Analysis of the Plant Geography of the Semideciduous Scrub and Forest and the Eucalypt Savannah near Port Moresby[1]

P. C. HEYLIGERS[2]

THE COASTAL LOWLANDS of southeastern Papua are subject to a monsoonal climate. Semideciduous scrub and forest, and eucalypt savannah are characteristic elements of the vegetation (Heyligers, 1965, 1966). During an investigation to determine whether the savannah is a climax vegetation or a disclimax caused and maintained by man and fire, I analyzed the geographical affinities of the species in these vegetation types to elucidate some aspects of their autecology and of the history of the area. Most of the literature on plant geography of neighboring areas, however, deals wholly or mainly with genera and, therefore, the distribution of the genera has been analyzed also. This lead to the discovery that in the Indo-Malesian Floristic Region the relationship between number of widespread genera and total number of genera could be expressed by a single logarithmic series.

DATA

During about 6 months' fieldwork in the dry seasons of 1965 and 1967, the numbers of trees, shrubs, and climbers were counted or estimated in about 180 plots of 150 m², and the density or cover of herbs was estimated in about 90 plots, the size of which depended on homogeneity of the vegetation. For each plot all the species were listed and the individuals belonging to each species were counted or their numbers estimated; for the herb layers the density or cover of each species was assessed. The plots were selected to represent the different types of forest, scrub, savannah, and their transitions and were located near Tovobada, near Tavai, and east of Mt. Lawes, 10 km NW, 45 km SE, and 23 km NNE, of Port Moresby, respectively. In the following pages these sites will jointly be referred to as "Port Moresby Area."

The 450 or so species of vascular plants found in or near the plots are considered to be a fair representation of their flora, because only a small number of species was added during the later stages of the fieldwork. It is emphasized that vegetation types such as seasonally flooded forests, swamps, and garden regrowth were not included in the investigation.

The basis for the geographical analysis is 292 identified species comprising 206 genera, and a further 73 identified genera.[3] Plant identifications were made with the cooperation of the staff of the Herbarium Australiense, Canberra; supplementary information from other herbaria has also been used.

Data on the distribution of genera were extracted mainly from Burbidge (1963), Good (1960), Kalkman (1955), and Willis (1966). Those for the species were collated from *Flora Malesiana,* Backer and Bakhuizen van den Brink (1963–1968), Burbidge (1963), Merrill (1923–1926), Specht (1958), and from serials

[1] Manuscript received 5 May 1971.

[2] Commonwealth Scientific and Industrial Research Organization, Division of Land Research, P. O. Box 109, Canberra City, A.C.T. 2601, Australia.

[3] This means that about 160 species (36 percent) and 62 genera (18 percent) were left unidentified. There are several reasons for not having been able to identify these plants. First, the knowledge of the New Guinea flora is very uneven, and identifications in several families, e.g., Annonaceae, Asclepidiaceae, and Cucurbitaceae, are often impossible because of the state of the taxonomy. Second, much of the unidentified material was obtained from sterile and, not uncommonly, juvenile plants. Any geographical treatment is bound to the state of the taxonomy (cf., van Balgooy, 1969), and I hold the opinion that my figures are quite comparable to these of neighboring areas. I do not think that identification of the inadequate material would have significantly altered the conclusions presented in this paper, because there is little reason to suppose that, for instance, endemic species would have gone undetected more often than species of wide distribution.

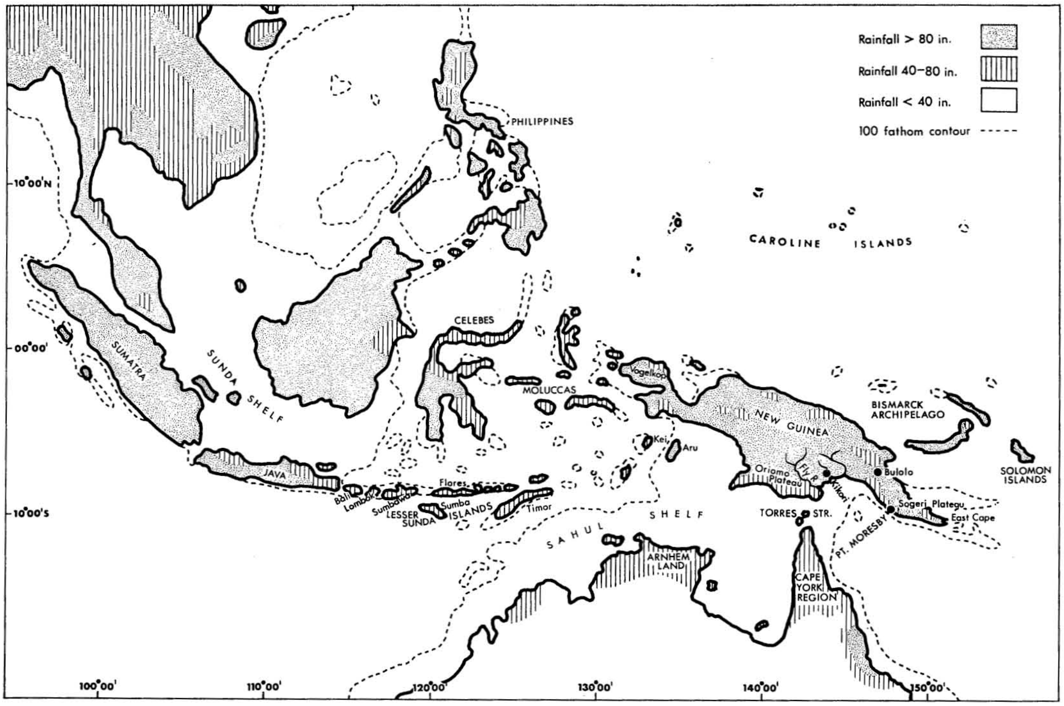

FIG. 1. Map of tropical southeastern Asia and northern Australia showing geographical names used in the text, average annual rainfall, and 100-fathom contour.

such as *Blumea, Nova Guinea, Botanische Jahrbücher*, and *Journal of the Arnold Arboretum*. Localities on exsiccatae in the Herbarium Australiense and the Queensland Herbarium, Brisbane, were also used. Technical Memorandum 72/1 documents the distribution data of the genera and species.[4]

To avoid ambiguities, the following geographical areas are defined (see Fig. 1):

Southeastern Papua: the coastal lowlands NW and SE from Port Moresby, subject to a seasonally dry climate.

New Guinea: the main island only.

Malesia: the archipelago between the Asian and Australian continents plus the Malay Peninsula.

Indomalesia: Asia from India eastward to include the archipelago mentioned above.

Pacific: the islands north and east of New Guinea and Australia.

GEOGRAPHICAL AFFINITIES OF THE GENERA

Port Moresby Area

The genera have been grouped according to geographical areas where most of their species occur. Table 1 lists the groups and the number of genera allocated to them. From this table it appears that:

1. Widespread genera (groups 1, 2, and 3) are predominant.
2. Only a few genera occur mainly in Australia (groups 8 and 9).
3. Very few genera are centered in Malesia (groups) or in the Pacific (group 10).
4. The Port Moresby Area has no local endemic genera, and that genera endemic to New Guinea (group 12) are very poorly represented.
5. Most of the genera found in the Port

[4] A list of all plants found in the plots is given in TM 72/2 which deals with life forms. Both memoranda are available upon writing to the Editor, CSIRO, Division of Land Research, P.O. Box 109, Canberra City, A.C.T. 2601, Australia.

TABLE 1

GENERIC DISTRIBUTION SPECTRUM OF THE PORT MORESBY AREA

			SEED PLANTS			
			INDIGENOUS NOT REPRESENTED IN			
GROUP	DESCRIPTION	TOTAL	AUSTRALIA	MALESIA*	INTRO-DUCED	FERNS
1	Pantropical or More Widespread Genera	115	2	–	5	6
2	Genera of the Old World Tropics	63	2	–	2	2
3	As 2, but Absent from the African Continent	33	–	–	1	–
4	Indo-Malesian Genera	11	5	–	–	–
5	Malesian Genera	3	–	–	–	–
6	Genera of Malesia and Australia	4	–	–	–	–
7	Genera of Malesia and the Pacific	8	–	–	–	–
8	Australian Genera	8	–	2	–	–
9	Genera of Australia and the Pacific	6	–	4	–	–
10	Pacific Genera	3	3	2	–	–
11	Genera Introduced from America	–	–	–	8	–
12	Genera Endemic to New Guinea	1	1	1	–	–
	Totals	255	13	9	16	8

* Outside New Guinea.

Moresby Area occur in Malesia as well as in Australia.

Comparisons with Other Areas

Comparisons are hampered in two ways. Classifications vary in degree of detail, and genera are placed in different geographical groups by different authors according to whether emphasis is placed on their overall distribution or on centers of species diversity. Only Kalkman (1955), in his study on the Lesser Sunda Islands, has published a list of the groups and the genera they comprise. Good (1960), writing on New Guinea, mentions quite a number of genera; but van Balgooy (1960) for the Pacific and van Steenis (1950, 1965) for Malesia and Java provide very little information on this point. I have tried to reconcile contradictory cases, and the figures for the Port Moresby Area have been adjusted to make them comparable as far as possible. Inasmuch as both Good and van Balgooy distinguish about 15 classes against van Steenis's and Kalkman's five or six, comparisons are made in two stages.

THE PORT MORESBY AREA COMPARED WITH NEW GUINEA

Table 2

The main points are:

1. The relative decrease in Indo-Malesian (type 5), Malesian (type 5*a*), and endemic genera is compensated by an increase in genera with wider distribution (types 1 and 4).
2. The percentages of Australian and Pacific elements (types 6 and 8) are only slightly larger than for New Guinea as a whole.

The low figure for the Australian element is somewhat unexpected in view of the similarity in climate and physiognomy of the vegetation between southeastern Papua and large areas of northern Australia. An analysis for these Australian vegetation types is not available, and this only would form a valid basis for comparison. It could well be that the Australian element in these types is not as prominent as one is inclined to surmise.

TABLE 2

GENERIC DISTRIBUTION SPECTRA OF NEW GUINEA AND SOME PACIFIC ISLANDS COMPARED WITH THAT OF THE PORT MORESBY AREA

CLASSIFICATION OF VAN BALGOOY (1960)		AREA*						APPROXIMATE EQUIVALENTS	
TYPE	DESCRIPTION	PM	NG	LOY	CAR	BIS	SOL	PM GROUPS (See Table 1)	NG CATEGORIES (See Good, 1960)
1	Worldwide Genera	44	20	47	42	38	35	1	b, d
1*a* + 2	Temperate Genera	–	6	1	–	<1	<1	–	a
4	Genera of Old-World Tropics, May be Absent from Africa	40	14	29	30	30	28	2, 3, 4 (types 4 and 5)	c
5	Indo-Malesian Genera, May be Present in Africa	2	28	3	13	14	10		e (part)
5*a*	Genera Centered in Malesia	2	7	1	8	10	13	5	e (part)
5*b*	Genera in Australia and Malesia	2	5	1	2	4	4	6	g^1, g^3 (part)
6	Australian Genera	5	4	5	<1	1	1	8, 9	f
7 + 7*b*	Subantarctic - Pacific Genera	<1	2	2	<1	<1	<1	†	g^2
8	Pacific Genera	4	3	8	3	2	5	7, 10	g^3 (part)
8*a*	Endemic Pacific Genera	–	–	–	<1	<1	<1	–	–
3, 7*a*, 9	Japanese, Indian Ocean, and American Genera	–	–	2	<1	–	<1	–	–
–	Genera Endemic to New Guinea	<1	10	–	–	–	–	12	h
	Total Numbers of Genera	255	1350	259	379	514	431		

NOTE: Number of genera per type is expressed as percentage of the total number in each area.

* PM, Port Moresby Area; NG, New Guinea (data from Good, 1960); LOY, Loyalty Islands; CAR, Caroline Islands; BIS, Bismarck Archipelago; SOL, Solomon Islands (data from van Balgooy, 1960).

† *Wahlenbergia* (from group 1) is allocated to type 7 by van Balgooy.

THE PORT MORESBY AREA COMPARED WITH SOME PACIFIC ISLANDS

The islands mentioned in Table 2 are chosen because they either belong to the same plant geographical subprovince as New Guinea, viz., the East Malesian, or, as in the case of the Loyalty Islands, have about the same number of genera with a similar distribution spectrum (van Balgooy, 1960).

The following points are of interest:

1. The Port Moresby Area has relatively more worldwide genera (type 1) than the Bismarcks or Solomons, and about as many as the Carolines and Loyalties.
2. The percentage of Old World tropic genera (type 4) is about 10 higher than for the other areas; the difference is largely accounted for in the Carolines, Bismarcks, and Solomons by a higher percentage of Malesian genera (type 5*a*) and genera with a wider distribution to the west (type 5), and in the Loyalty Islands by a higher number of Pacific and subantarctic genera (types 7, 7*b*, and 8).
3. The percentage of Australian elements in the Loyalty Islands equals that of the Port Moresby Area; it is very much lower in the other island groups.
4. Endemic genera are virtually absent.

The generic distribution spectrum of the Port Moresby Area appears to be rather similar to that of the medium sized islands in the East Malesian Subprovince. Its esential difference lies in a relative decrease in genera mainly distributed in Malesia and further west, and an increase in Australian elements, consistent with its proximity to the Australian Region. In this it is comparable with the Loyalty Islands, which are also situated close to the border of the Australian Region (van Balgooy, 1960).

COMPARISON OF THE PORT MORESBY AREA WITH JAVA AND THE LESSER SUNDA ISLANDS

Table 3

Westward from the Port Moresby Area the percentages of widely distributed (type 1) and Australian-Pacific genera (type 4) decrease progressively, whilst the percentages of Malesian-centered (type 3) or Asian-centered (type 2) genera increase. Endemism is low throughout.

The Number of Widespread Genera in Relation to the Total Number of Genera

The Port Moresby Area has a predominating representation of widespread genera. The relative number of genera of the Old World tropics, in particular, is greater than in other areas.

The figures in Tables 2 and 3 suggest an inverse relationship between the percentages of widespread genera (types 1 and 4 of Table 2 and type 1 of Table 3) and the total numbers of genera. To analyze this relationship, I plotted the actual numbers of widespread genera against the totals using the data from van Balgooy's tables for the Pacific islands and those given in Table 3 for the other areas (Fig. 2). The points for the Indo-Malesian and New Caledonian regions line up very well and fit the curve of a logarithmic series with an index of diversity of 400.[5] Originally the logarithmic series was found to express satisfactorily the relationship between the number of individuals and the number of species in a random sample of a mixed animal population. Later, amongst numerous other applications, it was demonstrated to fit well to the number of genera with different numbers of species in standard classifications of both animals and plants (Williams, 1947). From the fact that the relationship between number of widespread genera and total number of genera can be represented by a single curve can be deduced the theory that the genera of each of the plotted areas can be regarded as a sample of a single large generic population, viz., that of the Indo-Malesian and New Caledonian Floristic regions. The points for the New Zealand Subprovince of the Australian Region fall below the line. They suggest a similar relationship, but with a lesser influence of widespread genera. The different position of the curves for the New Zealand Subprovince and for the Indo-Malesian Region corroborates van Balgooy's (1960) evidence based on generic

[5] The reader is referred to Williams (1947) for the mathematical derivation and the characteristics of the index of diversity.

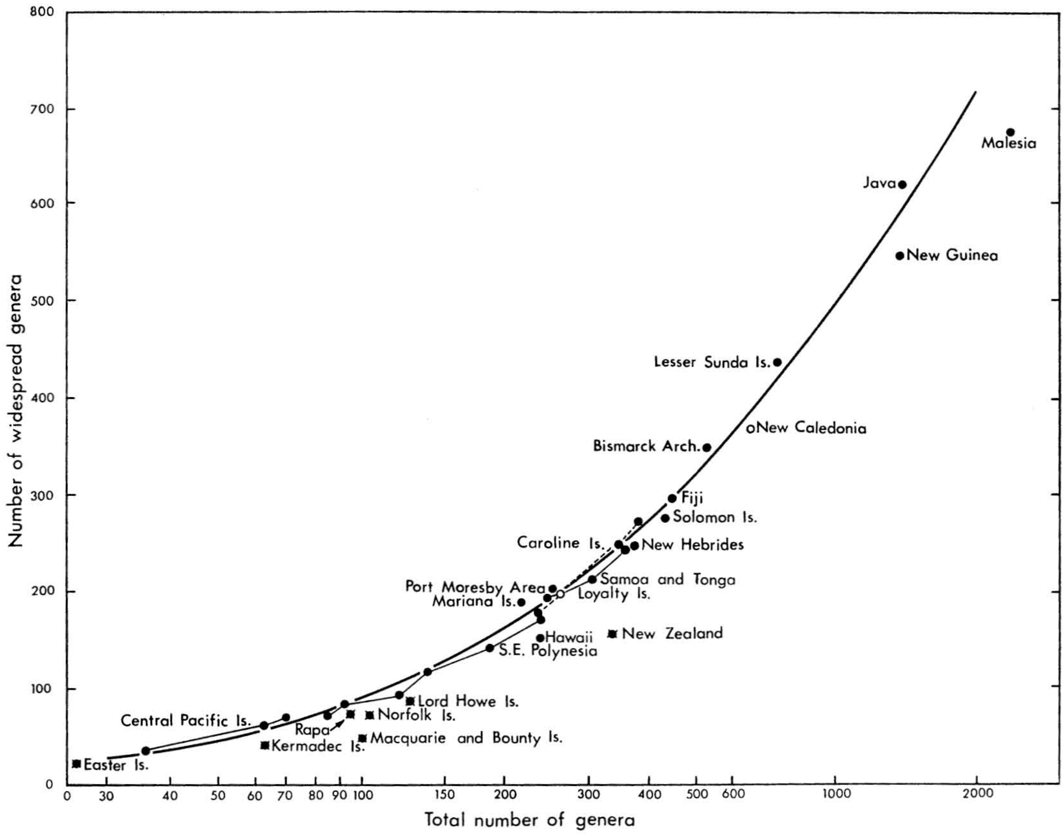

FIG. 2. Relationship between numbers of widespread genera and total numbers of genera in Malesia and the Pacific. Black dots relate to the Malesian and Southwest Pacific Subprovinces of the Indo-Malesian Region, open circles to the New Caledonian Region, and squares to the New Zealand Subprovince of the Australian Region. Dots connected by a line pertain to a particular group of islands and the dot with the highest value gives the total for the group. The curvilinear line represents the best fitting logarithmic series. Source of data: Pacific Islands, van Balgooy (1960); New Guinea, Good (1960); Lesser Sunda Islands, Kalkman (1955); Java and Malesia, van Steenis (1965).

distribution spectra, on which he divided the Pacific into an area predominantly under Indo-Malesian influence and one of significant Australian influence, roughly separated along the Tropic of Capricorn.

It also follows from the curvilinear relationship that, if the study had been extended over the rest of southeastern Papua and, for example, the number of genera had doubled, the number of widespread genera would increase from 201 to about 330 and, consequently, their percentage would drop from 80 to 65 percent. Because of this, figures for the Port Moresby Area do not apply automatically to the whole of monsoonal Papua.

DISTRIBUTION OF THE SPECIES

Species Distribution Spectrum of the Port Moresby Area

Table 4 summarizes the distribution of five ferns and 287 indigenous and naturalized seed plants. This latter number represents only a small fraction, about 3 percent, of the angiosperm flora of New Guinea, which has been estimated to comprise about 9,000 species (Good, 1960).

More than 60 percent of the species are found in both Australia and Indo-Malesia or are more widespread. The rest are divided about equally between endemic, Australian, and Indo-

TABLE 3

GENERIC DISTRIBUTION SPECTRA OF THE LESSER SUNDA ISLANDS, JAVA, AND MALESIA COMPARED WITH THOSE OF THE PORT MORESBY AREA AND NEW GUINEA

CLASSIFICATION OF VAN STEENIS (1950)		AREA*					APPROXIMATE EQUIVALENTS	
TYPE	DESCRIPTION	PM	LSI	J	M	NG	PM GROUPS (See Table 1)	NG CATEGORIES (See Good, 1960)
1	Widely Disributed Genera, Ranging from Australia to Asia or Farther	80	59	46	30	41	1, 2, 3	a, b, c, d
2	Center of Specific Distribution in Asia, Absent or Scarcely Represented in Australia	6	23	29	27	27	4	e (part)
3	Center of Development in Malesia, Some Outposts in Surrounding Regions	5	15	23	25	12	5, 6	e (part), g^1, g^3 (part)
3*A*	Genera Known from One Island or Group of Islands Only (Endemics)	<1	<1	<1	13	10	12	h
4	Center of Development in Australia or the Pacific, Absent or Scarcely Represented in Asia	8	3	1	6	9	7, 8, 9, 10	f, g^2, g^3 (part)
	Total Numbers of Genera	255	747	1370	2316	1350		

NOTE: Number of genera per type is expressed as percentage of the total number in each area.

* PM, Port Moresby Area; LSI, Lesser Sunda Islands (data from Kalkman, 1955); J, Java, and M, Malesia (data from van Steenis, 1965); NG, New Guinea (data adapted from Good, 1960).

TABLE 4

SPECIES DISTRIBUTION SPECTRUM OF THE PORT MORESBY AREA

DISTRIBUTION	TOTAL NUMBER OF SPECIES	NUMBER OF SPECIES EXTENDING INTO THE PACIFIC
Endemic to New Guinea	38(13%)	–
Found also in Other Parts of Indo-Malesia	33(11%)	5
Found in Australia and New Guinea, but Not in Other Parts of Malesia	39(13%)	5
Found in Australia and Indo-Malesia	104(36%)	28
Distributed beyond Indo-Malesia, but Not Found in Australia	5(2%)	–
Distributed beyond Indo-Malesia and Australia	73(25%)	17
Totals	292(100%)	55

Malesian species. The figure of 13 percent for endemic species contrasts sharply with the 94 percent for the whole of New Guinea given by Good (1960).

Of the 292 species found in the Port Moresby Area, 216 species are also found in Australia and 215 species in Malesia. Only 55 species are also found in the Pacific and these belong mainly to the groups with wide distributions.

Comparison with Arnhem Land and the Lesser Sunda Islands

The flora of Arnhem Land Aboriginal Reserve is composed of about 1,100 species of seed plants. Their distribution can be summarized as follows: 619 (57 percent) are confined to Australia, 102 (9 percent) extend to New Guinea and/or Timor, 156 (14 percent) are also found in Indo-Malesia, and 205 (19 percent) have a wider distribution (Specht, 1958).

The Port Moresby Area has 112 species in common with Arnhem Land. The distribution spectrum of the shared species is as follows: 24 percent is restricted to New Guinea and Australia, 32 percent is Indo-Malesian, and 44 percent is spread over the Old World tropics or farther. The shared species seem to be a random selection from the nonendemic Arnhem Land species for which the recalculated figures for occurrences in the above-mentioned areas are 22, 34, and 44 percent, respectively, rather than from the nonendemic species of the Port Moresby Area, for which the figures are 19, 49, and 32 percent.

Kalkman (1955) has calculated the species distribution spectra for the larger islands of the Lesser Sunda Group. He obtained data from taxonomic revisions published since 1925 and from lists of collections, covering 480 species or about 10 percent of the total flora. Of these, 27 are found also in the Port Moresby Area. The spectrum of the Port Moresby Area is most like that of Timor. Both areas have 42 to 45 percent of species occurring throughout the Old World tropics, and 10 to 13 percent of endemic species. The difference lies in a sharp decline of Indo-Malesian and Malesian species in the Port Moresby Area (from 37 to 13 percent) compensated by a rise in Malesian-Australian species (from 10 to 28 percent; the latter figure includes 13 percent of species which in the Malesian region occur only in New Guinea).

Group *C* in Table 5 shows that Malesian and Indo-Malesian species form the major component in the flora of the northern chain of the Lesser Sunda Islands, especially the western ones. They equal in importance the 57 percent of Arnhem Land species confined to Australia. In the southern islands about 10 percent of the Indo-Malesian species are replaced by more widespread species (group *B*) which are represented by a similar percentage in the Port Moresby Area. Indicated here is the transition zone between the Indo-Malesian and Australian Floristic regions. In the Port Moresby Area where, as mentioned above, the decrease in the numbers of Indo-Malesian species is strongest, species distributed over Australia and Malesia

TABLE 5

COMPARISON BETWEEN THE SPECIES DISTRIBUTION SPECTRA OF THE PORT MORESBY AREA, ARNHEM LAND, AND THE LESSER SUNDA ISLANDS

GROUP*	PORT MORESBY	ARNHEM LAND†	SOUTHERN ISLANDS‡		NORTHERN CHAIN OF ISLANDS‡			
			TIMOR	SUMBA	FLORES	SUMBAWA	LOMBOK	BALI
A	28	12	10	7	10	7	6	5
B	45	30	42	48	36	35	34	35
C	26	57	47	45	54	58	60	60

NOTE: Numbers per group are expressed as percentage of total number of species in each area.
* Group *A*, species found in Australia and Malesia; Group *B*, species distributed over Australia and Indo-Malesia or more widely; Group *C*, remaining species, viz., the local endemics, for Arnhem Land the endemics plus the species confined to Australia, and for the other areas the endemics and the species confined to Malesia or Indo-Malesia.
† Data for Arnhem Land extracted from Specht (1958).
‡ Data for the Lesser Sunda Islands from Kalkman (1955).

(group *A*) largely replace them. Group *A* shows a pronounced east–west gradient; it is strongest in the Port Moresby Area, still rather prominent in Arnhem Land and in Flores and Timor—the most eastern of the Lesser Sunda Islands, and tapers off over the western islands, including Sumba. It indicates that New Guinea has been and is in a more favorable position for the exchange between Australia and Malesia than the more western parts of the Malesian Region.

ECOLOGICAL SIGNIFICANCE OF SPECIES DISTRIBUTION PATTERNS

The species distributions have been used to determine drought tolerance. Species restricted to areas which are at least partly monsoonal, viz., Java, Celebes, Lesser Sunda Islands, Moluccas, Philippines, and continental Southeast Asia, were separated from species occurring also in wetter areas. (No species of the Port Moresby Area is confined beyond New Guinea to wetter areas.) This division is rather crude in view of the fact that van Steenis (1961) distinguishes six classes of increasingly drought-tolerant species interpreted from plotted distribution patterns. However, available data are too scanty to permit such plotting.

In New Guinea, the seasonally dry areas of southeastern Papua, southern New Guinea, and the northern parts of the island from the Vogelkop to the East Cape (Brookfield and Hart, 1966) were split off from the generally wetter parts of the island (Fig. 1). Four groups of species were distinguished on the basis of their distribution over these areas, as outlined in Table 6.

Table 6 can be summarized as follows: the general distribution of 169 species is restricted to regions where a periodically dry climate prevails; of these species, 108 are limited to the seasonally dry areas in New Guinea and 61 are not so limited. Not restricted to periodically dry regions are 123 species; of these, 36 are limited to seasonal areas in New Guinea and 87 are not.

The group of 61 species suggests that the separation of monsoonal from wetter regions is only an approximation. These species, although in their general distribution restricted to the monsoonal region, occur within this region also in local areas of higher rainfall. Examples are *Garuga floribunda, Rhus taitensis, Rhyssopteris timoriensis, Dianella odorata,* and *Eustrephus latifolius;* these species extend also into the wetter parts of the Pacific and *E. latifolius* to temperate Australia as well.

From ecological aspects, then, the species of the Port Moresby Area can be split into three groups: a group bound to seasonally dry conditions (108 species or 37 percent); a group indifferent to climate (87 species or 30 percent); and, between these, a group with intermediate requirements—either the species are in their general distribution restricted to monsoonal regions but occur also in locally higher rainfall areas, or they are restricted to seasonal areas in, but not outside, New Guinea (61 + 36 species or 33 percent).

TABLE 6

DISTRIBUTION PATTERNS IN NEW GUINEA OF THE FLORA OF THE PORT MORESBY AREA

TOTAL DISTRIBUTION AREA*	NUMBER OF SPECIES	DISTRIBUTION PATTERNS IN NEW GUINEA			
		SPECIES CONFINED TO MONSOONAL SOUTH-EASTERN PAPUA	SPECIES OCCURRING ALSO IN OTHER SEASONALLY DRY AREAS	SPECIES OCCURRING IN SOUTHEASTERN PAPUA AND IN AREAS OF HIGHER RAINFALL	SPECIES OCCURRING IN SEASONALLY DRY AREAS AND IN AREAS OF HIGHER RAINFALL
New Guinea	38	10	12	4	12
Australia and New Guinea	39	20	11	3	5
Monsoonal Indo-Malesia	19	5	3	1	10
Australia and Monsoonal Malesia	44	10	18	2	14
Australia and Monsoonal Indo-Malesia†	29	3	16	1	9
Subtotals	169	108		61	
Indo-Malesia†	19	4	1	5	9
Australia and Indo-Malesia	35	4	4	2	25
Old World Tropics or Wider	69	13	10	6	40
Subtotals	123	36		87	
Totals	292	69	75	24	124
Pacific*	55	6	10	4	35

* Species for which the distribution extends into the Pacific occur in most of the areas. They have been used in the calculations of the figures for these areas, but are also brought together at the end of the table.

† Some species are included for which the distribution extends to Africa.

HISTORICAL GEOGRAPHY OF SPECIES BOUND TO A SEASONALLY DRY CLIMATE

Van Balgooy (1969) remarked that the study of a group of plants bound to limiting ecological conditions may throw more light on historical geographical matters than would an analysis of the whole flora. In the last section of this paper I attempt to do this for the group of species bound to a seasonally dry climate. Table 7 gives in detail the distribution of these species. It is supplemented with nine species, which occur also under slightly higher rainfall on the Sogeri Plateau adjacent to the Port Moresby Area or at Bulolo north of the central range which has a low annual, if weakly seasonal, rainfall. Species known only from a single locality in northern drier areas have been included with species restricted to southern parts of New Guinea; they have also been listed separately.

The figures show: (1) a large number of local endemics, (2) a large number of Australian and Malesian species restricted to southeastern Papua, (3) a large number of widespread species common to southeastern Papua and the drier areas in the north, (4) relatively few species common to southeastern Papua and southern New Guinea.

The endemic species adapted to monsoonal conditions belong to genera which more often than not have their greatest number of species in areas of higher rainfall and are commonly spread throughout the Old World tropics. Several of the endemics, e.g., *Canthium suborbiculare, Jossinia desmantha, Psychotria lolokiensis, Colona discolor, Alectryon repando-dentatus, Panicum micranthum*, and *P. viale*, form predominant components in the present vegetation. Among the nonendemics there are 10 species or varieties which very likely evolved in southeastern Papua, e.g., *Alectryon connatus, Canarium australianum, Elaeocarpus brassii, Grevillea*

TABLE 7

DISTRIBUTION OF SPECIES BOUND TO A SEASONALLY DRY CLIMATE

TOTAL NUMBER OF SPECIES	DISTRIBUTION OUTSIDE NEW GUINEA WITH NUMBER OF SPECIES IN PARENTHESES	DISTRIBUTION IN NEW GUINEA: SOUTHEASTERN PAPUA ONLY	ALSO IN SOUTHERN NEW GUINEA	ALSO IN NORTHERN NEW GUINEA	SPECIES WITH ONLY A SINGLE LOCALITY IN NORTHERN NEW GUINEA
28	None	14	8	6	0
10	Very Limited, Species have Probably Spread From Southeastern Papua	5	4	2	1
35	Australia (27), Australia and Lesser Sunda Islands (8)	19	12	6	5
24	Malesia (3), Malesia and Australia (21)	17	7	7	4
23	Indo-Malesia (4); Indo-Malesia and Australia (14); Indo-Malesia, Australia, and Africa (6)	4	6	19	0

pinnatifida, *Jasminum aemulum*, and *Murraya paniculata* var. *ovatifoliolata*, and from there spread to the Cape York Region, Arnhem Land, Timor, and/or the Aru Islands (Fig. 1).

The endemic species, together with the species with a very limited distribution outside southeastern Papua, form one-third of the total number of species in the group. Their large number and prominent role in the vegetation point to a long history of seasonally dry conditions in southeastern Papua and to a relatively isolated position from ecologically similar areas. In contrast to surrounding areas at least parts of southeastern Papua have been above sea level since the Oligocene (Speight, 1965).

The remaining species have migrated to southeastern Papua. Van Steenis (1961) has pointed out that conditions for migration were favorable during the glacial stadia of the Pleistocene. The differences in the New Guinea distribution pattern of Australian and Malesian species on the one hand, and that of the more widespread species on the other, however, cannot satisfactorily be explained by Pleistocene migrations; it is not likely that Malesian and Indo-Malesian species would have migrated at different rates. It is presumed that there were at least two phases in migratory movements, which were separated by the Pliocene orogenesis, which formed the central cordillera of New Guinea.

The history of the Tertiary in relation to the interaction of southeastern Asia and Australia is complex and as yet only partly understood (Ripper, 1970; Veevers, 1969). It seems likely that the Australian continental plate, which includes New Guinea, has moved first east and later northeast with respect to the Asian continental plate. During the Tertiary there would have been several opportunities for interchange of species bound to seasonally dry conditions between both continents. Several of these species reached southeastern Papua.

Toward the end of the Tertiary and in the early Pleistocene, the main ranges in New Guinea were upthrusted and the Moluccas attained their present shape. In the northern parts of New Guinea the species bound to seasonally dry conditions found refuge in rain-shadow areas and became virtually isolated from the rest of Malesia when rain forest covered the ranges. Some of the species known from only a single northern locality could represent relicts which formerly had a larger distribution; others, pioneers which had just reached the area when conditions for migration became unfavorable.

During the Pleistocene, glacial periods alternated with interglacial ones, creating and cutting possibilities for the migration of plants bound to drier climatic conditions. During interglacials the Sahul Shelf was flooded and, at the climax of these periods, little land would have existed between the higher surfaces in Australia and the foothills of the main range in New Guinea, but during the peaks of the glacial periods large areas of the shelf were land that was subject to a monsoonal climate (van Andel et al., 1967; Specht, 1958; van Steenis, 1961). At the northeastern margin of the shelf the Fly, Kikori, and Purari river systems formed a vast delta with mangroves and freshwater swamps. Because of the seasonal climate, the latter were probably dominated by *Melaleuca* rather than by sago palms. Such an environment is only hospitable for monsoonal plants which can stand prolonged inundation and, of these, only a few occur in the Port Moresby Area. Higher ground, however, was found on and around the present-day islands and reefs of the Torres Strait and the Oriomo Plateau (Merauke Ridge). Land at the northern extremity of the Gulf of Papua receives at present much rain all the year round (5,761 mm per year in Kikori, 38 years of records, see Brookfield and Hart, 1966[6]). If this was so throughout the Pleistocene, then a distinct ecological barrier was still present between the shelf and southeastern Papua. The species which did cross were commonly of Australian origin. Malesian species represented an important second group and very likely came directly across the shelf. Only a few Indo-Malesian species entered along this route.

The events which followed the last glacial period can explain why at present southeastern Papua shares only a rather small number of species with southern New Guinea. After the last glacial period the sea level rose and attained a maximum of about 6 m above its present level (Specht, 1958; Williams, 1969). During this time, which was also one of increased rainfall, the dryland areas between New Guinea and Australia were reduced to small remnants surrounded by sea, and vast swamps built up in the lower Fly River area. Many, if not most, of the monsoonal dryland species in southern New Guinea would have been eliminated. Following the fall of the sea to its present level some species returned, but the old assemblage is still not fully replenished.

[6] The map in van Steenis, 1961, p. 426, is incorrect in this area.

SUMMARY

The geographical affinities of the flora of semideciduous forest and scrub and of eucalypt savannah in the Port Moresby Area have been analyzed. Of the 255 genera only 8 percent are centered in Australia and/or the Pacific, 12 percent are found in Asia and/or Malesia, and 80 percent occur in and often beyond Australia and Malesia. The first figure is almost the same as for New Guinea as a whole, indicating that the monsoonal conditions have not led to a stronger representation of Australian elements. The large percentage of widespread genera will decrease if the study is extended over the whole of monsoonal southeastern Papua. This assumption is based on a comparison with Pacific and Malesian islands which showed that the relationship between the numbers of widespread genera and the total number of genera can be expressed by a logarithmic series.

The distribution of 292 satisfactorily identified species is: endemic to New Guinea, 13 percent; occurring also in Australia, 13 percent; occurring also in Asia including Malesia, 11 percent; occurring in Australia and Asia, 36 percent; having a wider distribution, 27 percent. Compared with the Lesser Sunda Islands, the Port Moresby Area has a higher proportion of East Malesian–Australian species. Comparison with Arnhem Land shows a higher percentage of Indo-Malesian species.

Three groups of species based on the correlation of distribution areas with climatic regions can be distinguished: one (37 percent of the species) is bound to seasonally dry conditions, one (33 percent) shows only some preference for these conditions, and one (30 percent) occurs under monsoonal, as well as ever-wet, climates.

The history in southeastern Papua of species bound to a seasonally dry climate has been considered. Local endemism points to a dry local climate during the Tertiary. It is surmised that most of the widespread species reached southeastern Papua before the Pliocene via drier areas on the Asian and Australian continents. Mainly

the Australian and Malesian elements were enriched during the glacial periods of the Pleistocene, when the emerged Sahul Shelf effectively shortened the distance to southeastern Papua.

ACKNOWLEDGMENTS

The assistance of Mr. R. Pullen during field and herbarium work and of Mrs. M. Osins and Mrs. P. Colman in office work is gratefully acknowledged. The help and comments of other members of the staff of the Herbarium Australiense, especially of Dr. R. Schodde, and the hospitality given me by the Queensland Herbarium are also much appreciated.

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