

## **Macrofossils and pollen representing forests of the pre-Taupo volcanic eruption (c. 1850 yr BP) era at Pureora and Benneydale, central North Island, New Zealand**

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Micro- and macrofossil data from the remains of forests overwhelmed and buried at Pureora and Benneydale during the Taupo eruption (c. 1850 conventional radiocarbon yr BP) were compared. Classification of relative abundance data separated the techniques, rather than the locations, because the two primary clusters comprised pollen and litter/wood. This indicates that the pollen:litter/wood within-site comparisons (Pureora and Benneydale are 20 km apart) are not reliable. Plant macrofossils represented mainly local vegetation, while pollen assemblages represented a combination of local and regional vegetation. However, using ranked abundance and presence/absence data, both macrofossils and pollen at Pureora and Benneydale indicated conifer/broadleaved forest, of similar forest type and species composition at each site. This suggests that the forests destroyed by the eruption were typical of mid-altitude west Taupo forests, and that either data set (pollen or macrofossils) would have been adequate for regional forest interpretation.

The representation of c. 1850 yr BP pollen from the known buried forest taxa was generally consistent with trends determined by modern comparisons between pollen and their source vegetation, but with a few exceptions.

A pollen profile from between the Mamaku Tephra (c. 7250 yr BP) and the Taupo Ignimbrite indicated that the Benneydale forest had been markedly different in species dominance compared with the forest that was destroyed during the Taupo eruption. These differences probably reflect changes in drainage, and improvements in climate and/or soil fertility over the middle Holocene.

Keywords: macrofossil, litter, wood, buried forest, classification, Taupo Ignimbrite, Mamaku Tephra, pollen profile

### **INTRODUCTION**

Pollen assemblages from bog and lacustrine sediments are widely used in paleoecological studies for deriving vegetation history and documenting changes in plant species distribution (e.g., McGlone & Topping 1977; Delcourt et al. 1983). Plant macrofossils are used mainly to supplement the pollen data (e.g., Burrows & Russell 1990), because they are usually less frequent and less well preserved than pollen (Molloy & Cox 1972; Birks & Birks 1980). Opportunities to compare the information derived from microfossils of different plant parts are relatively rare.

Abundant and well-preserved leaves, seeds and wood buried together at Pureora and Benneydale during the Taupo eruption c. 1850 yr BP (Froggatt & Lowe 1990) enable a comparison of c. 1850 yr BP pollen assemblages with quantitative and semi-quantitative macrofossil data. The first part of the study investigated forest structure and composition at Pureora and Benneydale from the macrofossils (Clarkson et al. 1988 1992). This second part

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Fig. 1 – View of Pureora buried forest showing logs exposed along a ditch excavated through the wetland. The site is bounded by pine plantations on better-drained terrain. Photograph: H. Hemming, 1985.

examines the relations between the microfossil (pollen) and macrofossil (litter, wood) data sets from the two sites, and attempts to determine how accurately each of these measures taken separately reflects the local vegetation compositions.

In addition, the finding at Benneydale of a tephra layer in peat, 0.6 m below Taupo Ignimbrite, enables the chronology of development of the former forest there to be determined by pollen analysis between known time markers. Preliminary investigation indicated that it was Mamaku Tephra, which was to be confirmed (or otherwise) by radiocarbon dating and compositional analysis.

### STUDY SITES

The buried forest sites at Pureora (37 ha) and Benneydale (1.9 ha) are 20 km apart in the west Taupo region, central North Island, as described in Clarkson et al. (1988, 1992). At both sites, prone trees and intact litter layers, preserved beneath a layer of Taupo Ignimbrite up to 1 m thick, were exposed along ditches dug to drain post-Taupo eruption wetlands (Fig. 1). All the Pureora ditches except one were reflooded in 1985 in order to preserve the forest remains; the Benneydale ditches remain exposed. Both sites are now formally protected: Pureora buried forest is in Pureora Forest Park, which is administered by the Department of Conservation (cf. Clarkson et al. 1988); Benneydale buried forest is under an Open Space Covenant administered by the Queen Elizabeth II National Trust.

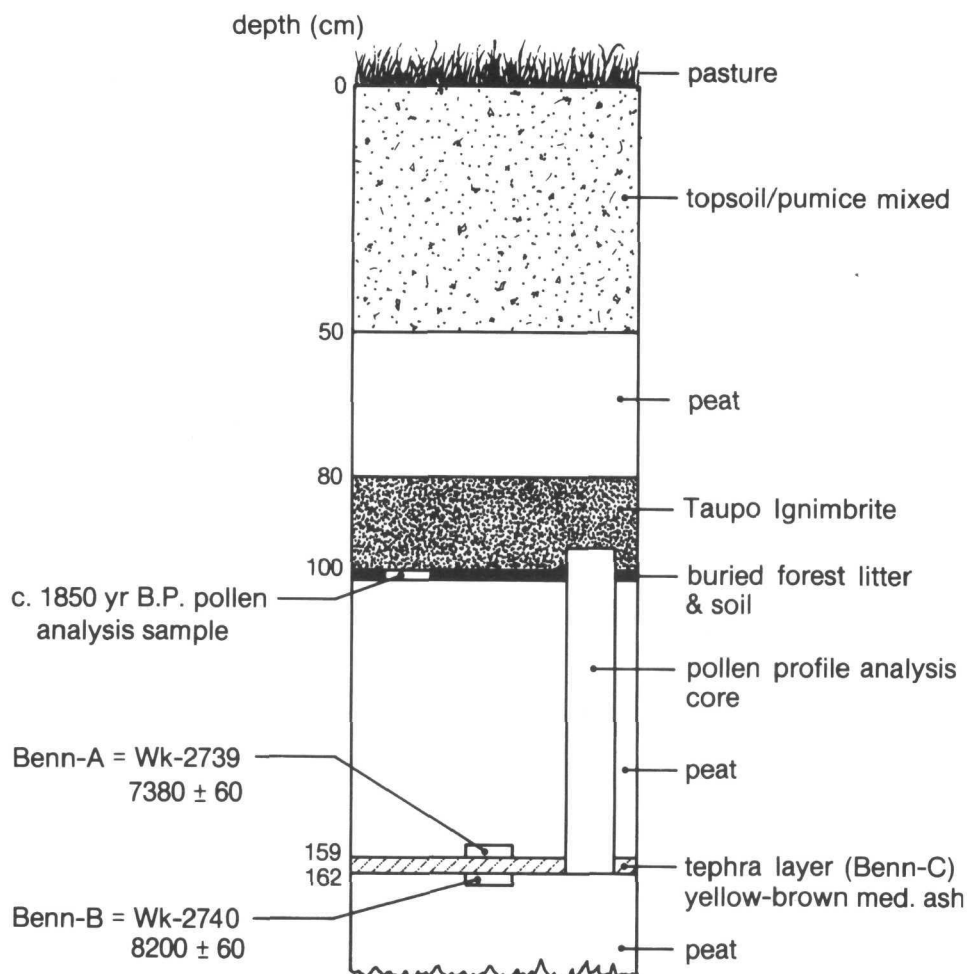


Fig. 2 – Stratigraphic column and sampling sites; eastern end of ditch adjacent Ohirea Road, Benneydale buried forest. Grid reference NZMS 260 (1:50,000 topographic map series) S17 158963.

All except one of the peat and tephra samples for pollen analysis, radiocarbon dating, and tephra composition were collected in Spring, 1992. Macrofossil samples for the forest reconstructions plus one peat sample were obtained between 1984 and 1987 and stored at New Zealand Forest Research Institute, Rotorua, and the former Botany Division, DSIR (now Manaaki Whenua – Landcare Research), Lincoln, respectively.

## METHODS

### Pollen analysis, radiocarbon dating, and tephra correlation

Three buried forest samples of c. 10 ml were collected at intervals c. 5 m apart, along the unflooded Tuarima ditch at the Pureora site. Three similar samples were obtained at Benneydale, from sites c. 5 m apart along the eastern end of the ditch nearest Ohirea Road (a total of six c. 1850 yr BP pollen samples). This ditch was the deepest, and the only place at which an unidentified tephra layer, approximately 3 cm thick and 60 cm below the Taupo Ignimbrite, was accessible. A 10 cm diameter core of the freshly-exposed peat from between, and including, these two tephras was extracted for pollen analysis for interpretation of vegetation changes. A c. 50 ml sample of the unidentified tephra was collected for mineralogical

Table 1 – Electron microprobe analyses\* of glass in the Benn-C tephra at Benneydale and comparisons with other tephra deposits. The analyses are normalised to 100% volatile free.

	Benn-C (This study) <sup>1</sup>	Okataina Volc. Centre <sup>2</sup>	Taupo Volc. Centre <sup>3</sup>	Mamaku Tephra <sup>4</sup>	Unidentified <sup>5</sup>
SiO <sub>2</sub>	78.08 ± 0.26	78.52 ± 0.32	76.90 ± 0.52	78.87 ± 0.50	78.47 ± 0.33
Al <sub>2</sub> O <sub>3</sub>	12.31 ± 0.16	12.32 ± 0.12	12.90 ± 0.25	12.05 ± 0.17	12.33 ± 0.17
TiO <sub>2</sub>	0.16 ± 0.04	0.11 ± 0.04	0.12 ± 0.04	0.12 ± 0.02	0.11 ± 0.04
FeO <sup>†</sup>	0.97 ± 0.07	0.90 ± 0.08	1.66 ± 0.15	0.87 ± 0.07	0.90 ± 0.08
MgO	0.14 ± 0.03	0.11 ± 0.02	0.17 ± 0.04	0.10 ± 0.02	0.11 ± 0.02
CaO	0.92 ± 0.08	0.78 ± 0.07	1.26 ± 0.13	0.69 ± 0.10	0.69 ± 0.08
Na <sub>2</sub> O	3.93 ± 0.09	3.55 ± 0.22	3.75 ± 0.25	3.80 ± 0.20	3.61 ± 0.15
K <sub>2</sub> O	3.38 ± 0.16	3.59 ± 0.26	3.04 ± 0.20	3.38 ± 0.43	3.66 ± 0.10
Cl	nd	0.12 ± 0.02	0.12 ± 0.02	0.12 ± 0.02	0.12 ± 0.01
Water <sup>‡</sup>	2.11 ± 1.12	nd	nd	1.13 ± 1.40	1.65 ± 2.38
n	10	111	76	14	10

\* Analyses made using a 8 nm beam current at 15 kV and defocussed to 10 µm on a Jeol JXA-733 Superprobe (see Froggatt 1983). Values are means of n analyses ± 1 standard deviation.

† Total Fe as FeO

‡ Difference between original analytical total and 100

n Number of analyses in mean

nd Not determined or not reported

1 Correlated with Mamaku Tephra; analysed by Dr P.C. Froggatt, Victoria University of Wellington

2 Mean analyses of Okataina-derived tephtras erupted since c. 18,000 yrs ago (except Rotorua Tephra) (from Lowe 1988b)

3 Mean analyses of Taupo-derived tephtras erupted since c. 10,000 yrs ago (from Lowe 1988b)

4 From Lowe (1988a)

5 Unidentified c. 8000 year-old tephra of uncertain stratigraphic status found in some Waikato lakes and bogs (D.J. Lowe, unpublished data)

and chemical compositional analysis (labelled Benn-C), plus one c. 500 ml peat sample (3 cm-thick slices) from each of the upper and lower contact of the tephra, for radiocarbon dating (labelled Benn-A and Benn-B; Fig. 2).

Pollen samples were prepared following the standard techniques of initial heating in potassium hydroxide, sieving, digestion in hydrofluoric acid, treatment with a mild chlorine bleach, then acetolysis (Moore & Webb 1978). Samples were counted until at least 400 grains (300 for the 1987 sample) of dryland plants were recorded. Then the slide was scanned and any taxa not recorded in the main count were noted.

A chronology of the samples was determined using radiocarbon dating and tephrochronology. The two samples for radiocarbon dating (Benn-A and Benn-B; Fig. 2) were prepared and assayed by the University of Waikato Radiocarbon Dating Laboratory, using 'Quantulus' liquid scintillation spectrometry (Lowe & Hogg 1992).

The tephra sample (Benn-C) was washed and cleaned using an ultrasonic probe and the 63 to 250 µm size fraction separated by sieving. This fraction was split, using a Frantz electromagnetic separator, into magnetic ('heavy') and non-magnetic ('light') fractions. The mineralogy of both fractions was determined with a polarising microscope; the non-magnetic fraction was mounted in araldite, polished, and carbon coated, and the major element composition of constituent glass shards analysed by electron microprobe (EMP) at Victoria University of Wellington (Table 1).

## Macrofossil/pollen comparisons

We systematically collected 48 four-litre litter samples from Pureora and 51 from Benneydale, plus 187 wood discs from Pureora and 30 from Benneydale. The data are detailed in Clarkson et al. (1988, 1992). Percentage litter cover for each species was defined as:

$$\text{Cover species } a \text{ at site } y = \frac{\text{sum of cover score} * \% \text{ midpoints for species } a \text{ at site } y \times 100\%}{\text{total cover score } \% \text{ midpoints for all species at site } y}$$

\* Cover score scale : 1=<1%; 2=1–5%; 3=5–25%; 4=25–50%; 6=75–100%

Midpoints : 1=0.5%; 2=3%; 3=15%; 4=37.5%; 5=62.5%; 6=87.5%.

and calculated for each site. Species occurrences from wood samples were expressed as percentages of the total occurrence at Pureora and again at Benneydale. Pollen percentages were calculated from the standard pollen sum, which includes all dryland plants except Pteridophytes.

Comparison of relative abundance data from pollen, litter, and wood by numerical analysis techniques was restricted to tree species (i.e., those potentially over 5 m tall in the Pureora-Benneydale district). Correlation tests on stand composition and litter representation in extant forest at Pureora indicated that only the canopy and subcanopy tree species tested were significantly correlated with corresponding litter layer. *Weinmannia racemosa* had a 1:1 cover class representation, and *Dacrydium cupressinum*, *Phyllocladus trichomanoides*, and *Podocarpus hallii* were under-represented in the litter by one cover class (Clarkson et al. 1988). In addition, trees were the only species well represented in all three data sets of leaf litter macrofossils, wood macrofossils, and pollen. Pollen and leaf macrofossil percentage abundance data were reworked to give tree species' relative abundances.

To investigate similarities between the three measures (pollen, macrofossils, and wood for each of Pureora and Benneydale), we used a cluster analysis based on the Canberra metric association measure and the UPGMA sorting strategy (Clifford & Stephenson 1975), and available as the PATN software package (Belbin 1989). We also ran a DECORANA (Hill 1979) ordination analysis on the data.

The predicted composition of the buried forest (Clarkson et al. 1988, 1992) incorporated all macrofossil data, i.e., leaves, seeds, and wood, and is assumed to be reasonably accurate, at least for tree species. This conclusion is based on the litter:tree cover analyses already described, and on the few published investigations relating modern plant macrofossil assemblages to the composition of nearby vegetation. In a detailed study, Dunwiddie (1987) showed that there is a virtual 1:1 relationship between coniferous forest tree basal area in USA, and potential macrofossils in lake sediments, whereas pollen percentages for most taxa were far from a 1:1 representation. He found that only 22% of the total local vascular flora was present as potential macrofossils, but 85% of tree species. Similar results were given by contemporary forest:litter composition tests at Pureora, where on average 28% of the total vascular flora, and 83% of the tree species, were present as litter (n = 10 plots; B.R. Clarkson unpublished, details in Clarkson et al. 1988). Studies of New Zealand lake/swamp sediments showed that 16% and 25% (McQueen 1969), and 18%, 32%, and 48% (Drake & Burrows 1980, as quoted in Dunwiddie 1987) of the local vascular flora were represented as potential macrofossils.

## RESULTS

### Chronology

The age of the Taupo Ignimbrite at 0.80–1.00 m depth (Fig. 2) is well defined by multiple radiocarbon samples with an error-weighted mean of  $1850 \pm 10$  yr BP\* (Froggatt & Lowe 1990; Wilson 1993), which we adopt here. It corresponds to a calendar (calibrated) date in the range AD 138–230 (Froggatt & Lowe 1990), consistent with possible calendar dates of

\* Ages reported and discussed in the text are conventional radiocarbon ages based on the Libby (old) half life of 5568 years (Hogg et al. 1987).

AD 177 (1 standard deviation range AD 166–195), obtained by dendrochronology (Palmer et al. 1988; Froggatt & Lowe 1990), and AD 181 ± 2 yr obtained from interpretation of sulphate concentrations in the GISP2 Greenland ice core (Zielinski et al. 1994).

The radiocarbon ages obtained above and below the tephra layer at 1.59–1.62 m depth are given in Fig. 2. Wk-2739 (7380 ± 60 yr BP), which provides a putative age for our earliest pollen sample, is about 800 years younger than Wk-2740 (8200 ± 60 yr BP) even though it might be expected to be essentially the same. Such a discrepancy may reflect variation in the rate of peat accumulation, or possibly minor contamination (e.g., see Lowe & Hogg 1986).

Mineralogical and chemical analyses of the tephra layer were therefore undertaken to try to verify, using tephrochronology, which of the two dates would be more accurate for our interpretation. The non-magnetic fraction of the tephra is dominated by clear or yellowish, vesicular volcanic glass shards with a small proportion of felsic minerals including plagioclase and quartz. The magnetic fraction comprises mainly orthopyroxene (hypersthene) with lesser amounts of calcic hornblende and Fe-Ti oxides (titanomagnetite); sparse amounts of pinkish-brown glass and zircon were also identified, and a few grains of ?cummingtonite. Such an assemblage of ferromagnesian minerals is consistent with a eruptive source in the Okataina Volcanic Centre (Lowe 1988a, 1988b; Froggatt & Lowe 1990).

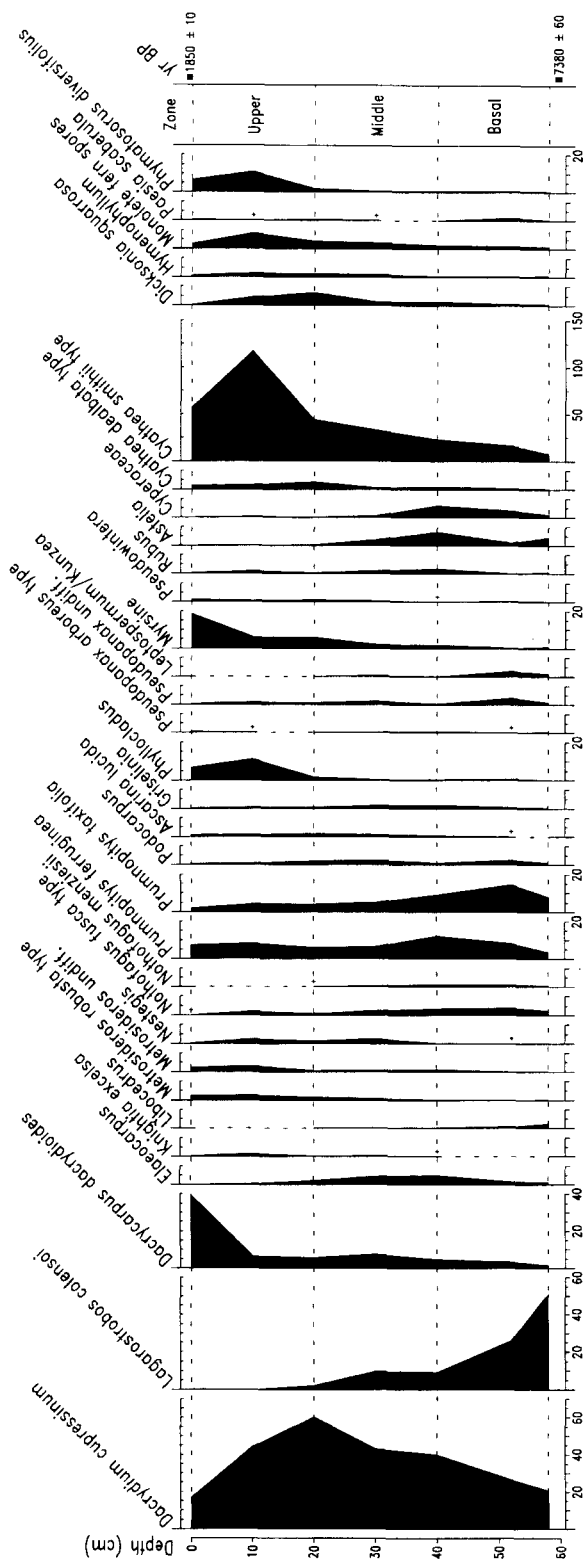
Analyses by EMP of the glass shards in the non-magnetic fraction support such a source (Table 1). The Mamaku Tephra, erupted from the Okataina Volcanic Centre, is the only eruptive from this source documented for the period from c. 7000–8000 years ago, and has an error-weighted mean age of 7250 ± 20 yr BP (Froggatt & Lowe 1990). (An earlier eruptive, Rotoma Tephra, aged 8530 ± 10 yr BP, is characterised by a dominance of cummingtonite and is therefore an improbable correlative.) The major element glass chemistry of the Benn-C tephra layer closely matches that of Mamaku Tephra as recorded in the Waikato region, although CaO is slightly higher in Benn-C (Table 1; Lowe 1988a, 1988b). However, several previous studies report sporadic records of another distal tephra layer in the Waikato region aged c. 8000 years old (Lowe 1988a; de Lange & Lowe 1990). It also has an Okataina-type glass chemistry (Table 1) similar to that of Benn-C. In the absence of any known Okataina eruptives of this age, however, Lowe (1988a) and de Lange & Lowe (1990) suggested that this layer was probably reworked and therefore of limited stratigraphic value. Thus, although we cannot rule out the possibility that the Benn-C tephra may represent a c. 8000 year-old eruptive, we currently favour correlation with the 7250 year-old Mamaku Tephra. Consequently, we have assigned an age of c. 7300 years to the earliest pollen sample in the succession analysed. Ages of the pollen samples between the Mamaku Tephra and Taupo Ignimbrite were calculated from sedimentation rates (assuming constant accumulation).

### **Vegetation changes from c. 7300 yr BP to c. 1850 yr BP, Benneydale**

The Benneydale pollen profile diagram (Fig. 3) depicts three zones: an early (=basal) zone of abundant *Lagarostrobos colensoi*, a middle zone of *Dacrydium cupressinum* dominance and of *L. colensoi* decline, and a late (=upper) zone in which *D. cupressinum* levels decline and *Dacrycarpus dacrydioides* levels rise sharply. In this last zone, which leads up to the Taupo eruption c. 1850 yr BP, *Myrsine*, *Phyllocladus*, and *Metrosideros* increase markedly: tree ferns, especially *Cyathea smithii*, are abundant, although their levels start to drop from a peak perhaps 1000 years before the Taupo eruption; *Prumnopitys ferruginea* and *Prumnopitys taxifolia* levels are also high. *P. ferruginea* levels are high throughout the profile, whereas *P. taxifolia* has gradually declined from an early post-deposition (c. 7300 yr BP) peak.

### **Comparison of c. 1850 yr BP pollen and macrofossil litter; all taxa**

Table 2 shows the relative abundances of taxa as represented by c. 1850 yr BP pollen and litter at Pureora and Benneydale buried forests. At both locations, more taxa are represented in the pollen samples, although macrofossils provide greater taxonomic resolution, e.g., *Metrosideros*, *Nestegis*. Composition of vegetation within each site as predicted by the



Analysis: MSM 1993

separate data sets is similar, in that most of the taxa are represented as both pollen and litter. But abundances can vary greatly, e.g., for *Dacrycarpus dacrydioides* and *Cyathea smithii*.

Scatter diagrams (Fig. 4) for pollen (x axis) versus litter (y axis) percentages of the dominant tree taxa recorded at Pureora and Benneydale indicate the degree of representation relative to these two measures. Points distributed along the  $y = x$  line indicate a 1:1 representation, which is rare: only *Nestegis* at Pureora shows this pattern, although abundances there are very low. Taxa having a higher macrofossil representation at both sites are *Dacrydium cupressinum* (particularly at Benneydale) and *Pseudowintera*, whereas *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, and *Phyllocladus* are better represented as pollen. The remaining five taxa are inconsistent, having higher litter levels at one site and higher pollen levels at the other. *Dacrycarpus dacrydioides*, for example, has much higher pollen representation at Benneydale, yet has slightly higher macrofossil representation at Pureora.

**Comparison of c. 1850 yr BP pollen, macrofossil litter and wood; tree taxa only**

Table 3 ranks the tree taxa at Pureora and Benneydale for pollen, litter and wood according to abundance. At Pureora, *D. cupressinum* is ranked first and *Phyllocladus* second for all three measures, with *Pseudowintera* the top ranked understorey small tree species (fifth in pollen, third in litter, ninth in wood). Rankings for Benneydale are more variable but overall *D. cupressinum* is the top ranked tree (second in pollen, first in litter, first in wood). Other highly ranked trees are *Metrosideros robusta* (seventh in pollen, second in litter, third

Fig. 3 – Pollen diagram, Benneydale buried forest site. Depths are from the Taupo Ignimbrite, c. 1850 yr BP. The earliest pollen samples are c. 7300 years old. Sampling interval is 10 cm. Pollen sum consists of all terrestrial taxa, excluding ferns. +=trace.

Table 2 – Pureora and Benneydale buried forests c. 1850 yr BP pollen and litter relative abundances; all taxa. Percentage pollen sums are based on terrestrial pollen types, excluding ferns. Data for each pollen sample are in Appendix 1.

Pollen taxa	Macrofossil taxa	Pureora		Benneydale	
		pollen	<i>litter</i>	pollen	<i>litter</i>
Agathis australis		+			
Alectryon excelsus		0.1		0.2	
Dacrydium cupressinum	<i>Dacrydium cupressinum</i>	36.3	41	16.2	54
Dacrycarpus dacrydioides	<i>Dacrycarpus dacrydioides</i>	0.9	4	37.6	4
Elaeocarpus	<i>Elaeocarpus dentatus</i> #	0.1	+		+
	<i>Elaeocarpus hookerianus</i>		+		+
Knightia excelsa	<i>Knightia excelsa</i>	0.1		1.2	2
Metrosideros umbellata type	<i>Metrosideros diffusa</i>	0.5	1	2.9	2
	<i>Metrosideros fulgens</i>				+
	<i>Metrosideros perforata</i>				+
Metrosideros robusta type	<i>Metrosideros robusta</i>	0.6	+	3.3	15
Nestegis	<i>Nestegis cunninghamii</i>	1.0		0.2	+
	<i>Nestegis lanceolata</i>				+
	<i>Nestegis montana</i>		1		+
Nothofagus fusca type		1.9		1.0	
Prumnopitys ferruginea	<i>Prumnopitys ferruginea</i>	11.3	1	9.5	2
Prumnopitys taxifolia	<i>Prumnopitys taxifolia</i>	12.4	1	3.6	+
Podocarpus	<i>Podocarpus totara</i>	1.2	+	0.7	+
Weinmannia		0.1			
Aristolelia		0.1		0.1	
Ascarina lucida		+		+	
Carpodetus serratus				+	
Syzygium maire				0.1	
Dodonaea viscosa				+	
Griselinia		0.5		1.1	
Halocarpus	<i>Halocarpus bidwillii</i>	0.1	+		
Neomyrtus type	<i>Neomyrtus pedunculata</i>	0.6	1		+
Hoheria				+	
Plagianthus				0.2	
Phyllocladus	<i>Phyllocladus trichomanoides</i>	26.1	17	4.2	2
Pittosporum		0.1			
Pseudopanax undiff.	<i>Pseudopanax anomalus</i>	+	+	0.5	
Pseudopanax arboreus				0.2	
Pseudopanax colensoi type	<i>Pseudopanax crassifolius</i>	0.3	2	0.1	
Schefflera digitata		0.1		+	
Coprosma	<i>Coprosma</i> sp. (t) of Eagle				
	1982	0.4	+	0.1	
Leptospermum		0.2		+	
Muehlenbeckia				0.4	
Myrsine	<i>Myrsine salicina</i>	1.8	5	14.3	7
Pseudowintera	<i>Pseudowintera axillaris</i>	2.7	+	1.0	3
	<i>Pseudowintera colorata</i>		9		
Dactylanthus taylori				+	
Rubus	<i>Rubus australis</i>	0.1	+	0.4	+
Tupeia antarctica		0.1			
Astelia	<i>Astelia grandis</i>		6	0.1	
Poaceae	<i>Microlaena avenacea</i> #	0.2	+		



Table 2 – contd

Pollen taxa	Macrofossil taxa	Pureora		Benneydale	
		pollen	litter	pollen	litter
Others	<i>Cordyline</i> sp.#		+		
	<i>Coriaria</i> sp. ( <i>arborea</i> ?)		+		
	<i>Dracophyllum</i> sp. ( <i>subulatum</i> ?)				+
	<i>Freycinetia baueriana</i>				
	ssp. <i>banksii</i>		1		
	<i>Libocedrus bidwillii</i> *		+		
Cyperaceae	<i>Libocedrus</i> sp. ( <i>bidwillii</i> ?)				+
	<i>Gahnia xanthocarpa</i>	0.1	4	0.1	
	<i>Uncinia</i> sp. ( <i>zotovii</i> ?)		+		1
Empodisma		+			
Lobeliaceae		+			
Cyathea medullaris				+	
Cyathea dealbata type		1.3		2.2	
Cyathea smithii type	<i>Cyathea smithii</i>	17.2	+	74.3	+
	<i>Cyathea colensoi</i>		+		
Dicksonia fibrosa		0.1			
Dicksonia squarrosa	<i>Dicksonia squarrosa</i>	0.1	+	0.6	1
Dicksonia lanata		+		+	
Blechnum capense type	<i>Blechnum</i> sp. 1 of Brownsey and Smith-Dodsworth (1989)		+	+	
Gleichenia	<i>Sticherus cunninghamii</i>	0.7	+		
Hymenophyllum type	<i>Hymenophyllum demissum</i>	0.8	+	0.7	+
	<i>Hymenophyllum</i> sp.		+		
Lycopodium varium		+		0.2	
Lygodium articulatum		+			
Monolete fern spores undiff.		2.1		2.9	
Phymatosorus diversifolius	<i>Phymatosorus diversifolius</i>	0.6	+	0.4	
Leptopteris	<i>Leptopteris superba</i>	0.2	1	0.1	
Tmesipteris tannensis		+			
Others	<i>Blechnum discolor</i>			2	5
	? <i>Blechnum</i> sp.			+	
	<i>Ctenopteris heterophylla</i>				+
Unidentified		0.7	+		+
Totals (%) for groups					
ferns		23.1		81.6	
herbs		0.2		0.1	
shrubs and small trees		3.5		1.9	
trees		96.3		98.0	
unknown and undetermined		0.7		0.0	
wetland		0.1		0.1	
Terrestrial pollen sum		463		428	
n		3	48	3	51

# only seed recorded

\* only wood recorded

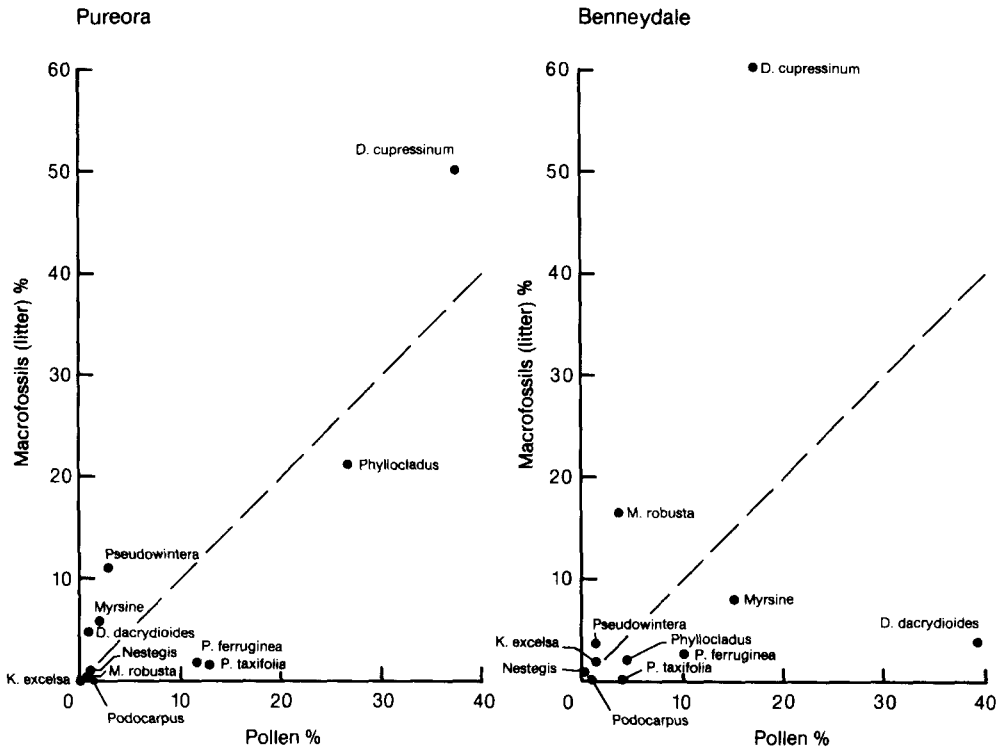


Fig. 4 – Comparisons of relative abundance of c. 1850 yr BP pollen and macrofossil (litter) representation for the dominant taxa at Pureora and Benneydale. Percentages for pollen (mean percentage) and litter are from Appendix 2.

in wood), *P. ferruginea* (fourth in pollen, sixth in litter, second in wood), and *D. dacrydioides* (first in pollen, fourth in litter, unrecorded here as wood; but was one of five species identified from Benneydale buried wood by Pullar & Patel 1972). *Myrsine* (third in pollen, third in litter, unrecorded as wood) is the top ranked understorey small tree.

Consistent differences between Pureora and Benneydale are generally reflected by all measures (Appendix 2, Table 3). Although *D. cupressinum* is the dominant at both sites, Pureora has more *Phyllocladus*, *P. taxifolia*, and *Pseudowintera*, and Benneydale has more *D. dacrydioides*, *Metrosideros robusta*, *Knightia excelsa*, and *Myrsine*.

Classification on relative abundance data separates the types of fossil material rather than the locations (Fig. 5): the two primary clusters comprise pollen (cluster A) and litter/wood (cluster B). Within the pollen cluster there is a marked difference between the locations, and Pureora pollen measurements vary less than those for Benneydale. In the litter/wood cluster the Pureora and Benneydale litters are very similar, but the Pureora wood is more similar to both litters than to the Benneydale wood. This is probably because the Benneydale wood sample size is too small ( $n = 30$  compared with  $n = 187$  at Pureora) to adequately represent tree composition there.

The DCA ordination (Fig. 6) clumps all Pureora measurements together at the start of axis 1, while the Benneydale ones are spread out along the rest of the axis. This indicates that there is greater variability within the Benneydale data than within the Pureora data: the Pureora site was better preserved and larger than the Benneydale site. Axis 2 separates the kinds of measurement within both locations, and there is some overlap between the two sites.

Table 3 Tree taxa ranked abundance for pollen, litter and wood.

Pureora			Benneydale		
Pollen	Litter	Wood	Pollen	Litter	Wood
1 <i>Dacrydium cupressinum</i>	1 <i>Dacrydium cupressinum</i>	1 <i>Dacrydium cupressinum</i>	1 <i>Dacrycarpus dacrydioides</i>	1 <i>Dacrydium cupressinum</i>	1 <i>Dacrydium cupressinum</i>
2 <i>Phyllocladus</i> <sup>1</sup>	2 <i>Phyllocladus</i>	2 <i>Phyllocladus</i>	2 <i>Dacrydium cupressinum</i>	2 <i>Metrosideros robusta</i> type	2 <i>Prumnopitys ferruginea</i>
3 <i>Prumnopitys taxifolia</i>	3 <i>Pseudowintera</i>	3 <i>Prumnopitys taxifolia</i>	3 <i>Myrsine</i>	3 <i>Myrsine</i>	3 <i>Metrosideros robusta</i> type
4 <i>Prumnopitys ferruginea</i>	4 <i>Myrsine</i>	4 <i>Dacrycarpus dacrydioides</i>	4 <i>Prumnopitys ferruginea</i>	4 <i>Dacrycarpus dacrydioides</i>	4= <i>Podocarpus</i>
5 <i>Pseudowintera</i> <sup>2</sup>	5 <i>Dacrycarpus dacrydioides</i>	5= <i>Podocarpus</i>	5 <i>Phyllocladus</i>	5 <i>Pseudowintera</i>	4= <i>Nestegis</i>
6 <i>Nothofagus fusca</i> type	6 <i>Pseudopanax colensoi</i> type	5= <i>Prumnopitys ferruginea</i>	6 <i>Prumnopitys taxifolia</i>	6 <i>Prumnopitys ferruginea</i>	6= <i>Knightia excelsa</i>
7 <i>Myrsine</i> <sup>3</sup>	7 <i>Prumnopitys ferruginea</i>	7= <i>Myrsine</i>	7 <i>Metrosideros robusta</i> type	7 <i>Phyllocladus</i>	6= <i>Libocedrus</i>
8 <i>Podocarpus</i> <sup>4</sup>	8 <i>Prumnopitys taxifolia</i>	7= <i>Nestegis</i>	8 <i>Knightia excelsa</i>	8 <i>Knightia excelsa</i>	6= <i>Phyllocladus</i>
9 <i>Nestegis</i> <sup>5</sup>	9 <i>Nestegis</i>	9 <i>Pseudowintera</i>	9 <i>Griselinia</i>	9 <i>Nestegis</i>	
10 <i>Dacrycarpus dacrydioides</i>	10 <i>Metrosideros robusta</i> type	10= <i>Metrosideros robusta</i> type	10 <i>Pseudowintera</i>	10 <i>Prumnopitys taxifolia</i>	
11 <i>Metrosideros robusta</i> type <sup>6</sup>	11 <i>Elaeocarpus</i>	10= <i>Libocedrus</i> <sup>10</sup>	11 <i>Nothofagus fusca</i> type	11 <i>Podocarpus</i>	
12 <i>Griselinia</i>	12 <i>Halocarpus</i>		12 <i>Podocarpus</i>		
13 <i>Pseudopanax colensoi</i> type <sup>7</sup>	13 <i>Podocarpus</i>		13 <i>Pseudopanax undiff.</i>		
14 <i>Elaeocarpus</i> <sup>8</sup>			14 <i>Pseudopanax arboreus</i>		
15= <i>Alectryon excelsus</i>			15= <i>Nestegis</i>		
15= <i>Aristotelia</i>			15= <i>Plagianthus</i>		
15= <i>Halocarpus</i> <sup>9</sup>			17 <i>Syzygium maire</i>		
15= <i>Knightia excelsa</i>			18 <i>Alectryon excelsus</i>		
15= <i>Pittosporum</i>			19 <i>Pseudopanax colensoi</i> type		
15= <i>Schefflera digitata</i>			20 <i>Aristotelia</i>		
15= <i>Weinmannia</i>			21= <i>Ascarina lucida</i>		
22= <i>Agathis australis</i>			21= <i>Hoheria</i>		
22= <i>Ascarina lucida</i>			21= <i>Schefflera digitata</i>		
22= <i>Pseudopanax undiff.</i>			21= <i>Dodonaea viscosa</i>		
			21= <i>Carpodetus serratus</i>		

For litter and wood data

- |   |   |
|---|---|
| 1 <i>Phyllocladus trichomanoides</i>  | 6 <i>Metrosideros robusta</i>   |
| 2 <i>Pseudowintera axillaris</i> , <i>P. colorata</i> (only at Pureora)                       | 7 <i>Pseudopanax crassifolius</i>   |
| 3 <i>Myrsine salicina</i>   | 8 <i>Elaeocarpus hookerianus</i>  |
| 4 <i>Podocarpus totara</i>  | 9 <i>Halocarpus bidwillii</i>   |
| 5 <i>Nestegis cunninghamii</i> (only at Benneydale), <i>N. lanceolata</i> , <i>N. montana</i> | 10 <i>Libocedrus bidwillii</i> at Pureora, <i>L. ?bidwillii</i> at Benneydale |

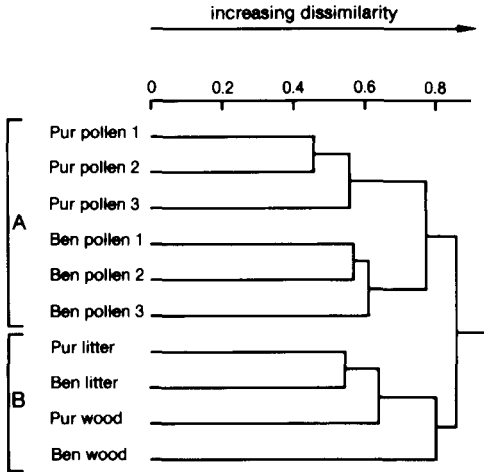


Fig. 5 – Phenogram of dissimilarity among c. 1850 yr BP macrofossil and pollen measures at Benneydale and Pureora using tree taxa percentage abundance (Appendix 2). Ben=Benneydale; Pur=Pureora.

## DISCUSSION

### Vegetation changes between c. 7300 yr BP and c. 1850 yr BP

The pollen trends depicted at Benneydale do not parallel those reported for the same time span in adjacent regions of Tongariro (McGlone & Topping 1977), Waikato (Newnham et al. 1989), or Taranaki (McGlone 1980). Similar rises and falls in *Lagarostrobos colensoi* levels were recorded at Tongariro and Taranaki, but the peaks occurred some 3000 years later, at around 4000 yr BP; there was also a small peak in the Waikato at that time. *Dacrydium cupressinum* peaks at Benneydale are similar to, but perhaps 2000 years later than, those in the Waikato pollen profiles. Rises and falls in *Prumnopitys taxifolia* and *Metrosideros robusta* are generally asynchronous. In the Tongariro pollen profiles, *D. cupressinum* rises and falls are asynchronous with those at Benneydale, and trends for other taxa represented are dissimilar. The abrupt increase in *Dacrycarpus dacrydioides* levels before the Taupo eruption is not mirrored in profiles from Waikato or Tongariro, nor in a shorter one from Rotorua (McGlone 1983).

These results suggest that the profile from Benneydale represents local (on-site) and extra-local (within c. 300 m of site) sources rather than regional sources (more than c. 300 m from site; Jacobson & Bradshaw 1981). Boggy conditions probably prevailed immediately after tephra deposition from the 7250 yr BP eruption, which favoured *Lagarostrobos colensoi* and, to a lesser extent, *Libocedrus* (probably *L. bidwillii*). The Benneydale buried forest site is relatively flat and occupies a small saddle perched several metres above a large area of alluvial terraces associated with a tributary of the Mangapehi Stream, so there was ample poorly-drained habitat close by. The pollen sequence of initial dominance by *L. colensoi*, then by *D. cupressinum*, and lastly by tree ferns and *D. dacrydioides*, probably indicates changes in drainage as well as improvements in climate, and/or soil fertility (species fertility/climate relationships within mires are discussed in Dobson 1979). There is some evidence that the pre-Taupo eruption climate was warmer and wetter than the present in the Tongariro region (McGlone & Topping 1977), at Pureora (Clarkson et al. 1988), and in the Rotorua district (McGlone 1978).

### Comparison of c. 1850 yr BP pollen and macrofossil data

The classification shows that the individual data sets (pollen, litter, wood) are more similar to each other than are the locations (Pureora, Benneydale). This indicates that the data derived

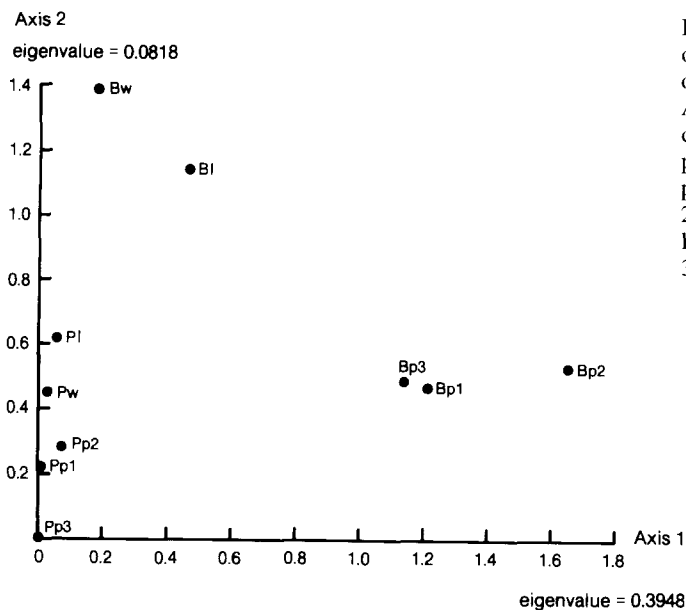


Fig. 6 – A two-dimensional ordination of the first two axes of a Detrended Correspondence Analysis ordination of the c. 1850 yr BP macrofossil and pollen measures using tree taxa percentage abundance (Appendix 2). B=Benneydale; P=Pureora; l=litter; p=pollen; w=wood; 1, 2, 3=sample number.

from the fossil material (pollen, litter/wood) are too dissimilar for reliable extrapolation from one data set to another within each site.

Rank abundance and presence/absence data, however, show that all plant subfossil samples exhibit differences between Pureora and Benneydale, and each clearly reflects the different nature of the sites. Species rankings and compositions derived from the individual measures agree on the forest type at each site. This is perhaps surprising considering the characteristically different ways in which pollen and macrofossils are dispersed and preserved (see Ogden et al. 1993).

### Representation of buried forest taxa in the c. 1850 yr BP pollen assemblages and interpretation of the regional vegetation pattern

Pollen representation in percentage terms is affected by several features of pollen grain structure, presentation and the parent plant. Pollen adapted to dispersal by animal, range in size from very small (<10  $\mu\text{m}$ ) to large (>150  $\mu\text{m}$ ), often have projections, and may have a sticky coating. There is no consistent trend in the amount of animal-dispersed pollen produced by any one species. It can range from only a few grains per flower (e.g., in *Beilschmiedia*) to large amounts per flower (e.g., in *Leptospermum scoparium*). Animal-dispersed pollen tends to be retained in the anther after dehiscence, and in many plants it drops to the ground when the flowers abscise if it has not been removed by animals. Wind-pollinated plants tend to have smooth, non-sticky pollen of intermediate size (20–100  $\mu\text{m}$ ), which is produced in great abundance, and is shed almost immediately the anther opens. Tall plants that form part of the canopy tend to have better-dispersed pollen than understorey or low growing plants, because the pollen is launched into turbulent air and can travel a greater distance before falling to the ground.

Studies in New Zealand on the representation of pollen in relation to source vegetation (summarised in Macphail & McQueen 1983; McGlone 1988; Bussell 1988) and observations on flower structure and pollen presentation, have generally confirmed the importance of these factors. Taxa can be placed into several groups according to their dispersal characteristics, as follows.

- 1 Taxa prominent in long-distance pollen rain – i.e., pollen that forms a normal and substantial part of the pollen content of the atmosphere above the vegetation cover – usually comes from wind-pollinated plants that make up the main canopy. Included in this group are the beeches, conifers, *Coprosma*, *Ascarina*, *Dodonaea*, tree ferns, bracken (*Pteridium esculentum*), grasses and sedges. However, representation in the long-distance pollen rain varies according to canopy height and pollen production. Generally, only a very small proportion of the abundant pollen produced by these plants reaches the long-distance pollen rain, and the rest (most of it) drops to the ground within a few hundred metres of the source plants. Hence, these plants are often over-represented close to the source vegetation
- 2 Some animal-pollinated taxa have high pollen production but extremely local pollen dispersion, and are well-represented only when samples are collected close to the source vegetation because the pollen is generally dispersed as part of the abscised flower (e.g., *Metrosideros*, *Weinmannia*, *Elaeocarpus*, *Leptospermum*).
- 3 A third group comprises animal-pollinated taxa which have low pollen production and are never well represented even in samples collected under their canopy (e.g., *Knightia excelsa*, *Nestegis*, *Pseudowintera*).
- 4 Some taxa cannot be easily placed in any category. For example, wind-pollinated *Dacrycarpus dacrydioides* has been reported as being both under-represented (Pocknall 1978; Macphail & McQueen 1983) and over-represented, because it is capable of long-distance dispersal (Bussell 1988). It is one of the tallest trees in the New Zealand flora, and is wind pollinated. Some individuals therefore reach situations from which they can get at least some of their pollen relatively high into the atmosphere. However, the pollen grains are large (larger than any other wind-pollinated tree with the exception of *Prumnopitys ferruginea*; Pocknall 1981) and therefore drop more rapidly and travel a shorter distance.

This study shows that the representation of c. 1850 yr BP pollens from buried forest taxa generally confirms the modern relationship between pollen:source vegetation, with a few notable exceptions (Table 4). For example, *Dacrydium cupressinum*, the dominant tree in the Pureora and Benneydale buried forests, was under-represented by pollen. It may have been even more abundant (in terms of relative cover) than the litter and wood samples indicate (Appendix 2) because of the slight under-representation in contemporary forests of *D. cupressinum* litter compared with canopy cover (Clarkson et al. 1988; buried forest wood sample basal areas could not be calculated, but 72% of logs more than 50 cm diameter were *D. cupressinum*). Pollen percentages of *Phyllocladus* (*P. trichomanoides* in macrofossils), although slightly over-represented compared with macrofossil litter, probably reflect the species' pre-Taupo eruption abundance fairly closely considering its slightly lower than expected litter production in contemporary forests. *Metrosideros (robusta)* and, to a lesser extent, *Elaeocarpus (hookerianus)* are under-represented as pollen even though sources were on-site. The extreme over-representation of pollen of *Dacrycarpus dacrydioides* at Benneydale supports McGlone's (1988) suggestion that it has abundant pollen but limited dispersal: a single very large tree, growing only a few metres from and no doubt overtopping the pollen

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Table 4 – On-site representation of tree taxa in c. 1850 yr BP pollen assemblages; Pureora and Benneydale buried forests.

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**1 Over-represented as pollen**

a Presumed absent from buried forests

*Nothofagus fusca* – type

*Griselinia*

*Alectryon excelsus*

*Syzygium maire*

*Plagianthus*

*Weinmannia racemosa*

b Present in buried forests

*Prumnopitys taxifolia*

*Prumnopitys ferruginea*

*Phyllocladus*

**2 Under-represented as pollen**

*Dacrydium cupressinum*

*Metrosideros robusta* type

*Pseudowintera*

*Nestegis*

*Knightia excelsa*

*Elaeocarpus*

**3 Inconsistent representation**

*Dacrycarpus dacrydioides*

*Myrsine*

---

collection sites, probably accounts for the high levels in our samples. *Myrsine*, cited as having low pollen production, has higher macrofossil (as *M. salicina*) representation at Pureora, yet has higher pollen representation at Benneydale.

Pollens of taxa that were not recorded in the buried forests were most likely to have been derived from extra-local and regional sources. *Plagianthus* (probably *P. regius*), *Hoheria*, and *Syzygium maire* probably grew on the alluvial terraces below the Benneydale site, and *Alectryon excelsus* on the adjoining hills. *Weinmannia* (probably *W. racemosa*) was likely to have been present on flattish terrain surrounding the Pureora site, and *Griselinia* (probably *G. littoralis*) was a likely component of the extra-local flora at both sites.

Interpretation of the regional vegetation pattern of the Pureora-Benneydale district is further enhanced by the pollen data, particularly with respect to non-tree species (see Table 2) which are usually severely under-represented in the litter (Clarkson et al. 1988). We can assume from the pollen data and from contemporary distributions that many additional taxa, including shrubs, e.g., *Pseudopanax arboreus*, *Schefflera digitata*, *Tupeia antarctica*; tree ferns, e.g., *Dicksonia fibrosa*, *Cyathea dealbata*; fern allies, e.g., *Lycopodium varium*, *Tmesipteris tannensis*; and lianes, e.g., *Muehlenbeckia*, grew in the forest understorey. There were probably scattered pockets of *Empodisma minus* and *Leptospermum scoparium* wetland around Pureora, and of *Nothofagus* forest at the regional extremities.

## CONCLUSION

The overall results of this study indicate that although pollen, litter, and wood analyses have their own inherent limitations in the interpretation of past vegetation patterns, conjoint analyses greatly enhance understanding (see also Newnham & Lusk 1990, and Ogden et al. 1993). Plant macrofossils represent mainly local vegetation, unless rivers redistribute them, and whereas trees are generally well preserved, other plant groups are not. Pollen assemblages represent a mixture of local, extra-local, and regional vegetation, and have the most taxa represented but with lower taxonomic resolution, so more caution is required for local interpretation.

On a wider scale, however, the pollen and macrofossil (particularly the litter) assemblages all tell essentially the same story – of a pre-Taupo eruption forest dominated by conifers with broadleaved associates. The similarity of the species compositions deduced from each site suggests that both the buried forests were typical of the broad Pureora-Benneydale forest pattern and that either measure alone would have been adequate to interpret them.

## ACKNOWLEDGEMENTS

Funds for this research were provided by The Foundation for Research, Science and Technology under Contract Number CLA202. DJL also acknowledges financial support from the University of Waikato Research Committee. Mr I. New granted permission to work on private land, Dr P.C. Froggatt analysed glass from the Benn-C tephra layer by EMP, and Dr T. Partridge carried out the multivariate analyses. Mr J.L. Nicholls, Dr W. Lee, Dr M. Pole, and an anonymous referee commented on the manuscript.

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## APPENDIX 1

Pollen (c. 1850 yr BP) percentages of peat samples collected from immediately beneath the Taupo Ignimbrite at Pureora and Benneydale buried forests. All samples were collected in 1992 except for Ben3 which was collected in 1987. Percentage sums are based on terrestrial pollen types, excluding ferns.

Taxa	Pureora			Benneydale		
	Pur1	Pur2	Pur3	Ben1	Ben2	Ben3
Agathis australis	+	0.0	0.0	0.0	0.0	0.0
Alectryon excelsus	0.0	0.0	0.2	0.2	0.0	0.3
Dacrydium cupressinum	40.6	40.7	27.6	19.0	10.8	18.9
Dacrycarpus dacrydioides	0.4	1.2	1.0	29.9	58.5	24.6
Elaeocarpus	0.2	0.2	0.0	0.0	0.0	0.0
Knightia excelsa	0.0	0.2	+	0.4	0.6	2.7
Metrosideros umbellata type	0.8	0.4	0.2	3.6	1.9	3.3
Metrosideros robusta type	0.6	0.8	0.5	1.7	2.9	5.4
Nestegis	0.2	1.2	1.7	0.6	+	0.0
Nothofagus fusca type	0.8	2.5	2.4	0.4	0.2	2.4
Prumnopitys ferruginea	10.5	11.3	12.0	12.0	6.8	9.9
Prumnopitys taxifolia	10.1	11.1	16.1	5.6	2.3	3.0
Podocarpus	0.8	1.2	1.7	1.1	0.8	0.3
Weinmannia	0.0	0.2	0.0	0.0	0.0	0.0
Aristotelia	0.0	0.0	0.2	+	0.0	0.3
Ascarina lucida	+	0.0	0.0	+	0.0	0.0
Carpodetus serratus	0.0	0.0	0.0	0.0	+	+
Syzygium maire	0.0	0.0	0.0	0.2	0.0	0.3
Dodonaea viscosa	0.0	0.0	0.0	0.0	+	0.0
Griselinia	0.4	0.6	0.5	0.4	0.4	2.7
Halocarpus	0.0	0.0	0.2	0.0	0.0	0.0
Neomyrtus type	1.0	0.6	0.2	0.0	0.0	0.0
Hoheria	0.0	0.0	0.0	+	0.0	0.0
Plagianthus	0.0	0.0	0.0	0.0	0.0	0.6
Phyllocladus	27.6	20.5	30.2	3.4	2.3	6.9
Pittosporum	0.0	0.0	0.2	0.0	0.0	0.0

## Appendix 1 (contd)

Taxa	Pureora			Benneydale		
	Pur1	Pur2	Pur3	Ben1	Ben2	Ben3
<i>Pseudopanax undiff</i>	+	0.0	0.0	0.0	0.0	1.5
<i>Pseudopanax arboreus</i>	0.0	0.0	0.0	0.4	0.4	+
<i>Pseudopanax colensoi</i> type	0.2	0.6	0.0	0.4	0.0	0.0
<i>Schefflera digitata</i>	0.2	+	0.0	0.0	+	0.0
<i>Coprosma</i>	0.8	0.4	0.0	0.0	0.0	0.3
<i>Leptospermum</i>	0.2	0.4	0.0	0.2	0.0	0.0
<i>Muehlenbeckia</i>	0.0	0.0	0.0	+	0.2	1.2
<i>Myrsine</i>	2.4	1.4	1.7	18.6	11.0	13.5
<i>Pseudowintera</i>	1.8	3.3	2.9	1.5	0.4	1.2
<i>Dactylanthus taylori</i>	0.0	0.0	0.0	+	+	0.0
<i>Rubus</i>	0.2	0.2	+	0.4	0.4	0.6
<i>Tupeia antarctica</i>	0.0	0.0	0.2	0.0	0.0	0.0
<i>Astelia</i>	0.0	0.0	0.0	0.0	0.0	0.3
<i>Collospermum</i>	0.0	0.2	0.0	0.0	0.0	0.0
Poaceae	0.0	0.6	0.0	0.0	0.0	0.0
Cyperaceae	0.0	0.0	0.2	0.0	0.0	0.3
<i>Empodisma</i>	0.0	0.0	+	0.0	0.0	0.0
Lobeliaceae	+	0.0	0.0	0.0	0.0	0.0
<i>Cyathea medullaris</i>	0.0	0.0	0.0	0.0	+	0.0
<i>Cyathea dealbata</i> type	1.2	1.0	1.7	1.7	0.2	4.8
<i>Cyathea smithii</i> type	6.3	16.0	29.3	40.8	30.1	152.1
<i>Dicksonia fibrosa</i>	+	+	0.2	0.0	0.0	0.0
<i>Dicksonia squarrosa</i>	0.0	0.0	0.2	0.0	+	1.8
<i>Dicksonia lanata</i>	+	+	+	+	+	0.0
<i>Blechnum capense</i> type	0.0	0.0	0.0	0.0	+	0.0
<i>Gleichenia</i>	0.0	+	2.2	0.0	0.0	0.0
<i>Hymenophyllum</i> type	0.4	1.4	0.7	1.1	0.6	0.3
<i>Lycopodium varium</i>	+	+	+	0.2	+	0.3
<i>Lycopodium scariosum</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lygodium articulatum</i>	+	0.0	0.0	0.0	0.0	0.0
Monolete fern spores undiff.	2.0	2.3	2.0	1.5	1.0	6.3
<i>Phymatosorus diversifolius</i>	0.4	0.2	1.2	0.4	+	0.9
<i>Leptopteris</i>	0.0	0.0	0.7	0.4	0.0	0.0
<i>Tmesipteris tannensis</i>	0.0	0.0	+	0.0	0.0	0.0
unidentified	1.0	0.8	0.2	0.0	0.0	0.0
<b>Totals (%) for groups</b>						
Ferns	10.3	20.7	38.3	46.2	32.0	166.5
Herbs	0.0	0.6	0.0	0.0	0.0	0.3
Shrubs and small trees	3.0	4.5	2.9	1.7	0.8	3.3
Trees	97.0	94.9	97.1	98.3	99.2	96.4
unknown and undetermined	1.0	0.8	0.2	0.0	0.0	0.0
Wetland	0.0	0.0	0.2	0.0	0.0	0.3
<b>Terrestrial pollen sum:</b>	493.0	487.0	410.0	468.0	482.0	334.0

## APPENDIX 2

## Pureora and Benneydale buried forests c. 1850 yr BP pollen, litter, and wood percentage abundances for tree taxa only

	Pureora						Benneydale					
	Pollen			Macrofossils			Pollen			Macrofossil		
	1	2	3	$\bar{x}$	Litter	Wood	1	2	3	$\bar{x}$	Litter	Wood
<i>Agathis australis</i>	+			+								
<i>Alectryon excelsus</i>			0.2	0.1			0.2		0.3	0.2		
<i>Aristotelia</i>			0.2	0.1			+		0.3	0.1		
<i>Ascarina lucida</i>	+			+			+			+		
<i>Carpodetus serratus</i>								+	+	+		
<i>Dacrydium cupressinum</i>	41.9	42.0	27.9	37.3	50.1	43	19.8	11.1	20.0	17.0	60.2	53
<i>Dacrycarpus dacrydioides</i>	0.4	1.2	1.0	0.9	4.7	6	31.2	60.0	26.0	39.1	4.0	
<i>Dodonaea viscosa</i>								+		+		
<i>Elaeocarpus</i> <sup>1</sup>	0.2	0.2		0.1	0.3							
<i>Griselinia</i>	0.4	0.6	0.5	0.5			0.4	0.4	2.9	1.2		
<i>Halocarpus</i> <sup>2</sup>			0.2	0.1	0.1							
<i>Hoheria</i>							+			+		
<i>Knightia excelsa</i>		0.2	+	0.1			0.4	0.6	2.9	1.3	1.9	3
<i>Libocedrus</i> <sup>3</sup>						+						3
<i>Metrosideros robusta</i> type <sup>4</sup>	0.6	0.8	0.5	0.6	0.4	+	1.8	3.0	5.7	3.5	16.5	10
<i>Myrsine</i> <sup>5</sup>	2.5	1.4	1.7	1.9	5.8	3	19.4	11.3	14.3	15.0	8.0	
<i>Nestegis</i> <sup>6</sup>	0.2	1.2	1.7	1.0	1.0	3	0.6	+		0.2	0.9	7
<i>Nothofagus fusca</i> type	0.8	2.6	2.4	1.9			0.4	0.2	2.5	1.0		
<i>Plagianthus</i>									0.6	0.2		
<i>Phyllocladus</i> <sup>7</sup>	28.5	21.1	30.5	26.7	21.1	25	3.6	2.4	7.3	4.4	2.0	3
<i>Pittosporum</i>			0.2	0.1								
<i>Podocarpus</i> <sup>8</sup>	0.8	1.2	1.7	1.2	+	4	1.2	0.8	0.3	0.8	+	7
<i>Prymnopterys ferruginea</i>	10.8	11.7	12.1	11.5	1.7	4	12.5	7.0	10.5	10.0	2.7	13
<i>Prymnopterys taxifolia</i>	10.4	11.5	16.2	12.7	1.5	10	5.8	2.4	3.2	3.8	0.1	
<i>Pseudopanax undiff.</i>	+			+					1.6	0.5		
<i>Pseudopanax arboreus</i>							0.4	0.4	+	0.3		
<i>Pseudopanax colensoi</i> type <sup>9</sup>	0.2	0.6		0.3	2.3		0.4			0.1		
<i>Schefflera digitata</i>	0.2	+		0.1				+		+		
<i>Syzygium maire</i>							0.2		0.3	0.2		
<i>Weinmannia</i>		0.2		0.1								
<i>Pseudowintera</i> <sup>10</sup>	1.9	3.4	2.9	2.7	11.0	2	1.6	0.4	1.3	1.1	3.7	
n				3	48	187				3	51	30

## For wood and litter data:

- <sup>1</sup> *Elaeocarpus hookerianus*
- <sup>2</sup> *Halocarpus bidwillii*
- <sup>3</sup> *Libocedrus bidwillii* for Pureora, *L. ?bidwillii* for Benneydale
- <sup>4</sup> *Metrosideros robusta*
- <sup>5</sup> *Myrsine salicina*
- <sup>6</sup> *Nestegis cunninghamii* (only at Benneydale), *N. lanceolata*, *N. montana*
- <sup>7</sup> *Phyllocladus trichomanoides*
- <sup>8</sup> *Podocarpus totara*
- <sup>9</sup> *Pseudopanax crassifolius*
- <sup>10</sup> *Pseudowintera axillaris*, *P. colorata* (only at Pureora)