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PALEO-ECOLOGICAL EVIDENCE FROM POLLEN AND SPORES

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RECONSTRUCTION OF CLIMATE AND VEGETATION HISTORY

I would like to regard the postglacial period as that following the maximum of the last major ice advance, or the last 18,000 years before the present, whichever proves to be the longer. The term postglacial implies that the present day climate differs essentially from a full glacial climate. The difference is such as to produce important changes in the vegetation, which will have adjusted itself to the altered conditions, or is in the process of becoming adjusted. Can we reconstruct this process to any great extent and if so, what do we learn about climate history up to the beginning of European settlement and of historical records? Inevitably time comes into consideration because if we want to reconstruct the pattern of vegetation change, and from this infer climate change, we must have some opinion about the chronological relationship between the pieces of evidence brought to light.

It can be seen at once that reconstruction of vegetation history over the past 18,000 years is an enormously difficult undertaking, since historical records cover only a very small fraction of that time, and the region is topographically complex. If ultimate success in such an undertaking were our only prospect of reward, we might well despair. We are encouraged to pursue this subject, however, by the fact that the project gives us a basis for coordinating a large number of independent observations, and is a means in particular of testing and extending our knowledge of the relation between organisms and environment.

In this very process we are building up a context in which certain types of observation find their significance. This context is probably in a large measure a by-product of various techniques and is in turn the means for improving techniques. To illustrate this, given a technique for extracting pollen from types of sediment which are sufficiently common, and the ability to distinguish the principal pollen types of New Zealand conifers, beeches and grass, let us take as a working hypothesis the generalisation that as beech pollen increases relatively to conifer, the climate is cooler, and when there is much grass pollen with little or no pollen of the beech and conifer types a cold climate is indicated. Here is a technique which is workable, though crude, and which will produce results sufficient to justify persevering with it and trying to improve it.

The underlying hypothesis may be regarded with suspicion by ecologists, and even with some misgiving by the palynologist, but the point has to be appreciated that the palynologist must have *some* hypothesis — or go out of business. The ecologist, on the other hand, makes deductions and inferences based on his own field studies, but these lack the support of historical evidence which, if obtainable at all, must come from a study of the fossil record. The question then arises as to whether the two techniques, that of the ecologist, and that of the palynologist can be mutually helpful, whether they can usefully exchange findings. It is this co-ordinated attempt to reconstruct vegetation and climate history which provides the framework within which the palynologist, as well as others, may seek a means for refining and perfecting his method.

PALYNOLOGY AND ECOLOGY

The two techniques, ecology and palynology, are quite distinct and independent. Judgments and intuitions are based on experience, and the experience in the one case is with pollen, in the other with plants. The palynologist is dealing with problems related to vegetation succession, though his field studies are necessarily very limited, but experience has shown that the interpretation of pollen results presents difficulties for the ecologist. A method is sometimes employed which helps to bridge the gap between the two techniques. A plant community is surveyed in the field and at the same locality the pollen which has accumulated in a suitable pollen trap, it may be a moss cushion, is investigated. Even this achieves only a partial reconciliation between the two techniques because of differences in perspective. Vegetation is dynamic and the palynologist deals with climaxes which develop over long periods, but which may not be well represented at a particular time.

It seems important to appreciate and even to emphasise the difference between these two techniques, more especially because to some extent the same names are used in a different context, and sometimes with a different significance. To give an example, there is a pollen type which, for convenience, the palynologist may call *Dacrydium bidwillii*. *Dacrydium biforme* has a similar pollen, though it is believed possible with care to distinguish them. *Dacrydium bidwillii* is the bog pine, and occurs in montane to subalpine scrub from 39° southwards, descending to lowland in the western South Island and in Stewart Island. *D. biforme*, though it ranges a little further northwards, has much the same distribution. Another species with a similar pollen type is *D. kirkii*, an occasional tree in lowland forest in the North Island between 35° and 37°, that is to say north of Auckland, and on Great Barrier Island. The third species is therefore quite different ecologically from the other two.

At the present stage of pollen research in New Zealand it is an unnecessary refinement to consider this pollen type as representing three species. If only a few grains are observed, judgment of climate will not be based on them but on the principal pollen types. If the pollen is relatively abundant, in no instance have all the facts taken together been consistent with the ecological conditions under which *D. kirkii* occurs today. When this pollen type is abundant, boggy soil conditions and cool to cold climate would better fit into the general picture. The *Dacrydium bidwillii* pollen type, then, is for the palynologist a unit, to be interpreted in relation to a context. It is unlike any corresponding unit of the ecologist.

This leads to the concept of frequency of association, which may give value to those pollen types which cannot be related to a single species in either the taxonomic or the ecological sense. From frequency of association it becomes possible to characterise assemblages, and as data accumulate and pollen assemblages are characterised in their climax forms, transitions between them can be recognised.

The ecologist and the palynologist can speak a common language when discussing climate or when there is a good correlation between the unit of the palynologist and the unit of the ecologist. The correlation might be considered good for the three species mentioned, *Nothofagus menziesii*, *Dacrydium cupressinum*, and *Podocarpus dacrydioides*, because the pollen type in each case represents a single species, which produces a large amount of wind-borne pollen, and is thus adequately represented. Among pollen assemblages, perhaps the beech pollen dominant assemblage approaches reasonable correlation with a plant community of the ecologist, though it is exceptional for comparable information regarding the species present to be attainable (Table 1). Some plant communities known to the ecologist may be unknown to the palynologist, for example tawa forest which is under-represented in the pollen record; on the other hand the palynologist may meet a pollen assemblage with no counterpart known to the ecologist, for example that dominated by the spore type *Trilites bifurcatus* Couper. The botanical relationship of this spore type is not yet known: its morphological affinity is with spores of the *Selaginella* type.

TABLE 1. *Comparison between tree counts and pollen counts — Little Barrier Island.*

Species or species groups	*Relative proportion of canopy trees* (1)	(2)	*tree pollens*
Quintinia acutifolia	22	32	17
Phyllocladus glaucus	14	2	4
Ixerba brexioides	14	16	—
Myrtaceae	20	22	51
Weinmannia silvicola	8	4	4
Ericaceae + Epacridaceae	10	8	6
Agathis australis	6	—	—
Podocarpus totara *Podocarpus hallii* *Podocarpus ferrugineus*	6	—	8
Other canopy components	—	16	10
	100%	100%	100%

NOTE: (1) and (2) are counts at different sites, the latter nearer to the site from which pollen counts were obtained. The above comparisons were kindly supplied by Mr I. A. Atkinson.

A recent study of frequency of association reveals patterns of association. Some pollen types increase in frequency with increasing warmth, among which are *Podocarpus dacrydioides* together with other Podocarpoid types, *Dacrydium cupressinum*, Nothofagus (*fusca* type) and *Laurelia novaezelandiae*. Other types are found less often and in lower frequencies with increasing warmth. Examples are *Dacrydium bidwillii* type, *Phyllocladus* type (in the Quaternary), *Agathis australis* (not found, however, in "cold" pollen floras), *Nothofagus menziesii*, Compositae and grass.

A typical sequence of pollen assemblages might be represented as follows:

Cold		*Cold*
Increasing warmth	Grass, herbs, shrubs. Little or no tree pollen.	*Decreasing warmth*
	Incoming/outgoing tree pollen esp. *Dacrydium bidwillii* & *Nothofagus menziesii*	
	Dominant *Nothofagus* (fusca type)	
	Dominant Podocarpoid	
	Dominant *Dacrydium cupressinum*	
Warm		*Warm*

CLIMATE HISTORY

Cranwell and von Post (1936) suggested a particular pattern of climate history which has been found in many parts of the world, and is widely accepted — a pattern of warming to a period of maximum warmth, followed by cooling to a less warm period. These periods have not been dated. Subsequent work seems to support this pattern and such carbon dates as are applicable also support the supposition that the period of maximum warmth roughly corresponds with the hypsithermal interval recognised elsewhere some 6500 to 2500 years B.P. It is not possible as yet to elaborate or extend this scheme with any certainty for the whole of New Zealand. Pollen results from the Hauraki Plains and from Wallaceville suggest that in the period of warming following the full glacial there was a climate oscillation possibly correlated with the Alleröd fluctuation, but so far it has not been possible to confirm this. A sequence of pollen zones has been proposed by the writer in accordance with this theory, which may be set out briefly as follows:

Zone	*Climate*	*Correspondence (tentative)*	*Age (Years B.P.)*
5a, b, c	Cooler	Period III NZ*	2,500—0
4	Maximum warmth	Hypsithermal interval of Europe. Period II NZ*	6,500— 2,500
3	Warming	Period I NZ*	10,000— 6,500
2	Oscillation	Alleröd of Europe.	c. 11,000
1	Warming		18,000—12,000
0	Cold, full glacial		18,000+

* NZB, after Cranwell & von Post, 1936.

The attempt has been made to subdivide zone 5 into a first part, zone 5a; a third part, zone 5C, which was the zone of European settlement with man induced changes in the vegetation; and an intermediate zone 5b. Zone 5c is readily recognisable in profiles in which it is preserved, not only by changes in the ratios of the principal pollen types but also by the incoming of exotic pollen. In many peats, however, this part of the record is seriously affected by draining and burning. Zone 5b seems to coincide roughly with the period of pre-European human occupation, and the question arises as to whether observed changes in the pollen assemblages,

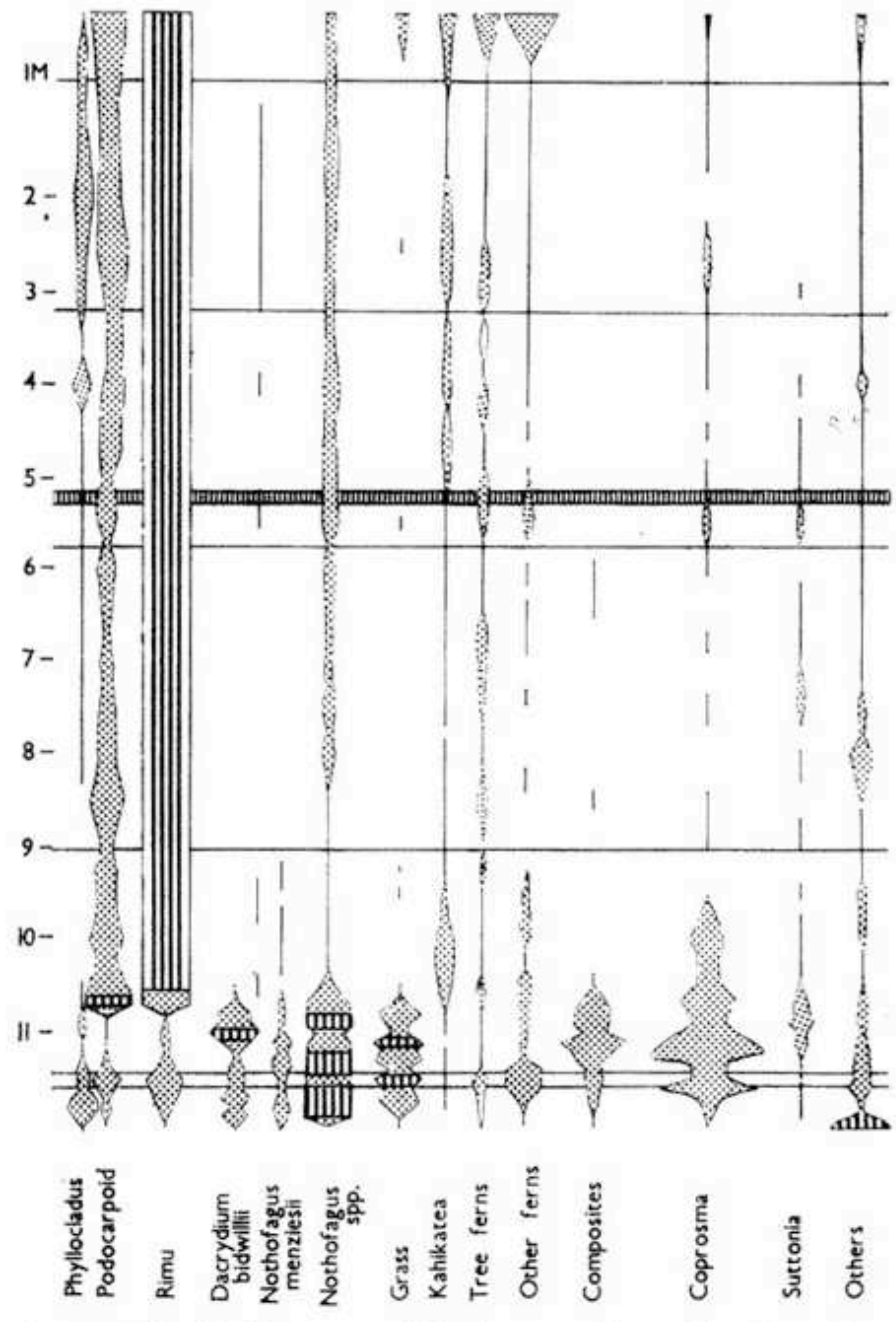

FIGURE 1. *Pollen profile from deep boring in peat, Hauraki Plains. A pumice layer is shown 5¼ metres below the surface which by radiocarbon dating may be correlated with the Taupo pumice, about 1700 years before the present. Diagrams show the ratio of each type when the dominant = 100. According to a tentative interpretation, boundaries between pollen zones are shown.*

when present, may not be attributable in large part at least to human influence, through imperfectly controlled burning. A pollen profile from a Hauraki Plains boring is shown in Figure 1.

An ash horizon was found in a Hamilton profile at a depth of from 5.25 to 5.5 metres, just over a metre above the substratum. This layer brought to a rather abrupt close the lowest pollen zone. The peat changed to a rush type and pollen of the Restionaceae type became abundant and continued as the dominant "bog pollen" type throughout the remainder of the profile.

The fire may have affected the vegetation on the neighbouring hilly area. The proportion of rimu to other conifers remained similar but tree fern spores became more abundant as also the pollen of *Nothofagus*, *Metrosideros* and *Ascarina*. The conifer pollen, though showing the same proportion among the individual pollen types, may have come from a slightly greater distance.

At a depth of just over 4.0 metres there was a marked change in the relative abundance of pollen of the rimu type in relation to that of other conifers. Rimu pollen became more strongly dominant and continued so throughout the remainder of the profile.

The pollen results, on this interpretation, suggest that during the period of deposition the vegetation had been affected locally by fire at an early stage in the record and more generally by forest succession, possibly in response to climate change. At the site of the borehole the peat had accumulated to a depth of one metre or more before the fire, to a depth of 2.25 metres before the subsequent change in the pollen rain (climate change?) and a further four metres since the change, plus the amount, unknown, lost by shrinkage and other causes since the area was drained for reclamation. The fire probably occurred in the pollen-zone 4 period, over 2500 years ago, and hence before human occupation (see Fig. 2).

No burnt horizon or evidence of fire was found at Pyramid Valley, in Canterbury, where a tentative correlation was made with a supposed climate change some 600–700

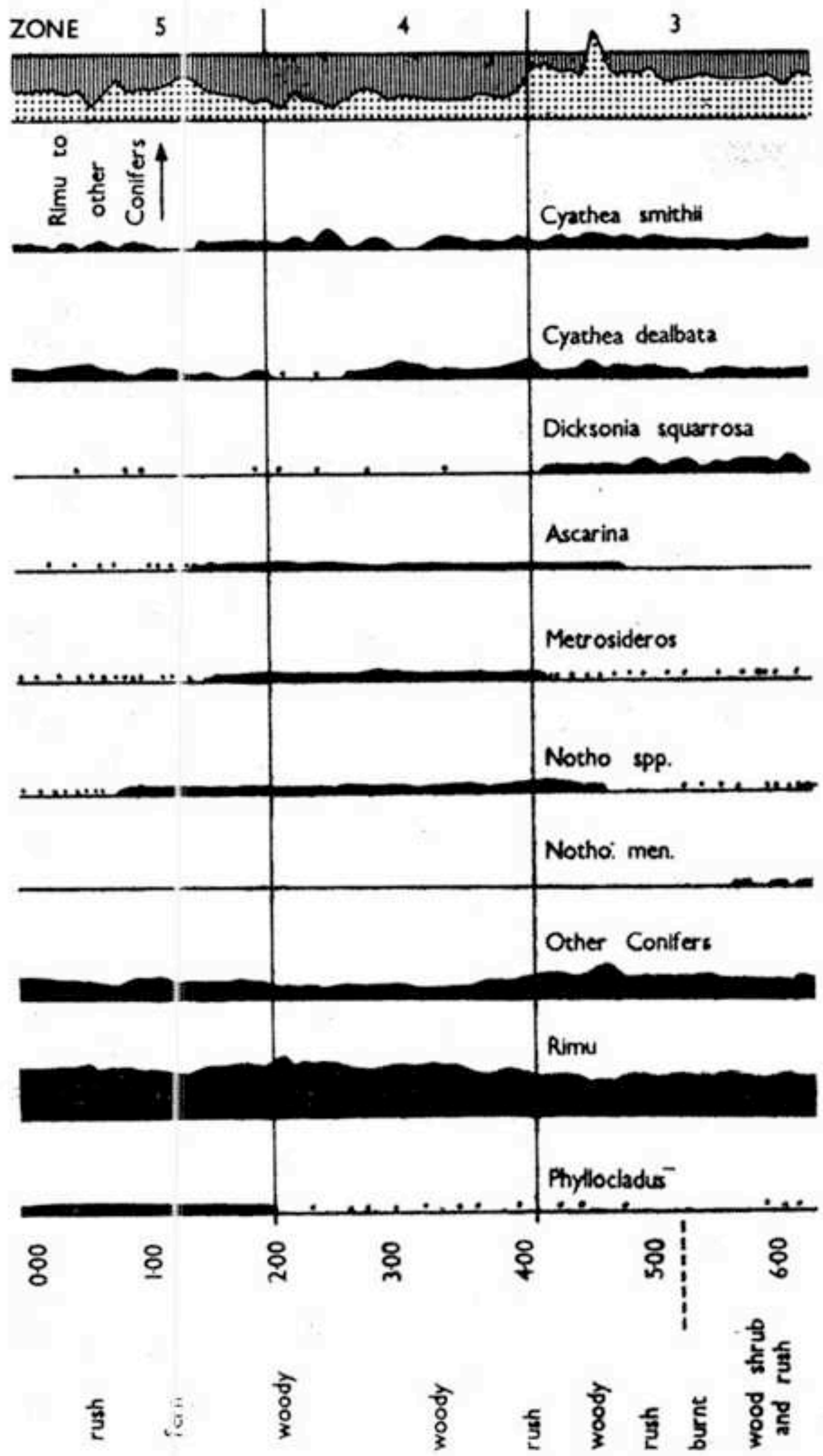

FIGURE 2. *Pollen profile from a boring in peat near Hamilton, made in 1949 in collaboration with Prof. Hugo Osvald. Plotted similarly to Fig. 1, but at the top the ratio* Dacrydium cupressinum *to "Podocarpoid" is shown, with a marked change at a depth of 4 metres.*

years ago. Close sampling was carried out in a borehole on the Hauraki Plains and the whole sequence was examined for pollen. It was possible to recognise a change in the pollen rain which was tentatively also correlated with this supposed climate change. There was no reason to suppose that it might be fire-induced. There was no evidence of an abrupt disturbance as in the Hamilton profile and elsewhere when exotic pollen enters the profile and the effects of European colonisation can be inferred. The rate and steadiness of the change suggest a factor more slow-acting than fire.

Among the postglacial series studied in most detail are the various profiles from the peat swamp at Wallaceville, near Wellington. Rimu pollen is dominant during the postglacial hypsithermal interval (zone 4), followed by beech pollen dominant. Subdivision of the beech pollen of zone 5 is not practicable, perhaps because the area, being a forest peat, is not suitable. Other Wellington profiles do not include that part of the postglacial, or when they do, as in the High Street, Lower Hutt, the sampling is not close enough for subdivision. Samples from a shallow peat on Mt. Cameron, a saddle above Lake Monk, show conifer pollen dominant in the oldest sample, changing to beech pollen very strongly dominant above (Tables 2 and 3). At first *Nothofagus menziesii* increases rapidly followed by greater increase of other species, apparently *N. fusca* and finally *N. solandri* var. *cliffortioides* which is also included in the *fusca* group in Table 2. Radiocarbon dates show that the oldest sample is between 5000 and 6000 years before the present, and thus within the hypsithermal interval. By about 2000 years ago there was as much beech as conifer pollen, and covering of the neighbouring mountain slopes by the mountain beech has taken place since then. Peat accumulated slowly at this site, possibly with an interval of standstill or even erosion, and the carbon dates show that very close sampling would be necessary to elucidate the relationship between climate and succession. The advance of beech forest seems to have begun at least 2000 years ago and may be a slow process, or from being purely local may be becoming more general. The results of Cranwell and von Post (1936) suggest that the advance has been from the west eastwards. Recent sampling of peat deposits in the southern part of the South Island shows that there has been as yet no strong increase of beech pollen and that in the younger part of the profile silver beech pollen has increased more than the other type (Fig. 3).

TABLE 2. *Comparison of pollen counts from two series of samples collected at the same depths on Cameron Mountain above Lake Monk.*

POLLEN/SPORE TYPES	DEPTH (*inches*)							
	19		*12*		*6*		*2*	
(a) Actual counts								
Nothofagus menziesii	11	6	55	136	56	87	23	91
N. spp. (*fusca* group)	9	2	45	119	155	150	76	150
"Dacrydioid"	200	150	150	150	76	49	15	36
"Podocarpoid"	18	15	48	75	36	33	9	22
Phyllocladus sp.	4	3	3	2	1	8	3	1
Weinmannia sp.	20	9	35	31	21	18	2	16
Metrosideros sp.	27	9	15	12	8	2	1	4
Araliaceae	8	5	2	6	10	1	1	1
Myrsine sp.	5	—	—	2	1	—	—	—
Others	49	22	51	39	24	20	12	29
Cyathea spp.	28	10	17	12	7	6	—	2
Ferns & Lycopods (except tree-ferns)	6	4	15	16	4	13	3	20
Grass	21	12	20	16	5	8	4	9
(b) Main groups as percentages								
Beeches	5	3	22	41	52	60	66	63
Conifers	54	67	45	37	28	22	18	16
Other trees and shrubs	27	19	22	14	16	11	11	13
Ferns	9	6	7	5	3	5	2	6
Grass	5	5	4	3	1	2	3	2

TABLE 3. *Pollen and spore types excluded in Table 2.*

POLLEN/SPORE TYPES	DEPTH (*inches*)							
	19		*12*		*6*		*2*	
Sedges	48	49	22	38	40	41	61	26
Leptospermum spp.	10	3	3	1	—	—	—	—
Phormium sp.	2	—	—	—	—	—	5	—
Typha muelleri	—	—	—	—	1	—	2	—
Hypolaena lateriflora	4	12	26	15	13	24	—	36
Dracophyllum sp.	4	3	5	5	8	—	2	7
Ericaceae	2	2	5	2	2	2	—	5
Orchidaceae	—	—	—	—	1	—	—	—
Coprosma spp.	8	3	7	8	—	2	2	9
Lycopodium fastigiatum	1	3	9	16	25	20	16	—
Myriophyllum spp.	1	3	4	1	1	—	—	—
Ferns	1	2	3	2	2	4	2	5
Podocarpus dacrydioides	4	4	2	2	—	—	—	—
Compositae	4	5	4	3	1	1	—	5
Others	11	11	10	7	6	6	10	7

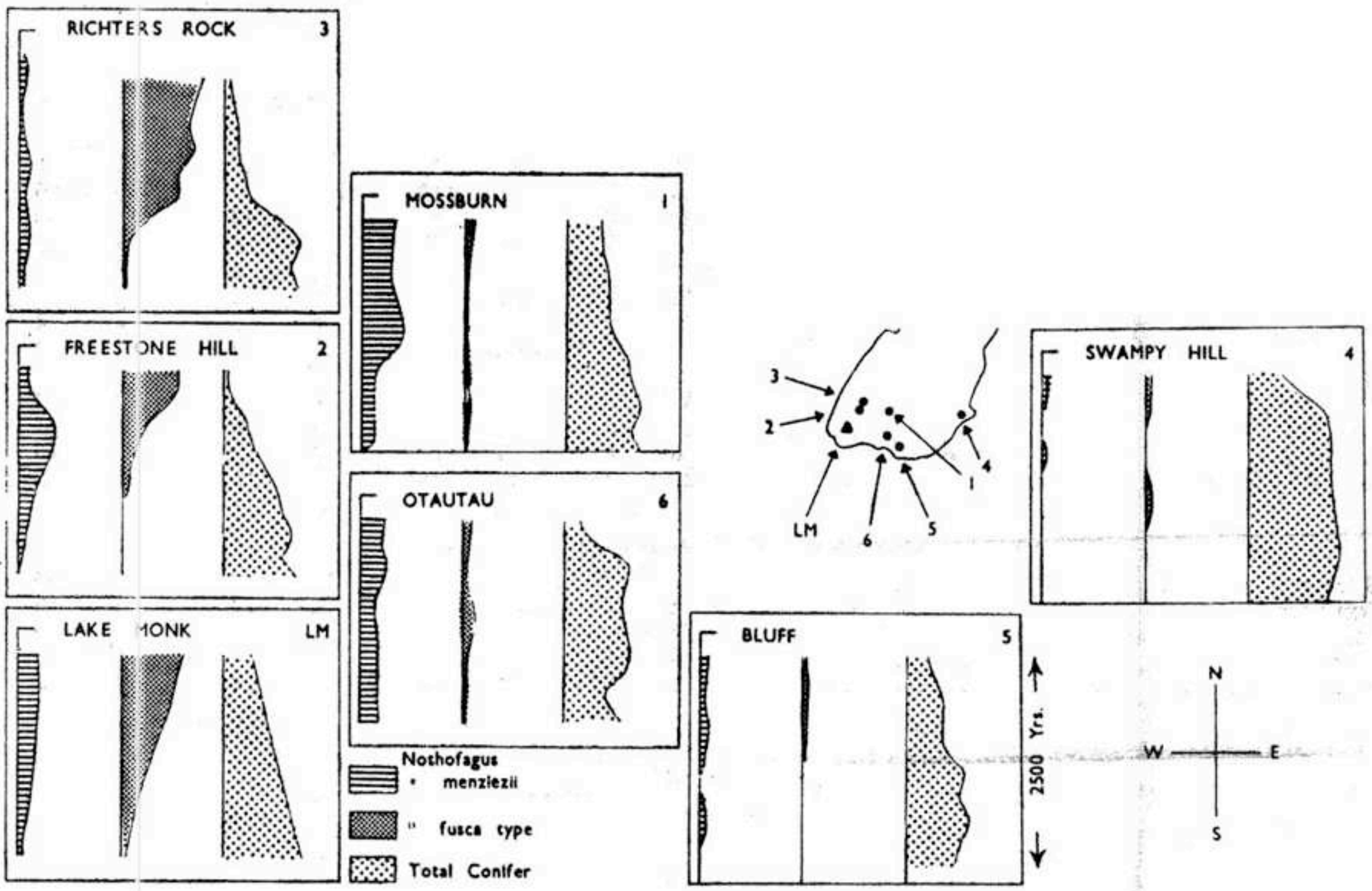

FIGURE 3 *Pollen diagrams arranged according to geographic relationships between stations, and showing that colonisation by beech is more advanced to the west. Colonisation appears to have been eastwards, with silver beech preceding red and/or mountain beech.*

SUMMARY

Analysis of acumulated data shows that on the basis of frequency of association, as distinct from botanical affinity, certain pollen types behave as follows:--

Increase with increasing warmth: Podocarpoid pollen in general as well as the easily distinguishable *Podocarpus dacrydioides* type, *Dacrydium cupressinum*, *Nothofagus* (*fusca* type) and *Laurelia novaezelandiae*.

Less frequent with increasing warmth: *Dacrydium bidwillii* type, *Phyllocladus* type (in the Quaternary), *Agathis australis* (not found in "cold floras"), *Nothofagus menziesii*, Composite and grass.

In a typical sequence of pollen assemblages, *Dacrydium bidwillii* type and *Nothofagus menziesii* appear with the incoming of tree pollen following a cold period, and as warmth increases a peak is reached in *Nothofagus* (*fusca* type), from then on Podocarpoid followed by *Dacrydium cupressinum*.

Climate change during the last 700 or 800 years cannot be demonstrated by pollen analysis except perhaps in certain areas, and interpretation would depend on the nature of the changes produced in the pollen profile.

Evidence from the southern part of the South Island indicates that beech forest began to replace coniferous forest some 2,000 years ago, has proceeded eastwards, and silver beech has tended to advance earlier than mountain beech. Evidence from pollen studies is not yet sufficient to show whether or not the process has been accelerated subsequently by fire and/or further climate change.

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