Development and Distribution of Vascular Epiphytes Communities on the Krakatau Islands, Indonesia

Tukirin PARTOMIHARDJO[1], SUZUKI Eizi[2] and YUKAWA Junichi[3]

1: Research & Development Center for Biology, LIPI, Bogor 16122, Indonesia
2: Faculty of Sciences, Kagoshima University, Kagoshima, 890-0065 Japan
3: Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan

Abstract

The development, diversity, vertical distribution and other ecological aspects of epiphyte communities were studied on the Krakatau Islands, Indonesia, which exhibit a primary succession since a catastrophic eruption in 1883. Compiled flora of epiphytes recorded in the studies from 1886 to 1993 by us and many scientists had 108 species in nine and six families of fern and seed plants, respectively, on the four islands of Krakatau: Rakata (98spp.), Sertung (32spp.), Panjang (28spp.) and Anak (7 spp.). The most diverse family in species number in epiphytic seed plants was Orchidaceae consisting of 37 species, followed by Asclepiadaceae and Moraceae with 8 and 6 species, respectively. The epiphytes occupied 5% of flora of the islands in the early 30 years after the eruption, and 20% in recent.

Our quantitative study in five plots from 10 to 700 m altitude on Rakata Island with summit of 813m in altitude showed that the fern epiphytes were more abundant than the seed plants. Upland had more epiphytes than lowland. In the lowland, epiphytes grew chiefly in the canopy layer and on the basal parts of the trees. The population of epiphytic fern *Antrophyum* decreased from the base of trunk to the canopy, whereas the population of orchids increased. Most of woody hemi-epiphytes, such as *Clidemia hirta* and *Schefflera polybotrya* preferred trunks and were found rooted in forks and crannies filled with humus.
Key words: dispersal mechanism, epiphyte, primary succession, species richness

Introduction

Epiphytes consist of some species of algae, bryophytes, lichens, ferns and spermatophytes. They have been distinguished from parasites and hemi-parasites by their ability to collect water and minerals from the air (HOSOKAWA 1968, RUINEN 1953). Although epiphytes are relatively small components among forest communities, they play an important role in characterizing tropical rain forests by having a specific nutrient cycle and life-support systems. For example, NADKARNI (1984), who studied the biomass and nutrient capital of vascular epiphytes in a neotropical elfin forest in northern Andes, reported that epiphytes produce relatively high amount of organic matter and had ability to fix atmospheric nitrogen. BENZING (1983) emphasized that tank epiphytes such as aroids, bromeliads and ferns are also very important in creating hiding and breeding sites for arboreal forest insects and amphibians. In spite of their importance in forest ecosystems, epiphyte communities have seldom been studied in relation to the tropical rain forest succession (WHITMORE 1975, 1984, WHITTAKER *et al.* 1989).

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The development of epiphyte communities on the Krakatau Islands, Indonesia have been paid little attention in the studies of re-colonization processes by plants and animals after the world famous volcanic eruption in 1883 except occasional collection of epiphyte specimens during general floristic surveys (*e.g.* DOCTERS van LEEUWEN, 1936). The only notable field survey was performed by FOSTER (1982), who recorded the altitudinal variation of the bryophytes on Rakata, one of the four Krakatau Islands in 1979. In contrast, the structure and development of tropical forest have been studied intensively on the Krakatau Islands, particularly in the past two decades (TAGAWA *et al.* 1985, WHITTAKER *et al.* 1989, BUSH *et al.* 1992, PARTOMIHARDJO *et al.* 1992, PARTOMIHARDJO 1995 and WHITTAKER *et al.* 1992). These studies now provide us with useful information about host plant species which can be substrates for epiphytes to grow in various places on the islands.

In order to know the re-colonization process of the Krakataus by plants and animals more precisely, intensive studies on epiphyte communities cannot be put on the side since they have close relationships with other plant communities and their associated animals. Such studies would contribute to the accumulation of general knowledge concerning the process of species enrichment in tropical forests. From these points of view, this paper reports the development, diversity, vertical distribution and other ecological aspects of vascular epiphyte communities on the Krakatau Islands.

STUDY SITES

The islands and eruption

Fig. 1. Map of Krakatau Islands. Squares and triangles show study plots and summits, respectively.

The Krakatau Islands are situated about in the middle of Sunda Strait between the West Java and South Sumatra (Fig.1). The Islands consist of four small islands *i.e.* Rakata, Panjang, Sertung and Anak Krakatau. The former three islands were remains of old Krakatau Island after the catastrophic eruption in 1883. Anak Krakatau appeared above sea level in the 1930s by submarine volcanic activity.

Vegetation succession

After the catastrophic eruption, many floristic surveys have been performed on the islands. Most scientists believed that Rakata, Panjang and Sertung had been sterilized by the 1883 eruption (DOCTERS van LEEUWEN 1936, BOORSUM WAALKES 1960, RICHARDS 1964, 1996, WHITTAKER and BUSH 1992). However, ERNEST (1908) suggested that the mantel of ash also provided a fertile substrate for colonization.

The first higher plants recorded from the three islands were 11 species of ferns and 13 species of spermatophytes. Gradually the islands accumulated a cover of grasses and scattered trees. By 1908, an open woodland existed along parts of the coast and the interior grassland was broken by patches of woodland consisting abundant *Ficus fulva* and *Macaranga tanarius*. The lowland forest of the three islands had similar succession paths over the first 50 years.

Rakata appeared to have advanced slightly to the closed forest by the end of 1920s. By the early of 1930s, Rakata was more or less completely forested with the most dominant trees species, *Neonauclea calycina* (DOCTERS van LEEUWEN 1936, WHITTAKER *et al.* 1989). On Rakata, a gradual change took place over the period from 1951 to 1983 from a poor mixed secondary forest to a taller forest with more diverse canopy. *Neonauclea calycina* still has been a principal canopy trees, being distributed from the coast to just below the summit. This vegetational development was accompanied by an increase of host plant species and provided epiphytes with diverse habitats.

Contrary to Rakata, forests were lower and less diverse on Panjang and Sertung, since these islands had been disturbed by eruptions of Anak Krakatau. Consequently, the vegetation succession on Panjang and Sertung is characterized to fragment, chronic and extensive disturbed, which mostly dominated by *Timonius compressicaulis* and *Dysoxylum gaudichaudianum*. In the coastal flat area, the forests consisted of the beach vegetation and typified by *Terminalia catappa*, *Calophyllum inophyllum*, *Barringtonia asiatica* and *Hernandia peltata* (DOCTERS van LEEUWEN 1936, BOORSUM WAALKES 1960).

The vegetation of Anak Krakatau has been restricted to eastern coast of the island, consisted mainly of *Casuarina equisetifolia* mixed with some young coastal trees such as *B. asiatica*, *C. inophyllum* and *T. catappa*.

Meteorological data

Only a few meteorological data are available for the Krakatau area. The data taken on Panjang in 1923 indicated that the mean monthly temperature was almost constant throughout the year, ranging from 26.9° C in July and December to 28.7° C in October (BAREN 1931). A series of temperature and humidity readings was taken on Rakata in September 1979 by FOSTER (1982). The lapse rate of mean annual air temperatures with altitude was calculated to be 0.8° C/100m based on the 75 cm depth soil temperatures in various places at different altitudes (WHITTAKER *et al.* 1989). The gradient in relative humidity indicated a fall from about 95% R.H. (relative humidity) at the summit to 75 - 80% R.H. in the lowland forest, and a further decline from the forest area to beaches (FOSTER 1982).

Methods

Literature survey for earlier colonization by epiphytes

In order to know the process of re-colonization by epiphytes until 1993, the following literature including floristic studies on the Krakataus was surveyed: DOCTERS van LEEUWEN 1936, BORSSUM WAALKES 1960, FOSTER 1982, WHITTAKER *et al.* 1989, WHITTAKER and BUSH 1993, and Partomihardjo 1995.

Study plots and field surveys

Nearly every year from 1982 to 1994, the first author visited the four Krakatau Islands for plant ecological and floristic studies, including epiphyte flora. The quantitative ecological study of epiphytes was conducted in the following plots on three islands (Fig. 1). On eastern side of Rakata, four study plots of 30 x 30m were established at 10, 100, 300 and 500m above sea level (asl) and one plot of 20 x 20m at 700m asl in July 1992. On the southwestern side, two plots of 20 x 20m were set up at 50 and 100m asl. Two plots of 20 x 20m were made at 100 and 150m asl on Sertung, and three on Panjang at altitudes of 50, 100 and 150m asl.

Observation was made on the occurrence of the vascular epiphytes on all trees bigger than 10 cm diameter at breast height (dbh) within the plots. The number of individual epiphytes of each species, percentage cover and the distribution on each tree were recorded. Similar measurements were also made on saplings between 1 and 9.9 cm in dbh. Herbarium specimens of both epiphytes and host plants were collected for identification. The population of vascular epiphytes associated with each tree was assessed in terms of floristic composition, size and distribution on the tree. The size of the epiphyte population was noted in terms of the number of individuals of each species present. For observations on distribution, the trees were divided into three epiphytic habitats: base of trunk, upper trunk, and crown. A single species clump was recorded as a single individual.

Results

Colonization by epiphytes

In 1886, hemi-epiphytic fern, *Nephrolepis biserrata* (Sw.) Schott was first found on the ground of Rakata Island (Appendix). The first seed epiphyte known to have arrived on the Krakataus was an orchid, *Cymbidium finlaysonianum*, a common epiphyte throughout the Indo-Malayan region. In 1896, BOERLAGE collected the specimen from a rock wall of Panjang and planted it in Bogor Botanical Garden for identification (DOCTERS van LEEUWEN, 1936). This species is not common on the Krakataus even now.

Table1. Species numbers of fern, orchids, and other seed plants on the Krakatau islands found in the three periods.

	Four islands	Rakata	Sertung	Panjang	Anak
1886-1933					
Fern	30	28	12	11	
Orchid	20	19	4	1	
Others	12	8	3	1	
Total	62	55	19	13	
1886-1982					
Fern	45	39	18	17	
Orchid	33	27	6	1	1
Others	19	17	7	3	1
Total	97	83	31	21	2
1886-1993					
Fern	49	43	18	20	3
Orchid	37	34	7	4	3
Others	22	21	7	4	1
Total	108	98	32	28	7

Actual and cumulative number of epiphyte species on the four Krakatau Islands from various expedition records is summarized in Fig. 2. In 1993, the actual and cumulative species number on the islands was 81, and 108, respectively (Appendix). Table 1 shows the change in species numbers of ferns, Orchids and others with time. Since the eruption in 1883, 49 ferns, 37 orchids, and 22 other spermatophytes have appeared on the islands. Over the period from 1922 to 1982, the rate of discovery of new epiphytes was relatively slow, compared to the total enrichment of vascular plants on the islands (Partomihardjo 1995). However, intensive field surveys by the authors in 1991 and 1992 increased the discovered species: six species of vascular epiphytes consisting of four orchids, *Eria verruculosa*, *Flikengeria angustifolia*, *Glomera erythrosma*, *Pholidota articulata* and two ferns *Asplenium tenerum* and *Oleandra neriiformis*, were newly recorded in these years. Based on herbarium collections, the two orchids, *E. verruculosa* and *G. erythrosma* are otherwise known so far only from Java.

Fig. 2-c shows the historic change of the percentage of epiphytes in the species number of all ferns and seed plants by Partomihardjo (1995) in cumulative and actual value. Before the 1920s, the percentages were around 5%. After the 1920s, epiphytes occupied about 15% and 20% of cumulative and actual species number of all plants. The increase of epiphyte percentage roughly coincided with the establishment of closed forest in most areas of Rakata in the 1930s (DOCTERS van LEEUWEN, 1936).

On Anak Krakatau Island, *Dendrobium crumenatum* was the first epiphytic seed plant recorded, and was found growing on the wall of cliff in an open area, whilst *Hoya diversifolia* was an early epiphytic colonizer growing on *Casuarina* trees (Partomihardjo 1995). In total, we found seven epiphyte species on Anak, and they were also found in every islands of the Krakatau (Appedix). Most of them were found growing on the ground surface due to the limited availability of their usual tree habitat. For example, *A. javanica* and *C. finlaysonianum* were found growing at the bases of *Saccharum spontaneum* clumps, whilst *D. denticulate* and *D. quercifolia* were found on the forest floor of *Casuarina* woodland. An epiphytic fern, *Pyrrosia lanceolata* began to colonize the stems of *Casuarina* trees by 1990.

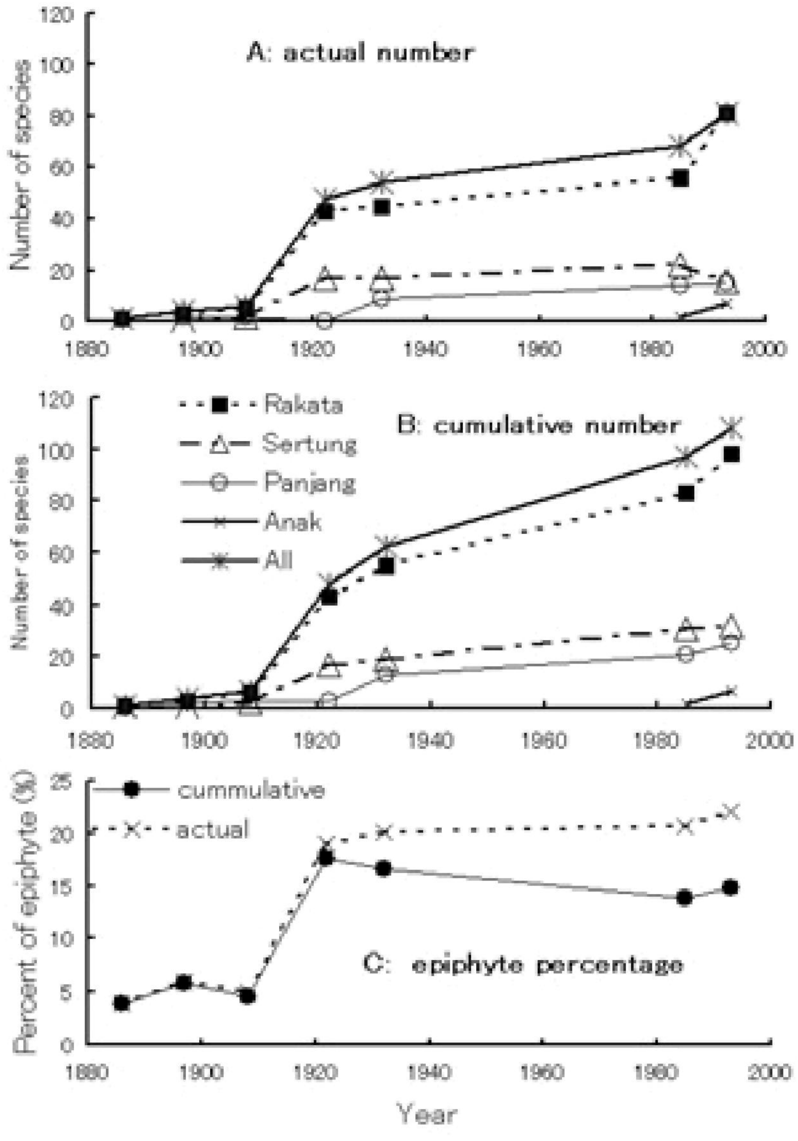

Fig. 2. Colonization curves of vascular epiphytes on each island of the Krakatau Islands from 1883 to 1993. **A**: Actual number which is species number found at the survey period. **B**: cumulative number which includes disappeared species. **C**: percentage of epiphytes to all flora in actual and cumulative number.

Epiphytes in the study plots

The species and abundance of the epiphytes were studied in plots on Rakata, Panjang and Sertung, whose total area was of 0.48 ha on Rakata, 0.08ha on Sertung and 0.12ha on Panjang. We found 65 epiphytic vascular plant species belonging to 42 genera within 16 families. This species number was equivalent to 60% of the known epiphytic flora of the Krakataus. These included 14 species of terrestrial plants and stranglers. They are usually not included in epiphytes but were occasionally found growing on the basal part of tree trunks in the plots.

Table 2. Total number of vascular epiphytes recorded on each plot in the forest of Rakata. **: Terrestrial plants which temporary recorded as epiphytes in the study plots.

Altitude (m asl) Plot size (m^2) Taxon	10 900	100 900	300 900	500 900	700 400
PTERYDOPHYTA					
Aspleniaceae					
Asplenium macrophyllum Sw.	0	14	7	32	14
Asplenium nidus L.	28	0	3	47	75
Asplenium tenerum L.	0	0	0	176	305
Asplenium thunbergii Kunze	0	0	0	79	37
Davaliaceae					
Davalia denticulata (Burm.f.) Merr.	0	12	17	100	0
Humata heterophylla (Sm.) Desv.	0	0	0	0	53
Humata repens (L.f.) Diels.	0	2	13	102	10
Hymenophyllaceae					
Crepidomanes bipunctatum (Poir.) Copel.	0	0	0	0	2
Lycopodiaceae					
Lycopodium carinatum Desv.	0	7	0	0	0
Lycopodium numularifolium Bl.	0	7	1	0	0
Lycopodium squarrosum Forst.	0	5	0	1	0
Oleandraceae					
Nephrolepis hirsutula (Forst.) Pr.**	0	0	1	2	200
Oleandra neriiformis Cav.	0	0	0	2	9
Polypodiaceae					
Aglaomorpha heraclea (Kze) Copel.	0	0	0	0	95
Belvisia revoluta (Bl.) Copel.	0	6	0	1	131
Crypsinus trilobus (Houtt.) Copel.	0	0	1	48	0
Drymoglossum piloselloides (L.) Pr.	0	0	0	12	2
Drynaria quercifolia (L.) J. J. Sm.	5	0	10	26	0
Lemmaphyllum accendens (Bl.) Donk	0	0	0	36	10
Loxogramae avenia (Bl.) Presl.	0	62	145	8	0
Microsium scolopendria (Burm.f.) Copel.	2	0	3	5	67
Microsium sp.	0	0	0	1	18
Pyrrosia lanceolata (L.) Farw.	76	28	19	10	0
Pyrrosia longifolia (Burm.f.) Morton	15	0	0	2	1

Pyrrosia numularia (Sw.) Ching	21	0	0	0	0
Vittariaceae					
Anthropyum reticulatum (Forst.) Kaulf.	87	144	343	189	3
Vittaria elongata Sw.	0	20	0	1	1
SPERMATOPHYTA					
Araliaceae					
Schefflera polybothrya (Miq.) Vig.**	0	0	0	4	32
Asclepiadaceae					
Dischidia cochleata Bl.	0	0	4	24	0
Dischidia rafflesiana Wall.	0	0	0	7	6
Hoya diversifolia Bl.	25	25	1	3	0
Hoya lacunosa Bl.	5	24	17	40	2
Commelinaceae					
Commelina benghalensis L.	0	0	0	0	1
Compositae/Asteraceae					
Gynura procumbens (Lour.) Merr.**	0	0	0	0	3
Gesneriaceae					
Aeschynanthus radicans Jack.	0	0	0	0	23
Cyrtandra sulcata Bl.**	0	0	0	0	5
Melastomataceae					
Clidemia hirta (L.) D. Don.**	0	0	0	0	144
Medinella eximia L.**	0	0	0	0	57
Medinella pterocaula Bl.	0	0	0	24	0
Graminae/Poaceae					
Pogonatherum paniceum (Lamk.)Hack.**	0	0	0	0	1
Moraceae					
Ficus ampelas Bl.**	0	0	0	0	1
Ficus ribes Reinw. ex Bl.**	0	0	0	0	1
Ficus subulata Bl.**	0	0	0	0	1
Ficus sumatrana Miq.**	1	0	0	0	0
Ficus tinctoria L. f.**	0	0	0	0	1
Orchidaceae					
Agrostophyllum bicuspidatum J. J. Sm.	0	0	0	2	5
Agrostophyllum denbergeri J. J. Sm.	0	0	0	4	0
Appendicula reflexa Bl.	0	0	0	0	66
Bulbophyllum purpurascens T. & B.	0	0	7	99	1
Bulbophyllum unguiculatum Rchb. f.	0	0	0	16	2
Bulbophyllum sp.3	0	0	3	0	8
Coelogyne rochussenii De Vr.	0	0	0	7	0
Dendrobium accuminatissimum (Bl.) Lindl.	0	0	0	14	1
Dendrobium crumenatum Swartz.	88	95	24	22	0
Dendrobium mutabile (Bl.) Lindl.	75	2	19	295	96
Dendrobium secundum (Bl.) Lindl.	0	0	3	0	1
Eria retusa (Bl.) Rchb.f.	0	0	0	0	1
Flikingeria angustifolia (Bl.) A.D.	0	0	0	2	14
Phaius tankervilliae (Banks ex I.Herit) Bl.**	0	0	0	0	1

Pholidota articulata Lindl.	0	0	0	0	5
Trixspermum merguens (Hook. f.) O. Kuntze	0	0	2	0	0
Number of species	12	15	21	36	44
Number of individuals/plot	428	453	643	1443	1512
Fisher's α	2.3	3.0	4.2	6.7	8.5

Table 2 shows the data in plots in Rakata, which includes 61 species. On Rakata, epiphytic orchids were most diverse and abundant among seed epiphytes. In particular two of them, *Dendrobium crumenatum* and *Dendrobium mutabile* were the commonest species. The majority of other families were represented by only one or two species. The families, Aspleniaceae, Polypodiaceae and Vittariaceae, comprised the bulk of the ferns encountered, with *Asplenium*, *Antrophyum*, and *Pyrrosia* occurring in each plot site.

Only four species of epiphytes were recorded from the study plots on Panjang and Sertung, as well as on the western part of Rakata. *Dendrobium crumenatum* and *Pyrrosia lanceolata* were the commonest epiphytes at these sites. In the three permanent plots on Anak Krakatau, four species of epiphytes were recorded. *Davalia denticulata, Drynaria quercifolia, Hoya diversifolia* and *Pyrrosia lanceolata* were growing on *Casuarina* and *Hibiscus* trees (Partomihardjo *et al.* 1992). All disappeared, however, after eruption of 1992/93 (THORNTON *et al.* 1994).

Change in density and diversity with altitude

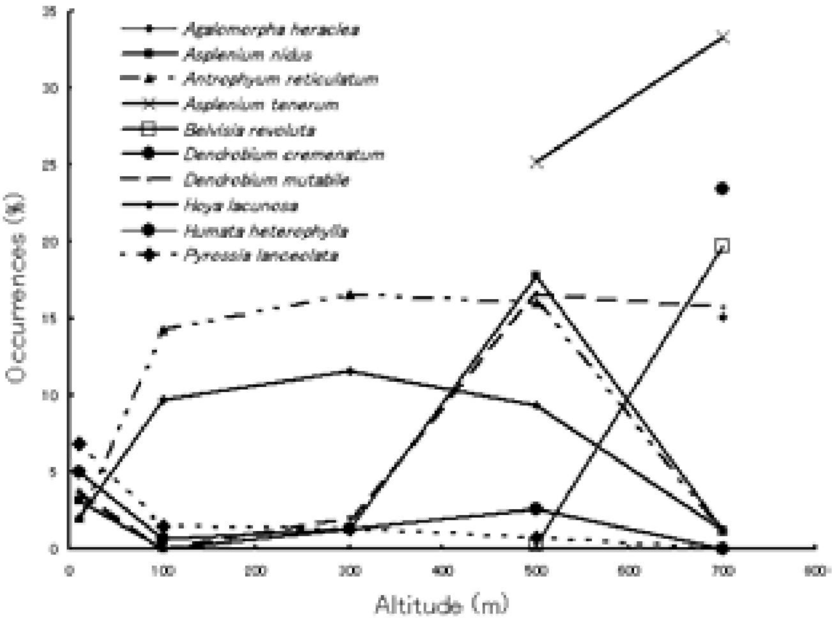

Fig. 3. The individual number of some important species of epiphytes at different altitudes: 10, 100, 300, 500 and 750m on Rakata.

The plots at higher altitudes on Rakata had a greater diversity than the lower plots. The total numbers of species in plot were 44, 36, 21, 15 and 12 species at 700m, 500m, 300m, 100m and 10m asl, respectively (Table 2). The diversity index, Fisher's α was 8.5, 6.7, 4.2, 3.0, 2.3 from upper to lower plots, respectively. Both population size and species diversity were the highest at the summit plot, with the number of individuals declining from 378 per $100m^2$ at the summit to 160 at 500m, 71 at 300m asl. At the 100m plot there were only 50 individuals per $100m^2$. An altitudinal preference was evident in some species (Fig. 3). The epiphytic ferns such as *Aglaomorpha heraclea, Belvisia revoluta* and *Humata heterophylla* were recorded at the highest plot only. The common orchids at the 700m plot were *Appendicula reflexa* and *Dendrobium mutabile*.

Distribution on the tree

The number of epiphytic species growing on trees on Rakata was not clearly correlated with tree size. The maximum number of epiphytic species noted on a tree was 14. These were growing on a relatively small tree of *Neonauclea calycina* with a diameter of 29.5cm, while the largest tree of *Calophyllum inophyllum* with a diameter of 102.5cm carried only two species. However, in general the average number of epiphyte species per tree rose with increase in tree size (Fig. 4).

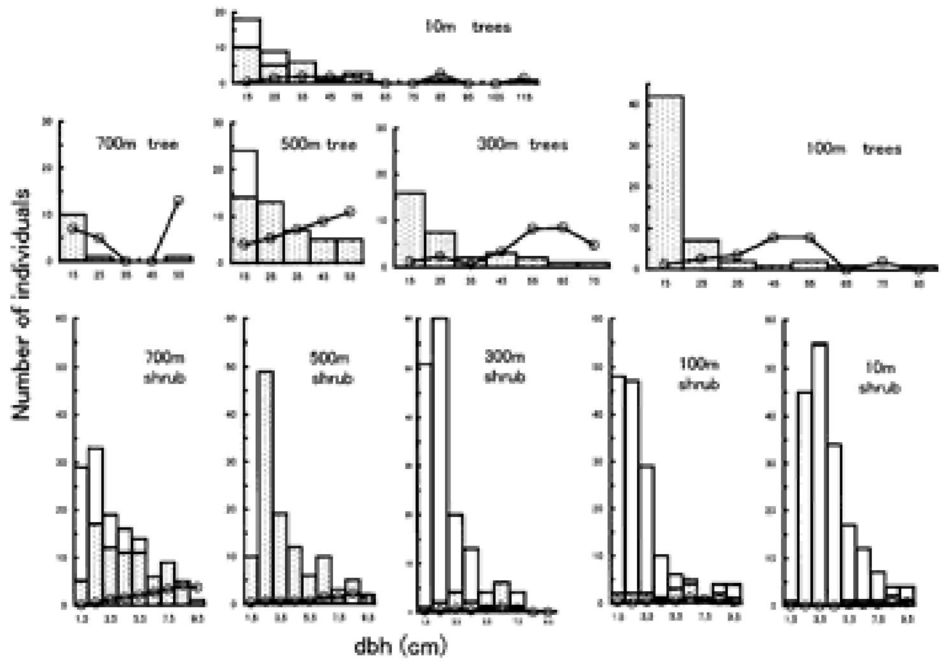

Fig. 4. Frequency distribution of epiphytes and their associated trees (dbh>10cm) and shrubs (dbh, 1- 9.9 cm) in the five plots at different altitudes. Shaded and open columns show the number of trees and shrubs with and without epiphytes, respectively. The polygonal lines show the average number of epiphytes on the given trees and shrubs. Numeric letters in each figure shows the altitude.

Table 3. Numbers of individuals(N) and species(s) of epiphytes recorded on various portions of trees within plots on the Krakatau Islands.

	Altitude	Basal		Trunk		Canopy	
Islands	(m)	N	S	N	S	N	S
Rakata (East coast)	10	112	7	73	8	236	11
	100	209	9	99	13	164	11
	300	376	7	148	14	118	15
	500	551	21	432	30	401	23
	700	672	23	414	32	442	13
Rakata (West coast)	50	0	0	10	2	27	3
	100	0	0	22	2	45	2
Panjang	50	0	0	8	1	54	3
	100	1	1	3	2	4	2
	150	2	1	11	5	5	2
Sertung	100	0	0	5	1	0	0
	150	0	0	17	4	0	0

There were three groups of epiphytes which had progressively colonized trees of the Rakata forest. Epiphytic colonizers of the canopy comprised mostly succulent orchids such as *Agrostophyllum* spp., *Bulbophyllum* spp., *Dendrobium crumenatum, D. secundum, Flikingeria angustifolia* and water collectors such ferns as *Aglaomorpha heraclea, Asplenium nidus* and *Drynaria quercifolia.* The second group consisted of epiphytes colonizing the large vertical boughs and the upper part of the tree trunk. The group consisted of relatively shade-tolerant forms such as *Davalia denticulata, Humata* spp., *Lycopodium* spp., *Pyrrosia* spp., *Oleandra neriiformis* and a group of orchids including *Appendicula reflexa, Coelogyne roschussenii, Dendrobium mutabile, Eria retusa* and *Trixspermum merguense*. This second group also included hemi-epiphytes or stranglers such as *Ficus* spp., *Schefflera polybotria* and *Medinilla pterocaula*. The third group of epiphytes comprised those growing on the lower part of the trunk and includes *Asplenium* spp. (except *A. nidus*), *Antrophyum reticulatum, Belvisia revoluta,* and *Vittaria elongata*. Few spermatophyte epiphytes belonged to this group, but some terrestrial plants grew temporarily on the mat of mosses at the tree trunks in the humid forest near the summit.

Table 3 shows the occurence of epiphytes in each part of the tree in plots at different altitudes. At 10m plot, the incidence of epiphytes on the basal part of the trees was less than that in the canopy, and there were more epiphytes on the basal part of the trunk in the high altitude plots than in the plots below 500m.

Dispersal mechanisms

The cumulative survey data of epiphytes from 1886 to 1993 comprise about 49 to 59 species of pteridophytes and spermatophytes, respectively (Table 1). Most of the epiphytes found in Krakataus are dispersed by wind (anemochorous). Only eight species of epiphytic spermatophytes were classified as being dispersed by birds or bats classified (zoochorous). These zoochorous epiphytes would be better described as hemi-epiphytes, which can grow as epiphytes, *e.g. Clidemia hirta* (Melastomataceae), *Schefflera polybotrya* (Araliaceae) and six species of *Ficus*. The *Ficus* species usually become stranglers after maturity. Over long distances, *Hoya lacunosa* is probably anemochorous, as indicated by the production of numerous seeds with a pappus at one end of each seed. However, the occurrence of *H. lacunosa* is associated with nests of an ant species of the genus *Crematogaster*, and ant-dispersal may be involved on a local scale.

Discussion

Colonization and development of vascular epiphytic flora

The first vascular epiphytes recorded as colonists on the Krakataus were *Cymbidium finlaysonianum* and *Nephrolepis biserrata* (DOCTERS van LEEUWEN 1936). In the early stages of succession on the Krakataus these plants did not grow on the trees that were not yet present. In the present study *C. finlaysonianum* and other epiphytic orchids such as *Acriopsis javanica* were recorded growing on the clump of *Saccharum* on the young island Anak Krakatau, where diversity of potential host trees was low (PARTOMIHARDJO *et al.* 1992). On *Casuarina equisetifolia* trees on the same island, the pioneer epiphyte is *Hoya diversifolia*. Both *Acriopsis* and *Cymbidium* collect water in their rosette leaves and *H. diversifolia* is succulent. These species are thus apparently adapted to survive in dry habitats. *Nephrolepis biserrata* is basically a ground fern, but is also commonly found as epiphyte on oil palm (WEE 1978). The presence of a depression in the axis of the main branches of some trees allows the accumulation of humus and thus paves the way for the establishment of other plants such as *Nephrolepis hirsutula* which is normally not epiphytic.

WHITTAKER *et al.* (1992) demonstrated that the forest communities on the Krakataus are still accumulating new families and genera of trees. Not only the forests are still relatively immature, both the potential pool of immigrants is far from exhausted. Among epiphytes a similar pattern exists: new species are still colonizing the islands (Appendix). Fifteen families are represented among the 108 species of epiphytes present on the Krakataus (1886-1993). The proportions of these families are, however, somewhat anomalous when compared with the distribution of epiphytes in surrounding islands. For example, orchids and pteridophytes comprise 62% and 30% respectively, of the 621 full- and hemi-epiphyte species in West Java, although they make up 34% and 45% respectively, of the 108 species on Krakatau Islands (Table 4).

Table 4. Number of species of higher plant epiphytes recorded from the Krakatau Islands and Java. Full=fully epiphyte; Hemi=hemi epiphyte species.

Group of taxa	Krakatau Islands		West Java		Total of Java
	Full	Hemi	Full	Hemi	
Pteridophyte	48	1	160	27	195
Piperaceae	0	0	1	0	1
Melastomataceae	1	1	9	4	13
Moraceae	0	6	4	1	5
Urticaceae	0	0	2	0	2
Araliaceae	0	1	5	1	7
Asclepiadaceae	8	0	15	1	18
Gesneriaceae	5	0	3	0	8
Orchidaceae	37	0	381	7	431
Total	99	9	580	41	680

As shown in Fig. 2-c, epiphytic species occupied only 5 % of flora on the islands until 1920s. By the early of 1930s, most area of Rakata, where most epiphytic plants were found, was forested (DOCTERS van LEEUWEN 1936, WHITTAKER *et al.* 1989). Because epiphytes need the host plants, the percentage of epiphytes increased with the recovery of forests. From the 1930s to 1993, it occupies about 20% of actual flora.

Altitudinal distribution and species richness

GRUBB *et al.* (1963) reported that the population density of epiphytes in the mountain forest in Ecuador at 1780m asl was nearly ten times that at 380m, and species diversity was 1.6 times greater. Generally the numbers of epiphyte species increase with wetness of climate in the tropics. Heavy rains in mountain forest have a constant leaching effect on the epiphytic habitat, but moisture makes epiphytes vigorous and healthy (STEENIS 1972). Therefore, montane habitats are more favorable for epiphytes than lowland habitats.

The greater number of epiphytic species in the upland of Rakata might be explained with the wetter conditions than on the lower slopes. Whittaker *et al.* (1989) pointed out that the forest above 500m asl is a cloud forest represented by moss communities, although in mainland areas (Java or Sumatra) such low altitudes are usually free from fog, and the cloud belt is usually situated at 2000m asl. Steenis (1972) stated that a sort of telescoping effect caused by mass-elevation on small island changes temperature, relative humidity and rainfall.

On Rakata there is an increase both in population density and species diversity of vascular epiphytes up to maximum at the summit plot of about 700m asl. The large increase in population and diversity at the 500m plot compared to the 300m plot was correlated with an increase of daily cloud cover at this altitude. Although the species diversity of epiphytes in the mossy forest of Rakata is not very different from that in the summit area, the population density on the latter is much higher. In the mossy forest at about 500m, average number of individuals was 3.9/sp/100 m^2 with maximum of 33. This finding can be compared with an average of 10/sp/100m^2 with a maximum of 76 in the summit area. Thus, while there is considerable overlap, only the maximum density encountered in the 500m plot approaches the mean density in the summit plot. The trees in the 500m plot mostly have a vertical bole with a broad-branched canopy. With increase of altitude canopy size did not decrease as much as bole length. In the 700m plot, the trees were smaller but usually twisted, inclined at all angles and branching in every direction. SUDDEN and ROBIN (1979) stated that inclined or horizontal branches and boles are more favorable to epiphytic growth than vertical surfaces.

They and WHITMORE (1992) noted that moisture from cloud and mist are important for colonization of epiphytes. The increase of daily cloud cover with altitude is accompanied by an increase in humidity. FOSTER (1982) determined the lapse rate of daily humidity and temperature with altitude. The increase in species diversity and abundance with altitude in the series of close forest plots on Rakata can be attributed to an increase in both average daily period of cloud cover and humidity with altitude. It is doubtful, however, that the humidity associated with cloud cover alone account for the high diversity of the vascular epiphytic flora on Rakata, for it is evident that many integrated factors affect the epiphytic population. Although there is no detail study, it seems that the abundance of mosses covering the bark, with their considerable water-holding capacity, promotes the germination of epiphyte seeds and spores. Consequently, some terrestrial plants are able to grow upon the lower tree trunks, and similarly a number of epiphytes can thrive on the mossy ground as well as they can on the trees.

Distribution on the tree

There are several important differences between growing on tree and in the ground. Light availability is an important difference, besides the physical properties of the bark of the host tree. A soft, spongy bark with roughened surface is the best for water retention and also provides cracks and crevices where epiphyte seeds easily lodge (DRESSER 1981). The spongy barks of *Neonauclea calycina* (Rubiaceae) in the higher area and of *Terminalia catappa* (Combretaceae) in beach areas are favorable for the growth of epiphytes on the Krakatau Islands. The horizontal branching of *T. catappa* also provides suitable habitats for epiphytic growth. Smooth and hard barks such as *Ficus* spp. and *Dysoxylum gaudichaudianum* in the inland forests and *Calophyllum inophyllum* in the beach area are less favorable for epiphyte establishment.

YEATON and GLADDSTONNE (1982) suggested that the effect of tree size on epiphytic diversity appears to be through the time available for colonization rather than through habitat diversity. They could not distinguish differences in physical habitat requirement between the common species of epiphytes growing on different-sized trees. The size of area to be colonized, representing habitat diversity did not appear to be main factor in the colonization of the epiphytic community. The age of substrate, its inclination, the amount of organic soil accumulation and climatic condition including light intensity are some of the variable that may contribute to the uniqueness of the inner canopy habitat (WALF 1994). JOHANSSON (1974) reported that physical condition varied greatly even within a single host tree, and usually showed a distinct zonation. A few epiphytic orchids such as *Appendicula, Pholidota* and *Podochyllus* thrive in the weaker light and greater moisture of the lower tree trunk. Some species, especially the more massive plants such as *Agrostophyllum, Cymbidium* and *Gramatophyllum* are usually found only on very large branches. Other species are more abundant on branches of moderate size, and many micro-epiphytes occur primarily on twigs just in leaf canopy. These patterns are largely controlled by physical factors such as light and moisture, which vary a good deal over short distances.

HOSOKAWA and ODANI (1957) identified three main arboreal habitats of epiphytic mosses and lichens: the stump, trunk and crown of the tree depending on the daily compensation period of the dominant species. Light-demanding species grow predominantly in the crown. Further, HOSOKAWA (1968) found that vascular epiphytes growing in the canopy are heliophilous, characterized by the creeping elongate stems and tufted elongate shoots. This type represented mostly by epiphytic orchids and some ferns. Epiphytes predominantly occupying the trunk of trees are probably adapted to grow under conditions of diffused weak light. This group was represented by acidophilus types with extremely shortened internodes of the creeping stems and a very short upright axes, both of which have tufted leaves. The epiphytes growing on the trunk consisted of a mixture of heliophilous cryptograms, suggesting that moisture availability and solar radiation intensity may determine the vertical distribution of species on the tree (HOSOKAWA and ODANI 1957).

Epiphytic communities composed of ecologically equivalent species. Benzing (1981) suggested that the arrival of propagules is the major factor determining the species quality of epiphytic communities. YEATON and GLADDSTONNE (1982) also believed that composition of vascular epiphytic communities is largely determined by the relative abundance of propagules of it species. On the Krakatau, the wide distributions of some species throughout the study areas indicate that dispersal is not limiting factor for their distribution. The distributions of individual species appear to be affected by moisture availability, and habitat quality. Though spore of ferns and very small seeds of orchids are dispersed by wind, the some spermatophyte epiphytes are dispersed by birds or fruit-eating bats. Both have potentials to be dispersed a long distance. The habitat of epiphytes is known to be very dynamic due to small disturbances such as by the activity of canopy animals, branch and tree falls and the expansion of the crown (PERRY 1978). The distribution of epiphytes on branch and trunk segments is also likely to be characterized by habitat properties. The lower and less diverse canopy on Sertung and Panjang compared to that on Rakata, is probably due to the frequent of heavy disturbances by ash fall from the volcanic activities of Anak Krakatau and low altitude. These are possibly important factors responsible for the relatively sparse epiphytic communities on these two islands.

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Appendix. The list of vascular epiphytes recorded on the Krakatau Islands (1883- 1993) from various expeditions. Survey data are combined as shown by the periods indicated as the years. Key: - = not reported, ? = uncertain identification, ! = identification to genus only, Upper case R,S,P, and A indicated species recorded from Rakata, Sertung, Panjang and Anak respectively. Lower case r, s and p indicate species recorded with some ambiguity in Docters van Leeuwen (1936) as to the year. * = terrestrial plants or stranglers usually occur as epiphytes during the young stage. L: Life form of plant. H,herb; Hw, herb with water collecting ability; Hs, herb with succulent tissue; W, woody plant; S, strangler.

Year* Species	L	1886	1897	1908	20/24	29/33	79/82	89/93
PTERIDOPHYTA								
ASPLENIACEAE								
Asplenium adiantoides (L.) Chr.	H	-	-	-	-	-	-	R
Asplenium longissimum Bl.	H	-	-	-	R	R	-	R
Asplenium macrophyllum Sw.	H	-	-	-	-	-	R	R
Asplenium montanum L.	H	-	-	-	-	-	-	R
Asplenium nidus L.	Hw	-	-	-	RS	RSP	RSP	RSP
Asplenium tenerum L.	H	-	-	-	-	-	-	R
Asplenium thunbergii Kunze	H	-	-	-	R	R	R	R
DAVALLIACEAE								
Davallia denticulata (Burm. f.) Merr.	H	-	-	-	RS	RSP	RSP	RSPA
Davallia solida (Forst.) Sw.	H	-	-	-	-	-	R	-
Davallia trichomanioides Bl.	H	-	-	-	-	-	SP	-
Humata heterophylla (Sm.) Desv.	H	-	-	-	R	R	R	R
Humata repens (L.f.) Diels.	H	-	-	-	-	-	R	R
Schyphularia pentaphylla F'ee	Hw	-	-	-	-	-	R	-
HYMENOPHYLLACEAE								
Hypenophyllum cf. *javanicum* Spr.	H	-	-	-	-	-	R	R
LYCOPODIACEAE								
Lycopodium carinatum *Desv.*	H	-	-	-	-	-	R	R
Lycopodium nummularifolium *Bl.*	H	-	-	-	-	-	R	R
Lycopodium squarrosum Forst.	H	-	-	-	R	R	-	R
OLEANDRACEAE								
Nephrolepis biserrata (Sw.) Schott *	Hs	R	RP	RSP	RS	RSP	RSP	RSP
Oleandra neriiformis Cav.	H	-	-	-	-	-	-	R
OPHIOGLOSSACEAE								
Ophioglossum pendulum L.	H	-	-	-	R	-	R	R
Ophioglossum reticulatum L.	H	-	R	-	RS	Rsp	-	-
Ophioglossum sp.	H	-	-	-	-	1951!	-	-
POLYPODIACEAE								
Aglaommorpha heraclea (Kze.) Copel.	Hw	-	-	-	R	R	R	R
Belvisia callifolia (Chr.) Copel	H	-	-	-	R	R	-	-
Belvisia revoluta (Bl.) Copel.	H	-	-	-	R	R	R	RP
Belvisia sp.	H	-	-	-	-	1951!	-	-
Crypsinus trilobus (Houtt.) Copel.	H	-	-	-	-	-	R	R
Drymoglossum piloselloides (L.) Pr.	H	-	-	-	R	-	RSP	RSP
Drynaria quercifolia (L.) J.Sm.	Hw	-	R	R	RS	RSP	RSP	RSPA
Lecanopteris sinuosa (Wall.ex Hk.) Copel.	H	-	-	-	-	R	RS	R
Lemmaphyllum accedens (Bl.) Donk.	H	-	-	-	R	R	R	R
Lepisous longifolius (Bl.) Holtt.	H	-	-	-	-	-	S	-

Loxogramma avenia (Bl.) Presl.	H	-	-	-	-	-	R	R
Microsorium linguiforme (Mett.) Copel.	H	-	-	-	-	-	R	-
Microsorium nigrescens (Bl.) Copel.	H	-	-	-	RS	Rsp	RP	R
Microsorium punctatum (L.) Copel.	H	-	-	R	RS	Rsp	RSP	RS
Microsorium rubidum (Kunze) Copel.	H	-	-	-	R	-	R	-
Microsorium scolopendria (Burm.f.) Copel	H	-	-	R	RS	S	RSP	R
Microsorium sp.	H	-	-	-	-	-	?	-
Pyrrosia lanceolata (L.) Farw.	H	-	-	-	RS	RSP	RSP	RSPA
Pyrrosia longifolia (Burm.f.) Morton	H	-	-	-	RS	sP	-	RS
Pyrrosia numularifolia (Sw.) Ching	H	-	-	-	S	RsP	-	R
PSILOTACEAE								
Psilotum complanatum Sw.	H	-	-	-	R	R	-	-
Psilotum nudum Griseb.	H	-	-	SP	S	Rsp	S	R
VITTARIACEAE								
Antrophyum reticulatum (Forst.) Kaulf.	H	-	-	-	R	R	RSP	RSP
Vittaria angustifolia Bl.	H	-	-	-	-	-	P	-
Vittaria elongata Sw.	H	-	-	-	-	-	RSP	RSP
Vittaria ensiformis Sw.	H	-	-	-	R	r	-	-
Vittaria zosterifolia Ching	H	-	-	-	R	R	-	-
SPERMATOPHYTA								
ARALIACEAE								
Schefflera polybotrya (Miq.)Vig.	W	-	-	-	-	R1951	R	R
ASCLEPIADACEAE								
Dischidia cochleata Bl.	Hs	-	-	-	-	R1951	-	R
Dischidia hirsuta (Bl.)Decne	Hs	-	-	-	-	-	R	-
Dischidia nummularia R.Br.	Hs	-	-	-	-	-	R	R
Dischidia rafflesiana Wall.	Hs	-	-	-	-	-	-	R
Heterostemma acuminatum Decne	Hs	-	-	-	-	S	RSP	R
Hoya diversifolia Bl.	Hs	-	-	-	-	-	RSPA	RSPA
Hoya lacunosa Bl.	Hs	-	-	-	-	-	RS	R
Hoya sp.	Hs	-	-	-	-	1951 !	-	-
GESNERIACEAE								
Aeschynanthus longiflorus (Bl.)DC.	Hs	-	-	-	-	-	R	R
Aeschynanthus pulchrum Bl.	Hs	-	-	-	R	R	-	-
Aeschynanthus radicans Jack.	Hs	-	-	-	-	R	R	R
Aeschynanthus volubilis Jack.	Hs	-	-	-	R	R	-	R
Marsdenia sp.	W	-	-	-	-	-	R	-
MELASTOMATACEAE								
Medinilla pterocaula Bl.	W	-	-	-		R	-	R
MORACEAE								
Ficus benjamina L.*	S	-	-	-	-	-	-	R
Ficus drupacea Thunb. *	S	-	-	-	-	-	-	R
Ficus elastica Nois.ex Bl.*	S	-	-	-	-	R1951	-	R
Ficus retusa L.*	S	-	-	-	-	-	S	R
Ficus sumatrana Miq.*	S	-	-	-	-	R1951	S	RSP
Ficus tinctoria L.f.*	S	-	-	-	S	Sp	RSP	RSP
ORCHIDACEAE								
Acriopsis javanica Reinw.ex Bl.	Hw	-	-	-	R	-	R	RSPA
Agrostophyllum bicuspidatum J. J. Sm.	H	-	-	-	R	R	-	R
Agrostophyllum denbergeri J. J. Sm.	H	-	-	-	R	-	R	R
Appendicula reflexa Bl.	H	-	-	-	-	R1951	R	R
Bulbophyllum purpuracens T. & B.	Hs	-	-	-	-	R	-	R
Bulbophyllum unguiculatum Rchb. f.	Hs	-	-	-	-	R1951	-	R
Bulbophyllum sp.	Hs	-	-	-	-	-	!	R

Coelogyne logifolia (Bl.) Lindl.	Hs	-	-	-	-	-	R	R
Coelogyne rochusseni De Vr.	Hs	-	-	-	-	-	R	R
Cymbidium aloifolium (L.) Sw.	H	-	-	-	-	-	R	R
Cymbidium bicolor Lindl.	H	-	-	-	R	S	-	R
Cymbidium finlaysonianum Lindl.	Hw	-	P	R	rs	r	R	RSPA
Dendrobium acuminatissimum (Bl.) Lindl.	Hs	-	-	-	-	-	R	R
Dendrobium crumenatum Swartz.	Hs	-	-	-	R	R	RSA	RSPA
Dendrobium mutabile (Bl.) Lindl.	Hs	-	-	-	R	R	R	R
Dendrobium secundum (Bl.) Lindl.	Hs	-	-	-	R	R	R	R
Dendrobium sp.	Hs	-	-	-	-	-	!	-
Eria oblitterata (Bl.) Rchb. f.	Hs	-	-	-	-	-	R	R
Eria retusa (Bl.) Rchb. f.	Hs	-	-	-	-	-	S	R
Eria verruculosa J.J.Sm.	Hs	-	-	-	-	-	-	R
Flickingeria angustifolia (Bl.) A. D.	Hs	-	-	-	-	-	-	R
Glomera erythrosma Bl.	H	-	-	-	-	-	-	R
Grammatophylllum speciosum Bl.	Hs	-	-	-	S	-	-	R
Liparis viridiflora (Bl.) Lindl.	Hs	-	-	-	R	R	-	R
Liparis wrayi Hook. f.	Hs	-	-	-	RS	RS	-	R
Liparis sp.	Hs	-	-	-	-	-	!	-
Malaxis latifolia J. E. Smith	Hs	-	-	-	R	R	-	-
Oberonia monstruosa (Bl.) Lindl.	Hs	-	-	-	R	R	R	R
Oberonia sp.	Hs	-	-	-	R	-	-	-
Pholidota articulata Lindl.	Hs	-	-	-	-	-	-	R
Pholidota imbricata W. J. Hooker	Hs	-	-	-	-	-	R	R
Podochilus bancanus J. J. S.	H	-	-	-	-	-	R	R
Taeniophyllum sp.	Hs	-	-	-	-	R	-	-
Thrixspermum merguens (Hk. f.) O. Kuntze	Hs	-	-	-	R	R	-	-
Thrixspermum sp.1	Hs	-	-	-	R	-	-	-
Thrixspermum sp.2	Hs	-	-	-	-	-	!	-
Trichotosia annulata Bl.	Hs	-	-	-	-	-	R	R
Total		1	4	6	48	45(9)	63(5)	81