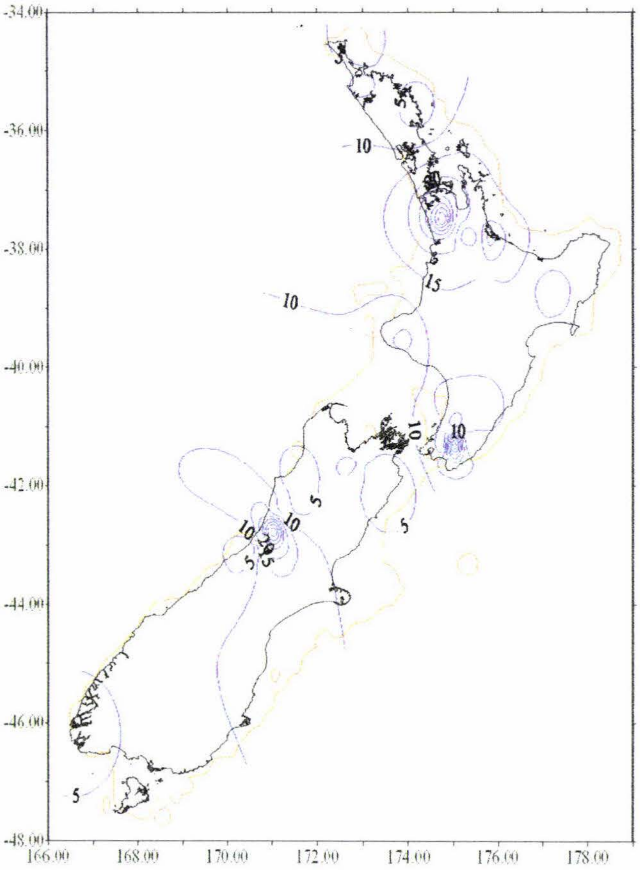
Dacrycarpus dacrydioides Modern



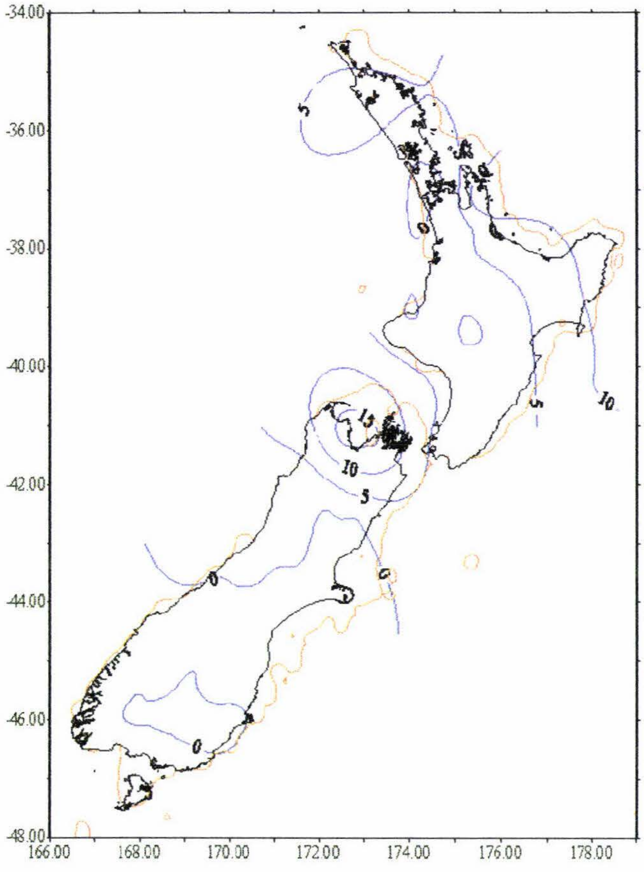
Libocedrus spp Isochrone Map 1% Critical Limit



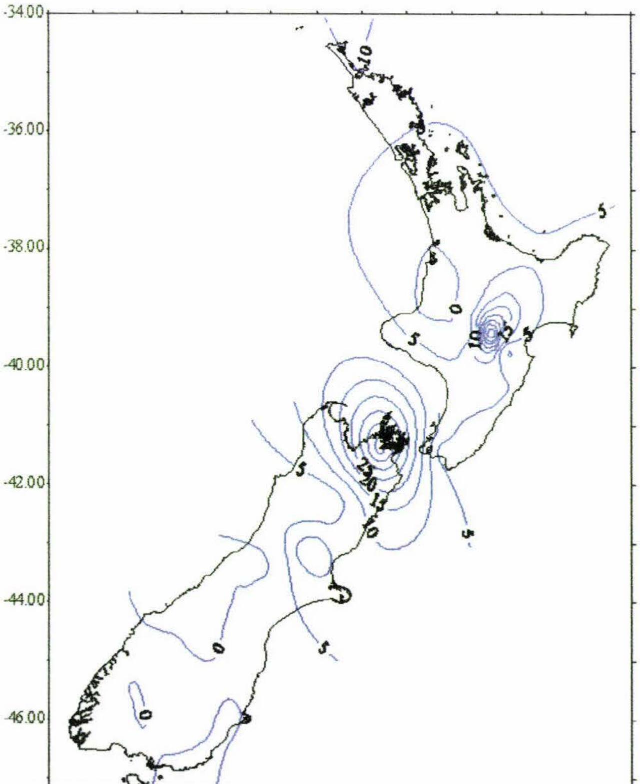
Nothofagus fusca Isochrone Map 5% Critical Limit



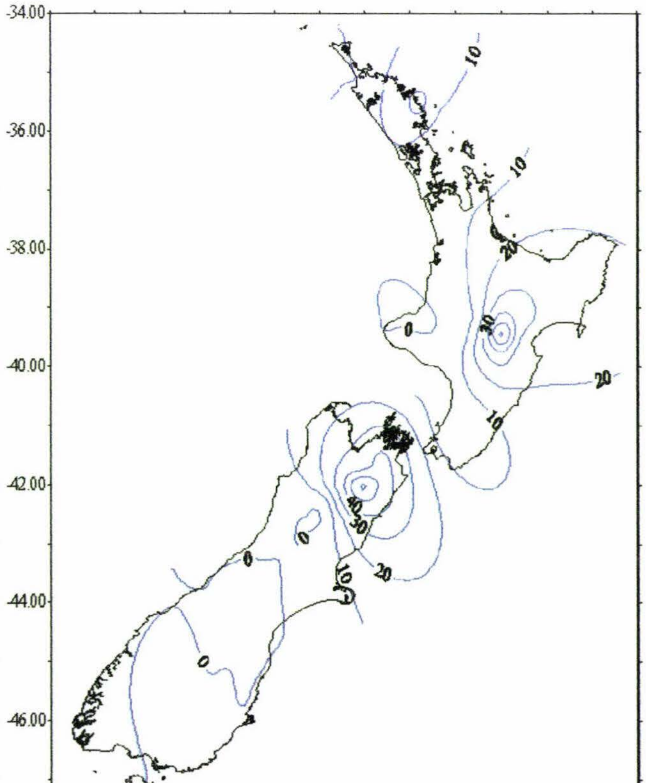
Nothofagus fusca 22,000 - 14,500 BP



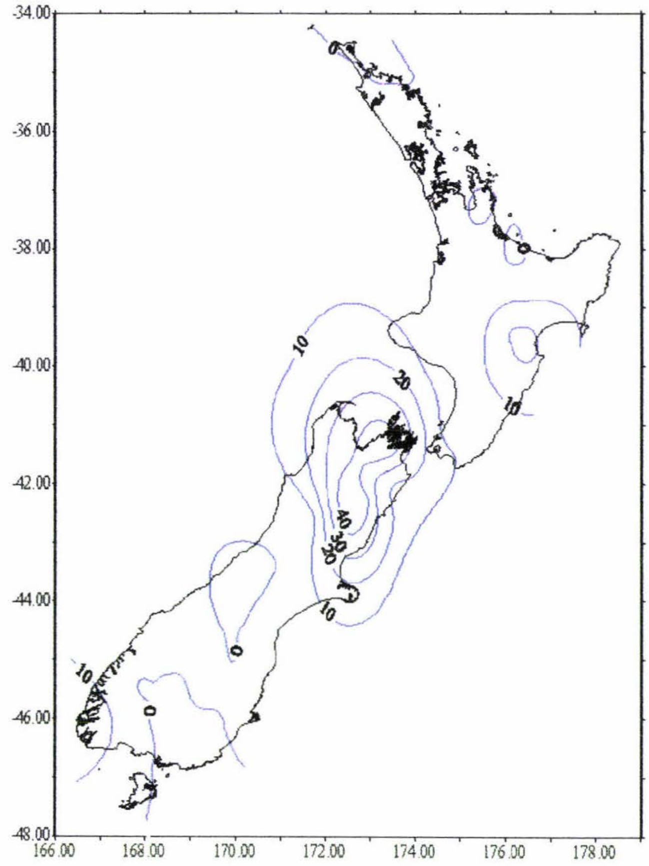
Nothofagus fusca 14,500 - 10,000 BP



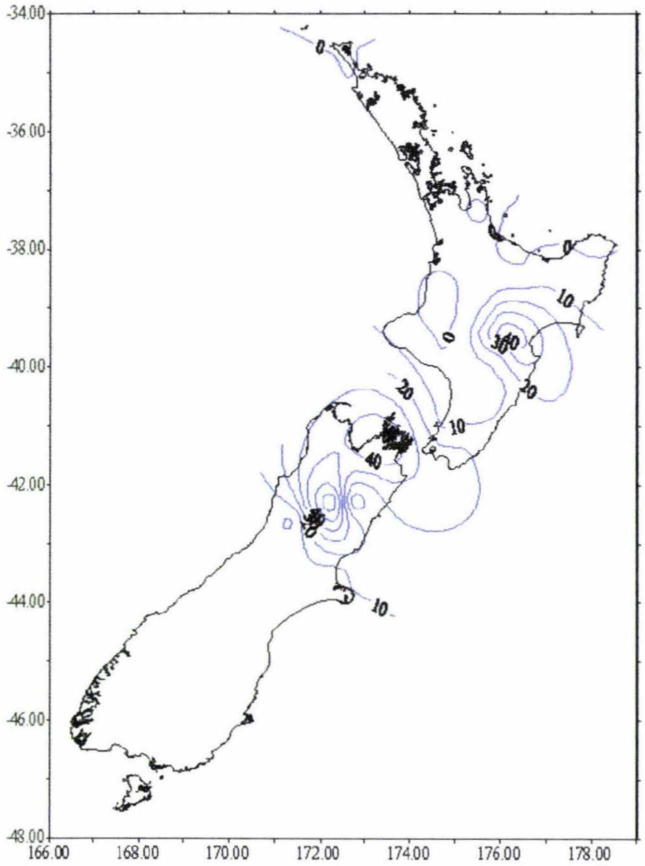
Nothofagus fusca 10,000 - 8,000 BP



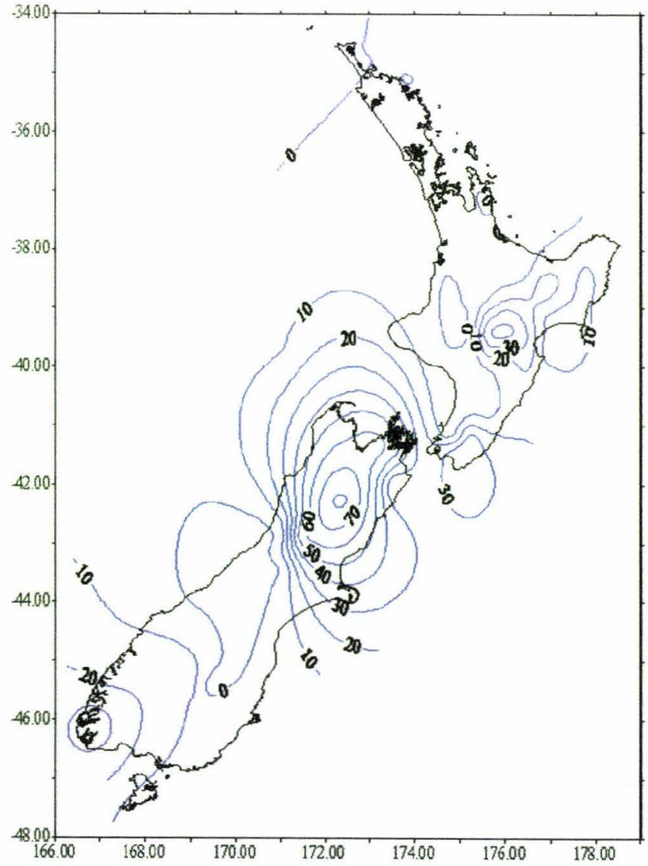
Nothofagus fusca 8,000 - 6,000 BP



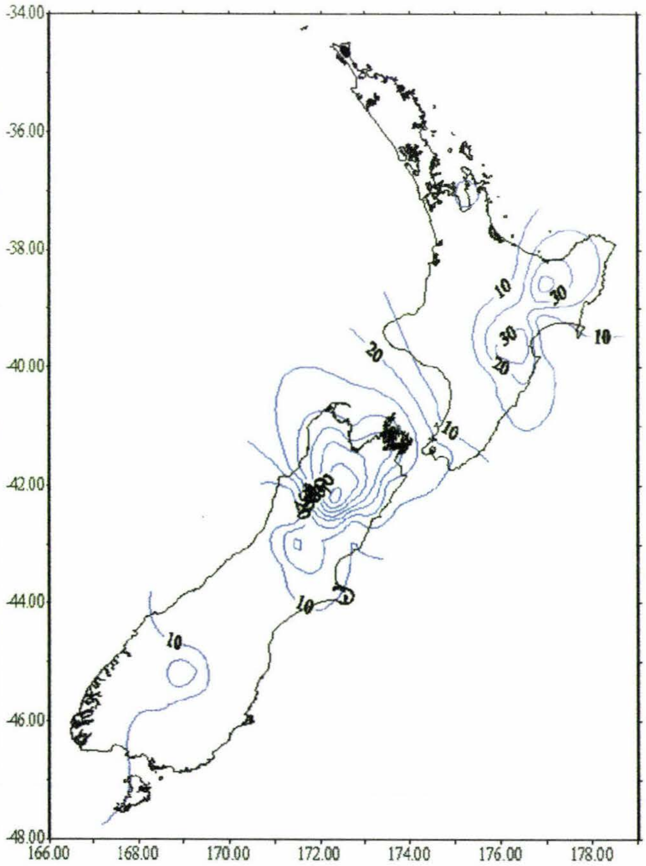
Nothofagus fusca 6,000 - 4,000 BP



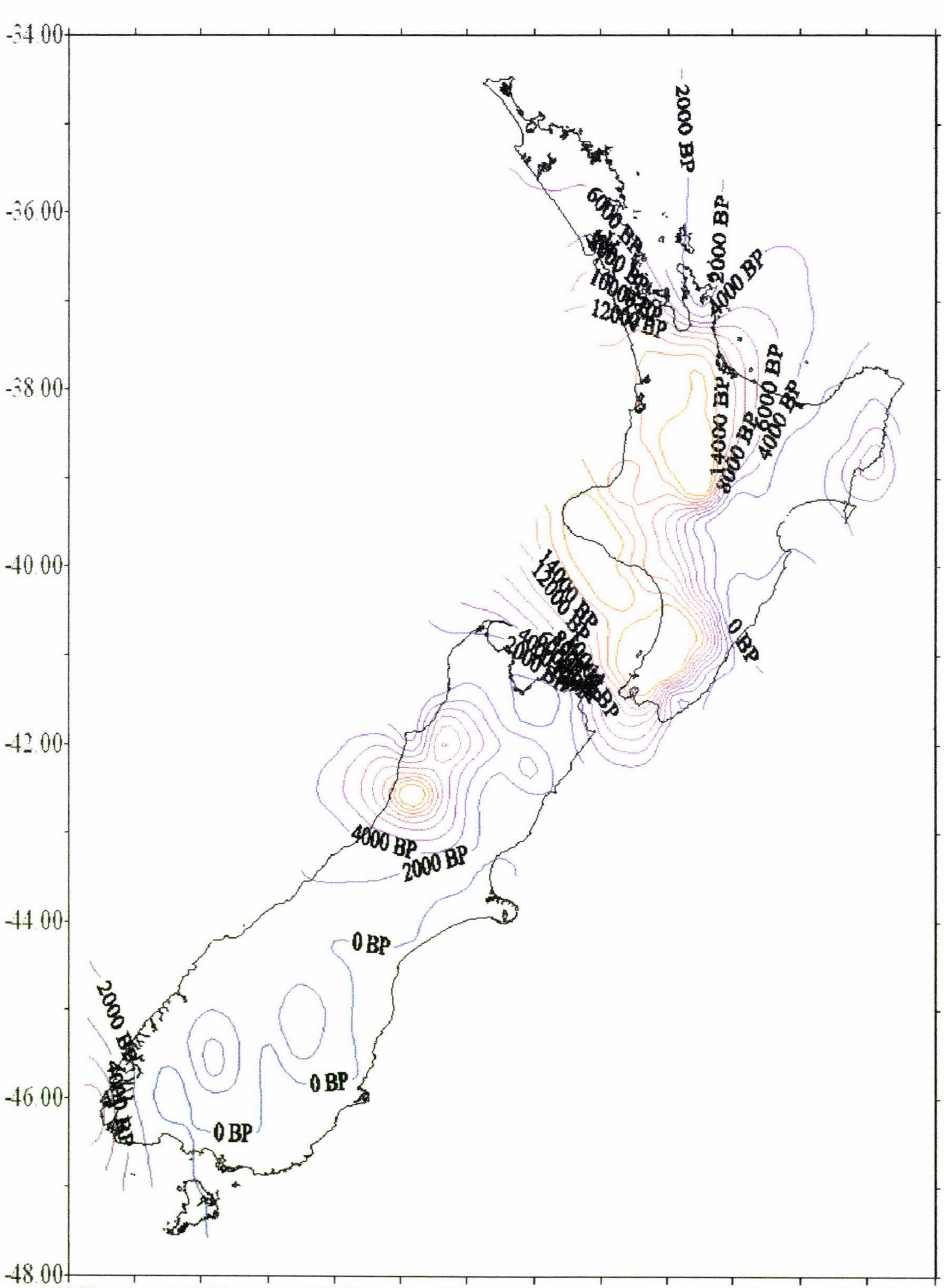
Nothofagus fusca 4,000 - 2,000 BP



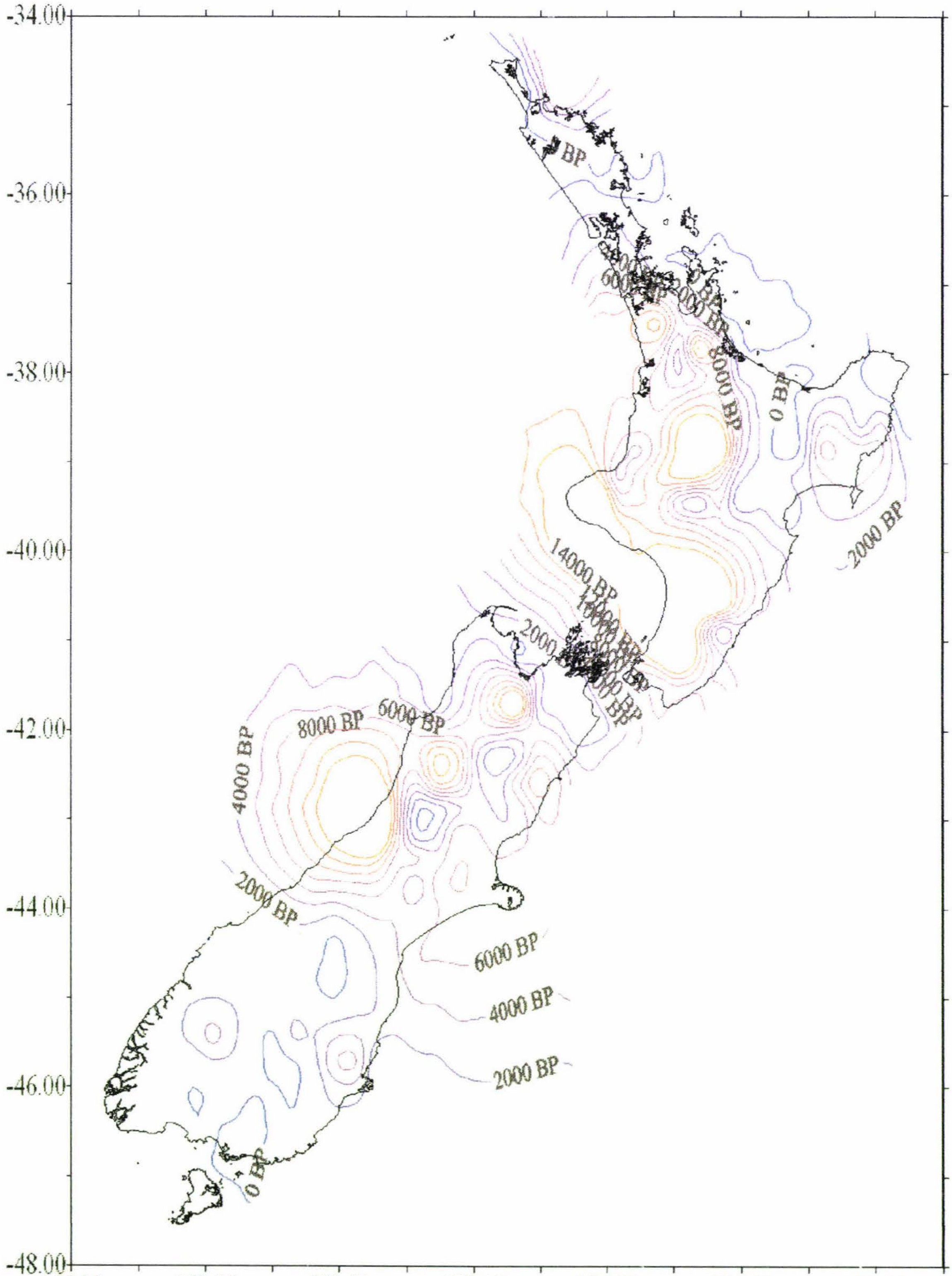
Nothofagus fusca 2,000 - 0 BP



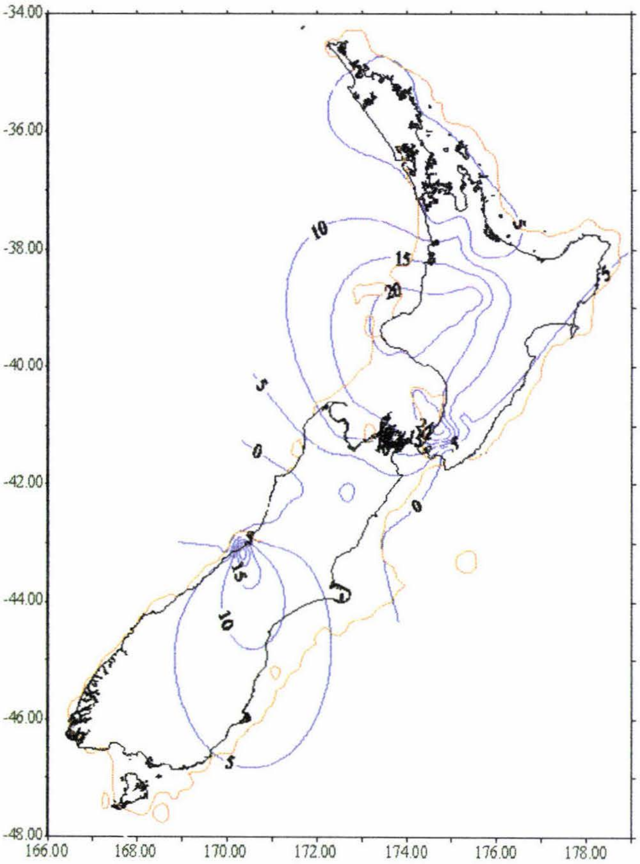
Nothofagus fusca Modern



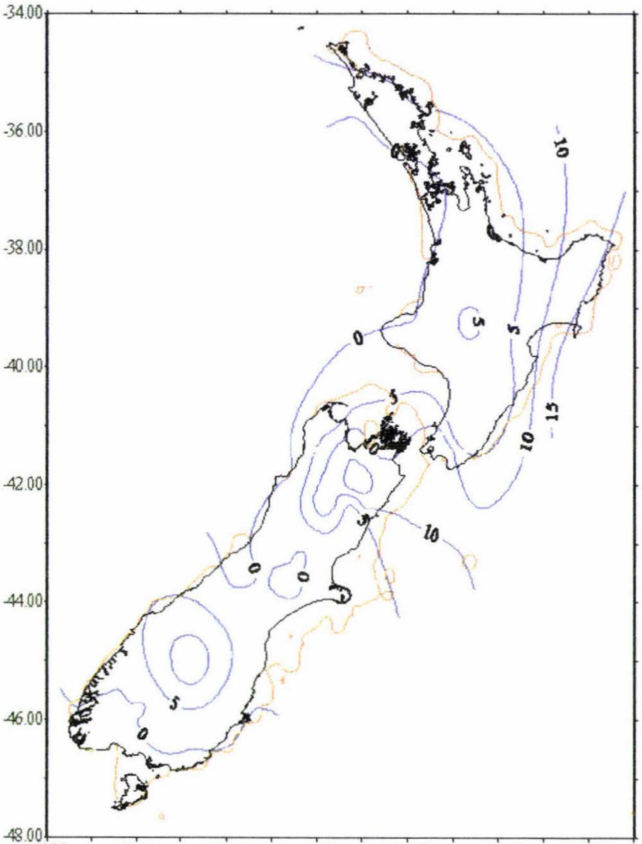
Nothofagus menziesii Isochrone Map 1% Critical Limit



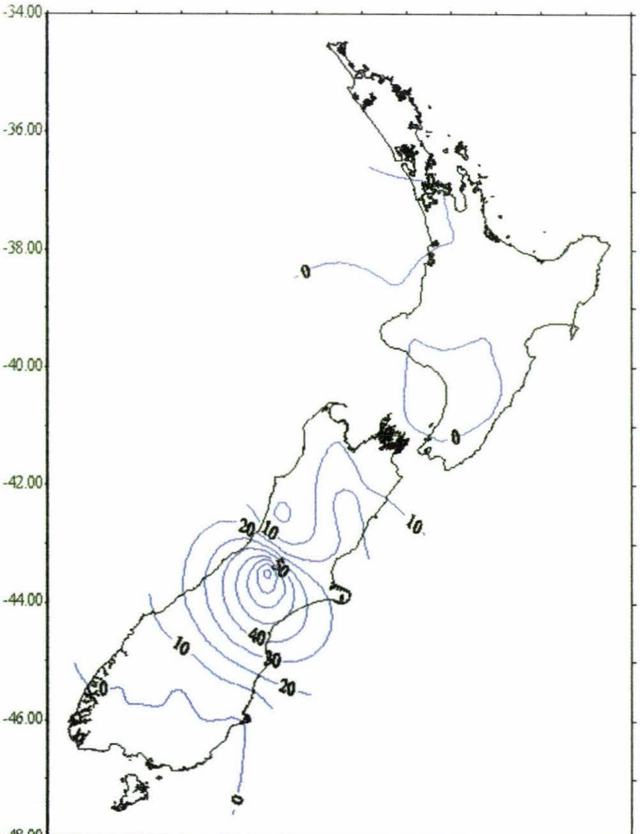
Phyllocladus spp Isochrone Map 1% Critical Limit



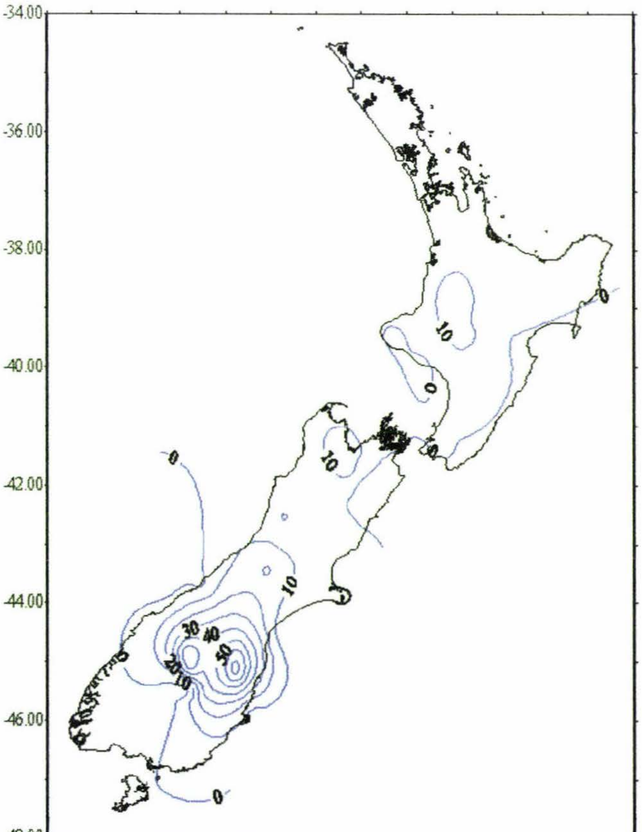
Phyllocladus spp 22,000 - 14,500 BP



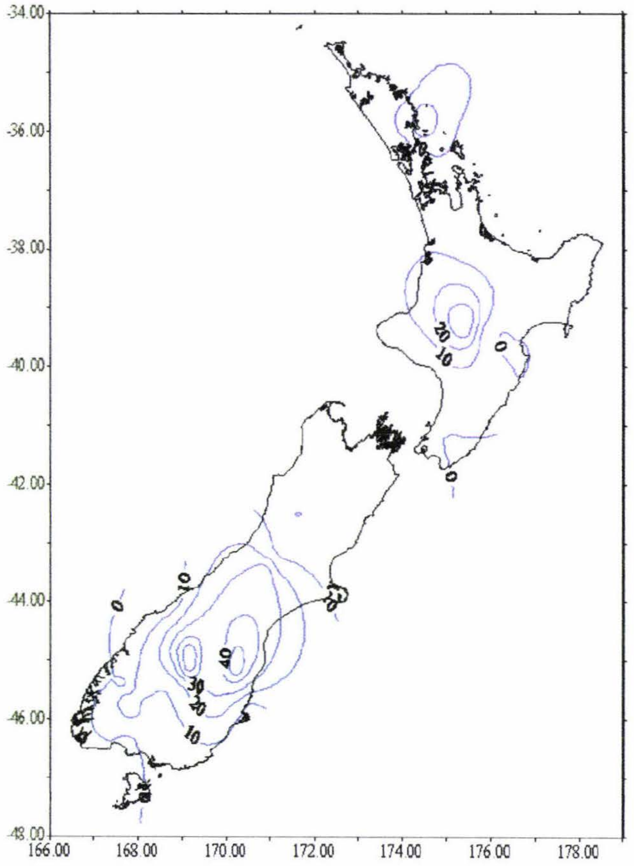
Phyllocladus spp 14,500 - 10,000 BP



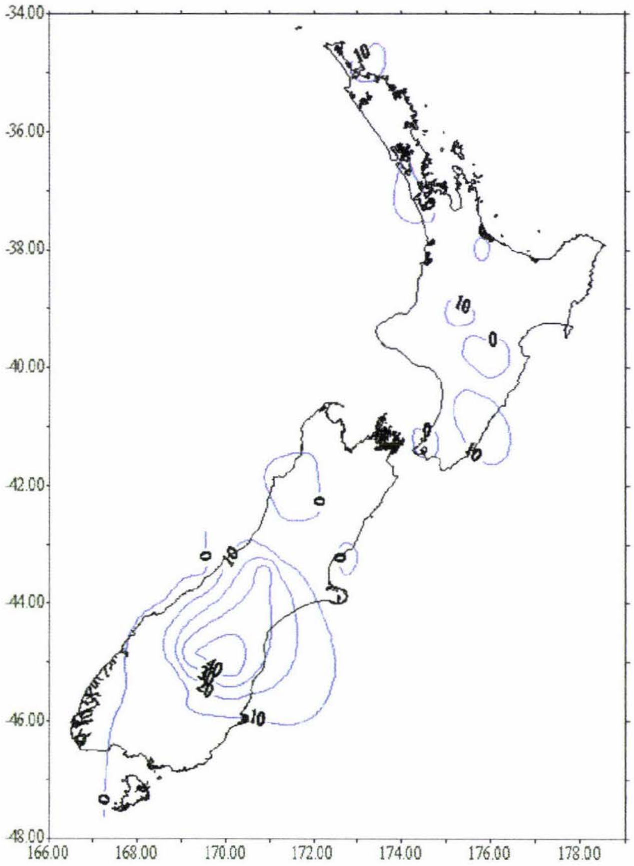
Phyllocladus spp 10,000 - 8,000 BP



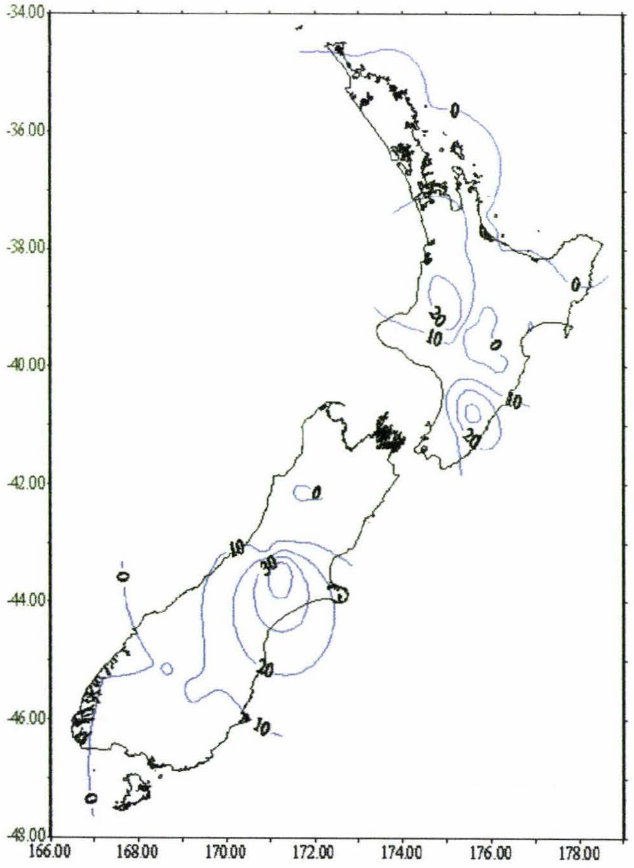
Phyllocladus spp 8,000 - 6,000 BP



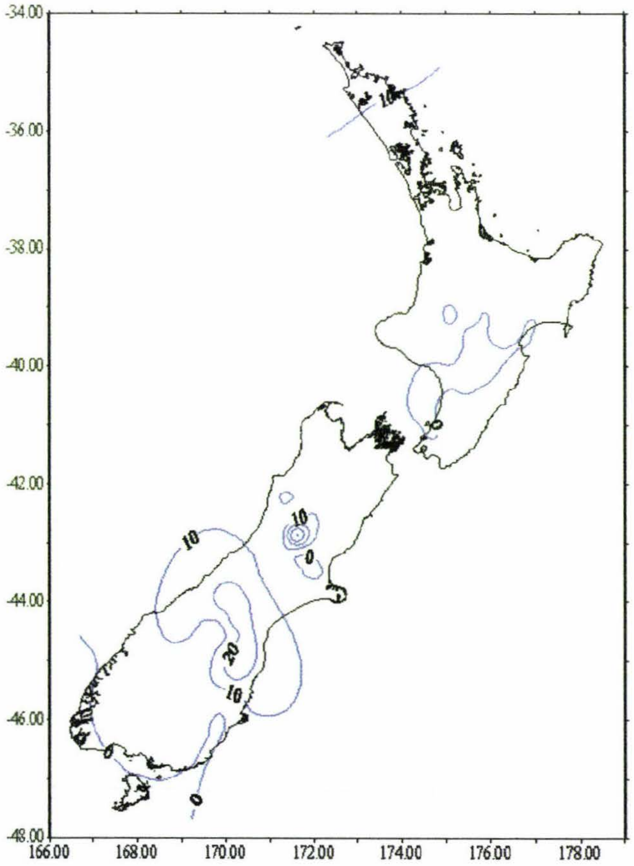
Phyllocladus spp 6,000 - 4,000 BP



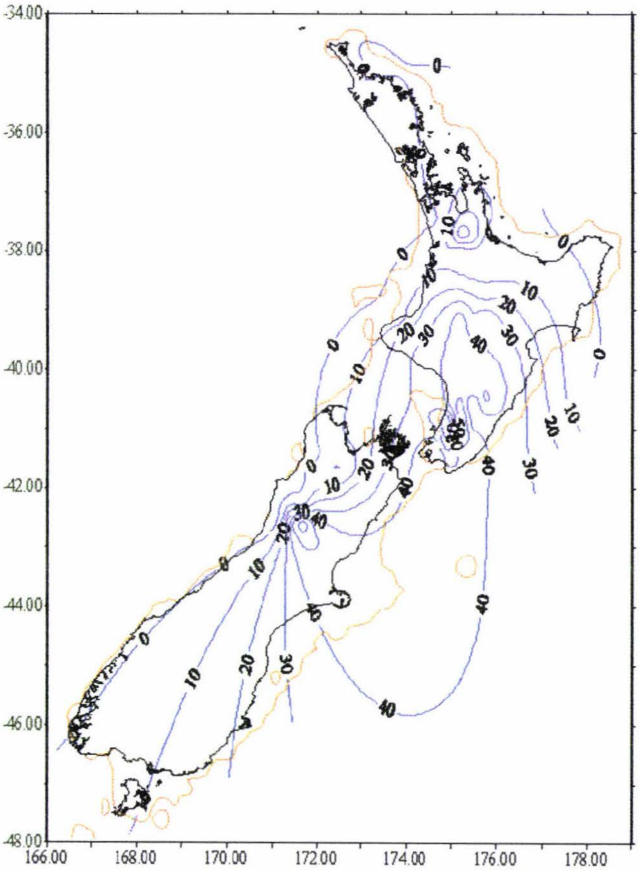
Phyllocladus spp 4,000 - 2,000 BP



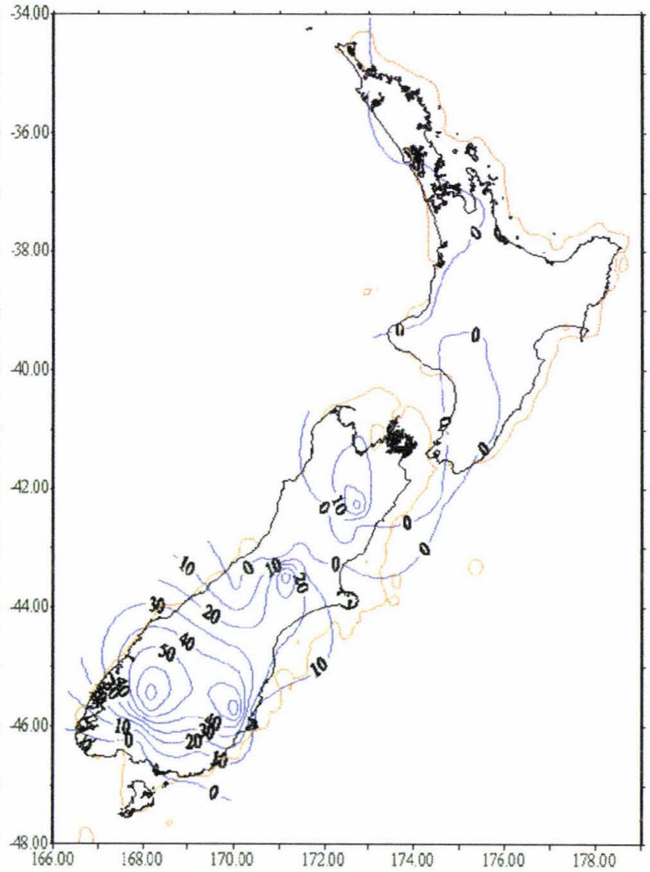
Phyllocladus spp 2,000 - 0 BP



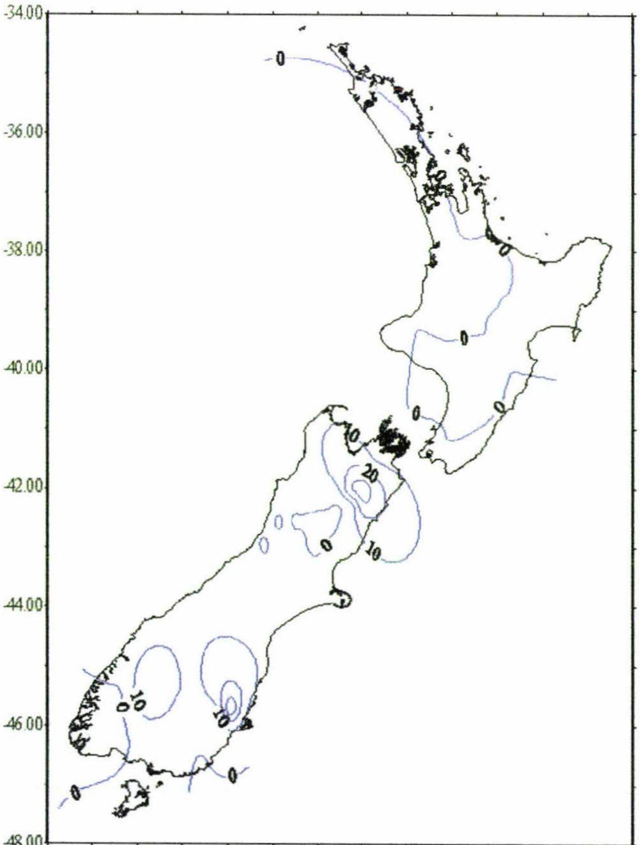
Phyllocladus spp Modern



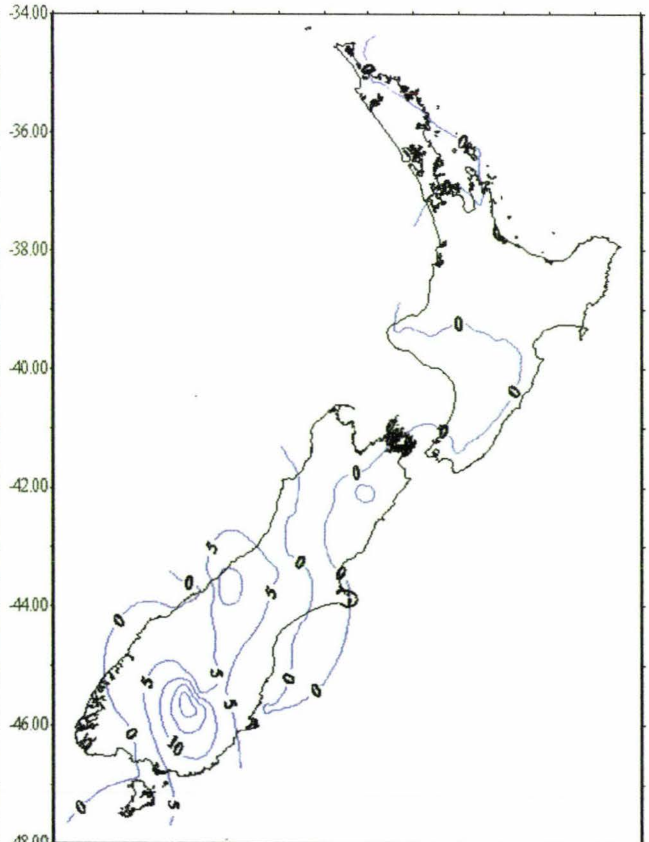
Poaceae spp 22,000 - 14,500 BP



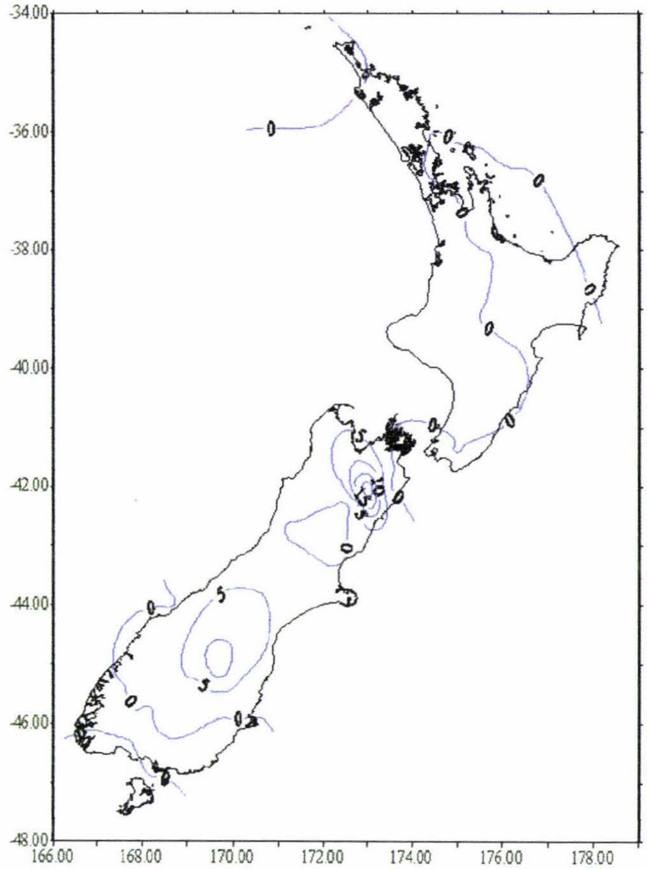
Poaceae spp 14,500 - 10,000 BP



Poaceae spp 10,000 - 8,000 BP



Poaceae spp 8,000 - 6,000 BP



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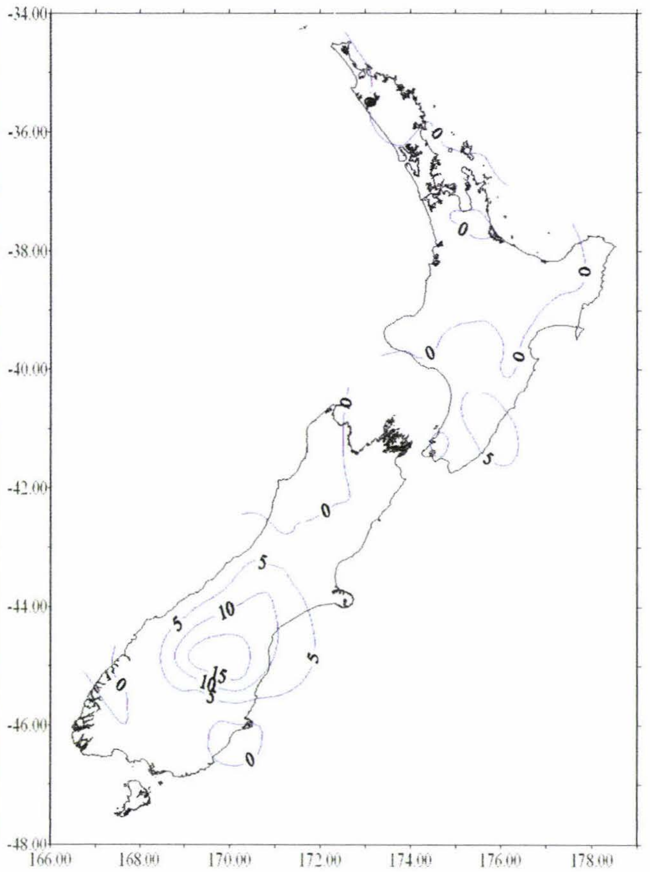
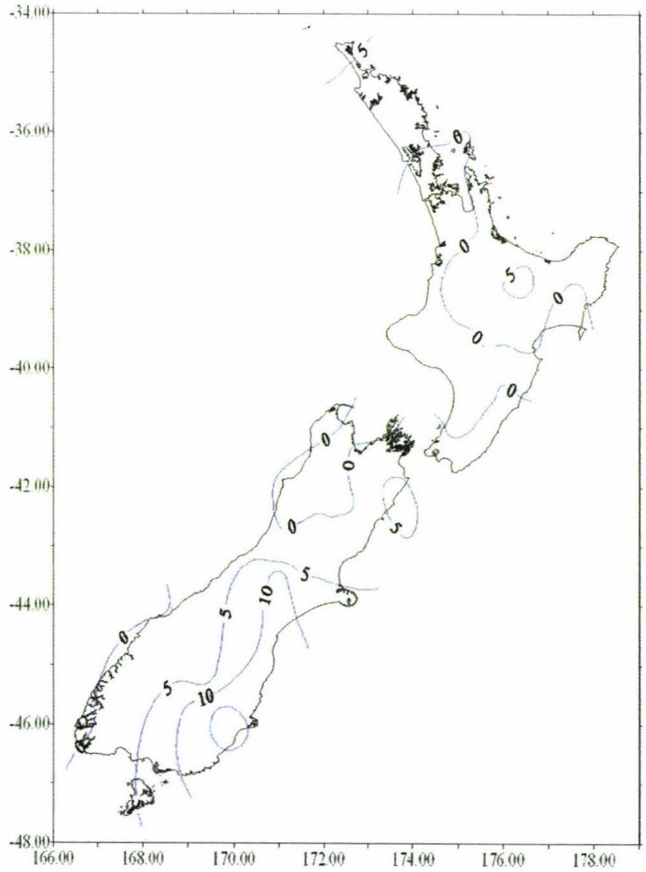


Poaceae spp 4,000 - 2,000 BP



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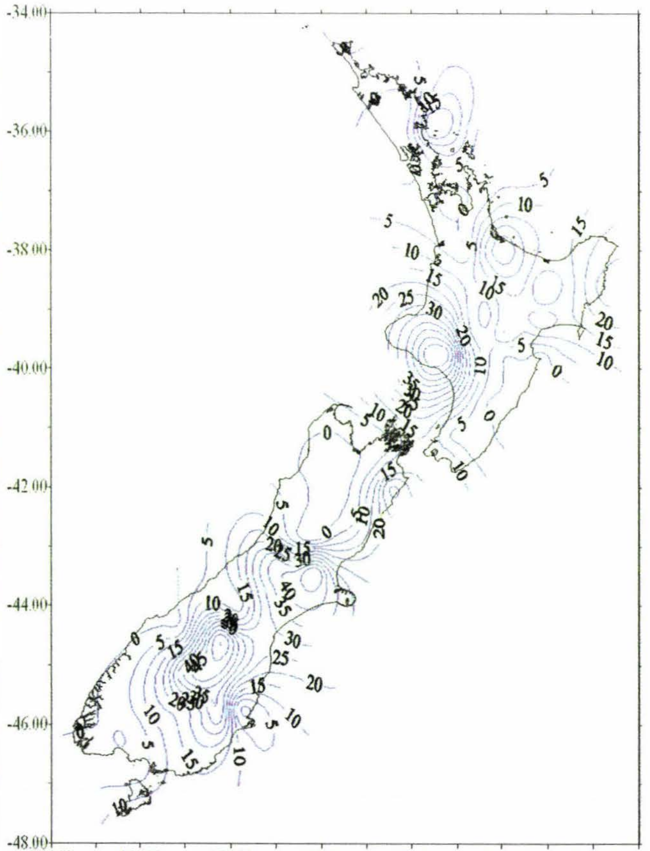
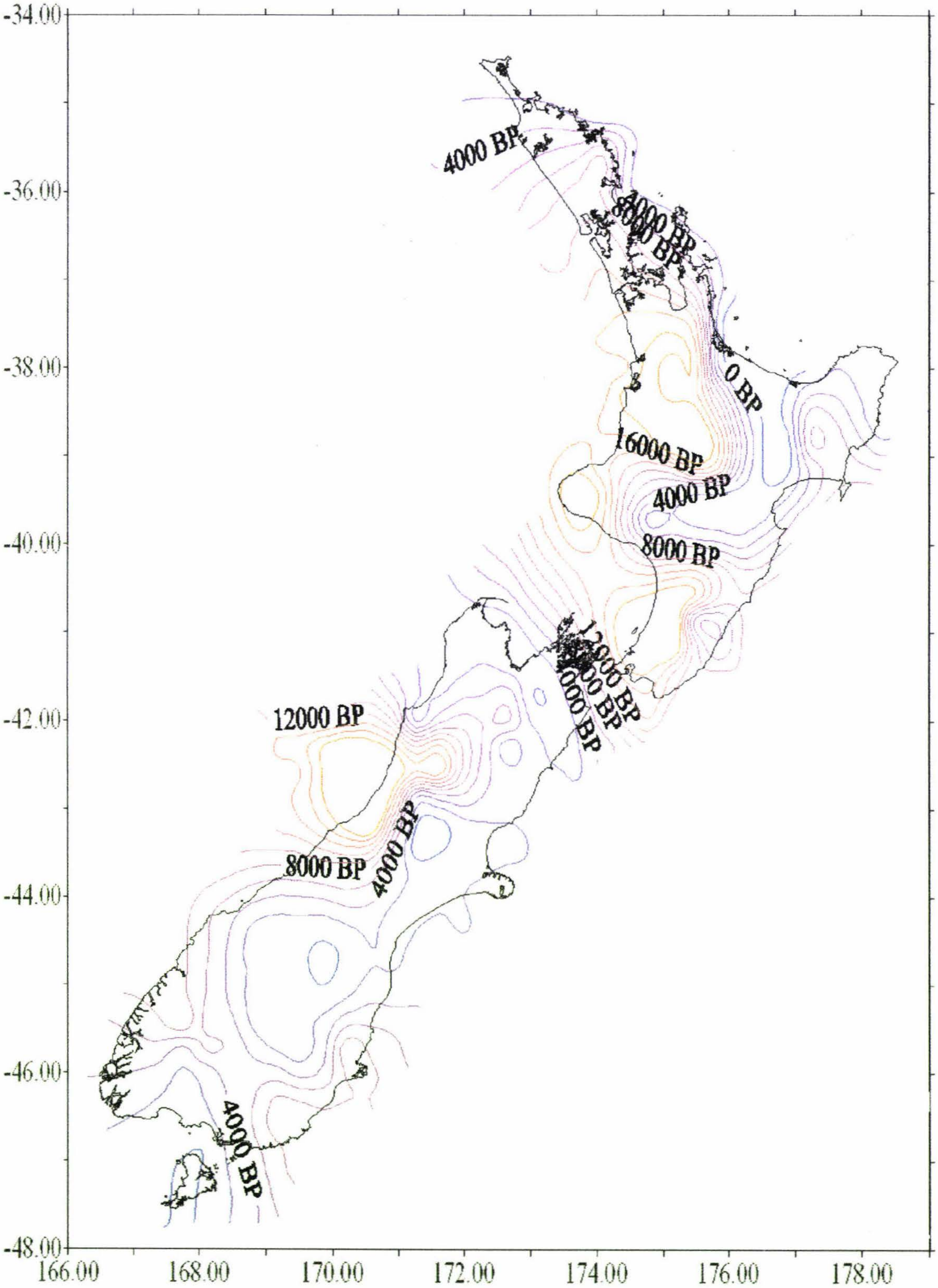
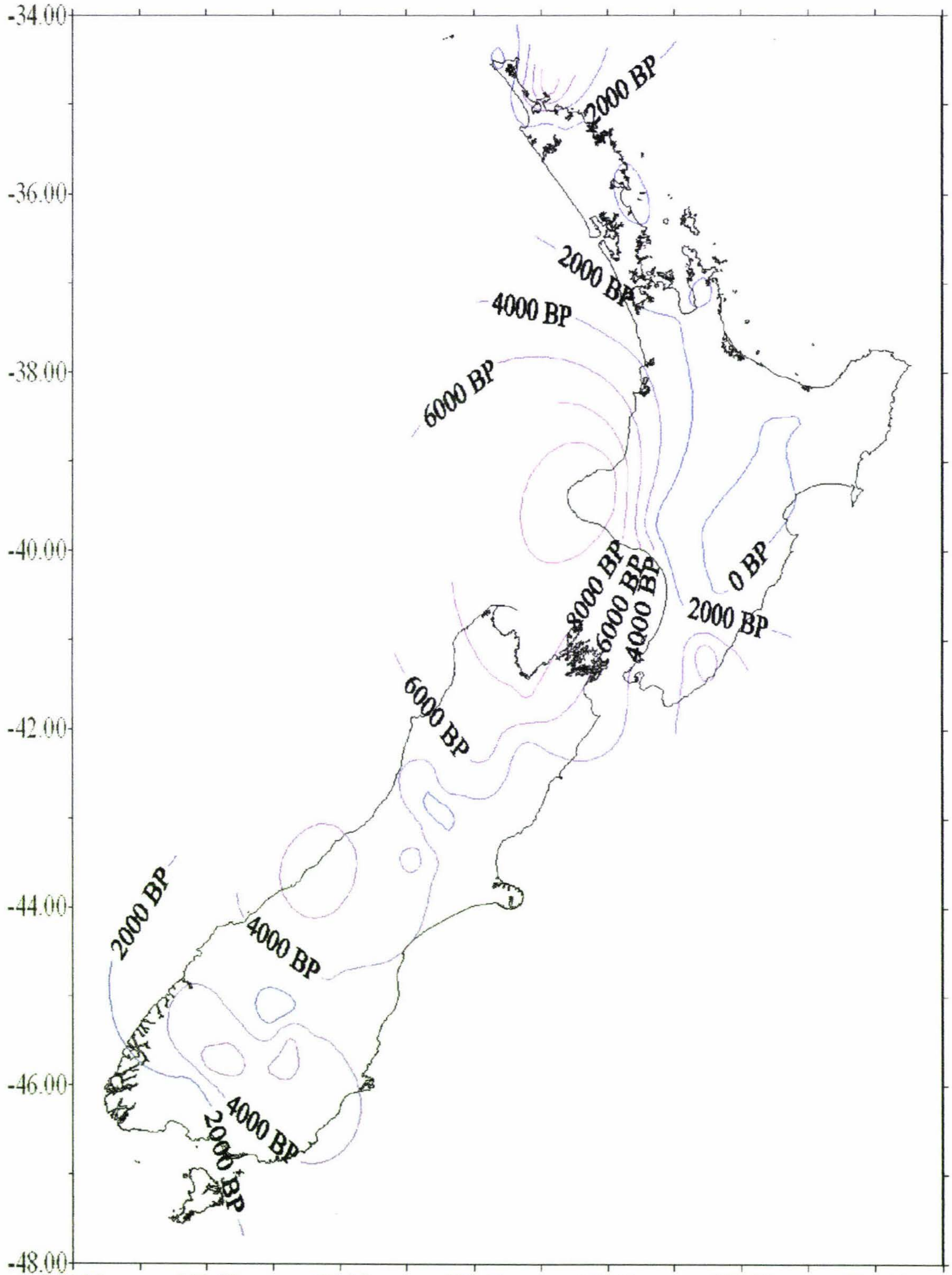


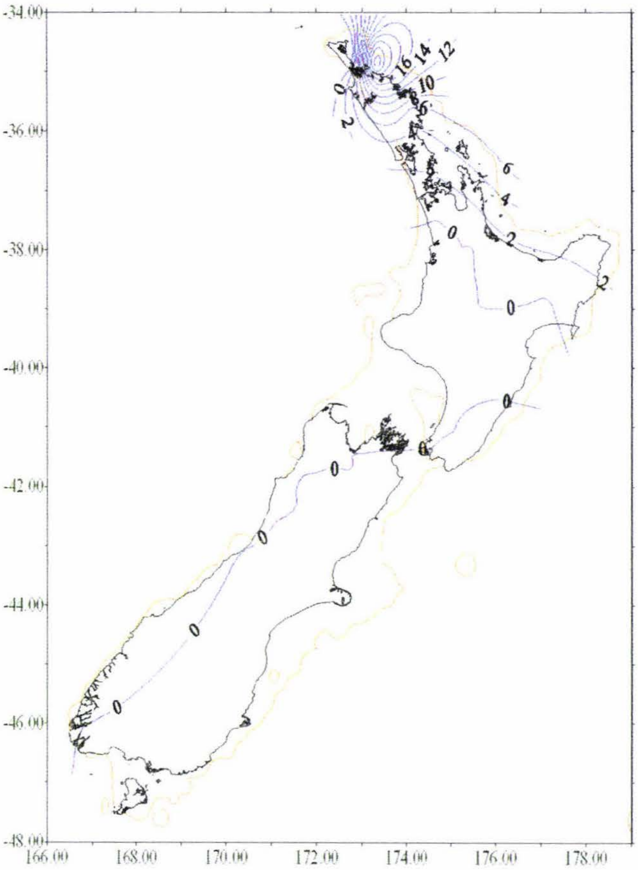
Poaceae spp Modern



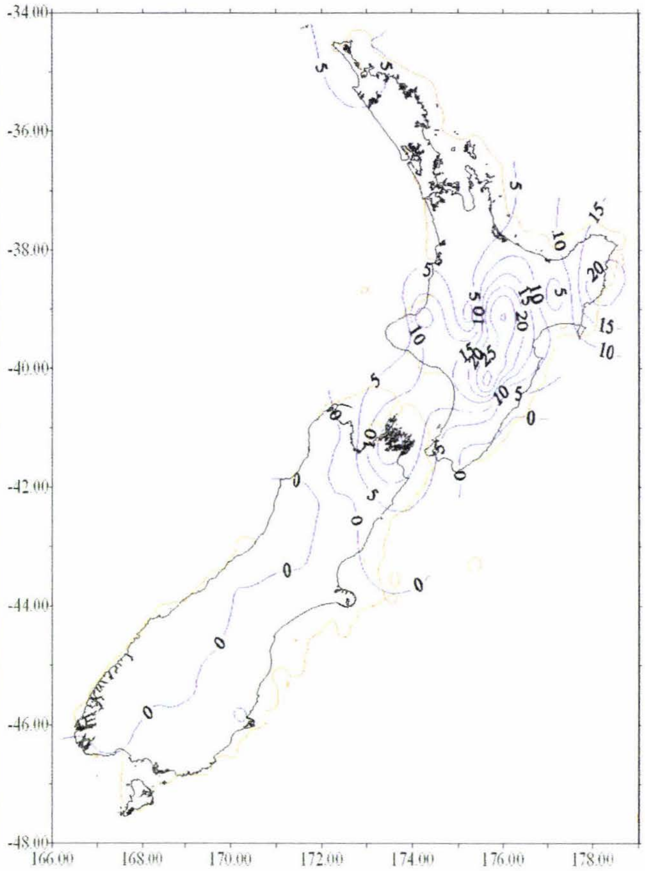
Poaceae spp Isochrone Map 1% Critical Limit



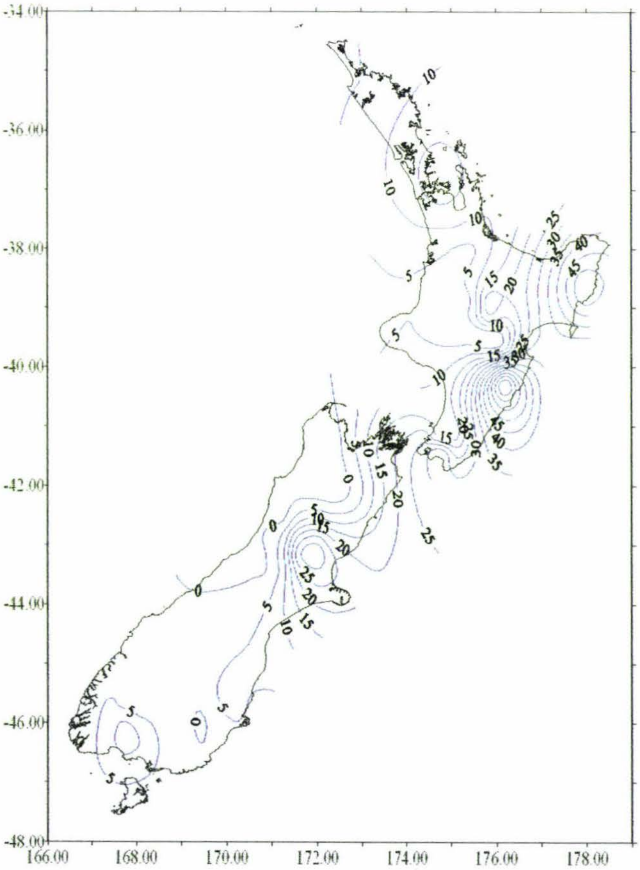
Podocarpus totara Isochrone Map 1% Critical Limit



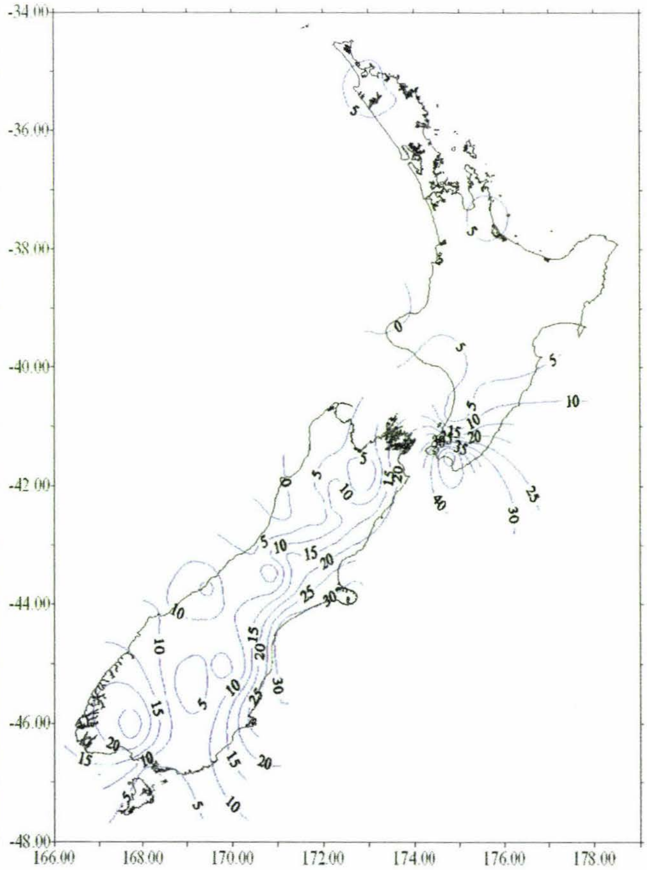
Podocarpus totara 22,000 - 14,500 BP



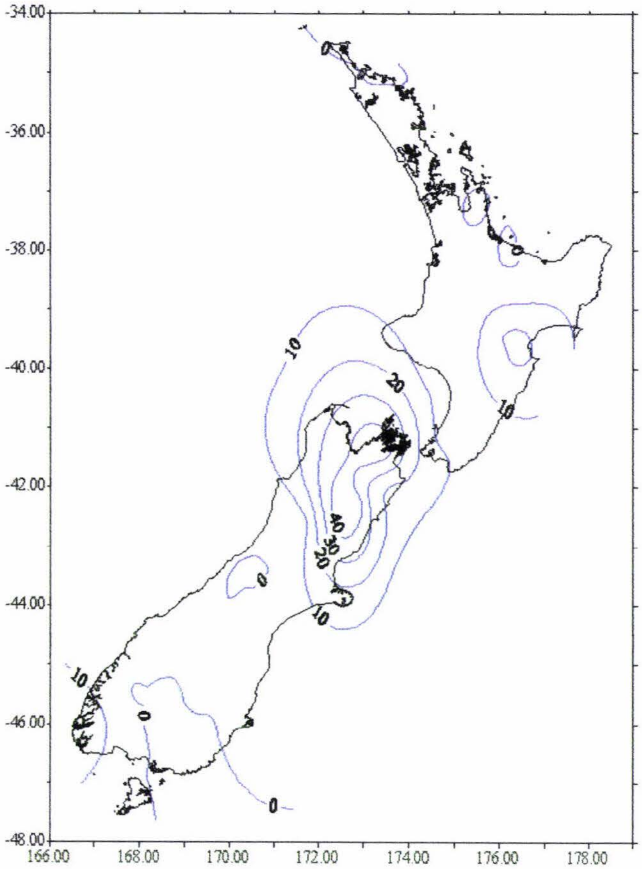
Podocarpus totara 14,500 - 10,000 BP



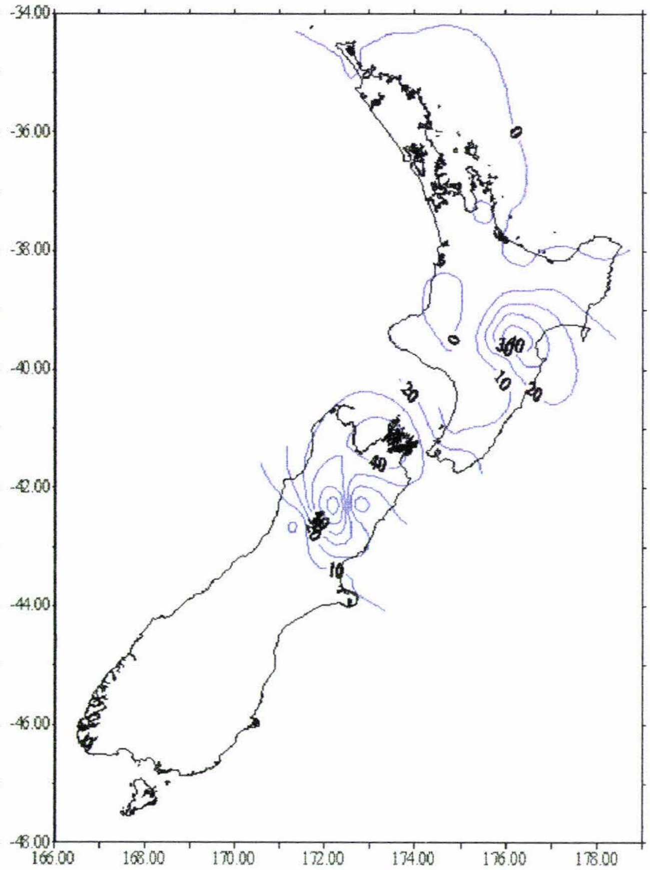
Podocarpus totara 10,000 - 8,000 BP



Podocarpus totara 8,000 - 6,000 BP



Podocarpus totara 6,000 - 4,000 BP



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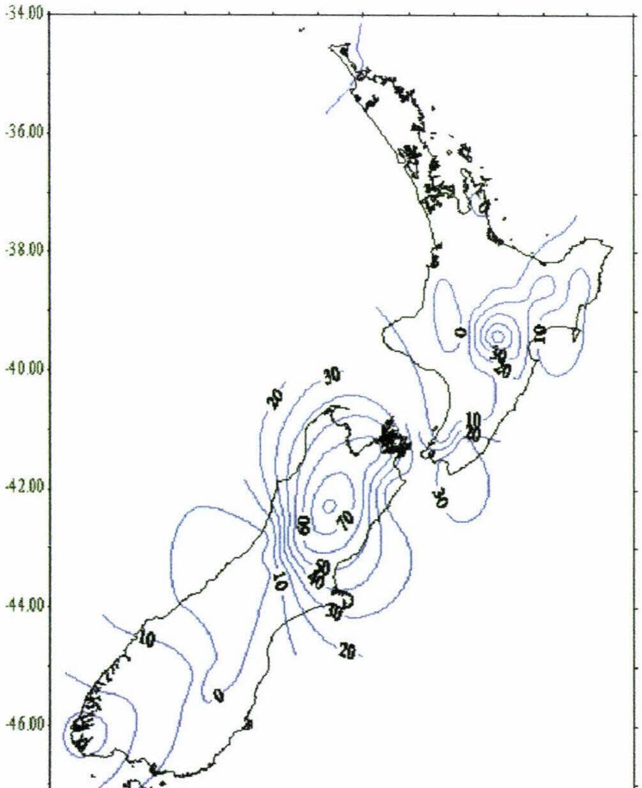
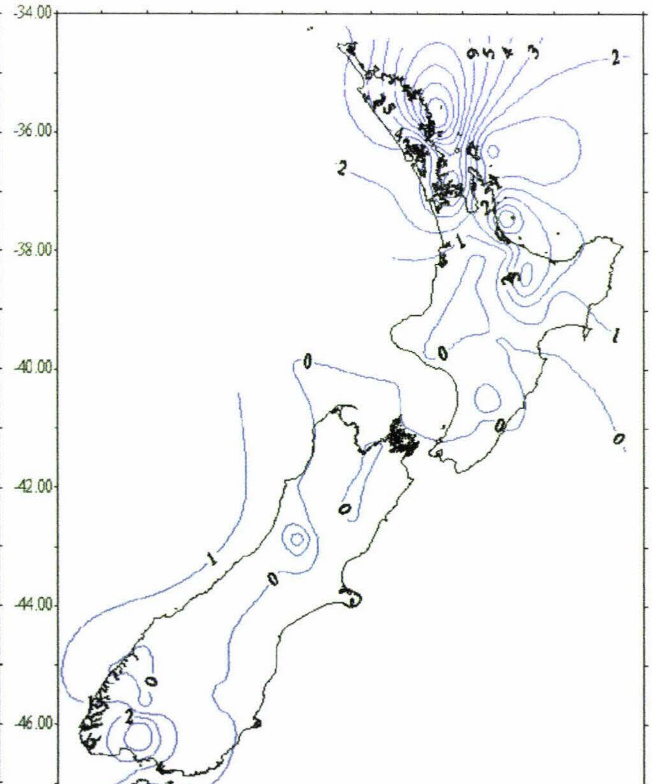
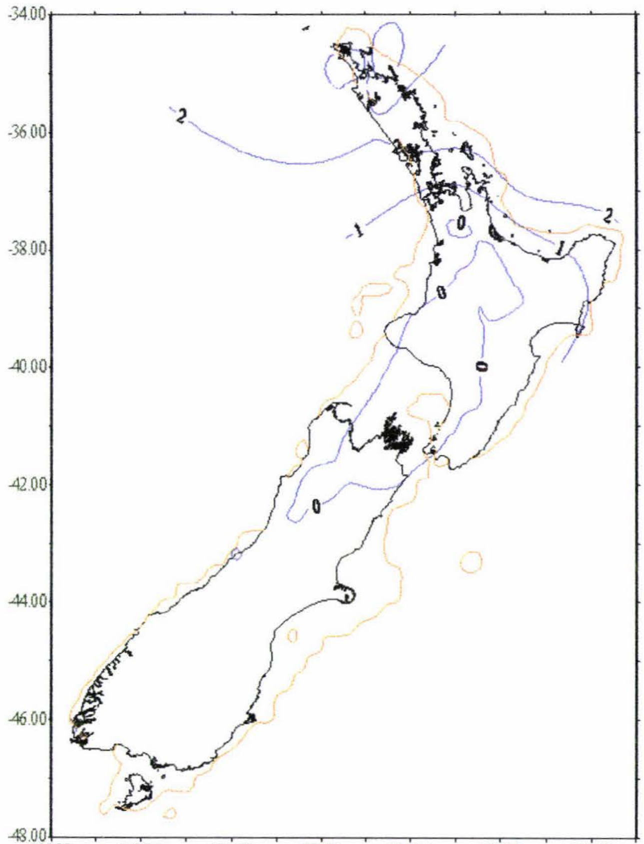


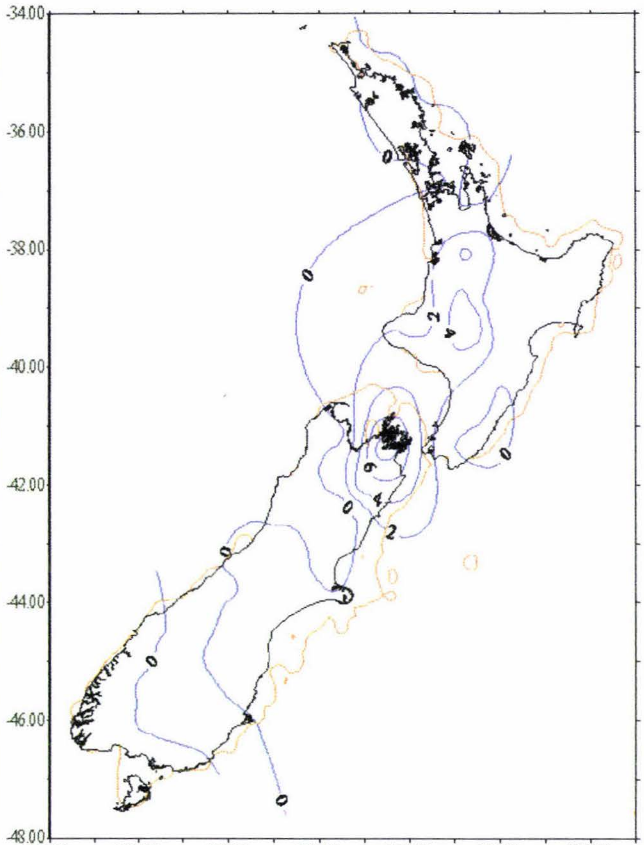
Podocarpus totara 2,000 - 0 BP



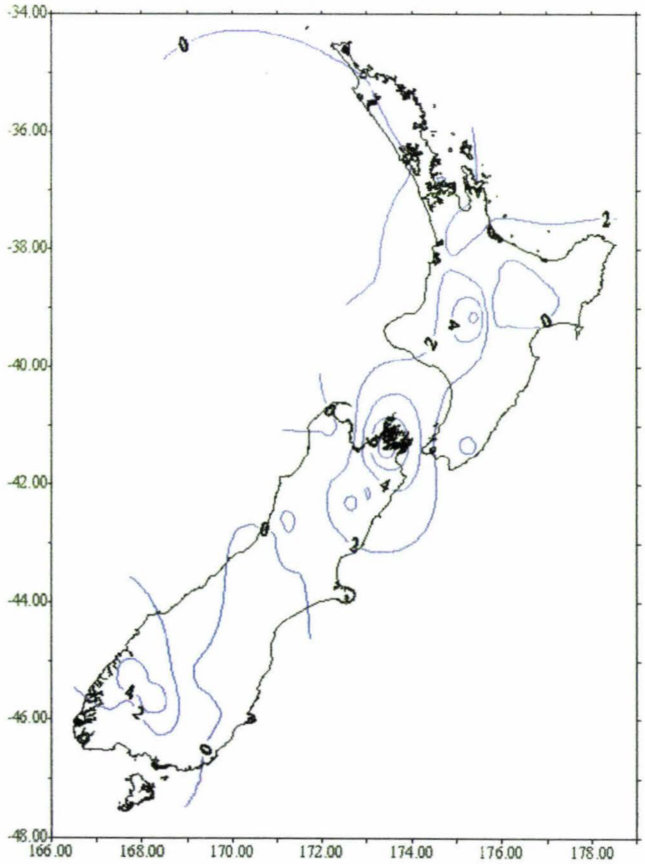
Podocarpus totara Modern



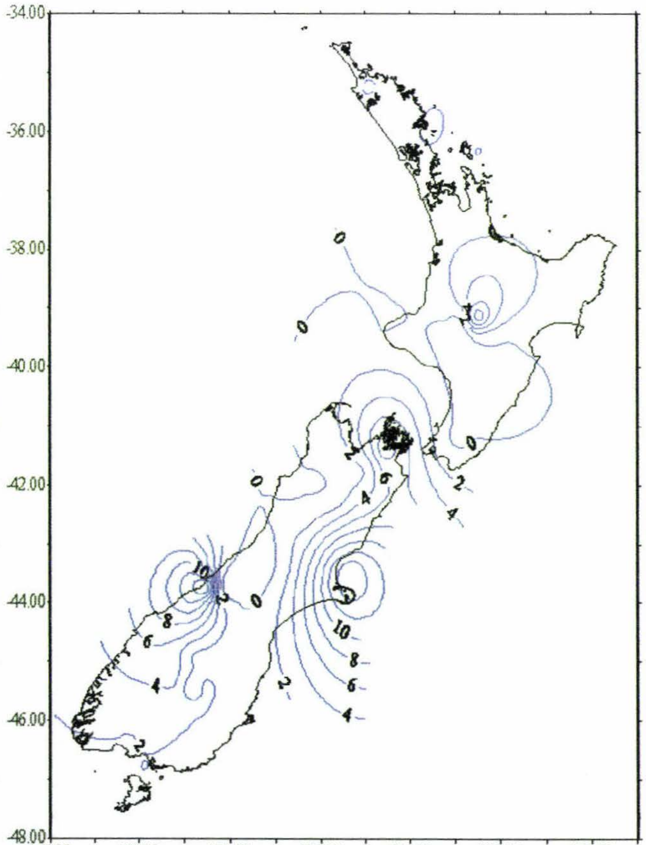
Prumnopitys ferruginea 22,000 - 14,500 BP



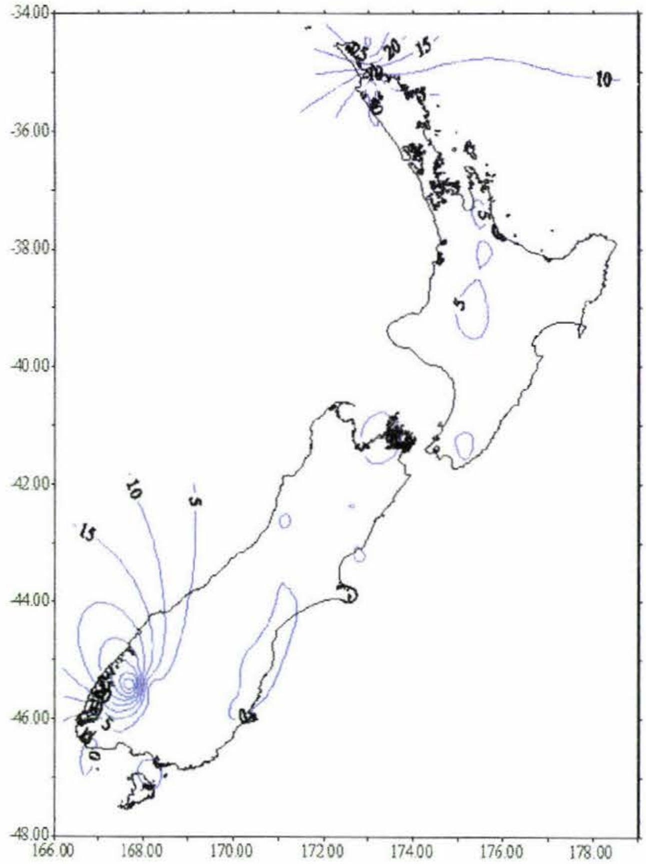
Prumnopitys ferruginea 14,500 - 10,000 BP



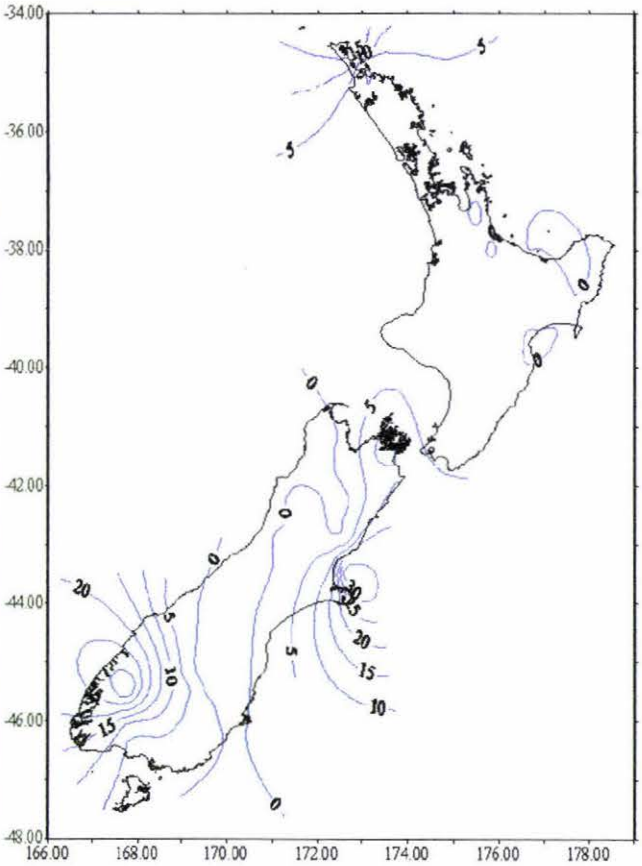
Prumnopitys ferruginea 10,000 - 8,000 BP



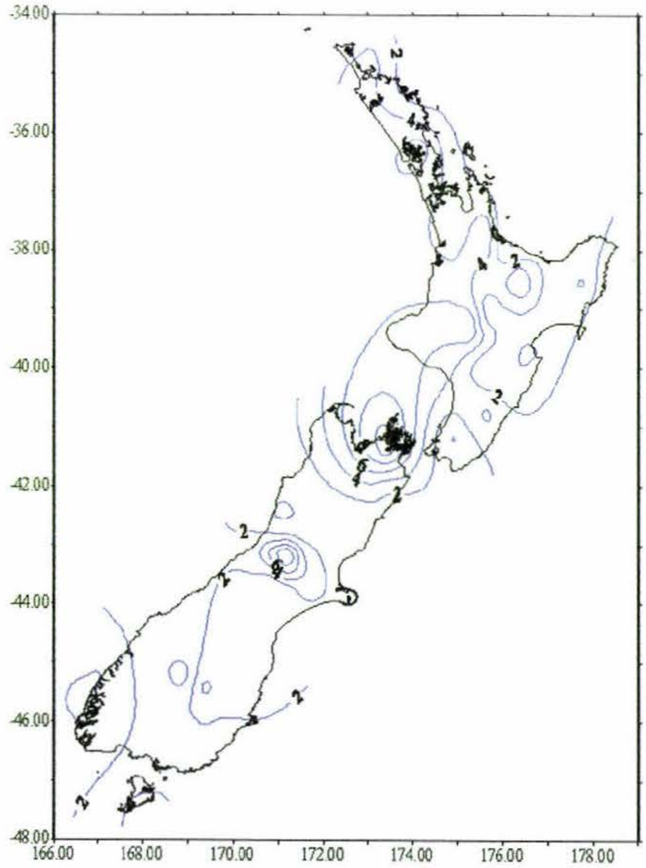
Prumnopitys ferruginea 8,000 - 6,000 BP



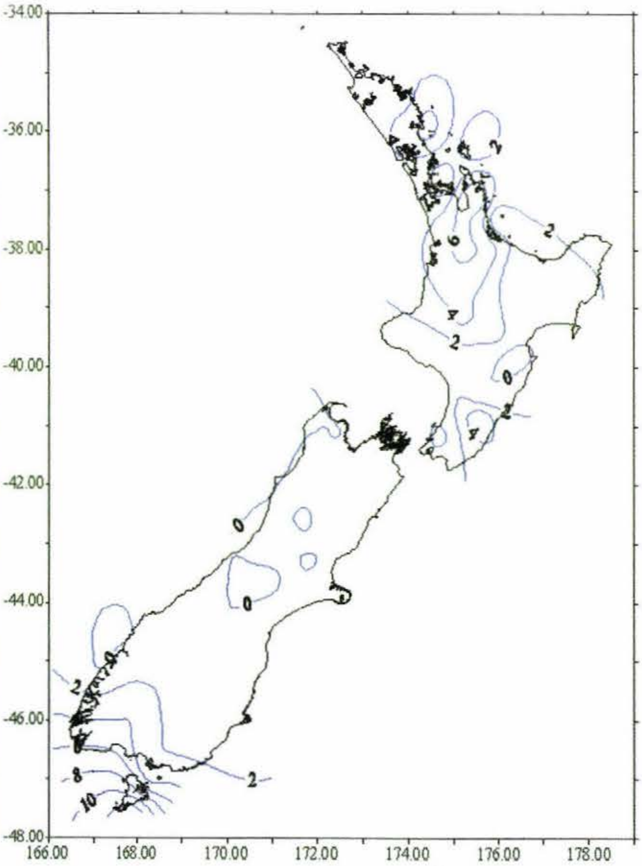
Prumnopitys ferruginea 6,000 - 4,000 BP



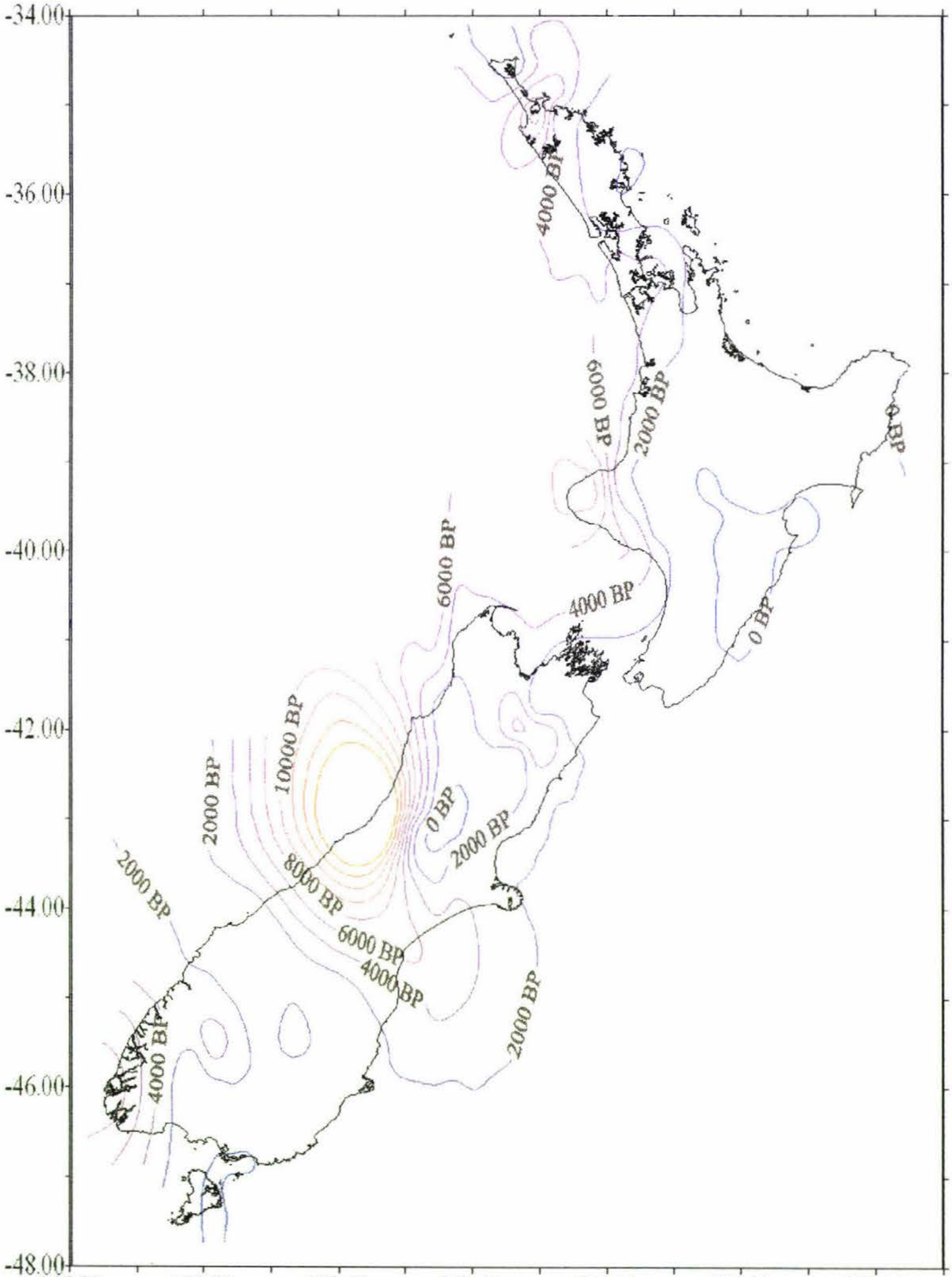
Prumnopitys ferruginea 4,000 - 2,000 BP



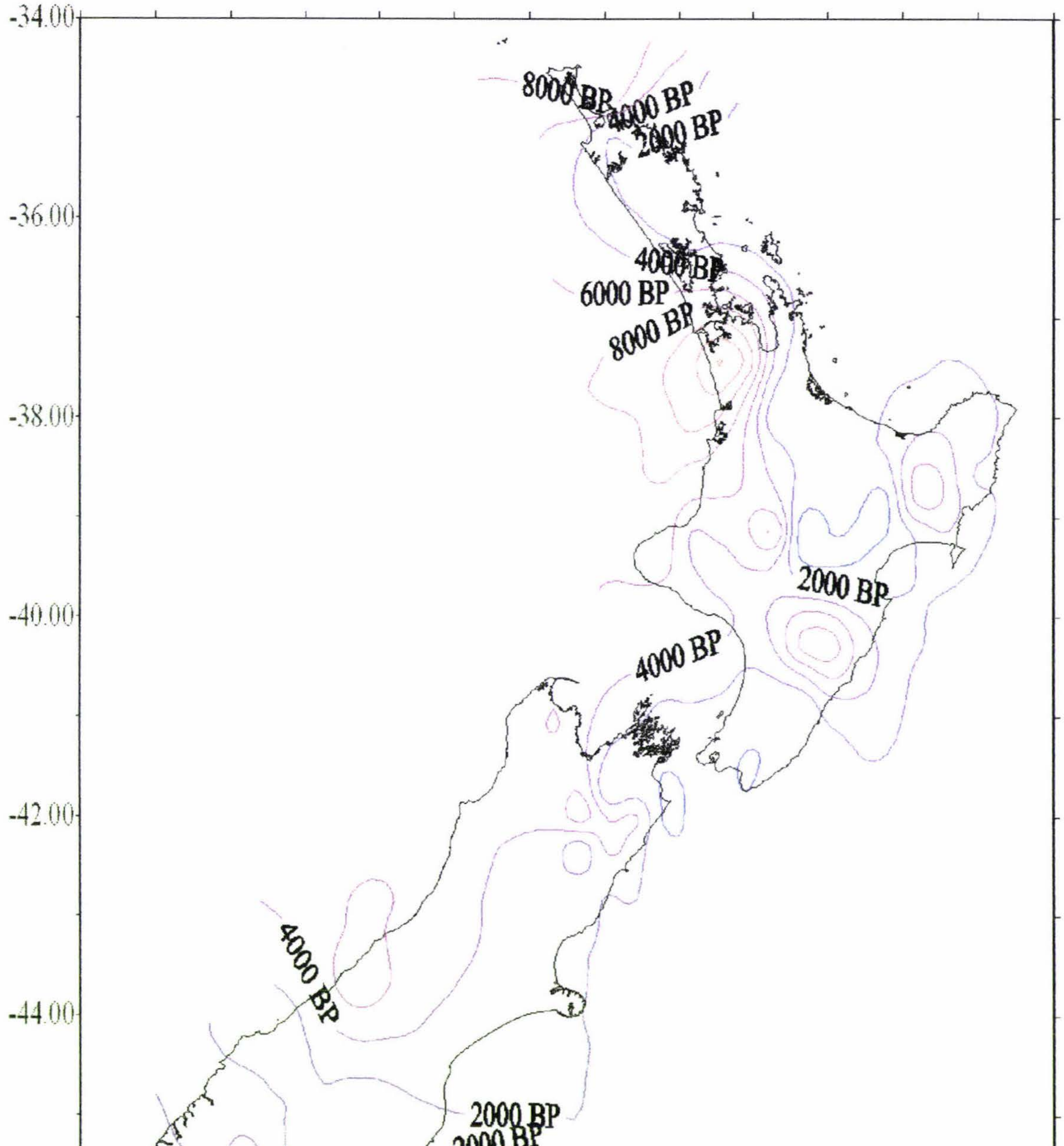
Prumnopitys ferruginea 2,000 - 0 BP



Prumnopitys ferruginea Modern



Prumnopitys ferruginea Isochrone Map 1% Critical Limit



Prumnopitys taxifolia Isochrone Map 5% Critical Limit

4 Interpretation of the Isopollen and Isochrone Maps

4.1 The Last Glacial Maximum 22,000 - 14,000 BP.

It is generally accepted that during the LGM much of the lowland vegetation present throughout New Zealand was comprised of alpine and sub-alpine taxa (McGlone 1988), with possibly only the central west coast of the South Island being completely unvegetated due to the glaciers extending to the sea (Ogden 1989). Low pollen percentages for large tree taxa throughout much of New Zealand are evident in the isopollen diagrams, supporting suggestions that the entire country was cooler (Hollin & Schilling 1981), drier and windier (Thiede 1979; Stewart & Neall 1984) than present. *Dacrycarpus dacrydioides* and *Dacrydium cupressinum* were almost completely absent south of Hamilton, except for small pockets in central Westland for *D.dacrydioides*, and in central Westland[141] and the paleo marine terraces east of Banks Peninsula for *D.cupressinum*.

The isochrone map for *Agathis australis* suggests that kauri was restricted to north of 35°S, and *Libocedrus* was restricted to small pockets near Hamilton, in southern Taranaki and Manawatu in the North Island, and central Westland in the South Island. *Prumnopitys ferruginea* was almost completely absent south of Auckland, apart from coastal areas and paleo plains in the Bay of Plenty. The isochrone map for *P.taxifolia* indicates the taxon was restricted to the south Auckland area at the LGM.

McGlone *et al* (1996) state that despite failing to dominate the pollen rain, *Nothofagus* is the most abundant taxon in LGM sites. Both the *Nothofagus fusca* and *N.menziesii* isochrone maps shows small pockets in North Westland-Buller 14,000 BP with no indication of the taxa existing earlier, although presumably they must have survived in numerous, widely dispersed refugia (McGlone 1985b; Ogden 1989) including Fiordland, where fossil woods (Johnson 1978) and leaves (Wardle & McKellar 1978) indicate the taxa survived the LGM. The restricted dispersal ability of *N.menziesii*[142] (relative to taxa

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[141] A refugium for *Ascarina lucida*, and possibly *Nothofagus fusca*, also occurred near Hokitika.

[142] Although the dispersal ability of *Nothofagus menziesii* is itself questionable; Haase (1989) examined isolated stands of *N. menziesii* near Otira and concluded that seed dispersal can only have occurred by wind, since dispersal by water was prevented by a 1500m mountain range en route. Therefore failure of *N.menziesii* to spread was not limited by low dispersal ability

with easily dispersed seed like *Dacrydium cupressinum*) along with its disjunct distribution in eastern Southland and Otago suggests that it also survived in the east during the LGM (McGlone 1980).

Grassland and shrubland are thought to have been the major vegetation cover south of 36°S (Moar & Suggate 1979; Markgraf *et al* 1992) or 37°S (McGlone 1995; Denton *et al* 1999) whereas McGlone *et al* (1993) claimed "Not enough dates or [pollen] diagrams are available to place a precise limit to continuous forest at this time, but south of 40.5°S forest was probably confined to discontinuous patches."

The isopollen map for *Poaceae* spp suggest that 39°S is a better estimate for the southern forest limit, with *Poaceae* spp making up >20% of the pollen sum between Taupo in the north and to the east of approximately 171°E, that is, all of Nelson, Marlborough, most of Canterbury and east Otago. Although *Poaceae* are typically undifferentiated below the family level, some inferences can be made about the types of grasses present based upon modern distribution. In general, grass species were predominantly tall tussocks such as *Chionochloa rubra* (red tussock) in wetter sites and short tussock species on drier sites, including *C.rigida* (narrow-leaved snow-tussock), *Festuca novae-zelandiae* (hard tussock), *Poa cita* (silver tussock) and *P.colensoi* (blue tussock). These species are now largely restricted to higher altitudes; *C.rubra* subsp. *rubra* var *rubra* is found between 550 and 1,400m and both *C.rubra* var *inermis* and var *cuprea* are found up to 1,500m (Edgar & Connor 2000). Where grasses have been identified, *Compositae* pollen is often present (Moar 1980), including *Taraxacum* and *Cotula* spp.

Coprosma spp show pollen percentages >5% for much of the northern and eastern North Island, supporting Moar & Suggate's (1979) and Markgraf's *et al* (1992) statements above. At the same time, cold-tolerant *Phyllocladus* spp were more common than present in the 'glaciated waist' of the South Island and to the west of Lake Taupo; these areas would have been cooler and displayed a greater seasonal temperature range than other areas due to continentality.

The temperature decrease at the LGM relative to present is uncertain; snowline depression of 800-850m below present (Porter 1975) implies, *ceteris paribus*, a temperature decrease of 4.5°C – 5°C[143]. Paleo SSTs discussed in this thesis indicate a cooling of 6°C in Auckland and 5.5°C in Christchurch and the northward-migration of *Zygochlamys deliculata* (Beu 1999) implies a cooling of 6°C. The LGM isopollen map shows that *Dacrycarpus dacrydioides* was virtually absent in the South Island; together with the 0% LGM isoline for *Dacrydium cupressinum* at the Otago Peninsula compared with the 10% modern day isoline for the same place would imply a 7-8°C cooling given the freezing temperatures of these taxa in Table 4, *ceteris paribus*[144]. However, temperature decreases of the order of 8°C would eliminate most arboreal taxa from upland areas throughout both islands; since pollen and macrofossil evidence suggest this did not occur (McGlone 1988), the temperature decline is likely to be closer to that implied by snowline depression or paleo sea surface temperatures, that is, in the range 4.5°C – 6°C cooler.

Newnham (1999) suggests a temperature decrease in the range discussed above is in itself insufficient to account for the Last Glacial Maximum vegetation pattern. Since mean temperature is only one component of climate, wind, precipitation and temperature extremes are also likely to be important contributors to New Zealand's factors affecting phytogeographical distribution in tandem with cooler temperatures.[145] Abundant charcoal deposits found in numerous sites throughout the country point to a drier climate (Newnham *et al* 1993; McGlone *et al* 1984), thus the virtual absence of *Ascarina lucida* in the southern North Island and the South Island in the LGM isopollen maps is likely to be due to both cool temperatures and drought. Furthermore, extensive ice cover in the South Island (Suggate 1990), lowered CO_2 levels in the atmosphere (Dodson 1998), edaphic factors (Wardle & Campbell 1976)[146] and extensive erosion (Nelson *et al* 1985) are also likely contributors to a reduction in forest cover.

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[143] Although the snowline depression may fail to take into account reduced precipitation, and therefore underestimate the temperature decrease.

[144] The temperature depression implied by the isopollen maps concords with McGlone's (1988) observation that "If the subalpine communities on the Taranaki lowlands at the [Last] glacial maximum grow under similar temperature regimes to present subalpine areas, the implied depression of annual temperature would be of the order of 8°C."

[145] It is also possible that some of the proxy temperature measures are at fault; for example Nelson *et al* (2000) suggested that 'enhanced leakage' of subantarctic water masses through the subtropical convergence zone (STC) proximal to the east coast of New Zealand may have occurred, without a large north-south shift of the oceanic STC itself. This would lead to an apparent cooling in the $\delta^{18}O$ signature. Nelson *et al* suggest that the leakage of cooler waters may have been caused by "...more compressed subantarctic water masses, lowered sea level and an expanded and stronger westerly wind system."

[146] Fresh alluvium rich in nutrients was common in the late glacial lowlands and upland basins (McGlone 1988) and taxa thought to be dominant in the late glacial such as *Prumnopitys taxifolia* and *Dacrycarpus dacrydioides* are today prominent on alluvial soils.

4.2 Late-Glacial Period 14,000 – 10,000 BP.

The late-glacial was characterised by rapid amelioration of the climate and retreat of the South Island glaciers; glacial westerly winds declined in intensity as the polar winds retreated to their present position (Stewart & Neall 1984) and the paleo-sea surface temperature maps (Appendix 5.3) suggest temperatures rose around 4°C from LGM temperatures for much of the country.

The southern hemisphere is thought to have lacked continental-scale migration events equivalent to the northern hemisphere in the late – post glacial, and forest taxa is thought to have spread from many microclimatologically favourable locations rather than a few refugia (Markgraf *et al* 1995). Thus in New Zealand, McGlone (1985b) claimed that the late glacial afforestation was "...no steady north-south progression of forest...afforestation occurred at roughly the same time throughout a district, regardless of latitude and altitude." Progressive afforestation, generally from north to south, resulted for small-tree and shrub taxa; this is seen clearly in the isochrone maps for *Ascarina lucida* and *Coprosma*, with the isolines in the South Island generally more widely spaced to the south than to the north. However this pattern is absent in the isochrone maps for *Dacrydium cupressinum*, *Dacrycarpus dacrydioides* and *Libocedrus*, supporting Markgraf *et al* (1995) and McGlone (1985b).

The late glacial afforestation is also thought to have been marked by its rapidity: McGlone (1985b) states that the South Island's revegetation took as little as 500 years, and the replacement of grassland-shrubland with lowland podocarp – hardwood forest, without undergoing a montane forest, intermediate phase. Although this is difficult to demonstrate with either the isopollen or isochrone maps since they lack the temporal resolution to detect such rapid change, the late-glacial to early post glacial sequence of Poaceae isopollen maps certainly indicate a rapid decline in grassland at that time.

Around 14,000 BP podocarp-hardwood forest was found throughout the North Island with the exception of the southwest part; by 12,500 BP the northern part of the southwest North Island was also forested (McGlone 1988; McGlone *et al* 1993). By 12,000 BP most lowland – lower montane regions in the North Island are thought to have been covered in dense forest except for the Wellington region (McGlone 1985a); in the South Island broadleaf forest was established along the West Coast and tall shrubland – low forest taxa began to replace grassland – shrubland communities (Markgraf *et al* 1992). This pattern of North Island revegetation is confirmed by the isochrone maps; *Nothofagus fusca* was in southern Taranaki by 12,000 BP and Manawatu by 10,000 BP; *Libocedrus* had expanded into eastern Taranaki by 12,000 BP and as far south as Wellington by 12,000 BP; *Dacrycarpus dacrydioides* expanded into NW Waikato. *Prumnopitys ferruginea* expansion lagged behind these other taxa, not reaching Taranaki until 10,000 years BP.

Temperatures are generally understood to have risen to within 2°C of present by 12,000 years BP (McGlone & Topping 1977) and the simultaneous development of large bog complexes on both the main islands[147] points to increased precipitation, however precipitation was very likely to have been lower than present in some areas, particularly in the east and in the south (Markgraf *et al* 1992). Burrows (1979) and McGlone (1988) argued that persistence of shrubland-grassland in central and south-east South Island until 10,000 years BP could not be explained by lower temperatures and precipitation alone, since all other things equal, temperature amelioration should have resulted in more widespread forest communities in the south. McGlone (1988) suggested that sporadic outbreaks of cold air from high latitudes, in tandem with lower temperatures and precipitation, would have restricted the growth of tall forests in the south and east.

Alloway *et al* (1992) state that in the western North Island late glacial conditions were still cool, and drier than present, however by 11,000 BP *Prumnopitys taxifolia* was replaced by *D.cupressinum*, suggesting warmer and wetter conditions, similar to present. The isochrone map for *P.taxifolia* shows this taxon was restricted to NW Waikato between 12,000 and 10,000 BP, whereas the late glacial isopollen map for *D.cupressinum* shows very high pollen percentages for the northern North Island except for East Cape and Bay of Plenty. In the South Island, *Libocedrus* extended from Greymouth in the north to southern Fiordland in the south by 10,000 BP.

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[147] For example Newnham *et al* (1995) dated the earliest basal peats at Kopouatai Bog in the Hauraki lowlands at 11,700 ± 80 years BP; McGlone & Wilmshurst estimated that sediments began to accumulate in Glendhu bog, east Otago, *c.* 12,000 years BP.

4.2.1 The Younger Dryas Stadial *c.* 11,500 – 10,500 BP.

In the latter part of the Late Glacial the general global warming was interrupted, at least in the Northern Hemisphere, by a cooling interval or stadial known as the Younger Dryas[148] or Greenland Stadial 1 (Björck *et al* 1998). Although there is good evidence for a stadial in the Northern Hemisphere, whether there was a coeval event in the Southern Hemisphere is highly debatable; however, determining whether a Younger Dryas – synchronous event occurred in the Southern Hemisphere is critical to understanding global paleoclimate change and modern climate modelling.

Although Barrows *et al* (2002) found no evidence of glacial readvance for the Younger Dryas in either the Snowy Mountains or the Tasmanian highlands, the only areas of LGM glaciation in Australia, researchers in other Southern Hemisphere sites have demonstrated climatic deterioration coeval with the stadial. Despite the existence of some evidence for cooling in South America broadly synchronous with the Younger Dryas, Rodbell & Seltzer (2000) suggest that "...disagreement over stratigraphic interpretations and a lack of tight age controls have hindered attempts to compare rigorously the glacial geologic record from the tropical Andes with events in extratropical regions."

An example of this is the different interpretations arising from analysis of sediments from the Rio Mocha valley in central Ecuador. Whereas Clapperton (1993) concluded there had been ice advances between 11,400 - 10,600 and 10,600 – 10,000 years BP, Heine (1993) argued that lake level changes may not have been the result of changes in glacial extent, and in any event the juxtaposition of radiocarbon dated peats and ice margin position was equivocal. Rodbell & Seltzer (2000) concluded from radiocarbon dated peats in glacial outwash on Cordillera Blanco in Peru that the ice rapidly retreated 10,900 BP; a similar retreat was noted by Abbott *et al* (1997) on the western side of the Cordillera Real in Bolivia. Heuser & Rabassa (1987) on the other hand, found radiocarbon dated glacial moraines in Tierra del Feugo, Argentina to be formed 11,580 – 10,510 years BP, a period of low pollen influx in cores from nearby Caleta Róbato.

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[148] According to Peteet (1995) the Younger Dryas was named after buried leaves and fruit of *Dryas octopetala* in Scandinavia: "....the reappearance of these tundra indicators after shrubs and trees had begun to colonise a glaciated landscape....suggested a reversion to colder conditions."

Given that these retreats were occurring at the height of the Younger Dryas in the Northern Hemisphere, and that "...at no time during the middle and latter part of the Younger Dryas were [the Peruvian and Bolivian] paleoglaciers more than several kilometres more extensive than they are today," (Rodbell & Seltzer 2000) doubts are raised whether the Younger Dryas was a global phenomenon.

Possibly the best evidence for YD synchronous glacial re-advance in New Zealand comes from the Waiho Loop moraine, a terminal moraine about 11km outside the present-day terminus of Franz Josef glacier, although like the South American studies discussed *supra*, "Dating this feature has proven difficult and controversial," (Fitzsimons 1997). Although Suggate (1990) found wood fragments in the Waiho Loop moraine to be ≥12,000 years old, Denton & Hendy (1994) dated wood-bearing diamicton from nearby Canavan Knob to 11,050 ± 14 years old. Denton & Hendy (1994) suggested the wood fragments were swept by avalanche or mass wasting on the valley walls onto the Franz Josef ice tongue and therefore should be derived from the trees coeval with Suggate's (1990) wood.

Ivy-Ochs *et al* (1999) compared ^{10}Be concentrations in quartz extracted from the upper surfaces of boulders in moraines in Julier Pass, Switzerland, and Lake Misery, near Arthurs Pass. The samples showed remarkable synchroneity, with boulders from the Swiss site indicating first exposure to cosmic rays 11,750 ± 140 years BP and the New Zealand site 11,720 ± 320 years BP. The New Zealand date offers support for Suggate (1990) although it is discordant with Denton & Hendy (1994); therefore the age of a glacial readvance coeval with the Younger Dryas remains inconclusive.

Palynological evidence is equally contentious. Although we might expect a strong correlation between glacier activity and the fossil pollen signature the correlation is weak in New Zealand. Singer *et al* (1998) found no evidence for a cooling event "during, before or after the YD," in pollen cores from NW Nelson, whereas Newnham & Lowe (2000) found "unequivocal evidence" for a 1,000-year cooling event at Kaipo Bog in the east of the North Island. Newnham & Lowe (2000) noted a decline in thermophilous taxa such as *Prumnopitys taxifolia*, *Fuscospora* and *Halocarpus*, and an increase in cold-tolerant taxa such as *Phyllocladus* and *Poaceae* between 11,600 and 10,700 years BP.

Although the temporal resolution of the isopollen maps may be too coarse[149] to show a YD-synchronous glacial readvance in New Zealand, the wisdom of basing conclusions about the occurrence or non-occurrence of the Younger Dryas in New Zealand upon a single site is questionable and is intuitively less palatable. The isopollen and isochrone maps can assist here by providing a perspective based upon multiple sites. If there was in fact a comparable cooling event in New Zealand, we would expect to see widespread retreats, or at least marked slowing, in the expansion rates of the thermophilous taxa identified by Newnham & Lowe (2000) and a corresponding expansion in cold tolerant species.

An examination of the isochrone maps for *Prumnopitys ferruginea*, *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Nothofagus fusca* and *Libocedrus* showed no obvious changes in expansion rate or direction (retreat); *Phyllocladus* showed no significant acceleration in its spread northward until after 10,000 years BP, and this was largely confined to spread into the King Country. Furthermore, the most cold-intolerant taxa such as *Ascarina lucida* continued to proceed southwards. Although *Poaceae* expanded between 12,000 and 10,000 years BP, rapid spread was restricted largely to southern Hawkes Bay and north Auckland. On balance, the pollen evidence does not indicate significant cooling synchronous with the Northern Hemisphere's Younger Dryas.

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[149] Since there were only a dozen or so sites with ^{14}C dates in the interval 11,500 – 10,500 years BP I was reluctant to establish a temporal interval for the Younger Dryas.

4.3 The Holocene: 10,000 BP - Present

4.3.1 Early Holocene 10,000 – 8,000 BP

The period 10,500 – 9,300 years BP is thought to have been characterised by the establishment of tall podocarp-hardwood forests, predominantly *Nothofagus menziesii*, *Libocedrus*, *Prumnopitys taxifolia* and *P.ferruginea*, established on the southern coast of the North Island and all of the South Island (Dodson 1978) except for the dry interior basins in the southeast, which remained in grassland – shrubland (Burrows 1979; Markgraf *et al* 1992); *Dacrydium cupressinum* became the dominant podocarp tree in western and northern North Island forests, whereas eastern forests continued to be dominated by podocarps and *Prumnopitys* (McGlone *et al* 1993).

The isopollen and isochrone maps partially support these claims. *Libocedrus* had extended its range in the South Island to Westland, Fiordland and western Southland by 8,000 years BP; the 10,000 - 8,000 years BP isopollen maps for *Dacrydium cupressinum* shows areas around the volcanic plateau and to the west achieved frequencies from 20% - 60% and in Northland around 20%.

The isopollen map shows that for the same period *Podocarpus totara* frequency increased in the east, comprising more than 20% of the pollen sum to the east of Lake Taupo and as high as 50% to the east of the Huiarau and Raukumara Ranges, and also to the east of the Tararua and Ruahine Ranges. The *Coprosma* genus was well-represented in the south-east, with relative pollen percentages exceeding 20% in central Otago, and nowhere south of Ashburton falling below 5%. The Poaceae isopollen map for 10,000 - 8,000 years BP shows ≥ 10% for southern Otago – northern Southland, in agreement with Burrows (1979) and Markgraf *et al* (1992).

In contrast, other taxa were not as widespread as Dodson (1978) or McGlone *et al* (1993) suggested; *Nothofagus menziesii* was limited to northern Westland – Buller by 8,000 years BP. *Prumnopitys taxifolia* was somewhat more restricted than Dodson's (1978) claim; the isochrone map demonstrates that in the North Island *P.taxifolia* was restricted to south

Nothofagus nca menziesii

Auckland and a small pocket in Manawatu, and was not evident in the South Island.[150] The distribution of *Prumnopitys ferruginea* does not match McGlone's *et al* (1993) claim; apart from a small area in eastern Waikato 10,000 – 8,000 years BP the taxon does not appear to dominate in the east in the isopoll maps until after 8,000 years BP.

Sakai *et al* (1981) suggest that the early Post-Glacial was characterised by a sequence of pollen dominance from *Dacrydium* (probably *D.bidwillii*) through *Phyllocladus* (most likely *P.asplenifolius* var *alpinus*) to *Podocarpus* and *Dacrycarpus*, "...and this sequence fits well with an order of decreasing freezing resistance." Given the frost and drought-tender species *Ascarina lucida* is presently uncommon or absent where rainfall is low, droughts are prevalent or winters are cold and frosty, its appearance at 9,600 years BP in central Taranaki suggests high, reliable rainfall and an absence of frosts. Some time between 10,000 (Wardle & Campbell 1976) and 9,000 years BP (Dodson 1998) the afforestation of New Zealand was thought to be complete, with the exception of the dry interiors in the South Island's central and south eastern districts.

This synopsis is supported by the isopollen maps and can be seen most clearly in the maps for *Dacrydium cupressinum* and *Nothofagus fusca* for 10,000 - 8,000 years BP. At this time the South Island showed a relative frequency of less than 5% for *N.fusca*, with the exception of the Nelson - Marlborough region. Similarly, for *D.cupressinum* the relative frequency south of Nelson-Marlborough was less than 10%, with zero frequency in the south-east interior. At the same time, the frequency of *Poaceae* and *Graminae* pollen was very much higher in these southern regions, offsetting the lower frequency of large taxa such as *D.cupressinum and N. fusca*.

The first postglacial forests on the west coast of South Island were thought to have been dominated by *D.cupressinum*, *Weinmannia* and treeferns with "These strikingly uniform podocarp-hardwood forests, differentiated into a wet western and dry eastern facies, extended throughout New Zealand." (McGlone *et al* 1993). The isopollen maps for *D.cupressinum* do not support this, with the taxon in the South Island restricted to North Canterbury and Marlborough. Not until after 8,000 years BP did *D.cupressinum* dominate on the west coast of the South Island.

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[150] In addition to possible under-representation, this could be the result of the difficulty in distinguishing *Prumnopitys taxifolia* from *P.ferruginea* (Pocknall 1981a) or, for weathered grains, from *Podocarpus totara*

The period between 10,000 and 7,000 BP is thought to have had milder winters with fewer frosts and less windy conditions than at present, and summers that were moister and cloudier (Newnham *et al* 1999) based on (i) increased pollen frequency of frost-sensitive trees such as *Ascarina lucida* in the west and in the south (McGlone & Moar 1977); (ii) restriction of *Nothofagus fusca* which are relatively frost-hardy; (iii) absence of wetlands in the east; and (iv) absence of forest in central south-eastern South Island (Cranwell & von Post 1936; Markgraf *et al* 1992).

Ascarina is absent from the South Island in the 10,000 – 8,000 years BP isopoll map but shows positive values in the 8,000 – 6,000 years BP isopollen map in South Westland and Fiordland in the South Island, and to the west of the Ruahine and Tararua Ranges and the Waikato lowlands in the North Island. By contrast, modern *Ascarina* percentages >1% are restricted to the southern Fiordland in the South Island, and around Lake Taupo and the Wairarapa in the North Island, but nowhere today are percentages as high as they were in the early post glacial.

The *Nothofagus fusca* isopollen maps also show broad agreement with McGlone *et al* (1993). The taxon continued to migrate south, however the rate of spread was relatively sedate, with the 10% isoline that runs in a NNW-SSE line from the Heaphy River to Kaikoura at 10,000 – 8,000 years BP moving around 80km south on the West Coast to Westport and 130km south on the east coast to Banks Peninsula in a NbyW-SbyE alignment by 8,000 – 6,000 years BP. The isochrone map also shows that the taxon expanded very slowly from its confines in north Westland - Buller, expanding southward by around 70km in three thousand years.[151]

(Wilmshurst *et al* 1999), whereby the taxa are often lumped into a catchall category, Podocarps.

[151] The different rates of expansion indicated by the isopollen and isochrone maps are discussed further in the conclusion.

4.3.2 Mid Holocene 8,000 – 4,000 BP

The mid- to late post glacial in New Zealand was characterised by the expansion of taxa that are more drought resistant and tolerant of cold, poor soils and disturbance including *Agathis australis* (Ogden *et al* 1992), *Nothofagus* and *Quintinia*, and decline of thermophilous taxa adapted to wet climates including *Ascarina* and tree ferns (McGlone 1988) and *Dodonaea viscosa* (Moar & Mildenhall 1988).

New Zealand's forest cover is thought to have undergone a series of changes in taxon composition and structure after around 7,000 BP. Although McGlone *et al* (1993) suggested that low forest was replaced by shrubland-grassland in central Otago, the isopollen maps for 8,000 – 6,000 years BP are inconclusive. Poaceae spp do not appear to have changed markedly in distribution, and *Coprosma* spp have declined. Forest species such as *Dacrycarpus dacrydioides*, *Podocarpus totara* and *Prumnopitys ferruginea* all increased their relative frequency since 14,500 - 10,000 BP indicating more favourable conditions for tree growth; the increased frequency for *Ascarina* is significant, indicating warmer temperatures and lack of droughts and frosts; conditions precisely the opposite of what we would expect to prevail if shrubland-grassland were to predominate. Countering this, the rise in *Phyllocladus* indicates cooling[152].

The isopollen map for *Nothofagus fusca* shows that the taxon increased a great deal in relative frequency between 8,000 and 6,000 years BP; the southern North Island shows 10-20% compared with around 5% for 10,000 – 8,000 years BP, strongly supporting McGlone *et al* (1993) claim that *Nothofagus* forest spread in many upland areas, especially in the northeastern sector of the South Island and southern North Island, in response to cooler temperatures and clearer skies.

Conifer and hardwood species including *Agathis australis*, *Libocedrus plumosa*, *Phyllocladus trichomanoides*, *Prumnopitys-Podocarpus*, *Knightia excelsa*, and *Nestigis* are believed to have increased in the North Island (McGlone *et al* 1993). The isopollen maps

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[152] Even the least cold-tolerant species of the *Phyllocladus* genus, *P.trichomaoides* is more tolerant to cooler conditions than the podocarps. Table 4 shows that bud freezing temperature is –10°C for this taxon, compared with *Dacrycarpus dacrydioides*, *Podocarpus totara*, and *Prumnopitys ferruginea* which all have a bud freezing temperature of –7°C.

support this; although *Agathis* registered no more than 1% relative frequency for the period 10,000 – 8,000 years BP along the east coast of the northern half of the North Island, by 8,000 – 6,000 years BP it was found as far south as Hamilton. The isochrone map shows that *Libocedrus* had migrated south from centres in the Waikato lowland, east from southern Taranaki and north from the Wairarapa, and *Dacrycarpus* increased significantly to the east of Lake Taupo.

McGlone *et al* (1993) stated that *Dacrydium cupressinum* and *Nothofagus menziesii* began to spread in the coastal districts of the South Island after 7,000 years BP; as discussed above, *D.cupressinum* is much more widespread after 8,000 – 6,000 years BP than in the previous time period particularly on the West Coast and coastal Nelson and Marlborough.

Between 6,000 and 5,000 BP the climate cooled by 1-1.5°C (Markgraf *et al* 1992) and the South Island glaciers advanced (Gellatley *et al* 1988). McGlone & Moar (1977) claim although *Ascarina lucida* became common around 10,000 years BP in the North Island, the first indications of its decline were noted around 5,000 years BP. The isopollen map for 6,000 – 4,000 years BP supports this, showing levels between 0 and 1% for much of the central North Island, with the 0% isoline covering a much greater part of the island in the period 4,000 – 2,000 years BP.

Although Wardle (1963) claimed there has been an average depression of the treeline of 160m over the last 7,000 years, Rogers & McGlone (1988) suggested that there is no evidence of the treeline descending in response to the cooler climate; the impact on vegetation of a temperature decrease may have been offset by increased solar radiation and clearer skies.

4.3.3 Late Holocene 4,000 BP – Present

According to McGlone *et al* (1996) "*Fuscospora* forest continued to spread in the southern North Island and northern South Island, and by 3,000 BP it was making inroads into lowland forest in the ranges immediately north of Wellington...and at the northern edge of Westland." This statement is supported by the *N.fusca* isochrone map; by 3,000 years BP *N.fusca* had migrated as far south as Manawatu; in the South Island, as far south as Fox Glacier At this time, between 85 and 90% of New Zealand's land cover was thought to be forested, with grassland and shrubland restricted to above the timberline (McGlone & Wilmshurst 1999).

McGlone & Moar (1977) claimed that *Ascarina* disappeared from the pollen record in the central North Island around the time of the Taupo eruption (1850 years BP), decreasing to modern levels in the southern North Island between 2,500 and 1,500 years BP. The isopollen map for 2,000 – 0 years BP strongly supports this, with a large portion of the central North Island showing 0% relative pollen frequency, and south of Manawatu displaying 1% frequency, very similar to the present day isopollen map.

Although frequent fires in the south after 2,500 years BP are thought to have promoted the replacement of scrub with grasslands (Markgraf *et al* 1992), temperate broadleaved and coniferous forests are believed to have covered as much as 90% of the land area prior to the arrival of humans in New Zealand (Leathwick 2001).

After around 1,000 years BP clear indications of anthropogenic impact are found in the fossil pollen record. The relative pollen percentage of tall forest taxa declined; *Pteridium esculentum* (bracken) spores and pollen from seral shrubs including *Coriaria*, *Aristotelia* and *Coprosma*, and grasses increased (Wilmshurst 1997). Sudden influxes in terrigenous sediments in lakes occurred at this time (Eden & Page 1998) and pollen cores displayed abnormally high amounts of charcoal. All these point to massive deforestation by way of burning following the arrival of Maori around 800 years BP (McGlone 1983b). Maori traditionally used fire to keep tracks clear, to exclude tall vegetation from dwelling areas, and to encourage growth of *Pteridium esculentum* (bracken), a major source of carbohydrate (McGlone & Wilmshurst 1999).

This pattern is seen very clearly in the 2,000 – 0 BP isopollen map for *Coprosma*, with high percentages indicated for Northland and the western North Island. Surprisingly, the Hawkes Bay area does not show an increase. This is unexpected given that Maori are likely to have settled early in this area given its favourable climate for horticulture. The isopollen map for the South Island is equally confusing; at 4,000 – 2,000 years BP the entire east coast south of Kaikoura had *Coprosma* pollen frequencies >5%, yet by 2,000 – 0 BP the 5% isoline had contracted southward and inland, which is somewhat contrary to expectations.

Although erosion pulses recorded in lake sediments and large quantities of charcoals on their own are not necessarily indicative of anthropogenic impact[153], taken together, along with the pollen record they provide a much more compelling case for deforestation by humans. Furthermore, since natural fires were rare in the western part of both islands, fires in moist rain forest were likely to have anthropogenic origins, particularly when these recurred with subdecadel return periods (McGlone & Wilmshurst 1999). According to McGlone (1983b) as much as 50% of the forest cover was destroyed before Europeans settled in New Zealand in the mid nineteenth century.

Removal of forest and scrub continued following European settlement; this is evident in the pollen record with increased frequency of Poaceae, *Taraxacum* and *Acaena* and the appearance of exotic taxa including *Pinus*, *Salix* and *Rumex*. At the same time, scrub taxa such as *Coprosma*, *Coriaria* and *Aristotelia* became less abundant (Wilmshurst 1997) as lowland areas were cleared to grow pasture.

The decline in *Coprosma* is seen very clearly in the isopollen maps, becoming virtually absent on the east coast of the South Island north of the Otago Peninsula. In the North Island the taxon was restricted to Manawatu and the volcanic plateau, and then achieved only 5% of the pollen sum. The isopollen maps for Poaceae clearly demonstrate the rise in grasses; the massive change between the 2,000 – 0 BP and the modern isopollen maps are in strong agreement with what is known from the historical record. As little as 25% of the original forest cover now remains (McGlone 1983b).

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[153] For example, severe storms and earthquakes can promote mass movement. Furthermore, dating charcoals produces some difficulties, for example humic acid contamination can lead to younging. More problematic

4.4 Conclusion

Overall, the isopollen and isochrone maps appear to be very plausible descriptions of New Zealand's paleoenvironment since the LGM, in that the pollen frequencies, migration direction and routes broadly agree with paleoenvironmental research conducted thus far.

In some cases the isochrone and isopollen maps at first glance appear to be contradictory. For example, *Dacrydium cupressinum* shows little expansion between 14,000 and 12,000 BP in the isochrone map although the isopollen map for 14,500 – 10,000 BP shows high pollen percentages in southern Waikato, northern Hawkes Bay and Northland. *Podocarpus totara* shows high percentages in Manawatu and East Cape in the late glacial isopollen map, yet the isochrone map fails to show the taxon before 10,000 BP. Similarly, the isopoll map for the period 10,000 - 8,000 BP shows a centre of *Nothofagus fusca* concentration around Picton, with between 0 and 5% relative frequency south of Westport. However, the isochrone map shows three distinct centres around Westport for 10,000 - 8,000 BP, and the taxon not reaching Picton until 2,000 BP. At first glance, this is contradictory.

There are three main reasons for this apparent incongruity. First, some of the discrepancy is an artefact of the time periods under consideration in the respective maps: whereas the isochrone maps are plotted at 2,000 year contour intervals, the isopollen maps cover a much wider time period, for example the late glacial (14,500–10,000 years BP) therefore they are not strictly comparable for this period of time. The different time intervals used was a compromise between having meaningful time periods for both types of map and having sufficient pollen sites to plot without excessive interpolation and extrapolation by the contouring program.

The second reason for the apparent discrepancy is that the contouring program used to produce the isopollen map utilises *all* sites to interpolate and extrapolate grid node values, even where these are recorded as 0% relative frequency[154]. Conversely, when constructing the isochrone maps, only sites with relative pollen frequencies ≥ the critical value are used.

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is that charcoals will be derived from woods of different ages: the longevity of many of our trees means that there can be a thousand-year age gap between living trees, with logs on the forest floor being even older.

[154] A 0% isoline is desirable where taxa boundaries are sharply demarcated, for example altitudinal limits.

Thus in a sense whereas the contouring program is interpolating and extrapolating grid values for isopollen map construction, in isochrone map construction it is interpolating only.

The third reason is that although using a critical value of, say 10% for taxon A gives equal weighting to all sites having greater than or equal to 10% in the isochrone map, the isopollen map does not treat the values as equal, and interpolates different valued isolines, depending on the desired interval specified in the contouring. Thus the critical value isoline in the isochrone map in a sense does not 'take into account' the variation in positive values, but simply contours on the basis of presence and absence in the data.

One way to evaluate the internal validity of the isopollen maps is to perform a sensitivity analysis, that is, assess the impact of adding or deleting sites on the contouring program. Appendix 5.5.1 shows *Dacrydium cupressinum* for the period 6,000 – 4,000 BP (a) compared with (b) which is derived from the same dataset, with another site added – Taieri Plains (O'Brien 2000). Clearly, adding a site influences the map, as evidenced by the new 10% isoline in SE Otago. However, kriging has 'reduced' the observed value (25% relative pollen frequency) to 10%. Thus although the surrounding grid nodes have moderated the new isoline value, the new site has had almost no discernible impact on the rest of the map. This is reassuring; one would be concerned if a single, high value distorted values at distal sites. At the same time, it would be equally disconcerting if adding a site with a high value had no impact on the map at all.

Appendix 5.5.2 shows the isopollen map for *Agathis australis* 4,000 – 2,000 years BP (a) compared with (b) which again is derived from the same dataset, with four additional sites: Waiatarua (Horrocks, Deng *et al* 2002), Harataonga (Horrocks, Nichol & Shane 2002), Ohinewai (McGlone *et al* 1984) and Tiniroto (Xun 2002, personal communication). Apart from 'forcing' the southern-most, 1% isoline to the west into Waikato, the addition of the four sites has had little impact on the resultant isopollen map.

In general the larger the sample set, the better the interpolation, since mean square error (discussed in Chapter 2.7) decreases. However, several researchers have found that once the sample set reaches a certain size, accuracy actually decreases. Eventually a point of diminishing returns occurs, beyond which the increased improvement is not worth the worth the extra effort to process the additional control points. According to Robinson *et al* (1978) "Certainly more control points that tend only to increase the clustering of the control points are not necessarily beneficial for surface portrayal, since this is more likely to lead to uneven generalisation." Thus the 'uneven generalisation' can outweigh the effect of the absolute number of samples, "... particularly when a reasonable density of data points has already been achieved," (Yang & Hodler 2000). In cases such as this, the researcher should focus on geometric (distribution of the samples) and quality attributes, leading Yang & Hodler (2000) to conclude that "... it is safe to say that a larger sample size (higher sample density) does not always ensure a higher accuracy of products."

One way of testing the external validity of the isopollen and isochrone maps is to compare them to similar maps that utilise data other than pollen. Ogden *et al* (1992) plotted a species range map for the Holocene expansion of *Agathis australis* based upon wood samples. The fossil wood species range map showed slightly different migration rates to the pollen isochrone map; Ogden *et al* (1992) showed kauri present as far south as Tauranga 3,500 years BP then retreating northward to Auckland by 1,500 BP. The *Agathis* isochrone map presented in this thesis shows the taxon at Tauranga 1,500 BP and as far south as Hamilton by 1,000 years BP (Appendix 5.5.3).

Given the limitations of palynology and carbon dating outlined in Appendix 5.4, the two paleo-reconstruction techniques show remarkably good agreement. The fossil wood species range map shows the modern southern limit in an arcuate shape running (from east to west) from Te Puke – Cambridge – Hamilton - Kawhia, which corresponds to the southern-most, 1,500 BP pollen isoline.

The modern isopollen map for *Ascarina lucida* can be compared to maps compiled by direct observation and sawmilling records (McGlone & Moar 1977) (Appendix 5.5.3). The isopollen map suggests that in the South Island, the taxon is largely restricted to southern Fiordland, however *Ascarina* is regularly present on the West Coast of the South Island and common in central Westland (McGlone & Moar 1977; Allan 1982). The reason for the discordance is almost solely attributable to the paucity of pollen sites, in particular modern pollen sites[155], for the West Coast. The *a posteriori* data (that is, the pollen frequency data) is overwhelmed by the *a priori* data (that is, sites assigned 0% pollen frequency on the basis of freezing temperatures), however the situation was scarcely improved by re-running the contouring program with the *a priori* data removed from the dataset. Thus the anomalous result appears to be an artefact of sample size rather than an inherent problem with either palynology or isopollen mapping. No doubt the situation would be remedied with more modern pollen data (*cf* Robinson *et al* 1978; Yang & Hodler 2000, *supra*.)

The major contribution that these isopollen and isochrone maps afford is that they demonstrate that adopting a holistic perspective and utilising an integrative approach can yield generally robust, coherent cartographic depictions of paleovegetation distribution. Of secondary importance is the alternative viewpoints that they imply and questions that they raise, such as shedding some doubt on the supposed southern limit of continuous forest at the LGM (McGlone *et al* 1993), the extent of forest cover in the South Island during the early Post-Glacial (Dodson 1978) or the existence of a Southern Hemisphere stadial coeval with the Younger Dryas (Newnham & Lowe 2000).

It would be useful to repeat the mapping exercise in the future as more fossil pollen data becomes available, particularly in areas where information is sparse such as the east coast of the South Island for the LGM, the west coast of the South Island for the late glacial and the early post glacial, and the east coast of the South Island for the period 2,000 – 0 years BP. Ideally, these maps would be supplemented with isophyte maps, however this would require much more modern pollen information to derive *R*-values than is currently available.

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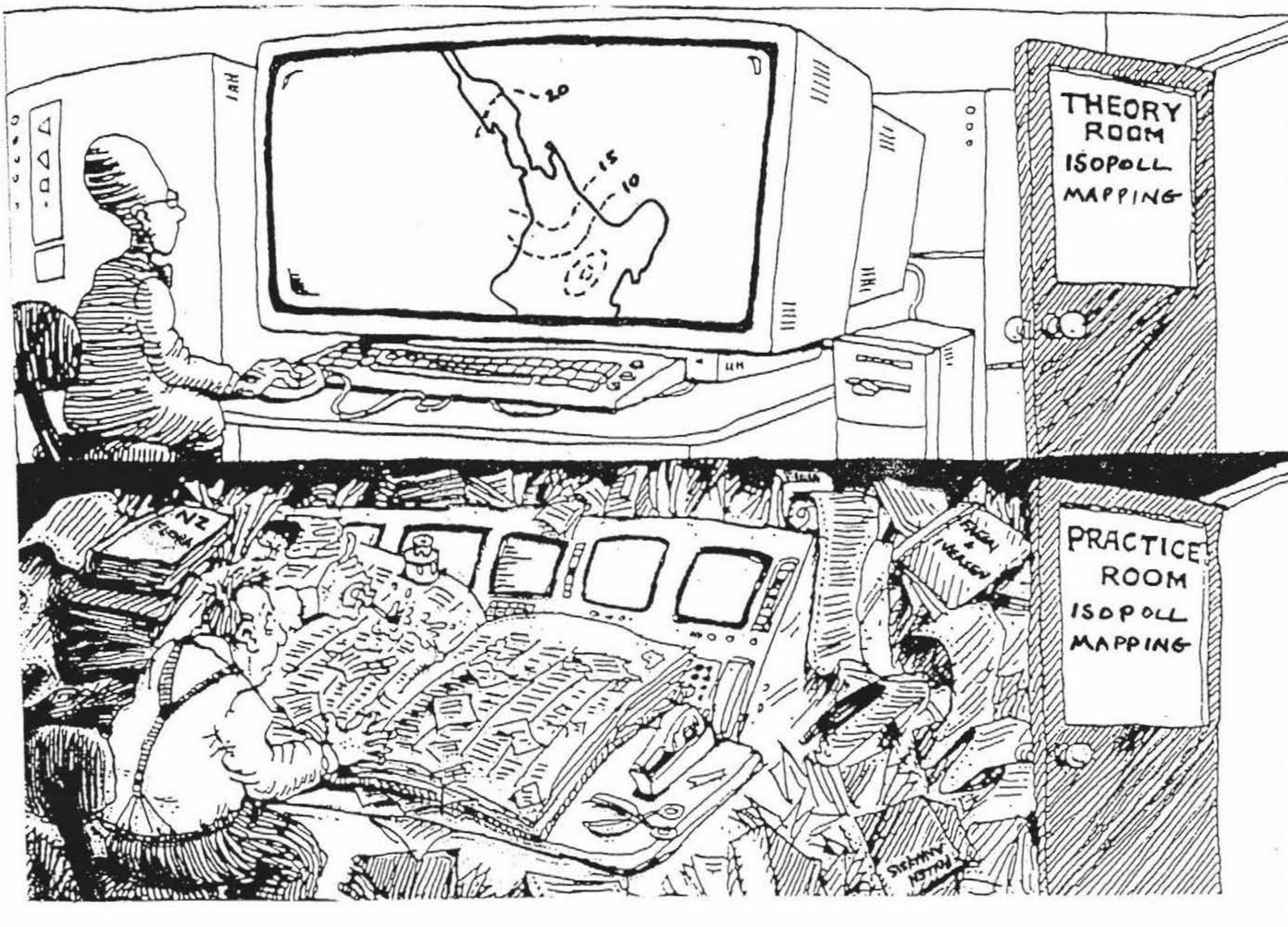
[155] Some fossil pollen diagrams do not report modern pollen data (Moar & Suggate 1973; Moar 1980); some do not record *Ascarina* (Moar & Suggate 1996) or record amounts <1% (Mildenhall 1978). Nowhere is *Ascarina* strongly represented.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15
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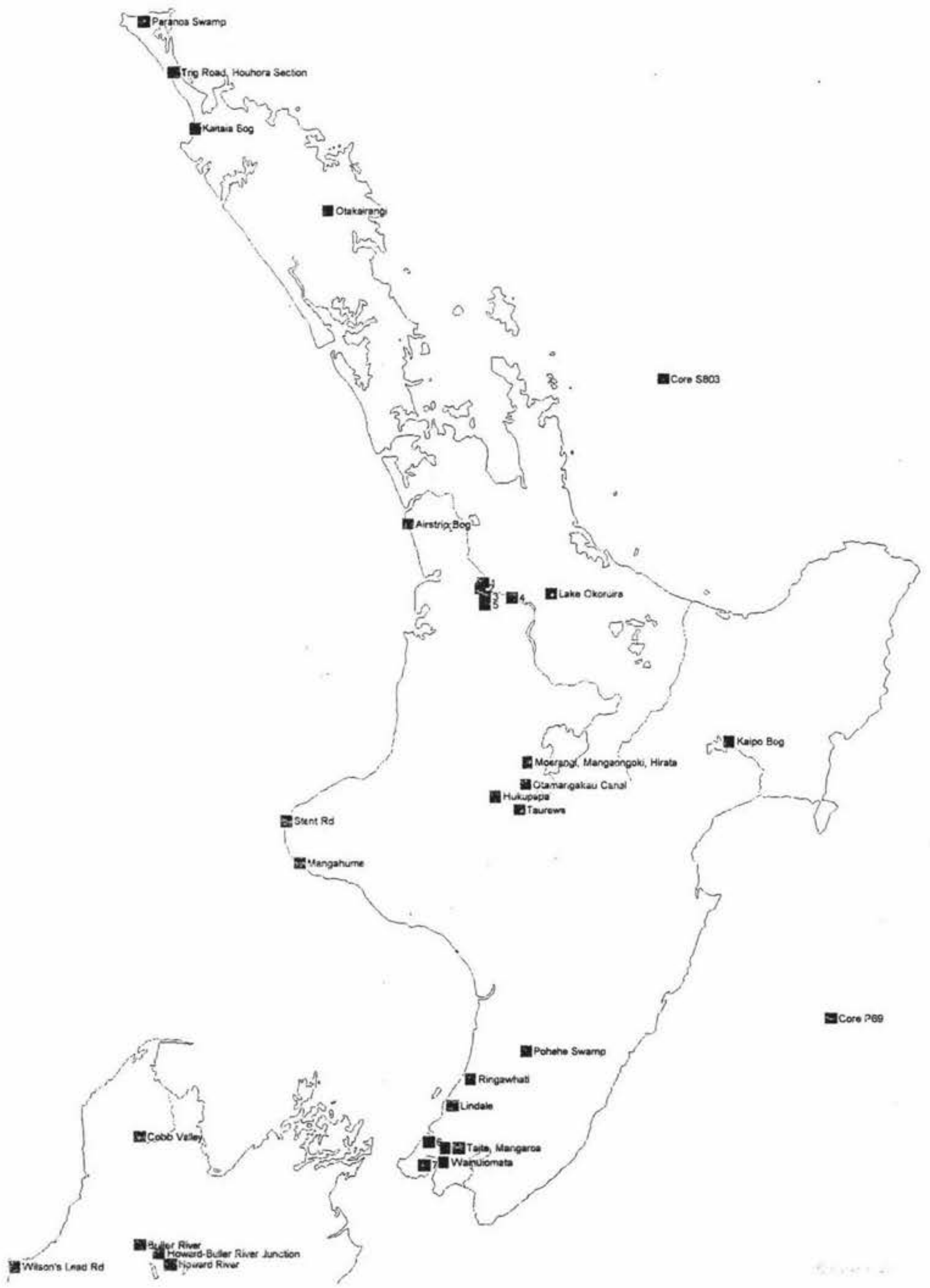
THEORY ROOM
ISOPOLL MAPPING
NZ FLORA
FAEGRI & IVERSEN
POLLEN ANALYSIS
PRACTICE ROOM
ISOPOLL MAPPING

5 Appendices

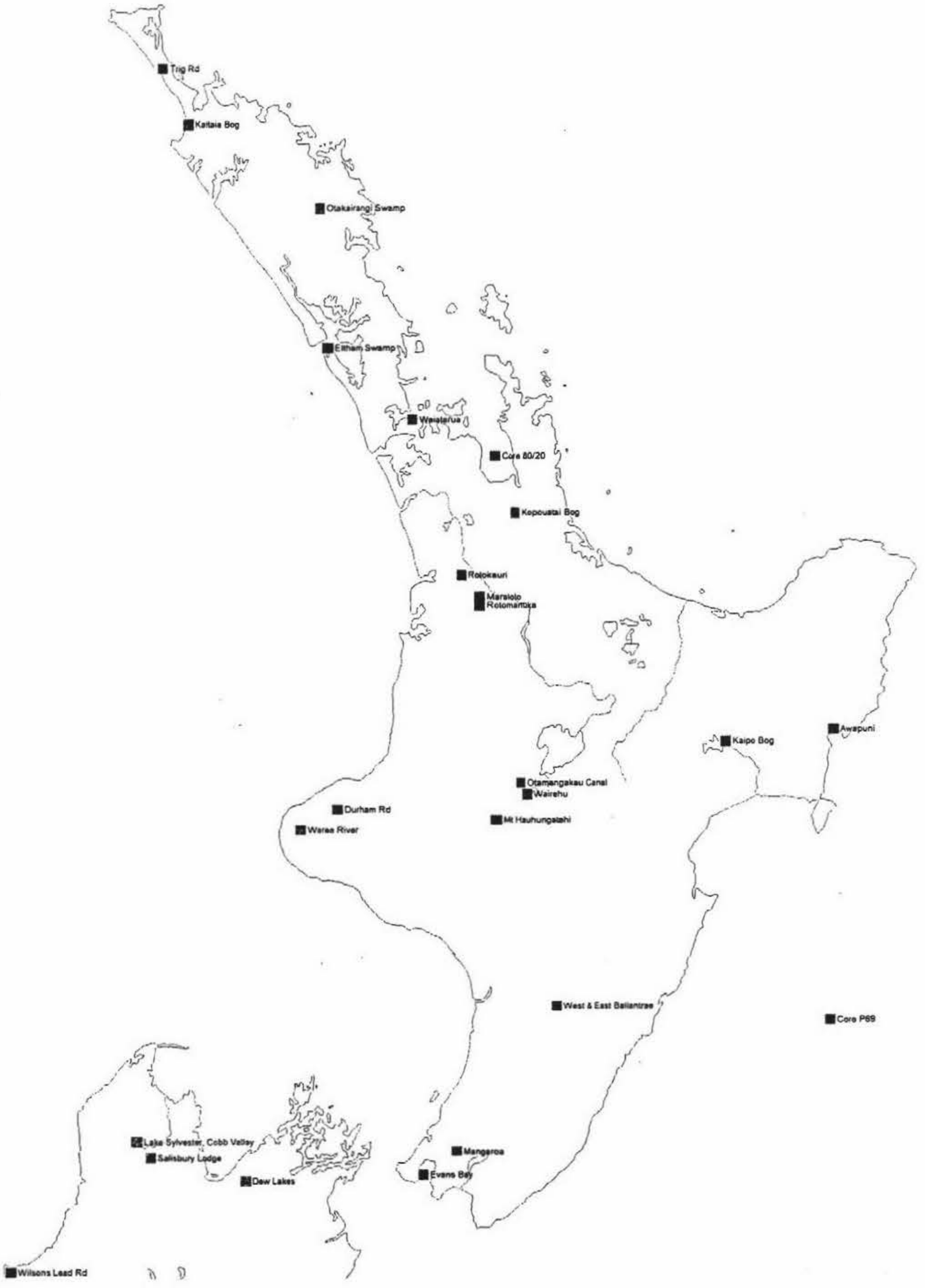
Appendix 5.1 Pollen Sites



Appendix 5.1.1.1 North Island Pollen Sites, 22,000 – 14,500 Years BP

1 = Waikato Hospital; 2 = Lake Rototuna; 3 = Lake Maratoto; 4 = Cambridge; 5 = Lake Rotomanuka; 6 = Porirua; 7 = Mirimar.

Appendix 5.1.1.2 South Island Pollen Sites, 22,000 – 14,500 Years BP



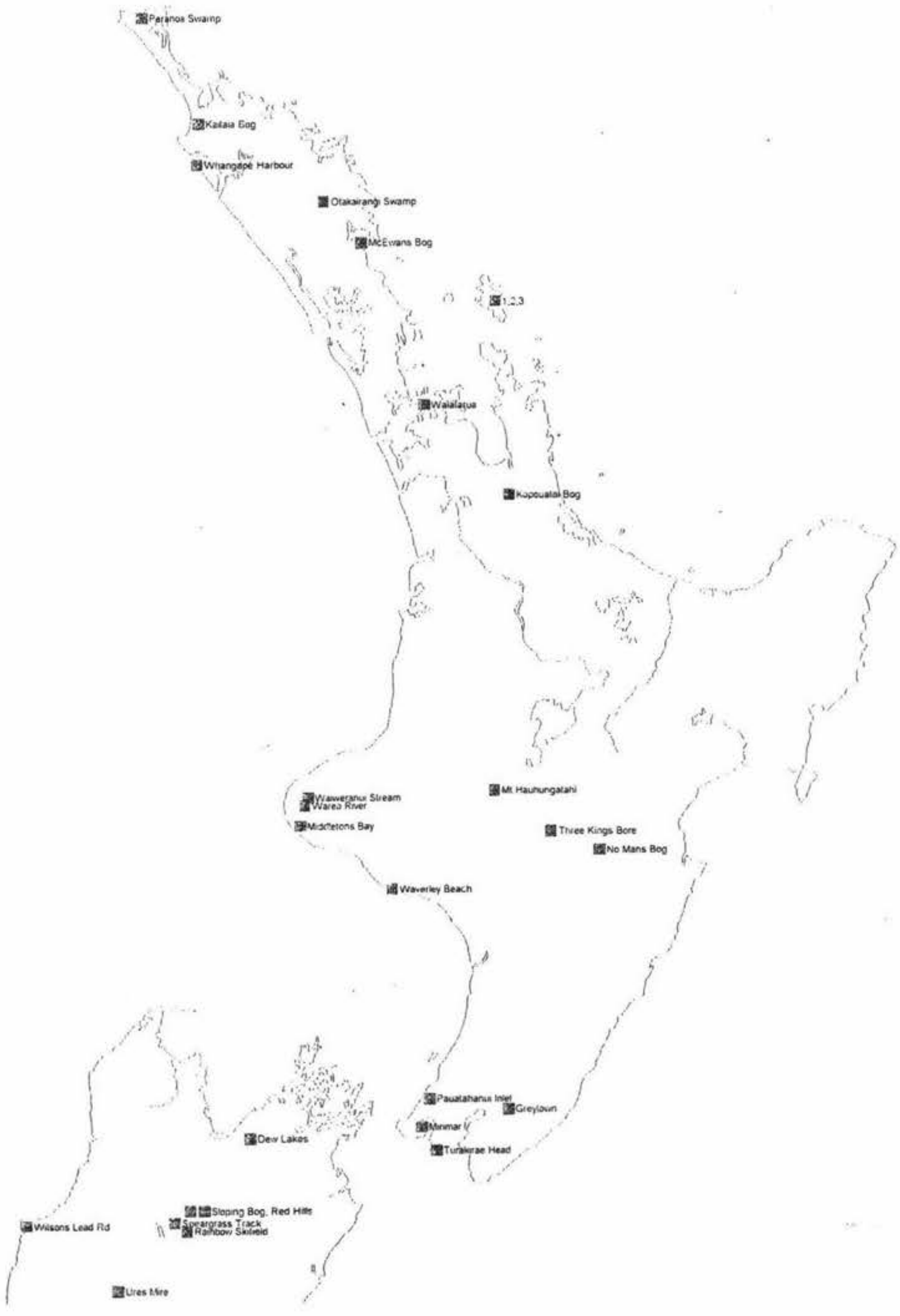
Appendix 5.1.2.1 North Island Pollen Sites, 14,500 – 10,000 Years BP

Appendix 5.1.2.2 South Island Pollen Sites, 14,500 – 10,000 Years BP

1= Windy Tarn; 2 = Quagmire Tarn; 3 = Wairau River; 4 = Upper Wairau River

Appendix 5.1.3.1 North Island Pollen Sites, 10,000 – 8,000 Years BP

Appendix 5.1.3.2 South Island Pollen Sites, 10,000 – 8,000 Years BP



Appendix 5.1.4.1 North Island Pollen Sites, 8,000 – 6,000 Years BP

1 = Forsythes Paddock; 2 = Kaitoke Swamp; 3 = Curreens Paddock

Appendix 5.1.4.2 South Island Pollen Sites, 8,000 – 6,000 Years BP

1 = Kawarau Gorge

Appendix 5.1.5.1 North Island Pollen Sites, 6,000 – 4,000 Years BP

1 = Reparoa Bog

Appendix 5.1.5.2 South Island Pollen Sites, 6,000 – 4,000 Years BP

1 = Nans Kettle; 2 = Kawarau Gorge; 3 = Ramparts

Appendix 5.1.6.1 North Island Pollen Sites, 4,000 – 2,000 Years BP

1 = Reparoa Bog; 2 = Lake Mangaratanui; 3 = Manawatu Gorge

Appendix 5.1.6.2 South Island Pollen Sites, 4,000 – 2,000 Years BP

1 = Nans Kettle; 2 = Nokamai Islands

Appendix 5.1.7.1 North Island Pollen Sites, 2,000 – 0 Years BP

1 = Lake Rotomanuka; 2 = Reparoa Bog; 3 = Lake Maratoto; 4 = Lake Okoroire; 5 = Lake Waikaremoana

Appendix 5.1.7.2 South Island Pollen Sites, 2,000 – 0 Years BP

1 = Nokamai Islands

Appendix 5.1.8.1 North Island Pollen Sites, Modern

1 = Lake Waikaremoana; 2 = Reparoa Bog

Appendix 5.1.8.2 South Island Pollen Sites, Modern

1 = Rakeahua Tarn

Appendix 5.1.9 Locations Mentioned in the Text (Excluding Pollen Sites)

Appendix 5.2 Pollen Morphology of New Zealand Taxa Discussed in the Text

Gymnosperms:

Family Araucariaceae. Genus ***Agathis*** The sole New Zealand representative of this genus[156] is *Agathis australis* (kauri), an easily recognised pollen grain described by Pocknall (1981c) as an apolar, spheroidal or occasionally ellipsoidal grain with a mean diameter of 46 μm. The exine[157] is approximately 2.5-3 μm thick, and the outer surface is scabrate[158] to papillate[159], features clearly seen in both Figures 14a and 14b.

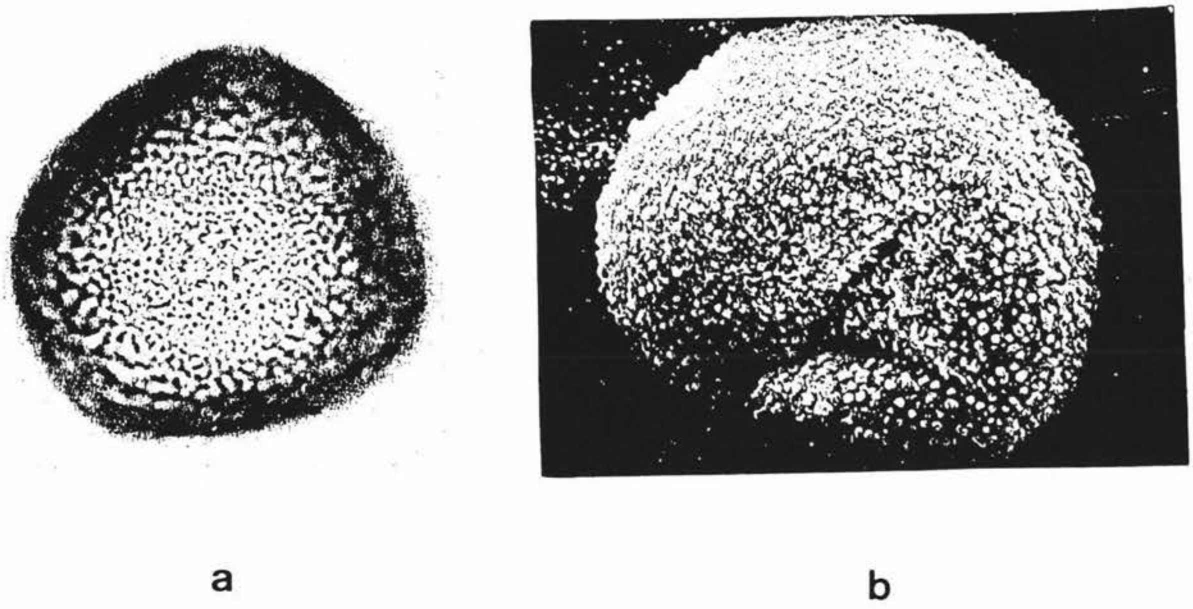


Figure 14: (**a**) Equatorial LM view of *Agathis australis* (× 750) (**b**) Equatorial SEM view of *A.australis* (× 800) *Source*: Pocknall (1981c)

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[156] *Agathis australis* is also the southernmost member of the genus (Owens *et al* 1995).

[157] The resistant outer wall of a grain of pollen which overlies the intine; subdivided into endexine and ectexine.

[158] Defined by Moar (1993) as a "....minute isodiametric element on the exine surface, usually < 1μm diameter."

[159] Papillate refers to parallel sided exinous elements with rounded apices < 1μm diameter (Hoen 1999).

Family Cupressaceae. Genus ***Libocedrus.*** *Libocedrus plumosa* (kawaka) pollen is described by Pocknall (1981c) as apolar, small (29μm mean diameter) spheroidal grain with a tectate-perforate sexine consisting of star-shaped orbicules [160]. Although the pollen grain preserves poorly[161], its under-representation in the fossil record is more likely due to the fact that it is often collapsed and distorted.

Because *L.plumosa* pollen is very similar to *L.bidwilli* (apart from size - *L.bidwilli* being around 25μm mean diameter); it is seldom identified to the species level (eg Moar 1967; Moar & Mildenhall 1988; McGlone & Moar 1998) and therefore not an ideal candidate for plotting as an isopollen map, given the different biogeographical distribution of the two species – Allan (1982) gives the distribution of *L.plumosa* as lowland forest, whereas *L.bidwillii* is montane to subalpine; furthermore, the former is found between 35 and 38°S whereas the latter is found south of 36° 50′S. An isochrone map was prepared for this genus however.

Family Phyllocladaceae: The genus ***Phyllocladus*** is comprised of five species, three of which are endemic to New Zealand. *Phyllocladus* pollen is generically distinctive: all grains are monads[162], heteropolar, bilateral, vesiculate[163] and bisaccate[164] (Pocknall 1981b), however pollen at the species level is difficult to distinguish. *Phyllocladus glaucus* can be relatively easily distinguished from *P.trichomanoides* and *P.aspleniifolius* var *alpinus* because of its smaller sacci and overall size (23.5μm total length versus 34.3μm and 34.2μm for *P.trichomanoides* and *P.alpinus* respectively); however distinguishing between *P.trichomanoides* and *P.alpinus* is more difficult: although

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[160] Tectate refers to the surface of a pollen grain that is covered by a continuous layer of exine. Perforate refers to a tectum with small perforations whose diameter is less than the interstitial spaces. Sexine refers to the outer, sculptured part of the exine. Orbicules or ubisch bodies are "Chunks of sporopollenin produced by the tapetum of the anther or prorangium but not 'used' in making exines," (Traverse 1988) that are often found attached to the pollen exines or as free bodies in polliniferous sediments.

[161] Horrocks & Ogden (1994) found that even for modern grains, most were partially or completely split open.

[162] Monads are pollen grains occurring singly, compared with tetrads, which are grains where separation of cells following division of the mother cell has not occurred. Tetrads occur in either tetrahedral or tetragonal forms.

[163] Heteropolar describes poles that are dissimilar with respect to shape, pattern or arrangement of apertures. Bilateral refers to two planes of symmetry. Vesiculate is a synonym of saccate, ie has a sac formed by the expansion of the exine (Hoen 1999).

[164] Bisaccate grains have two sacci or airsacs. Interestingly, *Phyllocladus* has been described as 'functionally non-saccate' by Tomlinson *et al* (1997) since unlike most other Podocarpaceae pollen bearing sacci, it is 'wettable' ie it sinks in water – a process that appears to be related to pollen capture by a pollination drop secreted by the ovule and exuded through the micropyle.

P.trichomanoides (Figure **15a**) is more spheroidal and has coarser sculpting of the cappa[165] and more folds in the sacci than *P.alpinus* (Figure **15b**), these distinctions are difficult to make under the light microscope due to the small size of the structural characteristics, as shown in Figures **15c** and **15d**.

This is unfortunate; most researchers therefore only identify grains to the genus level (Moar 1961; Soons & Burrows 1978; Burrows 1983; McGlone 1985), yet the geographical distribution of *P.trichomanoides* and *P.alpinus* is markedly different, as shown in Table 4. However, plotting *Phyllocladus* at the genus level could still provide useful information, for example Sakai & Wardle (1978) state that today, *P.alpinus* is not found south of 46°30′S. Therefore, fossil *Phyllocladus* pollen south of 46°30′S, for example, could indicate warmer temperatures.

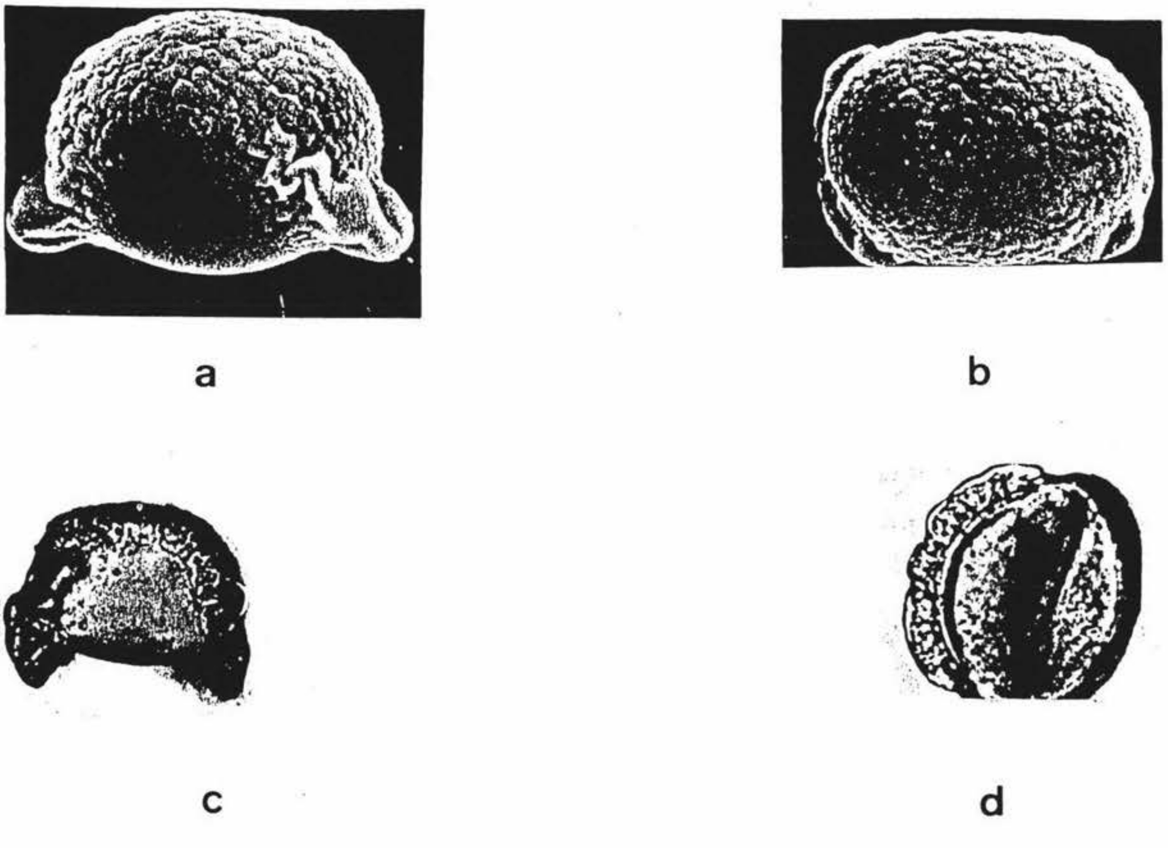

Figure 15: (**a**) Polar SEM view (proximal) of *Phyllocladus trichomanoides* (× 2000) (**b**) Polar SEM view (proximal) of *P.alpinus* (× 1750) (**c**) Lateral longitudinal LM view of *P. trichomanoides* (× 1300) (**d**) Lateral longitudinal LM view of *P.alpinus* (× 1300) *Source*: Pocknall (1981b)

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[165] Cappa refers to the round or elliptical area of the proximal surface, usually bounded by the marginal ridge (Cranwell 1940).

Family Podocarpaceae: Genus ***Dacrycarpus*** This genus consists of a single endemic species, *Dacrycarpus dacrydioides* (kahikatea)[166] whose pollen is easily identified since it is the sole modern, trisaccate (three airsacs) pollen in New Zealand (Pocknall 1980a) and therefore an excellent candidate for mapping since it is unlikely to be incorrectly identified, and has a distinct distribution. *D.dacrydioides* is monad, heteropolar and bilateral; the corpus is spheroidal or lens shaped (Figure **16b** shows the lenticular form very clearly); the cappa is finely tuberculate (Figure **16a**) terminating in a coarsely rugulate marginal ridge (Figure **16b**). Sacci are hemispherical and the furrow between them is triangular, which is best seen in Figure **16c**.

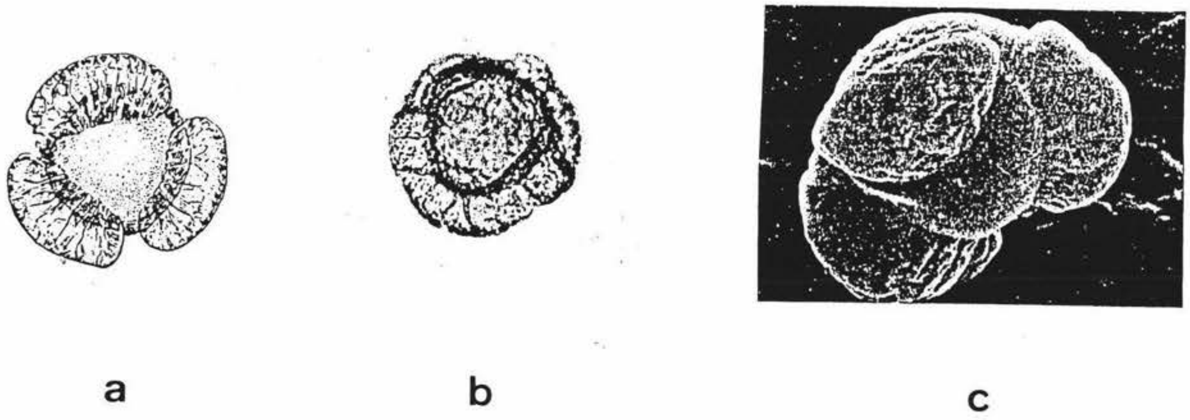

Figure 16: (**a**) Polar view (distal) of *Dacrycarpus dacrydioides* (× 790) (**b**) Polar LM view (proximal) of *D.dacrydioides* (× 790) (**c**) Polar SEM view (distal) of *D.dacrydioides* (× 1080) *Source*: Cranwell (1940); Pocknall (1981a)

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[166] Renamed from *Podocarpus dacrydioides* in Edgar (1971).

Family Podocarpaceae: The genus ***Dacrydium*** has a single species in New Zealand (Franklin 1968), *Dacrydium cupressinum* (rimu) that is easily distinguished in the fossil pollen record; it is similar in size to *Halocarpus kirkii* but can be differentiated on the basis of its saccus which does not protrude far from the corpus in polar view as seen in Fig **17a**, whereas it *H.kirkii* it does. Furthermore, the cappa is mostly coarsely tuberculate-rugulate[167] (seen clearly the SEM photo, **17b**) with an inconspicuous rugulate marginal ridge at the proximal roots of the sacci (most clearly seen in Fig **17c**), compared with *H.kirkii* (Figure **17d**) which is finely tuberculate in the centre with a marginal ridge near the proximal roots of the saccus. Again, *Dacrydium* is most amenable to plotting in isopollen maps.

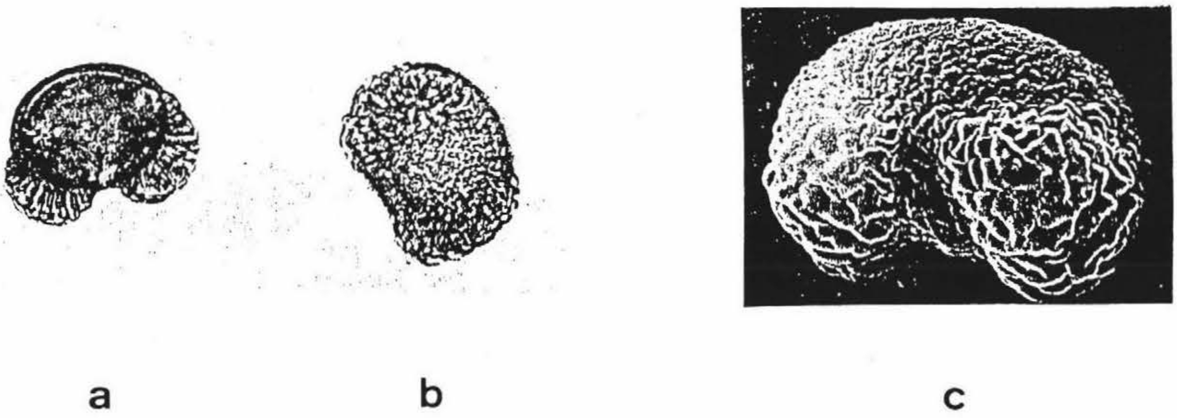

Figure 17: (**a**) Lateral longitudinal LM view of *Dacrydium cupressinum* (× 700) (**b**) Polar LM view (distal) of *D.cupressinum* (× 700). (**c**) Lateral longitudinal SEM view of *D.cupressinum* (× 1400). *Source*: Pocknall (1981a)

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[167] Tuberculate refers to a surface covered in knobbly projections; rugulate describes irregularly distributed, elongated strips of exine that are at least twice as long as they are broad (Moar 1993).

Family Podocarpaceae: Genus ***Halocarpus*** consists of three species, *Halocarpus bidwillii* (bog pine), *H.biformis* (pink pine) and *H.kirkii*[168] (monoao). According to Pocknall (1981a) pollen grains from these species are all monad, heteropolar, bilateral grains; vessiculate and bisaccate, at first glance making discrimination difficult, as seen in Figures **18a**, **18c** and **18d**.

Although *H.kirkii* has not been found in the fossil pollen record, and *H.biforme* and *H.bidwilli* can be distinguished from each other on the basis of size of the grain – *H.biforme* having a greater total length, corpus breadth and saccus length than *H.bidwillii* - most pollen diagrams only identify *Halocarpus* to the genus level (eg Dodson 1978; McLea 1996).

In any event the distinction is not particularly useful: since *H.biformis* and *H.bidwillii* are both montane-subalpine trees (Allan 1982) found from the central North Island to Stewart Island (Poole & Adams 1990) they do not elucidate paleoclimate characteristics as well as other taxa and therefore are not plotted.

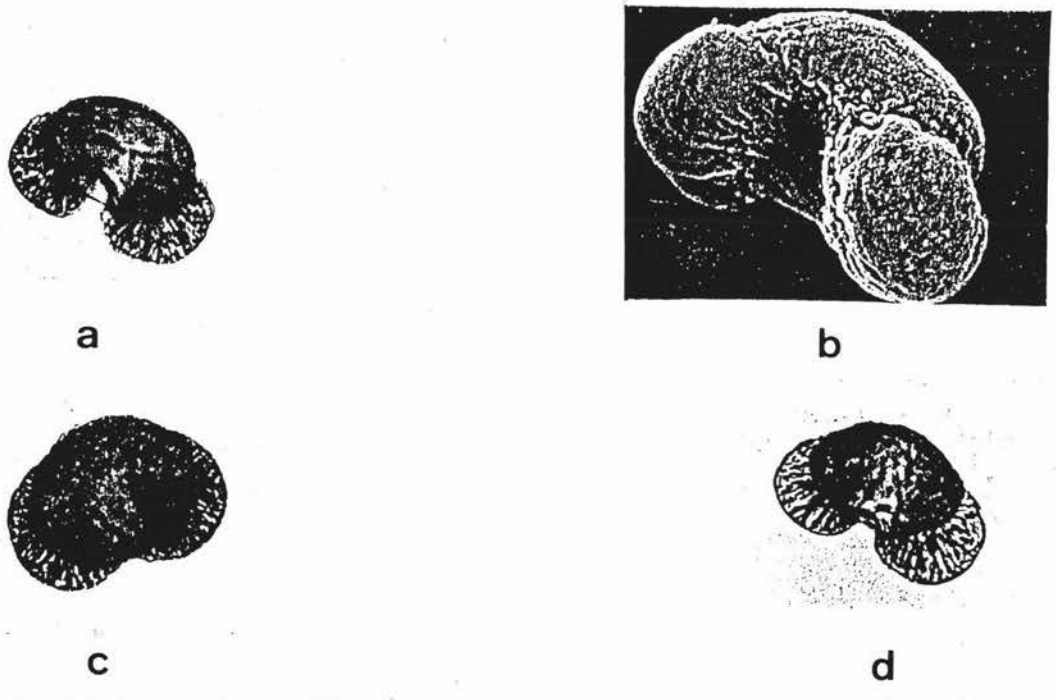

Figure 18: (**a**) Lateral longitudinal LM view of *Halocarpus bidwillii* (× 640) (**b**) Lateral longitudinal SEM view of *H.bidwilli* (× 1250) (**c**) Lateral longitudinal LM view of *H.biformis* (× 640) (**d**) Lateral longitudinal SEM view of *H.kirkii* *Source*: Pocknall (1981a)

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[168] Renamed from *Dacrydium bidwillii*, *Podocarpus biformis* and *Dacrydium kirkii* respectively in Edgar & Connor (1983).

Family Podocarpaceae The genus ***Lagarostrobos*** consists of one species *Lagarostrobos colensoi* (silver pine)[169] in New Zealand. The pollen of this genus is similar to the *Podocarpus* genus due to "...the absence of radial internal muri[170] of the sacci and the suggestion of a furrow[171] rim," (Pocknall 1981a). *L.colensoi* is relatively easily identified by its delicate reticulum which is clearly visible using both light microscopy (Figure **19a**) and scanning electron microscopy (Figure **19b**). Nevertheless, *Lagarostrobos* has not been mapped due to the small number of pollen diagrams that enumerate it.

Figure 19: (**a**) Polar LM view (distal) of *Lagarostrobos colensoi* (× 640) (**b**) Polar SEM view (distal) of *L.colensoi* (× 120) *Source*: Pocknall (1981a)

Family Podocarpaceae. Genus ***Podocarpus*** consists of four species in New Zealand: *Podocarpus acutifolius, P.hallii* (Hall's totara), *P.nivalis* (snow totara) and *P.totara*, (totara) and a variety *P.totara* var *waihoensis* (Wardle 1972[172]; Edgar & Connor 1983). Although these four species are often difficult to distinguish from each other on account of the similar morphological characteristics they share, in particular their spheroidal-ellipsoidal cappa and thick exine, Pocknall (1981a) states that they can be distinguished by their saccus size, shape and reticulation.

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[169] Renamed from *Dacrydium colensoi* in Edgar & Connor (1983).

[170] The murus is a ridge that is part of the pollen grain's ornamentation, separating the lumina in reticulate pollen grains or the striae in striate grains (Hoen 1999). It is a wall formed by the bacula or rod-like elements that extend between the endexine or inside layer of the exine, and the tectum or outermost layer or the pollen wall. The tectum and bacula together make up the ectexine. The lumina is the interstitial space formed in the reticulum by the enclosing walls of the muri.

[171] A furrow is an elongate aperture (Hoen 1999) lying latitudinally across the equator of the pollen grain.

P.acutifolius and *P.totara* var *waihoensis* both have discontinuous sacci lumina which can be discerned by comparing Figures **20a** and **20b** to Figure **20c**. However, *P.acutifolius* is infrequently identified in fossil pollen assemblages due to its lack of distinctive characteristics and limited distribution of the species. *P.nivalis* has a coarsely rugulate cappa (Figure **20c**) whereas *P.hallii* and *P.totara* have randomly distributed sacci lumina (Figures **20d**, **20e** and **20f**), although *P.hallii* is possibly more poorly preserved than the other podocarps, frequently collapsing when being prepared for scanning electron microscopy (Pocknall 1981a).

Thus although around 30% of pollen diagrams utilised in this thesis identified *Podocarpus* only to the genus level, there is a sufficient number of diagrams that are identified to the species level to construct isopollen maps for *P.totara*. This subset of diagrams may be augmented with pollen diagrams that adopt the nomenclature of Connor & Edgar (1987) since this would eliminate species previously classed in family Podocarpaceae: *Dacrycarpus dacrydioides* (renamed by Edgar 1971); *Prumnopitys ferruginea, P.taxifolia* (renamed by Edgar & Connor 1983) if the assumption is made that *P.halli* is generally not preserved and the majority of grains identified as *Podocarpus* are in fact *P.totara*.

Figure 20: (**a**) Polar LM view (distal) of *Podocarpus acutifolius* (× 860) (**b**) Polar LM view (distal) of *P. totara* var *wahoensis* (× 860) (**c**) Polar LM view (distal) of *P.nivalis* (× 860) (**d**) Polar LM view (distal) of *P.hallii* (× 860)

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[172] *Podocarpus totara* var *waihoensis* is thought to be a hybrid of *P.acutifolius* and *P.totara* (Wardle 1972).

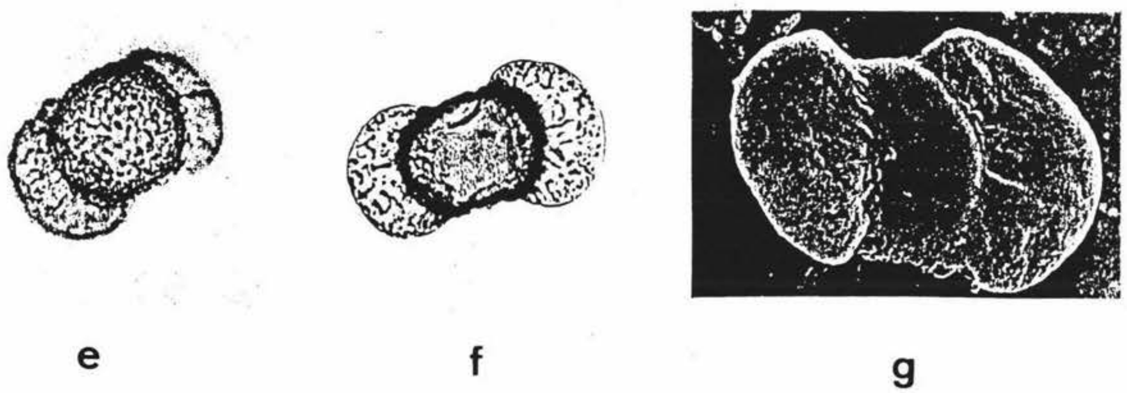

Figure 20 (continued): (**e**) Polar LM view (proximal) of *P. totara* (× 860) (**f**) Polar LM view (distal) of *P.totara* (× 860) (**g**) Polar SEM view (distal) of *P.totara* (× 1360) *Source*: Pocknall (1981a)

Family Podocarpaceae. Genus ***Prumnopitys*** consists of two species in New Zealand, *Prumnopitys ferruginea*, (miro) and *P.taxifolia* (matai). Pollen grains of both species are monad, heteropolar, bilateral; vesiculate and bisaccate. According to Pocknall (1981a) "Fossil [*P.taxifolia*] has usually been lumped with [*P.ferruginea*] in the one category 'Podocarpus.' " A review of the published pollen diagrams suggests otherwise; > 87% of diagrams do in fact distinguish *Prumnopitys* from other Podocarps.

Much of the difficulty in identification arises from the orientation of the pollen in fossil preparations as its limited diagnostic features are sometimes obscured. Saccus reticulation and size are the important factors in identification (Pocknall 1981a). *P.ferruginea* has a spheroidal cappa and ear-like saccus, clearly discernible in Figure **21c** but less clearly visible under light microscopy (Figure **21a**). The cappa of *P.taxifolia* is more rhomboidal in shape; as seen in Figure **21b**. Measurements from Pocknall (1981a) show that the pollen grain of *P.ferruginea* is much larger than *P.taxifolia*; the former has a mean total length of 89μm in a glycerine medium compared with 62μm for the latter, and a much longer saccus

- 35μm versus 22μm. Despite these difficulties, around 95% of diagrams that distinguish *Prumnopitys* from other Podocarpaceae also distinguish *P.ferruginea* from *P.taxifolia*. The isopollen and isochrone maps in this thesis utilise taxa level data.

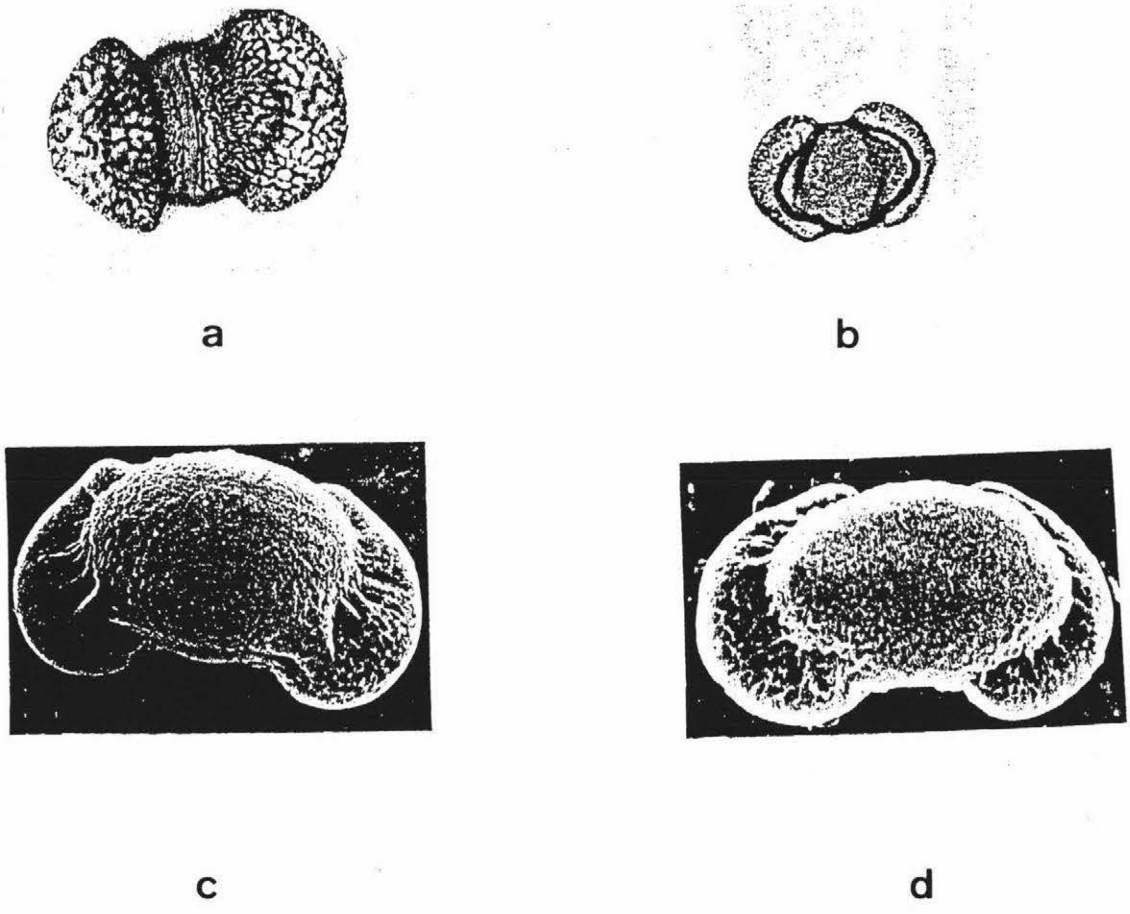

Figure 21: (**a**) Polar LM view of *Prumnopitys ferruginea* (× 540) (**b**) Polar LM view of *P.taxifolia* (× 540) (**c**) Lateral SEM view of *P.ferruginea* (× 800) (**d**) Lateral view *P.taxifolia* (× 1280) *Source*: Pocknall (1981a)

Dicotyledons

Family Avicenniaceae. Genus ***Avicennia***. *A.resinifera* (mangrove) is a monad, isopolar, tricolporate grain (Moar 1993). The ectoapertures[173] are slightly sunken along two-thirds of the length of the grain, very broad at the equator and rapidly narrowing towards the poles, and the endoapertures are often indistinct and slightly lalongate[174]. *A.resinifera's* exine is around 3μm thick, semitectate, baculate[175], and reticulate; the reticulum is heterobrachate[176]; lumina are very small, up to 2μm across; muri are normally coarse, up to 1μm across and sometimes duplibaculate[177]. *Avicennia resinifera* is subprolate[178] to spheroidal in shape, circular in polar view with convex amb[179]. The P axis is 33-35μm and E plane 29-33μm.

Because there have been relatively few pollen diagrams published for estuarine sites - isolated exceptions include Pocknall *et al* (1989) and Horrocks *et al* (2000b) - *Avicennia* is not identified in the fossil pollen record nor plotted. This is unfortunate since *Avicennia* would otherwise make an excellent paleoclimate indicator.

Family Chloranthraceae. Genus ***Ascarina***. The sole New Zealand species[180] of this genera, *Ascarina lucida* (hutu) produces a monad, anisopolar[181], bilaterally symmetrical, monocolpate pollen grain. According to Moar (1993) *A.lucida's* shape is "...ellipsoidal in proximal view, kidney shaped in long 'equatorial' plane, and spheroidal in short equatorial plane." The grain size is 37-40μm x 26-29μm, and the clavae or club-shaped sculptural elements are often decayed away in fossil samples. Due to *Ascarina's* invariably low

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[173] Ectoaperture refers to a colpus or furrow running along the pollen grain longitudinally, as opposed to endoapertures which run across the equatorial plane. The former arises due to reduction in the ectexine or outer layer of the exine, whereas the latter is formed by a thinning of the endexine or inner layer of the exine.

[174] Lalongate describes an endoaperture oriented at right angles to the colpus in the equatorial plane (Moar 1993)

[175] A grain with a cylindrical, free-standing exine element >1μm long and less than this in diameter (Hoen 1999)

[176] Heterobrachate refers to reticular sculpturing whereby the brochi or pattern formed by the lumen and murus are of an irregular size and shape.

[177] Duplibaculate describes the tectum in reticulate pollen grains that are supported by two or more rows of bacula beneath the muri, rather than a single row (simplibaculate) (Moar 1993).

[178] Subprolate describes an ellipsoid shape of the pollen grain where the Polar:Equatorial (P:E) ratio is between

8 : 7 and 8: 6. Prolate describes a grain with a P:E ratio of 8: 6 - 8: 4 and perprolate the P:E ratio is > 8 : 4

[179] The outline of the pollen grain viewed from the pole.

[180] A variety, *A.lucida* var *lanceolata* is found on Kermadec Island (Poole & Adams 1990).

[181] Anisopolar describes pollen grains whose hemispheres differ from each other; *cf* isopolar, where they are identical.

relative percentages in the pollen diagrams it is not particularly suitable for isopollen mapping, but because it is a useful paleoclimate I chose to construct isopollen and isochrone maps regardless.

Family Cunoniaceae. Genus ***Weinmannia***. The pollen of *Weinmannia racemosa* (kamahi) is described by Moar (1993) as monad, isopolar, and tricolporate. The shape is subprolate to spheroidal, rounded or pointed slightly at the poles, and circular in polar view. The polar axis ranges from 14 to 18µm, and the equatorial plane 11 to 16µm. *W.racemosa* displays slightly sunken ectoapertures which taper towards the poles and are constricted at the equator. The grain is costate[182] with fine costae; the exine is thin (<1µm), semitectate, baculate and reticulate; the reticulum is slightly heterobrochate; lumina are up to 1µm across and muri are very fine, <0.5µm. Unfortunately, *Weinmannia* is not identified in sufficient pollen diagrams to plot in isopollen maps; possibly due to the fact that it preserves poorly and can be confused with *Aristotelia fruticosa* and *Elaeocarpus hookerianus* (Cranwell & van Post 1936).

Family Elaeocarpaceae. Genus ***Elaeocarpus***. *E.dentatus* had a subprolate to spheroidal grain with a P axis of 13-15µm and an E plane of 13-14µm. Moar (1993) describes *E.dentatus* as monad, isopolar, tricolporate; ectoapertures are narrow; exine is thin (<1µm) and the surface of the grain is smooth. *E.dentatus* is similar in appearance to *Aristotelia serrata*, another species of family Elaeocarpaceae; the latter has a faintly reticulate surface and is slightly larger (the P axis 17-18µm, E plane 15-16µm) than *E.dentatus*. There is little evidence of this species in the fossil record, therefore isopollen maps were not created.

Family Escalloniaceae. Genus ***Quintinia***. *Q.acutifolia* is described by Moar (1993) as a monad, isopolar, tetra- to pentacoloporate grain, subprolate to spheroidal in shape, rounded at the poles and circular in polar view. Typically *Q.acutifolia* is 21-23µm along the polar axis and 18µm across the equatorial plane. The exine is very thin, <1µm, with a psilate (smooth) surface. *Q.acutifolia* is similar in appearance to *Q.serrata*. There is little evidence of this species in the fossil record, therefore isopollen maps were not created.

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[182] The rib-like appearance of a furrow edge caused by the thickening of marginal endexine (Moar 1993).

Family Lauraceae. Genus ***Beilschmiedia***. Macphail (1980) describes *Beilschmiedia tarairi* (taraire) pollen as monad, apolar[183], inapeturate with a spheroidal corpus 40-49µm long. *B.tarairi* has a very thin, intectate exine (0.5µm) bearing sharp, irregularly spaced spines up to 3µm long and gemmae[184] up to 1µm high. Moar (1993) suggests *B.tawa* (tawa) is morphologically similar although it lacks gemmae and the grains are somewhat smaller, typically 29-42µm in diameter. *Litsea calicaris* is similar in appearance to both *B.tarairi* and *B.tawa* but can be distinguished from them on account of shorter spines and smaller corpus than *B.tarairi.*

Unfortunately, although *B.tarairi* and *B.tawa* are very common trees, they are severely under-represented even in modern pollen studies, leading Macphail & McQueen (1983) to argue that the virtual absence of *Beilschmiedia* pollen in modern sediments, including litter beneath source trees, suggests that *Beilschmiedia* is a major 'blind spot' in the late Quaternary vegetation history of New Zealand; furthermore, some observations of *Beilschmiedia* in the fossil record are in fact mis-identifications.

Despite the fact that the extremely thin extine of these species must contribute to the meagre signature in the fossil pollen record, Macphail (1980) argues that the under-representation is due more to the fact that there is extremely limited production rather than poor dispersal or preservation. Given the lack of identification of *Beilschmiedia* in the pollen signature, it was not possible to construct isopollen maps for this genus.

Family Monimaceae. Genus ***Hedycarya***. *Hedycarya arborea* (pigeonwood) is a tetragonal tetrad with inaperturate (lacking apertures) members; the distal regions of the individual members are generally imperforate, tectate, papillate or scabrate. *H.arborea's* long axis ranges from 47 to 60µm and the short axis 38-44µm, and the species displays a thin exine, around 1µm (Moar 1993). This thin exine may contribute to the infrequency of *Hedycarya* occurring in the fossil record; it is not plotted in the isopollen maps presented here.

Family Myrtaceae. Pike (1956) described pollen of family Myrtaceae as being small to medium, radiosymmetrical, isopolar to slightly subisopolar, tricolporate, angulaperturate,

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[183] Moar (1993) suggests *B.tarairi* is anisopolar.

[184] Gemma is a sexine element which is constricted at its base, higher than 1µm and that has approximately the same width as its height [isodiametric] (Hoen 1999).

oblate, syncolpate or parasyncolpate[185], with a triangular amb and a smooth or faintly patterned exine.

The genus ***Metrosideros*** is often undifferentiated because it is difficult to distinguish its tricolporate, triangular pollen at the species level. *M.excelsa* and *M.umbellata* have grains with similar colpi, aperture, exine and tectum characteristics described by Moar (1993) as "Monad, isopolar, tricolporate, angulaperturate; with narrow and parasyncolpate ectoapertures; endoapertures are narrow and lalongate; very thin (around 1µm) excine; tectate, baculate; shape is oblate, triangular in polar view, angles rounded, amb[186] usually straight but sometimes slightly concave or convex." *M.excelsa* has grains whose polar axis is 15-17µm and equatorial plane 22-25µm[187], compared with *M.umbellata* with grains 14-16µm and 24-29µm respectively (Moar 1993).

Clearly the size ranges for *M.excelsa* and *M.umbellata* overlap on both planes, so size alone cannot be used to distinguish the grains. Moar (1993) states that the only distinguishing feature is that the tectum of *M.excelsa* is *usually* smooth but *sometimes* roughened in the mesocolpia, whereas *M.umbellata* has a "...tectum *often* faintly verrucate[188] in mesocolpia," (my emphasis). These uncertainties mean that *Metrosideros* is typically identified to the genus level only (eg Bussell 1988b; McLea 1990; McGlone 1995b). This is most unfortunate, since *M.excelsa* and *M.umbellata* have very different geographical preferences and would otherwise make excellent climate indicators; accordingly, they are not plotted in the isopollen maps here.

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[185] Angulaperturate refers to apertures situated in the angle or apex of the amb, as opposed to planaperturate where the apertures are located nearer the centre of the sides of the amb. Syncolpate is described by Moar (1993) as when the "...ectoaperture extends from the pole to fuse with extensions of other furrows," whereas parasyncolpate is where "...the ectoaperture ends bifurcate and branches fuse to form islands at the pole." Cranwell (1953) states that the fused furrows in *Metrosideros* "...run meridionally in true dicotyledonous fashion, where they form islands of ektexine over the poles."

[186] The outline of the pollen grain viewed when one of its poles are directed towards the observer (Pike 1956).

[187] Although Gadek & Martin (1981) suggest the equatorial plane dimensions are 17-21µm; the discrepancy may be due to different treatments or mounting mediums used which can cause swelling.

[188] A wart-like sexine element >1µm wide that is broader than it is high and is not constricted at its base (Hoen 1999)

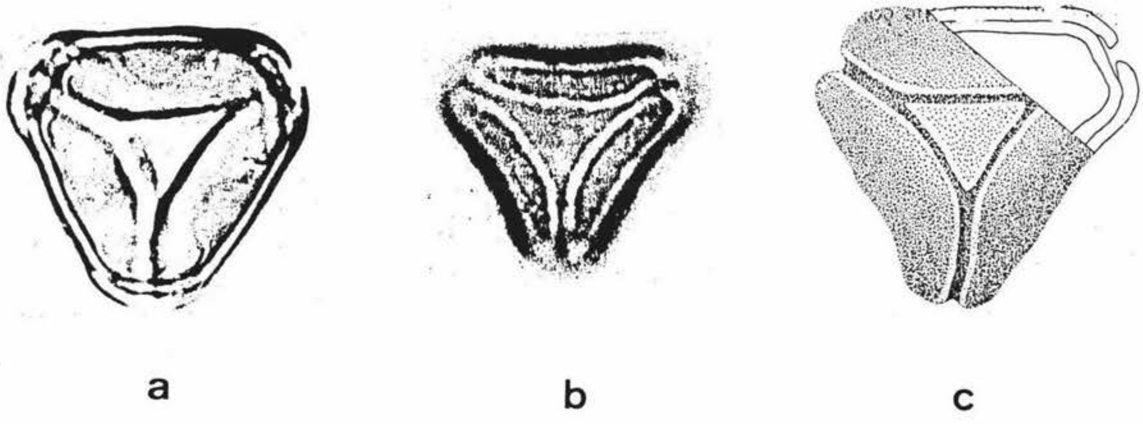

Figure 22: (a) Polar LM view of *Metrosideros excelsa* (b) Polar LM view of *M.umbellata* (c) Polar sketch of *M.robusta* showing exine and apertures. *Source*: McIntyre (1963)

Family Myrtaceae. Genus ***Leptospermum***. The pollen grains of *Leptospermum scoparium* (manuka) are slightly larger than kanuka, *Kunzea ericoides* and *K.sinclairii*[189]. Over 90% of *L.scoparium* have distinctly concave sides whereas *K.ericoides* and *L.sinclairii* have only 30% and 4% distinctly concave sides, respectively (McIntyre 1963). Nevertheless, because *Leptospermum* and *Kunzea* are typically only identified to the genus level, and since some species have an extremely wide geographical distribution (eg *L.scoparium* is found throughout New Zealand at lowland, montane, subalpine and alpine altitudes (Poole & Adams 1990) they are not a particularly useful climate indicator and are typically excluded from the pollen sum (eg Enright *et al* 1988; Moar & Suggate 1996). Accordingly, *Leptospermum* has not been plotted in isopollen maps.

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[189] Renamed from *Leptospermum ericoides* and *L.sinclairii* in Connor & Edgar (1987).

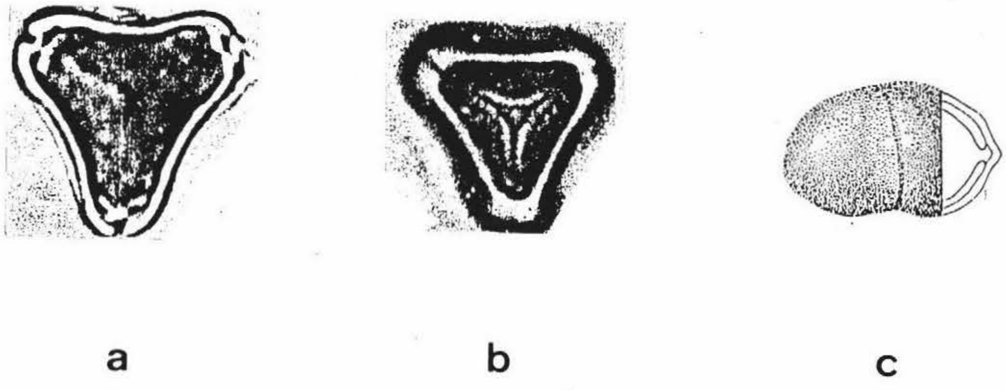

Figure 23 (**a**) Polar LM view of *Leptospermum scoparium* (**b**) Equatorial view of *L.scoparium* (**c**) Polar LM view of *Kunzea ericoides*) *Source*: McIntyre (1963)

Family Proteaceae. Genus ***Knightia*** Moar (1993) describes *Knightia excelsa* (rewarewa) pollen as triangular in polar view with the amb either straight or concave, peroblate (markedly flattened at the poles) with one pole more concave and longer than the other. The polar axis is 25-29μm long, and the equatorial plane is 40-47μm. The grain is typically monad, subisopolar, triporate[190], and angulaperturate. Moar (1993) notes the apertures are slightly lalongate (5x 3μm) or nearly circular; thick exine (around 2 μm), thinning towards the apertures, semitectate, baculate, reticulate; lumina <1μm, muri broad 0.5μm, duplibaculate, and the bacula is clearly visible in optical section. There is little evidence of this species in the fossil record, therefore isopollen maps were not created for *Knightia*.

Family Pittosporaceae. Genus ***Pittosporum***. Moar (1993) states that *Pittosporum tenuifolium* and *P.eugenioides*, like *P.colensoi*, *P.corifolium*, *P.crassiculae*, *P.crassifolium*, *P.huttonianum*, *P.kirkii*, *P.michiei*, *P.ralphii*, and *P.umbellatum*, is similar to *P.virgatum*. *P.virgatum* has very long ectoapertures which are up to 2μm across, tapering to a blunted end; costate; endoapertures are 8μm long; exine is 2μm thick in the mesocolpia, thinning

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[190] Having a circular or elliptic aperture with a length:breadth ratio <2.0 (Hoen 1999).

towards the apertures; bacula is clear, often in groups of 2 to 4; P-axis is 32-35μm, E-plane is 32-37μm. There is little evidence of *Pittosporum* in the fossil record, therefore isopollen maps were not created for this genus.

Family Fagaceae. Genus ***Nothofagus*** *N.fusca* (red beech) has a monad, isopolar pollen grain, with between five and eight colpi, although typically seven. Ectoapertures are short (5-6μm long); exine is 1-1.5μm thick; tectate, baculate; tectum has very short, evenly distributed spinules (Moar 1993). Harris (1956) noted that the shape is spherical or elongate in polar view and either elliptical, with outline convex between the apertures and the overall shape ranges from oblate, circular or polygonal in polar axis.

Moar (1993) notes that grains of *N.truncata* (hard beech), *N.solandri*, *N.solandri* var *solandri* (black beech) and *N.solandri* var *cliffortioides* (mountain beech) are all similar to *N.fusca*, making specific identification of *Nothofagus* difficult. Several researchers (Cranwell 1939; Harris 1956; Newnham 1992; Lees, Neall & Palmer 1998) have attempted to distinguish *Nothofagus* pollen by counting the number of pores in the grains and ascertaining the proportions of pores for each species; for example Harris (1956) found that 26% of *N.truncata* grains had six pores, 27% had seven pores, and 16% had eight pores. *N.fusca* however displayed 38, 43 and 13 percent respectively, with the comparable proportions for *N.solandri* and *N.cliffortiodes* being 20, 52 and 26% and 16, 58 and 25% respectively.

Six percent of *N.fusca*-type grains had five pores, and *N.solandri* was the only species to have nine pores, albeit a small proportion. Despite the fact that many researchers simply identify to the genus level only, or simply distinguish *Fuscospora* types from *N.menziesii*, there are sufficient pollen diagrams available that do distinguish *N.fusca* to create isopollen maps.

Nothofagus menziesii (silver beech) is a peroblate-shaped, monad, isopolar pollen grain, with between five and nine colpi, although typically seven. Moar (1993) describes *N.menziesii* as stephanocolporate and angulaperturate; tectum bearing short spinules. The *P* axis is typically 41-48μm and the equatorial plane 46-60μm. Although there is insufficient data available to plot isopollen maps for this taxon, an isochrone map was prepared.

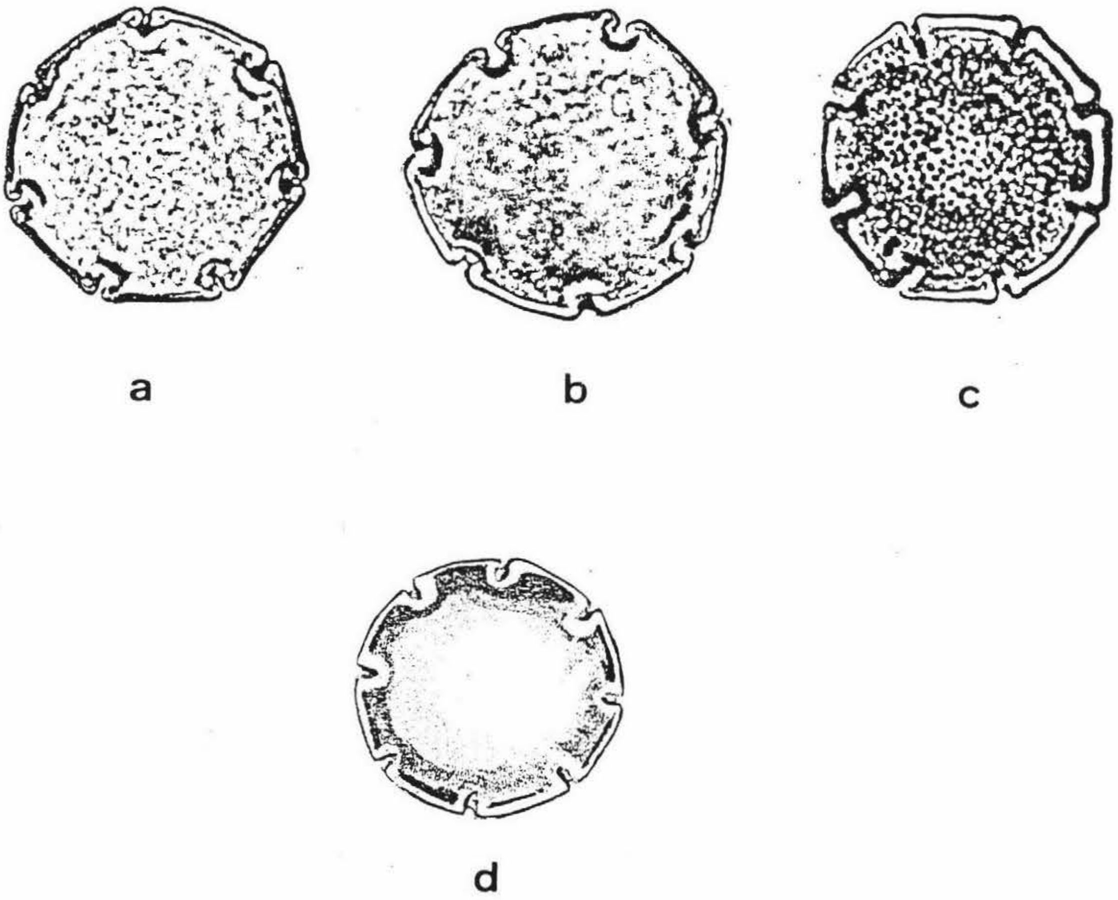
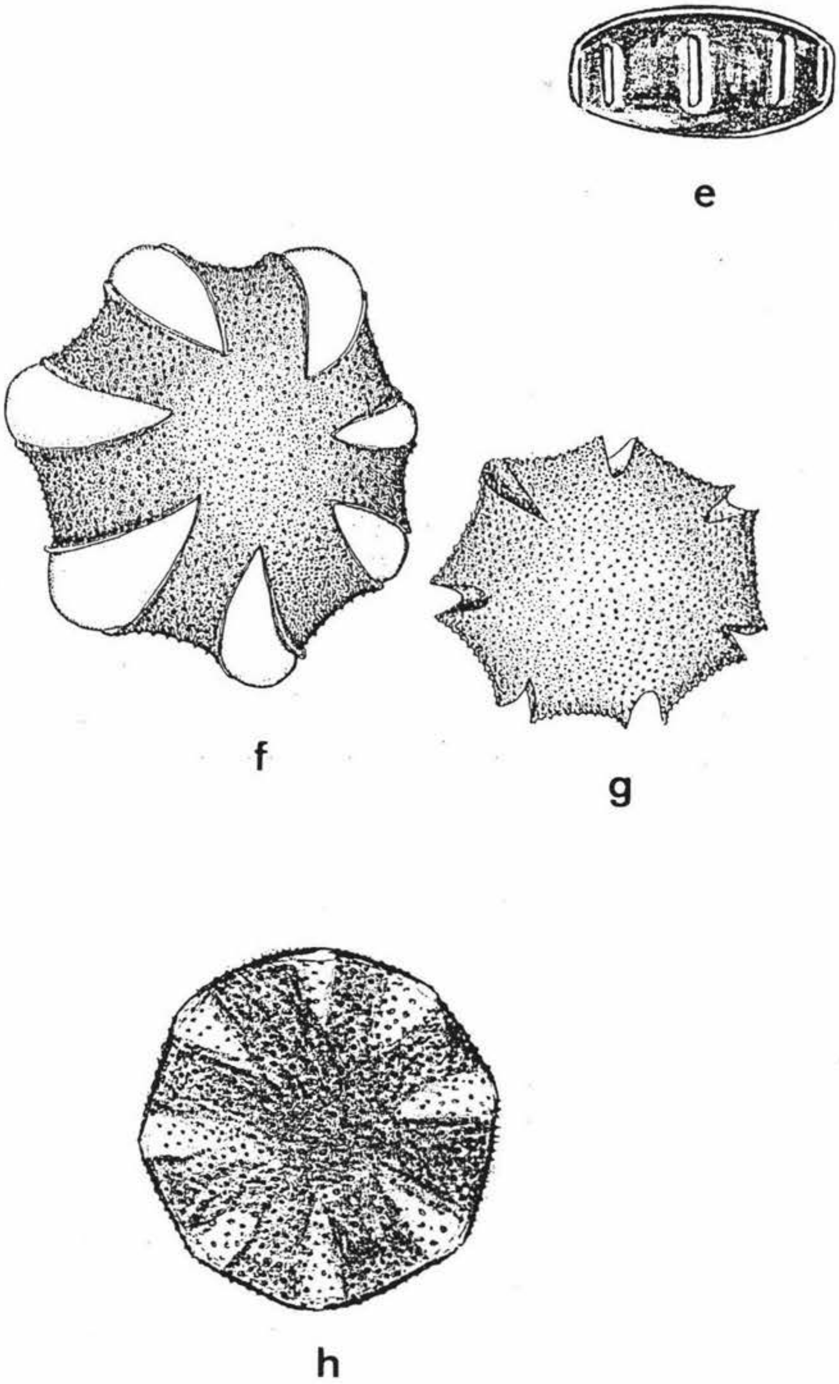


Figure 24 (**a**) Polar LM view of *Nothofagus truncata* x 1000 (**b**) Polar LM view of *N. solandri* var *solandri* x 1000 (**c**) Polar LM view of *N.solandri* var *cliffortioides* (**d**) Polar view of *N.fusca*



(**e**) Equatorial view of *N.fusca* (**f**) Polar view of *N.menziesii* in partly expanded condition (**g**) Polar view of *N.menziesii* in over-expanded condition; the ectexine is ruptured and endexine distended almost to rupturing point. (**h**) Polar view of *N.menziesii* in collapsed condition

Source: (a)-(c) Moar (1993); (d)-(f) Cranwell (1940); (g) - (h) Harris (1956)

Appendix 5.3 Sea Surface Temperatures

The reconstructed paleo sea surface temperatures show that temperatures on the west coast of New Zealand were not significantly cooler during the LGM relative to present whereas on the east coast the temperature difference was much more extreme. Nelson *et al* (1994) attribute the LGM disparity between the two oceans to differences in oceanic circulation: the Tasman Sea was apparently largely insulated from substantial cooling during the late glacial compared with the Holocene so that northward displacement of the Sub Tropical Convergence[191] was slight. In contrast, the southwest Pacific near-shore waters chilled between 4 and 8°C relative to present.

The SST maps show that temperatures on the east coast of both islands and the west coast of the North Island have gradually increased since the LGM. On the west coast of the South Island, however, temperature has oscillated by about 7°C with a 2,000 year periodicity. Although we might expect "...major shifts in average isotope values as well as distinct cyclic fluctuations in the $\delta^{18}O$ signal amplitude over time." (Head & Nelson 1994) oscillation of the signals that they refer to is related to Milankovitch forcing and therefore has a periodicity one or two orders of magnitude greater than the periodicity exhibited in these maps. For example, Head & Nelson (1994) found that glacial-interglacial events between 6.0 and 5.66, and 1.62 and 1.17 million years ago had a 40,000 year periodicity in the benthonic foraminiferal record at DSDP site 593 and therefore were likely to have been driven by the Earth's orbital obliquity.

In the planktonic foraminiferal record, Head & Nelson (1994) stated "...numerous low-amplitude, high frequency (~ 25 ky) cycles approximating the orbital frequency of precession (23 ky) that are superimposed on the high-amplitude ~ 100 ky eccentricity-driven cycles which otherwise dominate the isotope record from about 0.86 Ma."

Given that there is generally good agreement between isotopically-derived SSTs and measured SSTs – generally within 1°C in most cases (Nelson *et al* 1994; chapter 2.8.2),

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[191] The Sub Tropical Convergence (STC) is the frontal zone that separates the Subantarctic Surface Water that is driven north and east by the West Wind Drift south of Australia and New Zealand, form the Subtropical Surface Water in the north (Nelson *et al* 1994)

and since the SST fluctuation cannot be attributed to Milankovitch forcing, the ~ 2,000 oscillation remains problematic[192].

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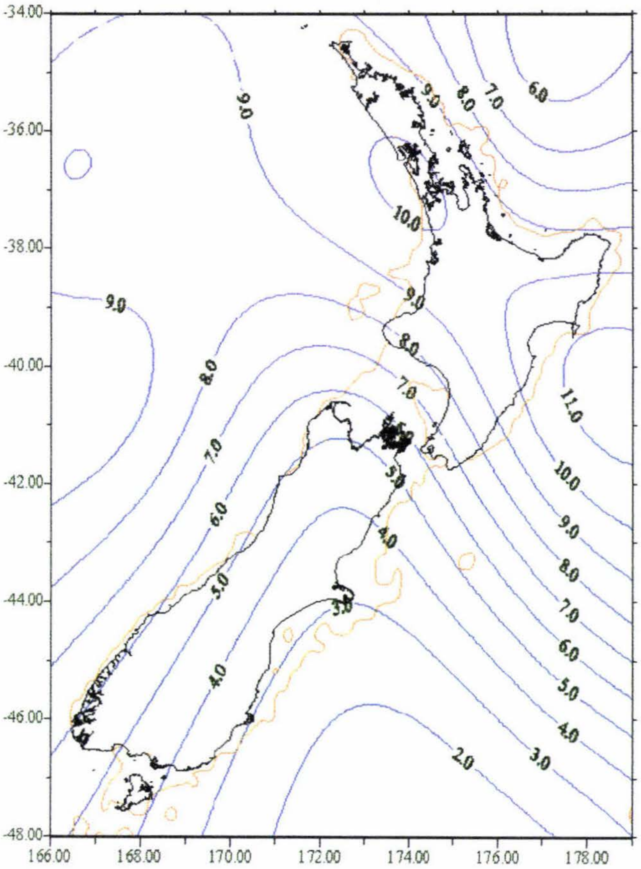
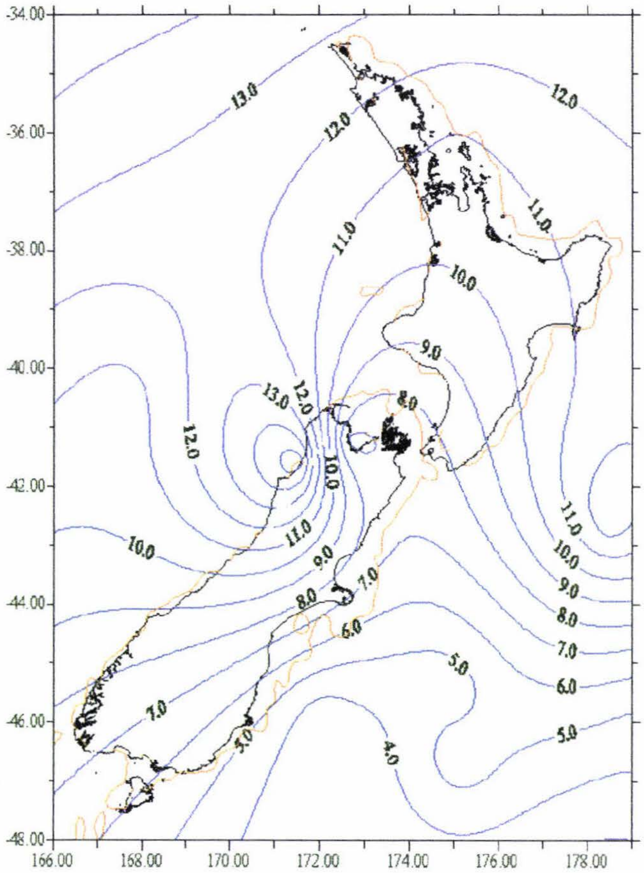
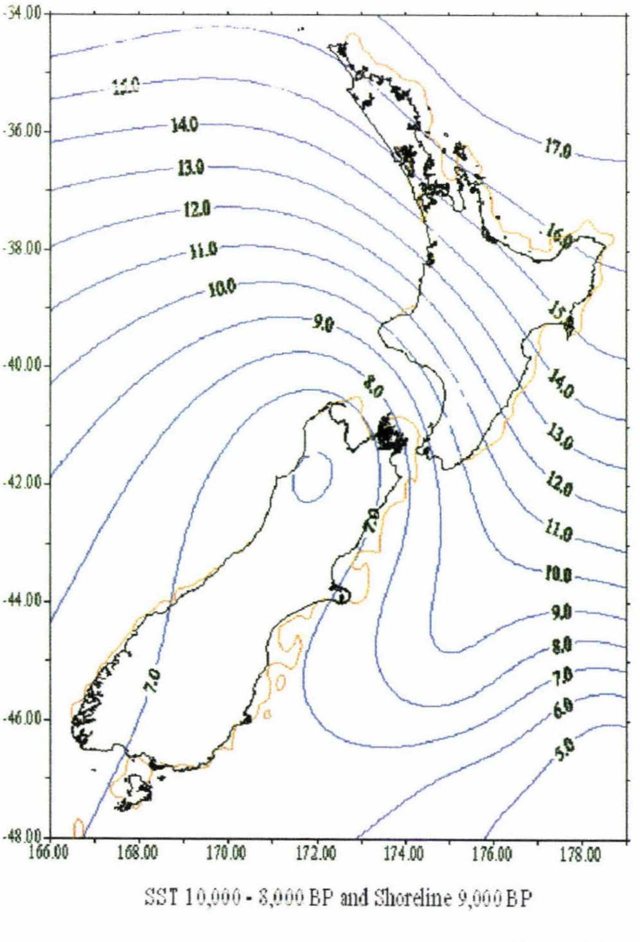
[192] Cam Nelson (personal communication 2002) stated "Apparently inshore temperature 'cycles' with 300 y periodicity are known from [the] West Coast, possibly related to changing wind patterns and whether N or S flowing inshore currents [prevail], in turn perhaps tied to ENSO events. Suspect that any 2 ky periodicity would be likewise linked to wind pattern change and/or oceanic current eddying."



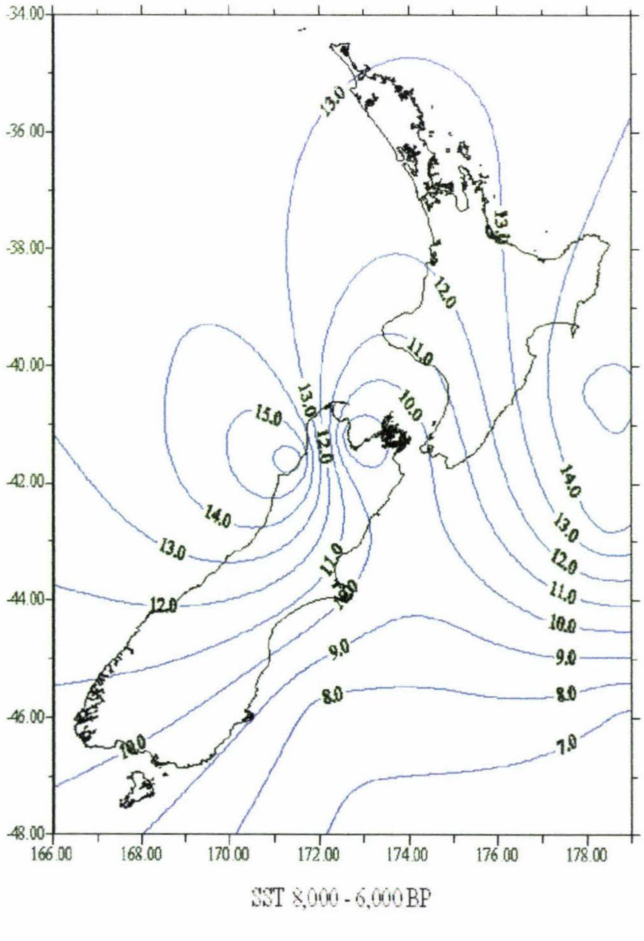
SST 22,000 - 14,500 BP and Shoreline 13,250 BP



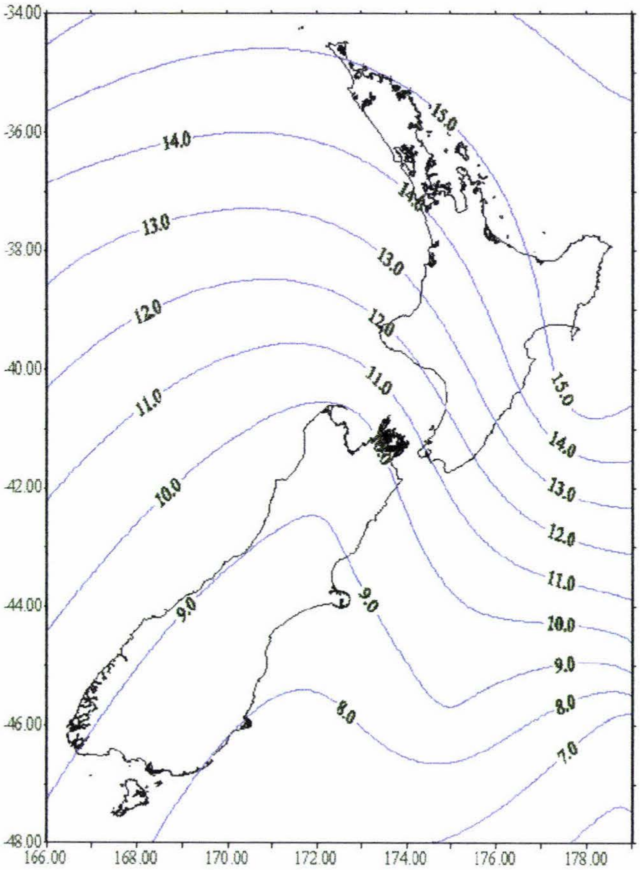
SST 14,500 - 10,000 BP and Shoreline 12,250 BP



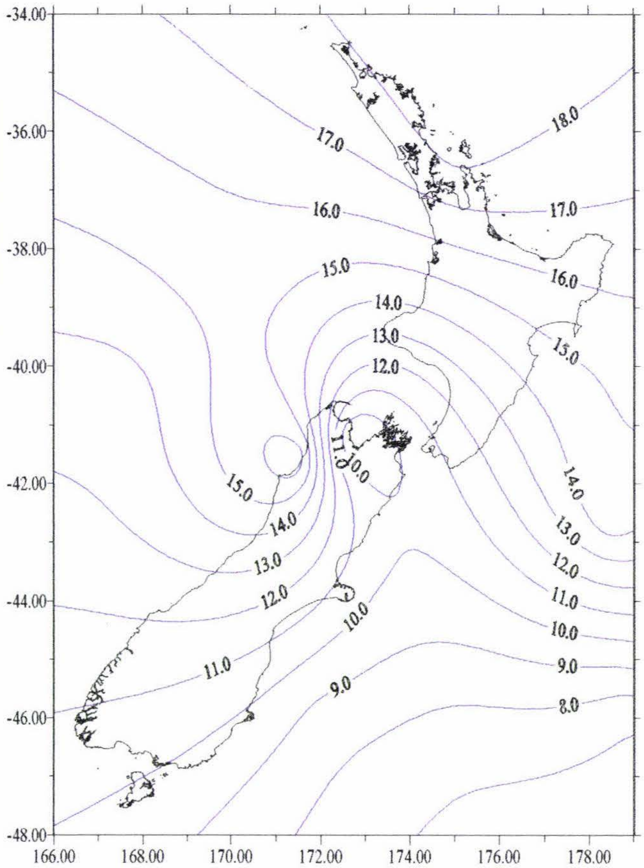
SST 10,000 - 8,000 BP and Shoreline 9,000 BP



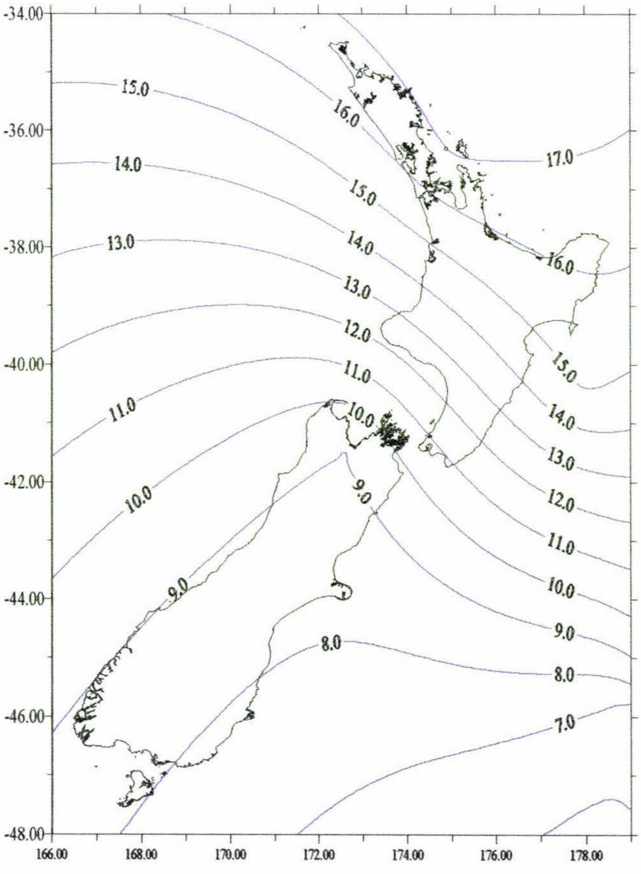
SST 8,000 - 6,000 BP



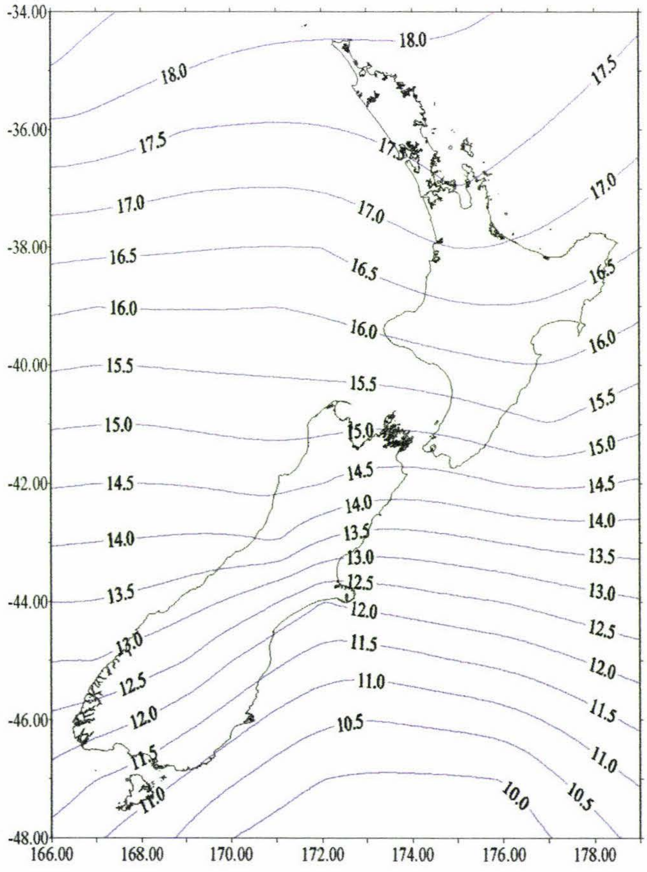
SST 6,000 - 4,000 BP



SST 4,000 - 2,000 BP



SST 2,000 - 50 BP



SST Modern (based on NOAA 2002)

Appendix 5.4 Cautions in Interpreting Isopollen and Isochrone Maps

A characteristic of any map is that it is an abstraction of reality, and is not truly objective since it focuses attention selectively on regions of space, features, objects and themes (Taylor 1991) accordingly one should interpret isopollen maps with caution. The various assumptions and weaknesses in deriving the post-LGM shorelines and timberlines have been discussed above, allowing the reader critically assess the premises used and make some judgement as to the validity of the results posted here. However, errors may also be introduced by the palynologist during coring, sampling, preparation, identification, counting graphing and dating the pollen. Construction of the pollen contour lines themselves introduces potential error, and this is also elaborated upon.

It follows then, that a review of the weaknesses and potential errors that may be associated with these maps is necessary in order to be as in order to be as transparent and as scientifically objective as possible.

5.4.1 Differential Pollen Production

The correlation between the relative pollen values in isopollen maps and actual taxon frequency is not perfect and the differential pollen production should be borne in mind when interpreting the isopolls. Anemophilous (wind pollinated) trees are the major pollen producers: according to Traverse (1988) the average hectare of anemophilous woodland in eastern North America produces at least 3,000 litres of pollen per year, varying with the specific composition of the forest. Zoophilous plants such as *Orchidaceae*, on the other hand, are very economical in pollen production[193], and their occurrence in the pollen record is typically disproportionately small. Zoophilous plants (eg *Weinmannia*, *Metrosideros* and *Elaeocarpus*) typically produce large pollinia in which all the pollen of one pollen chamber is shed as a cemented-together unit. Since such plants are adapted to pollination by animal vectors they are all under-represented outside the vegetation where they occur (Pocknall 1978). The relatively high importance of wind pollination is fortuitous for paleopalynological investigation in New Zealand.

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[193] Niklas (1985) suggests that wind-pollinated plants have pollen-ovule ratios that are one to three orders of magnitude greater than insect pollinated plants

5.4.2 Differential Pollen Dispersal in Air

Theoretically, pollen behaves like other small particles in the atmosphere, and palynologists have borrowed heavily from research in areas such as pollution monitoring, smoke stack design and travel of radioactive debris to understand the behaviour of pollen in the air, along with the implications for possible confounding factors in pollen analysis.

Tauber (1965) gives the equation for the average particle concentration immediately downwind of a continuously emitting point source situated at ground level (such as a prostrate shrub) as

$$x_{(z,y,O)} = \frac{Q}{\Pi \quad Cy \quad Cz \quad u \quad x^{2-n}}$$

where *Q* is the source strength in number of particles emitted per second, *Cy* is the diffusion coefficient for lateral direction, *Cz* is the diffusion coefficient for vertical direction[194], *u* is mean wind velocity, *n* is the degree of turbulence (related to the lapse rate)[195] and *x* is the distance downwind from the point source. This equation shows that maximum pollen concentration from a source at ground level occurs at the source itself, and the concentration of pollen downwind decreases rapidly with a power of the distance *x* from the source. The downwind concentration of pollen from a point at height *h* is given as

$$x_{(z,y,O)} = \frac{Q}{\Pi \quad Cy \quad Cz \quad u \quad x^{2-n}}\, e^{-} \quad \frac{h^2}{C_Z^2 \, x^{2-n}}$$

(Tauber 1965) which implies that there is zero concentration of pollen at the source itself.

Concentration declines slowly then rapidly with distance as a function of source height *h*, the vertical diffusion coefficient *Cz* and the turbulence parameter *n* so that maximum concentration occurs at d_{max} according to:

$$d_{\max} = \left(\frac{h^2}{C_Z^2} \right)^{\frac{1}{2-n}}$$

---

[194] In neutral conditions $Cy = 0.21\text{m}^{n/2}$ and $Cz = 0.12\ \text{m}^{n/2}$ (Tauber 1965).

[195] The degree of turbulence ranges from 0.15-0.20 in situations of high lapse rates, to 0.30-0.40 under inversion (Tauber 1965).

Taken together, the previous three equations show that pollen is dispersed further from an elevated height such as a tall tree (say, *Dacrydium cupressinum*) than a ground hugging species (say, *Sophora prostrata*). However, they imply that losses due to deposition are small relative to the concentration in the air immediately above the ground, therefore a fourth equation is necessary that takes into account the density of the pollen grains:

$$Q(x) = Qe^{-} \frac{4vg\ x^{n/2}}{n\ u\ \Pi^{1/2}\ Cz}$$

where $Q(x)$ is pollen quantity for a ground-level source, and vg is the velocity of deposition. The corresponding equation for an elevated source is given by Prentice (1983) as:

$$Q(x) = Q(0)e^{-} \frac{4vg}{n\ u\Pi\ Cz} \left[-x^{n2} e^{-\xi} + (h/Cz)^{2m} \left\{ \Gamma(-m+1) - \Gamma_{\xi}(-m+1) \right\} \right]$$

where h is source height, $m = n/(4-2n)$, $\xi = h^2/x^{2-n}\ Cz^2$ and Γx is the incomplete gamma function

$$\Gamma_x\ (a) = \int_0^x e^{-1}\ t^{u-1}\ dt$$

Both equations show that both the loss due to deposition, and the deposition rate, will be much greater for heavy pollen grains than light grains. According to Prentice (1983) deposition velocity v_g usually equals or exceeds the still-air sedimentation velocity, which increases with particle size according to Stokes' Law (discussed below).

However in nature things are more complicated and the equations above begin to break down. Trees do not act as 'true' elevated sources due to varying emission heights and unknown rates of reflotation and mesoscale[196] meteorological phenomena such as frontal

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[196] Mesoscale weather phenomena lie between synoptic and microscale atmospheric features, having spatial dimensions of a few hundred metres to 200km and temporal dimensions of an hour to days (Sturman *et al* 1999). In addition to fronts, mesoscale features include hurricanes, local winds and squall lines.

passages and orographic influences such as formation of lee waves and rotor systems which change in frequency and intensity throughout the year.

Furthermore, airflow is influenced by the structure and density of the vegetation which in turn acts as a 'particle sink' at source level, and the pollen is washed out of the canopy and trunk space, leading to quite different pollen dispersal outcomes[197]. Tauber (1965) cites the example of average wind velocities in the trunk space of an European oak forest as 1.25ms^{-1} prior to leafing and 0.75ms^{-1} with the trees in full leaf; in contrast, New Zealand has few deciduous trees[198] therefore it would be reasonable to expect that the effects of leaf fall would be relatively small. However, meteorological and orographic influences mentioned above may be more marked in New Zealand given its rugged topography.

The differing specific gravities and aerodynamics of the pollen grain leads to different rates of sinking through the air. Tauber (1965) estimated that most pollen taxa fall to the ground within 2,700m of the source however there is considerable variation within this, for example Tsukada (1982b) estimated that 90% of pollen from *Pseudotsuga menziesii* reaches the ground within 800 metres from the source. Myers (1973) found that *Nothofagus solandri* var *cliffortioides* pollen was an important component of the modern pollen rain at Bankside Scientific reserve, near Rakaia which was up to 60km away from its source in the foothills of the Southern Alps. Accordingly, caution should be exercised when interpreting pollen curves for taxa that are prone to long distance dispersal, since high values of these taxa do not necessarily imply local presence.

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[197] Tauber (1967), for example showed that filtration is affected by hairs and sticky compounds on branches of trees: whereas hairy *Salix* twigs had >40,000 grains on a sample of bark, birch twigs from the same area had only a few hundred grains

[198] Of the 10 or so deciduous species in New Zealand, *Plagianthus regius* (manatu or ribbonwood) is the only tall tree. Deciduous and evergreen forests differ in other ways; Randall (1991) found that only 3-10% of annual, modern pollen rain in Canterbury and Westland was redeposited, compared with over half in deciduous forests.

5.4.3 Differential Pollen Dispersal in Water

Pollen that has been transported by river is an important source of pollen deposition in alluvial deposits, open lake basins, and marine sediments, particularly nearshore sediments. In theory, once it is wet, pollen behaves like any other small particle, therefore sediment transport theory can be applied to pollen transport as well, which may assist in understanding fluvial transport and deposition. Unfortunately, however, palynmorphs often behave unpredictably in water. To calculate pollen fall velocity, Stokes' Law is used, which states that a small, smooth sphere[199] falling in a viscous fluid does so under the influence of gravity, ultimately acquiring a constant velocity, according to the formula

$$V = \frac{2\,ga^{2}\,2\,(d_{1} - d_{2})}{9\,\eta}$$

where a is the radius of the sphere (pollen grain), d_1 and d_2 the density or specific gravity of the sphere and the medium (water) respectively, g is the acceleration of gravity and the coefficient of viscosity. V will be in cm per second if g is in cm per sec^2, a in cm, d_1 and d_2 in g per cm^3 and η in dyne-sec per cm^2 or poises[200].

Particle concentration in a two-dimensional open channel is expressed as

$$\frac{c}{c_{a}} = \left\{ \frac{(y_{o} - y)\,a}{(y_{o} - a)\,y} \right\}^{Z}$$

where c = mean concentration of sediment at elevation y above the river bed; c_a = mean concentration of the same size sediment at elevation a; y_o is the total depth; Z = suspended load exponent, given by

$$Z = \frac{V}{\beta k u^{*}}$$

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[199] Because not all pollen grains are spherical and smooth, the extent to which Stoke's Law predicts falling pollen is debateable (Davis & Brubaker 1973).

[200] $g = 980.665$ cms^{-2}, $\eta = 0.0112$ poises (at 16°C); $d_2 = 1.12$ (at 16°C).

where V = terminal fall velocity of the pollen grain, β = the coefficient relating sediment diffusion coefficient to the momentum diffusion coefficient (usually this is assumed to be ≈ 1); k is a constant - the Von Karman coefficient 0.38, and u_* is shear velocity, given as

$$u_* = \sqrt{\gamma}\ \frac{RS}{\rho} = \sqrt{gRS}$$

where γ is the specific gravity of water, R is the hydraulic radius[201], S = slope, ρ = fluid density and g = acceleration due to gravity (980.665 cm^{-2}).

Laboratory simulations by Brush & Brush (1972) showed that the theoretical suspended load exponent Z is so small that the particulate concentration profile c/c_a is approximately 1 so that the concentrations throughout the water column will be virtually homogeneous. This prediction was matched for a large river (the Mississippi) by Smirnov *et al* (1996): using *Ambrosia* (ragwort) pollen[202] as an example, with an estimated fall velocity in water of 7.9×10^{-4} cm s^{-1}, "...the suspended pollen load exponent ($Z = v/ku_*$) for the Mississippi River ($u_* = 1.43$) is 1.5×10^{-3}. With the suspended load exponent being so negligible, the c/c_a ratio...tends to unity [and therefore pollen concentration will be uniform throughout the river cross section]."

In practice however, pollen concentrations within different regions of the hydraulic radius for the Mississippi differed by almost a degree of magnitude. Smirnov *et al* (1996) found that there was no correlation between flow velocity and pollen load in the Mississippi River, but that half of the variation in load could be explained by the depth of the river, and that likely factors contributing to the spatial heterogeneity of sediment load include the concentration of aerially deposited pollen on the water, and segregation of flow. Campbell & Chmura (1994) reported similar results from the Atchafalaya River, Louisiana, where again, the greatest concentration of pollen grains was found peripheral to the deepest part of the river.

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[201] The cross-sectional area of the stream or river, divided by the wetted perimeter (the length of wetted contact between the stream or river channel measured in cross section (perpendicular to flow).

[202] According to Harrington & Metzger (1963) *Ambrosia* has diameter of 0.001cm and specific gravity of 1.28 g cm^{-3}. These researchers required ragweed pollen density to assist in allergy research, since ragweed is one of the most serious aeroallergens.

This finding has an important bearing on differential pollen transport and deposition and therefore on selection of pollen sampling sites. Water transport of pollen and spores in NZ has been reported by Pocknall (1980) who found that *Quintinia* and *P.ferruginea* in Lady Lake, north Westland showed variation with depth; *Quintinia* increasing with water depth and *P.ferruginea* being more abundant in inshore sediments, possibly due to differential flotation. Mildenhall (1980) noted the same differential distribution amongst podocarp pollen in Caswell, Nancy and Milford Sounds.

5.4.4 Differential Lake Size

Pollen derived both locally and regionally will be present in all fossil pollen samples, but which component is most useful depends on the purpose of the study. According to Jacobson & Bradshaw (1981) "What may be considered 'noise' in the data being used for a regional paleoclimatic reconstruction may well be precisely the information most useful for developing the history of small scale patterns in vegetation." At first glance then, it would appear that larger sites are more amenable to regional paleoclimate reconstruction, by virtue of the greater proportion of regionally derived pollen, and small catchments are more suitable for local paleovegetation reconstruction; however this implies that lakes should ideally be of a similar size for comparative studies: Newnham & Lowe (1999) for example found a poor correlation between coeval pollen stratigraphy at Lake Rotomanuka (14ha) and Kopouatai Bog (9000ha) in Waikato.

Limnic sites in the New Zealand isopollen maps vary greatly in size[203], ranging from aapmires one or two hundred square metres in diameter (McGlone *et al* 1995) to lakes with an area of 215 km^2 (McGlone 1983). In addition, polliniferous cores have been obtained from marine cores from the Hauraki Gulf (Pocknall *et al* 1989) and Preservation Inlet (Pickrill *et al* 1992). There is a strong bias towards small bogs and swamps however, implying that ascertaining local paleovegetation is the primary focus for most palynological research in New Zealand, and reinforcing my earlier assertion that paleovegetation reconstruction in New Zealand is biased towards local reconstruction.

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[203] The majority of researchers do not report the area of the site; Enright *et al* (1988) and Newnham *et al* (1998) are amongst the few researchers to report both lake *and* catchment size.

5.4.5 Differential Pollen Sedimentation

Differential sedimentation of pollen in lacustrine environments can hinder interpretation of pollen diagrams. Davis *et al* (1971) found that in southern Michigan lakes small pollen grains and grains with air sacs were preferentially deposited in shallow water whereas larger grains were spread more uniformly throughout the lake basin. Davis *et al* (1971) state that "Many palynologists have thought that a sample or core taken from the deepest part of the lake basin is a 'standard' sample. Our study shows that the [relative] percentage of [a given taxon] is different even in adjacent lakes." suggesting that limnological factors are at least as important as the local floral assemblage in controlling relative pollen percentages.

De Busk (1977) found that pteridophyte spores in Lake Malawi were 10 times higher adjacent to river deltas than elsewhere in the lake, whereas the end of the lake with little forest had a low spore : pollen ratio. This discrepancy could reflect pteridophyte's preference for riparian habitats, but it could equally be due to the higher sporopollenin content in spores, making them more dense than pollen and consequently precipitating from the air more quickly, or even greater preservability of spores relative to pollen. De Busk also found forest- and woodland-derived pollen was found closest to source areas drained by high-gradient streams, differential settling was more important in Urticaceae whereas sedge and *Typha* spores were mainly deposited near their source, suggesting water was a more important transport vector than wind for those aquatic species.

Although the surface area of open water in a lake is a useful indicator of the size of the pollen-producing source area, the presence or absence of inflowing streams is a complicating factor. Bonny (1978) demonstrated the increase in 'effective surface area' brought about by streams flowing into a lake by comparing pollen influx via the air to pollen recruitment from inflowing streams in Blelham Tarn, England. Bonny found that only 15% of the influx came from airborne (local) sources thus the majority of the pollen was water-borne or regional.

5.4.6 Differential Pollen Preservation

The propensity of a given taxon's pollen spore to resist decay impacts upon absolute and relative pollen counts. A spore's preservability depends largely upon the sporopollenin content in the exine, which is partly a function of the thickness of the exine and partly a function of the division of the exine between endexine and ektexine: the more ektexine, the greater the amount of sporopollenin in the grain (Traverse 1988). Sporopollenin, an oxidative polymer of carotenoids and carotenoid esters, is one of the most resistant organic materials known (Brooks 1980) and pollen grains are known to remain viable even after passing through the gut of invertebrates (Chaloner 1976).

Other factors impacting on the pollen grains propensity for preservation include the nature of the substrate in which the pollen is deposited. In general pollen is preserved better in an acid than an alkaline environment, a reducing environment better than an oxidising one[204] and a sedentary environment better than an energetic environment. Thus the pollen count is biased towards more resistant spores in environments generally unfavourable for pollen preservation[205].

Various limnic types yield polliniferous sediments in New Zealand; each has different chemical and physical characteristics that influence pollen preservation. Raised bogs are mires in which peat[206] accumulates above the height of the surrounding substrate so that they become ombotrophic; that is, dependent upon precipitation for their nutrient and water supply.

Ombrogenous bogs[207] have a low pH[208] due to leaching and the acidifying effects of *Sphagnum* spp (Walker *et al* 2001) and are anaerobic due to the high water table. At the same time extreme nutrient deficiency retards microbial activity, and the high organic

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[204] Fire is an extreme case of oxidation, destroying or rapidly damaging pollen grains (Campbell 1999).

[205] Other processes that destroy sporopollenin (approximate empirical formula $C_{90}H_{142}O_{27}$) include carbonisation due to relatively low temperature elevation over time; exposure to high temperature over a short period of time (eg volcanic intrusion); and recrystallisation of minerals in sediments (Traverse 1988).

[206] Although only 0.7% of New Zealand's land area is peatland (Mark *et al* 1995) peatlands are much more significant from a palynological perspective given their propensity for pollen preservation.

[207] Damman (1986) suggests that ombrogenous (rain-made) peat bogs include ombotrophic (rain-fed) centres as well as minerotrophic borders separating the bog from the surrounding upland. Ombotrophic peat bogs, on the other hand, refer to only those parts of an ombrogenous bog not influenced by mineral soil water.

[208] For example, McQueen & Wilson (2000) found that Borland Bog, an ombotrophic bog in Southland, had a pH of <4.0.

content of the bog acts as an electron acceptor and a catalyst for hydrolysis (Eglinton & Logan 1991) therefore the potential for pollen preservation is high. Countering this is the fact that since they are raised, ombotrophic bogs are prone to drying out, desiccating the pollen grains.

Ombrogenous and topogenous bogs are at the middle of a continuum; at the topogenous extreme of the continuum are limnogenous bogs which receive their supply of nutrients and water from the surrounding substrate (or in extreme cases, entirely from rainfall) since they have a flat physiognomy. At the ombrogenous extreme are soligenous mires and fens, for example the Nokomai Island mires which are in strings called aapmires (McGlone *et al* 1995). Variations that lie in between these two extremes include mesotrophic sloping bogs in central Otago reported by McGlone *et al* (1997) and Papamoa Bog (Newnham *et al* 1995) which were not entirely ombrogenous but received some runoff from the surrounding catchment. Furthermore, bog chemistry and physiognomy may change over time; mires forming in valleys are generally rheotrophic early in their development and later may become domed and ombotrophic (Walker *et al* 2001).

Peat accumulation is substantially faster in basin or topogenous bogs than ombrogenous bogs (Froggatt & Rogers 1990); the implications for palynological studies are that age interpolation may be more accurate for topogenous bogs[209] since carbon dated materials are sufficiently separated in the core to enable interpolation procedures such as cubic splines or polynomial functions to be applied (*supra*). At the same time, bioturbation by burrowing invertebrates is generally less frequent in peat than other sediments because peats are virtually anoxic a few centimetres below the surface.

Oligotrophic lakes are infertile lakes where concentration of dissolved nutrients and therefore productivity is low, the water is clear and algal blooms and plankton are not visible (Edinvaux 1986). Pollen diagrams published for oligotrophic lakes in New Zealand include sedge mires at Eltham Swamp (McGlone & Neall 1994) and high moor swamp at Otakairangi, Northland (Newnham 1992). Eutrophic lakes, on the other hand, are fertile lakes where concentration of dissolved nutrients is high, the water is often opaque with

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[209] Although Rogers & McGlone (1989) found that the sedimentation rate for the ombrogenous bog at Three Kings deep bore of 0.41mm per year over the last 10,800 years was more rapid than that of the topogenous bogs at Three Kings shallow bore of 0.30mm per year over the last 4,470 years.

algal blooms and plankton and productivity is high (Edinvaux 1986). Lake Taumatawhana (Elliot *et al* 1995) appears to be an eutrophic lake since the material dated was gyttja, a typical eutrophic lake sediment; the status of Pyramid Valley swamp (Moar 1970) is uncertain since the dated sediments were "...jelly-like gyttja," or dy, typical of dystrophic lakes, and "...calcareous gyttja" or marl, which is associated with eutrophic lakes.

Although the higher, absolute number of aquatic pollen taxa found in eutrophic lakes relative to oligotrophic lakes may be compensated for by excluding aquatic pollen from the pollen sum, the different amount of carbon sequestration due to the different amount of plankton and invertebrates present may lead to anomalous ^{14}C dates. Furthermore, the high biological productivity may have palynological implications such as increased likelihood of bioturbation by invertebrates, leading to anachronisms within the pollen core.

Pollen studies have been conducted on several marine cores (Pocknall *et al* 1989; Pickrill *et al* 1992; Wilmshurst *et al* 1999). Marine environments are typically more energetic than terrestrial environments which can lead to physical weathering of pollen grains. For example, *Podocarpus totara* and *Prumnopitys taxifolia* were indistinguishable in a marine core from Poverty Bay due to poor preservation (Wilmshurst *et al* 1999). Tidal influences in estuaries complicate pollen deposition patterns; Clark & Patterson (1985) suggest that tide-borne pollen inputs into estuarine marshes may lead to over-representation of buoyant grains; at the same time turbulence in the epilimnion holds small grains in suspension whereas larger grains sink. The small grains are driven by wind currents to the littoral zone where they accumulate in excess of their relative abundance.

5.4.7 *R*-Values

It is theoretically possible to compensate for over- or under-representation of taxa in the pollen record by applying *R*-values which are correction factors that take into account differential pollen representation[210], however I chose not to do this since there is no comprehensive set of *R*-values for New Zealand taxa. The reasons for this appear to be that first, the results of relatively few modern pollen rain studies have been published for New Zealand, consequently quantifying the relationship between pollen and vegetation

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[210] Pollen percentages are not linearly related to tree proportions since pollen percentages for a given taxon also depend upon the relative abundances of other taxa – the so-called Fagerlind effect (Prentice & Webb 1986).

assemblages is difficult. Parsons & Prentice (1980) state that estimates of *R*-values based on single sites are likely to be statistically unreliable, unfortunately the scarcity of modern pollen data precludes the estimation of *R*-values based on many sites which would increase reliability.

Second, of those few studies where pollen: vegetation relationships have been quantified, results vary both between and within geographic localities to the extent that the usefulness of calculating and applying *R*-values is questionable, supporting Andersen's (1973) claim "*R*-values are not comparable from case to case, because they differ in various species combinations and vary with the species frequency." Schwartz (1989) for example, compared estimates of pre-settlement forest in Wisconsin based on pre-settlement pollen corrected with modern *R*-values to measured pre-settlement forest and found the estimates to be incongruous with the actual forest cover.

As a case in point, Pocknall (1978) used moss polsters and liverwort cushions to determine modern pollen rain characteristics at six sites in Hari Hari, South Westland, and combined this data with basal area of the taxa responsible from 150m² transects. At two sites, *Dacrydium cupressinum* pollen was slightly under-representative of the taxa present (R=0.7), but at another site it was over-represented (R = 1.9), possibly due to restricted air circulation because of the dense forest and an almost closed canopy which would prevent rainout of regional pollen of other taxa. Thus despite the fact that the bisaccate pollen morphology of *D.cupressinum* makes it amenable to long distance transport[211], local representation of *D.cupressinum* in the pollen assemblage was strongly influenced by the vegetation structure and the pollen dispersal characteristics of the other floral elements present.

Other taxa studied by Pocknall (1978) showed similar marked variation in the calculated *R*-values: *Dacrycarpus dacrydioides* ranged from 0.1 to 0.8; *Prumnopitys ferruginea* 0.03-0.6; *Pseudopanax* 0.2-0.6 and the ferns *Cyathea smithii* and *Dicksonia squarrosa* were always over-represented with calculated *R*-values as high as 3.0 and 1.5 respectively. Whereas *Dacrycarpus dacrydioides* was under-represented in Pocknall's (1978) study, Bussell (1988a) found that it was over-represented in the modern pollen spectrum in

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[211] For example, Moar (1970) found *Dacrydium cupressinum* pollen in Canterbury, derived from the West Coast; and Mildenhall (1976) found *D.cupressinum* in the Chatham Islands derived from the mainland, 725 km to the west.

central-western North Island. Although *Prumnopitys ferruginea* had a calculated *R*-value of 1.0 at Lady Lake, North Westland (Pocknall 1980), the value was 0.4 for Hari Hari and 0.7 for Northland (Elliot 1999).

One method of estimating the relationship between fossil pollen frequency and tree cover may be to compare pollen frequencies with plant macrofossil data. Ogden *et al* (1993) found that mean tree pollen percentage and macrofossil frequency were significantly correlated (r = .613) for a site on the Aupouri Peninsula in Northland (34,000 years BP). However taxon including *Dracophyllum* spp and *Astelia solandri* commonly occurred as macrofossils but were infrequent in the pollen record; conversely *Prumnopitys taxifolia* pollen was found but did not occur as a macrofossil.

Clarkson *et al* (1992) examined plant macrofossils (preserved leaves, wood and seeds) from forests in the Benneydale-Pureora district in the central North Island that had been overwhelmed and buried by ash from the Taupo eruption 1850 BP. Sites nearby for which coeval palynological analysis has been carried out include Erua Swamp (Horrocks & Ogden 1998) and Wairehu Swamp (McGlone & Topping 1977). Comparison of fossil pollen relative percentages from these two sites with the Benneydale wood is inconclusive; Table 7 shows that whereas 53% of the wood at Benneydale was *Dacrydium cupressinum*, only 22% and 35% of the pollen was of this taxon for Erua and Wairehu, respectively.

A study of phytoliths[212] from loess in Southland was also inconclusive; Carter (2000) found that the phytolith record prior to 12,000 BP was similar to that of the pollen record (McGlone & Bathgate 1983) in that it was dominated by chionochloid and chloridoid[213] phytolith forms, indicating *Chionochloa* and snow- and red tussock dominance. However the phytolith record also indicates persistence in grassland after 12,000 BP which is contrary to the pollen record for this time (McGlone & Bathgate 1983). Similarly, Horrocks *et al* (2000) compared the pollen record for Awana, Great Barrier Island with phytoliths; although grasses were well represented in both records, fern phytoliths were under-represented and gymnosperm phytoliths were almost absent. Thus although the two

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[212] Morphologically distinct, chemically resistant silica microfossils that originate in certain higher living plants, produced when soluble silica is absorbed along with ground water during plant growth. The soluble silica is eventually deposited as solid silica within and between plant walls, which are mostly deposited directly within the soil when the plant dies (Carter 2000).

[213] Chionochloid are spool-shaped phytoliths; chloridoid are battle-axed shaped and saddle-shaped phytoliths

techniques complement each other, the differences preclude the use of phytoliths (like macrofossils) to correct pollen percentages.

Given the foregoing discussion, I felt justified in leaving the pollen values in their raw form since any attempt to correct for over- or under-representation is likely to introduce more problems and would be somewhat misleading in that a greater degree of accuracy would be implied[214].

	Benneydale % Wood	Erua Swamp % Pollen	Wairehu Swamp % Pollen
Dacrydium cupressinum	53	22	35
Knightia excelsa	3	1	-
Metrosideros	10	1	1
Nestegis	7	1	-
Libocedrus	3	-	1
Prumnopitys	13	7	-
Podocarpus totara	7	5	-
Phyllocladus trichomanoides	-	5	-

Table 7. Comparison of the Relative Percentages of Fossil Wood and Fossil Pollen for three North Island sites, 1850 Years BP.

Source: Clarkson, Clarkson & Patel (1992); Horrocks & Ogden (1998); McGlone & Topping (1977).

5.4.8 Statistical Limitations

There is a certain amount of statistical error introduced into palynological analysis since invariably the analyst is deriving absolute or relative estimates based on samples. According to Moore & Webb (1978) "The process leading up to the preparation of slides containing concentrations of pollen is essentially one of sequential sampling and subsampling. Each sampling stage involves a successive approximation and hence a decrease in the accuracy of the ultimate representation." Sample error is propagated throughout the pollen analysis process because a sample of a core is taken, which is a sample of say, a small lake, which is a sample of a basin or catchment which may be a sample of a region. Since successive samples are not independent from their predecessors,

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[214] A strategy also utilised by Huntley & Birks (1983) in their isopollen maps of Europe.

the sample error grows with successive stages[215]. Even the use of *Lycopodium* tablets may introduce statistical error; according to Stockmarr (1971) "…the more pollen grains are counted the greater part of the error is due to the use of [*Lycopodium*] tablets although the total error decreases."

Brookes & Thomas (1967) argue that for pollen counted to be an accurate representation of the pollen assemblage, a number of assumptions have to be made: the pollen in the sediment are a random sample of the pollen rain during the time of deposition; pollen is not differentially preserved; the core sample is a random sample; the subsample take from the core is a random sample; slides prepared for examination are random samples; and the fraction of the slide counted is a random sample of the slide. Clearly, we cannot ensure that all these conditions are met, even if we take random samples in coring and examination, since whether or not the pollen in the sediment is a random sample of the prevailing pollen rain is beyond the palynologist's control. However, if these limitations are borne in mind then pollen analysis is an invaluable tool in calculating past vegetation distribution and climate inferences.

Since the isopoll maps are based upon relative pollen frequencies rather than absolute pollen counts, an increase in the value of one taxon's pollen will by necessity be offset by a decrease in the value of other pollen taxa in the sample. This obscures the absolute change in the respective pollen record. Fægri & Iversen (1989) call this effect the 'law of diminishing return' and cite as an example pollen of taxon A (say, *Nothofagus*) and taxon non-A (say, *Dacrydium*) who produce the same amount of pollen per unit area. If the proportion of *Nothofagus* to *Dacrydium* is 90% to 10% the area representation is the same. However, if *Nothofagus* doubled its output whereas *Dacrydium* stayed constant, *Nothofagus*' percentage would only increase to 95% of the pollen sum, whereas *Dacrydium* would reduce to only 5%. Fægri & Iversen (1989) suggest that this effect is most pronounced when the value of a pollen percentage nears 100%.

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[215] If the sample taken is a simple random sample, we can make the following generalisations: If the population variance is V, then the 95% sample error of the mean of the first sample of size n is $1.96^* \sqrt{(1-n/N)} * \sqrt{(V/n)}$. The 95% sample error of the mean of the second sample of size m is $1.96^* \sqrt{(1-m/N)}^* \sqrt{(V/m)}$, and so on, so that the sample error of the mean of the second subsample is $\sqrt{((N-m)/(N-n))}^* \sqrt{(n/m)}$ times the sample error of the mean of the first subsample.

5.4.9 Potential Errors in Sampling, Treatment & Counting Pollen

Errors can occur at any stage during sample collection, storage, treatment of the sample and counting. Coring can translocate modern pollen to older strata, contaminating the core, and leading to apocryphal pollen diagrams, and incorrect storage of cores and peat monoliths can lead to deterioration of the sediments and swelling of the pollen grains making analysis more difficult. For modern pollen rain, the type of pollen trap used can exert a strong influence on the apparent pollen assemblage; Myers (1973) found that samples from Tauber traps tended to have much higher percentages of *Nothofagus fusca* pollen than did samples from impact traps at the same site, whereas the opposite held for *Pinus* pollen.

Sample treatment to disintegrate and dissolve non-pollen components of the sediment can introduce errors; for example, during treatment with KOH to remove unsaturated organic soil colloids, boiling the solution to concentrate the solution to >10% KOH can lead to degradation of the exine of some pollen grains. Similarly, bromoform flotation to separate microfossils such as diatom frustules from mineral matter can result in clumping of pollen grains and fine organic particles, leading to loss of some pollen after filtration. Problems can occur during acetolysis to remove cellulose from the sample. Fægri & Iversen (1989) describe one study where a treatment sequence of HCl, HF then acetolysis resulted in the destruction of almost 100% of *Pinus* pollen. The resulting pollen slide becomes a palimpsest and is analogous to differential pollen preservation *in situ* and could result in misleading data.

Mounting the sample on a microscope slide can introduce bias; if the suspension holding the pollen grain is not spread evenly under the coverslip there can be differential migration of pollen grains under the coverslip - usually with the smallest grains migrating to the outside of the slide (Brookes & Thomas 1967).

5.4.10 Temporal Limitations

The majority of the published pollen diagrams for New Zealand have a small number of carbon dates associated with them, with several thousand years separating the verifiable dates, and there is a paucity of published, fine-resolution diagrams[216]. Unfortunately, this can mask rapid changes in the pollen spectrum; Allison *et al* (1986), for example, analysed varved[217] lake sediments in eastern North America and found that *Tsuga canadensis* (hemlock) declined by 75% in just a seven or eight year period[218]. Had fine resolution techniques not been used, and samples taken from the core at say 1000 year intervals, one might incorrectly conclude that the decline took place over several millennia.

5.4.11 Climate vs Edaphic Factors or Succession

Injudicious use of pollen analytical diagrams can lead the researcher to confuse vegetation change in response to climatic factors with edaphic or successional change. Clements (1904, cited in Tivy 1993) defined succession as a sequence or *sere* of floral communities (seral stages) that increase in complexity and replace each other until the climax vegetation is achieved. Climax vegetation in the Clementsian model is dominated by the largest plants capable of sustaining themselves in 'equilibrium' in the prevailing climatic and edaphic conditions.

During successional change there is a progressive alteration in the structure and species composition of the vegetation, whereas in cyclical change similar vegetation types recur in the same place at various intervals of time (Grime 1979). Succession can be further divided into the changes that occur during colonisation of a new and skeletal habitat initially lacking soil and vegetation (primary succession) and those which characterise the process of recolonisation of a disturbed habitat (secondary succession).

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[216] Exceptions include Horrocks & Ogden (1998) and Newnham & Lowe (2000).

[217] Distinct stratified sediments in lakes often reflecting seasonal cycles such as flooding or melting of winter snow.

[218] Presumably in response to a pathogen rather than climatic or even anthropogenic factors given both the severity and the suddenness of the decline, and given modern analogues such as *Castanea dentata* (American chestnut) or *Ophiostoma novo- ulmi* (Dutch Elm disease) spread by the beetle vector *Scolytus multistriatus* in New Zealand.

Whittington *et al* (1991) questioned Birks' (1989) interpretation of isochrone maps for Scotland, suggesting that climate was indirectly responsible for the changing dominance of *Betula* and *Corylus*, and edaphic factors were more important. Soils in Pickletillem (Fife, eastern Scotland) had developed on freely-draining fluvioglacial sands and gravels until iron precipitation and accumulation lead to iron pan development and subsequent waterlogging. This waterlogging was likely to have been modified and enhanced by changes in the water table in response to sea level fluctuations; together, the iron pan development and waterlogging are thought to have caused *Betula* and *Corylus* to reverse their relative dominance.

At Eltham Swamp, Taranaki, for example, a late glacial sequence of *Leptospermum* and *Phormium* → *Leptospermum-Gleichenia*-sedge → oligotrophic mire elements such as *Empodisma* may indicate an amelioration of climate, but could also signify a hydrosere or sedge mire succession (McGlone & Neall 1994). Most conventional pollen diagrams do *not* record successions because the source area normally encompasses many patches of vegetation in various successional stages (Prentice 1988) however it follows that a pollen diagram representing a very small basin or having very fine resolution (for example laminated sediments) could reflect a succession[219]. Furthermore, similar changes to vegetation in a region can occur asynchronously due to migration routes and colonisation speeds of different taxa, as well as local conditions such as topography, altitude, and so on.

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[219] According to John Ogden (personal communication 2002) "I think elements of succession are often included in pollen diagrams in New Zealand – most of which come from relatively small sites where marginal successions are occurring. However, over 2000 year intervals most 'successions' will be completed. Despite this, there could be a problem if 'succession' is occurring during a 2000 year slot at some sites, but more 'climate driven' change at another."

5.4.12 Potential Errors in Radiocarbon Dating & Tephrochronology

5.4.12.1 Introduction

Since a distinguishing feature of an isopollen map is its temporal dimension, a critical evaluation of the dating techniques used and their strengths and limitations is important when interpreting the credibility of the isopollen map. The predominant method of dating both terrestrial pollen cores and marine cores was radiocarbon dating; in addition, several techniques were utilised to assess the tephrochronology of the sites.

Most radiocarbon dating facilities prior to the early 1980s used either proportional gas counters or liquid scintillation techniques. In proportional gas counting, carbon is converted into one of methane, carbon dioxide (Grant-Taylor & Rafter 1962, 1971) or acetylene and then put into a proportional counter where the β particle emissions are counted. This was the technique used at New Zealand's Institute of Geological & Nuclear Science's Rafter Radiocarbon Laboratory until 1987.[220] Waikato Radiocarbon Dating Laboratory, in contrast, where around 3% of the radiocarbon dates used in the isopollen maps are derived, uses liquid scintillation.

This technique involves converting the carbon into benzene or, at Waikato, a mixture of benzene and toluene ($C_6H_6CH_6$). Benzene is preferred because it has excellent light transmission properties and a high chemical conversion yield of sample carbon to benzene (Waikato Radiocarbon Dating Laboratory 2000). The sample is first converted to carbon dioxide, then reacted with molten lithium to form lithium carbide, before being catalytically trimerised to benzene. The sample is then placed into a device that detects scintillations or flashes of light caused by the interaction of β particles and a phosphor added to the liquid. Like gas proportional counting, liquid scintillation requires either extensive shielding or the use of anti-coincidence rings to allow for extraneous background radiation or 'noise'.

Mass spectrometry promised much greater precision than conventional radiocarbon dating, with $^{13}C/^{14}C$ ratios accurate to 0.02 ‰, however the initial obstacle to this was low ^{14}C

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[220] Directors of the (then) DSIR's radiocarbon dating laboratory, Athol Rafter and Gordon Fergusson, were amongst the pioneers of the gas proportional counting technique, using CO_2 as the carrier gas.

content of most samples. A sample formed in the 19th century in equilibrium with the atmosphere, for example, would have only 1.4×10^{-12} g of ^{14}C per gram of carbon, whereas a sample 57,300 years old would have only 1.4×10^{-15}g (Stuiver 1978). Put another way, a 1gm sample of carbon with a ^{14}C content equivalent to modern levels produces around 15 β particles per minute as it decays, which is reasonably easy to count and therefore date accurately. However, 1gm of an organism that died 57,300 years ago produces only around 21 β particles per day, a level that is difficult to distinguish from background radiation which may be as high as 132 β particles per day (Bradley 1999). At the same time, the minute quantities of ^{14}C or $^{14}CO_2$ need to be distinguished from ^{14}N or $^{12}C^{16}O^{18}O$ respectively which are much more abundant.

In the late 1970s a new method of radiocarbon dating was developed; this involved coupling a particle accelerator to a mass spectrometer and is known as Accelerator Mass Spectrometry (AMS) dating. AMS dating involves measuring the concentration of ^{12}C, ^{13}C and ^{14}C ions rather than counting β particles. The carbon ions are produced from the sample, accelerated to high velocities through a tandem electrostatic accelerator[221] whereby a magnetic field separates the ions. As the negative carbon ions accelerate towards the positive potential, they pass through a 'stripper' comprised of a very thin carbon film or a tube filled with gas at low pressure, [222] which removes several electrons from the carbon ions, changing their polarity from negative to positive. The positive ions are then accelerated through the second stage of the accelerator, reaching kinetic energies of around 10 to 30 million electron volts.

Nitrogen anions are unstable and do not survive long enough to reach the accelerator terminal, and do not swamp the much rarer ^{14}C ions. The stripper also removes negatively charged molecules such as $^{13}CH^-$ and $^{12}CH_2^-$ which might otherwise be confused with ^{14}C ions. According to the Rafter Radiocarbon Laboratory (2001) "Provided three or more electrons are removed from the molecular ions the molecules dissociate into their component atoms at the stripping stage. The kinetic energy they had accumulated up to now is distributed among the separate atoms, none of which has the same energy as a

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[221] In essence two linear accelerators joined end-to-end via a terminal which is charged to a very high positive potential; according to the Rafter Radiocarbon Laboratory (2001) around 3 million volts or higher.

[222] Muller (1977) suggested that gold foil might also suffice as a stripper.

single ^{14}C ion. It is thus easy to distinguish the ^{14}C from the more intense 'background' caused by the dissociated molecules on the basis of their kinetic energy."

Much smaller samples can be successfully analysed using AMS than using the 'conventional' proportional gas counting or liquid scintillation techniques: as little as 1mg generally being adequate[223], compared with say 1g in Bradley's (1999) example *supra*. This allows more accurate dating of sediment core sequences if individual pollen grains, for example, can be isolated and dated, a task not possible using conventional radiocarbon dating, and means that samples of seawater need only be a 100 cm^3 or so rather than a few hundred litres previously required.

Whereas the analyst must wait for sufficient radioactive disintegrations to occur using radiometric techniques, AMS is a more 'proactive' technique in that it extracts and enumerates ^{14}C atoms in the sample, and at the same time determines the amount of the stable isotopes ^{13}C and ^{12}C. Therefore a measurement that may take 12 hours and require several grams of sample using conventional techniques may take only 30 minutes and consume a few milligrams using AMS. The Rafter Radiocarbon Laboratory acquired a six million volt tandem Van de Graaff accelerator which became operational in 1987, thus the bulk of dated cores used in the isopollen maps after this time have been dated using AMS.

Stuiver & Polach (1977) recommended using the 'Libby' or 'conventional' half life ($T^1/_2$) of 5,568 ± 30 years to report ^{14}C dates, with a statistical uncertainty of ± 1 standard deviation. Around 2% of the ^{14}C dates provided in the pollen diagrams were reported on a 'new date' or ^{14}C half-life of 5,730 ± 40 years; these were replaced with dates provided by Rafter Radiocarbon Laboratory based upon Libby half-lives and corrected for fractionation (discussed in Appendix 6.4.12.4)[224]. Also in accordance with Stuiver & Polach's (1977) recommendations, I elected not to use calibrated ^{14}C dates[225] in the isopollen maps.

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[223] Stuiver (1978) suggests samples as small as 20μg can be analysed using ion counting techniques.

[224] Initially I was tempted to convert to a Libby half life simply by multiplying by ($^{5568}/_{5730}$) however Roger Sparks (personal communication 2002) suggested using recalculated dates based upon Martin Manning's work at (the then) DSIR Institute of Nuclear Sciences in the 1980s that also correct for fractionation: "...while many of the ages measured here previously were corrected to d13C = -25 per mille, some were not. The correction has been properly taken into account in the recalculated ages we have recorded." At the Waikato Radiocarbon Dating Laboratory, on the other hand, dates have always been expressed using a Libby half-life (Alan Hogg, personal communication 2002).

[225] Calibration refers to the procedure of converting a ^{14}C age to a true or calender age by comparing the conventional radiocarbon age to wood samples whose precise age is known from counting the tree-rings.

Radiocarbon dates are reported as the midpoint of a Poisson probability distribution ±1 standard deviation, thus defining a known level of probability (Bradley 1999). A date from Cobb Valley of 17,720 ±100 yr BP (Singer *et al* 1998) for example indicates a 68% probability that the true age lies between 17,820 and 17,620 years BP. However, if two standard deviations are used, there is a 95% probability that the true age lies between 17,920 and 17,520 years BP. This implies that there is a trade-off between precision and accuracy when using radiocarbon dates. Furthermore, when assessing the goodness-of-fit for depth-age estimation using spline interpolation or polynomial line fitting (discussed in section 2.2) the goodness-of-fit will be unacceptably low if, *inter alia*, the associated errors are too small, since the fitted lines will have less room to move. Bennett (1999) recommends multiplying errors by two or three to improve the goodness-of-fit, which is the same as using two or three standard deviations. Accordingly, where the fitted curve from DEP-AGE appeared to be a poor model of deposition, I re-ran the program using the quoted error ×2 to achieve a 95% confidence interval.

In addition to radiocarbon dating peat and wood samples, dated tephras are often used to date polliniferous sediments in New Zealand (Newnham & Lowe 1992; Pillans *et al* 1993) particularly in the North Island. According to Boygle (1999) because tephra is an allochthonous input into a catchment that is geochemically and physically distinct from other sediments, it is amenable to dating deposits. Whereas the top of a tephra[226] formation may be time transgressive since it may incorporate material from other sources, the base of the tephra is in essence an isochronous plane (Froggatt & Lowe 1990) that provides more stringent dating than radiocarbon dating (Newnham & Lowe 1999). Rhyolitic tephra formations contain pyroclastic material from a single eruptive episode, generally separated by paleosols. In contrast, andesitic tephras typically contain material from more than one eruptive episode and therefore are less precise chronological markers than their rhyolitic counterparts.

Tephras are typically identified by the dominant ferromagnesium or titanomagnetic minerals present, or rare earths present in glass which can then be compared to published

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[226] Tephra refers to all unconsolidated, primary pyroclastic products of a volcanic eruption. Pyroclastic is a collective term for clastic or fragmentary material ejected from a volcanic vent (Froggatt & Lowe 1990).

data to enable their identification and a date[227]. According to Froggatt (1983) these bulk-sample techniques are prone to problems of contamination or weathering, particularly in older terrestrial deposits. This problem can be overcome by using electron microprobes which analyse polished internal surfaces of glass shards to deduce the glass chemistry. Once the tephra is identified, dates are available from published data [228].

5.4.12.2 Sample Selection & Contamination

According to Burrows (1988) "Contamination of radiocarbon date samples by young (or old) carbon is a possibility frequently ignored by Quaternary investigators in [New Zealand] accordingly a summary of potential dating errors would be instructive. Errors can occur during physical and chemical cleaning of the sample, chemical treatment to isolate the cellulose from the wood, converting the C to CO_2 and converting the CO_2 to graphite. Furthermore, since the majority of New Zealand radiocarbon dates are from a single laboratory (IGNS) there is a limited range of pre-treatment procedures used. Anderson (1996) for example suggested that pre-treatment of bone collagen from the Pacific rat *Rattus exulans* "...may not provide as 'clean' a product for combustion as the additional passage of soluble bone proteins through ion-exchange resins in the Oxford system," therefore there is some risk on relying upon a single laboratory's standard procedures. Nevertheless, errors are much more likely to be the result of contamination from natural sources.

Anomalous dates in, for example, Mildenhall (1978), Bussell (1988b) and Newnham & Lowe (1991) where apparent older wood samples were found above younger samples, suggest that either the wood has been translocated to anachronistic depths, or error has been introduced during radiocarbon dating itself. It is clear from the above discussion that since ^{14}C content of fossil samples is very low, introduction of additional 'young' carbon into a sample (eg by modern rootlets extending into a peat sample) may lead to an underestimate of the age of the sample.

An apparent younging of samples can also occur when dating samples containing carbonates; for example shells of molluscs are composed of $CaCO_3$ in the metastable form

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[227] Typically using techniques such as paleomagnetic dating or other radiometric techniques such as fission track dating for older tephras.

aragonite, which may dissolve and be redeposited in the stable form of calcite (Bradley 1999), and contamination with modern carbon can occur during solution and recrystallisation. Although this is not a great problem with respect to the carbon dating of pollen strata, since they are mostly dated by wood fragments, it may occur when dating marine organisms, for example foraminifera used for SST estimation or mollusca for paleo sealevels (*supra*). A third source of 'younging' can arise when weakly organic sediments are infiltrated by humic-rich groundwater; McGlone & Basher (1995) for example found silty loams at Winterton Bog, Inland Kaikoura Range which gave younger apparent ages than peats overlying them, possibly due to infiltration of waters saturated in young organic colloids.

The 'apparent age' or 'hard-water error' has the opposite effect, and can occur when marine molluscs or aquatic plants assimilate carbon from water containing bicarbonates from old sources. Old limestone and other calcareous rock is essentially free of ^{14}C and since the plants assimilate carbon in equilibrium with the soil and soil water as well as the atmosphere, the radiocarbon-derived or apparent age of the fossil sample is much older than the real age.

Shotton (1972) demonstrated this in late Quaternary sediments at Nørre Lynngby, Jutland whereby algae consistently showed dates 1,700 years older than contemporaneous woody twigs. Shotton (1972) concluded "...if the sample consists entirely of tree wood or macrofossils from wholly terrestrial plants then it can be assumed that no hard water error is present." Karrow & Anderson (1975) cited an even more extreme example, whereby bulk marl dates from Elice Bog in southern Canada had an apparent age of 33,900 years; based on the curve for spruce pollen, this is around 22,000 years in error.

Since samples for radiocarbon dating in New Zealand are often peats, it cannot be assumed that the hard-water error is absent. New Zealand peats are often composed of *Sphagnum cristatum* (Lintott & Burrows 1973; McGlone & Wilmshurst 1999b) *Empodisma minus*, *Gleichenia dicarpia*, the sedges *Cladium* spp and *Schoenus brevifolius* (Newnham 1992) all of which are either semi-aquatic or mire-dwelling taxa, and woody roots and fragments of *Leptospermum scoparium* and *Kunzea ericoides* (Newnham 1992). Shells are

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[228] Frequently there are numerous dates for the same tephra available; for example the mean radiocarbon age given for the Taupo tephra is 1850 years BP ±10 based on 41 radiocarbon ages (Froggatt & Lowe 1990).

sometimes used (eg Mildenhall 1994) or gyttja (Elliot *et al* 1995), and occasionally terrestrial woods, with some researchers identifying the species (eg McGlone *et al* 1988) which would tend to minimise hard-water error. On the other hand, erosional activity following deforestation may enable old carbonaceous rock or old leaf litter or charcoal to be deposited directly in the sedimentary column leading to anomalously old dates (McGlone & Wilmshurst 1999) and radiocarbon dates may be rejected in favour of tephra dates (Newnham *et al* 1998).

5.4.12.3 Long-term Changes in Atmospheric ^{14}C Content

A basic assumption in radiocarbon dating is that atmospheric concentrations of ^{14}C have remained constant over time, however clearly this is not so. According to Bradley (1999) "It is a sobering thought that fluctuations in the concentration of radiocarbon may help to explain the very paleoclimatic events to which radiocarbon dating has been applied to for so many years; there could be no better illustration of the essential unity of science."

Secular variations in ^{14}C have been attributed to changes in solar wind magnetic properties which modulate the deflection of galactic cosmic rays that travel towards the Earth, which in turn are responsible for ^{14}C production (Stuiver & Quay 1980). This was demonstrated by a significant correlation between the cosmic-ray flux modulation and the 11-year sunspot cycle: low ^{14}C levels in an 860-year tree ring sequence corresponded to an absence of sunspots observed between 1282 to 1342 AD (the Wolf minimum), 1416 to 1534 AD (the Spörer minimum) and 1654 and 1714 AD (the Maunder minimum).

Over the last century, two phenomena have contributed to fluctuating ^{14}C levels; first the 'Seuss effect' which refers to the reduced amount of ^{14}C in the atmosphere due to combustion of fossil fuels which are low in ^{14}C, leading to an apparent aging of samples that assimilate ^{14}C in equilibrium with the environment, and a countering process, the 'Nuclear bomb effect.' This refers to the extra ^{14}C released into the atmosphere following atmospheric detonation of nuclear bombs: the fission reaction releases vast quantities of neutrons, mimicking cosmic rays: $^{14}N + \text{neutron} \rightarrow {}^{14}C + \text{proton}$, leading to younger apparent ages.

Broecker *et al* (1985) showed that nuclear bomb-derived ^{14}C in the ocean varies geographically; for example to the east of New Zealand between 8.1 and 10.6×10^9 atoms of bomb-derived ^{14}C cm^2 were found compared with values of between 3 and 5×10^9 cm^2 along the equator in the Pacific, Atlantic and Indian Oceans.

5.4.12.4 Fractionation Effects

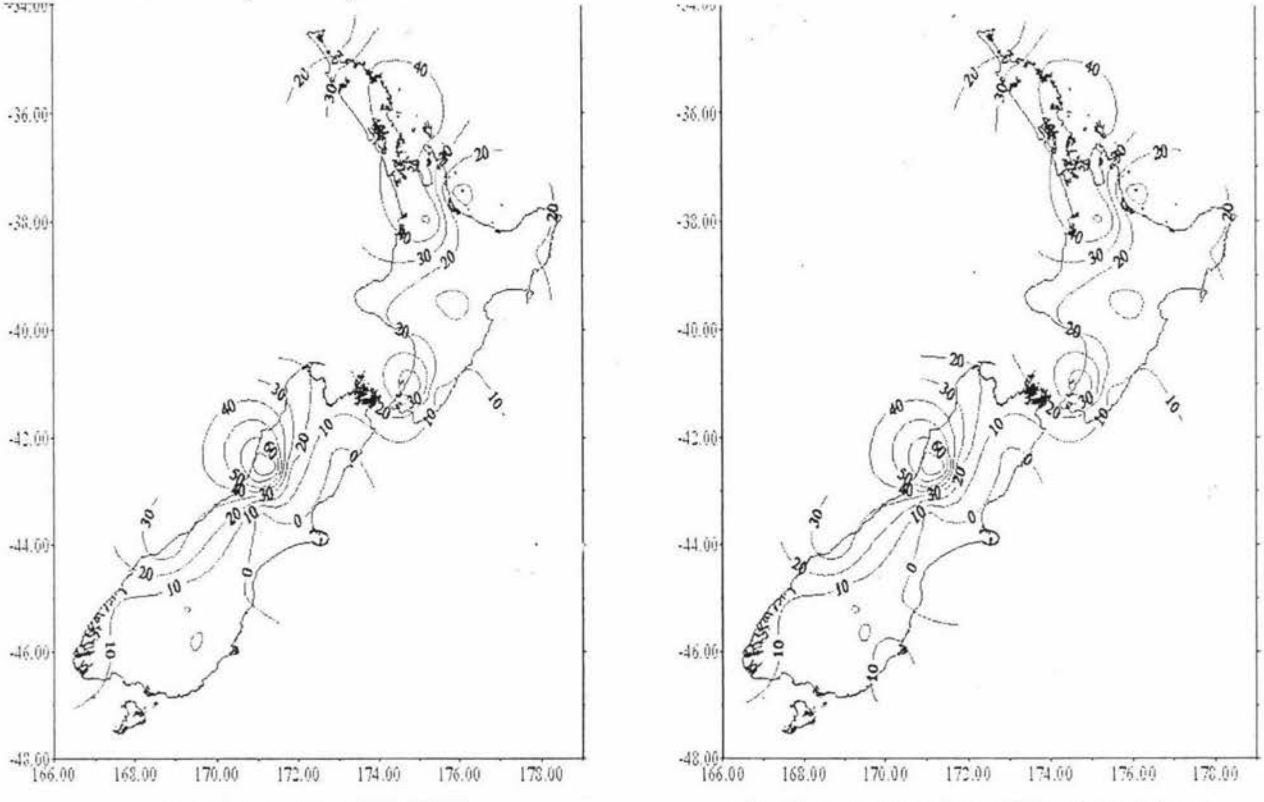
According to Lageard (1997) "Plant ^{14}C can be around 5% below atmospheric levels due to preferential assimilation of ^{12}C." Different organisms will contain different ^{14}C:^{12}C ratios because of differences in metabolism and chemical structure, due to ^{14}C and ^{13}C having a greater mass than ^{12}C. This phenomenon is known as fractionation, which can also occur in the dating laboratory. To correct for this, the ^{13}C:^{12}C ratio is compared to a standard which enables the ^{14}C : ^{12}C ratios of the sample to be corrected, since fractionation of ^{13}C is related to formation of ^{14}C.

The magnitude of fractionation that occurs in plants is due in part to the particular photosynthetic pathway utilised (Edwards & Walker 1983; Bradley 1999). The highest ^{13}C depletion occurs in plants that utilise the Calvin photosynthetic cycle; these so-called C_3 plants include large trees and peat forming taxa such as *Sphagnum*. The lowest ^{13}C depletion occurs in taxa utilising the Hatch-Slack (HS) photosynthetic cycle (C_4 plants) which include cereal grains and related grasses and sedges. Succulent plants fix carbon in their tissues by either the Calvin or Hatch-Slack cycle utilising crassulacean acid metabolism. The implications for accurate radiocarbon dating are that bulk samples require some identification of the component species, since uncorrected dates for sediments composed of HS plants would appear younger (to the order of 200 - 300 years) than Calvin cycle plants that are stratigraphically equivalent. Samples dated at Rafter Radiocarbon Laboratory are routinely corrected for fractionation effects, in accordance with Stuiver & Polach's (1977) recommendations (Roger Sparks, personal communication 2002).

5.4.12.5 Variations in ^{14}C Content of the Oceanic Reservoir

When CO_2 is absorbed in the oceans a fractionation occurs leading to an enrichment of 15‰ or an apparent age of minus 120 years. Countering this effect is the upwelling of ^{14}C-depleted water to the surface; this 'apparent age' or 'reservoir age' of ocean water varies geographically, and in the New Zealand region is between 350 and 400 years (Broecker *et al* 1985). The geographic variation in apparent age was also demonstrated by Mangeraud & Gulliksen (1975) who radiocarbon dated shells of molluscs collected alive before 1940 and found apparent ages of 440 years for samples from Norway, 510 years for shells from Spitsbergen, and 750 years for Ellesmere Island.

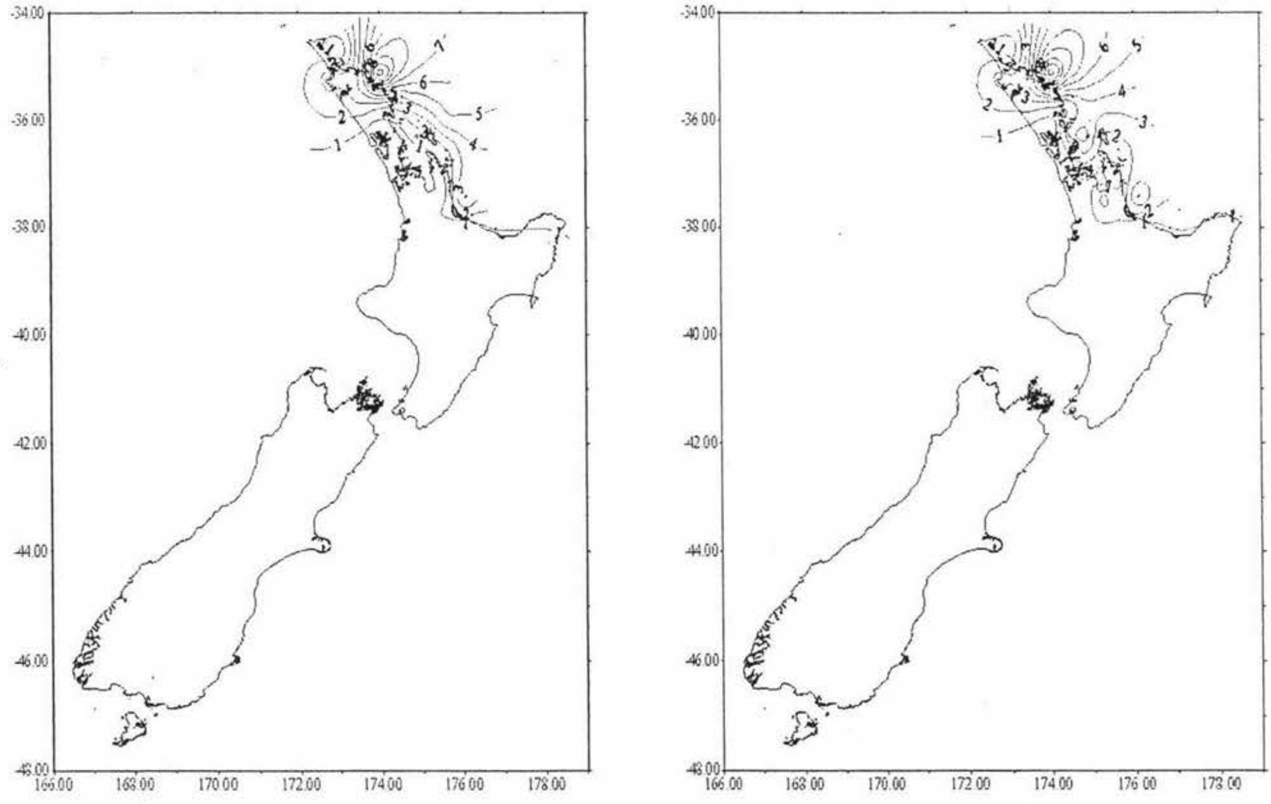
5.5 Sensitivity Analysis



Dacrydium cupressinum 6000 - 4000 BP

Dacrydium cupressinum 6000 - 4000 BP with Taieri Plains Core

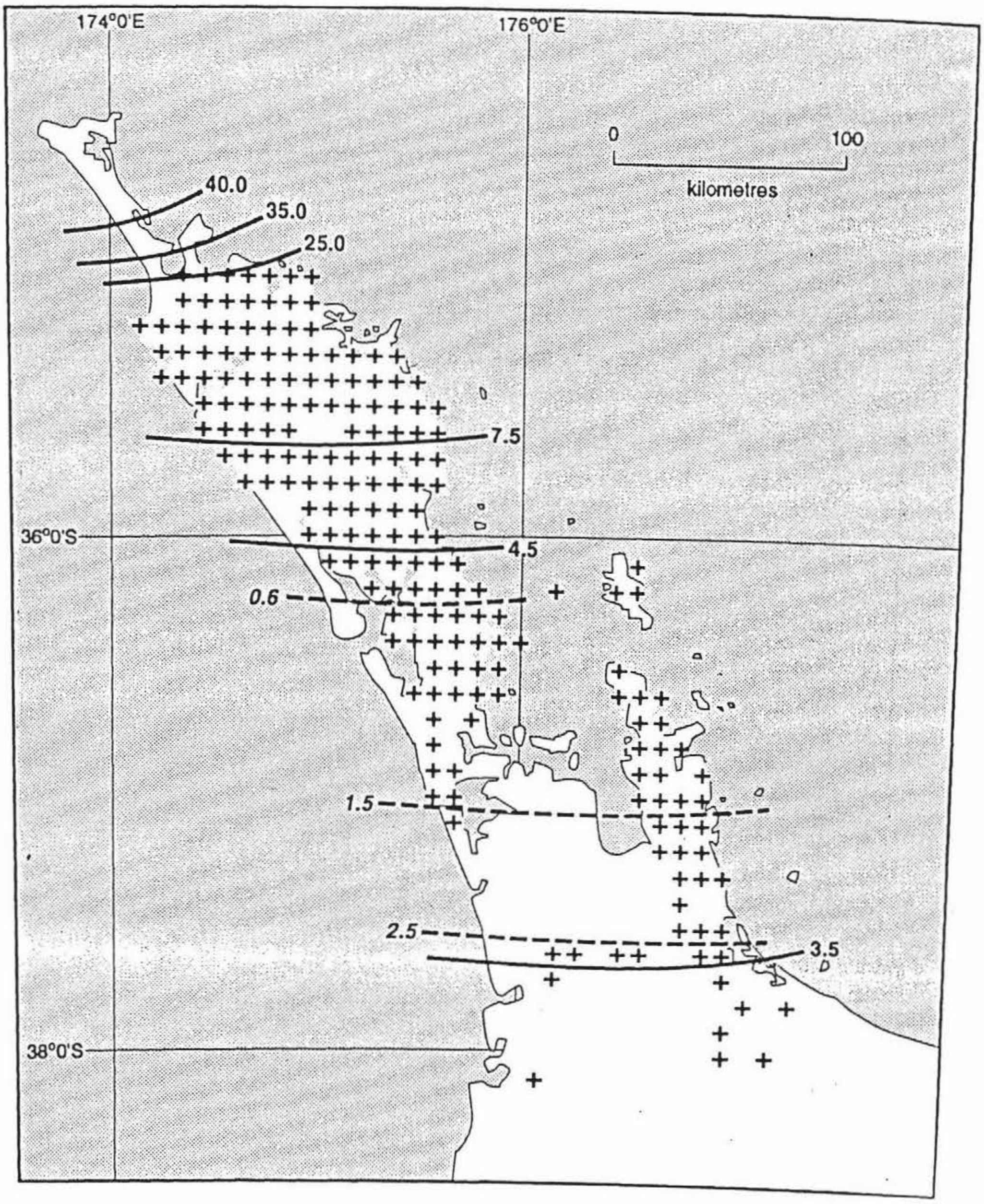
5.5.1 The impact of adding an extra site to the original *D. cupressinum* map.



Agathis australis 4,000 - 2,000 BP

Agathis australis 4,000 - 2,000 BP with additional sites

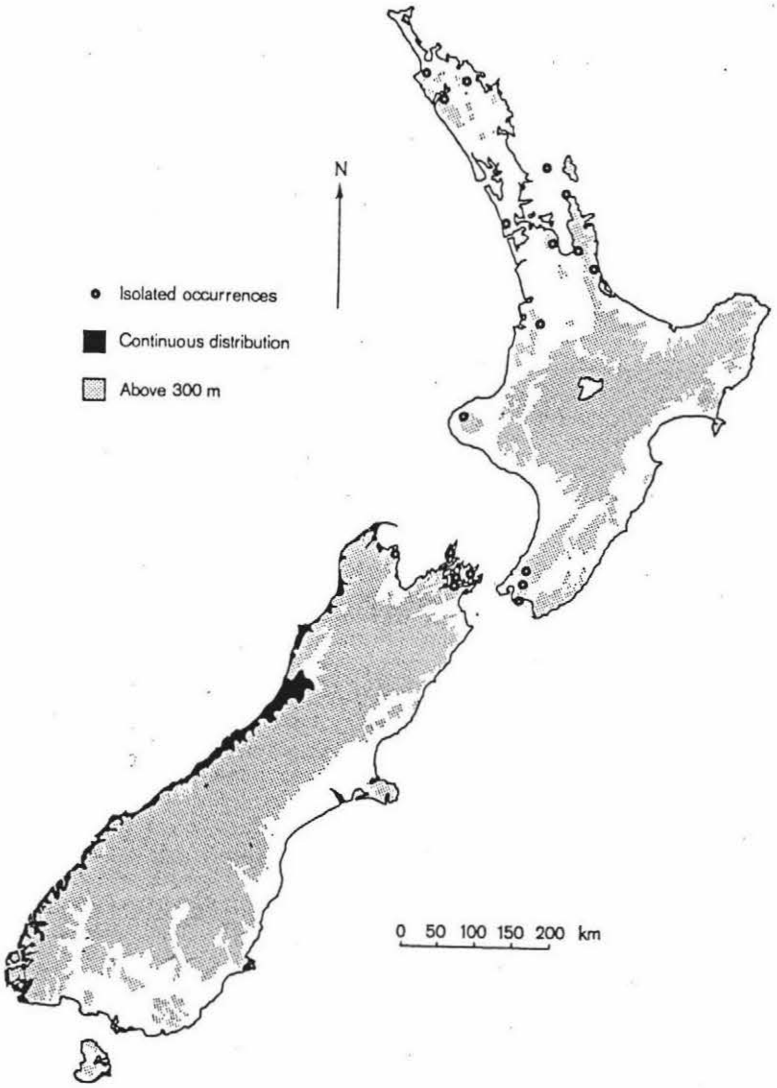
5.5.2 The impact of adding extra sites to the original *Agathis australis* map.



Appendix 5.5.3 (a) The Holocene Expansion of *Agathis australis*.

Crosses depict present distribution of *Agathis australis*. The figures on the lines are the median dates of the samples for the period. Solid lines represent southern expansion; dashed lines represent retreat to the north.

Source: Ogden *et al* (1992)



Appendix 5.5.3 (b) Modern Distribution of *Ascarina lucida*.

Source: McGlone & Moar (1977)

5.6 References

* = cited in the text; ‡ = data used in isopollen and isochrone maps

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5.7 Index