CHAPTER 7

CONTEMPORARY POLLEN DEPOSITION IN THE MARKHAM AREA

Pollen analysis as a tool of palaeoecology, rather than biostratigraphy, rests on a number of important assumptions concerning the production, dissemination and deposition of pollen grains and spores. In northern temperate regions studies on the dispersal of pollen grains under different conditions (e.g. Tauber, 1965, Andersen, 1973) have refined formerly intuitive models of pollen transfer. Further detailed work has elucidated the processes of pollen recruitment to lake sediments, and the mechanisms of deposition and redeposition (Davis and Brubaker, 1973, Davis *et al.*, 1973, and Bonny 1976, 1978).

Many empirical studies of regional contemporary pollen deposition have revealed facets of the relationship between pollen assemblages and the source vegetations crucial to the ecological interpretation of fossil palynological data. Recent approaches have employed multivariate statistical techniques to illuminate correlations between modern pollen spectra and vegetation composition (Kershaw 1973*a*, Webb, 1974, Davis and Webb, 1975, and Webb and McAndrews, 1976) or climate (Webb and Bryson, 1972).

A number of contemporary pollen deposition studies, reviewed by Flenley (1973), has been carried out in tropical regions, although the majority relate to predominantly upland or alpine, rather than lowland, areas. Of particular regional significance to lowland Papua New Guinea is the work of Hope (1973), Kershaw (1973*a*), Kershaw and Hyland (1975) and Morley (1976).

Despite these recent advances there still exists neither a sound theoretical basis for the interpretation of pollen analytical evidence from the tropical lowlands, nor a comprehensive regional study of contemporary pollen assemblages from any lowland tropical area. Investigations within the study area were therefore directed towards an understanding of the main aspects of pollen production and transfer, and of the nature of contemporary pollen assemblages in the environs of the Markham Valley.

SAMPLING CONTEMPORARY POLLEN DEPOSITION

The lack of pollen preservation in many situations proved a major problem in sampling pollen deposition in the diverse vegetation of the Markham Valley. As Flenley (1973) notes, moss polsters, commonly employed for their natural pollen-trapping properties, are surprisingly rare in lowland tropical forest. Damp moss tussocks from 'hill' forest between 180 m and 1 000 m altitude contained abundant well preserved pollen and spores. In lower altitude forests adequate samples could sometimes be obtained from the thin moss cover of tree trunks or rocks, provided several samples within close proximity were amalgamated for analysis. Pollen is generally not well preserved in lowland tropical soils (Hedberg, 1954, Hamilton, 1972). Some periodically inundated litter and surface-soil samples yielded small quantities of pollen, although spores were more abundant, perhaps suggesting differential destruction of pollen grains. Sediments from perennially water-logged swamps and lakes provided the most satisfactory natural traps for pollen and spores, although even here the concentration may be low due to rapid accumulation of the sediment. Such sites were unfortunately not widespread.

TABLE 7.1. Contemporary pollen samples from the Markham Valley

Sample No.	Type	Location	Alt. (m)	Vegetation type	Local plant taxa
PT 1	Pollen trap	Markham Point	180	Slightly disturbed 'hill' or 'ridge' forest	Aporosa papuana, Melicope (21144), Gnetum gnemon, Lucinaea (21146), Urophyllum (21149), Endiandra (21147), Dysoxylum (21148), Myristicaceae (21143)
PT 4	Pollen trap	Lake Wanum eastern shore c. 500 m from water	40	Lowland closed forest on gentle slope	Clerodendrum buchanii, ?Popowia (21130), Polyalthia (21131), Commelina (21132), Macaranga Alpinia (21127), Meliaceae (21129)
PT 5	Pollen trap	Lake Wanum, promontory at the western margin of north-east bay	40	Partially cleared, open forest	Asplenium nidus, Rhaphidophora (21108), Alpinia (21109), Diplocyclos palmatus, Mukia maderaspatana, Passiflora foetida, Mezonevron (21110), Malaisia scandens, ?Ganophyllum (21116), Cissus (21115), Celtis (21117), Murraya paniculata
PT 6	Pollen trap	Lake Wanum, on floating raft in centre of north-east bay; 250 m from shore	35	Open water	None
SQ 35	Litter and detritus, root mat	Lake Wanum, western margin of north-east bay, vegetation quadrat 35	35	Deep water floating root-mat (Group A) swamp vegetation	Nephrolepis hirsutula, Hypolytrum nemorum, Stenochlaena palustris, Microsorium (21067)
SQ 40	Lake sediment surface detritus	Lake Wanum, south swamp, vegetation quadrat 40	35	Hypolytrum nemorum association (Group B) swamp vegetation	H. nemorum, Cyclosorus (21050), Ceratophyllum demersum
SQ 50	Lake sediment surface detritus	Lake Wanum, south swamp, vegetation quadrat 50	35	Nelumbo nucifera association (Group E) swamp vegetation	N. nucifera, Leersia hexandra
SQ 51	Surface detritus and litter from root-mat	Lake Wanum, south swamp, vegetation quadrat 51	35	Leersia hexandra floating mat (Group D) swamp vegetation	L. hexandra, Phragmites karka, Nelumbo nucifera, Stenochlaena palustris, Hypolytrum nemorum
SS 13-15	Thin moss cover from dead tree trunks (3 samples, a few metres apart	Forest plot vicinity of lower Sankwep River	?50	Rain-forest	Homalium, Pometia, Artocarpus, Dysoxylum, Horsfieldia, Sterculia, Cryptocarya, Pangium, Antiaris, Gmelina, Gnetum, Gastonia, (identifications by R.J. Johns)

TABLE 7.1. (Cont.)

Sample No.	Type	Location	Alt. (m)	Vegetation type	Local plant taxa
SS 18	Leaf litter and surface soil	Markham river flood plain, about 0.5 km south of Markham bridge	?20	'Alluvium' forest; periodically inundated	*Antidesma* (21155), *Psychotria* (21156), *Voacanga papuana, Alpinia* (21154)
SS 20	Moss polster	Foothills of Hertzog ranges south of Gabensis	970	Tall 'hill' forest	*Acronychia trifoliolata, Aporosa papuana, Maesa* (21161) in area
SS 22	Moss polster	Foothills of Herzog ranges south of Gabensis	790	Tall 'hill' forest disturbed by logging	as above
SS 23	Organic detritus from swamp margin	Redhill swamp, eastern margin	35	Swamp margin vegetation under 20 cm of water	*Alyxia ?floribunda, Coleus scutellarioides, Dysophylla verticillata*
SS 27 + 28	Dry moss from tree roots and limestone boulders (2 samples, 100 metres apart)	50 m west of lake, Yanamugi	175	Semi-deciduous forest on thin soil on slope	-
LWMC 3 SS	Organic detritus and surface sediments	Short core LWMC 3, western margin of north-east bay, Lake Wanum	35	Open water	none
YANMC 1 SS	Calcareous surface mud	Short core YANMC 1, southern end of Yanamugi lake	170	Open water	none

Artificial pollen traps proved well suited to the collection of pollen and spores under a variety of conditions. Facilities were not available for the exclusive use of these devices, nor for monitoring rain-gauge catches, another alternative. Therefore both natural and artificial trapping methods were employed. A random collection scheme was thus not feasible, and most samples derive from either swamp or forest vegetation, leaving other dry land vegetation largely unrepresented. Open grassland areas remain unsampled, as the dry soil preserved no pollen, and placement of traps would have been futile in the annually fired vegetation.

The locations of the 16 samples analysed, four from pollen traps and 12 from surficial sediments or moss polsters, are given in Table 7.1. With the exception of four samples from swamp vegetation quadrats, no ecological measurements were made on the vegetation at these sites, although many plants from the vicinity of the samples were collected and identified.

Estimation of annual pollen deposition rates

In order to obtain estimates of annual pollen and spore deposition (PDR) rates under various conditions, pollen traps of the Tauber (1974) design were deployed. These consist of a PVC cylinder 10.1 cm internal diameter by 58.5 cm high, sealed at the base and with a circular aerodynamic lid having a 5 cm diameter orifice. The traps were stationed for 511 to 519 days between December 1974 and April/May 1976, and were not subsampled within this period.

Of six Tauber traps set, only four were recovered. One (PT 1) was located in 'hill' forest at an altitude of *c.* 180 m at Markham Point. The forest canopy, initially closed, was opened up

by the natural fall of a large tree immediately adjacent to the pollen trap prior to the recovery date. Three traps were situated in the vicinity of Lake Wanum, two on land and the third on an anchored raft. Trap PT 4 was located in closed forest at the base of Mount Misantum, about 500 m from the eastern shore of the lake. Open forest surrounded trap PT 5 on the narrow promontory west of the north-east bay. This site had been extensively cleared by 1976. All forest traps were located at ground level, with the trap lid about 30 cm above the forest floor. The floating trap (PT 6) was positioned in the centre of the north-east bay, at least 250 m from land, although it appeared to have drifted slightly by 1976.

On recovery the traps were sealed and shipped to Canberra intact. The entire contents were then consolidated by centrifugation and pollen slides prepared using the volumetric technique described previously.

A number of uncertainties are associated with the use of such pollen trapping methods. Human interference may be implicated in the disappearance of two of the traps, and might have affected the results from others, especially the highly conspicuous floating trap. In theory, a full year is the most appropriate sampling period, rather than 16 months. However, as the climate, and presumably flowering, is relatively aseasonal in this part of the valley, a reasonable estimation of annual PDR should be possible. The traps could accommodate up to 2390 mm of rainfall, equivalent to an annual precipitation of 1700 mm assuming zero evaporation. This figure is substantially lower than the actual rainfall over the whole area, and one trap (PT 1) was found full, and another (PT 4) nearly so. Estimates of PDR from these sites must therefore

represent minimum values. The two traps PT 5 and PT 6 from more exposed situations contained considerably less water, presumably due to greater evaporation, and had probably not overflowed.

Recently Krzywinski (1977) has questioned the utility of Tauber's pollen trap design, suggesting that inflated influx values may be produced due to rain-splash redeposition of pollen from the lid. The trap is however regarded as an inefficient collector in conditions of high wind speed (Peck, 1973). The size of errors is unknown, but can be presumed to be essentially similar for all traps in this study. In several cases the aerodynamic properties of the lid had been altered either by detrital twigs and leaves, or, in the floating trap, by bird excreta.

Estimates of total pollen content and annual PDR values are given for each of the trap sites in Table 7.2. Very great variations in PDR between traps are apparent. The two traps from closed forest sites, PT 1 and PT 4, give almost similar estimates of annual pollen and spore deposition at 132 000 and 102 000 cm^{-2} respectively. Figures for pollen alone are even closer, as the wetter site (PT 1) records over five times as many pteridophyte spores as the drier.

The highest influx estimates come from PT 5, the disturbed forest site west of the north-east bay. Here the annual PDR apparently exceeds 400 000, a figure that may have been inflated by the action of red ants, found infesting the trap, in importing appreciable quantities of pollen.

In contrast, the floating trap (PT 6) records a pollen influx one thousand times smaller than that of PT 5. Spores represent a higher proportion of the total catch in the floating trap, with an influx only 25 times lower than for the land trap. Despite the vulnerability of the raft trap, there was no evidence of overt

TABLE 7.2. *Annual pollen and spore deposition rates estimated from pollen traps*

Pollen trap no.	Location	Pollen and spores per trap	Spores cm^{-2} yr^{-1}	Pollen cm^{-2} yr^{-1}	Pollen and spores cm^{-2} yr^{-1}
PT 1	Hill Forest, Markham Point	3 638 568 ± 249 751	6 835 ± 2 061	125 056 ± 8 815	131 892 ± 9 053
PT 4	Closed forest, east shore, Lake Wanum	2 845 711 ± 220 870	1 228 ± 868	100 696 ± 7 830	101 924 ± 7 911
PT 5	Disturbed forest, prom-ontory, Lake Wanum	11 046 433 ± 688 054	1 945 ± 1 739	399 042 ± 24 915	400 986 ± 24 976
PT 6	Open water, north-east bay, Lake Wanum	10 057 ± 3 400	73 ± 55	293 ± 111	366 ± 124

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FIGURE 7.1. Major ecological groups represented in contemporary pollen samples
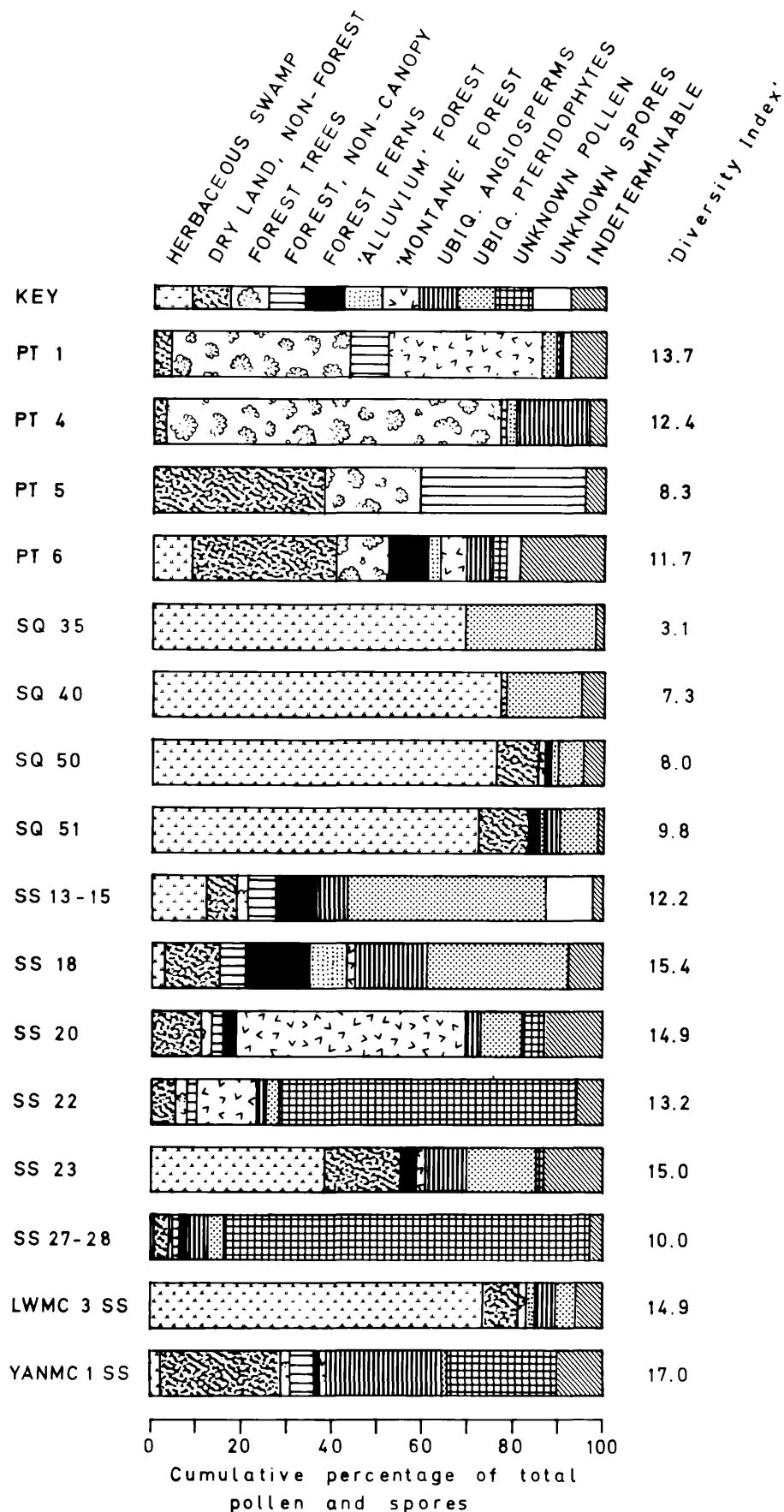
tampering and no reason to suspect that these figures do not rep-
resent a valid estimate of airborne pollen and spore deposition in
the central area of the north-east bay of Lake Wanum.

CONTEMPORARY POLLEN ASSEMBLAGES

Pollen assemblages from all traps and surface samples are
summarised in Fig. 7.1. Pollen and spore taxa are grouped[1] into
tentative ecological classes, based on known plant distributions
(Table II.1).

Herbaceous swamp taxa comprise over 70% of the total
count from all Lake Wanum swamp sites, with the exception of the
floating pollen trap where they represent only 9%. These taxa also
contribute 40% of the catch to the swamp marginal sample at Redhill.
Small percentages recorded from the 'alluvium forest' (SS 18) and wet
forest at Sankwep (SS 13-15) sites reflect the presence of
Nephrolepis, Stenochlaena palustris (SS 18) and *Uncaria* T.
(SS 13-15). Although these three taxa are included in the herbac-
eous swamp category, their sources are obviously not restricted to
this vegetation type.

The dry land non-forest category is harder to define.
Taxa included are those frequently represented in such situations,
although many show a more widespread distribution, either within
the single species or in other plant taxa contributing to the
pollen taxon. The group is represented to some extent in almost
all surface assemblages, being understandably more abundant in
disturbed forest and non-forest sites. Good representation occurs
in open lake catches also, e.g. pollen trap PT 6 and the surface

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[1] Lists of taxa comprising each group may be found in Table II.2

sediments from short cores, but not where samples are over-

whelmed by taxa from locally growing herbaceous swamp vegeta-

tion.

Included in the forest trees category are a number of

genera more common in the canopy of lowland forest, although again

many show a much wider distribution. This group of taxa appears to

reflect best the composition of the forest in the vicinity of Lake

Wanum, and is well represented in all pollen traps. The high

values of the group in PT 1 are primarily due to the inclusion of

Aporosa, a genus with a wide altitudinal range, and *Macaranga*

ovatifolia T. the source and range of which is unknown.

'Alluvium' forest is a group of taxa frequently found in

riparian, floodplain and mangrove environments, although many

constituent plants possess a much less restricted distribution than

this. The group is not particularly diagnostic as even at the

'alluvium' forest site (SS 18) its taxa make up less than 10% of

the total catch. The representation in open sites at Lake Wanum

may derive from nearby sources in the Markham and Oomsis valleys.

Non-canopy forest taxa include those trees restricted to,

or more common in, the understorey together with shrubs, palms and

vines. Components of the group are represented in all samples from

forest sites. A small but distinct group of taxa comprises the

forest ferns, although many such plants must also contribute to the

'ubiquitous pteridophytes' class. The highest proportions of

these spore taxa occur in the wetter lowland (SS 13-15) and 'alluv-

ium' forest (SS 18) samples.

Pollen taxa from plants not occurring in the lowest

altitude vegetation are included in the 'montane' forest category.

Some taxa, such as *Lithocarpus*, extend down to altitudes of 180 m

and lower, and *Castanopsis* T. pollen is found in trap PT 1 from
'hill' forest. Other taxa are more common above the 1 000 m alti-
tude of the highest site sampled, but contribute to pollen
assemblages at lower elevations.

The ubiquitous angiosperm and pteridophyte classes in-
clude pollen and spore taxa the sources of which are either
undetermined, or cannot be assigned with confidence to any ecologi-
cal category. Some such taxa embrace many plant genera or famil-
ies, e.g. Urticaceae/Moraceae pollen, or psilate monolete fern
spores. In other cases the pollen or spore taxon is identifiable
to the generic, or even specific level, but the plant occupies a
wide variety of different habitats. The ubiquitous pteridophytes
appear most common in the wetter forest types and in herbaceous
swamp samples where many spores from locally abundant ferns,
especially *Nephrolepis*, lose their diagnostic perisporia.

Pollen or spores not assignable to any lower level
taxonomic unit are included in the 'unknown' classes. The only
significant values are encountered in the two samples from
Yanamugi, where pollen type UK 194 is abundant, and in the 'hill'
forest site SS 22, where pollen type UK 106 dominates the assemb-
lage. Both taxa almost certainly derive from the local flora at
each site.

Most of the ecologically defined groups of pollen and
spores appear to characterise the vegetation type to some extent,
even though few taxa are restricted to a single habitat. Minor
refinements of the group allotment of taxa could be proposed, but
few would substantially alter the overall results.

*Diversity of contemporary pollen assemblages*

Diversity, or the relationship between numbers of taxa and individuals is a difficult measure to define for pollen spectra. The often non-specific composition of pollen and spore taxa and the vagaries of pollen dispersal render improbable a correlation between the diversity of a pollen assemblage, and that of the vegetation from which it derives. However, in some cases such a relationship does exist. Using Williams' (1964) index of diversity, Birks (1973) showed such a correlation in alpine and sub-alpine vegetation types of western Scotland. Williams' index is appropriate only where the assemblage contains a large number of taxa whose abundance follows a logarithmic series. As the number of taxa was limited for some of the Markham Valley samples a cruder index was calculated by

$$\frac{\text{no. of pollen and spore taxa}}{\text{log. total no. of individuals}}$$

to give relative measures of the diversity of catch in the contemporary pollen assemblages.

The lowest diversity values shown in Fig. 7.1 are recorded from herbaceous swamp sites where the number of local plant species is also low. A low value is also obtained from the disturbed forest site, PT 5. Highest indices of diversity are produced by samples from within forest vegetation, or from those open sites that might be expected to collect pollen and spores from a number of different vegetation types. Although no diversity measures for the vegetation exist for comparison, intuitively the diversity of the pollen assemblages appears to reflect, to some degree,

FIGURE 7.2. Contemporary pollen spectra (selected taxa) from herbaceous swamp sites
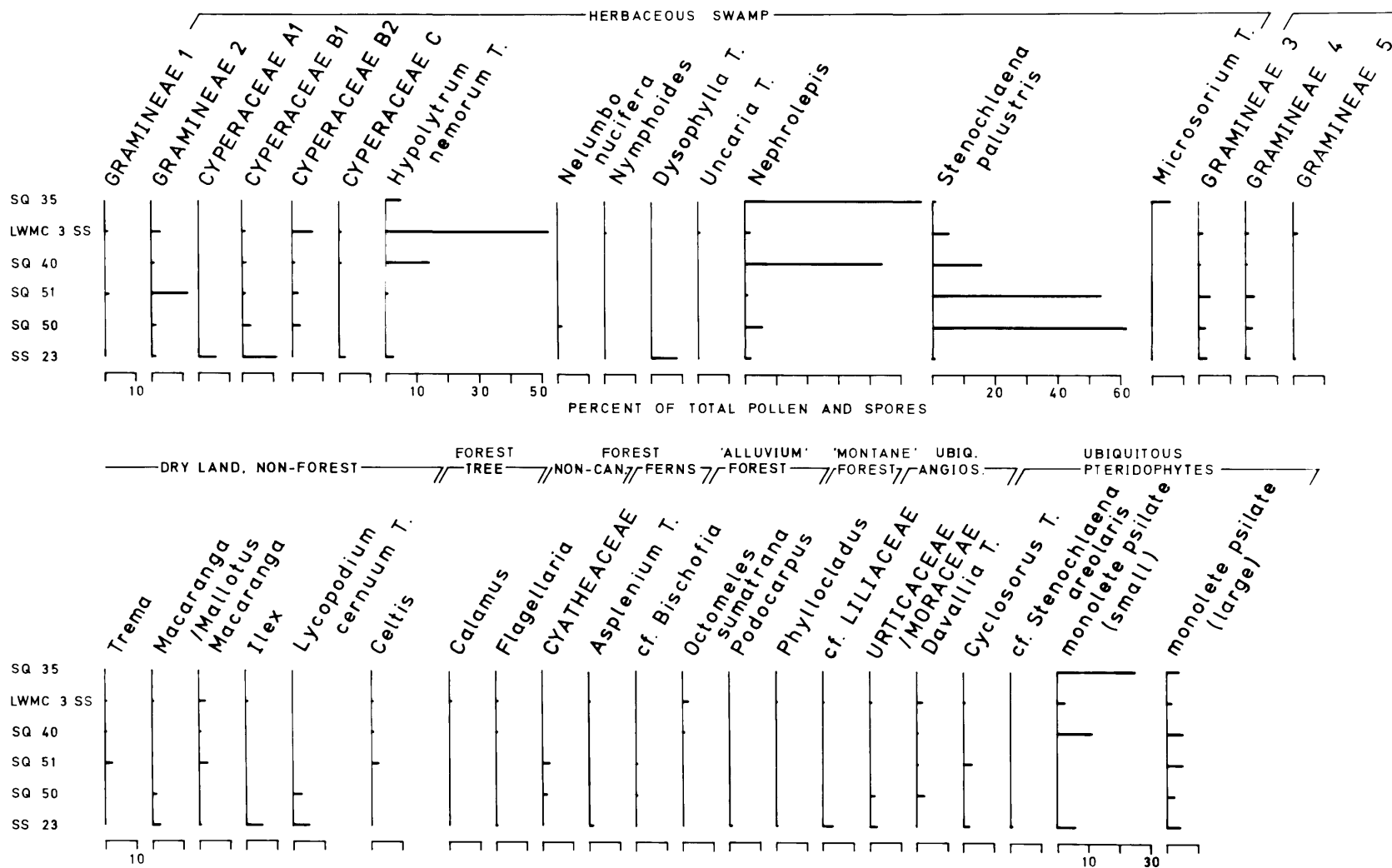
vegetation diversity, except where a pollen spectrum derives from a number of different vegetation types.

Herbaceous swamp site assemblages

The herbaceous swamp vegetation of the Lake Wanum area is one of the vegetation types better defined by its pollen spectra, although at Yanamugi there is poorer representation of the much less extensive swamp community. It is fortunate that 12 out of 37 plant taxa recorded in the vegetation quadrats at Lake Wanum and 7 out of 8 designated 'common' taxa produce recognisable and preservable pollen or spores. As herbaceous swamp vegetation associations have been previously described, it may be possible to characterise these by their pollen assemblages. Selected taxa recorded from surface spectra at Lake Wanum and Redhill are shown in Fig. 7.2 as percentages of the total pollen and spore count.

Samples SQ 35 and LWMC 3 SS both come from the western margin of the north-east bay of Lake Wanum. The first comprises surface litter from floating root-mat of Group A vegetation, whilst the second is surface detritus from a short core in open water, 15 m to the east. Both assemblages are dominated by the pollen and spores of herbaceous swamp taxa. The assemblage from SQ 35 consists almost exclusively of the four species dominating the root-mat vegetation: *Nephrolepis, Hypolytrum nemorum* T., *Stenochlaena palustris,* and *Microsorium* T. *Nephrolepis* is by far the most abundant, even more so if a proportion of the monolete fern spores lacking a perisporium is included. In contrast, the core surface sample reveals a very different pollen and spore assemblage despite its proximity to the same vegetation type. *Hypolytrum nemorum* T.

pollen dominates the count, with *Stenochlaena palustris* and *Nephrolepis* well represented. Also present is a number of pollen and spore taxa from other local swamp plants, including Gramineae 1 and 2 (probably *Leersia hexandra*), several Cyperaceae types and *Nymphoides*.

The root-mat litter sample is obviously dominated by extremely local taxa to a greater extent than the core sample that probably receives water-borne pollen and spores from a wider area. *Nephrolepis hirsutula* is found in the lower level of the root-mat vegetation and appears an abundant spore producer. In contrast *Hypolytrum nemorum* produces flowers above the general height of the dense vegetation mat, and was not observed in flower during 1974 when the litter sample was gathered. Profuse flowering did occur during 1976, when the short core was collected. These factors alone could account for observed differences in the two assemblages. It is also possible that the litter sample records a shorter time span than the surface detritus from the core and may thus be unduly influenced by temporary patterns of pollen and spore accumulation.

Four samples come from vegetation quadrats in the south swamp area of Lake Wanum. *Hypolytrum nemorum* dominates the (Group B) vegetation at the site of SQ 40. *H. nemorum* T. is well represented in the surface assemblage, but *Stenochlaena palustris* is equally so and the count is dominated by *Nephrolepis* spores although neither fern occurs in the quadrat. Pollen of grasses and of other sedges occurs in small proportions.

Vegetation of Group D (*Leersia hexandra* floating mat) occupies the site of sample SQ 51. *Stenochlaena palustris* spores dominate the count of litter from the root-mat. *Leersia hexandra*

is probably well represented in the Gramineae 1 and 2 grains, and *Phragmites karka* could account for a proportion of the larger grass pollen classes. *Nephrolepis* and various sedges are also represented despite their absence from the quadrat. No pollen of *Nelumbo nucifera* was encountered although the species occurs locally. *Nelumbo nucifera* and *Leersia hexandra* are the only species growing at the site of SQ 50, a quadrat of the Group E open water association. Both taxa are represented in the pollen assemblage, although the count is dominated by *Stenochlaena palustris* with *Nephrolepis* spores and various Cyperaceae pollen also present.

A sample of fine organic detritus from the margin of Redhill swamp (SS 23) contains herbaceous swamp taxa as 40% of the pollen assemblage. *Hypolytrum nemorum* T., *Nephrolepis* and *Stenochlaena palustris,* all components of the swamp vegetation, are represented together with a relatively high proportion of other Cyperaceae pollen. The small aquatic herb *Dysophylla verticillata* is abundant in the vicinity of the sample site and presumably contributes the proportion of *Dysophylla* T. pollen.

Surface pollen assemblages from swamp sites do reflect, to a limited extent, the herbaceous swamp vegetation associations described previously. Correlation between the floristics of the vegetation and of the pollen spectrum appears better where the sample analysed consists of litter or detritus from a floating mat. In the case of samples derived from the underlying sediment surface a number of factors may explain the less satisfactory correlation. The pollen assemblage is less dominated by very localised pollen and spore sources, and may also collect pollen from a larger area containing different vegetation types. A higher proportion of

water-borne pollen may also become incorporated into the sediment samples. The sediments may integrate several years' deposition, during which time the floristic composition of the adjacent vegetation may well have changed.

The surface pollen assemblages from swamp sites contain varying proportions of non-swamp taxa. In the sample from Redhill (SS 23), that with the highest proportion of non-swamp and ubiquitous taxa, a number of these taxa probably emanate from periodically inundated vegetation e.g. *Lycopodium cernuum* T., cf. Liliaceae, *Ilex, Cyclosorus* T., and *Asplenium* T.

The short core surface sample from Lake Wanum (LWMC 3 SS) shows the greatest diversity of pollen and spore taxa, despite consisting of over 50% of *Stenochlaena palustris* spores. Notable is the representation of sub-canopy components of the nearby forest, namely *Flagellaria, Asplenium* T. and probably *Davallia* T. Pollen assemblages from samples SQ 50 and SQ 51 reflect the influence of riparian and swamp forest along Oomsis Creek in the proportions of cf. *Bischofia* pollen and Cyatheaceae spores. The percentages of larger Gramineae pollen in these two samples may reflect the proximity of grassland. However, there are no patterned grains larger than 30 μm (Gramineae 5) typical of *Themeda australis*, the major dry land grass species in the area. In SQ 51 at least, the grass pollen may represent the local occurrence of *Phragmites karka*.

The remaining swamp site pollen assemblages contain few non-swamp taxa. This may be due either to the large distance from dry land vegetation (SQ 40) or to the intensely local representation and low total count (SQ 35).

FIGURE 7.3. Contemporary pollen spectra (selected taxa) from non-swamp sites
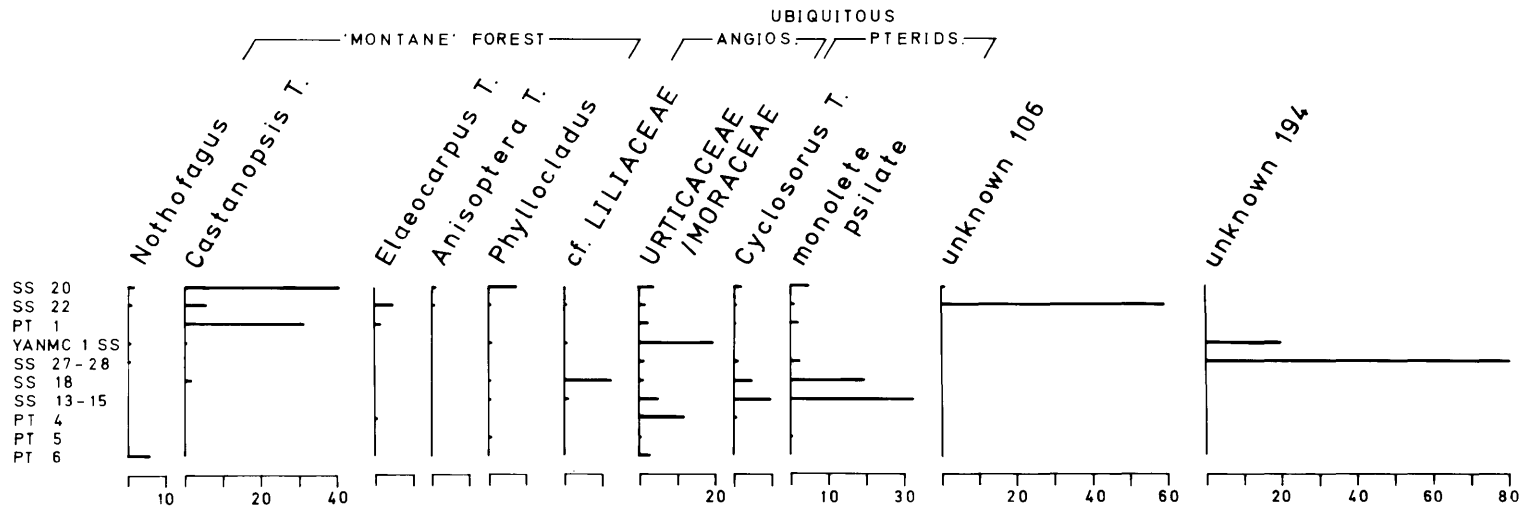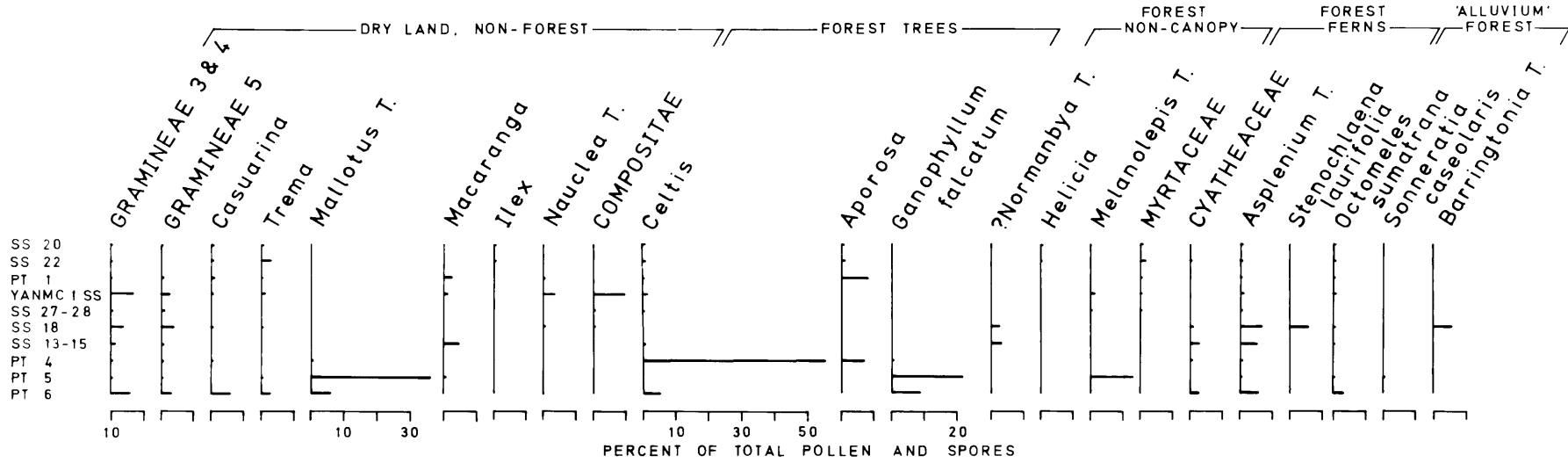
Non-swamp site assemblages

The composition of pollen assemblages from sites not dominated by herbaceous swamp taxa is very varied, as might be expected given the wide range of vegetation types encompassed. Selected taxa represented in these samples are shown, as percentages of the total pollen and spore count, in Fig. 7.3.

Many spectra, especially those from within forest, are dominated by one or more highly abundant taxa. In pollen trap PT 5, 80% of grains are from three taxa (*Hypserpa, Mallotus* T. and *Ganophyllum falcatum*), whilst *Celtis* comprises 54% of the catch in PT 4. Both samples from Yanamugi are dominated by the unidentified pollen type UK 194. In samples from higher altitudes *Castanopsis* T. is strongly represented with 31% in PT 1 and 41% in SS 20. The unidentified pollen taxon UK 106 accounts for 64% of the total in sample SS 22, also from high altitude 'hill' forest. Two extreme lowland forest sites (SS 13-15 and SS 18) are dominated by fern spores and other understorey components, such as cf. Liliaceae, rather than arboreal pollen.

In contrast to the forest and herbaceous swamp samples, non-forest site assemblages appear less dominated by a few locally occurring taxa. These samples include the floating pollen trap PT 6, the surficial sediment from Yanamugi, and the samples LWMC 3 SS and SS 23 that, although swamp dominated, include a wide variety of dry-land taxa also.

Few pollen or spore taxa are present in all dry-land assemblages. Those with the widest occurrence tend to be taxa such as Gramineae, Urticaceae/Moraceae, or monolete fern spores that represent a large group of plants from many ecological situations.

Nor are many taxa restricted to a single, well defined community, although a few such possible 'indicator' taxa may be identified. One group termed 'montane' (at least with respect to the present study) includes *Nothofagus, Podocarpus* and *Phyllocladus*. These three genera of trees are more common above 1 000 m, although all have been recorded growing at lower elevations. Both *Nothofagus* and *Phyllocladus* pollen are well represented in the higher altitude 'hill' forest samples SS 20 and SS 22, although neither tree appears to grow in the local forest. These taxa are also found in pollen spectra from much lower altitudes. *Nothofagus* occurs in both contemporary assemblages from Yanamugi and from the floating pollen trap PT 6, at Lake Wanum, whilst *Phyllocladus* is even more widespread occurring in over half the low altitude samples. *Podocarpus* pollen is represented by two grains from the swamp margin sample SS 23 at Redhill.

The designation of taxa restricted to lowland environments is more difficult. Two predominantly mangrove genera, *Sonneratia* and *Rhizophora* are sufficiently restricted to coastal habitats. The occurrence of considerable *Sonneratia caseolaris* pollen in trap PT 5 may be attributable to the action of red ants, although wind-borne influx cannot be excluded. The species does not grow at Lake Wanum today although it may occur nearby in the Markham Valley. The closest definite source is east of Labu, 13 km distant. A single occurrence of *Rhizophora apiculata* T. pollen from sample SS 20 at an altitude of 970 m is unlikely to be a misidentification as the genus is quite distinctive (Anderson and Muller, 1975). Although contamination cannot be ruled out, Muller and Caratini (1977) also report finding pollen of *Rhizophora* from a *Sphagnum* polster from 870 m altitude on Mount Santabong, West

Sarawak. *Octomeles sumatrana*, a species of large tree particularly common along lowland river channels, is also represented in the high altitude 'hill' forest pollen assemblages, although its pollen is less distinctive than the aforementioned taxa.

POLLEN PRODUCTION AND DISPERSAL IN THE MARKHAM VALLEY

Data presented above are too fragmentary to allow construction of an integrated model of contemporary pollen deposition in the area. They do however illustrate various aspects of pollen production and transfer in the lowland tropics that may be compared instructively with similar studies from other tropical and temperate regions.

Pollen production rates

The PDR estimates from the three pollen traps within arboreal vegetation suggest a high level of pollen production for at least some taxa. The maximum PDR for a single taxon is 143 000 grains cm^{-2} yr^{-1} for *Mallotus* T. in trap PT 5 although this value may have been inflated by insect activity. Estimates from undisturbed, although possibly overloaded, traps include 55 000 grains cm^{-2} yr^{-1} for *Celtis* in PT 4, and an annual deposition rate of 41 000 grains cm^{-2} in PT 1 for *Castanopsis* T.

The total PDR estimates from these three traps range between 100 000 and 400 000 grains cm^{-2} yr^{-1}. These figures are much higher than estimates from pollen trapping studies in a variety of other climatic and vegetation types (Table 7.3) although few of the tabulated samples derive from unroofed traps within forest. Intermediate PDR estimates have been calculated for lake sediments from deciduous forest sites in North America (Davis, *et al.*, 1973).

TABLE 7.3. *Comparative airborne pollen and spore deposition rates from other areas*

Author	Vegetation	Trap type and location	PDR, Pollen and spores cm^{-2} yr^{-1}
Flenley (1973)	Tropical rain-forest, Selangor, Malaysia	Oldfield traps Canopy Ground	800 1 100 - 2 020
Kershaw and Hyland (1975)	Tropical rain-forest margin, Atherton Tableland, Qld, Australia	Tauber traps floating on small lake Roofed Unroofed	90 - 124[a] 129 - 250[a]
Hope (1973)	Alpine and sub-alpine forest and non-forest, Mt. Wilhelm, Papua New Guinea	Tauber traps Roofed Unroofed Floating unroofed	40 - 710 750 - 6 450 750 - 900
Flenley (1973)	Montane forest, Papua New Guinea	Rain gauge sample	1 130
Hope (1968)	Forest and non-forest vegetation, Wilson's Promontory Vic., Australia	Tauber traps Unroofed	1 300 - 14 500
Tauber (1967)	Temperate broad-leaved forest, Zealand, Denmark	Tauber traps Unroofed floating on lake Roofed within forest	2 850 - 6 600[b] 788 - 825[b]
Berglund (1973)	Temperate forest and non-forest, Blekinge, south-eastern Sweden	Tauber traps floating on four lakes	2 000 - 4 400[c]

[a]Excludes aquatic, weed, and grass pollen
[b]Collection period March - November only
[c]Mean of roofed and unroofed traps. Unroofed traps collected 10 - 40% more pollen than roofed

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Investigations within Malaysian lowland forest (Flenley, 1973) produced PDR estimates of 1 100 and 2 020 grains cm^{-2} yr^{-1} from ground level traps. Although pollen traps of different design were employed, this factor alone is unlikely to explain the great difference between these figures and the values obtained in the current study. Estimates of contemporary PDR for Papua New Guinea highland areas (Hope, 1973, Flenley, 1973) indicate values in the range of 750 to 6 400 grains cm^{-2} yr^{-1}, only slightly lower than comparable northern European and temperate Australian situations (Tauber, 1967, Berglund, 1973, Hope, 1968).

Pollen dispersal

It is evident from the PDR results that pollen dispersal within the study area is a highly localised process. The very low annual influx values obtained from the isolated floating trap PT 6, one thousand times smaller than the maximum forest PDR estimates, can be explained only by an extremely low efficiency of aerial pollen transport. Values of a similar order of magnitude (hundreds of grains cm^{-2} yr^{-1}) are reported from floating pollen traps at other tropical sites (Hope, 1973, Kershaw and Hyland, 1975) and the canopy level trap of Flenley (1973). In contrast, from Blelham Tarn, a small lake in north-west England, Bonny (1978) reports an annual pollen influx rate to floating traps only twenty times less than the rate recorded from adjacent forest or lake-marginal sites.

A proportion of the pollen in the floating trap at Lake Wanum derives from vegetation types not immediately adjacent to the lake. A similar component is identifiable in surface assemblages from non-forested sites not overwhelmingly dominated by local herbaceous swamp taxa. Within the forest, a high proportion of taxa

derive from plants growing in the understorey. This situation is analogous with Tauber's three-component model of pollen transfer (Tauber, 1965). A 'trunk space' component is recognisable in forest sites, and a more regional 'rainout component' becomes significant in open sites where the pollen and spore influx from local vegetation is not overwhelming. Identification of an 'above the canopy' forest component is less satisfactory, as many canopy taxa are also common in the 'trunk space' component. Proportions of taxa thought to represent both of these components are found in open depositional sites adjacent to the forest and in the isolated floating pollen trap.

In a study of pollen transfer at sites in West Malesia Morley (1976) found that pollen from larger trees dominated assemblages in forest, although there was a substantial representation of trunk space taxa. Herbaceous swamp pollen was also found to predominate over forest pollen in swamp sites, although less so in open water. Unlike the situation in the Markham Valley there was little transfer of trunk space pollen and spores to swamp depositional sites, possibly due to the denser nature of the forest margin. Morley also found transport of *Trema* pollen above the altitudinal limit of the genus, but no evidence for downslope dispersal of any pollen taxa.

At Lake Euramoo, in north-east Queensland, Kershaw and Hyland (1975) identify a small 'rainout' component, with the 'above the canopy' component dominating pollen fallout onto the central lake surface. At Yanamugi, slightly smaller than Euramoo, the surface sediment assemblage contains some non-canopy forest taxa and a high proportion of non-forest taxa. The open nature of the semi-deciduous forest around the site could allow for significant transfer of 'trunk space' pollen and spores.

Pollen representation

Pollen 'representation' is an ill-defined concept depending as it does on the net outcome of pollen production, dispersal and preservation. In certain cases it may be feasible to compare frequencies of pollen in a modern assemblage with the proportions of source taxa in the surrounding vegetation (e.g. Davis and Goodlett, 1960). In the absence of comprehensive data on vegetation composition and floristics any such estimates here are highly subjective.

In the lowland tropical situation it could be argued that any pollen or spore taxa consistently encountered in sediments are 'over-represented'. Perhaps the majority of species hardly ever contribute to the pollen assemblage either because their pollen production is very low, maybe coupled with zoophilous pollination mechanisms, or because their wind-borne pollen is poorly dispersed or easily degraded by soil organisms. Nevertheless, certain pollen taxa possess a combination of production and dispersal abilities that enable them to be deposited well beyond the borders of the parent population. In tropical montane pollen studies these 'high relative export' taxa (*sensu* Flenley, 1973) are usually those found above the altitudinal limit of the source vegetation. In the present study pollen taxa similarly 'over-represented' are identified as those found either above or below the altitudinal limits of their source, or as pollen taxa much more widespread than the corresponding vegetation. Most noticeable are *Rhizophora apiculata* T. and *Octomeles sumatrana* (above alt. limit), *Nothofagus, Phyllocladus* and *Podocarpus* (below alt. limit) and *Trema* and *Casuarina* (generally widespread). With the exception of *O. sumatrana*, all taxa have been cited by other authors as showing

a similarly high relative export capacity (Hafsten, 1960,

Hamilton, 1972, Flenley, 1973, Hope, 1973, Morley, 1976, Colinvaux

and Schofield, 1976a, Caratini et al., 1973 and Muller and

Caratini, 1977).

Many other taxa show a locally very high representation

in the vegetation type in which the source plant occurs. Con-

versely some pollen taxa occur as very small proportions of the

total even when the source plants are abundant and close to the

sampling site. The best evidence comes from the herbaceous swamp

assemblages, from which comprehensive ecological data are also

available. Here taxa considered 'under-represented' include

Cyperaceae (excepting Hypolytrum nemorum T.), Nelumbo nucifera,

Nymphoides, and Gramineae. Hope (1973) and Colinvaux and

Schofield (1976a) also comment on the apparently poor dispersal

properties of grass pollen. It should be emphasised that these taxa

remain 'over-represented' in relation to the large number of

plants 'non-represented' in contemporary and fossil pollen assem-

blages.

POLLEN TRANSFER IN THE LOWLAND TROPICS

Flenley (1973) concludes that there appears to be no

fundamental difference between tropical and temperate pollen

'rain'. Whilst this is true, the current study reveals great diff-

erences in the degree of influence of various factors. Pollen and

spore production, at least in forest conditions, is shown to be

very high, whereas preservation and aerial dispersal are of a very

low order. At forest and herbaceous swamp vegetation sites the

great majority of the pollen appears to be derived from the local

vegetation within tens of metres. In more open sites the propor-

tion of taxa from increasingly distant sources is much greater.

Pollen is carried both upslope and downslope. Although downslope transport appears more significant, this may be due only to the number of distinctive taxa involved. With the steep altitudinal gradients of Papua New Guinea this process could produce considerable mixing of pollen from a wide range of vegetation types. Such a 'regional' component is nevertheless a much lower proportion of the total PDR than it appears to be in higher altitude sites (Hope, 1973).

Because of the generally low efficiency of aerial pollen dispersal, other routes for the incorporation of pollen into sediments may be important. Extensive water-borne influx of pollen has been demonstrated for temperate lakes (Bonny, 1976, 1978, Peck, 1973) and may be proportionally more important in the tropics (Germeraad et al., 1968). Although neither lake in this study possesses a permanent inflow stream, the effect of slopewash and periodic flooding on pollen transfer is unknown. Landslips and other natural or artificial erosional events could release large quantities of freshly deposited pollen from the soil surface into lakes or watercourses. These agents surely require investigation for a better understanding of pollen transfer and deposition in the tropical lowland environment.