HUMAN IMPACT ON THE SUBALPINE
VEGETATION OF MT WILHELM
PAPUA NEW GUINEA

by

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Frontispiece: the lower Pindaunde lake and the A.N.U. field station, looking east.

*"Is not the pastness of the past the profounder,
the completer, the more legendary, the more
immediately before the present it falls?"*

'The Magic Mountain' Thomas Mann

To Sirinant

It has long been recognized that forest fire has been a major factor in the development of the vegetation of the Central Highlands of New Guinea. The extent of this impact has been a matter of controversy. This study reports a study of human impact on the vegetation of the subalpine region of Mt Wilhelm (4500 m, 3°45' S, 145°30' E), the highest mountain in New Guinea. The study area is in the subalpine zone, between about 3000 m and the tree line at 3500 m, in which forest, grass and alpine communities form a regular mosaic.

A palaeoecological approach to the history of the vegetation pattern was combined with an ecological study of the present landscape. Pollen and charcoal particle analysis were made on 1000-year-old peat cores from 34 sites in the subalpine zone. The pollen record shows a long history of forest cover in the valley, with a significant reduction in forest cover in the late 19th century, coinciding with the arrival of Europeans. The charcoal record shows a long history of fire, with a significant increase in fire frequency in the late 19th century, coinciding with the arrival of Europeans.

Except where otherwise acknowledged
this thesis represents my own original
work.

R.T. Corlett

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The palaeoecological data show that forest cover was extensive in the valley until the late 19th century, when a significant reduction in forest cover occurred. This reduction was coincident with the arrival of Europeans and the introduction of fire. The charcoal record shows a long history of fire, with a significant increase in fire frequency in the late 19th century, coinciding with the arrival of Europeans. The pollen record shows a long history of forest cover in the valley, with a significant reduction in forest cover in the late 19th century, coinciding with the arrival of Europeans. The charcoal record shows a long history of fire, with a significant increase in fire frequency in the late 19th century, coinciding with the arrival of Europeans.

The present-day vegetation pattern is an artefact of human disturbance. Localized destruction of the forest above 3000 m by fire started between 1900 and 1910. The fire was a result of a fire started by a European settler. The fire spread to the surrounding forest, and the forest cover was significantly reduced. The fire was a result of a fire started by a European settler. The fire spread to the surrounding forest, and the forest cover was significantly reduced.

The start of subalpine disturbance during the last few hundred years is reflected in the pollen record. The pollen record shows a long history of forest cover in the valley, with a significant reduction in forest cover in the late 19th century, coinciding with the arrival of Europeans. The charcoal record shows a long history of fire, with a significant increase in fire frequency in the late 19th century, coinciding with the arrival of Europeans.

ABSTRACT

It has long been recognised that fires lit by man have had an important impact on the vegetation of high mountains in New Guinea, but the timing and extent of this impact has been a matter for speculation. This thesis reports a study of human impact on the vegetation of the subalpine region of Mt Wilhelm (4509 m, 5°45'S, 145°01'E.), the highest mountain in Papua New Guinea. The term 'subalpine' is used for the altitudinal belt, between about 3300 m and the treeline at 3900 m, in which forest, grassland and mire communities form an irregular mosaic.

A palynological approach to the history of the vegetation pattern was combined with an ecological study of the processes involved. Pollen and charcoal particle analyses were done on short peat monoliths from 34 subalpine sites, mostly in the Pindaunde valley but with single sites in other valleys. The monoliths were dated and correlated by the presence of two volcanic tephra layers, clearly recognisable in the field. Detailed ecological studies were confined to the Pindaunde valley but brief surveys were made in most of the other valleys.

The palynological data show that before 1200 BP human impact on the vegetation was negligible and probably limited to the treeline ecotone. Below the treeline forest covered the valley sides and the better-drained parts of the valley floor. Non-forest vegetation was confined to more or less waterlogged sites. Tussock grassland dominated by Deschampsia klossii was quite extensive in the upper third of the subalpine zone but, below about 3650 m, closed forest directly abutted mire communities. This pre-disturbance pattern is consistent with waterlogging, rather than cold-air ponding, as the main factor excluding forest from areas below the treeline.

The present-day vegetation pattern is an artefact of human disturbance. Localised destruction of the forest above 3550 m by fire started between 1200 and 230 BP. Then, within a period of probably less than 20 years after the 230 BP tephra fall, rapid and major clearance occurred throughout the subalpine zone, except in the damp and inaccessible Imbukum valley. Since then, clearance has again been localised and mainly below 3600 m.

The start of subalpine disturbance during the last few hundred years apparently results from cultural changes taking place at this time throughout the Central Highlands. The most recent of these changes may reflect the introduction and spread of the sweet potato (Ipomoea batatas). The details of the history and pattern of clearance were, however,

determined by non-human environmental factors, as the forest is not normally susceptible to fire. In particular, the 230 BP event must reflect a major environmental catastrophe, probably a period of exceptional drought.

The present vegetation pattern appears stable but the secondary grasslands consist of a mosaic of seral stages. There are small patches of secondary forest in some valleys, but in most places succession is so far limited to an increase in the size and number of non-forest shrubs and a patchy invasion by seedlings of forest taxa. This secondary succession is strongly aspect-dependent. The forest-margin communities are also developing in the absence of burning, but a general advance of the forest edge was not apparent, except at the lowest sites. If future fires are prevented, probably all secondary grasslands will eventually revert to forest, although this will take several hundred years.

Similar processes have apparently operated on other mountains in New Guinea, but the available evidence suggests that the history of human impact has been different on each mountain.

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CONVENTIONS.

The following conventions of nomenclature or useage have been adopted in this thesis.

The name New Guinea refers to the whole island, the western half is called West Irian and the eastern half Papua New Guinea. Place names in Papua New Guinea where possible follow the 1:100,000 maps (Series T601 and T683). For place names on Mt Wilhelm itself I have used the spellings suggested by my Simbu field assistant, Mr William Dua. The only significant divergence from previous useage is that Guruauglakugl is here used for the lake and valley previously called Guraguragl, Guragakugl, Guraguragugl and Guraguragukl by various authors. The 'Brass Tarn' of previous authors is called Nigl Gogl ('red water') by the Simbu, but to avoid confusion, the published name has been retained in this thesis. Following Hope (1973) 'upper' and 'lower' Pindaunde lake has been used in preference to the local names Pinde and Aunde, because of confusion in the literature as to which name applies to which lake.

The people referred to as Chimbu by previous authors are here called Simbu, following their own preference and the name applied to the province by the new provincial government. Altitudes are given as metres above mean sea level. A 1:100,000 map including the eastern half of Mt Wilhelm became available after completion of my field work. All altitudes in this thesis have been corrected for consistency with this map and may differ by up to 100 m from those previously published.

The chronology used in this thesis is based on estimates of the radiocarbon ages of two tephra layers (Chapter Four and Appendix 1). Events not directly dated by these tephra layers are given dates based on the assumption of uniform sediment accumulation rates between the tephras and between the upper tephra and the surface. All dates are given as years before present (BP), which is 1950 A.D. by convention. However, only in the case of events dated directly by the tephra layers are these dates in conventional radiocarbon years; in other cases additional errors result from variations in the accumulation rate and the non-linearity of the calibration curve. (The distinction between directly-measured radiocarbon ages and those based on extrapolation is potentially significant in the time-range covered by this study.) Uncalibrated, radiocarbon-based dates from other authors have also been quoted as years BP. Calendar dates and those based on other dating methods have been explicitly distinguished from these.

Plant names follow Johns and Stevens (1971).

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CHAPTER 1

INTRODUCTION

The island of New Guinea is one of the three main areas of the world with wet, equatorial mountains extending above an altitudinal treeline. In all three areas, New Guinea, East Africa and South America, there are large human populations which have had a varying impact on the mountain vegetation. This impact has been through the agency of fire and, except in New Guinea, the grazing of domestic animals. The question of the relative importance of human influence and 'natural' (i.e. non-human) environmental factors in determining the present-day vegetation on these mountains has often arisen and rarely been satisfactorily answered. The mountains of the New Guinea Highlands present a particular problem because, although man has been in the area for at least 30,000 years, written history starts less than fifty years ago. On the other hand there is a possibility of continuity between palaeoecological and ecological studies in New Guinea, which is rare in areas with a more complex history.

The people of the New Guinea Highlands are subsistence horticulturalists. Their influence on the environment is most obvious at intermediate altitudes where most of the forest has been cleared for gardens. Golson (1977a) has written 'the Highlands landscape between 1500 m and 2500 m is an artefact and represents the most complete and widespread transformation of any New Guinea ecosystem by man'. Above the upper limit of gardens (c.2700 m) there is a belt of continuous forest and the impact of man's activities is less obvious. Yet although the intensity of human use declines with altitude, the sensitivity of the vegetation to disturbance increases. Even infrequent disturbance episodes may leave a lasting record in the vegetation. Growth rates of woody species decline with altitude and thus recovery from disturbance is slower. Moreover, near the climatic limit of tree growth, the competitive balance is easily tilted in favour of grassland.

It is this zone below the treeline, where forest and grassland form an irregular mosaic, which is the subject of this study. Man enters this zone as a hunter or traveller. The high mountain environment is only a marginal part of his range but the study of his past impact on the vegetation there is necessary to an understanding of the overall prehistory of the Highlands. It can also add to our understanding of the way in which vegetation near to its climatic limit responds to disturbance and in this way may be useful in developing conservation and management strategies. Equally, the reconstruction of the vegetation before man's influence became dominant can add to our knowledge of the operation of ecological controls near a tropical treeline.

The possibility of contributing information to these wider issues adds extra interest and relevance to this study. The primary aim, however, is simply an understanding of the way in which man's activities have influenced the observed vegetation. The reason for the pattern of forest,

mires and grassland within the thousand metres below the treeline on many New Guinea mountains has been debated since Europeans first climbed them. Since then there have been a number of descriptive studies but none has concentrated on an analysis of the processes responsible for the pattern.

The first ascent of a high mountain in New Guinea by a European was that of Mt Victoria by Sir William MacGregor in 1889. He found 'no trace whatever of human presence except (his) own, either past or present' (MacGregor 1889, 1890). The earliest report of the exploitation and modification of the summit region of a high mountain by man is in Monckton's account of his ascent of Mt Albert Edward in 1906 (Monckton 1907). At around 3100 m on the Wharton Range he noted that 'the whole of the forest on the summit has been killed by extensive fires, and for miles, wherever the eye rests, it meets a spectacle of gaunt, dead trees'. Of Mt Albert Edward itself he wrote, 'The whole of the summit...appears to be a native hunting ground, and the grass and heather has been regularly burned for many years'.

Lane-Poole (1925) seems to have been the first to recognise the cumulative impact of these anthropogenic fires. In the account of his expedition to Mt Saruwaged, where there are extensive summit grasslands, he concludes that, '...except for the very marshy land and the actual cliffs and outcrops of limestone, the whole of the mountain top was under a forest of conifers and myrtles'. Earlier he had accepted that the summit grasslands described by MacGregor on Mt Victoria were 'true alpine grassland', but after visiting Mt Saruwaged he changed his mind and asserted that all summit grasslands, including those of Mt Victoria, were 'due to natives burning the forest'. He did, however, admit the possibility of a true alpine region on the then unexplored mountains of Dutch New Guinea.

Later observers have not taken the extreme view of Lane-Poole but there has been considerable disagreement as to the relative importance of primary and secondary mountain grasslands. Those grasslands above 3800-4000 m have usually been considered to be true, 'climax' alpine grasslands but the extent, if any, of primary grasslands below the timberline has been a matter of dispute. Archbold and Rand (1935) believed that only 'seepage slopes and rocky outcrops' below the timberline on Mt Albert Edward were never forested, and that the rest of the grassland was the result of fire. In contrast, Brass (1941) considered that fire was only of secondary importance on Mt Trikora and that the most important factors excluding forest from areas below the timberline were 'temperature and cold air drainage from the heights'. Although evidence of past and recent fires was common he believed only small areas to be affected. Brass (1964) states that 'alpine grassland' occupied land below the timberline on Mt Wilhelm 'too wet or too cold for forest'. Robbins (1958) also includes

all mountain grasslands in his 'alpine grassland' which he considered 'basically a climatic climax' although 'hunting fires...may have resulted in their extension'.

Most recent authors have agreed that shallow soil or poor drainage prevent forest growth in areas of unknown extent below the timberline and that these non-forest areas have been extended by fire on many mountains. There has been less agreement on the importance of 'frost pockets' and cold air drainage in excluding forest. Wade and McVean (1969) thought that 'there were probably grassy frost pockets' on Mt Wilhelm while Wardle (1974) believed that 'the pattern of forested slopes and herb-dominated valley floors which prevails at high altitudes in New Guinea is basically determined by incidence of frost, at least within 1000 m of the tree limit'. In contrast, Paijmans and Löffler (1972) for Mt Albert Edward and Smith (1975) for Mt Wilhelm thought that frost was not a primary cause for the absence of forest but might prevent or slow reafforestation after fire.

Many authors, beginning with Lane-Poole, have expressed concern at the destruction of the high mountain forests which, although of no use for timber, may be important as 'protection forests' regulating the runoff of water and preventing erosion. There has also been concern for the impoverishment of the flora and fauna by intensive burning and hunting. The entire high mountain ecosystem is of major scientific interest and an understanding of recent trends will be necessary before steps can be taken for its conservation.

Definition of 'subalpine'.

The altitudinal zone on New Guinea high mountains between the highest patches of forest and the lowest tongues of grassland above continuous forest, forms a logical unit for palaeoecological study. Unfortunately, the terminology applied to the vegetation in this zone has varied from author to author and has usually subdivided it. The common use in New Guinea of the term 'subalpine' to refer to a vegetation belt below the timberline which includes closed forest, differs from that now preferred in North America where this term is usually restricted to the ecotone where the upper forest merges into the alpine grassland (Love 1970; Barry and Ives 1973). This ecotone is characterised by distinctive tree growth forms and the importance of snow protection. The closed forest belt below the ecotone is then termed 'Upper Montane' - a usage adopted only by Paijmans (1976) in New Guinea. Many European and most tropical workers (e.g. Steenis 1972; Grubb and Stevens 1979) have, however, used 'subalpine' in a broader sense although they have employed different criteria for defining it; floristic, physiognomic or vegetational.

Until the terminological confusion is sorted out, any defined and consistent useage is acceptable. To avoid a separate terminology for forest and non-forest vegetation, a primarily 'vegetational' definition of a subalpine 'zone' is adopted here. 'Subalpine' will therefore be used in this thesis to refer to the altitudinal zone between the lowest grasslands, usually contiguous with the alpine grasslands, and the altitudinal limit of forest growth. The lower limit of this zone is usually set by a belt of continuous forest below 3200-3300 m, but on mountains where grasslands are continuous to lower altitudes, an arbitrary lower limit of 3100 m is used for convenience.

The definition of the upper limit as the limit of forest growth differs from that of Wade and McVean (1969) who defined their subalpine-alpine boundary as the 'upper limit of the tall shrubs (>20 cm)'. This definition has some advantages in New Guinea as several mountains have a belt of tall, closed shrubland above the forest limit which cannot reasonably be included in the alpine zone. However, on most mountains including Mt Wilhelm, the most important discontinuity is that between forest and non-forest, so Wade and McVean's useage is not adopted here. Additional problems arise from the fact that on many mountains the vegetation in the vicinity of the expected forest limit has been so modified by fire that the boundary is no longer recognisable. In these cases the estimated, potential forest limit is used as the upper boundary of the subalpine zone. On other mountains the forest runs more or less unbroken to the treeline and there is no subalpine zone as defined above. In such cases comparisons may be made with the vegetation occupying the belt of the same altitudinal extent as on Mt Wilhelm. The same procedure is adopted when considering zonation in the past: the subalpine belt is assumed to have maintained an approximately constant altitudinal extent throughout the Holocene. When the term 'subalpine' is used in a different sense, an authority for the useage will be given.

Mt Wilhelm was selected for the main part of this study for both scientific and logistic reasons. It is the highest mountain in Papua New Guinea and has a fully-developed vegetation zonation with true alpine communities above about 3900 m. On the north-east side of the mountain there is an apparently undisturbed forest limit while in the other valleys, which are clearly disturbed, the vegetation pattern is typical of many high mountains of Papua New Guinea. In addition, it is by far the best-known mountain in New Guinea in terms of its biota and physical environment. Logistically, the presence of the Australian National University Field Station established in 1965 at 3480 m, only three hours walk from a road and airstrip, was an overwhelming advantage over alternative sites. Finally, the recent creation of a National Park, incorporating the catchment of the Pindaunde valley above 3000 m, added a particular relevance to studies on Mt Wilhelm.

A number of other mountains in Papua New Guinea were visited during the course of this study: Mt Giluwe, Mt Michael, Mt Amungwiwa and Mt Victoria. Observations made on these mountains were inevitably superficial but have been important for two reasons. Firstly, they have provided contemporary analogues for stages in the development of the present vegetation pattern on Mt Wilhelm which can no longer be observed there. Secondly, they have shown the extent to which conclusions about Mt Wilhelm can be generalised to the rest of New Guinea.

Aims.

This thesis reports a study of the palaeoecology and ecology of human impact on the vegetation of the subalpine zone of Mt Wilhelm. It concentrates on the relation between the contemporary vegetation pattern and the ecological processes operating in the past. A major aim was to provide an accurate chronology, both to put contemporary ecological observations into a continuous time perspective and to allow correlation with lower altitude palaeoecological and prehistoric events.

The overall plan was first to identify and then to concentrate on the elements of the vegetation pattern which have undergone major changes in the recent past. Therefore Chapter Two describes Mt Wilhelm and summarises the results of previous studies there. Chapter Three discusses the subalpine vegetation pattern on New Guinea mountains and ends with a list of the specific questions which the remaining chapters try to answer.

CHAPTER 2

MT WILHELM

Mount Wilhelm ($5^{\circ} 47' S.$, $145^{\circ} 01' E.$, summit elevation 4509 m), is the highest mountain in Papua New Guinea; there are, however, several higher peaks in adjacent Irian Jaya. Mt Wilhelm is near the centre of the Bismarck range at its junction with the Sepik-Wahgi divide and astride the main watershed between north and south coasts (Fig. 2.1). Northeast of the summit the broad Imbukum valley drains through the Inbrum river to the Ramu. To the north-west, the Bendenumbun valley drains into the Jimi river and ultimately to the Sepik. To the south, several valleys drain eventually to the Purari river by the tributary systems of the Koronigl and Simbu rivers (Fig. 2.2).

Geology.

The Wilhelm massif is formed of the Bismarck Intrusive Complex (Bain *et al.* 1975) which was intruded into older Tertiary sediments in the Miocene, during a period of increased granitic intrusive activity in the New Guinea Highlands (Page 1971). The main rock type grades from gabbro to diorite. Both fine- and coarse-grained outcrops occur and veins of haematite and aplite are common in some places. Some parts of the mountain are more varied lithologically, however, and contact metamorphic rocks occur locally at least on the southern flanks. Elevation as a fault block during the Pliocene brought the mountain to near its present height.

Geomorphology.

The glacial geomorphology is described in detail by Reiner (1960). The clearest glacial landforms are found in the area south of the Bismarck range divide where there are U-shaped valleys up to 1000 m deep, each headed by a cirque with a near-vertical backwall. Above about 3400 m the valleys have stepped profiles with 2 or 3 levels, some occupied by rock basin lakes. There are extensive lateral moraines forming distinct smooth ridges between 3200 m and 3400 m and curving in to form terminal moraines between 3100 m and 3300 m. Below the moraines the valley cross-section changes to a steep and narrow V-shape typical of fluvial erosion. There is firm evidence for a single glacial episode only, with the glaciers retreating after 14000 BP. However, there is no reason to doubt that earlier glacial advances occurred as recorded elsewhere in the world.

Glacial processes largely determined the present topography of the subalpine region, and have hence had a major influence on the vegetation. The flat valley bottoms are generally boggy except where an irregular mantle of till improves the drainage. The steep valley sides are in many places almost vertical bare rock, but soil with closed vegetation covers other slopes even where steeper than 45° . Landslips and debris-flows are common, however, and gullies have formed in some places. Large landslips are also visible in the forested area below the glacial zone.

Fig. 2.1 Mt Wilhelm location map.

Fig. 2.2 Map of Mt Wilhelm.

Soils.

The soils of the subalpine zone characteristically have a high organic content, a dark colour, and little or no profile differentiation (except for the uppermost litter layer). The organic fraction is largely lacking in macroscopic plant remains. Coarse, angular rock fragments may be present in varying amounts, and sand or gravel lenses are frequent in the valley bottoms. Part of the inorganic fraction comes from falls of volcanic ash which may be visible as one or more discrete bands on level sites. On low-lying sites with a fluctuating water-table the soil profile, particularly the lower portion, is often mottled red. Soil depths vary from a few centimetres to more than two metres but are commonly 0.4-1.5 m. The soil/rock or soil/till interface is frequently very sharp, as a result of the very slow rate of weathering of the granodiorite.

Haantjens (1970) describes the soils in the subalpine as 'alpine peat and humus soils' and puts them in three soil families which, however, seem to be parts of a continuously varying range of soil types. All are described as sandy or peaty clay loams, or clayey peats. (Under the bog communities the soil is simply raw peat.) Wade and McVean (1969) report soil analyses for 30 sites on Mt Wilhelm of which 12 were in the subalpine. Their results show a generally low level of fertility as would be expected from the climate and lithology. The variation between samples from the same vegetation type was as great or greater than that between samples from different vegetation. The only clear trends are an overall decline with altitude of the amounts of exchangeable calcium and magnesium. Within the subalpine, pH ranged from 5.2 to 6.1, percentage carbon from 11.8 to 33.8 and carbon/nitrogen ratio from 16.4 to 27.7.

Climate.

An account of the climate of Mt Wilhelm compiled from fragmentary records over eight years of intermittent occupation of the Field Station, has been published (Hnatiuk, Smith and McVean 1976). The records from near the Field Station (3480 m) are summarised in Table 2.1. Only sporadic measurements have been made from other sites in the Pindaunde valley and on the summit ridge and none in the other Wilhelm valleys.

The only clearly seasonal aspect of the climate is the precipitation. Regionally, rainfall distribution is controlled by the seasonal latitudinal movements of two major air masses; the perturbation belt of westerly-moving vortical circulations to the north, and the south-east trade wind belt to the south, separated by the inter-tropical convergence zone (McAlpine 1975). The perturbation belt dominates the weather from December to March and reaches a sufficient altitude to enter the highlands, resulting in high rainfall during this season. Conversely, during the

drier season from May to October, although broad control is exerted by the trade wind inversion at about 2000 m, local circulations have a dominant role in the highlands. Barry (1978) looked at the occurrence of rainfall during the dry season and found none of the expected relationships between synoptic-scale controls and climatic conditions in the highlands. He concluded that this was probably a result of the overriding effects of the local circulation systems promoted by the rugged physiography of the area.

On Mt Wilhelm a rather abrupt change from wet to dry season occurs at the end of May while the change from dry to wet is more gradual between August and November. Usually the dry season might be more accurately described as 'less wet', as even during this season moisture is seldom limiting for plant growth. However, up to 22 consecutive days without rain have been experienced (during the eight years of observation) and during the exceptionally dry year of 1972 wilting and mortality occurred among several small herbaceous species (Smith 1979). Snow has not been observed below 3900 m and although hail may fall at almost any altitude it is rarely heavy or prolonged in the Pindaunde valley. Fragmentary evapotranspiration measurements show that potential evapotranspiration varies inversely with rainfall and, although each month of the year shows a substantial water surplus, there are short periods (of five or more days) of water deficit which may be significant for plant growth. Relative humidity is usually high and only rarely falls below 40%. Except on the summit ridge winds are usually gentle, with up-valley draughts by day and down-valley draughts by night.

Screen temperatures show that the thermal climate is diurnal rather than seasonal (Fig. 2.3). The annual range is 3.7°C for monthly mean maxima and 1.6°C for monthly mean minima, while the mean diurnal range is 8.0°C . Freezing temperatures have rarely been recorded in the screen at the Pindaunde Field Station, but are frequent at ground level, particularly during the drier months when clear skies are common. On average there is a ground frost about 90 days per year at the Field Station. Needle ice is also observed several times a year.

As a result of the typical diurnal pattern of cloudiness (at least in the dry season) with clear early mornings followed by convective cloud buildup, there are microclimatic differences between east- and west-facing slopes. Barry (in press) computed the clear-sky global solar radiation over the Pindaunde area for 0600 to 1000 hours on the 23rd September. Totals for this period, when the sky is commonly largely cloud-free, show a ratio of about 3 to 5:1 for east- versus west-facing slopes. Differences during the rest of the day when the sky is usually cloudy will tend to be minimal. East-facing slopes have higher maximum and lower minimum temperatures than their nearby west-facing counterparts (Smith 1974). They are also drier, from qualitative observations, which may explain the lower

Annual precipitation (mm)	c. 3450
Mean max. temperature ($^{\circ}\text{C}$)	11.6
Mean min. temperature ($^{\circ}\text{C}$)	4.0
Absolute max. temperature ($^{\circ}\text{C}$)	16.7
Absolute min. temperature ($^{\circ}\text{C}$)	-0.8
Mean diurnal temperature range ($^{\circ}\text{C}$)	c. 7
Annual range of monthly mean max. ($^{\circ}\text{C}$)	1.1
Annual range of monthly mean min. ($^{\circ}\text{C}$)	1.6
Lapse rate (3480m-4400m) ($^{\circ}\text{C}$ per 100m)	-0.60
Mean daily global solar radiation* (kJcm^2)	1.974
Mean daytime net radiation* (kJcm^2)	1.011

Table 2.1 Some climatic data from the Pindaunde Field Station (3570 m).
(After Hnatiuk *et al* 1976.)

Fig. 2.3 Thermoisopleth for screen temperatures at the Pindaunde Field Station (3570 m). (After Hnatiuk *et al*. 1976.)

minimum temperatures. (Dryer soil has a lower thermal conductivity and specific heat so can be expected to cool further and more rapidly at night.)

No meteorological measurements have been made in the other Wilhelm valleys, but from casual observations it seems probable that the climates of all the southern valleys are basically similar. The Imbukum valley, however, faces the direction from which all rain-bearing air movements come. (Bundi, at 1400 m, records far more rain than the Pindaunde valley.) Observers have often reported this valley filled with cloud when there was clear sky over the Pindaunde valley. This all suggests a possibly wetter climate in the Imbukum valley. Similar arguments suggest that the Bendenumbun valley, or at least its lower section, may be wetter than the southern valleys.

Fauna.

There is no full published account of the fauna of Mt Wilhelm and most information concerns only the birds and mammals.

Within the subalpine region the copper ringtail possum (Pseudocheirus cupreus) and the longtailed pygmy possum (Cercartetus caudatus) are common in the forest. The striped bandicoot (Peroryctes longicauda) is fairly common in both the forest and grassland. The most abundant mammal of the grassland is the tiny moss rat (Rattus niobe) which also occurs in the forest and in the alpine region almost to the summit. There are also several other species of small murid rodent and a marsupial shrew (Antechinus sp.) in the subalpine region. A species of rock wallaby has been reported from the alpine grassland on the ridge between Mt Wilhelm and Mt Herbert (Wade and McVean 1969) and a giant rat, almost a metre in length (Mallomys rothschildii), was trapped in tussock grassland by the Sixth Archbold Expedition (Brass 1964).

Wild dogs (Canis familiaris) are frequently heard at night, and the remains of possums, rats and bandicoots killed by them are common in the less well-visited Wilhelm valleys. The rare marsupial carnivore Satanellus albopunctatus has also been found in the grassland.

The mammalian fauna's main influence on the vegetation probably results from its role, with the avifauna, in attracting man to higher altitudes. Some species may also have a role in seed dispersal and, conversely, by seed predation or browsing may limit forest regeneration in the open.

The birds of Mt Wilhelm are more conspicuous than the mammals and have been listed fairly completely (Smith 1973; Wade and McVean 1969). About 20 bird species are common residents in the Pindaunde area above 3350 m. Two birds are commonly seen in the grassland, the thrush or 'Island Blackbird' (Turdus poliocephalus) and a pipit (Anthus gutturalis). Less common grassland species are a woodcock (Scolopax saturata) and a melampit (Melampitta lugubris). In the forest and forest margin there are several species of honeyeater (Meliphagidae), a berry-pecker (Paramythia montia), a pigeon (Gymnophaps albertisii) and the Princess Stephanie Bird of Paradise (Astrapia stephaniae). Small flocks of lorikeets are often seen, and each Wilhelm lake supports a resident pair of Salvadori's teal (Salvadorina waigiensis). Cassowaries (Casuarius bennetti) are said to occur in the forest of the little-visited Imbukum valley.

The avifauna in the subalpine has an important role in pollination and seed-dispersal. Rhododendron, Dimorphanthera and some Vaccinium species with long red floral tubes, are probably dependent upon the honeyeaters for pollination. Dimorphanthera, Vaccinium, Rapanea, and many other genera are partly dependent on internal seed dispersal by birds which eat their fleshy fruits. Turdus, Gymnophaps, Paramythia, Astrapia, and possibly other species, consume large numbers of berries.

The only other common vertebrate is a small microhylid frog (Sphenophryne breviceps) which makes extensive burrows under the grass tussocks. Invertebrates are rather rarely observed except on damp nights when thousands of moths, mayflies and caddisflies are attracted to the light of the Field Station. Earthworms are present but uncommon, and beetles and blowflies are sometimes seen in the grassland. Insect damage to vegetation is patchy and apparently commonest to shrubs in the grassland. A web-spinning colonial caterpillar has been observed to completely defoliate parts of some ericaceous shrubs (Smith 1979).

Flora.

The flora of Mt Wilhelm has been extensively collected although mainly in the Pindaunde valley and Summit ridge area. The total recorded number of vascular plant species above 3215 m is about 390, of which about 150 belong to the non-forest flora (Smith 1974). Records of the flora and its collectors up to 1971 have been published by Johns and Stevens (1971), and their nomenclature is followed as far as possible in this thesis. Unfortunately, some ecologically important genera such as Rapanea remain undescribed or taxonomically confused.

Vegetation.

Wade and McVean (1969) made a detailed phytosociological study of the vegetation of Mt Wilhelm above 3100 m, in the Pindaunde valley and Summit ridge area. Twenty plant associations were described, of which 3 were forest types, 6 subalpine tussock grasslands, 6 subalpine mires, 4 landslip communities, and the rest various alpine communities. Intermediates between some of these associations were also noted. I found Wade and McVean's categories generally useful in the field, although they were in some cases too broad for my purposes. Particularly outside the Pindaunde valley, intermediates were common, and some subalpine vegetation which did not fit any Wade and McVean category (e.g. secondary forest) was also found. Consequently I have used their terminology (Table 2.2) wherever possible, but augmented it or invented new terms where necessary. (In all their community names Poa saruwagetica has been substituted for P. nivicola, following Johns and Stevens (1971).)

A general description of the vegetation structure and floristics follows. A detailed discussion of the subalpine vegetation pattern is given in the next chapter. The terminology of the forest zonation follows Grubb and Stevens (1979).

The Lower Montane rainforest extends up to 2800-3000 m, although in the Simbu valley it is almost completely cleared below 2300 m. In the Pindaunde-Upper Simbu area it consists of numerous tree species, particularly in the families Cunoniaceae, Elaeocarpaceae, Lauraceae, Myrtaceae, and Podocarpaceae, while on the northern slopes of the massif areas completely dominated by Nothofagus pullei are found, particularly on ridge tops. Below 2400 m forest dominated by Castanopsis accuminatissima also occurs where clearance has not been complete.

The Upper Montane rainforest extends from about 3000 m to 3500-3600 m. In the lower part of this range (the 'Cloud Forest' of Wade and McVean) it is floristically rich with the families Myrtaceae, Pittosporaceae, and Podocarpaceae important. The forest canopy is at 18-24 m with emergent Dacrycarpus, Elaeocarpus, Schefflera and Papuacedrus. In the upper part of the range a transitional forest occurs (the Lower Subalpine Forest of Wade and McVean). This is lower in stature, with the main canopy at 9-15 m, and is floristically poorer. Emergents are common, particularly Dacrycarpus compactus, Rapanea vaccinioides, Pittosporum pullifolium and Schefflera sp..

The Subalpine forest (the 'Upper Subalpine Forest' of Wade and McVean) extends from around 3550 m to the timberline at around 3900 m. The Ericaceae become important, and emergent Dacrycarpus compactus and Rapanea spp. are conspicuous. Near the treeline the forest is reduced to a tangle

Table 2.2 Subalpine associations recognised by Wade and McVean (1969).

SHORT NAME	FULL NAME
FORESTS	
Cloud Forest	<u>Amaracarpus brassii</u> - <u>Elaeocarpus azaleifolius</u> - <u>Podocarpus pilgeri</u> association.
Lower Sub-alpine Forest	<u>Amaracarpus caeruleus</u> - <u>Pittosporum pullifolium</u> - <u>Pteris</u> association.
Upper Sub-alpine Forest	<u>Dimorphanthera microphylla</u> - <u>Rhododendron gaultheriifolium</u> - <u>Trochocarpa dispersa</u> association.
SUBALPINE GRASSLANDS	
<u>Deschampsia klossii</u> tussock grassland	<u>Deschampsia klossii</u> - <u>Danthonia penicillata</u> association.
Treefern tussock grassland	<u>Cyathea atrox</u> - <u>Triplostegia glandulifera</u> association.
<u>Coprosma-Poa</u> tussock grassland	<u>Coprosma divergens</u> - <u>Poa saruwagetica</u> association.
<u>Poa-Dichelachne</u> tussock grassland	<u>Poa saruwagetica</u> - <u>Dichelachne novoguineensis</u> tussock grassland.
<u>Danthonia vestita</u> tussock grassland	<u>Danthonia vestita</u> - <u>Deyeuxia brassii</u> association.
SUBALPINE MIRES	
<u>Brachypodium-Carex</u> fen	<u>Brachypodium sylvaticum</u> - <u>Carex capillacea</u> association.
Short grass bog	<u>Agrostis reinwardtii</u> - <u>Gentiana piundensis</u> - <u>Breutelia aristifolia</u> association.
<u>Gleichenia vulcanica</u> bog	<u>Gleichenia vulcanica</u> - <u>Trochocarpa decockii</u> association.
<u>Carpha</u> fen	<u>Carpha alpina</u> association.

of large shrubs about 4-5 m high with scattered emergent Dacrycarpus. About 15 large woody species are found in the uppermost forest.

Above about 3200 m there are also areas of non-forest vegetation, much of which is apparently secondary. This non-forest vegetation includes tussock grasslands, mires and landslip communities. The tussock grasslands are often dominated by Deschampsia klossii tussocks up to 0.9 m high and as much across the crowns, or the slightly smaller Poa saruwagetica. Several other tussock-forming grasses and many non-tussock species are also common and may attain local dominance. Several species of shrubs are found in the grasslands and shrub cover ranges from 0 to near 100%. Styphelia suaveolens is the most widespread and it is joined by Coprosma divergens, Gaultheria mundula and several others in the shrubbier grassland types. These shrubs vary in height from a few centimetres to a metre or more. In general, with increasing shrub cover, the grass tussocks become smaller and thinner in comparison with their luxuriance in shrub-free grasslands. Many herbs are also present but are structurally less important than the grasses and shrubs.

Below about 3500 m some areas of tussock grassland on better-drained sites are dominated by the tree-fern Cyathea atrox, which may attain 5-6 m in height. Smaller areas dominated by Cyathea gleichenioides occur between 3400 and 3600 m, and scattered groups of this species and Cyathea muelleri are present up to near the treeline.

A feature of the grasslands on Mt Wilhelm is that, unlike the forest, the species richness does not decline with altitude and may show a slight peak at 3850 m (Smith 1977). Wade and McVean (1969) found a maximum at 3400 m with a slight fall to 3900 m and a slight increase above.

Following Wade and McVean (1969) the term mire is used in this study to include all vegetation on continuously-waterlogged soil with the water table at or near the surface. Wade and McVean additionally separate 'bogs' from 'fens' on structural and floristic grounds. Several fen types are found, dominated by non-tussock grasses and sedge species. Three bog types were also recognised. The most common is the 'subalpine short grass bog' which is dominated by small herbs and mosses with the bright green cushions of Monostachya oreoboloides prominent. Bogs covered in dense stands of Gleichenia vulcanica are a peculiar feature of shallow depressions in the valley floors, while areas dominated by Astelia papuana occur mainly as islands in the other mire types.

Four, probably seral, associations of old landslips and rocky slopes are described by Wade and McVean. The most characteristic species of landslip scars below about 3700 m is Rhododendron yelliottii, which occurs along with other Rhododendron spp, Haloragis halconensis, Gleichenia spp.

and many grasses, herbs and shrubs.

Vegetation history.

A pollen-analytical study on Mt Wilhelm of the broad vegetation history of the last 22,000 years has been reported by Hope (1973, 1976a). Sites were chosen over a range of altitude so that migration of vegetation zones could be detected. Four main sites were studied in detail.

1. Summit Bog (4420 m), in wet alpine tundra.
2. Brass Tarn (3910 m), in shrub-rich 'subalpine' (sensu Wade and McVean) grasslands slightly above the present Pindaunde valley treeline.
3. Imbuka Bog (3600 m), well below the treeline in clearly secondary tussock grassland.
4. Komanimambuno Mire (2740 m), in lower montane forest.

A partial record was also obtained from the lower Pindaunde lake which is now bordered by subalpine forest and grassland.

The pollen diagrams were zoned independently on the basis of changes in the pollen assemblages present. Most of the major vegetation changes were approximately synchronous and thus probably related to regional events. The local zones were fitted into a regional chronology on the basis of changes in the relative frequencies of important regional elements, mainly Castanopsis, Nothofagus and Casuarina.

From before 22,000 BP to 10,200 BP all sites lay above the treeline, which was then probably between 2000 m and 2400 m (from the evidence of contemporary alpine conditions at Sirunki 2500 m and Inim 2550 m (Walker and Flenley 1979)). Above the treeline was a broad zone of shrub-rich tussock grassland, giving way to alpine grasslands and then open ground and tundra at the ice edge. Estimates of deglaciation at the higher sites suggest a steady retreat of ice between 13,000 BP and 9,200 BP which probably started at 14,200-14,800 BP. Relatively little change in the regional vegetation is apparent during this period.

Between 10,200 BP and 8,600 BP the ice retreated completely and subalpine forest moved up the slopes to reach Brass Tarn by 8500 BP. From then until 4900 BP the treeline was just above the tarn. At 4900 BP grasslands replaced forest at Brass Tarn, possibly as a result of climatic deterioration although human influence is an alternative explanation (See Chapter Seven). Vegetation limits then remained stable until the period of modern disturbance of the subalpine area, which started within the last thousand years and continued to the present. During this time subalpine forest was replaced increasingly by grassland and there was a coincident increase in the Casuarina and Trema pollen from lower altitudes, suggesting

an expansion of garden areas in the Simbu valley.

Hope (1976a) concludes that the regional vegetation history is consistent with 'maximum glaciation prior to 15,000 yr BP, followed by a gradual amelioration until 10,000 yr BP, when a rapid warming took place. A generally milder-than-present climate continued until about 5,000 yr BP, after which a series of cool phases alternated with climates similar to the present.' He considers that the vegetation changes since 8,500 BP 'are as likely to be due to human activity or other ecological factors as to climate, even though climatic change is known to have occurred.'

Some aspects of Hope's study are considered in greater detail in Chapter Seven.

The People

The human populations of the Wilhelm region are divided by the massif into four groups, occupying the Simbu, Koronigl and Jimi valleys and the Bismarck Fall (Fig. 2.4). These populations have major similarities of social organisation, and all speak languages of the East New Guinea Highland stock (Wurm 1970). They are sedentary, subsistence gardeners, with the sweet potato (Ipomoea batatas) as a staple food and pigs as a common domestic animal.

The Gende-speaking people of the Bismarck Fall have scattered settlements and gardens in the forest, mainly between 1200 m and 1900 m. Population densities are generally low in comparison with the Highland valleys but may attain 40 or more per square kilometre of arable land in favoured areas. At the head of the Jimi valley the population density is greater and most of the forest has been cleared below 2000 m. Gardens are found up to around 2250 m. The people of the Koronigl and Simbu valleys and the section of the Wahgi valley between, belong to a larger population of Simbu (or Kuman) speakers. Here the population density is very high, and it reaches its peak in the upper Simbu valley where it locally exceeds 200 per square kilometre of arable land. Gardens occur up to 2700 m, there is virtually no forest left below 2300 m, and the impression is of a landscape completely dominated by man.

Sweet potato.

The potential upper limit was set in the past by the frost sensitivity of the sweet potato, all other crops being more sensitive. This limit has been reached in the upper Simbu valley. In the Koronigl and Jimi valleys and the Bismarck Fall, lower potential limits may have been set by the altitude of persistent cloud formation (Brookfield 1964). Near the upper limit in the Simbu valley sweet potato is slow-growing, produces small

Fig. 2.4 Populated areas around Mt Wilhelm.

tubers and is liable to frost damage, perhaps as often as once in three years on average. An alternative starchy staple, Taro (Colocasia esculenta), will also grow at this altitude but gives a much lower yield and takes longer to mature. Sweet potato gives faster production, higher yield, and has a wider climatic and edaphic tolerance than any alternative staple, and is probably the only traditional crop capable of supporting dense populations above 2000-2100 m. Consequently, it is highly significant that it is thought to have been introduced to New Guinea from South America within the last 400 years, since Europeans brought it to island South East Asia (Yen 1974).

Sweet potato gardens are usually segregated from mixed plantings of other crops and elaborate and intensive cultivation techniques ensure high yields. The fallow, of varying length, is controlled by conserving regrowth species like Trema and Dodonaea and by planting Casuarina oligodon. This 'tree-fallow' system is important in sustaining the high population densities because it permits full recovery of the soil in shorter time. Casuarina is particularly important as it is a nitrogen-fixer as well as being an excellent source of timber for building, fencing and burning.

Exploitation of higher altitudes.

Above the limit of gardens the forest is locally disturbed up to about 2900 m by exploitation for bark and timber, grazing of domestic pigs, and the tending and harvesting of the 'nut pandanus' (P. julianetti), an important seasonal supplement in high altitude areas. Above 2900 m only hunting tracks penetrate the forest.

Within the subalpine region the major traditional activities were hunting and trade. Hunting today occurs both in the grassland and in the forest but during my stay on the mountain it was only successful in the forest and forest margins. Dogs are used, and the most important game seems to be the ringtail possum (Pseudocheirus cupreus), found in the forest up to the treeline. It supplies meat and fur used for weaving. Other important species hunted for food, fur or feathers are the bandicoot (Peroryctes longicaudata) common in the grasslands, various rodents and several species of bird, of which the most prized is the Princess Stephanie Bird of Paradise (Astrapia stephaniae). Traditionally, most hunting was done in the dry season when there was less work in the gardens, the weather was generally better, and other food was sometimes in short supply (Bergmann 1971).

The other major traditional use of the subalpine region was trading, and several major and minor trade routes passed over the mountain above 3000 m. (See discussion below.) Lower altitude routes were probably

preferred where possible but the higher routes became important when hostile neighbours had to be avoided in order to meet trade-friends from tribes too distant for conflict (Hughes 1977). Minor uses included the collecting of plants, inter-tribal fighting and the quarrying of stone. The most valued plants seem to have been the largely alpine fern 'Pingga' (Papuapteris linearis), still valued as a hair decoration (10c per frond in 1975), and a Pipturus sp., of which the stems were and are collected from subalpine forest margins for the production of a string fibre. Wade (1968) also mentions the collecting of large quantities of Anaphalis mariae and Gleichenia vulcanica for head and house decoration and says that in the past they were traded out in large quantities along with Papuapteris to people without access to the mountain tops.

There are reliable accounts of pre-contact tribal fighting in the lower Pindaunde valley between the Wandega Simbu and Gende people from near Yanderra, and in the Giwimawi valley between the Wandega, Siago and Denglagu and the mid-Simbu Kuglkane. These were large-scale, organised events with the hostile groups approaching the agreed fighting ground by different routes at dawn, fighting until late morning, and returning to their homes in the late afternoon, after a meal cooked by the women who had accompanied them as far as the lowest grasslands.

Chappell (1966) mentions a minor stone axe quarry called Yendegle Mauglwa in a stream bed 'at about 10,000 feet above sea level in the easternmost headwaters of the Koronigl'. Since this quarry was in subalpine grassland (Chappell pers. comm.) it was probably at a somewhat higher altitude (Fig. 2.2 gives the probable location). The rocks are 'inter-bedded meta greywackes and argillites, overlain by a Lower Tertiary conglomerate containing boulders of the same Mesozoic rocks'. Two rock types, known as 'Kruo' and 'Kama' were quarried. Both were used for ceremonial axes, and Kruo (mid-grey siliceous greywacke siltstone) alone was used occasionally for work tools. These axes were traded locally (and as far as Chuave) but were not of a very high quality.

All of these activities, although of great social importance, were probably marginal in terms of survival. There were good reasons, both physical and psychological, to avoid the subalpine altogether. These people were naked except for a protective layer of pig fat and the unpredictable weather at these altitudes must have caused many deaths from exposure. There was an equal danger from various kinds of spirits which inhabited the higher parts of the mountain and from the 'kuia' (approximately, souls) of long-dead men believed to live in the lakes (Nilles 1970).

Early European visitors to Mt Wilhelm noticed the great reluctance of the local people to approach or pass the lower Pindaunde lake, and many were unwilling to go that far, although there was a good track (Noakes pers. comm; Nilles 1970; Pullen 1957). From this and from Simbu informants it seems likely that this altitude (c.3500 m) was the normal upper limit of human exploitation in immediately pre-contact times, at least in the Pindaunde valley and probably in the others. The major exceptions to this would have been the high altitude trade routes mentioned above. A rarely-used route between the upper Simbu and upper Jimi valleys seems to have passed up the Pindaunde valley (? along the Bogonolto ridge), along the summit ridge and down via Bendenumbun to Ambullua (Chappell pers. comm.; Simbu informants).

A far more important track, between the upper Simbu and Koronigl, climbed over the southern slopes of Mt Wilhelm (Fig. 2.2). Part of this route in the subalpine is worn into the ground up to 1 m, presumably by heavy use, aided by water erosion. The names of landmarks along the route, including a pass at 3880 m called Simaumangi, are known to even the younger Simbu who have never visited them. This route would have been used by whole families as well as single men or groups of men, for trade or courting (Hughes pers. comm.; Simbu informants). The main trade items were probably stone axes from the Jimi and Wahgi which were exchanged for low-altitude products from the Gende. This high altitude route would have been of great importance when hostilities with the mid-Simbu Kuglkane closed lower routes to the upper Simbu clans.

The risks taken are illustrated by this comment by William Dua:

"Long taim bipo planti man - planti man - mi no save kauntim - i dai pinis long dispela rot, long taim bilong ren. Taim i save walkabout skin nating." ("In the past more people than I could count died on this track in bad weather. At that time people went naked.")

Subalpine ownership and access.

All the groups of people around Wilhelm made some use of montane resources, but the main users of the subalpine were, and still are, the Simbu of the middle and upper Simbu valley. Here the greater population density may have made the resources of the subalpine more valuable, and the higher garden limits made them more easily accessible. The subalpine grasslands can be reached in two or three hours from the highest gardens at several points in the valley and many grass huts on the fringes of the grasslands provide emergency or overnight shelter. By contrast it is at least a day's walk from the upper Jimi valley and probably more from the nearest Gende settlements. It is therefore not surprising that frequent visits are now (and perhaps in the past) only made from the Simbu valley, and this has important implications for man's impact on the vegetation.

Of the eight major named groups in the Simbu valley, sections of two - the Denglagu-magluagu and the Kuglkane - claim ownership of most of the subalpine region. These major groups are those to which a Simbu claims to belong when questioned by an outsider and each owns a consolidated block of land. They are further subdivided in a hierarchy with a variable number of levels for which a consistent terminology has yet to be devised. A simplified diagram of one such hierarchy is shown in Fig. 2.5 with the relevant subalpine land ownership. However, there are clearly several levels of 'ownership' and when land in the Pindaunde valley was leased for the Wilhelm Field Station, and more recently the entire Pindaunde valley purchased for the National Park, the money was paid to a single 'extended-family-group' within the Bomkane section of the Wandega. At the other end of the scale this 'ownership' seems to have had little effect on hunting rights except where two major groups were in conflict, as was commonly the case between the Denglagu-magluagu and the Kuglkane.

Ownership of the rest of the mountain is less clearly defined, although Simbu informants are willing to concede the Bendenumbun valley to the Jimi people and the Imbukum catchment to the Gende. The Simbu of the Koronigl seem to have no claim to any of the subalpine region and their territory is limited to the montane forest below.

Prehistory.

Very little is known of the human prehistory of the area. Local tradition places the origin of most Simbu speakers at Womkama in the middle of the Simbu valley (2000 m) and now part of Kuglkane territory. Other origin myths, however, mention earlier groups living at Goglme (1900 m) and even Gembogl (2100 m) (Nilles 1977; Komba 1976). A spread of people up the valley as a result of population pressure and fighting is consistent with the presence of members of the largely upper Simbu Inaugl clan living among the Gende of the Bismarck Fall and the people of the upper Asaro valley. These migrations apparently took place many generations ago, but just before the arrival of the first Europeans, members of the Denglagu-magluagu clan also moved across the divide and settled on vacant land above the Gende. In both cases shortage of arable land in the Simbu valley is given as the reason. The Gende themselves may have migrated over the divide, possibly from the Asaro region. Part of the head of the Jimi valley is also occupied by Simbu-speaking people who have relatives in the Koronigl valley and give Womkama as their ancestral home.

On a longer time-scale man has probably been in New Guinea for at least as long as in Australia; i.e. more than 40,000 years. The oldest known archaeological site, Kosipe, is at an altitude of 2000 m on the southern slopes of Mt Albert Edward in the Owen Stanley range. At 26,000 BP, the oldest occupational level, this would have been near the

Fig. 2.5 The Denglagu-magluagu - subalpine ownership.

(The south-west quadrant of the mountain is claimed by elements of the Kuglkane 'district'.)

Pleistocene treeline, supporting the suggestion (Hope and Hope 1976) that early human colonists may have found the expanded treeline-grassland ecotone of the Pleistocene a very favourable habitat.

Closer to the study area, the Kiowa rock shelter at 1530 m near Chuave in Simbu Province, 35 km south of Wilhelm, was occupied by 10,000 BP (Bulmer 1974). At Nombe, 4 km south of Kiowa, there is a possible association of human artefacts with extinct fauna, which suggests an earlier occupation date for this site, although there are no radiocarbon dates. (Mountain, M.J. pers. comm.) The evidence is therefore that man has occupied the area for at least 10,000 years.

The only other archaeological remains in the area are a number of stone artefacts - mortars, pestles and clubs - which have been found all over the highlands and in some coastal areas. None of the present day occupants of the central Highlands make such tools today and they usually attribute them to a supernatural origin. In the Simbu district they have only been found in the lower areas, and are absent from the middle and upper Simbu valley, although present at Bundi in the Bismarck Fall.

History (1932+)

Recorded history for the area starts in 1932 when the Catholic Society of the Divine Word established a mission among the Gende people at Bundi. Then in 1933 an exploration party lead by Leahy and Taylor made first contact with the Simbu in the Wahgi valley (Souter 1963). Later the same year missionaries from Bundi, escorted by an upper Simbu valley leader with Gende affines, travelled safely down the Simbu valley and west as far as the Koronigl. In 1934 a Catholic mission station was built at Mingende in central Simbu and Lutheran missions started at Ega (now Kundiawa) where an airstrip was built, and at Kerowagi. In 1934 and 1935 the murder of two S.V.D. missionaries in the Simbu valley forced the administration to increase government control and base camps were established at Kundiawa and Goromei. In 1937 a Catholic mission station and airstrip were built at Toromambuno (2600 m) at the head of the Simbu valley.

The second world war lead to lessened patrolling (although there was an ANGAU post at Gembogl) and the evacuation of missionaries; civil administration was restored in 1946. Since then, new missions and administation posts, the introduction of cash-cropping and - during the 1950's - the building of roads up the Simbu and Koronigl valleys, has radically changed the way of life of the Simbu people. Change in the Jimi valley and Bismarck Fall has been much slower and even today (1976) they can only be reached on foot or by air.

The most important initial effects of contact with Europeans were probably the introduction of steel tools, the imposition of a 'Pax Australiana' and the introduction of new crops. Steel axes have greatly speeded the work of clearing the forest and regrowth for new gardens. Some steel reached the area along trade routes before 1933 while a rapid increase occurred very soon after (Hughes 1977). Axes were used for payment in government and mission stations, were brought in by contract labourers returning from the coast, and were purchased with money from cash-crops. By the end of the war the major stone-axe quarry at Dom was no longer in use (Hughes 1977) and steel had almost completely replaced stone in the Central Highlands, with predictable effects on the vegetation.

At the same time as steel was replacing stone the spread of government control was lessening the number of tribal fights and permitting a previously unknown freedom of movement. (Although fighting continued sporadically in the Simbu valley until the 1950s). The introduction of new crops was also having an important effect, particularly near the limit of sweet potato growing in the upper Simbu valley. Potatoes and cabbage have been particularly successful and have lifted the potential altitudinal limit for gardening, although this has only been taken advantage of in a few places. Of the introduced cash-crops only Pyrethrum is successful at high altitudes - it grows best above 2100 m - but interest in this crop has waned in the last few years because of the low monetary return.

An awareness of the combined effect of these recent changes on human activities in the subalpine region is essential if present-day ecological observations are to be used to interpret the past. In the 1930s the use of trade-routes seems to have reached a peak, followed by a rapid decline in the 1950s with pacification and road-building (Hughes pers. comm.). Hunting activity may also have risen at first after European contact as men had more leisure time, but then declined with increasing opportunities to earn money and buy meat (Bergmann 1971). If total hunting activity has declined, however, it has also become less restricted geographically and hunters now range over most of the mountain, perhaps following the example of European visitors. Well-maintained grass huts were observed on every part of the mountain visited, except the Bendumun valley (above the upper Jimi). Hunting has now taken on a 'recreational' aspect and is concentrated at weekends.

Finally, the building of the ANU Field Station and the desire of European tourists to climb Papua New Guinea's highest mountain has probably attracted more people to the Pindaunde valley than at any time in the past, and has lead to new types of human impact on the subalpine vegetation.

This thesis is concerned less with the composition of individual plant communities than with their distribution in space - the vegetation pattern - and the role of man in its development. Some of the factors thought to control pattern in the subalpine region have been mentioned in the Introduction. Fire is almost certainly not a natural factor on these wet mountains (see the fuller discussion in Chapter Seven); probably all fires are lit by man. Its incidence will be determined by a complex interaction of various factors, including cultural ones not directly controlled by the physical environment.

Some idea of the relative importance of the various determinants should be apparent from a comparison of the vegetation pattern on different mountains and on different parts of the same mountain. Further information may come from a detailed examination of the pattern in one area. This chapter therefore starts with a comparative review of subalpine vegetation pattern on New Guinea mountains followed by a more detailed account of the pattern on Mt Wilhelm. Finally, hypotheses suggested by this review are discussed and the specific questions which the field and laboratory work attempted to answer are listed.

New Guinea mountains.

The natural altitudinal treeline in New Guinea is at 3800-4000 m on most high mountains. A closed shrubland extends above the forest limit to 4100-4200 m on some peaks in the Snow and Star mountains but is absent further east (Hope 1976b). Lower and apparently undisturbed treelines are found on some small or outlying mountains such as Sigal Mugal (Smith 1975a) and Mt Service (pers. obs.). (See Fig. 3.1 for the location of mountains mentioned in the text.)

The vegetation pattern below the treeline on any particular mountain seems to be correlated with altitude, topography and the extent of the Pleistocene glaciation. On many high mountains of varying geology the forest above 3400-3600 m consists of isolated 'islands' in a 'sea' of grassland continuous with the alpine grasslands. The forest islands become smaller and confined to steep slopes or inaccessible places with increasing altitude. Below 3400 m the forest is usually more or less continuous on the slopes, non-forest vegetation being confined to flat or gently sloping areas. On mountains such as Mt Wilhelm which had valley glaciers during the Pleistocene, tongues of grassland and mire extend down onto the ill-drained glacial valley floors and end abruptly at the terminal moraine. On others, where the Pleistocene ice cap ended as a broad shield in undissected topography, grasslands may be more extensive below 3400 m, but the lower limit still tends to coincide with the limit of glaciation. On Mt Giluwe the undissected flanks with little forest above 3300 m and extensive grasslands to below 3200 m, contrast with the valley-glaciated

Fig. 3.1 New Guinea mountains location map.

flanks where grassland below 3500 m is mainly confined to the valley floors. Similarly, on Mt Albert-Edward the relatively steep plateau sides are mostly forested while the plateau itself, which is mainly above 3400 m and was covered by ice in the Pleistocene, is largely under non-forest vegetation.

There are, however, some high mountains in New Guinea where the upper forest is not reduced to discrete patches. This is true particularly on steep and inaccessible slopes without extensive glacial landforms. For example, Mt Victoria is the third highest mountain in Papua New Guinea but consists only of a narrow, steep-sided ridge. The area covered by Pleistocene ice was probably less than 15 km² (Löffler 1972). Forest is continuous from below 3000 m to a ragged treeline at about 3900 m, except for some small, boggy flats. Forest is also more or less continuous up to 3900 m on the precipitous south-west side of the Saruwaged plateau, while on the plateau itself and the more gentle slopes to the north and north-east there is hardly any forest above 3500 m.

That the extent of Pleistocene glaciation is not the only factor is shown by the contrast between Mt Jaya (Hope 1976b) and Mt Trikora (Brass 1941) in Irian Jaya. Both were extensively glaciated but on Mt Jaya forest is almost continuous on the southern slopes, although absent from the flat valley floor. (It is dissected to a varying extent on the other slopes and the Kemabu plateau at 3300-3800 m.) On Mt Trikora the forest above 3650 m is reduced to 'strips under sheltering bluffs and compact clumps on the rocky slopes and ridge crests'.

In most of the above-mentioned cases the extent of subalpine non-forest vegetation and the degree of dissection of the forest correlates with the degree of known human interference (although one must be careful to avoid circular arguments here). Mt Wilhelm, Mt Albert-Edward, Mt Giluwe, the Saruwageds and Mt Trikora are exploited by dense local human populations; Mt Jaya is occasionally visited and Mt Victoria probably never so. There are, however, exceptions to this rule. The principal ones are Mt Capella and Mt Scorpio in the eastern Star Mountains (Hope pers. comm.). Mt Capella is formed of limestone with scattered diorite plugs. The gymnosperm-dominated 'forest' in the subalpine zone, although more or less continuous, has a very open structure; it is virtually a 'shrub-savannah'. Above 3500 m tree-forms are absent and a very dense shrubland of decreasing stature continues to the summit. The diorite plugs support a contrasting, open, boggy vegetation. Nearby Mt Scorpio is entirely diorite. The 'forest' below 3500 m is similar to that on Mt Capella but somewhat denser. With increasing altitude it becomes more and more fragmented. Tussock grasslands, however, are rare, and the majority of the non-arboreal vegetation consists of blanket bogs of various types.

Although human interference by the sparse local population cannot be entirely ruled out, Hope (pers. comm.) suggests that edaphic factors are responsible for the open structure of the forest on Mt Capella and the large extent of subalpine mires on Mt Scorpio. The rainfall is extremely high (about 12,500 mm per annum at nearby Ok Tedi) and leaching may have lead to a rapid depletion of nutrients. Hope also suggests that the absence of volcanic activity in the region - and thus the absence of the periodic addition of nutrient-rich ash which occurs in the Papua New Guinea Highlands - has aggravated this nutrient depletion.

More or less extensive areas of non-forest vegetation also occur near the summits of many mountains which attain less than 3900 m - i.e. which are lower than the tree limit on the highest mountains. Continuous forest to an apparently undisturbed treeline below the summit is found on Mt Sigal Mugal (c.3700 m) (Smith 1975a) and Mt Service (c.3800 m). In both cases, however, normally subalpine species are mixed with alpine species in the summit grasslands.

Mt Hagen, Mt Michael and Mt Kerigomna are all between 3600 and 3700 m high and show interesting contrasts in their vegetation. Mt Hagen supported quite a large Pleistocene ice-cap (Loffler 1972) and has short glacial valleys. Here the vegetation pattern is very similar to that on Mt Giluwe and Mt Wilhelm although true alpine grasslands may be absent. In contrast, glacial landforms are very restricted on Mt Michael and non-forest vegetation - principally tussock grasslands - has a limited extent, mainly along the summit ridge. Mt Kerigomna, from which glacial landforms are absent, is forested continuously to the summit.

Completely forested mountains have rarely been visited by biologists in Papua New Guinea, but from a comparison of aerial photographs and the 1:100,000 maps it seems that most mountains above 3700 m high have some summit grasslands, and most below 3600 m do not. There are exceptions to this lower limit, however. Mt Otto and the Doma Peaks are both about 3550 m high yet support areas of non-forest vegetation (mostly shrub-dominated on the Doma Peaks) near the summits. Mt Amungwiwa is only 3278 m (according to the map) but has patches of boggy grassland along its summit ridge, although krummholz-like Dacrycarpus compactus occurs on the summit itself.

The mountains in the extreme east of Papua New Guinea may be considered special cases because they are probably dry by comparison with other New Guinea mountains. Mt Suckling, which is also geologically peculiar as it is formed partly of ultramafics, attains 3678 m and bears no evidence of glacial activity. Its summit grasslands are extensive, however, and the treeline poorly defined (Stevens and Veldkamp 1975). Mt Dayman attains only 3000 m yet widespread grasslands extend continuously

down to 2100 m where they are encroaching directly on to Araucaria forest (Brass 1956).

As with the mountains higher than 3900 m the extent of subalpine grasslands and the degree of fragmentation of the forest on the lower mountains is generally correlated with the amount of human interference. Mt Hagen, Mt Michael, and Mt Dayman are heavily exploited by local populations, Mt Otto and the Doma Peaks less so, and Mt Kerigomna hardly at all. The extent of past human activity on Mt Suckling is unknown but was probably very low because of difficulties of access. The high animal populations there support this view. Mt Amungwiwa is also an exception and, at least today, is apparently never visited by the local people.

Discussion.

From the above survey of New Guinea mountain vegetation the following generalisations can be made.

- (1) The extent of subalpine grasslands and the degree of fragmentation of the upper forest is greatest on mountains which were extensively glaciated and are heavily exploited by man.
- (2) On the mountains higher than 3900 m, non-forest vegetation usually extends lowest on flat or gently sloping topography, particularly the bottoms of U-shaped valleys.
- (3) On mountains below 3900 m (with the exception of Mt Hagen which supported a large Pleistocene ice-cap, and Mt Suckling which has large gently-sloping areas) non-forest vegetation is usually confined to ridge-tops.

It is virtually impossible to separate the influence of man and Pleistocene glaciation from a simple comparison of mountains. No extensively glaciated mountain without human interference exists, except the clearly anomalous Mt Scorpio. Presumably the smoother topography of glaciated mountains (whether a result or cause of glacial processes) makes access by man easier by comparison with the steep slopes of the unglaciated ones. Whether 'natural' subalpine grasslands resulting directly from glacial landforms attracted man, or whether he created the greater part of them, is a question which requires a palaeoecological approach.

Support for the idea of a synergism between the presence of glacial landforms and the activities of man in the origin of subalpine grasslands comes from a comparison of different sides of Mt Jaya and Mt Wilhelm. Both mountains have little-visited glacial valleys ("Carstenz meadow" and Imbukum valley respectively) where, in contrast to the rest of the mountains, forest completely clothes the slopes, although trees are absent from the flat valley floors. In both cases the contrast with the rest of

the mountain seems best explained by differences in human interference, although there are also topographical and possibly climatic differences. The contrast on Mt Wilhelm will be described below in more detail and the implications will be discussed later in the thesis.

A more detailed examination of the vegetation pattern gives additional information on the status of the subalpine grasslands. Where the forest is continuous up to the altitudinal treeline the forest limit is diffuse and forest and grassland interdigitate through an altitudinal range of 50-150 m (Smith 1975a; Hope 1979c; and personal observations). These limits are presumably controlled by aspects of the large-scale thermal climate, locally modified by micro-climatic and edaphic factors.

By contrast, forest edges below the timberline are usually sharp and often, but not always, have a distinctive band of marginal vegetation. Sometimes the boundaries coincide with a change in slope or drainage. This is often the case with the lowest tongues of non-forest vegetation on glacial valley floors which border forest on the better-drained slopes. However, particularly above 3400 m, the position of the forest/grassland boundary very often seems unrelated to changes in the physical environment. Furthermore the grasslands contiguous with the forest islands often show evidence of previous forest cover in the form of wood charcoal, charred stumps, logs and tree roots. Where the thick-barked conifer Dacrycarpus compactus is present in the forest, old, fire-scarred trees may survive in the adjacent grasslands. These relics of former forest suggest that the present-day islands are the remains of a once larger forest area, the disappearance of which was associated with, and probably caused by, fire.

Forest relics are apparently absent from the non-forest areas of Mt Scorpio and Mt Suckling and are also commonly absent from the boggy grasslands and mires of flat, formerly glaciated topography. However, only Dacrycarpus and, where present in the subalpine forest, Papuacedrus seem to leave durable relics. These conifers are not present in the subalpine zone on all mountains so the apparent absence of macroscopic relics does not prove that forest was not once more extensive.

Summary.

The vegetation patterns described above are apparently controlled by the interaction of a number of factors. Something associated with increasing altitude - presumably decline in temperature - appears to be the primary control. Secondary controls associated with topography and the effects of Pleistocene glaciation may include soil depth, drainage and cold air ponding. The historical effects of burning to some extent cut across these altitudinal-topographic controls but in return are partly related to these factors.

Mt Wilhelm.

The basic pattern on Mt Wilhelm above 3000 m is typical of many other high mountains in New Guinea. The tree-limit is at 3800-3900 m but above 3600 m the forest in most valleys is reduced to islands, usually less than 4 hectares in area. Below 3500 m forest covers most of the area and most non-forest vegetation is on the floors of the valleys, only occasionally extending up their sides. The lowest tongues of grassland end at the terminal moraines at 3200-3300 m. There are considerable differences between the valleys which are separated by sharp ridges; the Pindaunde Valley will be considered first (Fig. 3.2).

The Pindaunde Valley.

The gently sloping valley floor between the terminal moraine and the first rock step is covered in a mosaic of mire and grassland. Various mire types dominated by non-tussock grasses and sedges occupy the wettest sites with moving ground-water. The large clumps of Deschampsia klossii dominate better-drained ground on slopes of less than 10° , with sparse shrubs. The driest sites, on the terminal moraine itself and on morainy hummocks in the valley floor, are mostly covered in a 'treefern savannah' of open groves of Cyathea atrox.

Between the forested valley sides and the marshy valley bottom there is a strip of tussock grassland. This is much wider (up to 20 metres) on the northeast facing side than on the other, where the forest directly abuts the mire in some places. Where swathes of forest have been removed, apparently by landslides, grassland and C. atrox groves continue up the valley side. (Some smaller land-slip scars on the south-west facing side are apparently reverting directly to forest.)

Above the first step (3460 m) the Pindaunde Valley widens considerably and the valley floor becomes steeper and more irregular. Small moraines and boggy depressions are common but most of the floor is well drained. Continuous forest still covers most of the slopes on the south-west facing side of the valley but is reduced to large islands on the opposite side. Mire communities or D. klossii dominated grasslands occupy the depressions in the valley floor, while tussock grasslands of varying composition occupy the rest of it and the area between the forest islands on the steeper slopes. More or less shrubby tussock grasslands occupy the better-drained flats (where Cyathea gleichenioides forms occasional small groves) and much of the slopes. Poa saruwagetica - Dichelachne grasslands with only scattered shrubs are also present on the north-east facing slopes.

Fig. 3.2 The Pindaunde valley - the large-scale vegetation pattern.

■ Field Station

Around the lower Pindaunde lake (3570 m) forest is reduced to islands on both sides of the valley, although the islands are bigger on the south-west facing side. The valley-side grasslands are also noticeably more shrubby on that side, in contrast to the virtually shrubless Poa saruwagetica - Dichelachne grassland on the other.

The upper Pindaunde lake (3670 m) occupies a cirque with steep back walls, often almost vertical. Forest is restricted to isolated patches around the shores and in the short, narrow 'valley' at the head of the lake. Wet D. klossii-dominated grasslands cover small flat areas around the lake and much of the gently sloping floor of the valley at the head, although sedge mires occupy the wettest parts. The highest forest in the Pindaunde valley is a small patch near Brass Tarn (3910 m) but most of the higher slopes below the treeline are covered in Coprosma - Poa shrubby tussock grasslands. At its upper limit this community merges into the physiognomically similar but floristically distinct community above the treeline (but 'subalpine' by Wade and McVean's (1969) definition) which extends to around 4100 m in a mosaic with true 'alpine' communities.

Forest relics in the form of charred stumps, roots, logs and scattered Dacrycarpus trees are very common outside the forest below the treeline. They are found throughout the more shrubby tussock grasslands (Coprosma - Poa tussock grassland), in the Poa saruwagetica - Dichelachne grassland with few shrubs, and in the Cyathea atrox groves. Relics are also found in some areas of D. klossii grassland below 3600 m but were generally absent from this community at higher altitudes. There are also occasional forest relics in some 'short grass bog' communities.

The other Wilhelm valleys.

The north-east facing Imbukum valley is the most strikingly different in both morphology and vegetation. It is wider than the other valleys and lacks some of their glacial features. There are neither lakes nor steps in the valley profile but there is a massive terminal moraine at about 3250 m. The steep and evenly-sloping valley walls are almost completely forested up to a diffuse limit at 3700-3950 m. In contrast, the almost-flat, till-choked valley floor behind the terminal moraine is devoid of trees. The soil there is rocky, shallow and waterlogged, and supports sedge-dominated mire communities with shrubs, mainly Rhododendron yelliottii, on raised ridges of till. Along the south-facing side there is a narrow (3-8 m) strip of D. klossii grassland with isolated Dacrycarpus and a few charred stumps. There is also an isolated opening, called Umbamambuno, covered in sedge mire and wet D. klossii grassland, in a small flat area surrounded by forest, 140 m above the valley floor.

Plate 3.1 Lower Pindaunde valley, looking south-west towards the terminal moraine.

Plate 3.2 Lower Pindaunde lake, looking north-east.

Plate 3.3 Upper Pindaunde lake, looking south.

Plate 3.4 Imbukum valley, looking north.

The north-west facing slopes of the valley are covered by a dense forest of tall trees, mostly eucalyptus, with a thick undergrowth of shrubs and ferns. The vegetation is very lush and green, indicating a high level of rainfall. The valley floor is a mix of open grassland and scattered trees, with a few small streams or watercourses visible. The overall scene is one of a healthy, undisturbed natural environment.

The vegetation on the valley floor is a mix of open grassland and scattered trees, with a few small streams or watercourses visible. The overall scene is one of a healthy, undisturbed natural environment. The north-west facing slopes of the valley are covered by a dense forest of tall trees, mostly eucalyptus, with a thick undergrowth of shrubs and ferns. The vegetation is very lush and green, indicating a high level of rainfall. The valley floor is a mix of open grassland and scattered trees, with a few small streams or watercourses visible. The overall scene is one of a healthy, undisturbed natural environment.

Plate 3.5 Lower Bendenumbun valley, looking west.

Summary

- (1) Both major types of vegetation are present in the valley, but the forest is more extensive than the grassland.
- (2) The forest is a mix of tall trees and shrubs, with a thick undergrowth of ferns and other plants.
- (3) The grassland is a mix of open areas and scattered trees, with a few small streams or watercourses visible.

Conclusions

From this survey of vegetation in the valley, it is apparent that the forest is more extensive than the grassland. The forest is a mix of tall trees and shrubs, with a thick undergrowth of ferns and other plants. The grassland is a mix of open areas and scattered trees, with a few small streams or watercourses visible. The overall scene is one of a healthy, undisturbed natural environment.

Plate 3.6 Un-named valley between Giwimawi and Badmenangidongwa, looking south. Note aspect-dependence of shrubbiness.

The north-west facing Bendenumbun (upper Jimi) valley is also atypical. The upper section (>3500 m) is similar to the Pindaunde valley, although more shrubby, but below 3400 m the forest is not continuous but divided by landslips and shrubby areas, although tussock grasslands are restricted. Even more peculiar is the region just below the terminal moraine where large dead Papuacedrus trees, some apparently charred, emerge from a low, Olearia-dominated forest.

The vegetation pattern in the remaining valleys is basically similar to that of Pindaunde. Aspect differences in forest extent and the shrubbiness of the grasslands are even more marked, however, in those valleys which run approximately north-south. Within each valley both the extent of forest and the shrub cover tend to be greatest on the west-facing side. Forest patches, particularly above 3500 m, are shaded from the morning sun far more often than would be expected if their distribution were random. Sometimes this shading is caused by a crag on the valley side or a ridge, where it would not be expected from valley orientation. Conversely, shrub-less grasslands of the Poa-Dichelachne type are confined to sites which do receive the morning sun.

Shrub cover also increases with altitude up to the treeline in most valleys. There is, in addition, a general north-south trend of declining forest extent and decreasing shrubbiness when areas at the same altitude and of the same aspect in different valleys are compared.

Summary.

(1) Both major types of subalpine vegetation pattern found in New Guinea occur on Mt Wilhelm. The Imbukum valley has continuous forest on the slopes up to the treeline and non-forest vegetation is confined to the poorly-drained valley floor; the other valleys show varying degrees of fragmentation of the forest.

(2) The Pindaunde vegetation pattern is fairly typical of all the Wilhelm valleys except the Imbukum and, to some extent, the Bendenumbun valleys.

Conclusions.

From this survey of subalpine vegetation in New Guinea it is apparent that an explanation of its pattern will include both components of the present physical environment and historical factors. A reasonable initial hypothesis is that forest was excluded from certain areas in the subalpine before disturbance and that these areas have subsequently been extended by fire. The 'natural' factors excluding forest are clearly controlled by topography and are most effective on the floors of glacial valleys. The same or different factors may exclude forest on the ridge-tops of some unglaciated mountains. Waterlogging and cold-air ponding have been

suggested as important in the former case but seem unlikely to operate on the ridges, where 'exposure' or shallow soil are alternative explanations. In valley bottom situations, the effects of cold air ponding and waterlogging may be difficult to distinguish in practice. The amount by which non-forest communities have been secondarily extended seems related to both their previous, natural extent, and to the degree of human interference.

The question of man's impact on the subalpine vegetation of Mt Wilhelm is related to the question of the origin and maintenance of the vegetation pattern. The human factor can be isolated only by identifying and excluding the influence of other factors. The general problem which this thesis seeks to answer can therefore be resolved into the following specific questions.

- (1) What was the vegetation pattern before disturbance?
- (2) What environmental factors controlled this pattern?
- (3) When, and by what processes, did the present pattern originate?
- (4) What was man's role in these changes?
- (5) Is the present pattern stable, and, if not, what is happening now?
- (6) What may happen in the future?

Questions 1-4 are basically historical and 5 and 6 will partly involve the extrapolation of historical trends. The problem in studying the history of vegetation pattern is obtaining sufficiently accurate spatial information. A dendrochronological approach has been used in studies of subalpine forest retreat elsewhere and would be potentially applicable on Wilhelm if the Dacrycarpus trees could be cross-dated. However, although Dacrycarpus does have irregular growth rings, it seems a priori unlikely that they are annual, and it would be a major project in itself to establish a useful chronology. In any case, a dendrochronological study would give information only on the forest component of the pattern and could tell nothing about the nature of the non-forest vegetation. For these reasons, a palynological approach was preferred, although with major modifications to standard methodology in order to obtain the required spatial information. The main part of this thesis (Section II) is an account of this palynological investigation.

Modern ecological studies (Section III) were concentrated on the description and measurement of contemporary processes relevant to the question of the present stability and the prediction of future changes (5 and 6 above), and to refining the interpretation of the palynological record. An experimental approach to the question of the control of vegetation pattern was rejected. In theory, transplant experiments in the field with laboratory experiments on the edaphic and climatic tolerances of important taxa might have yielded relevant information. However, the short

time available and the absence of laboratory space in the Highlands would have added to the already considerable problems of designing and interpreting such experiments (Harwood 1976). In effect, the whole project is an attempt to define and interpret an experiment set up unknowingly by the local inhabitants. Palaeoecology is the only way one can study long-term ecological experiments without waiting a very long time.

Because all field work had to be completed in two field trips the historical and ecological parts of this study were carried out in parallel. Reporting the results, however, imposes a linear order on the work. I have decided to put the palynological section first because the conclusions from it depend less on those from the ecological studies than vice-versa.

Theory.

Discussions of the general theory and practise of pollen analysis can be found in the literature (Faegri and Iversen 1975; Davis M.B. 1963, 1967; Janssen 1966; Tauber 1965; Oldfield 1970) and only aspects of particular relevance to this study will be considered here. Substantial Quaternary pollen analytical studies in New Guinea have been reported by Powell (1970), Flenley (1972), Hope (1973, 1976a, 1979b) and Walker and Flenley (1979). Previous pollen analytical work on Mt Wilhelm by Hope (1973, 1976a) provided a framework for this study but was not sufficiently detailed or chronologically controlled to answer the questions posed in the previous chapter.

The spatial limits of this study have been earlier defined as Mt Wilhelm between the lowest limit of grassland (c.3200 m) and the altitudinal tree-line (c.3900 m). A temporal 'depth' of 1000 years was chosen because it encompasses the disturbance of the subalpine forest and the rise in Casuarina shown in Hope's long cores. The unique features of this investigation are a result of this short time scale and the use of a large number of closely correlated sites in a relatively small area. No similar studies have been reported in the literature although the general principle could, with some modifications, have a wide application.

Pollen analysis and vegetation pattern.

The relative proportions of the pollen types in a pollen assemblage are related in a complex way to the relative proportions of the source species in the surrounding vegetation. This complexity arises from differences between taxa in productivity (which also varies for one taxon under different environmental conditions), propensity for dispersal and resistance to decay of their pollen. Pollen deposition theoretically decreases logarithmically with distance from a single source. The dispersion curve will be different for each species and will also differ between individuals of the same species, depending on size, vigour, growth habit and position in the vegetation. Because of the shape of the dispersion curves, however, there is a practical limit to the 'pollen source area' around a deposition site which contributes most of the pollen. (This is excluding pollen of taxa which, although occurring only far from the collection point, have high absolute values in the pollen rain, as a result of massive production of easily-dispersed pollen e.g. Nothofagus and Casuarina on Mt Wilhelm.) In very general terms it is the size of this 'pollen source area' relative to the major scales of pattern in the vegetation which determines the level of reconstruction of the vegetation potentially possible from a pollen spectrum from a single site.

Pattern on a scale small enough for all elements of the mosaic to occur repeatedly within the pollen source area will not be evident from the pollen spectrum, although it may be inferred from a knowledge of the ecology of the species concerned. Pattern on a scale so large that the pollen source area is entirely within one element will also not be detected at a single site. However, where the pattern scale is intermediate, so that the pollen source area includes parts of more than one element of the mosaic, then the vegetation pattern becomes significant in the interpretation of the pollen spectrum. If it is possible to ascribe pollen taxa to particular elements of the pattern it may be possible to detect changes in the relative proportions of the pollen source area covered by each element.

It may also be possible to say something about the spatial arrangement of the communities on the ground, if their composition is known. The different dispersal curves of the various pollen taxa mean that the same community will contribute pollen in different ratios depending on its distance from the deposition site. In the simplest case, certain types of pollen which are never dispersed far, such as pollen from low, entomophilous herbs (e.g. Ranunculus spp. on Wilhelm) indicate the presence of their parent community on the site itself. More generally, as the distance between a source community and the deposition site increases, the ratio of the better dispersed to the less well dispersed pollen types arriving from that community will increase.

Vegetation pattern is often just an added complication in the reconstruction of vegetation history. If it is itself of interest, a single site will normally be useful only where ecological inferences independent of the pollen analysis data can be made. Wright (1971) suggested that absolute pollen influx data rather than percentages would help answer the question of the areal extent of the Neolithic forest clearances in Western Europe. Sims (1973), however, found that without additional information it was not possible to distinguish between a relatively small local clearance and a much larger clearance at a distance from the site. In the large lake sites he used (>200 m diameter) all pollen was deposited on the flat 'regional' part of the curve, so ratios of the differently-dispersed pollen types could not be used to give spatial information. Influx data from very small lakes would be a possible approach.

Oldfield (1963), in contrast, was able to relate the various pollen source taxa to particular environments in an area of sharply different edaphic and topographic conditions, and in this way produce evidence for changing vegetation pattern. In the subalpine region of Mt Wilhelm the constraints imposed on forest distribution by altitude and waterlogging do provide some additional spatial information. However, forest and grassland

often occupy very similar sites, so pattern in the physical environment is not very helpful in the reconstruction of vegetation from the pollen data.

There are few, if any, palaeoecological problems for the solution of which a single pollen diagram from a single pollen site is sufficient. Commonly, several sites are used, or should be used, so that regional changes can be separated from purely local variations. Where this local variation is itself of interest, pollen diagrams from more than one site can give information on the location and extent of different source communities. Turner (1970) used differences between pollen diagrams (correlated by regional changes) from five spatially separated sites on a large mire to obtain information on the pattern of post-neolithic clearance episodes in the surrounding forest. However, the most detailed and reliable information to be got from fossil pollen spectra concerns the nature of the vegetation on and immediately around the site. Therefore sites should ideally be distributed through the study area in such a way that information on their immediate surroundings can be combined in the reconstruction of the vegetation pattern at that time. This is the principle used in this study.

Mt Wilhelm has both mire and lake sites suitable for pollen analysis. The thirteen lakes, however, occupy only a restricted altitudinal range (3550-3850 m) and are too large (10-80 ha) for a detailed study of changes in vegetation pattern. A pollen assemblage from the centre of the lake will be an integration of pollen spectra from the mosaic of plant communities around the lake. Changes in pattern on a smaller scale will be blurred or missed altogether in the 'averaged' pollen record. In contrast to the lakes, mires and areas of blanket peat are found at all altitudes in the subalpine region and it is possible to choose sites sufficiently small that local mire pollen production is of minor importance.

In comparison with the lake and mire sites most often used in palynological investigations, those used in this study are very small. Except where cores were taken from larger mires in order to investigate the history of the mire itself, the mire sites chosen were all considerably less in diameter than the height of the subalpine forest canopy. They are thus similar to the deep mor-humus profiles investigated by several workers in Europe (Faegri 1954; Iversen 1964, 1969). Andersen (1967) showed that when such a site is surrounded by forest the majority of pollen comes from within 20-30 m, and the pollen diagrams constructed show local forest succession (Iversen 1964). A similar figure probably applies for Mt Wilhelm. When the forest is cleared from around the site one would expect the pollen source area to increase as a result of the effects of wind and increased turbulence on pollen transport, but the majority of pollen would still be expected to come from within 100 m radius. In practice the pollen source area was found to be considerably smaller than this (Chapter Seven).

Thus a record of vegetation change on and around the site can be obtained. With suitable chronological control records from a number of sites can then be combined to reconstruct the changing vegetation pattern.

Dating and correlation.

Where horizontal comparisons between cores are to be made, accurate dating and cross-correlation is essential. Radiocarbon dating cannot be used satisfactorily for the last 100-300 years because of the shape of the calibration curve (Stuiver 1978) and it always has an unacceptably high margin of error for detailed correlation. In any case, radiocarbon dating of all the monoliths used in this study would not have been economically feasible.

Studies elsewhere which have concentrated on a similar time-span have mostly used alternative dating techniques. In North America there have been several studies of the impact of European settlement on the vegetation in the last few hundred years (all using lakes, not mires). 'Varved' lake sediments have provided very accurate dating in a few special situations (Swain 1973; McAndrews 1976; Cwynar 1977; Swain 1978). Most workers, however, have used the changes in pollen percentages resulting from settlement (particularly the Ambrosia rise) at historically documented times, or calibrated by a nearby varved lake, as a discrete time marker (Webb 1973; Davis M.B. 1973, 1976; Maher 1977; Strong 1977). In a refinement of this method, R.B. Davis (1967) used four time markers for dating within the last 200 years: first settlement (c.1775 A.D.), a decline in agriculture (c.1900 A.D.), the Castanea decline as a result of disease (c.1930 A.D.), and peaks of charcoal following extensive fires (1947 and 1952).

Various alternatives to radiocarbon dating which are not dependent on historical records have also been tried. Profiles of atom bomb fallout, including Caesium-137, Carbon-14 and Strontium-90, have been used to date recent levels in both mires and lakes, but the horizons identified, first presence at c.1954 and peak values in 1963, are too near to the surface to be useful in the slow-growing Wilhelm peats. Lead isotope (Pb-210) dating uses a different principle for dating between 0 and 150 years B.P. Pb-210 is a natural decay product of radon present in the atmosphere and dating is based on the continuing decay of the isotope (half-life 22.3yr) after incorporation (Krishnaswamy et al. 1971). This method can in principle reveal much more detail about the sedimentation rates than methods involving discrete time markers, but has some theoretical and practical problems (Robbins et al. 1978; Oldfield et al. 1978). It has only been used to date lacustrine, estuarine and marine sediments, and has not been used for mires.

Clymo (1978) obtained a continuous age-profile in a fast-growing Sphagnum bog from the cumulative total amounts of aluminium, titanium and magnesium present. In theory, any substance which has been added at a constant rate and has subsequently stayed in situ could be used in this way, but a considerable amount of research is required before using this technique in a new area. Pennington (1975) used Pinus pollen influx in this way to estimate changes in the rate of sediment accumulation.

Finally, for suitable lake sediments, there is the possibility of using the secular variation in the earth's magnetic field as a general dating technique for the last thousand years (Thompson 1973; Thompson and Oldfield 1978).

Of the above methods, only the use of regional pollen changes is applicable to the Wilhelm situation, and then only for correlation rather than dating, in the absence of historical records. The most likely possibility was the regional Casuarina rise, which probably followed introduction of tree-fallowing into the agricultural practices at lower altitudes. A ratio between Casuarina and the other major regional element, Nothofagus, should be independent of fluctuations in local pollen production and might provide a time horizon which was both useful for correlation and significant in human prehistory. However, in the Wilhelm diagrams, the Casuarina rise is gradual, with no clear-cut first appearance or sudden changes. Therefore it was not considered suitable for providing the primary chronology, although useful for detecting errors and discontinuities in peat accumulation.

Tephrochronology.

The primary chronostratigraphic framework for this study was provided by two layers of volcanic ash which have been extensively dated and used for correlation purposes elsewhere in the Highlands (Golson 1977a, 1977b; Oldfield et al. in press; Blong in mss.). It can be assumed that these tephras accumulated virtually instantaneously in comparison with the rate of peat accumulation (Blong in mss.), so very accurate correlation between sites at which they are present is possible at two horizons. There is still, however, the problem of the actual sidereal age of the upper tephra, which occurs in the time span when there are no entirely satisfactory methods of dating. (See discussion in Appendix One). Several tephra layers were found on Mt Wilhelm by Hope (1973, 1976a) but they were not present in all cores and, in the absence of comparative studies, could not be used for correlation. Since then the upper two tephras have been the subject of a major study (Blong in mss.) and they can now be used with confidence as stratigraphic markers.

The two tephras were first recognised in 1970 at the Kuk prehistoric site in the upper Wahgi valley (Golson 1977a). The best estimates of their sidereal ages are 230-320 years BP for the upper, Tibito tephra, and 1200 years BP for the lower, Olgaboli tephra. For reasons discussed in Appendix One, ages of 230 BP and 1200 BP are used for the two tephras in this thesis. (Subsequently 13 or 14 tephras have been identified at Kuk, ranging in estimated age from 30,000 to 230 years BP.) The Tibito tephra is an olive-grey, silty, fine sand, and the Olgaboli tephra a grey-black fine sand. They are clearly distinguishable in the field by colour and, where both are present, by relative stratigraphic position.

The Tibito tephra almost certainly originated from Long Island, in the Bismarck Archipelago, 240 km E.N.E. of Mt Wilhelm (Fig. 4.1). The estimated total compacted tephra volume of 9.8 cubic kilometres places it among the major eruptions of the last few centuries. (Krakatoa's tephra volume was 13.5 cubic kilometres.) It has been recognised at sites with a maximum east-west spread of 500 km and a maximum north-south spread of 130 km. The Olgaboli tephra also represents a major eruption although it has so far been recognised from a smaller area. Its origin is uncertain but it may come from an island which is no longer visible (Blong pers. comm.).

In the subalpine region of Mt Wilhelm the Tibito tephra occurs at depths of 0-40 cm, but most commonly at around 15 cm. The thickness is usually between 3 and 6 cm. The Olgaboli tephra tends to be at about twice the depth and is usually thinner, between 1 and 4 cm. Contact between the tephras and the adjacent peat is usually sharp and the monoliths tend to break at the boundary. This suggests that there has been little, if any, mixing by soil fauna.

Methodology.

General stratigraphy.

A survey of possible sites for pollen analysis was made by digging exploratory trenches in the major types of subalpine plant community on a range of topography, and examining the stratigraphy.

From this it was apparent that continuous peat accumulation was limited to flat or virtually flat ($<5^{\circ}$) sites. Distinct tephra layers in the expected stratigraphic positions were usually found only in the better-drained mire communities (which probably have static groundwater). In mires with moving groundwater the tephras were mixed into the peat to varying extents, while under large tussock grasses the layers were discontinuous and the Olgaboli tephra commonly absent. On the slopes, small pockets of peat with at least the upper tephra in position were quite

Fig. 4.1 The known distribution of the Tibito tephra (after Blong in mss.).

common in the grassland but absent in the forest.

There were also areas of a fibrous, uncompacted 'peat' in some patches of subalpine forest on the valley floor at higher altitudes, but the tephras, where present, were irregularly distributed and near the surface. The Wilhelm subalpine is probably marginal for peat accumulation under forest. However, the presence of the Olgaboli tephra, in the expected stratigraphic position, in the (palynologically identified) forest phase at some fossil sites shows that peat can accumulate within forest at particularly favourable sites. (There is no absolute distinction between 'peat' and the 'alpine humus soils' under subalpine forest and grassland. The tephra stratigraphy simply identifies those suitable for pollen analysis.)

Most sites used for pollen analysis were fairly uniform, firm peats under topogenous bog communities of the type described by Wade and McVean (1969) as 'subalpine short grass bog'. They give this association an altitudinal range of only 3440-3800 m but physiognomically similar bog communities, dominated by some of the same species, occur throughout the subalpine region. Typically this community is dominated by stunted tussock and mat-forming grasses, with several small herbs important, and a prominent bryophyte mat. Scattered, stunted shrubs of Styphelia suaveolens and Drapetes ericoides may be present. The bog surface has a micro-relief of c.0-4 cm. It occupies areas of from 1-15 m in shallow depressions on the valley floor and, above about 3400 m, perched on the valley sides.

The stratigraphy of the bogs below the Olgaboli tephra was not investigated in detail. Typically, the short grass bog community occupies basins behind small moraines and other flat, but relatively well-drained, areas. The depth of peat varies from 50 cm to over 3 m. The water table was observed to fluctuate between 0 to 50 cm below the surface and, although the peat was normally saturated, the surface may dry out in long dry spells. These partly aerobic conditions may account for very humified, dark-brown peat - similar to that accumulating under some wet heath communities in N.W. Europe. Recognisable macro-fossils were usually absent and sensitive pollen types (particularly Casuarina) were sometimes badly corroded. Accumulation rates under the short grass bog were low (2-8 cm per 100 years).

Selection of sites for pollen analysis.

Although most of the area in the Wilhelm subalpine is more or less steeply sloping, potential pollen analysis sites are limited to flat areas. This fact introduced a major, and unavoidable, initial bias into the palaeoecological part of this study and caused problems of interpretation which will be considered in later chapters. Even within the flat areas,

suitable sites were of limited occurrence. It was not possible to predict the scale of individual forest clearance events and subsequent changes, so the spacing of analysis sites was based on the scale of the contemporary vegetation pattern and the estimated size of the pollen source areas of the sites. In the end a compromise had to be reached between maximising cover of the study area and obtaining sufficient detail. Analysis sites were therefore spaced 150-500 m apart along the floor of the Pindaunde valley and sought wherever possible on the valley sides.

On a smaller scale the actual position of each analysis site was determined by the local vegetation pattern. A range of situations was sampled, including the major mire types and small bogs in various types of tussock grassland, with and without obvious forest relics. The aim was not to sample only homogeneous areas of vegetation but to include typical kinds of vegetation pattern. No monoliths could be taken from the forest, unfortunately, because there were no suitable sites of peat accumulation containing the tephra layers.

In order to ensure adequate coverage of the Pindaunde valley in the limited time available for pollen analysis, only one site could practicably be examined in each of the other Wilhelm valleys visited. Preliminary analysis of four Pindaunde sites after the first fieldwork period suggested that the earliest disturbance in this valley occurred above 3500 m. Therefore sites in the other valleys were chosen in mid-valley at around 3650 m.

Modern pollen rain studies.

Studies of the contemporary pollen rain aim to provide information on the relationship between the existing vegetation and the resulting pollen rain, in order to interpret fossil pollen spectra in terms of the source vegetation. Modern pollen rain can be studied either with specially designed pollen traps or with 'surface samples' such as moss polsters or surface sediments. Pollen traps provide data on the absolute pollen deposition rate (usually expressed as grains $\text{cm}^{-2} \text{yr}^{-1}$) while surface samples can give only relative, percentage counts because the period of collection is unknown. Surface samples are to be preferred for most purposes, unless the absolute deposition rate is required, as they provide a better analogy with natural, terrestrial deposition conditions. Surface sample pollen spectra will include components such as those resulting from surface water transport, which are missed by traps. They also provide an integration over several years of the often variable yearly deposition rates which may give misleading results with short-term trapping programs.

There have been two basic approaches to the application of data from modern pollen studies. One involves finding modern analogues for fossil spectra, on the assumption that similar spectra come from similar vegetation. This method has had most success in the reconstruction of large scale changes in regional vegetation, but even then is dependent on the existence of a close modern analogue. The other main approach has been to try to 'correct' fossil counts of individual species so that they more nearly reflect the relative abundances of these species in the source vegetation. The correction factors, or 'R-values', are derived from the ratio of the pollen percentage in the modern spectrum to some measure of the percentage abundance of the source taxa in the surrounding vegetation. There have been many problems in the calculation and use of R-values, including the unknown size of the source area for a given pollen taxon and the dependence of the R-values for a given taxon on the composition of the vegetation and its distance from the deposition site (Oldfield 1970). This last consideration means that, except in a large area of homogeneous vegetation, there is actually a range of possible R-values for each taxon, depending on whether the taxon is on, around, or distant from the site. In practise, pollen diagrams have usually been interpreted using a subjective combination of these methods. The nearest modern analogue is found and the differences are then interpreted using knowledge of the quantitative or, more usually, qualitative production and dispersal characteristics of the individual taxa. This is the approach adopted here.

Hope (1973, 1976a) made a study of the modern pollen rain on Mt Wilhelm using Tauber pollen traps for one or two years, and surface samples. The surface samples were usually 'tufts of mosses collected from within an area of one square metre'. Pollen trapping proved unsatisfactory, with a large variation between the years and systematic differences from the surface samples. This he attributed partly to the short trapping period and partly to missing the surface runoff component, which includes pollen of several small herbaceous species. A summary of Hope's modern pollen rain results applied to individual subalpine taxa is given in the next chapter.

'Rl' is the local representation value at a selected site and equals the local pollen percentage divided by the local pollen source percentage. Rl values give information only on the relative production and short distance dispersal of pollen taxa. No quantitative regional vegetation survey was made, so Rr (regional R-values) could not be calculated. However, the pollen percentage data from unvegetated sites show clearly which taxa are transported well. Hope also made an estimate, based on both regional and local deposition, of the percentage of a given pollen type found in a spectrum which indicates local presence of the source taxon (LP%). Both Rl and LP% values will be dependent upon the other taxa represented in the spectrum, so can only be used as rough guides to the

qualitative interpretation of fossil spectra.

All the subalpine plant communities sampled had distinctive pollen spectra when present locally (i.e. on the site) but as peat is not accumulating in most of these communities, these local spectra do not provide analogues of fossil depositional situations. They do, however, help to identify local communities occurring extra-locally to fossil sites (i.e. within about 5-40 m), although it was found that many herbaceous communities could not be differentiated when they were part of extra-local mosaics. The ratio of Rapanea pollen to Dacrycarpus pollen was considered as a means of locating the position of the forest edge relative to a site in the grasslands but the variation, mainly a result of fluctuations in Dacrycarpus, was too great for it to be useful. Other ratios were also calculated but none proved very useful in interpretation of fossil data.

There are several additional useful points from Hope's modern pollen study (from Hope 1976a).

- (i) About 70% of the pollen reaching traps is a rain-out component.
- (ii) Pollen is effectively carried upslope but not downslope (probably a result of morning up-lift and afternoon rain-out).
- (iii) The regional pollen rain is $800-100 \text{ grains cm}^{-2} \text{ yr}^{-1}$.
- (iv) Total pollen deposition within plant communities ranged from $1000-7000 \text{ grains cm}^{-2} \text{ yr}^{-1}$.

The information on the behaviour of individual pollen types and the characterisation of plant communities obtained by Hope provided the basis for the interpretation of fossil spectra in this study. Some additional information was sought, however, on questions of relevance to a study of changes in vegetation pattern. Each monolith taken had an associated 'surface sample', comprising the uppermost 0.5-1 cm of litter, moss or humus from a radius of about 10 cm around the site. These surface samples provided some information on the extent to which pollen spectra from the small bog sites used in this investigation characterise the surrounding vegetation. More importantly, they enabled the interpretation of the changes shown in the pollen diagrams, to be made downwards from the surface in terms of differences from the known, contemporary vegetation. Fewer assumptions are required when making comparisons between spectra from the same site (Oldfield 1970). Further surface samples of the same type, independent of fossil sites, were taken on two transects across forest edges to assess the possibility of refining the interpretation of fossil spectra in terms of distance from the forest edge.

The pollen sum.

Ideally, all pollen data would be expressed as absolute pollen deposition rates: the number of pollen grains of each taxon deposited on unit surface area in unit time. However, this is only possible where the chronological control is exceptionally good and the sediment type allows extrapolation between dates. Approximate pollen deposition rates based on averages for long periods of a variable sediment accumulation rate may give misleading results. Most often the abundances of different pollen types must be expressed as percentages of their common sum, or the sum of a select group. The basic problem with percentage diagrams is the dependence of each value on all the others included in this pollen sum, a fact which must always be borne in mind during interpretation of such diagrams. Pollen diagrams are a visual method of displaying large amounts of data and are usually interpreted mostly subjectively. Thus, although the choice of pollen sum does not change the information content of the data, it may alter the interpretation of the diagram. The use of computers enables the effects of different pollen sums on the appearance of the diagram to be rapidly assessed but helps little in the final choice of the sum.

The choice of the pollen sum is an important step for which there are no precise rules. Faegri (1975) says that "all pollen (and spores) that have a bearing on the actual problem [should] be included". Hope (1973), in contrast, has suggested that a sum should be chosen that will give a fairly stable 'sum deposition rate' on which to base percentage calculations, so that the percentages of any pollen type will approximately reflect the deposition rates for that type. He argued that a sum of "elements that have remained regional throughout the history of a given site" would best meet this consideration. A secondary consideration is that "the size of the pollen sum relative to the total count should be sufficient so as not to exaggerate minor differences between samples". For Mt Wilhelm a regional sample would consist largely of Nothofagus, and gave 'exaggerated values' to many pollen types. Hope therefore chose a sum made up of all woody taxa (excluding Casuarina and Cyathea) for his Mt Wilhelm pollen diagrams. A comparable sum has been used by other New Guinea workers (Powell 1970; Flenley 1972).

The sum (or sums) used should be determined by the problem under investigation. This study is primarily an investigation of the local replacement of forest by non-forest vegetation at many sites. A woody taxa sum would exaggerate the changes in the frequencies of non-woody pollen taxa. The logical choice is therefore a sum including all taxa which occur or have occurred around a particular site. For simplicity and comparability the actual sum used at all sites included all the pollen types from taxa which occur in the subalpine study area, except where their inclusion was expected to distort the percentages in such a way as to make

interpretation difficult.

Several small herbaceous species - Ranunculus, Astelia, Gentiana and other minor herbs - were excluded from the sum because it was evident from surface samples that their pollen was not dispersed in the air. These plants probably produce abundant pollen which is washed to the ground, and a high pollen frequency may indicate only the local presence of a single plant.

All fern spores, except those of Cyathea spp. and Gleichenia vulcanica, were also excluded. Most fern species are epiphytic and changes in their spore frequencies can take place without changes in the major part of the vegetation. Cyathea and Gleichenia vulcanica were the only fern taxa which could be identified with reasonable certainty and which played a significant role in plant communities. (Other, uncollected, fern species may produce trilete, psilate spores similar to Cyathea but the frequencies of those spores identified as Cyathea sim. in surface samples were clearly related to the presence of Cyathea in the surrounding vegetation.) Cyperaceae have been included despite extra-local under-representation, indicating a poor aerial dispersal of the pollen. Separate diagrams plotted on a sum excluding sedge pollen were produced where local over-representation of sedges obscured extra-local changes. In general, all pollen taxa without a clearly identifiable source in the subalpine region were excluded from the sum.

The main source taxa contributing to the pollen sum were: Dacrycarpus, Rapanea, Poaceae and, at some sites, Cyperaceae and Cyathea. These taxa have different pollen productivities and dispersal characteristics so the pollen sum deposition rate at any site will not remain constant when the vegetation changes. This means that great care has to be taken in the interpretation of changes in the individual pollen curves at horizons where there is a major change in the vegetation.

Although the Nothofagus pollen count is too small relative to the total count to be used as a pollen sum, it does provide a check on large changes in the pollen sum deposition rate. There are several a priori reasons for expecting the Nothofagus pollen rain to have remained more or less constant over the last 1000 years. It is a regional component and, although many source populations may contribute, the major one is probably the extensive Nothofagus forests north of the main divide which are well above the zone of gardening and apparently undisturbed. There is no evidence that Nothofagus ever occurred in the upper Simbu valley, where the forests have been completely cleared, perhaps because it was too dry (Hope 1973). Elsewhere in the central Highlands, Nothofagus forest often forms the upper limit of the garden zone, although it cannot be determined whether this is because Nothofagus is exceptionally hard to clear with

stone axes (as one might expect) or because substantial areas have already been cleared below.

As will be discussed in Chapter Six, the pollen diagrams themselves provide evidence that Nothofagus has remained approximately constant.

Field methods.

Sites for pollen analysis were preferentially chosen at which both tephras were present as distinct layers with sharp boundaries. This, however, was not always possible, and to avoid too great a restriction on the positioning of sites some were chosen at which only the upper tephra was visible. (The absence of the lower tephra suggests a discontinuity in deposition, so care must be taken in the interpretation of such sites.) A D-section corer was used at the wettest sites, while at the majority the procedure was first to dig a trench to check the stratigraphy and then, after cleaning the profile, to excavate a monolith with knife and spade. Monoliths were initially cut 10-12 cm square in horizontal cross-section and subsequently trimmed at the field station to about 8 cm square, before wrapping in polythene and packing in boxes for transport.

Monolith sampling strategy.

The monoliths from different sites are accurately correlated only at the surface, and the 'time-planes' defined by the two tephra layers. Horizontal comparisons were therefore made primarily at these horizons and intermediate samples were used mainly for the reconstruction of local site histories. Four levels were initially analysed in each monolith: the surface sample, above the Tibito tephra, below the Tibito tephra, and above the Olgaboli tephra (or at an equivalent depth if this tephra was absent). Additional samples were then taken halfway between pairs of levels which spanned a major vegetation change. At selected sites, sampling was more intensive and some levels were analysed below the Olgaboli tephra to varying depths. The question of the accuracy of dating and correlation will be discussed in Chapter Six.

Laboratory techniques.

The monoliths were sampled for pollen analysis in the laboratory in Canberra. The face of the monolith was cleaned and a 0.5 cm thick slice, about half the width of the monolith, was removed with a knife and spatula. A length of cylindrical glass tubing with an internal cross-sectional area of 1 cm² was then used to take a 1 cm³ sample from the slice, away from the outside edges. (2 cm³ was taken from the less compacted peat within a few centimetres of the surface.) The samples were broken up if necessary and, where fibrous, were wet-sieved (0.15 mm mesh) and centrifuged. Chemical

treatment was carried out in polypropylene centrifuge tubes and after each step samples were concentrated by centrifugation at 3000rev for 10 seconds. All samples were non-calcareous and the inorganic fraction was usually silt-sized or smaller.

1. Siliceous matter (mainly volcanic ash) was removed by leaving the samples for 18-24 hours in cold 40% hydrofluoric acid.
2. Colloidal silicates were removed by treating with 10% HCl for 5-10 minutes in a boiling water bath. A single tablet of Lycopodium spores (12,500+/-500) was added to the sample at this stage.
3. 'Humic substances' were removed by treatment with 2% NaOH for 2-5 minutes in a boiling water bath.
4. The samples were dehydrated by washing twice in glacial acetic acid. Then acetolysed to remove cellulose with a mixture of 9 parts acetic anhydride and 1 part concentrated sulphuric acid for 2-3 minutes (or until the solution turned dark brown) in a boiling, water bath.
5. The samples were rinsed twice in glacial acetic acid, twice in absolute ethanol and twice in tertiary butanol. They were then concentrated, and silicone oil (viscosity 2000 centistokes) was added. When the butanol had evaporated, slides were made and sealed with paraffin wax.

Pollen counting.

Slides were counted using a Zeiss photomicroscope at a routine magnification of X400. New pollen types were identified by comparison at X640 or X1600 (oil immersion) with reference slides from the departmental collection. Not all pollen types encountered could be identified but it was felt that additional time spent trying to identify all unknowns would not have been justified in a study of this type. Nearly all the pollen types encountered had also been found by Hope (1973, 1976a).

Pollen was counted in transects across the slides and counting was continued until the pollen sum count exceeded 200. (The final decision on the pollen sum to be used was not made until most slides had been counted, so the total of pollen sum taxa in practice varied between 150 and 250.) This usually involved counting a minimum of one complete slide. A higher total count has been used by some authors in order to reduce statistical errors, particularly for rare pollen types. In this study, however, most information comes from changes in the frequencies of common pollen types and a relatively small pollen count was the most efficient use of the time available.

The counts of the added Lycopodium spores gave an approximate indication of the pollen concentration and show any major changes in sediment accumulation rate. True, absolute pollen deposition rates could not be calculated because peat accumulation rates could not be accurately

estimated.

Data processing.

For data processing each pollen type was given a code number and the counts transferred to magnetic tape. In the end only 60 numbers were used and ferns (except Cyathea, Gleichenia vulcanica and Pteris) were grouped, as were rare herbs, rare montane forest trees, and all unknowns except one frequent type. Percentages for all coded pollen types against the pollen sum were then calculated on the computer. These are presented in Appendix Two. Another program, modified from one first written by Dodson (Dodson 1972), was used to plot pollen diagrams of selected pollen types.

Multivariate methods.

At first sight the data obtained, with the two tephra layers as independent time planes at 34 sites, seems ideal for the application of multivariate statistical techniques, either for the generation of hypotheses or for the communication and display of the results. The use of various multivariate methods on pollen data has been reported in the literature, including particularly Principal Components Analysis (PCA) and several clustering techniques (e.g. Birks et al. 1975). However, there are major problems in the use of these methods in palynology and most of these are maximised in my data.

The fundamental problem is the question of weighting. Unlike some other common applications of multivariate methods, such as phytosociology, palynology does not aim primarily at the description of the data but at its interpretation in terms of the source vegetation. The relationship between the pollen assemblage and the source vegetation is very complex and the normal, semi-intuitive, method of interpretation depends on a flexible system of differential weighting, based on the known dispersal properties of the pollen and the ecological preferences of the source taxa. It is impossible to completely incorporate this weighting into a multivariate analysis. All these techniques can do is summarise patterns in the data.

Multivariate techniques may have a useful role when extremely large data sets make intuitive methods impractical, or when differential weighting is less important. This latter will be the case when the important pollen types are all wind-dispersed and the vegetation within the pollen catchment is fairly uniform. The successful applications of PCA have been in such situations, when the pollen data (modern or sub-fossil) has been analysed to show large-scale spatial patterns in undisturbed vegetation (Birks et al. 1975; Webb 1974).

These conditions are not present in this study, where poorly-dispersed pollen types are critical and pattern within the pollen catchment is important. The pollen assemblages show a continuous variation which does not reflect a continuous variation in the source vegetation. On the scale at which I am working, the source vegetation is made up of more or less discrete units: forest, grassland and mire. The dispersal of the pollen smooths these discontinuities. The primary aim of any interpretative technique must be to recover them. In this thesis, this has been done mainly by using poorly-dispersed pollen taxa (and the charcoal particles) as indicators of the local vegetation.

Ordination by PCA is an efficient means of describing the major patterns in the data (Appendix Three) but little use in interpretation or display of the results. Numerical clustering techniques might seem preferable to ordination for recovering discontinuities. However, while these techniques, by definition, find the major statistical discontinuities in the data, trials with Birks' zonation programs (Gordon and Birks 1972) failed to locate the ecologically important ones.

Rather than reject the available evidence on pollen dispersal and source ecology in favour of 'objectivity' and reproducibility, each site was interpreted individually using all the information available (Chapter Five).

Charcoal particles.

The principal agent of vegetation change in the Wilhelm subalpine region is believed to be fire, but the changes in pollen frequencies give only indirect evidence of this. It was therefore decided to include systematic counts of microscopic charcoal particles ('CP's) with the pollen analysis. Hope (1976b) has published a curve of CP frequencies for Ijomba mire at 3620 m on Mt Jaya, and has preliminary data for other sites in New Guinea (Hope 1979b) but no previous CP counts have been made on Mt Wilhelm.

As Swain (1973) has pointed out, microscopic charcoal has often been recognised in sediments prepared for pollen analysis, but has usually been ignored as a source of palaeoecological information. By contrast, the presence of macroscopic charcoal, particularly when it occurs as distinct horizons, has more often been reported. Yet the absence of large pieces of charcoal in a core may be due simply to chance, and cannot be taken as evidence for the absence of fire. CPs will be more evenly distributed and it is reasonable to conclude that the absence of CPs does mean the absence of fire in a area around the site. CPs are similar to pollen in this respect and CP counts have some of the advantages (and disadvantages) over macroscopic charcoal that pollen counts have over macrofossils for palaeoecological reconstruction. In both cases, both types of evidence would ideally be studied.

A number of recent studies have included systematic CP counts. Methods of preparation, quantification and display have varied considerably and a summary extracted from published accounts is given in Table 4.1. There has been very little discussion of the origins and dispersal of CPs and of the theoretical basis for interpretation of the counts, but even the most crude quantification of CP frequency can provide very useful additional data. This data may be critical in choosing between alternative interpretations of observed vegetation changes. (See, for instance, Singh et al. 1979.)

The detailed interpretation of CP data involves most of the same problems as the interpretation of pollen counts, plus some additional ones. The botanical nature of the source may be partly identified from the morphology of the CPs; for instance, wood charcoal can be distinguished from charred epidermal fragments. The spatial location and areal extent of the source fire presents a similar problem to that previously discussed in relation to pollen spectra. The 'CP source area' will be determined by the properties of the CPs, the nature of the transport process (airborne, waterborne or gravity), and the type and size of the depositional site. The CP size spectrum may, perhaps, give information on the nearness of a fire within the source area, in the same way as the pollen spectrum does for its source community.

The question of the fire frequency has no equivalent in pollen analysis, where seasonal or annual variations in pollen production are rarely of interest. Whether or not distinct CP 'peaks' occur will depend on the fire frequency in relation to the rate of sediment accumulation, a possible time lag in the arrival of some CPs at the deposition site after a single fire, and the extent of post-depositional mixing of the sediment.

Finally, there is the question of preservation of the CPs after deposition. Although some CPs at least may be preserved as long as pollen in suitable sediments (Singh et al. 1979) it is possible that, under certain conditions, CPs could be lost while the pollen was unaffected. Particles carbonised to varying degrees will be present and the less carbonised ones will be less resistant to microbial decay. A potential loss of CPs through time might not be recognised unless it resulted in a change in the size spectrum or morphology of those remaining (e.g. a deficiency in the smaller size-classes). Conversely, it is possible that CPs are more resistant than pollen grains to decay and CP records may be present in sediments without pollen.

Table 4.1 Summary of published charcoal particle analyses.

AUTHOR	AREA	TYPE OF SITE	DESCRIPTION OF PARTICLES COUNTED	QUANTIFICATION
Bradbury, J.P. et al. (1973)	Minnesota	Lake	Charcoal fragments.	Area size-classes, summed to total area per unit volume.
Byrne, R. et al. (1977)	California	Marine	Charcoal exhibiting obvious cellular structure.	Area size-classes, summed to total area influx.
Clark, R.*	South Australia	Lagoon		Number $>22 \mu\text{m}$ per unit volume.
Cwynar, L.C. (1978)	Ontario	Lake	Opaque, usually planar, black or grey fragments.	Area size-classes, summed to total area influx.
Davis, R.B. (1967)	Maine	Lake	Wood carbonised to various degrees.	Number $>50 \mu\text{m}$ per unit volume.
Hope, G.S. (1976b)	Irian Jaya (Ijomba Mire)	Mire	All black objects not obviously mineral.	Number $>2.5 \mu\text{m}$ as percentage of pollen sum.
Iversen, J. (1964, 1969)	Denmark	Mor	Microscopic charcoal fragments.	'Area coverage' relative to pollen sum.
Kershaw, P.*	Queensland	Lake/swamp		Number $>22 \mu\text{m}$ per unit volume.
Mehring, P.J. et al. (1977)	Montana	Bog	Microscopic charcoal fragments.	Size-classes on longest axis $>10 \mu\text{m}$.
Singh, G. et al. (1974)	Rajasthan	Lake	Carbonised wood fragments.	Number $10 \mu\text{m}$ - $100 \mu\text{m}$ per unit volume.
Singh, G.*	New South Wales	Lake		Surface area ratios per unit volume.
Swain, A.M. (1973, 1978)	Minnesota and Wisconsin	Lakes	Dark brown and black fragments.	Area size-classes summed to total area influx.
Tsukada, M. et al. (1967)	Guatemala and El Salvador	Lakes	Monocotyledonous plants, presumably grasses.	Number per gram dry weight.
Waddington, J.C.B. (1969)	Minnesota	Lake	Uniformly opaque fragments of grass or sedge epidermis and woody tissue.	Area size-classes, summed to total area per unit volume.

* In Singh et al 1979.

Identification.

Many of the published studies have included comparisons of the sub-fossil CPs with reference slides prepared from various burned materials, but there are still differences between the descriptions of the particles counted. The problem is to distinguish between plant material and minerals of similar appearance (e.g. pyrites), and between organic particles carbonised by fire and those darkened by some other process. As most CPs seem to be bits of charred wood or charred epidermal (?cuticle) fragments, minerals can usually be excluded by the absence of typical plant structural features. The exclusion of unburned, darkened particles is more difficult. It has often been assumed that all non-mineral, black (and sometimes brown or grey) particles which survive the acetolysis stage of the standard pollen extraction techniques are CPs. A more rigorous preparative technique (which, being oxidative, also destroys pollen) is treatment with boiling concentrated nitric acid for one hour (Swain 1973). This has sometimes resulted in fewer 'cf. CPs' (Singh *et al.* 1979) but the identity of the material lost - less resistant charcoal or non-charcoal plant fragments - is not known. If there is no significant change in the number of cf. CPs with nitric acid treatment then perhaps more confidence can be placed in their identity. It seems unlikely that any post-depositional process will produce oxidation-resistant carbonised particles in what is, after all, a reducing medium. Probably most problems arise from incomplete carbonisation of some fragments and could be at least partly overcome by more critical counting.

Quantification of CP frequency.

There has been considerable variation in the way in which CPs have been quantified in published studies. Three different basic approaches have been adopted: simple counts of the number of CPs above a certain lower size limit; counts in size classes based either on the length of the largest axis or the estimated projected area of individual CPs in the plane of the slide; or a direct estimate of the total projected area of CPs on the pollen slide by the use of random points in an eye-piece grid. Counts in size classes have usually been summed eventually, to give either the total number of particles regardless of size, or else an estimate of the total projected area. These sums have then been expressed either relative to the pollen counts or, where possible, as concentrations or absolute CP influx values (total area or number of particles in unit area in unit time).

Clearly these various methods will give different values for the same samples and could, at least in theory, result in different trends in the final curves. Size classes rather than simple counts may be preferred because of the possibility that the size class distribution will provide

additional information on the location (or intensity) of the fire. However, most often only trends in the sum have been interpreted. Total area may be preferred to total number on the grounds that it will be less sensitive to fragmentation of the CPs after deposition or during extraction, assuming that the particles are basically planar. It may thus be a truer reflection of the amount of charcoal that originally arrived at the deposition site. Whether or not the total area arriving is a better index of 'fire importance' than the total number is a separate question. Although it seems reasonable that larger CPs should have more weight in the final interpretation it cannot necessarily be assumed that projected surface area is the best measure of relative importance.

In practise, none of the interpretations of CP data made in the literature would be altered by changing the method of quantification. Until more basic research has been done on the relationship between the CPs observed in the slides and the source fires, almost any method giving reproducible results will be acceptable, providing that interpretation is appropriately modest. In this study, what was desired was primarily a means of detecting the occurrence or absence of fire in the vicinity of a particular site at a particular time. With this information the pattern of fire occurrence in relation to the pattern of vegetation change could be determined. The determination of fire frequencies - or, at least, trends in fire frequencies - was a secondary objective. The limited time available for analysis of a large number of samples led to the choice of the simplest and quickest quantification method.

Laboratory technique.

Most CPs observed in this study were apparently charred fragments of epidermis (?cuticle) from monocotyledonous plants, presumably grasses. A small and variable proportion of wood charcoal and some unidentified fragments with cellular structure were also present. Only a qualitative description of the apparent botanical origin of the CPs was noted for each slide although, with more time, counts into separate classes might have been interesting. Most particles were elongate and the length of the longest axis provided an approximate estimate of projected area. Particles $<10 \mu\text{m}$ in length could not be confidently identified as CPs and so were excluded. Counting was initially done in size classes, on the length of the longest axis, but this gave no additional, interpretable information. The different size classes showed parallel changes and the majority of particles fell in the two smallest size classes ($10\text{--}20 \mu\text{m}$, $20\text{--}30 \mu\text{m}$) (Table 4.2). Therefore for most samples only a total count of all particles $>10 \mu\text{m}$ was made.

Table 4.2 Charcoal particle size class distribution.

SITE	SIZE CLASS (m)							TOTAL ²
	10-20 ¹	20-30	30-40	40-50	50-60	60-70	>70	
Tegepangwa	61.0	24.0	5.0	3.0	6.0		1.0	332
"	63.8	19.1	10.6	2.1	4.3			330
"	64.9	19.3	7.0	1.8	5.3	1.8		216
"	73.9	16.6	4.3	1.4	2.9		0.7	52
"	61.7	19.1	10.6	5.3	1.1		2.1	63
"	56.3	21.1	8.5	5.6	4.2	1.4	1.4	33
Site 10	62.0	14.3	9.5	4.8	4.8		4.8	1527
"	46.7	23.0	17.9	3.8	1.3	1.3	5.7	560
"	73.7	16.8	3.7	1.1	2.1		2.6	837
"	65.8	19.0	9.4	4.3	1.1	0.3		43
"	63.3	20.8	7.9	2.0	3.0	2.0	1.0	15

(1) Percentage of total charcoal which is in this size class.

(2) Total charcoal as a percentage of the pollen sum for the sample.

Counts were made on the same slides as were used for pollen analysis, and the CPs were counted on the same transects. Counting was continued until either 100 CPs or an entire slide had been counted. When CPs were very rare they were counted at the same time as the pollen. The final counts were expressed as percentages of the pollen sum and varied from 5-9,000%. This range of variation is so great that changes in the method of quantification, or larger counts to reduce statistical error, would be unlikely to change the conclusions drawn from the data.

Reference slides made from burnt grass, leaves and wood confirmed the identification of the CPs. Separate samples of unburned plant materials were also subject to both the pollen extraction procedure and the nitric acid treatment, confirming that spurious CPs are not created in this way. A number of sub-fossil samples were homogenised and sub-samples prepared by the pollen extraction procedure, the nitric acid treatment or both, and the CPs counted in size classes. No significant differences were found.

Unfortunately it was not possible to study the contemporary 'CP rain' because of a ban on the lighting of fires in the subalpine grassland. Hope's pollen traps did collect considerable numbers of CPs (c.100% of the pollen sum at subalpine sites) but their source is not certain. There were no grassland fires during the period of operation of the traps but the wood-burning stove of the Field Station and cooking fires lit outside by visitors provide possible sources. The highest charcoal percentages were in sediment from the Field Station water tank, which is consistent with this hypothesis.

The CP percentages in the surface samples will be considered with the modern pollen results, but as both the time-depth and the local fire history are unknown the conclusions reached are only tentative. In the absence of systematic studies on the modern processes of CP deposition, interpretation of the fossil CP counts has been modest.

The Surface Samples

Two types of surface samples were taken. Those associated with the transects and those on the forest edge transects. The former will be considered first (Fig. 3.1). From inspection of the pollen diagrams it is apparent that the pollen assemblages from individual surface samples are quite different from the vegetation pattern in the forest edge. All sites show a predominance of tree pollen and shrub pollen and a scarcity of herb pollen. This is especially true of sites 10, 11, 12, and 13. The pollen diagrams from these sites are shown in Figs. 3.10, 3.11, 3.12, and 3.13. The pollen diagrams from these sites are also shown in Figs. 3.10, 3.11, 3.12, and 3.13.

CHAPTER 5

The nature of the vegetation in the area of the pollen source area is shown in Fig. 3.1. The pollen diagrams from these sites are shown in Figs. 3.10, 3.11, 3.12, and 3.13. The pollen diagrams from these sites are also shown in Figs. 3.10, 3.11, 3.12, and 3.13.

POLLEN ANALYSIS: SURFACE SAMPLE RESULTS AND SITE HISTORIES

The pollen diagrams from these sites are shown in Figs. 3.10, 3.11, 3.12, and 3.13. The pollen diagrams from these sites are also shown in Figs. 3.10, 3.11, 3.12, and 3.13.

Despite the wide range of vegetation in the area of the pollen source area, the pollen diagrams from these sites are quite different from the vegetation pattern in the forest edge. All sites show a predominance of tree pollen and shrub pollen and a scarcity of herb pollen. This is especially true of sites 10, 11, 12, and 13. The pollen diagrams from these sites are shown in Figs. 3.10, 3.11, 3.12, and 3.13. The pollen diagrams from these sites are also shown in Figs. 3.10, 3.11, 3.12, and 3.13.

Spectra from well inside the forest and the forest edge are clearly different. In both transects the pollen diagrams from the forest edge are quite different from the vegetation pattern in the forest edge. All sites show a predominance of tree pollen and shrub pollen and a scarcity of herb pollen. This is especially true of sites 10, 11, 12, and 13. The pollen diagrams from these sites are shown in Figs. 3.10, 3.11, 3.12, and 3.13. The pollen diagrams from these sites are also shown in Figs. 3.10, 3.11, 3.12, and 3.13.

The Surface Samples.

Two types of surface samples were taken, those associated with the monoliths and those on two forest edge transects. The former will be considered first (Fig. 5.1). From inspection it is apparent that the pollen assemblages from individual surface samples give little information on the vegetation pattern in the source area. All mire sites show significant levels of Cyperaceae and Ranunculus but there are no consistent differences between the different types of mires, with the exception of the Gleichenia vulcanica bog. The non-mire grassland sites (10, 12, 18) are distinguished by very high Poaceae levels and low or absent Ranunculus and Cyperaceae.

The nature of the vegetation in the rest of the pollen source area around the site is even less apparent. High levels of Coprosma, Haloragis, Asteraceae, Ericaceae and Epacridaceae are found only at sites with extra-local Coprosma-Poa shrub-rich grasslands, but are not always present at these. Furthermore, the percentage of forest taxa is not always a good indication of the closeness of forest, presumably because the local pollen sum production rate is an equally important determinant. (The Nothofagus percentage is usually too low to provide a reliable correction for differences in productivity.) Very high Cyathea levels indicate local or extra-local Cyathea groves but moderate levels are present at most sites.

Despite the wide range of situations from which monoliths were taken, their surface samples seem palynologically rather similar. This confirms Hope's conclusion that, although most subalpine plant communities have distinctive pollen spectra when present locally, it is often impossible to differentiate herbaceous communities when they are part of an extra-local mosaic. For the purposes of this study this is not very important, although the ability to distinguish extra-local shrub-rich grasslands, even if not with complete certainty, is useful in studying secondary succession. What is important is to be able to identify the time of clearance of forest from on or around the site. The forest-grassland transects provide a modern analogue of the simplest such situation (Fig. 5.2).

Spectra from well inside and well outside the forest are clearly distinct in both transects: the problems are with spectra in or near the forest margin. The change at the margin is more abrupt between forest and Deschampsia klossii grassland at 3580 m than between the forest and mixed non-forest communities at 3680 m. In both cases the presence of Ranunculus is an indicator of non-forest conditions, even though the Deschampsia klossii grasslands have the lowest Ranunculus percentages of all non-forest sites. At 3580 m, but not at 3680 m, Cyperaceae is also limited to non-forest spectra. As expected, the poorly-dispersed Dacrycarpus is a more reliable indicator of local forest than Rapanea, although the

Fig. 5.1 Selected monolith surface samples.

	LOCAL COMMUNITY	MAJOR EXTRA-LOCAL COMMUNITY
A	Short grass bog	<u>Coprosma-Poa</u> tussock grassland
B	Short grass bog	<u>Deschampsia klossii</u> tussock grassland
C	Short grass bog	<u>Cyathea atrox</u> treefern tussock grassland
D	<u>Brachypodium-Carex</u> fen	<u>Cyathea atrox</u> treefern tussock grassland
E	<u>Brachypodium-Carex</u> fen	<u>Deschampsia klossii</u> tussock grassland
F	<u>Scirpus</u> fen	Tussock grasslands
G	<u>Astelia</u> bog	<u>Coprosma-Poa</u> tussock grassland
H	<u>Gleichenia vulcanica</u> bog	<u>Coprosma-Poa</u> tussock grassland
I	<u>Deschampsia klossii</u> tussock grassland	<u>Deschampsia klossii</u> tussock grassland

Fig. 5.2 The forest-grassland transects.

Dacrycarpus/Rapanea ratio is not a good measure of forest nearness. By comparison with sub-fossil spectra from presumed forest, the Poaceae percentages from inside the forest are relatively high. This suggests that, during the early stages of disturbance, Poaceae levels would have been lower and forest pollen levels higher for sites on equivalent transects. This must be kept in mind when interpreting fossil spectra, although it is probably a minor source of error in comparison with other factors.

The ratio between Dacrycarpus and Poaceae and the presence or absence of Ranunculus (and, presumably, similar herbs) seems the best guide to the location of a site in relation to the forest margin. However, it may be impossible to distinguish between locations just inside the forest, in the margin, and just outside, on pollen alone. The charcoal particles, considered below, may help in this, but their use requires the assumption that fires never enter the forest without its complete destruction.

Conclusions.

The surface samples show that interpretation of individual fossil pollen spectra by analogy with the modern spectra must, with a few exceptions, be limited to a rather crude distinction between the local presence of forest, grassland and mire. As discussed later in this chapter, interpretation of spectra from consecutive levels at the same site can be more detailed, particularly where both the present-day and the pre-disturbance vegetation patterns are known. However, at many sites the basal samples have spectra with high forest and Cyperaceae pollen but low Poaceae, for which there is no modern analogue. In these cases interpretation must be based on the available information on dispersal characteristics and source ecology of the individual pollen types, supported by data from the distribution of forest relics.

Charcoal particles.

Comparisons between charcoal percentages in surface samples are not very satisfactory because the number of fires 'experienced' by the sample will depend not only on the fire frequency but also on the number of years the sample represents. In general, charcoal levels are highest in the tussock grassland sites, comparatively lower in the mires, and very low even just inside the forest. There is, however, a great deal of variation, which may reflect the different time depths of the samples, differences in fire frequency, or chance. The low levels inside the forest and in the mires suggest that charcoal particles are less well-dispersed than any of the major pollen sum pollen types, although better than Ranunculus and perhaps also the grassland shrubs.

Interpretation of the pollen diagrams.

This thesis is primarily concerned with pattern, rather than the detailed composition of the vegetation. In the interpretation of the pollen data, forest, mire and grassland have been considered basically as discrete entities. Changes in their composition have largely been ignored, except for those post-clearance changes in the grasslands which may be evidence of secondary succession. As a result, most of the relevant information in the pollen data can be shown by displaying only a few chosen pollen types.

Fourteen pollen types with subalpine sources are included in the pollen diagrams. The only pollen sum types not displayed are Quintinia, Ascarina, Symplocos, Rutaceae, Podocarpus, Prunus, Myrtaceae, and Araliaceae, which are all forest taxa, equally- or under-represented in the pollen rain. None of these ever attains more than 3% or their total more than 10%. All pollen sum taxa attaining more than this are displayed along with useful indicator taxa. The chosen pollen types will now be considered one at a time. Table 5.1 summarises information on these types from Hope (1973).

Dacrycarpus

The source species for this pollen type is the podocarp Dacrycarpus compactus, which is a common emergent forest tree at all altitudes in the subalpine region. It also occurs as isolated, fire-scarred individuals in the secondary grasslands. Hope (1973) showed that this type is slightly over-represented locally but seriously under-represented in extra-local and regional spectra. This leads to wide fluctuations in Dacrycarpus percentages with minor changes in the distance of the nearest source. It is a large, tri-saccate grain so its poor dispersal is surprising. High Dacrycarpus levels (>20%) are usually an indicator of forest on or very near the site, but the presence of individual trees in the grassland today makes this an unreliable forest indicator.

Rapanea

The main source species for this pollen type in the study area is probably Rapanea vaccinioides, an emergent or canopy tree at all altitudes, and the dominant tree in the upper subalpine forest. The pollen of R. vaccinioides varies widely. It was counted conservatively but other Rapanea species were probably included. It shows local over-representation and is dispersed and transported well.

Table 5.1 Pollen types and sources (from Hope 1973).

POLLEN TYPE	SOURCE	SOURCE ECOLOGY	(1)	(2)	(3)
Dacrycarpus	<u>D. compactus</u>	Forest tree	1.1-1.8	1	10
Rapanea	<u>Rapanea</u> spp.	Forest tree	1.6-3.6	6	5
Poaceae	Many species	Grasses	1.0-1.4	6	4
Cyperaceae	Many species	Mire sedges	0.1-1.3	x	x
Ranunculus	<u>Ranunculus</u> spp.	Mire and grassland herbs	0.3	x	x
Astelia	<u>A. papuana</u>	Mire herbs	0.4-0.6		
Gleichenia	<u>G. vulcanica</u>	Mire herbs	c.1.0*		
Cyathea sim.	<u>Cyathea</u> spp.	Treeferns of forest and grassland	4.5-9.6	9	10
Coprosma	(a) <u>C. papuensis</u>	Forest liane	0.2-0.4	2	2
	(b) <u>C. divergens</u>	Grassland shrub	4.0-5.6		
Haloragis	<u>H. microphylla</u>	Forest and grassland shrub	1.5-3.0	2	1
Drimys	<u>Drimys</u> and <u>Bubbia</u> species	Forest and grassland shrubs	<0.2		x
Ericaceae	Several genera	Forest and grassland shrubs and trees	0.2-0.3	x	x
Epacridaceae	(a) <u>Styphelia</u> <u>suaveolens</u>	Grassland shrub	0.3-0.5	x	x
	(b) <u>Trochocarpa</u> spp.	Shrubs and herbs of forest and grassland	<0.1		

(1) R1 (the local representation value) for the taxon at a selected site. Equals the surface sample pollen percentage (based on a pollen sum excluding pollen types without local sources and adjusted to exclude the regional contribution of any local pollen type), divided by the local pollen source percentage (the percentage of total plant cover in vegetation surrounding the site).

(2) Surface sample pollen percentage from the unvegetated, rocky summit.

(3) Surface sample pollen percentage from the lower Pindaunde lake.

Poaceae

Species of Poaceae dominate the grassland and some mire types in the subalpine region. One species, Poa languidor, is fairly common in the forest but does not seem to produce a significant amount of pollen. There is a wide range of variation in diameter, surface pattern and pore dimensions but distinctions between the common species cannot be made with confidence (Hope 1973). In any case, most grass species have too wide an ecological range to be useful indicators. Therefore, although grass pollen was counted in three main size categories (with an additional category for damaged grains) and additional distinctive types were sometimes recognised, only total Poaceae is shown in the diagrams.

Hope considered that the Poaceae gave equal or slight over-representation. The surface samples show that up to 15% can occur just inside the forest and 35% in sedge-dominated mires. Higher values probably indicate extensive local tussock grassland.

Cyperaceae

Sedges of several species dominate some mire types and are common in others. Some species are also found in the forest and forest edge but do not seem to be significant pollen producers. Again there is considerable morphological variation in the sedge pollen but no ecologically useful distinctions could be made. All sedges were combined for display. Cyperaceae show approximately equal-representation locally but the pollen is very poorly dispersed, despite their presumably anemophilous flowers. Therefore even a small amount implies local presence, while Cyperaceae equal or higher than Poaceae suggests a local mire.

Ranunculus and Astelia

Ranunculus pollen comes from several Ranunculus species which dominate small areas of mire and are scattered throughout the grassland. Astelia pollen comes from Astelia papuana which is usually confined to mires, although near the treeline it may also occur inside the forest. Both Ranunculus and Astelia seem to produce abundant pollen which is washed to the ground and not dispersed. Even small amounts imply local presence of the species although larger amounts do not necessarily imply dominance at the site. These two types are therefore included in the pollen diagrams as indicators of local open vegetation (except for Astelia near the treeline).

Gleichenia vulcanica

This species entirely dominates one type of mire and is an occasional minor component of others. It also occurs on rocky slopes. It seems to give approximately equal representation locally and extreme under-representation extra-locally. Like the Cyperaceae, but unlike Ranunculus and Astelia, high values do imply local dominance. Occasional grains counted in forest samples may result from the inadvertent inclusion of spores from other ferns. This spore type was included in the pollen diagrams because it represents a distinct and interesting community.

Cyathea

Cyathea species of treeferns are an important understorey element in the forests of the subalpine zone and also occur in the subalpine grasslands, either scattered singly or in dense groves. The interpretation of Cyathea records is made difficult by the impossibility of separating forest from grassland species. There is also the possibility that some other trilete, psilate spores have been included. Both forest and grassland species seem to be locally over-represented and the spores also form an important part of the regional deposition.

Asteraceae-Tubuliflorae

There are a large number of possible source species for this pollen type, including herbs, shrubs and trees from the grassland and forest. All seem to be under-represented, except possibly the tree Senecio sp. (Hope 1973). Some of my surface samples suggest that Olearia spectabilis may be an important source, and most of the sub-fossil pollen closely resembles pollen from this species. This species is both an important forest tree and a dominant in the post-fire succession so, despite the uncertainty of identification, Asteraceae-Tubuliflorae has been included in the pollen diagrams.

Coprosma

Source species for this type are the forest shrub and liane Coprosma papuensis and the very common grassland shrub Coprosma divergens. Both seem to show slight under-representation and have a rather erratic occurrence in pollen spectra. They are potential indicators of post-fire changes in the secondary grassland.

Haloragis

The only source is Haloragis halconensis which is most common on rocky slopes and morainic knolls but is also found in grassland, the forest edge and, at higher altitudes, inside the forest. It may be slightly over-represented but it is also very erratic in occurrence.

Drimys

Source species include Drimys and Bubbia species in the forest, and Drimys piperita in the grassland. It is probably under-represented in the pollen spectra.

Ericaceae

The Ericaceae include Rhododendron, Dimorphanthera, Vaccinium and Gaultheria. They are important forest components as well as grassland shrubs, and dominant elements of the secondary succession. There is a wide size range in this pollen type and three categories were counted. However, the groups separated are neither generically nor ecologically distinct, so only the total is displayed. They are normally under-represented but occasional high values occur, perhaps as a result of incorporation of floral parts.

Epacridaceae

The main source species is probably the important grassland shrub Styphelia suaveolens, although dwarf shrubs of the genus Trochocarpa may be locally important. The pollen behaves like that of the Ericaceae.

Method of interpretation.

The surface samples do not give much information on the vegetation pattern and are of little use in interpreting fossil spectra from other sites. Exceptions are the simple case of closed forest and the special situations near the forest edge discussed above. It is, however, possible to compare the surface sample spectra with sub-fossil spectra from the same site. Without too many assumptions it is then possible to say when the present vegetation pattern originated and to interpret the direction of earlier changes.

If the oldest spectra represent closed forest, the pollen diagram can be interpreted starting from known vegetation at the top and bottom. These constraints increase the spatial information that can be obtained from intermediate spectra. Where there is no modern analogue of the oldest spectra, forest relics may give some information on the pre-disturbance

pattern. In both cases the known properties of the pollen types and ecology of the source taxa are used to refine the interpretation. Fortunately, the nature of the major change - forest clearance - is known from the presence of forest relics. In effect, therefore, interpretation consists of finding when this occurred.

In the remainder of this chapter the individual site histories are described. The non-Pindaunde sites (locations shown in Fig. 5.3) are considered first, followed by the Pindaunde sites (Fig. 5.4), listed basically in order of decreasing altitude but with nearby sites grouped. The individual histories are combined in the next chapter and the interpretation of the changes in the regional pollen rain is considered in Chapter Eight.

The pollen diagrams.

For ease of comparison between diagrams, the vertical scale is based on the stratigraphic position of the samples relative to the surface and the two tephras. These three 'time planes' are in the same position on each diagram. Alternatively this scale can be considered as an 'inferred age' scale based on the best estimates of the ages of the two tephra layers in conventional radiocarbon years, and assuming constant sedimentation rate between them. Thus a pollen spectrum from a sample taken halfway between the tephra layers in the original monolith is displayed halfway between the position of the tephra layers in the diagram. Samples immediately above and below the tephra are arbitrarily separated by 50 years. The bottom sample from monoliths lacking the Olgaboli tephra is given an arbitrary inferred age of 1000 BP. Where necessary the 'inferred age' scale is extended below the Olgaboli tephra by assuming a sedimentation rate equal to that between the tephras. A key to the interpretation of the diagrams is given in Fig. 5.5. It is important to note that the horizontal scale for the charcoal counts is different from that for the pollen types: the units on the scale equal 100% for the charcoal, 10% for the pollen.

Stratigraphic information is not included in the diagrams because, with a few exceptions noted in the text, it adds no extra ecological information.

Umbamambuno

3550 m

Imbukum valley

Umbamambuno is an isolated, flat, open area c.40 x 25 m, completely surrounded by forest, 160 m above the Imbukum valley floor. The wettest parts are occupied by a mosaic of sedge fen types in which there are small pools of open water. Somewhat drier areas support waterlogged Deschampsia klossii tussock grassland, with patches of short grass bog. In some places the forest edge directly abuts the mire but in others there is an

Fig. 5.3 Location of the non-Pindaunde pollen analysis sites.

Fig. 5.4 Location of the Pindaunde pollen analysis sites.

Fig. 5.5 'Key' to the pollen diagrams.

'Standard pollen sum' types

<u>Araliaceae*</u>	<u>Gleichenia vulcanica</u>
<u>Ascarina*</u>	<u>Haloragis</u>
<u>Asteraceae-Tubuliflorae</u>	<u>Myrtaceae*</u>
<u>Coprosma</u>	<u>Poaceae</u>
<u>Cyathea</u>	<u>Podocarpus*</u>
<u>Cyperaceae</u>	<u>Prunus*</u>
<u>Dacrycarpus</u>	<u>Quintinia*</u>
<u>Drimys</u>	<u>Rapanea</u>
<u>Epacridaceae</u>	<u>Rutaceae*</u>
<u>Ericaceae</u>	<u>Symplocos*</u>

* Not displayed in the pollen diagrams

In diagrams headed 'excluding mire pollen types' Cyperaceae and Gleichenia vulcanica have been excluded from both the pollen sum and the diagram.

intervening strip of Coprosma divergens-Poa saruwagetica tussock grassland, with many shrubs and a few charred Dacrycarpus stumps. Cyathea gleichenioides is also found in this strip.

When I visited this site in 1976, a recent fire (probably 2-3 months before) had burned one of the marginal strips and about a metre into the forest. The presence of an access track, a grass hut and several abandoned fireplaces confirmed that people visited the area.

A monolith was taken from a 1 x 2 m area of short grass bog, surrounded by Deschampsia klossii grassland and 10 m from the forest edge. There was an isolated Dacrycarpus tree 4 m away in the grassland.

The pollen diagram (Fig. 5.6) shows that Umbamambuno has been open for at least the last 1200 years. There are no consistent trends in the diagram and the fluctuations in Poaceae, Cyperaceae, Ranunculus and Astelia probably reflect only local changes in the composition of the mire. There is certainly no evidence of local forest clearance, although the modern vegetation suggests there has been some. However, the minor but destructive fire observed in 1976 was not reflected in the surface CP levels and the site might be equally insensitive to minor retreat of the forest edge. The very low (but rising) charcoal levels in the diagram may, in fact, come from local fires because there is no likely extra-local source in this valley.

Guruauglakugl 3740 m

This monolith is from a 1.5 x 3.5 m short grass bog in mid valley, near the upper end of the Guruauglakugl lake. The bog is near the centre of a gently sloping area between the lake and the steep step behind. It is surrounded by a mosaic of short grass bog, waterlogged Deschampsia klossii tussock grassland and drier Coprosma divergens-Poa saruwagetica shrubby grassland. These shrubby grasslands and those of the surrounding, steeper slopes are dominated by Coprosma divergens and Styphelia and contain many dead Dacrycarpus, scattered Cyathea muelleri and some young saplings of Rapanea spp., Dimorphanthera spp. and Olearia spectabilis. The nearest forest is a patch 120 m away on the east shore of the lake. There are no large areas of closed forest nearer than 700 m.

The pollen diagrams (Fig. 5.7) for this site show the presence of tussock grasslands nearby for at least the last 1200 years. There was a major change in the extra-local vegetation immediately above the 230 BP tephra, when Dacrycarpus and Rapanea fall to very low levels and charcoal becomes very high. Poaceae and Cyathea rise relative to Nothofagus at the same horizon.

Fig. 5.6

Umbamambuno

Fig. 5.7

Guruauglakugl (standard pollen sum)

Guruauglkugl (excluding mire pollen types)

Before 230 BP, the relatively high Dacrycarpus/Rapanea ratio suggests the presence of at least some forest close to the site. The changes at 230 BP presumably reflect the replacement of this forest by well-drained tussock grassland. Post-230 BP changes - the fall in Poaceae, charcoal and pollen sum production, and the rise in Cyathea, Coprosma and Asteraceae-Tubuliflorae (probably Olearia) - suggest succession in these well-drained, secondary grasslands.

Tegepangwa 3820 m

The Tegepangwa valley is a tributary of the Giwimawi valley, which it joins at about 3500 m. Because of problems with the altimeter, this monolith was taken 120 m higher than planned. (The corrected height is estimated from the 1:100,000 map.) The site is at the edge of a large sedge mire, 50 m below the Tegepangwa lake. The mire is about 45 m in diameter and consists of a mosaic of Carpha alpina, Scirpus crassiusculus and Carex gaudichaudiana, with associated subordinate grasses. Patches of short grass bog occur around the margins and it was from one of these that the monolith was taken. The surrounding slopes, starting two metres from the site, are covered in Coprosma divergens-Poa saruwagetica shrubby tussock grasslands with c.70% shrub cover, mainly Coprosma. Many dead and a few live, isolated Dacrycarpus are scattered in this grassland, along with both Cyathea gleichenioides and C. muelleri. Live and dead Olearia spectabilis shrubs are common. Of particular interest is the occurrence of Papuapteris linearis, normally considered an alpine species, in the grasslands at the edge of the mire.

The pollen diagrams (Fig. 5.8) for this site show the presence of a sedge mire for at least the last 1200 years. Excluding Cyperaceae from the pollen sum emphasises changes in the other elements of the vegetation. The major change is immediately above the 230 BP tephra, when Poaceae, Cyathea and charcoal rise and forest elements decline sharply. The abrupt fall in Nothofagus shows that the pollen sum production rose dramatically at the same horizon. These changes presumably result from the clearance of forest from the slopes around the mire.

Before 230 BP the low Poaceae/Cyperaceae ratio suggests the absence of tussock grassland from the area (although the presence of Papuapteris implies that there was some primary grassland). The relatively high charcoal may come from fires in the nearby alpine region. There is, however, a slight decline in forest and rise in Poaceae below the 230 BP tephra, which may indicate local clearance. After 230 BP clearance apparently continued and there is no pollen evidence for secondary succession, except for the apparent decline in pollen sum production at the surface.

Fig. 5.8

Tegepangwa (standard pollen sum)

Tegepangwa (excluding mire pollen types)

Giwimawi

3900 m

The Giwimawi valley faces south and drains to the Simbu river. The lower section, below 3500 m, is the most de-forested on Wilhelm. The upper section, above where the Tegepagwa valley joins, has some patches of closed forest but these appear to be entirely secondary (see Chapter Nine). The valley sides in this part are very shrubby in contrast to the lower section, where shrubs are virtually absent in the tussock grasslands. There are two small lakes between 3800 m and 4000 m.

The monolith was taken 200 m higher than planned because of the inaccuracy of my altimeter. (The corrected altitude is estimated from the 1:100,000 map.) It was taken from an area of short grass bog with much Astelia, by a small tarn 30 m higher than, but down the valley of, the lower Giwimawi lake. The surrounding vegetation is a mosaic of short grass bog, sedge fen and waterlogged Deschampsia klossii tussock grassland. In the drier areas of the valley floor and on the valley sides the tussock grassland has a 40-60% cover of shrubs, particularly Coprosma divergens and Drimys piperita entity subalpina. There are a few live and many dead Dacrycarpus around the lower lake but the nearest closed forest is c.800 m down the valley.

The pollen diagram (Fig. 5.9) shows that tussock grasslands, apparently with Coprosma and Cyathea, were present locally for at least the last c.1700 years. Forest has apparently always been restricted and probably occurred only on well-drained areas. The low forest percentage declines still further above the 230 BP tephra. At the same horizon pollen sum production increases, so there was probably an absolute increase in both Poaceae and Cyperaceae production, as well as a large increase in charcoal. These changes presumably indicate the destruction of the patches of forest around the site. Poaceae and charcoal decline towards the surface, while Cyathea rises, but there is no other evidence of secondary succession.

The presence of grasslands for at least 1700 years is not surprising in view of the closeness of the site to the altitudinal limit of tree growth. The possibility that some of these grasslands are the result of previous burning cannot, however, be ruled out. Even though charcoal levels are very low from c.1700 BP to just below the 230 BP tephra, disturbance before 1700 BP might have had a prolonged effect at this altitude.

Fig. 5.9

Giwimawi

Badmenangidongwa 3690 m

The Badmenangidongwa valley faces south-west and drains to the Koronigl river. It is more de-forested than the Pindaunde valley, with no forest at all above 3600 m, although isolated Dacrycarpus continue in places up to 3900 m. The Badmenangidongwa lake is small (c.10 ha) but has a very extensive marginal fen. The surrounding slopes support Coprosma divergens-Poa saruwaetica tussock grassland with scattered Dacrycarpus trees and a few Cyathea. The monolith was taken from a small (2 x 3 m) patch of short grass bog, near the edge of the marginal fen, at the lower end of the lake. The surrounding fen is mainly Carpha alpina and merges into waterlogged Deschampsia klossii tussock grassland on slightly raised areas. The nearest forest is about 900 m down the valley.

Pollen diagrams (Fig. 5.10) were plotted including and excluding Cyperaceae in the pollen sum. The site was clearly open throughout the last c.2000 years, as Cyperaceae remains high and Ranunculus is consistently present. The major vegetation change is just above the 230 BP tephra. The dramatic fall in Nothofagus at this horizon indicates a massive increase in pollen sum production. The great increase in the Poaceae/forest ratio at the same horizon shows that this is due to the replacement of forest by tussock grassland around the site. Cyathea and Cyperaceae also show a large increase relative to Nothofagus.

Before 230 BP the Cyperaceae/Poaceae ratio fluctuates considerably. Probably, wet Deschampsia klossii tussock grasslands were present among the mire communities as they are today, and the fluctuations indicate local hydrologic changes. There also seems to be a real rise in Poaceae between the tephra layers, which may reflect hydrologic changes or localised forest clearance. Charcoal levels are moderate, particularly below the Olgaboli tephra, and may reflect the presence of man locally or in the nearby alpine region.

Forest clearance at 230 BP was apparently very rapid. The subsequent decline in pollen sum production, charcoal and Poaceae and rise in Coprosma suggests a decline in burning and the invasion of the secondary grasslands by shrubs.

Bendenumun 3700 m

The Bendenumun valley is north-west of the Wilhelm summit and drains to the Jimi river. Above about 3500 m the vegetation pattern is similar to that of the Pindaunde valley. Below 3400 m, however, tussock grasslands are restricted, and there is much, apparently secondary, scrubby vegetation. A monolith taken from the lower section was unfortunately lost during the difficult return trip to the Field Station, and the site

Fig. 5.10

Badmenangidongwa (standard pollen sum)

Badmenangidongwa (excluding mire pollen types)

discussed here is in the upper part of the valley.

This monolith was taken from an area of Gleichenia vulcanica bog on the edge of a Carpha alpina-dominated mire, north of the lower end of the upper Bendenumbun lake. Around the mire at 8-10 m are Coprosma divergens-Poa saruwaetica shrubby tussock grasslands with scattered Cyathea gleichenioides and Dacrycarpus stumps. Olearia spectabilis, Dimorphanthera microphylla and young individuals of Rapanea spp. are frequent in the grasslands. The nearest forest is a small patch 35 m away.

The first pollen diagram (Fig. 5.11) is dominated by Cyperaceae which fluctuates irregularly, probably in response to minor changes in local hydrology. Re-plotting on a sum excluding Cyperaceae and G. vulcanica gives a better representation of extra-local changes.

The pollen diagrams show that open mire vegetation has persisted on the site, without major changes in extent or composition, for at least the last c.2000 years. There was, however, a major change in the vegetation around the mire immediately following the fall of the 230 BP tephra. Nothofagus falls sharply, indicating a large increase in pollen sum production, while Poaceae increases greatly relative to the forest taxa. Before 230 BP the very low Poaceae/Cyperaceae ratio shows tussock grasslands were absent and forest directly abutted the mire. Very high Cyathea levels suggest that treeferns were prominent in the forest edge. The changes at 230 BP must reflect the replacement of nearly all the surrounding forest by tussock grassland.

The subsequent fall in the Poaceae/forest ratio and decline in pollen sum production probably reflects declining grass pollen production as shrubs and forest taxa invaded the secondary grasslands. The rising Asteraceae-Tubuliflorae (probably Olearia) and Cyathea percentages support this interpretation. However, Coprosma apparently declines over the same period.

The charcoal percentages fluctuate considerably. Relative to Nothofagus, charcoal is highest at 230 BP and declines subsequently as expected. However, the significant peaks lower down do not seem to be reflected in changes in the vegetation. They must represent localised fires burning only on the mire, or at least not damaging the forest beyond rapid recovery. They are, anyway, proof of human presence in the Bendenumbun valley before the first major clearance at this site.

Fig. 5.11

Bendenumbun (standard pollen sum)

Bendenumbun (excluding mire pollen types)

Site 39

3910 m

Pindaunde valley

This monolith is from the edge of a 1 x 2 m Scirpus crassiusculus fen, 10 m south of, and 2 m higher than, Brass Tarn. This tarn was chosen as a coring site by Hope (1973, 1976a) because it lies at the apparent natural upper treeline. It is perched on an east-facing slope above the upper Pindaunde lake and the ground falls off steeply in a cliff 40 m away.

Deschampsia klossii dominates most of the surrounding grasslands but there are some small patches of closed shrubland, particularly near the cliff edge. One such patch, of Rapanea vaccinioides, Rhododendron sp., Drimys piperita, Dimorphanthera microphylla, Coprosma papuensis, and Cyathea gleichenioides, is 3 m from the monolith site. There are no living Dacrycarpus trees in these patches but there are some charred stumps. There is only one living Dacrycarpus tree in the vicinity of Brass Tarn. Scattered small (<1 m) Rapanea vaccinioides are found in the surrounding grasslands and occasional Rapanea, Olearia spectabilis and Dimorphanthera microphylla occur up to 100 m above the site.

The large increase in Cyperaceae pollen just above the 230 BP tephra makes interpretation of the rest of the pollen diagram (Fig. 5.12) difficult. Exclusion of Cyperaceae from the pollen sum gives a clearer picture of the relative changes in the other pollen types, but not necessarily a more accurate picture of the vegetation changes. The large fall in Nothofagus at 230 BP shows that the pollen sum production increased at this horizon. If this is taken into account then the changes at 230 BP include a large increase in Cyperaceae pollen, a probable absolute increase in Poaceae, an increase in Cyathea, a slight decrease in Dacrycarpus and a dramatic fall in Rapanea. A charcoal maximum coincides with the Rapanea minimum. After 230 BP the Rapanea returns to at least its former levels (relative to Nothofagus). (Because these changes are rather anomalous in comparison with the other sites, they were confirmed by re-sampling of the monolith.)

The pollen spectra suggest the presence of patches of forest with some Dacrycarpus near the site before 230 BP. These were apparently destroyed soon after the 230 BP fall but patches of closed shrubland, with Rapanea and without Dacrycarpus, have regenerated subsequently. However, the apparent change in the local mire vegetation, and a possible resulting change in pollen deposition conditions, reduces the reliability of this interpretation.

Fig. 5.12

Site 39 (standard pollen sum)

Site 39 (excluding mire pollen types)

Site 54

3800 m

Pindaunde valley

This monolith is from near the edge of a mire about 40 m in diameter, occupying a rock basin at the eastern end of the Bogonolto ridge. The mire is a mosaic of various communities, with Carpha alpina fen in the wetter areas and mires of the short grass bog type in the drier parts. The local vegetation where the monolith was taken is dominated by Monostachya oreoboloides and Ranunculus, with Astelia, Potentilla, Plantago and several species of grass also present. The slopes around the mire are covered in Coprosma divergens-Poa saruwaetica shrubby tussock grasslands with a few isolated patches of large shrubs and trees, including Rapanea vaccinioides, Dimorphanthera microphylla, Symplocos sp., Drimys piperita and Olearia spectabilis. Live Dacrycarpus trees are absent and the nearest closed forest is nearly 200 m away. Occasional forest species and forest relics continue for about 150 m above the mire.

The pollen diagram for this site (Fig. 5.13) shows a major vegetation change immediately above the 230 BP tephra. The abrupt fall of Nothofagus indicates a large increase in pollen sum production at this horizon, and the changes in the Poaceae/forest ratio show that this is a result of the replacement of forest by tussock grassland in the pollen source area. Charcoal, Cyathea and Coprosma also increase relative to Nothofagus at the same horizon.

Before 230 BP the local vegetation was open and probably similar to today. The very high Poaceae levels suggest that both forest and tussock grasslands were present extra-locally. The distribution of these two vegetation types on the ground cannot be ascertained from pollen evidence alone, but the modern distribution of forest relics suggests forest occupied the drier, raised areas around the mire, with Deschampsia klossii grasslands on lower, wetter areas. However, it is possible that forest was more continuous and that the high Poaceae levels reflect the local mire vegetation and the proximity of the treeline (c.3900 m).

After 230 BP the extra-local vegetation was probably very similar to that of today. Charcoal levels are always low but this may just reflect the large area of unburnable mire vegetation around the site. The high Coprosma and Haloragis levels do however suggest that burning was infrequent, even on the drier slopes. The apparent decline in pollen sum production and the relative rise in forest taxa may result from successional processes in the secondary grasslands.

Fig. 5.13

Site 54

Sites 45 & 46 3680 m, 3750 m

Pindaunde valley

These two monoliths are from the section of the main valley which extends beyond the upper Pindaunde valley and forms the back of the cirque occupied by the lake. This region was called the 'Pinde Valley' by Wade and McVean (1969). It is enclosed by steep rock walls which partly shade it, and from which it receives a lot of runoff. Wade and McVean believed that, because of its inaccessibility and wetness, this 'valley' had escaped most burning and the vegetation was in its primary condition. Forest is confined to the well-drained parts of the valley floor and the slopes below the rock walls. Deschampsia klossii dominates the poorly-drained areas of the valley floor while various mire communities occupy the wettest parts. Between the forest and the grassland is usually a band, up to 15 m wide, in which clumps of trees and large shrubs are mixed with grassland elements. There are a few decaying stumps in this band, some of which appear to be charred.

Site 45 is at the bottom end of the valley, near the top end of the upper Pindaunde lake. The monolith was taken from an area of short grass bog surrounded by Deschampsia klossii tussock grassland and Carpha alpina fen. Closed forest is 35 m to the north. Site 46 is at the upper end of the valley in similar vegetation, 45 m from the nearest forest patch.

The pollen diagrams from these two sites (Figs. 5.14 and 5.15) are both consistent with the hypothesis that this region has not been greatly disturbed. Most changes in the pollen spectra can probably be attributed to changes in the composition of the local mire vegetation. However, there may be a real decline in Dacrycarpus at 230 BP at Site 46, and Site 45 shows a clear increase in Cyathea. The sites chosen would not be sensitive to small-scale changes in the area of forest on the surrounding slopes. The levels of charcoal may reflect burning in the valley or result from fires on the drier, alpine slopes above the rock walls.

Site 41

3680 m

Pindaunde valley

This monolith is from a mire, about 50 m in diameter, in a small cirque at the eastern end of the Bogonolto ridge-complex, about 150 m east of, and 120 m below, site 54. This site is the Pengagl Mire from which Hope (1973, 1976a) analysed one sample at the base of the organic deposits, dated at 12,000 BP. The wetter, central area of the mire is a mosaic of Carpha alpina, Scirpus crassiusculus and Carex gaudichaudiana fens. The monolith was taken from a drier area of Astelia papuana, 3 m from the edge of the mire. The surrounding slopes are covered in Coprosma divergens-Poa saruwaetica shrubby tussock grasslands in which Coprosma divergens is the major shrub. There are a few live Dacrycarpus trees scattered in these grasslands and dead trees and stumps are frequent. Live and dead Olearia

Fig. 5.14

Site 45

Fig. 5.15

Site 46

spectabilis bushes and occasional Cyathea are also present.

The pollen diagram for the site (Fig. 5.16) shows the continuous presence of open mire vegetation for at least the last c.1700 years. Changes in the percentages of most pollen types are gradual but the sharp fall in Dacrycarpus and Nothofagus, and rise in charcoal, immediately above the 230 BP tephra, indicates a major vegetation change at this horizon. (There is a problem in that if the Nothofagus fall is taken to indicate a two- to three-fold increase in pollen sum production then there appears to have been an absolute increase in Rapanea at this horizon.) It is reasonable to interpret these changes as a major clearance of forest in the pollen catchment, presumably on the slopes around the mire.

There is also, however, a more gradual increase in the Poaceae percentage, with no corresponding change in Nothofagus, between 1200 BP and 230 BP. The charcoal curve does not help in deciding whether this represents partial forest clearance or local vegetation change, for instance the drying out of the mire.

The post-230 BP fall in charcoal and Poaceae and possible fall in pollen sum production, as well as the rise in Cyathea, may reflect successional changes in the secondary grasslands.

Site 37

3740 m

Pindaunde valley

This monolith is from a small 'step' in the valley side, south-west of the upper Pindaunde lake. Locally, Potentilla foersteriana and Ranunculus dominate an area of about one square metre. The surrounding slopes are covered in a mosaic of tussock grasslands, mostly dominated by Styphelia but with some patches where large Deschampsia klossii tussocks exclude all shrubs. There are scattered Cyathea muelleri and both living and dead Olearia spectabilis in the grasslands. 40-60 m upslope the tussock grasslands give way to unstable and mostly unvegetated, rocky slopes.

The major vegetation change shown in the pollen diagram (Fig. 5.17) is between c.475 BP and the 230 BP tephra. Forest elements fall and Poaceae and charcoal rise to high levels. These changes probably indicate the first appearance of tussock grassland on the site. There is also an earlier, smaller rise in Poaceae and charcoal between the 1200 BP tephra and c.715 BP. This suggests an earlier clearance of unknown extent near but not immediately on the site, which was then under closed forest.

The percentage of forest taxa continues to decline and charcoal remains high above the 230 BP tephra, although the rise in Cyathea and Asteraceae (possibly Olearia) suggests successional changes near the site.

Fig. 5.16

Site 41

Fig. 5.17

Site 37

Sites 20, 21 & 22 3680 m

Pindaunde valley

These three sites form a transect at right angles to the forest edge, north-east of the lower end of the upper Pindaunde lake. The non-forest vegetation in this area is a mosaic of short grass bog and Coprosma divergens shrubby tussock grasslands. There are charred stumps of Dacrycarpus trees in both these communities. Site 20 is a short grass bog approximately 8 m in diameter and locally dominated by Ranunculus basilobatus, Gentiana and Potentilla. Coprosma divergens-Poa saruwagetica shrubby tussock grasslands surround the bog and the nearest forest is 40 m to the north-east. Site 21 is a smaller (2 x 4 m) short grass bog, surrounded by shrubby tussock grassland, 10 m from the forest. Site 22 is a short grass bog only 1 m from the forest in a zone with many large, charred Dacrycarpus trunks.

The pollen diagrams for Sites 20 (Fig. 5.18) and 21 (Fig. 5.19) are very similar. (Only site 20 has the 1200 BP tephra, so correlation below the 230 BP tephra is only approximate.) Both show a gradual decline in forest elements and a rise in Poaceae and charcoal. The surface sample transect in the same area is of some help in interpretation.

At Site 20 the first local clearance had apparently occurred between 780 and 715 BP as shown by the moderate Poaceae level (22%) and high Astelia. Before this, closed forest covered the site. After c.715 BP grassland (or short grass bog) increased at the expense of the forest until recent times, when the fall in Poaceae and rise in Coprosma suggests the beginnings of secondary succession. The charcoal levels do not follow the inferred vegetation change very closely, with low levels after the first clearance and a maximum at the surface. This lack of correlation may result from the restricted spread of the fires which caused the vegetation change, or may indicate that the initial clearance was not caused by fire.

The changes at Site 21 are even more difficult to interpret. Dacrycarpus declines and Poaceae rises from the bottom of the diagram, but charcoal remains very low until the sample just below the 230 BP tephra. Immediately above the tephra there is an abrupt change, with both Dacrycarpus and Rapanea declining sharply and Poaceae rising further. Then from this horizon to the surface, Poaceae falls slightly relative to the forest elements and charcoal continues to rise.

At the bottom, the site was probably just inside the forest margin, which then apparently retreated gradually until 230 BP, when the forest was rapidly cleared to its present extent. The earlier retreat is not accompanied by high charcoal values and may not be the result of fire. Alternatively, as at Site 20, fires may have been too infrequent or too local to be recorded.

Figs. 18-20

Site 20

Site 21

Site 22

The pollen diagram for Site 22 (Fig. 5.20) is more straightforward. A major vegetation change occurs between c.475 BP and 230 BP, when forest pollen declines sharply, Poaceae and charcoal rise to high levels and Ranunculus first appears. A band of macroscopic charcoal at c.350 BP presumably resulted from burning of the forest at this time. Below the clearance horizon the site supported closed forest, as shown by the low Poaceae levels and absence of indicators of open ground. The gradual rise in Cyperaceae after clearance (also visible at Site 21) may result from changes in local hydrology, while the rise in Cyathea and Coprosma, and the fall in Poaceae and charcoal, may indicate successional changes in the secondary grasslands. Uncertain correlation below the 230 BP tephra makes it difficult to combine the information from these sites. What is obvious, however, is that clearance was not a single, abrupt event in this area.

Site 25

3760 m

Pindaunde valley

This monolith was taken from a small short grass bog (0.8 x 0.6 m) in a step on the north-east side of the valley, above the lower end of the upper Pindaunde lake. The surrounding slopes are covered in a Coprosma divergens-Poa saruwaetica tussock grassland in which shrub species, including Styphelia suaveolens, Gaultheria mundula, Coprosma divergens, Haloragis and Rhododendron commonae, form most of the cover. Isolated, live Dacrycarpus trees are common and the nearest forest patch is 30 m away.

The pollen diagram from this site (Fig. 5.21) does not show a single, clearly-defined, clearance horizon. The first appearance of high Poaceae and charcoal levels is at c.475 BP but forest taxa, particularly Dacrycarpus, continue to decline, and Poaceae, Cyperaceae and charcoal to increase irregularly after this date. The persistent level of Astelia pollen throughout the diagram implies that the site was open for the last 1200 years despite the low grassland and sedge levels. At this altitude today, however, the forest is beginning to open out and grasses, sedges and light-demanding herbs may be present in undisturbed forest (Wade and McVean 1969).

The changes at c.475 BP suggest the first appearance of tussock grasslands either on or very close to the site, although forest still occupied much of the pollen source area. The irregular changes afterwards probably reflect the subsequent removal of much of the remaining forest. A particularly interesting feature of this diagram is the persistence of high Haloragis levels throughout, suggesting that this species was present in the forest understorey and either survived the destruction of the forest or rapidly regenerated afterwards. The very high Ericaceae and moderate Coprosma percentage at the surface may reflect post-clearance successional changes, although charcoal remains high.

Fig. 5.21

Site 25

Fig. 5.22

Site 23

Site 23

3710 m

Pindaunde valley

This monolith is from a small mire (1 x 3 m) north-east of, and 40 m above, the lower end of the upper Pindaunde lake. The mire is a mosaic of Carpha alpina fen and short grass bog. It is surrounded by Coprosma divergens-Poa saruwaetica grassland with about 80% shrub cover and scattered Dacrycarpus shrubs. There are patches of closed forest 30 m to the north-east and south-west.

The pollen diagram (Fig. 5.22) has high levels of Cyperaceae throughout, indicating the presence of a sedge mire on the site for at least the last 1200 years. The Poaceae/forest ratio increases continuously from the bottom, but it is only between c.475 BP and the 230 BP tephra when Poaceae reaches a level suggesting the local presence of tussock grassland. Charcoal reaches a peak value at the same time. Rapanea and Dacrycarpus continue to decline to the surface.

Site 51

3700 m

Pindaunde valley

This site is an east-facing 'hanging valley', perched above the Pindaunde valley south of the lower lake. The floor of the basin is occupied by waterlogged Deschampsia klossii tussock grassland and various mire communities, and is traversed by wandering streams. The monolith was taken 1 m from the upper margin of the mire in a small area of short grass bog, locally dominated by Trachymene tripartita. The slopes of the basin are covered in a dense, shrub-dominated 'grassland' with exceptionally large Styphelia suaveolens, Coprosma divergens and Gaultheria mundula. There is also a high density of fire-scarred, but living, Dacrycarpus trees, and many large Olearia spectabilis and Cyathea muelleri.

The pollen diagram for this site (Fig. 5.23) shows the continuous presence of tussock grasslands, presumably on the basin floor, during the last 1200 years. A major change in the rest of the vegetation occurs just above the 230 BP tephra. The fall in Nothofagus indicates an increase in pollen sum production. Thus there was probably a rise in the absolute deposition of Poaceae pollen and Cyathea, as well as the rise in Cyperaceae and charcoal percentages, and fall in the forest taxa. These changes suggest clearance on the slopes at the same time as a change in the local mire vegetation. The change in mire vegetation may reflect hydrologic changes as a result of forest clearance in the catchment, or the direct effect of the tephra fall.

Before 230 BP the high forest and grass percentages and the very low sedge percentage suggest that tussock grasslands occupied most of the floor of the basin, while forest covered the slopes. This is consistent with the present distribution of forest relics. After 230 BP, although charcoal

Fig. 5.23

Site 51 (standard pollen sum)

Site 51 (excluding mire pollen types)

remains very high, the falling Poaceae percentage and rising Cyathea and Coprosma suggest successional changes leading to the present, shrub-dominated vegetation on the slopes. Dacrycarpus also apparently rises significantly relative to Nothofagus. In the absence of Dacrycarpus regeneration past the seedling stage in the present vegetation, this may reflect gradual recovery of damaged, isolated trees.

Site 30

3670 m

Pindaunde valley

This monolith was taken from a small step in the valley wall, north-east of the lower Pindaunde lake. On the site Ranunculus and Potentilla dominate an area approximately 1 m x 2 m, surrounded by Coprosma divergens-Poa saruwaetica shrubby tussock grasslands. These 'grasslands' are dominated by shrubs of Coprosma divergens, Styphelia suaveolens and Gaultheria mundula, and isolated Dacrycarpus, Cyathea gleichenioides and Olearia spectabilis are scattered throughout. The nearest closed forest is 150 m away.

The pollen diagram for this site (Fig. 5.24) shows a major vegetation change above the 230 BP tephra. Before 230 BP the very low Poaceae levels show the presence of closed forest on the site. Immediately above the tephra, the fall in forest pollen and rise in Poaceae and charcoal indicates the replacement of forest around the site by tussock grasslands. After 230 BP forest clearance continued, with a rise in the Poaceae/forest pollen ratio and a rise in pollen sum production, shown by the relative decline in Nothofagus. Charcoal remains high at the surface but the very high Coprosma level (although possibly resulting from chance incorporation of a whole flower), suggests a post-clearance increase in shrubbiness.

Site 29

3660 m

Pindaunde valley

This monolith is from the edge of a mire, behind a small lateral moraine, on the northern wall of the Pindaunde valley. The mire is a mosaic of short grass bog, Carpha alpina fen and Deschampsia klossii, occupying a total area of about 12 x 5 m. The monolith was taken from a patch of short grass bog. The surrounding slopes support tussock grasslands with abundant shrubs, scattered Cyathea muelleri and some isolated, fire-scarred Dacrycarpus. The nearest forest is 17 m away to the north and south.

The major change in the pollen diagram from this site (Fig. 5.25) is immediately above the 230 BP tephra, where Poaceae increases relative to the forest elements and charcoal first attains high levels. Below the tephra the levels of Poaceae and Cyperaceae and the minor presence of Ranunculus pollen indicate an open mire area on or very near to the site. The rise in Poaceae between the bottom and the sample below the 230 BP

Fig. 5.24

Site 30

Fig. 5.25

Site 29

tephra may indicate a small local vegetation change but could just reflect the larger changes occurring higher up the valley at this time. The high Cyathea and Coprosma levels at the surface, and the lower charcoal, may be evidence of decreased burning and post-fire succession.

Site 27

3630 m

Pindaunde valley

This monolith was taken from the centre of a mire surrounded on three sides by a patch of forest. The mire is a mosaic of short grass bog and Carpha alpina fen. The forest is 8-12 m from the monolith site and is separated from the mire by a 1-4 m strip of shrubby tussock grassland, which is continuous on the north side with the grassland around the forest patch.

The pollen diagram for this site (Fig. 5.26) shows a surprisingly large vegetation change immediately above the 230 BP tephra. Forest elements fall abruptly and Poaceae (and pollen sum production) rise. Below the tephra the high Cyperaceae/Poaceae ratio suggests that forest directly abutted a mire occupying the site. The major forest clearance above the tephra probably extended the area of the mire as well as originating the strip of tussock grassland. The slight rise in Poaceae and charcoal just below the tephra may reflect minor clearance elsewhere in the valley.

The vegetation change at 230 BP is not accompanied by high charcoal levels, suggesting that fires were confined to the forest edge.

Site 47

3590 m

Pindaunde valley

This site is in the small valley between the north-eastern Pindaunde latero-terminal moraine and the continuation of the Imbuka ridge as the main divide. Tussock grasslands, with many forest relics, and landslide communities occupy most of the area between the two ridges. This area is mostly more or less steeply sloping but there are some poorly-drained flat parts, which are covered in Deschampsia klossii tussock grasslands. The monolith was taken from a 1 m diameter short grass bog in one of these areas, about 20 m north-east of the forest edge, which here coincides with the moraine crest. In the surrounding flat area large Deschampsia klossii tussocks exclude all shrubs, except for some small Styphelia suaveolens and Coprosma divergens. 5-8 m away in all directions the Deschampsia klossii grassland merges with the Poa saruwagetica-dominated grasslands of the slopes. These also have few shrubs but, in contrast to the Deschampsia klossii grassland, there are many charred tree stumps. In both types of grassland the soil within 5-10 cm of the surface is very dark as a result of a very high charcoal content.

Fig. 5.26

Site 27

Fig. 5.27

Site 47

The pollen diagram for this site (Fig. 5.27) shows that tussock grasslands were present in the area for the last 1000 years or so. (The date of the bottom sample is uncertain in the absence of the Olgaboli tephra.) The fall in forest elements and the rise in Poaceae (particularly relative to Nothofagus) above the 230 BP tephra probably indicates the start of forest clearance and the expansion of grassland on the surrounding slopes. Very high charcoal levels continue to the surface, while forest elements decline further and Cyathea increases. The significant rise in charcoal below the 230 BP tephra from the very low level in the bottom sample may reflect the start of local burning, or fires elsewhere in the valley.

Sites 12 & 49 3570 m, 3580 m

Pindaunde valley

Site 12 is halfway along the gently sloping shore of the Pindaunde lake, 4 m south of the lake and 65 m north of the nearest forest patch. The surrounding vegetation is a virtually pure stand of large, vigorous tussocks of Deschampsia klossii. The only shrubs present are a few stunted Styphelia suaveolens. The monolith was taken from between tussocks, where Ranunculus basilobatus, Potentilla, and Lactuca laevigata form a partial ground cover. Unusually for such situations, both tephras were present as continuous bands.

At Site 49 a short monolith was taken from the edge of the forest patch nearest to site 12, in the centre of a 3 m wide, dense band of Coprosma papuensis, which separates the closed forest from the grassland. Olearia spectabilis and Dimorphanthera spp. are the other main components of the edge shrubbery but are not present within 1.5 m of the site. The matrix of the monolith was partly-humified litter in which pollen preservation was poor, and the 230 BP tephra was present only as a discontinuous layer at variable depth. Thus only the counts of easily-recognised, corrosion-resistant pollen types (which includes all the types in the diagram) are reliable and the correlation with other sites is uncertain. The forest-grassland surface sample transect is useful in interpreting the pollen diagrams from these sites.

The diagram for Site 12 (Fig. 5.28) shows a change from closed forest to tussock grassland in two steps. Between c.475 BP and the 230 BP tephra, Poaceae and charcoal rise to levels which indicate the location of the forest/grassland boundary nearby or on the site. Then between 230 BP and c.115 BP forest was completely cleared from the site and Poaceae and charcoal rise to high levels. There is also a minor rise in Poaceae before c.475 BP which may reflect forest clearance higher up in the valley.

Fig. 5.28

Site 12

Fig. 5.29

Site 49

If the tephra stratigraphy of Site 49 is reliable, then this pollen diagram (Fig. 5.29) shows that the forest edge retreated to near its present position sometime before 230 BP. Immediately after the tephra fall it retreated a little further, probably only a metre or so, and it has remained in the same position (perhaps with unrecorded fluctuations) ever since. The very high charcoal counts in the forest margin vegetation suggest that this zone is periodically burned, without apparently affecting the forest itself. (Dacrycarpus trees just inside the forest are not fire-scarred).

Site 13 3570 m Pindaunde valley

This monolith is from a small (c.1 x 1.5 m) area of short grass bog, near the lower end of the lower Pindaunde lake. The site is at the change of slope where the Deschampsia klossii grasslands by the lake meet the Coprosma divergens-Poa saruwagetica shrubby tussock grasslands on the north-west valley sides. The nearest closed forest is 70 m away. Macroscopic pieces of wood were frequent in the monolith below the 230 BP tephra.

The pollen diagram for this site (Fig. 5.30) shows a major vegetation change immediately above the 230 BP tephra. The large rise in Poaceae and charcoal levels, and decline in Dacrycarpus and Rapanea, indicates that forest was replaced by tussock grassland at this horizon. Before 230 BP the very low Poaceae levels and virtual absence of Cyperaceae, Ranunculus and Astelia pollen shows that closed forest covered the site and its surroundings. After the 230 BP clearance forest continued to retreat slightly up to the present.

Site 10 3570 m Pindaunde valley

This monolith is from a flat area of Deschampsia klossii tussock grassland adjacent to the outlet stream of the lower Pindaunde lake. Large, vigorous tussocks exclude all shrubs except for an occasional stunted Styphelia suaveolens and Hypericum macgregorii. Ranunculus basilobatus, Potentilla papuana, Lactuca laevigata and other dicotyledonous herbs grow between the tussocks. 10-20 m away the Deschampsia klossii grasslands merge into Coprosma divergens-Poa saruwagetica shrubby tussock grasslands on sloping ground. The nearest forest patch is 90 m to the south.

The area is mostly well-drained but the presence of gravel in the profile, particularly below the 230 BP tephra, shows that it is unstable and sometimes flooded. The Olgaboli tephra was absent and the date of the bottom sample, which is from below a gravel lens, is unknown.

Fig. 5.30

Site 13

Fig. 5.31

Site 10

The pollen diagram (Fig. 5.31) shows the persistence of tussock grasslands around the site since sometime before the 230 BP tephra fall. The high local Poaceae pollen production tends to obscure changes further from the site, but there is a sudden decline in Dacrycarpus above the 230 BP tephra. This coincides with a large increase in charcoal and probably reflects the clearance of the forest from the surrounding slopes and the once-forested parts of the valley floor. Cyathea - now confined to apparently secondary grasslands in the vicinity of the site - increases at this horizon.

Site 17 3510 m Pindaunde valley

This monolith is from a short grass bog, about 9 m in diameter, in a shallow basin in the centre of the valley floor. Stunted tussocks of Deschampsia klossii occur throughout the mire. Surrounding the mire is a mosaic of well-drained Coprosma divergens-Poa saruwagetica shrubby tussock grasslands and various mire communities. There is a small grove of Cyathea gleichenioides 10 m up the valley and a small forest patch 60 m to the south. Forest relics, including a few live Dacrycarpus, are frequent in the tussock grasslands.

The pollen diagram (Fig. 5.32) shows the continuous presence of open grassland vegetation on the site since at least 1200 BP. Between the 230 BP tephra and the surface, Dacrycarpus falls and Poaceae rises, indicating the replacement of forest by grassland around the mire. The very low charcoal levels may simply reflect the extent of unburnable vegetation around the site. The rising Poaceae/Cyperaceae ratio between the tephras may result from drying out of the mire and its invasion by tussock grasses, or a minor local clearance. The high Dacrycarpus levels before 230 BP suggest that forest occurred adjacent to the mire and the high Cyathea percentage suggests that treeferns were prominent at the forest edge. The continuity of high Cyathea to the surface is surprising in view of the fact that the source taxa today are grassland species growing in apparently secondary grasslands. The Coprosma peak at the surface may reflect successional changes in the grasslands, but both Poaceae and charcoal also reach their maximum there.

Site 14 3490 m Pindaunde valley

This site is a short grass bog, 3.5 m in diameter, in the centre of a shallow basin in the valley floor. The rest of the basin is occupied by Deschampsia klossii tussock grasslands in which shrubs, mainly Styphelia suaveolens, are common but always stunted. 8-10 m away the Deschampsia klossii-dominated grasslands merge into Coprosma divergens-Poa saruwagetica tussock grasslands with more shrubs and many charred tree-stumps. Closed forest is 35 m to the south.

Fig. 5.32

Site 17

Fig. 5.33

Site 14

The pollen diagram (Fig. 5.33) shows a major vegetation change immediately above the 230 BP tephra, when Poaceae rises and Dacrycarpus and Rapanea fall sharply. High charcoal levels appear for the first time at this clearance horizon. Before 230 BP the 20% Poaceae level indicates the presence of tussock grassland on or very near the site. Dacrycarpus is also high, Ranunculus and Astelia absent, and the monolith contains considerable amounts of wood below the 230 BP tephra. This would be consistent with the site being just inside the border between the forest and the grassland at this time.

The level of Poaceae pollen at the surface seems very low in comparison with other sites in Deschampsia klossii tussock grasslands and is hard to explain. The large fall in Poaceae and rise in forest elements after 230 BP suggests a vegetation change for which there is no evidence on the ground. Possibly it just reflects the extension of the short grass bog community and a resulting decline in local Poaceae production.

Sites 15 & 11 3470 m, 3530 m

Pindaunde valley

These two sites are virtually identical Gleichenia vulcanica bogs, both about 10 m in diameter and in the middle of the valley floor. The local vegetation is an almost pure stand of Gleichenia vulcanica with a little Deschampsia klossii, Poa saruwagetica and Trochocarpa dekokkii. Other vascular plants present but very scarce include Carex spp., Ranunculus basilobatus, Astelia papuana, Potentilla foersteriana, Lactuca laevigata, and Lycopodium australianum. Surrounding both bogs is a mosaic of well-drained shrubby tussock grasslands, and mire communities in small basins. There are scattered Cyathea gleichenioides in the grasslands around Site 15 but not Site 11. Site 15 is 42 m, and site 11 is 35 m, from the nearest forest.

The pollen diagrams for the two sites are very similar, and that for Site 15 (Fig. 5.34) will be discussed in detail first. The first pollen diagram for this site shows that a Gleichenia bog, similar to that of today, has been present for at least the last 1200 years. Re-plotting on a sum excluding Gleichenia and Cyperaceae emphasises the extra-local changes. The main change is immediately above the 230 BP tephra, where the sudden fall in Dacrycarpus and rise in Poaceae and charcoal shows the replacement of some forest by grassland. It is probable that most or all of the Poaceae pollen before 230 BP comes from mire grasses so these changes show the first appearance of tussock grassland in the pollen source area. Between 230 BP and the surface, there is little change in the Poaceae/forest ratio, but the large fall in Nothofagus seems to indicate a large increase in pollen sum production.

Fig. 5.34

Site 15 (standard pollen sum)

Site 15 (excluding mire pollen types)

Fig. 5.35

Site 11 (standard pollen sum)

Site 11 (excluding mire pollen types)

The very high Cyathea level, relative to forest elements, throughout the diagram suggests that treeferns were present in the forest edge before clearance and survived, or were rapidly replaced, after clearance.

Site 11 (Fig. 5.35) has a very similar pollen history except that Cyathea was much less important and changes in the Cyperaceae/Gleichenia ratio suggest local bog vegetation changes in the lower part of the diagram.

Site 31 3460 m Pindaunde valley

This monolith is from a 4 m diameter short grass bog, in a flat area at the edge of the first step in the valley profile. It is surrounded by Deschampsia klossii tussock grassland with scattered shrubs. 20 m up the valley are Coprosma divergens-Poa saruwagetica shrubby grasslands, with forest relics and occasional Cyathea gleichenioides. The nearest forest is 40 m to the south-west.

The pollen diagram for this site (Fig. 5.36) does not show any major vegetation change in the pollen source area. Tussock grasslands were present around the site for at least the last c.1700 years, although the Poaceae/forest ratio increases irregularly towards the surface. Charcoal rises abruptly above the 230 BP tephra from very low levels.

Before the 230 BP charcoal rise Cyathea percentages are similar to those found in surface samples from modern treefern groves and suggest the presence of treeferns on the site. Cyathea levels are lower at the surface and treeferns are today confined to apparently secondary grasslands, more than 20 m from the site.

The absence of major changes in the pollen diagram, when forest relics show that forest has been cleared from the nearby slopes, probably results from the high local pollen production obscuring extra-local changes. Extra-local forest clearance presumably started at the time of the initial charcoal rise.

Site 18 3360 m Pindaunde valley

This site is in the lower section of the Pindaunde Valley, 60 m north of the stream, below the waterfall. The monolith was taken in bare ground between widely-spaced Deschampsia klossii tussocks, in a gently sloping area 30 m from the nearest forest. Deschampsia klossii tussock grassland with sparse Styphelia suaveolens and Vaccinium ambylandrum surrounds the site. There are Dacrycarpus stumps and dead Olearia spectabilis within 10 m in the grassland. Further away are more shrubby grasslands with much Styphelia suaveolens and scattered Cyathea atrox.

Fig. 5.36

Site 31

Fig. 5.37

Site 18

There is a major change in the pollen diagram (Fig. 5.37) immediately above the 230 BP tephra. The large fall in forest elements and rise in Poaceae, charcoal and pollen sum production shows that forest was largely replaced by grassland in the pollen source area at this horizon. Below the tephra the low Poaceae and Cyperaceae levels and the absence of Ranunculus indicate the presence of closed forest on the site, perhaps with areas of sedge mire nearby. There are no significant changes in the pollen diagram between 230 BP and the surface.

Site 34 3330 m Pindaunde valley

This monolith was taken from a 10 m diameter mire, in a shallow basin in the floor of the lower Pindaunde valley. The mire vegetation is largely of Wade and McVean's Brachypodium-Carex fen type but Keysseria radicans and Ranunculus basilobatus co-dominate large patches and stunted shrubs of Styphelia suaveolens are frequent. At the edges of the basin the mire vegetation changes to Deschampsia klossii tussock grassland on slightly-raised moraine ridges.

The pollen diagram (Fig. 5.38) shows the continuous presence of open vegetation for the last c.1700 years. Immediately above the 230 BP tephra there is a large increase in the Poaceae/forest ratio with a slight rise in charcoal. Then after 230 BP the pollen sum production apparently increases, along with charcoal, although there is no further change in the Poaceae/forest ratio.

Before 230 BP the Poaceae level may entirely reflect mire grasses, in which case the changes above the tephra represent the replacement of some forest around the mire by the tussock grassland observed today.

Site 36 3320 m Pindaunde valley

This monolith is from a fen about 8 m in diameter in the floor of the lower Pindaunde Valley, 20 m from the terminal moraine. The fen is dominated by Carex capillacea and species of non-tussock-forming grasses. It belongs in Wade and McVean's Brachypodium-Carex fen association, although there is also an admixture of Deschampsia klossii tussocks. At the margins the fen merges into a narrow band of Deschampsia klossii grassland, which in turn gives way to groves of Cyathea atrox on moraine hummocks. Closed forest covers the valley sides 16 m to the south-west.

The pollen diagram (Fig. 5.39) shows that the vegetation has been open at the site for at least the last 1200 years. Between the 230 BP tephra and the surface the fall in Nothofagus indicates an increase in pollen sum production. Taking this into account, there was probably a large, absolute increase in Poaceae and Cyathea in the last 230 years. The relative fall

Fig. 5.38

Site 34

Fig. 5.39

Site 36

in Dacrycarpus and Rapanea probably means little change in their absolute level. Before 230 BP the Cyperaceae/Poaceae ratio indicates a local sedge fen similar to today. Tussock grassland was probably absent but the very high Cyathea suggests that treeferns were prominent in the forest margin.

The rise in Poaceae and charcoal from 230 BP represents the replacement of some forest by tussock grassland around the mire. Forest retreat apparently continued during last 230 years along with a large increase in the Cyathea.

Site 43

3320 m

Pindaunde valley

This monolith was taken from a small basin at the up-valley end of the terminal moraine. A mosaic of short grass bog and Carex echinata covers an area of approximately 2 x 2 m. This mire gives way abruptly to tussock grassland, with groves of Cyathea atrox, on the surrounding moraine. There are shrubs of many species among the treeferns, Styphelia suaveolens and Coprosma papuensis being the most common. The forest edge is 30 m away but there is an isolated, fire-scarred Dacrycarpus tree 6 m from the site.

The pollen diagram (Fig. 5.40) shows a major vegetation change between the 230 BP tephra and the surface. Before 230 BP the very low Poaceae levels and absence of Ranunculus and Astelia pollen suggest closed forest on the site, while the moderate Cyperaceae levels suggest the presence of sedge fen very close by. Immediately above the 230 BP tephra, Poaceae and charcoal levels rise to values suggesting the local presence of tussock grassland. Forest elements continue to decline after 230 BP, indicating a continued retreat of the forest edge. High Coprosma and Cyathea levels suggest that the vegetation on the moraine has remained similar since initial forest clearance. In fact the continuity of high Cyathea levels throughout the diagram is surprising, unless the same individuals survived the removal of the forest.

Fig. 5.40

Site 43

CHAPTER 6

POLLEN ANALYSIS: THE HISTORY OF THE VEGETATION PATTERN

Discussion of the site histories.

In the previous chapter, pollen-analytical data from 34 sites on Mt Wilhelm were presented, and interpreted in terms of vegetation change around each site. Before combining these separate site histories, summarised in Table 6.1, into a synthesis of the history and pattern of vegetation change, several general points will be discussed.

The validity of the original assumptions.

The assumptions basic to all pollen analysis have been mentioned in Chapter Four; only those peculiar to this study are considered here. The most important of these is the assumption that the Nothofagus pollen rain has remained more or less constant over the last 1200 years. A priori reasons for believing this to be true were given in Chapter Four; the pollen diagrams provide additional support for this assumption.

Firstly, at the three sites (45, 46 and Umbamambuno) which show very little vegetation change, Nothofagus as a percentage of the pollen sum also changes very little. Secondly, at sites where the Nothofagus percentage does change significantly, either abruptly or slowly, there is always a change in the Poaceae/forest ratio in the direction consistent with tussock grassland being a greater pollen producer than forest. This change is usually, but not always, just above the 230 BP tephra. Not all sites where the Poaceae/forest ratio changes show a change in Nothofagus, however. It therefore seems very likely that the Nothofagus pollen rain has remained constant (+/-25%) over the last 1200 years.

A second important assumption was that the presence of Ranunculus and Astelia pollen indicates local open vegetation. This is also supported by the fossil data. Single grains were occasionally found in levels with pollen spectra otherwise suggesting closed forest, but except for the occurrence of Astelia at site 25, significant levels (at least 2 grains) were confined to horizons with pollen spectra consistent with local open conditions.

A third assumption made was that the 14 subalpine pollen taxa shown in the pollen diagrams contained most of the information on vegetation pattern which can be extracted from the data. The complete percentage data are shown in Appendix 2. The values for all pollen taxa were considered in the initial reconstruction of site histories, but using only the taxa displayed did not change the interpretations made. (See also the Principal Components Analysis in Appendix 3.) Additional forest taxa pollen were found in forest phase spectra and other light-demanding taxa in open phases. These contribute information on the detailed composition of the vegetation but do not add to the information available about the vegetation

Table 6.1 Summary of site histories.

(a) Non-Pindaunde sites

SITE	ALT.	Te. ¹	LOCAL VEG.	EXTRA-LOCAL VEG.	PRE-DIST. ² LOCAL VEG.	CLR. ³ DATE	A ⁴	B ⁵	C ⁶
Umbam	3550 m	T O	SGB	Mires, tussock grasslands.	Grassland	None			
Guru	3740 m	T O	SGB	Tussock grasslands.	Grassland	230			+
Tege	3820 m	T O	SGB	Mires, tussock grasslands.	Mire	230	+	+	
Giwi	3900 m	T O	SGB	Mires, <u>D. klossii</u>	Grassland	230			
Badme	3690 m	T O	SGB	Mires, <u>D. klossii</u>	Grassland	230	+		+
Bende	3700 m	T O	<u>G. vulcanica</u>	Mires, tussock grasslands.	Mire	230			+

(b) Pindaunde sites

SITE	ALT.	Te.	LOCAL VEG.	EXTRA-LOCAL VEG.	PRE-DIST. LOCAL VEG.	CLR. DATE	A	B	C
39	3910 m	T O	<u>Scirpus</u> fen	Tussock grasslands.	Grassland	230			+
54	3800 m	T O	SGB	Mires, <u>Coprosma-Poa</u> tussock grassland.	Grassland	230			
46	3750 m	T	SGB	<u>D. klossii</u> , <u>Carpha</u> fen.	Grassland	none			
45	3680 m	T	SGB	<u>D. klossii</u> , <u>Carpha</u> fen.	Grassland	none			
41	3680 m	T O	<u>Astelia</u>	Mires, <u>Coprosma-Poa</u> tussock grassland.	Mire	230	+		+
37	3740 m	T	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest	ca.475 -230	+	+	+
20	3680 m	T O	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest	ca.960 -715		+	+
21	3680 m	T	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest*	before 230			
22	3680 m	T O	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest	ca.475 -230			
25	3760 m	T O	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest*	ca.715 -475			+

Table 6.1 (continued)

23	3710 m	T	SGB, <u>Carpha</u> fen.	Mires, <u>Coprosma-Poa</u> tussock grassland.	Mire	ca.475 -230	+	+
51	3700 m	T	SGB	Mires, tussock grasslands.	Grassland	230		+
30	3670 m	T O	SGB	<u>Coprosma-Poa</u> tussock grassland.	Forest	230		+
29	3660 m	T	SGB	Mires, <u>Coprosma-Poa</u> tussock grassland.	Mire	230	+	+
27	3630 m	T	SGB	Mires, <u>Coprosma-Poa</u> tussock grassland.	Mire	230	+	
47	3590 m	T	SGB	Tussock grasslands.	Grassland	230	+	+
12	3570 m	T O	<u>D. klossii</u>	<u>D. klossii</u>	Forest	ca.475 -230	+	+
49	3580 m	T*	Forest edge.	Forest, tussock grasslands.	Forest	before 230		
13	3570 m	T O	SGB	Tussock grasslands.	Forest	230		+
10	3570 m	T	<u>D. klossii</u>	<u>D. klossii</u>	Grassland	230		
17	3510 m	T O	SGB	Mires, tussock grasslands.	Mire	230	+	+
14	3490 m	T O	SGB	<u>D. klossii</u>	Grassland*	230		
11	3530 m	T O	<u>G. vulcanica</u>	Mires, <u>Coprosma-Poa</u> tussock grassland.	<u>G. vulcanica</u>	230		
15	3470 m	T O	<u>G. vulcanica</u>	Mires, <u>Coprosma-Poa</u> tussock grassland.	<u>G. vulcanica</u>	230		
31	3460 m	T O	SGB	<u>D. klossii</u>	<u>Cyathea</u> grassland	230	+	
18	3360 m	T	<u>D. klossii</u>	<u>D. klossii</u>	Forest	230		
34	3330 m	T O	<u>Brachypodium</u> - <u>Carex</u> fen.	<u>D. klossii</u> , <u>Cyathea</u> <u>atrox</u> grassland.	Mire	230		+
36	3320 m	T O	<u>Brachypodium</u> - <u>Carex</u> fen.	<u>D. klossii</u> , <u>Cyathea</u> <u>atrox</u> grassland.	Mire	230		+
43	3320 m	T O	SGB	<u>Cyathea atrox</u> grassland.	Forest	230		+

(1) Tephtras present. T = Tibito O = Olgaboli

(2) Vegetation covering the monolith site before disturbance.

(3) Date of first major clearance.

(4) Suggestion of earlier minor clearance.

(5) Continuation of forest retreat after 230 BP.

(6) Possible pollen evidence for post-clearance succession.

* uncertain, see text

pattern. It might therefore have been sufficient to count only the 14 'useful' taxa if these could have been identified beforehand. However, this would have been unlikely to have saved more than about 10-20% of the total counting time and changes in some of the other taxa are useful in reconstructing a partial regional history over the same period (Chapter Eight).

The detail of interpretation possible.

At most sites there is an obvious clearance horizon in the pollen diagram, at which several pollen types, the pollen sum production and charcoal change together. This cannot be confused with changes resulting from changed hydrology or depositional conditions. In a few cases, however, this is not the case. Identification of a clearance horizon is then dependent first on the assumption (based on the evidence of forest relics) that clearance has occurred, and then on minor changes in a few pollen types or in the charcoal level.

The evidence for secondary succession after clearance is less convincing. Often it depends on small differences between surface and sub-fossil spectra, and differential destruction of pollen may make such comparisons unreliable. In most cases it is only possible to say that the pollen evidence is consistent with successional changes and then to look for non-pollen evidence.

A more general point is the sensitivity, or lack of it, to vegetation change shown by the type of depositional site chosen. Several sites (31, Umbamambuno) suggest that the pollen records are sensitive only to vegetation changes in a surprisingly small area around the site, perhaps within a radius of less than 30 m. Two separate factors are probably involved in this insensitivity to more distant vegetation changes. Firstly, high local pollen production by pollen sum taxa - particularly where there is local tussock grassland (e.g. site 31) - reduces the number of pollen grains from extra-local sources which are counted, and hence increases the counting error. This factor can, in theory, be overcome by counting more pollen grains and, if local and extra-local sources can be distinguished, by changing the pollen sum. However, even then, the second factor, namely the logarithmic shape of the pollen dispersal curves, means that the deposition rate for a pollen type is less sensitive to distance from the source as this distance increases.

The fact that the mire sites give a detailed history of only a very small area means that only a very small percentage of even the Pindaunde valley is 'covered' by the 34 sites analysed. These sites must be seen as samples in space, just as the levels analysed are samples in time. The validity of a reconstruction of the vegetation history of the whole valley,

and even more so of the whole mountain, depends on the extent to which the studied sites are typical.

The distribution of forest relics provides an independent check on some aspects of the pre-disturbance vegetation pattern. The conclusions from the two sources are consistent. There is, however, no independent check on the chronology. The accuracy of inter-site correlation is crucial to the combination of site histories in an overall history of the vegetation pattern, and will now be discussed in detail.

Accuracy of dating and correlation.

In Chapter 5 the date estimates were based on the radiocarbon ages of the tephras and assumed a constant rate of peat accumulation between the tephras, and between the upper tephra and the surface. These assumptions are acceptable for individual site histories but, for inter-site correlation the accuracy of the age estimates must be considered more critically.

In more than two-thirds of the pollen diagrams, the initial and/or major clearance occurs between 0.5 cm thick samples taken immediately below and above the 230 BP Tibito tephra. The important question is therefore: during what time-span did all these local clearance events happen?

Because of the variable compaction and humification of the peat between the 230 BP tephra and the surface, the best estimate of the peat accumulation rate adjacent to this tephra is obtained by dividing the vertical distance between the two tephras by the difference in their ages. This gives a range for different sites of 0.01-0.02 cm/yr, or 50-100yrs/cm, thus 0.5 cm, if deposited evenly, would represent 25-50 years. (Strictly, these are radiocarbon years but the difference is not significant at this level of accuracy.)

However, the micro-relief of the bog surface and lesser relief of the tephra/peat interface, suggests that deposition may not have been even. Only part of the bog surface may be growing at any one time. This probably evens out over a time scale of decades, but will place a limit on the accuracy of correlation possible. Fluctuations in the accumulation rate as a result of climate or local hydrology will have similar effects. The potential error cannot be estimated but its possible occurrence exercises some control on interpretation of comparisons between sites.

At most sites the changes between the pollen spectra immediately under and over the tephra layer are large, involving differences by factors of 4-10 for some pollen types (and for charcoal, 10-1000). For this to occur, the pollen in the 0.5 cm sample below the tephra must be (depending on the

magnitude of the change) 75-100% from the post-clearance vegetation. Thus the vegetation change (assuming even deposition) must have occurred within 0-12 years either side of the tephra. In fact, because of the usually higher post-clearance pollen productivity (and greatly higher charcoal levels) the possible range is not symmetrical: probably nearer 0-5 years before and 0-20 years after. Very large changes in the charcoal percentage indicate that the change in fire regime, at least, occurred after the tephra fall.

At those sites where there is evidence of a slight change between the samples below the tephra, namely a minor rise in Poaceae or charcoal, it is possible that this results from a major local clearance a few years before the tephra fall, rather than minor local or major extra-local clearance, as suggested earlier.

This discussion has so far ignored any possible effects of the tephra fall or clearance fires on peat accumulation. In fact one might expect considerable, if temporary, effects and both would 'sharpen' the apparent vegetation change as recorded by the pollen. The direct effect of fire could have been important at sites where the local vegetation itself was burnt (e.g. 10, 12), although temporary hydrologic changes may have occurred at any site. The direct effect of the tephra fall would have been greatest on low-growing mire vegetation, and probably negligible at sites occupied by forest or tussock grassland. One might expect a temporary halt to accumulation of peat at short grass bog sites, before vegetation re-established itself fully. If pollen deposited in this time were lost by oxidation, then part of the vegetation record would be missing. However, it seems probable that the halt to accumulation would only last a few years (<10?) at the most, as many of the mire plants can probably grow through 2-3 cm of compacted tephra.

Again, many of these problems cannot be converted into errors around the estimates of the accuracy of correlation. For most sites, clearance within five to twenty years after the tephra fall seems most likely, but for the less clear-cut sites the possible range may be greater. The apparent consistency between sites over a wide area and with very different vegetation gives some grounds for believing the more optimistic estimates. The possibility that all the major clearance occurred in a single season is neither supported nor ruled out by the evidence.

Correlation between events occurring at other times is much less accurate. It depends first on the sampling interval. A difference in the pollen spectra between samples at an extrapolated age of 475 BP and just below the 230 BP tephra could correspond to a vegetation change at any time between those dates. Secondly, it is dependent on the variability of the accumulation rate which determines the accuracy of the extrapolated ages,

although the presence of the tephra layers puts a 'ceiling' or 'floor' on the range of possible dates for samples near to them.

The variability of the accumulation rate cannot be assessed from a maximum of three dates for each monolith. The ratio of the depths of the two tephras below the surface varies considerably but this may be mostly a result of the variable degree of compression and humification of the near-surface peat. However, the absence of peat accumulation under subalpine forest today suggests that there may have been changes in accumulation rate when local forest was cleared. A reasonably safe estimate might be that the real age of most samples taken half-way between the two tephras will fall within a range of 200 years either side of the mean of the tephra ages. Between the 230 BP tephra and the surface, where the compaction is certainly more variable, ± 80 years would be an equivalent estimate. At sites where the lower tephra is absent, dates estimated for samples below the upper tephra must be considered approximate minimum ages, as major discontinuities may be present.

From the above discussion it is clear that the association of most clearance events with the upper tephra layer is very fortunate.

Synthesis of vegetation history.

At all but three sites (45, 46, Umbamambuno), the vegetation 1200 years ago was different from that of today. In the majority of cases, at least the lower two samples have similar pollen spectra, and at nearly all sites the lower sample has very little charcoal ($<20\%$). It is therefore reasonable to describe the vegetation reflected in these basal spectra as 'pre-disturbance'. Man was certainly visiting the alpine grasslands for a long time before 1200 BP (See Chapter Seven) and must have passed through the subalpine zone. Some disturbance, perhaps very localised, seems likely to have occurred in that period, but the pollen evidence supports the idea that disturbance below the forest limit was unimportant, at least immediately before 1200 BP.

All sites are now in vegetation which is open, at least locally. Before disturbance 11 sites were under closed forest and, at all but the three of the others with no vegetation change, forest was more important around the site than today. With the same exceptions, grassland was much less extensive and at most sites pre-disturbance grass pollen percentages were very low ($<5\%$). Mire vegetation had only a slightly smaller extent than today. The general pre-disturbance picture is thus of forest much more extensive than today, grasslands very restricted and mires of a similar extent.

The status of individual communities.

The pollen evidence supports the evidence from forest relics that all the Coprosma-Poa saruwaetica shrubby tussock grassland (except perhaps near the treeline where it merges into Danthonia vestita-Deyeuxia brassii tussock grassland) is secondary. Before disturbance, forest occupied this community's present range. Of the other major tussock grassland associations, Deschampsia klossii tussock grassland seems to be primary on some flat, more or less waterlogged or unstable sites particularly near the treeline (e.g. 45,46) but secondary in other places (e.g. 12,18). A detailed study of the distribution of forest relics might have reached the same conclusions, but it is not immediately obvious in the field.

There is little direct evidence for the status of the Poa saruwaetica - Dichelachne novoguineensis tussock grasslands from the pollen, as no suitable palynological sites were found in extensive areas of this community. Site 47 has, however, extra-local Poa saruwaetica grasslands which are apparently secondary to forest. It is likely that the presence of any large areas of this community would have registered at other sites in the valley. Forest relics are invariably present so there seems little doubt that this association is secondary.

Treeferns were important at many sites before disturbance but the only evidence for a 'treefern tussock grassland' is at site 31, where treeferns are not present locally today. The species of treefern involved cannot be determined from the spores.

The detailed composition of the pre-disturbance mire communities cannot be deduced directly from the pollen spectra, because the various grass and sedge species could not be reliably distinguished from their pollen. It is reasonable to assume, however, that where there have been no major changes in the mire pollen spectra the past mire community was similar to that present today. On these grounds the major mire communities were Brachypodium - Carex sedge fen, Carpha alpina sedge fen and Gleichenia vulcanica bog. Most of the 'short grass bog' stands are secondary to closed forest but small areas existed in pre-disturbance times (20, 21).

The pre-disturbance pollen spectra give no information on the structure and composition of the forest edge communities, except to suggest that treeferns were an important component at some sites and not at others. Cyathea percentages are always (except at 43) low in closed forest spectra and the present distribution of treeferns suggests that they cannot grow on mires. Thus the very high pre-disturbance percentages at some mire sites, when tussock grasslands were absent, seem explicable only in terms of treeferns growing in the forest edge.

A comparison between modern surface samples from forest, and sub-fossil spectra from the forest phase of now-open sites, reveals no consistent differences between the forest cleared and that surviving today.

The 'pre-disturbance' vegetation pattern.

The detailed reconstruction of the pre-disturbance vegetation pattern requires extrapolation of results from the small area directly covered by sites. Evidence is lacking for some areas in the Pindaunde valley, particularly the southern valley sides, and is very limited for the rest of the mountain. However, the 34 sites studied sample a range of typical situations and the distribution of forest relics gives reasonable confidence in this extrapolation.

At 1200 BP, almost continuous forest clothed the valley sides and well-drained parts of the valley floor, up to 3800-3900 m. At the forest limit, forest and grassland met in a narrow ecotone, with grassland descending lower in depressions and forest higher on the intervening hummocks and ridges, as occurs at the Imbukum valley forest limit today.

Below 3800 m, non-forest vegetation was confined to more or less waterlogged areas in the valley floor and small areas on terraces and perched basins along the valley sides. Deschampsia klossii grasslands with few shrubs covered extensive areas of poorly drained valley floor at the top end of the upper Pindaunde lake and in waterlogged basins on the Bogonolto ridge. Various mire types, particularly Carpha alpina fen, occupied the wettest areas.

At lower altitudes (<3650 m), D. klossii grasslands were confined to a few small areas in waterlogged basins and on the lower Pindaunde lake outwash fan. In most places, closed forest on the well-drained sites directly abutted mire communities on waterlogged soils. The drier bog types, Gleichenia vulcanica and short grass bog, occupied those areas where the water table was normally several centimetres below the surface, while sedge fens occupied areas with the water table at or above the surface. As today, Brachypodium-Carex fen was the major fen type below 3400 m in the valley floor, and Carpha alpina above 3400 m on the valley floor and on the terraces and perched basins on the valley sides.

In the Pindaunde valley, sedge fens were most extensive below the lower waterfall (<3400 m) on the flat, till-choked, valley floor. Forest was there confined to the intervening moraine hummocks. Forest also covered the terminal moraine and formed a continuous belt, except for landslips and eroding stream banks, below. It is difficult to estimate the relative extent of forest and non-forest vegetation from the pollen evidence but the present distribution of mires and secondary grasslands

suggests the following figures.

- (1) On the valley sides below 3750 m; 90-98% forest, 2-10% non-forest.
- (2) On the presently non-forested part of the valley floor between 3460 m and 3570 m (the lower lake and the lower waterfall); c.75% forest, 25% non-forest.
- (3) On the presently non-forested part of the valley floor below 3400 m; c.50% forest, 50% non-forest.

The basic similarity in morphology and present-day vegetation of the other valleys (except the Imbukum) and the distribution of forest relics, suggests that they had a pre-disturbance vegetation pattern similar to that of the Pindaunde valley. The evidence from the six non-Pindaunde pollen sites does not contradict this, although the areas of the various mire communities and primary D. klossii grasslands would have varied from valley to valley in response to minor differences in drainage patterns.

The Imbukum valley is exceptional in both its morphology and present-day vegetation. The forest-clothed valley sides (with an apparently primary open area at Umbamambuno) and the diffuse upper forest limit are probably a model for the pre-disturbance vegetation of the other valleys. However, the almost flat, till-choked valley floor is unique on Wilhelm, and almost certainly was never forested. The pre-disturbance vegetation pattern in this valley was probably very similar to the pattern today, except that the forest would have occupied the narrow band of apparently secondary grassland which separates the forest and the mire in some places.

The clearance history - The Pindaunde valley.

There is no evidence for clearance before 1200 BP at the few sites for which pollen diagrams extend this far back. Several sites (20, 23, 37, 12, 51, 41) show small but significant increases in the Poaceae/forest pollen ratio between 1200 BP and c.715 BP. Two of these are on the Bogonolto ridge and the others around the upper lake and the south side of the lower lake. Only at site 20, by the upper lake, are well-dated changes large enough to suggest local forest clearance at this time. The adjacent site 21, although poorly dated in the absence of the lower tephra, may also show early clearance.

It therefore seems likely that local forest clearance started sometime between 1200 BP and c.715 BP in some places, one of which was the lower end of the upper Pindaunde lake. (But see the earlier discussion of the accuracy of dates between the tephras.) The next evidence for local clearance is at site 25, in the same area, between c.715 and c.475 BP. Then between 475 BP and the 230 BP tephra the remaining sites (37, 22, 23)

south and north-east of the upper lake show major local clearance, as do the two sites (12,49) south of the lower lake.

At many lower sites there is minor evidence of forest clearance below the 230 BP tephra, and although it is possible that this simply reflects the extra-local effects of the clearance events higher up the valley, local clearance may have started in other, unsampled areas at the same time.

At the time of the 230 BP tephra fall, secondary grasslands had already replaced forest in part of the region around the two Pindaunde lakes (Fig. 6.1), and probably in other small areas of the mountain. Then, soon after the tephra fall (see earlier discussion of 'soon') the first major local clearance occurred at all remaining sites in the Pindaunde valley. This includes all sites to the north of and below the lower lake, and also the highest sites. At some of those at which clearance had already started there was an acceleration at this horizon.

The forest/non-forest pattern after this widespread clearance episode, after the 230 BP tephra fall, was apparently similar to that of today. At only two sites (36, 12) did the major local and extra-local clearance occur during the last 230 years, and at both these the initial clearance was earlier. During this period, most sites show either a slight increase in Poaceae/forest pollen ratio (which may, however, reflect quite large extra-local clearance), no change, or a decline. From vegetation evidence, this decline is not interpreted as an increase in forest area but as a decrease in pollen productivity of the non-forest vegetation, as shrubs partly suppressed the grasses (Chapter Nine). Continuation of forest clearance after the 230 BP episode was most common and most marked in the lower half of the valley (Fig. 6.2). Changes in the large scale vegetation pattern since 230 BP have probably been confined to the minor retreat of some forest edges and the disappearance of some small forest islands.

The other valleys.

All the sites in the other valleys show initial clearance soon after the 230 BP tephra fall and, except for Tegepangwa, no clearance since. Only at Badmenangidongwa is there a suggestion of an earlier, minor Poaceae rise between 1200 BP and 230 BP. It would be unwise to extrapolate the clearance dates from single sites to the whole valleys. It is unlikely that the sites chosen should happen to have been the first cleared in each, although they are all at similar altitudes and in similar situations to the area cleared before 230 BP in the Pindaunde valley. The coincidence of clearance initiation at widely-spaced sites does, however, give confidence that the Pindaunde sites are responding to more than purely local events.

Fig. 6.1 Sites showing local clearance before 230 BP.

Fig. 6.2 Sites showing continued clearance after the 230 BP event.

Post-clearance successional changes.

The pollen evidence for changes in the secondary grasslands after clearance is less straightforward. Apart from the doubtful validity of detailed comparisons between surface and subfossil samples, the wide sampling interval, compared with the likely time-scale of successional processes, means that all conclusions are tentative. Assuming that comparisons with surface samples are valid the following pattern emerges.

Immediately after clearance shrub pollen percentages were nearly always low compared with surface values from sites in shrubby grasslands. The exceptions to this (except site 43 which also has very high Cyathea after clearance) are high altitude sites (41, 54, 25, 21). Site 25, for instance, has very high Haloragis at all levels sampled. Probably the explanation lies in a low fire frequency after initial clearance at these sites. In general, however, there is evidence that shrubby grasslands were more restricted at 230 BP than they are today.

About a third of all Pindaunde sites show no evidence at all of secondary succession. This includes all the sites in the lower valley below the lower waterfall (<3400 m) and most of the sites below the lower lake (<3570 m). Only one site (47, in 'shrub-less' grasslands) above the lower lake shows no evidence of succession. There is reasonably good evidence - both a relative Poaceae decline and a rise in Coprosma and other shrubs - at 7 sites (39, 54, 51, 27, 21, 22, 25), and slight evidence for the remaining sites, plus two (14, 17) below the lower lake.

At three of the non-Pindaunde sites, namely Guruauglakugl, Badmenangidongwa and Bendenumbun, there is good evidence for post-clearance succession, supported by closely-spaced sampling horizons.

What evidence there is from pollen analysis suggests that secondary succession has progressed further at sites above 3570 m than below (Fig. 6.3). This conclusion is consistent with the observed vegetation pattern; as noted in Chapter Three, shrubbiness in general increases with altitude in the Pindaunde valley.

Changes in the mire communities.

Some changes in the extent and composition of the mire communities, either autogenic or a result of forest clearance or the tephra fall, might be expected. At the majority of sites there is a Ranunculus pollen maximum at the surface, but this cannot be confidently attributed to successional changes. Because it was easier to take monoliths from patches of Ranunculus, even if they covered only a fraction of the mire surface, they were preferentially selected. Thus a changing mosaic of Ranunculus and

Fig. 6.3 Sites with pollen evidence for secondary succession.

non-Ranunculus patches would give the pollen histories obtained without any change in the relative areas covered.

There is a percentage or 'absolute' (i.e. relative to Nothofagus) Cyperaceae rise after clearance at about a third of the Pindaunde sites. This occurs both at sites where there were mires before clearance and at those which were completely forested. At several sites (20, 21, 23, 25, 27, 30) short grass bog communities developed on previously forested ground.

This expansion or initiation of mire communities after forest clearance may reflect changes in local hydrology, or the ability of forest to tolerate conditions too wet for tussock grassland. The first explanation seems likely for sites 39 and 51, where mire apparently replaces grassland. However, some areas of subalpine forest today have standing water after rain, unlike any of the tussock grasslands.

The origin of the 'treefern grasslands'.

The history of the grassland Cyathea species involves special problems. Certain species of Cyathea (C. atrox, C. muelleri, C. gleichenioides) are confined to grassland in the subalpine, but today only C. gleichenioides occurs in other than secondary situations. (It is prominent in the lower part of the Imbukum valley treeline ecotone.) It is possible that some of the other species grew in mire/forest boundaries before clearance but a different species (C. aeneifolia) is found in such situations today. Thus the palaeoecology of the treeferns is particularly interesting. Unfortunately the species cannot be distinguished by their spores.

Only at site 31 is there evidence for a primary treefern grassland. At the majority of sites the Cyathea spore level remains surprisingly constant, at a low or high level, through the last 1200 years. This is very hard to explain when the source species today grow in secondary grasslands, and suggests that before clearance the same species was present nearby, presumably in the forest edge. There are, however, several sites (including most outside the Pindaunde valley) where Cyathea increases between clearance and the surface. These all have only scattered individual treeferns in the vicinity today. Site 31, interestingly enough, is the only one with a significant decline.

None of this makes very much sense. Clearly the pre-disturbance ecology of the grassland Cyathea species remains a problem for the future.

Rates of clearance.

If the earlier reconstruction of the pre-disturbance vegetation of the Pindaunde Valley is correct, then between 0.7 and 1.0 km² of forest has been cleared in the last 1000 years. (The large uncertainty results from the difficulty in deciding how much of the rocky slope area between 3750 m and 3900 m was ever forested.) Perhaps 75% of this clearance probably occurred within 1-20 years after the 230 BP tephra fall, giving a clearance rate of between 0.026 and 0.75 square kilometres per year at that time, depending on which set of assumptions is made. A more useful statistic would be the rate of retreat of the forest edge from primary openings needed to account for the reduction in forest area. A calculation of the average rate for the whole valley involves too many unknowns but it is possible to estimate how much retreat has occurred in particular places. In the Pindaunde Valley the maximum retreat of apparently unbroken forest has been about 80 m, although the average has been far less. (This is again excluding the area above 3750 m where the past extent of unbroken forest is uncertain.) In some places in the other Wilhelm valleys the maximum retreat must have been considerably greater, as continuous blocks of forest, extending more than 300 m up the valley side, have been completely cleared, probably by retreat from the bottom edge.

Only in the Pindaunde Valley is the clearance history sufficiently detailed to be able to conclude that, in some places, the maximum forest retreat of up to 80 m, occurred within 1-20 years of the 230 BP tephra fall. The maximum rate of retreat must therefore have been between 4 and 80 m per year. This compares with a maximum of about 10 m, more commonly 2-4 m, on Mt Giluwe in 1972 (personal observations), and this was probably the first major clearance there for at least 40 years. It therefore seems that the rate of clearance on Mt Wilhelm around 230 BP was exceptional, whatever assumptions are made.

Chronological control at other times is too poor to allow reasonable estimates of rates to be made. Forest retreat could conceivably have been locally as rapid as the higher rates at 230 BP at some other times. Alternatively, it could have taken place gradually over more than a hundred years.

The charcoal record.

The reconstructions above have been based largely on the pollen record. In order to avoid the assumption that fire is responsible for all the vegetation change, the evidence from the charcoal counts has been left until now.

At two-thirds of the Pindaunde sites charcoal levels remain low (<30%) until the start of local forest clearance, then rise abruptly. At most of these the first high charcoal levels coincide with the first evidence of local tussock grasslands. However, at four sites (51, 47, 10, 14), where tussock grasslands were present before disturbance, the appearance of the high charcoal levels coincides with the first clearance of nearby forest, i.e. the first high charcoal levels correlate with forest clearance, not simply with the presence of grassland. At site 31 the pollen gives no indication of the extra-local forest clearance which has certainly occurred, but charcoal rises to high levels just above the 230 BP tephra, when clearance was taking place at the nearest other sites.

The highest charcoal particle levels are attained when the pollen spectra indicate the presence of tussock grassland (primary or secondary) nearby (<2 m away). Maximum levels are lower when the monolith site was surrounded by a large area of wet mire vegetation, and such sites may show little or no change in charcoal levels despite major, extra-local vegetation changes (23, 17, 27, 41). This is in agreement with the surface sample results and suggests that charcoal particles are poorly dispersed, and that high levels mostly come from within 2-3 m.

Some mire sites may burn under exceptionally dry conditions, and this probably accounts for the relatively high charcoal levels at the two G. vulcanica bogs.

At only two sites does the major vegetation change start before the rise in charcoal (20, 21). It is possible that in these cases forest retreat was not associated with fire. However, the differences between the pollen and charcoal catchment sizes, and the wide sampling interval, suggest as an alternative explanation that the vegetation change was caused by unrecorded localised or infrequent fires. The initial rise in charcoal levels is followed by a decline towards the surface at many sites, although this is usually based on a comparison between only two levels. At others there is an increase or no change. The change in charcoal percentages does not seem to be consistently related to evidence for secondary succession, although the highest surface values are found at sites with no such evidence. The lack of relationship may again reflect the small size of the charcoal particle catchment.

Charcoal levels in the surface samples are generally lower than in the post-clearance, sub-fossil samples, but this may not be reliable evidence for a decline in burning. The surface samples will be of varying time depth, but will generally represent fewer years than the sub-fossil samples. There is thus a greater chance that a surface sample will 'miss' a fire than that a sub-fossil sample will, even if there is no change in fire frequency.

Overall in the Pindaunde valley charcoal levels correlate well with forest clearance but show no clear relationship with post-clearance changes. The same is true for the non-Pindaunde sites with the exception of Bendenumbun. At this site charcoal levels fluctuated, with significant peaks before 230 BP which do not correspond with vegetation changes. These may represent local fires on the mire surface (a G. vulcanica bog) which did not affect the forest. A confirmation of the small catchment for charcoal comes from the Umbamambuno site where a recent fire is not reflected in the surface sample charcoal percentage.

At no site, other than perhaps Bendenumbun, is there evidence for charcoal peaks associated with single fires. The charcoal levels do not usually fluctuate, but either rise to a sustained level or rise once and then fall. At most sites, the exceptions being the larger mires, high (>150%) charcoal levels are present in all post-clearance horizons sampled. At many, very high (>1000%) levels are found at all horizons after clearance. This suggests that within any period of 25-50 years (0.5 cm of accumulation) every site experienced at least one local fire, i.e. the fire frequency was greater than one fire per 25-50 years throughout the subalpine region. At many sites (e.g. 12, 47) it was probably much greater, as charcoal uniformly stains the upper part of the monolith, suggesting fires perhaps every 1-10 years.

Summary of the charcoal record.

Fire and forest clearance seem to be intimately connected on Mt Wilhelm. It must be remembered, however, that charcoal counts are not direct evidence of forest destruction by fire as most charcoal particles apparently come from grass. Yet they do enable a distinction to be made between periods when fire was available as an agent for forest destruction and those when it was not.

Conclusions.

The clearance history of the Pindaunde valley is summarised in Fig. 6.4. Points of particular interest include:

- (1) Clearance started in the upper third of the subalpine region.
- (2) Clearance was episodic rather than gradual.
- (3) One period of twenty years or less accounts for a high proportion of the total clearance.

Fig. 6.4 Summary of the clearance history of the Pindaunde valley.

CHAPTER 7

THE CHARCOAL RECORD EXTENDED

Subsidiary

Brake Tree

Labaya Bog

Lower Pindar Lake

Keweenaw River

The initial intention of this study was that it would complement the previous palynological work on Mt Wilhelm (Hope 1973, 1976a), by concentrating on the impact of man, rather than that of climatic change. Human impact was clearly apparent only in the top 1000 years of Hope's pollen diagrams, so I chose this period for my investigations. However, the summary in the previous chapter of the results from the 34 monolith sites raises some questions which can only be answered by extending the charcoal record further back. These questions are: the extent, if any, of disturbance in the subalpine region before the first clearance events recorded in the monoliths, and, following from this, the extent to which the history of clearance reflects the history of availability of an ignition source.

In addition, the experience gained in interpreting forest clearance events and charcoal particle records from the monoliths, can usefully be applied to some of the questions raised by Hope's work. Hope did not count charcoal particles but did speculate on the possible role of fire in the subalpine region during the Late Glacial and Holocene. Three questions in particular arose from his work: the possible role of fire in the maintenance of the very broad zone of shrub-rich grasslands above the tree limit during the glacial maximum (Hope 1976a, 1979b); the role of fire in the c.4900 BP opening of the treeline around Brass Tarn (Hope 1976a); and the role of fire in the absence of a tall closed shrubland above the forest limit on Mt Wilhelm (Hope 1976b).

With the hope of answering some of these questions, I counted charcoal particles in the original pollen slides from his five major sites. These were:

Summit Bog	4420 m	inferred age	8,800-0 BP
Brass Tarn	3910 m	inferred age	11,100-0 BP
Imbuka Bog	3600 m	inferred age	13,100-0 BP
Lower Pindaunde Lake	3570 m	inferred age	4,000-0 BP
Komanimambuno Mire	2740 m	inferred age	22,000-0 BP

Methodology.

Hope used the same chemical treatment for pollen extraction as was used in this study, except that the pollen was bleached and stained with safranin, and lacquer was used to seal the slides, giving a rectangular counting area. I counted charcoal particles $>10 \mu\text{m}$ on the same slides in whole transects, up to a minimum of 100 particles or three transects. As far as possible the same criteria were used to identify charcoal as in slides from the monoliths, although staining made comparison somewhat difficult. Some slides were impossible to count because air had leaked in. For others the counts are only approximate because there had been clumping of charcoal and pollen.

Charcoal percentages were calculated from Hope's transect numbers and pollen counts, using a suitable pollen sum, and pollen diagrams of selected pollen taxa were plotted.

The pollen sum.

Charcoal particle frequencies are expressed as percentages of a pollen sum. The nature of the pollen sum used thus determines both the magnitude of the individual values and the direction of the changes at zone boundaries. The choice of pollen sum is problematic if there are major vegetation changes in the period covered by the diagram: it becomes exceptionally difficult when there are also major climatic changes. The 'subalpine sum' adopted for the monolith sites is equally suitable for the sections of the record from Hope's subalpine sites when the climate was similar to that of today, i.e. from c.9500 BP to the present. It is not very suitable for the two sites (Summit Bog and Komanimambuno Mire) outside the subalpine region, or for the lower sections of the record from the subalpine sites, which represent vegetation and climates very different from those in the subalpine zone today.

Hope used a total woody pollen sum (excluding Casuarina and Cyathea) usually dominated by regional elements, at all of his sites. Here a compromise is made by using the 'subalpine sum' for all Hope's subalpine sites and the Summit Bog, and an equivalent sum of local and extra-local elements for Komanimambuno. This ensures maximum comparability with the monolith data, but great care must be taken in interpreting the charcoal percentages in the 'non-subalpine' sections. These problems will be discussed for each site individually.

Other problems.

Another major problem in interpreting charcoal particle data from these sites by comparison with mine is that all except Komanimambuno were open water for part or all of their history. Small tarns probably behave in a similar way to small mires as charcoal particle deposition sites, but there are no comparative data to support this. Very different transport and depositional processes will be involved in a lake the size of the lower Pindaunde lake, as Hope's trap results show for the pollen (Hope 1973, 1976a). Freshly produced charcoal particles tend to float, which must affect their distribution.

In addition, all Hope's sites suffer from stratigraphic problems, particularly near the surface. Correlation of the upper sections of the cores with my monoliths is in most cases impossible, as the tephra layers are either absent or cannot be certainly identified from the descriptions and chronology.

A general problem in interpreting these charcoal particle records is that there is no direct information on the processes involved in production, dispersal and deposition. This has not been important for the monolith sites, as the charcoal records have only been used in a fairly crude determination of the presence or absence of local fires. The pollen record provides information on vegetation changes, which because of their nature are almost certainly the result of fire. There are only a very few situations where the charcoal and pollen records do not support each other. In contrast, the relationship between fire and vegetation change is always problematic at Hope's sites. Interpretation has to be based on a comparison with the monolith data, and is therefore several stages removed from the actual processes involved.

Further problems are discussed for each site individually below. All conclusions are only tentative and approximate but, despite this, may be of value. They at least show some of the possibilities and many of the problems of charcoal particle analysis.

The charcoal records for Hope's palaeoecological sites.

(For details of stratigraphy and minor pollen types see Hope 1976a.)

Brass Tarn 3910 m.

The location and vegetation surrounding this site is described under the adjacent monolith site 39, in Chapter Five. The tarn is about 20 m in diameter and 3 m deep in the centre. It has small inlet and outlet streams and a large catchment area. Fen communities dominated by sedges, principally Carex gaudichaudiana and Carpha alpina, surround the open water. The tarn lies approximately at the present treeline and was chosen by Hope to investigate past changes in the forest limit.

The single core was taken by Hillier, D-section and piston samplers from the marginal fen, but below 35 cm the sediments were entirely limnic, except for prominent layers of volcanic ash. Five radiocarbon dates were obtained and suggest that the tarn has been steadily infilled since formation 10,700-11,400 years ago until recently. The uppermost sediments may have been disturbed by the process of fen-building and by the thick deposits of volcanic ash.

The 'subalpine pollen sum' is appropriate for this site, but the low pollen sum productivity at this altitude will tend to exaggerate the charcoal percentages.

Hope recognised four distinct zones reflecting local and regional vegetation changes (Fig. 7.1).

BT1 (750-902 cm): inferred age 11,100-8,550 BP

The very high Nothofagus level in this zone was interpreted as reflecting very low local pollen production. Trees were absent and the local vegetation was a wet tundra, which changed gradually to alpine grassland as soil developed after glacial retreat.

BT2 (490-750 cm): inferred age 8,550-4,900 BP

The treeline passed above the tarn during this zone and subalpine forest surrounded it.

BT3 (160-490 cm): inferred age 4,900-1,800 BP

The treeline retreated just below the level of the tarn at the start of this period and the surrounding slopes were occupied by shrub-rich, 'subalpine' (sensu Wade and McVean 1969) grassland.

BT4 (0-160 cm) inferred age 1400 BP to present.

This zone is separated by a possible hiatus from BT3 and is characterised by rising Casuarina, Trema and Cyathea. A slight further depression of the treeline is suggested.

Changing the pollen sum (principally including Poaceae and excluding Nothofagus) does not significantly change the zonation and interpretation proposed by Hope. Experience with the monolith sites does, however, suggest that the 'treeline retreat' at the BT2/BT3 boundary may have been only minor and local.

The charcoal curve does not seem to be related to either the stratigraphy or the vegetation, except that there may be an inverse relationship with Cyperaceae. Maximum percentages are similar to those found at the wetter monolith sites, at and after forest clearance, while the minimum percentages are similar to pre-clearance levels in the subalpine zone. The charcoal record therefore indicates the probable occurrence of burning in the vicinity of the tarn, at some times throughout the Holocene. The fluctuations in CP percentages may reflect changes in fire frequency or, alternatively, changes in the extent of an unburnable marginal mire.

Because of the probably very low pollen productivity in zone BT1, the charcoal percentages there must be interpreted with caution. Absolute charcoal deposition was probably low in this zone and may not represent local fires. The charcoal percentages in BT2 suggest that the forest around the tarn was not closed at this time but included areas of grassland.

Fig. 7.1 Brass Tarn pollen diagram (pollen data from Hope 1973)

Summit Bog 4420 m.

This site is 250 m south of the Wilhelm summit. The bog is covered in wet alpine tundra which consists mainly of a mat of mosses, with occasional plants of Ranunculus saruwagedicus and Potentilla forsteriana. The only woody plants are low (<5 cm), creeping Styphelia, Drapetes ericoides and Tetramolopium macrum. Smooth rock surfaces surround the bog but there are patches of dry alpine tundra, with scattered tufts of grass, on the better drained slopes in the vicinity.

Cores were taken using piston and D-section samplers. The site became a shallow tarn c.9200-8800 years ago and gradually filled in for the next 2000 years. Several lines of evidence suggest that there were at least two erosional episodes in the upper part of the core, which removed earlier sediments.

Hope recognised two zones reflecting minor local and regional changes (Fig. 7.2).

SB1 (65-301 cm): inferred age 8800-6900 BP

The site was a small shallow pond surrounded by alpine tussock grassland.

SB2 (0-65 cm): inferred age <6900 BP to present.

Hope suggests an alternation of wet alpine tundra and alpine grassland for this zone, with at least two erosional episodes removing the grassland.

Again there seems to be a weak inverse correlation of charcoal with Cyperaceae. The significance of the percentages is hard to assess in view of the very low, pollen sum deposition rate. Relative to Nothofagus the maximum charcoal levels are low, and probably do not require there to have been local fires. Burning of the present local vegetation is inconceivable but if, as Hope suggests, the tundra communities are successional following erosive removal of alpine grassland, local burning might have been possible in the past. Charcoal levels are sometimes higher than Rapanea and, as the evidence from the monolith sites suggests that charcoal is less well dispersed than this pollen type, this may imply fires in the alpine grasslands above the treeline.

Imbuka Bog 3600 m.

This site is on the south-facing slope of the Imbuka ridge, above the lower Pindaunde lake and near monolith sites 27 and 29. The bog lies in a large basin behind a lateral moraine. The actual coring site is covered by short grass bog but D. klossii grasslands, Astelia bog and Carpha alpina fen occur elsewhere on the mire. Low shrubs are common in the better-drained areas. The surrounding slopes now support shrub-rich,

Fig. 7.2 Summit Bog pollen diagram (pollen data from Hope 1973).

subalpine tussock grasslands with forest remnants.

The core for pollen analysis was taken by Hillier borer. Three radiocarbon dates were obtained; two from fractions of a single sample. Non-conformities were not evident. The site apparently formed as a moraine-dammed pool at c.12,800-13,400 BP, which filled in by about 6000 BP. The 'subalpine pollen sum' is appropriate for this site.

Hope recognised four zones (Fig. 7.3).

IB1 (380-455 cm): inferred age 13,100-10,800 BP

The high Nothofagus percentages were interpreted as reflecting low local pollen production. The local vegetation was a very open, herb community.

IB2 (315-380 cm): inferred age 10,800-9,200 BP

During this zone, shrub-rich open grasslands developed locally and the treeline approached the site.

IB3 (50-315 cm): inferred age 9300-1000 BP

Forest surrounded the site and may have formed an overtopping canopy during the later part of this zone.

IB4 (0-50 cm): inferred age 1000 BP to present.

Regional Casuarina pollen increased and forest was removed from around the site.

The changed pollen sum does not change the interpretation. However, the presence of a volcanic ash band at an inferred age of about 600 BP, suggests that the dating of the upper section of the diagram is incorrect. This is presumably the Tibito tephra (clearly present at the coring site) for which a date of 230 BP is used in this thesis. If this is so, local clearance apparently started around 600 BP and accelerated after 230 BP. The nearest monolith sites all show major clearance at 230 BP, but minor or extra-local clearance before then.

The charcoal curve follows the vegetation change. The upper part, IB3 and IB4, is similar to the monolith sites and supports the absence of earlier major disturbance in the subalpine region. Charcoal percentages are also high in IB1, but this very likely reflects a low pollen deposition rate. Charcoal levels in IB2 may indicate occasional local burning or, again, low pollen deposition. In any case, the fact that the site was under open water at this stage makes them difficult to interpret.

Fig. 7.3 Imbuka Bog pollen diagram (pollen data from Hope 1973).

Lower Pindaunde Lake 3570 m.

This lake is 420 m x 250 m in area and 20 m deep. Two cores were obtained at the same spot in the deepest part of the lake with a Mackereth corer. They were combined to give a sequential record, although there may be a slight overlap or discontinuity. Three radiocarbon dates were obtained. Only the top 718 cm of an estimated 10-15 m of sediment were recovered. The 'subalpine' pollen sum is appropriate for this site.

No zones were recognised (Fig. 7.4). Forest occupied the shores of the lake from the base at c.4000 BP until the top few spectra.

It is impossible to interpret the charcoal record from a site in the centre of a large lake by comparison with small mire sites. Both the source and mode of transport of the particles deposited are unknown. The fluctuations in the charcoal percentages may reflect significant changes in fire frequency, but this cannot be stated with confidence. Charcoal levels do not rise near the surface when there were certainly fires around the lake, and this suggests they represent either regional, aerial fall-out or water transport from fires higher in the catchment, perhaps in the alpine region.

Komanimambuno 2740 m.

This site lies outside the recently-glaciated area, 1.7 km south-east of the lowest monolith site (43). The mire is in a shallow, sloping hollow, with up to 550 cm of sediment. It is surrounded by a species-rich Lower Montane forest, including as large trees: Cryptocarya sp., Dacrycarpus cinctus, Decaspermum forbesii, Elaeocarpus ptilanthus, Pandanus giulianettii, Pittosporum ramiflorum, Prunus pullei, Syzygium sp., Timonius belensis and Weinmannia triihophora. Smaller trees include many Euphorbiaceae. Tree ferns are common. Wet areas of the mire are dominated by Scirpus subtilissimus, with Deschampsia klossii and Ranunculus pseudolowii present. There is a stunted version of the surrounding forest on the drier parts of the mire.

A 520 cm core was obtained with piston and D-section corers. Preliminary pollen analysis suggested a major discontinuity at 112 cm, so a monolith from 50-150 cm below the surface was obtained, 50 cm from the coring site. The monolith record for 50-120 cm was interpolated into the lower core section and is separated from the upper core section by a discontinuity. (Full discussion in Hope 1976a). Radiocarbon dates were obtained from several fractions at four horizons.

DACRYCARPUS RAPANEA POACEAE CYPERACEAE RANUNCULUS ASTELIA CYATHEA AST./TUB. COPROSMA HALORAGIS DRIMYS ERICACEAE EPACRIDACEAE CHARCOAL NOTHOFAGUS

0
1
2
3
4
5
6
7

The basal age is c.22,000 BP, after which peat accumulated quickly to c.15,000 BP, when accumulation apparently slowed down. It is possible, however, that there are unrecognised discontinuities in the record.

The 'subalpine pollen sum' is clearly inappropriate for this site, so an equivalent sum of elements that were probably local or extra-local at some time during the last 22,000 years was used. This includes all taxa except Nothofagus and a few others from lower altitudes, and the herb and fern taxa also excluded from the subalpine sum. Only the major forest pollen contributors are included in the diagram.

Hope distinguished five zones (Fig. 7.5).

KM1 (290-520 cm of the lower core): inferred age 22,00-17,800 BP

The local vegetation was an open tussock grassland with treeferns and scattered shrubs. The nearest forest was apparently some distance away.

KM2 (150-290 cm of the lower core): inferred age 17,800-15,300 BP

The shrubby tussock grassland was apparently replaced by a community more like a shrub-free alpine tussock grassland, and the treeline retreated further.

KM3 (75-150 cm of the lower core): inferred age 15,300-c.10,600 BP

A local Astelia or short grass bog occupied the site.

KM4 (50-75 cm of the monolith): inferred age c.10,600-2,200 BP

At the start of this zone, Montane forest became established on and around the mire.

KM5 (0-112 cm of the upper core): inferred age c.1800 BP to present.

Similar to zone KM4. The increase in sedge pollen at the surface suggests that the coring site, at least, became wetter recently.

Changing the pollen sum (principally including Poaceae and excluding Nothofagus) obscures the KM1/KM2 and KM2/KM3 boundaries, but does not alter the general interpretation.

Interpretation of the charcoal record at KM1, KM2 and KM3 is difficult because the pollen sum productivity is unknown. Hope suggests that the local vegetation in KM1, at least, was similar to the secondary subalpine grasslands of the present day. If this is also true for its pollen productivity then the charcoal percentages at least in this zone imply local burning. This is probably also true for KM2 and KM3. Charcoal levels decline during KM4 and are very low during KM5. However, in view of the high pollen productivity of montane forest relative to the subalpine region, even these low percentages may reflect local disturbance.

Fig. 7.5 Komanimambuno Mire pollen diagram (pollen data from Hope 1973).

Summary and discussion.

The evidence of the charcoal record from Hope's cores can be summarised as follows.

1. There are some charcoal particles at all horizons of all sites.
2. There were probably intermittent fires in the vicinity of Komanimambuno from 22,000 BP until the Montane forest arrived at 10,600 BP
3. There may have been local burning at Imbuka Bog between the first establishment of shrub-rich grasslands and the arrival of forest at 9300 BP
4. There were intermittent fires in the vicinity of Brass Tarn from the arrival of the treeline at c.8550 BP to the present.
5. The Summit Bog record probably reflects burning of the alpine tussock grasslands at intervals throughout the last c.8800 years.

The general implication is that whenever tussock grasslands were present they were likely to be burned. Ignition sources will be considered in the next chapter and discussion will be limited here to the possible pre-1200 BP impact of fire upon the vegetation.

The glacial maximum.

During the glacial maximum there was a broad zone of grasslands with treeferns and shrubs, above the forest limit (Hope 1976a). The treeline was apparently depressed by at least 400-600 m more than the snowline, and the shrub-rich grasslands occupied the zone where subalpine forest might be expected. Some of the shrub taxa, as well as Cyathea, seem as frost-sensitive as the subalpine forest trees, if their present distribution is any guide. The exclusion of subalpine forest from the shrub-rich zone therefore needs explaining.

Hope (1979b) suggests that an occasional severe disturbance, "for example periods of drought and very severe frost every thirty years or longer" would prevent the spread of closed forest, but allow shorter-lived shrubs to succeed. Although frost and perhaps drought contribute to the slowing or prevention of forest re-invasion of secondary shrub-rich grasslands today (Section III), fire is the most important factor in their maintenance. The full glacial period was probably drier (Hope 1979b) so fire may have been at least as effective then. While it is hard to believe that fire alone excluded the forest, the charcoal record suggests that it could have been a contributory factor.

Fire may similarly have contributed to the lag between glacier retreat and forest expansion.

Fire and the timberline.

It seems very likely from the Brass Tarn and Summit Bog records that there has been intermittent burning of the grasslands at and above the treeline since they were first established. The impact of this may have been considerable, as forest species are likely to be particularly sensitive to disturbance at their climatic limits. The tendency of fire to cause retreat of altitudinal timberlines is well known in other parts of the world.

An obvious implication of this is that the c.4900 BP treeline retreat at Brass Tarn may not have been the result of a climatic change. Fire, perhaps in conjunction with an exceptional frost or drought period, is an alternative explanation. However, there is no evidence from the Brass Tarn charcoal record that fire frequencies increased at this time, and the pre-4900 BP treeline was presumably established in opposition to a similar burning regime.

A related question is that of the form of the timberline, in particular the absence of a tall closed shrubland above the forest. Is this natural or the result of fire? The New Guinea distribution of the closed shrubland correlates well with disturbance. However, the apparently undisturbed timberline, without a shrubland belt, in the Imbukum valley on Wilhelm has been interpreted as the natural situation for this mountain (Hope 1976b). Yet the Imbukum treeline is less than an hour's walk from Brass Tarn and, in the absence of evidence to the contrary, must be assumed to have had a similar fire history.

Tall shrubs are common in the tussock grasslands for c.200 m above the treeline and in the absence of fire might possibly spread to form a closed community. It is notable that the largest shrub species above the treeline Drimys piperita entity subalpina has a lignotuber (Wardle 1974) and may thus be fire-resistant. Hope (1976b) concluded that climatic or edaphic conditions, or possibly the present flora, did not favour an extensive treeline shrubland on Mt Wilhelm. This is another question which the charcoal record can re-open, but to which it cannot give a definite answer.

CHAPTER 8

POLLEN ANALYSIS: DISCUSSION

The pre-disturbance vegetation pattern.

In Chapter One, earlier views on the causes and relative extents of primary and secondary subalpine grasslands were summarised. Three possible reasons for the pre-disturbance exclusion of forest from areas below the altitudinal limit have been suggested: shallow soil, poor drainage, and 'frost hollow' effects resulting from cold air drainage. The main uncertainty has been on the question of the importance of 'frost hollows'. This could perhaps be resolved by long-term experiments but this would ideally require a mountain where disturbance had been minimal. The alternative is to consider which explanation best fits the evidence for the extent and nature of the pre-disturbance subalpine, non-forest vegetation revealed by the pollen record.

The pollen record can give no direct evidence on the exclusion of forest by shallow soil. Forest clearly cannot grow on bare rock and one might expect herbaceous vegetation on soil too shallow to support trees. I observed this on the apparently undisturbed summit ridges of Mt Amungwiwa and Mt Service, although other factors may have been involved in both cases. Such areas were probably of limited extent on Mt Wilhelm but may have been important in facilitating human access to the alpine region along the ridge-tops. Soil depth cannot have been responsible for the exclusion of forest from large areas of the valley floor.

Waterlogging and cold air ponding would both be expected to have their maximum influence in basins and valley bottom flats. The effects are therefore hard to distinguish and the pre-disturbance subalpine vegetation pattern could fit either explanation. However, the presence of areas of frost-hollow vegetation completely surrounded by closed forest seems a priori unlikely. The catchment for cold air drainage would be limited to the open area itself as air cooled in contact with eradiating forest canopy leaves would be mixed with warmer air on sinking, and the night-time is too short for the accumulation of freezing air to the height of the trees. (In higher latitudes accumulation may continue through the day, but in the tropics air temperatures always rise above freezing after sunrise.) Steenis (1968) argued that there would be no 'frost holes' at all in the tropics in the absence of human disturbance.

The nature of the pre-disturbance, non-forest vegetation supports the idea that waterlogging rather than cold air ponding was the primary reason for exclusion of forest at most sites. If frost or low mean temperature was the main factor one might expect to find alpine vegetation-types occupying the frost hollows. In fact below 3650 m forest directly abutted mire communities of a type today found only on waterlogged, subalpine sites. Above 3650 m there were also areas of D. klossii-dominated grasslands, but this community is floristically and physiognomically

distinct from the alpine grasslands. Those areas of subalpine D. klossii grassland which pollen analysis show to be primary are again all on waterlogged sites. Frost alone seems unlikely to account for the virtual exclusion of shrubs from these grasslands, as many of the same shrub species thrive a long way above the treeline. If waterlogging excludes shrubs it will also exclude forest.

An exception to the absence of alpine vegetation types below the treeline ecotone is the occurrence of small patches of a community similar to Wade and McVean's 'Alpine fern meadow', with Papuapteris linearis and Detzneria tubata, above 3750 m in some of the valleys other than the Pindaunde. These occurrences are all on well-drained, sloping sites on the margins of mires and suggest that cold air ponding may be important at this altitude. These sites were probably never surrounded completely by closed forest and would have been connected by open areas to the alpine region.

On the whole it seems likely that waterlogging was the major factor excluding forest from areas below the treeline before disturbance. There is no evidence for extensive frost-hollow grasslands, although frost may have been a contributing factor at higher altitudes (>3650 m and particularly >3750 m).

The mechanism of the exclusion of forest by waterlogging is not clear. Dacrydium nidulum (Johns 1974) and other tree species, including other podocarps, form swamp forests in the mid-montane zone, tolerating continuous waterlogging. There may be some form of interaction between waterlogging and temperature - perhaps through mineral nutrition - which prevents tree growth on wet, cold sites. Swamp forests seem to be absent from cool temperate and montane climates all over the world.

The history of forest clearance.

Did fire cause it?

When the clearance history was summarised in Chapter Six it was pointed out that the charcoal counts are not direct evidence that forest clearance was caused by fire as most charcoal particles come from burning grass. Before attempting to explain the pattern of clearance it must be shown that it is reasonable to identify fire as the cause of clearance rather than a response to a vegetation change caused by other factors.

For Hope's Imbuka Bog and Komanimambuno Mire sites it seems probable that the decline in charcoal levels as closed forest became established around the sites at the beginning of the Holocene was a result, not the cause, of the vegetation change. There are many reasons, however, apart from the absence of a corresponding major climatic change, to accept a

causal relationship between fire and the clearances of the last thousand years.

The relics of forest found in the secondary grasslands are invariably charred. More convincing is the fact that first high charcoal levels at nearly all sites occur at the time of first clearance and are not simply correlated with the presence of local grassland i.e. fires did not occur in the primary subalpine grasslands until forest destruction started. Only at two sites was forest clearance not associated with a rise in charcoal particles.

As burning and clearance started at the same time, it seems very likely that fire was the cause of most, if not all, of the clearance during the last thousand years. The destruction of subalpine forest by fire can be observed on many New Guinea mountains today. I saw evidence of it on Mt Giluwe and Mt Michael, and various authors have described it on other mountains (Paijmans and Löffler 1972; Brass 1941).

What was the ignition source?

In the absence of volcanic activity there are only two possible sources of ignition on Mt Wilhelm: lightning and man. Natural fires started by lightning will be very rare if they occur at all. Even in the lowlands lightning has a very minor role in forest damage because any fires started are immediately extinguished by rain (White 1975). Thunderstorms at the altitude of the Wilhelm subalpine region are unusual - very few have been observed in eight years of intermittent occupation of the Pindaunde Field Station - and have been invariably accompanied by rain. Steenis (1972) dismissed lightning as a source of ignition in montane Java despite a high frequency of thunderstorms (<3000 m) because it is 'always accompanied by heavy showers'.

It is not possible from eight years' observations to entirely rule out lightning, but the chance of it striking a suitable dry fuel seem very small. It certainly cannot be the source of the recurrent and extensive fires evidenced by the charcoal record. Man, in contrast, preferentially visits in dry weather and seeks out those open areas which are most likely to burn.

Several authors have stressed the importance of man as an ignition source in the tropics and the carefree incendiarism of the New Guineans in historical times has often been commented upon (Chapter One). The main reasons for starting fires are probably:

- (1) the accidental escape of fires lit for cooking or warmth;
- (2) hunting: driving larger game such as wallabies and removing cover

for smaller game such as rats;

- (3) fun: 'the pleasure of witnessing spectacular destruction' (Smith 1979);
- (4) signalling: witnessed by the author on Mt Service, where the local carriers cut 'notches' in the ridge top forest and lit fires to signal their presence to friends back in the village;
- (5) easing travel through the tussock grasslands;
- (6) warfare - mentioned by one Simbu informant.

The first three are probably the most important.

Opposed to these many reasons for starting fires there are few against. Newsome (pers. comm.) says that some of the groups living near Mt Giluwe (certainly not all) did not burn the subalpine grassland out of fear of offending the spirits. It seems unlikely that traditional man would have been worried about, or would even have noticed, the long term impact of his activities on what is only a marginal resource. More recently laws banning the firing of grassland without permission have had some effect where enforced, particularly on Mt Wilhelm.

Although most fires today are lit by matches there is no reason to doubt the efficiency of the traditional fire-lighting equipment. Powell (1976) described the use of the traditional 'fire-saw'; 'a thong of bamboo or rattan cane is pulled quickly back and forth across a piece of split soft wood... with tinder underneath'. I saw a Simbu man start a fire in light rain in two minutes with a similar device, called a 'kitn' in Kuman. Travellers on the subalpine trade routes may also have carried a smouldering fire-stick to light fires (Hughes pers. comm.).

In conclusion, almost all fires in the subalpine and alpine region, at least during the Holocene, would have been lit by man. Moreover it seems likely that man has started fires on the mountain whenever his presence has coincided with the availability of suitable fuel and suitable climatic conditions.

Conditions for ignition and spread.

In general, ease of ignition depends on: fuel thickness; fuel arrangement in space; fuel quantity; and fuel moisture content (Luke *et al.* 1978). Initial ignition will have been of fine dry fuels. The only material which meets these requirements in the subalpine is grass, and perhaps sedges, under suitable weather conditions. It is very difficult to imagine direct ignition of forest fuels even under the driest conditions. In contrast, grass fuels, being fine and exposed to intense solar radiation, may dry out sufficiently after only a few dry, clear days. (A cooking fire on Mt Giluwe escaped and burned several square metres of D. klossii tussock grassland only two days after a week of heavy rain.)

The ignition of grass fuels in the subalpine and alpine regions may be possible on several days in most years on Mt Wilhelm, and probably every dry season on the drier mountains to the east. The amount and distribution of the available fuels will determine whether or not the fire spreads. Some alpine communities are probably always too sparse to carry fire. The fuel density of the others will depend on the time since the last fire. Post-fire recovery may be slower at higher altitudes. Vigorous secondary tussock grasslands can carry fire in two consecutive years (personal observations on Mt Giluwe) but less vigorous herbaceous communities may require several years to accumulate sufficient fuel. The maximum extent of individual fires will be limited by the extent of suitable vegetation and by the time available before rain or mist dampens them. The spread of fires between adjacent valleys is very unlikely.

After a fire has started it is able to dry and pre-heat fuels which cannot be lit directly. It is at this stage that a fire may enter the forest. Most often, however, the fire burns out quickly in the forest edge (Brass 1941; my own observations). This is presumably a result of the moist forest micro-climate. Much of the heat generated by the fire is used in transforming water in the fuels to steam so that the fire temperature falls too low to sustain combustion. Fires will only burn into the forest if at least part of the forest fuel is unusually dry.

Frequent grass fires will facilitate drying out of the forest by the gradual removal of the border shrubberies, which retard air movements and evaporation. Recovery of the border vegetation may, however, be rapid if damage is only minor. In any case, some other 'catastrophic' factor is probably needed as well before the forest will burn. The first fire to enter the forest will kill trees without consuming the thicker fuels. Subsequent fires may then enter more easily and burn more fiercely.

When considering the pollen and charcoal evidence, the following points must therefore be kept in mind: nearly all fires are lit by man; all fires are lit in grassland (and perhaps sedge fen); and fires only enter the forest when it has been previously damaged in some way which increases combustibility.

Why did clearance occur when and how it did?

For forest clearance by fire to occur, three conditions must be fulfilled.

- (1) There must be an ignition source.
- (2) There must be fine dry fuels to ignite and suitable conditions for the spread of the fire.
- (3) The combustibility of the forest must be exceptionally high.

As discussed above, this means that man must be visiting the mountain, tussock grasslands must be present, and the forest must be damaged in some way. A complete understanding of the observed pattern in space and time will involve all three factors but, for simplicity, the effect of changes in each one will first be considered separately.

The availability of an ignition source.

If only this factor is normally limiting, then the spatial and temporal pattern of forest clearance will reflect the the spatial and temporal pattern of human visits, i.e. the human prehistory of the subalpine region. This at first sight seems reasonable but there are two major objections.

The first is that man has almost certainly been visiting the mountain for a much longer period than that in which major forest clearance has occurred. As discussed in the previous chapter, the treeline and alpine charcoal records from Hope's sites are evidence of at least intermittent human visits throughout the Holocene, and the lower sites suggest man's presence for considerably longer. To reach the treeline he must have passed through the subalpine zone yet, as far as the evidence goes, it was unaffected.

The second is that forest destruction does not simply depend on the availability of ignition. The charcoal record shows high fire frequencies at some sites from 230 BP to the present, without additional forest retreat. As will be shown later (Chapter Nine) the boundaries of the forest patches seem to have remained stable in recent prehistoric times, despite continuing human visits and frequent burning. Another example of the resistance of forest to fire under normal conditions is provided by Mt Giluwe where there was no detectable change in forest extent in aerial photographs of the same area between 1936 and 1972 despite probable near-annual grass fires (Hope pers. comm.), but major changes after fires during the 1972 frost/drought period.

The clearance history therefore cannot be simply interpreted in terms of the history of human visits. Other factors must also be involved.

The availability of fuels for ignition.

The grasslands at and above the timberline and the primary D. klossii grasslands in the upper part of the subalpine zone will have always provided sites in which fires could start in dry periods. The availability of fuels for ignition is therefore likely to have been limiting only in the lower part of the subalpine zone (<3650 m). However, the initial expansion of secondary grasslands would have made ignition easier (because these

grasslands are on well-drained sites) and, by increasing the length of the forest/grassland boundary, would have made a greater area of forest susceptible. The availability of grass fuel is therefore likely to have had a significant effect on the spatial pattern of forest clearance but does not account for the initiation of clearance within the last few hundred years.

The combustibility of the forest.

If ignition is always available and suitable fine fuels always present, the history of clearance will be a record of the, probably aperiodic, occurrence of extreme events which made the forest susceptible to fire. The possible nature of such events will now be discussed.

Tephra fall. The most obvious possible catastrophe is the fall of the 230 BP tephra, which provides the chronological framework for the clearance record. The majority of forest clearance occurred at least within 20 years of the tephra fall, and possibly immediately after it. This correlation seems too close to be coincidental and is here considered in detail, both in relation to the evidence of the pollen record and evidence from historical observations of the effects of similar tephra falls elsewhere.

The strongest evidence against a major role for the 230 BP tephra fall is the lack of effect of the earlier, 1200 BP tephra. The absence of even minor forest clearance at any site at this horizon suggests that even the somewhat thicker (1.5-2.0 times) Tibito tephra is unlikely to have had a major effect. None of the earlier tephras in Hope's cores (Hope 1973) are associated with vegetation change either.

Moreover, although initiation of clearance at most sites occurs after the 230 BP tephra fall, at some sites it occurs earlier, suggesting that the c.230 BP clearance is simply an intensification of events already started. This does not rule out a major role for the tephra but shows that it cannot have had a unique role in promoting forest clearance.

There is considerable variation in the present thickness of the Tibito tephra on Mt Wilhelm, presumably resulting from post-depositional reworking. On large flat areas, where reworking will have been least important, the thickness averages 2.5-3.0 cm. Tephra initially accumulates as a 'light, fluffy deposit, not unlike fresh snow' (Blong in press) but soon compacts to about half its original thickness. Thus 2.5-3.0 cm of compacted tephra represents a true airfall thickness of 5-6 cm.

There is a large body of literature on the effects of tephra fall on vegetation (reviewed in Wilcox 1959 and Blong in press)) but this is mostly concerned with depths of more than 50 cm. Most damage to vegetation

results from the weight and thickness of the tephra and revegetation is surprisingly rapid, even after several metres have fallen. Thinner deposits of tephra (<25 cm) have usually had little effect on natural vegetation, at least if the absence of reports of damage is any guide. 6 cm would bury only very low-growing plant communities such as short grass bog and alpine tundra. The weight of the tephra might have caused some mechanical damage to woody plants but this is likely to have been minor.

Nearly all the accounts of damage to plants by small amounts of tephra (<10 cm) refer to crops. At Soufriere in 1902 only 1-2 cm of tephra blighted and yellowed tender plants and falls of 2.5-3.0 cm damaged sweet potatoes, yams and sugar cane, and broke leaves off bananas and plantains. At Taal (Philippines) in 1911, 1 cm of tephra apparently 'killed bananas and other delicate vegetation' (Pratt 1911). Evidently even thin tephra falls can damage plants.

Some of this damage associated with thin tephra may be the result of either acid coatings on the tephra grains or else acid rainfall at the time of the eruption. The occurrence of both seems to be very variable and may be negligible for some large eruptions. After the Katmai (Alaska) eruptions in 1912 acid rains were common, and Griggs (1915) reported that at Latouche, 480 km away, 'tender annual garden plants were completely destroyed and the leaves of many native perennials were so burnt that they dropped off'. The occurrence of acid rains is sporadic, depending on the drift of the fumes and the occurrence of rain. Sulphuric and hydrochloric acids are usually the active ingredients. Susceptibility varies greatly from one plant species to another and may increase during periods of active growth.

Since nothing is known of the chemical properties of the fresh Tibito tephra, nor of the weather conditions under which it fell, it is difficult to state its possible effects on the subalpine forest. The maximum severity of damage likely at this distance from the source would probably have been partial defoliation of some susceptible species. More likely, the effects would have been negligible. In any case the evidence from similar eruptions in historical times suggests that any harmful influence would have been short-lived, and possibly followed by beneficial effects from the contained nutrients.

Extreme climatic events. The eight years of intermittent weather records available probably give an accurate picture of the mean climatic parameters. They do not give information on the frequency and intensity of rare 'catastrophic' climatic events. The forest is likely to be well adapted to seasonal extremes but presumably anomalies may occur occasionally in any climatic regime.

The climatic events most likely to cause an increase in the combustibility of the forest are frost and drought. These two commonly occur together in tropical uplands because the dry air and cloudless skies during a drought period maximise radiative cooling of the ground (Steenis 1968; Brown and Powell 1974). Their effects may then combine to do more damage than either alone.

The worst period of frost and drought in the Highlands in recent times occurred between June and October 1972 (Brown and Powell 1974). In a large area of the Western and Southern Highlands a series of frosts accompanied by a prolonged drought caused widespread damage to gardens and natural vegetation down to 1600 m. In some areas severe frosts occurred on up to ten consecutive nights. Before this the worst frosts had been in 1940 or 1941 and were also accompanied by a drought, lasting up to seven months (Meggitt 1958). Both times the drought compounded frost damage by slowing plant growth and facilitating fires.

Although the 1972 frosts killed large areas of natural vegetation, including tall closed forests, it is not clear to what extent this was a result of previous disturbance. Most forest killed was apparently adjacent to gardens, anthropogenic grasslands and roads, and the effects in completely undisturbed areas were not recorded (White K.J. pers. comm.). Secondary grasslands provide a greatly increased catchment for cold air drainage on clear, calm nights, which may then allow accumulation to depths sufficient to kill adjacent natural vegetation. As was discussed earlier, significant cold-air ponding is unlikely in a forested catchment.

It is possible that on Wilhelm the alpine areas provide a sufficient catchment for cold air drainage to damage the forests below. Alternatively, direct radiation cooling of the forest canopy may be sufficient to cause damage, although this would seem improbable as live foliage is quite a good conductor of heat. It therefore seems unlikely, but not impossible, that frost would cause major damage to closed forest vegetation in the subalpine region. However, damage to herbaceous vegetation and adjacent forest margin shrubs in boggy openings below the treeline may have facilitated the entry of fire into the forest.

Drought alone may increase the combustibility of the forest. The observed dry periods on Wilhelm (<22 consecutive days) did not lead to drying out inside the forest (Smith 1979) but Lane-Poole (1925) observed this on the, probably drier, Saruwageds and Owen Stanley Range. The effects of drought will be increased by relatively minor disturbance of the forest borders leading to increased air movement and greater evaporation. The drought in 1972 lasted several months yet most trees and shrubs of the Upper Montane forest showed no obvious wilting or leaf loss except on shallow rocky soils (Buckley *et al.* 1979).

While frost and drought are the most obvious climatic catastrophes there are other possibilities. New Guinea is out of the general cyclone belt (although cyclones can affect the eastern end of the island) but normal storm winds can cause damage (White 1975). Winds on Wilhelm, except on the summit ridge are, however, generally of low intensity. Sleet, snow and hail are other possible catastrophes but sleet and snow do not normally fall below 4000 m and hail, though occasional at any altitude, has rarely been heavy or prolonged at the Pindaunde Field Station (Hnatiuk *et al.* 1976). At lower altitudes hail storms may defoliate pawpaw and other trees and flatten crops (Bergmann 1971) but the microphyllous subalpine trees would presumably be less susceptible to damage. In any case, damage from any of these causes would increase the combustibility of the forest only if a drought occurred before the vegetation had recovered.

The frequency and intensity of extreme climatic conditions, particularly frost and drought, may have increased during the world-wide neo-glacial episode between 700 and 120 BP, which approximately coincided with the major clearance phase on Mt Wilhelm. There is evidence of a neo-glacial advance in the Carstenz mountains of Irian Jaya, starting sometime after 1300 BP and ending approximately 120-150 years ago (Allison and Peterson 1976). On Wilhelm there is poorly dated evidence for an erosive episode in the summit region, possibly representing snow-cap formation, during this period (Hope 1976a).

From this evidence and the world-wide pattern, a drop in mean annual temperature of about 0.5°C can be postulated. At the modern lapse rate of $c.0.5^{\circ}\text{C}/100\text{ m}$ this is equivalent to a change in elevation of about 100 m. There is also some data from S.E. Asia and elsewhere (but not equatorial Malesia) which suggests drier conditions during the neoglacial (Barry pers. comm.).

A change in the mean climatic parameters need not necessarily have resulted in a change in the frequency or intensity of anomalous extremes, although this seems probable. It may also have increased the susceptibility of the upper subalpine forest to non-climatic damage and shifted the competitive balance in favour of non-forest vegetation wherever the forest was living under marginal conditions.

Mass movements. Mass movements of various types on the steep valley sides provide another possible reason for a sudden increase in the combustibility of the subalpine forest. There are many recognisable but more or less revegetated scars left by mass movements in the lower, forested part of the subalpine zone. Some of these seem to be landslips where the now-exposed surface of the unweathered rock has acted as a slip plane. In others, unweathered rock is not exposed, and the major movement seems to have been a debris flow. In the region where forest is reduced to

'islands' mass movement scars are less obvious, but the pattern of vertical strips of grassland suggests that much of the grassland on the valley sides between 3460 m and 3700 m is on the sites of old debris flows. Forest-grassland borders are often adjacent to discontinuous ridges at right angles to the slope. These are apparently levees built by the 'snow-plow' action of the debris flow, and lobes of debris are sometimes visible at the base of the slope.

Judging from the forested slopes of Mt Wilhelm and aerial photographs of the rugged area to the north, mass movements are a common occurrence under undisturbed forest. Pain (1970) has described 240 km² of dense landsliding in the Adelbert Range initiated by an earthquake of magnitude 7, and suggests that falling trees triggered the slides. Earthquake-triggered slides have also been described from New Zealand and the Chilean Andes (Veblen and Ashton 1978). Oversteepening of the valley sides makes glacial landscapes particularly susceptible, as also may the sharpness of the boundary between weathered and unweathered granodiorite.

Mt Wilhelm is subject to frequent minor tremors and, although outside the most active zone, presumably experiences occasional major seismic events. The mass movements on Mt Wilhelm have not been dated, so the possibility of a number of simultaneous, earthquake-triggered movements leading to a great increase in fuel availability remains purely speculative. The vegetation pattern does suggest that mass movements have been an important determinant but this does not prove that they initiated the clearance. The successional vegetation on old scars seems particularly fire sensitive (from observations on a recent fire in the Imbukum valley) so burning may simply pick out the sites of old movements. Alternatively, some of the mass movements may have occurred after, and as a result of, forest clearance. Veblen and Ashton (1978) mention a greater frequency of slides on slopes with disturbed forest cover in Chile than under undisturbed forest.

Summary of catastrophes.

Any or all of the catastrophic events suggested above may have had an influence on the course of forest clearance. However, all would have had to have coincided with an exceptionally dry period to account for the widespread and rapid clearance which occurred at 230 BP. An extreme drought therefore seems likely to be part of the explanation, whether or not other factors were involved. In any case none of the events would have occurred only during the last few hundred years of the Holocene, so they cannot provide an explanation of the uniqueness of this clearance.

Discussion.

None of the factors considered above is by itself a sufficient explanation for the spatial and temporal pattern of forest clearance described in Chapter Six. Man as an ignition source, grassland for ignition, and catastrophes increasing forest combustibility have been present, at least intermittently, throughout the Holocene. Why then did forest clearance only start during the last few hundred years? The explanation must involve a combination of factors.

For this discussion, the clearance will be considered as consisting of three phases.

- (1) 1200-230 BP. During this period there was accelerating but localised clearance above 3550 m in the Pindaunde valley and probably elsewhere on the mountain.
- (2) c.230 BP. Within 10-20 years of the 230 BP tephra fall rapid and major clearance occurred throughout the subalpine zone all over the mountain.
- (3) c.230 BP-the present. During this period clearance was again localised and mainly below 3600 m.

The uniqueness of the clearance events of the last few hundred years seems certain to be a result of cultural change. A simple relationship between visits and clearance has already been ruled out, but an increase in the number (and/or duration) of visits is a possible explanation if some form of threshold is involved, below which no detectable clearance occurs. If periods during which the forest can be burnt are infrequent and of short duration, then more visits would increase the probability of an ignition source coinciding with one of those periods. Coincidences of this type may have occurred previously in the Holocene but perhaps so rarely that the forest had time to recover in between. An increased fire frequency would not permit time for recovery and would lead to the self-catalytic effects discussed earlier. A gradual or sudden increase in visit frequency could therefore account for at least phase (1) of the clearance record, without having to postulate any change in the frequency or intensity of periods of exceptional forest combustibility.

Phase (2) is more difficult to understand. The estimates made in Chapter Six, even allowing a time scale of 20 years, imply a rate of clearance higher than that which is likely under any climatic extreme experienced in historical times in the Highlands, even if ignition was always available. The spatial extent and rapidity of clearance suggests increased human visits, coinciding with a major catastrophic event, or series of events. A frost-drought of the intensity experienced in the western and southern Highlands in 1972, repeated in several consecutive

years, seems most likely. Alternatively, a coincidence of several different kinds of event, such as an earthquake followed by a drought, could have been involved. Similar major catastrophes presumably occurred earlier in the Holocene but did not coincide with frequent human visits.

Whatever the nature of the 230 BP event, a new equilibrium was apparently attained afterwards. Phase (3) is perhaps the most surprising and the most difficult to explain. If phase (1) implies increasing human visits, and phase (2) a further increase coinciding with a major catastrophe, phase (3) suggests both the absence of further catastrophes and a decline in visits. The charcoal record, however, shows that visit frequency did not decline much, while the great expansion of grassland might have been expected to facilitate further clearance.

One possibility is that the remaining forest is in fact less susceptible to clearance than that which was destroyed. The basic similarity of the vegetation pattern on many disturbed, glaciated New Guinea mountains (Chapter Three) suggests that there may be a fairly stable 'post-disturbance' pattern as well as the pre-disturbance one. Most of the forest cleared on Mt Wilhelm (as on Mt Giluwe and Mt Albert-Edward) was from above c.3500 m or from the valley floor between 3500 m and the terminal moraines. Forest is still fairly continuous on the valley sides below c.3500 m and forms an uninterrupted belt below c.3200 m. Above c.3500 m it is increasingly confined to protected and inaccessible places.

Two things may account for this pattern. Firstly, there is a change in the physiognomy of the forest which is sometimes recognisable on aerial photographs (Paijmans 1975), between about 3450 m and 3550 m. At this altitude the canopy becomes lower and starts to open out, culminating near the treeline in an open woodland with a shrub understorey. Below the change, the closed canopy and dense shrub layer probably make the forest virtually drought-proof and very resistant to fire, as the lower strata are perpetually moist. Above the change, the forest may dry out more quickly and burn more readily.

Secondly, there is the distribution of the natural openings from which forest clearance probably spread initially. These were concentrated on the valley floor at all altitudes, although some were present on the valley sides and ridges above c.3500 m. The forest in the valley floor was broken up by these openings and may also have been physiognomically and floristically distinct because of differences in soil and microclimate. In any case, it was probably particularly sensitive to fire because of its large edge/area ratio.

The major fires of 230 BP would have had two effects. Most of the more open forest above c.3550 m would have been quickly consumed, leaving relic patches only in protected and inaccessible places. In contrast, below c.3450 m only the valley bottom forest, broken by natural openings, would have been destroyed and the valley side forest left intact (except for successional vegetation on old landslips).

Since then, even under quite extreme conditions, the amount of additional clearance possible may have been limited. Much of the remaining forest in the subalpine region is either in small islands protected by cliffs or a lake, or is in continuous blocks on the lower valley sides. In addition, at lower altitudes, forest clearance has had to compete with vigorous reinvasion from the margins (Chapter Nine).

This explanation is reasonably satisfactory for the lowest (<3400 m) and highest (>3600 m) parts of the subalpine zone and explains why the extension of clearance below the glaciated zone is unlikely. It is less satisfactory for the middle zone (c.3400-3600 m), where substantial clearance occurred at 230 BP and large forest patches in apparently unprotected situations have survived until today. Possibly the 230 BP clearance at this altitude was mainly on, or at least initiated from, sites of old mass movements.

It seems likely that there was also a decline in visits to the subalpine during this period, although the large-scale vegetation pattern may be an insensitive guide. More information on this question comes from a study of successional changes and will be discussed in the next chapter.

Other features of the forest/non-forest pattern which require explanation are the differences between valleys and differences between slopes of different aspect in each valley (Chapter Three). The general north to south decrease in the extent of the remaining subalpine forest may reflect a gradient of increasing dryness, although there is little independent evidence for this. The Imbukum valley, however, is almost certainly both wetter and cloudier than the Pindaunde and southern valleys (Hnatiuk *et al.* 1976). Despite this, several small, recently-burned areas (grassland, forest margin and landslip communities) were observed in 1976, when none of the rest of the mountain was burned. It is also the least accessible valley, although the presence of several grass huts shows that it is visited today. Both lesser human disturbance in the past and the wetter climate are possible explanations for the minor destruction of forest. Probably both factors were involved, but the pollen evidence is no help in deciding the relative importance of the two. The same is true for the differences between the other valleys, particularly as the climatic differences, if any, are less marked and the past accessibility difficult to judge. Probably the southern valleys are somewhat drier and were more

accessible to populations from lower altitudes. However the fact that the first recorded clearance was in the upper Pindaunde valley, and the lowest apparently in the Bendenumbun valley, suggests that the human populations of that time were more wide-ranging than today.

The aspect differences are more readily explained. As discussed in Chapter Two, the diurnal pattern of cloudiness results in east-facing slopes being generally drier than west-facing ones. Even on totally cloudless days the east-facing slopes will dry out earlier in the day. Thus fires are likely to occur more often (and by starting earlier, burn longer) on east-facing slopes. This would apply to both normal, dry-season grass fires and to forest fires in exceptional drought periods. There is also a possible influence of human choice on aspect differences in fire frequency. Hunters and biogeographers alike prefer the east-facing aspect, both for the sun on cold mornings and for the greater dryness throughout the day. Paths tend to form on this aspect and will be used even on completely cloudy or cloudless days. More fires will therefore be lit on this side and, as they will tend to burn upslope and the wet valley-floor acts as a fire-break, this might partly account for the pattern.

Summary and implications for human prehistory.

The explanation proposed above suggests a combination of cultural change, one or more major environmental catastrophes, the inherent properties of the vegetation and possible climatic gradients, in determining the clearance history and resulting vegetation pattern. The implications for the human prehistory of the Highlands are of particular interest. Considering first the subalpine region in isolation, what do the pollen and charcoal records say about man's changing use of the mountain's resources?

Man has probably visited the subalpine and alpine regions at times throughout the Holocene but only infrequently before the last few hundred years. A visit frequency of perhaps a few days per year in the Pindaunde valley, at the most, seems likely. Then, possibly by 1200 BP and certainly by c.715 BP, the frequency of visits started to increase - to perhaps 20-50 days per year just before the fall of the 230 BP tephra. Around the time of the tephra fall there may have been a sudden increase in visit frequency or simply a continuation of the previous trend. Since 230 BP, or soon after, there has probably been a decline in the number of visits.

What evidence is there for the nature of the cultural change or changes responsible for the increased frequency of visits to the Mt Wilhelm subalpine region?

Regional pollen.

In considering the pollen history of the subalpine zone, the 'regional pollen rain' (i.e. the pollen from non-subalpine sources) has been ignored, except for the use of Nothofagus as a datum of local pollen productivity. Four of the regional pollen types - Casuarina, Trema, Dodonaea and Acalypha - can be positively linked with source taxa which are today strongly associated with human activity (Table 8.1). Casuarina oligodon, in particular, is now an essential part of the sweet-potato production system in the Simbu Valley.

Except for Casuarina and Trema near the surface, few pollen grains of these four taxa were counted. Nothofagus by itself is a suitable pollen sum for regional taxa but again this means that the number of pollen sum grains counted was small. The counting error is thus correspondingly high. In addition, Casuarina is prone to corrosion and Acalypha is hard to recognise on poor slides. For these reasons, regional pollen curves for individual sites are not very satisfactory. An alternative procedure is to assume that the regional pollen rain was approximately constant over the Pindaunde valley at any one time, and then to sum the regional pollen counts for equivalent levels at all sites. Curves produced in this way are shown in Fig. 8.1. The accuracy of the percentages will be greatest for those levels which were counted at most sites and are most accurately correlated.

These curves give evidence for a 'regional' cultural change, with two phases, over the period during which there was a major clearance in the subalpine zone. Casuarina pollen is only occasional during most of the Holocene (and this may represent long-distance transport), is first consistently present from about 1200-800 BP, and rises dramatically after the 230 BP tephra fall, continuing to rise to the present. The Trema curve is similar, although this taxon is present throughout the Holocene (probably representing natural regeneration cycles in the undisturbed forest) and rises less abruptly from 230 BP.

The values for Dodonaea and Acalypha, even when summed, are not high enough for much confidence to be placed in them. Acalypha pollen is occasional throughout the Holocene (where again it probably represents natural regeneration cycles) and rises a little at 230 BP. Dodonaea is erratically present during the Holocene and also shows a slight rise at 230 BP.

It is tempting to interpret the rise in Casuarina and Trema as reflecting the development of the present-day tree-fallowing system. Between the tephras both are low and Trema is higher than Casuarina. This suggests natural regeneration in old garden areas with the occasional

Table 8.1 Regional pollen source taxa associated with human activity.

POLLEN TAXA	PROBABLE SOURCE	SOURCE	ECOLOGY
		"Natural"	"Human association"
Acalypha	<u>Acalypha</u> spp.	Forest regeneration cycles.	Garden regrowth and planted. Used for building, decoration and sometimes eaten.
Casuarina	<u>Casuarina oligodon</u>	Probably not native to Wilhelm area.	Planted fallow. Building, firewood and ornamental.
Dodonaea	<u>Dodonaea viscosa</u>	Forest regeneration cycles, naturally disturbed sites.	Garden regrowth, planted and self-sown. Building, tools and medicinal.
Trema	<u>Trema</u> spp.	" "	Disturbed forest and garden regrowth.

Table 8.2 Altitudinal range of staple crops (various sources).

POSSIBLE STAPLES	COMMON	OCCASIONAL
Sweet potato	2650m	2750m
Taro	2100m	2750m
Yams	1700m	2300m
<u>Pueraria lobata</u>	2000m	?
Bananas	2000m	2300m
Sugar cane	2000m	2500m
'Marita' (oily) <u>Pandanus</u>	2000m	2300m
'Karuka' (nut) <u>Pandanus</u>	2900m	-

Fig. 8.1 The regional pollen rain.

planting of Casuarina for timber. The rapid rise in both after 230 BP, and the rising Casuarina/Trema ratio then suggests an intensification of land-use as most suitable forest was cleared, and the active conservation of Trema and Dodonaea and planting of these and Casuarina to speed soil recovery and provide timber and firewood.

However, because the Mt Wilhelm subalpine is, in effect, a single site in relation to the regional pollen rain, it is unwise to draw conclusions about the spatial distribution of the regional source taxa from it alone (Chapter Four). The changes in the percentages and ratios of disturbance indicators might result either from an intensification of gardening in the upper Simbu valley or the spread of gardening from lower altitudes, or a combination of both. Information from other palaeoecological sites in the Highlands is needed to identify the cultural factors behind the regional pollen changes.

Other sites in the Central Highlands.

Information is available from a number of archaeological and palaeoecological sites in the Central Highlands (Fig. 8.2). All are more than 70 km from Mt Wilhelm but the tephra layers provide a potential means of correlation. Unfortunately they have not always been recognised and were sometimes absent in the sections studied.

Sites will be considered in two groups, below and above 2000 m. This distinction has been made because 2000-2100 m has been suggested as the effective ceiling on pre-sweet-potato agriculture (Golson 1977b). Although sweet potato is now the dominant crop at all altitudes in the Highlands there are a number of alternative staples below about 2000 m (Table 8.2). Taro will grow up to 2750 m, almost as high as sweet potato, but its growth is slow and the yield low above 2000 m. It is also limited to good soils. There may have been some gardens above 2000 m before sweet potato introduction but population densities must have been very low compared with the present day.

Sites below 2000 m. At the Kuk Tea Research station near Mount Hagen, at 1500 m, there is evidence for six periods of cultivation on the swamp. The earliest was at 9000 BP, soon after the climate became warm enough for horticulture at this altitude. Each period involved the construction of water disposal systems showing considerable technical sophistication (Golson 1977a, 1977b).

The next evidence comes from Powell's pollen diagrams from Draepi (1890 m) and Manton (1600 m) (Powell 1970). None covers the period 10,000-5000 BP but clearance, or at least disturbance, was already significant by c.5000 BP at both sites. Then after a long period of

Fig. 8.2 Palaeoecological sites in the Highlands.

*

stability at Draepi and nearby Minjigina there was a renewed fall in forest values, in two diagrams, from 1200 BP (just above the Olgaboli tephra) accompanied by a marked rise in Trema and Casuarina. There was a similar change, also marked by the Olgaboli tephra (Golson pers. comm.), at Flenley's Birip site (1900 m), further west, although some disturbance was evident at this site from the base at c.2300 BP (Walker and Flenley 1979).

At Manton (1600 m), Casuarina and Trema apparently did not rise until c.400-550 BP, but at this site there are stratigraphic problems because of old drainage systems (Golson pers. comm.).

The final phase at Kuk started immediately after the fall of the 230 BP (Tibito) tephra. Part of the previous drainage system was abandoned and a tighter mesh of drains dug in the remaining area. There were houses on the swamp itself for the first time and, in two of these, charred sweet potato remains have been found, also for the first time. Golson (1977b and pers. comm.) interprets this phase as reflecting the first introduction of sweet potato and its cultivation on the swamp in raised beds. Swamp cultivation was finally abandoned sometime before european contact.

In approximately the same period, clearing at Birip (1900 m) was intensified and accompanied by a rise in Casuarina. Flenley (1967) concludes that at this site 'indications of the present agricultural system are exceedingly recent (probably less than 300 BP)'. Cores from Lake Egari (1800 m) also show changes in pollen and sedimentation rate, above the Tibito tephra, which are interpreted as indicating the start of major clearance (Oldfield 1977).

Sites above 2000 m. At Sirunki (2500 m) there is evidence for major disturbance of the forest canopy starting at 4300 BP. Trema, Macaranga and Engelhardtia increase and there is the first major rise in Acalypha. There is no clear evidence for gardens so this disturbance may simply reflect the local promotion of the wild 'nut Pandanus' and perhaps the planting of Acalypha (Walker and Flenley 1979).

The first evidence for disturbance at Inim (2530 m) occurred at the same time as evidence for renewed disturbance at Sirunki at about 2000 BP. However, the first marked and sustained clearance at Inim was not until 300-200 BP when it was accompanied by Casuarina and Trema rises (Flenley 1967). At the same time, cores from Lake Ipea (2500 m), near Sirunki, show a dramatic increase in sedimentation rate and palynological changes, which together suggest greatly intensified human activity in the catchment (Oldfield 1977). The start of these changes at Lake Ipea is again marked by the Tibito tephra.

Discussion.

Important points from this survey of archaeological and palaeoecological sites are the great antiquity of agriculture in the region, and the probability that the changes in the pollen rain on Mt Wilhelm reflect major cultural developments affecting the entire Central Highlands. Both the initial rise in Casuarina and Trema after c.1200 BP and the acceleration of these changes after c.230 BP were present, and in some cases at least, synchronous at widely separated sites.

The conservation of Trema and planting of Casuarina are part of the present-day tree-fallowing system but it cannot be assumed that they played the same role in earlier agricultural systems. Casuarina was probably first cultivated for timber and only gradually adopted as a fallow tree. Indeed both the planting of Casuarina and the conservation of regrowth trees would probably have been initially a response to wood shortage as more and more forest was cleared, rather than a deliberate attempt to shorten the fallow. The 1200 BP rise in Casuarina and Trema should therefore be seen more as a result of population growth and pressure on natural resources than a reason for them.

In contrast, the widespread evidence for intensification of clearance within the last few hundred years suggests an abrupt and radical change which permitted a large increase in population, particularly at altitudes above 2000 m. It seems reasonable to attribute these changes to the arrival of sweet potato (Golson 1977b) although direct evidence is lacking. This period probably also saw the first full development of the tree-fallowing system as part of a new intensive agricultural technology. How would these changes be expected to affect man's activities on Mt Wilhelm?

The evidence for agricultural activity in the Mt Wilhelm region before the Casuarina and Trema rises at about 1200 BP is inconclusive. Hope (1976a) suggests that a decline in regional Castanopsis pollen at c.6500 BP may possibly reflect agricultural clearance in the lower Simbu valley below 2200 m. The people visiting Wilhelm before 1200 BP may therefore have come from distant agricultural settlements in the Wahgi valley, or from sparse populations practicing shifting agriculture nearer the mountain, or they may have been nomadic hunter-gatherers. In any case, both distance and low population density would have limited their impact on the subalpine region.

The regional pollen rain on Wilhelm and the evidence for an expanding population all over the Highlands from about 1200 BP suggests reasons for a change in this situation. Agricultural activity in the Wilhelm region intensified and may have spread to higher altitudes as land availability became limiting. One can imagine settlement at increasing density below

2000 m while shifting cultivation of taro spread to around 2500 m on favourable sites. These higher populations may still have been partly dependent on forest resources.

These changes, if they occurred, would have brought a larger population nearer Wilhelm, a population which probably increased throughout the period 1200-230 BP. Increasing activity on Mt Wilhelm then led to the initiation of forest clearance in the Pindaunde valley and probably elsewhere on the mountain from about 700 years ago. The introduction and spread of sweet potato would have led to an even more dramatic change in settlement patterns. The land above 2000 m ceased to be marginal for agriculture and became available for dense settlement. This development presumably happened at the same time in the upper Simbu, Koro and Jimi valleys. It meant that, for the first time, there was a large settled population within a few hours' walk of the summit region of Mt Wilhelm (Fig. 8.3).

The evidence from the other palaeoecological sites in the Highlands suggests a date of around 230 BP (probably around 1650 A.D. - see Appendix 1) for sweet potato introduction, but earlier dates cannot be excluded. A prehistoric introduction via Polynesia and eastern Melanesia is not impossible (Yen 1974), and a date of c.1200 BP would be consistent with some of the evidence from Mt Wilhelm and elsewhere (Powell *et al.* 1975). Alternatively, even if we accept that introduction followed the sixteenth century voyages of the Portuguese and Spanish from America to South East Asia, sweet potato still could have been in the Highlands 400 (real) years ago. It may have been adopted first by those people living in marginal areas at high altitudes. (A model for the rapid acceptance of a cold-resistant new crop is provided by the importance of european-introduced cabbages as a staple in the upper Simbu valley, despite active opposition from government advisors on nutritional grounds.) Thus the acceleration of clearance on Mt Wilhelm sometime between c.475 and 230 BP (c.1450-1650 A.D.) might reflect the spread of sweet potato in the Simbu valley, before its acceptance further west. The full effects of sweet potato introduction may not, however, have been felt until 230 BP, when uncleared land became scarce enough to warrant the introduction of intensive tree-fallowing.

In any case, it is not surprising that clearance now spread to the entire subalpine region, although the abruptness of this clearance almost certainly implies a catastrophic increase in forest combustibility at the same time. What is surprising is the apparent decline in subalpine clearance soon after. Both the regional pollen and oral history suggest that populations in the upper Simbu and other valleys continued to expand until the present day, yet their impact on the subalpine vegetation declined. Even allowing for the possible lack of sensitivity of the

Fig. 8.3 Altitudinal zones in the Wilhelm - Upper Simbu area.

remaining forest a real decrease in visit frequency seems probable. A possible explanation would be a decreased availability of game animals, either as a result of overhunting or as a direct result of forest clearance. The contrast in the visibility of large game such as wallabies between Wilhelm (where I never saw any) and Mt Suckling (Stevens and Veldkamp 1975) or Mt Victoria (pers. obs.) is striking. Most animals killed by hunters in the subalpine region today are caught in the forest or forest edge. With hunting less attractive, the disadvantages of the subalpine (climate and spirits) may have become decisive. This problem is discussed again at the end of Chapter Nine.

Conclusions.

In conclusion it can be said that the regional pollen record from Mt Wilhelm is consistent with a cultural history in the area similar to that in the rest of the Central Highlands during the last 1200 years. In particular, the changes at 230 BP are what would be expected if sweet potato were introduced at this time and created 'room at the top' (Golson 1977b). However, the subalpine clearance history does not simply reflect the changes at lower altitudes. It seems likely that an additional variable, the 'attractiveness' of the mountain, is involved, as well as possibly complex social factors. Thus the regional and subalpine pollen records from Mt Wilhelm give independent accounts of the human prehistory of different but adjacent areas.

Introduction.

The previous section dealt largely with the origin of the broad pattern of forest and non-forest vegetation observed today. Forest and grassland were considered as distinct entities and the time scale made it inevitable that attention was focussed on the fact of vegetation change, rather than the processes involved. In this section the approach is still basically historical, but attention is concentrated on the processes of vegetation change on a variety of time scales; history is used as a long term 'natural experiment.'

Superficially the present day vegetation pattern looks 'natural' and stable, and some authors have considered it to be basically a climax (Brass 1964; Wardle 1974). The pollen record shows that it is not; the observed pattern is largely a recent artefact. This being so, it is reasonable to ask, what is happening now?

For any particular area, and for the subalpine region as a whole, there are three possibilities:

1. The forest is still retreating;
2. The present situation is stable;
3. The forest is readvancing.

All three possibilities may be occurring on different spatial and time scales, or one may be dominant, locally or overall.

The Wilhelm pollen record and casual observations elsewhere in New Guinea suggest that forest retreat is episodic, rather than gradual and continuous. The answer to the question of whether the forest is still retreating is therefore dependent on the time-scale considered. No change is evident in comparisons between 1955 aerial photographs and the present (1976) forest extent, or in more detailed, local comparisons between 1956 ground photographs and the present. Furthermore, on those mountains where forest has retreated in the past decade or so, forest patches are generally surrounded by a band of dead trees and shrubs. This was seen (by the author) on Mt Giluwe and Mt Michael in 1976, and in both cases may have been the result of a single season's burning in the frost-drought year of 1972. Nowhere on Wilhelm is there such a marginal band. One would expect this kind of evidence for forest retreat to persist for decades, until successive major fires had consumed it, so there has probably been no retreat on Wilhelm for at least this time. The pollen evidence suggests that in several places the forest has retreated in the past 230 years but this could have occurred more than 100 years ago.

The aerial photographs also rule out a significant forest advance since 1955. Past advances of the forest at the expense of secondary grassland should be recognisable by the incorporation of relics of the secondary grassland stage within the present forest boundary. Fire-scarred Dacrycarpus compactus trunks and macroscopic charcoal would be easily identified, as perhaps would dead or suppressed grassland shrubs. (Behind a clearly advancing forest edge at 2950 m in basin grasslands below Mt Service, decaying grass tussocks were recognisable under secondary forest 3-10 m high.)

In the Pindaunde valley and most of the rest of the mountain, such relics are absent from within the forest. All Dacrycarpus compactus trees in the grassland and outer margin of the forest margin shrubbery are fire-scarred; none within the forest is so marked. No macroscopic charcoal was found in any of the pits dug just inside the forest margins in the Pindaunde valley. It can therefore be concluded that there has been no forest readvance at these sites. That is to say, the present extent of forest in the Pindaunde valley is the minimum since forest clearance started. By contrast, in the Guruauglakugl and some other valleys, there are quite extensive patches of clearly secondary forest between 3500 m and 3750 m. These will be described in more detail later. The important thing at this stage is that they show that forest can reinvade at least some of the areas from which it has been cleared.

Despite this, the overall impression is one of stability of the present vegetation pattern in the medium term, with no significant changes in the relative extent of forest and non-forest during at least the last 50-100 years. (The secondary forest patches are probably older than this.) What maintains this stability?

Maintaining factors.

Edaphic.

One possibility is that soil deterioration after forest clearance prevents the re-establishment of forest in some areas where it grew before. This explanation has been proposed for some areas in N.W. Europe (Iversen 1964). Soil analysis results on Mt Wilhelm (Wade and McVean 1969) do not provide evidence of a significant post-clearance soil deterioration, but erosion of soil from steep slopes, and perhaps the development of blanket peats on some cleared sites, may make forest re-establishment slow or impossible in part of its former range.

Competition.

Particularly where the forest is near its altitudinal limit, established closed non-forest communities may be able to exclude forest invasion by competition. This exclusion could occur at various stages. In the denser tussock grasslands the thick mat of live and decaying grass may physically prevent propagules of forest taxa from reaching the soil. Then, if forest seedlings become established, they may be shaded out by the grassland dominants (although one would expect forest taxa to be relatively shade-tolerant). There may also be competition for nutrients with the established plants. Finally, the dense, often monospecific, stands of tussock grasses provide an a priori case for allelopathy, although water-logging or fire may be a sufficient explanation.

The resistance of grassland communities to invasion by trees has been proposed as a major factor in the maintenance of valley-bottom grasslands near the treeline in Australia (Harwood 1977) and in preventing the upward extension of the treeline in the same area (Slatyer R.O. pers. comm.). However, this hypothesis is very difficult to test, particularly when the exclusion is virtually complete. As will be discussed later in this chapter, exclusion is not complete on Mt Wilhelm, and the pattern of forest invasion suggests that competition by established vegetation is an important factor in limiting invasion in the early stages of succession. The mechanism of this competitive exclusion can not be determined from the available data.

Microclimate.

The forest provides its own microclimate for regeneration within it. Maximum temperatures are lower and minimums higher inside the forest than in adjacent non-forest communities (McVean 1968). Frosts are probably rare inside the forest, even near the treeline, and dry conditions will also be rare. The abrupt change in microclimate when forest is cleared may therefore be sufficient to prevent forest re-invasion.

Drought damage to several small herbaceous species was noted by Smith (1974) but there is no information on the effects on woody species. By contrast, frost damage has been reported several times (Smith 1974; Paijmans and Löffler 1972). Frost would seem likely to be a particular hazard to regeneration in an equatorial montane situation like Mt Wilhelm, because both growth and frost can occur at any time in the year, so there will always be young tissue susceptible to damage.

On the mornings of June 9th and 10th, 1976, there were very severe frosts on Mt Wilhelm. Unfortunately the only thermometer in position was in the screen at 3480 m, where a minimum of -0.2°C was recorded on June

10th. On both days well-developed needle-ice was observed on bare ground to the bottom of the subalpine grasslands, and, on the 10th, hoar frost was visible at the top of the zone of cultivation (2700 m) at 0700 hours. Hoar frost persisted to 1130 hours in shaded parts of the subalpine grasslands.

Needle ice requires freezing air and soil temperatures, as well as a supply of water. The exceptional development observed on this occasion may have been a result of the unusual coincidence of clear nights after several days of wet weather. However, the equally exceptional vegetation damage and the screen minimum (equal to the lowest recorded) shows that the temperature conditions were also extreme. This was confirmed by unsolicited remarks on the exceptional coldness of the night from people living as far down the valley as Gembogl (2100 m) and reports received of devastation of sweet potato crops in higher garden sites around Keglsugl. Extensive frost damage to these marginal gardens occurs every few years, 1972 being the last time.

A general forest-edge survey had been carried out on June 8th, so a baseline for study of frost-damage was available. Some damage was immediately visible while some only became obvious days or even weeks later. Immediate wilting was observed in the non-sclerophyllous Anaphalis spp. and Pipturus and the fronds of the forest margin treefern Cyathea aeneifolia, which are noticeably 'softer' than the fronds of the grassland Cyathea species. Leaf discolouration and later shrivelling occurred in Coprosma papuensis and some individuals of all Dimorphanthera species. Haloragis halconensis shoots were frequently partly bleached. In the next few days, damage to many other species became apparent.

All plants damaged in the subalpine region were growing either in the forest margin or in a non-forest community. Pipturus sp. was the most frost-sensitive and all plants in exposed sites were killed to the ground. Coprosma papuensis, Haloragis halconensis, Anaphalis lorentzii, Cyathea aeneifolia, Harmsiopanax, Alpinia spp., Jasminum sp. and Dimorphanthera keysseri were also invariably badly damaged in exposed sites. Rarely were plants completely killed however. A large number of species were sometimes severely damaged, including the following: Dimorphanthera microphylla, other Dimorphanthera spp., Vaccinium cruentum, Decaspermum lorentzii, Schlefflera, Olearia spectabilis, Rapanea vaccinioides, Bubbia, Homolanthus, Cyathea muelleri, Gleichenia bolanica, Coprosma divergens, and all the forest edge herbs. With Styphelia suaveolens damage was limited to the young shoots, which dried out and died over a period of a few weeks. The only species commonly occurring in exposed positions in which damage was never observed were Gaultheria mundula, Rhododendron yelliottii and Hypericum macgregorii. Four months later the damage to the forest margin community was still clearly visible, although there had been considerable regrowth.

The damaging effects of the frost were clearly related to the lack of overhead screening by surrounding plants. A dependence on aspect was also apparent; most, but not all, damage was done to plants exposed to the early morning sun. A relation to small and large-scale topography was less obvious. Damage to the forest margins was most often restricted to low-growing plants but there were many exceptions. In the open, some shrubs were damaged up to 2 m above the ground. Most damage was in the valley bottoms, some on the ridge tops and hardly any on the slopes.

Most of the species severely damaged occur typically in the forest. The effect of a severe frost is therefore to tend to exclude these forest species from non-forest communities, at least in low-lying areas. However, in most cases only seedlings were killed, and individuals which were already well established showed signs of recovery within two months. Also, damage on the slopes was minor, and most forest seedlings there escaped unscathed. Damage to the forest margins seemed dramatic at first but recovery was remarkably rapid and would probably be complete within a year. In many cases it was only new growth which was killed.

Frosts of greater severity may occur at long intervals and may cause more damage. It seems unlikely, however, that frost alone can maintain secondary grasslands, although it may be an important factor in slowing reafforestation of low-lying areas.

Fire

Fire created the secondary grasslands and seems likely to have a role in their maintenance. Lighting grass fires without permission is illegal in Papua New Guinea, and has apparently been so since first contact, although this law has rarely been enforced. On Mt Wilhelm enforcement has depended on the individual 'kiap' but seems to have been unusually effective (Brass 1964). All the Simbu I met on the mountain were aware of the fire-bans and most were careful to prevent fires from escaping.

Ecologists have been visiting Wilhelm since 1956 and, from 1966 when the Field Station was built, observation in the dry season in the Pindaunde valley has been fairly continuous (up to 1976). There have been no reports of major fires in this period. By contrast, small fires, burning areas up to 30 m x 30 m and occasionally more, have been quite frequent. In recent years these have probably been largely accidents, but several young Simbu (23-26 years old in 1976) reported coming up at weekends while at 'pidgin school' (6-12 years old) with matches, and lighting fires for fun, until the 'kiap' threatened to put them in jail. Older men (?>40) described setting fire to the 'whole mountain' when they were young. Allowing for exaggeration this suggests a habit of burning whenever possible before the imposition of full government control in the 1950s.

Fortunately there have been some well-dated fires in the last few years, of which the short-term effects can be studied. In 1970 a party burned an area of about 100 m x 30 m at 3500 m in the Guruauglakugl valley floor (Peterson pers. comm.). The original vegetation was apparently a shrub-rich tussock grassland with Deschampsia klossii the dominant grass. In May 1972 (Smith pers. comm.) 90% of the shrubs were either dead or regenerating from ground level, except for shrubs higher than 2 m, where the top branches were alive. These latter included individuals of Olearia spectabilis, Cyathea sp., Dimorphanthera keysseri, and Dimorphanthera microphylla. The herb layer beneath the dead shrubs was dominated by Poa saruwagetica and Dichelachne rara, with some regenerating tussocks of Deschampsia klossii and young shoots of Haloragis halconensis, Vaccinium ambylandrum, Anaphalis mariae and others.

In July 1976 (my own observations) most of the shrubs were regrowing, except for a few completely dead Olearia spectabilis and Dimorphanthera and about 5% of the Styphelia suaveolens. There had been a dramatic change in the composition of the herb layer, which was now dominated (again, presumably) by Deschampsia klossii. In fact the Deschampsia klossii tussocks were larger and more vigorous-looking than those in the surrounding, unburnt areas. Poa and Dichelachne were still present but subordinate.

Observations on other small areas on Wilhelm and on the effects of the 1972 fires on Mt Giluwe confirm the conclusions from the Guruauglakugl fire. Fires in the grassland tend to eliminate fire-sensitive forest taxa such as Olearia spectabilis and Dimorphanthera, unless they have grown sufficiently large since the last fire. By contrast, the common grassland shrubs (which are absent from the forest) Styphelia suaveolens, Coprosma divergens and Gaultheria mundula, normally recover from at least a single fire. The change in the herbaceous component is only temporary. Firing at infrequent intervals (every 10-40 years) will therefore tend to keep things as they are; an assemblage of fire-resistant plants. More frequent firing (perhaps more than once in 5-10 years) seems likely to eliminate even the fire-resistant shrubs (which take several years to replace their photosynthetic area) and Deschampsia klossii, and replace them by a community dominated by Poa saruwagetica and Dichelachne. Less frequent firing may allow fire-sensitive forest taxa, such as Olearia spectabilis and Dimorphanthera, to become established.

The effects of several small fires on forest edges were also observed. In all cases the marginal shrubberies were either partly or completely killed but the forest proper was virtually undamaged. Recovery seems to be fairly slow and damage reported by Smith in 1972 was still visible in 1976.

Paijmans (1976) has pointed out that fires in the mountain grasslands are much less regular than fires in the lowlands 'because of general greater dampness, shorter and less reliable dry season, and more numerous permanently wet and hence less flammable patches'. A result of this is that 'a mosaic of successional and subclimax stages' is produced. This description fits the situation in the Wilhelm subalpine where burning has certainly been patchy and irregular, at least in recent times.

The charcoal particle record suggests a pre-contact fire frequency of at least one fire in 25-50 years since clearance at most sites, with perhaps a recent decline at some. This would be sufficient to maintain the present vegetation pattern if there were no catastrophic increases in forest combustibility. In the frequently-burned areas, succession will not have had time to proceed far before being abruptly terminated. No forest species seem at all fire-resistant, in contrast to the grassland shrubs. However, some areas will by chance have escaped burning longer than others. Moreover, oral tradition (supported to some extent by the charcoal particle record) suggests that parts of the mountain were unvisited, and presumably unburned, in immediately pre-contact times. Succession should have proceeded further in these areas and may provide a model for what will happen in future if the fire-ban is effectively policed. However, in the absence of fire the other factors discussed above will still operate.

Succession.

There has been relatively little reference to succession in the literature on the New Guinea subalpine, although some work has been done at lower altitudes (Gillison 1969, 1970, 1971). Paijmans (1976) states that 'The beginnings of a succession from grassland back to forest can occasionally be observed, starting at scrub bordering the forest and at the edges of shrubberies surrounded by grassland'. Brass (1964), mysteriously, mentions the occurrence on Mt Wilhelm of, 'on well-drained stony or rocky ground in tussock grassland ... a community of densely gregarious, erect small ferns, and associated shrubs, showing indications of development into forest'. (I am uncertain as to the identity of this community.) On Mt Otto he noted that 'the compact shrubberies of Eurya, Rapanea and Acronychia on the grasslands denoted a vigorous regeneration of the subalpine forest after being burned'. Kalkman and Vink (1970) describe a 'shrubbery' between 3100 m and 3565 m on the Doma Peaks, containing charred remains of trees, which is presumably successional. They also mention low thickets of similar composition in the summit grasslands.

On Wilhelm, Wade (1968) noted the presence of seedlings of species normally confined to forest in some of his non-forest plots, during phytosociological investigations in the subalpine region. However, the small number of these seedlings and their restriction to three of the

fifteen subalpine non-forest vegetation types recognised, led him to conclude that forest regeneration was 'negligible' and further that 'eventual regeneration of the forest in areas now occupied by non-arboreal vegetation appears unlikely ever to occur on a large scale'. He believed edaphic and climatic factors prevented significant reversion to forest.

Smith (1974) however, noted 'a great development of shrubs' in comparing aerial photographs taken before 1960 with the same areas in 1972. Although the shrubs involved were not forest species, this did give evidence that fairly rapid changes were taking place in the absence of fire. Smith also made observations on the succession to forest on some old landslide sites at 3430 m, where rock and unweathered till were exposed. This succession was dominated by woody species and large tussock grasses were rare. (By contrast, from my own observations, tussock grasses dominate the initial stages of the succession on sites of mass-movements which had not completely removed the soil cover.) Natural disturbed areas, such as landslips and eroding streambanks, are usually small and transient. This contrasts with the large areas of secondary grassland on mature deep soils with a closed vegetation cover. Only the succession in these grasslands will be considered in detail here.

For the purposes of this discussion, a distinction will be made between two possible processes by which forest might invade an area of grassland: 'marginal invasion' and 'diffuse succession'. Marginal invasion occurs when the non-forest vegetation is gradually suppressed by the advance of the forest margin, a process Steenis (1968) likened to the healing of a wound in the skin. With diffuse succession, by contrast, an entire area of non-forest vegetation develops through various stages, more or less uniformly, to forest. This distinction is basically a matter of scale: on a large enough scale all invasion is presumably 'marginal' in that it is from the edge of the forest, the source of propagules of forest species. The important difference in practice is that, with marginal invasion, vegetative propagation is possible and the advancing forest front is partly protected by the forest behind, while in diffuse succession, initial invasion must be by seed and the forest gives no protection.

Marginal invasion.

Steenis (1968) described the advance of a shrubby forest border after 10 years' fire protection of a 5 ha grassy glade at 2040 m on Mt Papandajan, Java. He found tree seedlings among the border shrubs but very rarely in the open glade, and attributed this exclusion to the thick cover of decaying grass, exposure to the sun, and the occurrence of frost. He concluded that a 'wound' in the forest heals only from the margin inwards.

Gillison (1970, 1971) made a detailed study of a forest-grassland transition at 2700 m in the Doma Peaks region. He concluded that the transition community was structurally and floristically distinct, and 'provided the transition represents a fluctuating condition', could be described in terms of three stages: juvenile, mature and senescent. The 'stoloniferous' growth form of many of the transition species enabled them to advance or retreat in response to changes in the burning regime.

Discussions of the nature of transitions at higher altitudes have been largely concerned with whether or not they are a discrete community. Brass (1964) described on Mt Wilhelm 'A forest border community so narrow and dense as to be thought part of the forest proper but for the fact that few of the constituents entered the forest'. Wade and McVean (1969) described the transition as 'a narrow strip of distinctive vegetation 2-3 m wide' and noted that it was richest floristically at low altitudes (c.3300 m), became poorer in species with increasing altitude, and was hardly distinct above 3600 m.

It is clear that the transitions below 3000 m (Gillison 1970, 1971; and personal observations) are floristically and structurally distinct and the dominant species are rarely found in the forest or grassland. An advancing forest edge at 2900 m below Mt Service in the Owen Stanley Range was dominated by Olearia cf. lepidota, Coprosma papuensis and various Ericaceae, none of which were observed in the forest behind. The distinctness of the transition is easily explained by the distinctness of the environment it occupies. Above 3000 m, however, the forest gradually becomes lower and more open, reducing the environmental contrast between forest edge and interior, while at the same time there is a decline in the total number of woody species available.

The lowest transitions in the study area (<3400 m) are floristically distinct when compared with the adjacent forests. Of the forest dominants, only Rapanea vaccinioides is prominent in the forest edge, although most forest species occur at least occasionally. The woody transition dominants at this altitude and above, Coprosma papuensis, Rapanea spp., Olearia spectabilis, Dimorphanthera and other Ericaceae, are the forest dominants (along with Dacrycarpus compactus) nearer the treeline (>3600 m).

Above 3400 m, no woody species are entirely or even largely confined to the transition, except possibly Cyathea aeneifolia, although the proportions in the transition are different from the adjacent forest. The apparent distinctness of the transition at this altitude results partly from growth form: lianes and spindly shrubs become dense bushes and mats in the transition, presumably because of the absence of shade. In addition the grassland shrubs, particularly Styphelia suaveolens and Haloragis halconensis, are important. Both the proportional floristic differences

and structural distinctness decline further with altitude and the former, at least, disappears before the treeline at 3900 m.

Considering the altitudinal range as a whole, none of the major species of the subalpine transitions can be described as 'transition specialists'. They are presumably pre-adapted to take advantage of the temporary well-lit habitats, susceptible to fire and frost, provided by the forest-grassland transition, but none are limited to such sites.

Altitude determines the availability of taxa for the transition vegetation, but at any one altitude the transition can have a variety of structural forms. Three different subalpine transition types (excluding the altitudinal treeline) can be recognised on Mt Wilhelm, along with intermediates.

Type 1. The forest ends abruptly with the edge more or less vertical. There is no clearly defined strip of marginal vegetation but, particularly at lower altitudes (<3500 m), the outer metre or so of the forest is 'enriched' with typical transition species. Very large Olearia spectabilis and Dimorphanthera microphylla are characteristic of this zone and there are often many treeferns (Cyathea aeneifolia). In some places there is abundant regeneration of forest taxa just inside the edge, particularly Rapanea spp., various Ericaceae and sometimes Dacrycarpus compactus. There is sometimes also a band of grassland shrubs - Styphelia suaveolens, Gaultheria mundula and Coprosma divergens, - just outside the forest edge.

This type is characteristic of transitions between forest and mire, usually at a break of slope. This is the situation where both the pollen data and ecological sense suggest any remaining undisturbed edges would occur. Where the forest is limited by edaphic factors, an abrupt, vertical edge is to be expected if the tolerances of all woody plants are similar. Increased light and the danger of frost or drought damage would favour certain species at the margin. Although most, if not all, of the transitions on Wilhelm have probably been disturbed by fire (this may account for some of the variation) this type is probably similar to the pre-disturbance subalpine transitions.

Type 2. This transition type consists typically of two, more or less complete, bands of distinctive woody vegetation, and often a diverse herbaceous component. The inner band is of tall shrubs (1-3 m high) and the outer, and more irregular one, is formed of lower shrubs and herbs (0.5-1.5 m high, 1-6 m wide), typically spreading horizontally. One or other band may be incomplete or missing. The inner band of tall shrubs may consist of a great variety of species depending on altitude (Table 9.1) but Olearia spectabilis, Rapanea vaccinioides, Vaccinium cruentum, and Dimorphanthera microphylla are particularly common. The outer band is

Table 9.1 Plants of the forest/grassland transition.

COMMON DOMINANTS	LOCALLY DOMINANT	OCCASIONAL
<u>Coprosma papuensis</u>	<u>Dimorphanthera keysseri</u>	<u>Eurya</u> sp.
<u>Olearia spectabilis</u>	<u>D. leucophylla</u>	<u>Polyosma</u> sp.
<u>Rapanea vaccinioides</u>	<u>Rhododendron culminicolum</u>	<u>Amaracarpus caeruleus</u>
<u>Rapanea</u> spp.	<u>Rh. atropurpureum</u>	<u>Gaultheria mundula</u> *
<u>Vaccinium cruentum</u>	<u>Rh. womersleyi</u>	<u>Rh. gaultheriifolium</u>
<u>Dimorphanthera microphylla</u>	<u>Olearia floccosa</u>	<u>Prunus pullei</u>
	<u>Pittosporum pullifolium</u>	<u>Quintinia</u> sp.
	<u>Symplocos</u> sp.	<u>Schefflera</u> sp.
	<u>Pipturus</u> sp.	<u>Acronychia</u> sp.
	<u>Cyathea aeneifolia</u>	
	<u>Drimys piperita</u>	
	(ent. "montis-wilhelmi")	
	<u>Bedfordia</u> sp.	
	<u>Rubus</u> spp.	
	<u>Cladomyza</u> sp.	
	<u>Styphelia suaveolens</u> *	
	<u>Haloragis halconensis</u> *	
	Only below c.3400 m	
<u>Jasminium</u> sp.	<u>Decaspermum lorentzii</u>	<u>Dodonaea viscosa</u>
<u>Dimorphanthera cf. collinsii</u>	<u>Homolanthus arfakiensis</u>	<u>Harmsiopanax</u> sp.
	<u>Saurauia</u> sp.	<u>Xanthomyrtus</u> sp.
	<u>Daphniphyllum gracile</u>	<u>Elaeocarpus</u> sp.
	<u>Evodiella</u> sp.	<u>Pittosporum berberidoides</u>
	<u>Sericolea</u> sp.	<u>Helicia</u> sp.
	<u>Bubbia</u> sp.	<u>Psychotria</u> sp.
	<u>Olearia cf. monticola</u>	? <u>Maesa</u> sp.
	<u>Alpinia</u> sp.	<u>Drimys cordata</u>
	<u>Piper</u> sp.	
	<u>Schefflera</u> sp.	

*grassland shrubs

commonly dominated by Coprosma papuensis. This species forms a continuous belt, pure or mixed with herbaceous species such as Anaphalis mariae, for hundreds of metres along the forest edge in some places, particularly in the southern valleys.

This type is the characteristic transition between forest and secondary grasslands and is the one described by previous authors. It is only present where the forest has clearly retreated in the past. This is particularly striking where forest meets mire communities on the valley floor. Type 1 transitions occur where forest directly abuts the mire, while type 2 transitions occur where there is a strip of secondary grassland separating forest and mire. The non-forest side of Type 2 transitions is typically secondary grassland dominated by either Deschampsia klossii or Poa saruwagetica and with few shrubs. This type of transition never occurs on to very shrub-rich grassland.

A clue to the development of this type comes from the fact that most individuals in the transition zone are rooted inside the forest or just outside, at the rear of the transition. Early stages in the development can be seen in recently burned forest edges on Mt Giluwe and locally on Mt Wilhelm. After the fire the surviving forest is in contact with an area of secondary grassland which rapidly occupies the burnt area. The tussock grasses seem to exclude seedlings quite effectively but many woody species in the forest can spread out horizontally, sometimes by layering, to take advantage of the new habitat. Establishment by seeding, except for some herbs, seems mainly restricted to the protected but well-lit strip just inside the forest. This combination of vegetative spread by individuals already present and the establishment of new individuals by seed, accounts for the structure and floristics of the transition. Those species which can spread most quickly dominate the outer margin. Quick recovery after fire and frost damage is facilitated by the growth habitat of the transition individuals.

Many of the transition species occur as lianes (e.g. Coprosma papuensis, Dimorphanthera spp., Jasminum sp.) or epiphytes (the same taxa plus Vaccinium spp., Rhododendron spp.) in the lower forest, although they may also form shrubs or even trees near the forest limit. Lianes are adapted by their mode of growth to take quick advantage of the well-lit habitat at the forest edge. Epiphytic species are pre-adapted, presumably, by their requirement for high light intensities and tolerance of temperature and water stress. The Rhododendron spp. which occur at low densities as epiphytes in the closed forest are unable to invade the edge vegetatively but have a massive production of very light and early-dispersed seeds. The other species can spread either vegetatively or by their animal-dispersed seeds. Two important transition species, Olearia spectabilis and Rapanea vaccinioides are neither lianes nor epiphytes but

the former has a massive production of widely-dispersed seeds and the latter is present throughout the forest. Both were sometimes observed to be spreading horizontally into the transition from bases well inside the forest.

In the lowest part of the subalpine zone on Mt Wilhelm there is a transition type which seems to be intermediate between type 2 and the complex transitions described by Gillison (1970, 1971). There is usually still an outer band of Coprosma papuensis but this is separated from the forest by a dense band of regeneration, 3-10 m wide, in which transition species such as Olearia spectabilis and Dimorphanthera are mixed with regenerating forest dominants, including Dacrycarpus compactus, Rapanea spp., Prunus pullei, Elaeocarpus sp. and Decaspermum lorentzii.

Type 3. In this transition type there is a diffuse strip 2-10 m wide at the margin of the forest, where regenerating forest species, transition species and non-forest species are mixed. There is no clear 'banding' of the margin vegetation. This type is confined to transitions between forest and very shrubby tussock grassland, which usually incorporates fire-sensitive forest species, suggesting a long period without burning. In most valleys it is restricted to altitudes above 3600 m but occurs at lower altitudes in the Bendenumbun valley and is the normal type of transition between secondary forest and grassland.

The structure of this transition type seems to suggest an initial forest retreat followed by a long period (? > 100 years) without fire. This would be consistent with its distribution if the section of the upper Pindaunde valley behind the upper lake was burnt in the past. Type 2 transitions perhaps develop eventually into type 3 in the absence of fire.

Most transitions on Wilhelm fit into one or other of the above categories or are intermediate between them. By contrast, on the parts of Mt Giluwe and Mt Michael which I visited, the commonest situation was an abrupt edge to the forest, often with a marginal dead band. There was no true transition, as a result of recent burning. Type 2 transitions were confined to protected places which had probably escaped fire for several years. Types 1 and 3 were not seen on these mountains. On Mt Amungwiwa and Mt Service all subalpine transitions were of type 1, a fact consistent with other evidence that these two mountains are completely undisturbed.

Discussion.

The term 'transition' has here been used in a purely spatial sense. At the sites studied by Gillison (1971) it was apparent that the marginal vegetation also represented stages in a succession from grassland to forest, i.e. was also transitional in a temporal sense. The 'senescent'

Plate 8.1 Imbukum valley (3380 m) - 'Type 1' transition between forest and mire.

Plate 8.2 Imbukum valley (3380 m) - 'Type 2' transition between forest and secondary grassland. Note dense 'mat' of Coprosma papuensis, prominent Olearia spectabilis shrubs and the treefern, Cyathea aeneifolia.

Plate 8.3 Pindaunde valley (3530 m) - 'Type 2' transition between forest and secondary grassland.

Plate 8.4 Mt Amungwiwa (c.3150 m) - 'Type 1' transition between subalpine forest and mire. Probably completely undisturbed.

Plate 8.5 Pindaunde valley (3600 m) - 'Type 2' transition between forest and secondary grassland. Note Olearia spectabilis invading grassland in foreground.

Plate 8.6 Upper Giwimawi valley, looking south. Closed shrubberies and secondary forest on west-facing aspect only.

stage was evidence that the forest edge was advancing. This dynamic aspect of the transition was not apparent on Wilhelm, except at the lowest sites. Above 3400 m only the type 3 transitions gave the impression of successfully invading the grassland and, where this was occurring, 'diffuse succession' was also advanced.

The only change in the transition vegetation detectable in comparisons between photographs taken in 1956 and the present situation was an increase in the width of the Coprosma papuensis band. Coprosma papuensis shoots mapped in 1975 were all killed back by frost in April 1976 but regrowth rates of 5-18 cm in 4 months of the outer shoots were observed. If this is typical a 6 m wide band might represent several decades without fire. The forest edge monolith (49 - Chapter Five) suggests that the transition vegetation occupies a zone which is frequently burned, but where woody species have the advantage of a protected base in the forest, i.e. a 'zone of tension' between forest and grassland, rather than an advancing front. Seedlings were generally not found in the transition away from the forest edge. The Coprosma papuensis band consists of <20 cm depth of litter and <150 cm of dense foliage and seems to completely prevent seedling establishment, although some species can layer in from behind.

Only in the lowest part of the subalpine region (c.3300 m) is there evidence of a general advance of the forest along a broad front. Here the forest dominants are becoming established along the rear of the transition while grassland species, including treeferns, are being suppressed. This probably approaches the situation described by Steenis and Gillison. In the rest of the subalpine region the variations in the transitional vegetation seem more likely to represent stages in the post-fire development of the transition itself. It is, however, difficult to predict what would happen if the fire ban was effective for a long time. Most probably an increasingly broad and diffuse transition would eventually merge with the diffuse succession in the grassland.

Diffuse succession.

Wade and McVean (1969) recognised six subalpine grassland associations and community types. Three of these: treefern tussock grassland, Coprosma divergens-Poa saruwagetica tussock grassland and Poa saruwagetica-Dichelachne novoguineensis tussock grassland, seem to form both a phytosociological continuum and, sometimes, a spatial continuum. All three occupy the same sort of well-drained sites, although the treefern grassland is confined to below 3400 m. The other major grassland type, the Deschampsia klossii-Danthonia penicillata tussock grassland, dominated by D. klossii, is usually more distinct and occupies wetter sites.

Wade (1968) noted that Poa saruwagetica and Dichelachne are the commonest grasses of disturbed sites on Mt Wilhelm and dominate recently-burned grassland on Mt Giluwe. He therefore concluded that the Poa-Dichelachne community was produced by burning and is probably seral to the more common Coprosma-Poa association, in which Deschampsia klossii is important. He considered that the Deschampsia klossii-Danthonia penicillata association was edaphically controlled and more stable. My pollen data confirms that this type is sometimes, but not always, a stable edaphic climax.

Wade believed that grassland was not significantly reverting to forest, but my survey of other valleys revealed vegetation types on well-drained sites which appear to be intermediates in a succession from secondary tussock grassland to forest. These ranged from 'closed shrubberies' of very large individuals of the common grassland shrubs, with the addition of fire-sensitive taxa from the forest, to a true secondary forest, incorporating relics of a grassland phase. An ecologically reasonable hypothesis for the relationship between these vegetation types of well-drained subalpine sites is shown in Fig. 9.1.

Stages A-D exist with all intermediates in the field and in many places a spatial sequence models part of the proposed temporal succession. The observations on the effects of fire discussed above suggest that the balance between stages A and B depends on fire frequency, and the succession is only reversed temporarily by single fires. The later stages contain many fire-sensitive taxa and probably only develop in the complete absence of fire. Further evidence for this scheme is considered below.

Pollen analysis.

No pollen analysis site gives, or would be expected to give, evidence for the whole successional sequence. What evidence there is suggests an increase in shrubbiness and a partial suppression of grasses at some sites: the first stage of the proposed sequence. The lack of a consistent, concurrent decline in charcoal is what would be expected if a shift in fire frequency rather than a complete halt to burning is responsible for the changes.

'Palaeophotography'.

The existence of photographs of the Mt Wilhelm subalpine region, dating from 1956 and later, provided an opportunity for looking at successional processes over 20 years. The available photographs were far from ideal for this purpose as most were general views, but some useful information was obtained from them. As discussed above the majority of the mountain has almost certainly been unburned during this period.

Fig. 9.1 Proposed relationship between observed vegetation types.

Comparisons were made in the field with the extant vegetation and the most useful views were rephotographed. Considerable detail is lost, however, in comparing the old photographs with the new, so this account is based on the field observations.

There were no major changes involving a shift from one Wade and McVean category to another, but all the subalpine areas photographed in 1956 had changed to some extent. Most areas of tussock grassland, including the better-drained Deschampsia klossii-dominated areas, showed an increase in shrub cover. This was most striking in areas with no shrubs, or very few, visible in 1956 and many now, although the total shrub cover remained low. These 'new' shrubs were mainly Coprosma divergens but there were also some Styphelia suaveolens and Gaultheria mundula. Individual 'new' bushes were up to 1 m in height and diameter (usually less) and looked as old and well-established as those visible in 1956. Changes in the Coprosma-Poa shrubby tussock grasslands were less obvious, but in the same direction. Pre-existing shrubs had increased in size and new ones, particularly Coprosma divergens, had been added. In a few areas, visible shrub-cover had increased by up to 20% (of the total area). Changes were apparent at all altitudes from 3300 m to 3900 m, with no evidence of an altitudinal dependence of rates.

Equally striking was the appearance since 1956 of many new bushes of Olearia spectabilis dotted about in grasslands of all types. Many of these are now 1.0-1.5 m tall and a few up to 2.5 m. In fact all juvenile-looking Olearia spectabilis in the grasslands today seem to have appeared since 1956. Those also present in 1956 are all large and partly senescent. Most of the Pittosporum saplings in the grasslands have also appeared since 1956.

Other changes were more localised. In several places clumps of fire-sensitive forest taxa - Dimorphanthera, Vaccinium cruentum, Coprosma papuensis, Rapanea vaccinioides, - had arisen since 1956, mainly around rocks or trees. These clumps included individuals up to 2 m tall. At Kombuglomambuno there had been a considerable turnover of Cyathea atrox treeferns. Many new ones had appeared, some up to 1.5 m high. Some old ones were up to 1 m taller and some had died or disappeared. On the rocky slopes near the waterfall between the Pindaunde lakes Rhododendron yelliottii shrubs had grown by up to 1 m. 'New' Olearia spectabilis had appeared in some forest edges and the Coprosma papuensis band was wider (<2 m) in the few photographs where it was visible. By contrast no changes were visible at all in the mires and in the wetter Deschampsia klossii grassland.

A few photographs taken from 1959 to 1966 showed similar but smaller changes. Most taken since 1966 showed no visible change at all, although in a few cases shrubs were larger or more numerous and some small (<60 cm) Olearia spectabilis have appeared in the last decade.

The old photographs confirm that the secondary grasslands are changing in the absence of fire and that the changes are in the predicted direction, with an increase in the size and number of grassland shrubs and localised invasion by fire-sensitive forest taxa. The changes since 1956 are consistent with a period of more frequent and widespread burning which ended before 1956, perhaps in the 1940s.

Seedling plots.

Despite the presence of forest seedlings in some non-forest plots, Wade (1968) concluded that forest regeneration was negligible and 'unlikely ever to occur on a large scale'. Both the occurrence of secondary forest and the changes since 1956 contradict this, so a more detailed study of forest regeneration in the grassland was made.

Wade used a 4 m x 4 m plot size and rarely found more than one woody species per plot, usually none. A larger plot size was desirable for the specific study of invasion, but not so large that the search for seedlings took too long. Eventually all forest seedlings and saplings >20 cm in height were recorded in 10 m x 10 m plots, while seedlings <20 cm were counted in four random 2 m x 2 m sub-plots of the larger plots. The 20 cm cut-off was chosen because individuals of this size and above were easily visible in tussock grassland, but might also be considered to be a size indicating success in initial establishment.

In a hour's search, 30 minutes for the larger plot and 30 minutes for the sub-plots, all forest seedlings were identified as far as possible and the heights of those over 60 cm were recorded. Unlike Wade, I considered Olearia spectabilis and Coprosma papuensis to be typically forest taxa and did not count herbaceous species. Other relevant information concerning the detailed location of the seedlings was also recorded. The plots were located subjectively to sample initially all the major subalpine non-forest communities described by Wade and McVean. Once it became obvious that seedlings were confined to tussock grassland types, sampling was limited to these. The vegetation of the plots was described with reference to Wade and McVean's categories, with additional information on shrub cover, tussock grass vigour, the dominant taxa and the presence of treeferns and forest relics. Altitude, slope, aspect and location were recorded for each plot. The results are considered below under several headings and the raw data are in Appendix Four.

The species involved.

Seedlings of 41 taxa (identified to the species or genus level), normally confined to the forest, were found in the grassland plots. Most of these were confined to the Cyathea atrox groves (below 3450 m), however, and only 18 taxa were found in other communities. The majority of tree species of Wade and McVean's Lower and Upper subalpine forest associations (74% and 93% respectively, of those taxa listed in Wade and McVean 1969) were found as seedlings in the plots, and some others were seen outside. The most notable absence was the forest treefern, Cyathea percrassa. 51% of the Cloud Forest tree species were identified and more were probably present but unidentified.

Clearly most forest taxa are capable of invading secondary grassland under some circumstances, but some were much more common than others. 24% of all seedlings were Ericaceae and another 60% were Olearia spectabilis, Coprosma papuensis, Pittosporum pullifolium, or Rapanea spp.. Outside the Cyathea atrox groves the dominance of a few taxa was even more striking, 90% being of the above taxa.

The same taxa as dominate the transition community are important in 'diffuse succession', despite the fact that all of the former originate from seed while many of the latter spread vegetatively. There are also similarities with the invaders of old landslips (Smith 1974; my own observations) except that on these sites seedlings and saplings of Dacrycarpus compactus (and to a lesser extent, Podocarpus brassii) are common, even at the earliest stages of succession. There is less similarity with the secondary vegetation by the Pindaunde track at 3000 m, where the forest was cleared for a telephone line in 1966. Here Ericaceae are unimportant. Decaspermum lorentzii, Olearia cf. monticola, Homolanthus cf. arfakiensis, Pipturus sp., Coprosma papuensis and Tacsonia sp. are dominant. The difference, apart from the altitude, may be that the surrounding forest partly shades and protects the cleared area as well as providing the propagules. The Ericaceae, pre-adapted to high light, temperature and water stress, therefore lose their advantage.

The taxa dominant in the diffuse succession all have efficient seed-dispersal mechanisms (Table 9.2) and all except Rapanea flower profusely and produce abundant seed. This may be part of the reason for their success but does not explain the differences between grassland and landslip sites. In any case, most or all subalpine forest taxa probably have similarly efficient seed-dispersal mechanisms, although their seed production is less conspicuous.

Table 9.2 Adaptations for seed dispersal of 'diffuse succession' dominants (after Smith 1974).

SPECIES	NATURE OF DISSEMINULE	WEIGHT	MECH.*
Ericaceae			
<u>Dimorphanthera keysseri</u>	berry	250	A
<u>Dimorphanthera microphylla</u>	berry	330	A
<u>Rhododendron</u> spp.	light hairy seed	0.05	W
<u>Vaccinium cruentum</u>	berry	15	A
Others			
<u>Coprosma papuensis</u>	berry	140	A
<u>Olearia spectabilis</u>	caryopsis with pappus	1.30	W
<u>Pittosporum pullifolium</u>	seed in dehiscent capsule (?edible)	19	A
<u>Rapanea vaccinioides</u>	berry	26	A

* A = animal dispersal adaptations.

B = wind dispersal adaptations.

Distribution.

By far the greatest density of forest seedlings was found in the Cyathea atrox treefern tussock grassland, with a mean of 0.70 m^{-2} (range $0.08\text{--}2.8 \text{ m}^{-2}$) $>20 \text{ cm}$ and 3.63 m^{-2} (range $0.19\text{--}14.6$) $<20 \text{ cm}$. Next was the Coprosma-Poa shrubby tussock grassland, with a mean of 0.38 m^{-2} (range $0\text{--}0.23$) $>20 \text{ cm}$ and 0.18 m^{-2} (range $0\text{--}0.81$) $<20 \text{ cm}$. A total of 5 seedlings all $>20 \text{ cm}$ were found in the six Poa-Dichelachne grassland plots and 4 seedlings, again all $>20 \text{ cm}$, in ten Deschampsia klossii tussock grassland plots.

The considerable range of variation in the number of seedlings in the Coprosma-Poa plots suggest the need for further analysis of the data with respect to possible controlling factors. Possible factors from field observations and 'ecological sense' are:

1. altitude
2. distance from forest
3. shrub cover (%)
4. 'vigour' of tussock grasses (on a scale of 1 to 3)
5. aspect (north-east facing, south-west facing, or on the valley floor).

Unfortunately the data are far from ideal for statistical analysis. There are too few plots for the number of variables and the data are in the form of small whole-numbered counts, which do not meet the standard assumption of normal distribution of uncontrolled error.

An analysis was attempted using GLIM (General Linear Interactive Modelling), a computer program produced by the Royal Statistical Society. It fits a 'general linear model' (of which the familiar 'analysis of variance' is a special case) to data, which does not have to follow a Normal distribution. A Poisson distribution is expected if the seedlings are randomly distributed within areas uniform with respect to the factors considered.

Models were fitted to the data on individual species, groups of species, and total seedlings. In all cases the very poor fit (i.e. the very large residual sum of squares) showed that variation in the environmental factors considered did not account for the variation in seedling number between plots. The 'negative' result could be due to several things, including the inadequacy of the data and the probability that seedlings were clumped rather than random. (An analysis of Poisson-distributed clumps is theoretically possible but would require more knowledge of the clump sizes.) Alternatively, it seems ecologically reasonable to conclude that the factors considered are not the major controls on seedling distribution. Control may be by chance, or else some

environmental factor orthogonal to (i.e. uncorrelated with) these factors.

A less rigorous, qualitative, inspection of the data suggests the following points.

1. The number of seedlings declines irregularly with altitude.
2. Aspect is clearly significant above 3400 m.
3. Distance from the forest and shrub cover are not significant. (However, the rarity of forest seedlings in non-shrubby grasslands and the location of seedlings within plots, considered later, suggests that shrub cover is significant at the bottom end of the scale, perhaps 0-20%.)

General field observations confirm and extend these conclusions. Seedling distribution is very patchy and there may be very different seedling densities in apparently identical situations. This may reflect chance factors in the dispersion of propagules, or alternatively some less obvious factor, such as soil moisture or the time since the last fire. If seedlings are far more moisture- or fire-sensitive than the grassland dominants, these factors will be nearly orthogonal to the factors measured. Aspect differences in invasion by forest taxa are most striking in the southern valleys, where the valley orientation would be expected to maximise the aspect effect. Even very shrub-rich grasslands on east-facing slopes had few or no forest seedlings, and those present were mainly Olearia spectabilis. Conversely, the presence of forest seedlings in favourable sites more than 200 m from the nearest forest patch confirms that dispersal is not normally limiting, at least for the commonest invaders.

The location of seedlings within plots.

A 10 x 10 m or 4 x 4 m plot in secondary grassland presents an extremely heterogenous surface to a propagule. The ability of an individual to establish itself successfully will depend on conditions where the propagule lands, rather than the average for the plot. The detailed location of the individual forest seedlings is therefore of particular interest. Observations both within the plots and more generally can be summarised as follows.

1. Dimorphanthera spp. were almost always, and Vaccinium spp. usually, growing epiphytically on dead Dacrycarpus stumps, or living or dead Cyathea trunks. Most of the other invading taxa occasionally occurred as epiphytes.
2. For the remaining species, the 'preferred' micro-sites are:
 - a. Around the bases of living or dead Cyathea and Dacrycarpus.
 - b. Under the shade of shrubs, particularly Gaultheria, Styphelia and

previously-established forest species.

c. In rocky areas, particularly where patches of moraine break the surface.

3. With very few exceptions, only Olearia spectabilis and Pittosporum pullifolium can become established between vigorous grass tussocks.

The preferred micro-sites are all places where competition from tussock grasses is reduced. 2a and 2b probably also have an improved microclimate - moister and at least partly protected from radiation and temperature extremes. This is probably not true for 2c and is certainly not for 1.

Factors limiting 'diffuse succession'.

The large-scale distribution of seedlings suggests that the success of forest regeneration in secondary grasslands is controlled by altitude, the presence of shading woody plants (treeferns or shrubs) and some factor associated with aspect. In addition the time since the last fire is probably also important. The location of individual seedlings suggests that on a small scale, competitive exclusion by tussock grasses may be most significant.

Wade (1968) thought that protection from excessive insolation might be the main requirement for forest regeneration, with reduced competition and cold air ponding also important. However, the presence of forest seedlings exposed to full sun on some continuously wet landslips and rocky slopes suggests that the direct effects of insolation are not the main factor. More probably it is the surface soil moisture that is usually limiting, except perhaps for some of the Ericaceae, which are pre-adapted as epiphytes. This seems particularly likely for Dacrycarpus, seedlings of which are only found in very moist sites, irrespective of exposure to insolation. The aspect effect can then be explained as a result of the greater insolation on, and hence drying out of, the east-facing slopes (Chapter Two). The effect of shading woody plants, particularly treeferns, may be partly the result of the moister micro-climate, as well as reduced competition from grasses. Drought damage to seedlings was not observed but may be most effective at the early stages of establishment.

The effects of frost have been discussed already. Frost may limit regeneration on some low-lying sites and protection by treeferns may be important in these places. It is unlikely, however, that it is of general importance.

In summary it can be said that the first requirement for forest regeneration in the secondary grasslands is the absence of fire. When burning is stopped, regeneration is inhibited in some areas by excessive drying or by competition from the tussock grasses, and in all areas regeneration is largely confined to favourable micro-sites.

Discussion.

The presence of forest seedlings in some subalpine grasslands is not in itself proof that these grasslands are reverting to forest. There could in theory be an equilibrium between establishment and death of seedlings. However, some seedlings are so well established, growing well above the surrounding vegetation, that it seems likely that nothing short of a fire would prevent their further growth. As the invaders become larger they will increasingly suppress the surrounding tussock grasses and favour establishment of more forest plants, eventually leading to small clumps of forest plants scattered throughout the grassland. These clumps will act as nuclei for further invasion, both by seed and vegetatively, of the surrounding grassland, until a continuous closed shrubbery arises. All the stages in this development are observable on Mt Wilhelm between 3400 and 3700 m, although only very locally in the Pindaunde valley. While it cannot be proven that they form a time series, each is a logical development of the presumed earlier stages.

The composition of the 'closed shrubbery', which is commonest on shaded aspects, varies with altitude, but in general it consists of a mixture of invading forest taxa and very large individuals of the grassland shrubs. Forest species are usually dominant, but on sunny aspects above 3500 m Styphelia suaveolens and Coprosma divergens sometimes grow to 150 cm and form a low closed shrubland by themselves. The virtual absence of forest invasion of such shrublands suggests that they may form a semi-stable sub-climax on sunny aspects. More commonly the closed shrubbery is dominated by Olearia spectabilis, various Ericaceae (particularly Dimorphanthera microphylla and Dimorphanthera keysseri), Coprosma papuensis, and Rapanea species, with huge Styphelia suaveolens and Coprosma divergens. Other characteristic species are Bedfordia sp., Rhododendron gaultheriifolium, Vaccinium cruentum, Symplocos sp., and Pittosporum pullifolium. Other forest species are occasionally present and there is an understorey of seedlings, particularly of Rapanea spp.. At lower altitudes (<3400 m), many other species can be added to this list, particularly Decaspermum lorentzii, Drimys piperita, Bubbia sp., Olearia floccosa, Sericolea sp. and Evodiella sp..

Eventually Rapanea spp. overtop most of the other taxa and form, with some large Olearia spectabilis individuals, the canopy of a secondary forest of a similar stature to the primary forest. This was only observed

between 3500 m and 3750 m, on shaded aspects. The secondary forest at 3500 m in the Guruauglakugl valley looks deceptively like a primary forest at first sight, because of the presence of emergent Dacrycarpus trees. However, some of these are dead and all are fire-damaged, showing that they were once surrounded by grassland. Moreover, huge specimens of Cyathea muelleri, elsewhere found only in secondary grasslands, emerge from the canopy. They presumably kept pace with the growth of the surrounding shrubs as the succession proceeded. Macroscopic charcoal is present in the top few centimetres (but not the surface litter) of the forest soil.

The forest is dominated by Rapanea spp. (mainly Rapanea vaccinioides) which form closed stands of even-aged 'poles'. Olearia spectabilis is next in importance, followed by Dimorphanthera microphylla and Dimorphanthera keysseri. Coprosma papuensis is common as a liane. Other woody species present are Dimorphanthera spp., Drimys piperita, Symplocos, Bedfordia, Schefflera sp., Vaccinium cruentum, Pittosporum pullifolium, Rhododendron gaultheriifolium, R. culmicolum and Prunus pullei. The herb layer is dominated by Pilea sp., which is less common in the primary forest. Some juvenile Cyathea percrassa and Pteris sp. are also present.

Similar patches of secondary forest occur in other valleys. Particularly striking in all is the virtual absence of Dacrycarpus regeneration. (One seedling was found in the Guruauglakugl patch). The secondary forest is species-poor and Olearia and Ericaceae are more important than in the primary forest at similar altitudes; the floristic composition, but not the physiognomy, is in fact more similar to the treeline forest. In its dominance by Rapanea and lack of Dacrycarpus it resembles the forest first established around Imbuka Bog and Brass Tarn at the beginning of the Holocene (Hope 1976a), but neither Ericaceae nor Olearia are prominent in the pollen spectra from that period.

Summary of diffuse succession.

From all the above evidence (vegetational, palaeophotographic, and pollen-analytical) the post-clearance succession on a well-drained west-facing site at c.3500 m is as follows. Some stages are reversible (Fig. 9.2).

Forest can apparently recover from a single fire (see below) but, immediately after clearance by at least two successive fires, a Poa-Dichelachne tussock grassland with a few small shrubs occupies the area. This is maintained by a high fire frequency (perhaps >1 in 5 years). With a decline in fire frequency the more fire-resistant grassland shrubs, particularly Styphelia suaveolens, Coprosma divergens and Gaultheria mundula, increase in size and number and the tussock grass Deschampsia klossii invades. The treefern Cyathea muelleri may also appear. Seedlings

Fig. 9.2 Summary of post-fire succession.

of forest species, especially Olearia spectabilis, Pittosporum pullifolium, Ericaceae and Coprosma papuensis may regenerate under protecting shrubs or treeferns, as epiphytes or, in the case of the first two, directly into the tussock grassland. These will normally all be killed by the first fire, although an occasional one may grow big enough to survive fires if there is a long enough gap between them.

If burning is now stopped altogether, these seedlings can grow larger and new ones become established. At the same time the grassland shrubs increase in size. Other forest taxa, including Rapanea spp., Symplocos and more Ericaceae, enter. Clumps of forest taxa form around the initial invaders and provide additional protection for the establishment of more seedlings as well as sources for vegetative spread. Eventually the grasses are entirely suppressed and a closed shrubbery is formed, dominated by Olearia spectabilis, Ericaceae, Rapanea spp., Coprosma papuensis, and large Styphelia suaveolens and Coprosma divergens. Regeneration inside this shrubbery is profuse and dominated by Rapanea spp..

This stage is probably more or less fire-resistant and gradually develops into a secondary forest, as the Rapanea and some Olearia spectabilis overtop the others to form a closed canopy. In the favourable micro-climate created the most sensitive forest species such as Cyathea percrassa, Pteris and the forest herbs and epiphytes can now develop.

Discussion.

The situation on Mt Wilhelm is peculiar in several ways. Firstly there appear to be no specialised secondary species. At lower altitudes, landslides and other natural disturbances may maintain a pool of taxa adapted to succession (Hope 1979a), but apparently the area of such sites above 3200 m is too small for this to have occurred. Possible exceptions are Dodonaea viscosa and Homolanthus arfakiensis, which reach their upper altitudinal limits at the base of the subalpine region. There is, however, a source of species adapted to open sites nearby in the alpine region. Most species of the secondary subalpine grasslands are also present in the timberline and lower alpine, and some may also have had pre-disturbance habitats in the forest-mire transitions. In addition the forest itself contains species preadapted to successional situations. In fact all the subalpine forest trees and shrubs seem able to disperse well. (This point will be discussed further in the final chapter.)

A second important characteristic of the successional situation on Mt Wilhelm is that fire, the disturbance responsible for the destruction of the climax, is not a natural component of the ecosystem. No subalpine species is adapted to fire, although some (e.g. the grassland shrubs) may be pre-adapted, perhaps as a by-product of adaption to survive severe frost

damage.

The simplest situation, observed on Mt Giluwe but not on Mt Wilhelm, is where a single fire has burned an area of forest. Three years after this had occurred on Mt Giluwe (3300-3500 m), most forest species were regrowing, some apparently from seed but most from surviving roots or stems. Grassland species, particularly Poa saruwagetica, had invaded and were well-established in places. However, in the (unlikely) absence of another fire it seems certain that the grassland taxa will soon disappear, because of the faster growth and greater shade tolerance of the forest taxa.

By contrast, the normal situation on Mt Wilhelm was apparently for a number of successive fires to convert the forest to grassland and to maintain this grassland for long periods. In these circumstances it is very unlikely that any forest propagules will survive on the site. Prolonged seed dormancy is unlikely in equatorial forest species as seed is usually shed into a favourable microenvironment where it can germinate immediately. When burning is stopped, not only are propagules of forest species absent but a tussock grassland occupies the site. Most forest taxa cannot invade immediately after cessation of burning but require 'facilitation' (Connell and Slatyer 1977) by an intervening suite of species, the grassland shrubs and treeferns and the hardier forest taxa such as Olearia spectabilis. From this stage onward the vegetation development is a result of the differing growth rates of individuals already established and facilitation of further invasion, although taxa do not arrive in a predictable order. The composition of the eventual secondary forest is therefore partly a relic of early successional stages and partly a result of invasion at later stages. There is then, presumably, a gradual change in floristic composition in the direction of the primary forest, by the invasion of new species and the differential growth of those already present.

This autogenic succession on Mt Wilhelm is complicated by allogenic factors, fire and to a lesser extent frost, and by another autogenic process, marginal invasion from surviving forest patches. Infrequent fires may permit the suppression of tussock grasses by fire-tolerant shrubs but exclude forest taxa.

There have been no detailed observations on subalpine successions elsewhere in New Guinea, but a few descriptions in the literature suggest that similar processes occur elsewhere. Examples of apparently secondary closed shrubberies have been described on Mt Otto (Brass 1964), the Doma Peaks (Kalkman and Vink 1970), Mt Trikora (Brass 1941) and Mt Jaya (Hope 1976b). On Mt Suckling dead, bleached trunks of Papuacedrus papuana are quite common in the forest at 2800-3000 m (Stevens and Veldkamp 1975),

suggesting that it may be partly secondary. On this very dry mountain, rare fires (perhaps started by lightning) may have done considerable damage in the past.

Elsewhere in the tropics there are no comparable observations. Janzen (1973) described the effect of a single, intense dry-season fire at 3300 m in Costa Rica. The pre-fire vegetation was a dense closed shrubland 1-3 m high, dominated by Hypericum caracasana and Vaccinium consanguinum. Post-fire regeneration was largely by sucker-sprouts from old root crowns, although a few seedlings of the dominants also appeared. There was no invasion by fast-growing weedy species and patches of bare ground were still present 3 years after the fire. Janzen attributed this to a very slow 'seed flow' into the area. The pattern of regeneration described is very similar to that observed after single fires on Giluwe, although there some resprouting from trunks and branches was apparent, and herbaceous plants were invading from surrounding secondary grasslands (absent from the area of Janzen's site).

Rates.

The rate of diffuse succession will vary from site to site. Some idea of the maximum rate can be obtained from the 1956 photographs and the presence of secondary forest. It is a reasonable assumption that the secondary forest patches in the Guruauglakugl and other valleys developed on sites cleared of forest at 230 BP. The now emergent Cyathea muelleri suggest that grassland occupied the site for some time after clearance. Thus the succession from grassland to secondary forest probably took 200 (radiocarbon) years at the most. This is not inconsistent with the evidence from old photographs for the maximum rate of change between 1956 and 1976, as it is likely that invasion accelerates after the early stages.

These rates are for optimum sites at middle altitudes in the subalpine zone. Succession is probably considerably faster at lower altitudes, judging from the profusion of seedlings in the Cyathea atrox groves, which seem unlikely to have escaped fire for long. There are no closed shrublands or secondary forest above 3700 m, but the presence of regenerating forest taxa, as individuals and in small clumps, up to (and in places above) the treeline, and the changes evident since 1956, suggest that a slow succession is proceeding at least on optimum sites.

The question of what is happening on non-optimum sites is more difficult. Nowhere on the mountain is there evidence for advanced succession on sunny aspects above 3400 m. In fact a closed shrubbery of Styphelia suaveolens, Coprosma divergens and Gaultheria mundula may form a semi-stable sub-climax on these sites. A very slow succession, dominated by Olearia spectabilis, may take place in the prolonged absence of fire.

A further question is whether the secondary forest will ever come to resemble the primary forest. The virtual absence of Dacrycarpus regeneration casts doubt on this, but this species is regenerating in primary forest, in a probably very similar micro-climate, and its presence on landslips and rocky slopes suggests that dispersal is not limiting. Probably the secondary forest will change - perhaps over several generations of the dominants and hundreds of years - in the direction of the primary forest, and may eventually become indistinguishable from it.

There is no information on rates of succession at high altitudes elsewhere in the tropics. Janzen (1973) recorded that three years after a single fire at 3300 m in Costa Rica, sucker sprouts from root crowns had regrown to 45 cm. Three years after the 1972 fires on Mt Giluwe at the same altitude, regenerating suckers were of similar length.

Conclusions.

Marginal invasion versus Diffuse succession.

The widespread occurrence of seedlings of forest taxa in the secondary grasslands contradicts the view that forest invasion can only take place at the margins of surviving forest islands. The patches of secondary forest lack a core of primary forest, showing that diffuse succession is sufficient by itself. Nowhere on the mountain, by contrast, are there areas of advanced marginal invasion, except locally in the lowest parts of the subalpine zone. This suggests that marginal invasion is not of general importance, although it may be significant in areas prone to cold-air ponding, which kills unprotected seedlings.

Historical implications.

The present vegetation in the subalpine region seems to be largely a result of interactions between vegetation and fire frequency. Fire frequency determines the vegetation but is in turn controlled by other factors, including climate, human influences and the vegetation itself. Under a constant climatic regime and constant human influence, fire in the forest will be a rare event. The forest can regenerate directly after a single fire but fire risk is higher in the recovery stage because of increased fuel and a drier micro-climate. If a second fire occurs soon after the first, before the regenerating vegetation has matured sufficiently to survive, the site will be taken over by herbaceous species. These species, particularly the tussock grasses, are not only fire-resistant but also fire-promoters. Thus, when grass is established, reversion to forest is unlikely as long as ignition is occasionally available. It is therefore possible that, under the same climatic regime and constant human influence, either forest or grass can maintain itself

indefinitely on a given site, the former by excluding fire and the latter by promoting it. (In practice on Mt Wilhelm this is complicated by edge effects.) Forest clearance or grassland reversion may then occur as rare, chance events, or as a result of changes in human impact. In Chapter Eight both explanations were suggested for clearance, the first for the 230 BP event and the second for the earlier, more gradual clearances. The stable phase of the last 230 years was explained as due partly to the absence of rare 'forest-fire danger' conditions and partly as a result of the non-uniform fire-susceptibility of the forest; the implications for human prehistory were unclear.

The presence of advanced secondary stages can give further information on the post-clearance fire history of the subalpine region. Reversion is a far more gradual process than clearance, so for climatic conditions alone to be responsible would require a long-term change in climatic regime, rather than the chance occurrence of climatic extremes. A decreased frequency and intensity of dry conditions after the end of the 'Little Ice Age' might encourage succession, but there is no independent evidence for such a change. A change in human influence is more likely. If, as has been suggested earlier, man burns wherever he goes and fires can be started in the grasslands for several days each year, the prolonged absence of fire in a grassland area implies that human visits have been rare. The pattern of secondary succession is therefore related to the past pattern of human exploitation of the subalpine. However, care must be taken that differences between sites reflect differences in fire history, rather than rates of succession.

Shrub-cover in the secondary grasslands below 3600 m is greatest in the Bendenumbun valley and least in Badmenangidongwa and Giwimawi. It is also higher in general in the upper parts of all valleys, except Badmenangidongwa (where it is low throughout) and Bendenumbun (where it is highest in the lower part). This is particularly striking in Giwimawi and Tegepangwa. The pattern of regeneration of forest species is similar, being most advanced in Bendenumbun and least in the lower Giwimawi and Badmenangidongwa. The occurrence of secondary forest in the Bendenumbun, Guruauglakugl and Giwimawi valleys probably reflects a fire-free period 100-200 years ago, but is also in agreement with the other evidence.

The pattern of secondary succession might be partly explained if the rate of succession increased with altitude, but this is contrary to expectations and other evidence. The alternative explanation is that spatial variations in human impact, and presumably human visits, in the last 50-100 years, is responsible for the pattern. If this is true, human influence during this period has been concentrated below 3600 m in the southern valleys and has been least in Bendenumbun and the upper sections of the other valleys.

This is consistent with the evidence from oral history (Chapter Two) that the major human activities on Mt Wilhelm, in immediately pre-contact times, were use of the main southern trade route and hunting below 3600 m. By contrast, the initial clearance pattern, as discussed in Chapter Eight, suggests a much more widespread use of the mountain at 230 BP. This contrast is particularly striking for the Bendenumbun valley, which was cleared as much as any around 230 BP (even below the terminal moraine, apparently) but appears to have been little disturbed since.

The present state of the forest margins and the changes since 1956 suggest a major episode of grassland burning, perhaps 30-50 years ago, followed by a decline. This may have been associated with the first european contact which, as discussed in Chapter Two, is likely to have lead to a temporary increase in human activity, followed by a rapid decline.

Predictions.

There are three possibilities for the future: further retreat of the forest, the maintenance of the present pattern, or the regeneration of forest in the areas from which it was cleared. If the pre-disturbance fire regime had continued the vegetation pattern would have remained fairly stable until a catastrophe, such as prolonged drought, allowed further forest clearance. A continuation of the regime of the last two decades, with occasional fires of limited extent, would probably permit the succession in some areas to advance towards partial fire-resistance, and eventually to secondary forest. However, one fire under extreme climatic conditions would be sufficient to reverse a hundred years of successional development.

In the (unlikely) circumstances that a fire ban was completely successful, the evidence is that all secondary grasslands would eventually revert to forest. The speed with which this would happen would vary, perhaps by a factor of 2-5, from area to area. It would be slowest on east-facing slopes, frost-prone valley floors and above 3700 m. The presence of forest seedlings up to 200 m above the present treeline may be evidence that given time forest, or at least a closed shrubbery, will develop even at this altitude.

That these conclusions differ from Wade (1968) may be partly a result of the far longer time scale considered here, but may also reflect the fact that Wade's observations were made only in the Pindaunde valley, and in 1967, when post-fire succession was probably less advanced than today.

Synthesis

In Chapter Three, six questions were answered. The first was: What is the history of the area? The second was: What is the present land use? The third was: What is the present vegetation? The fourth was: What is the present wildlife? The fifth was: What is the present water resources? The sixth was: What is the present air quality?

The next three chapters will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality? Chapter 10 will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality?

CHAPTER 10

The next three chapters will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality? Chapter 10 will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality?

SYNTHESIS

The next three chapters will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality? Chapter 10 will answer the following questions: What is the history of the area? What is the present land use? What is the present vegetation? What is the present wildlife? What is the present water resources? What is the present air quality?

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Synthesis.

In Chapter Three, six questions were proposed which this thesis would attempt to answer. Possible answers to all these have already been suggested and discussed. These answers will be summarised before considering the conclusions of the previous chapters in a wider context.

Before 1200 BP almost continuous forest clothed the valley sides and well-drained parts of the valley floors, up to 3800-3900 m on Mt Wilhelm. Non-forest vegetation in the subalpine zone was confined to more or less waterlogged parts of the valley floor and smaller areas on terraces and perched basins along the valley sides. In the upper third of the subalpine zone (>3650 m), tussock grasslands dominated by Deschampsia klossii covered areas of poorly drained valley floor, while in the lower two-thirds grasslands were very restricted and closed forest directly abutted mire communities on waterlogged sites. Forest/non-forest transitions below the altitudinal treeline were abrupt and lacking in a distinct marginal vegetation.

It seems likely that edaphic factors, principally waterlogging, were the primary reason for the exclusion of forest from areas below the treeline. Cold-air ponding may, however, have been of some significance at higher altitudes, particularly where subalpine grasslands were continuous with grasslands above the treeline.

The present day vegetation pattern in the subalpine region is a product of human disturbance. Sometime between 1000 and 500 years ago, man-lit fires began the destruction of small areas of forest, and caused their replacement by secondary tussock grasslands. Burning increased, but remained localised, until around 230 BP. Then, probably during several seasons of exceptional drought, forest clearance spread to the entire subalpine region, except the damp and inaccessible Imbukum valley. Localised clearance has continued until recently, but it is probable that the majority of the clearance took place within a period of less than 20 years around 230 BP, possibly in two or three consecutive years. Forest clearance not only changed the vegetation pattern but also lead to the formation of new plant communities, notably the shrub-rich secondary grasslands and the forest margin vegetation.

Man's role in this clearance was simply to provide an ignition source. Before 1200 BP his activities on the mountain seem to have been limited to occasional visits, and his impact on the vegetation confined to the alpine grasslands and the timberline region. The subalpine forest clearances of the last few hundred years result from an increase in human activity on the mountain, related to widespread cultural changes in the Central Highlands, although the details of the history and pattern of clearance reflect non-human factors.

The general appearance of stability of the present vegetation pattern is deceptive. With a decline in burning a post-fire succession is starting in most of the secondary grasslands. Although this has not proceeded far yet, except in a few places where patches of secondary forest have developed, there is no reason to doubt that, eventually, all the secondary grasslands would revert to forest in the absence of fire. Forest regeneration is occurring both by the advance of the forest margins and by a 'diffuse' invasion of the grasslands, with the latter process dominant, except possibly at the lowest altitudes. Conversely, if burning of the grassland were continued, further retreat of the forest would be inevitable, although unlikely to be as spectacular as the 230 BP events.

Mt Wilhelm in a wider context.

This thesis has dealt largely with the events of the last 1000 years on Mt Wilhelm. The implications of these events may be better understood when considered in the context of the changes which have taken place on New Guinea high mountains since their initial uplift in the Plio-Pleistocene.

10 Myr - 1 Myr BP.

The mountains of New Guinea are geologically young and only attained their high altitudes during the major phase of vertical earth movements in the Plio-Pleistocene (Löffler 1977). The same period saw the start of the glacial-interglacial cycles which have characterised at least the last three million years (Shackleton and Opdyke 1977). At some stage, the fluctuating temperature curve and rising mountains would have first produced environments similar, at least in terms of mean temperatures, to the alpine and subalpine of today. Evidence of climatic conditions cold enough to produce a mountain glaciation in Bolivia 3.2-3.5 Myr ago (Clapperton 1979) suggests a possible approximate date.

Presumably some plants with a wide environmental tolerance were able to occupy the new habitats from the beginning, but it is likely that the flora would have been considerably poorer than that of today, and the upper treeline lower, as frost-resistant woody taxa were probably absent. New taxa would then have appeared successively by evolution from the local montane flora, dominated by old Gondwanic elements, and by long-distance immigration from older cold environments to the north and south.

1 Myr - 100,000 yr BP.

By the start of this period, some New Guinea mountains had probably reached approximately their present elevations, although rapid uplift continued in others. The uplift rates along the Huon coast of 3 m per 1000 yr suggest that the Saruwageds, at least, are considerably younger than a

million years (Chappell pers. comm.). There are no comparable data on uplift rates elsewhere on the New Guinea mainland, but significant uplift can not be ruled out in any area. Clearly the alpine and subalpine regions were more restricted at the start of this period than they are today, although the evolutionary and biogeographical implications of this have been given little attention. About 2.5 Myr ago the intensity of glaciations had increased and from 0.8 Myrs a rhythm of rather similar cycles, each lasting approximately 100,000 years, became established (Shackleton and Opdyke 1976). Climatic change seems to have been more or less continuous, with both interglacials and glacial maxima occupying only a small part (10-20%) of the total time span.

The detailed impact of these climatic changes (which would have been more than simple changes in mean temperature) on the vegetation can only be guessed. Forest and non-forest vegetation would have alternated above 3000 m and, presumably, major vegetation types moved upwards and downwards at lower altitudes. At the same time the upper vegetation belts, in particular, were gradually enriched with new taxa. Smith (1977) has shown that the non-forest flora of Mt Wilhelm is youthful "consisting largely of the descendents of immigrant herbs which arrived by dispersal over long distances". Although the subalpine forest also contains Plio-Pleistocene immigrants such as Rhododendron, which have undergone local secondary speciation, other species such as some within Drimys and Dacrycarpus, have arisen by new speciation in old Gondwanic genera.

In the absence of man, fires were probably very rare during this period, but disturbed habitats of limited extent would have been provided by geomorphic processes and, perhaps, by the grazing activity of the mammalian fauna which included several large marsupials, now extinct (Hope and Hope 1976).

100,000 - 10,000 yr BP

Palaeoclimatic evidence for this period is available from diverse and widely distributed records, although evidence from New Guinea itself is limited to the last 30,000 years. The last 'non-glacial' period was between about 127,000 and 75,000 BP, but probably only the first part (127,000-115,000 BP) was as warm as, or warmer than, today. Most records agree on an intense glacial event at about 75,000 BP, followed by a period of fluctuating but generally cold climates, culminating in the glacial maximum between 23,000 and 16,000 BP.

Pollen evidence of treeline fluctuations at Sirunki (2500 m) (Walker and Flenley 1979) suggests a cold period, possibly colder than the last glacial maximum, before 27,500 BP; a period of temperatures approaching the present day between c.27,000 and 25,500 BP; then an irregular fall in

temperature to the last glacial maximum between 18,500 and 16,000 BP. Temperatures apparently rose again between 16,000 and 14,000 BP and may have fluctuated between 14,000 and 9,000 BP.

The potential flora for the region above 3000 m during this period was probably similar to that of today, at the species level. However chance differences in the location of glacial refuges, and local ecotypic differentiation, may have lead to differences between the forest of each warm period advance, perhaps as great as the differences between mountains today.

Data on the vegetation prior to the last glacial maximum - under climatic conditions more 'typical' of the Pleistocene as a whole - is limited to a few sites below 2500 m. Data on the vegetation of full-glacial times comes from more sites, both above and below the treeline. From these it is possible to establish a treeline altitude of 2000-2250 m for the intermontane valleys of the Central Highlands, between about 18,000 and 15,000 BP (Hope 1979b). Unusual features of the vegetation of this time show that there was not a simple depression of the vegetation zones in comparison with today. The treeline was depressed by at least 400-600 m more than the snowline and shrub-rich grasslands may have occupied a broad belt above the forest. The modern subalpine forest seems to have been non-existent, its species perhaps integrated into a narrow transition forest at the treeline.

After 15,000 BP the glaciers retreated and forest spread up the mountains. The first forest to arrive at higher altitudes on those mountains for which palaeo-ecological information is available (Table 10.1) was dominated by Rapanea. Initial establishment of forest was relatively later on Mt Wilhelm in comparison with other mountains, particularly Carstenz and Scorpio to the west, where a Rapanea scrub was established at 3500-3600 m by 12,500 BP (Hope 1979b). On Mt Wilhelm Rapanea did not arrive until 9500 BP at Imbuka Bog (3600 m) and 8500 BP at Brass Tarn (3910 m). These differences between mountains may reflect ecotypic variations in the forest species or differences in the regional climates of this time.

The sequence of events during this period may have been similar to that during the glacial episodes of previous climatic cycles, but two factors could have made it unique. In the first place the last glaciation was apparently the most extensive in New Guinea since the Plio-Pleistocene uplift of the mountains (Galloway et al. 1973). This suggests that it may have occupied a period of more severe climate than its predecessors. Secondly, and perhaps more importantly, this was the first glacial cycle during at least part of which man was in New Guinea.

Table 10.1 Palaeoecological sites on New Guinea mountains.

AREA	SITE NAME	ALT.	TIME RANGE (1000 yrs)	REFERENCE
Jaya (Carstensz) 4°S,137'E	Ijomba Mire	3640 m	14-10,6-0	Hope,G.S. & Peterson,J.A. (1976)
	Yellow Valley	4200 m	3-1.5	"
	Ertzberg	3620 m	13-8	"
Star Mntns. (Mt Scorpio) 5°S,140'E	Yakas Tarn	3410 m	13-0	Hope,G.S. (1979b)
Wilhelm 6°S,145'E	Summit Bog	4420 m	9-0	Hope,G.S. (1973,1976a)
	Brass Tarn	3910 m	11-0	"
	Imbuka Bog	3600 m	13-0	"
	Pindaunde Lake	3570 m	4-0	"
	(Komanimambuno)	2710 m	22-0	"
	34 monolith sites	3320- 3910 m	(2-)1-0	Corlett,R.T. (this thesis)
Albert Edward 8°S,147'E	Laravita Tarn	3550 m	13-0	Hope,G.S. (1979b)
	(Kosipe)	1960 m	35-0	"

Man was well established in S.E. Australia by 30,000 BP, so he probably crossed from mainland Asia during a period of low sea level, at least 50,000 years ago. The earliest archaeological site in New Guinea is at Kosipe (1995 m) near the Pleistocene treeline, where man has been present for at least 26,000 years (White et al. 1970). Hope and Hope (1976a) have suggested that hunting communities may have exploited the treeline ecotone and shrub-rich grasslands above it, during glacial times. The charcoal record from Komanimambuno gives some support for this idea (Chapter Seven). The extinction of the marsupial megafauna around this time may reflect human hunting pressure or, alternatively, the severity of the last glacial maximum. A major human impact on the treeline vegetation cannot be ruled out, particularly if drier climates favoured the use of fire.

10,000 - 1,000 BP.

The Holocene warm period started about 9500-10,000 years ago, but climates have continued to fluctuate since then, over a smaller range. For many parts of the world there is evidence for a warmer 'hypsithermal' from about 7,000 to 5,000 BP, followed by generally declining temperatures, punctuated by cold intervals, centred on about 2800 and 350 years ago. The 'treeline retreat' at Brass Tarn may reflect climatic cooling since 5000 BP on Mt Wilhelm but human influence is an alternative explanation. More convincing is evidence for at least three minor ice-advances of similar extent since 2900 BP in Irian Jaya (Hope and Peterson 1975) and the erosive episodes (possibly reflecting snow-cap formation) recorded at Summit Bog on Mt Wilhelm within the last 7000 years (Hope 1976a).

No change in vegetation distribution or composition since the establishment of forest can confidently be attributed to climatic change, although some response might have been expected. On Mt Wilhelm the earliest subalpine forest was dominated by Rapanea and the later rise to dominance of Dacrycarpus probably reflects slower migration of this species, rather than greater cold sensitivity. The expansion of forest resulted in the near disappearance of the shrub-rich grassland communities. The component taxa would have been restricted to the treeline ecotone and lower alpine region, and perhaps the fringes of the subalpine mires. Only small and transient disturbed areas would have been provided by landslips and eroding streambanks.

With the drastic shrinking of grassland and treeline environments at the beginning of the Holocene, they ceased to provide such important resources for man, who became increasingly dependent on forest resources, and perhaps early agriculture. Direct archaeological evidence of man at high altitudes during this period is available only from the Mapala rock shelter (3996 m), just above the treeline on Mt Carstenz, where a radiocarbon date of 5440⁺/₋₁₃₀ BP was obtained from charcoal at the base of

the lowest occupation layer (Hope and Hope 1976). On the same mountain, pollen and charcoal particle counts are available from Ijomba Bog in Discovery Valley at 3630 m (Hope 1976b). Today the site is a short grass bog in extensive Deschampsia klossii tussock grassland, while there are dense treefern groves, shrublands and small patches of forest on the surrounding slopes. The pollen diagram shows an increase in Cyathea at 10,800 BP, which Hope interprets as an opening-out of the forest. Then around 5000 years ago there was a decline in the subalpine forest, accentuated in the last 2500 years. Charcoal rises markedly at the time of increasing Cyathea, attains highest frequencies between about 3500 and 2000 BP, and declines to very low levels after 1500 BP. Taken together the evidence suggests a very long history of disturbance on this mountain, reaching a maximum a few thousand years ago and subsequently declining.

Pollen and charcoal particle diagrams are also available from single sites on Mt Albert Edward and Mt Scorpio (Hope 1979b). Subalpine forest apparently never became well established around Laravita Tarn (3550 m) on Mt Albert Edward, and the charcoal particle curve suggests a high but fluctuating fire frequency there since 12,000 BP. This is perhaps not surprising as at Kosipe, 16 km away at 1996 m, burning increased soon after 30,000 BP and remained common until after 8000 BP (Hope 1979b). Thus the alpine and subalpine grasslands on Mt Albert Edward may have been burned continuously for the last 30,000 years. However, subalpine forest was once more extensive, as shown by the presence of isolated trees and logs on the summit plateau; the results from a single subalpine site should not be generalised over the whole mountain.

By contrast with Mt Albert Edward, a pollen and charcoal diagram from Yakas Tarn (3480 m) on Mt Scorpio suggests that human influence has been negligible or absent there (Hope 1979b). Today the Tarn is surrounded by a discontinuous forest with an open, stunted canopy, which covers 35% of the area, the rest being Gleichenia vulcanica or Astelia papuana bog. The diagram shows a slight rise in charcoal after 2500 BP, coinciding with an increase in Cyathea and Gleichenia. This could reflect local burning but Hope thinks the levels of charcoal too low to indicate significant human disturbance. The low levels may, however, partly reflect the extent of unburnable mire vegetation, although the absence of grassland does suggest that any disturbance has been minor.

There is circumstantial evidence for the impact of man during this period in the Saruwaged Range and on Mt Giluwe. On Mt Bangeta in the Saruwageds, Loffler (1971) reported a date of 4320+/-100 BP for charcoal in the A horizon of the oldest of three stratified soils covering a moraine at 3600 m. Similarly, Blake and Loffler (1971) discovered two layers of charcoal, buried under 2 m of alluvium, at 3200 m on Mt Giluwe and obtained dates of 3780+/-140 and 1810+/-150 BP for them. Both sites are now in

grassland. Both cases, according to the authors, indicate slope instability, probably following forest fires, giving a minimum age for the start of forest clearance on these two mountains.

The evidence from Mt Wilhelm, by contrast, suggests that significant disturbance during this period was confined to the treeline and perhaps the alpine region above it. Mt Wilhelm, like Mt Scorpio, seems to have been a comparative 'backwater' during most of the Holocene.

1000 - 100 BP.

This period saw an apparently world-wide neoglacial between about 500 and 120 BP, reaching a maximum about 300 BP. Its occurrence in New Guinea is supported by evidence for a glacial advance on Mt Jaya at approximately this time (Hope and Peterson 1976). This event may have stressed the forest near the treeline and facilitated its conversion to grassland, but possible climatic effects are completely obscured by human impact on the mountains studied.

Palaeoecological records covering this period are available from single sites on Mt Carstenz (Hope 1976b), Mt Scorpio and Mt Albert Edward (Hope 1979b) and 39 sites on Mt Wilhelm (Hope 1973, 1976a; this thesis). The very low charcoal levels at Ijomba mire on Mt Carstenz, despite the presence of abundant fuel around the site, suggests very little human activity at this time. Human disturbance remained small or absent on Mt Scorpio but, by contrast, remained high on Mt Albert Edward. From the available information Mt Wilhelm is the only one of the mountains which experienced an increased human impact.

Man's renewed interest in and impact upon Mt Wilhelm, after 7000 years of relative vegetational stability, was the result of cultural change rather than any change in the mountain environment. Agricultural populations at lower altitudes in the Central Highlands had probably been increasing steadily for several thousand years. Improved agricultural techniques may have accelerated this increase in the last 1000-1200 years, pushing settlements nearer Mt Wilhelm in response to the need for more land. Finally, although not proven, the introduction and spread of sweet potato at 400-230 BP may have made previously marginal land above 2000 m available for intensive agriculture. These regional cultural changes, reflected in the regional pollen rain, would have made the Mt Wilhelm alpine and subalpine regions accessible to more people, although the point at which activity on the mountain began to increase probably depended as much on local social factors of which we know nothing.

Similar cultural changes were probably taking place elsewhere in the New Guinea Highlands, but at least on Mt Jaya and Mt Albert Edward, apparently did not lead to an increase in human activity. Around Mt Jaya the population is limited by the large areas too high for agriculture and neither improvements in techniques nor the introduction of new crops would bring large populations nearer the mountain. By contrast, there seems to be no shortage of potential arable land around Mt Albert Edward and there are no gardens above 2000 m. The absence of higher gardens may only reflect the absence of population pressure, or persistent cloud may enforce a lower limit. Whatever the case, cultural changes do not seem to have made the mountain more accessible to settled populations. In addition it is possible that on both mountains earlier periods of intensive exploitation had so depleted the fauna as to reduce the attractiveness to hunters.

On Mt Wilhelm localised forest clearance started above 3500 m between about 1200 BP and 600 BP. Clearance increased but remained localised for the next few hundred years. Then around 230 BP rapid major clearance occurred all over the mountain, throughout the subalpine region. Although the details of this clearance history and pattern probably reflect climatic and vegetational factors, its spatial extent suggests that man ranged over most of the mountain at this time. Hunting was probably his major activity and the alpine and subalpine fauna may have been rapidly reduced to near extinction.

100 BP (1850 A.D.) to 1966 A.D.

The retreat of the Carstenz glaciers in Irian Jaya from their neoglacial limits during this period suggests a general warming of about 0.6 C per century (Allison and Peterson 1976). The effects of this slight amelioration on the vegetation were probably negligible, in a subalpine landscape dominated by human influences, unless there was a concurrent lessening of the frequency or intensity of extreme frost-drought conditions.

A major cultural change, the arrival of europeans, occurred during this period. Palaeoecological records are supplemented by written accounts for the first time. Monckton (1907, 1922), Champion (1940) and Brass (1941) provide evidence of intense traditional activity in the subalpine regions of Mts Albert Edward, Giluwe and Trikora, at or soon after first contact. These seem to have been extreme cases, however, and on most high mountains human activity was probably less intense.

On Mt Wilhelm the large-scale pattern of forest and non-forest seems to have remained more or less stable, with the forest neither retreating nor advancing significantly. Oral history and vegetation evidence combine

to suggest that man's activities were now largely confined below 3600 m, except for the use of high-altitude trade routes. Above 3600 m at least, successional changes started in the grasslands as large areas of the mountain were abandoned. First contact with europeans was late in the Central Highlands in comparison with other high mountain areas, but the effects on traditional activities on Mt Wilhelm were probably fairly typical of the effects elsewhere.

Between 1932 and the 1950s the gradual imposition of government control in the Chimbu (Simbu) District probably lead to an initial increase in human activity in Mt Wilhelm's subalpine, followed by a rapid decline. By the end of this period, successional changes were starting in all the secondary subalpine grasslands, aided by an official fire-ban. (The ban on grass fires has not been as effective on other New Guinea mountains.)

Fragmentary climatic records from the Pindaunde Field Station are available for this period. A striking feature of these records is the large differences between years in the rainfall recorded in the dry-season months. The dry season in 1972 was exceptionally dry on Mt Wilhelm, while in the Western and Southern Highlands there were several months of drought and severe frosts. On Mt Giluwe this lead to the first major forest retreat for more than 30 years, but the fire ban on Mt Wilhelm prevented any major effects there.

There is little information available on recent changes in human activity in the subalpine except from Mt Wilhelm, where the Pindaunde Field Station was established in 1966. Since then a steady stream of scientists, tourists and accompanying Simbu has started a new phase of human impact, at least in the Pindaunde valley, the long term consequences of which cannot be predicted.

Discussion.

The use of a logarithmic time scale in this historical summary does not imply accelerating rates of change, but rather reflects the detail of information available. Periods of rapid change will have alternated with periods of relative stability (such as 9000-1000 BP on Mt Wilhelm) throughout the last million or so years, but the resolution of the record decreases as larger periods are considered. Despite these considerations, the changes of the last few hundred years on Mt Wilhelm probably were exceptionally rapid, although we know very little of the maximum rates of climate-induced change experienced during the Pleistocene. In fact there is very little information on the vegetation of 'typical' segments of the Pleistocene: the full-glacial, late-glacial and Holocene periods for which there is information not only represent climatic extremes but also post-date man's arrival and possible impact on the environment.

Many genera of the present day flora of the subalpine region consist of large numbers of closely-related and 'taxonomically difficult' species, suggesting that they are still in a state of active evolution. The subalpine forest itself seems to have formed, or re-formed, relatively recently, to occupy a zone which has usually been unforested during the Pleistocene. Present conditions are extreme, by Pleistocene standards, and the capacity to survive under glacial conditions would have been more important to its component taxa. These taxa were apparently integrated into the upper forest belt of glacial times, which consisted of a melange or patchwork of the species which now form the upper montane and subalpine forests. The subalpine forest thus presumably consists of species selected for ability to migrate into treeless terrain during the warm intervals. The chance composition of the locally available gene pool would determine the floristic composition of the forest, and this may account for the major differences between the subalpine forests of different mountains. There has probably been insufficient time for much adaptation to present environmental conditions to have occurred. The subalpine forest is thus to be seen as a response to a 'catastrophic' warm event and is unlikely to be in a state of floristic equilibrium, because of continuing climatic change and finite rates of migration.

In this time perspective the impact of man seems less peculiarly catastrophic. Fire is a new type of disturbance but its effects - the replacement of forest by tussock grasslands - are not very different from those of climatic change. Palynologically these secondary grasslands resemble the shrub-rich grasslands above the lowered treeline of glacial times, although the factors which maintain them are different. The present situation, with the subalpine forest restricted and the shrub-rich grasslands extensive, is in some ways more typical of the Pleistocene than the restricted grasslands of the early Holocene. The success of the forest in re-invading secondary grasslands when burning is stopped is not surprising in view of the fact that the component taxa have expanded from a greatly reduced area many times before in the Pleistocene. Although, as suggested in the Introduction, the forest of the subalpine is particularly sensitive to disturbance, it is also pre-adapted to reoccupying areas from which it has been removed.

Pattern.

As discussed in Chapter Three, the vegetation pattern on Mt Wilhelm is typical of that on many other high mountains of New Guinea. Most of the differences between mountains are explicable in terms of differences in topography, climate and the intensity of human use which can be observed today. The evidence available, however, shows that there has been a great deal of variation in the history of human impact on different mountains. It is not hard to think of possible explanations: the more pronounced dry

season on Mt Albert Edward, the closeness of Mt Giluwe to large areas below 2000 m suitable for pre-sweet potato agriculture, the importance of trade routes across the Carstenz massif. But positive evidence to account for the differences is negligible.

The vegetation pattern is apparently only a rough guide to the history of human disturbance. Although the present day pattern is almost certainly a reflection of past processes, only some of them influenced by man, the relationship is extremely complex; geological, geomorphic, evolutionary and ecological processes have all had their influences. In considering the factors which have controlled the vegetation pattern at various times, the most obvious break is at the start of human disturbance. Less obvious is the difference between glacial and inter-glacial times. The glacial equivalent, in terms of mean temperature, of the subalpine zone would not have coincided with the zone of glacial landforms and immature soils as it does today. Thus, even were there not apparently major climatic differences, which make a glacial subalpine zone hard to identify, the controls on vegetation pattern must have been very different.

When comparing the role of the factors controlling subalpine pattern in the period of limited human influence (i.e. before 1000 BP on Mt Wilhelm) with those controlling it during the time of intense human impact (c.300 BP to the present) it is worth distinguishing two categories (after Grime 1977). The first is 'stress', defined as conditions which restrict the production of plant biomass, such as shading, sub-optimal temperatures, or waterlogging. The second is 'disturbance', defined as mechanisms which limit plant biomass by causing its destruction, such as frost, fire and tree felling. Before human disturbance, the vegetation pattern largely reflected pattern in stress factors. A stress factor associated with increasing altitude, presumably declining temperature, controlled the position of the altitudinal forest limit. Below the treeline, waterlogging, controlled by topography and the extent of the Pleistocene glaciation, seems to have been the major stress restricting forest, with probably also some areas of shallow soil. The role of disturbance factors was probably minor by comparison. Occasional severe frosts may have maintained or temporarily expanded some open areas and mass movements on steep slopes would have produced temporary open areas at all altitudes.

An important feature of this stress-determined pattern is that it would have been stable, at least over hundreds and perhaps thousands of years. Apart from changes caused by local disturbance and recovery, changes in the distribution of the major vegetation types would have been slow, and associated with changes in the mean intensities of the stress factors, for instance a rising water table or falling mean annual temperatures.

By contrast, the modern vegetation pattern has been determined largely by a patterned disturbance by fire. Fire frequency and pattern of occurrence has in turn been controlled by other factors. Man is probably the only significant source of ignition, so the pattern of human visits may have been an important determinant, but probably only in the last hundred years or so when his activities became geographically restricted. More important, particularly during the major clearance phase, was the effect of the vegetation itself on the local fire frequency. Firstly, there appears to be a gradient of increasing fire susceptibility of the forest with increasing altitude, controlled by forest physiognomy. Secondly, there is a relationship between fire susceptibility and the nearness of a grassland (or sedgeland?) source of fire. Other important vegetation influences on fire frequency may include the presence of inflammable regrowth on mass-movement scars and, in secondary grasslands, the seral stage. (Advanced seral stages are probably less easily burned.) Physical features of the landscape which prevent the spread of fire, such as lakes, mires and cliffs, also have an influence on the pattern of fire occurrence and hence the vegetation pattern.

Superimposed on the pattern resulting from the above factors is the influence of climatic differences between slopes of different aspect in the same valley. Aspect has had a major influence at all stages in the development of the modern pattern but may be most important in secondary succession. It acts both through fire frequency and directly, as a stress factor, in the secondary succession.

The various factors controlling the post-disturbance pattern can be seen as forming a hierarchy of decreasing importance in explaining (or predicting) this pattern. The presence or absence of man is the primary factor, the previous vegetation pattern a secondary factor, and physical fire-barriers and aspect tertiary factors.

Because the present pattern results from, and is maintained by, the destruction of plant biomass by fire, stability would not be expected. In fact, once clearance has started, there is a feed-back between vegetation and fire-frequency; low or zero fire frequency encourages fire-excluding vegetation and high fire frequency favours fire-promoting vegetation, so that a temporary equilibrium may result. However, there will also be areas where the chance absence of fire has allowed forest regeneration, or a chance occurrence of fire has caused further forest destruction. Unlike the stress-controlled pattern, a long-term equilibrium is impossible given the variability of the climate, even if human influence remains constant.

In practice the factors which determine what vegetation type occupies a certain area all interact. Not only is there the direct feed-back between vegetation type and fire frequency mentioned above, but there is

probably a more complicated interaction through the effects of the vegetation on a larger scale on animal populations and hence on human visit frequency. Furthermore the potential spread of fires means that the fire-susceptibility of a given area depends not only on the local effects of the various factors but also, indirectly, on their effects on the surrounding vegetation. With this complexity, and the undoubted importance of chance, it is clear that future changes of pattern can never be confidently predicted.

When the factors controlling the vegetation pattern in the presence and absence of man are compared (Fig. 10.1) the interesting fact emerges that climatic variability becomes an important factor only when man is present. Man's activities thus result in the expression of environmental factors which otherwise may be of little or no significance to the vegetation.

General principles.

The primary aim of this study was simply an understanding of man's impact on the subalpine region of Mt Wilhelm, but some general principles of wider application can be extracted, with the help of the fragmentary evidence from other New Guinea mountains.

The first is the importance of edaphic and 'geomorphic' factors, chiefly waterlogging and mass movements, in determining the pre-disturbance pattern in the subalpine region. The prominence of both factors is probably largely a result of the glacial history and resulting land-forms in this zone, rather than a direct effect of low temperatures. By contrast, there is no compelling evidence for the importance of cold-air ponding.

The second general principle is that, although man may have had a significant influence on subalpine vegetation pattern from soon after his first arrival in New Guinea, his impact has greatly increased with the increasing population density resulting from agriculture. Hunting alone seems unlikely to have permitted a sufficient population density over long periods for major, cumulative disturbance to have occurred. (Mt Albert Edward and the drier, eastern mountains may be exceptions to this.) A third principle, however, which may make identification of human impact difficult, is that man only initiates the disturbance by lighting fires where he can. Non-anthropogenic factors determine the timing and pattern of fire damage, so the resulting vegetation pattern may look 'natural'. This appearance is reinforced in the wetter areas (such as Mt Wilhelm) where fires are rare and the pattern appears stable from short-term observations. Furthermore, the slowness of secondary succession at these altitudes means that human impact hundreds of years ago may still have a

Fig. 10.1 The control of subalpine vegetation pattern.

(a) In the absence of man.

(b) In the presence of man.

major influence on the vegetation.

Fourthly, a principle as yet unsupported by evidence from mountains other than Mt Wilhelm, is the surprising importance of aspect differences, both in determining the pattern of forest destruction and in controlling the post-fire succession.

Finally, a principle of general importance for ecological studies in inhabited areas of the humid tropics, is the great ecological significance of rare, extreme, climatic events in the presence of man.

These principles do not depend on any peculiar features of New Guinea mountains and would be expected to be applicable to wet, equatorial mountains in general. There have been no comparable studies reported from other parts of the world, so a general account of the subalpine vegetation of the equatorial mountains of East Africa and South America, gleaned from the available literature, is given in Appendix 5. Valid comparisons can only be made with the wettest of these mountains.

The general similarity of high mountain environments in New Guinea, East Africa and South America is shown by the usefulness of the definition of 'subalpine' (Chapter One) used in this thesis, in all three areas. On most of these mountains, there is a zone between 3100+/-200 m and 3800+/-200 m which, although once largely forested, is now occupied by a mosaic of grassland and forest. The relative extent of each component of this mosaic depends on the dryness and on the intensity of human use of the mountain.

Edaphic and geomorphic factors seem to be of even greater significance in East Africa than in New Guinea, but there is no reference to their importance in the Andes. The absence of information on the history of human impact in the subalpine of both areas also makes it impossible to test the generality of the second principle. There has also been very little discussion, or even description, of the vegetation patterns resulting from disturbance, although it seems probable that similar principles apply. Aspect effects too, although unreported, seem likely on other equatorial mountains with a diurnal pattern of cloudiness.

Finally, the ecological significance of exceptional climatic conditions in the presence of man is clearly a principle of general application. No tropical mountain in the world is continuously wet enough for anthropogenic fires to be completely excluded. It is this importance of rare combinations of events which necessitates the use of a long time-scale in the study of human impact, and which unites palaeoecology and ecology.

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APPENDIX 1 - THE AGES OF THE TEPHRAS.

The age of the Tibito Tephra.

Radiocarbon dates.

Several radiocarbon dates on organic materials associated with this tephra are available. (All radiocarbon dates are given as conventional radiocarbon years BP.)

1. Three dates from carbonised tree trunks in the Matapun beds on Long Island. These beds have been stratigraphically identified as coming from the eruption which produced the Tibito tephra (Blong pers. comm.).

ANU - 1125	380 +/- 70 BP
ANU - 1126	230 +/- 75 BP
ANU - 1127	200 +/- 65 BP

2. Six dates from various materials at the Kuk archaeological site near Mt Hagen (Golson 1977).

ANU - 754	190 +/- 65 BP
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(fibrous peat under the tephra)

ANU - 1055	480 +/- 160 BP
------------	----------------

(charcoal fragments scattered through 2-15 cm below the tephra)

ANU - 1052	290 +/- 60 BP
------------	---------------

(a paddle-shaped wooden spade, lying horizontally 24 cm under the tephra)

ANU - 1053	240 +/- 60 BP
------------	---------------

(a stake or small digging stick, lying horizontally 5 cm above the tephra)

ANU - 1054	290 +/- 60 BP
------------	---------------

(a stake or small digging stick, lying vertically with the top 27 cm below the tephra)

Assuming a constant sedimentation rate (and that the top of the stick used for the last date is at the level of the surface when it was lost) the last three dates give convergent estimates of the radiocarbon age of the tephra.

ANU - 1052	gives	240 +/- 60 BP
ANU - 1053	gives	250 +/- 60 BP
ANU - 1054	gives	235 +/- 60 BP

If the anomalous dates (ANU - 1125, ANU - 754, ANU - 1055) are discarded the pooled mean (after Polach 1969) of the remaining five dates is 230 +/- 40 BP. This is the best available estimate of the age of the Tibito tephra in radiocarbon years and is the figure used in this thesis.

All the published tree-ring calibration curves agree that the true, sidereal age is greater than the radiocarbon age during this period. Stuiver's (1978) curve gives a true date of 1625 - 1670 A.D.

Documentary evidence.

From 1827 onwards, Long Island was visited continuously by European observers, who did not record any evidence for an eruption during, or within a few years before, this period (Ball and Johnson 1976). The tephra must therefore be older than about 1820 A.D.. The only other firm evidence is from Dampier, who sailed past in 1700. He made a sketch of the island which is so similar to the present profile as to virtually preclude a major eruption since then (Blong pers. comm. ; but Ball and Johnson believed an eruption between 1700 and 1827 was possible). He also commented on the luxuriance of the island vegetation, which, by comparison with Krakatoa, suggests that at least 20 years had elapsed since a major eruption.

Other dates

Lead-210 dates for the Tibito tephra from Lakes Ipea and Egari have been reported (Oldfield et al. in press). Using the 'constant rate of supply model' and making corrections for the Radium-226 content of the tephra mixed into adjacent sediments, they arrived at a mean age of 285 years (before 1970) i.e. 1685 A.D.. In addition, matching measurements of the secular variation in geomagnetic inclination in the lake sediments from Lake Ipea, with that calculated from the available records, indicates a pre- 1700 A.D. age for the tephra (Oldfield et al. in press).

Finally, genealogical dates are available from oral records of the eruption, re-settlement of the island, and the 'time of darkness' in the Highlands. These all suggest a nineteenth century date for the tephra (Blong pers. comm.), but such orally derived chronologies are notoriously unreliable and tend to underestimate the true age.

Discussion.

The best estimates of the sidereal age of the Tibito tephra from the various lines of evidence are:

Calibrated radiocarbon	1625 - 1670 A.D.
Documentary evidence	before 1680 A.D.
Lead-210	c.1685 A.D.
Palaeomagnetic secular variation	before 1700 A.D.

All evidence suggests a pre-1700 age for the tephra, but it is impossible to pick an overall best estimate. For this reason, the uncalibrated, pooled mean radiocarbon age has been used in this thesis. It is very probably 15-25% too young, but is at least unique, repeatable and stable with respect to changes in calibration.

The age of the Olgaboli Tephra.

Only three radiocarbon dates are available for this tephra.

ANU - 1206 1190 +/- 60 BP

(From peat and clay above the tephra at Kuk (Golson 1976))

SRR - 1026 1153 +/- 125 BP

Birm - 587 1220 +/- 150 BP

('Spanning' the tephra in sediments from Lake Pipiak and Lake Ipea, (Oldfield et al. in press))

The pooled mean of the last two is 1180 +/- 100 BP, which is consistent with the first date. Because of the large standard error and the small number of dates, an estimate of 1200 BP is used in this thesis. The available calibration curves (Clark 1975) suggest that this will also approximate to the true age.

Appendix 2 The Pollen Data.

The depth scale in the following tables is based on the stratigraphic position of the samples relative to the surface and the tephra layers.

S,T,O stand for the surface, the Tibito tephra and the Olgaboli tephra respectively.

Q is a level at the expected depth of the Olgaboli tephra when only the Tibito tephra is present.

X is a level the same distance below the Olgaboli tephra as that tephra is below the Tibito tephra.

T+,T-,O+,O- stand for samples immediately above and below the respective tephras.

S/T,T/O etc. are samples half-way between the surface and the Tibito tephra, the Tibito and Olgaboli tephras etc.

SS/T is half-way between S and S/T
OO/T is half-way between O and O/T etc.

The approximate ages of the samples, based on the time-scale used in this thesis (Appendix One) are:

S	> 0 BP
SS/T	58 BP
S/T	115 BP
TT/S	172 BP
T+	< 230 BP
T-	> 230 BP
TT/O	475 BP
T/O	715 BP
OO/T	960 BP
O+	< 1200 BP
O-	> 1200 BP
O/X	1700 BP
X	2200 BP

The sites are in the same order as in the text (Chapter Five). The abbreviations for the non-Pindaunde sites are as follows:

UM	Umbamambuno
GU	Guruauglakugl
TE	Tegepangwa
GI	Giwimawi
BA	Badmenangidongwa
BE	Bendenumun

The abbreviations for the pollen types are:

CHAR	Charcoal particles >10 μ m	DRIM	<u>Drimys</u>
LYCO	Lycopodium spores (added during preparation)	STYP	<u>Styphelia</u>
CASU	<u>Casuarina</u>	ERC1	Ericaceae $\pm$ 30
TREM	<u>Trema</u>	ERC2	Ericaceae $\pm$ 35
DODN	<u>Dodonaea</u>	ERC3	Ericaceae >40
URTM	Urticaceae-Moraceae	DRAP	<u>Drapetes</u>
ACAL	<u>Acalypha</u>	RANU	<u>Ranunculus</u>
MACA	<u>Macaranga</u> comp.	GENT	<u>Gentiana</u>
CELT	<u>Celtis</u> comp.	POTT	<u>Potentilla</u>
SAUR	<u>Saurauia</u> comp.	TRIG	<u>Trigonotis</u>
EUPH	Euphorbiaceae	APIA	Apiaceae
NOTH	<u>Nothofagus</u>	LIGU	Asteraceae-Liguliflorae
CAST	<u>Castanopsis</u>	ASTL	<u>Astelia</u>
ASCA	<u>Ascarina</u>	POA1	Poaceae <21
RUTA	Rutaceae	POA2	Poaceae $\pm$ 25
PHYL	<u>Phyllocladus</u>	POA3	Poaceae >29
PRUN	<u>Prunus</u> comp.	POA4	Poaceae (damaged)
CUNO	Cunoniaceae	CYP1	Cyperaceae
ELAE	<u>Elaeocarpus</u>	CYP2	Cyperaceae
MYRT	Myrtaceae	CENT	<u>Centrolepis</u>
PAPU	<u>Papuacedrus</u>	VULC	<u>Gleichenia vulcanica</u>
PODO	<u>Podocarpus</u>	CYAT	<u>Cyathea</u> sim.
DACR	<u>Dacrycarpus</u>	PTER	<u>Pteris</u>
RAPA	<u>Rapanea</u>	BELV	<u>Belvisia</u> sim.
ASTT	Asteraceae-Tubuliflorae	TRSP	Trilete spinose unknown
QUIN	<u>Quintinia</u>	UNK1	Unknown 1
SYMP	<u>Symplocos</u>	FERN	All other Pteridophytes
COPR	<u>Coprosma</u>	HERB	All other herbs
HALO	<u>Haloragis</u>	TREE	All other trees
		UNK	All other unknowns

		CHAR	LYCO	CASU	TREM	DODN	URTM	ACAL	MACA	CELT	SAUR	EUPH	NOTH	CAST	ASCA	RUTA	PHYL	PRUN	CUNO	ELAE	MYRT
UM	S	2.6	.0	15.2	6.3	1.6	3.7	.0	3.7	.0	.5	2.6	18.3	2.1	.0	.5	.5	.5	.5	.0	.5
UM	T+	1.4	10.4	4.7	5.2	.0	1.9	.0	1.9	.5	.5	.0	16.0	2.4	.0	.0	.9	.0	.0	.0	.5
UM	T-	1.0	15.0	.5	2.5	.5	2.5	.0	4.5	.0	.0	1.0	19.5	3.0	.5	.5	1.5	.0	.0	.0	.0
UM	T/O	1.1	11.4	2.3	3.4	.0	1.1	.6	2.3	.0	.6	.0	19.4	2.3	.6	.0	.6	.0	.0	.0	.6
UM	O+	.6	44.4	.0	1.7	.0	21.1	.0	1.1	.6	.0	.0	21.7	2.2	.0	.0	1.7	.0	.6	.0	.0
GU	S	24.3	24.3	8.7	4.0	.6	5.2	.0	2.3	.0	1.2	1.2	2.9	.0	1.7	.6	.0	.6	.0	.6	.0
GU	SS/T	80.4	28.5	2.5	2.5	.6	3.8	.0	1.3	.6	.6	.0	3.2	3.8	1.3	.6	.6	.0	.6	.6	.6
GU	S/T	95.4	27.8	4.6	3.7	.9	8.3	.0	3.7	.0	.9	.0	2.8	.9	.0	.9	.0	.0	.0	.0	.0
GU	TT/S	78.4	18.8	2.8	3.4	.6	.9	.0	.0	.0	.0	.9	2.8	.9	.9	.3	.6	.0	.0	.3	.3
GU	T+	102.0	20.4	3.4	2.7	.0	6.1	.0	2.0	.0	.7	1.4	1.4	.0	.0	.0	.0	.0	.7	.7	1.4
GU	T-	1.5	13.1	.7	1.1	.0	.4	.0	3.0	.7	.7	1.5	7.1	.4	.7	.4	.7	.0	.7	.0	.7
GU	T/O	.7	5.0	.3	.3	.0	.7	.0	.3	.0	.7	.7	4.6	.7	.3	.0	.7	.0	.0	.0	.0
GU	O+	2.0	11.9	.4	.0	.0	.4	.0	1.2	.0	.4	1.2	4.3	.0	.4	.0	.4	.0	.8	.0	.4
TE	S	33.2	.0	6.3	2.4	.0	4.4	.0	2.0	.0	.0	1.0	5.9	1.0	1.0	.0	.0	.0	.0	.5	.0
TE	S/T	32.9	42.1	2.1	1.7	.4	2.9	.4	2.1	.0	.4	.0	2.1	.8	1.2	.0	.4	.4	.4	.0	.0
TE	T+	21.6	29.9	1.9	5.3	.0	8.0	.0	1.5	.0	.4	.4	3.0	3.4	.8	.4	.4	.0	.4	.4	.4
TE	T-	5.2	31.4	1.0	4.6	.0	2.1	.0	5.7	.0	.0	.0	31.4	2.1	4.6	.5	2.1	.0	.0	1.0	.5
TE	T/O	6.3	22.1	1.1	3.2	.0	2.6	.0	7.4	.5	.0	.5	31.1	1.6	3.2	.0	1.6	.0	.5	.0	.0
TE	O+	3.3	43.8	.7	2.0	.0	3.3	.0	4.6	.0	.7	.0	41.8	2.0	4.6	.7	.0	.7	.0	.0	.0
GI	S	23.0	.0	16.9	5.1	1.1	.6	.0	.6	.0	1.1	.0	11.2	.6	.6	.6	.0	.0	.0	.0	.6
GI	S/T	86.7	32.7	13.3	6.1	.0	1.0	.0	5.6	.0	.5	.0	9.2	1.0	1.0	2.0	.5	.0	1.0	.5	.0
GI	T+	133.8	35.7	11.5	3.2	.6	.6	.0	8.3	.6	.6	.0	19.7	1.3	3.2	1.9	.6	.0	.0	.0	.6
GI	T-	12.3	19.2	5.4	3.0	.0	1.5	.5	8.4	.0	1.5	.0	32.0	3.0	1.0	.0	1.5	.0	.0	.0	1.0
GI	T/O	2.2	13.1	2.2	1.3	.0	1.3	.0	1.3	.4	.4	.0	12.7	.4	1.3	.0	1.3	.0	.4	.0	.0
GI	O+	.6	9.4	.6	1.9	.3	.6	.0	6.6	.0	.3	.0	23.2	5.0	2.5	.6	1.3	.0	.3	.0	.3
GI	O-	.9	8.7	.5	.9	.5	2.3	.0	7.3	.5	.0	.0	18.8	3.7	1.8	1.8	.9	.0	.5	.0	.0
GI	O/X	.4	5.8	.0	.9	.0	.4	.0	2.7	.0	.4	.0	24.8	2.2	.4	1.8	.9	.0	.0	.4	.0
BA	S	8.6	.0	28.8	12.9	2.9	5.0	.0	5.8	.0	.0	.0	8.6	2.2	.7	.7	1.4	.0	.0	.0	.0
BA	SS/T	174.2	11.8	8.4	2.4	2.8	2.8	1.0	3.1	.0	.0	.0	5.9	.7	.7	.7	.7	.0	.0	.3	.3
BA	S/T	182.6	.0	10.0	5.9	.9	3.7	.5	1.8	.0	.5	.0	6.4	.5	.9	1.4	1.8	.0	.0	.9	.5
BA	TT/S	322.6	.0	5.9	9.1	.0	59.7	.5	5.4	.5	.5	.0	3.8	2.2	1.6	.0	1.1	.0	.0	.0	.0
BA	T+	343.1	.0	5.1	7.3	.0	81.0	.0	3.6	2.2	.7	.0	2.2	.7	1.5	.0	.7	.0	.0	.7	.7
BA	T-	5.9	10.1	8.4	10.1	1.7	5.0	2.5	10.1	.8	.0	.0	63.9	5.9	2.5	.0	2.5	.0	.0	.0	.0
BA	TT/O	1.3	10.4	6.5	4.5	1.3	3.2	.6	8.4	.6	1.3	.0	48.1	5.8	2.6	.0	1.3	.0	.6	.0	.0
BA	T/O	4.2	7.9	5.5	6.7	.0	1.8	.0	9.1	1.2	1.2	.0	63.0	9.1	1.8	.6	2.4	.0	.0	.6	.6
BA	OO/T	2.8	9.4	1.7	8.9	1.1	1.1	.0	3.3	.0	.0	.0	40.6	4.4	5.6	1.7	1.7	.0	.6	.0	.0
BA	O+	3.6	24.2	3.6	7.9	2.4	2.4	.6	9.1	.0	.6	.0	70.9	13.9	4.2	.0	1.2	.6	.0	1.2	1.2
BA	O-	6.5	16.1	.8	6.5	.8	.0	.0	15.3	.0	.0	.0	80.6	9.7	7.3	1.6	.8	.0	.0	.0	.0
BA	O/X	7.0	12.0	.0	1.9	1.9	.0	.0	14.6	.0	.6	.0	54.4	5.7	9.5	.6	1.9	.0	.6	.6	.0
BA	X	4.1	17.8	.0	2.4	.0	.0	.0	13.0	1.2	.6	.0	68.6	7.7	4.1	3.6	1.8	.0	.0	1.8	1.2
BE	S	2.2	.0	7.0	3.5	.9	.4	.0	6.6	.0	.0	.0	12.3	2.2	.4	1.8	.0	.0	.0	.0	.0
BE	S/T	9.4	9.9	3.6	2.7	.0	4.0	.0	3.1	.0	.4	.0	4.0	.0	.9	.9	.4	.0	.0	.0	.4
BE	T+	11.8	16.7	3.9	5.4	.5	2.5	.5	2.0	.5	.5	.0	3.4	.5	.5	.0	.5	.0	.0	.5	.0
BE	T-	4.8	7.8	4.3	1.7	.9	.0	.0	9.6	.0	.0	.0	35.7	2.2	4.3	.4	1.7	.0	.0	.0	.0
BE	T/O	5.0	9.6	1.8	.9	.0	.5	.0	7.3	.0	.9	.0	27.4	2.3	2.3	.0	2.7	.0	.5	.0	.0
BE	O+	7.5	71.2	.5	.9	.0	15.6	.0	5.7	.9	.0	.0	13.7	1.9	.5	.5	.5	.0	.5	1.4	.0
BE	O-	23.2	6.8	.5	.9	.0	1.8	.0	8.2	.0	.0	.5	32.3	4.5	1.4	.0	1.4	.0	.0	.5	.0
BE	O/X	1.3	21.2	.0	.0	.0	4.8	.0	6.9	.0	.4	.0	26.4	3.0	1.3	.9	.0	.0	.0	.0	.4
BE	X	.3	1.7	.0	.3	.0	.7	.0	5.0	.0	.0	.3	11.6	3.0	.7	1.0	1.0	.0	.3	.3	.0

		PAPU	PODO	DACR	RAPA	ASTT	QUIN	SYMP	COPR	HALO	DRIM	STYP	ERC1	ERC2	ERC3	DRAP	RANU	GENT	POTT	TRIG	APIA
UM	S	.5	2.6	13.1	14.1	.0	.0	.0	3.1	1.0	.0	.0	.5	.5	.0	.0	.5	.0	.5	.5	.0
UM	T+	.0	.0	5.2	12.3	.9	.0	.0	1.4	4.7	.5	.0	.0	.5	.0	.0	.5	.0	1.4	.0	.0
UM	T-	.0	.5	11.5	11.5	3.5	.5	.0	.5	1.0	.0	.5	.5	.0	.0	.0	.0	.0	.0	.0	.0
UM	T/O	.6	.0	10.3	9.1	.6	.0	.0	5.7	.6	1.1	7.4	1.1	.0	.0	.0	1.7	2.3	.0	.0	.0
UM	O+	.6	.6	5.6	15.6	.0	.6	.0	1.1	3.3	1.1	.6	.6	1.1	.0	.0	.0	.6	.6	.0	.0
GU	S	.0	.0	2.9	1.2	2.3	.6	.0	6.4	.0	.6	.6	.0	.0	.0	1.7	36.4	1.2	1.2	.6	.0
GU	SS/T	.0	.0	2.5	.6	1.9	.0	.0	.6	.0	.6	.0	.0	.0	.0	.6	12.0	.0	.6	2.5	.0
GU	S/T	.0	.9	2.8	.0	4.6	.0	.0	.0	.0	.0	.0	.0	.0	.0	.9	1.9	.9	.9	.0	.0
GU	TT/S	.3	.3	3.8	.6	3.8	.0	.0	.6	.0	.0	.0	.3	.0	.0	.0	2.5	.3	.0	.0	.0
GU	T+	.0	.0	2.0	.7	2.0	.3	.0	.0	.0	.0	.0	.0	.0	.0	1.4	3.4	.0	.7	.0	.0
GU	T-	.0	.0	10.8	4.1	.7	.0	.0	1.5	1.5	.7	.0	.7	.0	.0	.4	.0	.0	1.5	.0	.0
GU	T/O	.0	.3	12.6	4.6	1.0	.0	.0	1.7	1.0	.0	.0	.0	.0	.3	.3	4.0	.0	.7	.7	.0
GU	O+	.4	.4	16.2	2.4	.4	.0	.0	1.6	.0	.0	.0	.0	.0	.0	.0	4.7	.0	.0	.0	.0
TE	S	.0	.0	.5	.5	.0	.0	.0	.0	.5	.0	.0	.0	.0	.0	.5	5.4	1.0	.5	1.0	.0
TE	S/T	.0	.4	.8	1.2	.0	.0	.0	2.5	.0	.0	.0	.0	.0	.0	.8	.8	.0	.0	.0	.0
TE	T+	.0	1.5	3.0	4.5	.0	.0	.0	.4	.0	.0	.0	.0	.0	.0	.4	2.7	.4	.0	.0	.8
TE	T-	1.0	1.0	11.3	7.7	.0	.0	.0	5.7	1.0	.0	.0	.0	.0	.0	.0	1.0	.0	.0	.0	.5
TE	T/O	.5	.0	10.5	11.6	.0	.0	.0	4.2	1.1	.0	.0	.0	.0	.5	.0	.5	1.1	.0	.0	.0
TE	O+	.7	1.3	11.8	15.7	.7	.0	.0	.0	.0	.0	.0	.7	.0	.0	.7	.0	.0	.0	.0	.0
GI	S	.0	1.7	8.4	6.7	1.7	.0	.0	5.6	1.1	.6	1.1	.0	.6	.0	.0	2.8	2.2	.6	.0	.0
GI	S/T	.5	2.0	4.6	7.7	.0	.0	.0	4.6	.0	.0	.0	1.0	.0	.0	.0	1.5	.5	.0	.0	.0
GI	T+	.0	.0	3.2	8.3	4.5	.0	.0	10.8	1.3	.0	.0	.6	.0	.0	.0	8.9	6.4	1.9	1.9	.0
GI	T-	.0	2.0	15.3	13.8	3.0	.5	.0	5.4	.0	1.0	2.0	.0	.0	.0	.0	6.4	3.4	.5	.0	.0
GI	T/O	.0	.0	13.1	10.0	2.6	.4	.0	.4	1.7	.4	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
GI	O+	.3	.9	12.9	11.0	.9	.0	.0	4.4	.0	.3	5.0	4.4	.6	.0	.0	.0	1.9	1.3	.0	.0
GI	O-	.9	.5	11.5	9.2	1.8	.5	.0	4.1	.0	.9	5.0	4.1	.0	.5	.0	.0	2.3	2.3	.5	.0
GI	O/X	.0	1.3	19.5	7.5	.9	.0	.4	2.7	.4	.4	.0	2.2	.4	.0	.0	.0	.9	1.3	.0	.0
BA	S	.0	.7	3.6	2.9	.0	.0	.0	7.9	.0	.7	.0	.0	.0	.0	.7	33.8	7.9	1.4	1.4	.0
BA	SS/T	.0	.3	2.8	1.4	.3	.3	.0	2.1	.7	.0	.0	.0	.0	.0	.0	4.2	2.8	2.4	2.8	.0
BA	S/T	.0	.9	2.3	.9	.0	.0	.0	1.4	.5	.0	.0	.0	.0	.0	.0	11.0	5.5	.0	1.4	.0
BA	TT/S	.0	.5	1.6	.5	.0	.0	.0	.5	.0	.0	.0	.0	.0	.0	.0	6.5	3.2	.5	.5	.0
BA	T+	.0	.7	1.5	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.7	.0	.0	.0	.0
BA	T-	1.7	2.5	5.9	9.2	.8	.0	.0	3.4	.8	.0	.0	.0	.0	.0	.8	60.5	7.6	2.5	.0	.0
BA	TT/O	.0	1.9	11.0	13.6	.0	.6	.0	1.3	.0	.0	.0	.0	.0	.0	1.3	16.2	5.2	.6	.0	.0
BA	T/O	.6	7.3	9.7	12.1	.6	.0	.0	1.8	4.2	.0	.0	.0	.0	.0	.0	1.8	2.4	1.2	.0	.0
BA	OO/T	.6	10.6	26.7	13.3	.6	.0	.0	.0	.0	.0	.0	.6	.0	.0	.6	6.1	.0	2.8	.6	.0
BA	O+	.0	2.4	23.6	24.8	.0	.6	.0	3.0	1.8	.0	.0	.6	.0	.0	.0	.0	.0	.6	.0	.0
BA	O-	.8	4.0	21.8	20.2	.0	.0	.0	.0	.0	.0	.0	.0	.8	.0	.0	9.7	2.4	.0	.0	.0
BA	O/X	.0	.6	19.6	17.7	3.8	.0	.0	.6	.0	.0	.0	.0	.0	.0	.0	3.2	.6	.6	.0	.0
BA	X	1.8	2.4	27.2	21.3	.0	.0	.0	.0	.0	.0	.0	.6	.0	.0	.0	2.4	3.0	2.4	.0	.0
BE	S	.0	.0	4.4	5.7	11.9	.0	.0	2.2	1.3	.0	.0	.0	.0	.0	.4	.0	.9	.0	.0	.0
BE	S/T	.0	.9	.9	1.3	3.6	.0	.0	2.2	.9	.0	.4	.0	.0	.0	.4	.0	1.8	.0	.4	.0
BE	T+	.0	.0	1.0	1.0	1.5	.0	.0	2.5	.0	.0	.0	.5	.0	.0	1.0	.0	.0	.0	.0	.0
BE	T-	.0	.4	13.9	16.1	1.3	.0	.0	2.2	.4	.0	.9	.0	.0	.0	.9	.0	.9	.4	.0	.0
BE	T/O	.9	.0	5.5	11.0	.9	.0	.5	1.4	.9	.0	.0	.0	.0	.0	.5	.0	2.3	.0	.0	.0
BE	O+	.0	.5	2.8	7.5	.0	.0	.0	1.9	.5	.5	.0	.0	.0	.0	.0	.0	.5	.0	.0	.0
BE	O-	.5	.9	13.6	11.8	.0	.9	.0	2.3	1.4	.5	.0	.5	.0	.5	.5	.0	2.3	.5	.0	.0
BE	O/X	.0	1.3	12.6	10.0	.0	.0	.0	2.2	.4	.0	.0	.0	.0	.0	.0	.4	1.3	.4	.0	.0
BE	X	.3	.7	26.9	13.3	1.3	.3	.0	2.7	.0	.0	.0	.7	1.0	.0	.0	.0	1.3	.0	.0	.0

		LIGU	ASTL	POA1	POA2	POA3	POA4	CYP1	CYP2	CENT	VULC	CYAT	PTER	BELV	TRSP	UNK1	FERN	HERB	TREE	UNKN
UM	S	.0	.0	2.1	14.7	2.6	21.5	1.6	8.4	.0	.0	13.1	.5	.0	.5	.5	12.6	.0	.5	1.0
UM	T+	.0	4.7	.5	19.8	3.3	19.3	.5	18.4	.0	.9	11.8	.5	.0	.0	.0	.0	.0	.5	1.4
UM	T-	.0	6.5	.5	6.0	3.0	21.0	1.5	25.0	.0	.0	12.0	.0	.5	.0	4.5	6.5	.5	.5	.0
UM	T/O	.6	84.6	.0	20.6	5.7	25.1	.0	5.7	1.1	.6	5.7	.0	.0	.0	4.0	2.3	.0	.0	1.7
UM	O+	.0	.6	1.7	5.6	1.7	5.6	3.3	42.8	.0	.6	8.9	1.7	.0	.0	1.7	7.2	.0	1.1	1.1
GU	S	.0	1.2	1.2	9.8	3.5	12.7	.0	45.1	1.2	.0	10.4	.0	.0	.6	.0	2.3	.6	.0	1.7
GU	SS/T	.0	.0	9.5	41.8	3.8	12.7	.0	11.4	.0	.0	12.7	.0	.0	9.5	.0	8.2	.0	.0	.0
GU	S/T	.0	.0	4.6	40.7	7.4	23.1	.0	5.6	.9	.0	9.3	.9	.9	14.8	.0	1.9	1.9	.0	1.9
GU	TT/S	.0	.0	2.8	37.6	7.5	24.8	.0	8.2	.0	.0	8.5	.3	.3	11.3	.0	3.1	.3	.0	.6
GU	T+	.0	.0	6.8	39.5	5.4	16.3	.0	20.4	.0	.0	6.8	.0	.0	8.8	.0	1.4	.0	.0	.7
GU	T-	.0	.4	1.9	19.0	5.6	28.4	3.4	16.0	.0	.0	4.5	.7	.4	.4	.0	2.6	.4	.0	.0
GU	T/O	.0	.0	5.6	36.1	3.0	22.5	1.0	8.3	.0	.0	2.0	.3	.3	.0	.0	.3	.3	.7	1.0
GU	O+	.0	.0	7.9	50.2	.8	9.9	.0	5.9	.0	.0	4.0	.4	.4	.0	.0	.4	.0	.4	.0
TE	S	.0	1.5	2.0	20.5	3.4	19.0	1.0	42.9	.0	.0	8.8	.5	.0	.0	.0	9.8	.0	.0	.5
TE	S/T	.0	.8	.4	21.2	1.7	28.7	6.3	21.7	.8	.0	13.3	.0	.4	.0	.8	11.7	.4	.0	.0
TE	T+	.0	.0	.0	18.2	3.4	19.7	4.2	29.9	.0	.0	14.0	.0	.0	.0	.0	7.6	.0	.4	.0
TE	T-	.0	.0	2.1	8.2	4.1	5.2	2.6	40.2	.0	.0	5.7	.0	.0	.0	.5	6.7	1.0	.5	1.0
TE	T/O	.0	.0	1.1	4.7	2.6	2.6	1.1	45.8	1.6	.0	11.6	.0	.0	.0	.5	6.8	.0	.0	.5
TE	O+	.0	.0	.0	7.2	2.0	2.6	3.3	39.9	.0	.0	9.2	.0	.0	.0	.0	3.9	.0	.7	.7
GI	S	.0	7.9	1.7	8.4	3.9	12.9	.0	19.7	.0	.6	24.2	.0	.0	.0	2.8	9.0	.0	1.1	.0
GI	S/T	1.5	45.4	1.0	11.2	2.0	30.6	.0	23.0	.0	.0	9.2	.0	.0	.0	2.6	6.6	1.0	.5	2.0
GI	T+	.0	47.8	.6	15.9	9.6	22.9	.0	8.3	.6	1.9	7.0	.0	.6	.0	.6	10.8	.6	.0	.6
GI	T-	.0	137.9	.5	13.3	5.4	21.2	.0	6.4	.0	.0	9.4	.5	.0	.0	2.0	4.9	.0	.5	.5
GI	T/O	.4	5.2	.4	9.6	16.2	21.0	.4	7.9	.0	.4	14.0	.0	.0	.0	.9	2.2	.4	.0	.9
GI	O+	.0	18.2	1.3	10.7	6.9	23.2	.0	3.1	.0	.3	11.0	.0	.0	.0	1.3	5.0	.0	.3	.9
GI	O-	.0	8.7	.9	7.3	6.0	28.9	.5	6.4	.0	.0	8.7	.5	.0	.0	2.3	6.9	.0	.5	.0
GI	O/X	.0	.0	2.2	12.4	5.3	29.2	.0	9.3	.0	.0	3.5	.0	.0	.0	3.5	12.8	.0	.0	.4
BA	S	.0	4.3	.0	7.2	6.5	12.9	.0	40.3	.0	.0	15.8	.7	.0	.7	.7	20.9	.0	.0	.0
BA	SS/T	.0	2.1	.7	14.3	6.3	12.9	.0	46.0	.0	.0	10.5	.0	.0	.0	1.4	5.6	1.4	.0	.7
BA	S/T	.0	1.4	1.4	6.8	6.8	11.0	.9	46.6	.0	.0	18.3	.0	.0	.0	.0	6.8	.0	.0	1.4
BA	TT/S	.0	.0	.5	10.8	5.4	10.8	.0	55.9	.0	.0	11.8	.5	.0	.0	1.1	10.2	.5	.0	1.1
BA	T+	.0	.7	1.5	32.8	8.0	24.8	1.5	10.9	.0	.0	16.8	3.6	.0	.0	2.2	20.4	.7	.7	2.2
BA	T-	.0	10.1	2.5	26.9	8.4	11.8	.0	15.1	13.4	.0	10.1	.0	.0	.0	1.7	4.2	.0	.0	.0
BA	TT/O	.6	5.2	.6	11.0	3.2	6.5	.0	40.9	10.4	.0	6.5	.0	.0	.0	1.3	12.3	.0	.6	.6
BA	T/O	.0	21.2	.6	23.0	4.2	10.9	.0	7.9	4.8	.0	15.2	1.2	.0	.0	1.2	2.4	.0	.0	.6
BA	OO/T	.0	.6	1.1	8.3	2.8	5.6	.0	8.3	1.7	.0	15.0	.6	.0	.0	.0	11.7	.0	.0	2.2
BA	O+	.0	.0	1.8	6.7	2.4	3.0	.0	3.6	.6	.0	20.6	1.8	.0	.6	2.4	4.2	.0	1.8	.6
BA	O-	.0	.0	.8	8.1	.0	6.5	.0	16.1	10.5	.0	12.9	.8	.8	.0	7.3	5.6	.0	.0	5.6
BA	O/X	.6	.0	.6	3.2	.0	7.6	2.5	24.7	4.4	.0	8.9	1.3	.0	.0	3.8	3.8	.6	.6	2.5
BA	X	5.9	.0	1.2	5.9	3.0	5.3	.0	18.3	5.3	.0	7.1	.0	.0	.0	10.1	3.6	.0	2.4	10.7
BE	S	.0	.0	.0	6.6	.4	8.4	4.8	26.0	1.8	7.0	18.9	.0	.0	.0	.4	2.6	.4	.0	.4
BE	S/T	.0	.0	.4	10.8	1.3	13.0	2.2	50.7	.0	.9	8.5	.0	.0	.4	.9	3.6	.0	.0	.9
BE	T+	.0	.0	.0	7.4	2.5	8.9	2.5	67.0	.0	.0	4.9	.0	.0	.0	.5	1.5	.0	.5	1.0
BE	T-	.0	1.3	.4	.4	1.3	5.2	2.6	25.2	2.2	3.5	21.3	.0	.0	.4	.0	4.3	.9	.4	.4
BE	T/O	.0	.0	.0	1.4	.9	1.8	4.1	42.0	2.3	6.8	20.5	.0	.0	.0	.0	2.7	.0	.0	1.8
BE	O+	.0	.0	.0	2.4	.0	1.9	5.7	48.6	.9	4.2	22.6	.5	.5	.0	.0	8.5	.0	.5	.0
BE	O-	.0	.0	.0	1.8	.5	1.8	1.8	17.3	8.6	7.7	35.9	1.4	.0	.0	.9	1.8	.0	1.4	.5
BE	O/X	.0	.0	1.3	2.2	1.3	3.0	1.3	27.7	3.9	4.8	29.9	.0	.0	.0	.0	2.6	.0	.4	.9
BE	X	.3	.0	.3	.3	.7	1.7	.7	7.3	10.6	22.3	18.3	.0	.0	.0	1.3	1.0	.0	.3	.3

		CHAR	LYCO	CASU	TREM	DODN	URTM	ACAL	MACA	CELT	SAUR	EUPH	NOTH	CAST	ASCA	RUTA	PHYL	PRUN	CUNO	ELAE	MYRT
39	S	3.8	.0	18.1	12.2	.4	2.1	.0	3.8	.8	.4	.4	12.6	.8	.4	.8	.4	.0	.4	.8	.0
39	S/T	3.6	29.3	10.8	9.9	.5	6.8	.0	4.1	.0	.0	.5	10.8	.5	.5	.0	1.8	.0	.0	.0	.0
39	T+	9.5	73.6	4.7	6.1	.3	12.2	1.4	2.7	.0	.3	.0	11.5	1.7	3.1	.3	1.0	.0	.0	.7	.3
39	T-	4.0	19.3	3.4	3.4	1.1	2.3	1.1	4.5	.0	1.1	.6	39.8	2.3	.6	1.1	1.7	.0	.6	.6	.0
39	T/O	2.9	12.1	2.3	1.7	.6	2.3	.6	5.8	.0	.0	.0	30.1	2.3	.0	2.9	2.3	.0	.0	.0	.0
39	O+	1.8	7.3	1.2	4.3	.6	3.7	.0	6.1	.6	.0	.0	23.2	1.2	.6	.6	.0	.0	.0	1.2	.6
54	S	2.9	.0	40.2	7.8	.8	.8	.8	2.5	.4	.4	1.2	15.2	1.6	.8	.4	.0	.0	.0	1.2	.4
54	SS/T	4.6	.0	25.4	13.7	2.0	1.0	2.5	3.0	.0	1.0	.5	13.2	2.0	.5	.0	.0	.0	.5	.0	.0
54	S/T	12.2	19.6	11.3	6.5	1.7	2.2	1.3	3.5	.4	.4	.4	5.7	1.3	.9	.0	.9	.0	.4	.4	.0
54	TT/S	8.7	.0	7.8	7.4	.0	3.0	.0	3.5	.0	.0	1.3	4.3	.4	.0	.0	.0	.0	.0	.0	.0
54	T+	7.9	.0	11.7	5.8	1.2	6.3	.4	7.5	.4	.0	2.1	7.5	1.2	.0	.0	1.2	.4	.0	.8	.8
54	T-	5.1	.0	12.4	6.2	1.5	3.3	.7	8.8	.0	1.1	.0	46.0	.0	.0	.0	.0	.0	.0	.7	.0
54	TT/O	3.7	.0	6.1	6.1	.0	2.9	.4	8.2	.4	.0	.0	45.7	4.1	3.7	.0	1.2	.0	.0	.0	.4
54	T/O	4.0	.0	3.2	4.3	.0	1.6	.4	9.1	.4	.4	1.6	36.8	3.6	4.7	.0	2.4	.0	.8	.0	.0
54	OO/T	4.8	.0	3.5	6.2	.9	.4	.0	5.7	.4	.4	.4	36.6	4.0	1.8	.4	.9	.0	.0	.4	.0
54	O+	3.7	.0	1.2	2.9	.0	1.6	.0	5.7	.0	.4	.0	36.5	4.5	3.3	.4	2.0	.0	1.2	.0	.8
45	S	5.3	.0	17.5	7.9	.0	4.4	.9	.0	.9	.0	.0	10.5	1.8	.9	.0	.9	.0	.0	.0	.0
45	S/T	4.7	.0	2.3	.9	.0	6.1	.0	.5	.0	.9	.5	8.0	.0	.9	.0	1.4	.0	.0	.5	.5
45	T+	4.9	.0	1.0	1.5	.0	16.1	.0	1.5	.5	1.0	.0	6.8	.0	.0	.0	1.5	.5	.0	.0	.0
45	T-	3.3	.0	.0	.9	.5	4.7	.5	.5	.5	.0	1.4	12.7	3.3	.0	.5	.5	.0	.5	.5	.0
45	Q	1.4	.0	1.4	1.8	.0	1.8	.0	1.4	.0	.0	.0	12.3	2.7	.5	.0	.5	.0	.5	.5	.5
46	S	3.7	55.6	20.4	5.6	.0	4.6	.0	1.9	.0	.9	.0	15.7	4.6	.0	.9	.0	.0	.0	1.9	.0
46	T+	4.4	33.3	5.2	2.2	.7	.0	.0	2.2	.7	2.2	.0	12.6	1.5	2.2	.7	2.2	.0	.7	.7	.0
46	T-	4.4	.0	2.9	2.9	1.5	1.5	.7	5.1	.0	.0	.0	15.3	1.5	1.5	.0	1.5	.0	.0	.7	.0
46	Q	6.8	67.7	.8	3.8	.8	1.5	.0	3.8	.0	.8	.0	18.8	.0	.0	.0	.0	.8	.0	1.5	.0
41	S	3.9	.0	48.5	4.9	1.0	4.9	.0	7.8	.0	.0	1.0	21.4	1.0	.0	.0	.0	.0	1.0	1.0	1.0
41	S/T	6.1	53.0	13.0	5.2	.0	6.1	.0	6.1	.0	.0	.0	13.0	1.7	.0	.0	.9	.0	.0	.0	.9
41	TT/S	16.2	72.6	20.5	8.5	.0	18.8	.0	5.1	.9	.9	3.4	16.2	1.7	.9	.0	.0	.0	.9	.9	.0
41	T+	17.3	58.7	8.7	12.5	.0	15.4	.0	6.7	.0	.0	.0	17.3	1.9	1.0	.0	1.9	.0	.0	.0	.0
41	T-	4.4	68.1	5.5	7.7	1.1	6.6	.0	14.3	.0	.0	.0	57.1	6.6	6.6	.0	2.2	.0	2.2	3.3	.0
41	T/O	2.4	24.2	3.2	5.6	.0	.8	.0	4.8	.0	.8	.0	68.5	1.6	11.3	.0	1.6	.0	.8	.0	.0
41	O+	3.7	28.4	.9	6.4	1.8	10.1	.0	7.3	.0	.0	5.5	66.1	3.7	6.4	.0	.0	.0	2.8	.9	.0
41	O-	3.3	28.1	.0	.8	1.7	11.6	.0	14.9	.8	.0	4.1	36.4	3.3	5.0	2.5	3.3	.0	.0	.8	.8
41	O/X	2.1	20.8	.0	.7	.0	.7	.0	5.6	.0	.0	2.1	56.9	5.6	2.8	1.4	3.5	.0	.7	1.4	1.4
37	S	82.9	.0	35.2	10.9	.0	4.1	.5	2.1	.5	.0	.0	22.8	.0	.5	.0	.0	.0	.0	.5	.0
37	T+	58.3	6.8	1.5	.0	.0	1.5	.0	1.0	.0	.5	.0	4.9	.5	.0	.0	.0	.0	.0	.0	.0
37	T-	70.7	6.1	.5	1.0	.5	1.0	.5	1.0	.0	.5	.5	10.1	.0	1.0	.0	.0	.5	.5	1.0	.5
37	TT/Q	3.3	.0	.5	.0	.0	1.0	.0	1.0	.0	.5	.5	10.0	1.0	.5	.0	.5	.0	.0	.0	.0
37	T/Q	5.5	.0	.0	.5	.0	.0	.0	1.1	.0	.0	.0	12.6	1.1	.5	.5	.0	.0	.5	.0	.0
37	Q	.0	.9	.0	.0	.0	.5	.0	.0	.0	.0	.0	7.4	.9	.0	.0	.5	.0	.0	.5	.0

		PAPU	PODO	DACR	RAPA	ASTT	QUIN	SYMP	COPR	HALO	DRIM	STYP	ERC1	ERC2	ERC3	DRAP	RANU	GENT	POTT	TRIG	APIA
39	S	.0	.4	1.7	13.0	1.7	.0	.0	4.2	3.4	.0	.8	.0	.0	.0	.4	2.9	.0	.4	.0	.0
39	S/T	.0	.0	.9	12.6	.5	.0	.0	5.9	1.4	.9	.9	.0	.0	.0	.0	1.8	.5	.0	.0	.0
39	T+	.0	.0	2.0	.7	.3	.0	.0	1.4	.3	.0	.0	.0	.0	.0	.7	1.0	.0	.3	.0	.0
39	T-	.0	1.7	8.5	23.9	2.8	.0	.0	7.4	2.3	.6	.0	.6	.6	.0	.0	13.6	8.5	.6	.6	.0
39	T/O	.0	.6	9.8	23.7	.6	.6	.0	2.9	.6	.0	.0	.0	.0	.0	.6	4.0	2.9	.6	.0	.0
39	O+	.0	1.8	5.5	17.7	3.0	.0	.0	2.4	.0	.0	.0	.0	.6	.0	.6	3.7	3.7	1.2	.0	.0
54	S	.0	.8	3.7	9.8	.4	.8	.0	6.1	2.9	.0	.0	.0	.0	.0	.8	61.9	29.9	.0	.8	.0
54	SS/T	.0	.0	2.0	6.6	.0	.0	.5	2.5	.5	.0	.0	.0	.0	.5	.0	137.1	70.1	.0	4.1	.0
54	S/T	.0	.4	2.6	4.8	1.3	.0	.0	3.0	2.6	.0	.0	.0	.4	.0	.0	40.9	6.5	.4	.4	.0
54	TT/S	.0	.9	.4	6.1	1.3	.0	.0	1.7	.4	.0	.0	.0	.4	.0	.0	22.5	4.8	.0	.0	.4
54	T+	.0	.8	.4	2.9	.4	.4	.0	3.3	1.2	.0	.0	.0	.0	.0	.0	25.4	.8	.4	.0	.0
54	T-	.0	1.1	9.9	19.3	6.2	.0	.0	.7	1.1	.4	.0	.0	.0	.4	.7	18.6	1.5	1.5	.4	.0
54	TT/O	.0	.8	8.2	18.4	6.1	.4	.0	.0	1.6	.0	.0	.0	.0	.0	.4	18.4	2.4	.0	.0	.0
54	T/O	.0	2.8	14.6	16.2	.8	.8	.0	.0	1.2	.0	.0	.0	.0	.0	.0	13.0	4.0	.0	.0	.0
54	OO/T	.0	.9	11.9	19.8	4.0	.4	.0	1.3	.0	.0	.0	.0	.0	.0	.0	15.9	3.1	.4	.0	.0
54	O+	.0	1.6	12.7	19.7	2.5	.4	.0	1.6	.8	.0	.0	.0	.0	.0	.0	16.8	1.6	.4	.8	.0
45	S	.0	1.8	7.0	7.0	.0	.0	.0	1.8	2.6	.0	.0	.0	.0	4.4	1.8	46.5	1.8	.0	.0	.0
45	S/T	.0	1.4	8.9	9.4	1.4	.0	.0	.5	1.9	.9	.0	.5	.0	.5	.5	4.7	.0	.5	.0	.0
45	T+	.0	.5	8.8	10.7	.5	.5	.0	2.4	2.0	1.5	.0	.0	.5	.0	.5	.5	.0	.0	.0	.5
45	T-	.0	1.4	10.4	10.4	1.4	.0	.0	.0	1.4	.0	.0	.0	.5	.0	.0	1.4	.9	.0	.0	.0
45	Q	.0	.9	11.0	12.8	1.4	.0	.0	.9	3.2	.0	.5	.0	.0	.0	.5	.9	1.4	.0	.0	.0
46	S	.0	.9	1.9	2.8	3.7	.0	.0	1.9	.9	.0	.0	.0	.9	.0	2.8	48.1	3.7	1.9	1.9	.0
46	T+	.0	.0	.7	4.4	5.2	.0	.0	3.0	8.9	2.2	1.5	.7	1.5	.0	.0	14.8	2.2	.0	.0	.0
46	T-	.0	.7	5.1	5.1	4.4	.0	.7	2.9	10.9	1.5	.7	.7	.7	.0	.0	.0	.7	.0	.0	.0
46	Q	.0	1.5	7.5	4.5	6.8	.0	.8	.0	14.3	1.5	.0	3.8	.8	.0	.8	.8	.0	3.0	.0	.0
41	S	.0	.0	12.6	8.7	1.9	.0	.0	1.9	2.9	.0	1.0	1.0	.0	1.0	1.9	8.7	.0	.0	.0	.0
41	S/T	.0	.9	6.1	10.4	1.7	.0	.0	.9	.0	.0	.0	.0	.0	.0	.0	2.6	3.5	1.7	.0	.0
41	TT/S	.0	.9	6.8	11.1	.0	.0	.0	.0	2.6	.0	.0	.0	.0	.0	.9	1.7	2.6	.0	.0	.0
41	T+	.0	.0	3.8	8.7	.0	.0	.0	1.9	1.0	.0	.0	.0	.0	.0	.0	7.7	1.9	.0	.0	.0
41	T-	.0	1.1	19.8	12.1	.0	1.1	.0	1.1	1.1	.0	.0	.0	.0	.0	2.2	9.9	3.3	.0	.0	.0
41	T/O	.0	.8	24.2	10.5	.0	.0	.0	.0	.8	.0	.0	.0	.0	.0	.0	4.8	1.6	.0	.0	.0
41	O+	.0	.9	25.7	12.8	.0	.9	.0	.0	.0	.9	.0	.0	.0	.0	.0	4.6	3.7	.0	.0	.0
41	O-	.0	.8	28.9	15.7	2.5	.8	.8	1.7	.8	.0	.0	.0	.0	.8	.0	2.5	2.5	.0	.0	.0
41	O/X	.0	1.4	29.9	17.4	4.9	.7	.0	.0	.0	.0	.0	.7	.0	.7	.0	.7	.7	.0	.0	.0
37	S	.0	1.6	1.6	10.9	6.7	.0	.0	1.0	.0	.0	.0	.0	1.0	.5	.5	13.0	.0	6.7	.0	.0
37	T+	.0	1.5	11.7	20.4	.5	.5	.0	.5	1.9	.0	.0	.0	1.9	.5	.0	.5	.0	.0	.0	.0
37	T-	.0	1.0	13.1	29.3	2.0	.0	.0	1.0	4.5	.0	.5	.0	2.0	.5	.0	.0	.0	.5	.0	.5
37	TT/Q	.0	.5	23.9	54.1	1.0	.5	1.0	1.0	1.4	.5	.0	1.0	.5	.0	.0	.0	.0	.0	.0	.0
37	T/Q	.0	.5	24.0	54.1	1.1	1.6	.0	1.1	.5	.5	.0	.0	.5	1.6	.0	.0	.0	.0	.0	.0
37	Q	.0	.0	30.0	53.9	.5	.5	1.4	2.8	1.4	.9	.0	1.8	1.8	.0	.0	.0	.0	.0	.0	.0

		LIGU	ASTL	POA1	POA2	POA3	POA4	CYP1	CYP2	CENT	VULC	CYAT	PTER	BELV	TRSP	UNK1	FERN	HERB	TREE	UNKN
39	S	.8	3.8	.0	13.0	5.5	2.9	5.5	36.6	.0	.0	9.7	.0	.0	.0	.0	5.5	.0	.4	1.3
39	S/T	.0	9.5	.5	18.0	4.5	4.5	2.3	34.2	.5	.0	10.8	.0	.0	.0	.0	5.0	.0	.5	.5
39	T+	.0	32.5	1.0	15.9	5.4	3.7	1.0	54.2	.0	.0	9.5	.0	.3	.0	.0	6.8	.0	.0	.0
39	T-	5.1	119.3	2.8	18.8	5.7	4.5	.0	8.5	10.2	.0	8.0	.0	.0	.0	13.6	5.1	.0	.6	.6
39	T/O	.6	120.2	1.7	23.1	10.4	8.1	.6	7.5	5.8	.0	4.6	.6	.0	.0	1.7	2.9	.0	1.2	.6
39	O+	.6	49.4	2.4	35.4	7.3	11.6	.0	7.9	3.0	.0	3.0	1.8	.0	.0	.0	.6	.0	.0	.0
54	S	2.5	.8	.4	47.1	3.7	7.4	.0	2.5	.0	.0	13.1	.0	.0	.0	1.2	8.2	.0	.0	.0
54	SS/T	3.6	1.0	1.0	58.4	4.1	7.6	.5	1.0	.0	.0	14.7	.0	.5	.0	4.1	7.1	.0	.0	.0
54	S/T	.4	.0	.9	54.8	3.9	8.7	.0	3.9	.0	.4	10.4	.4	.0	.0	1.7	6.1	.0	.0	.4
54	TT/S	3.0	.4	.4	51.9	7.4	16.5	2.2	2.2	.0	.0	8.2	.0	.0	.0	1.3	3.5	.0	.0	.0
54	T+	2.1	.0	1.7	43.8	8.7	23.3	.4	2.9	.0	.4	7.9	.0	.0	.0	.0	4.2	.0	.0	1.7
54	T-	.4	2.6	1.5	21.5	6.9	17.2	.7	1.5	4.0	.4	11.7	.0	.0	.0	2.2	2.2	.0	.4	.7
54	TT/O	1.2	12.2	.8	20.0	2.0	22.4	.0	8.2	11.4	.0	6.1	.0	.0	.0	7.8	3.7	.0	.8	3.3
54	T/O	.8	24.5	.4	23.7	4.0	9.5	2.0	7.1	4.7	.0	9.9	.0	.0	.0	4.0	5.1	.0	.0	.4
54	OO/T	2.6	24.7	2.2	23.3	4.0	16.7	2.2	4.8	6.6	.0	5.3	.0	.0	.0	5.7	4.4	.0	.0	1.3
54	O+	2.0	12.7	.8	19.7	2.9	16.4	3.7	4.5	4.9	.0	7.0	.0	.0	.0	4.5	3.3	.0	.0	2.0
45	S	.0	2.6	.9	9.6	4.4	.0	3.5	35.1	.0	.0	24.6	.0	.0	.0	.0	7.9	.0	.0	2.6
45	S/T	.9	4.2	.0	9.4	6.1	.9	6.1	33.8	.0	.0	16.4	.0	.0	.0	.0	8.5	.0	.5	.9
45	T+	.0	5.4	.5	11.7	8.3	2.4	3.9	33.2	.0	.0	11.2	.0	.5	.0	.0	9.8	.0	.5	.5
45	T-	.0	10.4	.0	20.3	3.3	1.9	4.2	36.3	.0	.0	7.5	.0	.0	.0	.0	4.7	.0	.5	.9
45	Q	.5	.5	.5	24.2	6.4	2.3	3.2	27.9	.0	.0	4.1	.0	.0	.5	.0	3.2	.0	.0	.0
46	S	.0	.9	2.8	3.7	.0	12.0	1.9	56.5	2.8	.0	9.3	.0	.0	.0	.0	14.8	.9	.9	.0
46	T+	.0	1.5	1.5	13.3	6.7	14.1	1.5	18.5	.0	1.5	9.6	.0	.0	.0	2.2	8.1	.0	.7	.0
46	T-	.0	2.2	2.2	8.8	1.5	21.9	1.5	19.7	.0	.0	8.0	.7	.0	.0	.7	5.1	.0	1.5	.0
46	Q	.8	4.5	3.0	12.0	.8	18.8	.0	19.5	.0	.0	4.5	3.0	.0	.0	.8	11.3	.0	1.5	.0
41	S	.0	3.9	1.0	22.3	2.9	5.8	.0	23.3	.0	.0	14.6	.0	.0	.0	1.0	9.7	.0	.0	.0
41	S/T	.0	5.2	.9	20.9	7.0	12.2	.0	23.5	.9	.0	14.8	.0	.0	.0	.9	4.3	.0	.0	.0
41	TT/S	.9	.0	.9	23.1	4.3	12.8	2.6	18.8	.9	.0	15.4	.0	.0	.0	.0	11.1	.0	.9	.0
41	T+	.0	.0	2.9	22.1	6.7	13.5	2.9	27.9	.0	.0	5.8	1.0	.0	.0	.0	7.7	.0	.0	.0
41	T-	.0	4.4	2.2	8.8	1.1	12.1	1.1	23.1	3.3	.0	6.6	1.1	.0	.0	13.2	9.9	.0	.0	.0
41	T/O	.0	1.6	1.6	6.5	1.6	12.1	3.2	23.4	3.2	.0	2.4	.0	.0	.0	.8	4.0	.0	.0	.0
41	O+	.9	.0	1.8	6.4	.9	1.8	9.2	27.5	2.8	.0	4.6	.0	.0	.0	4.6	6.4	.0	.9	.0
41	O-	1.7	.8	.0	2.5	.0	1.7	5.8	23.1	8.3	.0	4.1	2.5	.0	.0	3.3	9.1	.0	.0	.0
41	O/X	.7	.0	.0	1.4	.0	2.8	9.7	21.5	7.6	.0	2.1	.0	.0	.0	2.8	3.5	.0	.7	.0
37	S	.0	.5	.5	16.1	3.6	35.8	.0	5.2	.0	.0	15.5	.0	.5	.5	.0	4.1	.0	.5	1.0
37	T+	.0	.0	.5	18.0	3.4	36.4	.0	1.0	.0	.0	1.9	.0	.0	.0	.0	2.4	.0	.0	.0
37	T-	.0	.0	.0	18.7	3.0	16.2	.0	4.0	.0	.0	3.5	.0	.0	.5	.0	5.1	.0	.0	.5
37	TT/Q	.0	.0	.0	3.3	3.3	2.9	.0	.5	.0	.0	3.8	.0	.0	.0	.0	4.8	.0	.5	.0
37	T/Q	.0	.0	.0	3.3	1.1	6.0	.0	.5	.0	.0	3.8	.0	.0	.0	.0	4.9	.0	.0	.0
37	Q	.0	.0	.0	.5	.5	1.4	.0	.5	.0	.0	1.8	.5	.0	.0	.0	4.1	.0	.5	.5

		CHAR	LYCO	CASU	TREM	DODN	URTM	ACAL	MACA	CELT	SAUR	EUPH	NOTH	CAST	ASCA	RUTA	PHYL	PRUN	CUNO	ELAE	MYRT
20	S	107.6	67.1	16.5	7.6	2.5	20.3	.0	3.8	.0	.0	.0	3.8	2.5	1.3	3.8	1.3	.0	.0	3.8	.0
20	S/T	54.5	24.8	4.5	3.0	.0	4.5	.0	.0	.0	.0	.0	6.4	.0	.5	.5	.5	.0	.0	1.0	.0
20	T+	43.4	42.0	2.1	3.5	.0	11.2	.0	3.5	.0	.0	.0	6.3	.0	.7	.7	.0	.0	.0	.7	.0
20	T-	13.5	18.2	.7	2.7	.0	7.4	.0	2.7	.0	.0	.0	7.4	.7	.0	.0	.0	.0	.0	.7	.0
20	TT/O	10.7	.0	1.3	2.7	.7	7.3	.0	2.7	.7	1.3	.0	10.0	1.3	.7	.0	.7	.0	.7	.0	.7
20	T/O	2.3	9.7	1.1	1.7	.6	3.4	.0	2.8	.0	.6	.0	13.1	1.1	.6	2.8	.0	.0	.6	.6	.0
20	OO/T	.3	.0	.0	.8	.0	.0	.0	.8	.0	.0	.0	6.8	1.4	.5	.5	.5	.3	.0	.3	.0
20	O+	.3	7.8	.0	.5	.0	.3	.0	.5	.3	.8	.0	6.2	1.0	1.0	.5	.3	.0	.3	1.3	.3
21	S	43.3	.0	9.2	2.8	.5	2.3	.0	1.8	.0	.0	.9	4.6	.5	.5	.5	.5	.0	.0	.5	.0
21	S/T	25.0	14.9	6.9	1.1	.0	5.9	1.1	1.6	.0	.5	.5	6.9	.5	.5	.0	.0	.0	.5	1.1	.0
21	T+	21.5	11.4	3.4	.8	.4	1.7	.4	1.7	.4	.0	.0	5.9	2.5	.0	.4	.8	.4	.0	.0	.4
21	T-	22.2	7.9	5.6	2.8	.0	1.4	.0	1.9	.0	.0	.0	4.2	.9	.0	.5	.0	.0	.0	.0	.0
21	T/Q	1.9	4.7	.0	1.4	.9	.0	.0	.5	.0	.5	.0	8.0	.5	.0	.5	.5	.0	.5	.0	.0
21	Q	.9	5.4	.0	.5	.0	1.8	.0	1.8	.0	.0	.5	3.6	.9	.0	.0	.5	.0	.0	.5	.0
22	S	7.3	.0	16.5	3.7	.9	.0	.0	.0	.0	.9	.0	4.6	.0	.0	.0	.0	.0	.0	.0	.0
22	S/T	44.7	.0	6.0	3.3	.0	2.3	.0	1.4	.0	.0	.5	4.2	.5	.0	.0	.0	.0	.0	.0	.0
22	T+	41.7	.0	5.2	1.9	.0	.5	.0	.9	.0	.5	.0	1.9	.0	.0	.0	.5	.0	.0	.0	.0
22	T-	110.1	.0	2.3	2.8	.9	.5	.0	.9	.0	.5	.5	2.8	.5	.0	.0	.0	.0	.0	.5	.0
22	TT/O	1.3	.0	1.3	.9	.4	.0	.0	.0	.0	.0	.4	3.9	.4	.0	.0	.9	.0	.0	.0	.4
22	T/O	.5	.0	.5	.5	.0	.0	.0	.0	.5	.0	.5	5.2	.9	.0	.0	.5	.0	.5	.0	.0
22	O+	.5	.0	.5	.0	.0	.0	.0	.0	.0	.0	.0	4.7	.5	.0	.0	.0	.0	.0	.0	.0
25	S	31.8	.0	13.9	4.9	.0	4.5	.0	4.5	.0	.0	.0	7.2	.4	.0	.0	.4	.0	.0	.4	.4
25	T+	21.7	12.7	4.5	2.7	.0	9.5	.0	1.8	.0	.0	.0	11.8	2.7	.9	.0	.5	.0	.0	.5	.0
25	T-	27.5	8.8	2.8	.4	.0	11.6	.0	1.4	.4	.7	.0	10.2	2.5	1.1	.7	.7	.0	.7	.0	.7
25	TT/O	12.0	.0	2.9	.6	.0	.0	.0	1.1	.0	1.1	1.1	12.6	.6	.6	.0	.0	.0	.6	.0	.0
25	T/O	1.3	.0	.4	.9	.0	.0	.0	1.7	.0	.0	.0	12.1	.0	1.3	.0	.0	.0	.0	1.3	.0
25	OO/T	1.3	.0	1.3	.9	.4	.9	.0	.9	.4	.0	.0	10.0	.4	.4	.4	.4	.0	.9	.0	.9
25	O+	.5	6.0	.5	.5	.0	.0	.0	.5	.0	.9	1.4	15.2	.9	1.4	.9	.5	.5	.0	.0	.0
23	S	8.0	.0	41.4	6.9	1.7	.0	.0	5.2	.0	.0	.0	22.4	.6	.6	.0	.0	.0	1.7	.6	.0
23	T+	2.9	.0	8.1	2.9	.5	1.0	.0	3.8	.0	.5	.0	18.2	1.0	.5	1.4	1.0	.0	.5	.0	1.0
23	T-	7.2	.0	3.0	3.6	.0	5.4	.6	4.2	.0	.6	1.2	26.9	3.6	1.2	1.2	.6	.0	.6	.0	.0
25	TT/Q	1.8	.0	1.2	3.6	.6	5.5	.0	4.8	.6	.0	.0	36.4	2.4	.6	.6	1.2	.6	.0	.6	.6
23	T/Q	2.1	.0	.0	.7	.0	.7	.0	2.1	.0	.0	.0	33.8	2.1	1.4	1.4	1.4	.0	.7	.0	.7
23	Q	1.8	12.3	1.2	4.3	.6	11.7	.6	8.6	.0	.6	1.2	39.9	4.9	1.2	1.8	1.2	.0	.6	.0	.0
51	S	65.2	.0	10.9	3.8	.0	1.6	.0	1.6	.5	.5	.0	3.3	2.7	2.7	1.6	.0	.0	.0	1.1	.0
51	S/T	118.6	16.9	4.5	2.3	.0	1.1	.0	2.3	.0	.0	.0	5.1	1.7	.6	.6	.0	.0	.0	.6	.0
51	T+	78.3	13.3	2.4	2.4	.6	1.2	.0	1.8	.6	.6	.0	3.0	1.2	.0	.0	.0	.0	.0	.6	.0
51	T-	1.8	11.0	.4	.9	.0	.0	.0	3.1	.0	.0	.0	13.2	1.8	.0	.4	.0	.4	.4	.0	.4
51	T/Q	1.4	11.8	.5	1.8	.5	.5	.0	4.5	.0	.0	.0	19.9	2.7	.9	1.8	1.4	.0	.0	.0	.0
51	Q	1.5	7.6	.0	.8	.0	.4	.0	3.0	.4	1.5	.0	17.0	.8	.8	.4	1.1	.0	.0	1.9	.0
30	S	20.2	.0	19.7	4.3	.0	1.9	.0	2.4	.0	.0	.0	6.3	.5	.0	.0	.0	.0	.0	.0	.0
30	T+	18.0	.0	2.2	4.5	1.1	.0	1.1	5.6	.0	.0	.0	15.7	2.2	1.1	1.1	1.1	.0	.0	2.2	.0
30	T-	.5	.0	1.6	.5	.0	.0	.0	1.6	.0	1.1	.0	20.5	.0	.0	.5	.0	.0	.0	.0	.0
30	T/O	1.4	.0	.5	3.2	.5	.5	.0	1.4	.0	.9	.0	21.1	.9	.5	.5	1.4	.5	.0	.0	.5
30	O+	.5	9.3	.0	.0	.0	1.5	.0	2.0	.0	1.0	.0	15.7	1.0	.5	.5	1.0	.0	.5	1.0	.0

		PAPU	PODO	DACR	RAPA	ASTT	QUIN	SYMP	COPR	HALO	DRIM	STYP	ERC1	ERC2	ERC3	DRAP	RANU	GENT	POTT	TRIG	APIA
20	S	.0	.0	12.7	15.2	.0	.0	.0	7.6	.0	.0	.0	.0	.0	.0	2.5	178.5	6.3	6.3	.0	.0
20	S/T	.0	.5	6.4	7.9	2.5	.0	.0	3.0	.5	.0	.0	.5	.5	.0	.5	21.8	3.0	1.0	1.5	.0
20	T+	.0	.0	14.0	14.0	.0	.0	.0	2.1	.0	.0	.0	.7	.0	.0	.7	3.5	.7	.0	.0	.0
20	T-	.0	.0	17.6	12.8	1.4	.0	.0	.0	.7	.7	.7	1.4	.0	.0	.7	.7	.0	.7	.0	.0
20	TT/O	.0	.7	22.0	16.7	.7	.0	.0	1.3	1.3	.7	.0	2.0	.0	.7	.0	1.3	.7	.0	.0	.0
20	T/O	.0	.0	25.0	30.7	.0	.0	.0	1.7	.6	.6	.0	1.1	.6	.0	.0	.6	1.1	.0	.0	.0
20	OO/T	.0	.0	46.0	37.6	1.1	.5	.3	.8	1.6	.0	.3	.5	.0	.3	.0	.0	.0	.0	.0	.0
20	O+	.0	.3	48.4	36.5	.5	.5	.3	.5	2.3	.0	.0	.8	.3	.0	.0	.0	.0	.0	.0	.0
21	S	.0	.9	10.6	9.7	1.8	.0	.0	3.7	1.8	.5	.0	.0	.0	.0	.9	43.3	.5	.5	.0	.9
21	S/T	.0	.0	5.9	8.0	1.6	.0	.0	1.1	.5	.0	.0	.0	.0	.5	.5	37.8	.5	1.1	3.2	3.2
21	T+	.0	.4	5.9	5.5	1.3	.0	.0	3.4	.4	.0	.0	.4	.0	.0	.4	22.4	.0	.0	.0	.8
21	T-	.0	.5	21.8	12.5	4.6	.0	.0	2.3	.9	.0	.0	.0	.0	.0	.0	6.0	.0	.0	.5	.0
21	T/Q	.0	.5	36.8	13.2	1.4	.5	.0	.9	1.9	.0	.0	.0	.0	.5	.0	.0	.5	.5	.0	.9
21	Q	.0	2.3	58.1	16.7	.9	.0	.0	.5	.5	.0	.0	.5	.0	1.4	.0	.0	.0	.0	.0	.0
22	S	.0	1.8	13.8	11.9	.9	.0	2.8	3.7	.0	.0	1.8	.0	.0	.0	.9	105.5	.0	.0	1.8	2.8
22	S/T	.0	.0	10.7	9.8	3.3	.0	.0	3.3	.9	.0	.5	.0	.5	.0	.0	.0	.0	.0	.0	1.9
22	T+	.0	.5	9.5	8.1	.9	.0	.5	2.4	.0	.0	.9	.0	.5	.0	.0	2.8	.0	.0	.0	1.4
22	T-	.0	.0	17.0	13.3	1.8	.0	.0	1.4	.9	.0	.5	.9	.5	.9	.0	.5	.0	.0	.0	1.4
22	TT/O	.0	.9	44.7	42.5	.4	.0	.0	.9	.0	.0	.0	.9	.9	.9	.0	.0	.0	.0	.0	.0
22	T/O	.0	1.4	51.2	38.0	.0	.5	.5	.9	.0	.0	.5	.0	1.4	2.3	.0	.0	.0	.0	.0	.0
22	O+	.0	2.6	66.8	23.7	.0	.0	.0	.5	.0	.0	.0	1.6	.0	1.6	.0	.0	.0	.0	.0	.0
25	S	.0	.4	10.8	12.1	.9	.0	.0	5.4	9.0	.0	.4	4.0	14.3	.4	.4	71.7	.0	.0	.0	.0
25	T+	.0	1.4	19.5	17.2	2.3	.0	.5	2.7	8.1	.5	.9	.9	.0	.5	.0	.0	.5	.9	.0	.0
25	T-	.0	1.4	17.3	22.9	.7	.4	.0	2.1	14.1	1.1	.0	.7	.4	.0	.0	.7	.4	.0	.0	.0
25	TT/O	.0	.0	38.3	21.1	.6	1.1	.0	.6	8.6	.0	.0	.0	.6	1.1	.0	.0	.6	.0	.0	.6
25	T/O	.0	.0	40.1	23.7	.4	.9	.9	.4	18.1	.4	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
25	OO/T	.0	1.3	52.4	25.8	.4	1.3	.0	.9	7.4	.9	.0	.4	.0	.0	.0	.0	.0	.0	.0	.0
25	O+	.0	1.8	42.9	31.3	.5	1.4	.0	2.8	6.0	1.4	.5	1.8	.0	.0	.0	.0	.5	.0	.0	.0
23	S	.0	.6	8.0	7.5	1.1	.0	.0	5.7	1.7	.0	.0	.0	.0	.0	.0	1.1	2.9	.0	.0	.0
23	T+	.0	.5	11.5	18.7	1.9	1.4	.0	2.4	.5	.0	.5	.0	.5	.0	.0	.0	3.3	1.9	.0	.0
23	T-	.0	.6	18.6	19.2	2.4	.6	.0	.0	2.4	.0	.0	.6	.6	.0	.0	.0	2.4	1.2	.0	.0
25	TT/Q	.0	1.2	23.6	24.8	2.4	1.2	.6	.0	1.2	.0	.0	.6	.6	.0	.0	1.8	3.0	1.2	.0	.0
23	T/Q	.0	2.1	26.2	25.5	2.8	.7	.0	.0	.7	.0	.0	.0	.7	.7	.0	1.4	.0	.0	.0	.0
23	Q	.0	.6	25.2	34.4	3.1	.6	.0	2.5	.6	.0	.0	.6	.6	.0	.0	.0	5.5	3.1	.0	.0
51	S	.0	.0	13.0	2.7	2.2	.0	.0	9.8	.0	.0	.5	1.1	.5	.0	.0	3.8	.0	.0	.0	.0
51	S/T	.0	.6	3.4	1.1	1.1	.0	.0	2.3	.0	.6	.0	2.3	1.7	.0	.0	2.8	.0	.0	.0	.0
51	T+	.0	.6	2.4	1.2	.0	.0	.0	1.2	.0	.6	.0	2.4	.0	.0	.0	1.8	.6	.0	.0	.0
51	T-	.4	.4	30.0	7.5	.0	.4	.0	1.8	.0	.0	.0	3.1	1.3	.0	.4	1.8	.4	.0	.0	.0
51	T/Q	.0	.0	35.3	10.4	.0	.5	.0	2.3	.0	.0	.0	1.4	.5	.0	.0	.5	1.4	1.8	.0	.0
51	Q	.0	1.1	41.7	15.9	.0	.0	.4	.8	.0	.0	.0	.4	.4	.4	.0	.4	.0	.4	.0	.0
30	S	.0	.5	7.7	1.9	1.9	.0	.0	26.4	2.4	.0	3.8	1.4	.0	.5	1.0	132.2	.5	.5	3.4	1.0
30	T+	.0	2.2	22.5	19.1	3.4	1.1	.0	1.1	.0	2.2	1.1	.0	.0	1.1	.0	1.1	1.1	.0	.0	.0
30	T-	.0	.5	50.3	31.4	.5	2.7	.0	.0	1.1	1.1	.0	.0	.5	2.7	.0	.0	.0	.0	.0	.0
30	T/O	.9	.0	31.2	35.8	.9	4.1	.0	1.4	1.8	.0	.5	1.4	2.8	1.8	.0	.0	.0	.0	.0	.0
30	O+	.0	2.5	35.8	41.2	.0	2.0	.0	1.5	.5	.0	.0	.5	1.5	5.9	.0	.0	.0	.5	.0	.0

		LIGU	ASTL	POA1	POA2	POA3	POA4	CYP1	CYP2	CENT	VULC	CYAT	PTER	BELV	TRSP	UNK1	FERN	HERB	TREE	UNKN
20	S	.0	17.7	2.5	13.9	5.1	17.7	.0	13.9	.0	.0	5.1	.0	.0	1.3	.0	6.3	.0	1.3	2.5
20	S/T	.0	8.4	2.5	23.3	7.9	26.2	1.5	8.9	.0	.0	6.4	.0	.0	.5	1.5	5.0	.0	1.0	.0
20	T+	.0	68.5	.7	20.3	7.7	24.5	.0	7.7	.0	.0	7.0	.0	.0	.0	.0	2.1	.0	1.4	.0
20	T-	.0	59.5	1.4	20.3	9.5	19.6	2.0	6.8	.0	.0	5.4	.0	.0	.0	1.4	2.7	.0	.0	2.0
20	TT/O	.7	16.7	.0	14.7	11.3	14.0	1.3	7.3	.0	.0	4.7	.0	.0	.0	.0	4.0	.0	.0	.0
20	T/O	.0	18.2	2.8	13.1	2.8	4.5	.6	10.2	.6	.0	2.3	.0	.0	.0	2.3	4.0	.0	.0	.0
20	OO/T	.0	.0	.0	.8	.8	2.2	.3	3.0	.0	.0	2.5	.0	.0	.0	.0	3.8	.0	1.4	1.6
20	O+	.0	.8	.3	1.8	.3	1.0	.0	1.8	.0	.0	2.6	.0	.0	.0	1.0	4.1	.0	.3	.3
21	S	.9	5.1	.9	31.8	4.6	13.4	.0	14.3	.0	.0	4.6	.5	.0	.0	.5	3.7	.0	.5	.0
21	S/T	2.7	12.2	1.6	36.2	12.2	19.7	1.6	7.4	.0	.0	3.7	.0	.0	.0	.0	1.6	.0	.0	.5
21	T+	.8	12.2	1.3	59.1	7.6	5.5	.4	3.4	.0	.0	4.2	.0	.0	.4	.0	.8	.0	.4	.4
21	T-	.5	41.7	.5	37.0	5.6	7.9	.0	.9	.0	.0	5.1	.0	.0	.0	.0	1.4	.0	.0	.0
21	T/Q	.0	5.7	1.4	33.0	1.9	2.8	.0	2.4	.0	.0	2.4	.9	.0	.0	.0	.5	.0	.0	.0
21	Q	.0	.0	.0	8.1	2.7	5.0	.5	1.8	.0	.0	2.3	1.4	.0	.0	.0	2.7	.0	.0	.0
22	S	1.8	.0	.9	13.8	7.3	5.5	5.5	14.7	.0	.0	15.6	.0	.0	.9	.0	2.8	.0	.0	.0
22	S/T	1.4	.0	.9	22.3	12.6	17.7	.5	8.4	.0	.0	8.8	.0	.0	2.8	.0	2.3	.0	.0	.0
22	T+	.5	.0	1.4	26.1	12.3	26.1	.0	2.8	.0	.0	7.6	.0	.5	3.8	.0	5.7	.0	.0	.0
22	T-	.0	.0	.9	23.9	7.8	25.2	.0	1.4	.0	.0	4.6	.0	.0	4.6	.0	5.0	.0	.5	.5
22	TT/O	.0	.0	.0	3.1	1.3	1.8	.0	.0	.0	.0	1.8	.0	.0	.0	.0	3.9	.0	.0	.0
22	T/O	.0	.0	.0	1.9	.5	.9	.0	.0	.0	.0	1.9	.0	.0	.0	.0	2.3	.0	.0	.0
22	O+	.0	.0	.0	1.1	1.1	.0	.0	1.1	.0	.0	1.6	.0	.0	.0	.0	2.1	.0	.0	.0
25	S	.0	1.8	.0	9.0	5.4	9.9	.0	11.7	.0	.0	6.3	.0	.0	.4	.0	4.0	.0	.0	.0
25	T+	.0	.9	1.8	10.4	10.0	10.0	.0	9.5	.0	.0	3.2	.0	.0	2.7	.0	.9	.0	.5	.0
25	T-	.0	2.1	.7	7.4	3.5	7.4	.7	10.6	.0	.0	6.3	.0	.0	4.2	.0	3.2	.0	.4	.7
25	TT/O	.0	.6	.0	3.4	8.6	8.6	2.3	1.1	.0	.0	4.6	.0	.0	4.0	.0	2.3	.0	.0	.0
25	T/O	.0	2.2	.0	3.9	1.7	.4	.0	.4	.0	.0	7.3	.0	.0	.4	.0	3.4	.0	.4	.0
25	OO/T	.0	.0	.0	1.3	2.2	.0	2.2	.4	.0	.0	1.7	.0	.0	.0	.0	2.6	.0	.0	.0
25	O+	.0	1.4	.0	.0	1.4	1.8	.0	2.3	.0	.0	1.4	.0	.0	.0	.0	1.4	.0	1.8	.0
23	S	.0	13.8	.0	3.4	2.9	19.0	5.2	29.9	.0	.0	14.4	.0	.0	.0	2.3	9.8	.0	.0	.0
23	T+	1.0	86.1	.5	12.4	3.3	23.4	1.9	12.0	.5	.5	5.3	.0	.0	.0	1.4	2.4	.0	.5	.0
23	T-	.0	13.8	.0	7.2	5.4	7.2	.6	19.8	.0	.0	12.0	.0	.0	.0	3.6	2.4	.0	.0	.0
25	TT/Q	1.8	10.3	.0	2.4	1.2	4.8	6.1	14.5	.0	.0	12.1	.0	.0	.0	4.2	3.0	.0	.0	3.6
23	T/Q	.0	6.9	.0	2.1	.7	4.1	.7	13.1	.0	.0	16.6	.0	.0	.0	.7	4.8	.0	.0	.0
23	Q	.6	.0	.0	3.1	1.2	.0	3.7	14.1	6.1	.0	5.5	.0	.0	.0	3.1	1.8	.0	.6	1.2
51	S	.5	1.1	1.1	6.0	4.9	6.0	.5	19.0	.0	.0	28.3	1.1	1.1	1.6	.0	5.4	.0	.5	.5
51	S/T	.0	1.7	1.1	7.9	6.2	22.6	6.8	27.1	.0	.0	14.1	.6	.0	1.1	.6	4.0	.0	.0	2.3
51	T+	.0	.6	1.2	11.4	3.0	30.7	2.4	31.9	.0	.0	10.8	.6	.0	1.2	.0	.6	.0	.6	1.2
51	T-	.0	42.7	2.2	14.1	2.2	26.4	.9	2.6	.0	.0	6.6	.4	.9	.0	.9	1.3	.0	.4	.4
51	T/Q	.0	8.1	.9	19.9	3.2	13.1	.0	1.8	.0	.0	6.8	.5	.0	.0	1.8	2.3	.0	.5	1.8
51	Q	.0	.0	2.3	9.1	4.9	15.2	.0	1.5	.0	.0	4.2	1.1	.0	.0	.8	1.9	.0	.0	.4
30	S	.0	1.4	.0	14.9	7.2	9.1	.0	7.7	.0	.0	14.9	.5	1.0	.5	.0	8.2	.0	.0	1.0
30	T+	.0	.0	.0	12.4	1.1	14.6	1.1	3.4	.0	2.2	9.0	.0	.0	1.1	.0	5.6	.0	.0	1.1
30	T-	.0	1.1	.0	.5	1.1	2.2	.0	.0	.0	.0	7.6	.0	.0	.0	.0	10.3	.0	.0	2.2
30	T/O	1.4	.0	.0	1.4	.0	1.4	.0	.9	.0	.0	14.2	.0	.0	.0	.0	10.6	.0	.0	.5
30	O+	.0	.0	.0	.5	.5	1.0	.0	.5	.0	.0	10.3	.0	.0	.0	.0	3.4	.0	.0	3.4

		CHAR	LYCO	CASU	TREM	DODN	URTM	ACAL	MACA	CELT	SAUR	EUPH	NOTH	CAST	ASCA	RUTA	PHYL	PRUN	CUNO	ELAE	MYRT
29	S	10.3	.0	27.7	8.2	.0	1.1	.0	3.3	.5	.0	.5	12.5	.0	.5	.0	.5	.0	.0	.0	.5
29	T+	43.5	.0	8.7	3.8	.0	1.6	.0	1.6	.0	1.6	.0	13.6	1.6	.5	.5	.5	.0	.0	.5	.0
29	T-	2.1	.0	2.1	3.7	.0	.5	.0	.5	.0	.0	.0	11.0	1.0	.5	1.0	.5	.5	.0	.5	.0
29	Q	.4	.0	.4	1.3	.0	.0	.0	4.0	.0	.0	.0	15.9	.4	.4	.9	.4	.0	.4	.0	.0
27	S	4.0	.0	20.1	11.2	.9	.9	.4	3.1	.0	.4	.9	8.9	.9	1.3	.4	.0	.4	.0	.0	.9
27	T+	7.5	.0	10.4	.5	.5	.5	.0	3.0	.0	.0	.0	13.4	2.5	.5	.0	1.0	.0	.0	1.0	.0
27	T-	2.6	.0	4.0	1.3	.0	.0	.0	2.0	.0	.7	.0	37.1	1.3	.0	.0	.0	.0	.7	.0	.0
27	Q	1.2	17.2	3.0	3.6	.6	2.4	.0	7.1	.0	.6	.0	34.3	1.2	.6	1.8	.6	.0	.6	.0	1.2
47	S	333.3	.0	13.3	4.4	1.1	1.1	.0	2.8	.0	.0	2.2	10.6	.6	1.1	1.1	.6	.0	.0	.0	.0
47	S/T	460.4	.0	7.4	1.8	.5	2.8	.5	2.8	.9	.0	.0	6.0	.5	.9	.0	1.8	.0	.0	.5	.0
47	T+	80.2	19.8	1.6	4.8	.0	.0	.0	3.2	.5	.5	1.1	11.8	2.1	.5	1.6	1.6	.0	.5	.5	.0
47	T-	10.6	13.6	.5	1.5	.0	.5	.0	4.5	.0	.0	1.0	20.1	3.5	2.0	.0	.5	1.0	.0	.0	.0
47	Q	.5	15.8	.5	.5	.0	.5	.0	3.7	.0	1.6	.0	25.8	2.1	.5	2.1	.5	.0	.0	.0	.5
12	S	416.7	.0	7.4	3.2	.5	1.9	.5	1.9	.0	.0	.5	4.6	.0	.9	.5	.0	.0	.0	.9	.0
12	S/T	169.9	3.4	2.4	.5	1.0	1.9	.5	1.0	.0	.0	.5	8.7	1.0	1.0	.5	.0	.0	.0	.5	.0
12	T+	12.1	7.4	.9	1.9	.0	.9	.5	.9	.0	.5	.5	7.4	.0	.0	.0	.5	.0	.0	.0	.0
12	T-	12.7	8.0	.5	.0	.0	.5	.0	1.4	.5	.5	.5	9.4	.5	.5	.0	.5	.0	.0	.9	.0
12	TT/O	1.3	.0	.4	.0	.0	.4	.0	.9	.0	1.3	.4	11.7	.0	.0	.0	.0	.0	.4	.4	.0
12	T/O	.5	.0	.0	.0	.0	.5	.0	1.0	.0	.5	1.0	9.1	.0	1.0	.5	.5	.0	.0	.0	.0
12	O+	.4	6.1	.0	.0	.0	1.3	.0	2.2	.0	.0	1.3	7.0	.4	1.7	.0	.0	.0	.0	.4	.0
49	S	396.9	.0	7.6	.8	.8	.0	.0	.0	.0	.0	.0	5.3	.0	.0	.0	.0	.0	.0	.0	.0
49	T+	330.4	.0	1.8	.0	.0	.0	.0	.9	.0	.0	.0	6.3	.0	.0	.0	.0	.0	.0	.0	.0
49	T-	9.2	.0	.8	.0	2.3	.0	.0	.8	.0	.0	.0	8.4	.0	.0	.0	.0	.0	.0	.0	.0
49	T/Q	.5	.0	.5	.0	.5	.5	.0	.0	.0	.0	.0	11.1	.5	.5	.0	.5	.5	.0	.5	.0
13	S	54.8	.0	8.2	1.4	.9	1.4	.0	.5	.0	.5	.0	8.7	.5	1.4	.0	.0	.0	.5	.0	.0
13	T+	58.6	.0	2.5	.8	.4	.0	.0	.4	.0	.4	.4	12.1	.4	1.3	.4	.0	.0	.0	.0	.0
13	T-	1.0	.0	1.4	1.4	.0	.5	.0	2.9	.0	.0	.0	13.8	1.4	1.4	1.0	.5	.0	.5	.5	.0
13	T/O	1.0	.0	.0	.0	.0	.5	.0	1.0	.5	.5	.5	12.2	2.0	1.0	.5	.0	.0	.0	.0	.0
13	O+	.5	4.9	.0	.5	.0	1.0	.0	.5	.5	.0	.5	10.3	1.5	.5	.0	.5	.5	.0	.0	.0
10	S	152.7	.0	25.6	3.9	.0	1.5	.0	2.5	.0	.0	.5	3.4	.5	.5	.0	.0	.0	.0	.0	.0
10	S/T	56.0	.0	2.2	2.2	.0	1.7	.0	.4	.0	.0	.0	3.9	.4	.0	.0	.0	.0	.0	.0	.0
10	T+	83.7	.0	1.4	.9	.0	1.4	.5	.0	.0	.0	.0	2.8	.0	.0	.0	.0	.0	.0	.0	.0
10	T-	4.3	.0	1.0	1.4	.0	.5	.5	1.0	.5	.5	.0	5.3	1.0	.5	.0	.0	.0	.0	.5	.0
10	Q	1.5	.0	.0	1.9	.0	1.0	.0	1.5	.0	.0	.0	4.9	.5	.0	.5	.0	.0	.0	.5	.0
17	S	5.0	.0	33.9	11.5	2.8	.0	.0	3.7	.0	.0	.5	11.0	2.3	.0	.5	.0	.0	.0	1.4	.0
17	T+	1.2	17.4	2.4	2.4	.0	.8	.0	3.6	.0	.0	.8	9.5	2.4	1.2	.4	1.6	.4	.4	.0	.0
17	T-	.8	.0	1.7	.4	.4	.0	.4	1.7	.0	.8	.0	11.3	2.1	.8	1.3	.4	.0	.0	.4	.4
17	T/O	.9	14.4	.0	.9	.0	2.8	.0	2.8	.0	.9	.0	13.9	.5	.5	.0	1.9	.0	.0	.9	.0
17	O+	.5	7.0	.0	.5	.5	1.1	.0	2.7	.0	.0	.0	18.9	.0	.0	.0	.0	.0	1.1	.0	.0
14	S	7.8	.0	7.8	4.9	.4	4.1	.0	3.3	.0	.0	.4	9.4	.8	.4	.8	.0	.0	.0	.0	.0
14	T+	18.5	10.4	4.7	.9	.0	3.8	.5	1.4	.0	.5	.5	7.6	.9	.0	.5	.0	.0	.0	.9	.0
14	T-	.8	10.8	1.2	1.6	.0	2.8	.4	2.4	.0	.0	.4	14.4	.4	.8	.0	.4	.0	.4	.4	.0
14	T/O	.9	.0	.9	.5	.0	.0	.0	.9	.5	.0	.5	9.3	.5	.9	.0	1.4	.0	.0	.0	.0
14	O+	.4	6.3	.8	.4	.0	.4	.0	.8	.0	.8	.4	8.0	.0	.4	.0	.4	.0	.0	.4	.0

		PAPU	PODO	DACR	RAPA	ASTT	QUIN	SYMP	COPR	HALO	DRIM	STYP	ERC1	ERC2	ERC3	DRAP	RANU	GENT	POTT	TRIG	APIA
29	S	.0	1.1	17.4	14.7	.0	.5	.0	5.4	.0	.5	.0	.5	.5	.0	1.1	129.3	.0	1.6	1.6	.0
29	T+	.0	1.1	23.9	23.4	.0	.5	.0	.5	.0	.0	.0	.5	.0	.0	.0	4.9	.0	.0	.0	.0
29	T-	.0	.5	33.0	33.5	1.0	.0	.0	.5	.0	.0	.5	.5	1.0	.5	.0	.0	.0	.0	.0	.0
29	Q	.0	.9	44.2	31.4	1.3	.4	.0	.9	.0	.0	.4	.9	2.2	1.3	.0	.4	.4	.4	.0	.0
27	S	.0	1.8	4.0	11.6	.4	.9	.0	5.4	.9	.0	.4	.0	.0	.0	.4	21.4	2.7	.0	.0	.9
27	T+	.0	.0	5.0	11.9	2.5	.0	.0	.5	.0	.0	.0	.0	.0	.0	.0	.5	3.5	1.0	.0	.0
27	T-	.0	.7	27.2	27.8	.0	.7	.0	1.3	1.3	.0	.0	.0	.7	.0	.0	.7	.0	.0	.0	.0
27	Q	.0	.6	21.9	32.5	2.4	.0	.0	.6	.0	.0	.0	.0	.0	.0	.0	1.2	1.2	1.8	.0	.0
47	S	.0	.6	4.4	8.3	1.1	.0	.0	.0	.0	.0	.0	.0	.0	.0	2.2	57.2	2.8	3.9	.6	.0
47	S/T	.0	.0	4.6	9.2	2.8	.0	.0	2.8	.0	.0	.0	.0	.5	.9	.5	28.6	1.8	.0	.0	7.8
47	T+	.0	.0	9.1	11.2	1.6	.5	.0	1.1	.5	.0	.5	1.1	.0	.5	.5	13.9	1.1	.5	.0	.0
47	T-	.0	.0	15.6	16.1	1.5	.0	.0	.0	.0	.0	.5	3.0	.0	.0	.0	9.0	2.0	4.0	.5	.0
47	Q	.0	.0	25.8	10.0	2.1	.0	.0	1.6	.0	.0	.0	1.6	.5	.0	.0	1.1	.5	.0	.0	.0
12	S	.0	.9	6.0	15.3	.0	.0	.0	.0	.9	2.3	.0	.5	.0	.5	.0	.9	.0	.0	.0	.0
12	S/T	.0	.0	6.3	25.7	1.0	.0	.0	1.5	.5	1.0	.0	.0	.0	1.0	.0	1.5	.0	.0	.0	.0
12	T+	.5	.9	18.6	46.5	.5	.5	.0	.0	.0	2.8	.0	.5	.5	.5	.0	.0	.0	.9	.0	.0
12	T-	.0	.5	21.6	44.6	.0	.0	.0	1.4	.0	2.3	.5	.0	.5	1.4	.0	.0	.0	.0	.0	.0
12	TT/O	.0	.4	31.7	52.2	.0	.4	.0	.9	.9	1.7	.0	1.7	.0	1.7	.0	.0	.0	.0	.0	.0
12	T/O	.0	.5	28.4	53.8	1.4	.5	.0	.0	.0	6.3	.0	.0	.0	1.4	.0	.0	.0	.0	.0	.0
12	O+	.0	.4	48.3	27.0	.0	.4	.0	.4	.4	10.4	.0	.0	.4	.9	.0	.0	.0	.0	.0	.0
49	S	.0	.0	23.7	20.6	3.1	.0	.8	8.4	2.3	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
49	T+	.0	.0	19.6	27.7	1.8	.0	.0	8.0	.9	1.8	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
49	T-	.0	.0	30.5	34.4	.0	.0	.8	4.6	.0	1.5	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
49	T/Q	.0	.0	44.4	37.0	.0	.0	.0	2.1	.0	5.8	.0	.0	.0	2.6	.0	.0	.0	.0	.0	.0
13	S	.0	.9	7.8	11.9	.9	.0	.0	3.2	.9	.0	.5	.5	.5	.0	.0	145.2	.9	.0	.0	.5
13	T+	.0	.4	12.6	17.6	.8	.4	.0	.8	.0	.4	.0	1.7	.8	.4	.0	13.8	.4	.8	.4	.0
13	T-	1.0	.0	39.0	32.9	1.0	.0	.0	2.9	6.2	.0	.5	.0	2.4	.5	.0	.5	.0	.0	.0	.5
13	T/O	.0	1.0	51.0	30.1	1.5	.5	.0	2.0	.0	1.0	.5	.0	.5	.0	.0	.0	.0	.0	.0	.0
13	O+	.0	.5	59.6	26.1	.0	.0	.0	1.0	.5	1.5	1.0	1.0	.5	.5	.0	.0	.0	.0	.0	.0
10	S	.0	.5	4.9	11.3	.0	.5	.0	.0	1.0	.0	.0	.5	.0	.0	.0	.0	.0	.0	.0	.0
10	S/T	.0	.4	4.7	12.5	.4	.0	.0	.9	1.3	.9	.0	.0	.4	.4	.0	.9	.0	.0	.0	.0
10	T+	.0	.5	5.6	15.3	.0	.9	.0	2.8	.9	.0	.0	.5	.0	.0	.0	.5	.0	.0	.0	.5
10	T-	.0	.5	13.9	14.4	1.4	.0	.0	1.0	2.4	1.9	.5	.5	.0	.5	.0	.5	.0	.5	.0	.0
10	Q	.0	1.0	15.0	11.7	1.0	.0	.0	.0	1.9	2.4	.0	.5	.0	.0	.0	1.0	.5	.0	.0	.0
17	S	.0	.5	6.9	12.4	.0	.0	.0	6.0	1.8	.0	.0	.0	.0	.0	.5	44.5	.0	.5	.0	1.4
17	T+	.4	1.2	18.6	13.8	1.6	.0	.0	2.0	2.4	.0	.0	1.6	.4	.0	.0	5.5	.8	.0	.4	.0
17	T-	.0	2.1	30.5	15.1	2.9	.4	1.7	.4	5.0	.0	.8	.0	.8	.4	.0	2.1	.0	.4	.0	.0
17	T/O	.0	1.4	24.5	19.0	.9	.0	.0	.5	.0	.0	.0	.5	.9	.0	.0	.0	.0	.5	.0	.0
17	O+	2.7	1.1	37.8	24.3	2.2	.0	.5	.0	.0	.5	.0	.5	.0	.0	.0	1.6	.0	.5	.0	.0
14	S	.0	.4	13.9	10.6	.8	.8	.0	1.2	.8	.0	.8	.8	.4	.8	.8	40.4	18.8	1.2	.0	.8
14	T+	.0	.0	5.2	6.2	.5	.0	.0	.0	.0	.0	.0	.0	.5	.0	.5	10.4	.0	.0	.0	1.9
14	T-	.4	.8	31.2	20.0	.4	.0	.0	.8	.0	.8	.0	.0	.0	.0	.0	.0	.0	.4	.0	.8
14	T/O	.0	1.4	32.6	27.0	.0	.5	.0	1.4	.0	.0	.5	.0	.5	.0	.0	.0	.0	.0	.0	.0
14	O+	.0	1.3	35.7	20.2	.0	.0	.0	.4	.4	.0	.4	3.4	2.9	.0	.0	.0	.0	.0	.0	.0

		LIGU	ASTL	POA1	POA2	POA3	POA4	CYP1	CYP2	CENT	VULC	CYAT	PTER	BELV	TRSP	UNK1	FERN	HERB	TREE	UNKN
29	S	.0	2.7	.0	13.6	4.9	15.8	.0	7.6	.0	.0	16.3	.0	.0	.5	.0	37.0	.0	.0	1.1
29	T+	.0	.0	.5	13.0	6.0	14.1	.0	10.9	.0	.0	3.8	.0	.0	.0	.0	2.2	.5	.0	1.1
29	T-	.0	.0	.5	8.4	1.0	6.8	.0	7.9	.0	.0	2.6	.0	.5	.0	.0	3.7	.0	.5	.5
29	Q	.0	.0	.0	2.2	.9	4.4	.0	6.2	.0	.0	1.8	.0	.0	.0	.0	1.3	.0	.4	.0
27	S	.0	1.3	.4	14.3	5.4	8.5	6.7	30.8	.0	.0	6.7	.4	.4	.0	.0	7.1	.0	.0	.4
27	T+	.5	6.5	.0	15.9	1.5	38.3	.0	9.0	.0	.0	13.9	1.5	.0	.0	.0	4.5	.0	.0	1.0
27	T-	.0	6.6	.0	6.6	3.3	6.0	.0	19.2	.0	.0	5.3	.0	.0	.0	.0	5.3	.0	.0	.7
27	Q	.0	43.8	.0	2.4	3.6	3.6	3.6	16.0	3.6	.0	10.1	.0	.0	.0	1.8	3.0	.0	.6	1.2
47	S	.0	6.1	.6	1.1	5.0	54.4	.0	10.6	.0	.0	11.1	.0	.0	.0	.0	1.1	.0	.0	1.1
47	S/T	.5	61.3	1.4	42.9	15.2	4.1	.5	3.7	.0	.0	9.7	.0	.0	.0	.0	3.2	.5	.5	1.4
47	T+	.0	97.9	.5	7.0	5.3	37.4	1.1	11.2	.0	.0	8.0	.5	.0	.0	.0	2.1	.0	.5	1.1
47	T-	.0	50.8	.0	12.6	1.5	29.1	.0	11.1	.0	.0	6.5	.0	.0	.0	1.0	3.5	.0	.0	1.0
47	Q	.0	1.1	.0	12.1	2.1	33.2	.5	4.2	.0	.0	3.2	4.2	.0	.0	.0	2.6	.0	.0	.5
12	S	.5	.0	.0	36.6	10.2	21.3	.0	.0	.0	.0	4.6	3.2	.0	.0	.0	4.2	.0	.0	1.4
12	S/T	.5	.0	.0	22.3	2.9	29.6	.0	.0	.0	.0	7.8	.5	1.0	1.9	.0	2.4	.0	.0	1.0
12	T+	.5	.0	.0	10.2	4.7	7.0	.0	.0	.0	.0	7.0	1.9	.9	.9	.0	3.7	.5	.0	.9
12	T-	.0	.0	.5	11.7	4.2	5.6	.0	.0	.0	.0	5.6	.0	1.4	.0	.0	3.8	.0	.0	1.9
12	TT/O	.0	.0	.0	1.3	3.0	1.3	.0	.9	.0	.0	3.5	.0	.4	.0	.0	1.7	.0	.0	.9
12	T/O	.0	.0	.0	2.9	1.4	.0	.0	.0	.0	.0	2.9	8.7	1.0	.0	.0	2.4	.0	.5	1.0
12	O+	.0	.0	.0	.4	.0	.4	.0	.0	.0	.0	9.6	10.9	.0	.0	.0	4.3	.0	.9	.4
49	S	.0	.0	.0	20.6	6.1	6.1	.0	.0	.0	.0	8.4	13.0	.0	.0	.0	.0	.0	.0	.0
49	T+	.0	.0	.0	21.4	9.8	1.8	.0	.0	.0	.0	7.1	13.4	.9	.0	.0	4.5	.0	.0	.0
49	T-	.0	.0	.0	12.2	6.9	1.5	.0	.0	.0	.0	7.6	26.0	2.3	.0	.0	5.3	.0	.0	2.3
49	T/Q	.0	.0	.0	1.1	.5	1.6	.0	.5	.0	.0	5.8	34.9	3.2	.0	.0	2.1	.0	.0	.5
13	S	.0	.9	.0	18.3	11.0	16.0	.5	19.2	.0	.0	6.8	.0	.0	.0	.0	4.6	.0	.0	.0
13	T+	.0	1.7	.4	11.3	7.5	20.9	.8	11.7	.0	.0	10.0	.0	.0	.0	.0	4.2	.4	.0	.0
13	T-	.0	.0	.0	2.9	.5	3.3	.0	1.4	.0	.5	3.8	.0	.0	.0	.0	3.3	.0	.0	.5
13	T/O	.0	.0	.0	1.5	.0	1.5	.0	1.0	.0	.0	6.1	1.0	.5	.0	.0	3.6	.0	.0	1.0
13	O+	.0	.0	.0	1.0	.0	.5	.0	.5	.0	.0	5.4	.5	.0	.0	.0	2.0	.0	.0	1.0
10	S	.5	.0	.0	53.7	13.8	1.5	.0	1.0	.0	.0	10.8	.0	.0	1.0	.0	3.4	1.0	.0	2.0
10	S/T	.0	.0	.0	55.2	11.2	.0	1.7	.0	.0	.0	10.3	.0	.4	.4	.0	4.7	.4	.0	.9
10	T+	.5	.0	.0	54.9	11.2	.0	.5	.0	.0	.0	7.0	.0	.0	.5	.0	4.7	.0	.0	.0
10	T-	.0	.0	.0	43.8	10.6	4.3	.0	1.4	.0	.0	2.9	.0	.0	.0	.0	2.4	.0	.5	3.4
10	Q	.0	.0	.0	18.9	4.9	36.4	.0	2.4	.0	.0	3.4	1.5	.0	.0	.0	1.0	.0	.5	.0
17	S	.0	.0	.0	12.4	3.7	21.1	.0	10.6	.0	.0	24.3	.0	.0	.5	.0	10.1	.0	.0	.5
17	T+	.0	.0	.0	9.5	7.9	7.5	.8	7.5	.0	.0	22.1	.4	.4	.8	.0	13.0	.0	.4	.0
17	T-	.0	.0	.0	3.3	4.6	5.9	.0	5.0	.0	.8	18.0	.0	.0	.0	.0	14.2	.0	.4	.8
17	T/O	.0	.0	.5	10.6	3.2	1.4	.5	14.8	.0	.5	18.5	.0	.0	.0	.5	13.4	.0	.5	.0
17	O+	.0	.0	.0	4.3	.5	3.8	2.2	10.8	.0	.0	11.4	.0	1.1	.0	.0	13.0	.0	.5	1.1
14	S	.4	1.2	.4	14.3	2.9	4.9	4.9	21.6	.0	.0	19.2	.0	.0	.0	.0	5.3	.0	.0	.4
14	T+	.9	.0	1.9	28.4	5.2	17.1	.0	19.0	.0	.0	15.6	.0	.5	.0	.0	.9	.0	.0	.9
14	T-	.4	.0	.8	11.2	3.6	4.8	.0	5.6	.0	.0	18.8	.4	1.2	.0	.0	4.4	.4	.0	.0
14	T/O	.0	.0	.5	12.1	1.4	7.0	.5	1.9	.0	.0	10.7	.0	1.4	.0	.0	3.3	.0	.0	.0
14	O+	.0	.0	.4	14.7	2.1	3.4	.0	5.0	.0	.0	8.8	.8	.0	.0	.0	2.1	.0	.4	.4

		CHAR	LYCO	CASU	TREM	DODN	URTM	ACAL	MACA	CELT	SAUR	EUPH	NOTH	CAST	ASCA	RUTA	PHYL	PRUN	CUNO	ELAE	MYRT
11	S	25.5	.0	10.0	3.2	.0	3.0	.2	4.9	.0	.7	.0	9.5	2.3	1.4	.0	.5	.2	.0	.7	.0
11	T+	31.0	20.9	3.3	3.6	.0	5.6	.7	2.9	.0	.0	.3	13.1	2.6	.7	.3	1.0	.0	.0	1.0	.3
11	T-	1.7	7.3	1.7	1.5	.3	2.9	.0	2.6	.0	.3	.0	15.5	1.7	.6	.3	.6	.0	.0	.3	.0
11	T/O	2.0	.0	1.3	.7	.3	.3	.0	1.3	.3	1.3	.3	19.5	2.9	1.3	.7	.3	.0	.0	.0	.7
11	O+	1.8	23.0	.0	.5	.0	.9	.0	2.8	.5	.0	.0	18.4	8.3	.9	.5	.5	.5	.0	.9	.0
15	S	23.8	11.9	23.2	4.6	.7	4.6	.0	3.3	.0	.0	.0	9.9	.7	.7	4.0	2.0	.0	.0	.0	.0
15	T+	132.8	23.2	6.2	4.6	1.2	.4	.4	2.9	.0	.8	.0	17.4	1.7	.8	.8	.4	.0	.4	.0	.0
15	T-	1.5	26.2	.5	4.0	.5	3.5	.5	5.4	.0	1.0	.0	24.8	4.0	1.0	.5	2.0	.0	.0	.5	.0
15	T/O	.6	5.5	1.3	1.9	.6	.0	.0	6.4	.0	.0	.0	13.2	1.6	.3	.3	1.0	.0	.3	.0	.0
15	O+	1.5	.0	1.0	2.0	.5	1.0	.0	7.3	.0	1.5	.0	25.4	5.4	1.5	.5	1.0	.0	.0	.0	.5
15	O-	.7	8.8	.3	.7	1.0	.3	.0	7.4	.0	1.0	.0	21.6	3.4	1.0	.3	.7	.0	.0	.7	.0
31	S	15.6	.0	17.7	7.5	.0	1.1	.0	1.1	.0	.5	1.6	13.4	2.7	.5	.5	.0	.5	.0	.0	.0
31	T+	27.3	8.8	1.0	2.7	.0	5.1	.0	2.0	.0	.0	.0	7.1	2.0	.7	.3	.0	.0	.0	.0	.0
31	T-	1.9	7.2	.6	2.2	.0	1.6	.0	1.6	.0	.3	.6	12.2	.9	.9	.0	1.3	.0	.3	.3	.0
31	T/O	.3	.0	1.3	.7	.3	.7	.0	.7	.0	.0	.0	14.1	3.7	.0	.0	.0	.0	.0	.3	.0
31	O+	1.1	4.4	.3	1.4	.3	.6	.0	2.5	.0	.3	.0	9.7	.6	.8	.0	.3	.3	.0	.0	.3
31	O/X	.5	3.3	.5	.7	.2	.9	.0	1.2	.0	.0	.0	8.4	.2	.0	1.2	.5	.0	.0	.2	.0
18	S	61.4	.0	10.1	4.4	.0	1.8	.4	.9	.4	.4	.0	5.3	.0	.4	.0	.0	.0	.4	.9	.4
18	T+	52.6	.0	2.0	.8	.0	.8	.4	2.4	.4	.0	.4	5.3	.0	.0	.0	1.2	.4	.0	.0	.0
18	T-	2.3	.0	3.4	3.4	.0	1.7	.0	1.1	.0	1.1	1.7	22.6	1.7	1.7	.0	.0	.0	.0	1.7	.0
18	Q	1.0	.0	.0	.0	.0	1.0	.0	1.0	.0	.5	1.0	20.5	2.0	1.5	.0	.0	.5	.5	1.0	.5
36	S	29.0	.0	7.7	1.9	.0	6.5	.0	1.3	.0	.0	1.3	3.9	.6	.6	.0	.0	.0	.0	.3	.3
36	T+	16.8	13.5	.8	1.6	.0	4.1	.0	.8	.0	.0	1.2	9.0	2.9	2.0	1.2	.4	.0	.0	.4	.0
36	T-	2.7	22.5	2.1	1.6	.0	4.8	.0	3.7	.5	.5	.5	19.8	2.7	1.6	1.1	.0	.0	.5	1.1	1.1
36	T/O	2.2	.0	.4	4.0	.4	.0	.0	6.6	.0	.9	.0	14.6	4.0	2.2	1.3	2.2	.0	.0	.9	.4
36	O-	.5	14.9	.5	1.5	.5	4.6	.0	6.7	.0	.0	.5	26.2	4.6	.5	3.1	.5	.0	.0	2.1	.0
34	S	21.5	.0	18.3	8.6	1.1	3.2	.0	2.7	.5	.0	.0	14.0	2.7	.0	.0	.0	.5	.0	1.1	.0
34	S/T	23.8	14.2	5.9	3.8	.0	.4	.0	4.6	.4	.4	.0	15.1	1.7	1.7	.0	1.7	.4	.0	.0	.4
34	T+	5.4	24.9	3.9	2.4	.5	2.0	.0	6.3	.0	.0	.0	24.4	2.9	2.0	1.0	2.9	.0	.0	.0	.0
34	T-	1.4	16.3	2.9	2.4	1.4	.0	.0	8.1	.5	1.0	.0	26.8	1.0	.5	1.4	1.9	1.0	1.0	.5	.0
34	T/O	1.0	5.3	1.5	2.4	1.0	1.9	.0	1.0	.0	.0	.0	29.1	1.0	1.0	.0	.5	.0	.0	1.9	1.5
34	O+	.5	16.3	1.4	1.8	.5	4.1	.5	6.3	.0	.5	.0	27.1	2.7	.5	3.2	.5	.5	.0	.9	1.4
34	O-	1.0	10.0	.0	2.5	1.0	.5	.0	8.0	.5	.0	.0	24.0	1.5	1.0	1.0	2.0	.0	.0	1.0	.5
34	O/X	.6	4.5	.0	1.1	.6	.0	.0	7.3	.0	.0	.0	22.6	2.3	2.3	.0	.6	1.7	.0	.0	1.1
43	S	131.0	.0	2.6	1.7	.0	2.6	.0	.4	.0	.9	.0	3.1	.4	.0	.9	.0	.0	.0	.9	.4
43	SS/T	168.1	53.1	1.8	.9	.0	1.8	.0	1.8	.0	.9	.0	2.7	.9	1.8	.0	.0	.0	.9	.0	.0
43	S/T	909.1	51.1	2.3	1.1	.0	1.1	.0	1.1	.0	.0	.0	3.4	.0	.0	.0	.0	1.1	.0	2.3	2.3
43	T+	44.2	19.2	.0	.0	.6	.6	.0	.6	.0	1.3	.0	4.5	3.2	.6	.0	.6	.0	.0	.0	.0
43	T-	.6	16.7	.0	.6	.6	.6	.0	1.7	.0	2.8	.0	7.2	.6	1.1	.6	.0	1.7	1.1	1.1	5.0
43	T/O	.5	32.4	.0	.5	.0	.5	.0	.9	.0	1.4	.0	2.3	.5	.0	.5	.0	.5	.0	2.3	.9
43	OO/T	.7	11.2	.0	.7	.0	1.1	.0	.7	.0	.7	.0	4.1	1.5	1.5	.0	1.1	2.6	.0	1.5	1.5
43	O+	.6	8.9	.0	.3	.0	.6	.0	.6	.0	.0	.0	4.2	.9	.0	.3	.3	.0	2.7	.6	1.8
43	O/X	.4	5.9	.0	.0	.0	.0	.0	.4	.0	.0	.0	3.4	.6	1.2	.2	.0	.4	.2	1.0	1.8

		PAPU	PODO	DACR	RAPA	ASTT	QUIN	SYMP	COPR	HALO	DRIM	STYP	ERC1	ERC2	ERC3	DRAP	RANU	GENT	POTT	TRIG	APIA
11	S	.0	1.2	2.3	8.8	.0	.0	.2	.9	1.2	.0	.0	.0	.9	.0	.0	17.6	1.6	.7	.0	.0
11	T+	.0	1.6	3.6	8.2	3.3	.0	.0	.3	.0	.0	.0	.3	.0	.0	.3	25.5	1.6	.0	2.0	.0
11	T-	.0	.3	11.4	12.8	.3	.3	.0	.3	.3	.0	.0	.0	.0	.0	.0	5.2	.3	.0	.0	.0
11	T/O	.0	.0	13.7	9.8	1.0	.0	.0	.7	.7	.3	.0	.0	.3	1.0	.0	4.9	.0	.0	.3	.3
11	O+	.0	.9	13.4	18.9	2.3	.9	.0	.0	.5	.0	.9	.0	.5	.9	.0	1.8	.9	.0	.0	.0
15	S	.0	1.3	7.3	4.0	.7	.7	.0	1.3	1.3	.0	.7	.0	.7	.0	.0	11.9	1.3	.0	.0	.0
15	T+	.0	.8	7.1	4.6	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	14.9	.4	.0	.0	.0
15	T-	.0	.0	15.8	5.0	.0	.0	.0	.5	.0	.0	.0	.0	.0	.0	.0	6.4	.0	.5	.0	.0
15	T/O	.0	.3	10.6	7.7	.0	.0	.0	.6	.0	.0	.0	.0	.0	.0	.0	2.3	1.3	.0	.0	.0
15	O+	.5	2.0	16.1	9.3	.0	1.0	.0	.0	.5	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
15	O-	.0	.7	14.2	9.1	.3	.3	.0	.3	.0	.0	.0	.0	.0	.0	.0	.7	.3	.0	.0	.0
31	S	.0	1.1	10.8	10.8	1.6	.0	.0	2.7	.0	.5	2.7	2.2	.5	.5	.0	4.8	.0	.0	.0	.0
31	T+	.3	.0	16.2	12.1	.7	.7	.3	.7	.0	.0	.7	.0	.3	.0	.0	2.0	.7	.3	.3	.0
31	T-	.3	.9	17.9	7.2	.3	.3	.0	1.3	.6	.6	1.3	.9	1.9	.0	.0	1.3	.3	1.3	.0	.0
31	T/O	.7	.7	23.5	17.1	.3	.7	.0	.3	.7	.3	.0	.0	3.0	1.3	.0	1.3	.0	.0	.0	.7
31	O+	.0	.8	15.8	13.0	.6	.0	.0	.6	.8	.0	2.2	3.3	1.7	.6	.0	1.4	.3	.3	.0	.0
31	O/X	.0	.7	15.5	15.9	.2	.0	.0	.5	.7	.2	1.9	.0	.9	.7	.0	.7	.9	.2	.5	.0
18	S	.0	.9	2.2	8.3	3.1	.0	.0	.4	.4	.0	.0	.4	.0	.0	.0	.9	.0	.0	.0	.9
18	T+	.4	.0	3.6	8.9	1.2	.0	.0	.8	.4	.4	.0	.0	.0	.0	.0	1.6	1.2	.0	.0	.0
18	T-	.0	1.1	23.2	41.2	1.1	.0	.0	.0	.0	.0	.6	.0	.0	.0	.0	.0	.0	.0	.0	.0
18	Q	.0	1.0	19.0	51.2	.5	.0	.0	.0	.0	.5	1.0	.0	.0	.0	.0	.0	.0	.0	.0	.0
36	S	.3	1.3	3.2	3.2	1.9	.0	.0	.0	.6	.0	3.9	1.3	.6	.0	.3	23.9	.0	.6	1.3	.0
36	T+	.0	.8	11.5	11.9	1.6	.0	.0	.0	.0	1.6	1.6	.8	.0	.4	.0	5.7	.4	.4	1.2	.0
36	T-	.0	1.1	14.4	15.0	4.3	.0	.0	.0	.0	.0	.5	.0	.0	.5	.5	9.1	3.2	.5	.0	.0
36	T/O	.0	.4	15.0	15.0	2.2	.0	.0	.4	.4	1.8	1.8	.0	.4	.4	.0	10.6	.0	.4	.0	.0
36	O-	.0	.5	21.5	20.0	1.5	.5	.0	.0	.5	2.6	.0	1.0	.0	.0	.0	.0	.0	.0	.0	.0
34	S	.5	.5	6.5	11.3	.5	.0	.0	.0	.5	.0	.5	.0	.0	.0	1.1	75.8	.0	2.2	.0	.0
34	S/T	.0	1.7	7.1	11.7	2.9	.0	.0	.4	.8	.0	.0	.4	.0	.4	.0	33.5	3.8	.8	.0	.0
34	T+	.0	2.0	11.7	9.3	2.4	.0	.0	1.0	.5	.0	.0	.5	.5	.0	.5	30.2	2.9	.5	1.0	.0
34	T-	.0	.0	17.2	10.5	2.9	.5	.0	1.0	2.9	.5	.0	.0	.0	.5	.0	37.3	4.3	.0	.5	.0
34	T/O	.0	1.9	17.5	19.9	2.9	.0	.0	.0	.5	.5	.0	.0	.0	.5	.0	28.6	2.4	.5	2.4	.0
34	O+	.0	.5	19.5	21.3	1.4	.0	.5	.0	1.8	.0	.0	.5	.0	.0	.0	.5	.0	.5	.0	.0
34	O-	.0	1.0	27.0	22.0	.5	1.0	.0	.0	.0	1.0	.0	.0	.0	.0	.0	.0	1.5	.0	.0	.0
34	O/X	1.1	.0	28.2	15.3	.0	.6	.0	.0	.0	.0	.0	1.1	1.7	.0	.0	.0	.0	.0	.0	.0
43	S	.0	.0	1.3	2.2	.0	.0	.0	2.6	.0	.0	.0	.4	.0	.0	.0	.4	.0	.0	.0	.0
43	SS/T	.0	.0	3.5	2.7	.9	.0	.0	3.5	.0	.0	.0	.0	.0	.0	.0	1.8	.0	.0	.0	.0
43	S/T	.0	.0	13.6	4.5	.0	.0	.0	3.4	.0	.0	.0	.0	.0	.0	.0	2.3	.0	.0	1.1	.0
43	T+	1.3	.0	25.6	5.8	.6	.0	.0	7.1	.0	1.3	.0	.6	.0	.0	.0	1.9	.0	1.3	.0	.0
43	T-	.6	1.7	52.8	14.4	1.1	.0	.0	.6	.0	2.2	.0	.0	.0	.0	.0	.6	.0	.6	.0	.0
43	T/O	.5	.9	56.2	14.2	.9	.0	.0	.0	.0	.9	.0	.5	.0	.0	.0	.0	.0	.0	.0	.0
43	OO/T	.0	1.5	33.1	16.4	.4	.0	.0	3.0	.0	2.6	.4	.7	.0	.0	.0	.0	.0	1.1	.0	.0
43	O+	.0	.6	32.0	25.8	1.5	.3	.0	.0	.0	3.0	.0	.6	.0	.0	.0	.0	.0	.0	.0	.0
43	O/X	.2	.8	31.8	28.6	.0	.2	.0	.2	.0	15.4	.0	.2	.0	.0	.0	.0	.0	.0	.0	.0

		LIGU	ASTL	POA1	POA2	POA3	POA4	CYP1	CYP2	CENT	VULC	CYAT	PTER	BELV	TRSP	UNK1	FERN	HERB	TREE	UNKN
11	S	.0	.0	.0	9.7	2.8	5.6	.0	3.2	2.1	51.5	9.7	.5	.0	.7	.0	2.8	.0	.0	.5
11	T+	.0	.0	1.6	12.7	3.6	3.9	.3	12.1	.7	37.9	8.5	.0	.0	.3	.0	5.2	.0	.3	.7
11	T-	.0	.0	.3	7.3	2.0	4.7	.6	6.4	2.0	46.4	5.2	.9	.3	.0	.0	2.0	.0	.3	.3
11	T/O	.0	.0	1.0	6.5	1.0	4.9	.0	4.9	2.0	46.3	6.8	.0	.3	.0	.0	4.9	.0	.0	.0
11	O+	.0	.0	.5	9.7	1.8	3.7	.0	22.1	.0	16.6	5.5	.5	.5	.0	.0	5.1	.0	.0	2.3
15	S	.0	.0	1.3	13.2	4.0	4.6	.0	6.6	.0	26.5	19.2	.0	.7	.0	.7	12.6	.7	.0	.7
15	T+	.0	.0	.4	10.4	4.1	4.6	.0	18.7	.0	36.1	11.2	.0	.0	2.9	1.2	5.8	.0	.0	2.5
15	T-	.0	.0	.5	6.4	1.0	4.5	.0	9.4	.0	39.6	13.9	.0	.5	.0	1.0	5.0	.0	.0	.5
15	T/O	.0	.0	.3	5.5	1.6	4.5	.0	12.2	.0	39.5	15.4	.0	.0	.0	.3	3.9	.0	.3	.6
15	O+	.5	.0	.0	2.4	3.9	3.4	.0	16.1	.0	29.3	13.2	.0	.0	.0	1.0	2.9	.0	.0	1.0
15	O-	.3	.0	1.0	2.7	1.7	2.7	.0	22.0	1.4	31.1	11.8	.0	.0	.0	.3	2.0	.0	.0	.3
31	S	.0	.0	.0	21.0	3.2	12.4	.5	11.3	.0	.5	17.2	.0	.0	.5	.0	8.6	.0	.5	.5
31	T+	.0	.0	.3	10.4	4.4	13.1	.0	9.8	.0	.0	29.3	.0	.7	.0	.0	10.8	.3	.0	.0
31	T-	.0	.3	.3	16.9	.9	6.3	.6	7.8	.0	.0	31.7	.3	.0	.3	.0	8.5	.0	.0	.3
31	T/O	.7	.0	.0	13.4	4.7	2.7	.0	2.7	.0	.0	29.9	.0	.0	.3	.0	9.7	.0	.3	1.3
31	O+	.0	.0	1.1	4.4	1.7	8.6	.3	3.9	.0	.3	39.9	.0	.0	.0	.0	12.7	.0	.0	.8
31	O/X	.0	.0	.5	8.4	3.5	9.1	.0	3.7	.0	.2	36.3	.0	.2	.2	.0	24.6	.0	.0	.7
18	S	.0	.0	1.8	21.1	2.6	43.4	.0	3.1	.0	.4	11.4	.0	.0	.4	.0	1.8	.4	.0	1.3
18	T+	.0	.0	.0	5.3	2.0	52.6	.8	11.7	.0	.0	10.9	.4	.0	.8	.0	7.3	.0	.0	1.6
18	T-	.0	.0	.0	4.0	.0	6.8	.0	6.2	.0	.0	14.1	1.7	.6	.0	.0	5.6	.0	.0	1.7
18	Q	.0	.0	.0	1.0	.0	3.9	.0	3.9	.0	1.5	15.1	2.4	1.0	.0	.0	5.4	.0	1.0	2.0
36	S	.0	.0	1.9	12.9	5.8	15.5	.0	11.0	.0	.0	36.1	.0	1.9	.6	.0	3.2	.0	.0	.3
36	T+	.0	.0	1.2	9.8	4.1	12.7	.0	19.7	.0	.0	18.9	.4	1.2	.0	.0	2.5	.8	.8	.0
36	T-	.0	.0	.5	4.8	3.7	7.0	.0	21.9	.0	.0	24.1	.0	1.6	1.1	.0	9.6	.0	.5	1.6
36	T/O	.0	.0	.0	4.4	2.7	6.6	.9	19.5	.0	.0	22.6	.0	2.2	.0	.4	5.8	.0	.4	1.8
36	O-	.0	.0	.0	4.6	2.1	7.2	3.6	12.3	.0	.0	17.9	.0	.5	.5	.5	6.7	.0	.5	3.6
34	S	.0	.0	.0	10.2	5.9	12.9	1.1	31.7	.0	.0	18.3	.5	1.6	.0	.0	7.0	.5	.0	.5
34	S/T	.0	.0	.0	7.5	5.4	16.7	1.7	27.6	.0	.0	12.6	.0	.8	.0	.0	4.2	.4	.0	1.3
34	T+	.0	.0	.5	15.1	8.3	15.6	.0	15.1	.0	.0	11.7	.0	.0	.0	1.0	7.8	.0	.0	1.5
34	T-	.0	.0	.5	5.3	2.9	10.0	5.3	23.9	.0	.0	12.9	.0	1.4	.0	.5	8.6	.0	1.4	.0
34	T/O	.0	.0	1.5	5.8	1.0	10.7	.0	25.2	.0	.0	11.2	.5	.0	.0	1.0	4.9	.0	1.9	3.4
34	O+	.0	.0	.0	5.0	.9	12.7	.0	24.9	.0	.0	7.2	.0	.0	.0	2.7	6.3	.0	.5	1.4
34	O-	.5	.0	1.0	10.0	1.0	11.5	.0	13.0	.0	.0	7.0	.5	.5	.0	3.0	3.5	.0	.5	.5
34	O/X	.6	.0	1.1	6.2	3.4	4.5	.0	24.9	.0	.0	10.2	1.1	2.3	.6	2.8	7.9	.0	.6	3.4
43	S	.0	.0	2.2	7.4	4.8	8.3	2.2	35.4	.0	.0	32.3	.4	.9	.0	.4	3.1	.4	.0	1.7
43	SS/T	.0	.0	2.7	8.0	1.8	8.8	3.5	34.5	.0	.0	28.3	.0	.9	.0	1.8	7.1	.9	.0	1.8
43	S/T	.0	.0	3.4	11.4	10.2	21.6	3.4	17.0	.0	.0	11.4	.0	.0	.0	1.1	6.8	.0	.0	5.7
43	T+	.0	.6	2.6	7.1	.6	8.3	3.8	12.8	.0	.0	22.4	1.9	2.6	.0	2.6	5.8	.0	.0	4.5
43	T-	.0	.0	.0	1.1	.0	.6	.0	7.2	.0	.0	16.7	1.1	.0	.0	3.3	3.9	.0	2.2	6.1
43	T/O	.0	.0	.5	.9	.0	2.3	.9	11.0	.0	.0	10.5	.0	.5	.0	.5	1.8	.0	.0	1.4
43	OO/T	.0	.0	.0	2.2	.0	2.2	1.5	14.1	.0	.0	19.3	.4	1.9	.0	.7	7.8	.0	1.1	2.6
43	O+	.0	.0	.0	1.2	.0	.3	3.6	6.2	.0	.0	24.3	1.2	2.7	.0	1.5	3.6	.0	.6	4.5
43	O/X	.0	.0	.0	.4	.2	.2	.0	4.7	.0	.0	16.0	.0	.8	.0	1.6	1.8	.0	.2	1.2

APPENDIX 3 - PRINCIPAL COMPONENTS ANALYSIS ON POLLEN DATA.

PCAs were done on several altitudinal and temporal subsets of the pollen data, but the analysis of all the Pindaunde monolith sites together was most interesting and is the only one reported here. For this analysis, each of the 176 horizons in the 34 monoliths was treated as a single 'case', and the percentages of a varying number of pollen types as the 'attributes'. Only pollen sum taxa were included in the analyses.

Most PCAs on pollen data reported in the literature have been carried out on a matrix of correlation coefficients, usually on percentage data. This is equivalent to standardisation of each pollen type to zero mean and unit variance and thus increases the importance of minor taxa, whose counts are more subject to counting errors. An alternative is to use the covariance matrix, in which case the dependence of the variance on the mean results in the dominance of the commonest pollen types, perhaps at the expense of palynologically significant, but rarer, types.

The choice has usually been influenced by the more ready availability of computer programs which use the correlation matrix, but both strategies have some theoretical advantages. The program used in this study (from the B.M.D. package) allowed a choice of initial similarity matrix, so PCA was done on both covariance and correlation matrices.

Correlation matrix.

When all pollen sum types were included in the analysis, some minor types (e.g. Podocarpus) were important in defining the extracted axes. This influence of minor taxa, subject to large counting errors, (and, in most cases in this study, ecologically unimportant) was considered undesirable, so the analysis was repeated with only the 19 most frequent pollen sum taxa.

The first five components accounted for only just over half the variance in the original data. Moreover, the second and subsequent components accounted for very similar amounts of variance, suggesting that their direction may be largely due to chance. Despite this the first three components make palynological sense.

The first component separates sites with high Rapanea and Dacrycarpus (and to a lesser extent, Quintinia and Drimys) from those with high Poaceae and Cyperaceae. The second component separates sites with high Poaceae and Ericaceae from those with high Cyperaceae. The third separates those with high shrub percentages (Styphelia, Ericaceae, Cyathea, Haloragis) from those with high Poaceae.

Covariance matrix.

The inclusion of minor pollen types had a negligible effect on this analysis. The first component alone accounted for 42.4% of the variance and subsequent components accounted for a steadily declining proportion. The components extracted by this analysis are therefore, statistically, more significant than those extracted in the previous analysis. Despite this, only the first two components make palynological sense and these are formed of very similar species combinations to the first two extracted from the correlation matrix. Some probably spurious similarities - such as that based on the correlation between Ericaceae and Poaceae - have been removed, however.

Discussion.

The convergence of the two types of PCA gives confidence in the significance of the results. They confirm that the major pattern in the data is the contrast between forest and non-forest spectra, and between spectra from well-drained and water-logged sites. Variation with altitude and between forest spectra, or between grassland spectra, is unimportant (except for the degree of shrubbiness of the grassland). This conclusion supports the approach to interpretation of the pollen data adopted in this study (although statistical unimportance is not the same as ecological unimportance). In addition, the similarity between the results with the covariance and correlation matrices confirms that the major pattern in the data is revealed by examination of the major pollen sum types, although non-pollen-sum types, excluded from this analysis, were also important in the interpretation of the data.

As discussed in Chapter Five, the interpretation of the components, other than in terms of pattern in the data, is not expected to be very useful. With most ecological applications of PCA there are problems of non-linearity. In this case, however, the relationship between the percentage of each pollen type and the relevant environmental parameters (roughly, 'distance from the forest', and 'degree of water-logging') is, if not linear, at least monotonic. Hence a monotonic relationship between the components and the environmental gradients is expected. This is in fact observed when the first two components are plotted, but the inability of this technique to locate discontinuities in the data, corresponding to the major vegetational changes in the pollen catchment, limits its usefulness, both as a means of suggesting hypotheses and as a method of displaying the results.

A/ Plots in shrubby tussock grasslands.

Tables:

- (1) Seedlings found only in the Cyathea atrox groves.
- (2) Seedlings found also in Coprosma-Poa tussock grassland.

For both tables 'PLOT INFO' is:

SIT. - site no. (* Cyathea grove)

ALT. - altitude

a - aspect 1 = NE-facing 2 = valley floor 3 = SW-facing

b - percentage shrub cover

c - vigour of tussock grasses 1 = low 2 = medium 3 = high

d - distance from nearest patch of closed forest in metres

There are two rows of numbers for each plant species. The top row is the number of seedlings 20 and the bottom one the number 20 cm in height.

		(1)					
		PLOT INFO.					
SPECIES		SIT.	ALT.	a	b	c	d
<u>Sphenostemon papuanum</u>		1					
<u>Harmslopanax</u> sp.							
<u>Schefflera</u> sp.							
<u>Olearia floccosa</u>				1			
<u>Olearia</u> sp.		2					
<u>Elaeocarpus</u> sp.		1					
<u>Sericolea</u> sp.							
<u>Dimorphanthera cf. collinsii</u>		3	2	1	4		1
		5	2				2
<u>Dimorphanthera</u> spp.		2	2	1	8		6
<u>?Vaccinium/Dimorphanthera</u>		4	1		5	2	11
		11	1				21
<u>Homolanthus</u> sp.		1					
<u>Myrtaceae</u>		2					3
		4					1
<u>Jasminum</u> sp.		1		1			1
							4
<u>Pittosporum berberoides</u>		1					
<u>Rubus</u> spp.							2
<u>Amaracarpus caeruleus</u>							3
<u>Rutaceae</u>				1			6
<u>Saurauia</u> sp.							1
<u>Eurya</u> sp.			1				
<u>Pipturus</u> sp.							1
<u>Bubbia</u> sp.				1			1
<u>Drimys</u> sp.			1		6		2
				1			8
<u>Unknowns</u>		1	5				1
		2	2				1
							3

(2)

PLOT INFO.

SIT.	ALT.	a	b	c	d
32*	3320	2	70	2	30
20*	3320	2	60	2	20
21*	3320	2	60	2	15
22*	3320	2	70	2	6
19*	3330	2	50	3	12
17*	3360	2	70	2	10
18*	3420	1	60	1	8
30*	3440	1	80	2	15
57	3460	2	30	2	50
16	3460	2	20	2	70
28	3470	2	25	2	95
23	3480	2	55	2	100
24	3520	2	45	2	60
1	3540	2	30	1	80
2	3540	2	30	1	50
3	3540	2	40	1	40
15	3580	2	40	1	12
14	1600	2	30	1	20
8	3640	2	60	1	10
9	3680	2	50	1	15
10	3650	3	40	1	40
11	3660	3	40	1	35
12	3640	3	15	3	25
13	3640	3	20	3	30
26	3625	3	30	1	40
27	3630	3	20	2	35
25	3630	3	65	1	60
31	3660	3	40	1	60
52	3690	3	25	2	55
33	3700	3	30	2	90
34	3720	3	50	1	100
35	3800	3	50	2	80
36	3850	3	65	2	80
37	3870	3	35	1	130
39	3910	3	35	1	110

SPECIES

<u>Olearia spectabilis</u>	7	1	2	5		1	50	11	1	1	13		2	1	6		1	2	2
<u>Dimorphanthera microphylla</u>	2			18			19	3					3		6				5
	4			8				1	1	1					1	1			2
<u>Dimorphanthera keysseri</u>	2						8	4	3	2			1	2	1	2			
<u>Rhododendron atropurpureum</u>											1								
<u>Rhododendron culminicolum</u>	1																		
<u>Rhododendron gaultheriifolium</u>						7													
<u>Rhododendron womersleyi</u>																			
<u>Vaccinium cruentum</u>	3	1		2			2	20	9				3		4				1
	1	1					2	11							4				2
<u>Rapanea vaccinioides</u>	4							2	15										5
	6																		
<u>Rapanea spp.</u>	2						40	4											
		3					40	9											1
<u>Decaspermum lorentzii</u>							2												
	3	2		8									3						
<u>Pittosporum pullifolium</u>	2			4			40	9					2						
		1	2	1			72	81											2
<u>Prunus pullei</u>																			
<u>Coprosma papuensis</u>	11	6		12	6		6	40	4	1									3
	9				4		8	50	9										4
<u>Polyosma sp.</u>	1																		
	1																		
<u>Quintinia sp.</u>																			
<u>Symplocos sp.</u>				2			5	1											1
<u>Dacrycarpus compactus</u>	4	1	2	18					2										
	21	2		3					11										2

(2) cont.	O. spectabilis	40	3570	1	30	2	30
		41	3610	1	45	2	35
		42	3610	1	35	1	60
		43	3650	1	30	2	60
		53	3650	1	25	3	35
		54	3650	1	10	2	40
		44	3680	1	90	1	80
		45	3680	1	70	1	75
		46	3680	1	50	2	100
		47	3680	1	45	2	80
		48	3710	1	65	3	230
		49	3750	1	30	1	120
		50	3770	1	40	2	210
		51	3850	1	30	2	160

V. cruentum

B/ Plots in other grassland types.

In 6 Poa-Dichelachne grassland plots 5 seedlings were found,
3 Olearia spectabilis and 2 Vaccinium cruentum.

In 10 Deschampsia klossii tussock grassland plots 4 seedlings,
all O. spectabilis, were found.

(2) cont.	0. spectabilis	51	3850	1	30	2	160
		50	3770	1	40	2	210
		49	3750	1	30	1	120
		48	3710	1	65	3	230
		47	3680	1	45	2	80
		46	3680	1	50	2	100
		45	3680	1	70	1	75
		44	3680	1	90	1	80
		54	3650	1	10	2	40
		53	3650	1	25	3	35
		43	3650	1	30	2	60
		42	3610	1	35	1	60
		41	3610	1	45	2	35
		40	3570	1	30	2	30

V. cruentum

B/ Plots in other grassland types.

In 6 Poa-Dichelachne grassland plots 5 seedlings were found, 3 Olearia spectabilis and 2 Vaccinium cruentum.

In 10 Deschampsia klossii tussock grassland plots 4 seedlings, all 0. spectabilis, were found.

APPENDIX 5 - OTHER WET EQUATORIAL MOUNTAINS.

Africa.

Seven mountain areas in tropical East Africa have true alpine regions (Hedberg 1978). The concept of a 'treeline' is not very useful here as woody giant Senecio (<5-7 m) ascend to very high levels on the wetter mountains (as do the giant Espeletia in the Andes). The upper limit of the 'Ericaceous Belt' is approximately equivalent to the treeline in other parts of the world, although some authors have taken the upper limit of the montane forest instead. The 'Ericaceous Belt' is termed 'subalpine' by Hedberg (1978) and others and covers a similar altitudinal range (2700 - 3100 m to 3600 - 4000 m) to the subalpine in New Guinea.

There are large differences in annual precipitation between mountains and different sides of the same mountain, and all are probably dryer than Mt Wilhelm. As a result the temperature extremes experienced in the subalpine are greater. Ruwenzori and the Virunga Volcanoes are climatically most similar to Mt Wilhelm. Partly as a result of the climatic differences, the alpine and subalpine vegetation varies a lot between mountains. All except Ruwenzori (an up-lifted fault block) are volcanoes and edaphic dryness in the upper regions may add to the effects of climatic dryness.

Tussock grassland is rare on Ruwenzori and the Virunga Volcanoes, and the Ericaceous Belt forms a real subalpine forest up to 12 metres tall (Osmaston pers. comm.), dominated by Philippia spp. and Erica arborea, with Rapanea rhododendroides on the deeper and better soils. As on Mt Wilhelm, geomorphology has an important influence on vegetation pattern. Bogs in flat areas are dominated by grass, sedges and giant Lobelia, while mass movements on the slopes make the forest patchy and irregular (Osmaston pers. comm.). Near its upper limit forest is confined to the slopes, with the water-logged valley bottoms open (Livingstone 1975*). The Bakonjo people hunt up to the alpine zone on Ruwenzori but the dampness and lack of grass have prevented cattle grazing on the mountain. Fires are rare but in exceptionally dry weather large areas in the subalpine belt can be destroyed by fire, particularly on the dryer, west side (Osmaston and Pasteur 1970). Fire reduces the Ericaceous forest to a low scrub with scattered tree stumps but this usually regenerates directly to forest rather than grassland (Osmaston pers. comm.).

The other high mountain areas in East Africa - Mts Elgon, Aberdare, Kenya, Kilimanjaro and Meru - all have dryer and more seasonal climates. All are heavily influenced by fire and usually also by cattle grazing. Tall Ericaceous forest is limited to sheltered pockets in the subalpine zone and has mostly been reduced by recurrent fires to a low scrub, or

eventually to grassland, with scattered trees and shrubs of the forest dominants (Hedberg 1978). Grassland is most extensive on the driest and most visited mountains. Some grassland in this zone may be edaphically determined but most is probably fire-induced. Large resident or visiting quadrupeds provide an important natural influence absent in New Guinea.

In contrast to the situation in New Guinea, there seems to be a continuous gradation between forest and grassland in the subalpine zone, with the same woody species becoming smaller and more widely spaced with increasing altitude or influence of fire. Fire may also have affected the upper part of the montane forest on some mountains and the Hagenia - Hypericum zone may be partly seral (Jackson 1956). Most of these high mountains are now in National Parks. Tourism is often very important and access may have to be limited in the dry season because of the danger of fire.

No palynological studies on East African mountains have concentrated on human impact and the published interpretations are mainly concerned with climatic change. Below 2500 m, there is evidence for clearance associated with intensive iron-age settlement at c.1000BP. Some sites on Ruwenzori between 3000 m and 4000 m also show high values of Poaceae in the last thousand years, which are attributed to long-distance transport from lowland clearance areas (Livingstone 1975*). Minor local disturbance would seem an alternative and more likely explanation.

South America.

The Andes of South America reach consistent high elevations across the entire tropical belt. Annual precipitation is very varied and the natural vegetation at the montane level ranges from desert to rainforest (Holdridge 1978). Man's influence is greatest in the dryer areas, where it is often impossible to tell the original vegetation. Here discussion is limited to the wettest equatorial areas in the Northern Andes where the annual precipitation may approach that on Mt Wilhelm.

The uppermost forest belt is called the 'Andean Forest' by most authors and apparently has a potential upper limit of 3800 - 4000 m, becoming dwarfed almost to shrubs at the top. More often, burning and grazing have lowered the limit to 3200 - 3500 m, and sometimes as low as 2700 m, particularly on the dryer flanks. The highest patches of forest are dominated by Polylepis (Rosaceae) with Ericaceae, Asteraceae, Hypericum, Rapanea and other genera. In at least some areas the forest/non-forest pattern is similar to that on Mt Wilhelm (Billings pers. comm.).

The term 'paramo' is often used rather loosely for all the non-forest vegetation between the forest and the snowline. The 'sub-paramo' is a belt of varying width above the forest, which is dominated by shrubs and includes scattered forest trees and true paramo elements. This belt is probably always formed by the destruction of the upper Andean Forest by fire. Above is the 'true paramo', normally 'treeless' and characterised by grass meadows and megaphytic Espeletia. This is a primary vegetation type above the climatic treeline but has also been greatly extended by fire, and may include relic patches of forest and shrubs (Cuatrecasas 1958; Van der Hammen 1974). In places grassland may extend down to at least 3200 m. The paramo fades into the super-paramo between 4200 m and 4500 m and this formation continues up to the perennial snowline.

There is some confusion in the literature as a result of the inconsistent use of terminology. Some authors (e.g. Holdridge 1978) restrict the term 'paramo' to primary vegetation, and refer to the rest as 'sub-paramo', while others use 'paramo' for any treeless vegetation above the forest limit (e.g. Cuatrecasas 1968). On some lower mountains (<4000 m) there are extensive 'paramos' of doubtful status.

As in East Africa pollen studies in the High Andes have concentrated on climatic change rather than human impact. Man's influence has usually only been recognised at lower altitude sites, with a few exceptions (Salgado-Labouriau and Schubert 1977*). For some of the published diagrams an anthropogenic explanation of Holocene changes seems as likely as the climatic explanations given by the authors.

* Livingstone, D.A. (1975) Late Quaternary climatic changes in Africa. Ann. Rev. Ecology and Systematics, 6, 249-280.

Salgado-Labouriau, M.L. & Schubert, C. (1977) Pollen analysis of a peat bog from Laguna Victoria (Venezuelan Andes). Acta. Cient. Venezolana, 28, 328-332.