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Modern pollen-vegetation relationships in Northland, New Zealand

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INTRODUCTION

Information gained from modern pollen rain studies has become routinely used in the interpretation of Quaternary fossil pollen records, and is the first step towards reconstructing the vegetational history of a region. Data from modern pollen studies are used to clarify relationships between the relative frequency of pollen/spores and species abundance in the present vegetation so that one can make a more informed and accurate interpretation of the fossil pollen record. Proportions of taxa in pollen records are not assumed to correspond with vegetation percentages. This is because pollen spectra are known to be biased according to pollen production and dispersal (Prentice 1985; Prentice & Webb 1986). A number of models have been proposed to explain the pollen-vegetation abundance relationship and pollen source area (e.g., Davis 1963; Tauber 1965, 1967; Jacobson & Bradshaw 1981; Prentice 1985; Sugita 1993, 1994). Although traditional interpretation of pollen frequencies, which assumes a linear relationship between pollen and tree abundance, is still the first choice approach in Quaternary pollen analysis (Prentice & Webb 1986), most New Zealand contemporary pollen rain studies have shown that given proportions of pollen taxa do not bear a linear relationship to their representation in the vegetation (McGlone & Wilson 1996). This paper seeks to establish the relationships between various plant communities in Northland and their respective contemporary pollen rain.

Early work on the relationship between recent or modern pollen deposition and the contemporary vegetation of New Zealand was published in Moar (1970, 1971), Dodson (1976), Pocknall (1978, 1980, 1982), Macphail (1980), and McGlone (1982). Modern pollen studies published since include those of Bussell (1988) on central-western North Island,

Abstract The pollen and spores from surface samples consisting of moss polsters and soils collected from 15 sites in Northland and Rangitoto Island were analysed. Sample sites were chosen to be representative of differing plant communities in the Northland region. Major plant communities could be distinguished by their characteristic pollen spectra but minor associations were difficult to distinguish. Gymnosperms (anemophilous) are generally proportionately or over-represented compared with zoophilous taxa. A notable exception to this is *Agathis australis* which is typically grossly under-represented. Angiosperm elements of Northland forests are generally very poorly represented, the exception being *Metrosideros* spp. which are either well or over-represented. In contrast to reports from other parts of New Zealand, moderate to high values (>5%) of *Nothofagus* subgenus *Fuscospora* pollen in Northland spectra suggest local presence. Poaceae pollen records only low frequencies in forest spectra, but dominates grassland sites. Bracken (*Pteridium esculentum*) spores record low frequencies at most sites but are well represented where bracken is present on forest margins, or in surrounding open grassland/scrub.

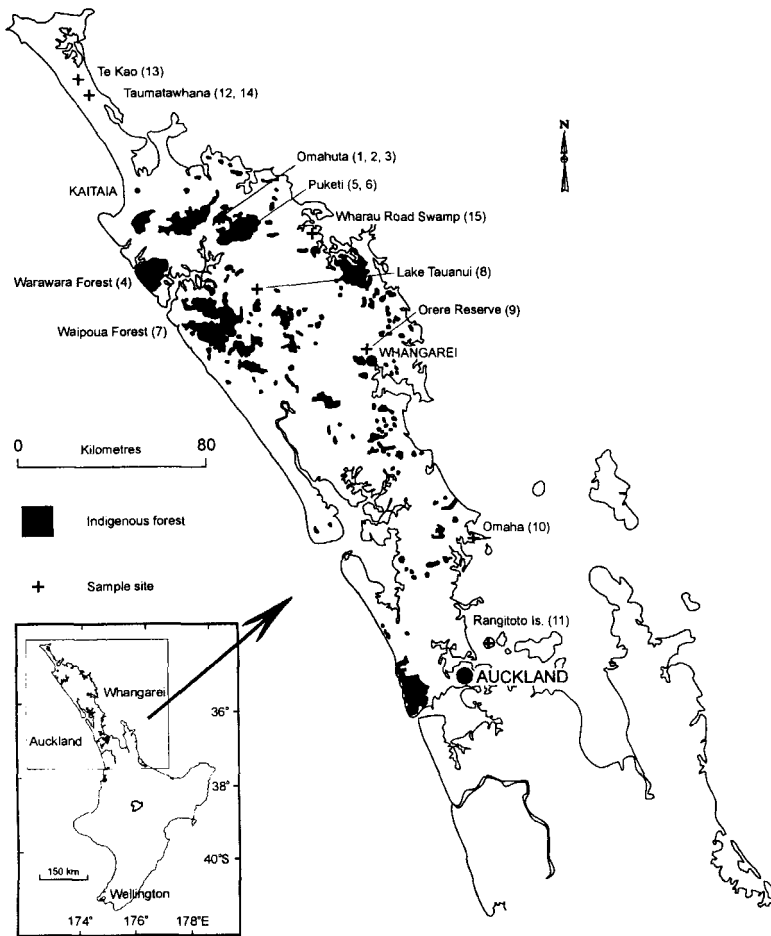


Fig. 1 Modern pollen sample sites in northern New Zealand.

Randall (1990, 1991) on the Southern Alps of the South Island, Horrocks & Ogden (1994) on Mount Hauhungatahi, Central North Island, McGlone & Wilson (1996) on Stewart Island, and McGlone & Moar (1997) on the Auckland Islands. None of these papers examines the modern pollen rain of Northland, and only the unpublished work of Newnham (1990) on Waipoua Forest and Chester (1986) on Bay of Islands examines northern forest sites in any detail. Generally, previous studies have involved the analysis of surface samples, and this study continues that tradition. Carroll (1943) demonstrated the value of bryophytic polsters and mats for analysing recent pollen deposition, concluding that the relative proportions of pollen types trapped were similar regardless of moss species (see also Bradshaw 1981). Boyd (1986) showed that, providing the establishment of absolute quantities of pollen is not the primary interest, mosses are useful

indicators of pollen rain. Others have also successfully used surface soils and litter (e.g., Crowley et al. 1994; Kershaw & Bulman 1994).

METHODS

Forest, grassland, and swamp sites were selected as being representative of major vegetation types in Northland. The sites chosen for this study (Fig. 1, Table 1) are intended to reflect a wide variety of plant communities, particularly forest types, to provide modern analogues for vegetation reconstruction work.

Forest sites were surveyed by random selection of 20 m² plots in areas considered representative of the forest association. Vegetation within these plots was surveyed by recording diameter at breast height (1.2 m, dbh) of all individuals >10 cm dbh. The

dominance of individual trees is related to bulk, which can be illustrated by a number of parameters, e.g., tree height, basal area, total weight, foliage weight, etc. Of these, height and basal area can be measured non-destructively. Basal area is thought to be more proportional than height to tree foliage, which is thought to be most closely correlated with total pollen production of a tree (Ogawa et al. 1965 in Morley 1976), and dominance can therefore be estimated from basal area measurements. The measure also takes account of the higher pollen production of bigger trees (Davis & Goodlett 1960). At each site at least 6 samples were collected from within 20 m² forest plots and combined to form a single sample. Only moss growing on level or near-level surfaces was collected, and always the thickest portions were taken as these could be expected to be most effective as pollen traps. Generally the mats were only c. 1 cm thick, so the entire depth of mat was collected. Although the time span over which these moss polsters have collected pollen cannot be determined, it can be assumed that their pollen assemblages represent several seasons/years of deposition (Bradshaw 1981). Thus, their respective pollen spectra provide an average which reduces the effects of any annual or seasonal fluctuations in pollen production.

Swamp vegetation was surveyed by estimating cover abundance based on field observations of the sample site. Although the method is one of subjective estimation and is necessarily general, its application has been successfully used by other palynologists (e.g., Maloney 1979). A plot size of

10 m² at each site was randomly selected from the study area where core samples for fossil pollen analysis had been recovered (Elliot et al. 1995, 1997). The surface swamp sediment samples were collected from the top 1–2 cm of sediment.

The herb flora of the grassland-shrubland sites at Taumatawhana and Te Kao was surveyed using the line intercept method of Canfield (1941). Tauber (1965) suggested that the majority of herb pollen will be deposited within 5 m of its source, so the sampling site was based on a radius of 5 m from a central randomly selected point. Eight radiating transect lines 5 m long, aligned to the major points of the compass, were measured out, and all contacts of stem, leaf, pinnule, or flower along each line were recorded for each 0.5 m interval. The surface soil samples were collected from the top 1–2 cm of soil at unimproved pasture sites from a central position in the 5 m radius circular plots.

In all, surface samples were collected from 15 sites, as 11 moss polster sites, 2 surface soil sites, and 2 surface swamp sites (Table 1). In the laboratory, modern pollen samples from each site were homogenised and a sub-sample taken which was broken down in a "Waring" commercial blender so as to provide a larger surface area for chemical attack during chemical preparation. Pollen extraction followed standard chemical preparation techniques (Moore et al. 1991) of disaggregation of samples in hot 10% KOH, digestion in 40% HF, oxidation with a chlorine bleach, and acetolysis. Clay-rich samples were treated with sodium pyrophosphate (Bates et al. 1978). Residues were stained with basic fuchsin

Table 1 Site locations and their plant communities.

Site	Location	Grid reference NZMS 260	Altitude m a.s.l.	Vegetation type
1	Omahuta State Forest 1	O05/676623	320	Kauri-podocarp-hardwood forest
2	Omahuta State Forest 2	O05/665621	200	Kauri-beech-podocarp-hardwood forest
3	Omahuta State Forest 3	O05/666618	180	Kauri-podocarp-hardwood forest
4	Warawara State Forest	O05/365423	240	Kauri-podocarp-hardwood forest
5	Puketi State Forest 1	P05/830653	300	Kauri-podocarp-hardwood forest
6	Puketi State Forest 2	P05/837664	300	Kauri-podocarp-hardwood forest
7	Waipoua State Forest	O06/616166	100	Kauri-podocarp-hardwood forest
8	Lake Tauanui	P06/887332	230	Podocarp-hardwood forest
9	Orere Reserve	O06/274127	160	Podocarp-hardwood forest
10	Omaha	R09/695387	5	Kahikatea forest
11	Rangitoto Island	R11/739885	5	Pohutukawa forest
12	Taumatawhana 2	N03/128204	50	Grassland-shrubland
13	Te Kao	N03/098261	40	Grassland-shrubland
14	Taumatawhana 1	N03/128204	60	<i>Typha-Eleocharis</i> swamp
15	Wharau Road	P05/052635	15	<i>Typha-Eleocharis</i> swamp

and mounted in glycerine jelly on glass microscope slides for pollen counting by light microscopy at 450× magnification. The pollen sum consists of all dryland taxa excluding ferns, fern allies, and wetland species. These are excluded because of their tendency to overpower the pollen signal from dryland taxa which are generally of principal interest for Quaternary pollen analyses. In almost all cases a sum of 250 or more was used for percentage calculations. Nomenclature follows Allan (1961), Moore & Edgar (1970), and subsequent revisions made by Brownsey et al. (1985), Connor & Edgar (1987), Webb et al. (1988), and Molloy (1995). *Nothofagus* classifications follow Hill & Read (1991) and Hill & Jordan (1993) and *N. fusca*-type pollen species are designated *Fuscospora* (after McGlone et al. 1996).

SITE DESCRIPTION

In the following section the values in parentheses represent % total basal area of taxa >30 cm in girth at breast height at the forest sites (1–11), and % cover in grassland (12 and 13) and swamp (14 and 15) sites.

1, 2, & 3. Omahuta Forest

Three sites lie in the Omahuta Forest which forms part of the Omahuta-Puketi conjoint forests. In the more inaccessible upland parts the forests are unexploited, dense kauri (*Agathis australis*) forests. *Halocarpus kirkii* may sometimes be prominent in the upper tier and in the sub-canopy; *Ixerba brexioides* and *Toronia toru* are locally common. The more accessible areas have been logged. The Kauri Sanctuary site (Site 1) is on an elevated plateau and is dominated by *Agathis australis* (83.7%). These kauri are large, mature trees up to 2.5 m diameter. Few other mature forest trees are present at this site: *Podocarpus totara* (6.9%), *Prumnopitys ferruginea* (4.8%), and *Elaeocarpus dentatus* (1%). Sub-canopy trees comprise *Caldcluvia rosifolia* (0.3%), *Toronia toru* (0.1%), and the tree fern *Dicksonia squarrosa* (0.6%). At lower levels there are abundant *Coprosma lucida*, *Leucopogon fasciculatus*, *Freycinetia baueriana*, and *Astelia trinervia*. *Myrsine australis*, *Olearia rani*, and seedlings of *Caldcluvia* and *Elaeocarpus* are common. *Metrosideros robusta* is present on some trees as a liane.

The other sites, near the junction of the two main tributaries of the Pukekohe Stream, form part of an association which is now rare in Northland (Wardle

1984), kauri-hard beech (*Nothofagus truncata*) forest. Site 2, on the west side of the Pukekohe Stream, contains no hard beech, but consists of an angiosperm canopy dominated by *Weinmannia silvicola* (29.3%) and *Caldcluvia rosifolia* (19.4%). Other common trees include *Dysoxylum spectabile* (9.8%) and *Knightia excelsa* (12.3%). Lesser amounts of *Beilschmiedia tarairi* (2.3%), *Hedycarya arborea* (2.2%), *Rhopalostylis sapida* (2.5%), and *Metrosideros robusta* (2.8%) as strangling lianes, were recorded. Tree ferns, *Cyathea medullaris* (16.4%) and *Dicksonia squarrosa* (3.1%), are abundant. Understorey species include *Rhopalostylis sapida*, as well as the tree ferns. Site 3 is on a steep spur about 20 m above the east bank of Pukekohe Stream and about 100 m from Site 2. The dominant canopy tree is *Nothofagus truncata* (61.5%), with *Agathis* (2.5%) and *Podocarpus hallii* (7%) also present. The sub-canopy is dominated by *Weinmannia* (14.1%) and *Caldcluvia* (5%), with *Hedycarya* (2%), *Phyllocladus* (0.6%), and *Elaeocarpus* (1.7%). *Olearia rani* (0.5%) and *Cyathea dealbata* (1.5%) contribute to the understorey.

4. Warawara Forest

The remote uplands of Warawara Forest are typified by dense stands of mature kauri (*Agathis australis*), many of which are stunted or stag-headed. In places these trees reach heights of 35–45 m, forming an almost complete canopy. Below is usually a tier of smaller diameter podocarps, mainly *Prumnopitys ferruginea*, *Dacrydium cupressinum*, and *Phyllocladus trichomanoides*. Kauri is locally absent at the Warawara sample site. The canopy is dominated by *Beilschmiedia tarairi* and *B. tawa* (16.1%), *Phyllocladus trichomanoides* (14.9%), *Knightia* (11.9%), and *Prumnopitys ferruginea* (6.8%). *Weinmannia silvicola* (9.4%) dominates the sub-canopy, with *Olearia rani* (2.9%), and *Pseudopanax ferox* (0.7%). *Coprosma arborea* (24.5%) is the dominant understorey taxon, contributing significantly to the total basal area of the plot, and *Dicksonia fibrosa* (11.9%) is also abundant. *B. tarairi* and *B. tawa* saplings are common.

5 & 6. Puketi Forest

The two sites within the Puketi Forest are kauri-podocarp-hardwood forest. *Agathis australis* (kauri) is common throughout in small clumps or as widely spaced single trees, with an assortment of locally frequent trees and tree ferns.

Site 5 (Puketi Forest Headquarters) is dominated by *Weinmannia silvicola* (37%) near the margin of

the forest. There are appreciable amounts of *Podocarpus hallii* and *P. totara* (13.3%), *Cyathea dealbata* (11.7%), *Prumnopitys ferruginea* (9.3%), *Dacrydium cupressinum* (9.2%), *Dysoxylum spectabile* (8.2%), and *Hedycarya arborea* (4.9%). Scattered individuals of *Beilschmiedia tawa* (1.8%), *Coprosma arborea* (2%), *Dacrycarpus dacrydioides* (1.4%), *Olearia arborescens* (0.5%), and *Rhopalostylis sapida* (0.6%) occur. The forest floor cover consists of numerous seedlings of the above as well as various ground ferns such as *Blechnum* spp. and *Asplenium* spp., including *A. bulbiferum* and *A. polyodon*.

Swampy ground occurs in the lower third of Site 6 at Manginangina Scenic Reserve. The canopy is dominated by a single *Agathis australis* tree (75.9%). Below it are scattered individuals of *Weinmannia silvicola* (5.3%), *Syzygium maire* (7.6%), *Knightia excelsa* (4.1%), and one *Halocarpus kirkii* (2.9%), a relatively uncommon tree. *Cyathea dealbata* (2.7%) is common. Also present are *Dysoxylum* (0.9%), *Laurelia novae-zelandiae* (0.3%), *Rhopalostylis* (0.2%), and *Dicksonia squarrosa* (0.2%). The forest floor is rich in bryophytes, pteridophytes, especially *Blechnum* and *Asplenium* spp., many tree seedlings, and scattered individuals of *Ripogonum scandens*.

7. Waipoua Forest

The locality is dominated by large kauri and *Beilschmiedia tarairi*, with *Weinmannia silvicola* and *Prumnopitys ferruginea* locally common. Site 7 is notable for a marked dominance by *Agathis* (87.8%) with appreciable amounts of *Beilschmiedia* (6.2%) and *Weinmannia silvicola* (2.5%). Also present are *Prumnopitys ferruginea* (1%), *Caldcluvia* (0.3%), and *Coprosma arborea* (0.1%). Tree ferns, though not abundant, are represented by *Cyathea dealbata* (0.3%), *Dicksonia fibrosa* (0.8%), and *D. squarrosa* (1%).

8. Lake Tauanui

This site is on the crest of a small island in the lake and is dominated by *Vitex lucens* (58.6%), *Knightia* (20.2%), and *Beilschmiedia tarairi* (9.7%). The understorey mostly consists of *Rhopalostylis* (4.6%), *Myrsine australis* (3.8%), and *Melicytus ramiflorus* (2%). Small trees of *Dacrycarpus* (0.7%), *Dysoxylum* (0.5%), and sapling *Podocarpus totara* are present. *Dicksonia squarrosa* (0.5%) is recorded, and *Cyathea medullaris* is present in adjacent bush. Ground cover includes abundant *Paesia scaberula* in forest openings along with *Pteris macilentata*.

Collospermum hastatum is a common epiphyte, and *Metrosideros robusta* occurs as juvenile lianes.

9. Orere Reserve

The Orere Reserve near Kamo, Whangarei, is a podocarp-hardwood mosaic dominated by *Podocarpus totara*. Site 9 is predominantly *Podocarpus totara* (80.1%), with significant amounts of *Cyathea dealbata* and *C. medullaris* (8.6%), *Coprosma arborea* (4.2%), *Dysoxylum spectabile* (2.4%), *Beilschmiedia tarairi* (2.9%), and *Corynocarpus laevigatus* (1.9%). The understorey contains numerous seedlings of these trees plus abundant *Macropiper excelsum*, *Melicytus ramiflorus*, *Myrsine australis*, and ground ferns including *Phymatosorus diversifolius* and *Adiantum hispidulum*. The sub-canopy includes numerous tree ferns, mainly *Cyathea medullaris* and *C. dealbata*, and small trees or shrubs such as *Melicytus ramiflorus*, *Macropiper excelsum*, *Coprosma arborea*, *Rhopalostylis sapida*, *Cordyline australis*, and *Myrsine australis*. Other common canopy trees nearby include *Vitex lucens*, *Dacrycarpus dacrydioides*, *Knightia excelsa*, and lesser amounts of the liane *Metrosideros robusta*.

10. Omaha kahikatea forest

At Omaha, kahikatea (*Dacrycarpus dacrydioides*) forest forms a band some 1.5 km long and up to 200 m wide, and is recognised as the only remaining unmodified site of its type in Northland (K. Parnell pers. comm. 1992). Site 10 lies in what was probably a former back-dune swamp, and *Dacrycarpus dacrydioides* (42.3%) is the most common tree species. Within this dense assemblage there are significant amounts of *Cordyline australis* (19.7%), *Rhopalostylis sapida* (13.8%), *Corynocarpus laevigatus* (11.7%), and *Vitex lucens* (11.3%). *Cyathea dealbata* (1.2%) is also present. The understorey vegetation is diverse and includes various fern and *Coprosma* species. Present in adjacent bush are *Leucopogon fasciculatus*, *Leptospermum scoparium*, *Kunzea ericoides*, *Myrsine australis*, *Pseudopanax crassifolius*, and immature *Dacrydium cupressinum*, *Podocarpus totara*, *Agathis australis*, and *Beilschmiedia tarairi*.

11. Rangitoto Island

The pohutukawa (*Metrosideros excelsa*) forest site (Site 11) is characteristic of most of the vegetated parts of Rangitoto Island. The vegetation is almost entirely *Metrosideros excelsa* (97.1%). The remainder is *Melicytus ramiflorus* (2.9%). The understorey consists largely of *Myrsine australis*. *Griselinia*

lucida is present nearby. The location is notable for a lack of soil development and xeric conditions.

12 & 13. Taumatawhana and Te Kao grassland-shrublands

The grassland sites at Taumatawhana Pa and Te Kao are typical of the Aupouri Peninsula where only isolated pockets of indigenous forest remain. They consist chiefly of a variety of introduced herbs and scattered shrubs. Site 12 at Taumatawhana is within a historic reserve, and Site 13 at Te Kao is in an open field of unimproved pasture. The grassland-shrubland heath at Te Kao is dominated by grasses (89.3%). The remainder of the cover comprises *Hypochaeris radicata* (4%), *Juncus tenuis* (2%), *Isolepis* sp. (2%), and a few of each of *Gnaphalium subfaculatum*, *Lotus suaveolens*, *Plantago lanceolata*, *Pratia* sp., *Rumex acetosella*, and *Anagallis arvensis*. Grasses (86.5%) also dominate the Taumatawhana site, and *Pteridium esculentum* (7.8%), *Juncus* sp. (3.2%), *Hypochaeris radicata* (1.0%), and *Lepidosperma laterale* (1.0%) comprise the rest of the ground cover.

14 & 15. Taumatawhana and Wharau Road swamps

Swamps are widespread throughout Northland. The Taumatawhana and Wharau Road swamps are typical, dominated by *Eleocharis acuta* and *Typha orientalis*. At Taumatawhana (Site 14), *Typha orientalis* (85%) is the dominant species. Significant cover is also given by *Eleocharis acuta* (10%), a sharp spike-sedge of the Cyperaceae family. The remaining significant cover is provided by *Gleichenia dicarpa* (3%) and *Phormium tenax* (2%). Other swamp tolerant plants recorded as trace values are *Conyza canadensis*, *Hypochaeris radicata*, and *Isachne globosa*. The swamp and its drier margins are surrounded by *Leptospermum* scrub, with scattered *Cordyline australis* and *Coprosma tenuicaulis*. *Blechnum minus* is common. The enclosing dunes are in pasture dominated by *Anthoxanthum odoratum* and *Pennisetum clandestinum*. Wharau Road swamp (Site 15) is an extensive valley-dammed wetland with a diverse flora. Surrounding hillsides are mostly in pasture with patches of gorse (*Ulex europaeus*) and *Leptospermum* scrub. The site is dominated by *Eleocharis acuta* (55%), but *Typha* (20%), and the swamp-tolerant shrubs *Leptospermum scoparium* (10%), *Coprosma tenuicaulis* (8%), and *Cordyline australis* are common. Other species recorded are *Gleichenia dicarpa* (1%), *Isachne globosa* (1%), and traces of *Calystegia*

silvatica, *Conyza canadensis*, *Crepis capillaris*, and *Senecio minimus*.

RESULTS AND DISCUSSION

Comparative sets of data relating pollen and spore frequency to basal area for forest types are summarised in Table 2 and Fig. 2, those for swamp plants in Table 3, and those for grassland-scrub taxa in Table 4. Vegetation at sampling sites for the swamp and grassland plots is summarised in Appendices 1 and 2. The pollen diagrams are shown in Fig. 3 as percentage data.

Dacrydium cupressinum is generally over-represented in the pollen spectra, and is recorded even when absent from the sample plots. This supports earlier studies by Moar (1970) and Mildenhall (1976), who noted long distance transport of *Dacrydium* pollen in the South Island and on Chatham Island, respectively. Therefore, the presence of *Dacrydium* in the pollen spectra cannot necessarily be seen as evidence of local occurrence. *Dacrydium* is found throughout Northland forests. It is common in all types of *Agathis australis* (kauri) forest, and is a characteristic dominant in podocarp-*Beilschmiedia tarairi* associations though seldom abundant (Franklin 1968). However, the results from Omahuta-Puketiki Forest imply that high frequencies are indicative of local or extra-local representation. *Dacrydium* is capable of producing large quantities of pollen which are widely dispersed. Most studies have shown the taxon to be well or over-represented in the pollen record (e.g., Macphail & McQueen 1983; Bussell 1988; McGlone 1982; McGlone & Wilson 1996).

Prumnopitys ferruginea (miro) representation is variable. At some sites (Pukekohe Stream, Lake Tauanui, and Omaha) it is recorded in the pollen rain even though it is absent from the site, implying its presence in the nearby forest, but at other sites the tendency is for under-representation. At Warawara no miro pollen is recorded in spite of its significant presence at the site. This may be because of the upland nature of the site and exposure to prevailing westerly winds which would carry pollen away from the sample site. Pocknall (1978) reported under-representation of this species from Westland forest, although Newnham (1990) considered that miro tends to be over-represented. Results here indicate that deposition of miro pollen may be quite variable depending on local factors, though the general tendency is for under-representation.

Table 2 Total basal area (BA) in m² and pollen percentages (P%) for tree types at forest sites.

	Omahuta 1		Omahuta 2		Omahuta 3		Warawara		Puketi 1		Puketi 2		Waipoua		L. Tauanui		Orere Res.		Omaha		Rangitoto Is.	
	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%	BA	P%
<i>Agathis</i>	83.7	27.0	—	2.6	2.5	0.9	—	0.2	—	1.7	75.9	14.0	87.9	35.3	—	—	—	0.3	—	0.3	—	0.3
<i>Beilschmiedia</i>	2.7	—	2.3	—	3.4	—	15.8	—	1.8	—	—	—	6.2	—	9.7	—	2.9	—	—	—	—	—
<i>Caldcluvia</i>	0.3	—	19.4	3.2	5.0	—	—	—	—	—	—	—	0.3	—	—	—	—	—	—	—	—	—
<i>Corynocarpus</i>	—	—	—	—	—	—	—	0.1	—	—	—	—	—	—	0.4	1.9	—	11.7	1.7	—	—	—
<i>Dacrycarpus</i>	—	0.6	—	2.0	—	0.7	—	0.2	1.4	1.2	—	2.8	—	1.1	0.7	0.8	—	1.0	42.3	27.3	—	—
<i>Dacrydium</i>	—	11.9	—	2.0	—	0.5	—	0.5	9.2	19.0	—	13.1	—	2.0	—	3.1	—	—	—	4.7	—	1.1
<i>Dysoxylum</i>	—	—	9.8	0.3	—	—	—	—	8.2	—	0.9	—	—	—	0.5	—	2.4	—	—	—	—	—
<i>Elaeocarpus</i>	1.0	0.6	—	0.3	1.7	0.2	—	—	—	3.0	—	1.8	—	3.1	—	—	—	—	—	—	—	0.9
<i>Fuscospora</i>	—	1.7	—	7.8	61.5	72.0	—	—	—	—	—	—	—	—	—	—	—	—	—	0.6	—	0.6
<i>Halocarpus</i>	—	2.4	—	0.3	—	0.4	—	0.1	—	—	2.9	0.7	—	2.8	—	1.1	—	—	—	—	—	—
<i>Hedycarya</i>	—	—	2.2	—	2.0	—	—	—	4.9	—	—	0.2	—	—	—	—	—	—	—	—	—	—
<i>Knightia</i>	—	1.1	12.3	4.6	—	1.2	12.0	0.4	—	4.3	4.1	4.2	—	1.7	20.2	6.1	—	0.3	—	0.3	—	—
<i>Laurelia</i>	—	—	—	—	—	—	—	—	—	—	0.3	1.2	—	0.3	—	—	—	0.3	—	1.1	—	—
<i>Metrosideros</i>	—	2.2	2.8	3.5	—	2.7	—	0.3	—	5.8	—	7.6	—	3.6	—	1.9	—	0.7	—	2.5	97.1	61.1
<i>Phyllocladus</i>	—	2.8	—	4.6	0.6	2.2	15.1	88.2	—	16.5	—	2.8	—	0.6	—	1.9	—	—	—	1.1	—	0.9
<i>Podocarpus</i>	6.9	7.8	—	2.6	7.0	1.5	—	0.2	13.3	7.8	—	2.3	—	5.6	—	9.5	80.1	47.9	—	1.9	—	0.9
<i>Prumnopitys f.</i>	4.8	3.2	—	2.9	—	1.1	6.9	—	9.3	3.3	—	1.4	1.0	3.9	—	3.8	—	—	—	0.3	—	0.9
<i>Prumnopitys t.</i>	—	2.4	—	2.9	—	1.1	—	0.7	—	4.5	—	4.8	—	14.0	—	8.8	—	1.4	—	1.9	—	—
<i>Syzygium</i>	—	—	—	—	—	—	—	0.1	—	0.2	7.6	4.2	—	0.3	—	—	—	—	—	0.3	—	1.7
<i>Vitex</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	0.3	58.6	3.1	—	0.7	11.3	0.6	—	—
<i>Weinmannia</i>	—	0.6	29.3	29.6	14.1	2.2	9.4	0.1	37.0	7.7	5.3	5.5	2.5	2.2	—	—	—	—	—	—	—	—
<i>Coprosma</i>	—	1.9	—	2.9	—	1.1	25.1	7.4	2.0	3.8	—	0.9	0.1	0.6	—	0.4	4.2	2.1	—	3.3	—	—
<i>Cordyline</i>	—	—	—	—	—	—	—	0.2	—	0.7	—	0.2	—	—	—	2.3	—	2.1	19.7	5.0	—	0.3
<i>Melicytus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.0	—	—	—	—	—	2.9	—
<i>Myrsine</i>	—	0.2	—	—	—	0.1	—	—	—	0.2	—	0.2	—	0.3	3.8	0.8	—	—	—	1.1	—	4.0
<i>Olearia</i>	—	—	—	—	0.5	—	2.9	—	0.5	—	—	0.2	—	—	—	—	—	—	—	—	—	—
<i>Pseudopanax</i>	—	0.2	—	0.9	—	0.4	0.7	0.4	—	1.2	—	0.5	—	—	—	—	—	—	—	0.3	—	—
<i>Rhopalostylis</i>	—	—	2.5	—	—	—	—	—	0.6	0.5	0.2	3.0	—	—	4.6	3.8	—	0.7	13.8	2.8	—	0.3
<i>Toronia</i>	0.1	0.6	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cyathea d. type</i>	—	5.7	16.4	63.3	1.5	9.2	—	9.3	11.7	26.6	2.7	22.0	0.3	20.0	—	14.0	8.6	25.6	1.2	2.0	—	1.1
<i>Dicksonia fibrosa</i>	—	—	—	2.1	—	0.4	12.0	—	—	0.3	—	0.1	0.8	—	—	—	—	—	—	—	—	—
<i>Dicksonia sq.</i>	0.6	4.7	3.1	0.8	—	0.9	—	—	—	—	0.2	6.0	1.0	6.7	0.5	1.0	—	1.1	—	—	—	—

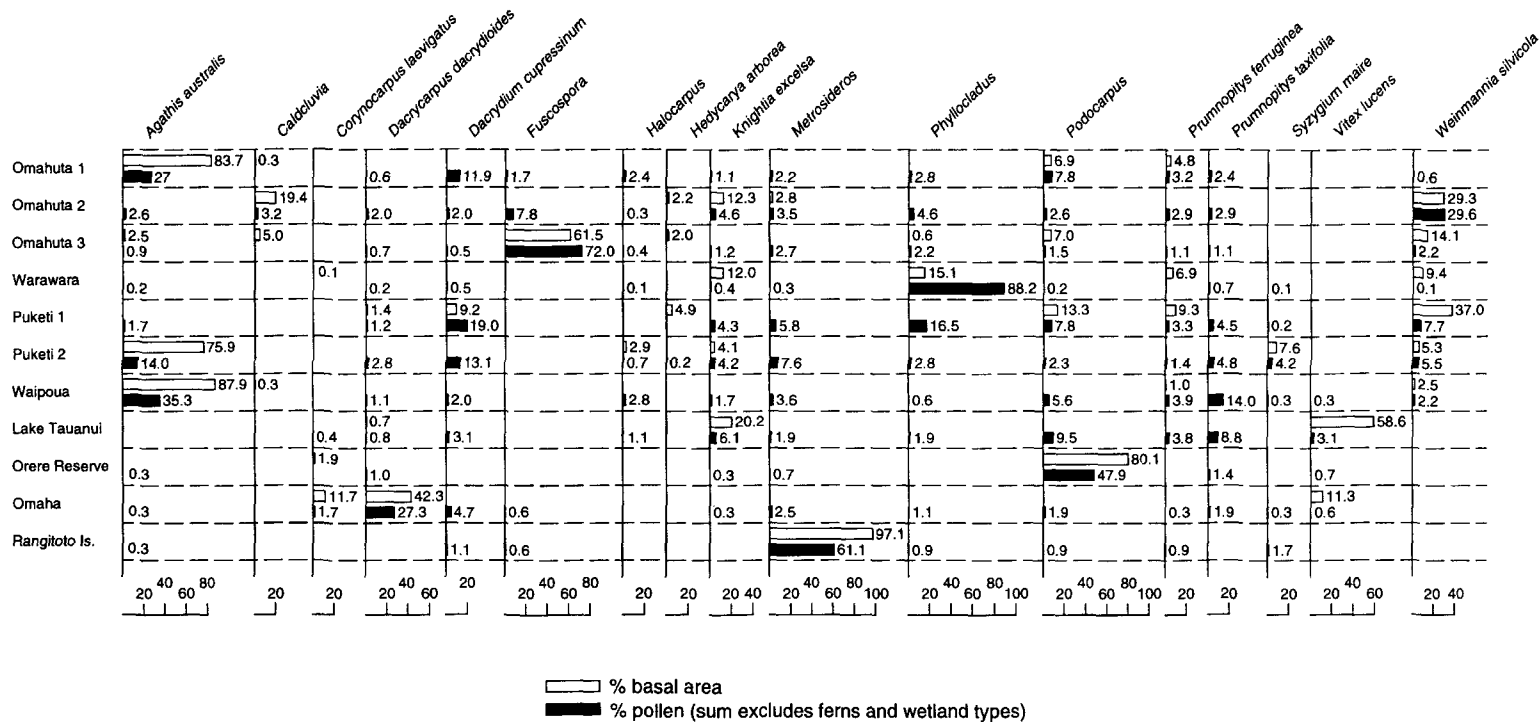


Fig. 2 Relationship between pollen rain and forest composition for main tree types.

Prumnopitys taxifolia pollen was consistently recorded at all forest sites even though no individual trees were found within the forest plots. High frequencies of pollen were recorded at Puketi (Site 5, 6), Waipoua (Site 7), and Lake Tauanui (Site 8). Moar (1970) observed that both *Prumnopitys* species tend to over-representation. Pocknall (1978) has suggested that low frequencies do not imply rarity in the vegetation and that high frequencies suggest presence at or near the site of deposition. Results from this study support that finding.

Dacrycarpus dacrydioides, when present, is always under-represented. This finding is in agreement with that of Pocknall (1978, 1980) who argued that this is because of low pollen production. The Omaha result shows that high frequencies of *Dacrycarpus* pollen indicate local presence. Other sites often record low values in spite of its absence from basal area analyses. This suggests that although the taxon

may be a low producer, it is capable of wide dispersal.

Podocarpus-type is generally well represented in the pollen spectra but this does not always reflect its importance in the local vegetation. In Orere Reserve, where *Podocarpus totara* is the dominant tree, the pollen values under-represent its occurrence in the local forest. At Omahuta, in the *Nothofagus truncata* plot (Site 3), *Podocarpus hallii* is very under-represented. At the Puketi Forest Headquarters site (Site 5), where mixed populations of *P. hallii* and *P. totara* occur, pollen values also indicate under-representation. Pocknall (1982) and McGlone & Wilson (1996) have suggested that *P. hallii* pollen has poor dispersal but is represented roughly proportionately when present locally. These results tend to support that conclusion, e.g., Site 1 at Omahuta. Its presence in the pollen spectra at other sites where it is not recorded in the basal area analyses reflects its wide-

Table 3 Plant group representation and their respective pollen percentages at swamp sites. Asteraceae are *Taraxacum*-type. + = <1%.

	Taumatawhana Swamp		Wharau Road Swamp	
	% Cover	% Pollen	% Cover	% Pollen
<i>Coprosma</i>	—	6.2	8	10.8
<i>Cordyline</i>	—	3.4	5	—
<i>Leptospermum</i>	—	6.5	10	21.1
Asteraceae	+	6.7	+	1.7
Convolvulaceae	—	—	+	—
Cyperaceae	10	4.2	55	14.7
Poaceae	+	23.6	1	32.9
<i>Phormium</i>	2	—	—	—
<i>Typha</i>	85	65.0	20	12.2
<i>Gleichenia</i>	—	—	1	3.3

Table 4 Plant group representation and their respective pollen percentages at grassland-shrubland sites. Asteraceae are *Taraxacum*-type. + = <1%.

	Te Kao		Taumatawhana	
	% Cover	% Pollen	% Cover	% Pollen
Asteraceae	4.3	4.6	1.0	7.0
Epacridaceae	+	0.7	—	—
Leguminosae	+	—	—	—
Lobeliaceae	+	—	—	—
<i>Plantago</i> spp.	+	—	—	—
Polygonaceae	+	—	—	—
Poaceae	89.3	54.7	86.5	44.3
Cyperaceae	2.0	0.9	1.0	0.0
Juncaceae	2.0	—	3.2	—
<i>Pteridium esculentum</i>	—	5.3	7.8	3.8

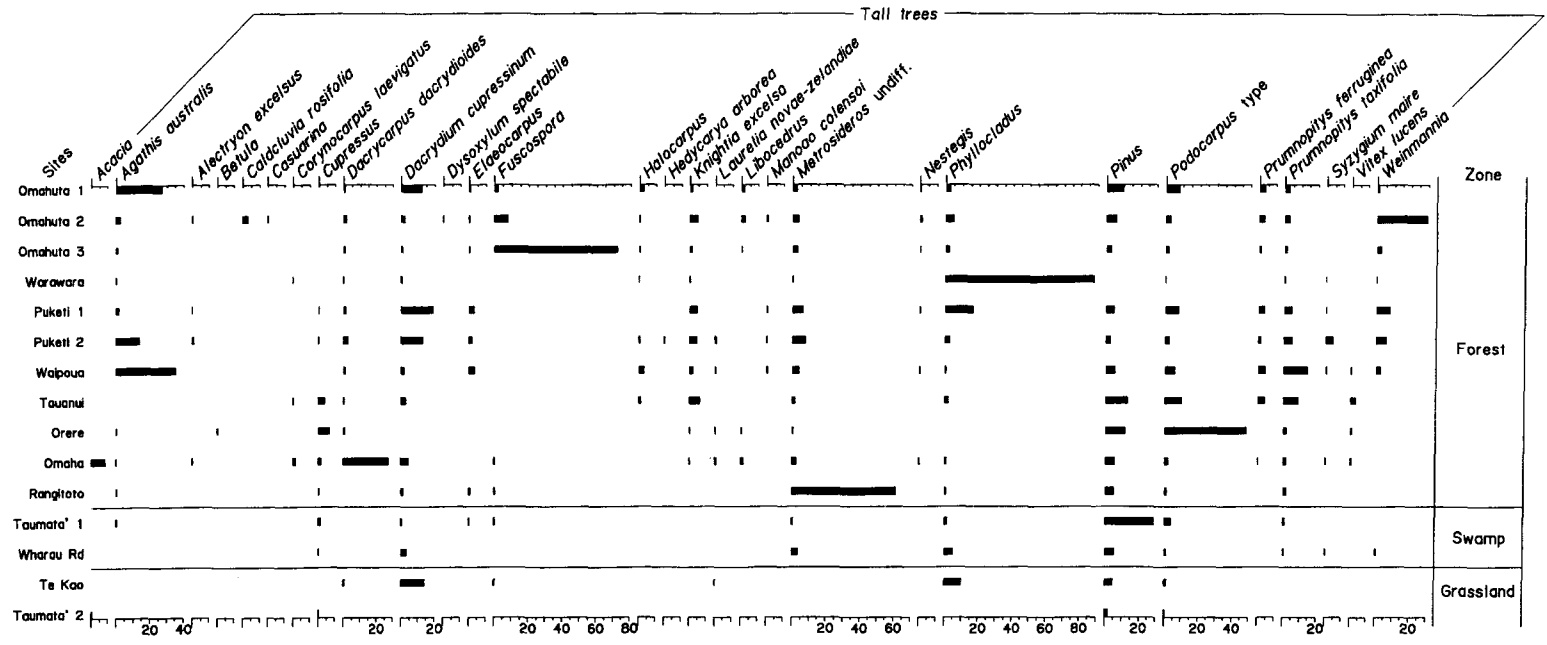


Fig. 3 Percentage pollen at all sites. Open bars indicate taxa not included in pollen sum.

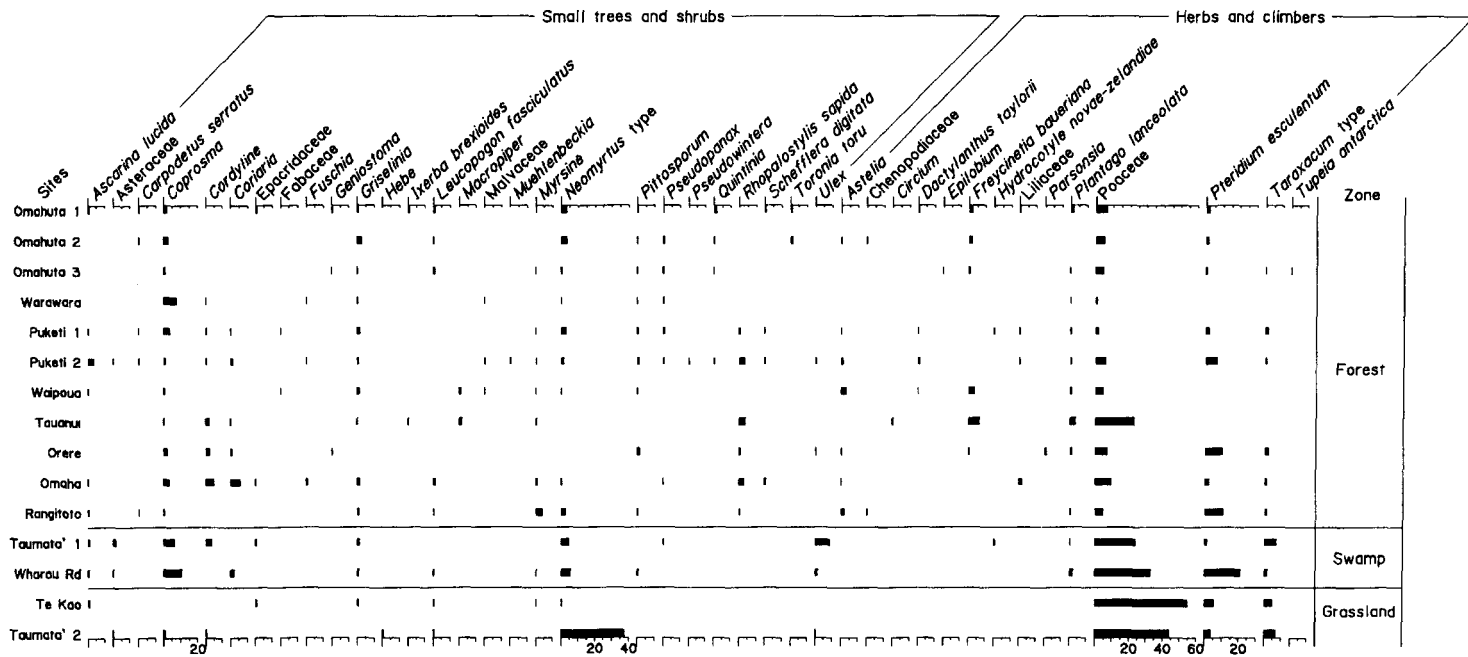


Fig. 3 (cont'd)

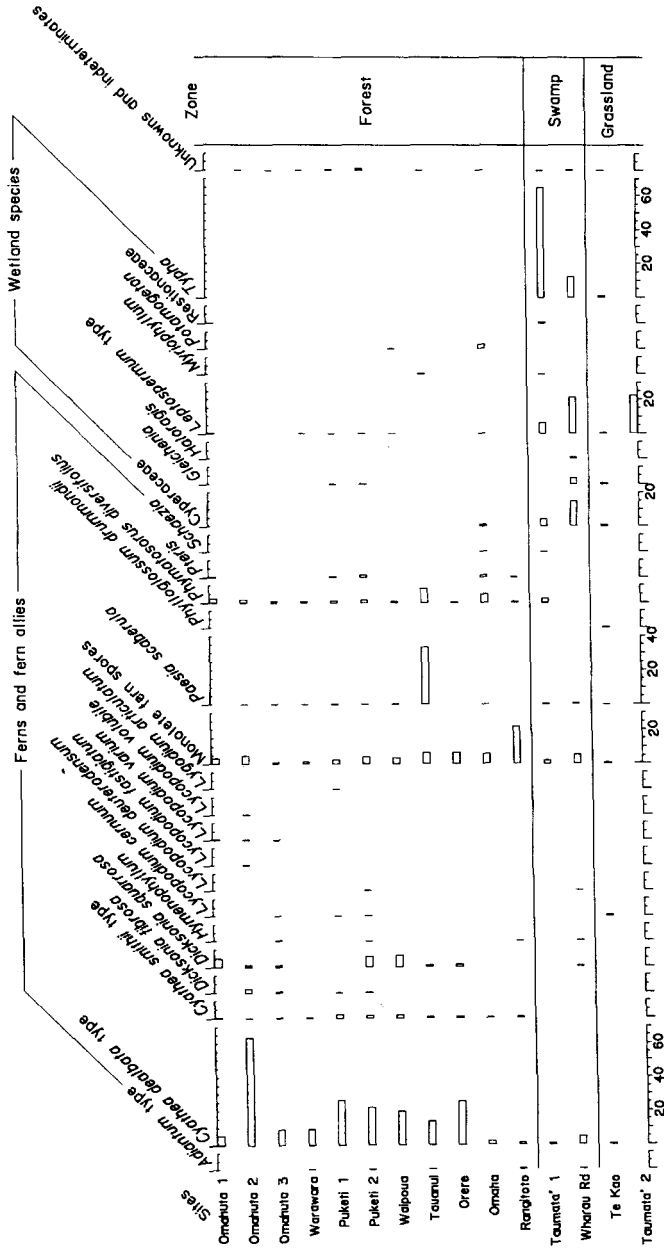


Fig. 3 (cont'd)

spread occurrence throughout Northland, both in forest and as open woodland on farmed landscapes.

Phyllocladus is generally well to over-represented. The results from Warawara (Site 4) are clearly an extreme case. Pocknall (1982) described similar pollen dominance from Westland samples and argued that such results could occur where there is a lack of air circulation under the canopy. This may

be the case for this site, and also for Site 5 at Pukehi Headquarters where high values are also recorded. Elsewhere, *Phyllocladus* is generally well represented given its common occurrence in Northland forests, especially in association with *Agathis australis*. It is less well represented farther from source, indicating that its pollen is not widely dispersed. This finding is at variance with Newnham

(1990) who suggested that *Phyllocladus* is widely dispersed but consistently under-represented (note also McGlone & Basher 1995).

Agathis australis, though it may dominate the pollen spectrum, is almost invariably under-represented, sometimes extremely so. Even where this taxon constitutes nearly 90% of the basal area it does not achieve more than about one third of the pollen sum. When *Agathis* is not present, or comprises only a small part of the local vegetation, the pollen values range from zero to low. The results imply that when pollen values exceed 5–10%, *Agathis* is common in the local/extra-local vegetation. This agrees with observations made by Newnham (1990) at Waipoua and Newnham et al. (1993), although Wilmshurst (1995) and McGlone et al. (1988) reported long-distance transport of *Agathis* pollen in Hawke's Bay and Taranaki, respectively.

Weinmannia silvicola is well represented when present locally, but pollen values decline rapidly with distance from source or when its presence is only a small proportion of the local vegetation. This indicates that, although it is an abundant producer, *Weinmannia* has poor dispersal power. Pocknall (1980), McGlone (1982), and Newnham (1990) reported similar results.

Pollen of *Elaeocarpus dentatus* is generally quite indicative of its representation in the vegetation, though it can be over-represented when locally abundant. Like *Weinmannia*, it produces copious pollen but has limited dispersal.

Knightia excelsa is a common tree in Northland forests, particularly in secondary regrowth areas where it can be a dominant successional tree. The recent pollen spectra indicate that it can be well represented when locally common, but generally *Knightia* is under-represented. In some cases, even where the tree is common, pollen is scarce. So, although high values are possible where it is locally abundant, it is otherwise under-represented and has poor dispersal.

Metrosideros pollen (cf. *M. robusta*) tends to be proportional to its presence where it is recorded in the basal area analyses, but otherwise is generally over-represented. McGlone (1988) described the genus as an abundant producer with poor dispersal characteristics. Its frequent occurrence in Northland pollen spectra suggests that the over-representation may result from the importance of *Metrosideros* lianes and their abundance in the flora, although they are under-represented in basal area analyses. Newnham (1990) recorded similar results. Because species identification of *Metrosideros* pollen is not

readily achieved, pollen counts may include a number of species (*M. albiflora*, *M. carminea*, *M. colensoi*, *M. diffusa*, *M. fulgens*, *M. perforata*, and *M. robusta*). Although many of these species are commonly found in northern forests, much of this pollen is probably *M. robusta*, which usually begins life as an epiphyte and eventually becomes an emergent tall tree. Like its southern equivalent, *M. umbellata*, *M. robusta* bears many flowers producing abundant pollen, whereas other *Metrosideros* species are less common or scarce and may also bear fewer flowers, e.g., *M. diffusa* (McGlone & Wilson 1996).

Nothofagus truncata (hard beech) is well to over-represented at Omahuta. The genus is a prolific pollen producer and capable of long-distance dispersal (Mildenhall 1976). Newnham (1990) reported that, even with localised distribution in Waipoua Forest, *Fuscospora* pollen (which might include a long-distance transport component of other members of this subgenus, e.g., *Nothofagus fusca*) is recorded in 4 out of 12 samples. He argued that the pollen is regionally dispersed and consistently over-represented. Bussell (1988) found that *Fuscospora* pollen masks pollen of other taxa when locally abundant. However, the results in this study generally show that pollen values fall sharply with distance from source. At Site 3 at Omahuta, where *Nothofagus truncata* dominates the vegetation (61.5%), *Fuscospora* pollen reaches 72%, yet at Site 2 (only 50–100 m from Site 3) only 7.8% *Fuscospora* pollen was recorded. The Site 1 (Omahuta) pollen rain has only 1.7% *Fuscospora* pollen. Although high values of beech pollen have been recorded elsewhere in spite of local absence (e.g., McGlone & Wilson 1996), when values exceed 5% in Northland it is likely that the *Nothofagus* is locally present.

Vitex lucens is a common canopy tree in many parts of Northland yet its pollen is rarely recorded. Even where it dominates the local vegetation, such as the Lake Tauanui site (Site 8), this taxon exhibits extreme under-representation.

Rhopalostylis sapida demonstrates variable frequencies in the pollen rain but is generally under-represented. At Puketi (Site 6), where it is over-represented, the species is abundant in the surrounding vegetation. Conversely, at Omaha (Site 10) where *Rhopalostylis* is very under-represented, it forms an important component of the vegetation. In the latter case, *Rhopalostylis* pollen appears to be masked by other species, especially by introduced taxa such as *Acacia*, *Pinus*, and grasses.

Cordyline pollen was recorded at several forest sites, either as a trace (<1%), or in only low frequencies. Even where abundant in the vegetation at Omaha (Site 10), this genus is very under-represented.

Coprosma is generally well to over-represented at most sites. The genus is anemophilous and a high pollen producer. Pocknall (1978) recorded the genus as being over-represented. The Warawara sample (Site 4) greatly under-represents its importance at the site. This is probably attributable to the masking effect of *Phyllocladus* discussed above.

Pollen percentages for *Dysoxylum spectabile*, *Hedycarya arborea*, *Syzygium maire*, *Beilschmiedia tarairi*, and *B. tawa* do not reflect their importance in Northland forests. *Beilschmiedia* pollen is almost never recorded, even from litter on and beneath the tree (Macphail 1980). The results in this study confirm that finding. Low pollen production (e.g., *Beilschmiedia*), entomophily, ornithophily, and extremely local dispersion (e.g., *Syzygium*) are factors accounting for low representation of these species.

Cyathea dealbata-type and *Dicksonia squarrosa* are consistently over-represented, which is typical of tree fern representation reported elsewhere (Moar 1970; Dodson 1976; Pocknall 1978). However, their dispersal power appears to be limited. Ground ferns are often extremely over-represented when locally common, e.g., *Paesia scaberula*, but may be scarce when the sample site is distant from source. *Pteridium esculentum* (bracken) spores record low frequencies at most forest sites. The exceptions are Puketiti (Site 6, 6.3%), Orere (Site 9, 9.8%), and Rangitoto (Site 11, 10.3%). At these sites bracken is common on the forest margins providing a local source for spores. At the grassland sites bracken is under-represented at Taumatawhana (Site 12) where it is a common local element, but recorded 5.3% at Te Kao (Site 13) where it was absent from the site. The Te Kao abundance may be derived extra-locally from nearby scrubland. The swamp sites also gave contrasting results for *Pteridium* spores. Wharau Road (Site 15) recorded almost 21%, yet Taumatawhana (Site 14) had only 1%. The abundance of spores at Wharau Road is probably derived from scrubland surrounding the swamp, both local and extra-local. Wilmshurst (1995) has reported similar variable results for *Pteridium esculentum*. Some writers report under-representation of fern spores, particularly *Cyathea dealbata*-type, *Dicksonia* spp., and *Pteridium esculentum* (e.g., Macphail & McQueen 1983), but others describe them as either well or over-represented (e.g., Dodson 1976; Bussell

1988; McGlone 1982). Wilmshurst (1995) has suggested a number of explanations for the contradictory reports of bracken spore representation, including variable fertility and spore production of bracken colonies. The age of a moss polster and therefore the duration of pollen accumulation in it may influence pollen and spore preservation. The importance of wind dispersal at exposed sites may also be a factor, carrying spores over long distances from source. This study suggests that fern spores in general are well to over-represented on a local scale, but only adequately to under-represented on an extra-local to regional scale.

Typha representation at Taumatawhana (Site 14) and Wharau Road (Site 15) swamps is good but rarely recorded elsewhere, indicating that the species has limited dispersal. Cyperaceae pollen is only moderately represented even when abundant at Site 15 (Wharau Road). *Leptospermum* is well to over-represented at both swamp sites and the Taumatawhana grassland site (Site 12).

Poaceae pollens are generally represented at less than 5% in forest spectra despite large areas of pasture land in surrounding areas. Similar observations were made by Pocknall (1978) and Randall (1990), suggesting that local vegetation may inhibit rainout of regional pollen. Where sample sites are in more open situations, such as the swamp sites and Lake Tauanui, grass pollen influx is considerably greater.

CONCLUSIONS

The pollens of anemophilous taxa are generally proportionately represented or over-represented when compared with the entomophilous and ornithophilous taxa. However, there are some exceptions, most notably *Agathis australis* which is typically grossly under-represented. Other anemophilous taxa that form important components of Northland forests which are often under-represented are *Prumnopitys ferruginea* and *Dacrycarpus dacrydioides*. Pocknall (1978) reported similar findings from Westland, and concluded that a low frequency of these species is not necessarily indicative of rarity in the vegetation. *Podocarpus* is regularly under-represented even when it is the dominant forest tree, particularly where *P. hallii* is common, concurring with McGlone & Wilson's (1996) report of *P. hallii* being under-represented in Stewart Island spectra.

The angiosperm elements of Northland forests are generally very poorly recorded. The exception to this is *Metrosideros*. This pollen type is either well or

over-represented. *Weinmannia* and *Elaeocarpus* may form significant proportions of pollen spectra, but only when close to source. *Knightia excelsa* is consistently under-represented. Its presence in pollen spectra indicates local occurrence. Other angiosperm taxa are either recorded only sporadically, e.g., *Dysoxylum spectabile* and *Hedycarya arborea*, or not recorded at all, e.g., *Beilschmiedia* spp. The extreme under-representation of the angiosperm vegetation in general is a major problem for New Zealand Quaternary pollen analyses.

Tree ferns and ground ferns are often over-represented, particularly when the sample site is close to source, e.g., *Dicksonia squarrosa* and *Paesia scaberula*. Most produce vast numbers of spores, but the majority of these fall to ground close to source and dispersal is reduced with distance.

The non-forest sites show markedly different pollen spectra, and the comparison between the vegetation composition and the pollen frequencies is necessarily somewhat subjective. Grass pollen is always well represented, though it under-represents the proportion of grass in the grassland-shrubland sites. At Taumatawhana, shrub pollen forms an important component of the pollen sum. This is represented mainly by large amounts of *Neomyrtus*-type and *Leptospermum*-type pollen. These pollen types both represent genera belonging to the Myrtaceae family. They are prolific pollen producers but have low dispersal ability. The pollen source for these groups is quite local. At Te Kao much of the non-herbaceous pollen is derived from trees, particularly *Dacrydium* and *Pinus*, demonstrating their wide dispersal characteristics. The records for *Pinus* in most samples, including indigenous forest sites, reflect the widespread occurrence of this introduced species throughout the country and the high productivity and wide dispersal of its pollen.

The swamp sites indicate a general tendency for emergent species such as *Typha* to be under-represented. The swamp-tolerant woody taxa, such as *Leptospermum* and *Coprosma*, tend to be over-represented. Poaceae pollen is recorded at high frequencies in swamps but the source for this pollen is mostly from the surrounding slopes in pasture, and this feature indicates that grasses are high producers.

In general, the pollen profiles presented here are reflective of their respective plant communities, and results are comparable with other modern pollen studies.

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Appendix 1 Percentage cover of recorded species at swamp sites. + = <1%

	Taumatawahana Swamp	Wharau Road Swamp
<i>Coprosma tenuicaulis</i>	–	8
<i>Leptospermum scoparium</i>	–	10
<i>Conyza canadensis</i>	+	+
<i>Crepis capillaris</i>	–	+
<i>Hypochoeris radicata</i>	+	–
<i>Senecio minimus</i>	–	+
<i>Isachne globosa</i>	+	1
<i>Cordyline australis</i>	–	5
<i>Eleocharis acuta</i>	10	55
<i>Phormium tenax</i>	2	–
<i>Typha orientalis</i>	85	20
<i>Gleichenia dicarpa</i>	3	1

Appendix 2 Percentage cover of recorded species at grassland-shrubland sites, (+ = <1%; ⊗ = presence recorded).

	Te Kao	Taumatawhana
<i>Agrostis capillaris</i>	4.9	—
<i>Anagallis arvensis</i>	+	—
<i>Anthoxanthum odoratum</i>	74.1	27.9
<i>Axonopus affinis</i>	10.3	—
<i>Briza minor</i>	—	+
<i>Centella uniflora</i>	⊗	—
<i>Coprosma</i> sp.	—	⊗
<i>Cyathodes junipera</i>	—	⊗
<i>Dactylis glomerata</i>	—	1.0
<i>Gnaphalium subfaculatum</i>	+	—
<i>Hypochaeris radicata</i>	4.3	1.0
<i>Isolepis</i> sp.	2.0	—
<i>Juncus</i> sp.	2.0	3.2
<i>Lepidosperma laterale</i>	—	1.1
<i>Leucopogon fraseri</i>	⊗	—
<i>Lolium</i> sp.	—	+
<i>Lotus suaveolens</i>	+	—
<i>Muehlenbeckia complexa</i>	—	+
<i>Paspalum dilatatum</i>	+	2.0
<i>Pennisetum clandestinum</i>	—	54.3
<i>Phleum pratense</i>	—	1.3
<i>Plantago lanceolata</i>	+	—
<i>Pomaderris phyllicifolia</i>	—	⊗
<i>Pratia</i> sp.	+	—
<i>Prunella vulgaris</i>	⊗	—
<i>Pteridium esculentum</i>	—	7.8
<i>Rumex acetosella</i>	+	—
<i>Sacciolepis indica</i>	+	—
<i>Schoenus maschalinus</i>	⊗	—
<i>Sysyrrinchium iridifolium</i>	+	—