ORIGINS AND ECOLOGY OF
THE NON-FOREST FLORA
OF MT WILHELM, NEW GUINEA

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CORRIGENDA

Among many minor errors and omissions in this thesis the following of more serious nature require correction.

Page	Position	Correction
iv	Top line	"correlations" should read "differences".
41	Fig. 3.2	Mean max. for Sep and Yr should be 11.9 and 11.3 respectively, and ½ (max.+ min.) for the same periods should both be 7.6.
46	Fig. 3.4	Mean max. temperature for Pindaunde should be 11.3.
47	Bottom para., line 5	"eastern" should read "northeast-facing".
62	Second para., line 8	"photographs" should read "photographs taken before 1960".
68	Top para., line 7	"3100" should read "4100".
82	Top para., line 3	"about 14" should read "about 14 excluding tree-ferns".
82	Third para., assumption 1	"Pacific islands" should read "tropical Pacific islands".
100	Top para., line 3	"are known" should read "are not known".
110	Fig. 4.10	The figures in the following columns should be:

P :	1	2	-	2	-	1	-	-	1	-	2	3	6	9
E,C,R,T :	3	1	4	12	7	3	4	1	1	-	1	8	29	37
Total :	6	6	6	39	15	7	6	5	9	1	9	18	91	109

Page	Position	Correction
135	Top line	"median"should read "intermediate".
174	Third para., line 3	"greater frequency" should read "lesser frequency".
217	Para (d), item (v)	"lower mean" should read "higher mean".
219	Item 11	">2600m" should read "<2600m", and "<4050m" should read ">4050".
226	Fourth para., line 9	"distributions" should read "distinctions".
244	Smith, J.M.B., 1974d	"Pac.Sci. (in press)" should read "Unpubl. MS".
246	Went, F.W. 1964	"alpine forests" should read "alpine plants".

J.M.B. Smith December, 1974

Frontispiece: Mt Wilhelm summit from the upper Jimi valley near Lake Bendenumbun, looking southeast [from Smith, 1974a].

ORIGINS AND ECOLOGY OF THE NON-FOREST FLORA OF MT WILHELM, NEW GUINEA

J.M.B. Smith, Ph.D. Thesis, Australian National University,
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x + 270 pages, including 80 figures, 16 photographs,
8 appendices and a bibliography of 246 publications.

ABSTRACT

Mt Wilhelm (4510 m) is the highest point in Papua New Guinea. Non-forest vegetation extends unbroken down to the forest limit at 3810 m, and in areas of impeded drainage or shallow soil down to the Pleistocene terminal moraines at about 3200 m. The area of grassland has been greatly expanded by man through fire. Below 3200 m some areas of anthropogenic grassland occur, and river-banks, landslips and paths provide other sites for colonization by non-forest plants.

It seems probable that the non-forest flora of Mt Wilhelm is of largely Plio-Pleistocene immigration, though some gondwanic and endemic taxa occur and a few alien species have become widespread. Floristic elements within the flora were tentatively defined upon mainly geographic and taxonomic criteria. These elements were assessed according to several ecological parameters. It was postulated that characteristics associated with good colonists of island and other situations, and others appropriate to seasonal daylength and climate conditions, would be present in the putatively most ancient immigrants to the least degree, and in aliens to the greatest.

Good colonist ability, rapid growth rate, continuous flowering and growth in the field, successful flowering under cultivation, vulnerability to frost, lack of preference for slopes of particular aspect, and wide and generally low altitudinal range were all present to a greater extent in elements of more recent immigration. Dispersal ability was not significantly correlated with floristic elements. The largest number of significant correlations was found between aliens and natives and between the peregrine element (of supposed Plio-Pleistocene immigration) and more ancient immigrants. Ecological distinctions between geographic groupings of species within the peregrine element were few.

It was concluded that the non-forest flora of Mt Wilhelm is a youthful one consisting largely of the descendants of immigrant herbs which arrived by dispersal over long distances in the past 5 million years. Prior to this New Guinea was largely or almost entirely forested; a few forest taxa of ancient status in New Guinea have become adapted to the tropicalpine environment. Several successful alien species provide indications of migration ability, lost to varying extents by members of the native flora. The non-forest flora consists largely of adaptable and unspecialized species occurring in a variety of habitats, this being a reflection of the relative recency of arrival of most or all of its constituents to their present peculiar environment.

This thesis represents the original research of the author except where otherwise acknowledged in the text.

JMB Smith

J.M.B. Smith

3 April 1974.

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CHAPTER 1

INTRODUCTION

1-A THE BOTANY OF TROPICAL MOUNTAINS

Though generally remote and inaccessible from centres of scientific enquiry, tropical mountains have exerted a fascination upon scientists since their early exploration by man like Humboldt and Bonpland. Of particular interest have been their floras which, even to the casual observer, proclaim a stronger link with distant temperate regions than with the lowland forests below them.

The vegetation zonation of tropical mountains has been described in general terms by many authors [e.g. Hall, 1973; Hedberg, 1964; Steenis, 1962a; Troll, 1959] and various points of similarity between different areas have been highlighted by Troll [1959]. In general forest extends up to 3500-4000 m above which lie communities dominated by herbaceous plants. The forests are evergreen and species-rich, emergent trees often having shield-shaped crowns, but becoming floristically and physiognomically simpler with increasing altitude.

Above about 3000-3300 m the forests are low in stature and often consist of intertwined shrubs, Ericaceae predominating, with scattered emergent trees, often coniferous. At these altitudes grasslands also occur, especially on ridges [Troll, 1959], in boggy sites or where man has repeatedly burned the vegetation [Smith, 1974d]. Shrubby species of *Hypericum* appear characteristic of this grassland belt in several areas [Troll, 1959].

Above the forest limit lies a belt of vegetation often numerically dominated by tussock grasses, but most notable especially in East Africa and the Andes for the bizarre megaphytes [Hedberg, 1964; Troll, 1959] which are however lacking in New Guinea. Above 4300-4600 m a belt of tundra vegetation growing on ice-shattered ground occurs, and above 4600-4900 m, permanent snow.

Troll [1959] attempts a classification of tropical mountain vegetation applicable to all mountainous regions of the tropics. He stresses the contrasting ecological factors operative in temperate and tropical mountains and proposes the abandonment of the misleading terms alpine and subalpine for the latter. However this classificatory scheme, based as it is on scanty and generalized data in several areas, seems premature for all tropical mountains and I prefer to use the rather neutral term "tropicalpine" to refer to vegetation and environments above tropical mountain forests.

The origins of tropicalpine floras have aroused much discussion because of their obvious if diverse affinities with distant temperate zone regions. Despite arguments involving former lowered vegetation zones, connections and stepping stones [e.g. Moreau, 1963; Morton, 1972; Steenis, 1964a] it is hard to avoid the conclusion that there has been at least some dispersal over fairly long distances in the geologically recent past [Hedberg, 1969; Holloway, 1970]. The importance of "stepping-stone" areas of tropicalpine environment during glacial maxima which are no longer present today should not be minimized. As further discussed in sections 2-D and 2-E, migration may have been more frequent during the Pleistocene than previously, including from the cool temperate zones to tropical mountains: Morton's [1972] "constipated duck" may have achieved intercontinental significance as an agent of seed dispersal during this period even if she has lost it today.

Speciation on tropical mountains is likely to be unusually fast. Here small populations occur in fairly simple and often open environments, where morphological adaptive changes manifest themselves more rapidly than in larger populations in stable and complex environments. Pleistocene fluctuations of climate probably led to repeated local migrations and extinctions as well as migration of plants over long distances, so that the "founder effect" was operative [see Cain, 1944; Stebbins, 1950]. Furthermore most tropicalpine plants are herbaceous and reach reproductive maturity within one or at most a very few years, resulting in a shorter generation time and more rapid potential evolution than would be possible in slower maturing plants. Morton [1972] explains a high rate of endemism in mountain grassland floras in West Africa by assuming rapid evolution of small but fluctuating populations during Quaternary climatic oscillations.

If speciation on tropical mountains is indeed rapid, as seems likely especially for short-lived herbaceous plants, then the existence of many taxa on such mountains apparently conspecific with similar taxa in distant places reaffirms the conclusion that much migration has taken place in the relatively recent past. Conclusions of this sort have been drawn for the high mountain floras of several areas, including New Zealand [Fleming, 1963b; Raven, 1973], California [Chabot and Billings, 1972] and Borneo [Holloway, 1970]. All these mountains, like those of New Guinea and several other regions, are of fairly recent uplift (post-Oligocene and perhaps mostly Plio-Pleistocene), but as Steenis [1967a] and Melville [pers. comm., 1972; quoted by Whyte, 1972] have argued for Mt Kinabalu, Borneo, the flora need not necessarily postdate orogeny. The evidence nevertheless seems to me to support the conclusion that in large part tropicalpine floras are of allochthonous origin. Some distributional data for the non-forest flora of Mt Wilhelm are given in Fig. 1-1 for comparison with similar data for the tropicalpine flora of East Africa [after Hedberg, 1969]. The low rate of species endemism on Mt Wilhelm is clear.

	Total Flora	Single Mountain Endemic	Regional Endemic	More Widespread
Tropicalpine flora of East Africa (above 3000 m)	101	65 (64%)	33 (33%)	3 (3%)
Non-forest flora of Mt Wilhelm (excluding aliens) (above 3215 m)	163	4 (2%)	117 (72%)	42 (26%)

Fig. 1-1: Extent of distribution of the species in two tropicalpine floras.

Polyploidy appears to be intrinsically more common in some cool climate taxa than in most tropical lowland ones. An increase in ploidy can be due to a variety of genetic and perhaps environmental factors, but it seems that in at least many cases polyploids have wider tolerance limits than related (including parental) diploids, and are frequently self-compatible or able to reproduce vegetatively [Stebbins, 1950]. Such characteristics may have been of great selective advantage under tropicalpine environmental conditions during the Quaternary. Morton [1966] gives the percentage of polyploids in the Cameroons Mts flora as 49% (156 spp.) compared with 45% for the East African mountains (122 spp.). Borgmann's [1964] study of nearly 200 species in the New Guinea highlands shows 59% of polyploids, including 67% of 75 members of Mt Wilhelm's non-forest flora.

Ecological features of the tropicalpine environment have been discussed by Coe [1967], Hedberg [1964], and Salt [1954] for East Africa and by Troll [1958; 1959; 1960] for the Andes. The high mountain environments of Malesia including New Guinea are less harsh than in these regions due to generally higher and less seasonal rainfall and a greater degree of cloudiness, reducing diurnal irradiation and nocturnal eradiation, and resulting in less violent fluctuations in temperature during the daily cycle of weather. The main climatic features are similar however: Mt Wilhelm's climate is summarized in section 3-B. In order to flourish in tropicalpine environments, especially at higher altitudes, plants must be able to cope with freezing temperatures alternating with growth temperatures throughout the year, frost-heaving of soil except where sheltered, cold soils, high irradiation levels, high leaf temperatures, and very variable atmospheric humidity and soil water content. Daylength on Mt Wilhelm varies by only 75 minutes throughout the year. Life forms characteristic of tropicalpine environments are listed and discussed by Hedberg [1964; 1971].

Man has added a new and potent ecological factor to many tropicalpine environments in the form of fire [Hall, 1973; Hedberg, 1964; Paijmans and Löffler, 1972; Smith, 1974d]. Natural fire in such situations is probably rare, at least in New Guinea. The usual effects of repeated fire in these environments are to replace shrub- or tree-dominated communities by grasslands and to reduce species diversity.

1-B THE STUDY AREA

New Guinea is an island of considerable diversity physically, biologically and ethnically. Its rugged topography and a reputation for ferocity little deserved by most of its inhabitants caused it to be one of the last great regions unexplored by western man. The large populations of the main highland valleys were quite unsuspected prior to

1933 [Leahy, 1936]. Since this time the highlands have undergone radical social and technological change [Brown, 1972], and the world has learnt much concerning the people and their unique environment.

One of the leading interests in New Guinea biology has been the mountain flora which, perhaps more obviously than at lower altitudes, displays affinities with both Australasia to the south and Malesia and mainland Asia to the west and north. Furthermore, temperate man transplanted to the tropics yearns for the cool of the mountains, which has more than compensated for the difficulties and discomforts attendant upon mountaineering in New Guinea. Our present knowledge of the high mountain peaks and their botany is therefore greater than that of the forested lower slopes and coastal areas.

Nevertheless this knowledge is scanty. Of all the mountains in New Guinea, Mt Wilhelm (at 4510 m the highest in Papua New Guinea) is the best known. Between 1956 and 1971 over forty botanical collections were made there [Johns and Stevens, 1971] yet during the present study three native species and many aliens were collected from the mountain for the first time. In many cases species have been collected several times but remain undescribed, unrecognized or taxonomically confused. A checklist of the flora produced recently [Johns and Stevens, 1971] is of considerable value, but cannot be regarded as definitive.

Between 1956 and 1973 a small research station was maintained beside the lower lake in the Pindaunde valley by the Department of Biogeography and Geomorphology of the Australian National University. Research topics already complete or nearly so include studies of the plant associations above 3200 m [Wade and McVean, 1969], the productivity of herbaceous vegetation [Walker, 1968] and in particular of tussock grasses [Hnatiuk, in prep.], the vegetation history since 12,000 yr B.P. [Hope, 1973], mammals [Hope, in prep.] and meteorology [McVean, 1968; Hnatiuk and others, in prep.]. Unpublished research includes work on glacial land-forms [J.A. Peterson] and the morphology of tree-ferns [H.E. Reeve]. Some publications deriving from earlier research on Mt Wilhelm concern glacial land-forms [Reiner, 1960], high altitude flora [Hoogland, 1958], plant chromosome numbers [Borgmann, 1964], lacustrine algae [Thomasson, 1967] and a general expedition account [Brass, 1964].

The intention of the present study is to examine the non-forest angiosperm flora of Mt Wilhelm in order to elucidate possible ecological differences between plants of different geographical origin and/or time of immigration to New Guinea. Mt Wilhelm was selected as the site of the main part of the study for both scientific and logistic reasons. As the highest mountain in Papua New Guinea and one not recently subject to severe burning or other human disturbance, it seemed likely to offer sufficient range of ecological and vegetational variations. The plants and other organisms as well as most aspects of the physical environment are better known on Mt Wilhelm than on any other mountain in the Malesian tropics. Logistically the presence of an established research station at 3480 m altitude only three hours' walk from a roadhead and airstrip was of inestimable value, and it is hard to imagine the present study being at all possible without it.

Colour photographs of Mt Wilhelm have been published recently by Mossel [1972] and Smith [1974a]. Other photographs are incorporated into this thesis, and the environment and biota of Mt Wilhelm are discussed in greater detail in chapter 3.

1-C THE ECOLOGY OF GEOGRAPHIC ELEMENTS

Early phytogeographers tended to define geographic elements and their migration routes on the evidence of the ecology, especially thermoecology, of their constituent taxa. Forbes [1846] in his classic memoir upon the origins of the British flora described a series of migrations to the British Isles each at a different time, from a different source and under different climatic conditions. His Lusitanian element, found today in the mild moist southwest of the British Isles, was suggested to be of southern preglacial origin while arctic-alpine plants immigrated during the glacial period [West, 1968].

Most later phytogeographers have preferred to deduce migration routes through the medium of taxonomy, arguing that populations with relatively close similarities must have had a common origin in the past [e.g. Steenis, 1964a]. A few recent authors [e.g. Raven and Axelrod, 1972] have stressed ecological aspects of migration while basing actual migration routes (or their absence) upon both taxonomic and geological criteria.

The two approaches find common ground in the genotypes controlling the identity and behaviour of plant taxa. The ecological attributes of plants upon which Forbes concentrated are largely reflections of their physiological characteristics, while taxonomy has been based mainly upon morphology. Both physiology and morphology are controlled by genotype, so that geographic elements based upon either are founded on different aspects of the same fundamental basis, and should ideally be identical.

The schools of thought represented by Forbes and Steenis stand together on the issue of migration of entire communities rather than as a series of individual and independent migrations by each constituent species. This view is opposed by other biogeographers especially those with experience in the study of island biota [e.g. MacArthur and Wilson, 1967]. Migration of communities implies near continuity of favourable habitat, and is difficult to believe in the case of isolated habitats like oceanic islands. On the other hand plant migration *en masse* has probably occurred elsewhere both as a result of continental drift and across "land-bridges".

This phytogeographic controversy has been paralleled and influenced by a similar one in plant ecology, whose extreme viewpoints have been championed by Clements [1916] and Gleason [1926]. Clements compared plant associations with organisms and regarded them as the inevitable and unchanging results of particular environmental conditions. To him the migrations of plants would involve a steady spread of the whole integrated ecosystem in response to a geographic shift in the environmental conditions under which it flourished. Gleason, by contrast, considered vegetation to be the fortuitous result of immigration acting with a variable and fluctuating environment; all communities have resulted from the independent spread of individual plants so that vegetation is a flux, with every bit unique and impossible of prediction [Gleason and Cronquist, 1964; Watt, 1964].

In this thesis an attempt will be made to relate physiology (as behaviour) to morphology (as taxonomy), in that some ecological attributes of members of a diverse flora will be compared with its division into floristic elements on taxonomic and distributional criteria. The phrase floristic element has been used in preference to the more usual geographic element because there is an important temporal as well as geographic basis to the definition of such elements. Phytogeographic hypotheses with a particular bearing upon New Guinea are reviewed and discussed in chapter 2.

Ecological segregation of geographic elements has been reported several times and is obvious in northern Australia where the "Malesian" element is restricted to wetter and/or more eutrophic sites and the "Australian" element to drier, less fertile places, the two types of community showing a sharp boundary, emphasized by fire [Beard, 1967; Herbert, 1966; H.E. Reeve, pers. comm., 1973]. Herbert also points to an Australian element in Malesian forests which shows a strong tendency to be ecologically segregated in seral situations and includes taxa like *Tristania* and Proteaceae. A similar situation has been reported by Gilbert [1959] in Tasmania, where *Eucalyptus*, *Acacia*, *Pomaderris* and other members of the "Australian" element generally occur only in disturbed sites. After repeated fires this element becomes predominant at the expense of "Subantarctic" *Nothofagus*-dominated rainforest which occupies undisturbed areas.

In New Guinea Schodde [1973] mentions a floristic and faunistic break in the forests of New Guinea at an altitude of 1200-1500 m, with austral (gondwanic) taxa predominant above this division and oriental below: he also regards the herbaceous biota growing above the forest limits as being relatively poor in forms and of diverse geographical affinity suggesting a history of itinerant colonization.

It is within the last-named high altitude flora that this thesis seeks to establish ecological variations related to geographic and/or temporal elements. Apart from the observation that aliens seldom grow away from sites of disturbance, no obvious distinctions exist within the vegetation which can be related to geographic affinity. The ecological variations being sought are therefore of a far subtler nature than those reported by Schodde and the Australian authors mentioned above.

The high mountains of New Guinea can be regarded as insular environments for plants requiring low temperatures since they are surrounded by expanses of hot lowlands and ocean. They are thus separated from each other and from other comparable environments in southeast Asia and Australasia. In many regards the situation of plants in the non-forest flora of New Guinea mountains can be closely compared with that of plants on islands.

MacArthur and Wilson [1967], in a theoretical study of island biota, have deduced that species most likely to be able to colonize islands from a distant source have the following ecological characteristics:

1. Live in open or species-poor habitats
2. Have good dispersal ability
3. Have wide ecological tolerance
4. Display rapid growth and development and produce numerous disseminules.

These conclusions agree well with botanists' lists of adaptations possessed by very good plant colonists, namely the weeds of man-disturbed sites [e.g. Baker, 1972; Ehrendorfer, 1965]. To exemplify this some ecological characteristics of two species of *Ageratum*, the weedy *A. conyzoides* and a plant of stable environments *A. microcarpum*, grown under uniform conditions are copied from Baker [1972] in Fig. 1-2. The ecological tolerance and the rapid growth and development of *A. conyzoides* need no emphasis, while its description as a widespread weed implies efficient dispersal and the colonization of open habitats created by human disturbance, in contrast to the "scarcely weedy" *A. microcarpum*.

Ageratum microcarpum (scarcely weedy)	*Ageratum conyzoides* (widespread weed)
Light requirement for germination	No light requirement for germination
Perennial	Life span 1 year
Flowers in second season of growth	Germination to flowering in 6-8 weeks
Flowering inhibited by high night temperatures	Flowering at low (10 °C) or high (27 °C) night temperatures
Flowering better with long (12 hour) nights	No photoperiodic control of flowering
Mesophyte	Tolerates waterlogging, drought
Self-incompatible	Self-compatible (largely self-fertilized)
Not very phenotypically plastic	Phenotypically plastic
$n = 10$	$n = 20$

Fig. 1-2: Comparative features of *Ageratum microcarpum* and *A. conyzoides* revealed by controlled environment experiments [from Baker, 1972].

MacArthur and Wilson [1967], whose views concerning characteristics of colonists of insular situations have been summarized above, have also discussed the evolutionary changes likely to occur after successful colonization. The initial population, unrestrained by competition or population pressure, will expand quickly, genotypes being favoured which make maximal if wasteful use of available resources including light, water and mineral nutrients. Such individuals have rapid growth rates and produce numerous offspring. However, when competition between individuals or species becomes acute those genotypes able to persist at the lowest levels of resource availability will survive while their more prodigal and formerly more successful fellows perish.

Margalef [1959; 1968] has reached similar conclusions. He states that pioneer species are short-lived but quick-growing, producing large numbers of well-dispersed offspring, and tending to evolve quickly. With increasing competition, as in seral succession, the opposite characters become important. Such thoughts are again echoed by Baker [1972] who mentions the replacement of general purpose genotypes by those giving close local adaptation when a weed lingers in an area.

In the Mt Wilhelm context I have hypothesized:

1. Some elements of the flora are of ancient status in the New Guinea area while others are of relatively recent immigration, most of all the alien plants introduced by man. An attempt is made to identify floristic elements in chapter 2 and to define them within the non-forest flora of Mt Wilhelm on objective criteria in section 3-G.

2. Various ecological attributes associated with good colonists, in particular of insular situations, should be present in the supposedly most recent immigrants to the greatest extent, and that conversely these should be most completely lost in the descendants of the most ancient arrivals.

3. In addition to these attributes appropriate to colonization of insular situations, others appropriate to the peculiar tropicalpine climate were considered. Most immigrants are likely and appear to have reached the young mountains of New Guinea from older areas of thermally comparable climate to north or south. These plants after arrival and in order to survive must have adapted themselves to daylength changing

little throughout the year, and to a diurnal rather than seasonal fluctuation of climatic conditions. I have hypothesized that plants descended from the most ancient immigrants are likely to have adapted furthest towards such environmental conditions.

Research topics arising out of this series of hypotheses are examined in more detail in the next section.

1-D RATIONALE, METHODOLOGY AND ORGANIZATION OF THE THESIS

As argued in section 1-C the characteristics of species expected and discovered to be good colonists of insular situations are comparable with those enabling species to be efficient weeds of sites of human activity. Such characteristics include:

good dispersal
good ability to colonize open sites
rapid growth rates
wide ecological tolerance
poor adaptation to specialized ecological niches.

Since a majority of the species of the non-forest flora of the New Guinea mountains may be of relatively recent immigration, it is postulated that they will exhibit some or all of the characteristics above in proportion to their time of occupancy of the area. As most immigrant plants appear to have their origins in one of the temperate zones other characteristics inappropriate to the tropicalpine environment may persist, like seasonal daylength-adapted phenology.

This thesis examines most species of the non-forest flora of Mt Wilhelm in respect of some or all of these characteristics in an attempt to find some correlation between autecology and history of migration. Specifically, the following questions are examined.

1. What is the history of the tropicalpine environment in New Guinea and of its biota?

2. Is there a correlation between the apparent age of residence and/or place of origin of floristic elements in the New Guinea mountains and:

(a) dispersal ability
(b) colonist ability

(c) growth rate
(d) periodicity of growth and flowering
(e) vulnerability to frost
(f) preference for slopes of particular aspect
(g) range of altitudinal distribution
(h) mean of highest and lowest altitude records?

3. In the light of the above what are the likely origins of the non-forest flora of Mt Wilhelm?

Methods employed in both field and laboratory have been uncomplicated. Wide collections of pressed plant material were made in the field, as well as of disseminules and wood samples preserved in ethanol, and disseminules and live material for propagation in Canberra. Numerous observations of local plant distribution were made employing only compass, pocket barometric altimeter and the usual recording and collection gear. Measured quadrats were studied on slopes of opposing aspect (see chapter 7). Standard meteorological equipment was used to measure temperatures and rainfall. Most field research was undertaken using the research station as a base, but camps were also set up for brief periods at various times in 1972, at Saddle Camp (4300 m on the summit path) and in the Imbukum, Guraguragugl and upper Jimi valleys of Mt Wilhelm, at Kombugli and Kuraglumba, and on Mt Sigal Mugal in the Kubor range.

Cultivation of plants in Canberra was achieved in an enclosed area of glasshouse heated in winter and air-conditioned in summer. A sledge microtome was used to cut wood sections which, like the preserved disseminules, were examined microscopically as well as with the unaided eye. Preserved disseminules and oven-dried aerial plant parts were weighed using a Mettler H20T balance. Herbarium material, in particular that of the Forests Department Botany Division at Lae, was invaluable both in the confirmation of the identity of plant taxa encountered in the field and in the compilation of distributional data (see chapter 8).

The written thesis is organized under the following headings:

Chapter 1. Introduction. A discussion of the botany of tropical mountains and the ecology of geographic elements, especially in the context of New Guinea, and a brief description of the aims of the thesis.

Chapter 2. Phytogeography of New Guinea. A review and discussion of literature pertinent to the plant geography of the Malesian and Australasian regions, in particular of the high mountains of New Guinea.

Chapter 3. Mount Wilhelm. A description of the geography and geology, climate, soils, biota and non-forest vegetation of Mt Wilhelm, with some discussion of possible disharmony of the flora and a tentative definition of floristic elements.

Chapter 4. Dispersal Ability. An account of the dispersal abilities of the floristic elements in the non-forest flora of Mt Wilhelm, as shown both by size and morphology of disseminules and by local distribution.

Chapter 5. Colonist Ability. An account of seral succession on Mt Wilhelm and of colonist abilities of floristic elements as shown by adventiveness.

Chapter 6. Growth Rate and Phenology. An account of growth rates of short-stemmed herbs, and of various aspects of phenology as seen both in the field and in cultivation in Canberra, and their relationship with floristic elements.

Chapter 7. Distribution on Slopes of Different Aspect. An account of the different thermal micrometeorology and flora of slopes of opposing eastern and western aspects, and of their ecological and phytogeographic implications.

Chapter 8. Distribution in New Guinea. A description of distribution patterns, both lateral and altitudinal, of herbaceous plant species in the non-forest flora of New Guinea mountains, and a discussion of these with regard to ecological, evolutionary and phytogeographic factors.

Chapter 9. Integration, Discussion and Conclusions. A summary of conclusions and a discussion of their mutual relationships and their significance to the elucidation of the history of the non-forest flora of Mt Wilhelm.

CHAPTER 2

PHYTOGEOGRAPHY OF NEW GUINEA

2-A REVIEW OF THE LITERATURE

New Guinea lies geographically and floristically between Asia and Australasia. The affinities of its lowland flora are predominantly with the Indomalesian region to the northwest, but its highland flora especially within the forests displays clear southern links, in particular with eastern Australia, New Caledonia, New Zealand and southern South America. Present day geography offers possible migration routes through the Indonesian archipelago to account for the former affinities, but the latter have been less easy to explain.

Since the days of early scientific travellers over a century ago, including Darwin, Hooker and Wallace, there has been considerable interest in the distributions of organisms in the southern hemisphere. While the many unique features of the biotas of the various southern lands startled north temperate eyes, it was the web of similarities between the widely separated land masses which aroused the greatest controversy. The realization that continental drift is of profound biogeographical significance, and a growing awareness of the importance to some organisms of dispersal over long distances, have today brought some understanding to the question. Nevertheless this understanding is at best a sketchy one, and we have almost no direct evidence to help account for the distribution of the majority of southern plants and animals.

With regard to the origin of transoceanic disjunct distributions of plants, as between Africa and Australia or Chile, New Zealand and New Guinea there have always been two schools of thought. One preferred to postulate dispersal of plants across long distances to reach their present distributions, the other suggested changing geography so that organisms were able to achieve present distributions without recourse to long distance dispersal. Darwin and Hooker respectively championed the two causes during the last century, followed in each case by a succession of later workers [Wace, 1965]. As with most deep-seated controversies the truth lies neither in one camp nor the other, each explanation probably being true in some cases but not in others.

Various agencies have been suggested as providing the means for dispersal of seeds over long distances including the sea [Darwin, 1968], birds [Falla, 1960] and "the wild west wind" [Gibbs, 1920]. In certain cases probably all these agencies are effective as has been shown in some specific instances. Experiments with the viability and flotation of disseminules in sea-water [Darwin, 1968; Ridley, 1930] have shown that those of some species can float and survive for long periods, and Sykes and Godley [1968] have shown that dispersal of viable seeds of the small tree *Sophora* has almost certainly occurred over very great distances by flotation in the sea. Taylor [1954] has shown that seabirds can carry seeds between oceanic islands at subantarctic latitudes. It is generally accepted that waterfowl, by adherence of disseminules to foot and feather, are largely responsible for the wide distribution of many aquatic and marsh plants; but internal transport of viable seeds by birds over long distances seems less likely to have occurred [Löve, 1963]. Whyte [1972] suggests bird transport of grasses to Malesian mountains from both north and south temperate zones. Wind is probably of greater importance to plant dispersal though perhaps only of applicability to those taxa with small or peculiarly adapted disseminules. However wind can act indirectly by blowing disseminule-carrying birds for long distances, and as Holloway [1970] points out "it would be foolish to underestimate the power of the typhoon. A heavy seed may sink in wind and water but the branch bearing it may not". Cyclones have been suggested by Hedberg [1969] as being of possible importance to the migration of the East African tropicalpine flora.

The dispersal capacity of many plants seems restricted to only very short distances, as for example the beeches and podocarps of New Zealand [Holloway, 1954; Preest, 1967; Wardle, 1963]. Nevertheless that subantarctic islands which were quite buried by ice during the Pleistocene support vegetation today demonstrates that long distance dispersal must be effective for some plants [Dawson, 1958]. On the other hand the disharmonic flora of Hawaii, lacking even mangroves though they thrive when introduced [Stone, 1967], shows that such dispersal is not effective for all plants even over a period of several million years.

Biogeographers favouring changes in geography to account for plant distribution have themselves been divided into two groups. The land-bridge theory has been strongly proposed and defended by Steenis [1962b] who visualizes vertical tectonic movements producing mountain chains, peninsulas and archipelagos along which organisms migrate, these structures later foundering and disappearing. Central America can be regarded as a land bridge today, and a former land bridge spanned the Bering Strait. However, a complex of transoceanic land bridges such as have been suggested, receiving little or no support from geological evidence, seems most improbable.

Gondwanaland is no new idea to biogeographers. Joseph Hooker wrote in 1860 "the many bonds of affinity between the three southern Floras, the Antarctic, Australian and South African, indicate that these may all have been members of one great vegetation, which may once have covered as large a southern area as the European now does a northern." Similarly H.F. Osborn wrote in 1910, five years before the publication of Wegener's famous book, "One of the greatest triumphs of recent biological investigation is the hypothetical reconstruction of a great southern continent ... through the concurrence of evidence derived from botany, zoology and palaeontology". But continental drift was regarded by most biologists until quite recently either as inherently unlikely or as having occurred too long ago to be of relevance to modern plant or animal distributions. Only Good [1947; 1958] has consistently argued the case that plant distributions are explicable in terms of continental drift, though often with scant regard for the details of geological conclusions.

Today many biogeographers have appreciated the demonstration by geologists that most of the lateral crustal movements resulting in the wide separation of Gondwanaland fragments are post-Jurassic [Heirtzler and others, 1968; Smith and others, 1972] and therefore within the time span of modern groups including angiosperms and mammals, as shown by a recent spate of publications on the subject [Fooden, 1972; Jardine and McKenzie, 1972; Kurtén, 1969; Schuster, 1972]. However there is perhaps now, after years of rejection of continental drift, a danger that biogeographers will attempt to explain too much by the fashionable paradigm, although Raven and Axelrod [1972] and Smith [1974b] have recently emphasized that southern floras are influenced by Quaternary migrations as well as the Mesozoic and Tertiary dispositions of land masses.

Earlier workers [e.g. Merrill, 1926; Steenis, 1964a] looked for affinities and defined elements with little regard for the rank and age of the plant taxa concerned, species distributions being equated with those of genera and even families. Though it is difficult to assess and equate rates of evolution in different taxa, it is hard to regard in the same light (for example) the transatlantic distribution of the related ericaceous genera *Agauria* and *Agarista* [Stevens, 1970] with that of infrageneric sections of *Bromus*, *Gossypium* and *Solanum* [Hawkes and Smith, 1965] or of single species such as *Bacopa egensis*, *Dioclea reflexa* and *Parinari excelsa* [Hepper, 1965].

The differentiation of disjunct south temperate plants into two elements, the pre-Pleistocene element consisting of taxa having achieved their distribution overland or across only small sea gaps and the post-Pleistocene consisting of species of recent long distance dispersal, was first made by Dawson [1958]. These two elements have been called palaeoaustral and neoaustral respectively by Fleming [1963a] and the taxa of each have been tentatively listed by Wace [1965] who points out that the two groups are not necessarily mutually exclusive. The neoaustral element consists typically of widespread southern species, occurring on subantarctic islands and exhibiting good dispersal mechanisms. The palaeoaustral plants on the other hand are typically disjunct genera with different species on each land mass, not found on oceanic islands and not showing mechanisms clearly adapted to long distance dispersal. It is amongst the palaeoaustral element that we may expect to find plants with direct Gondwanaland ancestry, though many other Gondwanaland-derived plants have no doubt proved more successful and achieved such a widespread distribution that there is now little clue to an initially southern origin.

The distinction between temporal floristic elements already made for the southern cool climate flora is probably applicable to and important in defining phytogeographic elements in all parts of the world. Oceanic islands and areas formerly made devoid of vascular plants by ice or vulcanism have floras only of the modern long distance dispersed type (though evolution over long periods may have modified them as in Hawaii). More stable continental land masses are predominantly covered by a more ancient and conservative vegetation with modern adventive immigrants and their descendants found especially in sites of current or recent disturbance (shores, moraines, etc.).

Phytogeographic hypotheses as applied to New Guinea have been reviewed by Robbins [1971], who discusses each without reaching any firm conclusions.

2-B GEOLOGICAL HISTORY OF NEW GUINEA

The southern part of New Guinea is geologically stable, old (Palaeozoic) and a part of Australia [Glaessner, 1950; Page, 1971], the Torres Strait and Arafura Sea being shallow, and in fact dry during parts of the Pleistocene and earlier periods [Doutch, 1972; Jennings, 1972]. However, the bulk of the island, north of the southern lowlands, is more rugged in topography and younger in age.

During the Mesozoic, Australia as part of the rifting southern supercontinent, Gondwanaland, lay south of its present position [Smith and others, 1972]. During the early Tertiary, rifting between Antarctica and Australia led to the northward drift of Australia which continues today [Vogt and Connolly, 1971]. The Australia Plate with what is now New Guinea as its leading edge has therefore probably been forced over the Pacific Plate causing the development of a subduction zone, Pacific oceanic crust being forced below the continental crust of New Guinea, accompanied by folding and faulting, uplift, vulcanism and the development of geosynclines [Davies and Smith, 1971].

Tectonic activity reached a peak in the Oligocene when a large block of arched ocean floor was faulted and thrust upwards, perhaps to give New Guinea its first highland area [Thompson, 1967]. Metamorphism and isostatic uplift of this block in the Miocene was followed by further folding and vulcanism continuing to the present day, as evidenced by post-Miocene marine limestones forming the Sarawaket mountains over 4000 m high, and a measured rate of uplift of 4 mm p.a. on the north coast of the Huon Peninsula [J.M.A. Chappell, pers. comm., 1973].

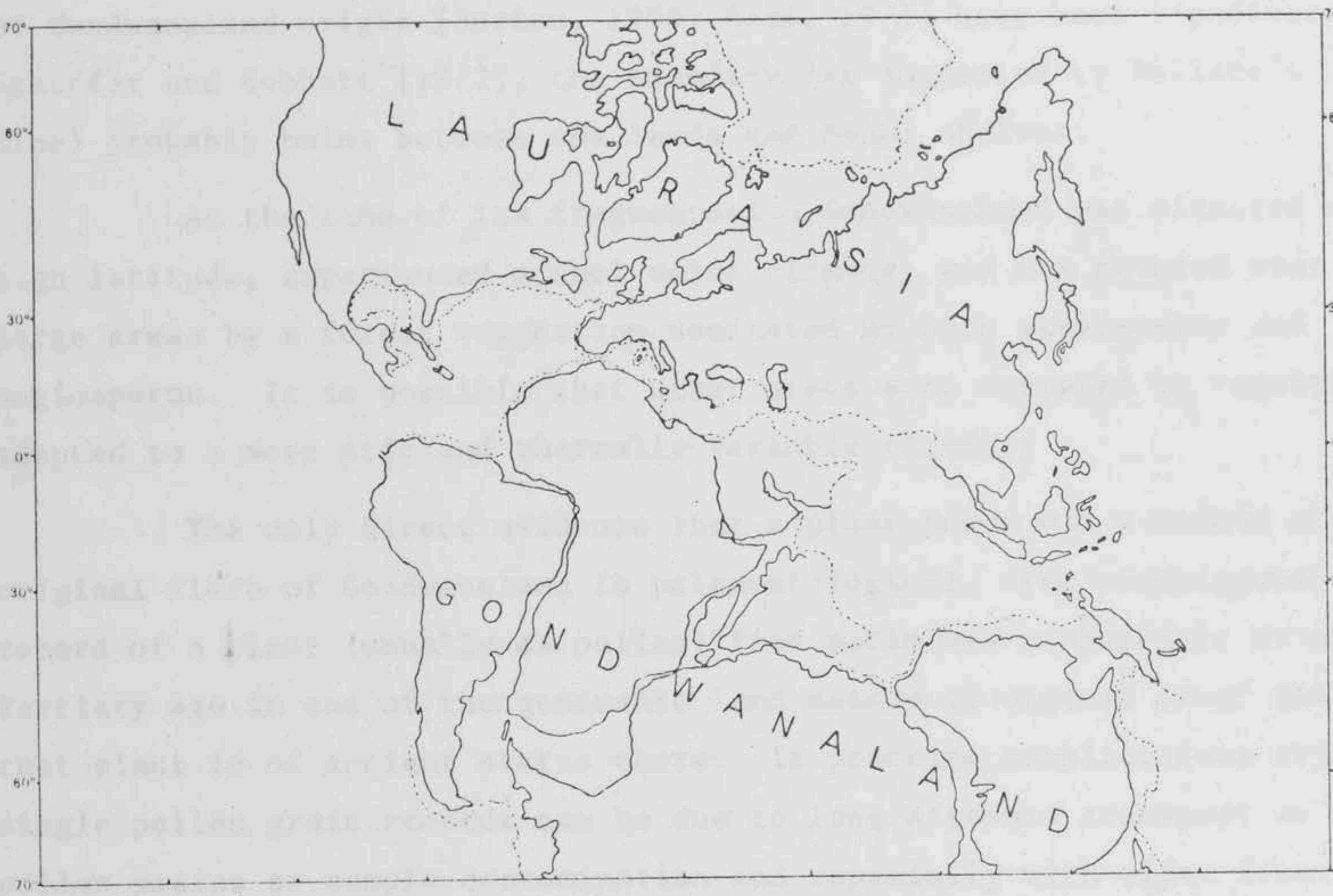
The contact between the Australia and Pacific Plates lies at present roughly along the north coast of New Guinea. South of this line the mountain ranges, trending west-east or northwest-southeast, become progressively greater in age until the old stable platform rocks are encountered at the southern margin of the highlands [Davies and Smith, 1971; Page, 1971].

Although palaeogeographers cannot agree on the Mesozoic position of southeast Asia [Ridd, 1971], it seems probable that Australia and New Guinea (which have been a part of the same continental region at least since the late Palaeozoic) have been remote from Asia and the Malesian region continuously until the late Tertiary. On the other hand they were contiguous with Antarctica until about 45 m. yr ago, and the approach towards Asia was the result of the same movement that caused the separation from Antarctica.

Recent palaeogeographic maps [Smith and others, 1972] show three periods of contact between the Australia-New Guinea landmass and other terrestrial regions either overland or across only short water gaps (see Fig. 2-1). Until the latter part of the Cretaceous period contact was maintained with Antarctica, and *via* Antarctica with other areas of Gondwanaland including India, Africa and South America. There was probably slight and interrupted indirect communication with northern Laurasian regions *via* Central America and North Africa. The second period lasting up to about 45 m. yr ago involved direct contact with Antarctica, and with only short sea gaps separating Australia from New Zealand and Antarctica from South America. The third period, that of direct contact northwards to southeast Asia but none with southern lands, has, geologically speaking, only just begun: direct terrestrial contact has not yet been made but the short sea gaps between the existing islands (or at least between the exposed areas of the Sunda and Sahul shelves at glacial maximum) have presented no barrier to the migration of many organisms.

2-C GONDWANALAND AND THE FATE OF ITS FLORA

It is probable that much of the flora of New Guinea had its origin in the rifting Gondwanaland of the Cretaceous. The evidence for post-Jurassic rifting and drifting of continental land masses [Takeuchi and others, 1967; Tarling and Tarling, 1971] and its significance for southern biogeography [Jardine and McKenzie, 1972; Raven and Axelrod, 1972; Schuster, 1972; Smith, 1974b; 1974c] have been summarized in several reviews. The present land masses derived from Gondwanaland are generally agreed to be the continents of South America, Africa, Australia



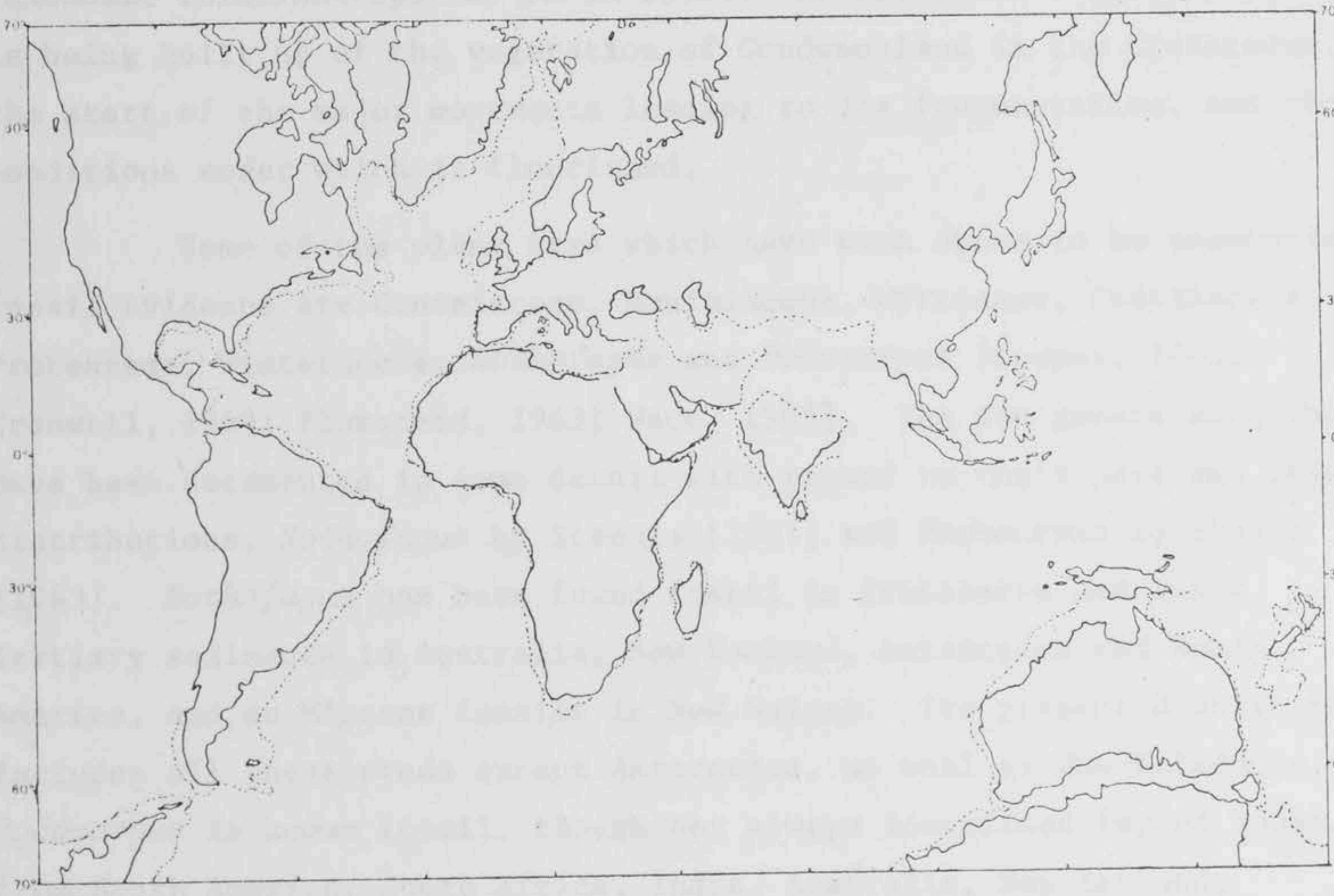


Fig. 2-1: World palaeogeography in the Cretaceous (100 m. yr ago, top) and Eocene (50 m. yr ago, bottom), after Smith and others [1972]. 60° of longitude omitted in the Pacific region.

and Antarctica, the Indian peninsula, and the islands of Malagasy, the Seychelles, Sri Lanka, Kerguelen, New Guinea, New Caledonia, New Zealand and the Falklands. Suggestions that parts of southeast Asia may also be of Gondwanaland origin [Burton, 1970; Ridd, 1971] have been repudiated by Stauffer and Gobbett [1972], the boundary (as suggested by Wallace's Line) probably being between the Sunda and Sahul shelves.

At the time of its fragmentation Gondwanaland was situated at high latitude, experienced a cool moist climate, and was covered over large areas by a forest vegetation dominated by both gymnosperms and angiosperms. It is possible that other areas were occupied by vegetation adapted to a more arid and thermally variable climate.

The only direct evidence that a plant taxon was a member of the original flora of Gondwanaland is palaeontological. The unambiguous record of a plant (usually as pollen) from sediments of Mesozoic or early Tertiary age in one of the gondwanic land masses is virtual proof that that plant is of ancient status there. In practice complications arise: single pollen grain records can be due to long distance transport of pollen grains or sample contamination and especially with older fossils taxonomic relationships may be in doubt. Nevertheless a sketchy picture is being built up of the vegetation of Gondwanaland in the Cretaceous, at the start of the major movements leading to its fragmentation, and the conditions under which it flourished.

Some of the plant taxa which have been shown to be gondwanic by fossil evidence are Cunoniaceae, Monimiaceae, Myrtaceae, Pedaliaceae, Proteaceae, Winteraceae, *Nothofagus* and *Podocarpus* [Couper, 1960; Cranwell, 1969; Plumstead, 1963; Wace, 1965]. The two genera mentioned have been documented in some detail with regard to their past and present distributions, *Nothofagus* by Steenis [1971] and *Podocarpus* by Florin [1963]. *Nothofagus* has been found fossil in Cretaceous and early Tertiary sediments in Australia, New Zealand, Antarctica and South America, and as Miocene fossils in New Guinea. Its present distribution includes all these areas except Antarctica, as well as New Caledonia. *Podocarpus* is known fossil, though not always identified beyond doubt, from South America, South Africa, India, Australia, New Zealand, Antarctica and Kerguelen. Its present distribution covers areas of the same land masses excluding the last two named but including Malagasy, several west Pacific islands, and with northern extensions into southeast

Asia, central America and the West Indies. Both genera are considered to show unusually poor dispersal ability [Preest, 1963].

The difference between the distributions of these two genera is interesting. Both are successful trees finding their optimum expression under conditions of moist and isothermal cool temperate climate. *Podocarpus* occupies areas in Africa and India from which *Nothofagus* is absent and has extended into southeast Asia and central America, though elsewhere the ranges of the two genera are roughly coincidental. The explanation of the difference probably lies in the different ages of the genera and in the slightly greater dispersal ability of *Podocarpus*. Palaeogeographic maps [Smith and others, 1972] show Gondwanaland virtually intact in mid-Cretaceous, but with Africa and India separate by the Eocene. The earliest fossils of *Nothofagus* (except perhaps in New Zealand) are upper Cretaceous, so it is possible that when Africa and India became separated from the other parts of Gondwanaland their floras included *Podocarpus*, which is older, but the later evolving and spreading *Nothofagus* "missed the boat".

It is relevant to point out that the very primitive angiosperm family Winteraceae, which by its northern extensions into southeast Asia and central America displays a similar dispersal ability to *Podocarpus*, occurs not only in South America and the Australasian area but also, as a single species of *Bubbia*, in Malagasy. Although this can be explained as the result of chance long distance dispersal, it seems more reasonable to accept this species as a relic of a formerly contiguous population of Winteraceae in Cretaceous Gondwanaland.

Late Palaeozoic sedimentary rocks in gondwanic land-masses include tillites and coal, both strongly indicative of a cool wet climate over large areas of the supercontinent at that time [Hamilton, 1964]. This is despite suggestions that a land area of such size would be arid in all but the coastal regions [Meyerhoff and Teichert, 1971], a view receiving some support from the present aridity of Antarctica. During the Mesozoic world temperatures were higher than those of today, as evidenced both by oxygen isotope studies [Lowenstam, 1964] and perhaps by the wide distributions of poikilothermic reptiles [Colbert, 1964]. Gondwanaland was seasonally arid over wide areas during the Triassic and Jurassic periods, but became wetter in the Cretaceous [King, 1961] as drift began on a large scale. The Cretaceous was also cooler than the earlier Mesozoic periods, although forest was still able to grow at the north pole [Bain, 1969].

Palaeontological data [Axelrod and Bailey, 1969; Kremp, 1963; Martinez-Pardo, 1965] and oxygen isotope data [Emiliani, 1954; Devereaux, 1967; Dorman, 1966; Stonehouse, 1969] both suggest temperatures warmer than today until Pliocene times. Rather moister climates are also indicated for both Australia [Gentilli, 1961] and southern Africa [Gill, 1961] during most of the Tertiary. *Nothofagus* forests, now almost completely restricted to the extreme southeast of the continent, grew in many parts of southern Australia during the early Tertiary [Keast, 1959] and even during the late Pliocene southeast Australia was moister than today [Turnbull and Lundelius, 1970]. Relict populations in isolated moist habitats in both Africa [Levyns, 1964] and Australia [Gentilli, 1961] provide further evidence for the relatively recent spread of more arid conditions.

It seems likely that parts of South America and New Guinea, suffering considerable orogeny, and island fragments of Gondwanaland, including Malagasy, New Caledonia and New Zealand, maintained moist isothermal conditions throughout their histories. Climate controls to a very great extent the distribution and separation of geographic elements in the southern hemisphere. Hence climate seems to have been the main factor involved in the selection of different taxa in different areas from an originally common, though not necessarily uniform, flora of Cretaceous Gondwanaland. Axelrod and Bailey [1968] have stressed the importance of isothermal climate to a variety of organisms, and Raven and Axelrod [1972] and Smith [1974b] have emphasized its significance for the survival of relict plants in parts of the southern hemisphere.

Thus while taxa like the Philesiacease and Proteaceae are typically common in those areas of the southern continents which are less wet and have high maximum temperatures [Wild, 1968], Winteraceae, *Nothofagus* and *Podocarpus* typify wetter more isothermal areas [Moore, 1972; Steenis, 1971]. Even the physiognomy of the forests composed of the latter element appears to be peculiarly southern [Dawson, 1970]. The Indian element in northern Australia [Herbert, 1966] is partly the result, on both continents, of selection of the same elements from the same basic flora under the same monsoonal conditions. Likewise the formerly mysterious floristic relationship between Malagasy and New Caledonia

[Good, 1950] becomes explicable when both islands are seen as fragments of the same original land mass having experienced similar climatic conditions since their separation. Floristic and physiognomic affinities between the Himalayas and the west Pacific area are explicable by reference to continental drift, especially as these may formerly have been the areas of most oceanic climate in the undrifted Gondwanaland [Schuster, 1972]. The present distributions of some cryptogamic plants can also be explained by the fragmentation of Gondwanaland and its flora [Fulford, 1951; Lovis, 1959; Schuster, 1972].

The richest recognizable gondwanic floras today are in the moist isothermal areas of cool temperate Australasia (New Guinea highlands, southeast Australia, New Zealand) and South America; clear gondwanic elements are also discernible in the floras of the extreme south of Africa, Malagasy, New Caledonia and various high Pacific islands. The paucity of clearly gondwanic plants in India and most of Africa probably reflects the early separation of these areas from the rest of the supercontinent as well as contact over a long period with Laurasian floras. There may also have been migration between cool temperate parts of Australasia and South America *via* Antarctica during much of the Tertiary [Moore, 1972].

2-D NEW GUINEA DURING TERTIARY AND QUATERNARY TIMES

It is probable that the increasingly equatorial position of north Australia and New Guinea during northward movement in the Tertiary was at least partly compensated for in climatic terms by the decrease in world temperature and by the uplift of highland areas in New Guinea. If this were so a gondwanic flora could have survived *in situ* with little extinction throughout the Tertiary. Walker [1972] has suggested that late Tertiary uplift in New Guinea could have provided a refuge for moisture-loving temperate vegetation of northern Australia threatened by increasing aridity as the area moved into the "horse latitudes". Migration of organisms overland between Australia and South America *via* Antarctica could have taken place until about 45 m. yr ago [Moore, 1972].

However, the origins of the New Guinea flora are not of course exclusively southern. The mixing of gondwanic with Laurasian floras is perhaps more recent and less complete in the New Guinea-southeast Asia region than in South America, Africa or India. This factor together with the geomorphically diverse and dissected nature of the region may explain its great biotic richness. Schuster [1972] suggests that this richness may be the result of a double injection of southern flora at different times (*via* India and Australasia) into a northern flora. The lack of complete mingling of northern and and southern flora is shown by the forests of New Guinea, whose geographical affinities are predominantly northern at altitudes below 1200-1500 m and southern above [Schodde, 1973].

The northward movement of Australia and New Guinea has not yet provided a direct terrestrial connection with Asia, but an insular "stepping-stone" link has been effective from about the Pliocene for the migration of some organisms, perhaps acting as a two-way "filter-bridge" for both plant and animal taxa. Rodents probably reached Australia from Malesia in the Pliocene [Turnbull and Lundelius, 1970], and the widespread genus *Acacia* made its first appearance in the West Australian fossil record in late Miocene times [B.E. Balme, pers. comm., 1973]. Muller [1966] has shown palynologically that the highland vegetation of Borneo included northern genera (*Alnus*, *Ephedra*, *Picea*, *Pinus*, *Tsuga*) from Eocene to Miocene times but that these became extinct and were replaced in the Pliocene by some southern taxa including the still extant genera *Phyllocladus* and *Podocarpus*.

A relatively rapid cooling through the Pliocene culminated in the glaciations of the Pleistocene. Firm evidence has only been presented so far for a single major glacial advance in New Guinea [Löffler, 1972], lasting to about 10,000 yr ago [Hope, 1973]. However, there is no reason to suppose that earlier cold periods recorded elsewhere were not effective in New Guinea. Depression of snowline during the last glaciation was 1000-1100 m (relative to the present snowline on Mt Carstensz at about 4600 m) to 3500-3600 m, probably caused by a drop in mean temperature of 5-6 °C [Löffler, 1972]. Terminal moraines on Mt Wilhelm occur at about 3200 m, though they have been identified at much lower altitude on Mt Carstensz [Peterson and Hope, 1972].

As New Guinea was approaching the islands of the Indonesian archipelago at the end of the Tertiary, vegetation belts were being lowered and mountain ice-caps formed by a process of world cooling. At the same time sea-level was lowered and the New Guinea highlands experienced considerable vulcanicity. All these factors led to a burst of plant migration between New Guinea and Asian regions. The various land masses were closer than ever before (although New Guinea and Asia were still separated at all times by the strait between the Sunda and Sahul shelves), areas of montane vegetation were enlarged, and natural "seed-beds" were provided by the products of glacial erosion and volcanic eruption.

Holloway [1970], in suggesting that much migration of plants growing today above 2000 m in Malesia occurred during the Pleistocene, has pointed out that if vegetation belts are lowered by 1000 m, areas of montane vegetation are enlarged and become closer to each other facilitating migration. This is not so to any great extent if plants growing above the forest limit are considered (see Fig. 2-3), although many species at present mainly occurring above the forests can also occur occasionally in open situations at lower altitudes (see section 8-C). However, areas of lowland forest must have been considerably closer as a result of lowering of sea-level. Many lowland plants probably migrated between New Guinea and Asia at this time, exemplified by the Asian family Dipterocarpaceae which, though poorly adapted to dispersal [Wyatt-Smith, 1953] is represented by four genera in New Guinea. Their failure to spread into Australia suggests that their migration as far as New Guinea has been a fairly recent phenomenon.

Most of the mountains over 3000 m high in Papua New Guinea (and probably also Irian Jaya) supported ice-caps often feeding valley glaciers during the Pleistocene [Löffler, 1972]. Moraines are still visible today and much fluvioglacial material has been deposited as fans and braided river beds in the valleys of the highlands. In addition even larger natural "seed-beds" were provided in Plio-Pleistocene times by volcanoes in the highlands of Papua New Guinea [Bain and others, 1970; Taylor, 1969]. Some of these mountains were volcanically active concurrent with being glaciated [e.g. Giluwe; Blake and Löffler, 1971] while others were too low to support ice-caps. Large areas of lava were extruded and yet larger areas periodically blanketed by ash showers, leading to lahars and other geomorphic processes of rapid erosion and deposition [Pain, 1973].

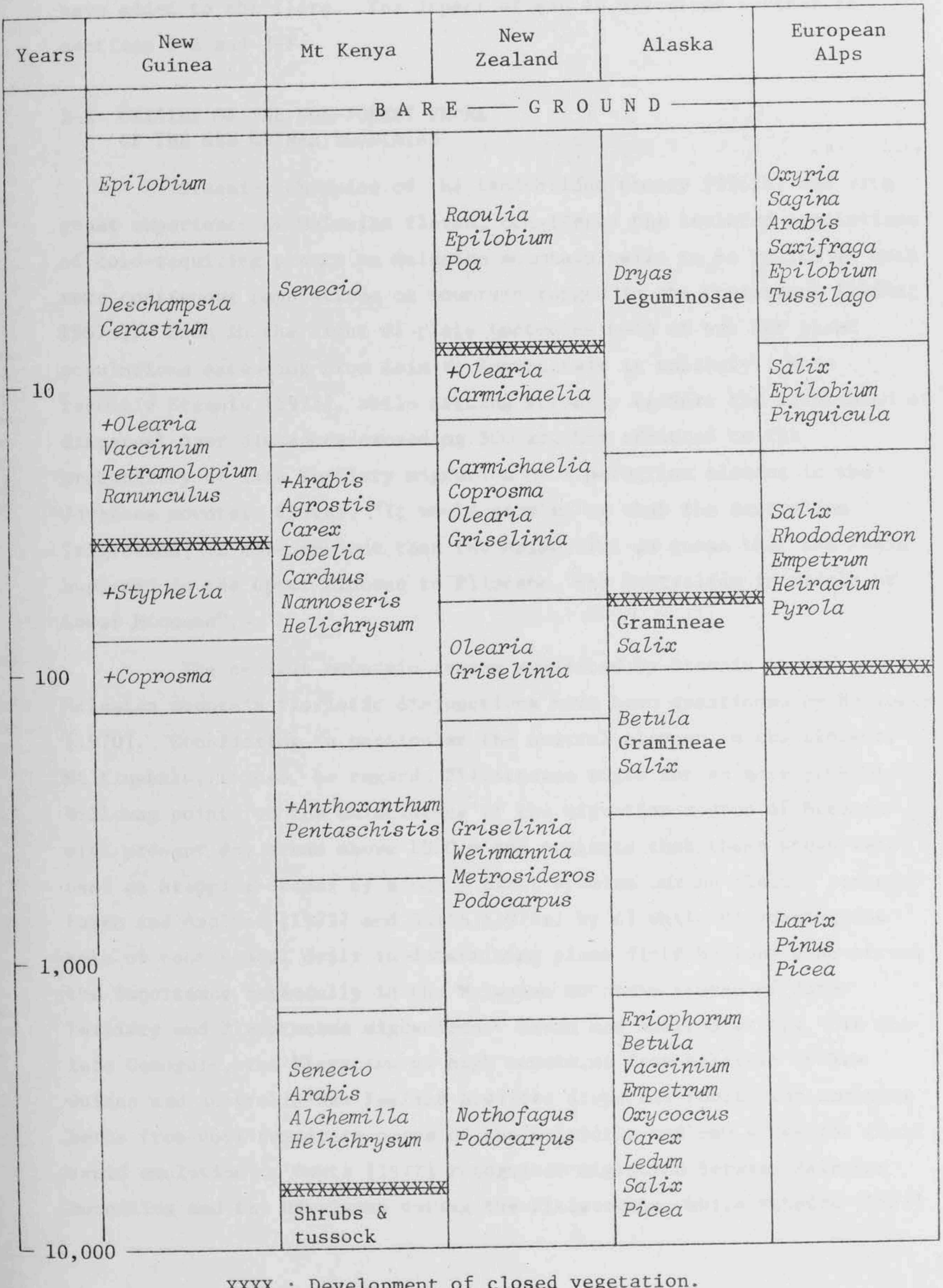
Morainic material is rich in mineral nutrients, though poor in nitrogen, and scattered erratic boulders offer niches at their bases sheltered from damaging winds, where insolation is more effective, and where windblown debris including seeds tends to collect [Swan, 1961]. Volcanic ash is similarly rich in mineral nutrients and may be deposited at any altitude. The occurrence of areas of mineral soil was probably of importance to plant immigration to New Guinea. Most plant species especially of the pioneer type are not usually able to establish themselves in closed stands of vegetation, whereas open habitats may be readily colonized. Dispersal of disseminules is of no avail in increasing the range of a species if successful germination, establishment and reproduction do not follow. On Mt Wilhelm today several native species (e.g. *Gnaphalium involucratum*, *Sagina papuana*, *Senecio glomeratus*) are seldom found other than in sites of natural or human disturbance such as landslips, streambanks and paths, and alien species show the same behaviour. In northwest Europe the earliest vegetation to colonize the moraines of the last glacial period included a large number of species which can only be described as ruderals, many now common and widespread as garden weeds [Godwin, 1960]. The probable importance of both glacial and volcanic activity in producing sites suitable for the establishment of immigrant plants has been emphasized for East African mountains by Hedberg [1971].

Accounts of seral succession on recently exposed moraines have been written for several regions. The achievement of a closed sward may take less than ten years (Franz Josef glacier, New Zealand; Stevens [1963]) or several thousand (Mt Kenya; Coe [1967]), notable pioneer species including Compositae (Mt Kenya, New Zealand), Gramineae (New Guinea, Mt Kenya, New Zealand), Leguminosae (New Zealand, Alaska), *Epilobium* (New Guinea, New Zealand, European Alps) and *Dryas* (Alaska) (see Fig. 2-2).

Ecologically important in New Zealand and Alaska are nodulated species which fix nitrogen, mainly *Carmichaelia* and *Coriaria* [Stevens, 1963] and *Dryas* and *Alnus* [Lawrence and others, 1967] respectively. Since *Coriaria papuana* does not grow above 3230 m on Mt Wilhelm today and was not recorded in the Mt Carstensz moraine succession [G.S. Hope, pers. comm., 1972] it is hard to see what vascular plants if any may be nitrogen-fixing on New Guinea moraines.

Man has been present in the highlands of New Guinea for at least 25,000 years [White and others, 1970] when the forest limit was depressed to at least 2400 m and perhaps below 2000 m [Hope, 1973]. The

Fig. 2-2: Vegetation succession on glacially deposited material in various regions. Data for New Guinea (Carstensz) from G.S. Hope [pers. comm., 1972], for Mt Kenya from Coe [1967], for New Zealand from Stevens [1963; 1968], for Alaska from Viereck [1966], and for European Alps from Lüdi [1945].



XXXX : Development of closed vegetation.

effects of agriculture and replacement of forest by grassland through the medium of fire have been man's principal influences upon highlands vegetation, while numerous introductions especially in the last 50 years have added to the flora. The impact of man is discussed further in sections 3-E and 3-F.

2-E ORIGINS OF THE NON-FOREST FLORA OF THE NEW GUINEA MOUNTAINS

Steenis, champion of the land-bridge theory [1962a] and with great experience of Malesian floras, considered the isolated populations of cold-requiring plants on Malesian mountain peaks to be relics of much more continuous populations on mountain ranges in the Cretaceous [1964a; 1967a]. Seen in the light of plate tectonics such an age for plant populations extending from Asia to Australasia is unlikely. More recently Steenis [1972], while arguing strongly against the likelihood of dispersal over distances exceeding 500 km, has admitted to the probability of late Tertiary migration of a peregrine element in the Javanese mountain flora: "It would seem to me that the Australian [migration] is more ancient than the Asian, let us guess that the Asian happened in the Upper Miocene to Pliocene, the Australian in Middle or Lower Miocene".

The ancient mountain ranges suggested by Steenis to account for Malesian mountain floristic disjunctions have been questioned by Holloway [1970]. Considering in particular the austral element in the flora of Mt Kinabalu, Borneo, he regards Pleistocene migration as more probable. Holloway points to the coincidence of the migration routes of Steenis with present day areas above 1000 m and suggests that these areas were used as stepping-stones by montane plant species during glacial periods. Raven and Axelrod [1972] and Smith (1974a; b; c] while discussing the role of continental drift in determining plant distributions also stress the importance especially in the Malesian mountain floras of late Tertiary and Pleistocene migrations. Raven and Axelrod write: "In the late Cenozoic, the elevation of high mountains from Malaysia to New Guinea and Australia-New Zealand provided dispersal routes for numerous herbs from cool-temperate parts of the Holarctic and new sites for their rapid evolution". Gupta [1972] recognizes migration between Malesian mountains and the Himalayas during the Pleistocene, while Schodde [1973] considers the diverse geographical affinities of the fauna and flora above the New Guinea forest limit suggestive of "itinerant colonization".

Consideration of the apparent geographical affinities of the New Guinea non-forest mountain flora together with the region's geological and geographical history leads me to suggest three main elements:

1. Gondwanic. Having origins in Gondwanaland and having remained in the New Guinea area or nearby in north Australia or New Caledonia throughout the Tertiary.

2. Peregrine. Having migrated from temperate areas both north and south in Plio-Pleistocene times.

3. Alien. Having been introduced by man from most parts of the world, in particular from the long-cultivated Eurasian region.

The gondwanic element dominates the mountain forest most of whose trees belong to southern families or genera (e.g. Cunoniaceae, Monimiaceae, Pittosporaceae, Podocarpaceae, *Nothofagus*). Some members of such taxa occur above the forests as grassland shrubs or trees, like *Dacrycarpus compactus* and *Drimys piperita*, and some non-forest herbaceous genera have distributions suggestive of a gondwanic origin, like *Oreomyrrhis*. It is possible that alpine/tropicalpine herbs have survived *in situ* on low peaks in north Australia/New Guinea since the uplift of the Oligocene and perhaps since the end of the Cretaceous, together with the mountain forest taxa (e.g. *Nothofagus*) which have in some cases subsequently evolved species of tropicalpine tolerance (e.g. *Drimys*). But the tropicalpine flora did not develop a large area or species richness until the major uplifts of the Miocene.

During the earlier Tertiary, when world climate was warmer and New Guinea topography less elevated, even allowing for its more southerly position, the New Guinea region may have supported only small areas of mountain non-forest vegetation. The same can be said with more certainty of New Zealand, where it has been postulated that the alpine flora is partially derived from a well-developed late Tertiary antarctic-alpine flora in Antarctica [Fleming, 1963b] as well as having an important immigrant element which has arrived from Australia since the Miocene [Raven, 1973]. So although it seems unlikely that the gondwanic forests are the result of upper Tertiary migration from the far south (southern

Australia, New Zealand or Antarctica) it is possible that apparently gondwanic elements in the tropicalpine flora like *Coprosma* are so, and possibly better included in the peregrine element. My gondwanic element is the equivalent in part of the palaeoaustral element of New Zealand [Fleming, 1963a] and the continental element of the south temperate zone [Wace, 1965].

The peregrine element includes most of the non-forest mountain flora, embracing species found both outside New Guinea and endemic to it. It is postulated that these plants immigrated during Miocene, Pliocene and Pleistocene times, after major uplift (Miocene) and at an increasing rate as New Guinea moved nearer Asia, as further uplift increased the highland area, and as cooling climate expanded the area of tropicalpine vegetation. Probably most immigration took place during the Pleistocene glacial periods.

Fig. 2-3 shows the location of areas in Malesia and Australia likely to have been above the maximum forest limit at the time of the glacial maximum. Distances (km) are given beside some gaps. The longest gap, apart from to Japan and New Zealand, is between New Guinea and the New England highlands of eastern Australia. Furthermore this gap is least likely to have had many if any small areas of alpine/tropicalpine vegetation to act as stepping-stones during plant migration. Throughout Malesia however there are liable to have been small areas of tropicalpine vegetation on peaks which were below the maximum forest limit, just as mountains in Sumatra, Java and Sulawesi support non-forest vegetation today though below forest limit (see Fig. 2-4). The migration tracks of Malesian mountain plants of Steenis [1964a] are shown in Fig. 2-5, from which and by comparison with Fig. 2-3 it can be seen that the tracks follow the rows of "stepping-stones" presented by current topography and that there is little need for recourse to past mountain chains which have since eroded away. The considerable importance of stepping-stones for migration has been demonstrated by MacArthur and Wilson [1967].

The peregrine element includes taxa of various geographical affinities. A group of plants having close links with the cool wet areas of the south temperate zone [e.g. *Acaena*, *Nertera granadensis*) can be equated with Fleming's [1963a] neoaustral element. Other taxa like the Epacridaceae and *Centrolepis* are distinctly Australian, and yet others are of northern affinity and origin such as *Rhododendron*, *Potentilla* and

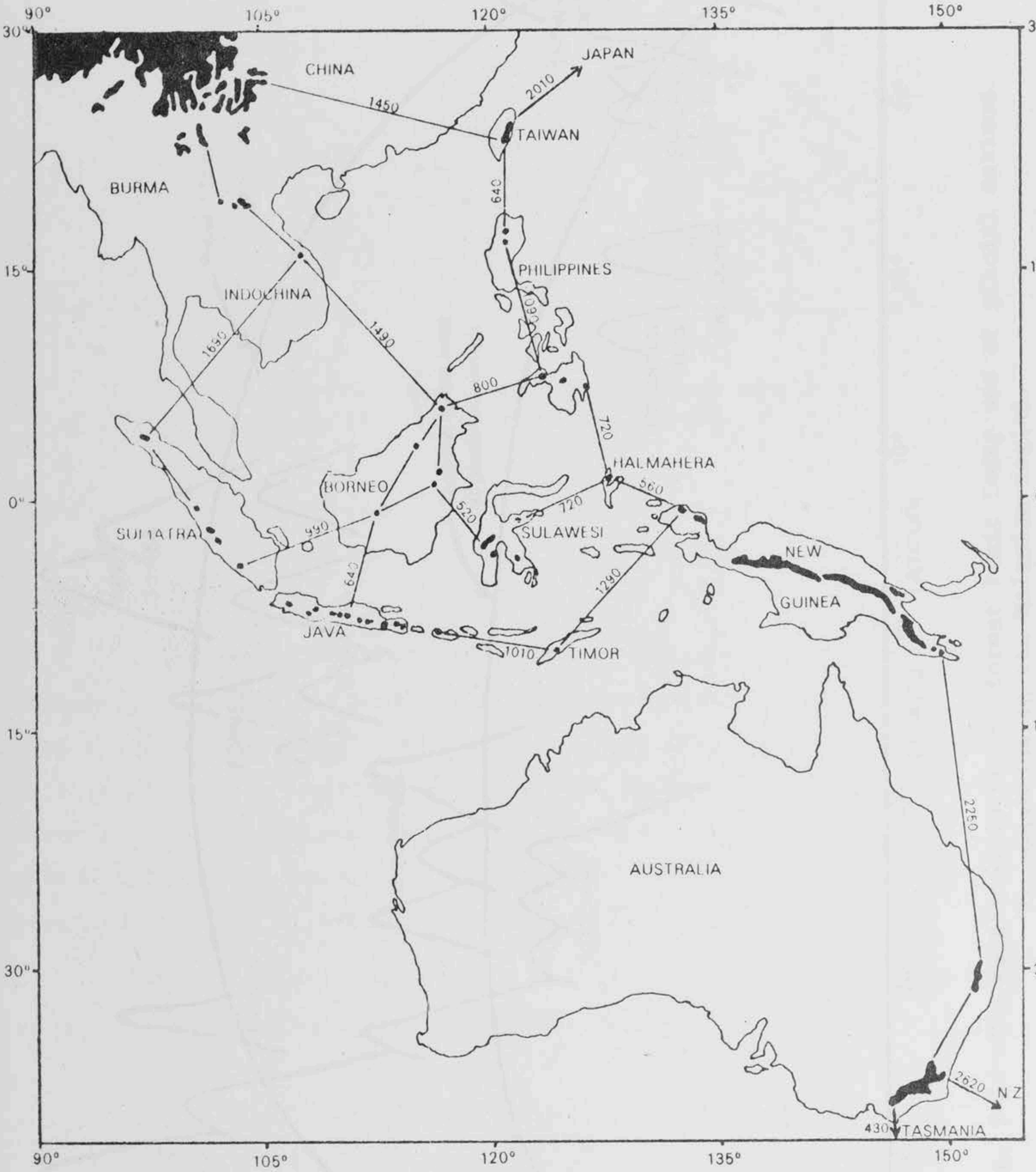


Fig. 2-3: Land in the Malesian region probably lying above the forest limit at the time of glacial maximum.

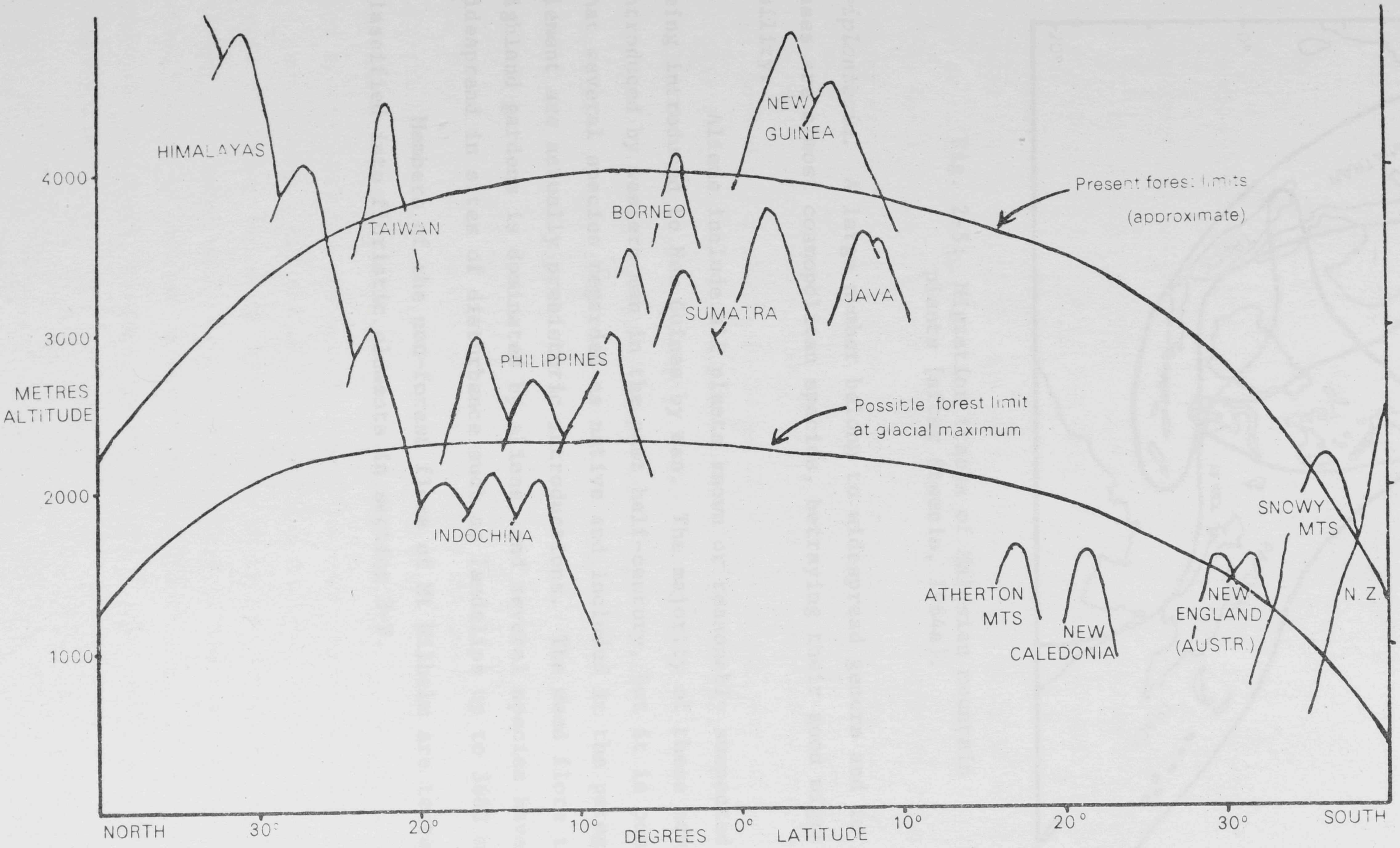


Fig. 2-4: The relationship of the forest limit today and at glacial maximum to mountains in the Malesian region.

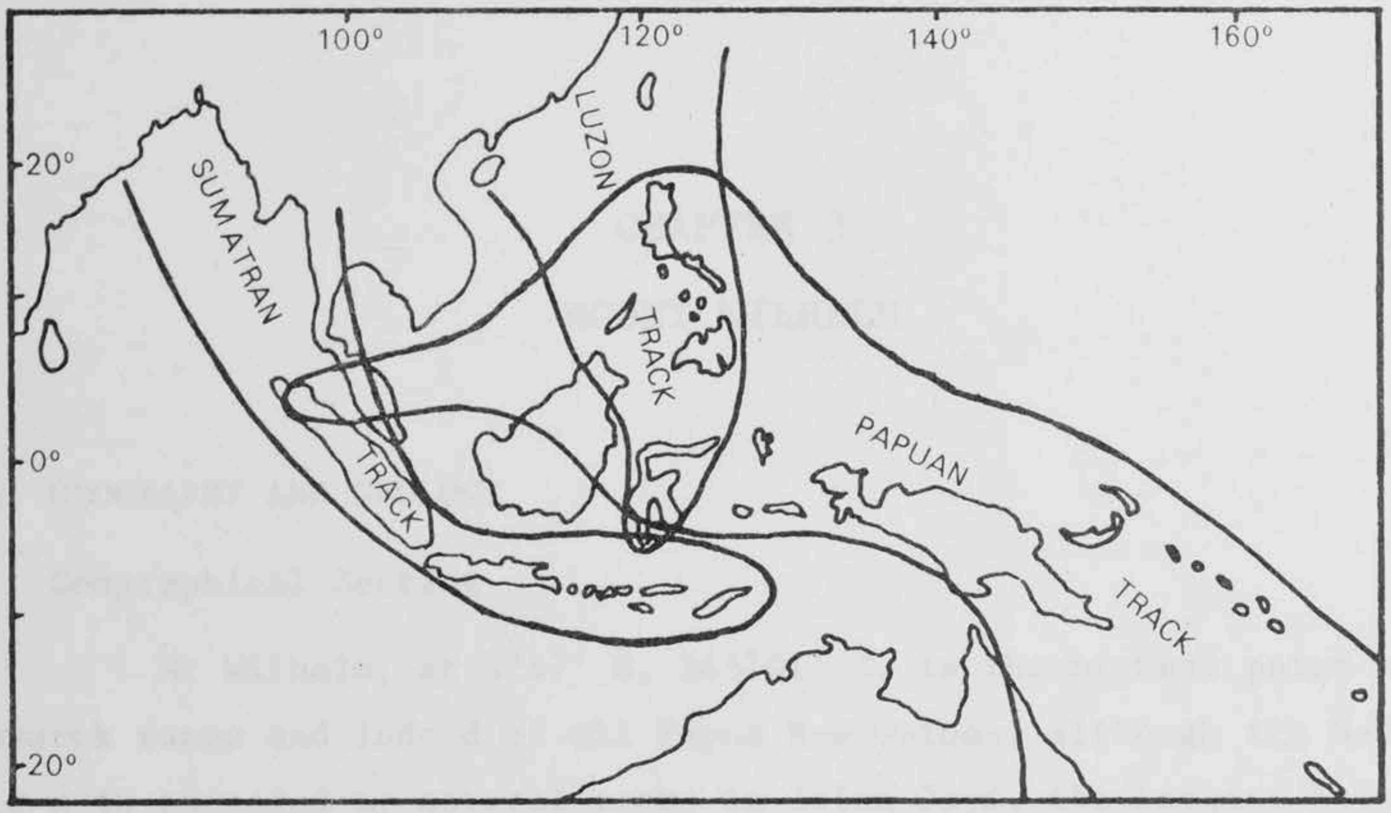


Fig. 2-5: Migration tracks of Malesian mountain plants [after Steenis, 1964a].

Triplostegia. A large number belong to widespread genera and in some cases are almost cosmopolitan species, betraying their good migration ability.

Aliens include all plants known or reasonably suspected of being introduced to New Guinea by man. The majority of these have been introduced by western man in the past half-century, but it is possible that several species regarded as native and included in the peregrine element are actually prehistoric introductions. The weed flora in highland gardens is dominated by aliens, and several species have become widespread in sites of disturbance such as landslips up to 3688 m.

Members of the non-forest flora of Mt Wilhelm are tentatively classified into floristic elements in section 3-F.

CHAPTER 3

MOUNT WILHELM

3-A GEOGRAPHY AND GEOLOGY

(a) Geographical Setting

Mt Wilhelm, at 5°47' S, 145°01' E, is the highest point of the Bismarck range and indeed of all Papua New Guinea, although its height of 4510 m is exceeded by several peaks in Irian Jaya, the largest being Carstensz (4884 m). Mt Wilhelm is situated at the junction of the Bismarck range (running northwest and southsoutheast from the mountain) and the Sepik-Wahgi divide (to the west), lying astride the watershed dividing drainage to the Bismarck Sea northwards and the Gulf of Papua southwards. To the northwest the Bismarck range drops to about 3700 m before rising again to form Mt Herbert (about 7 km distant and 4200 m high), beyond which the range loses altitude and does not exceed 3000 m. The same range to the southsoutheast forms Kombugli Hill (3260 m, about 6 km from Mt Wilhelm) and maintains a height of about 2800 m until reaching Mt Otto 55 km distant and 3569 m high. The Sepik-Wahgi divide loses altitude away from Mt Wilhelm but does not drop below 2500 m for a distance of over 35 km.

The deployment of ridges divides the drainage of Mt Wilhelm into four systems. To the westnorthwest of the summit ridge (see Fig. 3-1) the upper Jimi valley with its two lakes, Bendenumbun (3572 m) and Bandenumbun (3530 m), drains to the Jimi, Yuat and Sepik rivers. Northeast of the mountain the wide and deep Imbukum valley leads to the Inbrum and Ramu rivers. All the southern valleys drain ultimately to the Purari river but in the Mt Wilhelm area there are two distinct tributary systems, the Wahgi which receives the waters of the Koronigl (with several lakes in smaller valleys) and the Chimbu which drains the Pindaunde (2 lakes), Pengagl, Guraguragugl (1 lake) and Giwimawi (3 lakes) valleys.

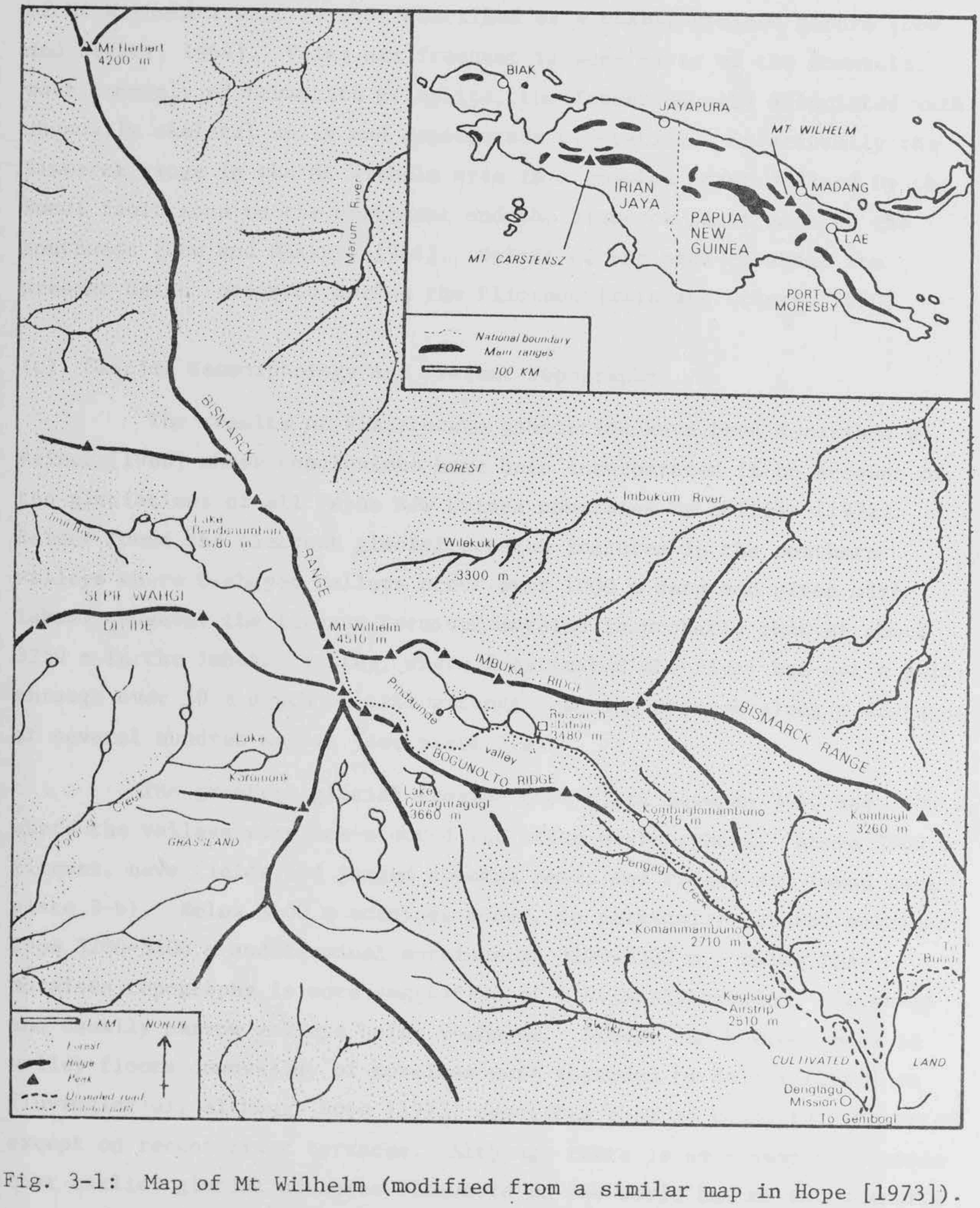


Fig. 3-1: Map of Mt Wilhelm (modified from a similar map in Hope [1973]).

(b) Geology

The lithology of Mt Wilhelm is fairly uniform, the area consisting entirely of Bismarck granodiorite [Rickwood, 1955], dated radiometrically as Miocene in age [Page and McDougall, 1970]. The chemical and crystalline structure of the rock is not uniform, and that of Mt Wilhelm itself is best described as a coarse-grained gabbro [Dow and Dekker, 1964]. Veins are frequent in some parts of the mountain, most commonly of haematite or aplite, the former usually associated with unusually skeletal soils and depauperate vegetation. Structurally the Bismarck range in the Mt Wilhelm area is a complex horst defined by the Bundi fault zone to the northeast and the Bismarck fault zone to the southwest [Dow and Dekker, 1964]. Uplift of the area to about its present height occurred during the Pliocene [Bain and others, 1970].

(c) Glacial Geomorphology and Present Topography

The results of Pleistocene glaciation have been described by Reiner [1960] whose conclusions have been incorporated in an account of the glaciations of all Papua New Guinea mountains by Löffler [1972]. Reiner found the clearest glacial erosion features in the southern valleys where U-shaped valleys occur over 1000 m deep and often with lakes. However the largest terminal moraine is probably that at about 3250 m in the Imbukum valley, where I estimated the river had cut a gully through over 50 m depth of till without reaching bedrock along a distance of several hundred metres (see plate 3-a).

The greatest glacial erosion took place between 3400 and 3900 m, where the valleys were ice-scoured and often overdeepened. Above 3900 m cirques, neve fields and jagged nunatak peaks and ridges are found (see plate 3-b). Below 3400 m moraines occur, in particular lateral moraines from 3200-3400 m and terminal moraines at 3200-3300 m. Below the moraines topography is more suggestive of fluviatile erosion, the steep and usually narrow valleys being V-shaped. Gravel and boulder beds in valley floors downvalley of moraines were regarded by Reiner [1960] as fluvioglacial, although Hope [1973] describes them as completely unsorted except on recent river terraces. Although there is no reason to suppose that earlier glacial advances elsewhere in the world had no counterparts in New Guinea, firm evidence has been obtained for only a single glacial period [Löffler, 1972; Reiner, 1960], the ice reaching its maximum extent

Plate 3-a: The Imbukum valley terminal moraine.

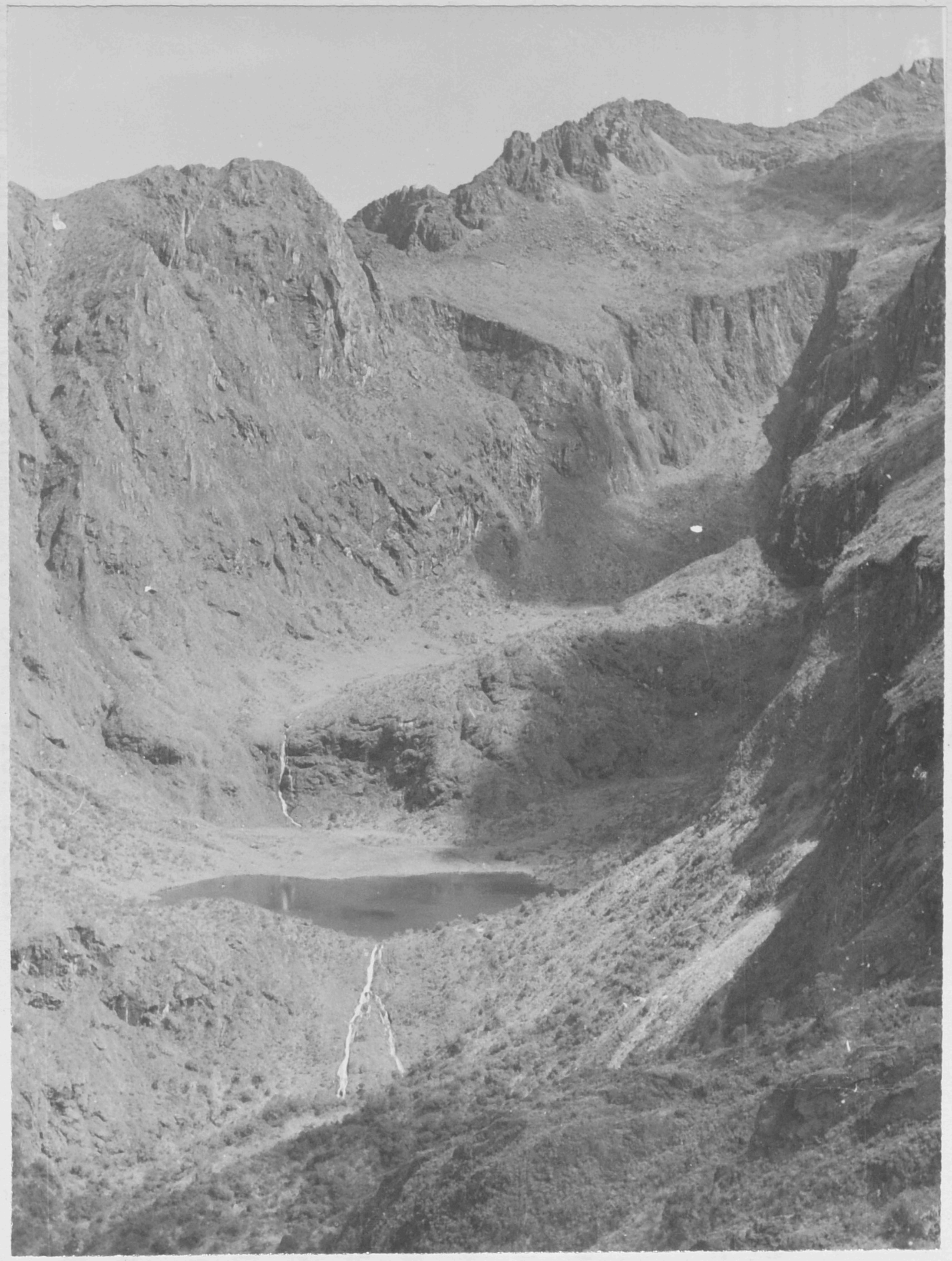


Plate 3-b: The Guraguragl valley, with its lake at 3660 m.

about 14,500 yr ago and climate becoming similar to that of today about 8,600 yr ago [Hope, 1973].

Present topography above 3215 m is largely the result of glacial geomorphology. Jagged peaks and ridges sometimes with screes or blockstreams below them overlook sloping but not precipitous former neve fields, usually with only a thin skeletal soil.

The valleys are steep-sided and flat-bottomed. The sides are frequently almost vertical and of bare rock, but other slopes, even at angles steeper than 45°, are generally soil-covered and support closed vegetation, often tussock grassland. However landslips are frequent off such slopes, often beginning as a slippage of waterlogged peaty soil lubricated by seeping water at the soil/till or soil/rock interface which leads to a mudflow down to the valley floor. Large or repeated slips can result in deep gullies with banks raised by debris deposited along them from the mudflows in a way analogous to levee formation on floodplains. Valley bottoms, flat and often mantled irregularly by till, are ill-drained and boggy (or submerged) over wide areas.

Judging by the clarity of the streams and lakes and by the small size of deltas at lake inflow points, erosion is generally proceeding slowly. However, landslips can be large and are not restricted to the glaciated valleys above 3215 m. Brass [1964] reported that a large landslip in forested country in the Pengagl valley between 3050 and 3120 m, still active in 1972, occurred in 1958. This choked the bed of Pengagl Creek with boulders, gravel and wood for more than 1 km (see plate 3-c) in a similar way to landslides described and illustrated from the Adelbert range by Pain [1972].

3-B CLIMATE

Meteorological measurements were made periodically between 1966 and 1972, mainly near the Australian National University research station (3480 m) but with spasmodic measurements of various climatic parameters down to 3215 m in the Pindaunde valley and up to 4400 m on the summit ridge. A summary of the research station observations is provided in Fig. 3-2. Previous publications on the climate include two papers by McVean [1968; and in press] while other authors notably Hnatiuk [in prep.] and Hope [1973] have included climatic data in accounts of

Plate 3-c: Pengagl Creek at 2810 m.

Plate 3-d: Pindaunde valley near Kombuglomambuno, 3250 m.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Yr	Monthly Range
Temperature (°C)	Mean max.	11.7	8.3	10.8	11.7	11.5	11.6	11.2	11.8	9.6	11.6	11.7	11.7	11.1	3.5
	Mean min.	4.4	3.8	4.8	4.3	4.4	3.9	3.5	3.2	3.4	3.9	3.0	4.1	3.9	1.8
	½ (max. + min.)	8.0	6.0	7.8	8.0	7.9	7.7	7.3	7.5	6.5	7.7	7.3	7.9	7.5	2.0
	Highest max.	13.4	11.1	12.8	14.4	13.9	15.0	14.3	15.0	14.4	15.5	14.2	13.2	15.5	4.4
	Lowest min.	2.7	1.7	3.4	0.8	0.6	-0.4	-0.2	-0.8	-0.3	-0.1	-0.2	2.7	-0.8	4.2
	Lowest max.	10.1	5.6	8.6	8.3	7.2	7.3	7.8	8.6	6.8	7.8	8.4	9.2	5.6	4.5
	Highest min.	6.7	5.3	5.9	7.2	6.1	8.7	6.1	6.1	7.6	6.2	6.2	6.2	8.7	3.4
	Lowest grass min.	-2.1	?	-2.6	-6.0	-3.3	-4.7	-6.9	-6.9	-6.8	-3.3	-9.1	-2.1	-9.1	7.0
	Highest grass max.	?	?	23.5	26.8	26.3	29.4	23.3	27.0	27.0	24.4	25.9	?	29.4	6.1
Rainfall (mm)		365	(285)	205+	200+	212+	96	91+	120	165	207+	238	398	2583+	307
Lowest relative humitidy (%)		?	50	?	45	45	25	30	30	30	30	30	55	25	30
No. days with ground frost		3+	?	1+	7+	7+	17+	9+	14+	14+	6+	9+	2+	89+	-
No. days without cloud		?	?	?	?	3	6	3	5	3	?	?	?	20+	-
Max. no. months of observation		1	1	1	3	4	5	6	5	5	4	3	1	-	-

Fig. 3.2: Summary of meteorological records, Mt Wilhelm, 3480 m, 1966-72.

biological research. A comprehensive paper on the climate of Mt Wilhelm is currently in preparation [Hnatiuk and others, in prep.].

(a) Precipitation, Runoff and Evapotranspiration

Rain falls throughout the year on Mt Wilhelm, but shows a pronounced peak from December to March in common with lower altitude areas surrounding the mountain [Brookfield and Hart, 1966]. Above 4000 m much of the precipitation is snow, usually of the translucent pellet (sago) variety but also flake snow, but it quickly melts. Hail, usually light, may fall at any altitude.

It has not been possible to accurately measure the total rainfall for a whole year, but the use of a non-standard long-term rain-gauge during the wet season of 1971-72 produced a probable rainfall figure of 3356-3537 mm for the year beginning 1 September 1971 at the research station at 3480 m. From fragmentary records the annual rainfall at Kombuglomambuno (3215 m) was estimated to be 2400 mm [McVean, 1968]. Annual precipitation at the Saddle Camp (4380 m) may be slightly less than at the research station (3480 m).

Up to 22 consecutive dry days have been recorded, and over 40 consecutive rainy days. Periods of more than a few dry days are not usual and are confined to the dry seasons of particular years (e.g. 1970 and 1972) of drought throughout the highlands. The highest rainfall recorded for a single day in over 40 months of records was 58.4 mm, on 1 May 1972. Most rain is not of high intensity, fine drizzle being common. Runoff, at least from unforested slopes above 3500 m, is rapid and lake level responds to precipitation within about 24 hr. Potential evapotranspiration [McVean, 1968] varies inversely with rainfall, lying between 19 and 57 mm per month at the research station and 39 and 66 mm at Kombuglomambuno (3215 m).

Relative humidity seldom falls below 40% and is usually much higher. As well as predictable diurnal minima, low humidities frequently occur at night, usually after midnight, probably explicable by "dry föhn" winds as described for Mt Kenya by Hedberg [1964] [R.J. Hnatiuk, pers. comm., 1973]. Stiff winds often from the northeast are commonly experienced at the summit, but at lower altitudes most winds are gentle upvalley draughts by day and downvalley draughts by night.

(b) Radiation and Temperature

Mean daily sunshine calculated from data gathered over 7 months in 1968-69 is less than 3 hours (D.N. McVean, pers. comm., 1973] and the average rate of radiant energy input over 7 months of 1970 was 0.56 ± 0.05 cal/cm^2/min, about a quarter of incoming daytime radiation being reradiated at night [R.J. Hnatiuk, pers. comm., 1973].

Temperatures vary little through the day and hardly at all from month to month, as shown by the thermoisopleth [Troll, 1943] derived from screen temperature records at 3480 m during 1970 (Fig. 3-3) [R.J. Hnatiuk, pers. comm., 1973]. Although the temperature range is small it is clear that the thermal climate is diurnal and not seasonal, as befits the mountain's tropical position. Temperature range beneath a forest canopy is yet smaller [McVean, 1968].

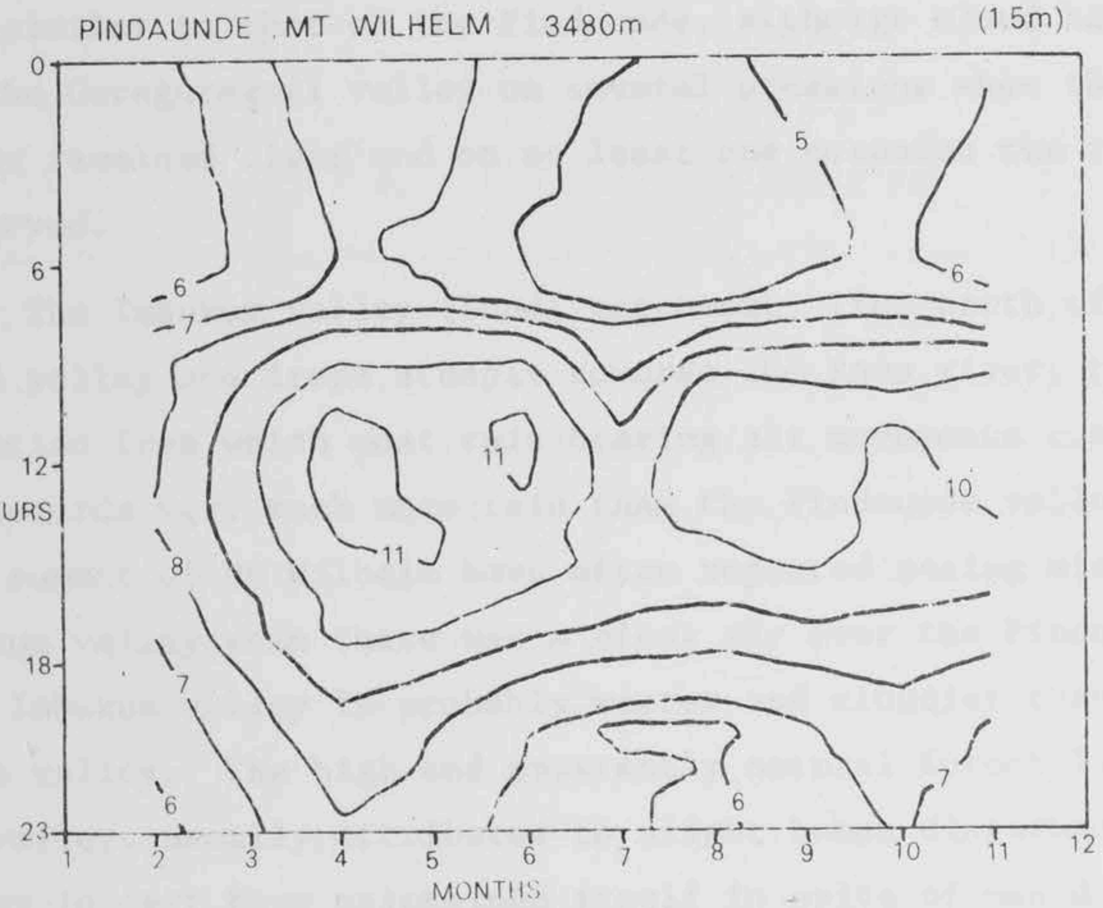


Fig. 3-3: Thermoisopleth for screen temperatures at Pindaunde research station (3480 m).

Near or at ground level in grassland the range of temperatures is greater (see also section 7-B). Frosts occur at ground level near the research station on most clear nights but only rarely does air temperature at 1.5 m height fall to freezing point. Similarly the mean maximum temperature at ground level is 19.7 °C compared with 11.1 °C at screen height. Soil temperatures at and below 15 cm depth remain continually between 7 °C and 8 °C.

Ground frosts occur almost nightly above 4300 m, on between a quarter and a half of all nights at 3480 m, and occasionally at 3215 m. On areas of bare wet soil, especially above 4000 m but sometimes at 3480 m, needle ice (pipkrake) may form on frosty nights, heaving surface particles of soil (and seedlings) up to 5 cm above ground surface.

(c) Variation and Comparisons

To date, all meteorological measurements on Mt Wilhelm have been made in the Pindaunde valley or on its adjacent ridges. Only casual observations have been made in other valleys. A summary of these observations is presented below to indicate the extent to which observations in the Pindaunde valley reflect the climate everywhere on Mt Wilhelm. It seems probable that the climates of the southern valleys are very similar to that of the Pindaunde, although cloud has been seen to fill the Guraguragugl valley on several occasions when the Pindaunde valley has remained clear and on at least one occasion the reverse has been observed.

The Imbukum valley (Bundi catchment) lies north of the Pindaunde valley and drops steeply towards the Ramu river, thus facing the direction from which most rain-bearing air movements come. Bundi, at 1400 m, records very much more rain than the Pindaunde valley. Observers near the summit of Mt Wilhelm have often reported seeing mist or cloud in the Imbukum valley when there was a clear sky over the Pindaunde valley. Thus the Imbukum valley is probably wetter and cloudier than the Pindaunde valley. The high and apparently natural forest limit in the Imbukum valley, usually attributed to slight human disturbance [Smith, 1974d] may in part have maintained itself in spite of man due to a wetter climate.

The Bendenumbun or upper Jimi valley may be divided into two climatically different sections which are separated by a narrow and precipitous right-angled bend in the valley between the two lakes (i.e. between 3572 m and 3530 m). Frequent observations from the summit area of Mt Wilhelm suggest that the upper section is probably climatically similar to the Pindaunde valley but that the lower section is mistier and moister. Cloud has been seen here when the whole summit area was clear.

There is botanical evidence in support of the hypothesis of a cloudier and milder climate for the lower section of the upper Jimi valley. *Agapetes vitis-idaea* is common from below 3170 m to 3650 m, this being the only valley on Mt Wilhelm where it has been found (except for a single record from Imbuka Ridge). Elsewhere in New Guinea (e.g. Kubor range and Mt Ialibu), it is a plant of moist habitats. Many of the upper Jimi valley plants were suffering frost or drought damage in August 1972. *Hypericum papuanum* was found up to 3322 m in the upper Jimi valley but elsewhere on the mountain it occurs much lower down (e.g. up to only 3026 m in the Pengagl valley). Trees and other shrub taxa, restricted to the forests in the Pindaunde valley, are found in the grasslands of the lower valley section below Lake Bandenumbun.

In Fig. 3-4 some climatic parameters for Mt Wilhelm at 3480 m are compared with those for some other tropical mountains.

3-C SOILS AND BIOTA

(a) Soils

The soils of Mt Wilhelm above the upper limit of continuous forest (3215 m) are described as alpine peat and humus soils [Haantjens, 1970]. The Pinde Family of soils occurs beneath grasslands on gentle to steep slopes between 3350 and 3960 m, while the Pompameiri Family occurs on various slopes under forest or, rarely, grassland between 2135 and 3660 m. It may be that Pinde soils occur beneath natural non-forest vegetation while the Pompameiri soils occur beneath forest or anthropogenic grassland. A third family of alpine peat and humus soils, the Tomba, is found more commonly on weathered volcanic ash but can also occur on weathered coarse-grained rock, and may underlie either forest or grassland between 2135 and 3660 m. Pinde and Tomba soils are between 0.4 and 0.8 m deep and Pompameiri soils between 0.9 and 1.2 m. All are clayey or loamy and very rich in organic matter.

Soil analyses are reported by Wade and McVean [1969] for 30 sites on Mt Wilhelm between 3470 and 4350 m. They found a generally low level of soil fertility. Amounts of exchangeable calcium and magnesium decreased with altitude, while pH and phosphorus levels showed no altitudinal trend. Carbon contents ranged from 3.1 per cent to 33.8 per cent, carbon/nitrogen ratios from 13.0 to 27.7 and pH from 4.7 to 6.7. Soils are not entirely autochtonous since traces of several showers of

Region	Site	Altitude (m)	Mean Max. Temperature (°C)	Mean Min. Temperature (°C)	Mean Daily Temperature Amplitude (°C)	Absolute Max. Temperature (°C)	Absolute Min. Temperature (°C)	Annual Precipitation (mm)
New Guinea	Pindaunde, Mt Wilhelm	3480	11.1	3.9	3-4 (1970) *c.* 7 (1972)	15.0	-0.8	*c.* 3450
Borneo	Panar Laban, Mt Kinabalu	3353	*c.* 15	5.3	*c.* 8	18	0.6	*c.* 3300
Java	Summit, Mt Pangrango	3025	?	?	2-5	12.8	6.5	*c.* 3500
Ecuador	Cotopaxi	3600	7.5	5.4	8.6	17.3	-1.5	500-1000?
	Cruz Loma	3950	6.8	5.9	6.4	14.0	1.5	?
	Gomessiat	4750	0.9	0.7	2.5	3.5	-2.0	?
Mt Kenya, East Africa	Naro Moro Trk	3048	16.2	1.7	16.2	19.4	-1.6	1397
	Teleki Valley	4191	5.3	-3.6	5.3	11.0	-6.7	889

Fig. 3.4: Summary of climatic data for eight tropicalpine sites, based on a table compiled by R.J. Hnatiuk. (Kinabalu data from my observations, Aug. 1967, temperature data for only 14 days, rainfall extrapolated from only 23 days; Pangrango data from Troll [1964]; Ecuador temperature data from Troll [1959]; Kenya data from Coe [1967]; Cotopaxi precipitation estimate from Oxford Atlas, 1966).

volcanic ash up to about 3 cm thick can be found in sections of bog peat postdating glaciation.

(b) Vegetation

Wade and McVean [1969] in a detailed study of phytosociology in the Pindaunde valley-summit ridge area above 3100 m have described 29 plant associations. Of these 3 are forest types, 6 "subalpine" tussock grasslands, 9 mires, 4 landslip communities and 7 "alpine" associations. As recognized by these authors not all these associations are natural and intermediates exist between many of them. An earlier and less detailed study by Walker [1968] distinguished on both floristic and structural grounds four non-forest vegetation types, but the possibility of further subdivision or redefinition was admitted as more data accumulate.

I believe that the categories of Walker are too general and ill-defined to be of great utility during field studies while those of Wade and McVean, although undoubtedly real, are not sufficiently distinct from each other to be always readily recognizable under field conditions. Only a few relatively rare species are restricted to a single association, most being found in many different associations, only their relative proportions differing. Accordingly neither system of vegetation classification was adhered to in the present study. Non-forest vegetation is described and discussed further in sections D - E below.

Walker [1968] found very high above-ground standing crop weights in all non-forest vegetation types examined compared with their north temperate analogues. Hnatiuk [in prep.] confirms this for *Deschampsia klossii* tussock grassland, although he found productivity in subantarctic tussock grasses to be higher. Productivity of *Deschampsia* at higher altitudes may have been greater than at lower. High standing crop and productivity rates on Mt Wilhelm are probably associated with the non-seasonal thermal climate which allows perpetual growth.

The lowest tongues of mountain grassland on Mt Wilhelm are on the ill-drained terminal moraines as at Kombuglomambuno at 3215 m in the Pindaunde valley (see plate 3-d). Here the vegetation is dominated by tussock grasses, mainly *Deschampsia klossii* but with *Poa saruwagetica* on better-drained slopes. Tree-ferns of *Cyathea atrox* along the eastern side of the valley floor provide a bright green contrast to the varied but darker green of the forest on the valley sides and the predominantly

Plate 3-e: Cascade between the Pindaunde lakes: dead *Harmsiopanax ingens* in the foreground.

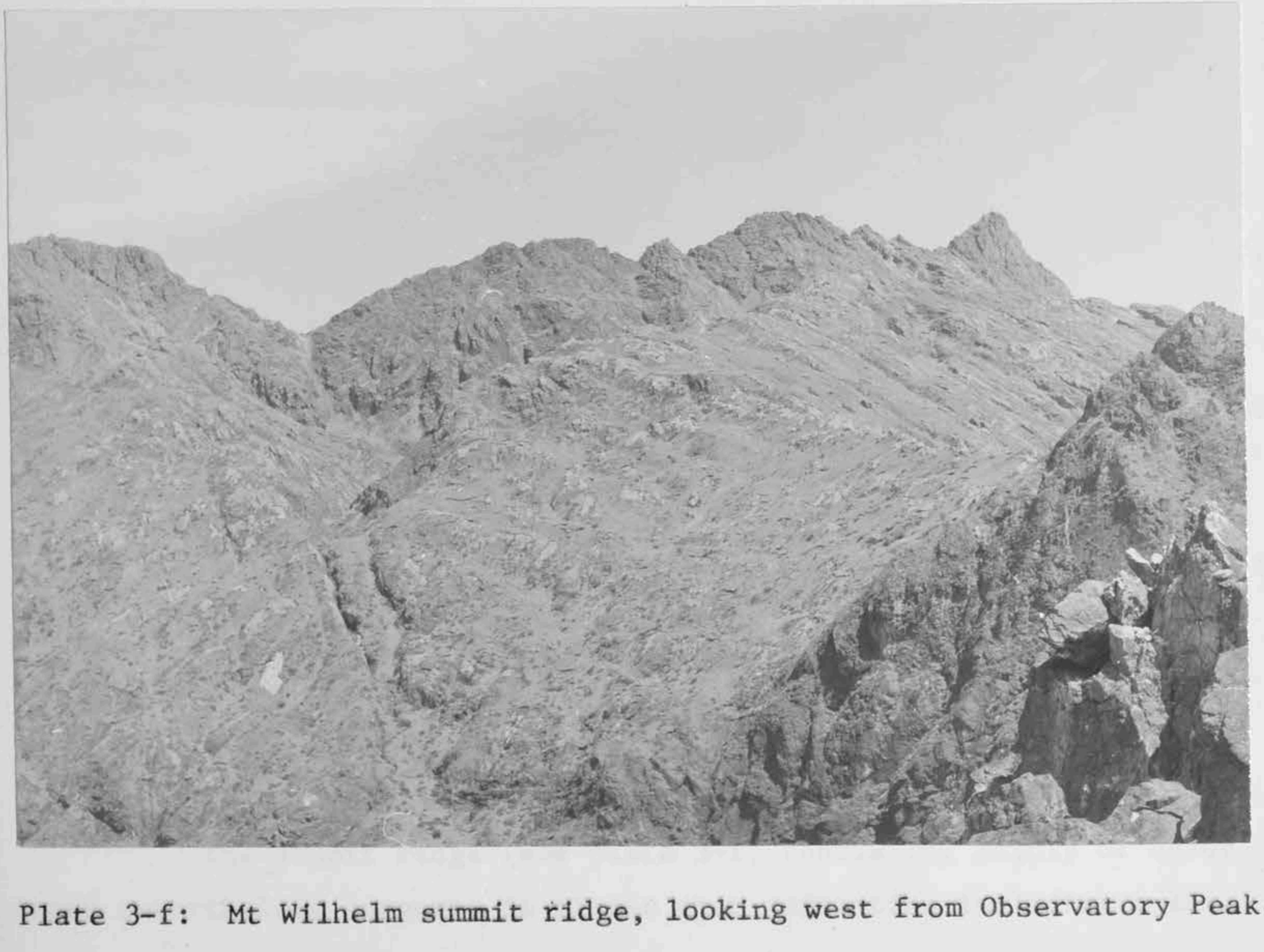


Plate 3-f: Mt Wilhelm summit ridge, looking west from Observatory Peak.

ochre shades of the tussock. As the climber ascends the valley other plant communities will be noticed especially on old landslips where small shrubs of *Haloragis halconensis* and *Vaccinium amblyandrum* as well as the taller *Rhododendron yelliottii* and *R. womersleyi* are often prominent. The forest margins are often choked by trailing stems of the shrubby *Coprosma papuensis* and the woolly-leaved herb *Anaphalis mariae*. Shrubs in the tussock grassland commonly include the red and cream flowered *Dimorphanthera microphylla*, *Gaultheria mundula* and *Styphelia suaveolens*.

As the altitude of the lower lake (3480 m) is approached, areas of flat boggy ground become increasingly frequent (see plate 3-e), lacking tussock grasses and woody plants and covered by small herbs and mosses, the former including cushions of *Monostachya oreoboloides* and *Astelia papuana*, many sedges, and providing colour in the form of yellow buttercups (*Ranunculus pseudolowii* and *R. wahgiensis*), blue and white gentians (*Gentiana ettingshausenii* and *G. piundenis*) and mauve daisies (*Keysseria radicans*). Most species here are not restricted to this habitat but occur elsewhere including at higher altitudes wherever a sufficient area and depth of soil exists which is not shaded by woody plants or tussock grasses. The lake itself is clear and cold, the only aquatic vascular plants being a few individuals of *Callitriche verna* and *Scirpus subtillissimus*.

Above this level the forests, still floristically rich but consisting merely of tangled shrubbery about 5 m high with scattered emergent *Dacrycarpus compactus* trees, is limited in extent to discrete thickets often in inaccessible places. Tussock grasslands predominate, often with many shrubs and scattered small trees of *Olearia spectabilis* and larger ones of *Dacrycarpus*. Above 3800 m however forest does not occur although shrubs of *Coprosma divergens* and other taxa continue but are of ever decreasing stature to over 4300 m. Small trees of *Drimys piperita* entity *subalpina* are found up to 4100 m. At these altitudes short grassland rich in species and often dominated by *Danthonia vestita* tends to replace the ubiquitous tussock grassland, perhaps associated with shallower soils. However *Deschampsia* still remains dominant over large areas up to 4400 m, often in association with the spiky rufous fronds of the alpine finger fern, *Papuapteris linearis*.

The summit ridge (see plate 3-f) consisting mainly of naked rock nevertheless supports in places open vegetation including a low heath of *Styphelia suaveolens* and *Tetramolopium macrum* and a sparse cover of bryophytes, lichens and small herbs, often including the yellow blooms of *Ranunculus saruwagedicus*, which has been described as tundra. Some plants (e.g. *Styphelia*) grow to within a few metres of the summit itself (4510 m), showing that though the mountain is probably less than 200 m below the snowline it does not exceed the upper limit of vascular plant occurrence.

(c) Flora

The flora of Mt Wilhelm, especially above the forests, has been fairly extensively collected although new species continue to be found. Three native and many alien species were found for the first time during my own fieldwork. Over 6000 specimens have been collected and some 390 native species of vascular plant have been recorded, as well as about 40 aliens: records of the flora and its collectors up to 1971 have been published by Johns and Stevens [1971]. The non-forest flora above 3215 m includes about 148 species, mostly herbs, excluding those found only occasionally in the lowest parts as "strays" from a basically lower altitude adventive flora (e.g. *Hypericum japonicum*, *Imperata conferta*, *Viola betonicifolia*).

Though moderately well collected the flora of Mt Wilhelm is not so fully described. Revisions have been recently published of several groups, for example in Flora Malesiana, but only rather piecemeal descriptive work has been completed on others. Several species remain to be described although in most cases at least as far as Mt Wilhelm is concerned the species limits are quite clear. In this thesis nomenclature follows Johns and Stevens [1971] wherever possible, even to the point of using their numbered but unnamed species (e.g. *Poa* sp.1, *Senecio* sp.2) and using the suffix "sp.1" for those species which are the only ones undescribed in their genera and so unnumbered by Johns and Stevens. Therefore *Lactuca* sp.1 refers to the high altitude species of *Lactuca* recognized by Johns and Stevens although undescribed, leaving *Lactuca* sp. to be used in any case in which I was unable to identify a specimen beyond generic level.

The following native species were omitted from Johns and Stevens [1971] or have been collected since its publication.

Alpinia sp.3	Zingiberaceae	3000 m
Blechnum vulcanicum (Bl.) Kuhn	Blechnaceae	2770 m
Brachycome papuana Mattf.	Compositae	3307 m
Cardamine africana L.	Cruciferae	2743-3050 m
Currania sp.1	Aspidiaceae	2770 m
Gentiana sp.1	Gentianaceae	4300 m
Gleichenia sp.1	Gleicheniaceae	3353 m
Hypolepis sp.2	Dennstaedtiaceae	2985 m
Macaranga rhodonema Airy Shaw	Euphorbiaceae	2800-3100 m
Mazus pumilus (Burm. f.) Steen.	Scrophulariaceae	2600-3480 m
Mecodium archboldii Copel	Hymenophyllaceae	2770 m
Microlepia sp.1	Dennstaedtiaceae	2985 m
Montia fontana L.	Portulacaceae	3200 m
Muhlenbergia arisansis Hayata	Gramineae	2933 m
Myriactis cabrerae Koster	Compositae	3350 m
Nasturtium backeri O.E. Schultz	Cruciferae	2700-2911 m
Pterostylis sp.1	Orchidaceae	3644 m
Saurauia rufa Burk.	Saurauiaceae	2593-2773 m
Scleranthus singuliflorus (F.v.M.) Mattf.	Caryophyllaceae	4400 m
Syzygium adelphicum Diels	Myrtaceae	2850-3150 m
Syzygium alatum (Laut.) Diels	Myrtaceae	3050-3560 m
Syzygium sp.1	Myrtaceae	2650-3048 m
Trichomanes sp.3	Hymenophyllaceae	3048 m
Trochocarpa papuana (Wright) Sleum.	Epacridaceae	3429 m

The following species through taxonomic revisions or new identifications have acquired new names since the publication of Johns and Stevens [1971].

Anaphalis hellwigii	becomes	*A. lorentzii* Lautb.
Breynia cernua	"	*B. collaris* Airy Shaw
Corsia sp.1	"	*C. unguiculata* Schltr. in K.Sch. & Laut.
Cyrtandra sp.2	"	*C. tarsodes* B.L. Burtt.
Dryopteris sp.1	"	*D. ?hirtipes* (Bl.) C.Chr.
Gnaphalium clemensiae	"	*G. breviscapum* Mattf.
Harmsiopanax sp.1	"	*H. ingens* Philipson
Hymenophyllum sp.2	"	*H. physocarpum* C.Chr.

Hypericum habbemense	becomes	*H. papuanum* Ridl.
Lactuca sp.2	"	*Senecio* sp.5
Myosotis saruwagedica	"	*M. australis* R. Br.
Phyllanthus nervosus	"	*P. flaviflorus* (Laut. & K.Sch.) Airy Shaw
Pilea sp.2	"	*Pilea* sp. cf. *johniana* Stapf
Polystichum sp.1	"	*Rumohra adiantiformis* (Forst.) Chin.
Polystichum sp.2	"	*?Stenolepia tristis* (Bl.) v.A.v.R.
Ranunculus sp.1	"	*R. schoddei* Eichler (ined.)
Riedelia sp.2	"	*R. monticola* Val.
Trichomanes pallidum	"	*Hymenophyllum* sp.4
Trichomanes sp.1	"	*Hymenophyllum* sp.5
Vaccinium amplifolium	"	*Dimorphanthera amplifolia* (F.v.M.) Stevens (ined.)
Vaccinium keysseri	"	*Dimorphanthera keysseri* (Schltr. ex Diels) Stevens (ined.)

A full list of alien species recorded above 2515 m on Mt Wilhelm is given in Fig. 3-8.

Some variable taxa occur on Mt Wilhelm which have been described either as single species with or without forms or varieties, or as more than one species. In all cases I have treated such taxa as single species, which has involved the merging of the following taxa:

Cerastium keysseri	is included in	*C. papuanum*
Geranium monticola	" " "	*G. potentilloides*
Scirpus ?aucklandicus	" " "	*S.* cf. *subtillissimus*
Viola ?kjellbergii	" " "	*V. arcuata*

Difficulty was experienced in the identification of a few species under field conditions so that their names are not reliable, as indicated by a "?":

Carex ?celebica *Carex ?finitima* *Carex ?perciliata*	—	Some confusion between these species during early part of fieldwork.
Danthonia ?penicillata	—	Some early data under this name may include records of *D. vestita*.
Epilobium ?hooglandii	—	Data probably include records at lower altitudes of *E. prostratum*.

Potentilla ?foersteriana — Data probably include some records of *P. parvula*.

Due to their having been collected and identified far less fully than flowering plants, pteridophytes were not included in most aspects of this thesis. Apart from tree-ferns only about 15 species of pteridophytes are full members of the non-forest flora above 3215 m, although a far greater diversity inhabits the forests.

Thomasson [1967] has given an account of the algae of some Mt Wilhelm lakes.

(d) Fauna

Information on Mt Wilhelm animals, where it exists at all, is scattered and often unpublished. A study of the mammals is in preparation by J.H. Hope and the birds have probably been listed fairly completely, but despite several large collections of invertebrates having been made knowledge of most groups is scanty.

The forest fauna is far richer than that of the grasslands, including arboreal mammals such as ring-tailed possums (*Pseudocheirus cupreus*) and tree kangaroos (*Dendrolagus*) which are much sought after by hunters. The avifauna is also rich, including cassowaries in the Imbukum valley although these have probably been hunted to extinction in the southern valleys. Small birds and mammals (both rodents and marsupials) are present in great variety and numbers.

The lakes are oligotrophic and support little life. One species each of small gastropod and lamellibranch as well as larvae of caddis-flies are common in the shallow waters of the lower Pindaunde lake, while an oligochaete worm is abundant in the sediments of deeper areas of the lake. Introduced brown trout have grown rapidly in this lake but became rare in 1972 probably due to an inability to breed except in the small outlet stream. Each of the Mt Wilhelm lakes supports a resident pair of Salvadori's teal (*Salvadorina waigiuensis*).

The commonest vertebrates of tussock grassland are probably the moss rat (*Rattus niobe*), which is equally at home in forested and unforested places and occurs almost if not actually to the summit, and the small burrowing microhylid frog (*Sphenophryne breviceps*), whose calls after rain can be heard in tussock grassland up to 4000 m. Packs of feral dogs, extremely shy and rarely seen, may be heard howling at night, and footprints are often found especially above 3500 m. A rock wallaby has been reported from the ridge between Mt Wilhelm and Mt Herbert [Wade and McVean, 1969] and formerly may have been common, as it or a similar species still is on the unhunted Mt Suckling [P.F. Stevens, pers. comm., 1973]. Other mammals of the grasslands below 3800 m include the rare marsupial carnivore *Satanellus albopunctatus*, the bandicoot *Perorycytes longicauda*, a marsupial shrew (*Antechinus* sp.) and a variety of rodents.

The only two common grassland birds, both occurring up to the summit ridge, are the pipit *Anthus gutturalis* and the thrush *Turdus poliocephalus*. The East Indian woodcock (*Scolopax saturata*) and lesser melampitta (*Melampitta lugubris*) are both residents of the grassy valley floor below the Pindaunde lakes though neither is seen frequently. A swiftlet (*Collocalia ?esculenta*) is often seen hawking for flying insects around the lower Pindaunde lake and elsewhere in large numbers. Birds of prey are scarce: I disturbed an owl (*?Tyto tenebricosa*) on one occasion from forest edge vegetation at 3430 m, and saw a large hawk about five times in over 9 months' residence in the Pindaunde valley. Several forest birds may be seen feeding in forest edge and grassland shrub situations including honeyeaters (Meliphagidae), a berry-pecker (*Paramythia montia*) and the Princess Stephanie bird of paradise (*Astrapia stephaniae*). To a short list of vagrant birds given by Wade and McVean [1969] can be added a cormorant (*?Phalacrocorax sulcirostris*) seen flying from the upper to the lower Pindaunde lake and, after disturbance, away downvalley one day in August 1971.

Invertebrates in the grassland include moths, blow-flies, beetles and earthworms as well as mites and other smaller animals. Grasshoppers and butterflies are unknown except as rare vagrants. Damage to vegetation by insects has been described as almost completely absent by Wade and McVean [1969] although leaves of *Olearia spectabilis* may be badly holed, and a web-spinning colonial caterpillar can completely defoliate parts of some ericaceous shrubs including *Dimorphanthera microphylla* and *Gaultheria mundula*.

3-D GRASSLANDS

Several general accounts exist of mountain grasslands in various parts of New Guinea [e.g. Brass, 1964; Coode and Stevens, 1972; Hoogland, 1958; Lam, 1945; Robbins, 1960; 1970; Royen, 1967] but the report of Wade and McVean on the grasslands of Mt Wilhelm above 3215 m is the only one that provides a detailed description of the vegetation. Paijmans and Löffler [1972] provide an anthropogenic explanation for the bulk of the grasslands of Mt Albert Edward, and other authors [e.g. Lane-Poole, 1925; Wade and McVean, 1969] also stress the importance of fire in producing and maintaining grasslands. In this section four grassland areas are described from and near Mt Wilhelm, and in the next a discussion of their origin, history and nomenclature is provided.

(a) Imbukum Valley Above Forest Limit

All the southern valleys of Mt Wilhelm lead to heavily populated areas below 2500 m from which hunters and gatherers of various plant products habitually ascend the mountain. In addition an important trade route now disused climbed across the main divide from the Jimi valley (northwest of Wilhelm summit) southwards to Kerowagi. Only the Imbukum valley (Bundi catchment) leading steeply towards Bundi and the Inbrum river to the northeast is remote from human populations, seldom visited and little disturbed, and only here can a natural forest limit be observed (see plate 3-g).

The Imbukum valley was approached in April 1972 from the summit ridge at its head. The vegetation down to 3810 m is more or less as described by Wade and McVean [1969] from similar altitudes in the Pindaunde valley of Mt Wilhelm. Between *c.* 3810 and 4000 m large erect shrubs of *Drimys piperita* entity *subalpina* and smaller shrubs of *Coprosma divergens*, *Detzneria tubata* and *Styphelia suaveolens* are prominent in vegetation types dominated by tussock and other grasses. Between 3760 and 3810 m altitude a mosaic of vegetation types occurs, with small gullies and depressions (usually only a few metres wide) being occupied by *Deschampsia klossii* tussock grassland with shrubs including *Coprosma divergens*, *Eurya brassii*, *Haloragis halconensis* and *Styphelia suaveolens*. On the intervening hummocks and small ridges a forest community grows, with emergent *Dacryarpus compactus* and smaller trees of species including *Dimorphanthera microphylla*, *Olearia floccosa*, *O. spectabilis*, *Rapanea*

Plate 3-g:

Forest limit in the Imbukum valley, 3800 m.

Plate 3-h:

Imbukum valley seen from the south, showing the grassy areas of Wilekukl and Umbamambuno.

vaccinioides and *Symplocos* sp. Tree-ferns, mainly *Cyathea gleichenoides*. are conspicuous along the margins of the two interdigiting communities. Below 3760 m there is almost continuous forest except where waterlogged ground or rocky outcrops prevent tree growth.

A similarly diffuse forest limit occurs on Mt Sigal Mugal in the Kubor range (*c*. 6°04' S, 144°19' E), a mountain of about 3700 m rather remote from sizeable human populations. The forest limit is, however, about 300 m lower than in the Imbukum valley, at about 3530 m on ridges but 100 m lower in and below cirques. Although physiognomically similar the two situations are not comparable floristically, many species occurring above the Mt Sigal Mugal forest limit which are restricted to areas below it on Mt Wilhelm. For example a healthy specimen of the conspicuous *Rhododendron atropurpureum* was flowering and fruiting in a small gully within a few metres of the Mt Sigal Mugal summit, this species having been collected only below the forest limit on Mt Wilhelm.

(b) Wilekukl, Imbukum Valley

Wilekukl is an area of till-choked valley floor measuring *c*. 200 × 1000 m and situated in the Imbukum valley at 3300-3350 m (see plate 3-h) crossed by several anastomosing stream beds which probably change course periodically. It is approximately horizontal in transverse section but slopes gently and consistently downvalley. The ground is ill-drained and supports a predominantly miry vegetation often dominated by *Carex gaudichaudiana*, with small raised "islands" of till on which are scattered shrubs, mainly *Rhododendron yelliottii*. The slopes at either side of Wilekukl are clothed with almost continuous forest, except at the base where a strip of *Deschampsia klossii*-dominated tussock grassland *c*. 5-10 m wide abuts the mire. However, isolated old *Dacrycarpus compactus* trees in this strip suggest that it was formerly forested. The forest margin is abrupt and marked by a band of shrubs, *Coprosma papuensis* and *Haloragis halconensis* predominating. The presence of a dilapidated shelter (in April 1972) showed at least some penetration by man, and two local informants who accompanied me on this trip confirmed that hunters from Bundi and the upper Chimbu valley occasionally visit Wilekukl although they never climb to the higher treeline at 3760-3810 m.

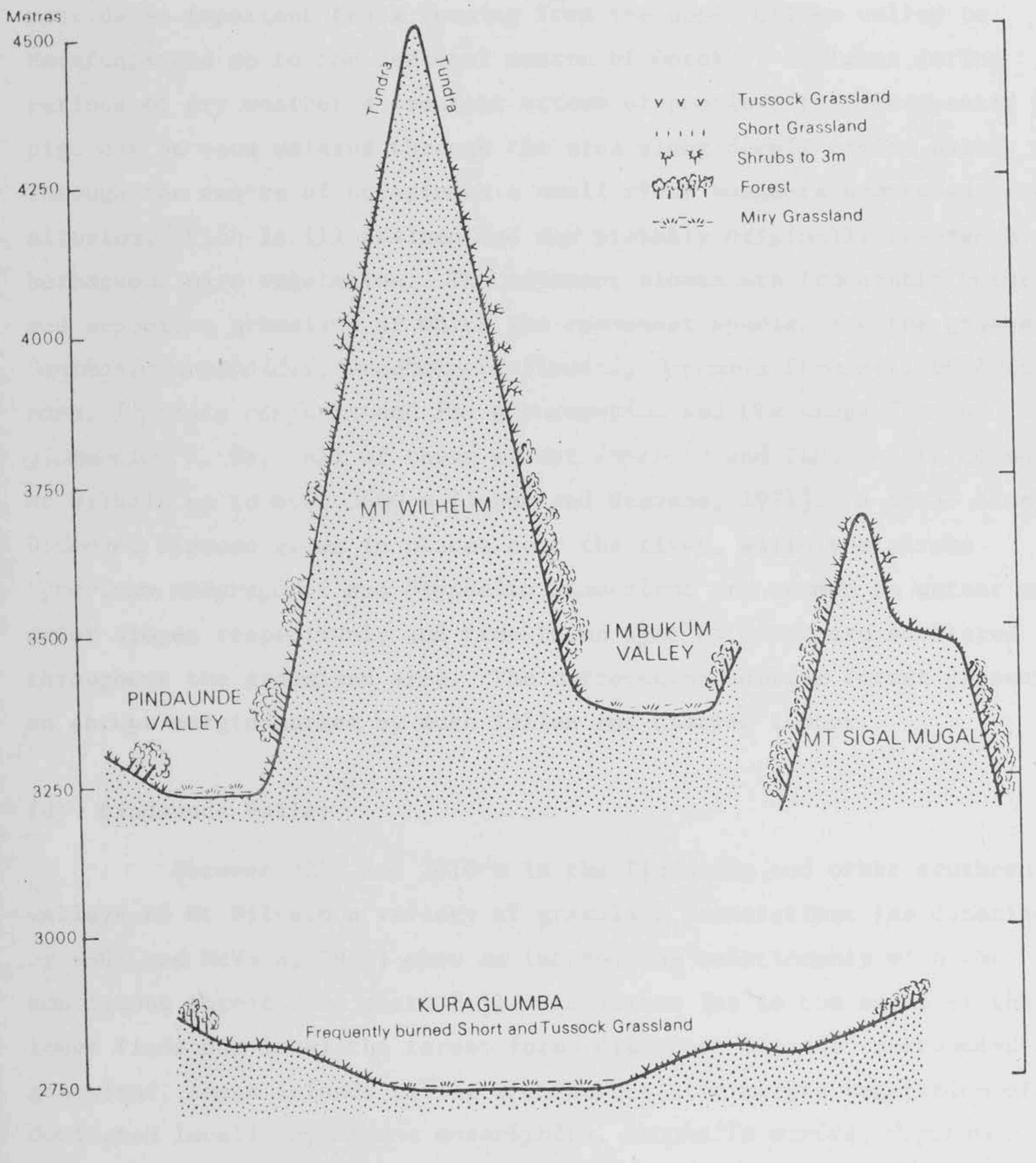


Fig. 3-5: Diagrammatic representation of some mountain grassland situations.

(c) Kuraglumba, Upper Chimbu Valley

Kuraglumba is an intermontane basin at 2730-2850 m altitude above Pompameri village *c*. 20 km southeast of Mt Wilhelm summit (see plate 3-i). It is a large area of grassland, measuring *c*. 3 × 8 km lying astride an important track running from the upper Chimbu valley to Marafunga and so to the regional centre of Goroka. At least during periods of dry weather a constant stream of people often accompanied by pigs can be seen walking through the area along deeply eroded paths. Through the centre of Kuraglumba a small river meanders across an area of alluvium, which is ill-drained and was probably originally covered by herbaceous mire vegetation. The adjacent slopes are frequently burned and support a grassland of which the commonest species are the grasses *Danthonia archboldii*, *Deschampsia klossii*, *Deyeuxia ?brassii*, *Dichelachne rara*, *Imperata conferta* and *Poa saruwagetica* and the sedge *Cladium glomeratum* R. Br. All of these except *Imperata* and *Cladium* are common on Mt Wilhelm up to over 3600 m [Johns and Stevens, 1971]. A small tree *Dodonaea viscosa* grows in places near the river, while the shrubs *Hypericum macgregorii* and *Styphelia suaveolens* are common on wetter and drier slopes respectively and tree-ferns *Cyathea atrox* are scattered throughout the grassland area. The surrounding montane forest presents an abrupt margin marked by much fallen and charred timber.

(d) Pindaunde Valley

Between 3215 and 3810 m in the Pindaunde and other southern valleys of Mt Wilhelm a variety of grassland associations [as described by Wade and McVean, 1969] show an interesting relationship with the contiguous forest (see plate 3-j). In places (as to the south of the lower Pindaunde lake) the forest forms discrete "islands" surrounded by grassland, these islands having a characteristic margin vegetation often dominated locally by *Acaena anserifolia*, *Anaphalis mariae*, *Coprosma papuensis*, *Dimorphanthera* spp., *Myosotis australis*, *Rhododendron* spp., or one of several ferns [Wade and McVean, 1969]. In places the forest edge appears to be advancing (in the absence of recent burning) largely by layering, as documented for the Doma Peaks area at lower altitude (2700 m) by Gillison [1970].

Elsewhere in the valley, for example north and east of the lower lake, the grassland contiguous with forest "islands" includes

Plate 3-i: Kuraglumba.

Plate 3-j: Relict distribution of forest near the lower Pindaunde lake.

numerous shrubs and several old trees of *Dacrycarpus compactus*. Only in the valley bottoms (apart from at very high altitude) are no trees or large shrubs found. The presence of charcoal, charred stumps and tree-roots in the better drained grasslands [Walker, 1968], the isolated *Dacrycarpus* trees often with fire-damaged bases, and the relict distribution of forest suggest a formerly larger forested area whose contraction was associated with burning. Confirmation for this view is provided by the palynological examination of grassland peats which show forest vegetation replaced in relatively recent times by grassland (G.S. Hope, pers. comm., 1973].

As pointed out by Wade and McVean [1969], the climate of the Pindaunde valley is less cloudy and probably less rainy than that of the adjacent Imbukum valley which may partly explain the difference observed in their forest/grassland relationships. The vegetation of the sites described above is shown diagrammatically in Fig. 3-5.

3-E STATUS AND NOMENCLATURE OF THE GRASSLANDS

(a) Influence of Past Climate Upon the Extent of the Grasslands

Hope [1973] has made a study of the postglacial vegetation history of Mt Wilhelm and reviewed earlier work on vegetation history at lower altitudes in New Guinea. He suggests that for probably more than 20,000 years prior to 10,000 yr B.P. mountain grasslands with scattered shrubs and tree-ferns were widespread above an altitude of about 2400 m, the snowline being reduced from *c*. 4700 m to 3600 m altitude [Löffler, 1972]. Between 10,000 and 8,400 yr B.P. climatic amelioration allowed a rapid advance of forest to the present or higher than present level. Today Brass Tarn in the Pindaunde valley (*c*. 3900 m) is at or slightly above the forest limit and surrounded by grassland with scattered shrubs and a few trees in a sheltered east-facing gully: between 8,400 and 5,000 yr B.P. the tarn was surrounded by forest, which has since been absent from this site.

The recent retreat of the forest limit so demonstrated is open to conflicting interpretation. Man was present long before 5,000 yr B.P. in the New Guinea highlands [White and others, 1970] and, through fire, may have artificially lowered the forest limit. Whether or not this was so, the initial invasion of the site by forest 8,400 yr B.P., since it is apparently unable to reoccupy the site today, may indicate a warmer "hypsithermal" period at that time. If this is the case, and if it is true that grassland cannot (at least at higher altitudes) revert to forest, we are forced to the conclusion that the "natural" forest limit (in for example the Imbukum valley) is in a sense a fossil one, owing its position to colonization under earlier less rigorous conditions and able to persist today only through the development of seedlings in the shelter of the parental trees. Wardle [1971] considers that failure to ripen new growth due to low temperature is the factor which prevents trees from growing above their usual limits, at the forest limit or treeline. If this is so, and since the most extreme temperatures occur at ground level outside the forest, it is easy to see how forest can perpetuate itself, yet be unable to recolonize grassland formerly forested and at the same altitude.

Against this it can be argued (at least for altitudes lower than *c.* 3700 m) that the reversion from grassland to forest is a slow process dependent upon the suppression of tussock grasses by shrubs, beneath which seedlings of forest taxa can develop. If this is the case, the process would hardly be apparent yet. Burning of vegetation on Mt Wilhelm has been banned by the Administration since 1959 or earlier [Brass, 1964] and there have probably been only local fires during this period. Comparison of photographs with the same areas (at 3480-3600 m) in 1972 shows a great development of shrubs of for example *Coprosma divergens*, *C. papuensis*, *Gaultheria mundula* and *Styphelia suaveolens*. That fire was previously keeping them in check is indicated by an area at 3350 m in the Guraguragugl valley of Mt Wilhelm which was burnt an estimated 2 years prior to observation in May 1972. The area had previously been dominated by *c.* 1 m high shrubs, mainly *Coprosma papuensis*, *Dimorphanthera keysseri*, *D. microphylla*, *Gaultheria mundula*, *Olearia spectabilis* and *Styphelia suaveolens*. Of these *c.* 90% were dead or only regenerating from the base, the area being dominated by the grasses *Dichelachne rara* and *Poa saruwagetica*.

(b) The Impact of Man

In many parts of the highlands of eastern New Guinea below 2000 m there are currently fairly large populations of people subsisting primarily on sweet potato as well as on a variety of other food crops, with meat from domesticated pigs and hunted forest animals. The earliest date for the presence of man in the region so far obtained is *c*. 25,000 yr B.P. [White and others, 1970]. Hope [1973] has found a rise in *Casuarina* pollen in Mt Wilhelm bog and lake sediments commencing from 900 yr B.P., probably derived from trees of *C. oligodon* introduced to areas below 2500 m as a source of timber and firewood and as a fallow crop improving soil by nitrogen fixation. This probably marks the beginning of widespread agriculture in the upper Chimbu valley at 1500-2500 m, although gardens may have been present there from as early as 6,500 yr B.P. The Wahgi valley experienced widespread agriculture from before 5,000 yr B.P. [Powell, 1970].

Only two animals were successfully introduced to the Mt Wilhelm area in prehistoric times, the wild "singing" dog and the pig. Rootling by semi-domesticated pigs causes extensive damage to the forest floor environment in areas not far from human settlement, as in the Pengagl valley up to about 2900 m. Feral pigs are said to inhabit the forests of the Imbukum valley. Brown trout in the lower Pindaunde lake and its outlet stream were introduced as fry in 1969 but do not breed well. Plant introductions are discussed in section 3-F.

The digging activities of man in the past few years, restricted almost completely to the Pindaunde valley, have created new habitats for pioneer plant colonists including both native and alien species. Most aliens recorded above 3200 m have been found only in disturbed sites including landslips and stream-banks, and in several cases only in sites of human disturbance like path-sides, campsites and rubbish pits. Human trampling has also created a new habitat along paths, favouring some short-stemmed herbaceous species which become abundant there. Probable hybrids in *Galium*, *Hypericum*, *Rhododendron* and *Vaccinium* [P.F. Stevens, pers. comm., 1973] have all been collected only from anthropogenic grassland or its margin with forest, perhaps illustrating the principle that hybridization of plants only follows "habitat hybridization", usually as a result of human activity [Anderson, 1949].

The most important effect man has had upon mountain grasslands is through fire. Two sites providing an understanding of how this takes place are Kuraglumba and Wilekukl described above.

Fire is a dominating ecological factor at Kuraglumba, producing vegetation changes perhaps comparable to those described at Doma Peaks by

Gillison [1969]. In August 1972, during an unusually dry season, over a quarter of the area had been very recently burned, and several fires were deliberately lit during my brief (30 hr) visit. In places grassland fires had reached the margin of the forest killing or at least severely damaging trees and shrubs. It is clear that most or all of the Kuraglumba grasslands are induced, maintained and expanded by fires set by man, which destroy tree seedlings and kill the forest edge, so maintaining and expanding the area dominated mainly by grass species which are both combustible and fire-tolerant.

Wilekukl provides an example of the process in an early stage, showing that areas of mainly herbaceous vegetation in ill-drained sites provide natural routes for travellers and hunters. These become combustible during dry periods when hunting activity is at a peak and are set alight for warmth or simple pleasure, or possibly to drive out or kill small game. This leads not only to modification of the herbaceous vegetation but also to a progressive increase in its area as the forest margin is repeatedly damaged by the fire. A similar explanation has been proposed for the Neon grasslands of Mt Albert Edward, comparable to Kuraglumba in altitude, physiography and floristics [Paijmans and Löffler, 1972] though probably not subject to such intensive human activity and frequent burning [G.S. Hope, pers. comm., 1973]; and for grasslands up to 3565 m in the Doma Peaks area [Gillison, 1969; Kalkman and Vink, 1970].

Although an Administration ban on grass burning has been largely effective on Mt Wilhelm since 1959 [Brass, 1964], the same is not true of other mountains where human destruction of forest vegetation continues unabated. Writing of Mt Giluwe, Bowers [1968] states

> "At the upper limits of montane forest where environmental conditions are critical for the survival of ligneous species, hunters fell the forest trees more rapidly than colonization can take place. Both montane forest and alpine shrubbery retreat, while the area occupied by alpine grassland expands".

During the unusually dry season of 1972 very large areas of grassland above the Mt Giluwe forests were burnt [P.F. Stevens, pers. comm., 1972], resulting in places in burning of peat to a depth of over 5 cm accompanied by almost total local destruction of vegetation [G.S. Hope, pers. comm., 1973].

(c) Inverted Treelines

The ecological factors causing the development of grassy vegetation in areas of impeded drainage are in dispute. Wardle [1971], by comparison with similar areas in New Zealand and southeast Australia, favours frost as the agency preventing most woody plant growth, through the phenomenon of cold air drainage on windless nights. In possible support of this, Wade and McVean [1969] report an almost total absence of forest tree seedlings in most herbaceous associations in the Pindaunde valley between 3260 and 4100 m altitude, in contrast with forest associations, and ascribe this to the influence of frost. During 1972 exceptional frosts at lower altitudes (1800-2500 m) caused extensive damage to areas of forest adjacent to basin grasslands in the western and southern highlands of Papua New Guinea [C.F. Pain, pers. comm., 1973].

On the other hand it seems to me that grassland sites over such a large range of altitude (*c.* 2800 m at Neon Basin and Kuraglumba, to 3215 - *c.* 3750 m on Mt Wilhelm) can hardly be explained by a thermal factor, frosts being occasional and mild at the lower altitudes by comparison with sites near the Imbukum valley forest limit. Furthermore herbaceous vegetation may occupy flat areas entirely surrounded by forest, as at Umbamambuno at *c.* 3500 m on the south side of the Imbukum valley, where cold air drainage cannot easily be invoked. It appears more likely that waterlogged soil conditions provide a better explanation of the observed distribution of "inverted treelines". Frost may well play a part in preventing forest from reoccupying burnt slopes, but even this may be dependent upon the periodic destruction by fire of shrubs which may shelter tree seedlings during the critical first few years of life.

Whatever the origin of "inverted treelines", it is clear that fire is responsible for enlarging areas of grassland, beginning in such unforested basin sites and extending progressively upslope. It is interesting to note that inverted treelines, common in New Guinea, are generally typical of temperate rather than tropical mountains [Troll, 1959]. Steenis [1968; 1972] has described the influence of frost on mountain vegetation in Java and deduced that "without the intervention of man there would be no frost holes at all". He considers that areas of grassy vegetation surrounded by forest, occurring in Java down to 900 m and common above 2000 m, are the result of human burning of natural herbaceous vegetation in marshy areas which damages the forest edge causing progressive expansion of the grassland area.

(d) Floristic Considerations

Definitions of altitudinal vegetation zones based on physiognomy in New Guinea prove to be not only impossible to apply consistently, but also to have no floristic constancy and so no clear climatic basis. As well as the problems associated with human disturbance discussed above there is the observation that treeline is lower on smaller mountains (see section 8-C).

The example of Mt Sigal Mugal mentioned above shows that the lowering of forest limit on smaller mountains is largely a physiognomic and not a floristic effect. Unless it is postulated that the many species which occur above the forest limit on Mt Sigal Mugal but only below it on Mt Wilhelm are represented on the two mountains by very distinct physiological races, we must conclude that the two forest limits are not governed by the same environmental (presumably climatic) factors.

Even within one valley of a single mountain, floristics (except in a very arbitrary and imprecise fashion) do not help define altitudinal vegetation belts. In the Pindaunde valley of Mt Wilhelm several species can be said not to occur above an altitude marking the natural forest limit, or conversely not below the same altitude. However, the same could probably be said for any altitude selected, there being no sudden change in flora across a relatively small change in altitude except where this coincides with a major ecological or physiognomic boundary. Furthermore species may grow occasionally well above their usual range (the zones of temporary establishment of Steenis [1961]), making nonsense of any attempted qualitative floristic definition of a subalpine/alpine margin. For example in a sheltered gully at 4085 m facing northeast across the Imbukum valley of Mt Wilhelm I found *Acaena anserifolia*, *Cardamine altigena* and *Oxalis magellanica*, none of which had previously been recorded above 3658 m [Johns and Stevens, 1971].

The lower limit of Wade and McVean's subalpine grassland coincides with, and is determined by, the terminal moraines of Pleistocene valley glaciers. Tongues of grassland extend down the valleys well below the forest/grassland margin elsewhere, terminating abruptly where the flat-bottomed, ill-drained, till-choked glacial valley changes to the steeper, better-drained fluvial valley lower down. Several species characteristic of disturbed areas at lower altitudes, possibly intolerant of severe frosts, occur in these lower tongues of mountain grassland. Between 3215 and 3380 m in the Pindaunde valley *Hypericum japonicum* var. *humifusum*, *Imperata conferta*, *Lobelia angulata* and *Viola betonicifolia* have all been recorded. Of the vascular plant species recorded at Kuraglumba (2730-2850 m), *c*. 45% appear to be more characteristic of grasslands above 3200 m on Mt Wilhelm and *c*. 55% of the agricultural area below 2500 m in the upper Chimbu valley.

(e) Nomenclature of Vegetation Types

In writing general accounts of New Guinea vegetation, most authors [e.g. Brass, 1964; Hoogland, 1958; Robbins, 1960; Royen, 1967] have described grasslands of mountain summits as alpine, though such vegetation may extend below 3000 m, well below the upper limit of closed forests. In the only detailed study so far made of mountain grassland communities Wade and McVean [1969] reject the use of the word alpine to cover such a range of plant associations, and describe communities below the upper limit of large shrubs (4100 m) but above about 3215 m as subalpine. The same usage of the terms alpine and subalpine has been followed by Hope [1973], Johns [1972] and Robbins [1970]. These authors do not clearly define the lower limit of their subalpine belt, but include all grasslands above the highest continuous forest (above 3215 m), and Wade and McVean find a floristic break in the forest at similar altitude which they take as the division between cloud forest and subalpine forest.

Lam [1945] writes of both subalpine and alpine flora in New Guinea without definition. Coode and Stevens [1972] refer to vegetation on Mt Strong (3550 m) above 3200 m as subalpine, and Henty [1972] describes all grasslands in New Guinea above 3048 m as subalpine.

Löve [1970b] has criticized use of the limit of large shrubs as the upper margin of the subalpine belt. She refers to her own definition, after Meusel and others [1965] and other European authors, and recommends it [1970a] to workers specifically in north temperate regions and by inference throughout the world. She writes "The subalpine belt is the natural belt below the treeless belt from the upper altitudinal treeline to the closed montane forest at lower elevations. It is an ecotone, a mosaic of biota from the treeless alpine belt above and the forested belt below".

Löve's [1970b] main criticism of Wade and McVean's definition of the subalpine belt centres around the use of the "upper limit of large shrubs" to mark the top of the belt. Her own description [1970a] of the subalpine belt as "mixed meadow- and heath-like vegetation and islands of trees or krummholz or small shrubs" raises the possibility that this difference may be simply one of interpretation. The largest shrub between 3810 and 3100 m, above all stands of forest on Mt Wilhelm but within the subalpine belt of Wade and McVean, is *Drimys piperita* entity *subalpina*, which frequently exceeds 3 m in height [Wardle, 1971] and often has a single main trunk though admittedly usually branching in the lowest metre. Such a plant by most definitions would be described as a tree, or at least (as suggested by Wardle) as a woody krummholz, thereby giving this belt subalpine status by Löve's definition. What may possibly be regarded as more appropriate in the New Guinea context with problems of this kind is the use of the term "lower alpine", meaning the belt of vegetation quite without stands of forest but including shrubs more than a few centimetres tall [Wardle, 1971]. The vegetation belt on Mt Wilhelm perhaps conforming most closely to Löve's definition of subalpine is the narrow (50 m altitude) belt in the Imbukum valley displaying an interdigitation of forest and grassland vegetation.

No definition of alpine, subalpine or montane vegetation belts used to date in connection with non-forest vegetation in New Guinea has proved satisfactory, at least for more than a very local situation, not comparable to other areas of New Guinea or the world. Furthermore it appears that as grasslands may vary in their origins and history as well as in their floristics, and that since altitude is not correlated consistently with vegetation, no definition of more than very local significance can be attempted. Inevitably most current ideas of altitudinal zonation of vegetation have their roots in work on mountains of the temperate zones. The wet tropics present a superficially similar situation but with two important differences, namely that the climate is virtually non-seasonal and that the forests have far greater floristic and ecological diversity. In New Guinea there is the added complication of considerable prehistoric human disturbance.

It is proposed that the terms subalpine and alpine as referred to mountain grasslands in New Guinea be, as far as is practicable, abandoned. To use them implies a degree of knowledge and of certainty of correlation with similarly named vegetation belts elsewhere that cannot at the present time be upheld. Such terms borrowed from the temperate zone, which has marked seasons and where factors such as period of snow lie are of ecological importance, tend to convey a false impression of tropical mountains with daily, non-seasonal climates [Troll, 1959].

I have elsewhere [Smith, 1974d] proposed a classification of mountain vegetation in New Guinea based upon physiognomy and fully recognizing the role of man (see Fig. 3-6). The units represented on Mt Wilhelm with which this thesis is concerned are:

Ais : Belt of periglacial action and sparse vegetation above 4300 m.

Pinga : Short or tussock grassland with scattered small woody plants between the above and the forest limit at 3810 m.

Diwai maunten : Mountain forest.

Gras maunten : Grasslands between 2500 m and 3810 m.

  (i) *Bipo* : Natural, as in miry and rocky sites.

  (ii) *Manmeri* : Anthropogenic, derived from forest by burning.

Except for the mountain forest these categories are not easy to demarcate exactly. Accordingly, and since this thesis is concerned with autecology and phytogeography rather than with vegetation studies, no more than passing mention will be made of them. I use the word *tropicalpine* to refer to flora or vegetation occurring naturally above or outside the forest above 3215 m, which is the lowest altitude in the Pindaunde valley of Mt Wilhelm at which grasslands contiguous with those of the summit area occur. *Non-forest* vegetation or flora refers to that occurring outside the shade of the forests anywhere above 2500 m, including *adventive plants* on local and rather temporary sites of disturbance such as riverbanks, pathsides and landslips, and *mountain grasslands* which are defined as more extensive and permanent areas of non-forest vegetation usually dominated by grasses.

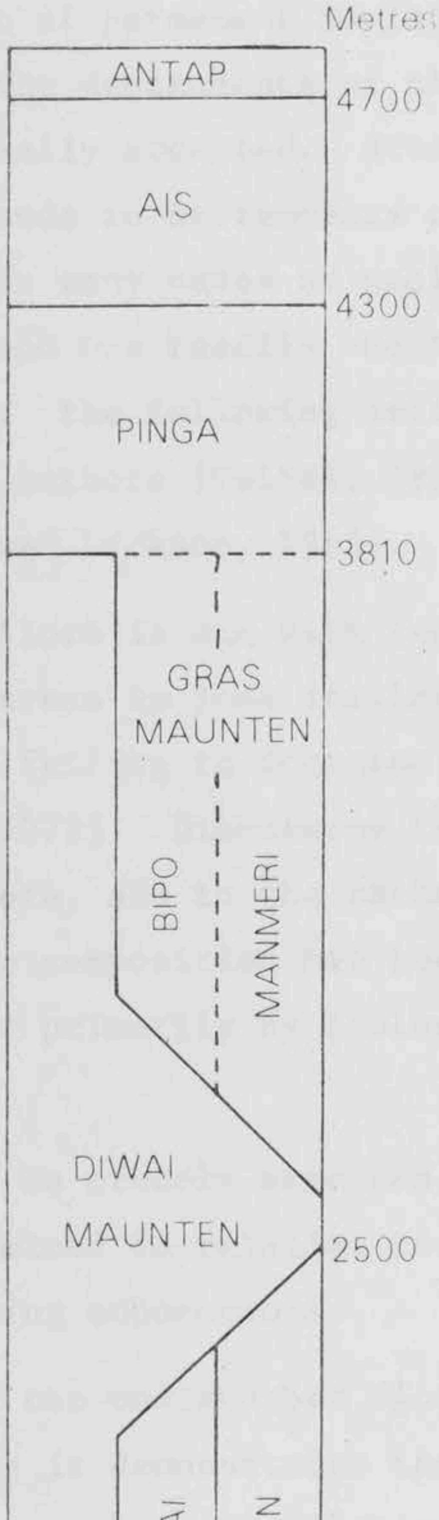


Fig. 3-6: A classification of vegetation above 1500 m in New Guinea [from Smith, 1974d].

3-F POSSIBLE DISHARMONY OF THE FLORA

The floras of isolated environments, in particular of oceanic islands, have often been described as disharmonic. This description rests upon the assumption of permanent isolation of such environments, whose floras consist of the descendants of chance immigrants. This assumption is not universally accepted. Steenis [1964b] has stated that he considers oceanic islands to be remnants of foundered continental areas, a view receiving in many cases no geological support. Disharmony, though a useful concept and one readily understood in general terms, has not been clearly defined: the following definition encompasses its understanding by several authors [Gulick, 1932; Macarthur and Wilson, 1967; Stone, 1967; Wace and Dickson, 1965].

A disharmonic flora is one with fewer species than floras of ecologically comparable areas in less insular locations, the species occupying less fully and failing to increase as much the available "niche hyperspace" [Whittaker, 1972]. Disharmony is considered to be due to the relative youth of the flora, and to the rather small number of its immigrant ancestors whose composition has been largely determined by dispersal ability and not primarily by ecological adaptation to the insular environment.

Disharmony can be crudely assessed in two main ways. Both are described below, and examined in relation to the non-forest flora of Mt Wilhelm in the following subsections.

1. Invasibility of the undisturbed flora by introduced plants suggests disharmony since it demonstrates that species from similar environments are able to occupy incompletely filled niches in the insular ecosystem. Probably every flora is invasible in time by at least some alien species, but most closed vegetation without disturbance successfully resists invasion. Thus although tree seedlings may grow readily on ploughed ground they may be unable to do so in grassland [Egler, 1954], even though the same trees form the climax vegetation of the area, and the grassland flora can be considered disharmonic in lacking tree species. Examination of the position of alien plants in environments allowing the development of closed vegetation usually shows them to be restricted to sites of disturbance involving vegetation damage. This may be the case even where the only disturbance is natural and where

the native flora may reasonably be described as disharmonic, as on Gough Island [Wace and Dickson, 1965]. Invasibility therefore, at least as it is applicable in usual field situations, can only be used to reveal very extreme cases of disharmony, where closed vegetation has hardly developed. The susceptibility of the formerly possibly unvegetated upper slopes of Tristan da Cunha to invasion by *Rumex acetosella* [Wace and Dickson, 1965] may be a case in point.

2. Inspection of the flora, and its comparison with floras in ecologically similar but less insular environments especially with regard to the following criteria, may indicate disharmony.

   (i) Size of the flora in relation to the area occupied by it.

   (ii) Degree of integration and specialization of members of the flora.

   (iii) Taxonomic content of the flora.

Such inspection and comparison is bound to some extent to be subjective, not only in the measures used but also in the selection of ecologically similar areas. However in practical terms this approach seems likely to provide a better understanding of the extent of a flora's disharmony because it does not rely upon assessment of such an easily fulfilled requirement as closed vegetation or such a difficultly evaluated one as invasibility over time.

Mountain peaks in the tropics are islands of cool climate and non-forest vegetation in an ocean of hot tropical lowland forest: the nearest comparable "islands" to the New Guinea mountains are in southeast Australia to the south, a few small peaks in Malesia to the west and northwest, and beyond them distant mountains on the Asian mainland. Furthermore the non-forest habitat above treeline may be relatively young by comparison with similar habitats in other regions since the principal phases of geological uplift in New Guinea were in Miocene and later times [Thompson, 1967] prior to which forest may have covered the entire area. It is therefore appropriate to search for indications of disharmony in the flora of the non-forest areas of Mt Wilhelm.

However, problems immediately arise in the definition of the "island's" flora which do not apply to oceanic islands. Definition of the species occupying the area under consideration is not easy since it is not bounded by a non-terrestrial but only a forest environment. In this discussion I have restricted myself to native species as far as possible and except where explicitly stated. For Mt Wilhelm only those species occurring commonly or solely in non-forest habitats above 3215 m are considered here, this altitude including the lowest Pleistocene moraines and the lowest grasslands areally continuous with those above climatic forest limit. It seems most unlikely that any appearance of disharmony in the flora of this area can be explained by environmental uniformity.

(a) Invasibility by Aliens

On Tristan da Cunha there are as many introduced as native flowering plants, and of the *c*. 42 alien species recorded by Wace and Dickson [1965], 12 are successful invaders not only of habitats disturbed by man and his animals but also of native vegetation suffering natural disturbance.

In the Mt Wilhelm area 54 alien species have been collected above 2515 m (Keglsugl) and 24 above 3215 m (Kombuglomambuno). All the higher altitude colonists are herbaceous and most are very widespread weeds of cultivation. They can be divided into the following categories:

1. Collected once, not recorded for several years, probably extinct in the area.

   Linum usitatissimum
   Phalaris tuberosa
   Vicia sativa

2. Unable to reproduce and dependent upon repeated reintroduction.

   Cordyline fruticosa
   Brassica oleracea
   Lupinus sp.
   Pisum sativum
   Tacsonia mollissima
   Verbena bonariensis

   to which may be added a few deliberately planted species at the research station including:

   Fuchsia ?magellanica

Petroselinium crispum
Allium sativum
Solanum tuberosum
Vicia faba

3. Able to reproduce only vegetatively, spread slowly, and only occurring (to date) in disturbed habitats.

   Nasturtium officianale (common in Gwaki creek to 3055 m)
   Mentha sp.

4. Newly arrived species of unknown potential spread.

   Plantago lanceolata (probably already extinct due to collection of only plants present)
   Lolium rigidum
   Vulpia bromoides

5. Successful colonists only of sites disturbed by man.

   Tritonia X *crocosmaeflora*
   Poa annua
   Stellaria media
   Bidens pilosa
   Veronica cf. *persica*

6. Occasional colonists of natural habitats, mainly streambanks and landslips, as well as of pathsides, etc.

   Crassocephalum crepidioides
   Erigeron canadensis
   E. sumatrensis
   Sonchus oleraceus
   Fragaria cf. *vesca*.

Many species may be regarded as successful invaders at lower altitudes, where riverbanks and landslips as well as man-disturbed sites are often colonized by a predominantly alien vegetation. But in non-forest habitats above 3215 m only the five species in the last category can be so considered. Of these the four Compositae are found as scattered individuals in early seral situations. All, especially *Crassocephalum*, are prone to frost damage, and without disturbance on a larger scale than at present it is doubtful whether their populations could survive in the absence of a seed source at lower altitudes.

Fragaria cf. *vesca* is common between 2500 m and 2900 m on pathsides, and specimens planted beside the research station at 3480 m are healthy and fertile. There are also a few individuals in apparently little disturbed grassland habitats in the general vicinity of the research station, perhaps owing their presence to dispersal in human faeces. *Fragaria vesca* has been firmly established on Mt Pangrango (around 3000 m) in Java since its deliberate introduction in *c*. 1840 [Kalkman, 1968]. The most aggressive introduced plant in both the Snowy Mts and the Tristan da Cunha islands, *Rumex acetosella*, is so far absent from New Guinea. Only 14 alien species are regarded as being members of the non-forest flora of Mt Wilhelm (see section 3-G).

It therefore appears that the vegetation of Mt Wilhelm generally resists invasion by alien plants except at sites of soil or vegetation disturbance either natural or by man.

(b) Inspection of the Flora and Its Comparison with Similar Floras

(i) Size of the flora

Central to the concept of disharmony is the small number of species in the flora by comparison with ecologically comparable areas elsewhere. McVean [1969], writing of the Snowy Mts of southeast Australia by comparison with north temperate alpine areas, states "The alpine flora ... is not a rich one, which is only to be expected from the small and isolated area available. There are about twenty-two species of 'obligate' alpines and about 180 'facultative' alpines among the vascular plants. The general impression is of a restricted number of species displaying wide ecological amplitude to fill the available niches ...".

The difficulty of comparing New Guinea vegetation belts with those elsewhere has already been remarked. However, an alpine belt is defined as being above the upper limit of forest growth. The total number of species occurring above the forest limit on Mt Wilhelm is even smaller than in the alpine floras of either the Snowy Mts of southeast Australia or the mountains of Otago in South Island, New Zealand, as shown in Fig. 3-7.

The flowering plant flora of non-forest environments above 3215 m numbers about 143 species. This estimate is in rough accord with

	Mt Wilhelm		Snowy Mts		Otago
	Only Above 3800 m	Above and Below 3800 m	Obligate Alpine	Total Alpine	"High Alpine"
Flowering plants	12	108	?no.	196	160
Vascular plants	16	120	22	202	166

Fig. 3-7: Numbers of species in three Australasian high mountain floras. Data for Mt Wilhelm partly from Johns and Stevens [1971]; for Snowy Mts from McVean [1969] and A.B. Costin [pers. comm., 1973]; and for Otago from Mark and Bliss [1970].

that of Wade and McVean [1969] of 160 species of vascular plants. Johns and Stevens [1971] list 311 flowering plants and 387 vascular plants occurring above 3200 m, but probably over half of these are found mainly or exclusively in the floristically diverse forest. Although the total number of species is smaller than might be expected, approximately the same numbers of species per 2-4 m^2 releve occur in comparable vegetation types on Mt Wilhelm, in the Snowy Mts, in Norway and in Scotland [Wade and McVean, 1969].

However, the floras of oceanic islands may be considerably poorer, and more disharmonic, than this. Easter Island, the most isolated of all islands, has 42 species of vascular plant of which 30 are flowering plants [Gulick, 1932]. The Tristan da Cunha islands, climatically comparable with Mt Wilhelm, have 74 vascular plant species of which 41 are flowering plants [Wace and Dickson, 1965]. Some species/area curves are plotted to the same scale in Fig. 3-8.

If the glaciated area of Mt Wilhelm, 107 sq. km [Löffler, 1972] is taken as the area of grassland above the treeline, the number of flowering plant species per sq. km is 1.3. By comparison Easter Island and the Tristan da Cunha islands, with total areas of 117 and 159 sq. km respectively, both have densities of 0.26 species of flowering plant per sq. km. If only the Pindaunde valley with adjacent ridges is considered, an area of *c*. 20 sq. km from which most Mt Wilhelm plant records come, the density rises to *c*. 7. By comparison Gough and Inaccessible islands in the Tristan da Cunha group, with areas of 57 and 12 sq. km respectively, have densities of 0.54 and 0.46. In about 100 sq. km of

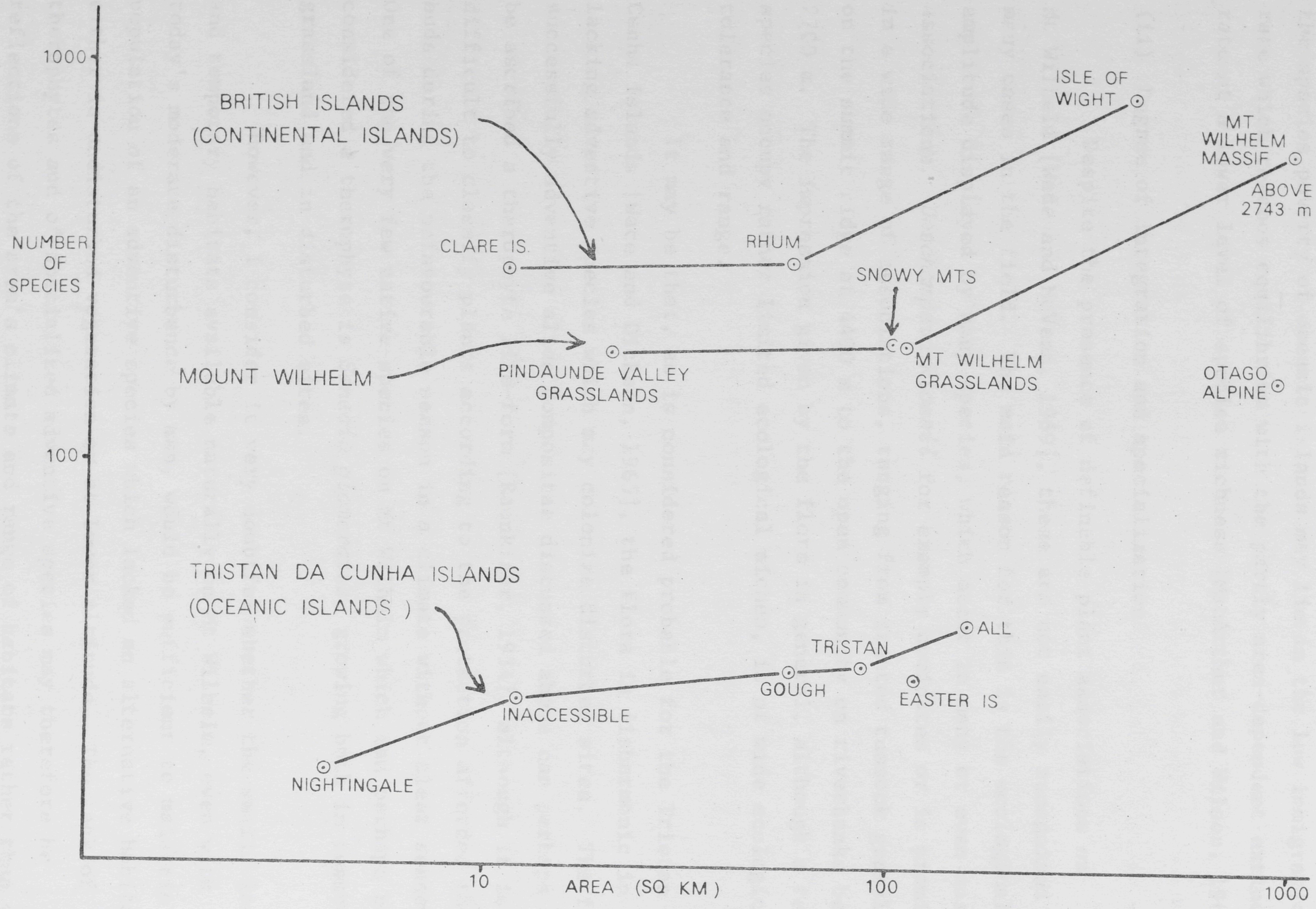


Fig. 3-8: Area occupied by and number of species in several floras of insular situations.

alpine vegetation in the Snowy Mts, about 196 flowering plant species occur [A.B. Costin, pers. comm., 1973] giving a species density of 2.0 spp. per sq. km, similar to the Mt Wilhelm figure. An explanation of the species poverty of oceanic islands may lie in the low immigration rate which reaches equilibrium with the partly area-dependent extinction rate at a lower level of species richness [MacArthur and Wilson, 1967].

(ii) Degree of integration and specialization

Despite the presence of definable plant associations on Mt Wilhelm [Wade and McVean, 1969], these are not easily recognized in many cases in the field. The main reason for this is the ecological amplitude displayed by many species, which occur in many or even most associations. *Deschampsia klossii* for example dominates or is prominent in a wide range of associations, ranging from stunted tussock grassland on the summit ridge at 4400 m to the open community on riverbanks below 2700 m. The impression given by the flora in general, although a few species occupy rather limited ecological niches, is of wide ecological tolerance and range.

It may be that, as is considered probable for the Tristan da Cunha islands [Wace and Dickson, 1965], the flora is disharmonic in lacking adventive species which may colonize disturbed sites. The four successfully adventive alien Compositae discussed above can perhaps best be ascribed a therophyte life-form [Raunkiaer, 1934], although it is difficult to classify plants according to the protection afforded the buds during the unfavourable season in a climate without clear seasons. One of the very few native species on Mt Wilhelm which can perhaps be considered a therophyte is *Senecio glomeratus*, growing both in tussock grassland and in disturbed sites.

However, I consider it very doubtful whether the small, local and temporary habitats available naturally on Mt Wilhelm, even with today's moderate disturbance by man, would be sufficient to maintain a population of an adventive species which lacked an alternative habitat either in undisturbed vegetation or at lower altitude. The lack of therophytes and of specialized adventive species may therefore be reflections of the area's climate and range of habitats rather than of its floristic disharmony.

If the vegetation of the high mountains of New Guinea is compared with that of other tropical mountains, it becomes apparent that a peculiar life-form common to Africa, South America and Hawaii is absent. Above the limit of forest growth in these places, in the *paramo* belt of Troll [1959], small trees or "giant herbs" occur of pachycaulous habit and with their growing points often insulated by hair or dead plant parts. These include the *Senecio* and *Lobelia* "trees" of the mountains of East Africa, *Argyroxiphium* in Hawaii, and members of the genera *Espeletia* and *Puya* in the Andes. On Mt Wilhelm the only tree found above the highest stands of forest is *Drimys piperita* entity *subalpina* which is not pachycaulous. An arboreal species of *Senecio*, little branched and with large woolly leaves, is one of the earliest colonists of newly exposed moraines on Mt Carstensz [G.S. Hope, pers. comm., 1972]. Though we know little of the ecological factors which allow "megaphytes" to thrive in their peculiar habitat, it appears that in New Guinea this life-form has not yet evolved despite conditions similar to, for example, megaphyte localities in Ecuador [R.G.A. Feachem, pers. comm., 1971]. Lack of megaphytes may indicate disharmony of the New Guinea tropicalpine flora.

(iii) Taxonomic content

A low proportion of species per genus and genera per family may indicate disharmony [Wace and Dickson, 1965]. The figures in Fig. 3-9 suggest that the Mt Wilhelm flora may be rather less disharmonic than insular floras, though very similar to the Snowy Mts and Otago alpine floras.

	Mt Wilhelm Non-forest Flora	Snowy Mts Alpine Flora	Central Otago High Alpine Flora	Tristan da Cunha Islands	Easter Island	New Guinea and Southwest Pacific	World
Spp./genus	1.6	1.6	2.5	1.4	1.2	?	18
Genera/family	2.4	2.4	2.4	1.7	1.7	9.3	33

Fig. 3-9: Proportions of taxa of different rank in several flowering plant floras. Data for Snowy Mts from McVean [1969], for Otago from Mark and Bliss [1970], for Tristan da Cunha from Wace and Dickson [1965], for Easter Island from Gulick [1932], for New Guinea and Southwest Pacific from Division of Botany [1969], and for the world from Good [1953].

These figures are perhaps a reflection of the age of floras, since with time a small number of immigrants by adaptive radiation will evolve into a variety of taxa occupying more efficiently the range of habitats available. The low numbers of species per genus and genera per family in the Mt Wilhelm flora indicate a small degree of radiation, though endemic species especially at high altitude show that some recent speciation has occurred, for example in *Danthonia*, *Gnaphalium*, *Lactuca*, *Lobelia*, *Senecio*, *Ranunculus*, *Rubus*, *Trachymene* and *Uncinia*. The only flowering plant genera endemic to New Guinea and occurring in the high grasslands of Mt Wilhelm are *Detzneria*, *Ischnea* and the orchids *Giulianettia* and *Pedilochilus*.

Raunkiaer [1934] estimated the ratio of phanerogam to pteridophyte species in the world as being about 25:1, and on this basis defined a "pteridophyte quotient" for floras derived by dividing 25 times the number of pteridophyte species in the flora by the number of phanerogam species. By calculating this figure for a number of floras he discovered that it is generally higher than unity, and tends to be very high in both wet climates and isolated islands. He explained these observations by saying that pteridophyte species generally occur over a greater geographic range than phanerograms, that they are favoured by wet climates, and that their spores are more easily dispersed over long distances than the seeds of phanerograms. If as has been widely assumed pteridophytes are indeed more readily dispersed, the pteridophyte quotient may provide an indication of poverty and disharmony in the phanerogam flora.

The figures below show the pteridophyte quotients for several floras (data largely from Wace and Dickson [1965]). The highest figures are for islands, especially Tristan da Cunha with an ever-wet climate. The figures for Mt Wilhelm (data modified from Johns and Stevens [1971]), are lower than those for wet islands, but higher than those for part of an alpine flora in Scotland (data from Poore [1955]), the Snowy Mts alpine flora (data from McVean [1969] and A.B. Costin, pers. comm. [1973]) and the Otago alpine flora (data from Mark and Bliss [1970]). This could possibly indicate a more disharmonic flora on Mt Wilhelm than in the Snowy Mts or Otago though not as much as on oceanic islands: on the other hand the low figure for the Snowy Mts and Otago could perhaps be taken as showing a disharmonic pteridophyte flora there. Insufficient information is available for calculation of Mt Wilhelm's bryophyte quotient [Raunkiaer, 1934].

Pteridophyte Quotients	$\frac{25 \times \text{No. spp. Pteridophytes}}{\text{No. spp. Phanerogams}}$
Tristan da Cunha islands	20.1
Easter Island	10.0
Juan Fernandez	9.0
Hawaii	5.1
Mt Wilhelm above 2743 m	5.0
" " " 3800 m	3.3
" " " 4000 m	2.7
Madeira	2.7
Breadalbane, Scotland	2.4
World	1.0
Central Otago high alpine	0.9
Snowy Mts alpine	0.8 - 0.9

Although not to a greater extent than on most oceanic islands, the flora of Mt Wilhelm does appear to be disharmonic, suggesting that its component species have immigrated too recently to have undergone sufficient adaptation and diversification to occupy fully all the available ecological niches. As a result of this, it is to be expected that the vegetation and the flora are in changing balance with the environment, their components being as yet only partly adapted to present conditions, and partly retaining adaptations to former conditions obtaining prior to immigration to New Guinea. Disharmony tends to confirm the view that this flora is probably to a large extent of fairly recent immigrant derivation.

3-G GEOGRAPHIC AND TEMPORAL ELEMENTS IN THE NON-FOREST FLORA

The non-forest flora of Mt Wilhelm is here defined as including all species occurring commonly or solely in the grasslands above 3215 m or commonly in other non-forest habitats above 2500 m on Mt Wilhelm or in localities in its immediate neighbourhood. It includes both natives and aliens, a few species with only a single collection from the mountain and some species found in forest as well as non-forest environments. Pteridophytes are not considered due to their small number (about 14 although there are many in the forests), poor taxonomy and doubts concerning their phytogeographic comparability with flowering plants. The non-forest flora consists of 178 species in 112 genera, including 163 native species in 100 genera, and 15 introduced species. The largest genera are *Carex* and *Rhododendron* (8 species each), *Poa* (6 species) and *Ranunculus* and *Trigonotis* (4 species each), while *Danthonia*, *Dimorphanthera*, *Epilobium*, *Gentiana*, *Gnaphalium*, *Olearia*, *Oreomyrrhis*, *Parahebe*, *Potentilla*, *Scirpus* and *Senecio* all have 3 species.

The geographic elements likely to be recognized in this flora have been discussed in section 2-E. The purpose of this section is to clarify these with particular regard to the individual species occurring on Mt Wilhelm. I am not suggesting that on the geographical and taxonomic bases used the migrational histories of all these plants can be determined. However, it is on such bases that phytogeography has leaned heavily in the past, and it is necessary to form some idea of the identity of the floristic elements in order to examine their ecological characteristics. The elements identified below will be re-examined in chapter 9 in the light of my ecological and other data presented in chapters 4 - 8.

Two basic assumptions have been made.

1. That distributions outside Malesia (including for present purposes Pacific islands) indicate source regions.
2. That species also occurring outside Malesia are of more recent immigration than Malesian endemic species.

Both of these assumptions are open to criticism. Caughley [1964] has warned against the unadmitted principle of biogeography that forms always migrate from elsewhere to the region bring considered. In this case the relatively small areas of Malesia available to cold-demanding plants (especially by comparison with Eurasia) and the youth of these elevated areas make it appear more probable that taxa shared between Malesia and one or both of the temperate zones have their origins in the latter and have migrated to Malesia rather than vice-versa. Rates of speciation are not known and clearly differ between taxa. It is logical nevertheless to assume that geographically separated populations of an originally single species diverge progressively with time, so that more distinct taxa have been geographically separate for longer than less distinct ones.

With these admittedly imperfect assumptions in mind a key was devised to separate the flora into its component elements, based upon the geographic distributions of both the genera and the species (see Appendix 1 and Fig. 3-10). Malesia rather than New Guinea has been used as the smallest geographic unit because of the strong and probably recent floristic links between different Malesian mountain floras. Distributions within New Guinea are discussed in chapter 8. In the key below abbreviations of floristic elements are introduced and are as follows:

A - alien
P - peregrine (N - northern, S - southern, W - widespread)
G - gondwanic
E - endemic.

1.	Species introduced by man	A
	Species native	(2)
2.	Species occurring outside Malesia	(3)
	Species endemic to Malesia	(5)
3.	Genus occurring only in Malesia and Eurasia	PNN
	Genus occurring only in Malesia and Australasia	PSS
	Genus more widespread	(4)
4.	Species occurring only in Malesia and Eurasia	PWN
	Species occurring only in Malesia and Australasia	PWS
	Species more widespread	PWW
5.	Genus occurring in Malesia, Eurasia and Australasia	PW
	Genus occurring only in Malesia and Eurasia	PN
	Genus occurring only in Malesia and Australasia	PS
	Genus occurring only in Malesia, Australasia and South America (sometimes also Africa)	G
	Genus endemic to Malesia	E

The resulting floristic elements are discussed and in some cases slightly modified below.

Species Distribution	Genus Distribution				
	Endemic to Malesia and Pacific islands	Southern disjunct (Malesia, Australasia and South America, sometimes also Africa)	Northern (Malesia and Eurasia, sometimes also North America)	Southern (Malesia and Australasia	Widespread (Malesia, Eurasia and Australasia at least)
Endemic to Malesia and Pacific islands	E	G/?G	PN	PS	PW
Northern (Malesia and Eurasia, sometimes also North America)	–	–	PNN	–	PWN
Southern (Malesia and Australasia, sometimes South America)	–	PSS	–	PSS	PWS
Widespread (Malesia, Eurasia and Australasia at least)	–	–	–	–	PWW
Introduced to mountains of New Guinea	–	–	A	A	A

Fig. 3-10: Geographic basis for the definition of floristic elements in the non-forest flora of Mt Wilhelm.

(a) Species of Ancient Status in New Guinea

Included provisionally within this category are all species which key out as gondwanics (G) or endemics (E).

The gondwanic element consists of 19 species in 14 genera. Three genera, *Nertera*, *Oreobolus* and *Uncinia*, have species in the peregrine as well as the gondwanic element.

Several of the species in the gondwanic element as defined here appear unlikely, however, to have been in the New Guinea area throughout the Tertiary without spreading into Eurasia in Plio-Pleistocene times. *Astelia papuana*, *Coprosma divergens*, *Coprosma papuensis*, *Nertera* cf. *nigricarpa*, *Pipturus* sp.1, and *Uncinia* sp.1 have apparently good dispersal mechanisms perhaps enabling long distance dispersal. *Oreobolus ambiguus* is of wide distribution within Malesia also suggesting good dispersal ability, and species of *Parahebe* as well as having very small seeds belong to a genus of northern affinity, part of the "*Veronica-Hebe-Parahebe-Detzneria*" complex [Steenis, 1971]. These species are hereafter grouped as the "?G" element, leaving the following in the "G" element: *Abrotanella papuana*, *Dacrycarpus compactus*, *Drapetes ericoides*, *Drimys piperita* "entity" *subalpina*, *Haloragis halconensis*, species of *Oreomyrrhis* and *Pittosporum pullifolium*. It is worth pointing out that the genera *Dacrycarpus*, *Drimys* and *Pittosporum*, all woody plants, find their best development in the forests on Mt Wilhelm, while other gondwanic taxa occur without near allies in non-forest habitats.

The endemic element (E) includes 11 species in 8 genera. Two of these genera have strong northern affinity (*Detzneria* and *Dimorphanthera*) and most of the others belong to the Compositae or Orchidaceae, both advanced and mainly herbaceous families of rapid and recent evolution. This leaves the araliaceous *Harmsiopanax*, a pachycaulous and hapaxanthic forest tree often colonizing non-forest sites below 3300 m, as the only probable ancient endemic. Members of the endemic element are listed below.

Ceratostylis sp.2
Detzneria tubata
Dimorphanthera amplifolia
D. keysseri
D. microphylla
Harmsiopanax ingens
Ischnea elachoglossa
Keysseria radicans
Pedilochilus sp.1
Tetramolopium alinae
Tetramolopium macrum

(b) The Peregrine Element

The majority of the non-forest flora, 133 species in 81 genera, key out as members of the peregrine element. 42 of these species occur outside Malesia, 8 to the north, 23 to the south, and 11 to both north and south, while 91 are species endemic to Malesia. Of the genera in the peregrine element, 10 are predominantly Eurasian, 18 Australian and 53 very widespread. The peregrine element is divided into the following categories.

PW - Malesian endemic species of genera widespread both north and south of Malesia: 58 species as follows:

Agrostis reinwardtii
Anaphalis lorentzii
Anaphalis mariae
Anthoxanthum angustum
Cardamine altigena
Carex celebica
Carex euphlebia
Carex neoguineensis
Cerastium papuanum
Coleus scutellarioides
Cotula cf. *leptoloba*
Cynoglossum javanicum
Danthonia archboldii
Danthonia vestita
Deschampsia klossii
Deyeuxia brassii
Epilobium detznerianum
Epilobium hooglandii
Epilobium keysseri
Eriocaulon montanum
Euphrasia mirabilis
Eurya albiflora
Eurya brassii
Festuca crispate-pilosa
Festuca papuana
Galium novoguineense
Gaultheria mundula
Gentiana cruttwellii
Gentiana ettingshausenii
Gentiana piundensis
Gnaphalium breviscapum
Habenaria (Platanthera) sp.
Hypericum macgregorii
Imperata conferta
Lactuca laevigata
Lactuca sp.1
Lobelia archboldiana
Phreatia sp.1
Pilea cf. *johniana*
Plantago aundensis
Poa callosa
Poa crassicaulis
Poa epileuca
Poa saruwagetica
Poa sp.1
Polygonum runcinatum
Ranunculus pseudolowii
Ranunculus saruwagedicus
Ranunculus schoddei
Ranunculus wahgiensis
Rapanea vaccinioides
Rubus papuanus
Sagina papuana
Saurauia sp.2
Schoenus curvulus
Senecio papuanus
Senecio sp.5
Symplocos sp.3

PN - Malesian endemic species in predominantly northern (Eurasian) genera: 22 species, as follows:

Agapetes vitis-idaea
Anotis sp.1
Decaspermum lorentzii
Miscanthus floridulus
Myriactis cabrerae
Potentilla foersteriana
Potentilla papuana
Potentilla parvula
Rhododendron atropurpureum
Rhododendron beyerinckianum
Rhododendron commonae
Rhododendron culminicolum
Rhododendron gaultheriifolium
Rhododendron inconspicuum
Rhododendron womersleyi
Rhododendron yelliottii
Trigonotis inoblita
Trigonitis papuana
Trigonotis sp. aff. *papuana*
Trigonotis procumbens
Vaccinium amblyandrum
Vaccinium cruentum

PS - Malesian endemic species in predominantly southern (Australasian) genera: 11 species, as follows:

Centrolepis philippinensis
Monostachya oreoboloides
Olearia floccosa
Olearia monticola
Olearia spectabilis
Pterostylis sp.2
Quintinia sp.1
Thelymitra cf. *papuana*
Trachymene tripartita
Trochocarpa dekockii
Trochocarpa dispersa

PWW - Widespread species (to both north and south of Malesia) in widespread genera: 11 species, as follows:

Callitriche verna
Carex capillacea
Carex gaudichaudiana
Carex perciliata
Dichrocephala bicolor
Dodonaea viscosa
Gnaphalium japonicum
Hydrocotyle sibthorpioides
Juncus effusus
Luzula campestris
Montia fontana

PWN - Species occurring also in Eurasia in widespread genera: 7 species, as follows:

Brachypodium sylvaticum
Carex echinata
Carex finitima
Deyeuxia arundinacea
Polygonum nepalense
Scirpus subcapitatus
Viola arcuata

PWS - Species occurring also in Australasia in widepsread genera: 12 species, as follows:

Agrostis avenacea
Danthonia penicillata
Geranium potentilloides
Gnaphalium involucratum
Hierochloe redolens
Lobelia angulata
Myosotis australis
Oxalis magellanica
Schoenus maschalinus
Scirpus crassiusculus
Scirpus cf. *subtillissimus*
Senecio glomeratus

PNN - Species occurring also in Eurasia in predominantly northern genera: 1 species:

Triplostegia glandulifera

PSS - Species occurring also in Australasia in predominantly southern genera: 11 species, as follows:

Acaena anserifolia
Carpha alpina
Dichelachne rara
Gaimardia setacea
Libertia pulchella
Microlaena stipoides
Nertera granadensis
Oreobolus pumilio
Styphelia suaveolens
Trachymene saniculifolia
Uncinia riparia

(c) The Alien Element

The alien element (A) consists of 15 species in 14 genera, only this number being members of the non-forest flora from a total list of 45 introduced species recorded from above 2515 m on Mt Wilhelm. The full list with details of authority and distribution on Mt Wilhelm is given in Fig. 3-11. All species known or reasonably suspected of having been introduced to New Guinea by man are described here as alien. The degree of certainty of their alien status, their probable dates of introduction, and their uses or external transport by man are given in Fig. 3-12. Also included in this table are several species possibly introduced before 100 years ago but here regarded as native. I am indebted to E.E. Henty for his views on the alien or native status in New Guinea of species in the Mt Wilhelm flora.

The species in the alien element of the non-forest flora are listed below. Two genera, *Plantago* and *Poa*, include both native and introduced species.

Bidens pilosa
Crassocephalum crepidioides
Erigeron canadensis
Erigeron sumatrensis
Fragaria cf. *vesca*
Lolium rigidum
Plantago lanceolata
Poa annua
Sonchus oleraceus
Stellaria media
Tacsonia mollissima
Tritonia X *crocosmaeflora*
Verbena bonariensis
Veronica cf. *persica*
Vulpia bromoides

Most of these are apparently well established and widespread in the Mt Wilhelm area. *Plantago lanceolata* and *Vulpia bromoides* were both recorded for the first time in New Guinea in 1972, the former represented by a few individuals beside the research station probably already extinct there as all plants were collected, the latter known from single clumps at only two places. *Lolium rigidum*, though multiplying, is also known from only two places on Mt Wilhelm, having first been collected in 1971.

Colour photographs of four plants representing different floristic elements in the Mt Wilhelm flora are provided in plate 3-1.

Fig. 3-11: Plant species alien to New Guinea growing in the Mt Wilhelm area, 1972.

Family	Species	Occurrence at Sites													Specimen Number	Earliest Collection	Highest Record	Frost	Notes
		1	2	3	4	5	6	7	8	9	10	11	12	13					
Gramineae	*Eragrostis tenuifolia* Hochst. ex Steud.	+		+			+								ANU 15348	1959	2819	?	1
	Lolium rigidum Gaud.								+				+		ANU 15303	1971	3481	H	
	Phalaris tuberosa L.													(+)	NGF 39562	1955	3536	?	
	Poa annua L.	+		+			+		+						ANU 15079	1959	3481	H	2
	Pennisetum clandestinum Hochst. ex Chiov.	+		+			+		+						ANU 15079	1962	2911	?	
	Vulpia bromoides (L.) S.F.Gray						+						+		ANU 15301	1972	3481	H	
Iridaceae	*Tritonia* X *crocosmaeflora* Nichols	+	+		+	+	+				+		+		ANU 15302	1953	3481	S	3
Liliaceae	*Cordyline fruticosa* (L.) Gepp.	+	+	+	+	+	+	+	+				+		ANU 15353	1930	3481	S	4
Caryophyllaceae	*Dianthus* sp.	+					+								ANU 15411	1972	2667	?	
	Stellaria media L.	+	+	+	+		+						+		ANU 15153	1959	3481	H	
Casuarinaceae	*Casuarina oligodon* Johnson	+		+			+								ANU 15456	1951	2819	?	5
Compositae	*Ageratum conyzoides* L.	+					+								ANU 15365	1950	2576	?	
	Bidens pilosa L.	+	+	+			+	+	+				+		ANU 15205	1953	3490	S	6
	Chrysanthemum cinerariifolium (Trev.) Bocc.	+					+								ANU 15519	1972	2539	?	7
	Conyza aegyptica Ait.						(+)	(+)							Brass 30526	1957	2713	?	
	Cosmos ?bipinnatus Cav.	+		+			+	+							ANU 13013	1971	2819	?	
	Crassocephalum crepidioides (Benth.) S.Moore	+	+	+			+	+	+	+				+	ANU 15244	1957	3414	S	8
	Erechtites valerianifolia (Wolf.) DC.		+	+			+	+							ANU 15373	1953	2880	?	
	Erigeron canadensis L.	+	+	+	+		+	+		+	+	+	+	+	ANU 15261	1957	3688	H	
	Erigeron sumatrensis Retz.	+	+	+		+	+	+	+	+	+	+	+	+	ANU 15148	1950	3688	H	
	Galinsoga parviflora Cav.	+		+	+		+								ANU 15253	1959	2966	?	
	Gynura procumbens (Laur.) Merr.			+			(+)	(+)							ANU 15250	1959	2850	?	
	Siegesbeckia orientalis L.	+					+	+							ANU 15363	1947	2728	?	
	Sonchus asper (L.) Hill		+	+			+	+							ANU 15201	1963	2911	?	
	Sonchus oleraceus L.	+	+	+			+	+	+	+	+	+	+	+	ANU 15382	1950	3688	H	
	Tagetes minuta L.	+					+	+							ANU 15349	1959	2728	?	
	Tagetes sp.	+		+			+								ANU 15361	1972	2667	?	
Cruciferae	*Brassica oleracea* L.	+		+									+		ANU 15321	1972	3481	H	9
	Cardamine hirsuta L.	+		+			+								ANU 15252	1960	2911	?	
	Nasturtium officinale R.Br.	+		+			+	+			+	+			ANU 15424	1960	3240	?	10
	Rorippa sp.						+								ANU 15357	1960	2667	?	
Labiatae	*Coleus* sp.	+					+								ANU 13011	1971	2661	?	
	Mentha sp.	+											+		ANU 15512	1972	3481	H	11
	Stachys arvensis L.	+			+		+	+							ANU 15342	1957	2966	?	
	Thymus ?vulgaris L.	+					+								ANU 15359	1968	2667	?	12
Leguminosae	*Cassia tomentosa* L.f.	+					+								ANU 15351	1959	2713	?	
	Lathyrus ?sativus L.	+					+								ANU 15399	1960	2530	?	
	Lupinus sp.	+	+	+									+		ANU 15249	1959	3481	S	
	Pisum sativum L.	+										+	+		ANU 15300	1972	3481	H	13
	Trifolium repens L.	+					+	+	+						ANU 15200	1960	2911	?	
	Vicia sativa L.												(+)		ANU 7033	1966	3481	?	
Linaceae	*Linum usitatissimum* L.													(+)	NGF 35093	1968	3535	?	
Passifloraceae	*Passiflora* sp.						+								ANU 15517	1972	2713	?	
	Tacsonia mollissima Kunth.	+	+	+	+		+	+	+			+	+		ANU 15304	1959	3481	S	14
Plantaginaceae	*Plantago lanceolata* L.												+		ANU 15477	1972	3481	H	
	Plantago major L.	+		+			+								ANU 15189	1967	2804	?	
Rosaceae	*Fragaria* cf. *vesca* L.	+		+			+	+	+				+	+	ANU 15078	1971	3484	H	15
Scrophulariaceae	*Veronica* cf. *persica* Poir.	+					+	+					+		ANU 15117	1957	3481	H	
Solanaceae	*Cestrum ?elegans* Schlecht.	+					+								ANU 15360	1966	2667	?	16
	Nicotiana tabacum L.	+					+								ANU 15455	1961	2633	?	17
	Physalis peruviana L.	+	+	+			+	+							ANU 15179	1954	2728	?	18
	Solanum nigrum L.						+	(+)							ANU 15352	1956	2713	?	
Verbenaceae	*Verbena bonariensis* L.	+	+	+			+						+		ANU 15350	1953	3481	S	
Pinaceae	*Pinus* sp.	+					+								ANU 15457	1972	2515	?	19

Sites:

1. Gardens, upper Chimbu valley, 2100-2510 m.
2. Kuraglumba, 2730-2850 m.
3. Mondia road, 2800-2900 m.
4. Clearing on Keglsugl-Kombugli track, 2970 m.
5. Kombugli, 3240-3270 m.
6. Wilhelm summit track (Keglsugl-Komanimambuno), 2510-2710 m.
7. Wilhelm summit track (Pengagl creek: old route), 2710-2900 m.
8. Wilhelm summit track (old route), 2900-3200 m.
9. ?Banks of Pengagl creek, 2900-3050 m.
10. Gwaki creek and Guraguragugl valleys, 2900-3560 m.
11. Wilhelm summit track (Pindaunde mountain grassland), 3200-3480 m.
12. Near Pindaunde huts, 3480-3490 m.
13. Landslips and other natural habitats, 3200-3700 m.

\+ indicates occurrence during 1972.
(+) indicates an earlier record not repeated in 1972.

Notes:

1. Probably favoured by trampling.
2. Favoured by pollution at 3480 m.
3. Favoured by pig disturbance of soil below 2750 m.
4. Commonly planted as stem cuttings along paths.
5. Commonly planted as seedlings below 2500 m.
6. Hooked fruits often carried in clothing.
7. Pyrethrum: occasional wild seedlings found near cultivated plots.
8. Very good colonist of newly bared ground.
9. Often grows from discarded cabbage stalks.
10. Watercress: commonly planted as stem cuttings in wet places.
11. Mint: never flowers but reproduces by stolons.
12. Thyme: only found near abandoned home sites.
13. Seeds often carried by children for food.
14. Fruits eaten by man and pigs; seeds germinate in old pig faeces.
15. "Fruits" eaten by man and pigs.
16. Ornamental shrub commonly planted near houses.
17. Tobacco: only found near abandoned home sites.
18. Fruits sometimes eaten by man.
19. Pine: planted as seedlings.

All plant specimens quoted are lodged in the Forests Department herbarium, Lae. Earliest and highest records are those represented by collections in Lae from all of Papua New Guinea and from the Mt Wilhelm area respectively. Altitudes are in metres. H indicates that the species is hardly damaged by frost on Mt Wilhelm; S indicates that the species is frost-sensitive.

Excluded from the table are species growing only below 2510 m (site 1), and species growing only as deliberately planted specimens near the Pindaunde research station showing no sign of spread or already extinct (including *Fuchsia ?magellanica*, *Petroselinum crispum* and various vegetables).

Fig. 3-12: Times of introduction and uses of alien plants growing in the Mt Wilhelm area, 1972.

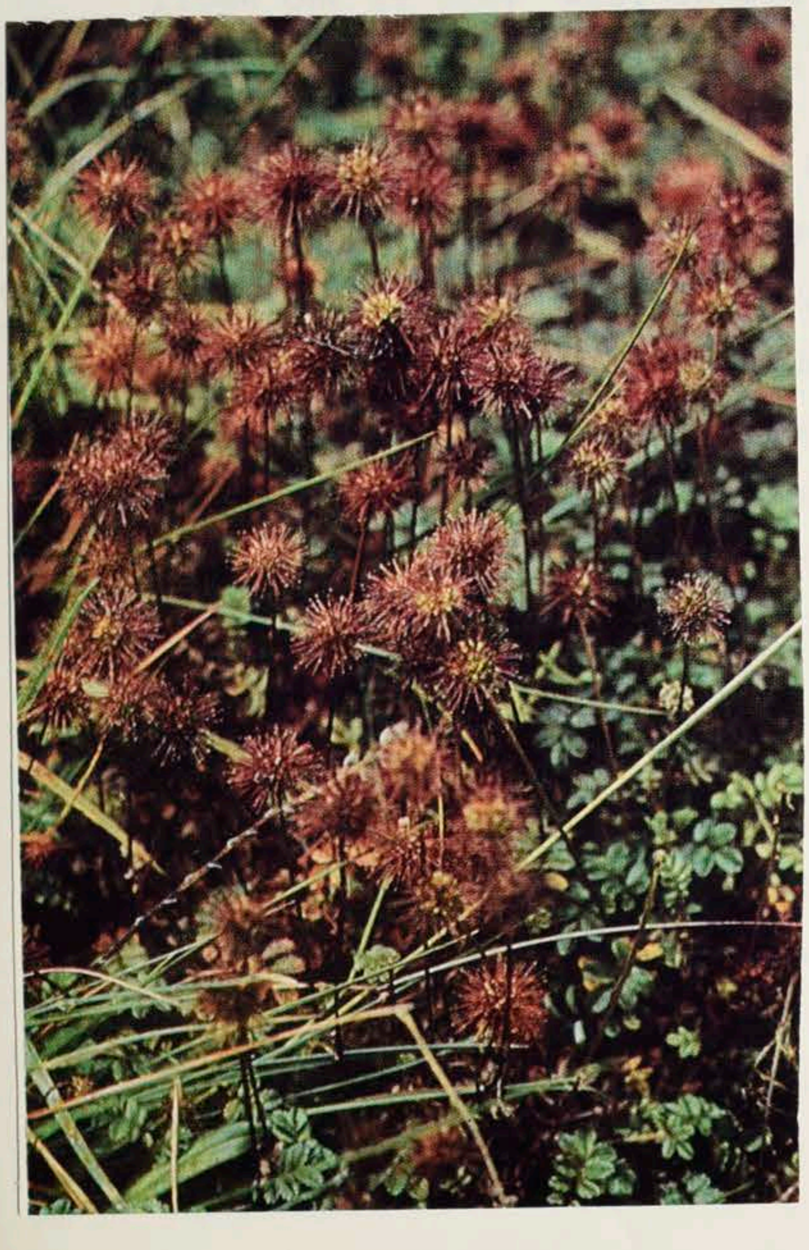
Time of Introduction	Woody Plants	Monocotyledons	Compositae	Other Dicotyledons
Possibly pre-European (before about 100 yr ago)		*Isachne myosotis* *Juncus effusus* *Juncus prismatocarpus* *Microlaena stipoides* (1)	*Dichrocephala bicolor* (1) *Gnaphalium japonicum*	*Coleus scutellarioides* (4) *Cynoglossum javanicum* *Mazus pumilus* *Oenanthe javanica* (2) *Oxalis corniculata* *Polygonum nepalense* *Wahlenbergia marginata*
Probably pre-European	*Casuarina oligodon* (4) *Cordyline fruticosa* (4)		*Gynura procumbens*	*Nicotiana tabacum* (4) *Plantago major* *Rorippa* sp. (2) *Solanum nigrum*
Probably European (after about 100 yr ago)	*Cassia tomentosa* (3) *Cestrum elegans* (3)	*Eragrostis tenuifolia* *Poa annua* *Tritonia* X *crocosmaeflora* (3)	*Ageratum conyzoides* *Bidens pilosa* (1) *Conyza aegyptica* *Cosmos ?bipinnatus* (3) *Erechtites valerianifolia* *Erigeron canadensis* *Erigeron sumatrensis* *Galinsoga parviflora* *Siegesbeckia orientalis* *Sonchus asper* *Sonchus oleraceus* *Tagetes minuta* *Tagetes* sp. (3)	*Cardamine hirsuta* *Coleus* sp. (3) *Lathyrus sativus* *Lupinus* sp. (4) *Mentha* sp. (2) *Nasturtium officinale* (2) *Physalis peruviana* (2) *Stachys arvensis* *Stellaria media* *Tacsonia mollissima* (2) *Thymus ?vulgaris* (2) *Verbena bonariensis* *Veronica* cf. *persica*
Certainly European	*Pinus* sp. (4)	*Lolium rigidum* *Pennisetum clandestinum* (4) *Phalaris tuberosa* *Vulpia bromoides*	*Chrysanthemum cinerariifolium* (4) *Crassocephalum crepidioides*	*Brassica oleraceus* (2) *Dianthus* sp. (3) *Fragaria* cf. *vesca* (2) *Linum usitatissimum* *Passiflora* sp. (2) *Pisum sativum* (2) *Plantago lanceolata* *Trifolium repens* (4) *Vicia sativa*

KEY:
1. Disseminules cling to clothing.
2. Eaten by man as fruit, herb or vegetable.
3. Planted for decorative qualities.
4. Used for timber, grazing of domestic animals, dyeing, manufacture of pyrethrum or tobacco, etc.

Plate 3-k: Four plants from Mt Wilhelm.

Top left: *Podocarpus brassii.*
Top right: *Rhododendron womersleyi.*
Bottom left: *Acaena anserifolia.*
Bottom right: *Tacsonia mollissima.*

[From Smith, 1974a.]



CHAPTER 4

DISPERSAL ABILITY

4-A THE SIGNIFICANCE OF DISPERSAL ABILITY

Vestigial organs have long provided one of the pillars supporting classical evolutionary theory, and the belief that organs which cease to be advantageous progressively decline in size in successive generations by a process of natural selection was propounded by Darwin in *The Origin of Species*. He considered the flightlessness of many species of beetle on the island if Madeira to be mainly due to

> "the action of natural selection, but combined probably with disuse. For during thousands of successive generations each individual beetle which flew least, either from its wings having been ever so little less perfectly developed or from indolent habit, will have had the best chance of surviving from not being flown out to sea; and, on the other hand, those beetles which most readily took to flight will oftenest have been blown to sea and thus have been destroyed." [Darwin, 1968].

Carlquist [1966a; 1966b] has extended these observations to insular plant populations. Using evidence provided by *Bidens* and other Compositae occurring on Pacific islands he argues that although efficient dispersal mechanisms are of paramount importance to species colonizing small oceanic islands, this does not remain so after establishment of the population. Almost all disseminules "exported" from an island are doomed, and even if they are able to develop into mature plants elsewhere such plants would be most unlikely to cross-pollinate with the parent population, so that effectively all disseminules leaving the island are lost to the remaining gene-pool. Therefore a selective pressure exists curbing the dispersal ability of species of plants which have succeeded in colonizing oceanic islands. Carlquist claims to have established a progressive loss of dispersal mechanisms in island populations of Compositae notably of hooks on the fruits of *Bidens*. Gillett [1972], while accepting a progressive loss of such hooks, does not agree that the evolutionary role of this trend is fully explained by the theory of loss of dispersal ability, at least in Hawaiian species of *Bidens*.

However MacArthur and Wilson [1967] agree that "In order to adapt to the insular environment, species will on the average incur a loss of dispersal power". Pijl [1969] remarks upon the apparently poor dispersal ability of members of floras of some oceanic islands, and quotes Guppy [1906] as noting an increase in seed size in insular plants compared with their continental relatives. Ridley [1930] has observed that grasses with plumed seeds although common in continental areas are markedly rare on islands. Whether there is a selective pressure against dispersal mechanisms or whether their loss is simply due to no selective pressure in their favour is not relevant to the present argument.

Tropical mountains can be compared with oceanic islands, though their "shores" cannot be easily defined, as they are in effect islands of cool climate and associated vegetation in oceans of hot tropical lowland forest. Carlquist's argument concerning loss of dispersal mechanisms in plants adapting to the insular situation can be applied here also, and a parallel exists between the flightlessness of Madeiran insects remarked upon by Darwin and of insects on Mt Kilimanjaro [Salt, 1954].

It is easy to imagine vegetative reproduction being of great survival value to a colonist species, at least in the initial establishment of a local colony. Insofar as division of the growing point or growth from axillary buds together with development of adventitious roots can lead to a clumped or tufted habit, vegetative reproduction is found in a majority of the non-forest flora of Mt Wilhelm, and is responsible for growth forms like the tussock (e.g. *Deschampsia klossii*, *Poa saruwagetica*) and cushion (e.g. *Astelia papuana*, *Centrolepis philippinensis*, *Monostachya oreoboloides*). Runners are important in *Acaena anserifolia*, *Gnaphalium breviscapum*, *Nertera granadensis*, *Senecio papuanus*, *Trigonotis papuana*, *Trigonotis procumbens* and *Viola arcuata*, and lead to the formation of mats in *Pilea* cf. *johniana* and *Poa crassicaulis*. Subterranean stolons are developed by *Nertera nigricarpa* and *Oxalis magellanica*. Layering is important to most woody plants within the forests and can result in spread of forest into grassland in the absence of burning [Gillison, 1970]. Layering also enables the decumbent shrubs *Trochocarpa dekockii* and *Vaccinium amblyandrum* to spread across bare sites from non-forest vegetation at their margins (see section 5-B). However, partly because of the difficulty in its measurement and assessment, vegetative reproduction *per se* has not been considered here.

In an analysis of 104 native plant species growing above 3000 m on mountains in East Africa, Hedberg [1971] has concluded that 37 were probably carried there by wind, 14 were carried externally by animals, probably by birds, and that 53 (31%) having no identificable mechanism must have been carried in mud on the feet of birds or mammals. In a similar study of the flora of the summit zone of Mt Kinabalu, Stapf [1894] found that 74% of species growing above about 3350 m lacked recognizable mechanisms, the remaining 26% being wind-dispersed: a larger proportion of the flora at lower altitudes possessed dispersal mechanisms. On Mt Pangrango, a smaller mountain in Java (3025 m), Leeuwen [1933, quoted by Steenis, 1972] concluded that 58 of 152 species were potentially animal-dispersed, 42 wind-dispersed (including small-seeded ones) and 52 had no mechanism. I examined 113 non-forest species from Mt Wilhelm, mostly growing above 3215 m. The disseminules of 31 showed adaptations to wind dispersal or had seeds weighing less than 0.1 mg, 30 were potentially dispersed either internally or externally by animals, and 52 had no clear mechanisms for dispersal. Of 100 native species in this total, 44 had no dispersal adaptation.

MacArthur and Wilson [1967] have stressed that most immigrants to insular localities are organisms with efficient means of dispersal which tend to establish themselves initially in open habitats such as shores and streambanks where they behave as pioneers. Margalef [1959; 1968] has pointed out that such species produce large numbers of disseminules with good dispersal mechanisms, often being wind-dispersed. After successful establishment there is an evolutionary trend towards reduction both in the number and effectiveness of dispersal of disseminules, which often become larger and animal-dispersed or with no obvious means of dispersal.

It is therefore logical to expect dispersal mechanisms to be most efficient and obvious in plants which are of most recent immigration to insular situations. Members of the Mt Wilhelm non-forest flora were examined with this in mind. Two assumptions have been made:

1. That morphology and size provide information concerning dispersal, i.e. that hooks or sticky secretions facilitate external

animal dispersal, that fleshy fruits facilitate internal animal dispersal, that plumes and pappuses facilitate wind dispersal, and that disseminules weighing less than 0.1 mg are easily carried by wind.

2. That dispersal mechanisms effective over short distances (up to a few km) also render disseminules more likely than disseminules without such mechanisms to be dispersed over longer distances, up to over 1000 km.

Neither assumption appears unreasonable although neither can be proven as fact upon present information.

Dispersal ability is examined below, both by the investigation of disseminule characteristics (section 4-B) and by observation of the distribution of taxa in areas from which they may have been excluded by barriers to dispersal.

4-B WEIGHTS AND ADAPTATIONS OF DISSEMINULES

Disseminules of 112 species of angiosperm were collected on Mt Wilhelm and preserved in 70% ethanol, and those of one further species were collected subsequently from plants in cultivation in Canberra. They were examined both fresh and when preserved for the presence of probable dispersal mechanisms including fleshy edible tissue, hooks, sticky secretions, pappuses and plumes. Preserved disseminules were surface-dried in the laboratory and weighed in grams to five decimal places. Fig. 4-1 shows drawings of some disseminules with probable mechanisms for dispersal, and in Appendix 3 weights of disseminules are tabulated. In a subsidiary experiment disseminules of some New Guinea species in cultivation in Canberra and some other species were collected, weighed fresh, and then weighed (surface-dried) after several days preservation in 70% ethanol. The latter weights with a single exception were all within 36% of the fresh weight, averaging a gain of about 10% during preservation as shown in Fig. 4-2. As a result of this experiment I believe that the preserved weights given in Appendix 3 provide an approximation to the live weights of the same disseminules.

65% of the 113 Mt Wilhelm species examined had disseminules weighing between 0.1 and 10 mg. The proportion exhibiting no apparent dispersal mechanism is highest over the same range. Of those disseminules heavier than this, 90% have fleshy edible tissue implying

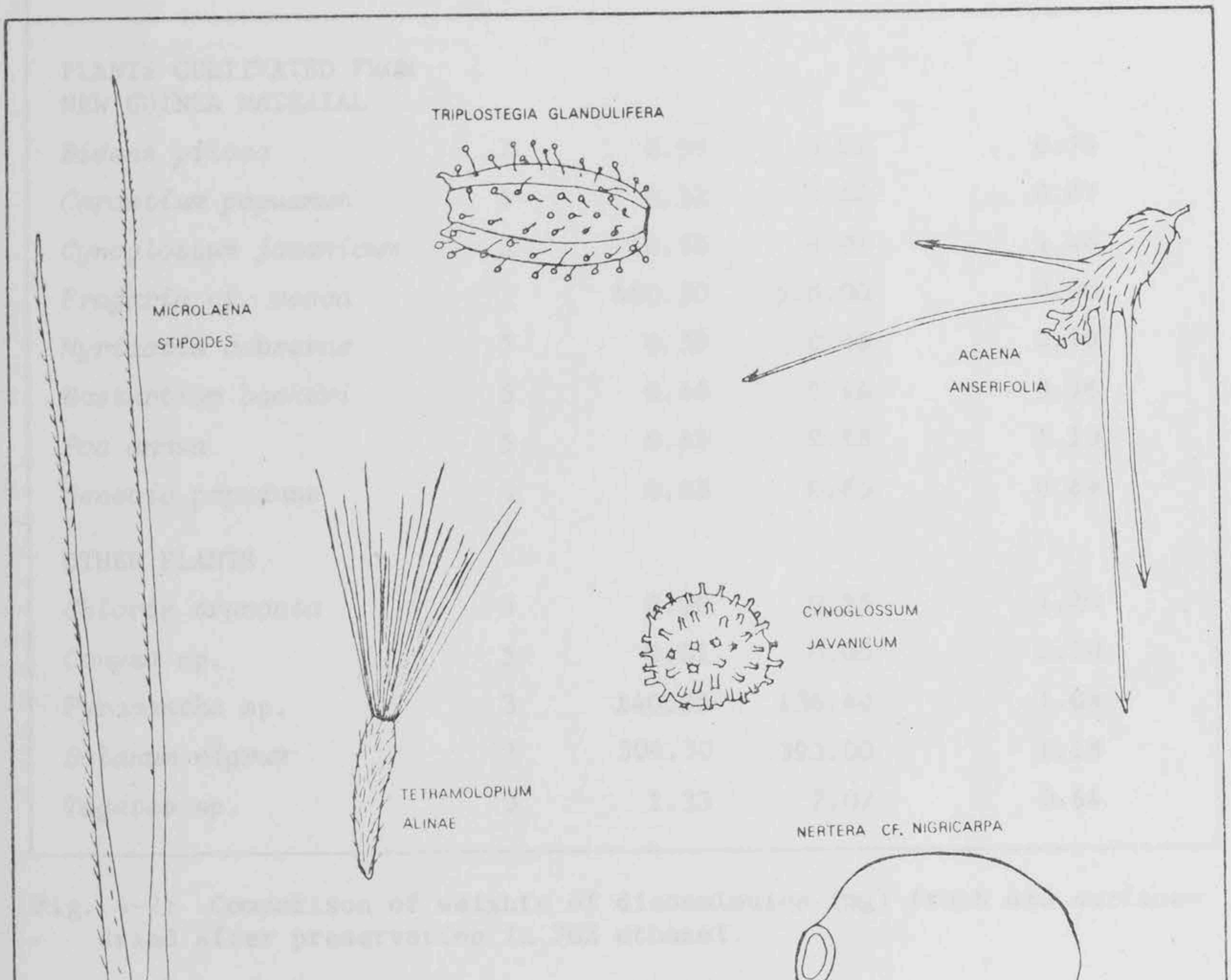


Fig. 4-1: Disseminules of some species in the non-forest flora of Mt Wilhelm showing dispersal mechanisms.

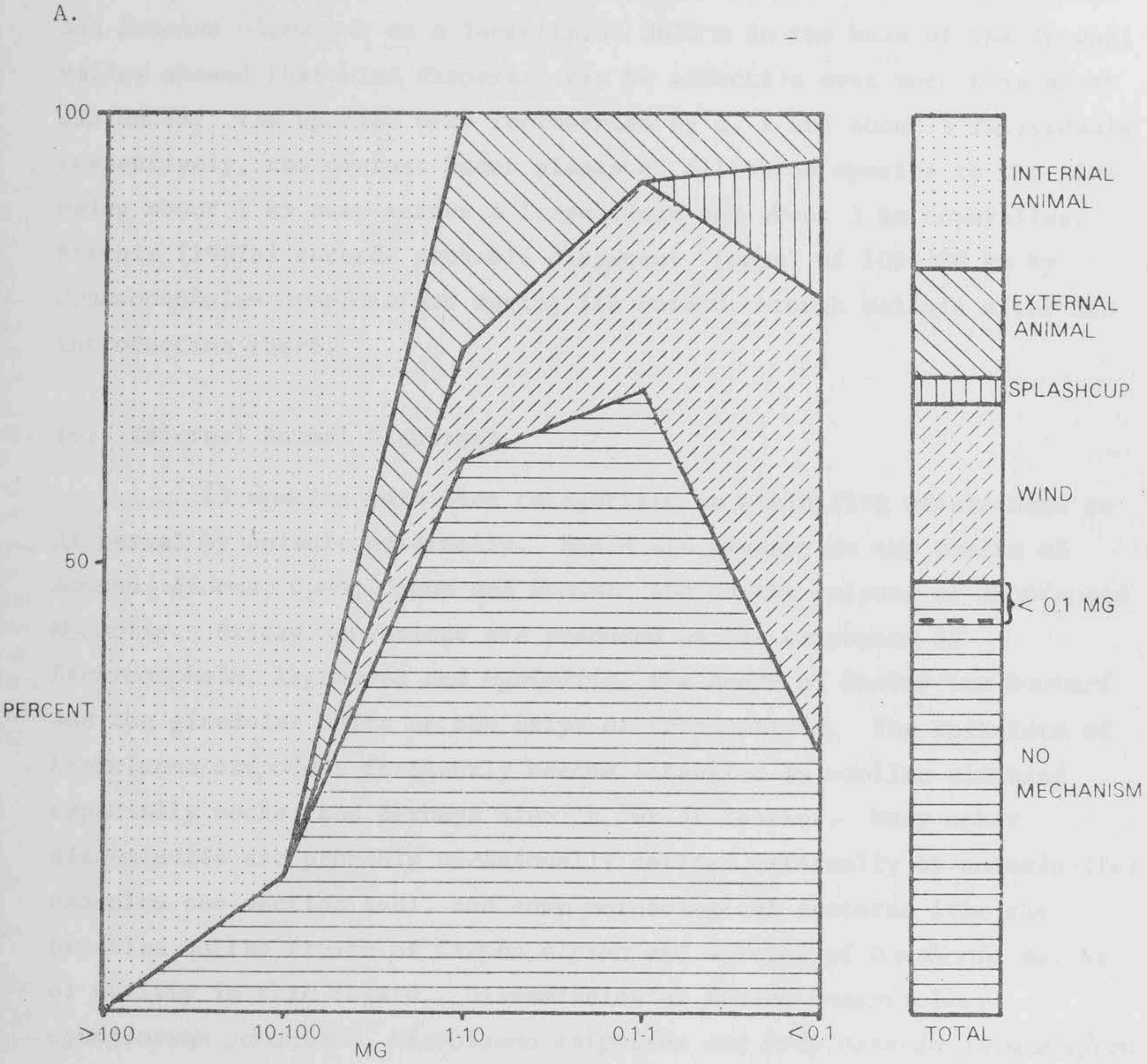
Species	No. Weighed	Fresh Weight	Preserved Weight	Fresh Wt ÷ Preserved Wt
PLANTS CULTIVATED FROM NEW GUINEA MATERIAL				
Bidens pilosa	7	2.99	4.02	0.74
Cerastium papuanum	6	0.52	0.60	0.87
Cynoglossum javanicum	3	10.33	8.07	1.28
Fragaria cf. *vesca*	1	460.30	510.00	0.90
Myriactis cabrerae	5	0.38	0.48	0.79
Nasturtium backeri	5	0.44	0.46	0.96
Poa annua	5	0.63	0.58	1.10
Senecio papuanus	4	0.45	0.65	0.69
OTHER PLANTS				
Chloris truncata	5	0.30	0.25	1.20
Conyza sp.	5	0.01	0.05	0.20
Pyracantha sp.	3	140.20	136.40	1.03
Solanum nigrum	2	504.30	393.00	1.28
Tagetes sp.	3	1.33	2.07	0.64

Fig. 4-2: Comparison of weights of disseminules (mg) fresh and surface-dried after preservation in 70% ethanol.

internal transport by animals. The proportion of disseminules with pappuses or hairs enabling wind dispersal increases with decrease in disseminule weight (see Fig. 4-3).

(a) Wind Dispersal

23 species of the 113 examined had clear adaptations towards wind dispersal in the form of a pappus in many Compositae or hairs attached to the testa as in species of *Epilobium*, *Imperata*, *Miscanthus*, and *Rhododendron*. Wind-dispersed disseminules of *Imperata conferta* and *Tetramolopium alinae* are drawn in Fig. 4-1. A further 5 species, in *Hypericum*, *Lobelia*, *Parahebe* and *Sagina*, without special adaptations have "dust seeds" weighing less than 0.1 mg which may also be predominantly wind-dispersed, while 3 have seeds of the same size dispersed from a splashcup (see below).



B.

Weight (mg)	> 100	10-100	1.0-10	0.1-1.0	< 0.1	Total
Internal animal	8	11	-	-	-	19
External animal	-	-	9	3	1	13
Splashcup	-	-	-	-	3	3
Wind	-	-	4	9	10	23
No adaptation	-	2	21	27	5	55
Total	8	13	34	39	19	113

Fig. 4-3: Numbers of disseminules examined in various weight classes and with adaptations to dispersal: A - by proportion; B - actual numbers.

The occurrence in 1972 of *Erigeron canadensis*, *E. sumatrensis* and *Sonchus oleraceus* on a landslip at 3670 m in the head of the Pengagl valley showed that wind dispersal can be effective over more than short distances. The species were represented by 2, 1 and about 5 individuals respectively, the nearest known plants of all three species to the site being about 1 km away across a large ridge and about 3 km downvalley. Steenis [1967b] records probable dispersal "jumps" of 100-300 km by *Crassocephalum crepidioides* during its spread through Malesia after its introduction there.

(b) External Animal Dispersal

13 species have been categorized as exhibiting adaptations to dispersal by animals externally. Hooks are present on the fruits of *Acaena*, *Bidens*, *Cynoglossum* and *Uncinia* and on the calyces of *Anotis* and *Myosotis*. Sticky secretions are produced on the caryopses of *Dichrocephala*, *Keysseria* and *Myriactis*, the seeds of *Nasturtium backeri* and the glandular hairs on the calyx of *Triplostegia*. The spikelets of *Microlaena stipoides* frequently become entangled in woollen clothing especially socks, and perhaps also in fur or feather. Many other disseminules are probably occasionally carried externally by animals (for examples see section 4-D), and some morphological features like the bristles on the fruits of *Carpha alpina* and species of *Danthonia* may be of utility in this regard. Disseminules of *Acaena anserifolia*, *Cynoglossum javanicum*, *Microlaena stipoides* and *Triplostegia glandulifera* are drawn in Fig. 4-1.

(c) Internal Animal Dispersal

19 species had fleshy fruits apparently adapted to internal transport of seeds by animals. They are mostly shrubs, mainly Epacridaceae, Ericaceae and Rubiaceae, but also include species of *Astelia* and *Nertera* and the aliens *Fragaria* cf. *vesca* and *Tacsonia mollissima*. In *Gaultheria mundula* the "fruit" can dry out and dehisce if not eaten by a bird: the fleshy pink calyx shrivels allowing the capsule within to open releasing the seeds.

Apart from man (see section 4-D) the animals which eat fleshy fruits most commonly are birds. Of the grassland birds the thrush *Turdus poliocephalus* which is common consumes very many berries, while in forest edge habitats *Paramythia montia* and *Astrapia stephaniae* subsist almost entirely on fruits. The dispersal activities, if any, of small mammals are known.

(d) Splashcup Dispersal

3 species, *Euphrasia mirabilis*, *Gentiana ettingshausenii* and *G. piundensis*, were recognized as having a special splashcup mechanism derived from the fruit wall to facilitate dispersal by raindrops (see Fig. 4-4). The mechanism provides an interesting example of convergent evolution with the bird's nest fungi [Ingold, 1953]. I have shown that the splashcups of *E. mirabilis* and *G. piundensis*, at least, are hygroscopic, only opening during damp conditions. Splashcups placed in sunshine on the research station bench closed but reopened when transferred to a damp filter paper in a Petri dish.

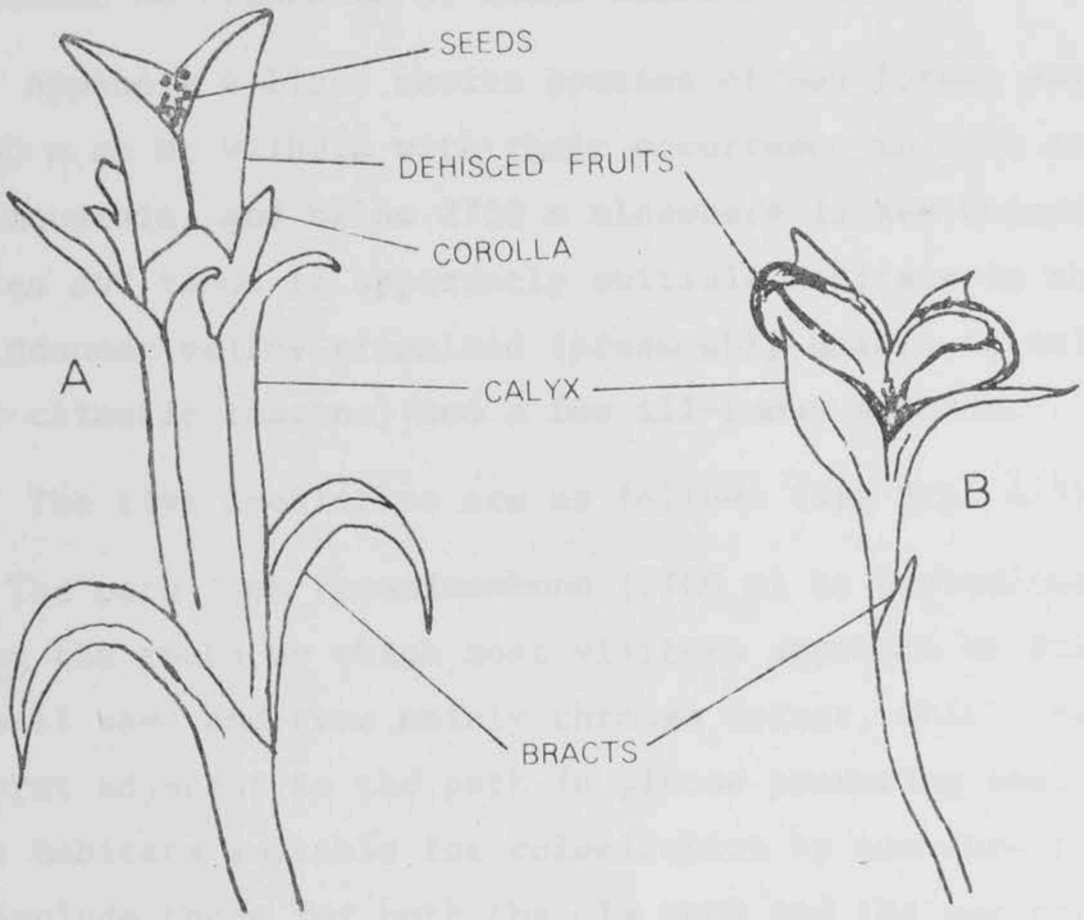


Fig. 4.4: Splashcups of: A - *Gentiana ettingshausenii*;
B - *Euphrasia mirabilis*.

This is the only dispersal mechanism discussed here which cannot by itself be of significance to dispersal over long distances. However in all 3 cases the seeds weigh less than 0.1 mg which suggests that they may be carried by wind following a splashcup "launching" into the air.

(e) Occasional Dispersal

50 of the 113 species examined have disseminules weighing more than 0.1 mg and without apparent dispersal mechanisms. However as pointed out by many authors [e.g. Darwin, 1968; Hedberg, 1971; Ridley, 1930] there are effective means of dispersal requiring no morphological adaptations which may occasionally disperse almost any species, such as typhoons and adherence in mud to birds' feet. The fact that alien species without apparent dispersal mechanisms like *Poa annua*, *Stellaria media* and *Veronica* cf. *persica* have spread widely and rapidly through the New Guinea highlands shows that lack of clearly discernible dispersal mechanisms does not necessarily preclude active dispersal.

4-C DISPERSAL AS EVIDENCED BY LOCAL DISTRIBUTION

Appendix 4 lists native species of non-forest environments above 3200 m on Mt Wilhelm with their occurrence in five other localities near the mountain, and below 2750 m elsewhere in New Guinea. Excluded are species not found in apparently suitable habitats in the lower parts of the Pindaunde valley grassland (presumably unable to colonize the sites for climatic reasons) and a few ill-known orchids.

The five localities are as follows (see Fig. 4-5).

1. The path from Komanimambuno (2700 m) to Kombuglomambuno (3200 m), this being the route by which most visitors approach Mt Wilhelm. The path is well used and runs mainly through forest, which has been cleared and/or burnt adjacent to the path in places producing small and rather transient habitats suitable for colonization by non-forest plants. Records include those for both the old path and the new one, cut early in 1972 along a substantially different line between 2750 and 3080 m, except where the old path forms part of the next category.

2. Pengagl Creek between 2700 and 3140 m. The creek has a rubbly bed and eroding banks of fluvioglacial material up to 10 m high, offering sand and shingle banks and cliffs and slumps of ill-sorted debris for colonization by plants of non-forest environments. From 2700 to 2910 m the creek bed formed part of the old path to the Pindaunde valley, but

above this it is rarely visited by man. Though Pengagl Creek has a long history, the present habitats for light-demanding plants are fairly young, constantly being replaced by slumping, and in no case older than 14 years when a catastrophic flood occurred, following a landslip above 3140 m [Brass, 1964] which remains active.

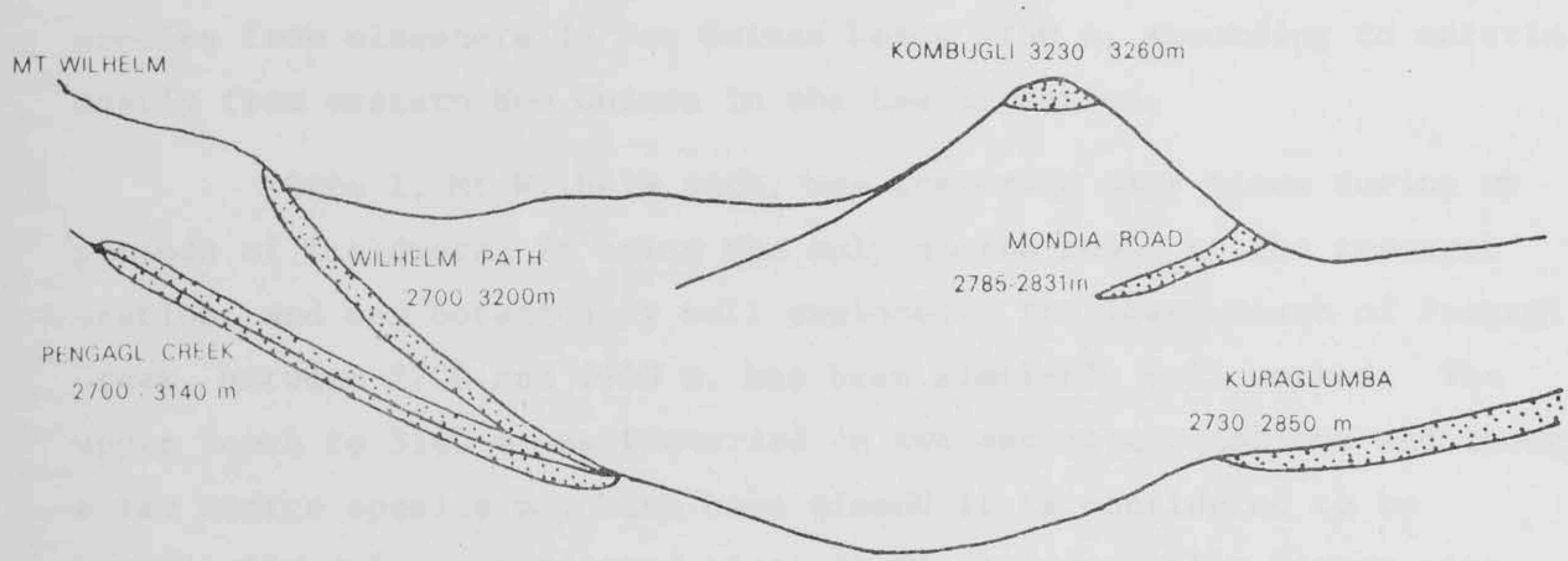


Fig. 4-5: Diagrammatic sketch of the head of the upper Chimbu valley showing positions of sites discussed in section 4-C.

3. Mondia road between 2785 and 2831 m. This earth road, dug since 1960 but scarcely used by vehicles due to recurrent landslips, forms an important pedestrian route between the upper Chimbu valley and Bundi. The records are from the section which runs on the Chimbu side of Iwam Pass between the old sawmill and Mondia village, about 10 km eastsoutheast of Mt Wilhelm summit. Earth banks both *in situ* and of dug material as well as the compacted earth of the road surface are available for colonization by non-forest plants.

4. Kombugli is a hill lying on the Chimbu/Bundi divide between Mt Wilhelm and the Mondia road, about 6 km eastsoutheast of Mt Wilhelm. Formerly a much used track, still used occasionally, ran across the hill's summit. At the top of the hill, between 3230 m and 3260 m, is an area of anthropogenic grassland measuring about 100 × 300 m, subject to a variable extent to both rootling by pigs and burning. Though high in altitude the site is exposed and it is probable that winds make frost an unusual event.

5. Kuraglumba is a grassy intermontane basin between 2730 and 2850 m. The basin has been described in section 3-D. It is subject to considerable disturbance mainly by burning, to which most of the grassland owes its origin. An area of ill-drained alluvium probably supported non-forest vegetation in the centre of the present area of Kuraglumba even before the initial impact of man several centuries ago.

6. In this column of Appendix 4 are recorded any collections of the species from elsewhere in New Guinea below 2750 m, according to material mostly from eastern New Guinea in the Lae herbarium.

Site 1, Mt Wilhelm path, was traversed many times during my periods of fieldwork, it being the only access route to the research station, and was botanically well explored. The lower reach of Pengagl Creek, between 2700 and 2900 m, has been similarly well worked. The upper reach to 3140 m was traversed on two separate occasions and though a few scarce species may have been missed it is considered to be botanically well investigated since it is an essentially linear site. Similarly Mondia road was traversed three times and, being linear, is fairly well explored. I spent one night encamped at Komblugli and as the area of grassland is fairly small I succeeded in covering it quite intensively. However the same cannot be said for Kuraglumba with its very large area although in the course of two visits encompassing three days a large species list was compiled.

Of these sites Mondia road, Kombugli and Kuraglumba represent places surrounded by forest vegetation with no direct contact with other mountain grassland, and the link is tenuous in the cases of the Wilhelm path and Pengagl Creek localities. All are artificially open sites and with the exception of the central miry area of Kuraglumba were forested prior to human disturbance, or in the case of Pengagl Creek, recent geomorphic events.

Occurrence of mountain plants at these sites is therefore suggestive of good dispersal ability since it is unlikely that seed could have been available *in situ*, except for some plants of mires at Kuraglumba. Therefore, after excluding those species which are probably prevented by ecological or climatic rather than dispersal factors from colonizing the sites considered, a rough measure of dispersal ability is possible.

The occurrence of a species below 2750 m elsewhere in New Guinea is regarded as evidence that the species is able to tolerate the climate of the sites being considered. Species not recorded in this column and which are also not found in the other sites are categorized as being contained by a climatic barrier (C). Miry habitats do not occur in the sites being considered (except at Kuraglumba where they are subject to frequent burning) and so species of such habitats are categorized as being excluded by a non-climatic ecological barrier (E). A small group of species is unclassified (U) because of taxonomic uncertainties.

The remaining species, all apparently able to grow at the sites being considered and prevented from doing so only by dispersal barriers, were initially classified into those of good (G), medium (M) and poor (P) dispersal ability according to whether they were recorded in over 3, 1-2, or none of the five sites. Upon inspection two further groups of species were removed from the third of these categories due to rarity (R) in the area including Mt Wilhelm, or due to the belief, based upon observations on Mt Wilhelm, that the species were prevented by a climatic barrier from growing at lower altitude despite the occurrence elsewhere below 2750 m of apparently specifically identical taxa (T).

From this analysis 27 species are ascribed a good, 30 a medium, and 9 a poor dispersal ability (see Appendix 4).

The five sites considered here can be compared floristically by using Colgan's Index of Floral Diversity [Praeger, 1911; Wace and Dickson, 1965] for all pairs of sites, the index being calculated as $\frac{a+b}{a+b+x}$ where a is the number of species found in flora A but not B, b is the number in B but not in A, and x is the number of species common to both floras. The index was calculated for all pairs of sites and for four groupings of species within each site's flora: plants found commonly above 3215 m (62 spp.); alien species (34 spp.); other plants, mostly typical of open sites below 2500 m (47 spp.); and total flora (143 spp.). The indices are tabulated in Fig. 4-6: totally different floras would have an index of diversity of unity and identical floras one of zero.

The most similar floras overall are those of Pengagl Creek and Mondia road, both rather shady and generally unburnt sites, and there are also close similarities between these sites and Wilhelm path and between Mondia road and Kuraglumba. The greatest differences in flora are between Kombugli and both Mondia road and Wilhelm path.

Sites Compared	Species Common Above 3215 m on Mt Wilhelm	Aliens	Other Species	Total Angiosperm Flora
1/2	0.49	0.67	0.50	0.54
1/3	0.59	0.67	0.38	0.55
1/4	0.65	0.85	0.77	0.72
1/5	0.58	0.70	0.56	0.66
2/3	0.47	0.58	0.41	0.49
2/4	0.43	0.90	0.63	0.59
2/5	0.47	0.62	0.65	0.57
3/4	0.67	0.92	0.75	0.76
3/5	0.66	0.48	0.54	0.53
4/5	0.51	0.80	0.84	0.67

Fig. 4-6: Colgan's Index of Floral Diversity, calculated for sections of the floras of five non-forest sites not in direct contact with grasslands above 3215 m on Mt Wilhelm.

Sites:
1. Wilhelm Path 2700-3200 m
2. Pengagl Creek 2700-3140 m
3. Mondia Road 2745-2831 m
4. Kombugli 3230-3260 m
5. Kuraglumba 2730-2850 m.

This pattern of similarities in the total flora is not reflected in all of its component parts. The most striking contrasts concern Pengagl Creek and Kombugli (similar in species occurring commonly above 3215 m but dissimilar in aliens) and Mondia road and Kuraglumba (similar in aliens but dissimilar in species occurring commonly above 3215 m). This may in part reflect a poverty of aliens on Kombugli and a small list of species occurring commonly above 3215 m from Mondia road.

Kuraglumba has a long species list by comparison with the other sites. This is due to its greater area which includes a diversity of habitats not found at the other sites, such as mires, grasslands and forest edge habitats showing very divergent degrees of disturbance by fire, pigs and earth movements.

4-D DISPERSAL BY MAN

In both 1971 and 1972, disseminules were collected from footwear and clothing (especially from socks) of climbers reaching the research station from Keglsugl or lower in the upper Chimbu valley. Attempts were made to germinate seeds, and in addition the number of disseminules of each species were counted from six individual climbers at various dates during 1972. In this way 12 species (identified as disseminules or as large seedlings) were shown to have disseminules dispersed externally by man, those most commonly so being *Acaena anserifolia*, *Bidens pilosa*, *Cynoglossum javanicum*, *Microlaena stipoides* and *Uncinia* spp. (see Fig. 4-7). In addition it is probable that viable seeds of *Fragaria* cf. *vesca* and *Tacsonia mollissima* are carried internally by man: healthy seedlings of *Tacsonia* have been found growing from old pig dung along Pengagl Creek at 2790 m.

	Seeds Germinated		Disseminules Counted (1972)					
	1971	1972	14/4	14/4	4/5	15/5	12/6	3/7
Acaena anserifolia	–	+	29	4	59	56	1	11
Bidens pilosa	–	+	2	–	53	51	–	39
Cynoglossum javanicum	–	+	13	–	10	–	–	11
Deschampsia klossii	+	–	–	–	–	–	–	–
Desmodium sp.	+	–	–	–	–	74	–	–
Microlaena stipoides	–	+	–	–	–	–	–	–
Myosotis australis	–	+	11	2	–	–	–	–
Poa annua	+	–	–	–	–	–	–	–
Ranunculus sp.	–	–	–	–	1	–	–	–
Triplostegia glandulifera	–	–	–	–	1	–	–	–
Uncinia spp.	–	?	–	–	–	15	7	5
Unidentified Gramineae	+	+	–	2	25	10	5	8
Unknown	–	?	–	–	–	12	–	2

Fig. 4-7: Disseminules carried by man on clothing or footwear from the upper Chimbu valley at or below 2515 m to the research station, 3480 m, 1971-72.

An analysis of the distribution of seven species probably commonly man-transported between open sites at 2642-2792 m is shown in Fig. 4-8, together with seven common wind-dispersed species for comparison. Sites are grouped under four geographical heads: the Wilhelm path and Mondia road are both commonly used paths along which man may disperse disseminules. Pengagl Creek is not now often visited by man though up to early 1972 part of it was used as a section of the path to the Pindaunde valley. All the sites from Kuraglumba are landslips or streambanks well away from paths. It can readily be seen that the man-dispersed plants, though generally common along Wilhelm path and Mondia road, are infrequent along Pengagl Creek and absent from the Kuraglumba sites. On the other hand the wind-dispersed species are common in all four areas as would be expected.

4-E DISPERSAL ABILITY AND FLORISTIC ELEMENTS

The numbers of species in each floristic element with disseminules possessing different types of dispersal mechanisms are tabulated in Fig. 4-9. 61% of the floristic elements of putatively oldest residence in New Guinea (G+?G+E) have apparent dispersal mechanisms as do 58% of the total peregrine element and 54% of the alien. Of those species with dispersal mechanisms a higher proportion of the putatively oldest residents (10/14) are animal dispersed than of the peregrines (19/42) or aliens (3/7). This recalls Margalef's [1968] statement that "In initial plant communities in the succession, a major proportion of the diaspores are carried away by wind, but in later stages plants with seeds dispersed by animals are more numerous", and perhaps indicates a better adaptation amongst members of the oldest elements to climax vegetation conditions. However a χ^2 test on the table shows that neither this nor other distinctions between floristic elements are significant at the 5% level.

Turning to dispersal ability as suggested by distribution in discrete, anthropogenic or transient non-forest sites, the occurrences of the categories defined in section 4-C in floristic elements are tabulated in Fig. 4-10. If as I have suggested dispersal ability should be greatest in the most recently immigrant floristic elements, the anticipated result should show a higher proportion of the peregrine element with good dispersal ability than of the other older elements.

	Mt Wilhelm Path (Used Path) 16 Sites	Mondia Road (Used Path) 14 Sites	Pengagl Creek (Streambank, Occasional Path) 27 Sites	Kuraglumba (Streambanks, Landslips Away from Paths) 10 Sites
MAN-DISPERSED				
Acaena anserifolia	4 (25%)	0	0	0
Bidens pilosa	9 (56%)	6 (43%)	3 (11%)	0
Cynoglossum javanicum	6 (38%)	4 (29%)	1 (4%)	0
Fragaria cf. *vesca*	5 (31%)	2 (14%)	2 (7%)	0
Microlaena stipoides	10 (63%)	4 (29%)	3 (11%)	0
Tacsonia mollissima	6 (38%)	3 (21%)	3 (11%)	0
Uncinia ohwiana	2 (13%)	0	0	0
Average	6.0 (38%)	2.7 (19%)	1.7 (6%)	0
WIND-DISPERSED				
Anaphalis lorentzii	3 (19%)	5 (36%)	18 (67%)	2 (20%)
Crassocephalum crepidioides	7 (44%)	9 (64%)	15 (56%)	3 (30%)
Epilobium keysseri	2 (13%)	4 (29%)	19 (70%)	9 (90%)
Epilobium ?prostratum	6 (38%)	6 (43%)	20 (74%)	6 (60%)
Erigeron canadensis	2 (13%)	5 (36%)	18 (67%)	0
Erigeron sumatrensis	10 (63%)	14 (100%)	17 (67%)	6 (60%)
Sonchus oleraceus	7 (44%)	8 (57%)	7 (26%)	2 (20%)
Average	5.3 (33%)	7.3 (52%)	16.3 (60%)	4.0 (40%)

Fig. 4-8: Distribution of some commonly man-dispersed and wind-dispersed species beside and away from paths in the Mt Wilhelm area, 2642-2972 m.

Floristic Element	Adaptation								
	Wind	External Animal	Internal Animal	Splashcup	< 0.1 mg	Wind + Splashcup + < 0.1 mg	Total Animal	No Adaptation	Total
G	–	–	–	–	–	–	–	6	6
?G	–	1	5	–	2	2	6	2	10
E	2	1	3	–	–	2	4	1	7
PW	10	1	4	3	2	15	5	15	35
PN	2	3	2	–	–	2	5	4	11
PS	1	–	1	–	–	1	1	2	4
PWW	2	1	–	–	–	2	1	2	5
PWN	–	–	–	–	–	–	–	4	4
PWS	2	1	–	–	1	3	1	4	8
PNN	–	1	–	–	–	–	–	–	1
PSS	–	3	2	–	–	–	5	4	9
A	4	1	2	–	–	4	3	6	13
Ancient Immigrants	2	2	8	–	2	4	10	9	23
Peregrine element	17	10	9	3	3	23	19	35	73
Aliens	4	1	2	–	–	4	3	6	13
Total	23	13	19	3	5	31	32	50	113

Fig. 4-9: Numbers of species in floristic elements with disseminule adaptations to dispersal.

Within the peregrine element the highest rate of dispersal ability should be amongst those species occurring also outside Malesia and therefore of putatively most recent migration. It can also be argued that species removed from consideration on grounds of ecological or climatic specialization have lost the "weedy" character of pioneer species and have evolved to fit particular ecological niches, and that the proportion of these plants should be highest amongst the oldest elements. Examination of the table in Fig. 4-10 shows all these trends to be present though none clearly. χ^2 testing shows no part of the table to be significant at the 5% level.

Floristic Element	Dispersal Ability Category					
	G	M	P	E,C,R,T	U	Total
G	-	2	1	3	-	6
?G	3	-	2	1	-	6
E	-	1	-	4	1	6
PW	15	9	3	12	1	40
PN	-	6	-	7	2	15
PS	-	2	2	3	1	8
PWW	1	1	-	3	-	5
PWN	2	2	-	2	-	6
PWS	3	4	-	1	-	8
PNN	-	1	-	1	-	2
PSS	3	3	1	1	-	8
Ancient immigrants	3	3	3	8	1	18
Peregrine element	24	28	6	30	4	92
Total	27	31	9	38	5	110

Fig. 4-10: Numbers of species in floristic elements in the dispersal ability categories defined in section 4-C.

Disseminule adaptations to dispersal are positively correlated with low mean of highest and lowest records, and dispersal ability as evidenced by local distribution is positively correlated with both this and with colonist ability. These other ecological characteristics are both positively correlated with floristic elements (see sections 9-A and 9-B). However despite this slight indication, it cannot be firmly concluded that there is any link between apparent dispersal ability and supposed recency of immigration to the New Guinea mountains.

There is therefore little evidence for loss of dispersal ability with time, yet a large proportion of the Mt Wilhelm non-forest flora (like other tropicalpine floras) has no apparent disseminule adaptations and generally poor dispersal ability. It appears likely that dispersal mechanisms and ability operative over short distances do not significantly enhance a plant species' chances of long distance dispersal. Such dispersal must therefore be by agencies for which no mechanisms are required and which perhaps act only occasionally. Possibly responsible in the case of tropicalpine plant immigration are cyclones [Hedberg, 1969; Holloway, 1970] and mud adhering to the feet of migrating birds [Hedberg, 1971], the latter perhaps being particularly efficaceous for plants of aquatic or miry sites.

CHAPTER 5
COLONIST ABILITY

5-A THE SIGNIFICANCE OF COLONIST ABILITY

In order successfully to migrate to an island or to an isolated mountain region plant species must not only display efficient dispersal but also be able to germinate, develop and reproduce in a new and probably different habitat. Such colonization is most commonly in open habitats either natural, like shores [MacArthur and Wilson, 1967] or artificial, like cultivated land [Wace and Dickson, 1965], where mineral soils often occur. This was the case in the Plio-Pleistocene mountains of New Guinea where glacial, fluvioglacial and volcanic deposits provided large areas of open ground (see section 2-D). The ability to grow in open habitats on humic or clastic substrata including parts of the banks and beds of streams, the scars and debris of landslips, and areas of human digging as along roads is here described as colonist ability, and species with this ability are described as adventives.

The ecology of such adventive species is very different from that of species adapted to more precise and stable niches in the environment. Several studies [e.g. Holt, 1972; Miles, 1972; Putwain and others, 1968] have shown that the rate of establishment of particular species in the early stages of succession may be considerably reduced with the progressive development of closed vegetation. The resistance of closed natural vegetation, whose flora is closely adapted to its environment, to invasion by adventive species, in contrast with the susceptibility of open habitats to invasion by the same species, is a simple example of what has been described as vegetation inertia by Pearsall [1959].

The importance of open habitats as "staging posts" [MacArthur and Wilson, 1967] for immigrants is emphasized in the Mt Wilhelm situation by the observation that only one alien species out of many recorded above 3215 m has succeeded in establishing itself in closed vegetation. *Fragaria* cf. *vesca* occurs mainly as a pathside plant but a few individuals are also to be found in tussock grassland (even here perhaps affected by trampling) in the vicinity of the research station. Some striking instances of vegetation inertia are given by Steenis [1972] for Javanese mountains. There the alien *Rumex alpinus* fully fertile and 90 years after its introduction remains restricted to only the few square metres where it was originally planted on Mt Pangrango. Seed of various species scattered in apparently suitable sites failed to establish populations on mountains not naturally occupied by those species, while entire plants of Sumatran *Impatiens* and *Anemone* in clods of soil were successfully transplanted to Tjibodas but have not spread. By contrast plants of good colonist ability can spread between disturbed sites with speed and efficiency, as documented for *Crassocephalum crepidioides* by Steenis [1967b].

MacArthur and Wilson [1967] and Margalef [1959; 1968] have stressed the different selective pressures acting upon species in unstable and stable situations. Adventive species in open habitats are favoured by a rapid and prodigal use of resources to produce many offspring of good dispersal, and rapid population increase. As the population increases and vegetation becomes closed, competition between individuals increases and selection begins to favour those making more efficient use of the resources including mineral nutrients, water and light. In order to survive and maintain themselves in such a situation, species may either produce seeds or fruit which are not dispersed over wide areas and are capable of producing vigorous seedlings, or else reproduce vegetatively *in situ*. In the former case seeds are usually large and as a result relatively few in number. Evolution therefore tends progressively to transform the adventive species into a plant of lesser colonist ability but better adapted to survive in closed vegetation and to occupy a particular niche; the generalist becomes changed to a specialist.

Some species are well adapted to pioneer situations and survive by virtue of efficient dispersal mechanisms enabling them to colonize new open sites as old ones become overgrown by vegetation. For example *Tussilago farfara* L., a primary colonist of moraines in the European Alps [Lüdi, 1945], has been shown by Ogden [1974] to invest a higher proportion of its energy in rhizome production in open situations than under conditions of crowding. Seed production continues unchanged however, so that while rapid vegetative local spread takes place in the earliest stages of succession, dispersal by airborne seeds to other open sites is possible throughout the life of the plant until it is killed through overtopping by larger species. Until the arrival of man in the New Guinea highlands open sites were probably too few and transient, at least at high altitudes, to support obligate pioneer plant species. Immigrant species adapted to pioneer conditions evolved to survive in closed vegetation or became extinct. But there is no evidence from the pollen record for extinction during the past 10,000 yr in the Mt Wilhelm flora [Hope, 1973].

The concept of progressive loss of colonist ability after immigration to an insular situation is perhaps incompatible with the view expressed by Wace and Dickson [1965] that lack of native adventive species is a sign of disharmony of a flora. I consider it probable that in areas where the mature vegetation consists of permanently closed communities, a rich flora of obligate adventives is unlikely to maintain itself indefinitely. The scarcity, smallness and temporary nature of sites of natural disturbance and open vegetation may lead in time to the extinction of an adventive species lacking a population in more stable vegetation, despite the survival for many years of several alien adventive species on Gough Island, undisturbed by man [Wace and Dickson, 1965]. In such areas a rich adventive flora (composed mainly of therophytes) is probably an artefact resulting from human disturbance. As Raunkiaer [1934] has written,

> "... steppes and deserts are comparatively rich in therophytes. This life-form occurs also indeed in many other situations, but especially on cultivated land where there is much open ground. ... Most of the plants which grow as annuals (in Denmark) are not native ... . If the ground were left to itself most of the annuals would succumb in the battle with other life-forms".

It is no coincidence that the vast majority of the world's widespread weeds of tillage appear to be native to areas where agriculture has been widely practised for millennia. Prior to the development of agriculture man favoured adventive species through forest clearance and burning [Smith, 1970]. Yet earlier wide areas of Eurasia were clothed by till and loess which supported many adventive plants later to become weeds [Godwin, 1960] and perhaps provided the environment in which adventiveness first evolved as a feature of these plants. But in the absence of widespread disturbance of habitat by glaciation, vulcanism or man (or where open habitats are maintained by climatic factors), selective pressures are against adventiveness. As MacArthur and Wilson [1967] have shown one of the changes undergone by an organism following colonization of an island is migration from unstable to stable habitats.

In the Mt Wilhelm area sites of natural disturbance (landslips, streambanks) are small and usually transient, closed vegetation developing within a fairly short time depending upon altitude and substratum. By cultivation and the creation of paths and roads, and also by fire, man has very greatly enlarged the areas of open vegetation present at any one time especially below 2500 m. A large proportion of the commonest weeds of New Guinea highland gardens [Walker, 1966] are undoubtedly alien species. At higher altitudes most are native, but none of these is notably common or widespread as an adventive and all also occur in closed vegetation types nearby.

It seems unlikely that a purely adventive species could survive in the small and temporary areas of disturbance existing naturally under present environmental conditions. However a species which could persist, in the temporary absence of open habitats, in more permanent closed vegetation, would more likely survive and evolve further towards being a member of a stable vegetation.

Following these arguments I suggest that plant immigrants to the New Guinea highlands were initially adventives often colonizing sites with largely mineral substrata. These immigrants gradually adapted to conditions of closed vegetation and as part of this evolutionary process lost much of their colonist ability. Hence it is to be anticipated that those species showing best colonist ability today are those of most recent immigration.

Several genera in Mt Wilhelm's non-forest flora include species which are good colonists of open sites as well as more specialized species of closed vegetation. Examples include *Danthonia*, *Gnaphalium*, *Lactuca*, *Nertera*, *Parahebe*, *Ranunculus* and herbaceous *Senecio*, in all of which the generalists have lower altitudinal ranges than the specialists. In several cases (e.g. *Danthonia*, *Gnaphalium*, *Nertera*) the species with colonist ability are found also outside Malesia while the specialist species are endemic to New Guinea, which may suggest that the ancestors of both immigrated separately. In others (e.g. *Parahebe*, *Ranunculus*) all species are endemic to the island and sometimes to rather limited areas, perhaps suggestive of recent evolutionary radiation from a single immigrant ancestral species.

The gondwanic element may not have migrated far, only locally and overland, having been in the north Australia-New Guinea region since the fragmentation of Gondwanaland. Until late Tertiary times the distance between New Guinea and Asia was great, and high mountains did not exist in New Guinea until the Miocene (see section 2-B). However in Plio-Pleistocene times the distance became progressively reduced, high mountains were present, and vulcanicity and glaciation occurred, these factors favouring immigration of cool-tolerant plants from both north and south. During late Quaternary times man's digging and burning activities provided further sites suitable for immigrant adventives, and especially in the past century man has provided a flood of alien species to help exploit these and other open sites.

Some rare species on Mt Wilhelm may be of recent natural immigration. *Brachycome papuana* is known outside the Sarawaket Mts only from the Imbukum valley. It was present there when discovered in 1972 only as a small fertile colony in an anthropogenic forest margin locality, and as two seedlings on the debris resulting from a fairly recent landslip and mudflow. Similarly *Trochocarpa papuana*, widespread in the mountains of eastern New Guinea, is known from Mt Wilhelm only as a single bush found in 1971 on an overgrown landslip site in the Pindaunde valley. The occurrence of these species only in formerly open habitats raises the possibility of recent immigration to these sites. Other rare species like *Lobelia archboldiana*, *Montia fontana* and *Scleranthus singuliflorus* have probably been missed by collectors due to their inconspicuous appearance. It is worth noting here that aliens newly recorded from Mt Wilhelm and New Guinea like *Lolium rigidum*, *Plantago lanceolata* and *Vulpia bromoides* occur, like most introduced species, in disturbed and open habitats.

5-B SUCCESSION AND CLIMAX ON MT WILHELM

(a) Some General Considerations

Selleck [1960] and Whittaker [1953] have reviewed concepts of climax vegetation and shown the confusion prevailing in their definition and use. Whittaker suggests recognition of climax patterns with gradients between different climax vegetation types. Margalef [1968] suggests use of the phrases less mature or more mature ecosystems in preference to nomenclature incorporating the word climax.

Egler [1954] has pointed out that it is the initial floristic composition of bared sites which may determine subsequent succession. Individuals of all successional stages invade abandoned arable land in North America, and the succession is determined by the varying rates of development of different species. The more traditional idea, that each successional stage so modified the habitat as to allow the invasion of individuals of the next stage, is shown experimentally to be false under these circumstances. Tree saplings when removed by herbicidal poisoning do not reappear by fresh invasion, and instead an almost stable vegetation type dominated by herbaceous or shrub species results.

Kellman [1970] has presented results in partial support of Egler from his study of succession on abandoned areas of shifting cultivation at about 1000 m in Mindanao. He shows that secondary regrowth plants of a variety of life-forms become simultaneously established. These, by their different rates of development, undergo successional changes with dominance shifting to progressively larger plants. However it is only within this regrowth that individuals of the final stage (forest dominated by hardwood trees) can establish and develop.

On Mt Wilhelm the type of succession described by Egler may obtain below 3000 m on bared soil. Clearings in forests quickly develop a mixed vegetation cover in which herbs are overtopped by quick-growing small trees and lianes which are in turn choked out by saplings of taller trees. By contrast where burning kills most woody plants, grass-dominated communities with scattered tree-ferns and shrubs result. Other factors beside the killing of woody seedlings are probably operative here, however, including humus content of the soil, degree of shading by adjacent forest and extent of rootling by pigs. My own observations are not precise enough at these lower altitudes to further clarify the matter.

Above 3000 m, except perhaps in small forest clearings protected from severe frost, each stage in the succession is probably dependent upon development of earlier stages. This development is in turn dependent upon two principal factors, protection from frost and accumulation of soil. Frost protection is probably important for the establishment of forest taxa in non-forest communities, especially on gentle slopes liable to nocturnal cold air ponding.

Soil accumulation, often largely in the form of peat, is an essential prerequisite for any vascular plant community on exposed unfractured rock or till. Clearly plants of forest or grassland communities cannot establish themselves on such substrata until an initial population of cryptogams and crevice-living vascular plants has formed and trapped sufficient unconsolidated material to provide for their water and nutrient requirements. Above 3810 m the climax vegetation appears to be a mosaic of tussock grassland with shrubs and *Papuapteris* fernfield. These communities only occur on deep soils. Succession on scree or rock cannot reach this climax stage until soil development beneath a different vegetation type such as short grassland has proceeded for a considerable period of time.

Succession determined by initial floristic composition as described by Egler can only occur when edaphic and microclimatic conditions at the beginning of the succession are suitable for taxa of all stages of that succession, and is therefore restricted to secondary successions. In particular this requires a mature soil and a climate lacking thermal or xeric extremes. Where soil is lacking or inadequate, its development and accumulation by a combination of biotic and geomorphic factors beneath a "subclimax" vegetation is essential for establishment of taxa of the "climax". Where drought or extremes of temperature occur subclimax vegetation may be essential as a protective layer before climax vegetation taxa can invade as seedlings beneath it.

On the other hand it is clear that vigorous subclimax vegetation can also competitively exclude climax vegetation species under some circumstances. An example is provided by Egler's herb- and shrub-dominated fields in which he poisoned the initial crop of tree saplings which did not reinvade. Another example may perhaps be the tussock grass- and shrub-dominated communities resulting from forest burning below 3700 m on Mt Wilhelm. However these subclimax vegetation types cannot be stable over long periods, if for no other reason than that they will be progressively overtaken from the margins of adjacent forest [Gillison, 1970]. It may be significant that in both cases cited above the succession has been interfered with by man to the extent of producing a vegetation type not originally known from the area in question, so that the observations are upon unnatural situations.

(b) Observations Upon Some Sites on Mt Wilhelm

On Mt Wilhelm insufficient study of phytosociology and, more particularly, ecosystem dynamics precludes clear identification of climax vegetation types. At present forest vegetation extends upwards to about 3810 m except under the following conditions:

1. where edaphic conditions do not permit forest growth, usually due either to impeded drainage in basin sites or to shallowness of soil on rocky ridges and elsewhere (gras maunten bipo).

2. where forest has been replaced by grassland due to cutting and, more importantly, burning of vegetation by man (gras maunten manmeri).

The forest becomes simpler both in terms of floristic diversity and physiognomic complexity with increasing altitude. Although Wade and McVean [1969] distinguished two floristic associations above 3590 m, the simplification of the forest seems to be fairly gradual without abrupt floristic, physiognomic or ecological boundaries. Near its upper limits forest appears unable to recolonize areas where it has been destroyed by man, and the present forest limit may reflect formerly warmer climatic conditions and not the present climatic limit of forest climax vegetation (see section 3-E).

At lower altitudes forest is certainly the endpoint of succession, but there are various non-forest associations which are relatively stable and which are here described as subclimax. These include short grass bog on ill-drained peaty soils, anthropogenic grassland under conditions of repeated burning, and the communities occupying the crevices and moss layer of old landslip sites. A general scheme of succession above 3000 m on Mt Wilhelm is presented in Fig. 5-1.

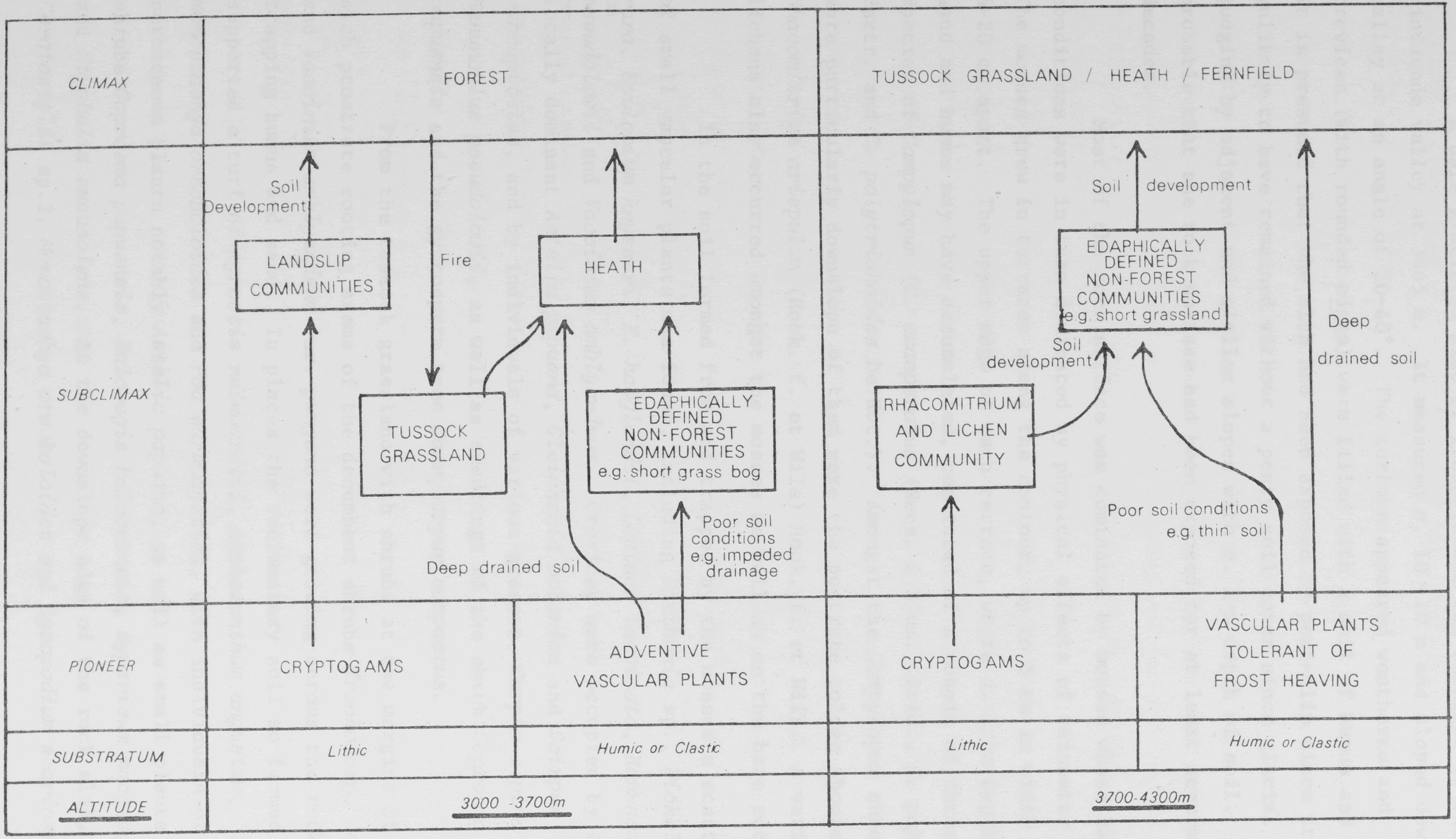


Fig. 5-1: Succession on Mt Wilhelm above 3000 m.

A bare glaciated slab of granodiorite was examined in the Pindaunde valley at 3445 m. It measured *c*. 10 × 10 m and sloped down-valley at an angle of 20-40°. The surface appeared weathered and crevices (with rounded edges) were filled with a soil of humus and sand. It is presumed that the slab had been exposed by peat-slip since it is unlikely to have remained without a peaty soil cover since glacial times, judging by adjacent and similar slopes with *c*. 1 m depth of soil. It is probable that the rock surface had been exposed for at least several decades.

Most of the rock surface was dominated by mosses whose habitat conditions were in turn dominated by physical effects of rainwater runoff. The mosses grew in terraces along the contour, up to 5 cm in width and 5-20 cm apart. The upper edge of each terrace, where *c*. 1 cm depth of sand and humus may have accumulated, consisted of a mosaic of three species of *Campylopus* (*C. exasperatus* (Nees. & Blum.) Brid., *C. papuensis* Partr. and *C. polytrichoides* De Not.). Amongst the *Campylopus* shoots and more particularly downslope of them were the postrate golden shoots of *Rhacomitrium crispulum* (Hook. f. et Wils) Hook. f. et Wils. A variety of lichens also occurred amongst the mosses as well as on the bare rock.

In the soil formed from and trapped by the mosses a scattering of small vascular plants was found, including *Danthonia* sp., *Dichelachne rara*, *Epilobium keysseri*, *E. hooglandii*, *Lactuca laevigata*, *Ranunculus pseudolowii* and *Vaccinium amblyandrum*. Crevices were occupied by the locally dominant *Astelia papuana*, *Gleichenia bolanica* and *Scirpus subcapitatus*, and by individuals of various grasses, *Carpha alpina* and *Ranunculus pseudolowii*, as well as seedlings of the shrub *Coprosma papuensis* and the gymnosperm tree *Dacrycarpus compactus*.

From the tussock grassland with shrubs at the margins of the slab prostrate rooting stems of the decumbent shrubs *Trochocarpa dekockii* and *Vaccinium amblyandrum* var. *pungens* were growing across the rock, trapping humus and sand. In places the rudimentary soil so formed supported a turf of *Agrostis reinwardtii*, *Anthoxanthum angustum*, *Monostachya oreoboloides* and *Poa saruwagetica*, with individuals of other herbaceous plants notably *Astelia papuana*, as well as small plants of the shrubs *Coprosma papuensis*, *Haloragis halconensis*, *Hypericum macgregorii* and *Styphelia suaveolens*. At the downslope edge of the rock slab, *Ceratostylis* sp.2, *Monostachya oreoboloides* and *Lycopodium scariosum* formed locally pure stands. This site, typical of many similar ones, shows the beginning of soil formation and the development of closed vegetation on bare rock.

A similar rock face examined at much higher altitude (4175 m in the head of the Guraguragugl valley), probably bare of vegetation since deglaciation over 8,000 yr ago, supported no vascular plants although moss terraces (of *Rhacomitrium ?crispulum* only) and a variety of lichens were present. At an intermediate altitude (3960 m) west of the upper Pindaunde lake, crevices in slabs sloping west at 45° supported 16 vascular plant species, all angiosperms and including 5 shrubs, though none was abundant.

Later stages in succession on a rocky substratum are shown by a transect of 10 × 10 m squares across landslips on the northeast side of the Pindaunde valley at 3430 m. The slips, which may have been simultaneous, were of till, compacted and infertile but by its roughness more conducive to soil development than rock. Between quadrats C and E the solid rock was exposed, while the depauperate forest in quadrats F and G was perhaps growing on an old soil, only part of which was stripped during the landslip: the forests in and beyond quadrat L may also be secondary but that in A and B appeared quite undisturbed (see Fig. 5-2). It is probably reasonable to assume that the sequence C-D→H-K→F-G→L→A-B represents a seral succession. Measured quadrats 10 m square constituted the transect, arranged linearly along the contour. Each quadrat was laid out and examined in turn, the presence of every vascular plant species within each quadrat being recorded.

Fig. 5-3 shows the species found along the transect, excluding 25 species occurring in only one or two of the 11 quadrats. The majority of excluded species are herbs occurring only outside the forests; 5 species were restricted to one or two forest quadrats including *Trochocarpa papuana* mentioned in section 5-A above; 3 species were restricted to one or two depauperate forest or forest edge quadrats.

The remaining species have been grouped after inspection of the data into 4 categories in Fig. 5-3. Category 1 consists of 18 species found on landslip sites which are not heavily shaded and carry a predominantly herbaceous vegetation, but not found in forested quadrats. All but the rather soft-stemmed *Haloragis halconensis* and the decumbent

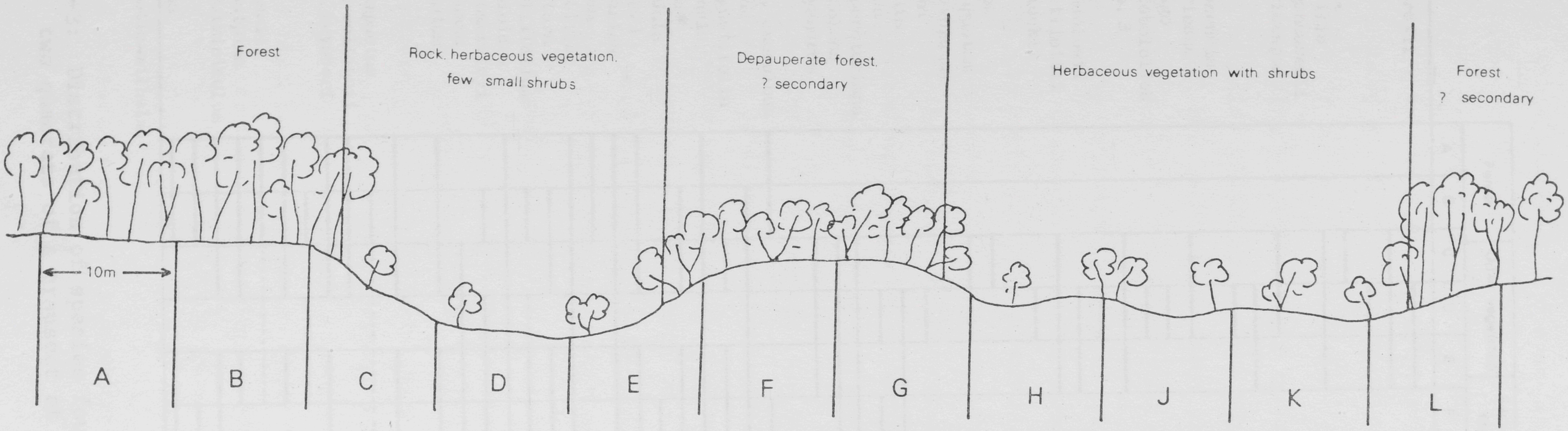


Fig. 5-2: The vegetation of a transect across old landslips in the Pindaunde valley, 3430 m. The transect runs along the contour, this diagrammatic view being from upslope.

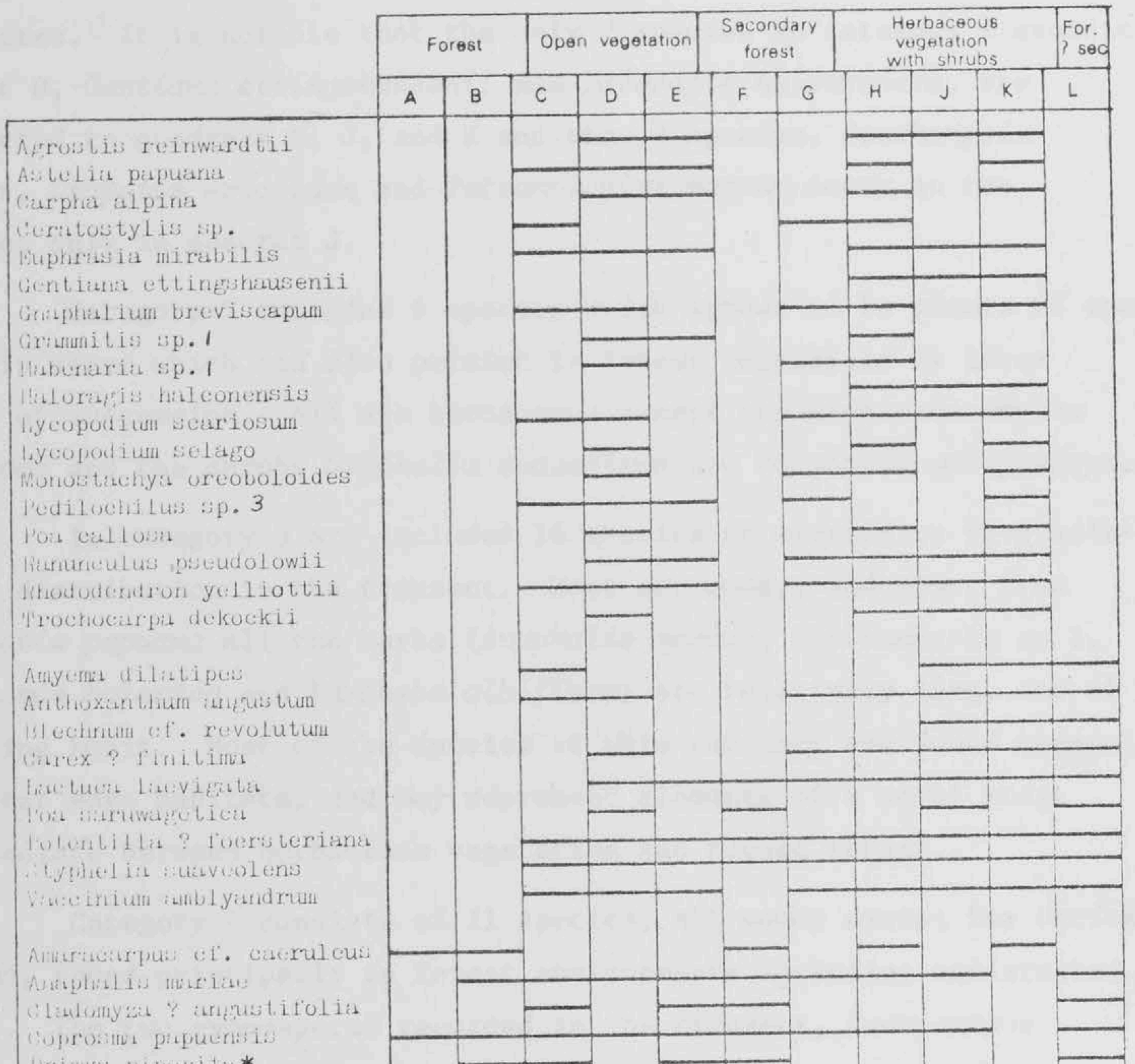


Fig. 5-3: Distribution of species found in more than two quadrats of a transect at 3430 m.

Trochocarpa dekockii are herbs. Many of these species avoid quadrat J which was noted in the field as having a deeper soil than the other landslip sites. It is notable that the only 2 species in category 1 avoiding quadrat D, *Gentiana ettingshausenii* and *Haloragis halconensis*, are restricted to quadrats H, J, and K and that 3 species, *Deschampsia klossii*, *Drapetes ericoides* and *Tetramolopium macrum* occur in the transect only in quadrat J.

Category 2 contains 9 species which appear to be plants of open landslip sites which can also persist in forest vegetation at later stages of succession. All are herbaceous except the mistletoe *Amyema dilatipes* and the shrubs *Styphelia suaveolens* and *Vaccinium amblyandrum*.

In category 3 are included 16 species of erratic or very widespread distribution in the transect. Most are woody, and apart from *Trigonotis papuana* all the herbs (*Anaphalis mariae*, *Giulianettia* sp.1, *Gleichenia bolanica* and *Parahebe albiflora*) are relatively large and of a sprawling habit. Most of the species of this category are found commonly in forest edge habitats, and may represent elements of a seral stage intermediate between herbaceous vegetation and closed forest.

Category 4 consists of 11 species, all woody except for *Uncinia ohwiana*, found principally in forest environments including undisturbed forest. The two gymnosperms recorded in the transect, *Dacrycarpus compactus* and *Podocarpus brassii*, belong here but are notable for their ability to establish themselves as small slow-growing seedlings in unshaded landslip sites with predominantly herbaceous vegetation.

As already mentioned, succession on bare rock surfaces at 4175 m has not proceeded beyond a cryptogram-dominated stage. However on substrata which provide a less inhospitable rooting environment the climax vegetation between 4100 and 4300 m is tussock grassland dominated by *Deschampsia klossii* and including occasional shrubs of *Coprosma divergens*, *Detzneria tubata* and *Styphelia suaveolens* less than 1 m high. Hope [1973] suggests that tundra vegetation above 4300 m may be a stage in seral succession towards tussock grassland. *Deschampsia klossii* will only grow on substrata providing relatively great rooting depth [pers. obs.; and Hnatiuk, in prep.].

Results of a transect of 2 × 2 m quadrats across a partly stabilized and vegetated scree at 4190 m in the Guraguragugl valley are given in Fig. 5-4. The scree, of stones not exceeding *c*. 10 cm in diameter, sloped at *c*. 30° southsoutheast. Tussock grassland grew upon a peaty soil *c*. 20 cm deep on top of parts of the scree. The quadrats were laid out linearly along the contour, all vascular plant species occurring in each being recorded.

Species occurring in the transect have been grouped after inspection of the data into 3 categories. All species are herbaceous except for *Styphelia suaveolens*, which at this altitude rarely grows higher than 50 cm and is often decumbent; *Drapetes ericoides* has rather woody stems but does not grow higher than 25 cm. The largest plant is the tussock grass *Deschampsia klossii*. Category 1 includes 7 species growing only on scree and avoiding tussock grassland, while category 3 includes 11 species of tussock grassland many of which also occur on stabilized scree though not on loose scree. The remaining 7 species, in category 2, are of wide or erratic distribution in the transect.

Between 2900 and 3200 m disturbance of forest during path maintenance and, especially, the unsuccessful erection of a telephone line in 1969 has resulted in rapid regrowth. After initial colonization by mainly herbaceous species (as outlined in section 5-D), seedlings of woody plants became dominant, resulting in a thicket over 2 m high after only 3 years. Species of *Amaracarpus*, *Evodiella*, *Harmsiopanax*, *Macaranga*, *Melicope*, *Olearia*, *Saurauia* and *Schefflera* are prominent in this secondary forest growth, together with the lianes *Jasminum*, *Rubus* and the alien *Tacsonia*.

5-C INFLUENCE OF MAN ON SUCCESSION

Apart from areas of more purposeful disturbance (cultivation, roads and paths, and rootling by domestic pigs below 2500 m) in the Mt Wilhelm area, man's greatest impact upon seral succession is by fire. The anthropogenic origin of many grasslands in the area has been discussed in section 3-E. Succession in gardened areas at 2500 m near Lake Ipea, 200 km west of Mt Wilhelm, has been described by Walker [1966], and the situation in the upper Chimbu valley is similar.

Firing of grasslands is traditional throughout the New Guinea highlands, and despite Administration discouragement continues today. A ban on grass fires on Mt Wilhelm initiated in or before 1959 [Brass, 1964]

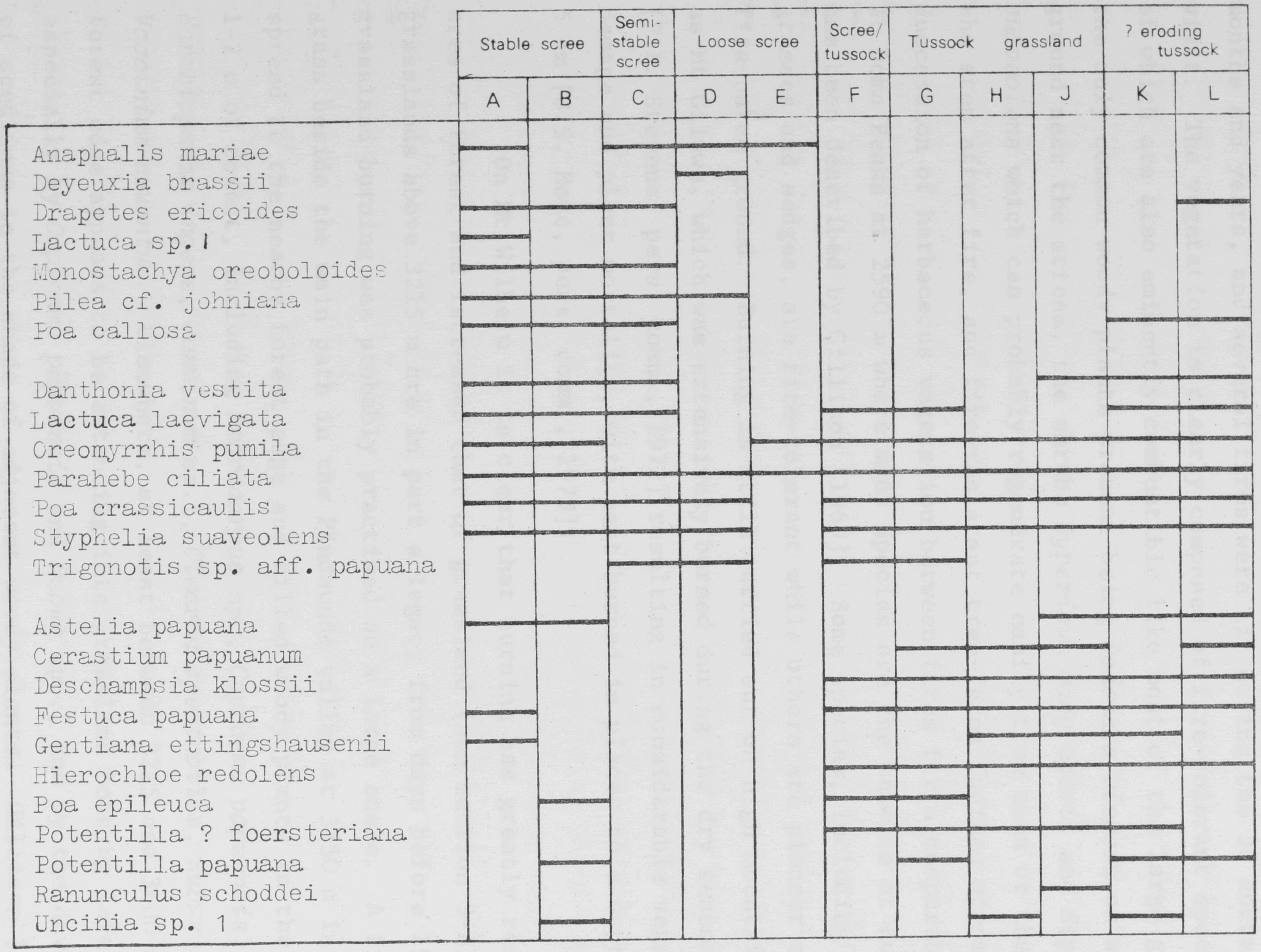


Fig. 5-4: Species found along a transect at 4190 m.

has largely been respected, although lower altitude areas such as Kuraglumba are frequently burned. In August 1972 during an unusually dry period over a quarter of the area of Kuraglumba had been recently burned, most of the remainder showed direct evidence of burning in previous months and years, and several fires were lit during the 36 hours of my visit. The vegetation is clearly composed of fire-tolerant species (many of which are also eminently combustible like most of the large grasses), the only common woody plants present being *Dodonaea viscosa* on wetter ground near the stream, the shrubs *Hypericum macgregorii* and *Styphelia suaveolens* which can probably regenerate easily from seed or the base of the stem after fire, and fire-resistant tree-ferns *Cyathea atrox*. Succession of herbaceous vegetation between fires for a comparable area at Doma Peaks at 2590 m where many species are the same as at Kuraglumba has been described by Gillison [1969]. Some species, including several grasses and sedges, are fire-tolerant while others are pioneer species on fire-bared ground. Burning is still carried out on high mountains such as Mt Giluwe, which was extensively burned during the dry season of 1972 [P.F. Stevens, pers. comm., 1972] resulting in considerable vegetation damage and plant mortality, with peat burned in places to a depth of over 5 cm [G.S. Hope, pers. comm., 1973].

On Mt Wilhelm it is clear that burning has greatly reduced the area of forest and increased that of grassland (see section 3-E). The grasslands above 3215 m are in part a legacy from days before 1959 when grassland burning was probably practised on a large scale. A fire in grass beside the main path in the Pindaunde valley at 3350 m in 1972 spread to the nearby forest edge and killed woody plants in the outer 1-2 m of forest, including *Amaracarpus* sp., *Coprosma papuensis*, *Harmsiopanax ingens*, *Jasminum* sp.1, *Olearia spectabilis*, *Rubus* sp. and *Vaccinium cruentum*. Elsewhere, at least between 3215 and 3600 m, the forest edge appears to be extending into grassland both by layering, especially by *Coprosma papuensis* and *Rubus* spp., and by the development of seedlings in the shade of adjacent woody plants. Gillison [1970] found layering to be important in forest edge extension at Doma Peaks, and it is true that in the cool wet climate of Mt Wilhelm virtually all woody plants are capable of this method of vegetative reproduction.

Between the same altitudes there has been an increase in the number and size of shrubs in grassland in recent years, as shown by comparison of photographs taken before 1960 and the same areas in 1972. A parallel development has taken place in the Snowy Mts alpine areas since the cessation of grazing and firing there [Costin, pers. comm., 1973]. Also present in the grasslands are pioneers of the small trees *Olearia spectabilis* and, less commonly, *Pittosporum pullifolium*. That fire is potent in excluding or at least severely damaging shrubs in grassland is shown by an area measuring *c*. 150 × 50 m at 3550 m in the Guraguragugl valley, burned an estimated 2 years prior to my visit in May 1972. The area was formerly covered by a community dominated by shrubs over 1 m tall, mainly *Coprosma papuensis*, *Dimorphanthera keysseri*, *D. microphylla*, *Gaultheria mundula*, *Olearia spectabilis*, *Styphelia suaveolens* and *Vaccinium amblyandrum* var. *pungens*. About 90% of the shrubs had been killed or were regenerating only from the base, and it was only shrubs and trees higher than 2 m whose top branches were alive. The grasses *Dichelachne rara* and *Poa saruwagetica* were dominant in the new plant community. It is these two species, together with the composites *Anaphalis lorentzii* and *Gnaphalium japonicum*, which are characteristic of sites of past disturbance within grasslands between 3215 and 3600 m. Wade and McVean [1969] consider that grasslands dominated by *Poa saruwagetica* (misnamed *P. nivicola* by these authors) are almost certainly a secondary development throughout their range.

Whether anthropogenic grassland on Mt Wilhelm if left to itself would revert to forest is an open question. The development of increasingly shrub-rich communities is already evident, but tree seedlings are rare outside the forest. However it is possible that trees will be able to grow beneath shrubs though unable to do so in grassland. Wade and McVean [1969] observed tree seedlings outside forest only in communities affording some shade by woody plants. If shrubs provide greater protection against frost and/or less competition for light or nutrients than tussock grasses, tree seedlings may in future develop in areas at present under tussock grass from which they are now absent.

Between *c*. 3600 m and the forest limit at 3810 m the grasslands appear to be stable and the forest stands not to be extending into grasslands. This may indicate a very slow succession to forest which is not yet obvious, or a genuine stability with neither expansion nor extinction of forests. If the latter is true, then it is possible that the forest limit in undisturbed sites like the Imbukum valley is a fossil one, developed during a hypsithermal period [Hope, 1973] and maintained only through development of tree seedlings within the shelter of the forest environment which would again exemplify Pearsall's [1959] concept of vegetation inertia.

5-D ADVENTIVE VASCULAR PLANTS ON MT WILHELM

(a) Situations Available for Colonization by Adventives

In section 5-A colonist ability was defined as the ability to grow in open habitats on humic or clastic substrata, and plants possessing such ability were identified as adventives. In the same section the significance of such ability to migration, and of its persistence in Mt Wilhelm taxa to the possible elucidation of times of migration, were discussed. The position of adventives in seral succession is shown in Fig. 5-1.

Open habitats colonized by adventive species in the Mt Wilhelm area are of several kinds. On Mt Wilhelm itself, above 3500 m, almost the only open habitats are provided by landslips, usually small and resulting from slippage of peat off an ice-smoothed rock-surface lubricated by percolating rain-water. Occasional rock-falls and screes occur on steeper slopes, and old talus slopes probably inactive since a colder climate was operative are common on the flanks of summit ridges. Between 3215 and 3500 m slips of till from valley sides have occurred, and at these altitudes also occur the highest open habitats directly attributable to man in the form of cleared pathsides and various small dug and burned areas. Some landslips in the past have led to mudflows which have flanked gullies with "levees" of unsorted debris.

At lower altitudes the impact of man becomes progressively greater until cultivated land is reached. Though mainly forested, the slopes between 2500 and 3215 m are transversed in places by much used paths and even roads (Mondia) as well as including areas of anthropogenic grassland, foraging by domestic pigs and another disturbance. Here too the streams become large enough to erode steep banks and deposit sand and gravel along their beds.

A variety of habitats is therefore available to adventive plants, providing various combinations of area, substrate, altitude, shade, soil water, and other factors. Substrates vary from bare granodiorite through compacted mineral till and resorted mineral particles to humic soil. All sites examined had an area of *c*. 5-100 sq. m, there being no relationship between area and altitude, and none was heavily shaded. There is no correlation between the adventive flora of a site and its aspect or altitude, although aspect has a significant effect upon the flora of sites with closed non-forest vegetation (see chapter 7). Perhaps the microclimatic effects of aspect are too subtle to influence plants without the additional pressure of competition.

Substratum and, to an even greater extent, altitude appear to be closely related to the rate of colonization and development of closed vegetation, and of which species take part. Above 3500 m, and especially above 3900 m, frost-heaving of the ground and the frequent development of needle ice pose severe problems to plant seedlings. Consequently at these altitudes ability to survive such unfavourable climatic/edaphic conditions is at least as important as ability to colonize open habitats in determining whether a species will occur as an adventive. Billings and Mooney [1968] consider that seedling establishment under such conditions is rare and very slow, several years having to elapse before a seedling is safely established.

Between 3000 and 3500 m frost is still frequent though not so severe, and may exclude many alien and other adventive species common at yet lower altitudes. Here colonization of open habitats is not noticeably interrupted by frost-heaving of the soil, and most of the species taking part are natives occurring in adjacent or nearby stands of closed vegetation. Below 3000 m a greater variety of species participates in colonization of open habitats, a few aliens being prominent, and a closed sward of vegetation develops within a few months where edaphic conditions allow.

(b) Methods of Study

Over 200 open habitats were examined at altitudes ranging from 2642 to 3993 m. In every case areas of about 5-100 sq. m were examined, each being fairly uniform over its entirety, and all species occurring as adventives recorded. These species were each allocated to one of two abundance classes, "common" and "present", subjectively. Also recorded were nature of substratum, altitude and proportion of available ground with plant cover. Sites were subsequently grouped into different altitude, maturity and substratum categories.

Altitude: C - 3500-4000 m
B - 3000-3499 m
A - 2600-2999 m

Ecosystem maturity: III - subclimax, 100% vegetation cover
II - 50-100% vegetation cover
I - pioneer vegetation, < 50% cover

Substratum: S - humic soil
L - loose mineral soil, e.g. river gravel
T - compacted till, etc.
R - rock, plants in crevices or in thin moss or humus layer.

The number of sites examined in each of the resulting categories are:

	A I	A II	A III	B I	B II	B III	C I	C II	C III
S	14	25	0	9	3	0	13	22	0
L	16	4	0	1	10	2	0	3	5
T	1	7	0	0	2	9	1	10	11
R	0	0	0	0	1	11	0	5	17

The numbers of occurrences of all species were tabulated for all site categories. For those site categories including at least five examined sites, figures were made more readily comparable by providing each species present with a measure of frequency of occurrence within the site category:

4 - occurring in 50-100% of sites
3 - occurring in 25-49% of sites
2 - occurring in 12-24% of sites
1 - occurring in fewer than 12% of sites.

Upon inspection it was found that site categories with a rock substratum (R) or subclimax vegetation (ecosystem maturity class III) tended to have a very different flora from other categories, confirming an impression gained in the field. Rocky sites are probably all "old" and in those cases where they were classified in ecosystem maturity class II plant cover was probably low due to lack of suitable rooting substratum. Non-rocky sites in ecosystem maturity class III are all on infertile and usually compacted mineral substrata. Therefore it seems likely that all these sites have the flora they do because of edaphic factors, and do not give any indication of the colonist ability of species present. Accordingly all R and III sites were excluded from later stages of data analysis.

155 species were recorded in at least one of the remaining 141 sites examined. Good colonists were then arbitrarily defined according to both abundance and number of site categories occupied, the two measures giving very similar results. 79 species occurred in three or more of the nine site categories, excluding those on rock (R) or of ecosystem maturity class III and categories with fewer than five recorded sites each. 62 species had sums of frequency of occurrence measures of 6 or more. The combined lists include 80 species of good colonist ability. Of these 21 occurred in 7 or more of the nine site categories, and 22 have sums of frequency of occurrence measures of 15 or more, giving a combined list of 24 species of very good colonist ability (see Appendix 5). Remaining species were regarded as displaying poor colonist ability.

(c) Adventives in Field Situations

Of the 80 species of good colonist ability derived from the data as outlined above, none are gymnosperms and only three are pteridophytes. 11 woody plants are included as well as 4 partly woody species (*Haloragis halconensis*, *Harmsiopanax ingens*, *Rubus papuanus*, *Tacsonia mollissima*). 31 species are both of wide substratum tolerance and of wide or median altitude range. 22 species grow only at lower altitudes, 20 at higher, 19 on loose humic substrata, and none on compacted mineral substrata (see Fig. 5-5). Of the 20 higher altitude species 6 do not occur in the earliest stages of seral succession, before half the available ground space has been covered by vegetation.

The impression gained in the field is that the range of altitude of most species is considerably greater in colonist sites than in closed vegetation. In particular species typical of mountain grassland habitats may grow well below their "normal" altitudes on streambanks and pathsides. Calculation of average species' diversity for sites in each category represented shows that the largest number of species occurs

	Occurring Mainly at Low Altitudes (A,AB)	Wide or Median Altitudinal Range (ABC,B,AC)	Occurring Mainly at High Altitudes (BC,C)
Preferring loose humic substrata (S,SL)	*Bidens pilosa* *Carex neoguineensis* *Coleus scutellarioides* *Cynoglossum javanicum* *Harmsiopanax ingens* *Juncus effusus* *Lobelia angulata* *Microlaena stipoides* *Polygonum nepalense* *Saurauia* sp. *Tacsonia mollissima*	*Anthoxanthum angustum* *Cerastium papuanum* *Gnaphalium japonicum* *Pilea* cf. *johniana* *Pipturus* sp.1 *Schoenus maschalinus* *Scirpus* cf. *subtillissimus*	*Carex ?perciliata* *Danthonia archboldii*
Wide tolerance of substrata (SLT,ST)	*Agrostis avenacea* *Crassocephalum crepidioides* *Dichrocephala bicolor* *Dodonaea viscosa* *Equisetum debile* *Erigeron canadensis* *Gnaphalium involucratum* *Imperata conferta* *Miscanthus floridulus* *Nertera granadensis* *Olearia monticola* *Trigonotis inoblita*	*Acaena anserifolia* *Agrostis reinwardtii* *Anaphalis lorentzii* *Anaphalis mariae* *Brachypodium sylvaticum* *Carex euphlebia* *Coprosma papuensis* *Deschampsia klossii* *Deyeuxia brassii* *Dichelachne rara* *Epilobium ?hooglandii* *Epilobium keysseri* *Erigeron sumatrensis* *Haloragis halconensis* *Hierochloe redolens* *Hydrocotyle sibthorpioides* *Hypericum macgregorii* *Lactuca laevigata* *Libertia pulchella* *Parahebe albiflora* *Poa saruwagetica* *Polygonum runcinatum* *Potentilla papuana* *Ranunculus pseudolowii* *Sagina papuana* *Schoenus curvulus* *Senecio papuanus* *Sonchus oleraceus* *Trigonotis papuana* *Viola arcuata*	*Carex ?celebica* *Carpha alpina* *Coprosma divergens* *Danthonia penicillata* *Epilobium detznerianum* *Gaultheria mundula* *Gleichenia bolanica* *Gnaphalium breviscapum* *Grammitis* sp. *Ischnea elachoglossa* *Monostachya oreoboloides* *Oxalis magellanica* *Pedilochilus* sp.3 *Potentilla ?foersteriana* *Rhododendron yelliottii* *Rubus papuanus* *Styphelia suaveolens* *Vaccinium amblyandrum*
Preferring compacted mineral substrata (LT,L)	Nil	Nil	Nil

Fig. 5-5: Altitudinal and substratum preferences of adventive plant species of good colonist ability on Mt Wilhelm, 2600-4000 m.

at median altitudes (3000-3499 m), perhaps demonstrating an overlap between the ranges of species typical of mountain grasslands and of the cultivated zone (see section 8-C). Species diversity appears to be proportional to ecosystem maturity of site (assessed by plant cover) for all substrata and altitudes (see Fig. 5-6).

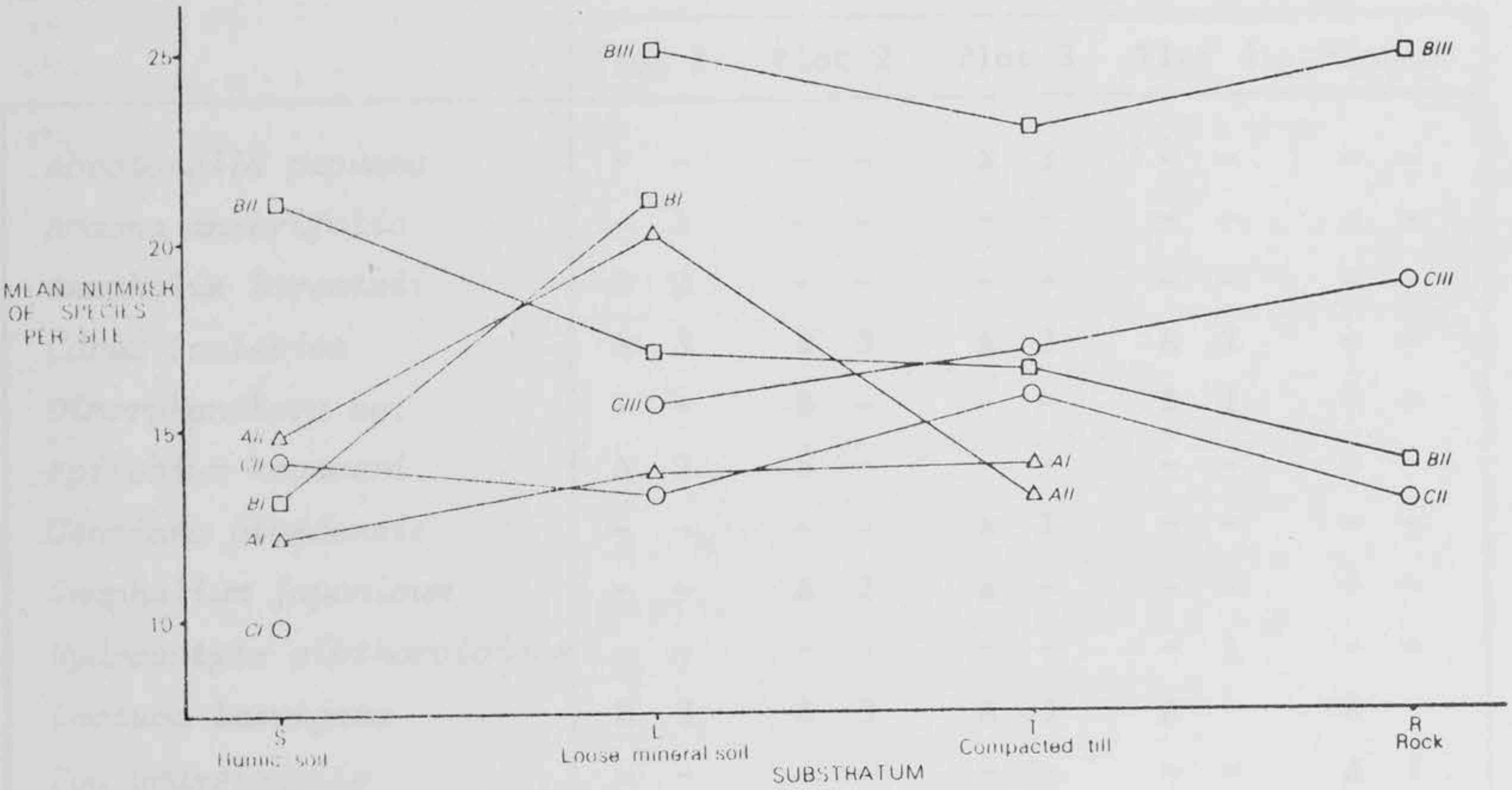


Fig. 5-6: Mean numbers of species found at sites within different site categories.

(d) Recolonization of Dug Plots

5 plots measuring 2 × 2 m were dug in 1971 and examined for plant colonists in 1972. At each site the top soil (upper 20-30 cm of soil) and vegetation were removed and later buried in the same plot beneath the deeper soil (a further 30 cm depth being dug and collected on a tarpaulin for this purpose). Prior to this operation the flora of the plot was recorded together with species in immediately adjacent areas. It is unlikely that living seeds were present in the soil constituting the surface 30 cm immediately after preparation of the plots, as accumulation of the peaty soil is slow and mixing by earthworms or other animals negligible.

Several seedlings were identified in 1972 from all sites except the highest, at 4023 m, which only supported a single small plant of *Poa crassicaulis*. The surface soil of this plot was loose and fine-grained and clearly subject to frequent development of needle ice, which is the probable reason for the paucity of colonists. Full results of the experiment are shown in Fig. 5-7. *Carex ?celebica*, *Lactuca laevigata*,

Fig. 5-7: Recolonization of dug plots, Pindaunde valley.

	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Abrotanella papuana	- -	- -	A 3	- -	- -
Acaena anserifolia	- 1	- -	- -	- -	- -
Anaphalis lorentzii	B 2	- -	- -	- -	- -
Carex ?celebica	A 3	B 3	A 3	A 2	- -
Dimorphanthera sp.	- -	B -	- -	B 1	- -
Epilobium keysseri	A 2	B -	- -	- -	- -
Gentiana piundensis	- -	- -	A 1	- -	- -
Gnaphalium japonicum	- -	A 2	A -	- -	- -
Hydrocotyle sibthorpioides	- -	- -	- -	- 1	- -
Lactuca laevigata	B 3	A 3	A 3	A -	A -
Poa crassicaulis	- -	- -	- -	- -	A 1
Poa saruwagetica	A 3	A 3	- ?	A 3	- -
Potentilla ?foersteriana	B -	A 1	- 1	A -	A -
Potentilla papuana	A -	A 2	A -	A -	B -
Ranunculus pseudolowii	A 3	A -	A 3	A 1	- -
Viola arcuata	- 1	- 3	- -	- -	- -

Key: A - present on plot before digging
B - adjacent to plot
1 - 1 colonist individual
2 - 2-5 colonist individuals
3 - more than 5 colonist individuals.

Plot details:
1. Trampled ground, Kombuglomambuno, 3215 m, dug 14/10/71, examined 4/9/72.
2. Tussock grassland with tree-ferns, Kombuglomambuno, 3215 m, dug 14/10/71, examined 4/9/72.
3. Short grass bog, near lower Pindaunde lake, 3475 m, dug 4/8/71, examined 4/9/72.
4. Tussock grassland, near lower Pindaunde lake, 3485 m, dug 20/8/71, examined 4/9/72.
5. Tussock grassland, Pindaunde valley, 4025 m, dug 15/10/71, examined 2/9/72.

Poa saruwagetica, *Ranunculus pseudolowii*, *Schoenus maschalinus* and *Viola arcuata* appear to be the most efficient of the 15 colonist species recorded under these conditions. *Hydrocotyle sibthorpioides*, *Potentilla ?foersteriana*, *Schoenus maschalinus* and *Viola arcuata* are notable for their ability to colonize one or more of the sites without being present in the former or adjacent vegetation.

Some Mt Wilhelm species under cultivation in Canberra showed good colonist ability by growing widely as seedlings in pots other than those of the parent plants, by contrast with the scarcity or absence of seedlings of other species which also produced viable seed. The species showing these contrasting modes of behaviour are tabulated below.

	Good Colonists	Poor Colonists
Native species	*Cerastium papuanum* *Dichrocephala bicolor* *Myriactis cabrerae* *Nasturtium backeri* *Senecio glomeratus* *Viola arcuata*	*Carex celebica* *Cynoglossum javanicum* *Danthonia penicillata* *Myosotis australis* *Oreomyrrhis papuana* *Ranunculus pseudolowii* *Scirpus* cf. *subtillissimus* *Senecio papuanus* *Triplostegia glandulifera*
Alien species	*Bidens pilosa* *Poa annua* *Stellaria media*	*Fragaria* cf. *vesca*

After serious burning of Mt Giluwe grasslands in 1972 most shrubs and tussock grasses were killed although individuals of *Trochocarpa dekockii* and *Danthonia archboldii* survived where other species were exterminated. Commonest colonists of the bared surfaces in 1973 were the native adventives *Agrostis reinwardtii*, *Deyeuxia brassii*, *Dichelachne rara*, *Lactuca laevigata*, *Senecio glomeratus* and *Swertia papuana* Diels, with the sedge *Cladium glomeratum* R.Br. on ill-drained ground [G.S. Hope, pers. comm., 1973].

5-E COLONIST ABILITY AND FLORISTIC ELEMENTS

The numbers of species in each floristic element (defined in section 3-G) with poor, good and very good colonist ability (as defined in section 5-D(b)) are shown in Fig. 5-8. As discussed in section 5-A, it might be expected that taxa of most recent immigration would show best colonist ability. This would mean that aliens would be better colonists than the peregrine element, which would be better than gondwanics and endemics; within the peregrine element those species occurring outside Malesia would show better colonist ability than Malesian endemic species.

Floristic Element	Poor Colonist Ability	Good and Very Good Colonist Ability	Very Good Colonist Ability	Total Element
G	8	1	1	9
?G	6	4	3	10
E	8	3	0	11
PW	28	30	13	58
PN	15	7	1	22
PS	9	2	0	11
PWW	5	6	1	11
PWN	4	3	0	7
PWS	4	8	1	12
PNN	1	0	0	1
PSS	4	7	1	11
A	9	6	3	15
Ancient immigrants	22	8	4	30
Peregrine element	70	63	17	133
Native flora	92	71	21	163
Total	101	77	24	178

Fig. 5-8: Numbers of species in each floristic element with different degrees of colonist ability.

Aliens do not show a significantly different colonist ability from native species. This may in part be due to the fact that the definition of the number of alien species included in the non-forest flora is somewhat arbitrary, especially considering that some are of very recent arrival in the area and have not spread to the limits of their ecological potential.

Amongst the native species the total peregrine element has a higher proportion of good colonists than the notionally more ancient immigrants (G+?G+E), significant at the 5% level ($\chi^2 = 4.1$, $n = 1$). The level of significance is yet greater if those gondwanics suspected of being of less ancient immigration (?G, see section 3-G) are excluded since these include 4 of the 8 good colonists in the composite ancient element, but only 6 of the 22 poor colonists. There are no significant variations within the peregrine element.

CHAPTER 6

GROWTH RATE AND PHENOLOGY

6-A THE SIGNIFICANCE OF GROWTH RATES

Although rapid growth rate and high yield have been widely assumed to be of competitive advantage to plants growing under any conditions, Bradshaw and others [1964] have suggested that on soils of low fertility the reverse is the case. These authors have said that species of low yield are at a selective advantage under conditions of low soil nutrient levels since they do not outstrip the nutrient supply and can metabolize normally at even very low nutrient levels. Fast-growing plants have higher nutrient requirements than slow-growing ones, and will be more adversely affected by a small supply of nutrients. Such supply, from rock weathering and decomposition of plant and animal bodies and excretion materials, is likely to be continuous even if it is small and perhaps fluctuating, so that slow-growing plants will be able to satisfy their minimal requirements while fast-growing ones perish from nutrient deficiency.

This argument has been widened by Parsons [1968] who has considered growth rates under limiting conditions of temperature and aridity as well as of soil fertility. Parsons concludes that evolutionary selection of plants with slow growth rates is common under severely limiting levels of any environmental factor, and that slow growth rates represent a simple and frequent adaptation by plants to such conditions.

In the Mt Wilhelm environment, especially at higher altitudes and outside the forests, cold and soil fertility are probably especially limiting to plant growth. A correlation between plant species distributions and maximum temperatures is shown in chapter 7, and the damaging effects of frost mentioned in section 6-G. Soil fertility has been examined by Wade and McVean [1969] who report 30 soil analyses and state

> "The general level of soil fertility is low ... The local plant species would appear to be well adapted to the low level of soil fertility and the scarcity of calcium and phosphorus. Top dressings of calcium hydrogen phosphate were applied to a number of plots of short grass bog ... without producing any change in colour or increase in growth rate."

Many native species respond to increase in soil nutrient status in the long term, as shown by luxuriant specimens of *Keysseria radicans*, *Potentilla papuana*, *Senecio glomeratus*, *Viola arcuata* and other species in a small cultivated and fertilized plot beside the research station.

It may therefore be expected that plants growing on Mt Wilhelm with slow growth rates would be at a selective advantage over otherwise similar plants with more rapid growth rates, especially at times of unusual stress such as during prolonged rainless spells or periods of extreme temperatures or nutrient insufficiency. This may not have been so, at least to the same degree, in the environments whence many species of Mt Wilhelm's non-forest flora migrated in Plio-Pleistocene times. Furthermore some of the most efficient colonizing species today, the cosmopolitan weeds of agriculture, may be fast-growing plants, but may become more closely adapted to a particular environment when lingering in an area [Baker, 1972].

I suggest therefore that most of the successful immigrants to Mt Wilhelm and to the New Guinea highlands were initially fast-growing plants, but that with time a progressive adaptation to the environment took place including the evolution of slower growth rates. I would expect plants of putatively most ancient status in the area to show as a group the slowest growth rates and aliens of recent immigration the fastest.

In an attempt to test this, growth rates of a variety of plants were measured at altitudes from 3390 to 4410 m. Organs were periodically measured and marked, and samples taken for dry weight determination. Some difficulty was experienced under field conditions in the measurement of stem dimensions and to a lesser extent the number and size of flowers and fruits. In addition to these problems damage to and mortality of plants under observation occurred, for both natural and human reasons: in particular most of the conspicuously marked twigs of observed shrubs were removed by unknown persons, and several herbs were killed or injured during the very dry year of 1972 by drought or frost. As a result of these difficulties only the computed growth rates of short-stemmed herbs are regarded as being at all precise, and discussion is limited to these, a total of 23 species.

6-B GROWTH RATES OF SHORT-STEMMED HERBS ON MT WILHELM

Plants of various species and at various localities were examined periodically, the sizes and number of aerial parts being recorded and leaves marked by pinprick. It was possible by this procedure to trace the development, longevity and mortality of each aerial organ of a range of plants for up to 397 days. At the end of the observation period the observed plants were collected, similar plants of the same species being collected at the same localities wherever observed individuals had died. By measurement of dimensions and of dry weight of this collected material, the dry weights of the plants at the times of observation in the field were estimated.

Growth rate data are given for short-stemmed herbaceous plants in Appendix 6, and the means of various groupings of species in Fig. 6-2. Fig. 6-1 provides some details of the plots in which growth measurements were made, whose numbers are quoted in Appendix 6. Species means were

Plot	Altitude (m)	Habitat
1	3490	Shallow wet soil on old landslip
2	3470	Short grass bog
3	3470	Wet tussock grassland
4	3480	Heath and short grassland
5	3490	Short grass bog
6	3480	Tussock grassland
7	3390	Tussock grassland
8	3480	Dry tussock grassland
9	3480	Tussock grassland subject to disturbance
11	4000	Tussock grassland
12	4030	Short grassland
13	4030	Wet short grassland
14	4400	Tundra
15	4410	Shaded tundra

Fig. 6-1: Habitat details of growth measurement plots.

calculated as $\frac{\Sigma(g\cdot d)}{\Sigma d}$ where g is the growth rate of each individual plant measured and d is the number of days of observation. All growth rates are expressed as per cent daily increment of dry weight of aerial parts.

Total (23)	0.60
Dicotyledons (19)	0.63
Monocotyledons (4)	0.41
Ancient immigrants (7)	0.50
Peregrine element (14)	0.63
Ancient immigrants, dicotyledons only (5)	0.61
Peregrine element, dicotyledons only (12)	0.65
Aliens, both dicotyledons (2)	0.67
Species measured only above 3950 m (4)	0.61
Species measured above 3950 m and below 3500 m (7)	0.56
Species measured only below 3500 m (12)	0.61

Fig. 6-2: Mean growth rates of various groupings of species.

Individual growth rates vary from 0.10% to 1.74% and species mean growth rates from 0.20% to 0.93%. The mean growth rate of all 23 species measured is 0.60%. With the exception of *Poa crassicaulis* the monocotyledons examined (*Astelia papuana*, *Carpha alpina*, *Pedilochilus* sp.3) grow more slowly than the dicotyledons.

There is no consistent trend of growth rate variation either with altitude or with size of plant. Species at high altitude grow as a group neither more nor less quickly than those at low altitude. Of those species measured both above 3950 m and below 3500 m, *Ischnea elachoglossa* and *Trachymene tripartita* may grow faster at higher than at lower altitudes, and *Potentilla ?foersteriana* and *Potentilla papuana* may show the opposite trend (see Fig. 6-3). The three species of *Ranunculus*, each growing over a different altitudinal range from the others have almost identical growth rates. In *Fragaria* cf. *vesca* and *Oreomyrrhis papuana* large plants appear to have faster growth rates than small ones, while the opposite may be true of *Ranunculus pseudolowii* and *Trachymene tripartita*. In a larger number of species (*Astelia papuana*, *Keysseria* *radicans*, *Lactuca laevigata*, *Oreomyrrhis linearis*, *Poa crassicaulis*, *Potentilla ?foersteriana*, *Potentilla papuana*, *Viola arcuata*) large and small plants show similar growth rates.

Species	Plants Measured Below 3500 m	Plants Measured Above 3950 m
Astelia papuana	0.29	0.25
Ischnea keysseri	0.53	0.83
Keysseria radicans	0.42	0.46
Poa crassicaulis	0.83	0.80
Potentilla ?foersteriana	0.65	0.57
Potentilla papuana	0.70	0.60
Trachymene tripartita	0.43	0.59

Fig. 6-3: Growth rates of plants of seven species growing both below 3500 m and above 3950 m.

When the growth rates are examined by floristic element it is found that those species of presumed longest residence in the New Guinea highlands (G, ?G and E; 7 spp.) give a mean growth rate of 0.50%; the total peregrine element (P; 14 spp.) one of 0.63%; and the two alien species a mean of 0.67%. If only dicotyledons are considered the figures are 0.61%, 0.65% and 0.67% respectively. While not markedly different the growth rates do nevertheless vary in accordance with the hypothesis that the taxa of longest residence in the region have as a group the slowest growth rates, and the aliens of recent introduction the fastest.

In order to test the significance of the figures they were grouped into growth rates faster and slower respectively than 0.60%, and by element into ancient (G+?G+E) and modern (P+A). A χ^2 test on the resulting table shows the variation to be significant at the 10% level ($\chi^2 = 2.9$, $n = 1$).

6-C THE SIGNIFICANCE OF SEASONALITY

Schodde [1973] has recognized three main geographic categories in the New Guinea flora, separated from each other altitudinally. From sea-level up to 1200-1500 m is dominated by mixed forest taxa of Malesian affinity and origin, including for example oaks and dipterocarps. Above this and up to the forest limit the forests tend to be dominated by taxa of gondwanic origin including podocarps and *Nothofagus*. Finally mountains rising above the forests are clothed by a mainly herbaceous vegetation consisting of plants of varied temperate affinity, described as itinerant by Schodde and equivalent to the peregrine plants of Steenis [1972].

Of these three broad categories only the last, with which I am concerned here, has probably resulted from relatively recent and abrupt migration from a seasonal into a largely non-seasonal environment. The gondwanic element has probably moved more or less *in situ* as Australia with New Guinea drifted slowly northwards during the Tertiary, providing in all likelihood a very gradual transition from temperate to tropical conditions. Plio-Pleistocene migration of the Malesian element was across lines of longitude rather than latitude, so that no temperate zone seasonality was involved.

Holttum [1940] has pointed out how great a barrier a non-seasonal environment can be to the spread and migration of plant species adapted to a seasonal one, and has given several examples (mostly trees) of plants from seasonal regions failing to grow or at least to flower in Singapore. Steenis [1972] has mentioned the specimen of *Fagus sylvatica* L. on Mt Pangrango in Java, whose periodicity in producing new leaf was in complete disorder and which remained a stunted shrub after many decades. Similarly most European fruit trees failed to flower in Java, and this has generally been attributed to the tropical daylength regime. However Steenis also mentions apple, pear, plum and peach trees fruiting successfully in Timor where daylength is uniform but where the year is divided into marked wet and dry seasons; and apples being induced to flower and fruit in Java by artificial defoliation of part of the tree.

Therefore it appears that at least for many north temperate trees a requirement for successful establishment is an annual alternation of seasons favourable and unfavourable for growth, regardless of daylength. Clearly the same is not true for many herbaceous species of temperate zone regions which have very successfully established themselves as aliens in tropical mountain regions, their number including species regarded in their lands of origin as perennial or biennial as well as annual. Perhaps the problems associated with a well developed perennating mechanism are greater in the case of trees migrating (or transplanted) to the tropics than for herbaceous plants.

Went [1964], from experimental as well as observational data on the plants of Charleston Peak in Nevada, has defined two classes of mountain plants according to their differing temperature requirements. The first, exemplified by species of *Pinus* and *Yucca*, requires a long cold resting season but can tolerate high temperatures during the growing season. The second class, exemplified by species of *Aquilegia* and *Physaria*, requires a cool growing season. Only plants in the latter class will be able to establish themselves without modification on tropical mountains which lack thermal seasons. The examples quoted for this group are all herbs whereas the two plants given as examples of the other season-demanding class are both woody. It is easy to equate the class of plants requiring low growing season temperatures with microtherm plants of Malesian mountains discussed by Steenis [1962a; 1972].

Most of the plants whose photoperiod requirements for flower initiation have been examined are herbaceous. There is considerable variation of response to daylength both between species and in some cases within species (e.g. *Fragaria chiloensis*, *Nicotiana tabacum*), often modified by temperature [Salisbury, 1963]. Nevertheless it appears that most plants investigated have requirements which would be satisfied by a daylength varying little from twelve hours throughout the year, such a figure exceeding the minimum requirements of most long-day plants and being less than the maximum of most short-day plants. At 29° latitude the longest and shortest days of the year do not deviate from twelve hours by more than two hours [List, 1968] (see Fig. 6-4). Such latitudes include parts of the Himalayas and West China mountain regions and of the mountains of New England (eastern Australia), both of which probably supported alpine vegetation during the glacial maximum and could have acted as source areas of plants migrating to New Guinea.

Although the number of introduced plants, if any, which have failed to establish themselves in New Guinea for photoperiod reasons can never be known, the great majority of aliens there today flowers almost continuously. The only exception to my knowledge is *Mentha* sp. (garden mint) a not uncommon garden escape in the New Guinea highlands and growing beside the Mt Wilhelm field station, which only reproduces in New Guinea vegetatively and never flowers. *Mentha piperita* is listed by

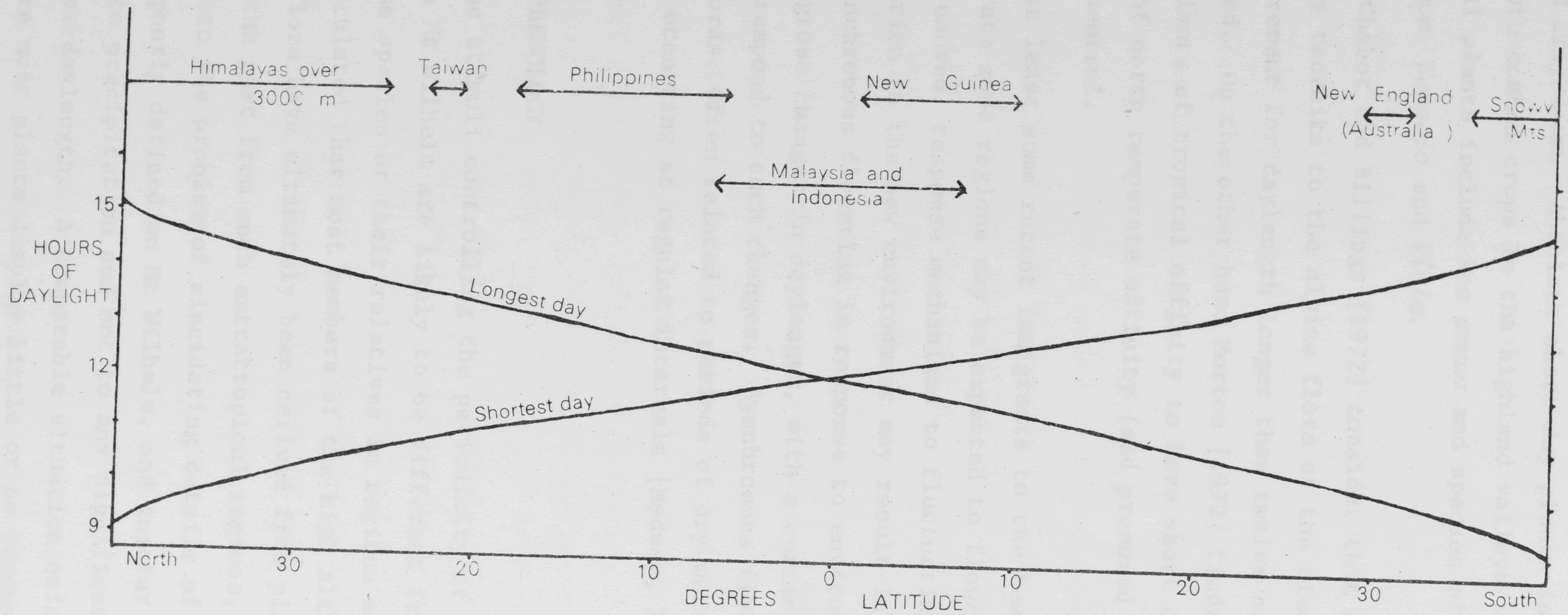


Fig. 6-4: The relationship between latitude and daylength in the Malesian region.

Salisbury [1963] as being an absolute long-day plant. Another absolute long-day plant is *Phalaris arundinacea* which has been collected in flower near the lower Pindaunde lake, as are species of *Agrostis*, *Festuca*, *Lolium* and *Trifolium*. Absolute short-day plants include sweet potato and coffee, both common crops in the highland valleys surrounding Mt Wilhelm. Day neutral plants include *Poa annua* and species of *Cardamine*, *Fuchsia*, *Rhododendron*, *Senecio* and *Viola*.

Chabot and Billings [1972] consider that one of the adaptations acquired by recruits to the alpine flora of the Sierra Nevada, California, is a requirement for daylength longer than twelve hours for flowering to be initiated. On the other hand Morton [1972] finds West African mountain plants of tropical affinity to have short daylength requirements, but those of north temperate affinity (and presumed origin) to be daylength-neutral.

At least some recent immigrants to the New Guinea mountains from temperate zone regions may be expected to flower continuously while retaining, unused, response mechanisms to fluctuating daylength. With time adaptation to the new environment may result in the evolution of periodic synchronous flowering in response to environmental factors other than gross changes in daylength, with a corresponding loss of ability to respond to such changes. Synchronous flowering is frequent in tropical floras, often related to periods of dry weather and not necessarily occurring at regular intervals [Medway, 1972; Steenis, 1972; Yong, 1971].

6-D FIELD PHENOLOGY

The stimuli controlling the periodicity of growth and flowering of plants on Mt Wilhelm are likely to be different from those operative upon the same species or their relatives in regions at higher latitudes. As it is postulated that most members of the high altitude non-forest angiosperm flora have ultimately been derived from plants which have migrated in the past from such extratropical regions, their phenology is of relevance to the problem of elucidating details of these migrations. Seasons are poorly defined on Mt Wilhelm, and insofar as they do exist are related to precipitation and not to any significant extent to either temperature or daylength. A comparable situation exists on Mt Kinabalu (Borneo) where most plants display little or no seasonal behaviour, exceptions being *Diplycosia kinabaluensis*, *Habenaria* (*Platanthera*) *kinabaluensis* and *Ilex revoluta* [Smith, 1972]. On Mt Pangrango (Java), where a dry season is more pronounced, only four of seventeen species listed by Steenis [1972] flower continuously, eight flowering mainly during the dry season and five during the wet. Synchronous flowering is likely to be of selective advantage in the tropicalpine environment since cross-pollination is not an easy matter there. Insect pollinators are few and often inactive, while the frequency of mist and rain may militate against effective pollination by wind.

Almost all alien species present on Mt Wilhelm flower and grow continuously, suggesting that these recent immigrants have not developed mechanisms sufficiently subtle to control phenology under the prevailing meteorological conditions. At least one native species, *Styphelia suaveolens* (occurring also in Australia and Borneo), shows periodic flowering and growth on Mt Wilhelm but with different and often adjacent individuals out of phase with each other. But many other species do show to some extent synchronous phenology and periodic observations were made to gain some idea of the extent of this.

In three different areas on Mt Wilhelm species present were examined to discover the occurrence of new vegetative growth and reproductive structures. These observations were made on several occasions between May and September 1972 near the research station (3480 m), near Ridge Camp (4020 m) and near Saddle Camp (4350 m). Although my observations only extended over half a year I believe that the conclusions resulting from them may be tentatively extended to cover the entire annual cycle. Dated herbarium material shows that there is no period during the year including the wet season when many species do not flower. Daylength during the wet season when I was absent is similar to that during the dry while climatic extremes are less severe, so that any tendency toward seasonality is less likely to manifest itself at that time than during the period of my observations.

Analysis of the assembled data showed that 60 species exhibited negligible seasonality in growth or reproduction (seven of them being aliens), while 52 species (all native) displayed synchronous seasonal behaviour to some extent. These latter were allocated to four categories, listed below. Nine species were clearly seasonal in both vegetative and reproductive development: 16 showed a clear "burst" of flowering during one period but individuals could be found in flower at other times: eight stopped flowering almost completely after unusually dry weather in 1972 but appeared to flower continuously under more normal weather conditions: and 19 species gave some slight indication of periodic rather than continuous flowering.

1. Species with almost entirely synchronous periodic flowering.

Danthonia vestita
Dimorphanthera keysseri
Habenaria sp.1
Monostachya oreoboloides
Myriactis cabrerae
Parahebe ciliata
Pittosporum pullifolium
Senecio sp.2
Vaccinium cruentum

2. Species with mainly synchronous and periodic flowering but with some individuals in flower at other times.

Acaena anserifolia
Carpha alpina
Dimorphanthera leucostoma
Dimorphanthera microphylla
Gaultheria mundula
Olearia spectabilis
Parahebe tenuis
Plantago aundensis
Potentilla papuana
Rapanea vaccinioides
Rhododendron atropurpureum
Rhododendron commonae
Rhododendron culminocolum
Trochocarpa dekockii
Uncinia sp.1
Vaccinium amblyandrum

3. Species which flowered only rarely during prolonged dry weather in July-August 1972 but which probably flower continuously under wetter climatic conditions.

Dichelachne rara
Gnaphalium japonicum
Keysseria radicans
Olearia floccosa
Poa languidior
Tetramolopium alinae
Trachymene tripartita
Uncinia ohwiana

4. Species with generally continuous or unsynchronized flowering but with some variation.

Anaphalis mariae
Astelia papuana
Carex ?echinata
Deschampsia klossii
Lactuca laevigata
Oreomyrrhis linearis
Oreomyrrhis pumila
Poa crassicaulis

Deyeuxia brassii
Dimorphanthera collinsii
Euphrasia mirabilis
Gnaphalium breviscapum
Haloragis halconensis
Hierochloe redolens
Polygonum runcinatum
Potentilla ?foersteriana
Ranunculus schoddei
Rhododendron womersleyi
Rhododendron yelliottii

5. Species flowering quite unsynchronously or continuously.

Abrotanella papuana
Agrostis reinwardtii
Anaphalis lorentzii
Anthoxanthum angustum
Anotis sp.1
Cardamine altigena
Carex capillacea
Cerastium papuanum
Coprosma divergens
Coprosma papuensis
Danthonia penicillata
Detzneria tubata
Drapetes ericoides
Drimys piperita (entities *montis-wilhelmi* and *subalpina*)
Epilobium detznerianum
Epilobium hooglandii
Epilobium keysseri
Eurya brassii
Festuca crispate-pilosa
Festuca papuana
Fragaria cf. *vesca*
Fuchsia ?magellanica
Gentiana cruttwellii
Gentiana ettingshausenii
Gentiana piundensis
Hypericum macgregorii
Ischnea elachoglossa
Lactuca sp.1
Lolium rigidum
Mazus pumilus
Myosotis australis
Nertera nigricarpa
Oreobolus ambiguus
Oreomyrrhis papuana
Oxalis magellanica
Parahebe albiflora
Pilea johniana
Poa annua
Poa callosa
Poa epileuca
Poa saruwagetica
Quintinia sp.1
Ranunculus pseudolowii
Ranunculus saruwagedicus
Ranunculus wahgiensis
Sagina papuana
Schoenus curvulus
Schoenus maschalinus
Senecio glomeratus
Senecio papuanus
Senecio sp.5
Sonchus oleraceus
Stellaria media
Styphelia suaveolens
Tetramolopium macrum
Trigonotis papuana
Trigonotis aff. *papuana*
Trigonotis procumbens
Uncinia riparia
Veronica cf. *persica*

It is interesting to note that species of *Habenaria* are amongst the most seasonally adjusted plants on both Mt Wilhelm and Mt Kinabalu. While species of *Polygonum* and *Ranunculus* show similarly slight seasonality in both Java and New Guinea and species of *Vaccinium* are much more seasonal in both places, *Anaphalis*, *Eurya*, *Gentiana* and *Hypericum* appear to behave differently, flowering seasonally in Java but not or only very indistinctly so on Mt Wilhelm.

6-E PHENOLOGY UNDER CONDITIONS OF CULTIVATION IN CANBERRA

A large proportion of temperate herbaceous plants responds to daylength as a control of flowering, and it is postulated that recent immigrants to New Guinea may retain such response mechanisms despite having migrated to an only slightly seasonal environment. Therefore it was decided to cultivate plants from Mt Wilhelm in Canberra under conditions of temperate zone daylength but continuously favourable temperature. Related species were collected from the Snowy Mts and cultivated alongside the New Guinea plants as controls. Daylength on Mt Wilhelm fluctuates from about 11 hr 47 min to 12 hr 28 min and in Canberra from 9 hr 48 min to 14 hr 31 min.

Seed samples were collected from Mt Wilhelm and despatched to Canberra by airmail in four batches in October 1971 and between May and September 1972. Whole plants were airfreighted on three occasions during the same period. Plants were gathered from the Snowy Mts mainly as transplants in November 1972 and January 1973. All plants were grown in a sealed part of a glasshouse heated to prevent frost during winter and cooled by airconditioner in summer. The resulting temperature regime, though not closely matching that of any locality on Mt Wilhelm, proved favourable for the growth and flowering of most of the New Guinea plants and perhaps approximated to that at an altitude of about 2500 m. However the winter temperatures were generally lower than during summer as shown by the failure of *Fragaria* cf. *vesca* to ripen fruits, and the development of open rather than cleistogamic flowers by *Viola arcuata*, during winter. No artificial lighting was employed. Daily watering ensured perpetually moist soil in the 4 inch and 5 inch pots used. Humidity in the glasshouse was high.

Seed of 74 species was despatched from Mt Wilhelm, of which that of 42 species germinated (see Fig. 6-5). Except for *Rhododendron atropurpureum* (seed sent by request to Edinburgh) seedlings of all species were obtained in Canberra, but in the cases of *Anaphalis lorentzii*, *Epilobium detznerianum*, *Epilobium keysseri*, *Euphrasia mirabilis*, *Gnaphalium japonicum*, *Ischnea elachoglossa*, *Lactuca laevigata* and *Parahebe albiflora* all the seedlings died. Several other species never reached sexual maturity during the period of observation which extended throughout 1973.

Whole plants airfreighted to Australia from Mt Wilhelm had to be scrupulously cleaned of all soil and after arrival be grown for several weeks in a quarantine glasshouse. Considerable mortality accompanied this process, but individuals of 17 species survived and were later released by the quarantine authorities, 3 being shrubs. 28 species were transplanted from the Snowy Mts to Canberra and 1 propagated from seed. Most of these were collected in the Charlotte Pass area (about 1800 m) and a few near Jindabyne (about 1300 m).

A complete year's observations were made of the plants at weekly intervals from 2 January 1973 to 1 January 1974. Each individual was examined for buds, flowers and undried fruits which were recorded if present. A total of 72 species were kept under observation, 47 from Mt Wilhelm and 29 from the Snowy Mts, 4 (*Acaena anserifolia*, *Carpha alpina*, *Poa annua* and *Scirpus* cf. *subtillissimus*) being collected from both sites.

19 New Guinean and 9 Australian species failed to develop any sexual reproductive organs at all, while *Keysseria radicans* from Mt Wilhelm and 10 Australian species were transplanted with buds, flowers or fruits but developed no further ones in the glasshouse. In some of these cases, especially of plants grown from seed, the plants were unable to reach maturity in the time available, but in others some factor in the glasshouse environment appeared inimical to bud initiation. 4 species from Mt Wilhelm and 2 from the Snowy Mts began flowering only near the end of 1973, so that their reproductive behaviour in relation to day-length cannot be determined. All these species, excluded from further consideration here, are tabulated in Fig. 6-6.

Fig. 6-5: Germination of seed sent from Mt Wilhelm mainly to Canberra.

Seed Batch	1971	1972A	1972B	1972C	Various
Days between collection and planting	*c.* 35	?10	47	*c.* 34	Various
Acaena anserifolia	+	+ G	+ G		
Agrostis reinwardtii				+ G	
Anaphalis lorentzii			+ G		
Anaphalis mariae	+				
Anthoxanthum angustum				+	
Astelia papuana	+				
Bidens pilosa			+ G		
Cardamine altigena	+	+ G			
Carpha alpina	+	+ G			
Cerastium papuanum		+	+ G		
Coprosma divergens	+	+			
Crassocephalum crepidioides			+		
Cynoglossum javanicum			+ G		+ G
Danthonia penicillata				+ G	
Deschampsia klossii	+ G			+ G	+ G
Dichrocephala bicolor			+ G		
Dimorphanthera keysseri	+				
Epilobium detznerianum		+ G			
Epilobium hooglandii	+				
Epilobium keysseri	+	+ G			
Euphrasia mirabilis	+	+ G			
Erigeron sumatrensis			+		
Fragaria cf. *vesca*		+ G			
Gaultheria mundula	+				
Gentiana ettingshausenii			+		
Gentiana piundensis			+		
Gnaphalium breviscapum	+		+		
Gnaphalium japonicum		+ G			
Haloragis halconensis	+				
Hierochloe redolens				+	
Hydrocotyle sibthorpioides		+ G	+ G		+ G
Hypericum macgregorii	+	+	+		
Ischnea elachoglossa	+	+ G			
Keysseria radicans			+		
Lactuca laevigata		+ G			
Lactuca sp.1			+		
Myosotis australis	+	+ G	+ G		

+: seed collected and planted
G: seed germinated.

1971 seed subjected to methyl bromide fumigation.

Fig. 6-5 (cont'd).

Seed Batch	1971	1972A	1972B	1972C	Various
Days between collection and planting	*c.* 35	?10	47	*c.* 34	Various
Nasturtium backeri			+ G		
Nertera granadensis			+ G		
Olearia spectabilis	+				
Oreomyrrhis linearis		+ G			
Oreomyrrhis papuana	+ G	+ G			
Oreomyrrhis pumila		+ G			
Oxalis magellanica	+	+			
Parahebe albiflora	+	+ G			
Parahebe ciliata		+			
Poa annua	+ G			+ G	
Poa saruwagetica	+				
Potentilla papuana		+ G	+		
Ranunculus pseudolowii	+	+ G	+ G		+ G
Ranunculus schoddei	+	+ G			
Rhododendron atropurpureum					+ G
Rhododendron womersleyi	+				
Sagina papuana		+ G	+ G		
Schoenus curvulus	+				
Senecio glomeratus		+ G			
Senecio papuanus	+	+ G			
Senecio sp.5			+		
Sonchus oleraceus				+	
Stellaria media				+ G	
Styphelia suaveolens	+	+			
Tacsonia mollisima					+ G
Tetramolopium alinae	+	+ G			
Tetramolopium macrum		+ G			
Trachymene saniculifolia		+ G			
Trachymene tripartita	+ G	+ G			
Trigonotis aff. *papuana*			+		
Trigonotis inoblita			+		
Triplostegia glandulifera			+ G		
Uncinia riparia	+				
Vaccinium amblyandrum	+				
Viola arcuata		+ G			
Youngia japonica			+		

+: seed collected and planted
G: seed germinated.

1971 seed subjected to methyl bromide fumigation.

	Mt Wilhelm		Snowy Mts	
	No.	Species	No.	Species
No sexual reproduction	A5	*Acaena anserifolia*		
	C2	*Agrostis reinwardtii*		
	D3	*Astelia papuana*		
	H5	*Brachycome papuana*		
	A20	*Carpha alpina*		
	F2	*Deschampsia klossii*	E14	*Acaena anserifolia*
	D5	*Drimys piperita subalpina*	E2	*Astelia psychrocharis* F.Muell.
	G1	*Haloragis halconensis*	E5	*Carex gaudichaudiana*
	A21 +B9	*Hydrocotyle sibthorpioides*	E4	*Carpha alpina*
	B11	*Nertera granadensis*	E3	*Oreomyrrhis ciliata* Hook.f.
	A6	*Oreomyrrhis linearis*	E11	*Oreomyrrhis eripoda* (DC.) Hook.f.
	A19 +G3	*Potentilla papuana*	E13	*Parahebe derwentiana* (Andr.) B.Briggs et Ehrend.
	D4	*Potentilla parvula*	J4	*Plantago muelleri* Pilger
	A13 +H3	*Ranunculus schoddei*	J8	*Poa* sp.
	A14	*Sagina papuana*		
	A18	*Tetramolopium alinae*		
	A17	*Tetramolopium macrum*		
	A10	*Trachymene tripartita*		
	G4	*Vaccinium amblyandrum*		
No initiation of flower buds after transplanting			J6	*Agrostis parviflora* R.Br.
			E12	*Brachycome* sp. (ANU 15631)
			E6	*Caltha introloba* F.Muell.
			E9	*Helichrysum scorpioides* Labill.
			J3	*Schizeilema fragoseum* (F.Muell.) Domin.
	H1	*Keysseria radicans*	J2	*Plantago* sp. (ANU 15637)
			E15	*Ranunculus pimpinellifolius* Hook.
			E1	*Ranunculus muelleri* Benth.
			E7	*Senecio gunnii* (Hook.f.) Belcher
			J1	*Viola betonicifolia*
Sexual reproduction only late in the year	H7	*Carex celebica*		
	A7	*Oreomyrrhis pumila*	J7	*Carex jackiana* Boott.
	F1	*Tacsonia mollissima*	K1	*Cerastium fontanum* Baumg.
	A9	*Trachymene saniculifolia*		

Fig. 6-6: Species under cultivation in Canberra which failed to flower before late 1973.

The remaining plants fell into 5 classes.

a. Hapaxanthic plants, dying or at least dying back to a considerable degree after fruiting. *Bidens pilosa* and *Cynoglossum javanicum* as well as the two species of *Gnaphalium* from the Snowy Mts needed to be regrown from seed periodically, while *Myosotis australis* and *Senecio glomeratus* produced new young shoots from the base of the dying stems after fruiting.

b. Continuously flowering plants, showing no response to different daylengths. This category includes 13 species from Mt Wilhelm but only *Carex hebes* and the alien *Poa annua* from the Snowy Mts, the latter species being collected from both sites and behaving similarly in both cases.

c. Plants which flowered in both summer and winter but which declined progressively in vigour and became infertile before the end of the year. Only 3 species are included, all from Mt Wilhelm, probably belonging to category (b) though on present data this cannot be certain.

d. Plants flowering only in winter and spring, apparently requiring a short day for flower bud initiation. Only *Libertia pulchella* from Mt Wilhelm is included.

e. Plants flowering only or mainly in summer, apparently requiring a long day for flower bud initiation. *Myriactis cabrerae* and *Senecio papuanus* belong here, as do 4 species from the Snowy Mts, including *Scirpus* cf. *subtillissimus* although plants of this species from Mt Wilhelm flower continuously.

Periods of reproduction are given for all species in classes a - e above in Fig. 6-7. The general picture to emerge is that while the majority of the Snowy Mts taxa which flowered are long-day plants as regards initiation of flower buds, most of the Mt Wilhelm taxa are daylength-neutral, even though several are congeneric and one conspecific with the Australian plants. This conclusion is in general agreement with that of Morton [1972] who found species in the West African mountain flora of north temperate affinity to be daylength-neutral. The long-day requirement of most of the Snowy Mts plants is also in accord with the same phenomenon in other temperate alpine floras like that of the Sierra Nevada [Chabot and Billings, 1972].

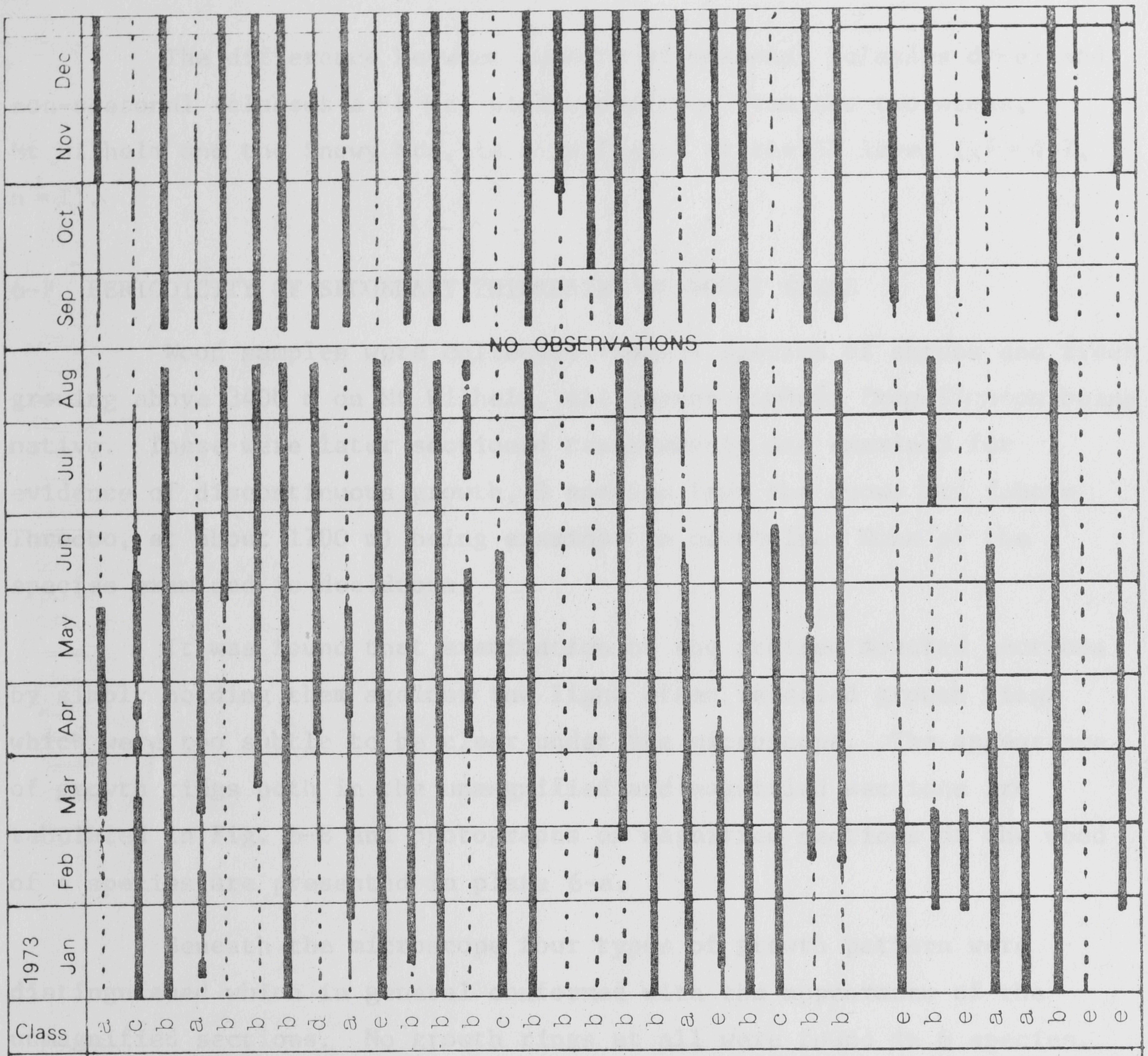


Fig. 6-7: Periods of reproductive organ development by species from Mt Wilhelm (top group) and the Snowy Mts, cultivated in Canberra. Thick lines indicate buds, flowers or unripe fruits on at least half the observed plants, thin lines on less than half and broken lines on none.

The difference between numbers of seasonal (classes d + e) and non-seasonal (classes a + b + c) plants observed from the two areas, Mt Wilhelm and the Snowy Mts, is significant at the 5% level ($\chi^2 = 4.7$, $n = 1$).

6-F PERIODICITY OF SECONDARY THICKENING OF WOODY STEMS

Wood samples were collected from 21 species of shrubs and trees growing above 3400 m on Mt Wilhelm, all except *Fuchsia ?magellanica* being native. These were later sectioned transversely and examined for evidence of discontinuous growth, 3 species from the Snowy Mts (above Thredbo, at about 1700 m) being examined as controls. None of the species examined is deciduous.

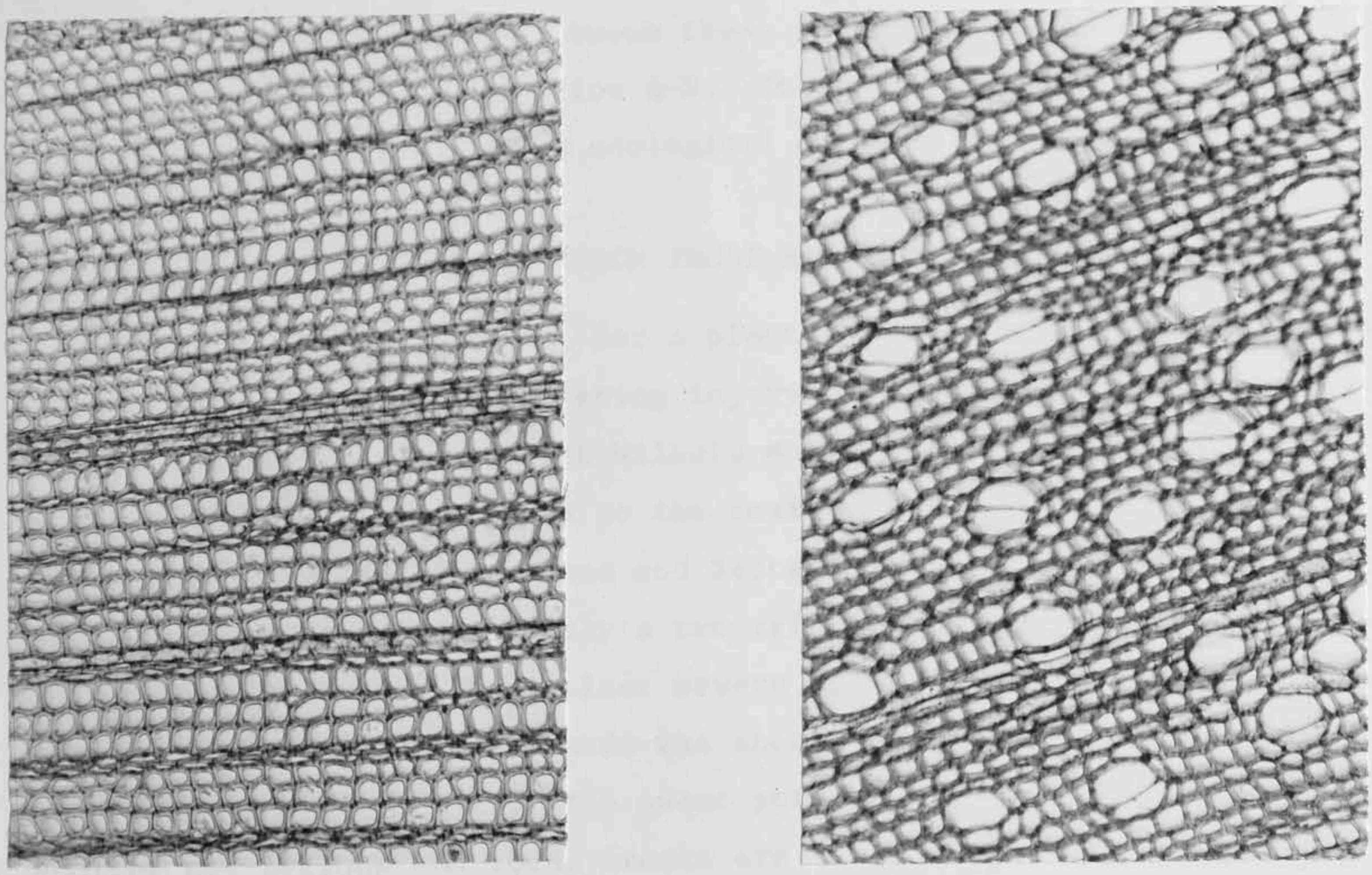
It was found that examination of the stained mounted sections by simply holding them against the light often revealed growth rings which were too subtle to be clear under the microscope. The appearance of growth rings both in the unmagnified and magnified sections are tabulated in Fig. 6-8 and photographs of magnified sections of the wood of 4 species are presented in plate 6-a.

Beneath the microscope four types of growth pattern were distinguished which in general conformed with the appearance of the unmagnified sections. No growth rings at all were found in 6 species, suggesting even and uninterrupted growth. At the other end of the scale 4 species from Mt Wilhelm including the only alien, *Fuchsia ?magellanica*, as well as all 3 Snowy Mts specimens, showed abrupt growth rings indicating periodic cessation and recommencement of growth. The presence of *Fuchsia* in this final category may be due entirely to periodic defoliation of the plant, growing beside the research station, by hard frosts. All the Australian specimens showed much clearer growth rings than any of those from New Guinea.

Two intermediate categories were also recognized. 5 species showed a general absence of growth rings except for a single one, suggesting that normally continuous growth was interrupted once by an exceptional event such as drought. And six species showed a fairly regular alternation of wood types with large and small cells but without any abrupt transition between them, suggesting a periodic deceleration but never total cessation of growth.

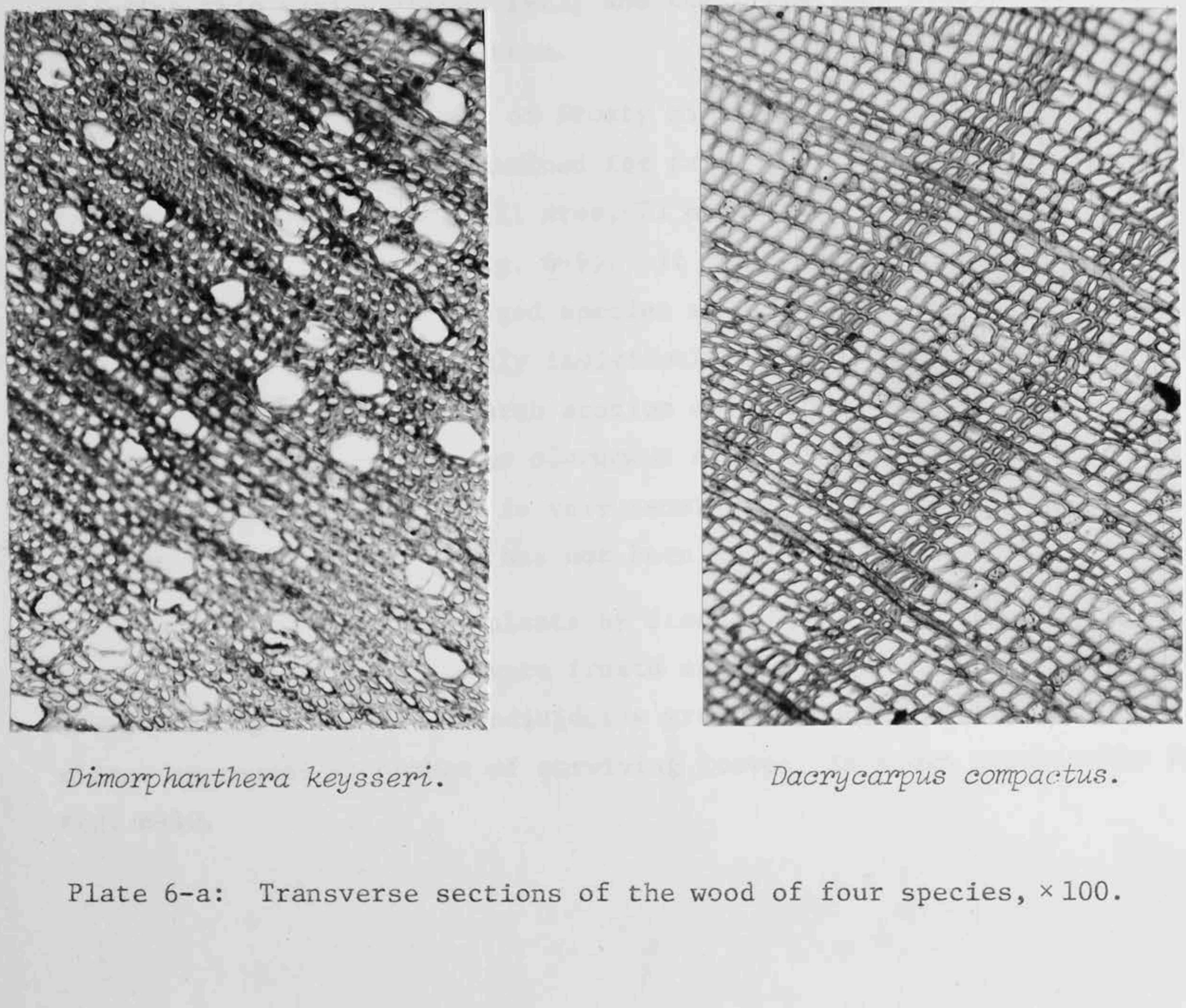
	Floristic Element	Year of Collection	Growth Rings in Unmagnified Section	Growth Pattern Shown Under Microscope
1. Species showing uninterrupted growth:				
Drimys piperita subalpina	G	1971	None	1
Pipturus sp.1	?G	1972	None	1
Rapanea vaccinioides	PW	1971	None	1
Rhododendron womersleyi	PN	1971	None	1
Schefflera chimbuensis	PW	1971	Faint	1
Vaccinium cruentum	PN	1971	None	1
2. Species showing growth interrupted only once:				
Drimys piperita montis-wilhelmi	G	1972	Faint	2
Eurya brassii	PW	1972	Faint	2
Olearia spectabilis	PS	1971	Faint	2
Quintinia sp.1	PS	1972	None	2
Rhododendron yelliottii	PN	1971	Faint	2
3. Species showing periodic fluctuations in growth:				
Coprosma divergens	?G	1971	Faint	3
Decaspermum lorentzii	PN	1972	Clear	3
Dimorphanthera microphylla	E	1971	Faint	3
Pittosporum pullifolium	G	1971	Faint	3
Senecio sp.2	PW	1972	Clear	3
Trochocarpa dispersa	PS	1972	Clear	3
4. Species showing periodic cessation of growth:				
Dacrycarpus compactus	G	1971	Clear	4
Dimorphanthera keysseri	E	1971	Clear	4
Fuchsia ?magellanica	A	1971	Clear	4
Styphelia suaveolens	PSS	1971	Clear	4
Drimys xerophila Parment.	Snowy Mts	1971	Clear	4
Olearia phlogopappa (Labill.) DC.	Snowy Mts	1971	Clear	4
Styphelia suaveolens	Snowy Mts	1971	Clear	4

Fig. 6.8: Secondary growth characteristics of woody stems.



Drimys piperita entity *montis wilhelmi*.

Quintinia sp.1.



Dimorphanthera keysseri.

Dacrycarpus compactus.

Plate 6-a: Transverse sections of the wood of four species, × 100.

The relationship between these growth categories and floristic elements is discussed in section 6-H. There are no clear relationships between growth categories and ecological or taxonomic groupings.

6-G INJURY AND MORTALITY THROUGH FROST AND DROUGHT

It is arguable that for a plant to be unresistant to frost and drought to the extent of suffering injury or mortality indicates a poor degree of adaptation to the Mt Wilhelm environment and may thus imply relatively recent immigration to the region. Frost and drought to the extent experienced between June and September 1972 occur only every several years but are certainly a recurring feature of the present Mt Wilhelm environment. The last severe drought and frost year prior to 1972 in the New Guinea highlands was about 1941, remembered because of its devastating effect upon the sweet potato crop below 2500 m, but shorter dry periods and local frosts are frequent [E.W. Waddell, pers. comm., 1973]. However whether arguments concerning adaptations by plants to frost and drought have any validity when related to migrations older than 10,000 yr ago is dubious, considering the great climatic changes preceding this period [Hope, 1973] and the migrations within New Guinea which must have accompanied them.

After a succession of frosty nights, plants in the vicinity of the research station were examined for frost damage on 13 June 1972. Of 49 species listed from a small area, 21 had suffered injury to foliage and 28 were unharmed (see Fig. 6-9). It is perhaps significant that while 9 (43%) of the 21 damaged species were aliens, only 5 (18%) of the undamaged ones were. The only individuals known to have been completely killed by frost in the research station area were of alien species, *Erigeron sumatrensis*, *Sonchus oleraceus* and *Tacsonia mollissima*. *Crassocephalum crepidioides* is very sensitive to frost although, and perhaps for this reason, it has not been found above 3414 m.

Severe injury to plants by freezing also occurred at high altitude although fairly severe frosts are of almost nightly occurrence there. Damage to several individuals growing at 4400 m on the summit ridge, expressed as number of surviving leaves, is shown graphically in Fig. 6-10.

Floristic Element	Damaged by Frost	Unharmed by Frost
Ancient immigrants	*Keysseria radicans*	*Ceratostylis* sp.2 *Coprosma divergens* *Detzneria tubata* *Haloragis halconensis* *Pittosporum pullifolium*
Peregrine element	*Acaena anserifolia* *Anaphalis lorentzii* *Epilobium keysseri* *Eriocaulon montanum* *Potentilla ?foersteriana* *Ranunculus pseudolowii* *Senecio glomeratus* *Senecio papuanus* *Vaccinium amblyandrum* *Sagina papuana* *Schoenus maschalinus*	*Anaphalis mariae* *Carex celebica* *Danthonia penicillata* *Deschampsia klossii* *Euphrasia mirabilis* *Gaultheria mundula* *Gnaphalium japonicum* *Hierochloe redolens* *Lactuca laevigata* *Myosotis australis* *Hypericum macgregorii* *Olearia spectabilis* *Plantago aundensis* *Poa saruwagetica* *Potentilla papuana* *Styphelia suaveolens* *Trigonotis papuana* *Vaccinium cruentum*
Aliens	*Cordyline fruticosa* *Fragaria* cf. *vesca* *Fuchsia ?magellanica* *Mentha* sp. *Plantago lanceolata* *Raphanus sativus* *Sonchus oleraceus* *Stellaria media* *Tritonia* X *crocosmaeflora*	*Brassica oleracea* *Petroselinum crispum* *Poa annua* *Solanum tuberosum* *Veronica* cf. *persica*

Fig. 6-9: Extent of frost damage to plants growing near research station, 3480 m, 13 June 1972.

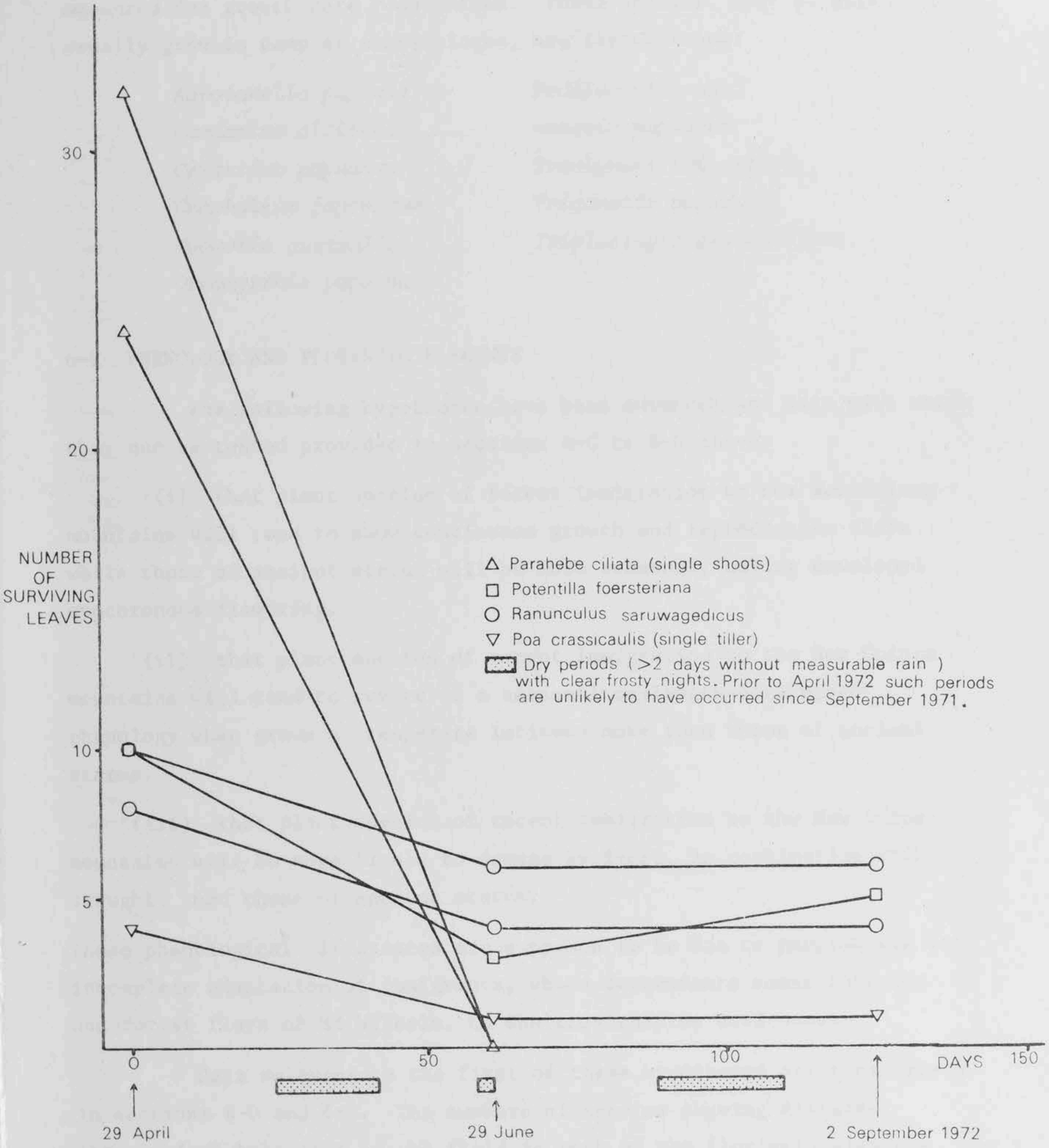


Fig. 6-10: Injury by frost to six individuals of four species growing at 4400 m, expressed as number of surviving leaves.

Mortality of individuals through drought was noted in several species growing at 3350-3500 m, the plants having been periodically measured for growth rate computation. These species, most of which usually grow in damp or shady places, are listed below:

Abrotanella papuana
Cardamine altigena
Cerastium papuanum
Gnaphalium japonicum
Myosotis australis
Oreomyrrhis papuana
Pedilochilus sp.3
Senecio papuanus
Trachymene tripartita
Trigonotis papuana
Triplostegia glandulifera.

6-H PHENOLOGY AND FLORISTIC ELEMENTS

The following hypotheses have been advanced and data with which they can be tested provided in sections 6-C to 6-G above:

(i) that plant species of recent immigration to the New Guinea mountains will tend to show continuous growth and reproduction there while those of ancient status will be more seasonal, having developed synchronous flowering.

(ii) that plant species of recent immigration to the New Guinea mountains will tend to revert to a seasonal daylength-determined phenology when grown at temperate latitude more than those of ancient status.

(iii) that plant species of recent immigration to the New Guinea mountains will be more liable to damage by frost, in combination with drought, than those of ancient status.

These phenological differences are supposed to be due to progressive but incomplete adaptation of immigrants, whose descendants constitute the non-forest flora of Mt Wilhelm, to the tropicalpine environment.

Data relevant to the first of these hypotheses are those given in sections 6-D and 6-E. The numbers of species showing different phenological behaviour in the field in each of the floristic elements (see section 3-G) are tabulated in Fig. 6-11. There is negligible difference between the proportions of the peregrine and more ancient elements which show some as opposed to no indication of seasonality. However the total native flora appears to show a significant difference

	1 Clearly Seasonal Flowering	2 Seasonal Flush of Flowering	3 Cessation of Flowering After Drought	4 Slight Indication of Seasonal Flowering	1 + 2 + 3 + 4	No Indication of Seasonal Flowering	Total
G	1	–	–	3	4	5	9
?G	1	2	1	1	5	5	10
E	–	2	2	1	5	3	8
PW	3	3	1	9	16	28	44
PN	3	5	–	3	11	4	15
PS	1	2	2	–	5	1	6
PWW	–	–	1	–	1	1	2
PWN	–	–	–	1	1	–	1
PWS	–	–	–	1	1	4	5
PNN	–	–	–	–	–	–	0
PSS	–	2	1	–	3	2	5
A	–	–	–	–	–	7	7
Members of peregrine element in widespread genera	3	3	2	11	19	33	52
Members of peregrine element in northern or southern genera	6	9	3	3	19	7	26
Ancient immigrants	2	4	3	5	14	13	27
Peregrine element	7	12	5	15	39	39	78
Aliens	–	–	–	–	–	7	7
Total	9	16	8	19	52	60	112

Fig. 6-11: Numbers of species in floristic elements showing different degrees of seasonal flowering in the field.

from the aliens which, though only 7 were examined, all flower continuously ($\chi^2 = 6.7$, $n = 1$; significant at the 1% level). An unexpected difference within the peregrine element occurs between species in widespread genera (PW, PWW, PWN, PWS) and species in more restricted genera (PN, PNN, PS, PSS); a significantly higher proportion of the former flowers continuously, possibly reflecting the superior migration abilities of these widespread genera ($\chi^2 = 9.2$, $n = 1$); significant at the 1% level).

Data concerning secondary growth of woody stems is presented by floristic element in Fig. 6-12. More members of the ancient element show discontinuous than continuous growth while the reverse is true for members of the peregrine element. Although this tends to support the field phenology data in verifying hypothesis (i) above, numbers are small and the difference is only just significant at the 10% level ($\chi^2 = 1.7$, $n = 1$; $\chi^2 = 2.6$ if the two "entities" in *Drimys piperita* are regarded as conspecific).

Fig. 6-12: Numbers of species in floristic elements showing different secondary growth behaviour.

Floristic Element	Continuous Growth (1 and 2)	Discontinuous Growth (3 and 4)
Ancient immigrants	*Drimys piperita* "*montis-wilhelmi*" *Drimys piperita* "*subalpina*" *Pipturus* sp.1	*Coprosma divergens* *Dacrycarpus compactus* *Dimorphanthera keysseri* *Dimorphanthera microphylla* *Pittosporum pullifolium*
Peregrine element	*Eurya brassii* *Olearia spectabilis* *Quintinia* sp.1 *Rapanea vaccinioides* *Rhododendron womersleyi* *Rhododendron yelliottii* *Schefflera chimbuensis* *Vaccinium cruentum*	*Decaspermum lorentzii* *Senecio* sp.2 *Styphelia suaveolens* *Trochocarpa dispersa*
Aliens		*Fuchsia ?magellanica**
Snowy Mts plants		*Drimys xerophila* *Olearia phlogopappa* *Styphelia suaveolens*

* Periodic growth perhaps due to periodic defoliation by frost.

Numbers are also too small to reveal phenological differences between elements within the group of species from Mt Wilhelm cultivated with flowering success in Canberra. However if these species are compared as a group by floristic elements with species failing to flower in Canberra at least until late in 1973, it is found that there is a tendency for species of more ancient status in the New Guinea mountains to be reproductive failures in Canberra. The figures are given in Fig. 6-13, the whole table showing differing trends between the "successes" and "failures" significant at the 5% level ($\chi^2 = 8.5$, $n = 3$). A complex of factors are no doubt responsible for lateness or absence of flowering, including slow growth rate and lack of adaptability of the plants themselves. I have already suggested (see section 1-A) that such characteristics are the antithesis of those expected in a good colonist species, so that their occurrence amongst the more ancient immigrants to New Guinea is not surprising as these plants may have lost some colonist attributes during adaptation to the tropicalpine environment.

	Species Flowering Well	Species Flowering Late or Not at All	Total
Ancient immigrants	1	8	9
Malesian endemic spp. in peregrine element	9	10	19
More widespread spp. in peregrine element	9	5	14
Aliens	4	1	5

Fig. 6-13: Number of species in floristic elements flowering well or poorly under cultivation in Canberra.

Hardiness to frost of 48 species has been tabulated in Fig. 6-9. There is no significant difference between ancient and peregrine elements in proportion of frost sensitive species; the difference between natives and aliens is not quite significant at the 5% level, the aliens as a group being less hardy ($\chi^2 = 3.7$, $n = 1$).

CHAPTER 7

DISTRIBUTION ON SLOPES OF DIFFERENT ASPECT

7-A THE SIGNIFICANCE OF ASPECT

Duration of insolation may control the local distribution of species whose ecological requirements include temperature as a limiting factor. Especially in the temperate zones slopes of different aspect will experience different amounts of insolation, equator-facing slopes receiving more than poleward ones. Aspect differences have been related to vegetation differences by many authors [e.g. Conolly and Dahl, 1970; Specht, 1972; Whittaker, 1953; Wilson, 1970] in a variety of temperate zone regions.

However in the tropics the sun climbs daily to a position close to the vertical and therefore slopes of different aspect may not be expected to differ in the insolation they receive. As Seddon [1971] has written in a recent biogeography textbook,

> "The microclimate as it affects plants on a rock-face is obviously very different on south and north exposures and even great differences in altitude cannot entirely compensate for aspect differences in high latitudes. Such differences are much less pronounced in mountains in low latitudes".

Many, perhaps most, tropical mountains display aspect differences in terms of precipitation differences on different flanks of peaks and ranges [e.g. Coe, 1967; McVean, 1968; Steenis, 1972]. The eccentric ice-cap of Mt Kilimanjaro has been explained in terms of variation in precipitation rather than insolation [Salt, 1951]. The importance of slope aspect in the tropics has been recognized in connection with insolation in early morning and late evening by Garnier and Ohmura [1969]. To my knowledge this has not been related to a regularly changing cloud pattern, resulting in different total insolation and vegetation characteristics of tropical slopes of different aspect.

Observations upon the daily march of weather on Mt Wilhelm [e.g. McVean, 1968] suggested that insolation on west-facing slopes may be significantly reduced by build-up of cloud during late morning and afternoon, by comparison with east-facing slopes receiving early morning sunshine. Hnatiuk [in prep.] in an attempt to demonstrate this at 4300 m, found no difference between maximum temperatures on slopes of different aspect, but a site sloping steeply westwards had minimum temperatures over 3 °C higher than three other sites with lesser slopes and other aspects. Wardle [1971] has stated that *Drimys piperita* entity *subalpina* (as *D. brassii*) grows on Mt Wilhelm "mainly on cold aspects on deep soil".

Although they were not obvious an investigation was carried out to elucidate microclimatic and floristic distinctions between slopes of opposing aspect. When this investigation was planned it was not known whether these distinctions existed but I believed that some species could be shown to grow preferentially on warmer and drier eastern or cooler and wetter western slopes. I considered it possible that such preferences could be related to floristic elements in that plants of particular geographic origins may be commoner under the microclimatic conditions provided by slopes of particular aspect.

7-B THE CLIMATE OF SLOPES OF DIFFERENT ASPECT ON MT WILHELM

At 3480 m (site 1) "Dobbie" maximum and minimum thermometers were placed at ground level, exposed to the sky except for a shield of thin corrugated aluminium sheet *c*. 1 cm above the instruments, on opposing slopes of a small ice-rounded hillock covered by peaty soil and tussock grassland. The hillock lay near the research station in the bottom of the Pindaunde valley and the slopes where the thermometers were placed had aspects of precisely 90° and 270°.

Two higher sites lay astride ridges, near Ridge Camp on the Bogunolto ridge at 4025 m (site 2) and on a col of the main summit ridge *c*. 500 m northwest of Saddle Camp at 4300 m (site 3). U-tube max/min thermometers were placed as described for the lower altitude site *c*. 10 m below the ridge crest in each case. At 3480 m the thermometers were observed and reset almost every day for nearly 14 weeks. At both higher sites they were observed at intervals of 1-18 and 1-25 days and for 19 and 10 weeks respectively. The aspects of the slopes at site 2 were 35° and 210° and at site 3, 65° and 245°.

All thermometers used were calibrated under identical conditions in the research station and found to agree with each other to within one degree. A "Dobbie" maximum thermometer, shielded as it had been on Mt Wilhelm, was also compared with an aspirated thermistor in Canberra in January 1974 to check radiation error. Several measurements were made at two times of day in both sunshine and shadow at ground surface on a rough lawn. Under these conditions the aspirated thermistor showed fairly consistently a temperature 7.5 °C higher in the sun than in shade, while the thermometer gave a figure, also fairly consistently, 16.0 °C higher. The two instruments agreed exactly upon shade temperatures, so that the thermometer was exaggerating ground surface air temperatures in sunshine by 8.5 °C. Therefore while the maximum temperatures recorded in the field cannot be taken as accurate, they do provide a reliable indication of relative temperature and a measure of degree of insolation.

Minimum temperatures were generally lower on slopes facing east at all altitudes. Almost all the minimum temperature records from site 1, a majority from site 2 and all from site 3 show this trend (see Figs. 7-1A and 7-2). The average differences between minimum temperatures on eastern and western slopes at sites 1, 2 and 3 respectively are 1.5 °C, 0.2 °C and 1.7 °C. At site 1 the difference is despite nocturnal cold air drainage, as the less cold westerly slope is the one facing upvalley. Maximum temperatures by contrast are higher on eastern than on western slopes: all records at site 2 and almost all at site 3 support this expected conclusion (see Fig. 7-2). The situation at site 1 is less clear (see Fig. 7.1), although the average of all recorded maxima on the eastern slopes (29.31 °C) is higher than that for the western (28.51 °C). However a factor complicating this investigation is that the period in 1972 during which observations were made was unusually dry and cloudless by comparison with "typical" weather. For example McVean [1968] writes

> "A typical day on the mountain begins with clear skies ... Updraught on the valley walls, with consequent cloud formation, begins about 0800, with intermittent mist and showers of rain at station level by 1100. Showers die out by sunset and the sky clears completely by 2100."

By this definition, supported by numerous other observers, most days during the observation period were atypical. If only days recorded as being cloudy in the afternoon are considered, a maximum temperature

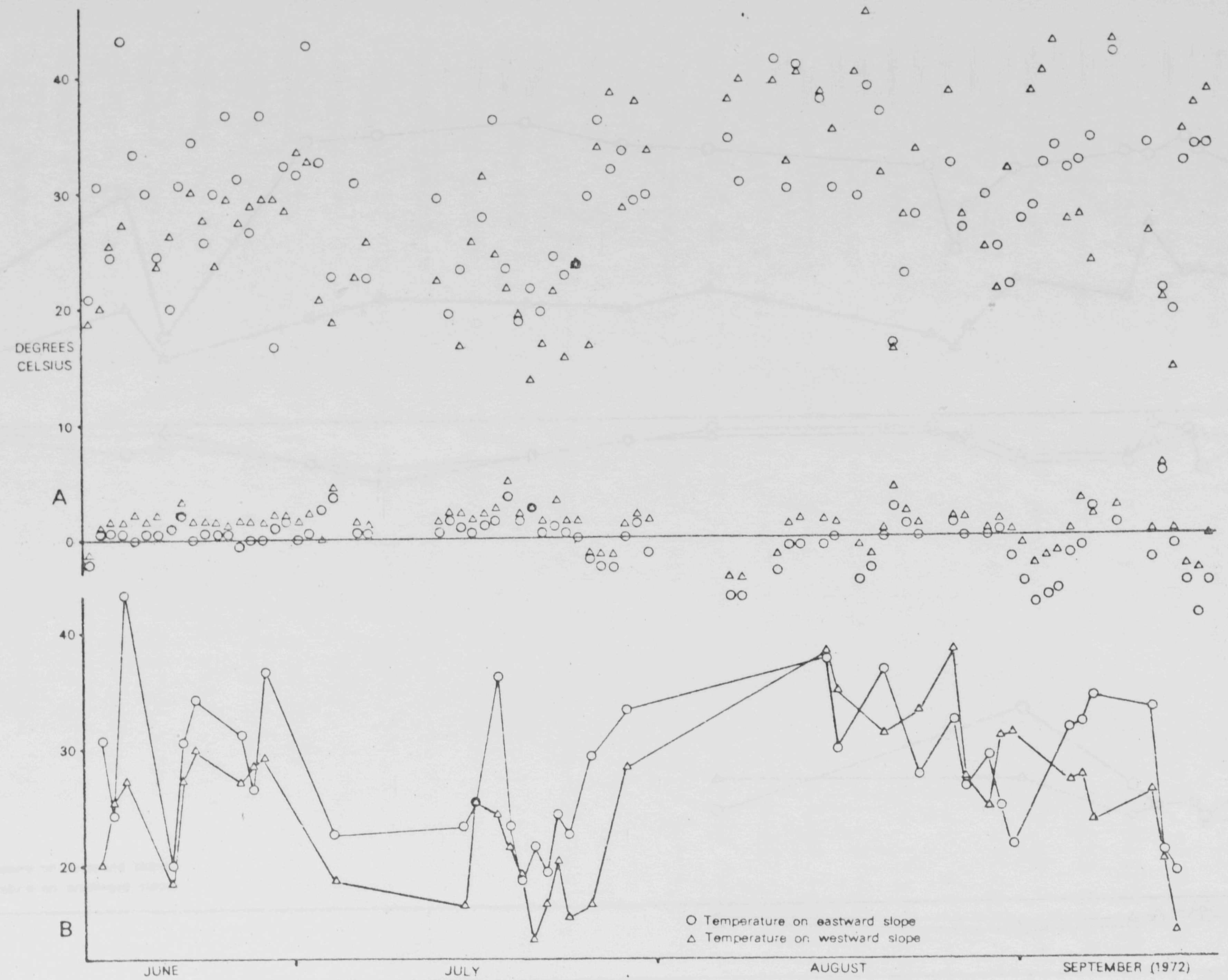


Fig. 7-1: Temperatures on slopes of opposing aspect, site 1, 3480 m.
A : all records; B : records for days with cloudy afternoons.

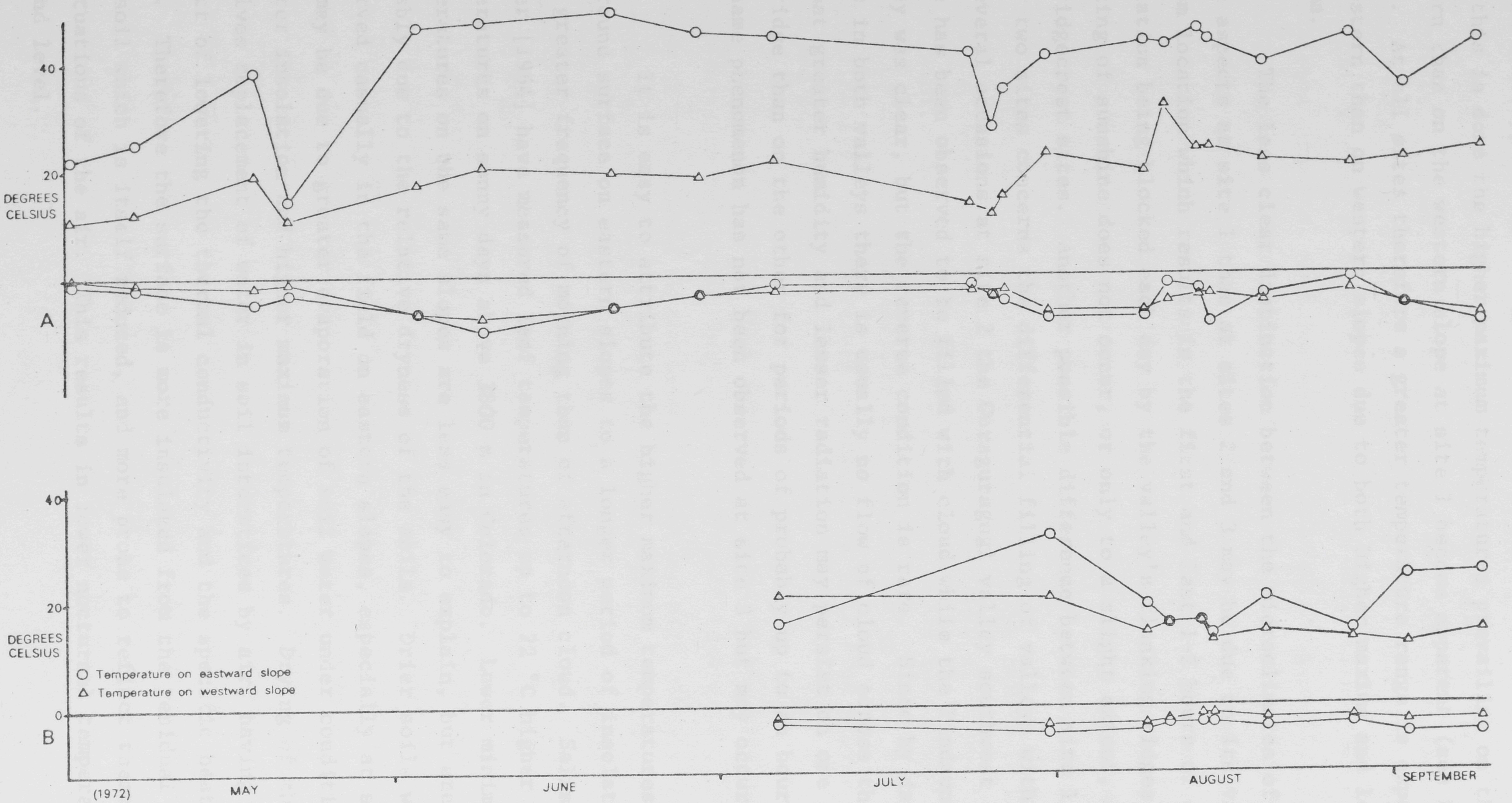


Fig. 7-2: Temperatures on slopes of opposing aspect.

A : site 2, 4025 m; B : site 3, 4300 m.

pattern more typical of the general climate might be expected to result. When this is done the higher maximum temperatures prevailing on the eastern than on the western slope at site 1 become apparent (see Fig. 7-1B). At all sites therefore a greater temperature range is experienced on eastern than on western slopes due to both higher maxima and lower minima.

The less clear distinction between the microclimates of the two slope aspects at site 1 than at sites 2 and 3 may be due to its valley bottom location which results in the first and last 1-2 hours of direct insolation being blocked each day by the valley's flanking ridges. Such blocking of sunshine does not occur, or only to a slight extent, at the two ridgecrest sites. Another possible difference between site 1 and the other two sites concerns the differential filling of valleys with cloud. On several occasions at site 2 the Guraguragugl valley southwest of the ridge has been observed to be filled with cloud while the Pindaunde valley was clear, but the reverse condition is rare. Since by day air rises in both valleys there is usually no flow of cloud across the ridge, so that greater humidity and lesser radiation may persist on one side of the ridge than on the other for periods of probably up to an hour or more. The same phenomenon has not been observed at site 3 but may occur there also.

It is easy to attribute the higher maximum temperatures of air at ground surface on eastern slopes to a longer period of insolation due to a greater frequency of morning than of afternoon cloud. Salisbury and Spomer [1964] have measured leaf temperatures up to 22 °C higher than air temperatures on sunny days above 3800 m in Colorado. Lower minimum temperatures on the same slopes are less easy to explain, but are probably due to the relative dryness of the soils. Drier soils were observed casually in the field on eastern slopes, especially at site 2, and may be due to greater evaporation of soil water under conditions of greater insolation and higher maximum temperatures. Drying of the soil involves replacement of water in soil interstices by air, having the dual effect of lowering the thermal conductivity and the specific heat of the soil. Therefore the surface is more insulated from the residual heat in the soil which is itself reduced, and more prone to reflect thermal fluctuations of the air. This results in lower nocturnal temperatures at ground level.

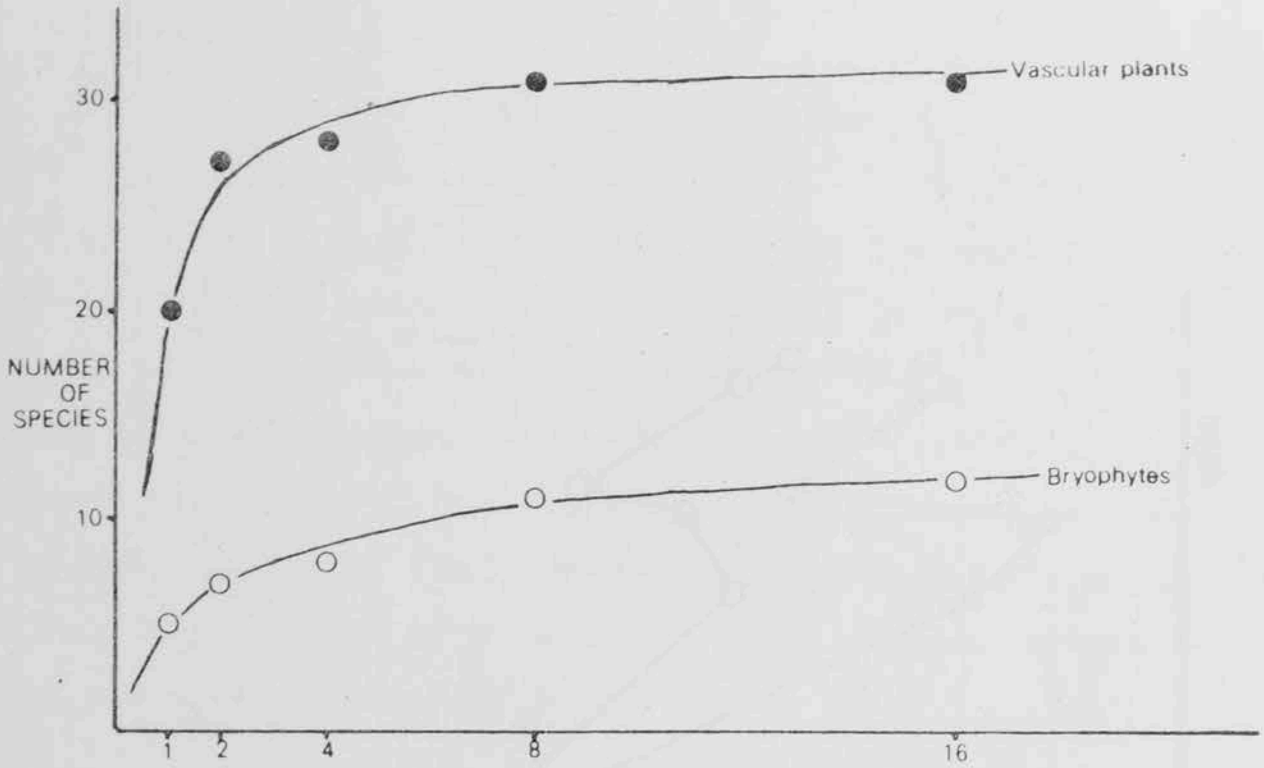
7-C FLORA OF SLOPES OF DIFFERENT ASPECT

Although it was not noticed before the start of the investigation, it soon became clear that opposing east/west slopes with comparable vegetation differed from each other floristically to some extent. For example at Ridge Camp (site 2) it was noticed that west-facing slopes supported many individuals of *Oreomyrrhis pumila*, a generally higher altitude species, but none of *O. linearis*, the latter species being common however on the eastern slopes which also had a few individuals of *O. pumila* but only in the shade of small shrubs. In particular it was noticed that many species (for example in the genera *Agrostis*, *Festuca*, *Oreomyrrhis*, *Papuapteris* and *Uncinia*) appeared to occur mainly on east-facing slopes in the upper parts of their ranges.

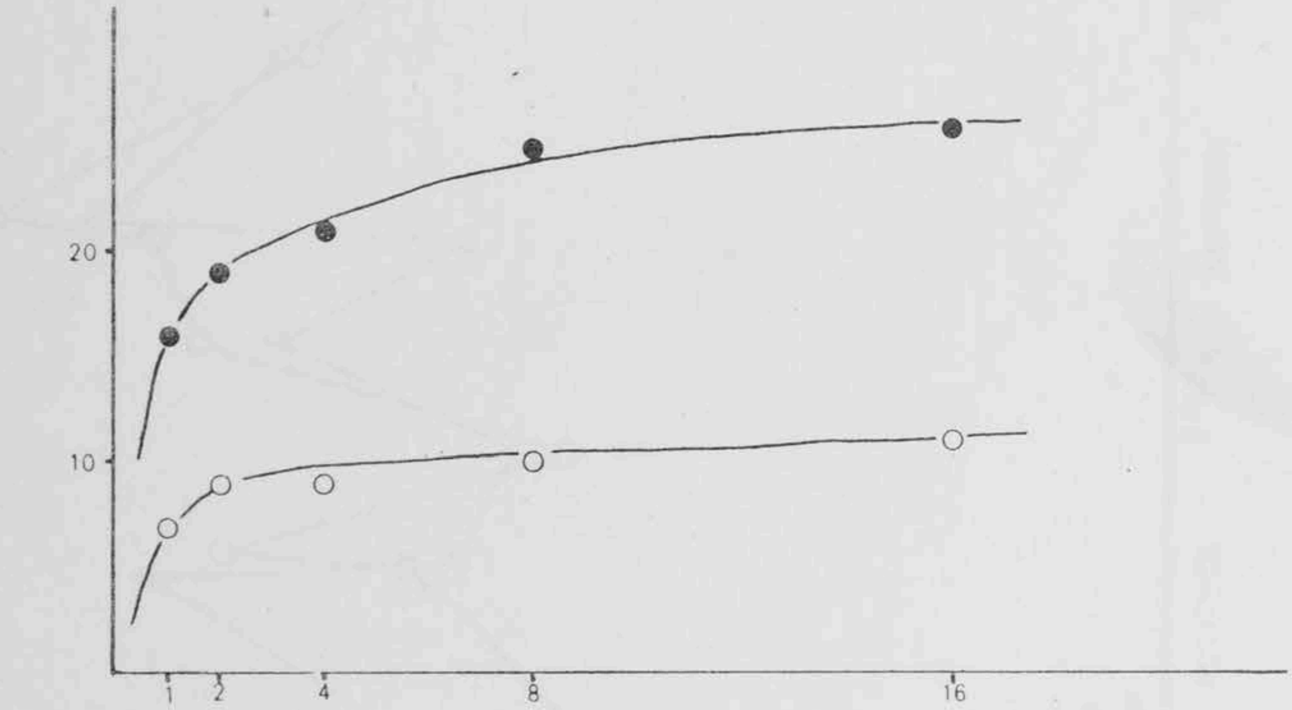
On the other hand no similar impression was gained in the field for opposing slopes of north/south aspect, whose vegetation and flora appeared similar or not consistently different. This impression was confirmed by more detailed inspection of the assembled data, and subsequent analysis was therefore restricted to data from slopes of eastern and western aspect.

33 pairs of sites were examined with slopes of opposing aspect of which 21 pairs had slopes facing east (45°-135°) and west (225°-315°). All pairs of slopes were at the same altitude and with closely comparable vegetation, and were generally within 100 m of each other on either side of a ridge or small valley. Each slope was examined by recording species present in each of 10 quadrats measuring 2×2 m above and 3×3 m below 3800 m as suggested by species/area curves (see Fig. 7-3).

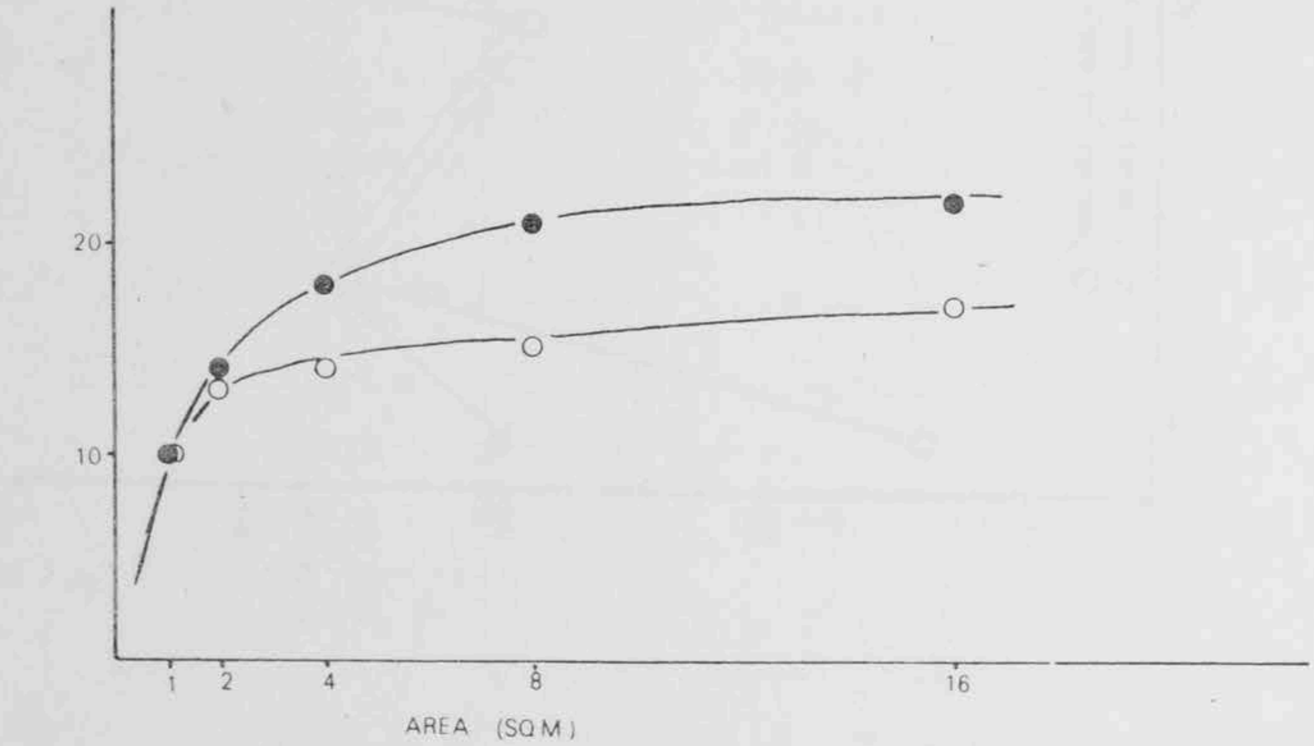
Numbers of species occurring in the tens of quadrats analysed on eastern and western slopes were plotted against altitude (see Fig. 7-4). The resulting graph shows the non-forest flora reaching a peak of richness at *c.* 3850 m altitude, corresponding to the highest stands of forest (3810 m) and confirming a similar conclusion reached by Wade and McVean [1969] who found a peak of grassland species richness at 3900 m. This may be related to the history of the grasslands concerned, as those above the forest limit are natural and probably represent climatic climax vegetation while those below are mostly anthropogenic, derived from forest by human destruction of vegetation mainly by fire.



Short grassland, 4020 m, northeast aspect.



Short grassland, 4020 m, southwest aspect.



Tussock grassland, 3640 m, eastern aspect.

Fig. 6-3: Numbers of vascular plant and bryophyte species in different areas of three communities.

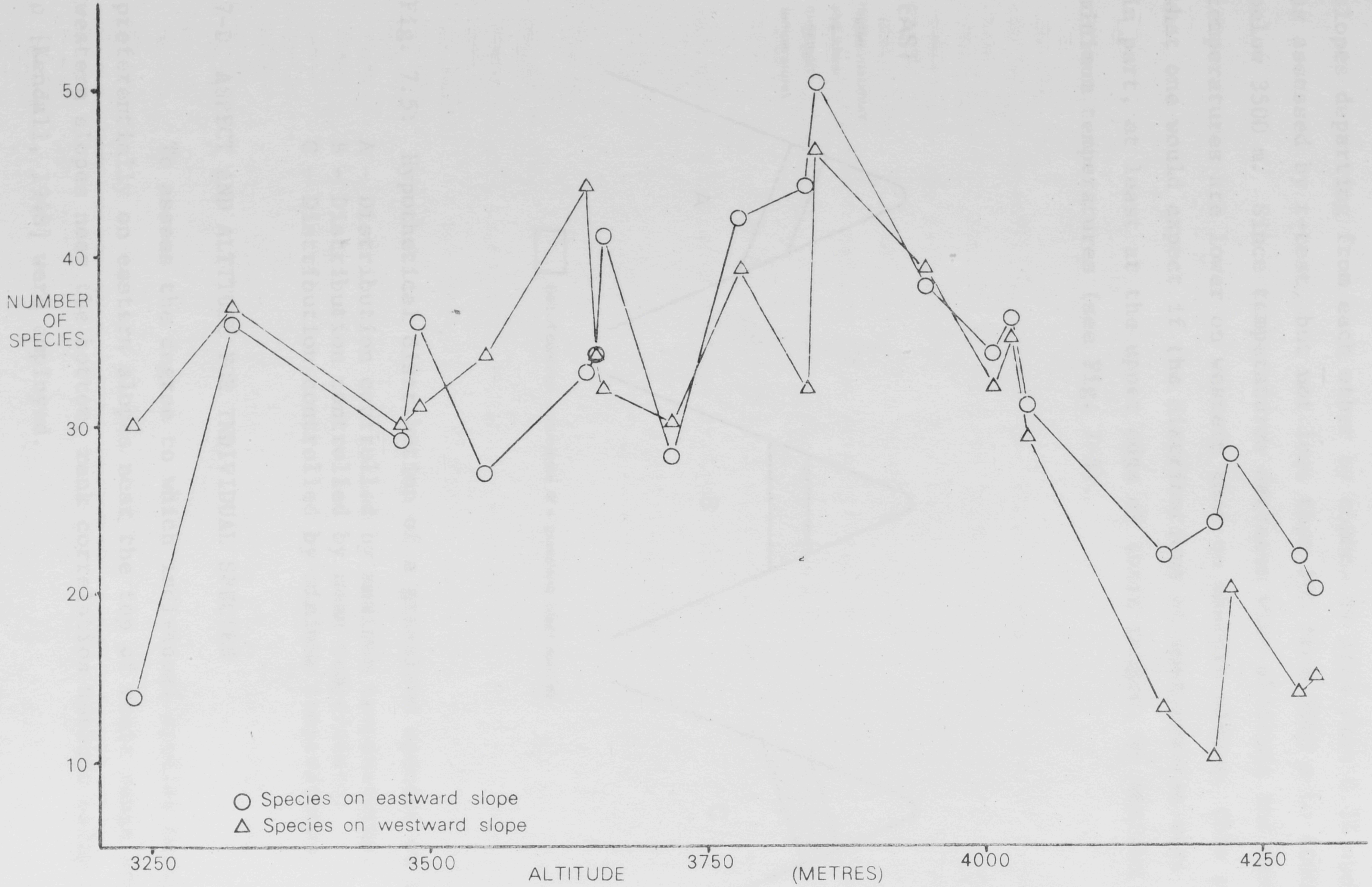


Fig. 7-4: Numbers of species occurring in tens of quadrats on slopes of eastern and western aspect at 21 sites at various altitudes.

This graph also shows that the flora of eastern slopes tends to be richer than that of western slopes above 4000 m and perhaps poorer below 3500 m. The probability of the figures for western and eastern slopes departing from each other by chance is less than 0.2% above 4000 m as assessed by t-test, but not less than 10% from 3500 m to 4000 m and below 3500 m. Since temperatures decrease with altitude and maximum temperatures are lower on western than on eastern slopes, this pattern is what one would expect if the distributions of most species were limited in part, at least at the upper edge of their ranges, by maximum and not minimum temperatures (see Fig. 7-5).

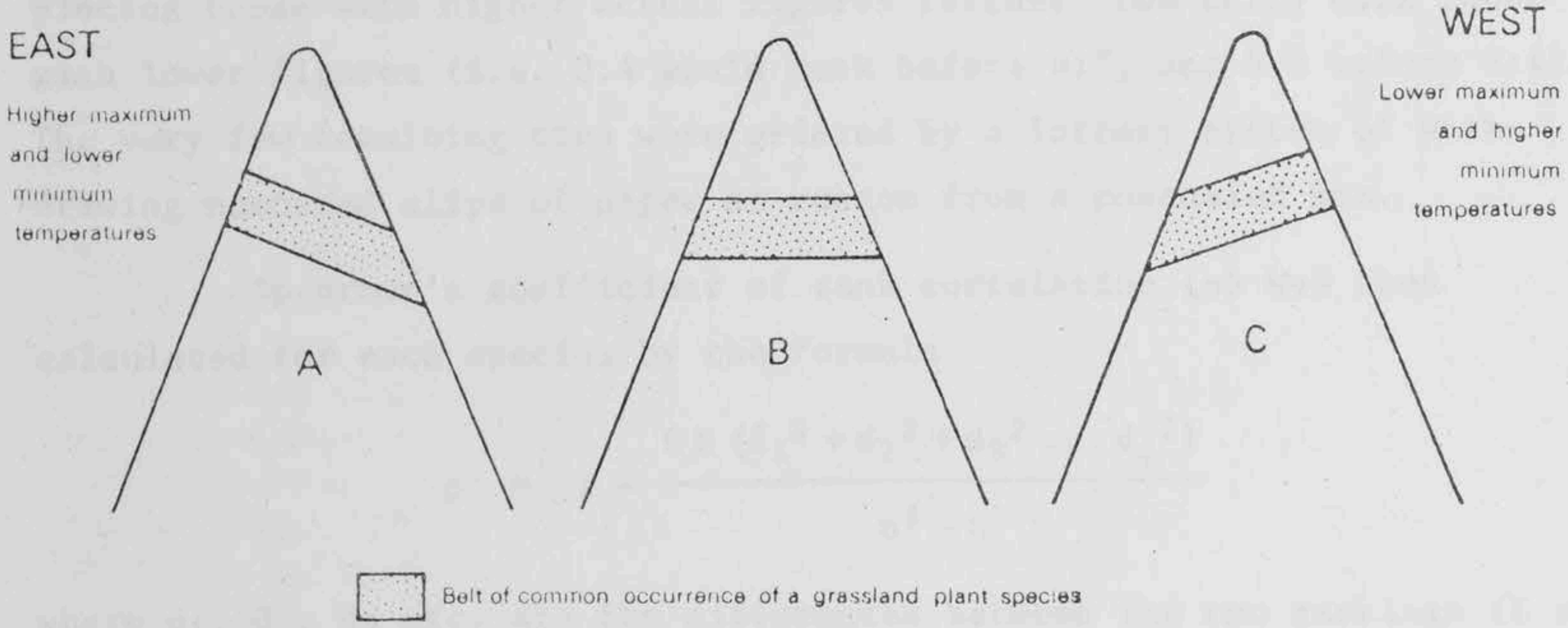


Fig. 7.5: Hypothetical distribution of a grassland species on Mt Wilhelm.
A - Distribution controlled by maximum temperatures.
B - Distribution controlled by mean temperature.
C - Distribution controlled by minimum temperatures.

7-D ASPECT AND ALTITUDE FOR INDIVIDUAL SPECIES

To assess the degree to which individual species occurred preferentially on eastern slopes near the top of their range and on western slopes near the bottom, rank correlation methods using Spearman's ρ [Kendall, 1948] were employed.

All species occurring at five or more sites with both eastward and westward slopes were ranked according to the proportion of 10 quadrats occupied on the eastward slope divided by that on the westward.

This ranking was then compared with direct ranking of sites by altitude.

For example for *Coprosma papuensis*:

A: Site number:	031	032	020	008	007
B: No. quadrats occupied on eastern slopes:	5	1	4	0	1
C: No. quadrats occupied on western slopes:	5	6	3	2	0
D: B ÷ C:	1	0.2	1.3	0	∝
E: Altitude ranking:	1	2	3	4	5
F: Ranking by D:	3	2	4	1	5

To avoid unnecessary statistical complexity tied ranks according to proportion of eastern to western quadrats occupied (D) were ordered by placing those with higher actual figures further from unity than those with lower figures (i.e. 0:4 would rank before 0:2, and 4:2 before 8:4). The very few remaining ties were ordered by a lottery system of withdrawing numbered slips of paper at random from a concealed box.

Spearman's coefficient of rank correlation (ρ) was then calculated for each species by the formula

$$\rho = 1 - \frac{6\,\Sigma\,(d_1{}^2 + d_2{}^2 + d_3{}^2 \ldots d_n{}^2)}{n^3 - n}$$

where d_1, d_2, d_3 etc. are the differences between the two rankings (E and F above) for each site, and n is the number of sites considered. Therefore for the example of *Coprosma papuensis* considered above,

$$\rho = 1 - \frac{6 \times (4 + 0 + 1 + 9 + 0)}{125 - 5}$$

$$= 1 - 0.70 = +0.30 \; .$$

Significance of the 66 figures of ρ thus calculated was worked out by deriving t from the formula

$$t = \rho\sqrt{\frac{n-2}{1-\rho^2}} \; ,$$

t then being converted to y by reference to the table in Appendix 4 of Kendall [1948], and the per cent probability of such a value being obtained by chance being simply calculated $2(1-y) \times 100$.

Values of n, ρ and per cent probability are provided for 66 species in Fig. 7-6. It can be seen that 56 of these are positively

Fig. 7-6: Preference by species for slopes of particular aspect: rank correlation between site altitude and tendency to grow preferentially on eastern slopes.

Species	No. Sites n	Spearman's Coefficient of Rank Correlation ρ	Probability of Obtaining Rank by Chance (%)
Acaena anserifolia	5	+0.300	64
Agrostis reinwardtii	16	+0.733	0.2
Anaphalis lorentzii	5	-0.500	40
Anaphalis mariae	12	-0.175	56
Anthoxanthum angustum	16	+0.495	5.2
Astelia papuana	15	+0.799	< 0.1
Carex ?celebica	7	+0.464	32
Carex ?perciliata	6	-0.029	48
Carpha alpina	5	+0.400	50
Cerastium papuanum	8	+0.571	14
Coprosma divergens	16	+0.844	< 0.1
Coprosma papuensis	5	+0.300	64
Danthonia penicillata	8	+0.215	63
Danthonia vestita	10	+0.552	9.4
Deschampsia klossii	19	+0.582	0.8
Detzneria tubata	9	+0.133	70
Deyeuxia brassii	16	+0.471	6.6
Dichelachne rara	11	+0.345	30
Drapetes ericoides	11	+0.745	0.8
Epilobium keysseri	8	+0.484	21
Euphrasia mirabilis	10	+0.164	62
Eurya brassii	7	+0.036	92
Festuca crispate-pilosa	6	+0.143	78
Festuca papuana	13	+0.769	0.2
Gaultheria mundula	15	+0.068	84
Gentiana cruttwellii	6	+0.771	8.0
Gentiana ettingshausenii	18	+0.203	44
Gentiana piundensis	9	+0.583	10
Geranium potentilloides	8	+0.666	7.0
Gnaphalium breviscapum	13	+0.582	3.6
Gnaphalium japonicum	5	-0.300	65
Haloragis halconensis	12	+0.378	22
Hierochloe redolens	14	-0.380	19

Fig. 7-6 (cont'd)

Species	No. Sites n	Spearman's Coefficient of Rank Correlation ρ	Probability of Obtaining Rank by Chance (%)
Hypericum macgregorii	7	-0.071	85
Lactuca laevigata	21	+0.594	0.4
Lycopodium clavatum	6	+0.200	70
Lycopodium selago	10	+0.564	9.4
Monostachya oreoboloides	9	+0.300	45
Olearia spectabilis	9	+0.150	70
Oreomyrrhis linearis	10	+0.855	0.2
Oreomyrrhis papuana	8	+0.789	2.2
Oreomyrrhis pumila	9	+0.617	7.4
Oxalis magellanica	7	0	100
Papuapteris linearis	6	+1.000	< 0.1
Parahebe ciliata	10	+0.588	7.0
Pedilochilus sp.3	7	+0.679	7.4
Pilea cf. *johniana*	13	+0.484	10
Poa callosa	12	-0.208	50
Poa crassicaulis	14	+0.088	77
Poa epileuca	9	+0.250	51
Poa saruwagetica	16	+0.326	21
Potentilla ?foersteriana	21	+0.094	69
Potentilla papuana	19	+0.442	6.2
Ranunculus pseudolowii	10	-0.030	92
Ranunculus saruwagedicus	5	+0.200	72
Ranunculus schoddei	6	+0.600	21
Schoenus maschalinus	8	+0.096	85
Senecio papuanus	10	+0.188	63
Styphelia suaveolens	21	+0.310	18
Tetramolopium macrum	15	+0.442	9.6
Trigonotis papuana	16	-0.113	70
Trochocarpa dekockii	8	+0.079	85
Uncinia riparia	11	+0.491	12
Uncinia sp.1	11	+0.409	23
Vaccinium amblyandrum	20	+0.238	33
Viola arcuata	6	+0.657	16
Average	10.67	+0.345	35 (n = 10) 30 (n = 11)

correlated and only 9 negatively, suggesting that most species favour eastern slopes at the top of their range and western at the bottom. 3 species are positively correlated at the 0.1% level of significance, a further 6 at the 1% level, and a further 15 at the 10% level, comprising 36% of all species examined. These are listed below. None of the 9 species showing negative correlations is significant at the 10% level.

Probability < 0.1%

Astelia papuana
Coprosma divergens
Papuapteris linearis

Probability 0.1 - 1.0%

Agrostis reinwardtii
Deschampsia klossii
Drapetes ericoides
Festuca papuana
Lactuca laevigata
Oreomyrrhis linearis

Probability 1.0 - 10%

Anthoxanthum angustum
Danthonia vestita
Deyeuxia brassii
Gentiana cruttwellii
Gentiana piundensis
Geranium potentilloides
Gnaphalium breviscapum
Lycopodium selago
Oreomyrrhis papuana
Oreomyrrhis pumila
Parahebe ciliata
Pedilochilus sp.3
Pilea cf. *johniana*
Potentilla papuana
Tetramolopium macrum

Therefore all species for which sufficient data have been assembled (66) either grow preferentially on eastern slopes at high altitudes and western at low (24 at less than the 10% probability level of significance), or show no significant aspect preference with altitude. Since both maximum and minimum temperatures fall with increasing altitude, and since eastern slopes have higher maxima but lower minima than western slopes, these results suggest a strong tendency for species distribution to be controlled by critical maximum temperatures, but none for them to be controlled by minima, within the area above 3230 m on Mt Wilhelm.

On the other hand several species growing in the mountain grasslands of Mt Wilhelm are damaged severely by frost during spells of unusually clear weather. Individuals of some alien species, including *Crassocephalum crepidioides*, *Erigeron sumatrensis* and *Tacsonia mollissima*, but no natives, have been observed to be completely killed by frost between 3400 m and 3480 m. After heavy frost during and preceding the night of 12-13 June 1972, 11 of 34 native species growing in the immediate vicinity of the research station at 3480 m were noted as suffering light or moderate damage (see section 6-G). At higher altitudes on other occasions fairly severe frost damage was observed to several species especially *Gaultheria mundula* at 4036 m and *Ranunculus saruwagedicus* at 4300 m. Presumably individuals occurring above the usual range of their species would be liable to repeated frost damage and therefore be at a competitive disadvantage.

Nevertheless, despite observations of frost damage and although distributions of species on Mt Wilhelm are no doubt controlled by a complex of factors of different importance to each, it seems clear that maximum temperatures are of general ecological importance. It is also possible that total radiation is important in itself as well as in its thermal effect upon the plants' environment. Hnatiuk [in prep.] has shown that *Deschampsia klossii* on Mt Wilhelm has low carbohydrate reserves and that its photosynthetic system is probably not light-saturated on cloudy days. This raises the question whether light itself can, with competition, be limiting to some species on slopes of western aspect receiving less insolation than those of eastern aspect.

There is no clear relationship between growth form and a species' display of an aspect preference shifting with altitude. Of the species listed above *Coprosma divergens* is a shrub and *Drapetes ericoides* though small has woody stems. Many growth forms are present among the herbs, from the small creeping *Pilea* cf. *johniana* to the large tussock grass *Deschampsia klossii*. The 24 species listed include two pteridophytes, *Lycopodium selago* and *Papuapteris linearis*.

The conclusion that maximum but not minimum temperatures are limiting to most grassland plant species on Mt Wilhelm is matched by similar conclusions from other high mountain regions. Billings and Mooney [1968], writing mainly of north temperate mountain and arctic plants, state "Higher day time temperatures are closely allied with photosynthetic processes and thus it is day time temperature that marks the real boundary between the true arctic or alpine tundra and subarctic or subalpine meadows." Dahl [1951] and Conolly and Dahl [1970] have shown that maximum temperatures limit the distributions of mountain plants of northwest Europe.

7-E ASPECT OF SLOPE AND FLORISTIC ELEMENTS

Mt Wilhelm has a highly oceanic, or perhaps more correctly quasioceanic, climate. Poore and McVean [1957] in discussing oceanic climates of northwest Europe provide figures of Kotilainen's Index of Oceanicity up to 417 for Norway and to 452 for Scotland. This index is calculated from the formula

$$k = \frac{N \cdot dt}{100\Delta}$$

where N is precipitation in mm, dt is the number of days each year with mean temperature between 0 and 10 °C, and Δ is the difference between the mean temperatures of the coldest and warmest months. Kotilainen's index (although admittedly devised for temperate zones only) calculated for the Pindaunde research station is about 6,200!

Most of the plants of probable Plio-Pleistocene immigration to the New Guinea highlands probably came from regions of, to varying extents, more continental climate. Since the microclimate at ground level is drier and has a larger range of temperature on eastern slopes than on western, I considered it possible that some floristic elements, in particular geographic divisions within the peregrine element, may show consistently a preference for eastern slopes.

All species occurring at five or more of the 21 sites with opposing east and west aspects examined and which occur on more than twice as many eastern aspects as western, or vice-versa, are tabulated in Fig. 7-7. 13 species of which 2 are pteridophytes are listed as possibly preferring eastern slopes at all altitudes examined, and 9 species, all angiosperms, as possibly preferring western slopes.

The angiosperms preferring eastern slopes are all of putative Plio-Pleistocene immigration, as are those on western slopes except for the three species of *Oreomyrrhis* which belong in the gondwanic element. This may lack significance, though interesting in itself, because if altitudinal ranges are examined an ecological explanation appears as described below. Within the peregrine element there is no pattern of

	No. sites with more eastern quadrats occupied than western	No. sites with same no. quadrats occupied on both aspects	No. sites with more western quadrats occupied than eastern	Total no. eastern quadrats occupied	Total no. western quadrats occupied	Floristic element	Altitudinal range in Mt Wilhelm area (m)	Mean of extremes of altitudinal range on Mt Wilhelm (m)
Preferring eastern slopes								
Anaphalis lorentzii	4	-	1	18	9	PW	2700-3718	3209
Danthonia penicillata	5	1	2	25	18	PWS	2582-3901	3241
Dichelachne rara	8	2	1	63	39	PSS	2738-3658	3198
Epilobium keysseri	6	1	1	33	21	PW	2896-4035	3465
Gnaphalium japonicum	4	-	1	17	3	PWW	2750-3560	3155
Hypericum macgregorii	5	2	-	38	18	PW	2740-4115	3427
Lycopodium clavatum	6	-	-	18	5	-	2740-3800	3270
Papuapteris linearis	4	1	1	34	14	-	3600-4400	4000
Pilea cf. *johniana*	8	2	3	76	53	PW	2740-4298	3549
Poa saruwagetica	10	5	1	123	80	PW	2753-4207	3480
Schoenus maschalinus	6	1	1	40	16	PW	2770-4000	3385
Senecio papuanus	6	2	2	47	34	PW	2900-3600	3250
Viola arcuata	4	1	1	25	12	PW	2440-3920	3180
Preferring western slopes								
Festuca papuana	4	-	9	57	56	PW	3962-4390	4176
Oreomyrrhis linearis	3	-	7	42	48	G	3170-4030	3600
Oreomyrrhis papuana	-	2	6	27	50	G	3200-3800	3500
Oreomyrrhis pumila	1	2	6	51	71	G	3600-4500	4050
Poa callosa	2	4	6	66	76	PW	3413-4500	3956
Poa crassicaulis	4	1	9	71	87	PW	3450-4450	3950
Poa epileuca	2	1	6	23	37	PW	3541-4115	3828
Potentilla ?foersteriana	5	4	12	100	134	PN	3230-4460	3845
Uncinia riparia	3	-	8	25	41	PSS	3170-4115	3642

Fig. 7-7: Species possibly occurring preferentially on either eastern or western slopes at all altitudes sampled (3230-4297 m).

geographic elements significantly different from their distribution within the total element amongst species on either eastern or western slopes.

Most of the species preferring eastern slopes in the altitudinal range sampled (3230-4297 m) grow also at levels lower than 3000 m, and are therefore being examined only in the upper parts of their vertical ranges. As already shown, species tend to occur preferentially on slopes of eastern aspect at the tops of their ranges, and therefore their apparently consistent preference for such slopes is probably an artefact resulting from sampling only above 3230 m. Similarly most of the species apparently preferring western slopes are species of high altitude not found below 3200 m, and are being sampled over most or all of their ranges and perhaps most intensively in the lower parts. Altitudinal ranges of all species possibly consistently preferring either eastern or western slopes are given in Fig. 7-7, together with the means of highest and lowest records for each species. The mean of these means for the eastern species is 3370 m and for the western ones, 3839 m. Altitudinal ranges are discussed in more detail in section 8-C, and their relationship with floristic elements in section 8-E.

Since maximum temperatures are apparently of greater ecological importance than minima to plants of arctic and "alpine" environments generally [Billings and Mooney, 1968], and since I have shown that eastern slopes have higher maximum temperatures than western, it can be argued that a shifting preference with altitude from western to eastern slopes shows a high degree of adaptation to the environment of Mt Wilhelm's grasslands. In this regard it is of great interest to find that species of presumed longer history in the area are better represented amongst those which display this trend to a significant degree than are more recent immigrants.

Fig. 7-8 shows the numbers of species in the different floristic elements (as defined in section 3-G) amongst the 63 angiosperm species occurring in at least 5 of the 21 sites of opposing east/west aspects examined; and amongst the 22 species which, of the 63, show to a significant extent an increasing preference for eastern slopes with increasing altitude. Angiosperm species with significantly shifting aspect preferences are listed below by floristic element.

	Number of Species in 5 or More Sites with Opposing East/West Aspects Examined	Number of Species Showing Significantly Increasing Preference for Slopes of Eastern Aspect with Increasing Altitude	Number of Species Not Showing Significantly Increasing Preference for Slopes of Eastern Aspect with Increasing Altitude
E	3	2	1
G	5	4	1
?G	5	3	2
PW	32	12	20
PN	4	1	3
PS	3	0	3
PWW	2	0	2
PWN	0	0	0
PWS	4	0	4
PNN	0	0	0
PSS	5	0	5
A	0	0	0
Malesian endemic species in peregrine element	39	13	26
More widespread species in peregrine element	11	0	11
Ancient immigrants	13	9	4
Peregrine element	50	13	37
Total	63	22	41

Fig. 7-8: Numbers of species in floristic elements showing and failing to show a shifting preference for slopes of eastern aspect with altitude.

G: *Drapetes ericoides*
Oreomyrrhis linearis
Oreomyrrhis papuana
Oreomyrrhis pumila

?G: *Astelia papuana*
Coprosma divergens
Parahebe ciliata

E: *Pedilochilus* sp.3
Tetramolopium macrum

PW: *Agrostis reinwardtii*
Anthoxanthum angustum
Danthonia vestita
Deschampsia klossii
Deyeuxia brassii
Festuca papuana
Gentiana cruttwellii
Gentiana piundensis
Geranium potentilloides
Gnaphalium breviscapum
Lactuca laevigata
Pilea cf. *johniana*

PN: *Potentilla papuana*

Considering those elements of presumed longest residence in New Guinea, 2 of 3 endemics (E) and 7 of 10 gondwanics (G+?G) common enough to be considered showed a significant change in aspect preference with increasing altitude. By contrast only 13 of 50 species of presumed Plio-Pleistocene immigration did so. This is significant at the 1% level ($\chi^2 = 8.66$, $n = 1$). Within the peregrine element all species showing shifting aspect preference are Malesian endemic species; none of the eleven species found also outside Malesia occurring in at least five quadrats show this. Though numbers are not large this is nevertheless easily significant at the 5% level ($\chi^2 = 6.59$, $n = 1$): it is reasonable to presume that the Malesian endemic species have a longer history within the region than species also occurring elsewhere. Evidently the fine adaptation to the tropicalpine environment reflected in a shifting aspect preference with altitude is a process accompanying speciation and continuing to the point of generic differentiation.

CHAPTER 8

DISTRIBUTION IN NEW GUINEA

8-A THE DATA

Herbarium material of almost all herbaceous angiosperm taxa in the New Guinea mountain grassland flora was examined in the Botany Division herbarium, Forests Department, Lae, Papua New Guinea, and it is mainly upon data so derived that this chapter is based. Some further distributional data were gleaned from Flora Malesiana and from G.S. Hope [pers. comm., 1973], Koster [1966; 1972], Raven [1967] and Royen [1964a; 1964b]. However all these data display some substantial shortcomings, both in numbers of specimens collected and in their taxonomic treatment.

Davis and Heywood [1963] consider that knowledge of a region's flora progresses through four overlapping phases, the pioneer or exploratory, consolidation, biosystematic, and encyclopaedic phases. The flora of New Guinea is definitely in the first phase, the pioneer or exploratory one, primarily concerned with identification, in which "The flora is known mainly from limited herbarium material, often provided with meagre field data though usually well localised." The Pindaunde valley of Mt Wilhelm is the most intensively collected small area in the whole of New Guinea [J.S. Womersley, pers. comm., 1971] yet even here a new native species record was made during my own fieldwork, and two other species were found in the area for the first time in adjacent valleys; several species are still known from Mt Wilhelm from only single specimens.

Collections are fairly numerous from the Bismarck, Sarawaket and parts of the Owen Stanley ranges and from several mountains in the Mt Hagen area. The Kubor range and Krakte Mts are less well known floristically and the Star Mts hardly at all. Collections from the various mountains of Irian Jaya are scattered and few, many of which I have not been able to examine.

A second shortcoming is taxonomic. Many species remain to be described, and distribution studies are at times bedevilled by the use of different names for the same species in different localities. Very variable taxa occur which have in the past been described either as single species (e.g. *Haloragis halconensis*, *Hydrocotyle sibthorpioides*) or as several species (e.g. *Cerastium keysseri* and *papuanum*, *Geranium monticola* and *potentilloides*, *Viola arcuata*, *kjellbergii* and *lagaipensis*) depending upon the perceptions of the various taxonomic botanists who have described them. Some problems of taxonomy and species nomenclature relating to the non-forest flora of Mt Wilhelm have been discussed in section 3-C.

Therefore as with most other plant distributional studies this discussion rests on data derived from incomplete collections and inconsistent taxonomy. I have attempted to minimize these difficulties by adopting a fairly uniformly wide species concept and by restricting discussion in some of the following sections to the flora of the best-known mountains in New Guinea or to Mt Wilhelm alone. I believe that the data are of adequate quantity and quality to result in reliable conclusions, albeit of a tentative nature.

8-B COMPARISON OF NEW GUINEA MOUNTAIN GRASSLAND FLORAS

For comparative purposes the mountains of Papua New Guinea were divided into several more or less natural regions as shown in Fig. 8-1, of which the extent of knowledge of their floras has been indicated above. What data were available for the West Irian mountains were lumped as an eighth category, but this and the limited collections from the Star Mts were considered inadequate for more than superficial comparison.

A full list of plant taxa considered is given in Appendix 7. An attempt was made to include all herbaceous angiosperm species found commonly or solely in non-forest habitats above 3000 m, excluding known aliens. A total of 252 species in 75 genera is involved.

The number of species held in common by all pairs of mountain regions considered is shown in Fig. 8-2A, together with total herbaceous angiosperm floras and numbers of species endemic to particular regions. It can be seen at once that the Star Mts have a small collected flora, while that of Irian Jaya, an area as large and diverse as all Papua New

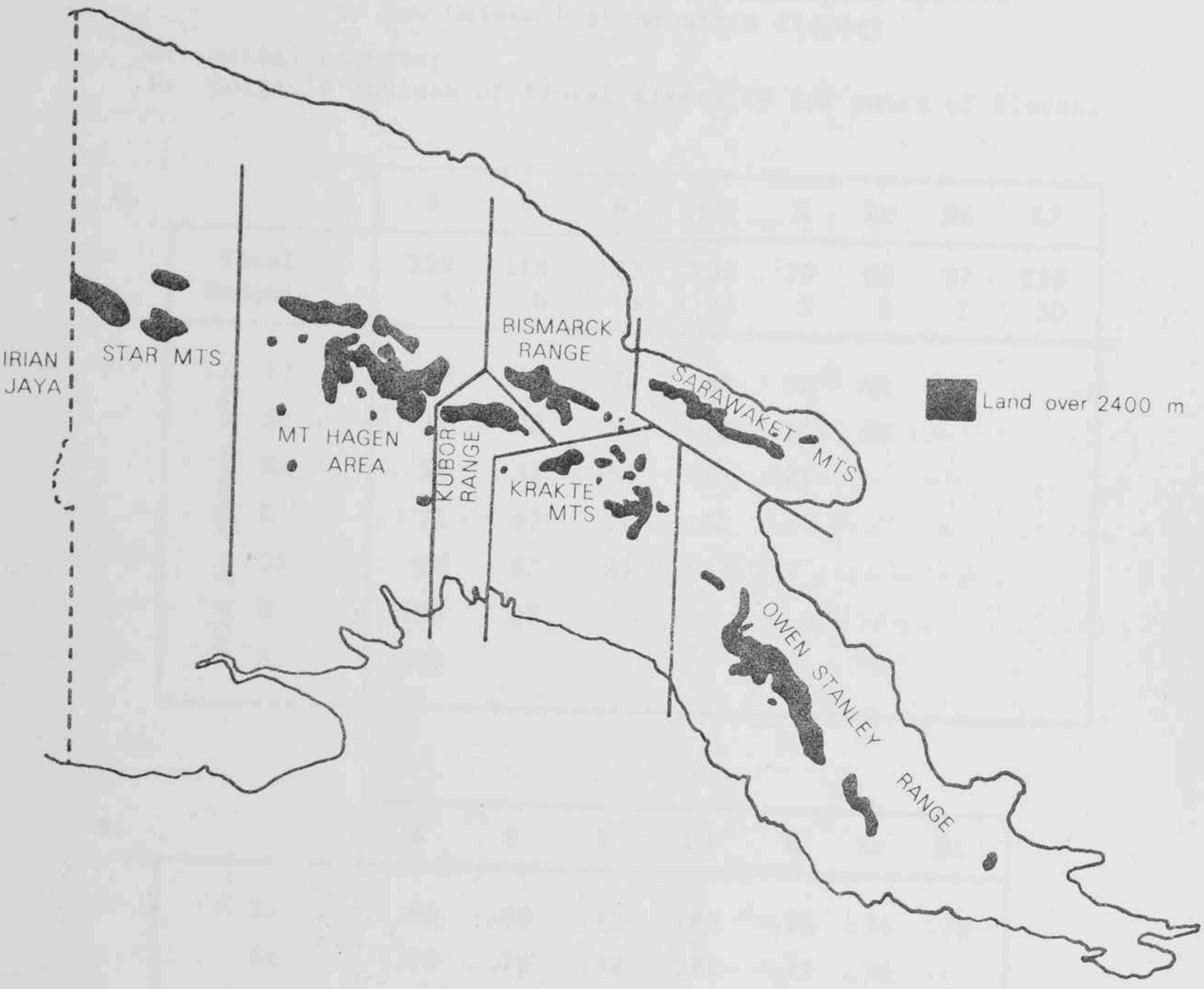


Fig. 8-1: Mountain areas of eastern New Guinea [map after Brown and Pain, 1970].

Guinea, has a recorded flora only about the size of each of the better collected regions within Papua New Guinea. Particularly in these areas many species probably remain to be discovered. It is also clear that the largest numbers of endemic species are in Irian Jaya (50 of 139) and the Owen Stanley range (25/135) which are at the western and eastern limits of the region being considered and are the most fragmented areas. The lowest number of endemics is found in the Kubor range (2 of 79) and the Krakte mountains (1 of 60) which are most central.

More detailed comparison between the floras can be made by calculating Colgan's Index of Floral Diversity for every pair of areas. This index [Praeger, 1911; Wace and Dickson, 1965] puts a numerical value upon the degree of difference of pairs of floras such that the index of

Fig. 8.2: Numbers of herbaceous angiosperm species in New Guinea high mountain floras:

A: actual numbers;
B: Colgan's indices of floral diversity for pairs of floras.

A.

		B	S	H	OS	K	Kr	St	IJ
Total		129	118	123	135	79	60	37	139
Endemic		4	6	6	25	2	1	1	50
Held in common with	IJ	69	66	72	68	50	42	32	
	St	30	28	32	28	25	19		
	Kr	55	51	54	53	42			
	K	71	67	70	62				
	OS	94	83	87					
	H	103	87						
	S	99							

B.

	B	S	H	OS	K	Kr	St
IJ	.65	.66	.63	.68	.71	.74	.78
St	.78	.78	.48	.81	.72	.76	
Kr	.59	.60	.58	.63	.56		
K	.48	.48	.47	.59			
OS	.44	.51	.49				
H	.30	.44					
S	.33						

B - Bismarck range
S - Sarawaket Mts
H - Mt Hagen area
OS - Owen Stanley range
K - Kubor range
Kr - Krakte Mts
St - Star Mts
IJ - Irian Jaya

identical floras is zero and of totally different floras, unity. Its calculation has been described in section 4-C. Other less simple methods for comparing insular floras [e.g. Tobler and others, 1970; Williams, 1947] have not been used due to paucity of data on not only the floras considered but also the areas occupied by them.

Colgan's Indices calculated from the present data are presented (for species) in Fig. 7-2B. These figures are largest for pairs one or both of which have not been well explored botanically, notably Irian Jaya (0.63-0.78) and the Star Mts (0.48-0.81), as well as the Krakte Mts (0.56-0.76) and the Kubor range (0.47-0.72). These high indices of diversity are probably due in large part to their floras being incompletely known.

The other four mountain areas considered, the Mt Hagen area, Sarawaket Mts and the Bismarck and Owen Stanley ranges, are relatively well known botanically, and share indices of species diversity of 0.30 to 0.50. These indices are correlated with least distance, *via* "stepping-stone" areas in some cases, across land lower than 2400 m between the mountain areas being considered, using Spearman's ρ as a measure of correlation between the ranking of pairs by species indices of floral diversity and by distance of separation (see section 7-D). The probability of such correlation of ranking occurring by chance is 4% ($\rho = 0.83$).

However the distribution of genera (see Fig. 8-3A) presents a different picture. Only Irian Jaya has genera (3) not found in any of the other areas considered. As with species the highest indices of diversity (see Fig. 8-3B) involve pairs including undercollected areas, notably the Star Mts but also Irian Jaya, the Krakte Mts and the Kubor range. However if the indices of generic diversity for pairs between the four better known areas are considered, no correlation with distance of separation emerges ($\rho = 0.43$, probability 40%), and there is only weak correlation with ranking by species indices of diversity ($\rho = 0.71$, probability 12%). The lowest indices of generic diversity are for pairs including the Bismarck range (including Mt Wilhelm) which is located fairly centrally and has the second highest number of recorded genera of all the areas considered.

Ordination of the indices of species diversity of these floras [mainly after Bray and Curtis, 1957] shows the four well-collected floras of the Mt Hagen area, Sarawaket Mts and Bismarck and Owen Stanley ranges to lie consistently together. The Bismarck range, including Mt Wilhelm, falls in a central position within this cluster in all three ordination plots as well as geographically (see Fig. 8-4).

Fig. 8-3: Numbers of herbaceous angiosperm genera in New Guinea high mountain floras:

A: actual numbers;
B: Colgan's indices of floral diversity for pairs of floras.

A.

		B	S	H	OS	K	Kr	St	IJ
Total		68	63	64	69	52	46	31	61
Endemic (within N.G.)		0	0	0	0	0	0	0	3
Held in common with	IJ	56	55	55	56	46	43	30	
	St	30	30	29	30	27	21		
	Kr	45	43	44	45	39			
	K	52	49	49	52				
	OS	66	60	61					
	H	58	58						
	S	61							

B.

	B	S	H	OS	K	Kr	St
IJ	.28	.24	.25	.27	.34	.36	.54
St	.57	.53	.56	.57	.52	.62	
Kr	.35	.35	.33	.36	.34		
K	.24	.26	.27	.25			
OS	.07	.17	.15				
H	.14	.16					
S	.13						

B - Bismarck range
S - Sarawaket Mts
H - Mt Hagen area
OS - Owen Stanley range
K - Kubor range
Kr - Krakte Mts
St - Star Mts
IR - Irian Jaya

It appears from this analysis that the distribution of species on mountains within New Guinea can be largely or fully explained in terms of present geography. Since several of the mountains, like the Sarawaket Mts and several peaks in the Mt Hagen area, are entirely of Plio-Pleistocene uplift or origin, we are led to look for the origins of these floras at species rank within only the last few million years. This

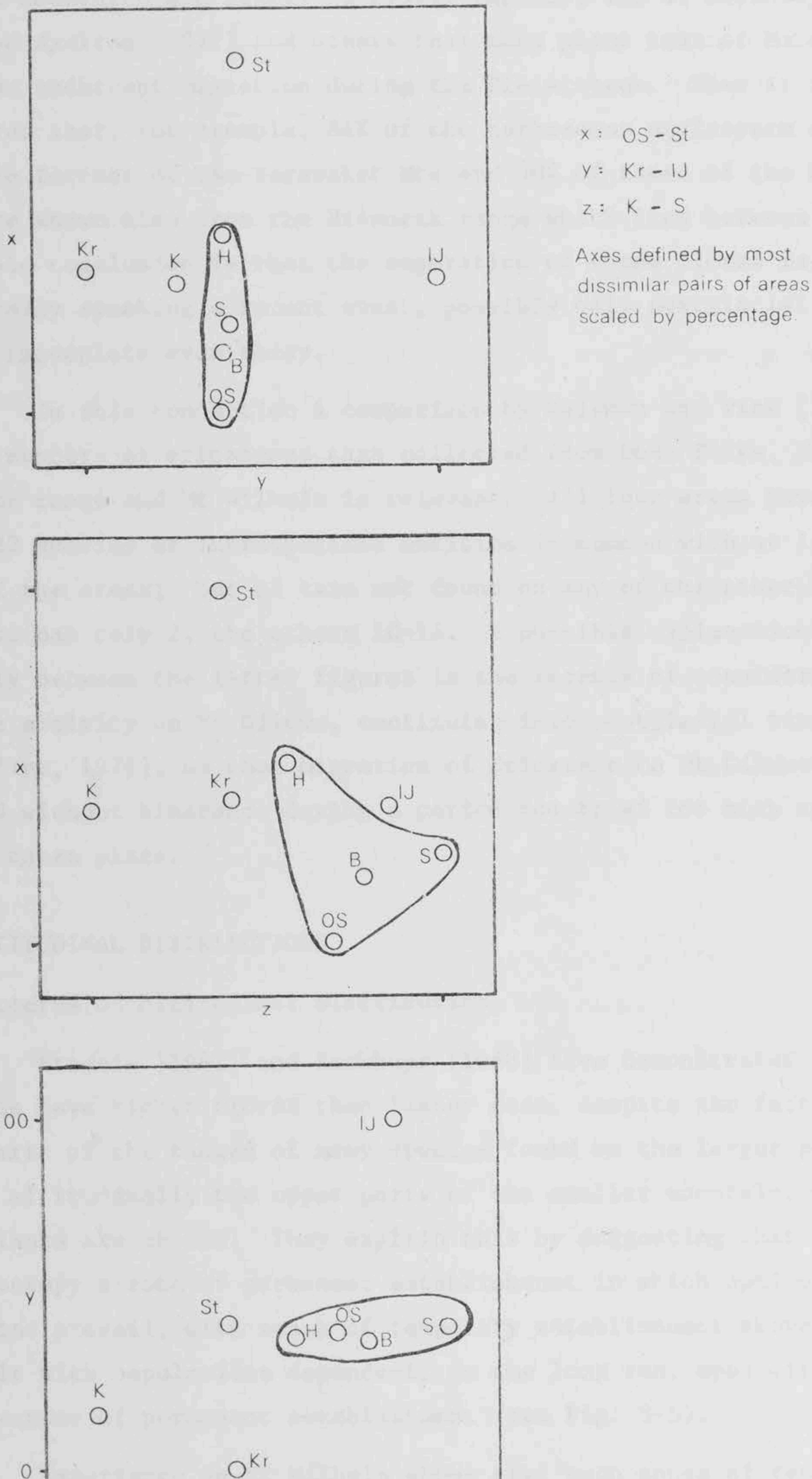


Fig. 8-4: Ordination of New Guinea mountain grassland floras. Abbreviations of areas as in Fig. 8-2, page 192.

recalls the arguments of Morton [1972] that small isolated populations on tropical mountains are likely to evolve rapidly, and of Holloway [1970], Raven and Axelrod [1972] and others that many plant taxa of Malesian mountains underwent migration during the Pleistocene. When it is considered that, for example, 84% of the herbaceous angiosperm species above the forests of the Sarawaket Mts and 90% of those of the Kubor range are known also from the Bismarck range which lies between them, a reasonable conclusion is that the separation of these floras is geologically speaking a recent event, possibly only postglacial and perhaps incomplete even today.

In this connection a comparison by Kalkman and Vink [1970] between numbers of ericaceous taxa collected from Doma Peaks, Mt Giluwe, the Kubor range and Mt Wilhelm is relevant. All four areas have between 19 and 22 species or intraspecific entities in common with at least one other of the areas; but of taxa not found on any of the other mountains Mt Giluwe has only 2, the others 10-14. A possible explanation of the disparity between the latter figures is the recency of considerable volcanic activity on Mt Giluwe, continuing into postglacial times [Blake and Löffler, 1971], so that migration of Ericaceae to Mt Giluwe may have occurred without hindrance during a period too brief for much speciation to have taken place.

8-C ALTITUDINAL DISTRIBUTIONS

(a) Patterns of Altitudinal Distribution

Steenis [1961] and Backhuys [1968] have demonstrated that high mountains have richer floras than lesser ones, despite the fact that the lower parts of the ranges of many species found on the larger peak overlap altitudinally the upper parts of the smaller mountain, where these plants are absent. They explain this by suggesting that mountain plants occupy a zone of permanent establishment in which optimum conditions prevail, with zones of temporary establishment above and below this belt with populations dependent, in the long run, upon disseminules from the zone of permanent establishment (see Fig. 8-5).

Experience on Mt Wilhelm shows that such zones of temporary establishment are a reality for at least some species. The upper zone of temporary establishment is especially clear for some wind-dispersed alien species. For example plants of *Crassocephalum crepidioides* and *Erigeron sumatrensis* not infrequently establish themselves on landslip sites above 3300 m. Such plants are commonly damaged or killed by frost before seeding, however, and it is clear that the continued presence of these species at such altitudes is dependent upon an inflow of disseminules from below 3000 m, where both are locally abundant. Native species may show the same phenomenon. In a sheltered gully facing northeast at 4085 m at the foot of Observatory Peak, *Acaena anserifolia*, *Cardamine altigena* and *Oxalis magellanica* were all growing more than 400 m above their usual altitudinal limits. Each species was represented by only a few individuals and it is not easy to imagine such colonies persisting for long periods without immigration of disseminules from the larger populations below 3650 m.

The lower zone of temporary establishment is well illustrated by scattered individuals well below their usual ranges growing on streambanks and in similar temporarily open habitats. For example individuals of *Agrostis reinwardtii*, *Cardamine altigena* and *Haloragis halconensis* grow below 2910 m along Pengagl Creek, and the artificially cleared path between 2910 and 3050 m supports single small colonies of *Gentiana ettingshausenii*, *Keysseria radicans* and *Triplostegia glandulifera* along its sides. *Carex echinata* reported by Brass [1964] near Pengagl Creek in 1959 had apparently died out there by 1972.

Wood [1971] points out that the "elevation effect", explained by Steenis and Backhuys in terms of zones of temporary establishment, can equally well be explained in terms of a raising of vegetation belts during a hypsithermal period, followed by a cooling to today's climate (see Fig. 8-6). Hope [1973] has provided some evidence of a hypsithermal period on Mt Wilhelm at about 5,000 yr ago. However Wood also points out that the two hypotheses are not contradictory, and that both effects may apply to any mountain species.

A separate phenomenon is the lowering of vegetation belts on isolated peaks, which is perhaps due in part to exposure to wind [Richards, 1964] or to soil factors [Grubb, 1971]. This lowering is largely a physiognomic phenomenon, the floristics of the same formation at different altitudes on different mountains being dissimilar. When a species is largely controlled in its distribution by biotic factors, a

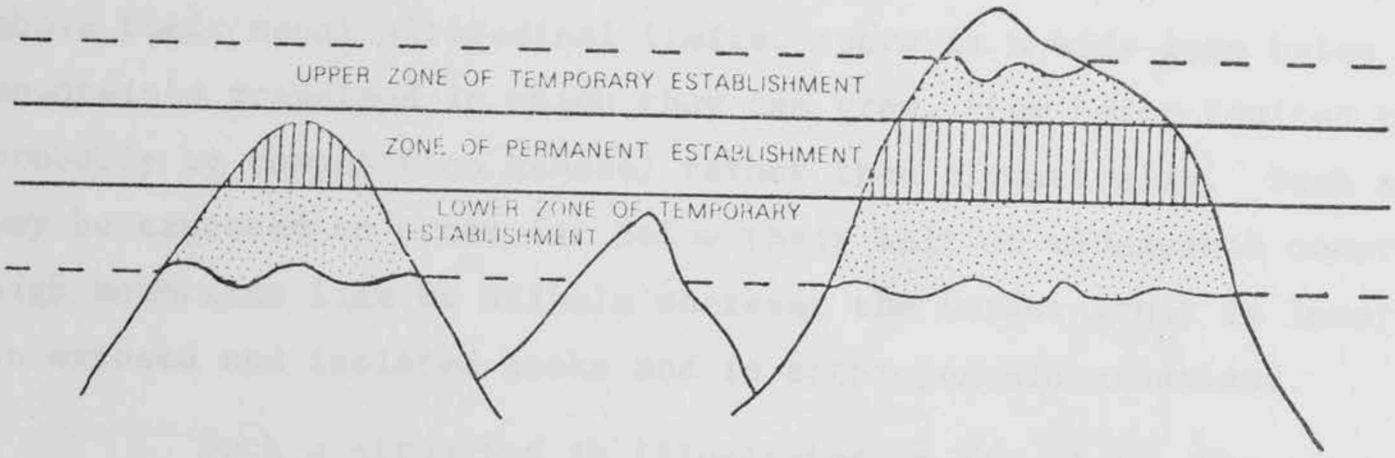


Fig. 8.5: Zones of permanent and temporary establishment [after Steenis, 1961].

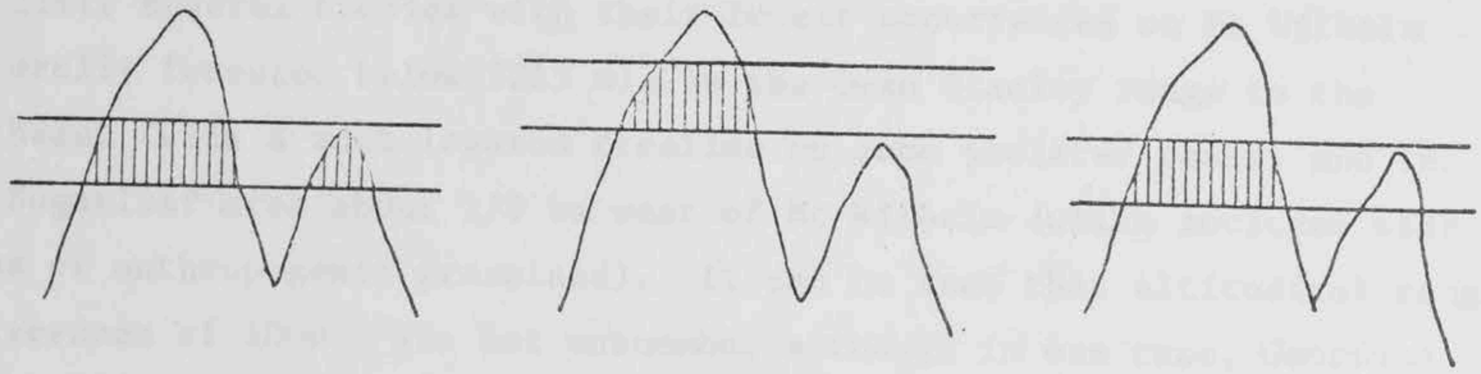


Fig. 8-6: The effect of a raising of the level of a limiting environmental factor upon the distribution of a species on two mountains [after Wood, 1971].

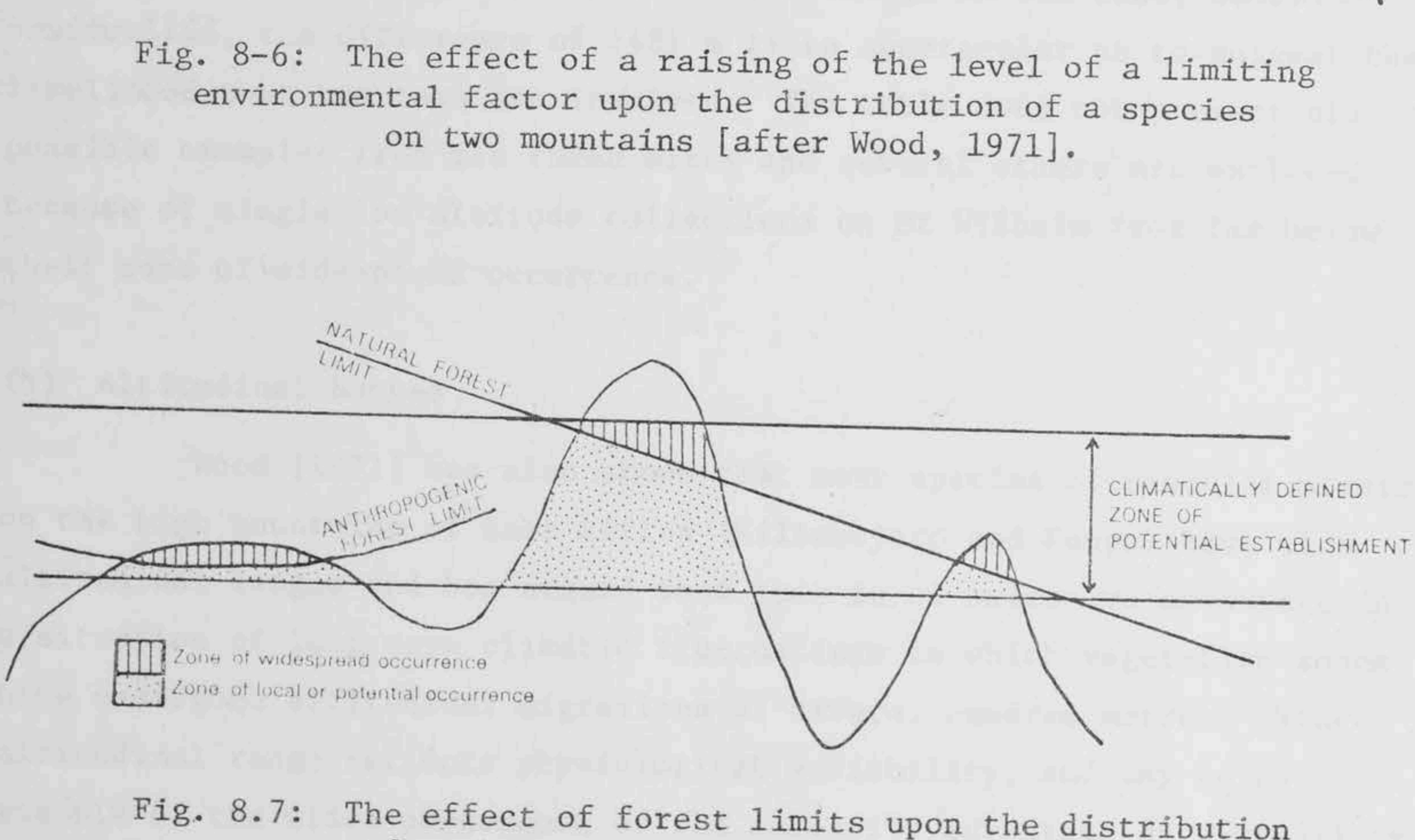


Fig. 8.7: The effect of forest limits upon the distribution of a shade-intolerant mountain plant.

change in physiognomy may result in its occurrence at lower altitudes on smaller mountains. This may be potentially so for the bulk of species of the New Guinea mountain grasslands.

It is my impression on Mt Wilhelm that although most species are only able to occupy very limited areas of favourable microclimate above their usual altitudinal limits, there is a wide zone below the mountain's grassland in which they can grow, they being limited there probably by competition (shade) rather than climatically. Such species may be expected to occur far below their belt of widespread occurrence on high mountains like Mt Wilhelm wherever the forest limit is lowered, as on exposed and isolated peaks and in anthropogenic grassland.

Such a situation is illustrated in Fig. 8-7. The zone of local or potential occurrence can perhaps be equated with Steenis' lower zone of temporary establishment. This phenomenon of apparently varied altitudinal ranges has been pointed out for several genera by Balgooy [1973] who compares stations in Malesia and the Western Pacific. Fig. 8-8 lists several species with their lowest occurrences on Mt Wilhelm (generally forested below 3215 m), in the Owen Stanley range to the southeast (with a much lowered treeline on some isolated peaks) and in the Sugarloaf area about 170 km west of Mt Wilhelm (which includes wide areas of anthropogenic grassland). It can be seen that altitudinal range differences of 1000 m are not uncommon, although in one case, *Gentiana cruttwellii*, the difference of 2481 m is so spectacular as to suggest the likelihood that two taxa are involved. The table does not present all possible examples from the three sites and several others are excluded because of single low altitude collections on Mt Wilhelm from far below their zone of widespread occurrence.

(b) Altitudinal Ranges

Wood [1971] has also shown that most species of vascular plants on the high mountains of East Africa (Kilimanjaro and Kenya) have wide altitudinal ranges and has argued that this is of selective advantage in a situation of long term climatic fluctuations in which vegetation zones have undergone altitudinal migrations of several hundred metres. Wide altitudinal range reflects physiological variability, and may be an example of the wider phenomenon of the selective advantage of variability in any situation of long term environmental fluctuation [Margalef, 1959].

Species	Owen Stanley Range	Sugarloaf Area	Mt Wilhelm
Anotis sp.1	2780	2530	3300
Anthoxanthum angustum	1524	2896	3109
Carex echinata	-	2530	3000
Carex gaudichaudiana	-	2530	3611
Centrolepis philippinensis	2743	-	3700
Danthonia archboldii	2250	2836	3300
Drapetes ericoides	1981	2896	3293
Gentiana cruttwellii	869	-	3350
Gentiana ettingshausenii	2833	2743	3063
Geranium potentilloides	2050	2896	3350
Oreobolus ambiguus	2515	-	3658
Poa crassicaulis	-	2896	3450
Potentilla foersteriana	2230	2700	3535
Potentilla parvula	2591	2560	3063
Scirpus subcapitatus	-	2896	3535
Senecio glomeratus	-	2591	3048
Tetramolopium macrum	-	2529	3535

Fig. 8-8: Lowest altitude records from three areas (m).

It is possible in altitudinally wide-ranging plant species for ecotypes to migrate up or down by gene flow, without the need for seed dispersal, by pollination of plants at one altitude by those of a different ecotype of the same species at another. No relationship between altitudinal range and pollination mechanism on Mt Wilhelm or elsewhere has been shown.

The altitudinal ranges of herbaceous angiosperm species occurring above 3215 m on Mt Wilhelm also tend to be wide, and are listed in Appendix 8. These ranges are displayed as a series of histograms in Fig. 8-9 together with corresponding data [from Wood, 1971] for vascular plants on Mt Kilimanjaro and Mt Kenya. The ranges presented here give no information on actual altitudes but only the altitudinal distance between the highest and lowest records. The Mt Wilhelm data are for all native herbaceous angiosperm species growing above the limit of unbroken forest (3215 m) and include records from all New Guinea (the highest collection usually being from Mt Wilhelm).

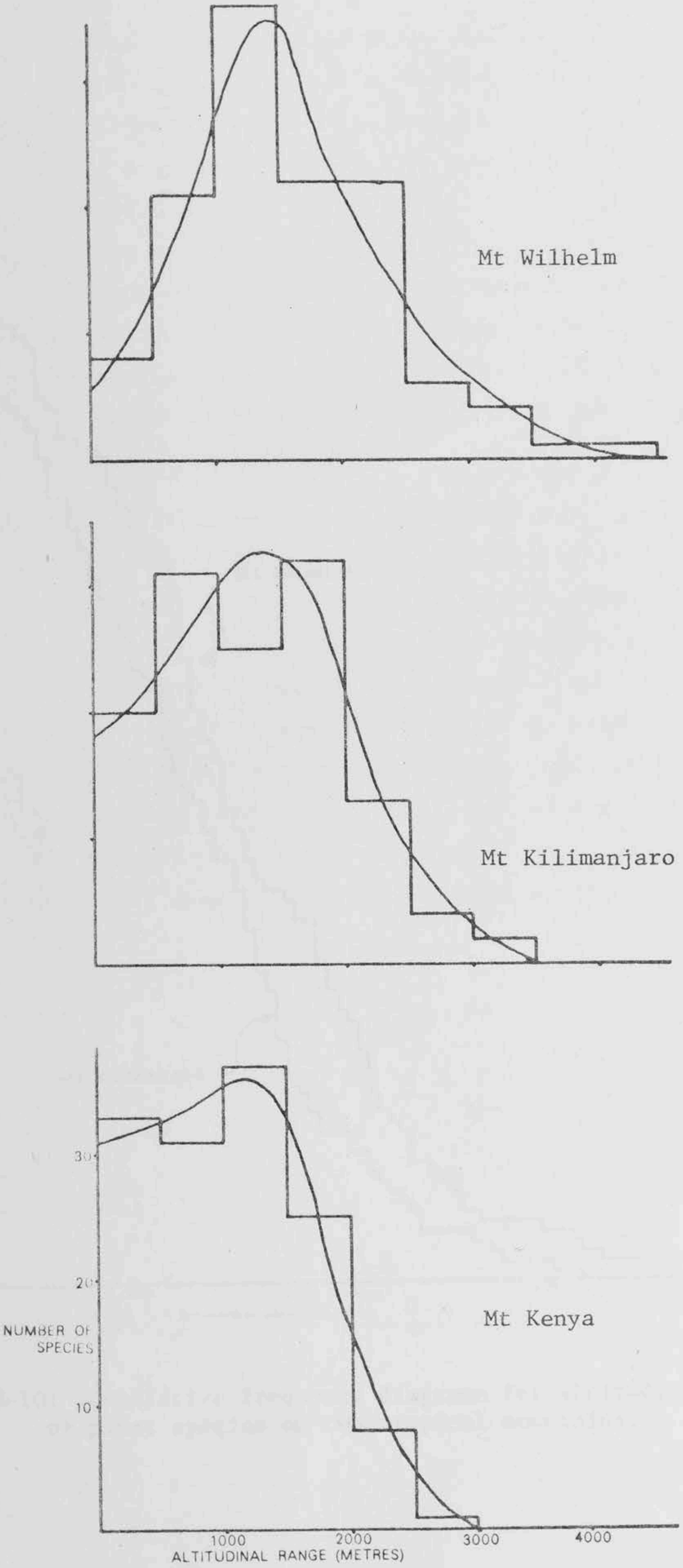


Fig. 8-9: Altitudinal ranges of plant species on three tropical mountains (curves drawn by eye).

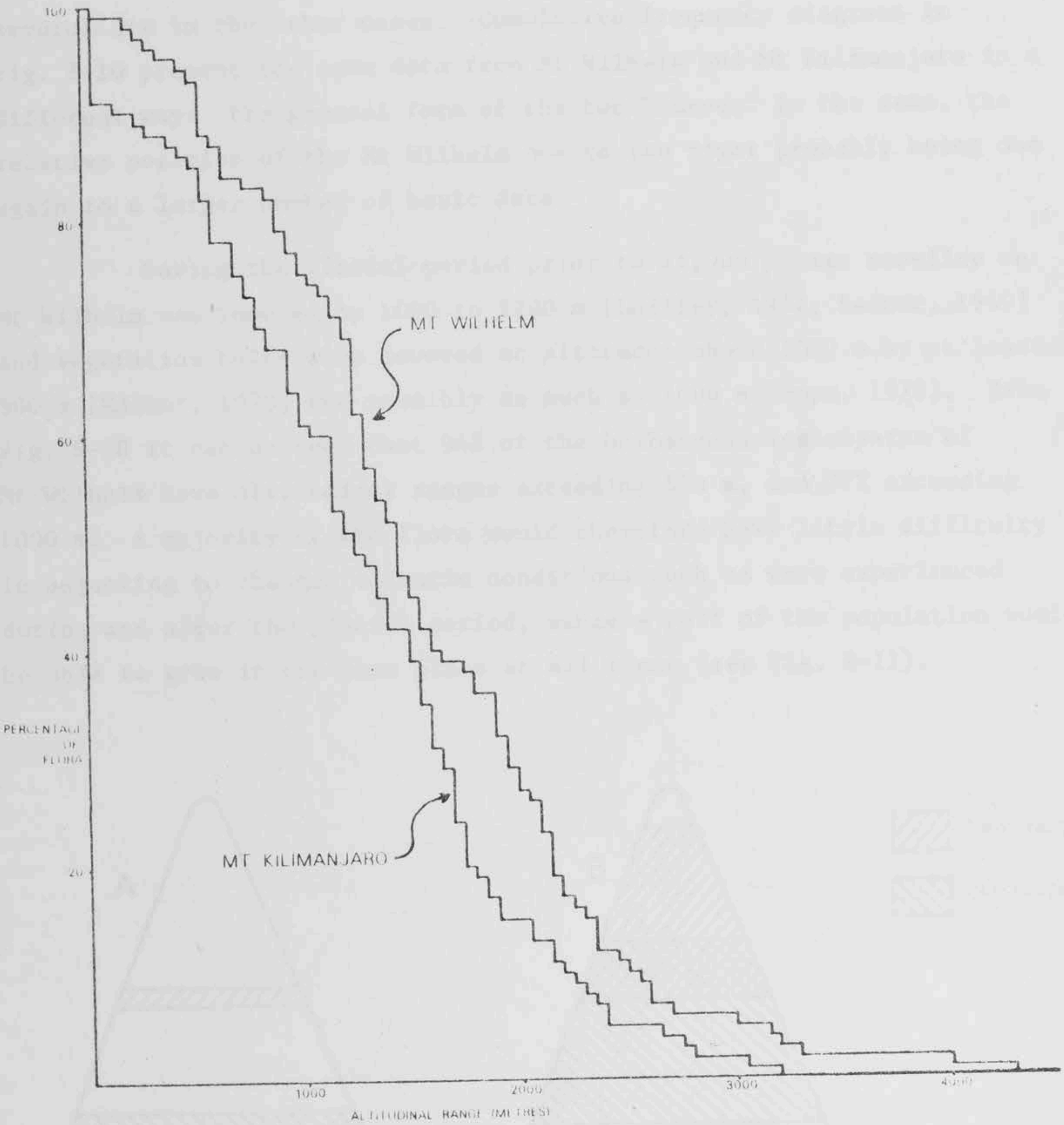


Fig. 8-10: Cumulative frequency diagrams for altitudinal ranges of plant species on two tropical mountains.

In all three cases the altitudinal ranges are generally great. The distribution of ranges approaches normality on Mt Wilhelm more nearly than for the African mountains, and the peak of distribution is further to the right, but this probably reflects no more than the larger number of collections from New Guinea: no species contributing to the Mt Wilhelm diagram are represented by only single collections whereas several are in the other cases. Cumulative frequency diagrams in Fig. 8-10 present the same data from Mt Wilhelm and Mt Kilimanjaro in a different way: the general form of the two "curves" is the same, the relative position of the Mt Wilhelm one to the right probably being due again to a larger number of basic data.

During the glacial period prior to 12,000 yr ago snowline on Mt Wilhelm was lowered by 1000 to 1200 m [Loffler, 1972; Reiner, 1960] and vegetation belts were lowered at altitudes above 2000 m by at least 500 m [Walker, 1970] and possibly as much as 1000 m [Hope, 1973]. From Fig. 8-10 it can be seen that 94% of the herbaceous angiosperms of Mt Wilhelm have altitudinal ranges exceeding 500 m, and 77% exceeding 1000 m. A majority of the flora would therefore have little difficulty in adjusting to changed climatic conditions such as were experienced during and after the glacial period, since a part of the population would be able to grow in the same place at all times (see Fig. 8-11).

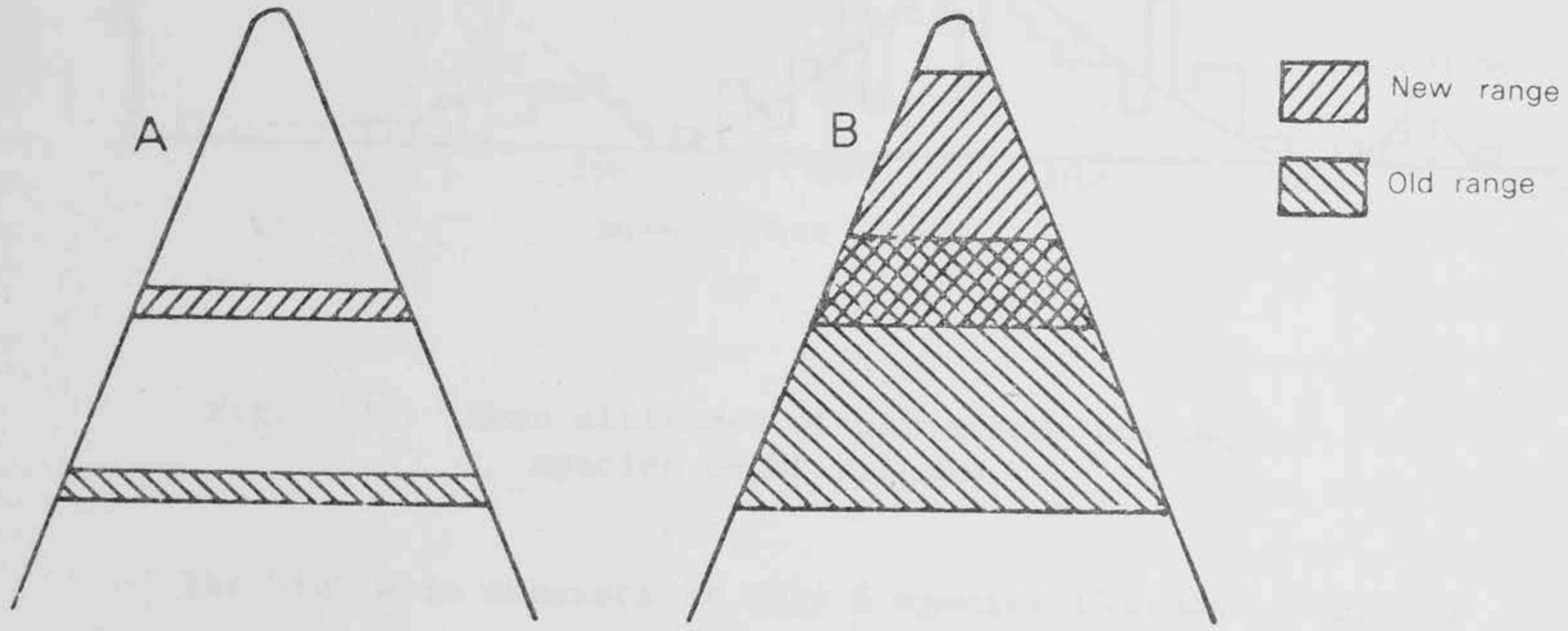


Fig. 8-11: Effect of a rise in altitude of limiting factors (e.g. warming of climate) upon A: a narrow-ranging, and B: a wide-ranging species [after Wood, 1971].

It is worth noting here that alien species tend to have even wider ranges than natives. Of 24 aliens found above 3215 m on Mt Wilhelm, 7 (29%) have altitudinal ranges in New Guinea exceeding 2500 m, while only 12 and 119 native species (10%) do so. If 6 alien species collected in New Guinea only once, on Mt Wilhelm, are excluded the proportion of aliens with such wide altitudinal ranges increases to 39%. No native species are included with only single records.

(c) Actual Altitudinal Distributions

As discussed in section 3-E the altitudinal distributions of individual species show considerable overlap in any single area, with no clear breaks marking floristic altitudinal belts. However if mean altitudes (average of highest and lowest records) and arranged in histogram form the resulting distribution can be arbitrarily interpreted as a trimodal one using class intervals with zero frequency as cutoff points (Fig. 8-12). A majority of species contributes to the middle of these three modes and shows a peak at about 3350 m. However, two exceptional groups form smaller high and low modes.

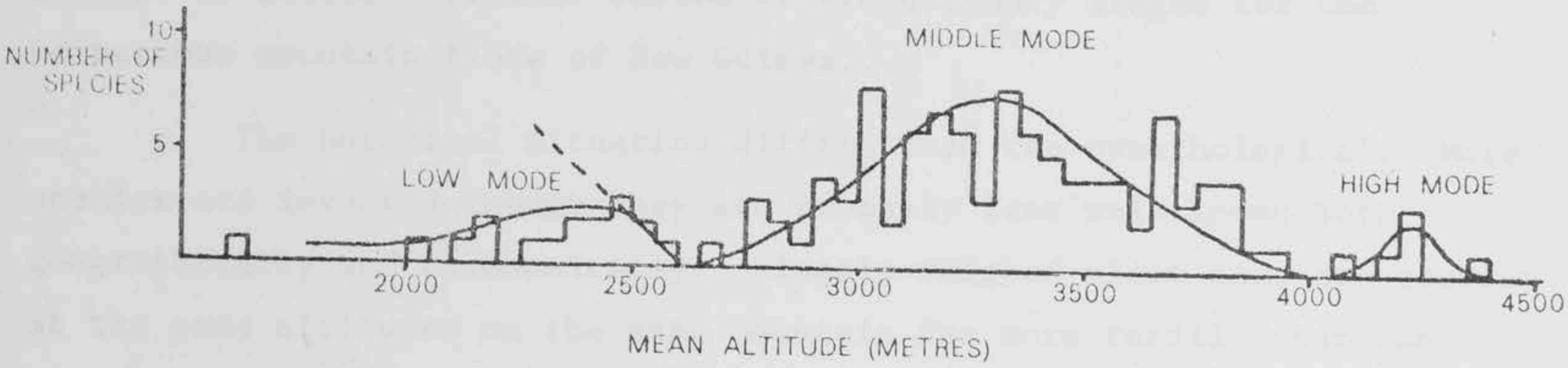


Fig. 8.12: Mean altitudes of herbaceous angiosperm species on Mt Wilhelm.

The high mode consists of only 6 species (*Lactuca* sp.1, *Poa* sp.1, *Ranunculus saruwagedicus*, *Senecio* sp.5, *Trigonotis* sp. aff. *papuana*, *Uncinia* sp.1) all of limited altitudinal range (< 600 m) and endemic to Mt Wilhelm or known also from a very few similar high peaks.

The low mode is less uniform but includes five species (*Gentiana cruttwellii*, *Haloragis halconensis*, *Lactuca laevigata*, *Ranunculus pseudolowii*, *Schoenus curvulus*) which are the obverse of the high mode, having very wide altitudinal ranges (> 3000 m and in the case of *Lactuca laevigata*, 4267 m). The other 12 species in this mode all seem to belong primarily to lower altitude floras, occurring only occasionally or in sheltered conditions above 3215 m: 4 are primarily herbs of the forest edge (*Cardamine africana*, *Galium rotundifolium*, *Polygonum runcinatum*, *Trigonotis procumbens*), and 8 are representatives of an adventive flora richly developed below 2500 m (*Carex euphlebia*, *Dichrocephala bicolor*, *Hypericum japonicum*, *Imperata conferta*, *Lobelia angulata*, *Miscanthus floridulus*, *Viola betonicifolia*, *Wahlenbergia marginata*).

8-D THE EVOLUTION OF NEW GUINEA MOUNTAIN GRASSLAND FLORAS

Diamond [1973], using the taxonomic and geographical relationships of bird populations in the mountains of New Guinea, has defined a series of stages of evolution from single bird species to two or more widespread and altitudinally separate species, each stage exemplified by several present day examples. This section represents an attempt to define a similar series of evolutionary stages for the herbaceous mountain flora of New Guinea.

The botanical situation differs from the ornithological. More species are involved though they are probably less well known both geographically and taxonomically. Closely related plant taxa can coexist at the same altitudes on the same mountain far more readily than can birds, perhaps due to the availability of a greater variety of ecological niches. Geographically separate plant populations can be in genetic contact with each other by pollination across distances greater than the usual dispersal range of either birds or plants. So it is not surprising that stages of evolution of flora are not directly comparable with those of the avifauna.

Nevertheless, certain stages can be defined. Fig. 8-13 illustrates these stages, the diagrams showing the types of distribution found at each stage in a hypothetical situation of three mountain areas rising to altitudes of 4500, 3500 and 4000 m respectively.

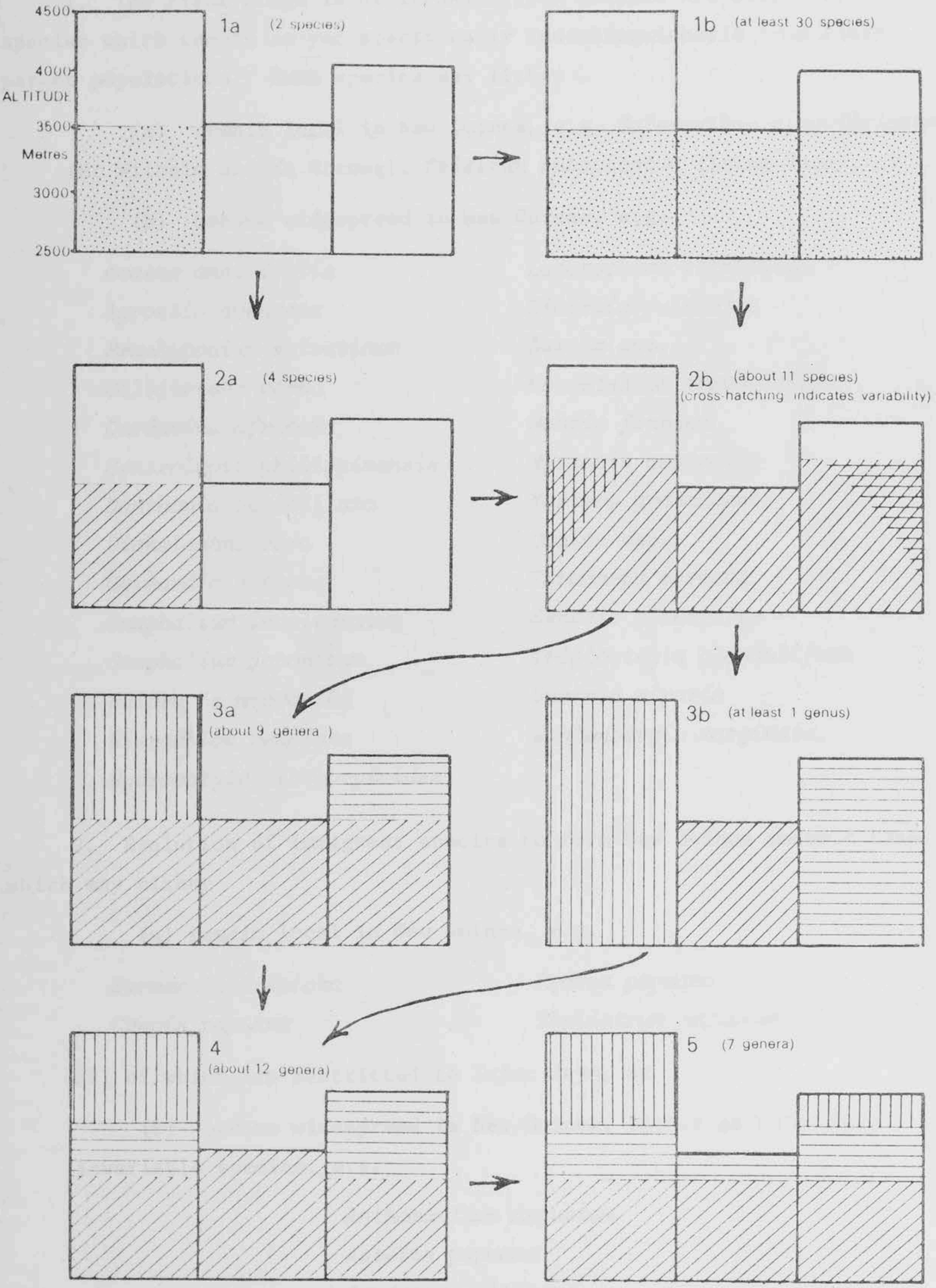


Fig. 8-13: Postulated stages in the evolution of New Guinea mountain grassland plant taxa.

1. The first stage is of invasion from outside New Guinea by species which remain as yet specifically indistinguishable from their parent populations. Such species may either

(a) remain local in New Guinea, e.g. *Scleranthus singuliflorus* (Mt Wilhelm and Mt Strong), *Trisetum subspicatum* (Irian Jaya), or

(b) become widespread in New Guinea, e.g.

Acaena anserifolia
Agrostis avenacea
Brachypodium sylvaticum
Callitriche verna
Cardamine africana
Centrolepis philippinensis
Danthonia penicillata
Dichelachne rara
Gaimardia setacea
Gnaphalium involucratum
Gnaphalium japonicum
Haloragis micrantha
Hierochloe redolens
Hydrocotyle sibthorpioides
Lagenophora stipitata
Libertia pulchella
Luzula spp.
Monostachya oreoboloides
Montia fontana
Myosotis australis
Nertera granadensis
Oxalis spp.
Peracarpa carnosa
Senecio glomeratus
Triplostegia glandulifera
Uncinia riparia
Wahlenbergia marginata.

2. Evolution of immigrant species to form New Guinea endemic taxa which may either

(a) remain local in New Guinea, e.g.

Burmannia disticha
Crepis papuana
Pratia papuana
Thalictrum papuanum,

all of which are restricted to Irian Jaya, or

(b) become widespread in New Guinea, either as relatively invariable species, e.g.

Anthoxanthum angustum
Astelia papuana
Cardamine altigena
Polygonum runcinatum

and perhaps *Anotis* sp.1

or as very variable species, e.g.

Cerastium papuanum	*Geranium potentilloides*
Cotula cf. *leptoloba*	*Gnaphalium breviscapum*
Drapetes ericoides	*Viola arcuata.*

3. (a) Evolution of local high altitude species from widespread and variable lower altitude species. Two good examples of genera showing this pattern, *Parahebe* and *Ranunculus*, are tabulated in Fig. 8-14. Other examples may include *Anaphalis*, *Lactuca*, *Lobelia*, *Sagina*, *Senecio*, *Uncinia* and *Wahlenbergia.*

(b) Evolution through geographical isolation of distinct species with no range of overlap. The two species of *Brachycome* provide a clear example:

B. elegans: Wharton range (part of Owen Stanley range) and Mt Giluwe, 2896-3200 m

B. papuana: Sarawaket Mts and Mt Wilhelm, 3353 m.

4. Limited migration between mountains in a mixed pattern of local and widespread species. In *Keysseria*, 3 species are restricted to Irian Jaya, 3 to the Owen Stanley range and 1 to the Krakte Mts while *K. gibbsiae* occurs in the Kubor and Owen Stanley ranges and in the Mt Hagen area as well as on Mt Kinabalu, and *K. radicans* is found in all the main mountain areas of New Guinea. The distribution of species of *Tetramolopium* in New Guinea is shown in Fig. 8-15. Other examples of this stage are:

Abrotanella
Euphrasia
Gentiana
Ischnea
Oreomyrrhis
Plantago
Trachymene

and perhaps *Deyeuxia*, *Eriocaulon* and *Papuzilla.*

5. Further migration between mountains leads to widespread sympatry as in:

Danthonia (*archboldii* & *vestita*)
Epilobium
Festuca
Galium
Poa
Potentilla
Trigonotis.

GENUS	WIDESPREAD SPECIES	Altitudinal Range (m)	LOCAL SPECIES	Distribution	Altitudinal Range (m)
PARAHEBE	*albiflora*	2438-3658	*ciliata*	Sarawaket Mts, Bismarck range, Mt Hagen	3231-4466
			polyphylla	Sarawaket Mts	?
			rigida	Mt Strong	3475-3505
			rubra	Owen Stanley range	2743-3100
			tenuis	Sarawaket Mts, Mt Wilhelm	3480-4100
			thymelioides	Kubor range	4163
			sp.	Mt Simpson	1169
RANUNCULUS	*pseudolowii* (including *basilobatus* and *brassii*)	869-4029	*amerophyllus*	Owen Stanley range	2896
			bidens	Kubor range	3590-4020
			keysseri	Sarawaket Mts, Bismarck and Owen Stanley ranges	2591-3505
			saruwagedicus	Sarawaket Mts, Mt Wilhelm	3962-4481
			schoddei	Mt Wilhelm	3643-4060
			wahgiensis	Bismarck range, Mt Hagen area	2700-3810
			sp.	Owen Stanley range	?

Fig. 8-14: The distribution in Papua New Guinea of two genera each with single widespread low altitude species and several local higher altitude species.

Fig. 8-15: Distribution of *Tetramolopium* in New Guinea.

	West Irian	Sarawaket Mts	Bismarck range	Mt Hagen area	Star Mts	Kubor range	Krakte Mts	Owen Stanley range
T. alinae	+	+	+				+	+
T. bicolor	+							
T. ciliatum		+						
T. cinereum								+
T. corallioides	+							
T. distichum	+							
T. ericoides	+							
T. fasciculatum	+							
T. flaccidum								+
T. gracile				+				
T. klossii	+				+			
T. lanatum	+							
T. macrum	+	+	+	+		+	+	+
T. piloso-villosum	+							
T. procumbens				+				
T. prostratum	+							
T. pumilum								+
T. spathulatum		+						
T. tenue	+							
T. virgatum	+				+			
T. wilhelminae	+							

Nomenclature after and data mainly from Koster [1966].

Migration may also result in spread beyond New Guinea, for example in:

Agrostis reinwardtii	*Haloragis halconensis*
Anthoxanthum angustum	*Keysseria gibbsiae*
Bromus insignis	*Poa epileuca*
Deschampsia klossii	*Potentilla parvula*

Drapetes ericoides *Trachymene saniculifolia.*
Epilobium prostratum

Stages 1, 2 and 5 above are stages of migration, or at least have implicitly the assumption of genetic contact between populations either by migration or long distance pollination. Stages 3 and 4 are stages of speciation, denying the possibility of migration or long distance pollination to more than a very limited extent. Although considerable speciation has taken place under conditions of geographical isolation the number of taxa which have remained geographically discrete is not large: this contradictory evidence may be a reflection of alternating glacial periods (with migration) and interglacial periods (with isolation) during the Pleistocene.

8-E DISTRIBUTION PATTERNS AND FLORISTIC ELEMENTS

(a) Altitudinal Ranges

In Fig. 8-16A the numbers of species within each floristic element with altitudinal ranges of four different magnitudes are tabulated. Percentages of the total elements in each altitude range category are plotted on a graph in Fig. 8-16B. All herbaceous angiosperm species considered, 119 native and 18 alien, are listed in Appendix 8, 6 alien species being omitted due to their being represented by only single records. It is immediately obvious that there is a strong tendency for aliens to have the widest altitudinal ranges and for putatively most ancient immigrants to have the narrowest. The probability of the pattern observed occurring by chance is less than 0.1% ($\chi^2 = 25.5$, $n = 6$). This shows that more recent immigrants in the flora have greater adaptability and a lesser degree of specialization towards occupation of a restricted ecological niche than plants of more ancient status.

(b) Actual Altitudinal Distributions

When actual altitudes as represented by averaged highest and lowest records are examined, it is found that a slightly higher proportion of the peregrine element than of those species of putatively more recent immigration is present in the lowest distribution mode, while the 18 aliens considered show a far greater tendency to grow at lower altitude. The figures are tabulated in Fig. 8-17A and presented

A.

Floristic Element	Altitudinal Ranges				Total
	0-999 m	1000-1499 m	1500-2499 m	2500-4267 m	
E	-	3	1	-	4
G	1	3	2	1	7
?G	2	6	-	-	8
PW	15	8	21	8	52
PN	2	1	6	-	9
PS	1	1	2	-	4
PWW	2	3	4	2	11
PWN	2	4	2	-	8
PWS	1	3	4	-	8
PWN	1	-	-	-	1
PSS	2	2	2	1	7
Aliens	2	3	6	7	18
Ancient immigrants	3	12	3	1	19
Peregrine element	26	22	41	11	100
Total	31	3	50	19	137

B.

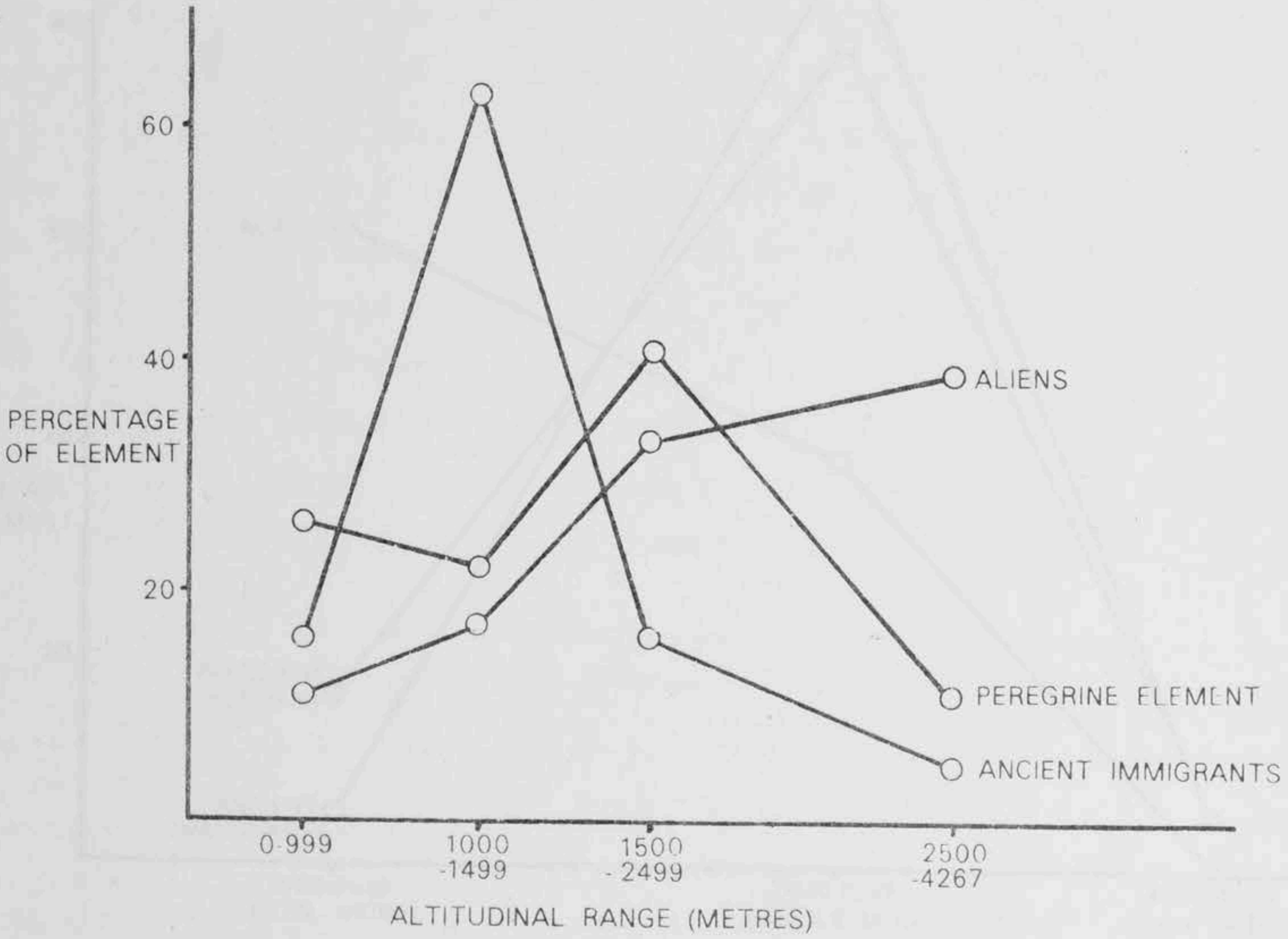


Fig. 8-16: Numbers of species in floristic elements with altitudinal ranges of different magnitudes;

A: tabulation of actual numbers;
B: percentages of elements displayed graphically.

A.

Floristic Element	Mean Altitudes Low 1600-2599 m	Middle 2600-3999 m	High 4000-4400 m	Total
E	-	4	-	4
G	1	6	-	7
?G	-	7	1	8
PW	9	39	4	52
PN	2	6	1	9
PS	-	4	-	4
PWW	4	7	-	11
PWN	1	7	-	8
PWS	-	8	-	8
PNN	-	1	-	1
PSS	-	7	-	7
Aliens	11	7	-	18
Ancient immigrants	1	17	1	19
Peregrine element	16	79	5	100
Total	28	103	6	137

B.

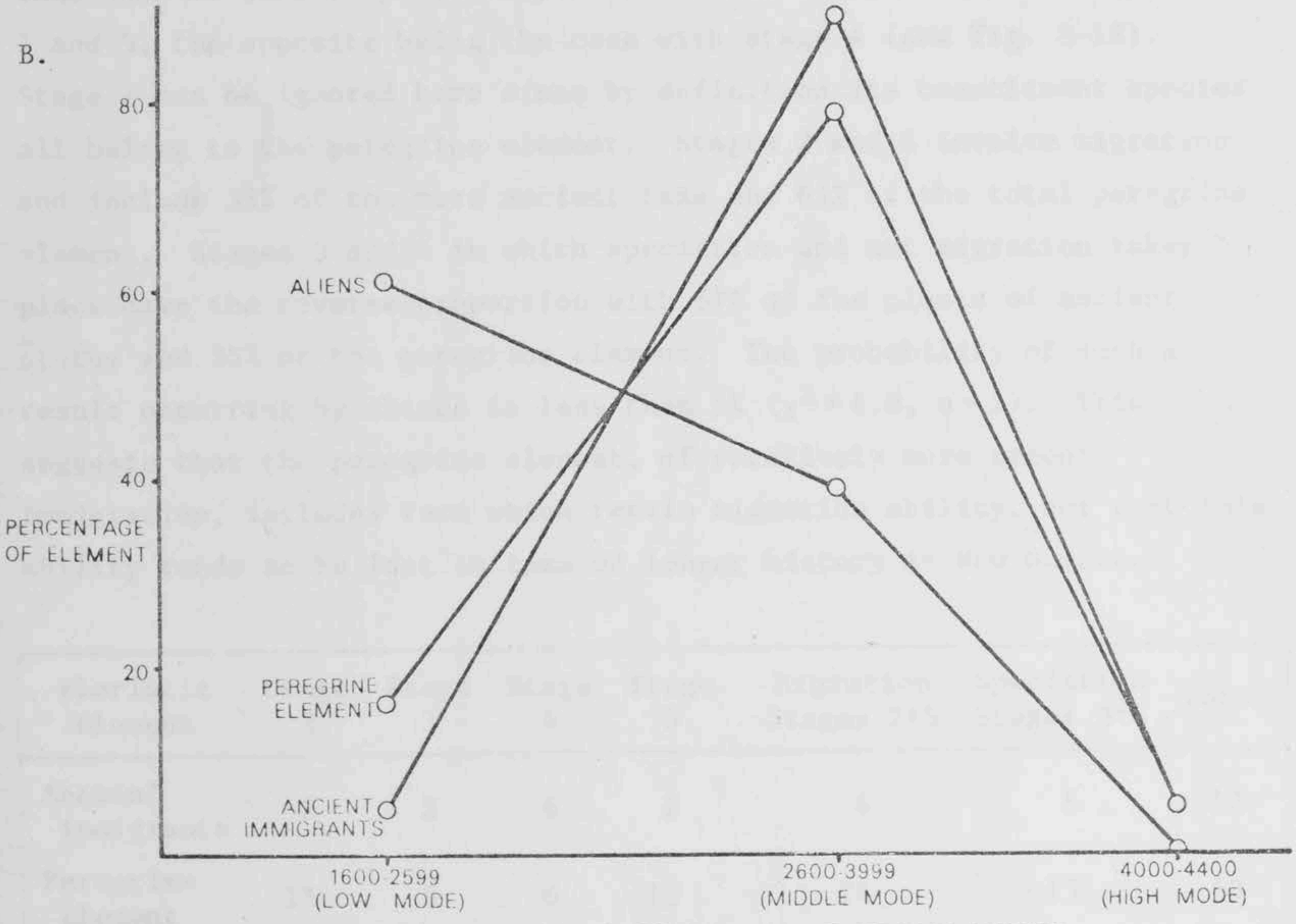


Fig. 8-17: Numbers of species in floristic elements with mean altitudes of different magnitudes;
A: tabulation of actual numbers;
B: percentages of elements displayed graphically.

graphically by percentage of total element in each altitude mode in Fig. 8-17B. The probability of such a pattern emerging randomly is less than 0.1% ($\chi^2 = 21.5$, $n = 4$), due to the great divergence between alien and native species' altitudes. The implication is that plant species may initially migrate to New Guinea best adapted to grow at lower altitudes and with time evolve to survive under more rigorous conditions at higher altitudes. It should be pointed out that specialization towards lower altitude niches may also occur but would not appear from this study which only embraces plants growing above 3215 m on Mt Wilhelm.

(c) Stages in Evolution of Mountain Grassland Floras

Taxa representing possible stages in the evolution of the mountain grassland flora (as outlined in the previous section) may be assigned to floristic elements, though with less precision than in other cases because the taxa concerned are of different ranks, including both species and genera. It is found that a higher proportion of peregrine taxa than of taxa of putatively more ancient immigration fall into stages 2 and 5, the opposite being the case with stage 4 (see Fig. 8-18). Stage 1 can be ignored here since by definition its constituent species all belong to the peregrine element. Stages 2 and 5 involve migration and include 33% of the more ancient taxa and 65% of the total peregrine element. Stages 3 and 4 in which speciation and not migration takes place have the reverse proportion with 67% of the plants of ancient status and 35% of the peregrine element. The probability of such a result occurring by chance is less than 5% ($\chi^2 = 4.0$, $n = 1$). This suggests that the peregrine element, of putatively more recent immigration, includes taxa which retain migration ability, but that this ability tends to be lost in taxa of longer history in New Guinea.

Floristic Element	Stage 2	Stage 3	Stage 4	Stage 5	Migration Stages 2+5	Speciation Stages 3+4	Total
Ancient immigrants	2	2	6	2	4	8	12
Peregrine element	15	9	6	13	28	15	43
Total	17	11	12	15	32	23	55

Fig. 8-18: Taxa representing different stages in the suggested evolution of mountain grassland floras tabulated by floristic element, excluding alien and stage 1 species.

Woody plants occurring above 3215 m on Mt Wilhelm which are not obligate forest inhabitants appear (from less detailed data) to fall mainly in the last two stages of evolution of the mountain grassland flora. Only *Styphelia suaveolens* is a member of stage 1 and *Detzneria*, *Pipturus* and perhaps woody *Hypericum* of stage 2. All other genera (*Agapetes*, *Coprosma*, *Dimorphanthera*, *Drimys*, *Eurya*, *Gaultheria*, *Pittosporum*, *Rapanea*, *Rhododendron*, *Vaccinium* and *Xanthomyrtus*) have two or more species which show to some extent sympatric distributions. Their possibly better dispersal mechanisms and/or longer history in New Guinea may contribute to the concentration of woody non-forest taxa in the suggested later stages of grassland flora evolution.

CHAPTER 9

INTEGRATION, DISCUSSION AND CONCLUSIONS

9-A SUMMARY OF CONCLUSIONS REACHED IN PREVIOUS CHAPTERS

The following conclusions concerning ecological attributes of floristic elements in the non-forest flora of Mt Wilhelm have already been reached.

(a) By comparison with the peregrine element, plants of notionally more ancient immigration display as a group:

(i) poorer colonist ability (significant at the 5% level; see section 5-E)

(ii) slower growth rate (significant at the 10% level; see section 6-B)

(iii) lesser ability to flower under cultivation in Canberra (significant at the 2% level; see section 6-H)

(iv) a greater tendency towards discontinuous secondary growth (significant at the 10% level; see section 6-H)

(v) clearer preference for slopes of western aspect at lower and eastern aspect at higher altitudes (significant at the 1% level; see section 7-E)

(vi) smaller altitudinal ranges (significant at the 2% level; see section 8-E).

(b) By comparison with species in the peregrine element found also outside Malesia, species in the same element endemic to Malesia display as a group:

(i) clearer preference for slopes of western aspect at lower and eastern aspect a higher altitudes (significant at the 2% level; see section 7-E).

(c) By comparison with species in the peregrine element belonging to genera found both north and south of Malesia, species in the same element in genera known only from Malesia and either the region to its north or to its south display as a group:

(i) lesser ability to flower under cultivation in Canberra (significant at the 5% level; see section 6-H).

(d) By comparison with aliens, native species display as a group:

(i) a greater tendency towards synchronous and discontinuous flowering (significant at the 1% level; see section 6-H)

(ii) lesser ability to flower under cultivation in Canberra (significant at the 10% level; see section 6-H)

(iii) a greater resistance to injury by frost (significant at the 10% level; see section 6-H)

(iv) smaller altitudinal ranges (significant at the 5% level; see section 8-E)

(v) lower mean of highest and lowest altitude records (significant at the 0.1% level; see section 8-E).

	Dispersal adaptations	Dispersal ability	Colonist ability	Growth rate	Field phenology	Cultivation phenology	Secondary growth	Frost vulnerability	Aspect preference	Altitude range	Mean altitude
Ancient immigrants/ Peregrine element	-	-	5	10	-	2	10	-	1	2	-
Endemic peregrine spp./ widespread peregrine spp.	-	-	-		-	-			2	-	-
Peregrine species in widespread/northern or southern genera	-	-	-		-	5			-	-	-
Natives/Aliens	-		-		1	10		10		5	0.1

Fig. 9-1: Probability of ecological differences between floristic elements resulting by chance.

These results are tabulated in Fig. 9-1, in which probabilities exceeding 10% of the data resulting by chance are signified by a dash. Of 11 ecological attributes tabulated, 2 (dispersal adaptations and dispersal ability) failed to provide any correlation with floristic elements (see section 4-E). Two others (growth rate and secondary growth) provided correlations at only the 10% significance level, perhaps due in part to fairly small numbers of species examined.

9-B SUMMATION AND COMPARISON OF ECOLOGICAL ATTRIBUTES AND THEIR PHYTOGEOGRAPHIC SIGNIFICANCE

All species in the non-forest flora of Mt Wilhelm and additional species considered by floristic element in chapters 4-8 have been listed in Appendices 1 and 2, together with their generic and specific distributions which together define the elements to which they belong. Each species in the lists was given a score for each ecological attribute examined, supposed migration ability indicating recency of immigration being signified by higher scores in every case. Scoring was as follows.

1. Disseminule adaptations to dispersal (see section 4-B).

Dispersal by wind or disseminules weighing less than 0.1 mg - 2

Dispersal by animals either internally or externally - 1

No adaptation - 0

2. Dispersal ability as evidenced by local distribution (see section 4-C).

Good - 2

Medium - 1

Poor - 0

3. Colonist ability (see section 5-D).

Very good - 2

Good - 1

Poor - 0

4. Growth rate (see section 6-B).

More than 0.70% - 2

0.60 - 0.70% - 1

Less than 0.60% - 0

5. Field phenology (see section 6-D).

Continuous flowering - 2

Partly synchronous and discontinuous flowering (classes 3 and 4) - 1

Clearly synchronous and discontinuous flowering (classes 1 and 2) - 0

6. Phenology under cultivation in Canberra (see section 6-E).

Seasonal flowering (classes d and e) - 2

Continuous flowering (classes a, b and c) - 1

Failure to flower before late 1973 - 0

7. Secondary growth of woody stems (see section 6-F).

Continuous growth (class 1) - 2

Partly periodic growth (classes 2 and 3) - 1

Clearly periodic growth (class 4) - 0

8. Injury by frost (see section 6-G).

Damaged by frost - 2

Unharmed by frost - 0

9. Shifting preference with altitude for slopes of eastern or western aspect (see section 7-D).

No shifting preference ($p > 10\%$) - 2

Shifting preference (p 1-10%) - 1

Clearly shifting preference ($p < 1\%$) - 0

10. Altitudinal distribution range (see section 8-C).

> 2500 m - 2

1000-2500 m - 1

< 1000 m - 0

11. Mean of highest and lowest altitude records (see section 8-C).

> 2600 m - 2

2650-4000 m - 1

< 4050 m - 0

Mean scores were then derived for all species scored for 4 or more ecological attributes.

The mean scores of each of the major floristic elements are shown as percentage histograms in Fig. 9-2. The generally lower scores of the ancient immigrants and higher scores of the aliens are apparent, although there is considerable overlap; only 3 species of supposedly ancient immigrants (12%), all in the ?G element, have mean scores of 1.25 or more, compared with 6 aliens (36%). The only 3 species with the maximum mean score of 2.0 are aliens (*Crassocephalum crepidioides*, *Erigeron sumatrensis*, *Sonchus oleraceus*).

Mean scores of floristic elements are displayed in a different way in Fig. 9-3 in which the percentages of mean score classes belonging to the main floristic elements are presented in histogram form. The concentration of ancient immigrants to the left of the diagram (lowest mean scores) is clear, as to a lesser extent is that of aliens to the right. Averaged mean scores of the main elements reflect the trend; ancient immigrants average 0.813 (26 species), the peregrine element 1.051 (92 species) and aliens 1.144 (17 species). Within the peregrine element species of genera found both north and south of Malesia show a higher average mean score (1.117, 65 species) than those of genera known from Malesia and regions either to its north or to its south (0.893, 27 species), recalling a similar distinction in field phenology (see section 6-H).

However the tabulated data show only low significance levels when tested by χ^2. Division into species with mean scores less than 0.80, between 0.80 and 1.20, and more than 1.20 results in three classes of roughly equal size. The difference between numbers of putatively ancient immigrants and peregrine element species within these classes is significant only at the 10% level ($\chi^2 = 5.69$, $n = 2$), and that between native and alien species not at all.

Similarly, a comparison of the highest (≥ 1.5) and lowest (≤ 0.5) scoring species is not quite significant at the 10% level either between ancient and peregrine plants ($\chi^2 = 1.86$, $n = 1$) or between natives and aliens ($\chi^2 = 2.56$, $n = 1$). However inspection of the two lists reveals some interesting ecological facts. The 18 lowest scoring species are almost all plants showing a high degree of ecological specialization, some being relatively rare. Five (*Danthonia vestita*, *Oreomyrrhis linearis*, *Parahebe tenuis*, *Trigonotis* sp. aff. *papuana*, *Uncinia* sp.1) are of restricted and high altitudinal ranges, five are mainly forest and

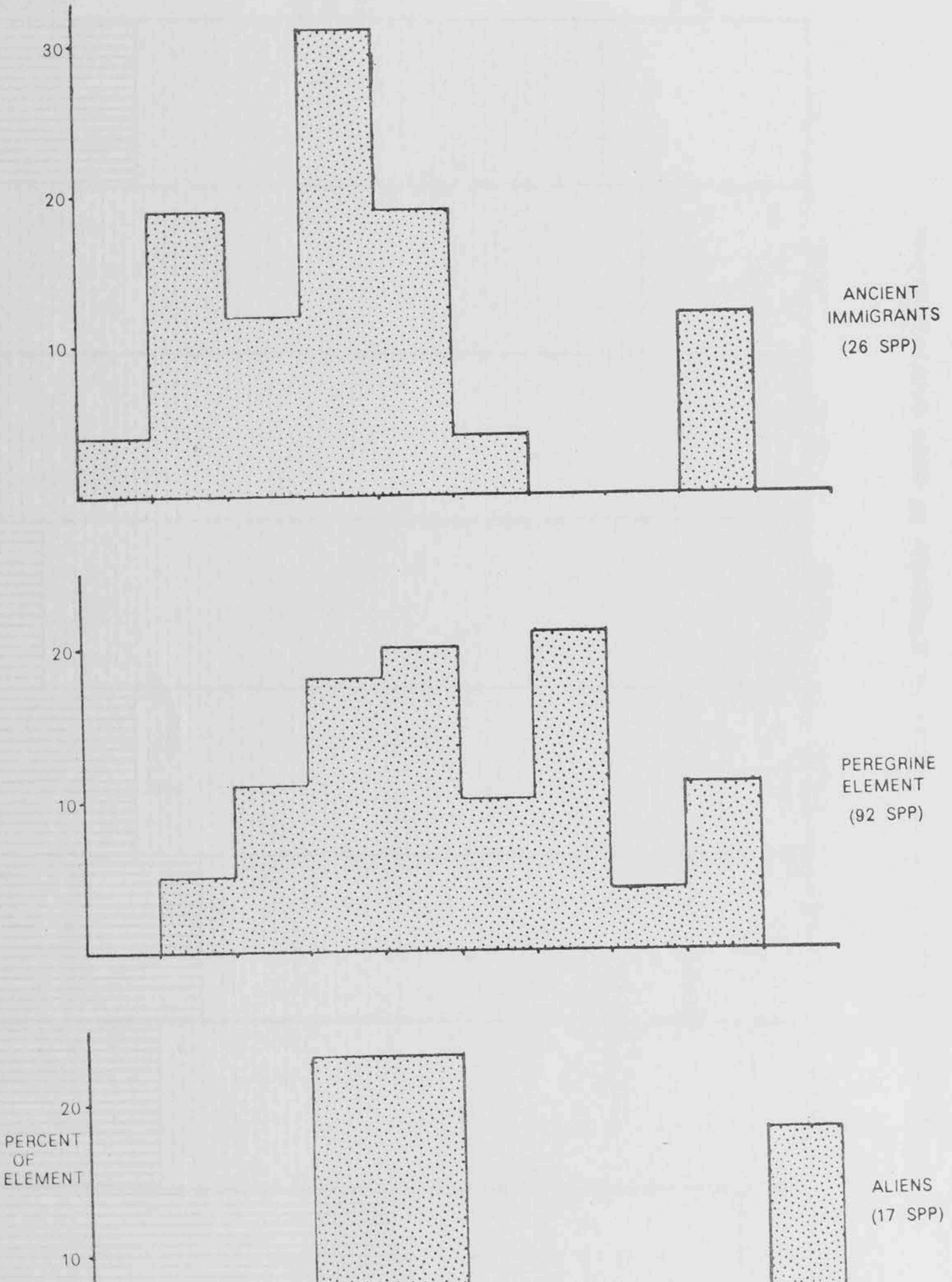


Fig. 9-2: Mean scores of floristic elements.

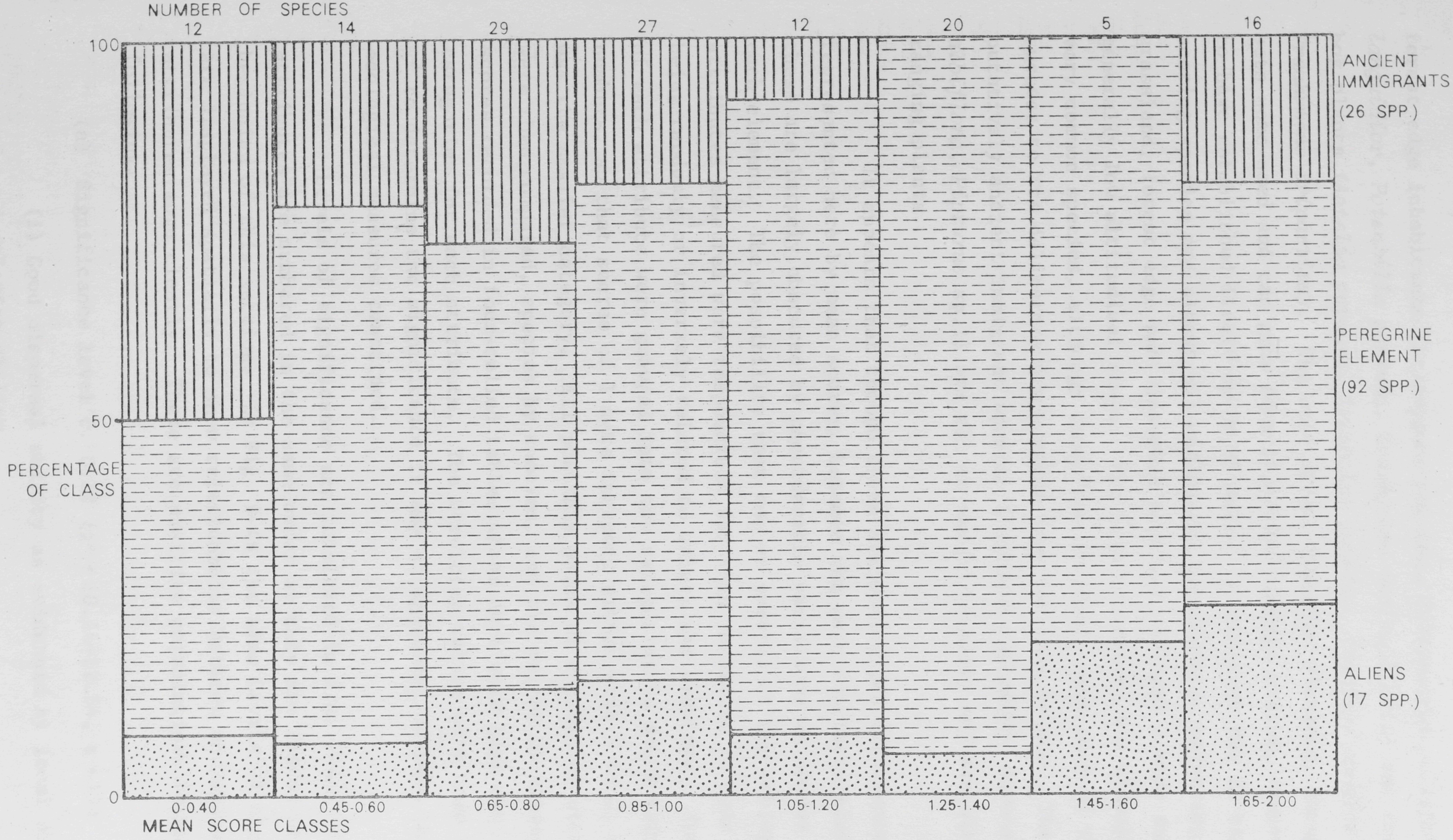


Fig. 9-3: Proportions of floristic elements in mean score classes.

forest edge inhabitants (*Brachycome papuana*, *Pittosporum pullifolium*, *Poa languidior*, *Potentilla parvula*, *Trachymene saniculifolia*) and four are bog plants (*Astelia papuana*, *Oreobolus pumilio*, *Plantago aundensis*, *Trachymene tripartita*). The only alien, *Brassica oleracea*, though it sets some seed and can grow from discarded cabbage stalks, cannot be said to have established itself on Mt Wilhelm. By contrast the 21 highest scoring species are almost all ecological generalists, occurring alike in grassland, forest edge and disturbed habitats and over a wide and often generally low altitudinal range. The five aliens are all widespread and very common species, although *Cordyline fruticosa* owes much of its success to its deliberate propagation from cuttings by man. The three putatively ancient immigrant species (*Coprosma papuensis*, *Parahebe albiflora*, *Pipturus* sp.1) are all in the ?G category and are also wide-ranging plants.

It appears that though there are ecological differences, as represented here by mean scores, between the main floristic elements, these are largely obscured by considerable variations in scores within each element. The possibility that one or several of the ecological attributes measured were responsible for this variation in mean scores by being randomly or inversely related to others was examined. The scores of each attribute were grouped into two categories to avoid very small numbers, so that scores of 1 were included either with 0 or 2, whichever was the smaller category. All possible pairs of ecological attributes were then compared, species by species, and the degree of agreement in scores recorded in four-celled tables whose axes were high and low score categories for each attribute. The resulting tables were then tested by χ^2 to determine the significance if any of agreement between the ecological measures concerned.

Levels of significance are tabulated in Fig. 9-4A. Ecological attributes are numbered in the same order as they are listed at the beginning of this section. In Fig. 9-4B the same levels of significance are displayed spatially to show relationships between ecological attributes more clearly. There are positive correlations between the following.

(a) Significance level *c.* 0.1% ($\chi^2 = 10.16\text{-}12.34$, $n = 1$):

(i) Good dispersal ability as evidenced by local distribution, and good colonist ability

(ii) Good colonist ability, and wide altitudinal range

(iii) Continuous flowering in the field, and flowering under cultivation in Canberra

(iv) Wide altitudinal range, and low mean of highest and lowest altitude records.

(b) Significance level 5-10% ($\chi^2 = 2.86\text{-}4.01$, $n = 1$):

(i) Disseminule adaptations to dispersal, and low mean of highest and lowest altitude records

(ii) Good dispersal ability as evidenced by local distribution, and low mean of highest and lowest altitude records

(iii) Good colonist ability, and lack of shifting preference for slopes of western aspect at lower and eastern at higher altitudes

(iv) Good colonist ability, and low mean of highest and lowest altitude records

(v) Continuous flowering in the field, and vulnerability to frost.

The arrangement of these correlations in Fig. 9-4B shows them to fall into two groups of related ecological attributes. There are also two uncorrelated attributes, growth rate and secondary growth of woody stems, whose lack of correlation can be explained in terms of the relatively small number of species examined in both cases. The larger group embraces dispersal and colonist ability, slope aspect preference and altitudinal distribution, while the smaller includes phenology in the field, flowering under cultivation and vulnerability to frost. Both ecological attributes which showed no correlation with floristic elements, disseminule adaptations to dispersal and dispersal ability as evidenced by local distribution, are correlated with other attributes which themselves show correlations with floristic elements.

Both groups include ecological attributes which are strongly correlated with floristic elements (see section 9-A). It can be tentatively concluded, therefore, that in all these ecological ways plant species immigrant to the mountains of New Guinea have undergone evolutionary changes. Such a conclusion receives some support from a

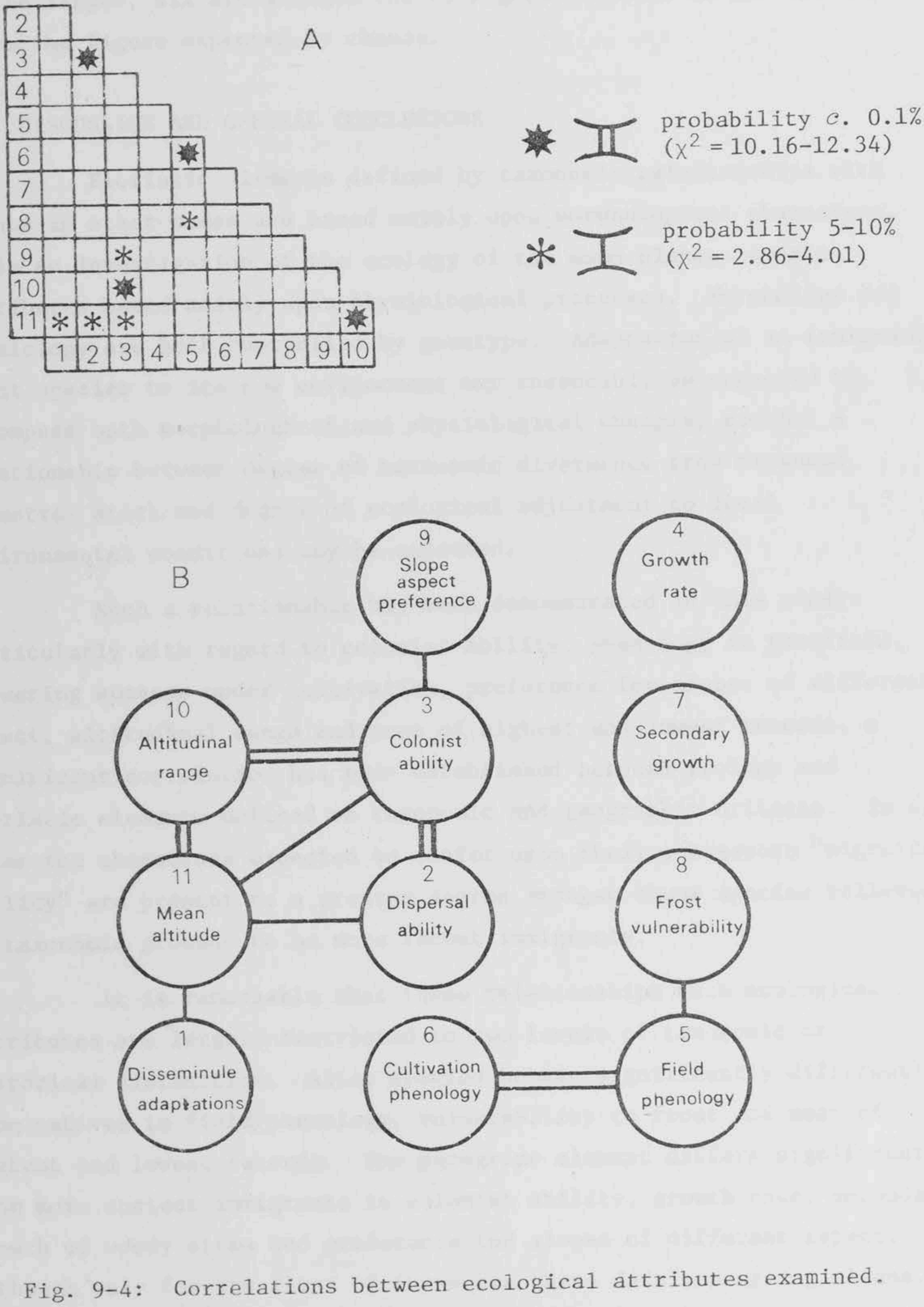


Fig. 9-4: Correlations between ecological attributes examined.

A: tabulation.
B: spatial arrangement of correlated attributes.

comparison of the top scoring species within each group. Of the 11 species with the highest mean score in the smaller which are also scored in the larger, six are amongst the 45 highest scorers in the latter, twice the figure expected by chance.

9-C DISCUSSION AND GENERAL CONCLUSIONS

Floristic elements defined by taxonomic relationships with plants in other areas are based mainly upon morphological characters, while an investigation of the ecology of the same plants reveals attributes based mainly upon physiological processes. Morphology and physiology are both controlled by genotype. Adaptation of an immigrant plant species to its new environment may reasonably be expected to encompass both morphological and physiological changes, so that a relationship between degree of taxonomic divergence from presumed ancestral stock and degree of ecological adjustment to local environmental conditions may be expected.

Such a relationship has been demonstrated in this study. Particularly with regard to colonist ability, phenology in the field, flowering success under cultivation, preference for slopes of different aspect, altitudinal range and mean of highest and lowest records, a significant correlation has been established between ecology and floristic elements defined on taxonomic and geographic criteria. In all cases the characters expected to confer upon their possessors "migration ability" are present to a greater degree amongst those species believed on taxonomic grounds to be more recent immigrants.

It is remarkable that these relationships with ecological attributes are largely restricted to two levels of taxonomic or historical distinction. Alien species behave significantly differently from natives in field phenology, vulnerability to frost and mean of highest and lowest records. The peregrine element differs significantly from more ancient immigrants in colonist ability, growth rate, secondary growth of woody stems and preference for slopes of different aspect, although only for the first of these are there data concerning aliens. Both these floristic element distributions prove ecologically significant in the cases of flowering success under cultivation and altitudinal range.

At the intermediate level of taxonomic distinction, between species in the peregrine element occurring also outside Malesia and species in the same element endemic to Malesia, a significant ecological difference is found only in preference for slopes of different aspect. Another significant distinction within the peregrine element concerns phenology in the field and is between species in widespread genera and species in genera absent from regions either north or south of Malesia.

The implication is that morphological and physiological adaptations proceed at different rates. A first period of physiological adaptation takes place before speciation as shown by distinctions between natives and aliens (if aliens are compared with peregrine species occurring also outside Malesia, significance is reduced partly due to low numbers in the cases of phenology in the field, flowering success in Canberra, and vulnerability to frost, but not in the cases of altitudinal range and mean of highest and lowest records). A second period accompanies or follows the evolution of distinct genera. The evolution of sufficient morphological distinctness for Malesian endemic species to be recognized appears to coincide with little physiological change.

When scores for all ecological attributes examined are averaged, species can be arranged on a gradient of "migration ability", which shows no significant correlation with floristic elements. Both measures are crude, however, the one confused by probably greatly different evolution rates and by doubts concerning the degree of migration ability initially possessed by immigrants, the latter by difficult interpretation of taxonomic relationships and incomplete geographical knowledge due to extinction or inadequate collection of some populations.

Migration ability so defined arranges species clinally so that they can only be grouped arbitrarily. However inspection of the species at extremes of the cline shows that those with highest ability are the most adaptable and ecologically and altitudinally widespread species; those of lowest ability are those species most closely associated with a single type of habitat and usually found over a limited and often high altitude range.

It is possible that floristic elements, defined partly upon geographic criteria, provide an indication of source areas of immigrant plants; while the gradient of migration ability, being a compound of attributes likely to have changed with time, gives an indication of age of residence in New Guinea.

Pursuit of this line of reasoning leads to anomalies, since we find some gondwanic plants of recent immigration, and aliens and species in the peregrine element of ancient immigration, as suggested by migration ability. These anomalies may be partly explained as follows.

1. Some gondwanic plants, present in the mountain forests of New Guinea and connected areas since the end of the Mesozoic, became evolutionarily "rejuvenated" in Plio-Pleistocene times with the creation of a new and incompletely exploited environment by orogeny, vulcanism, glaciation and, latterly, man. Rejuvenation of plants by rejuvenation of habitat has its parallel in Anderson's [1949] description of plant hybridization following habitat hybridization. Margalef [1968] has stressed the acceleration in evolution caused by the creation of pioneer environments.

Some taxa to which this may apply in the present context are *Coprosma*, *Haloragis* and *Pipturus*. Whether the rejuvenation took place in New Guinea or whether their presence there is due to post-rejuvenation migration from Australasia cannot be decided. P.F. Stevens [pers. comm., 1973] says of the undoubtedly gondwanic genus *Drimys*:

> "It is best to consider *Drimys* in Papua New Guinea as being in a state of active evolution, with the local populations not being notably stable. The total variation encompassed by the entities is considerable; the mountains on which *Drimys* grows are geologically young yet the variation pattern within and between the local species in Papua New Guinea to a considerable degree reflects the spatial arrangement of the mountains."

2. Some gondwanic plants, so defined by generic and species distributions, are not so in origin, but instead are genera newly evolved from immigrant stock which have migrated to occupy a range including New Guinea and south temperate regions, the New Guinea species being endemic to Malesia. This appears likely in the case of *Parahebe*, closely related to the cosmopolitan *Veronica* and also the New Guinea endemic *Detzneria* [Steenis, 1971], and of apparently quite recent migration in south temperate regions [Raven, 1973; Wace, 1965]. It is quite possible that *Parahebe* evolved from immigrant *Veronica* in New Guinea, later migrating through Australia to New Zealand and South America in the Pleistocene. Raven [1973] has argued convincingly that the large number of species of *Parahebe* and some other genera in New Zealand is due to

Plio-Pleistocene evolutionary radiation of immigrant species from Australia, and does not suggest an ancient site of generic origin there.

3. Some peregrine plants, though in some cases of the same species as plants distant to north or south, have been resident in New Guinea for a considerable time, possibly since the Cretaceous. This has been suggested in the case of Mt Kinabalu's flora by Steenis [1964a; 1967a] which has several species in common with Mt Wilhelm. Such an explanation would certainly account for the low migration ability of plants like *Carpha alpina*, *Geranium potentilloides*, *Oreobolus pumilio*, *Trachymene saniculifolia* and *Triplostegia glandulifera*, but I find it hard to believe that small populations of herbaceous species like these could remain specifically unchanged for over 50 million years.

4. Several alien species with apparently low migration ability show by their occurrence on Mt Wilhelm in small numbers a good migration ability, finding their optimum environment at far lower altitudes. Such species should not be included in comparisons as they are not established on Mt Wilhelm. This argument gains force when it is realised that three of the five aliens described in section 3-F as colonists of natural habitats above 3215 m have the highest migration ability of all species assessed. All five species have an average mean score of 1.75 (maximum 2.0) compared with an average of 1.00 for all native species (see section 9-B).

On geological grounds it seems probable that the tropicalpine environment in New Guinea is only of Plio-Pleistocene age, and I believe that the geographical relationships and ecological characteristics of its flora agree well with this interpretation.

True gondwanic taxa like *Dacrycarpus*, *Drimys* and *Pittosporum* are primarily plants of the mountain forests, which have an ancient history in the region, extending back to the Cretaceous. With the creation of a new environment above the forests some gondwanic taxa became "rejuvenated", such as *Drimys*, which went into a phase of rapid evolution enabling it to develop species adapted to occupy tropicalpine habitats. The rejuvenation of other gondwanic plants may have included the development of dispersal mechanisms (*Astelia*, *Coprosma*, *Nertera*, *Pipturus*, *Uncinia*) or good colonist ability (*Haloragis halconensis*) so that their presence in New Guinea may easily be due to Plio-Pleistocene migration from areas to its south. Yet other apparently gondwanic taxa which are neither forest inhabitants nor possessing good migration ability (*Abrotanella*, *Drapetes*, *Oreobolus*, *Oreomyrrhis*) give no clue as to their history in the New Guinea mountain flora.

In addition to the rejuvenation of forest inhabitants and the immigration of other apparently gondwanic plants from the south, there was a great influx of plants from both north and south constituting the peregrine element. Nearly two thirds of these plants are in genera which are almost cosmopolitan and include species well-known as pioneer plants of open habitats or as weeds of tillage. Some taxa have remained specifically identical with populations outside Malesia, others like the Ericaceae have undergone considerable speciation in New Guinea.

Most of the genera endemic to Malesia and occurring in the tropicalpine flora of Mt Wilhelm are probably neo-endemics, the descendants of late Tertiary immigrants, including *Detzneria*, *Dimorphanthera*, *Ischnea*, *Keysseria* and *Tetramolopium*. After their probable initial evolution in New Guinea some genera spread elsewhere, such as *Keysseria* to Borneo, *Tetramolopium* to Hawaii and *Parahebe* to Australasia and South America. Only *Harmsiopanax* and possibly the orchids *Ceratostylis* and *Pedilochilus* represent an ancient endemic element which has encroached upon the tropicalpine areas from the forests below rather than by long-distance immigration.

The most recent step in the phytogeographic history of the flora is further disturbance especially below 2500 m, and greatly increased opportunities for both long- and short-distance dispersal, by man. The result has been the establishment of a number of alien species. None has yet established itself in closed vegetation in the tropicalpine environment and most of the species found frequently there are opportunist pioneers. These most recent immigrants provide some clues as to the ecology of earlier immigrants and the degree to which they have become adapted to their environment since initial establishment.

By comparison with the mountain forest flora the non-forest flora remains to a large extent a collection of opportunist and generalist species, most of which occur in a variety of habitats and are not specialized to the occupation of particular ecological niches. There is nevertheless an evolutionary trend evident away from the adaptable and generalist to the limited and specialized. Although many species are found in a wide range of associations others, often of apparently more ancient immigration, are more restricted [Wade and McVean, 1969], and a few species can be found only in particular and specialized niches. Examples are *Abrotanella papuana* and *Plantago aundensis* only in short grass bog below 4100 m, *Lactuca* sp.1 and *Trigonotis* sp. aff. *papuana* in rock crevices and shallow gravel above the same altitude, *Lobelia archboldiana* beneath overhangs and at the base of tussocks from 3500 m to 4000 m, and *Myriactis cabrerae* on slightly raised sites in ill-drained tussock grassland at about 3350 m.

Clements [1916] regarded climax communities as quite invariable entitles, analogous to organisms, their succession analogous to organisms' ontogeny. Gleason [1926] on the other hand considered vegetation to consist of continua and to be the result of immigration combined with a variable and fluctuating environment. This conflict of views has underlain much of the discussion in plant ecology in past years, but as Watt [1964] has pointed out the reality of any situation probably lies between the divergent viewpoints of Clements and Gleason.

On Mt Wilhelm the tropicalpine vegetation tends to support the Gleasonian concept. It is a series of indistinctly separable associations sharing many species and probably not keeping a stable pattern. However, the existence of some specialist plant species shows that the situation does include pattern dependent upon the interaction of environmental factors with plant genotypes, and between genotypes, in a rather inflexible way. Tropicalpine areas in New Guinea have had a short and geomorphically violent history so that their flora of immigrants may have had neither time nor environmental stability in which to achieve a maximal occupation of available ecological niches.

By contrast the mountain forests, ancient and controlling to a great extent their own sub-canopy environment, appear more stable and permanent and to reflect the Clementsian view. Yet even here the presence of Plio-Pleistocene immigrant taxa like *Rhododendron*, *Saurauia* and many others shows the essential impermanence of the community, and the occurrence of floristic variations without definable associations in the forests [D. Walker, pers. comm., 1973] belies the organismal analogy.

Pattern and order exist to some extent in all vegetation, but equally all vegetation is to some extent the result of the operation of chance factors. Different environments support plant communities with different degrees of pattern and randomness. Part of the reason for the difference lies in the age of the communities involved. Just as there is a large element of chance in the composition of the pioneer community upon a landslip and a smaller one in the forest that ultimately replaces it, so the random element is stronger in communities composed of relatively recent immigrants than in ancient and mature ecosystems. In examining relationships between morphological and physiological expressions of genotypes, this thesis has explored a meeting point of the two sciences of plant ecology and historical phytogeography.

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Appendix 1: The non-forest flora of Mt Wilhelm, with distributions and floristic elements (see section 3-G) and scores (see section 9-B).

Species	Genus distribution	Species distribution	Floristic element	1. Disseminule adaptations	2. Dispersal ability	3. Colonist ability	4. Growth rate	5. Field phenology	6. Cultivation phenology	7. Secondary growth	8. Frost vulnerability	9. Slope aspect preference	10. Altitudinal range	11. Mean actual altitude	Mean score
Abrotanella papuana	8	1	G	0	0	0	0	2					1	1	0.60
Acaena anserifolia	5	4	PSS	1	2	1		0	0		2	2	1	1	1.10
Agapetes vitis-idaea	6	1	PN			0									
Agrostis avenacea	9	4	PWS			1									
A. reinwardtii	9	2	PW	0	2	2		2	0			0	1	1	1.00
Anaphalis lorentzii	9	3	PW	2	2	2		2			2	2	1	1	1.75
A. mariae	9	1	PW	2	2	2		1			0	2	1	1	1.40
Anotis sp.1	6	?1	PN	1	1	0		2					1	1	1.00
Anthoxanthum angustum	9	2	PW	0	1	1		2				1	1	1	1.00
Astelia papuana	8	1	?G	1	0	0	0	1	0			0	1	1	0.40
Bidens pilosa	Introduced		A	1		1			1				2	2	1.40
Brachypodium sylvaticum	9	6	PWN	0	2	1							1	1	1.00
Callitriche verna	9	9	PWW			0							1	1	
Cardamine altigena	9	1	PW	0	2	0		2	1				0	1	0.90
Carex capillacea	9	7	PWW			0		2					1	1	1.00
C. celebica	9	2	PW	0	1	1			0		0	2	0	1	0.60
C. echinata	9	6	PWN	0	1	0		1					1	1	0.70
C. euphlebia	9	?2	PW	0	2	1							1	2	1.20
C. finitima	9	6	PWN			0							0	1	
C. gaudichaudiana	9	7	PWW			0							1	1	
C. neoguineensis	9	1	PW			1							1	1	
C. pereiliata	9	?7	PWW			1						2	0	1	1.00
Carpha alpina	8	4	PSS	0		1	0	0	0			2	1	1	0.60
Centrolepis philippinensis	7	2	PS			0							1	1	
Cerastium papuanum	9	1	PW	0	2	1		2	1			2	2	1	1.40
Ceratostylis sp.2	2	1	E			0					0				
Coleus scutellarioides	9	?2	PW			1									
Coprosma divergens	5	1	?G	1		1		2		1	0	0			0.80
C. papuensis	5	1	?G	1	2	2		2				2			1.80
Cotula cf. *leptoloba*	9	?1	PW			0							1	1	
Crassocephalum crepidioides	Introduced		A	2		2							2	2	2.00
Cynoglossum javanicum	9	?2	PW	1		1			1						
Dacrycarpus compactus	8	1	G			0				0					
Danthonia archboldii	9	1	PW	0	1	1							1	1	0.80
D. penicillata	9	4	PWS	0	2	1		2	1		0	2	0	1	1.00
D. vestita	9	1	PW	0		0		0				1	1	1	0.50
Decaspermum lorentzii	6	?1	PN			0				1					
Deschampsia klossii	9	2	PW	0	2	2		1	0		0	0	1	1	0.80
Detzneria tubata	1	1	E			0		2			0	2			1.00
Deyeuxia arundinacea	9	6	PWN		1	0							0	1	0.50
D. brassii	9	1	PW		1	1		1				1	1	1	1.00
Dichelachne rara	4	4	PSS	0	2	2		1				2	1	1	1.30
Dichrocephala bicolor	9	7	PWW	1		1			1				2	2	1.40
Dimorphanthera amplifolia	2	1	E			0									
D. keysseri	2	1	E	1		0		0		0					0.25
D. microphylla	2	1	E	1		0		0		1					0.50
Dodonaea viscosa	9	9	PWW			1									
Drapetes ericoides	5	2	G			0		2				0	1	1	0.80
Drimys piperita subalpina	5	4	G	0		0		2	0	2					0.80
Epilobium detznerianum	9	1	PW	2		1		2					1	1	1.40
E. ?hooglandii	9	1	PW			2		2					1	1	1.50
E. keysseri	9	1	PW	2	2	2		2			2	2	1	1	1.75
Erigeron canadensis	Introduced		A	2		1							2	2	1.75
E. sumatrensis	Introduced		A	2		2							2	2	2.00
Eriocaulon montanum	9	1	PW			0					2		0	1	0.75
Euphrasia mirabilis	9	1	PW	2		0		1			0	2	0	1	0.90
Eurya albiflora	9	1	PW			0									
E. brassii	9	1	PW	1		0		2		1		2			1.20
Festuca crispate-pilosa	9	1	PW	0		0		2				2	0	1	0.80
F. papuana	9	1	PW			0		2				0	1	1	0.80

Distribution key:

1. New Guinea endemic
2. Malesian endemic
3. Malesia and Pacific islands
4. Malesia and Australia and/or New Zealand
5. Malesia to South America
6. Malesia to Eurasian mainland and sometimes Africa
7. Malesia, Eurasia and Australasia
8. Mainly Africa, South America and Australasia
9. Very widespread

Appendix 1 (cont'd)

Species	Genus distribution	Species distribution	Floristic element	1. Disseminule adaptations	2. Dispersal ability	3. Colonist ability	4. Growth rate	5. Field phenology	6. Cultivation phenology	7. Secondary growth	8. Frost vulnerability	9. Slope aspect preference	10. Altitudinal range	11. Mean actual altitude	Mean score
Fragaria cf. *vesca*	Introduced		A	1		0	1	2	1		2		1	2	1.00
Gaimardia setacea	7	4	PSS			0							0	1	
Galium novoguineense	9	?1	PW			0							0	1	
Gaultheria mundula	7	1	PW	1	1	1		0			0	2			0.80
Gentiana cruttwellii	9	1	PW			0		2				1	2	2	1.40
G. ettingshausenii	9	1	PW	2	1	0		2				2	1	1	1.30
G. piundensis	9	1	PW	2		0		2				1	1	1	1.20
Geranium potentilloides	9	4	PWS		0	0						1	1	1	0.60
Gnaphalium breviscapum	9	1	PW	2	0	1	1	1				1	1	1	1.00
G. involucratum	9	4	PWS	2		1							1	1	1.25
G. japonicum	9	9	PWW	2	1	1		1			0	2	1	1	1.10
Habenaria (Platanthera) sp.1	9	?1	PW			0		0							
Haloragis halconensis	8	2	G	0	1	2		1	0		0	2	2	2	1.10
Harmsiopanax ingens	2	?1	E			1									
Hierochloe redolens	9	5	PWS	0	2	1		1			0	2	1	1	1.00
Hydrocotyle sibthorpioides	9	9	PWW	0	2	2			0				2	1	1.70
Hypericum macgregorii	9	1	PW	2	1	2		2			0	2	1	1	1.40
Imperata conferta	9	1	PW	2		1							2	2	1.75
Ischnea elachoglossa	1	1	E	0		1	1	2					1	1	1.00
Juncus effusus	9	7	PWW	0		1									
Keysseria radicans	3	1	E	1	1	0	0	1	0		2		1	1	0.80
Lactuca laevigata	9	2	PW	2	2	2	2	1			0	0	2	2	1.40
Lactuca sp.1	9	1	PW	2		0		2					0	0	0.80
Libertia pulchella	5	4	PSS	0	1	1			2				0	1	0.80
Lobelia angulata	9	5	PWS	2		1							1	2	1.50
L. archboldiana	9	1	PW			0							0	1	
Lolium rigidum	Introduced		A	0		0		2					0	1	0.60
Luzula campestris	9	9	PWW			0							1	1	
Microlaena stipoides	4	4	PSS	1		1									
Miscanthus floridulus	6	3	PN	2		1							1	2	1.50
Monostachya oreoboloides	4	2	PS	0	0	1		0				2	1	1	0.70
Montia fontana	9	9	PWW			0							0	1	
Myosotis australis	9	4	PWS	1		0		2	1		0		1	1	0.90
Myriactis cabrerae	6	1	PN	1		0		0	2				0	1	0.70
Nertera granadensis	8	5	PSS	1	2	1			0				2	1	1.70
N. cf. *nigricarpa*	8	?1	?G	1		0		2					1	1	1.00
Olearia floccosa	4	1	PS			0		1							
O. monticola	4	1	PS			1									
O. spectabilis	4	1	PS	2	1	0		0		1	0	2			0.90
Oreobolus ambiguus	5	2	?G	0	0	0		2					1	1	0.70
O. pumilio	5	4	PSS		0	0							1	1	0.50
Oreomyrrhis linearis	5	1	G	0		0	0	1	0			0	1	1	0.40
O. papuana	5	1	G	0	1	0	2	2	1			1	0	1	0.90
O. pumila	5	1	G	0		0		1	0			1	1	1	0.60
Oxalis magellanica	9	5	PWS	0	1	1	2	2	1			2	1	1	1.20
Parahebe albiflora	5	1	?G	2	2	2		2					1	1	1.70
P. ciliata	5	1	?G	2		0		0				1	1	1	0.80
P. tenuis	5	1	?G			0		0					0	1	0.25
Peditochilus sp.3	1	1	E			1	0					1			
Phreatia sp.1	7	?1	PW			0									
Pilea cf. *johniana*	9	2	PW		1	1		2				1	1	1	1.70
Pipturus sp.1	8	?1	?G	1	2	2				2					1.75
Pittosporum pullifolium	8	1	G	0		0		0		1	0				0.20
Plantago aundensis	9	1	PW		0	0	0	0	1		0		1	1	0.40
P. lanceolata	Introduced		A	0		0	1				2		0	1	0.70
Poa annua	Introduced		A	0		0		2	1		0		1	1	0.70
P. callosa	9	1	PW			0		2				2	1	1	1.20
P. crassicaulis	9	1	PW			0	2	1				2	1	1	1.70
P. epileuca	9	2	PW			0		2				2	1	1	1.20

Distribution key:

1. New Guinea endemic
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3. Malesia and Pacific islands
4. Malesia and Australia and/or New Zealand
5. Malesia to South America
6. Malesia to Eurasian mainland and sometimes Africa
7. Malesia, Eurasia and Australasia
8. Mainly Africa, South America and Australasia
9. Very widespread

Appendix 1 (cont'd)

Species	Genus distribution	Species distribution	Floristic element	1. Disseminule adaptations	2. Dispersal ability	3. Colonist ability	4. Growth rate	5. Field phenology	6. Cultivation phenology	7. Secondary growth	8. Frost vulnerability	9. Slope aspect preference	10. Altitudinal range	11. Mean actual altitude	Mean score
P. saruwagetica	9	1	PW	0	2	2		2			0	2	1	1	1.25
Poa sp.1	9	1	PW			0							0	0	
Polygonum nepalense	9	6	PWN			1									
P. runcinatum	9	?1	PW		2	1		1					1	2	1.40
Potentilla ?foersteriana	6	1	PN			1	1	1			2	2	1	1	1.30
P. papuana	6	2	PN	0	1	2	1	0	0		0	1	1	1	0.70
P. parvula	6	2	PN			0			0				1	1	0.50
Pterostylis sp.1	4	?1	PS			0									
Quintinia sp.1	4	?1	PS			0		2		1					
Ranunculus pseudolowii	9	1	PW	0	2	2	1	2	1		2	2	2	2	1.60
R. saruwagedicus	9	1	PW			0	1	2				2	0	0	0.80
R. schoddei	9	1	PW	0		0	1	1	0			2	0	1	0.60
R. wahgiensis	9	1	PW			0		2							
Rapanea vaccinioides	9	1	PW	1		0		0		2					0.75
Rhododendron atropurpureum	6	1	PN			0		0							
R. beyerinckianum	6	1	PN		1	0									
R. commonae	6	1	PN			0		0							
R. culminicolum	6	1	PN			0		0							
R. gaultheriifolium	6	1	PN			0									
R. inconspicuum	6	1	PN			0									
R. womersleyi	6	1	PN	2		0		1		2					1.25
R. yelliottii	6	1	PN		1	1		1		1					1.00
Rubus papuanus	9	1	PW	1	1	1									
Sagina papuana	9	2	PW	0	2	2		2	0		2		2	1	1.40
Saurauia sp.2	9	?1	PW			1									
Schoenus curvulus	9	2	PW	0	2	2		2					2	2	1.70
S. maschalinus	9	4	PWS	0	1	1		2			2	2	1	1	1.25
Scirpus crassiusculus	9	4	PWS			0							1	1	
S. subcapitatus	9	6	PWN			0							1	1	
S. cf. *subtillissimus*	9	4	PWS		2	2			1				1	1	1.40
Senecio glomeratus	9	4	PWS	2	1	0		2	1		2		1	1	1.25
S. papuanus	9	1	PW	2	2	2		2	2		2	2	0	1	1.70
Senecio sp.5	9	1	PW	2		0	0	2					0	0	0.70
Sonchus oleraceus	Introduced		A	2		2		2			2		2	2	2.00
Stellaria media	Introduced		A	0		0		2	1		2		1	2	1.10
Styphelia suaveolens	4	4	PSS	1	1	1		2		0	0	2			1.00
Symplocos sp.3	9	?1	PW			0									
Tacsonia mollissima	Introduced		A	1		1			0				1	2	1.00
Tetramolopium alinae	3	1	E	2		0		1	0				1	1	0.80
T. macrum	3	1	E	2		0		2	0			1	1	1	1.00
Thelymitra cf. *papuana*	4	?1	PS			0									
Trachymene saniculifolia	4	4	PSS	0	0	0			0				1	1	0.30
T. tripartita	4	1	PS	0		0	0	1	0				0	1	0.30
Trigonotis inoblita	6	1	PN	0		1									
T. papuana	6	1	PN	0	1	1		2	1		0	2	1	1	1.10
Trigonotis sp. aff. *papuana*	6	1	PN	0		0		2					0	0	0.40
T. procumbens	6	1	PN			0		2					1	2	1.25
Triplostegia glandulifera	6	6	PNN	1	1	0			1				0	1	0.70
Tritonia X *crocosmaeflora*	Introduced		A			0					2		1	1	1.00
Trochocarpa dekockii	4	1	PS	1	1	0		0				2			0.80
T. dispersa	4	1	PS			0				1					
Uncinia riparia	5	4	PSS	1	1	0		2				2	1	1	1.10
Uncinia sp.1	5	1	?G			0		0				2	0	0	0.40
Vaccinium amblyandrum	6	1	PN	1	1	1		0	0		2	2			1.00
V. cruentum	6	1	PN	1		0		0		2	0				0.60
Verbena bonariensis	Introduced		A			0							2	2	
Veronica cf. *persica*	Introduced		A	0		0		2			0		1	1	0.70
Viola arcuata	9	6	PWN	0	2	1	0		1			2	1	1	1.00
Vulpia bromoides	Introduced		A			0							0	1	

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6. Malesia to Eurasian mainland and sometimes Africa
7. Malesia, Eurasia and Australasia
8. Mainly Africa, South America and Australasia
9. Very widespread

Appendix 2: Species not in the non-forest flora but considered by floristic elements in chapters 4-8, with distributions and floristic elements (see section 3-G) and scores (see section 9-B).

Species	Genus distribution	Species distribution	Floristic element	1. Disseminule adaptations	2. Dispersal ability	3. Colonist ability	4. Growth rate	5. Field phenology	6. Cultivation phenology	7. Secondary growth	8. Frost vulnerability	9. Slope aspect preference	10. Altitudinal range	11. Mean actual altitude	Mean score
Brachycome papuana	9	1	PW			0			0				0	1	0.25
Brassica oleracea	Introduced		A			0					0		0	1	0.25
Cardamine africana	9	9	PWW			0							1	2	
Cordyline fruticosa	Introduced		A			0					2		2	2	1.50
Dimorphanthera collinsii	2	1	E			0		1							
D. leucostoma	2	1	E			0		0							
Drimys piperita montis-wilhelmi	5	4	G			0		2		1					
Epilobium prostratum	9	2	PW			0									
Eragrostis tenuifolia	Introduced		A	0		0									
Fuchsia ?magellanica	Introduced		A			0		2		0	2				1.00
Galium rotundifolium	9	6	PWW			0							1	2	
Hypericum japonicum	9	7	PWW			0							1	2	
Linum usitatissimum	Introduced		A			0							0	1	
Lupinus sp.	Introduced		A			0							1	2	
Luzula effusa	9	6	PWN	0		0									
Mazus pumilus	7	4	PW			0		2							
Mentha sp.	Introduced		A			0					2		0	1	0.75
Nasturtium backeri	6	2	PN	1		0			1						
N. officinale	Introduced		A			0							2	2	
Petroselinum crispum	Introduced		A			0					0				
Pisum sativum	Introduced		A			0							0	1	
Phalaris tuberosa	Introduced		A			0							0	2	
Poa languidior	9	1	PW			0		1					0	1	0.50
Raphanus sativus	Introduced		A			0					2				
Schefflera chimbuensis	9	1	PW			0				2					
Senecio sp.2	9	1	PW			0		0		1					
Sericolea sp.	1	1	E	1		0									
Siegesbeckia orientalis	Introduced		A	0		0									
Solanum tuberosum	Introduced		A			0					0				
Uncinia ohwiana	5	1	?G	1		0		1					1	1	0.80
Vicia sativa	Introduced		A			0							0	1	
Viola betonicifolia	9	7	PWW			0							1	2	
Wahlenbergia marginata	9	7	PWW			0							1	2	
Youngia japonica	7	7	PWW	2		0									

Distribution key:

1. New Guinea endemic
2. Malesian endemic
3. Malesia and Pacific islands
4. Malesia and Australasia and/or New Zealand
5. Malesia to South America
6. Malesia to Eurasian mainland and sometimes Africa
7. Malesia, Eurasia and Australasia
8. Mainly Africa, South America and Australasia
9. Very widespread

Appendix 3: Weights and nature of disseminules.

Species	No. Disseminules Weighed	Disseminule Weight (mg)	Nature of Disseminule	Category
Abrotanella papuana	5	0.14	Caryopsis	-
Acaena anserifolia	4	4.60	Hooked achene	E
Agrostis reinwardtii	4	0.40	Spikelet	-
Anaphalis lorentzii	5	0.04	Caryopsis with pappus	W
Anaphalis mariae	5	0.08	Caryopsis with pappus	W
Anotis sp.1	2	8.00	Fruit in bristly calyx	-
Anthoxanthum angustum	5	1.90	Awned spikelet	-
Astelia papuana	1	160	Berry	I
Bidens pilosa	4	2.10	Hooked caryopsis	E
Brachypodium sylvaticum	2	4.40	Spikelet	-
Cardamine altigena	5	0.76	Seeds in dehiscent siliqua	-
Carex celebica	4	0.71	Dry fruit with bracts	-
Carex echinata	5	0.42	Dry fruit with bracts	-
Carex euphlebia	10	0.80	Dry fruit with bracts	-
Carpha alpina	3	3.30	Bristly dry fruit	-
Cerastium papuanum	4	0.75	Seeds in dehiscent capsule	-
Coprosma divergens	1	68	Berry	I
Coprosma papuensis	1	140	Berry	I
Crassocephalum crepidioides	8	0.08	Caryopsis with pappus	W
Cynoglossum javanicum	4	6.00	Hooked nutlets	E
Danthonia archboldii	4	2.10	Awned bristly spikelet	-
Danthonia penicillata	5	2.30	Awned spikelet	-
Danthonia vestita	3	2.00	Bristly spikelet	-
Deschampsia klossii	6	0.23	Spikelet	-
Dichelachne rara	10	0.39	Awned spikelet	-
Dichrocephala bicolor	6	0.08	Viscid caryopsis	E
Dimorphanthera keysseri	1	250	Berry	I
Dimorphanthera microphylla	1	330	Berry	I
Drimys piperita subalpina	6	0.83	Seeds in dehiscent follicle	-
Epilobium detznerianum	7	0.07	Hairy seed	W
Epilobium keysseri	7	0.10	Hairy seed	W
Eragrostis tenuifolia	2	0.45	Spikelet	-
Erigeron canadensis	4	0.01	Caryopsis with pappus	W
Erigeron sumatrensis	5	0.02	Caryopsis with pappus	W
Euphrasia mirabilis	7	0.08	Seeds in splashcup	D
Eurya brassii	3	72	Berry	I
Festuca crispate-pilosa	4	2.40	Spikelet	-
Fragaria cf. *vesca*	3	0.50	Achene	
ditto (receptacle)	1	600	Fleshy receptacle	I
Gaultheria mundula	1	230	Capsule in fleshy calyx	I
Gentiana ettingshausenii	9	0.03	Seeds in splashcup	D
Gentiana piundensis	9	0.02	Seeds in splashcup	D
Gnaphalium breviscapum	5	0.06	Caryopsis with pappus	W
Gnaphalium involucratum	14	0.02	Caryopsis with pappus	W
Gnaphalium japonicum	5	0.01	Caryopsis with pappus	W
Haloragis halconensis	4	0.92	Dry fruit with calyx	-
Hierochloe redolens	6	2.70	Spikelet	-
Hydrocotyle sibthorpioides	4	1.20	Mericarp	-
Hypericum macgregorii	6	0.03	Seeds in dehiscent capsule	-
Imperata conferta	10	0.23	Hairy seed	W
Ischnea elachoglossa	6	0.80	Caryopsis	-
Juncus effusus	5	0.43	Dry fruit with bracts	-
Keysseria radicans	1	0.75	Viscid caryopsis	E
Lactuca laevigata	5	0.59	Caryopsis with pappus	W
Lactuca sp.1	3	0.43	Caryopsis with pappus	W
Libertia pulchella	4	1.20.	Seeds in dehiscent capsule	-
Lobelia angulata	11	0.04	Seeds in dehiscent capsule	D
Lolium rigidum	2	3.90	Spikelet	-

W: Wind-dispersal adaptations
D: Dust seeds
E: Adaptations to external animal dispersal
I: Adaptations to internal animal dispersal

Appendix 3 (cont'd)

Species	No. Disseminules Weighed	Disseminule Weight (mg)	Nature of Disseminule	Category
Luzula effusa	3	3.40	Dry fruit with bracts	-
Microlaena stipoides	4	5.30	Awned spikelet	E
Miscanthus floridulus	10	0.80	Hairy spikelet	W
Monostachya oreoboloides	6	0.58	Spikelet	-
Myosotis australis	4	0.10	Nutlet	
ditto (empty calyx)	1	6.00	Bristly calyx	E
Myriactis cabrerae	5	0.48	Viscid caryopsis	E
Nasturtium backeri	5	0.46	Viscid seeds	E
Nertera granadensis	3	16	Berry	I
Nertera nigricarpa	4	21	Berry	I
Olearia spectabilis	2	1.30	Caryopsis with pappus	W
Oreobolus ambiguus	1	4.30	Dry fruit with bracts	-
Oreomyrrhis linearis	2	1.60	Mericarp	-
Oreomyrrhis papuana	4	0.88	Mericarp	-
Oreomyrrhis pumila	4	1.00	Mericarp	-
Oxalis magellanica	5	0.80	Seeds in dehiscent capsule	-
Parahebe albiflora	10	0.06	Seeds in dehiscent capsule	D
Parahebe ciliata	12	0.02	Seeds in dehiscent capsule	D
Pipturus sp.1	2	43	Berry	I
Pittosporum pullifolium	3	19	Seeds in dehiscent capsule	-
Plantago aundensis	4	0.36	Seeds in dehiscent capsule	-
Poa annua	6	0.62	Spikelet	-
Poa saruwagetica	5	0.58	Spikelet	-
Potentilla papuana	6	0.27	Achene	-
Ranunculus pseudolowii	6	1.30	Achene	-
Ranunculus schoddei	3	1.20	Achene	-
Rapanea vaccinioides	3	26	Berry	I
Rhododendron womersleyi	11	0.05	Hairy seed	W
Rubus papuanus	1	410	Compound drupe	I
Sagina papuana	10	0.02	Seed in dehiscent capsule	D
Schoenus curvulus	1	1.20	Dry fruit with bracts	-
Schoenus maschalinus	2	0.25	Dry fruit with bracts	-
Senecio glomeratus	4	0.60	Caryopsis with pappus	W
Senecio papuanus	5	0.76	Caryopsis with pappus	W
Senecio sp.5	3	1.70	Caryopsis with pappus	W
Sericolea sp.	5	59	Berry	I
Siegesbeckia orientalis	5	1.30	Caryopsis	-
Sonchus oleraceus	3	0.63	Caryopsis with pappus	W
Stellaria media	4	1.20	Seeds in dehiscent capsule	-
Styphelia suaveolens	2	33	Berry	I
Tacsonia mollissima	1	62	Seed with juicy endocarp	I
Tetramolopium alinae	4	1.10	Caryopsis with pappus	W
Tetramolopium macrum	3	1.10	Caryopsis with pappus	W
Trachymene saniculifolia	4	2.10	Mericarp	-
Trachymene tripartita	6	1.70	Mericarp	-
Trigonotis inoblita	3	0.17	Nutlet	-
Trigonotis papuana	4	0.25	Nutlet	-
Trigonotis aff. *papuana*	4	0.15	Nutlet	-
Triplostegia glandulifera	2	3.30	Fruit with viscid calyx	E
Trochocarpa dekockii	3	67	Berry	I
Uncinia ohwiana	2	1.90	Dry hooked fruit	E
Uncinia riparia	1	1.40	Dry hooked fruit	E
Vaccinium amblyandrum	3	100	Berry	I
Vaccinium cruentum	2	15	Berry	I
Veronica cf. *persica*	3	0.48	Seeds in dehiscent capsule	-
Viola arcuata	5	0.36	Seeds in dehiscent capsule	-
Youngia japonica	2	0.15	Caryopsis with pappus	W

W: Wind-dispersal adaptations
E: Adaptations to external animal dispersal
D: Dust seeds
I: Adaptations to internal animal dispersal

Appendix 4: Dispersal of Mt Wilhelm mountain grassland species to other sites. Included are all species occurring commonly or solely in non-forest environments above 3215 m, except those not present in the lowest parts of these environments or below 2750 m elsewhere, and some ill-known orchids.

Species	Wilhelm path 2715-3200 m	Pengagl Creek 2715-3140 m	Mondia road 2785-2831 m	Kombugli 3230-3260 m	Kuraglumba 2730-2850 m	Elsewhere in New Guinea below 2750 m	Category (see section 4-C)
Abrotanella papuana						+	P
Acaena anserifolia	+	+		+	+	+	G
Agrostis reinwardtii		+		+	+	+	G
Anaphalis lorentzii	+	+	+	+	+	+	G
Anaphalis mariae	+	+		+	+	+	G
Anotis sp.1					+	+	M
Anthoxanthum angustum					+	+	M
Astelia papuana						+	P
Brachypodium sylvaticum	+	+		+	+	+	G
Callitriche verna						+	E
Cardamine altigena		+	+		+	+	G
Carex capillacea						+	E
Carex celebica	+						M
Carex echinata		(+)			+	+	M
Carex euphlebia		+	+	+	+	+	G
Carex finitima							C
Carex gaudichaudiana					+	+	E
Carpha alpina							C
Centrolepis philippinensis						+	E
Cerastium papuanum	+	+	+		+	+	G
Coprosma papuensis	+	+		+	+	+	G
Danthonia archboldii				+	+	+	M
Danthonia penicillata	+			+	+	+	G
Deschampsia klossii	+	+	+	+	+	+	G
Deyeuxia arundinacea		+					M
Deyeuxia brassii					+		M
Dichelachne rara		+		+	+	+	G
Dimorphanthera keysseri							C
Dimorphanthera microphylla							C
Drapetes ericoides							C
Epilobium detznerianum						+	T
Epilobium hooglandii	?	?	?		?	+	U
Epilobium keysseri	+	+	+	+	+	+	G
Euphrasia mirabilis							C
Eurya albiflora							C
Eurya brassii							C
Festuca crispate-pilosa							C

(+) Records from Brass [1964].

Appendix 4 (cont'd)

Species	Wilhelm path 2715-3200 m	Pengagl Creek 2715-3140 m	Mondia road 2785-2831 m	Kombugli 3230-3260 m	Kuraglumba 2730-2850 m	Elsewhere in New Guinea below 2750 m	Category (see section 4-C)
Gaultheria mundula				+	+		M
Gentiana cruttwellii						+	T
Gentiana ettingshausenii	+			+		+	M
Gentiana piundensis						+	E
Geranium potentilloides						+	P
Gnaphalium breviscapum						+	P
Gnaphalium japonicum				+	+	+	M
Haloragis halconensis	+	+				+	M
Hierochloe redolens	+	+		+	+	+	G
Hydrocotyle sibthorpioides	+	+	+	+	+	+	G
Hypericum macgregorii				+	+	+	M
Keysseria radicans	+						M
Lactuca laevigata	+	+	+	+	+	+	G
Libertia pulchella	+			+		+	M
Luzula campestris						+	R
Monostachya oreoboloides						+	P
Myosotis australis	+					+	M
Myriactis cabrerae						+	R
Nertera granadensis	+	+	+		+	+	G
Nertera nigricarpa						+	R
Olearia floccosa							C
Olearia spectabilis				+			M
Oreobolus ambiguus						+	P
Oreobolus pumilio						+	P
Oreomyrrhis papuana	+						M
Oreomyrrhis pumila						+	T
Oxalis magellanica		(+)	+	+		+	M
Parahebe albiflora	+	+	+	+	+	+	G
Pedilochilus sp.3				+		?	U
Pilea cf. *johniana*					+		M
Pipturus sp.1	+	+	+	+		?	G
Pittosporum pullifolium							C
Plantago aundensis						+	P
Poa callosa							C
Poa crassicaulis							C
Poa epileuca						+	T

(+) Records from Brass [1964].

Appendix 4 (cont'd)

Species	Wilhelm path 2715-3200 m	Pengagl Creek 2715-3140 m	Mondia road 2785-2831 m	Kombugli 3230-3260 m	Kuraglumba 2730-2850 m	Elsewhere in New Guinea below 2750 m	Category (see section 4-C)
Poa saruwagetica	+	+		+	+	+	G
Polygonum runcinatum	+	+	+	+	+	+	G
Potentilla foersteriana				?	?	+	U
Potentilla papuana				+	+	+	M
Potentilla parvula	+	(?)		?	?	+	U
Ranunculus pseudolowii	+	+	+	+	+	+	G
Ranunculus wahgiensis							C
Rapanea vaccinioides							C
Rhododendron atropurpureum							C
Rhododendron beyerinckianum		(+)		+			M
Rhododendron commonae							C
Rhododendron gaultheriifolium							C
Rhododendron inconspicuum							C
Rhododendron womersleyi							C
Rhododendron yelliottii		+		+			M
Rubus papuanus	+						M
Sagina papuana	+	+	+		+	+	G
Schoenus curvulus	+	+	+	+	+	+	G
Schoenus maschalinus	+				+	+	M
Scirpus crassiusculus					+	+	E
Scirpus cf. *subtillissimus*	+	+	+	+	+	+	G
Senecio glomeratus					+	+	M
Senecio papuanus	+	+	+	+		+	G
Styphelia suaveolens		(+)			+		M
Tetramolopium alinae							C
Tetramolopium macrum						+	T
Thelymitra cf. *papuana*					+		U
Trachymene saniculifolia						+	P
Trachymene tripartita							C
Trigonotis papuana		+		+			M
Triplostegia glandulifera	+					+	M
Trochocarpa dekockii				+			M
Uncinia riparia	+					+	M
Vaccinium amblyandrum					+		M
Vaccinium cruentum							C
Viola arcuata	+	+		+	+	+	G

(+) Records from Brass [1964].

Appendix 5: Adventive species (see section 5-D).

Species	Occurrence frequencies in site categories with 5 or more sites									Sum of occurrence frequencies ≥ 6 (+) or ≥ 15 (++)	No. site categories occupied ≥ 3 (+) or ≥ 6 (++)
	A I S	A II S	B I S	C I S	C II S	A I L	B II L	A II T	C II T		
Acaena anserifolia	1	2			1		2		3	+	+
Agrostis avenacea	1	4				2		2		+	+
Agrostis reinwardtii	1	3	3	4		1	3	3	4	++	++
Anaphalis lorentzii	3	3	2	3	3	3	4	4	4	++	++
Anaphalis mariae			3	4	4		4	3	4	++	+
Anthoxanthum angustum	1		2	3	3					+	+
Bidens pilosa	2	4	2			2				+	+
Brachypodium sylvaticum		1		1	1			2	1	+	+
Carex ?celebica			4	2	2		2		3	+	+
Carex euphlebia	3	1	2			2	4		2	+	+
Carex neoguineensis	2	3	1			1		2		+	+
Carex ?perciliata				1	2				1		+
Carpha alpina				2	1				1		+
Cerastium papuanum	2	1	2	1		1				+	+
Coleus scutellarioides	1	1				1					+
Coprosma divergens				2	4				1	+	+
Coprosma papuensis		2	2	2	2	2	4	2	2	++	++
Crassocephalum crepidioides	4	3	1			4	1	3		++	+
Cynoglossum javanicum	2	3				1				+	+
Danthonia archboldii			1	1	1						+
Danthonia penicillata			1	3	3		1		4	+	+
Deschampsia klossii	4	4	3	3	3	4	4	4	4	++	++
Deyeuxia brassii	1			1	1			3	2	+	+
Dichelachne rara		3	1	2	3	1	4	3	3	++	++
Dichrocephala bicolor	3	4				2		2		+	+
Dodonaea viscosa	2	2				3	3	2		+	+
Epilobium detznerianum			1	2	2		1		3	+	+
Epilobium ?hooglandii	4	4	3	2	2	4	3	3		++	++
Epilobium keysseri	4	3	3	2	2	4	4	4	3	++	++
Equisetum debile	2	2				4	1	4		+	+
Erigeron canadensis		3	3		1	4		3		+	+
Erigeron sumatrensis	4	4	3	2	1	4	2	2		++	++
Gaultheria mundula				3	3			2	3	+	+
Gleichenia bolanica				1	2		1		1		+
Gnaphalium breviscapum				2	3				3	+	+
Gnaphalium involucratum	3	4	2			3		2		+	+
Gnaphalium japonicum	1		2				2				+
Grammitis sp.					1		1		2		+
Haloragis halconensis		2	3	3	4	1	4	3	3	++	++
Harmsiopanax ingens	2	1				1					+

Appendix 5 (cont'd)

Species	Occurrence frequencies in site categories with 5 or more sites									Sum of occurrence frequencies ≥ 6 (+) or ≥ 15 (++)	No. site categories occupied ≥ 3 (+) or ≥ 6 (++)
	A I S	A II S	B I S	C I S	C II S	A I L	B II L	A II T	C II T		
Hierochloe redolens			2	1			4	2	2	+	+
Hydrocotyle sibthorpioides	3	1	1	2	1	2	2	2	1	++	++
Hypericum macgregorii	1			3	2	1	1	2	2	+	++
Imperata conferta	2					3		3		+	+
Ischnea elachoglossa				1	2				1		+
Juncus effusus	1	2				2					+
Lactuca laevigata	3	3	4	4	4	4	4	4	4	++	++
Libertia pulchella	1						1		1		+
Lobelia angulata	2	3				1				+	+
Microlaena stipoides		4				2				+	
Miscanthus floridulus	1	1	1			3	2	3		+	+
Monostachya oreoboloides					2		1		1		+
Nertera granadensis	2	2	1			3				+	+
Olearia monticola	1					1	1	2			+
Oxalis magellanica					1		1		2		+
Parahebe albiflora	2	2	2	1		3	3	3	3	++	++
Pedilochilus sp.3					1		1		1		+
Pilea cf. *johniana*		1		1	2						+
Pipturus sp.1	4	2	1	1	2	2	4			++	++
Poa saruwagetica	3		4	4	4	2	4	4	4	++	++
Polygonum nepalense		3	1			1				+	+
Polygonum runcinatum	3	2			1					+	+
Potentilla ?foersteriana			1		3	1	3		2	+	+
Potentilla papuana			2	3	3		3		4	++	+
Ranunculus pseudolowii	2	4	3	3	3	4	4	4	4	++	++
Rhododendron yelliottii					1		4		2	+	+
Rubus papuanus			1	1	1				2		+
Sagina papuana	2	3	2	1	1	3	2	3	4	++	++
Saurauia sp.		2				2	3			+	+
Schoenus curvulus	2	2	4	3	4	2	4		4	++	++
Schoenus maschalinus	1		2	1	2		2			+	+
Scirpus cf. *subtillissimus*	2	3	1	1		3	2	2		+	++
Senecio papuanus	2	3	4	3	2		1	2	3	++	++
Sonchus oleraceus	4	4	3		1	2	2	2		++	++
Styphelia suaveolens				2	3			3		+	+
Tacsonia mollissima	1	3	1			2				+	+
Trigonotis inoblita	2	1	1								+
Trigonotis papuana				3	3		2		3	+	+
Vaccinium amblyandrum					1			3	2	+	+
Viola arcuata		2	2		1	1	1			+	+

Appendix 6: Growth rates of short-stemmed herbs (see section 6-B).

Species	Plant No.	Plot	Year	Period (days)	Dry Weight of Aerial Parts (mg)	Growth Rate (daily %)	Species Mean Growth Rate
Abrotanella papuana	APA	8	71/72	378	17.1	0.43	0.47
	AP4B*	8	71/72	378	34.3	0.47	
	AP2A	5	71	57	7.5	0.64	
	AP2B	5	71	57	8.5	0.64	
Astelia papuana	AP1A	1	72	138	150.2	0.46	0.29
	AP1B	1	71/72	273	8.4	0.27	
	AP3	1	71/72	325	65.9	0.23	
	AP5	11	71/72	373	205.7	0.10	
	AP6A	13	71/72	257	42.3	0.26	
	AP6B	13	71/72	257	55.4	0.26	
	AP7A	12	71/72	322	151.7	0.42	
	AP7B	12	71/72	322	59.1	0.24	
Carpha alpina	CA1	1	72	130	44.9	0.46	0.34
	CA6	1	72	130	16.5	0.32	
	CA3	1	72	66	30.1	0.28	
	CA4*	1	72	130	22.0	0.26	
Fragaria cf. *vesca*	FS1	9	72	132	1770.6	0.70	0.65
	FS2	9	72	131	212.0	0.55	
	FS3	9	72	131	177.1	0.45	
	FS4	9	72	131	1750.4	0.91	
Gnaphalium breviscapum	GB3A	2	71	70	10.9	0.76	0.65
	GB3B	2	72	139	12.1	0.71	
	GB4A	2	71	70	7.6	0.75	
	GB4B	2	72	139	11.2	0.84	
	GB1A	1	71	70	8.6	1.13	
	GB1B	1	72	75	4.5	0.48	
	GB2	1	71/72	397	13.3	0.47	
Ischnea elachoglossa	IE1A	6	71	52	48.8	0.28	0.62
	IE1B	6	72	68	65.2	0.61	
	IE2A	6	71	52	41.5	0.59	
	IE2B	6	72	68	23.1	0.59	
	IE3	11	71	48	43.3	0.82	
	IE4	11	71	48	28.9	0.85	
Keysseria radicans	KR1*	5	71/72	385	772.7	0.40	0.44
	KR2	5	71/72	385	623.7	0.41	
	KR3	5	71	57	52.6	0.58	
	KR4	12	71/72	322	514.0	0.45	
	KR5	12	71/72	322	424.7	0.48	

* Growth rate is an underestimate due to inadequate measurement of certain organs, e.g. fruits, branch tillers.

Appendix 6 (cont'd)

Species	Plant No.	Plot	Year	Period (days)	Dry Weight of Aerial Parts (mg)	Growth Rate (daily %)	Species Mean Growth Rate
Lactuca laevigata	LL3	7	72	134	16.8	1.00	0.78
	LL1A	1	71	70	51.6	0.95	
	LL1B	1	72	138	60.2	0.62	
	LL2A	8	71	48	76.2	0.29	
	LL2B	8	72	68	275.2	0.83	
Oreomyrrhis linearis	OL1	12	71/72	199	19.5	0.37	0.57
	OL3	12	72	123	106.8	0.73	
	OL4	12	72	123	54.7	0.74	
Oreomyrrhis papuana	OP5*	7	72	103	31.3	1.05	0.93
	OP1A	2	71	70	5.6	0.61	
	OP1B	2	72	139	4.6	0.19	
	OP2	3	71	67	534.6	1.74	
	OP3	3	71	67	727.7	1.49	
	OP6*	6	72	132	37.1	1.05	
	OP7	8	72	132	26.9	0.95	
Oxalis magellanica	OM1	9	72	76	3.9	0.93	0.87
	OM2	9	72	131	12.6	0.83	
Pedilochilus sp.3	PS1	4	71/72	249	69.2	0.15	0.20
	PS2	4	71/72	249	52.6	0.25	
Plantago aundensis	PA1*	2	71/72	397	112.4	0.56	0.54
	PA2*	4	71/72	328	88.0	0.49	
	PA3*	4	71/72	390	96.6	0.55	
	PA4	5	71/72	385	99.2	0.54	
Plantago lanceolata	PL1	9	72	120	1852.0	0.64	0.69
	PL2/3	9	72	120	1740.9	0.60	
	PL4	9	72	120	741.0	0.85	
	PL5	9	72	120	1667.0	0.67	
Poa crassicaulis	PC1A	4	71	60	21.0	0.69	0.81
	PC1B	4	72	138	26.2	0.89	
	PC5	11	72	65	33.2	0.62	
	PC6	15	72	126	1.8	0.89	
Potentilla ?foersteriana	PF4	7	71	53	740.6	0.82	0.61
	PF2A	2	71	70	454.6	0.43	
	PF2B	2	72	139	331.8	0.67	
	PF1A	1	71	70	135.1	0.54	
	PF1B	1	72	138	112.6	0.83	
	PF3	6	71	52	2765.0	0.41	
	PF5A	11	71	48	1672.6	0.89	
	PF5B	11	72	123	893.6	0.86	
	PF6	12	71/72	322	272.9	0.47	
	PF8	15	72	126	1236.2	0.43	

* Growth rate is an underestimate due to inadequate measurement of certain organs, e.g. fruits, branch tillers.

Appendix 6 (cont'd)

Species	Plant No.	Plot	Year	Period (days)	Dry Weight of Aerial Parts (mg)	Growth Rate (daily %)	Species Mean Growth Rate
Potentilla papuana	PP2	6	71/72	380	1320.0	0.64	0.66
	PP3	8	71/72	329	1194.9	0.50	
	PP1A	4	71	60	260.7	0.89	
	PP1B	4	72	138	312.4	1.25	
	PP4A	11	71	48	860.5	0.45	
	PP4B	11	72	123	500.6	0.62	
	PP5	12	71/72	322	395.0	0.73	
	PP6A	14	72	126	385.0	0.49	
	PP6B	14	72	126	249.2	0.43	
Ranunculus pseudolowii	RP5	7	71/72	327	867.8	0.46	0.66
	RP2	2	71/72	397	50.6	0.95	
	RP1	1	71/72	366	122.6	0.60	
	RP6	8	71/72	378	236.0	0.57	
	RP3	4	71/72	390	23.3	0.64	
	RP4	5	71/72	385	78.2	0.72	
Ranunculus saruwagedicus	RS1	14	71/72	324	85.4	0.47	0.63
	RS2	15	72	126	101.7	0.77	
	RS3	15	72	126	159.3	0.62	
	RS4	15	72	126	86.4	0.89	
Ranunculus schoddei	RK3	13	72	123	15.5	0.95	0.66
	RK4	13	72	123	4.0	0.66	
	RK1	12	71/72	199	28.4	0.30	
	RK2	12	72	123	6.6	0.97	
Senecio sp.5	LS1	14	72	126	16.6	0.52	0.59
	LS2	14	72	61	7.0	0.55	
	LS3	14	72	126	17.6	0.67	
Trachymene tripartita	TT1	1	71/72	397	2.5	0.27	0.46
	TT2	1	71/72	397	1.9	0.33	
	TT3A*	5	71/72	385	19.7	0.56	
	TT3B	5	71/72	385	14.3	0.50	
	TT3C	5	71	57	0.7	0.99	
	TT4	13	71/72	322	22.8	0.52	
	TT5	13	72	65	0.5	0.96	
Viola arcuata	VS3A	7	72	128	13.9	0.65	0.57
	VS3B	7	72	128	13.9	0.78	
	VS3C	7	72	128	13.9	0.39	
	VS1	4	71	60	0.2	0.50	
	VS2	4	71	60	0.9	0.42	

* Growth rate is an underestimate due to inadequate measurement of certain organs, e.g. fruits, branch tillers.

Appendix 7: Distributions of 252 herbaceous angiosperm species in mountain regions of New Guinea.

	IJ	S	B	H	St	K	Kr	OS
Abrotanella papuana S.Moore	+		+	+			+	+
Abrotanella sp.				+		+		
Acaena anserifolia (G.Forst.) Domin.	+	+	+	+		+	+	+
Agrostis reinwardtii van Hall	+	+	+	+		+	+	+
Anaphalis lorentzii Lautb.	+	+	+	+		+	+	+
Anaphalis mariae F.v.M.	+	+	+	+		+	+	+
Anaphalis monocephala S.Moore	+							
Anotis sp.1		+	+	+		+		+
Anthoxanthum angustum (Hitchc.) Ohwi	+	+	+	+		+	+	+
Astelia papuana Skottsb.	+	+	+	+		+	+	+
Brachycome elegans Koster								+
Brachycome papuana Mattf.		+	+					
Brachypodium longisetum Hitchc.			+	+				+
Brachypodium sylvaticum (Huds.) P.Beauv.	+	+	+	+			+	+
Bromus insignis Buse	+							
Callitriche verna L.		+	+	+				+
Cardamine africana L.		+	+	+				+
Cardamine altigena Schltr. ex Schultz			+	+				+
Carex acrophila S.T.Blake	+							
Carex celebica Kük.		+	+	+		+		
Carex capillacea Boott.		+	+	+		+		
Carex echinata Murr.			+	+		+		
Carex eremostachya S.T.Blake	+							
Carex euphlebia S.T.Blake	+		+	+	+		+	+
Carex finitima Boott.		+	+					
Carex gaudichaudiana Kunth.	+		+	+				
Carex melanophora S.T.Blake	+		+					
Carex neoguineensis C.B.Clarke	+	+	+	+		+		+
Carex perciliata (Kük.) Nelmes		+	+			+		+
Carex sarawaketensis Kük.		+						+
Carex tricuspidatum Kük.	+							
Carpha alpina R.Br.	+	+	+	+		+	+	+
Centrolepis fascicularis Labill.	+							
Centrolepis philippinensis Merr.	+	+	+	+		+	+	+
Cerastium papuanum Schltr.	+	+	+	+		+	+	+
Cotula cf. *leptoloba* Mattf.	+	+	+	+			+	+
Danthonia archboldii Hitchc.	+	+	+	+	+	+	+	+
Danthonia penicillata (Labill.) P.Beauv.			+	+				+
Danthonia vestita Pilg.	+	+	+	+		+		+
Deschampsia flexuosa (L.) Trin.	+							
Deschampsia klossii Ridl.	+	+	+	+	+	+	+	+
Deyeuxia arundinacea (L.) Jansen		+	+	+		+	+	+

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 7 (cont'd)

	IJ	S	B	H	St	K	Kr	OS
Deyeuxia australis (Zoll. et Mor.) Jansen		+						
Deyeuxia brassii (Hitchc.) Jansen	+	+	+	+		+	+	+
Deyeuxia macgregorii Jansen				+				
Deyeuxia ?stenophylla Jansen		+	+					
Dichelachne rara (R.Br.) Vickery			+	+			+	+
Drapetes ericoides Hook. f.	+	+	+	+	+	+	+	+
Epilobium detznerianum Schltr. ex Diels	+	+	+	+	+	+		
Epilobium hooglandii Raven	+	+	+	+				+
Epilobium keysseri Diels	+	+	+	+		+	+	+
Epilobium prostratum Warb.	+	+	+	+		+		+
Eriocaulon montanum Royen	+	+	+	+	+	+	+	+
Euphrasia bangetensis Royen		+						
Euphrasia callosa Penn.		+		+				+
Euphrasia culminicola Wernham	+							
Euphrasia curvifolia Penn.								+
Euphrasia humifusa Penn.	+			+				
Euphrasia mirabilis Penn.	+	+	+	+		+	+	+
Euphrasia cf. *rectiflora* Penn.								+
Euphrasia scutellarioides Wernham	+							
Euphrasia spatuliflora Penn.	+							
Euphrasia sp.					+			
Festuca crispate-pilosa Bor.		+	+					
Festuca nubigena Jungh.	+	+		+				
Festuca papuana Stapf		+	+	+			+	+
Gahnia javanica Zoll. et Mor. ex Mor.	+			+	+			+
Gaimardia setacea Hook. f.			+	+		+		+
Galium bryoides Merr. et Perr.								+
Galium novoguineense Diels		+	+	+		+		
Galium rotundifolium L.	+	+	+	+	+	+	+	+
Galium subtrifidum Reinw. ex Bl.	+	+	+	+	+	+	+	+
Gentiana carinicostata Hemsl.	+							
Gentiana cinereifolia Royen								+
Gentiana cruttwellii H.Sm.		+	+			+		+
Gentiana dimorphophylla F.v.M.	+							
Gentiana ettingshausenii F.v.M.		+	+	+		+	+	+
Gentiana giulianettii Hemsl.								+
Gentiana igitii Royen								+
Gentiana juniperina H.Smith								+
Gentiana lorentzii Koord.	+			+	+			
Gentiana macgregorii Hemsl.	+			+				+
Gentiana nerterifolia Royen	+				+			
Gentiana papuana Royen	+				+			

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 7 (cont'd)

	IJ	S	B	H	St	K	Kr	OS
Gentiana piundensis Royen		+	+	+	+	+	+	
Gentiana protensa Royen	+							
Gentiana pungens Royen	+							
Gentiana recurvifolia Royen				+		+		+
Gentiana saginifolia Wernham	+	+		+				
Gentiana sclerophylla Royen	+							
Gentiana vandewateri Wernham in Ridl.	+							
Gentiana wollostonii Wernham in Ridl.	+							
Gentiana sp.						+		
Geranium potentilloides L'Herit. ex DC.	+	+	+	+		+	+	+
Gnaphalium brassii Mattf.								+
Gnaphalium breviscapum Mattf.		+	+	+		+		+
Gnaphalium involucratum G.Forst.	+	+	+	+				+
Gnaphalium japonicum Thunb.			+	+			+	+
Haloragis halconensis Merr.	+	+	+	+	+	+	+	+
Haloragis micrantha (Thunb.) R.Br.	+	+		+			+	+
Hierochloe redolens (Vahl.) R. et S.	+	+	+	+			+	
Hierochloe sp.				+				
Hydrocotyle sibthorpioides Lamk.	+	+	+	+		+		+
Hypericum japonicum Thunb.	+	+	+	+	+			+
Ischnea elachoglossa F.v.M.	+	+	+	+	+	+		+
Ischnea linifolia Koster				+				
Ischnea sp.	+							
Ischnea sp.		+				+		
Ischnea sp.	+							
Keysseria bellidiformis (F.v.M.) Mattf.								+
Keysseria extensa Koster	+							
Keysseria fasciculata Koster							+	
Keysseria gibbsiae (Merr.) Cabrera ex Steen.				+		+		
Keysseria radicans (F.v.M.) Mattf.	+	+	+	+	+	+	+	+
Keysseria rosulans Koster								+
Keysseria tomentella Mattf.								+
Keysseria wollastonii (S.Moore) Mattf.	+							
Lactuca dentata (Thunb.) C.L.Rob.	+							
Lactuca laevigata (Bl.) DC.	+	+	+	+		+	+	+
Lactuca sp.1			+					
Lagenophora lanata A.Cunn.	+	+		+				+
Lagenophora stipitata (Labill.) Druce		+	+					+
Libertia pulchella (R.Br.) Spreng.	+	+	+	+	+	+	+	+
Lobelia archboldiana (Merr. et Perr.) Moeliono			+	+		+		+
Lobelia conferta Merr. et Perr.								+
Luzula campestris (L.) DC.	+		+	+				+

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 7 (cont'd)

	IJ	S	B	H	St	K	Kr	OS
Luzula effusa Buch.			+					+
Monostachya oreoboloides (F.v.M.) Hitchc.	+	+	+	+	+	+	+	+
Montia fontana L.			+					+
Myosotis australis R.Br.	+	+	+		+	+		+
Myriactis cabrerae Koster	+	+	+	+				+
Myriactis mindanaensis Elm.	+							
Myriophyllum pedunculatum Hook. f.		+		+				+
Myriophyllum pygmaeum Mattf.		+						+
Nertera granadensis (L.f.) Mutis ex Druce	+	+	+	+	+	+	+	+
Nertera cf. *nigricarpa* Hayata		+	+	+				+
Oreobolus ambiguus Kük. et Steen.	+		+	+	+	+		+
Oreobolus pumilio R.Br.	+	+	+	+		+		+
Oreomyrrhis azolleracea Buw.								+
Oreomyrrhis buwaldiana Matth. et Const.	+							
Oreomyrrhis linearis Hemsl.			+	+			+	+
Oreomyrrhis papuana Buw.	+	+	+	+		+		
Oreomyrrhis pumila Ridl.	+	+	+					+
Oreomyrrhis sp.								+
Oxalis magellanica G.Forst.	+	+	+		+	+		+
Papuzilla lataeviridis Royen	+	+						
Papuzilla minutiflora Ridl.	+			+				
Parahebe albiflora (Penn.) Royen et Ehrend.		+	+	+			+	
Parahebe carstensensis Diels	+							
Parahebe ciliata (Penn.) Royen et Ehrend.		+	+	+				
Parahebe polyphylla (Penn.) Royen et Ehrend.		+						
Parahebe rigida (Penn.) Royen et Ehrend.								+
Parahebe rubra (Penn.) Royen et Ehrend.								+
Parahebe tenuis (Penn.) Royen et Ehrend.		+	+					
Parahebe thymelioides (Penn.) Royen et Ehrend.						+		
Parahebe vanderwateri (Penn. ex Wernham) Royen et Ehrend.	+							
Parahebe sp.								+
Peracarpa carnosa (Wall in Roxb.) Hook. f.		+	+	+	+			
Piora ericoides Koster							+	+
Plantago aundensis Royen	+	+	+	+		+	+	
Plantago depauperata Merr. et Perr.	+		+	+		+		
Plantago sp. aff. *depauperata*						+	+	+
Plantago papuana Royen				+				
Plantago stenophylla Merr. et Perr.	+	+	+				+	+
Plantago trichophora Merr. et Perr.								+
Poa callosa Stapf		+	+	+		+	+	
Poa crassicaulis Pilg.	+	+	+	+				+
Poa egregia Chase	+							

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 7 (cont'd)

	IJ	S	B	H	St	K	Kr	OS
Poa epileuca (Stapf) Stapf	+	+	+	+	+	+	+	+
Poa erectifolia Hitchc.	+							+
Poa languidior Hitchc.		+	+	+		+	+	+
Poa longiramea Hitchc.		+						+
Poa nivicola Ridl.	+	+	+	+				
Poa saruwagetica Pilg.		+	+	+				
Polygonum decipiens R.Br.	+			+				
Polygonum runcinatum D.Don	+	+	+	+	+	+		+
Potentilla foersteriana Lautb.	+	+	+	+	+	+		+
Potentilla ?habbemana Merr. et Perr.	+							+
Potentilla papuana (Focke) Hook. f. ex Stapf	+	+	+	+		+	+	+
Potentilla parvula Hook. f. ex Stapf	+	+	+	+	+	+	+	+
Pratia papuana S.Moore	+							
Ranunculus amerophyllus F.v.M.	+							+
Ranunculus bidens Eichl. ined.						+		
Ranunculus habbemensis Merr. et Perr.	+							
Ranunculus keysseri Eichl.		+	+					+
Ranunculus lappaceus Sm.	+							
Ranunculus papuanus Ridl.	+							
Ranunculus perindutus Merr. et Perr.	+							
Ranunculus pseudolowii Eichl.	+	+	+	+		+	+	+
Ranunculus saruwagedicus Eichl.		+	+					
Ranunculus schoddei Eichl. ined.			+					
Ranunculus tridens Ridl.	+							
Ranunculus wahgiensis Eichl.			+	+				
Ranunculus sp. aff. *wahgiensis*								+
Sagina belonophylla Mattf.	+							
Sagina monticola Merr. et Perr.	+							
Sagina papuana Warb.	+	+	+	+	+		+	+
Schoenus curvulus F.v.M.		+	+	+	+	+	+	+
Schoenus maschalinus R. et S.	+	+	+	+		+		+
Schoenus setiformis S.T.Blake	+	+						
Scleranthus singuliflorus (F.v.M.) Mattf.			+					+
Scirpus crassiusculus (Hook. f.) Benth.		+	+	+		+		+
Scirpus inundatus (R.Br.) Poir.			+	+				
Scirpus subcapitatus Thwaites			+	+				+
Scirpus subtillissimus Boeck.		+	+	+				+
Senecio glomeratus Desf. ex Poir.		+	+	+				
Senecio papuanus (Lautb.) Belcher		+	+	+		+	+	+
Senecio sp.5			+	+				
Tetramolopium alinae (F.v.M.) Mattf.	+	+	+				+	+
Tetramolopium bicolor Koster	+							

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 7 (cont'd)

	IJ	S	B	H	St	K	Kr	OS
Tetramolopium ciliatum Mattf.		+						
Tetramolopium cinereum Koster								+
Tetramolopium corallioides Koster	+							
Tetramolopium distichum (S.Moore) Mattf.	+							
Tetramolopium ericoides Mattf.	+							
Tetramolopium fasciculatum Koster	+							
Tetramolopium flaccidum Mattf.								+
Tetramolopium gracile Koster				+				
Tetramolopium klossii (S.Moore) Mattf.	+				+			
Tetramolopium lanatum Koster	+							
Tetramolopium macrum (F.v.M.) Mattf.	+	+	+	+		+	+	+
Tetramolopium piloso-villosum (S.Moore) Mattf.	+							
Tetramolopium procumbens Koster				+				
Tetramolopium prostratum Mattf.	+							
Tetramolopium pumilum Mattf.								+
Tetramolopium spathulatum Mattf.		+						
Tetramolopium tenue Koster	+							
Tetramolopium virgatum Mattf.	+				+			
Tetramolopium wilhelminae Koster	+							
Thalictrum papuanum Ridl.	+							
Trachymene adenodes Buw.		+	+	+			+	+
Trachymene flabellifolia Buw.	+							
Trachymene koebrensis (Gibbs) Buw.	+							
Trachymene novoguineensis (Domin.) Buw.	+	+	+		+		+	+
Trachymene papillosa Buw.	+							
Trachymene rosulans (Dans.) Buw.								+
Trachymene saniculifolia Stapf			+	+				+
Trachymene tripartita Hoogl.		+	+	+		+		
Trigonotis inoblita F.v.M.		+	+	+		+	+	+
Trigonotis papuana (Hemsl.) Johnston	+		+	+		+		+
Trigonotis sp. aff. *papuana*			+					
Trigonotis pleiomera Johnston		+						
Trigonotis procumbens (Warb.) Johnston	+	+	+	+		+	+	
Triplostegia glandulifera Wall.	+	+	+	+	+	+		+
Trisetum subspicatum (L.) P.Beauv.	+							
Uncinia ohwiana Koy		+	+			+		+
Uncinia riparia R.Br.		+	+			+		+
Uncinia sp.1			+					
Viola arcuata Bl.	+	+	+	+	+	+		+
Wahlenbergia confusa Merr. et Perr.	+							+
Wahlenbergia marginata (Thunb.) DC.		+	+	+	+	+	+	+
Wahlenbergia sp.								+

IJ	Irian Jaya	St	Star Mts
S	Sarawaket Mts	K	Kubor range
B	Bismarck range	Kr	Krakte Mts
H	Mt Hagen area	OS	Owen Stanley range

Appendix 8: Altitudinal distributions in New Guinea of herbaceous angiosperm species growing above 3215 m on Mt Wilhelm (m).

	Lowest Record	Highest Record	Altitudinal Range	Mean of Highest and Lowest Records
NATIVE SPECIES				
Abrotanella papuana	2591	4000	1409	3295
Acaena anserifolia	2230	4085	1855	3157
Agrostis reinwardtii	1890	4206	2316	3048
Anaphalis lorentzii	1800	3700	1900	2750
Anaphalis mariae	2560	4400	1840	3480
Anotis sp.1	2286	3901	1615	3093
Anthoxanthum angustum	1524	4115	2591	2819
Astelia papuana	2926	4420	1494	3673
Brachycome papuana	3353	3353	0	3353
Brachypodium sylvaticum	2560	3810	1250	3185
Callitriche verna	2103	4115	2012	3109
Cardamine africana	1311	3650	2339	2480
Cardamine altigena	3200	4085	885	3642
Carex capillacea	2603	3810	1207	3206
Carex celebica	3270	3749	479	3509
Carex echinata	2591	3810	1219	3200
Carex euphlebia	1400	3536	2136	2468
Carex finitima	3048	3597	549	3322
Carex gaudichaudiana	2530	3800	1270	3165
Carex neoguineensis	2042	3560	1518	2801
Carex perciliata	3383	4176	793	3779
Carpha alpina	3200	4481	1281	3840
Centrolepis philippinensis	2000	4252	2252	3136
Cerastium papuanum	1524	4510	2986	3017
Cotula cf. *leptoloba*	2835	3850	1015	3342
Danthonia archboldii	1981	3840	1859	2910
Danthonia penicillata	2682	3560	878	3121
Danthonia vestita	3475	4481	1006	3978
Deschampsia klossii	1981	4300	2319	3140
Deyeuxia arundinacea	3078	3673	595	3375
Deyeuxia brassii	2804	4280	1476	3542
Dichelachne rara	1981	3840	1859	2910
Dichrocephala bicolor	840	3535	2695	2187
Drapetes ericoides	2896	4510	1614	3703
Epilobium detznerianum	2316	4350	2034	3333
Epilobium hooglandii	2743	4085	1342	3424
Epilobium keysseri	1981	4035	2054	3008
Eriocaulon montanum	3050	3950	900	3500
Euphrasia mirabilis	3200	4115	915	3657
Festuca crispate-pilosa	3000	3840	840	3420
Festuca papuana	3200	4390	1190	3795
Gaimardia setacea	3353	4000	647	3686
Galium novoguineense	3225	3760	535	3492

Appendix 8 (cont'd)

	Lowest Record	Highest Record	Altitudinal Range	Mean of Highest and Lowest Records
Galium rotundifolium	1370	3500	2130	2435
Gentiana cruttwellii	869	4161	3292	2515
Gentiana ettingshausenii	2134	4328	2194	3231
Gentiana piundensis	2700	4480	1780	3590
Geranium potentilloides	2591	4328	1737	3460
Gnaphalium breviscapum	2835	4420	1585	3627
Gnaphalium involucratum	1524	3575	2051	2550
Gnaphalium japonicum	2286	3650	1364	2968
Haloragis halconensis	975	4115	3140	2545
Hierochloe redolens	2712	4450	1738	3581
Hydrocotyle sibthorpioides	1646	4221	2575	2933
Hypericum japonicum	1433	3292	1859	2362
Hypericum macgregorii	1981	4115	2134	3048
Imperata conferta	20	3257	3237	1639
Ischnea elachoglossa	3048	4420	1372	3734
Keysseria radicans	3048	4267	1219	3657
Lactuca laevigata	0	4267	4267	2133
Lactuca sp.1	4100	4350	250	4225
Libertia pulchella	2743	3688	945	3170
Lobelia angulata	1067	3300	2233	2183
Lobelia archboldiana	3500	4008	508	3754
Luzula campestris	2530	3871	1341	3200
Miscanthus floridulus	1219	3500	2281	2359
Monostachya oreoboloides	2500	4481	1981	3490
Montia fontana	3200	3444	244	3322
Myosotis australis	2743	3950	1207	3346
Myriactis cabrerae	2530	3505	975	3017
Nertera granadensis	1433	4115	2682	2774
Nertera nigricarpa	2591	3925	1334	3258
Oreobolus ambiguus	2500	3780	1280	3140
Oreobolus pumilio	2600	4000	1400	3300
Oreomyrrhis linearis	2835	3950	1115	3392
Oreomyrrhis papuana	3048	3658	610	3353
Oreomyrrhis pumila	2743	4680	1937	3711
Oxalis magellanica	2200	4085	1885	3142
Parahebe albiflora	2438	3658	1220	3048
Parahebe ciliata	3231	4466	1235	3848
Parahebe tenuis	3840	4008	168	3924
Pilea cf. *johniana*	3050	4267	1217	3658
Plantago aundensis	2700	4115	1415	3407
Poa callosa	3170	4500	1330	3835
Poa crassicaulis	2896	4450	1554	3673
Poa epileuca	2591	4115	1524	3353
Poa languidior	3048	3650	602	3349
Poa saruwagetica	2100	4206	2106	3153
Poa sp.1	3962	4481	519	4221
Polygonum runcinatum	1372	3550	2178	2461
Potentilla foersteriana	2230	4460	2230	3345

Appendix 8 (cont'd)

	Lowest Record	Highest Record	Altitudinal Range	Mean of Highest and Lowest Records
Potentilla papuana	2134	4221	2087	3177
Potentilla parvula	2591	4115	1524	3353
Ranunculus pseudolowii	869	4029	3160	2449
Ranunculus saruwagedicus	3962	4481	519	4221
Ranunculus schoddei	3643	4060	417	3851
Sagina papuana	1524	4050	2526	2787
Schoenus curvulus	30	4000	3970	2015
Schoenus maschalinus	2230	3749	1519	2989
Scirpus crassiusculus	2560	3810	1250	3185
Scirpus subcapitatus	2896	4000	1104	3448
Scirpus cf. *subtillissimus*	1676	4115	2439	2895
Senecio glomeratus	2591	3810	1219	3200
Senecio papuanus	2896	3600	704	3248
Senecio sp.5	4000	4300	300	4150
Tetramolopium alinae	3048	4115	1067	3581
Tetramolopium macrum	2530	4300	1770	3415
Trachymene saniculifolia	2225	3658	1433	2941
Trachymene tripartita	3109	4000	891	3554
Trigonotis papuana	2896	4115	1219	3505
Trigonotis sp. aff. *papuana*	4250	4481	231	4365
Trigonotis procumbens	1524	3658	2134	2589
Triplostegia glandulifera	2591	3560	969	3075
Uncinia ohwiana	2447	3640	1193	3043
Uncinia riparia	2680	4115	1435	3397
Uncinia sp.1	3764	4343	579	4053
Viola arcuata	1433	3932	2499	2682
Viola betonicifolia	1311	3300	1989	2305
Wahlenbergia marginata	1067	3505	2438	2286
ALIEN SPECIES				
Bidens pilosa	15	3490	3475	1752
Cordyline fruticosa	10	3481	3471	1745
Crassocephalum crepidioides	30	3414	3384	1717
Erigeron canadensis	354	3688	3334	2021
Erigeron sumatrensis	152	3688	3536	1920
Fragaria cf. *vesca*	1585	3484	1899	2434
Lolium rigidum	3180	3481	301	3330
Lupinus sp.	1920	3481	1561	2700
Nasturtium officinale	1905	3240	1335	2572
Phalaris tuberosa	1905	3536	1631	2521
Poa annua	2438	3481	1043	2959
Sonchus oleraceus	914	3688	2774	2301
Stellaria media	1820	3481	1661	1650
Tacsonia mollissima	1981	3481	1500	2731
Tritonia X *crocosmaeflora*	1829	3481	1652	2655
Verbena bonariensis	914	3481	2567	2197
Veronica cf. *persica*	2133	3481	1384	2807
Vulpia bromoides	2539	3481	942	3010