



Plant Recolonization and Vegetation Succession on the Krakatau Islands, Indonesia

R. J. Whittaker; M. B. Bush; K. Richards

Ecological Monographs, Vol. 59, No. 2. (Jun., 1989), pp. 59-123.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28198906%2959%3A2%3C59%3APRAVSO%3E2.0.CO%3B2-1>

Ecological Monographs is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

PLANT RECOLONIZATION AND VEGETATION SUCCESSION ON THE KRAKATAU ISLANDS, INDONESIA¹

R. J. WHITTAKER

School of Geography, University of Oxford, Mansfield Road, Oxford, OX1 3TB, United Kingdom

M. B. BUSH²

Department of Geography, University of Hull, Cottingham Road, Hull, HU6 7RX, United Kingdom

AND

K. RICHARDS

Robertson Research International, Llandudno, Gwynedd, LL30 1SA, United Kingdom

Abstract. The development of the vegetation and floras of the Krakatau Islands in the Sunda Straits, Indonesia, since their "sterilization" in 1883 is described. Key features of the post-1883 environment, such as pedogenesis, geomorphology (coastal change), human influence, and recent volcanic activity are detailed, and their possible influence on spatial and temporal patterns in both vegetation and flora is discussed.

Field work conducted in 1979, 1983, and 1984 has enabled an assessment of the present state of vegetation development, aided by plot-based sampling and analysis of the arboreal component, employing numerical classification (by TWINSpan) and ordination (by DCA). The coastal communities were established early and have remained little changed, although the distribution of the various components has changed according to the influence of a dynamic coastal geomorphology. Fifty years after forest closure, the forests of the interiors remain species-poor and composed of typical early-seral species. Rakata was dominated inland by *Neonauclea calycina* and *Ficus pubinervis* up to ≈ 550 m altitude, above which a mossy forest of *Ficus* spp. and *Schefflera polybotrya* scrub was recorded. The main inland forest types on Rakata Kecil and Sertung were of young, even-aged stands of *Timonius compressicaulis* (extensive) and older stands of *Dysoxylum gaudichaudianum* (often with a *T. compressicaulis* understory). The principal axes of variation within the data were found to be between extremes of the Rakata forest types, with Sertung and R. Kecil stands remaining undifferentiated until lower levels of the analyses. These patterns were ascribed to a mix of environmental variation (coastal and altitudinal factors), chance variations in colonization, and to volcanic action following the emergence of Anak Krakatau in 1927. Disturbance by volcanism (e.g., in 1930, 1934-1936, 1939, 1952-1953, 1961) has resulted in the deflection of vegetation succession on R. Kecil and Sertung into a different pathway from that followed on Rakata, which has remained unaffected by the activity. On Anak Krakatau, volcanic action has prevented successful colonization away from accreting coastal deposits, and has several times eliminated the entire flora. In addition, the major source of propagules for Anak Krakatau is from within the group, and for these several reasons the new island is shown to be a poor analogue for the early recovery phases of the other islands.

Complete floral lists are given for each recorded survey for each island in the group, including data from surveys in 1979, 1982, and 1983. These data have been revised from previous publications on the basis of recent herbarium work and literature searches. The data are analyzed according to several different models: cumulative species totals, species totals for particular combinations of surveys, and totals calculated on the assumption of minimum turnover. The early beach spermatophyte assemblages of Rakata have undergone relatively few losses in comparison to the assemblages of the interior, while within the latter there has been a relatively high proportion of losses among the pioneering pteridophytes. The possession of major habitat types has been identified as critical in determining the shape of the overall colonization curve, through the passive sampling of different source pools. The diversity of the floras of the group as a whole and of Rakata and Anak Krakatau has continued to increase. The curves of species present on Sertung and R. Kecil have levelled and fallen respectively, as a result of the volcanic activity of Anak Krakatau.

It is shown that the number of animal-transported species on the Krakatau group has continued to increase over the last 50 yr, and that this accounts for the majority of the increase in the size of the spermatophyte flora. The animal-transported species and the early sea-dispersed species appear to be species-stable groups. Later sea-dispersed species included ephemerals and species of temporary habitats, and have experienced a relatively high proportion of losses. Few beach species that have established on all of the three main islands have subsequently become extinct from the group. The number of pteridophytes on the islands has increased over the last 50 yr, mainly through the addition of forest species. A large proportion of plant species has been found only on Rakata, which samples an upland source pool not represented on the other islands. It is argued that the assumptions of "classical" island biogeography are inappropriate to these data and that the pattern in floral recolonization can best be understood as a successional process involving broad habitat and dispersal mechanism determinants. The implication of these findings is that community dynamics are highly significant in determining rates of immigration, colonization (i.e., successful immigration), and extinction, and that the probabilities of each vary among different groups of species and through time.

Key words: disturbance; island biogeography; Krakatau; plant recolonization; tropical forest; vegetation succession; volcano.

¹ Manuscript received 29 May 1987; revised 6 June 1988; accepted 13 June 1988.

² Present address: Department of Zoology, The Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210 USA.

INTRODUCTION

The Krakatau (Krakatoa) islands (Fig. 1) have been the subject of a unique combination of long-term studies on tropical succession and of studies of the re-assembly of island biotas. Despite the objections of Backer (1929, 1930), the sterilization of the islands by the eruptions of May to 27 August 1883 can be assumed to be essentially complete. Certainly no significant vestige of the former soil and vegetation cover remained on the greatly re-shaped and ash-covered islands (Verbeek 1885, Steenis 1930, 1931, Docters van Leeuwen 1936). The principal seral sequences can therefore be viewed as primary successions. This paper reports a comprehensive spatial description of the vegetation of the islands of the group up to 1983–1984, requiring new interpretations of successional pathways and of the role of disturbances. The floral recolonization data are examined with a critical view to the relevance of island biogeographical theory (*sensu* MacArthur and Wilson 1967), with the analysis being directed toward an understanding of the influence of habitat type, changing environment, and succession on the patterns in the floristic data.

The largest island of the group, the remnant from the active volcano of 1883, is Rakata (Pulau Rakata Besar, or Krakatau). The other pre-1883 islands are Sertung (Verlaten Island) and Rakata Kecil (Lang Island, or Panjang). A new volcano, Anak Krakatau, established in the center of the group between 1927 and 1930, and has since grown to become a substantial island. It adds an extra dimension to this "natural experiment," both by creating new habitats and by disrupting the vegetation of Sertung and R. Kecil.

This paper details the first comprehensive description of the flora and vegetation of the Krakatau islands since the work of Docters van Leeuwen (1936), integrating results of investigations in 1951–1952, 1979, and 1982–1984 (Borssum Waalkes 1960, Flenley and Richards 1982, Tagawa 1984, Tagawa et al. 1985, 1986, Bush et al. 1986a).

PHYSICAL ENVIRONMENT

Climate

Few meteorological data are available from Krakatau, although from readings taken on R. Kecil in 1929, the mean monthly temperature was found to be almost constant throughout the year, varying from 26.9° (July and December) to 28.7°C (October), (Fig. 2A; Baren 1931). The climate has been classified as "Afa" in the Koppens world system, i.e., as a tropical rainy climate with few dry months (Subagio and Reuler 1985), with the west monsoon bringing heavy rains from the Indian Ocean and the east monsoon relatively dry air from Australia (Dammerman 1948). The dry season, between May and October, is of variable duration and timing, and can be extreme (Fig. 2A).

A series of temperature and humidity readings was

taken on Rakata in September 1979 (Fig. 2B; Forster 1982). The lapse rate of mean annual air temperatures was calculated to be 0.8°C/100 m from the regression line of soil temperatures at 75 cm depth, according to the method of Mohr and Baren (1954). Personal observation suggests that the highest altitudes on Rakata experience a much greater diurnal range in temperatures than the lowlands, although this has not been quantified. The gradient in relative humidity at 1300 (Fig. 2B) indicates a fall from about 95% at the summit to 75–80% in the lowland, and a further decline from the forest to the beaches (Forster 1982). Gradients in precipitation are doubtless associated with the humidity and temperature patterns (Borssum Waalkes 1960), so rainfall may be anticipated to be higher on Rakata (highest point > 735 m) than on Sertung (182 m) or R. Kecil (142 m).

Caldera development

Verbeek (1885) described the development of the Krakatau caldera from a prehistoric volcano at least 2000 m high, formed along the Sunda Fault. This volcano collapsed $\approx 60\,000$ yr ago (Ninkovich 1979, Camus and Vincent 1983) to form a caldera wall of which four pieces emerged above sea level. Subsequently from Rakata peak and the craters Danan and Perboewatan, the main island rebuilt towards the center of the caldera. Eruptions of Perboewatan in May 1680 resulted in the ejection of pumice and possibly of lava. Contemporary accounts describe the island as "burned and barren" (Berg 1884). The volcano remained dormant until 20 May 1883, when Perboewatan and later Danan became active. After eruptions of increasing violence, there occurred the catastrophic collapse of 27 August, repeating the prehistoric collapse. The eruption terminated on 28 August, although further minor activity took place in September or October of that year (Verbeek 1885). The islands remained dormant until June 1927 (Simkin and Fiske 1983).

Coastal change since 1883

The 1883 coastlines of pyroclastic deposits have been subject to continuous reshaping (Docters van Leeuwen 1936, Dammerman 1948) and have retreated by as much as 2.5 km, the most extensive recession being in southwest Sertung and west Rakata (Bird and Rosengren 1984). Rates of recession in these deposits, at 6.6 m/yr, are among the most rapid recorded worldwide. As a result of the predominant monsoon pattern, wave action is generally stronger from a westerly direction. This has resulted in higher cliffs than found on eastern shores, with incised gullies emerging as v-shaped notches in the upper cliff. In places the more resistant underlying rocks (of pre-1883 age) have been exposed, as on the southwest coast of R. Kecil, where andesitic lavas form a structural bench (Bird and Rosengren 1984). The cliffs of the west coast of R. Kecil receded by as much as 1.5 km between 1883 and 1928, although

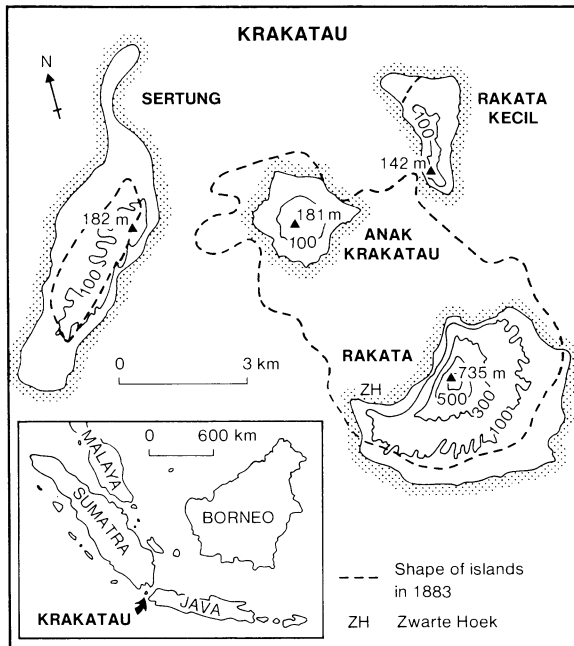


FIG. 1. The location of the Krakatau Islands, Indonesia. The 1983 coastline (—) of Rakata Kecil coincides with the coastline as of this writing (— — —) except in the northwest.

since the emergence of Anak Krakatau to the west, this rate has greatly diminished. In contrast, erosion of the southern end of Sertung is currently extremely rapid and can reach rates as high as 3.0 m/mo (Bird and Rosengren 1984).

From the northern end of Sertung there extends a broad spit nearly 2 km long, fed by longshore drift along the island. The spit has been subject to continual change. By a combination of erosion of the western shore and accretion on the eastern side, the spit has migrated 1 km eastward, and suffered a 1 km loss of length between 1945 and 1982 (Bird and Rosengren 1984, Rosengren 1985). These changes have resulted in the breaching and loss of two small lagoons present on the spit in the early part of the century. (Compare Fig. 1 and Fig. 3.) The eastern side of the promontory has formed a sheltered bay with a shallow shelving beach. The western shoreline is steeper as the spit is being undercut, so that the *Casuarina equisetifolia* trees appear stilt-rooted. Above the slope the spit is flat and for 30 m inland is generally littered with pumice and flotsam, indicating periodic inundation. Overtopping of the beach at Zwarte Hoek on Rakata (Fig. 1) was

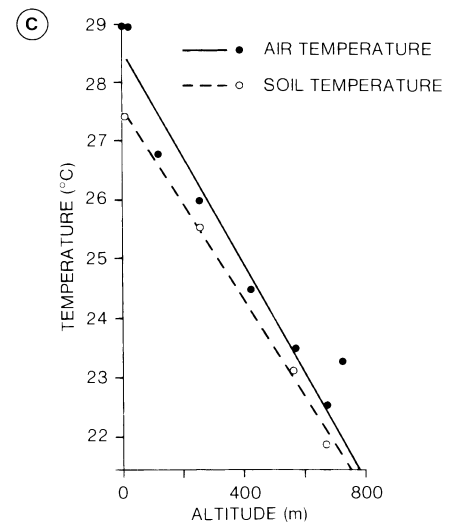
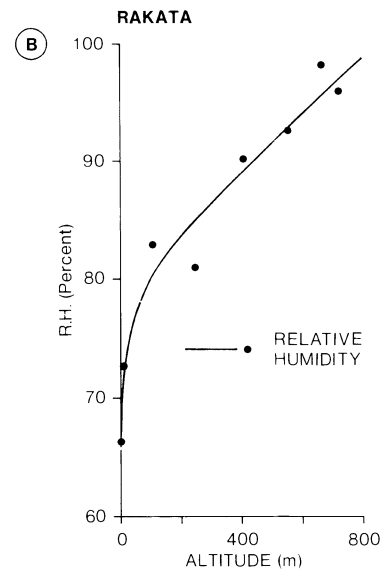
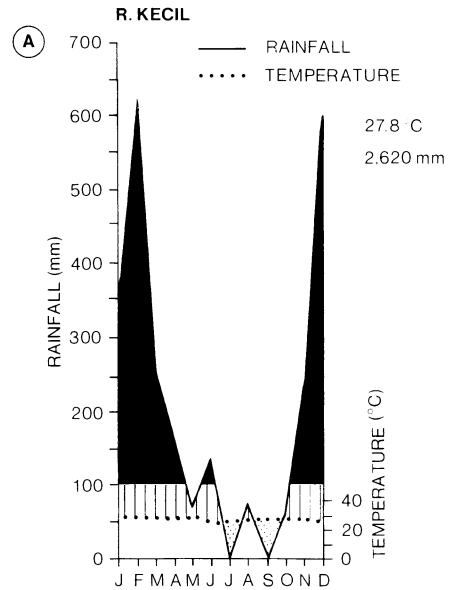


FIG. 2. (A) Climate diagram of R. Kecil from observations by Stehn in 1929 (after Tagawa et al. 1985). (B) Pattern of variation in relative humidity with altitude on Rakata. (C) Temperature variation with altitude on Rakata. (B) and (C) recorded at 1300 in September 1979 (from Forster 1982).

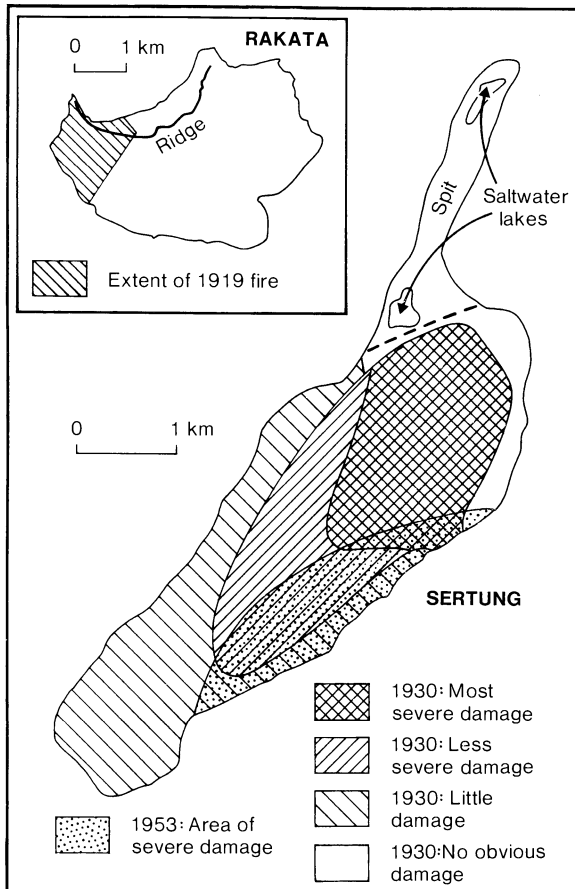


FIG. 3. The distribution of volcanic damage on Sertung in 1930 and 1953, and of the 1919 fire on Rakata. Sertung has been hit by eruptive activity at other points since 1927, as has R. Kecil, but these events have not been mapped. See pages 65–66. After Docters van Leeuwen (1936) and De Neve (*personal communication* 1984).

observed in 1984, with drift being deposited in runnels behind the strand bank. Undercutting of established trees was noted here as in other places on the islands, suggesting lateral migration in conditions of erosion and accretion in the medium term. On Anak Krakatau there have been additions due to volcanism and rapid erosion of coastlines of pyroclastic materials. Where lava has been extruded on the western coast, the erosion rate has been much slower. In general, material drifts to the sheltered eastern coastline of this island, where cusped forelands have formed (Bird and Rosengren 1984).

Topographic development

The 1883 eruptions resulted in both the removal of a large part of the main island and the addition of new territory. The additions took the form of ejecta, a mixture principally of pumice blocks and fine porous ashes. The depth of the ash layer in the lowlands appears on average to have been 60–80 m, although depths of as

much as 150 m were reported locally, and the existing coastlines were extended laterally by as much as 700 m (Verbeek 1885, Docters van Leeuwen 1936, Simpkin and Fiske 1983). Immediately following the eruption, the ash was subject to rapid gullying, to the extent of several metres downcutting by 28 October 1883 (Verbeek 1885). Although the layers of ash and pumice were not as thick near the summit and were subject to rapid erosion in the early years, Docters van Leeuwen (1936) recorded a 5 m depth of 1883 ejecta at a point on the summit of Rakata as late as 1929.

The islands remain characterized by steeply dissected topography, with innumerable deep gullies. Slope instability, landslides, and rockfall have been a continuous feature of the post-1883 physical environment (Docters van Leeuwen 1936, Bush 1986a), although the deep gully systems characteristic of these islands represent the product of the intense early post-eruptive phase of erosion and are now essentially fossil features (Stehn 1929, Newsome 1982). There is a marked break of slope on Rakata at ≈ 400 m altitude, above which the dominant topography consists of narrow ridges divided by deep v-shaped gullies; slopes of 40–70% are common. Below 100 m, the ridge-gully system is generally less pronounced, with 25–40% slopes (Subagio and Reuler 1985). Small streams flow in some of the gullies following prolonged downpours, but usually the porous ash is so permeable that it prevents any surface flow. Many gullies appear to have become slightly infilled as a result of slope retreat, with interfluvial areas often reduced to very narrow ash walls, protected by the forest cover (Richards 1982).

The north face of Rakata consists of a precipitous cliff marking the edge of the 1883 caldera (Fig. 4). Rockfall down this face has been observed frequently since 1883 (e.g., Ernst 1908, Docters van Leeuwen 1936). The altitude of the summit was 830 m in October 1883 (Verbeek 1885) and 813 m in 1928 (Stehn 1929). Recent survey data are lacking, but photographic evidence suggests no more than a slight decline since then. The altimeter readings of 735 m used here must therefore be viewed as provisional, subject to revision by proper survey data. The profiles of Sertung and R. Kecil also slope steeply from the summit ridge to the center of the prehistoric caldera, with more gentle outer slopes. Although relatively low islands, both are deeply dissected by gullies which, combined with the sheer cliffs of the eroding coastlines (Fig. 5), have prevented exploration of some areas.

Soils

The vitric ash (hypersthene-augite association) of 1883 provided a nutrient-rich substrate and an excellent rooting medium. Nevertheless, it lacked organic matter and some minerals may not have been available in soluble form (Ernst 1908, Baren 1931). The initially homogeneous ash cover quickly became more varied, and by 1886, sand and organic debris had become



FIG. 4. The sheer north face of Rakata (>735 m), viewed from Anak Krakatau (unvegetated foreground) (T. Richards 1983).

mixed with the pumice along the coast. Inland the larger ravines had cut through the new ash, in places exposing the older buried material.

By 1979 there was some evidence of weathering in the form of mineral decomposition and associated cation release (Newsome 1982, 1986). Particle size data showed low overall percentages of clays, but there was evidence of crystalline clay minerals (smectite and traces of chlorite, vermiculite, and mica), which were attributed principally to geo-hydrothermal alteration in the course of the 1883 eruption. Organic matter incorporation and decomposition at the soil surface has given rise to well-developed A horizons, especially in more stable gullies. Subagjo and Reuler (1985) indicate a solum depth of 20–30 cm, and occasionally as much as 35–40 cm, but with only thin A1 horizons (2–8 cm), overlying weak gravelly silt/loam AC horizons. In some places a B1 or weak B2 horizon could also be distinguished. Subagjo and Reuler (1985) classify these soils as Typic or Andeptic Troporthents and Eutropepts, while Shinagawa et al. (1984) classify all seven samples located between 2 and 730 m on Rakata as Andeptic Troporthents. The soils of Rakata are highly permeable, as indicated by a low bulk density of $<0.82 \text{ g/cm}^3$ and high total pore space ($>69\%$) (Hardjosoestastro and Dai 1985, Newsome 1986). Nevertheless, the micropores of this relatively silt-rich soil have a higher capacity for water retention and are less subject to des-

iccation than, for example, the sandy soils sampled on the vegetated parts of Anak Krakatau in 1979 and 1983 (Newsome 1986).

The soils of Rakata also show some variation with altitude. For example, there is a decrease in the concentration of sodium in the A horizon with increasing altitude (Flenley and Richards 1982), although this may be largely due to the decreasing coastal influence. Above $\approx 530 \text{ m}$ altitude, soil organic matter appeared distinctly black and well decomposed, but mixed with fibrous organic material, in contrast to the thin, ashy soils of the lowlands. High levels of calcium in the topsoil and high carbon/nitrogen values of the upland soils indicated a mull humus (Newsome 1982). Soils with buried horizons were estimated subjectively to cover $<10\%$ of the area in 1982 (Subagjo and Reuler 1985), and were found primarily within the upland gullies ($>400 \text{ m}$ altitude). The buried brown soils were developed from older basalto-andesitic ash, perhaps related to the 1680 eruption. Compared to the post-1883 soils, the buried soils displayed more advanced weathering and appreciable amounts of clay (7–15%). Some had become incorporated into contemporary soils, due to downcutting, slumping of gully sides and re-deposition on the lower slopes (Subagjo and Reuler 1985).

Shinagawa et al. (1984) classify soils sampled from Sertung (four sites), R. Kecil (five sites) and Anak Krak-



FIG. 5. A high-energy beach environment on Rakata, typical of many of the unsheltered beaches of the islands. This steeply shelving eroding beach is unsuitable for *pes-caprae* establishment and is backed by sheer ash cliffs and hanging gullies, exposing forest of the interior at the cliff-edge. The stacks, once a part of the western portion of Rakata, are now a considerable distance out to sea (T. Richards 1983).

atau (two sites) as Typic (as opposed to Andeptic) Tro-porthents. The samples from Sertung and R. Kecil were found to have lower contents of soil organic matter, clay, and free iron and aluminum hydroxides than those from Rakata. They describe five or six phases of soil development, interrupted by deposits of volcanic ash and scoria originating from Anak Krakatau. These include very recent deposits in the cases of at least one profile from both R. Kecil and Sertung (cf. Simkin and Fiske 1983:359). Carbon, exchangeable and water-soluble potassium, and clay and silt contents revealed a gradient from Anak Krakatau soils, which were similar to those of Sertung and R. Kecil, through to Rakata soils. Shinagawa et al. (1984) suggest that these variations, in particular those relating to the ejecta from Anak Krakatau, could have provided a significant influence on the patterns of vegetation succession within the islands.

The soils from Anak Krakatau, developing in coarse to medium scoria, fragments of lava, or even lapilli, were the least developed of all those sampled in 1982

by Shinagawa et al. (1984). Newsome (1986) found that the soils of the vegetated areas were almost entirely composed of sand-sized particles ($> 50 \mu\text{m}$). Formation of the A1 horizon has been very weak, with low carbon exchange capacity, organic carbon, and total nitrogen (Barker and Richards 1982). The samples taken by Shinagawa et al. (1984) ranged from pH 6 to 7.3, little different from the other islands, but Barker and Richards (1982) reported slightly lower values of pH 5.3 to 6.8 for six near-coastal sites sampled in 1979. The surface environment on Anak Krakatau is distinct within the group on account of the lack of a complete vegetation cover. High surface temperatures and a macroporous structure render this soil prone to desiccation, and unsuitable for nonxerophyte colonization.

Volcanic and tectonic activity since 1883

After 1883, no major volcanic episodes occurred until 1927, when a new cone began to build at the edge of the 1883 caldera. A permanent presence was estab-



FIG. 6. Sertung following the 1952 eruption. Notes by De Neve on back of photograph: "Sertung, 19th October, 10.30 hrs. Volcanic ash on the broken trees and other vegetation has been washed away by rains. The thickness of new ash at this locality c. 40 cm; distance from beach 250 m. (De Neve)."

lished (Anak Krakatau IV) on 12 August 1931. By September 1932 the island was 47 m high. It has continued to grow rapidly as a result of successive eruptive phases (including several lava flows), and in 1985 was 190 m high and 2 km in diameter (Bird and Rosengren 1984, Thornton 1986). The new volcano has directly affected the other islands of the group by such influences as wave damage, ash fall, fire damage, gas poisoning, and earthquakes. Although incompletely documented, the major recorded events are as follows.

Ash fall and blast damage.—Ash fall and blast damage are known to have affected Sertung in 1930, 1934, 1935 (Docters van Leeuwen 1936, Dammerman 1948), 1952 (Fig. 6 and Borssum Waalkes 1954, 1960) and 1953 (G. A. De Neve 1953a, b, 1982, *personal communication* 1984, 1985). Dammerman (1948) recorded violent eruptions in July 1939 that totally buried the pioneer vegetation on Anak Krakatau, and there were eruptions during World War II of unknown effect on the other islands (Borssum Waalkes 1960). It is clear that R. Kecil received ash fall in the early years of activity, e.g., in 1932 (Dammerman 1948), and in 1952–

1953 (Hoogerwerf 1953, Borssum Waalkes 1960). There have undoubtedly been other occasions on which Sertung and R. Kecil have been affected by ash fall (see Sudrajat 1982), one of the most recent being a light fall on Sertung in 1981 (Simkin and Fiske 1983:359). Indeed, in 1982 Shinagawa et al. (1984) recorded five or six separate layers of post-1883 volcanic ash and scorias on both islands, including very recent deposits. Eruptions in 1961 are known to have produced andesitic lava flows as well as pyroclastic fallout (Bird and Rosengren 1984), and there were substantial eruptions in the early 1970s, unfortunately without direct observations of the impact on the other islands. The available evidence (observational and stratigraphic), however, is that Rakata has not been affected by significant ash fall from the new volcano. The prevailing winds tend to carry ash clouds away from Rakata and towards Sertung in the dry season and towards R. Kecil in the wet season (Dammerman 1948).

Gas damage.—Gases produced by Anak Krakatau may have significantly influenced the vegetation of Sertung in 1930 (Docters van Leeuwen 1936), and of both

Sertung and R. Kecil in 1952–1953 (Borssum Waalkes 1954, 1960), but Dammerman (1948) argued that the damage of the 1930s might have been the direct product of ash-fall (and rain-wash).

Earthquakes.—Landslides, and in particular, rock-fall down the north face of Rakata, have often been associated with earth tremors centered within the group. Several such events were witnessed in the early years of Anak Krakatau's activity (Stehn 1929, Docters van Leeuwen 1936) and were also observed in 1984.

HUMAN INFLUENCE

One of the most significant features of Krakatau in the present context is how little the islands have been affected by human disturbance. During the period 1916–1922, Rakata was inhabited by a small group employed by a Mr. Handl in pumice extraction. A garden was planted around their cottage on the southeast side, and several weed species were introduced en route from the landing stage. Most were lost soon after the concession was abandoned (below), and none has had a significant role in the vegetation communities of Rakata. In 1919, visiting scientists accidentally started a fire that burned a sizeable part of the west side of the island (Fig. 3). The vegetation of the area consisted predominantly of grass-steppe, which at the end of the dry monsoon formed a highly flammable mass. It was principally this material that burned, rather than the woody parts of trees and shrubs. According to Docters van Leeuwen (1936:193), "After but a few years not a single trace of the fire was discernable. . . ." That is not to say, however, that it had no medium-term effect on the vegetation composition (and successional direction) of the affected area. For example, *Ficus* spp. and *Macaranga tanarius* apparently survived the fire better than other tree species (Docters van Leeuwen 1936: 134). Nonetheless, it was his view that neither the fire nor the inhabitants had more than a temporary effect on vegetation development. Small-scale interference has continued on the island, although without the establishment of dwellings. In the early 1950s, a limited amount of shifting cultivation was reported, including an area of 500 × 50 m on the southeast side, which had been cleared for growing coconuts (Hoogerwerf 1953, Borssum Waalkes 1960).

Ernst (1908) speculated that a party of surveyors might have been responsible for planting coconut away from the beach on Sertung and for introducing *Carica papaya*. In 1951, a small garden was found on Sertung, but both the garden and an accompanying dwelling were destroyed in the 1952 eruptions of Anak Krakatau (Borssum Waalkes 1960). Between August 1896 and January 1897, a small topographical survey team was stationed on R. Kecil, and in the period 1928 to 1931, the Volcanological Service had an official observation post there (Dammerman 1948). A few weeds were found along the paths of the latter (Docters van Leeuwen 1936), but apparently none has survived. The Japanese

are reported to have had an observation post on R. Kecil in the early 1940s (undocumented) and pumice extraction is also reported from the island in 1951 (Borssum Waalkes 1960).

Although the islands have a protected status (Geno-laganni 1985), it is probable that intermittent small-scale interference continues at and near the coast at convenient landing points. These events constitute only short-term, localized disruptions to the vegetation. One way in which people may have provided a significant influence on plant community dynamics is by introducing certain animals, e.g., *Rattus* spp. to each island (Dammerman 1948) and possibly pigs to R. Kecil (Bush et al. 1986b), but their impact on the vegetation succession, if any, remains unknown.

PRE-1883 VEGETATION

Very little is known concerning the 1680–1883 Krakatau flora. Docters van Leeuwen (1936) listed six species known from the coastal vegetation. These were *Intsia amboinensis*, *Mucuna gigantea* (Leguminosae), *Dendrophloe pentandra* Miq., *Viscum articulatum* Burm. (Loranthaceae), *Dysoxylum arborescens* (Meliaceae) and *Dendrobium uncatum* Lindl. (Orchidaceae). In addition, carbonized remains of *Macaranga tanarius* (Baas 1982) have been identified from this period (Switsur 1982). Of these species, both Leguminosae plus *D. arborescens* and *M. tanarius* have all been found on the group since 1883.

HISTORY OF VEGETATION SUCCESSION ON RAKATA, SERTUNG, AND R. KECIL, 1883 TO 1953

Rakata

The first explorations of Rakata took place in October 1883 (when the summit was reached) and in May 1884. No plant life was detected on either occasion. By September 1884 a few sporadic blades of grass had appeared (Verbeek 1885), and in 1886 the pioneers of the new vegetation could be seen from the coast to the summit (Treub 1888), although the upper reaches were only examined through binoculars (Docters van Leeuwen 1936). Among the colonists were six species of blue-green algae, forming a gelatinous layer, suggested to have been important in improving conditions for the establishment of ferns which, at this early stage, almost exclusively covered the interior. Only a very few angiosperms were observed, most of which were restricted to the beach.

By 1897 the interior of Rakata was clothed in a dense savanna-type grassland, dominated by *Saccharum spontaneum* and *Imperata cylindrica*, interspersed with small clusters of trees. Ferns dominated only the higher regions and the balance of species had also greatly shifted in favor of the flowering plants. On the beaches a *Pes-caprae* formation (a typical tropical formation named after the creeper *Ipomoea pes-caprae*) was already prevalent, backed in many places by the first

signs of the coastal *Terminalia/Barringtonia* and *Casuarina* communities. By 1906, the vegetation had become further enriched (99 species of angiosperms) and the coastal vegetation had developed into discontinuous young woodland, incorporating a large proportion of *Casuarina equisetifolia*, with scattered *Barringtonia asiatica*, *Terminalia catappa*, *Calophyllum inophyllum*, and *Hibiscus tiliaceus* (Ernst 1908). During this period there developed among the lowland grasslands, patches of woodland containing *Ficus* spp., *Macaranga tanarius*, and other secondary forest species (Backer 1909). The shrub *Cyrtandra sulcata* was common within a particularly luxuriant patch of woodland, in a ravine between 300 and 400 m altitude. Above 400 m, the fern communities were slowly receding upwards and also contained a scattering of trees (Docters van Leeuwen 1936).

Over the period 1919 to 1934, a gradual change took place from savanna grassland and *Casuarina equisetifolia* woodland to a species-poor but mixed secondary forest. Since *C. equisetifolia* cannot regenerate under a closed canopy, the woodlands of the lowland regions rapidly developed into a mixed *Macaranga-Ficus* (especially *F. fulva*) forest, with, for example, *Pipturus argenteus*. Altitudinal differentiation was noted at an early stage of forest development, in 1921, when *Villebrunea rubescens* and *Neonauclea calycina* were found only above 300 m (Docters van Leeuwen 1921, 1936). Both are common in the upland forests of Java. Above this altitude, the trees remained rather more scattered, while *Cyrtandra sulcata* formed a thick, almost monospecific scrub from ≈ 360 m to the summit. The young trees observed among the *C. sulcata* included many bird- and bat-dispersed *Ficus* spp., commonly *F. ribes*, *F. lepicalpa*, and some already huge specimens of *F. pubinervis*. At this stage, the forest was still very poor in tree species; only 47 had been found, 20 of which were members of the coastal flora (Docters van Leeuwen 1923). While the composition of the coastal communities remained little changed throughout, the fern and grass savanna communities continued to decline throughout the 1920s and early 1930s, remaining only in small patches in the lowlands, on some upland ridges, and on the summit. By 1929 the region from 400 m altitude up to within 60 m of the summit (previously *Cyrtandra* scrub), had become forest consisting mainly of *Neonauclea calycina*. These developments were accompanied not only by the decline, and in some cases the loss of pioneer species, but also by the provision of new habitats and by a peak in species immigration (below, Whittaker and Flenley 1982). The epiphytic vegetation was greatly enriched from that previously described, and lianes, orchids, forest ferns, mosses, liverworts and lichens, all increased in number of species throughout this formative phase of forest development (Docters van Leeuwen 1923, 1929, 1936, Boedijn 1940).

By 1951, *Neonauclea calycina* had become the principal canopy tree from near the coast up to just below

the summit (Borssum Waalkes 1960). This is an interesting development, in that all other marked changes in community type involving an altitudinal progression have been of lowland forms spreading up the island. *Neonauclea calycina* mostly occurs in secondary forest. When full grown it reaches a height of 20 m, with a girth of 2 m and a rather dense crown (Borssum Waalkes 1960). The relatively sparse undergrowth of this forest was characterized by the shrubs *Leea sambucina* (in ravines) and *Leucosyke capitellata* (on ridges), with *Nephrolepis biserrata* also very common in the ground flora at lower altitudes. The 1951 *Neonauclea* forest displayed a gradation with altitude, similar to that emerging in the 1920s and 1930s. In coastal localities and up to 50 m altitude, *Terminalia catappa*, *Ficus fulva*, *F. fistulosa*, *F. hispida*, *Macaranga tanarius*, *Tarennia fragrans*, and *Melochia umbellata* were found. From 50 to 200 m, *N. calycina* was practically the only species in the tree layer. Other species of the zone included *Tectaria polymorpha*, *Ficus ampelas*, *F. annulata* and *Villebrunea rubescens*. Between 200 and 500 m, the forest included *Ficus variegata*, *F. retusa*, *F. gibbosa*, *F. quercifolia*, *F. pubinervis*, and *Parinarium corymbosum*. The ground flora (e.g., *Selaginella plana*) and the cover of epiphytic mosses and ferns (e.g., *Antrophyum reticulatum*, *Crepidomanes bipunctatum*) were also much denser than in preceding zones. The forest above ≈ 500 m was characterized by a thick moss layer, much stouter trees, and ferns such as *Asplenium nidus*, lending it the appearance of a montane rain forest.

The summit vegetation consisted of a dense shrub layer, scattered trees and some dense patches of *Saccharum spontaneum*. The early dominant shrub *Cyrtandra sulcata* had declined in importance, while *Schefflera polybotrya*, a species not previously recorded on the island, was found to have replaced it at the highest altitudes. Other species of this zone included *Leucosyke capitellata*, *Neonauclea calycina*, *Macaranga tanarius*, *Piper blumei*, *Blumea riparia*, *Aeschynanthus volubilis*, and *Medinilla speciosa*. The moss flora was very rich, covering ground and higher plants alike.

Sertung

The first description of the vegetation of Sertung was provided by Penzig (1902), who landed briefly in 1897. He found a small woodland of 5–6 m high *Casuarina equisetifolia* on the south point of the island. There was a beach vegetation of *Pes-caprae*, and some of the constituents of the present *Terminalia* forest, e.g., *Terminalia catappa* and *Pandanus tectorius*. Although unable to explore the interior, Penzig described the vegetation as consisting of closed stands of grasses, as found on Rakata. In 1906, patches of *Casuarina equisetifolia* were found on the east coast, between which were groups of trees and shrubs typical of the later *Terminalia* forest (Ernst 1908). Most of the interior was covered by savanna grassland similar to that of

Rakata, and containing ferns, Compositae, terrestrial orchids, and some scattered shrubs and trees, such as *Ficus fulva*, *F. septica*, *F. hirta*, and *Melastoma affine*.

By 1919 the hills of Sertung had become entirely covered by grass-steppe, within which were scattered trees. In the ravines, *Macaranga tanarius*-*Ficus fulva* forest was already the dominant cover type. The coastal *Pes-caprae* and *Terminalia* communities were well developed, especially on the level northern part of the island. Sertung lacked the upland communities of Rakata, but held a small area of mangrove in a lagoon, a habitat absent from Rakata. Apart from these habitat-based differences, vegetation succession continued to follow a similar course on both islands during the rest of the 1920s.

During the period 16 July to 7 August 1930, Sertung was affected by directional eruptions from Anak Krakatau (Fig. 3). The depth of ash deposited was not great in comparison with the 1883 covering (Docters van Leeuwen 1936), and the full impact of the eruptions was not immediately obvious. By March 1931, half the trees had died in some areas, and the most disturbed parts resembled "a European wood in winter." Much of the damage was suggested to have been caused by poisonous gases or some sort of acidic washout. At earlier stages of the emergence of Anak Krakatau, the northern coastal forest of Sertung was damaged by high waves associated with the eruptions of 1928 (Stehn 1929).

By 1931, a mixed forest, densely festooned with climbers, had replaced the earlier *Casuarina* woodland on the northern part of the island. In the northeast there were large marshy patches covered with *Ischaemum muticum* and *Hibiscus tiliaceus*, while the main saltwater lake still contained a small area of mangrove. Inland the damage was found to be greater (Fig. 3). The ravines were the most disrupted areas, a pattern attributed to landslides associated with earth-tremors and to windthrow (Stehn 1929, Docters van Leeuwen 1936). Some of the standing trees had begun to sprout again, and numerous seedlings had responded to the break in the canopy. High *Saccharum* covered much of the ground surface, probably largely from rhizomes that had persisted through the preceding period of shade. Those areas in the hills that had not been badly affected were almost completely covered with a *Macaranga tanarius*-*Ficus fulva* woodland, with only patches of grasses and ferns.

Subsequent eruptions in the 1930s also hit Sertung, although these events were not well documented. For example, in 1934, a visitor described the island as having a "wintry" aspect. Further damage occurred in 1935, and Stehn wrote that Sertung "... looked grey and disconsolate. Heavy showers of ash and sand have swept across it . . ." (reported in Docters van Leeuwen 1936). The damage was unlikely to be comparable with the devastation of 1883, but the effect on the vegetation was likely to have been compounded by the short in-

tervals between the events. It should be emphasized that the map reproduced in Fig. 3 was drawn in relation to the 1930 eruption, and that no such data exist with regard to these later and possibly more serious eruptions.

The next documented visit by a botanist was not made until 1951 when Borssum Waalkes (1960) spent 2 h collecting on the island. There followed a period of volcanic activity which culminated on 10-11 October 1952 with extensive damage to the forests of both Sertung and R. Kecil (Fig. 6). Estimates of the depth of ash-fall on Sertung vary from 0.5 m (Borssum Waalkes 1954, 1960), to a range of from 0.5 to >1.5 m by De Neve (1953a, b, *personal communication* 1984). De Neve reported an almost complete destruction of the foliage, while Borssum Waalkes described the island as looking as if a big fire had ravaged it, with only the trunks and the thickest branches of the trees remaining. This initial impression of devastation was moderated by a closer examination. *Casuarina* forest on the spit was found to be damaged, but apparently as a consequence of storm or wave action, rather than of ash-fall. On moving southwest along the beach, however, the physical damage to the vegetation was seen to have been tremendous, trees having been "broken like matchsticks." Most also looked scorched (Borssum Waalkes 1954). The coastal vegetation had been largely defoliated, but already many shrubs and small trees were sprouting from axillary buds. In addition, two species of the *Pes-caprae* formation (*Ischaemum muticum* and *Canavalia maritima*) had already reached the surface again, having grown through 15 cm of ash. The inland forest was also badly damaged, although the higher parts appeared to be becoming green again in places. Despite the extent of the damage, Borssum Waalkes (1960) concluded that the vegetation cover would have "recovered" within a couple of years, providing no other violent eruptions took place. That view does not, however, preclude the possibility of effects on the direction or rate of compositional changes. In fact, further disturbance did occur in September 1953 (Fig. 3 and De Neve 1953a, b, *personal communication* 1984), and has occurred subsequently, unfortunately without close documentation as to the ecological impact.

Rakata Kecil

In 1896-1897, a dense vegetation cover was described from the beach and parts of the interior of R. Kecil (Penzig 1902). A few groves of *Casuarina equisetifolia* were noted near the beach along with species of the *Pes-caprae* formation. The communities described were comparable with Rakata, although ferns appeared less important. Ernst (1908) noted that R. Kecil, with its steep coast, was almost without strand vegetation in 1906. Trees and shrubs were sparsely scattered among the grass savanna of the interior, but the vegetation appeared less advanced than on either of the other

islands. Backer (1909) collected from the beach flora in 1908, but no further details are available of the vegetation succession until Docters van Leeuwen's (1936) studies of 1928–1932. *Pes-caprae* and *Terminalia* woodland were well developed by 1928, but were restricted to the small areas of gently shelving beach. Mixed forest had developed in near-coastal areas, but the hills were mostly covered by grass-steppe, dominated by *Saccharum spontaneum* with *Imperata cylindrica*. Scattered trees, mainly *Macaranga tanarius* and *Ficus fulva*, were widespread within the grassland and provided the dominant community type in the ravines. Once underway, this stage of the succession proceeded very rapidly, and by 1932 the grass-steppe had mostly disappeared, except from a few ridges and recent landslide scars. As on Sertung, the inland forest remained poorer in species than the mixed near-coastal forest. *Timonius compressicaulis* was already common in the inland forest of R. Kecil, while the grasses had been replaced in the undergrowth by *Nephrolepis* sp.

After the 1952 eruption, Borssum Waalkes (1954, 1960) described damage similar to that observed on Sertung, although he did not actually land on R. Kecil. De Neve (*personal communication*) recorded that 0.7 m of fresh ash had fallen on the northern end of the island and that 90% of the vegetation of the island appeared scorched. Approaching the island from the west in November, Borssum Waalkes observed that some greenery was visible near the coast and to the south. Rounding the southern tip of the island, the east side (farthest from Anak Krakatau) was found to be much less damaged. Some trees (mainly in coastal areas) appeared completely unharmed. Eruptive activity affected R. Kecil again in 1953, although the damage appeared to be restricted to the southern part of the island (De Neve 1953a, b, *personal communication* 1984).

Succession 1883–1953 on Rakata,

Sertung and Rakata Kecil: concluding remarks

Until 1928, each island experienced similar vegetation successions, with the exceptions of the differing proportions of particular habitats noted. In particular, Sertung and R. Kecil are considerably lower than Rakata, and this may be one of the reasons that the 1920s *Neonauclea* forests of Rakata, which developed first in the uplands, were absent from the other islands. During the 1920s, many species that were bird or bat dispersed (e.g., *Ardisia humilis*, *Cyclea barbata*, *Dysoxylum gaudichaudianum*, and *Melia azedarach*) arrived on the group, as the habitat for these fauna became more suitable, constituting a mutually reinforcing effect (Hoogerwerf 1953). Docters van Leeuwen (1936) suggested that some differences between the three islands may have been related to the time of arrival of particular species to each island. In particular, *Timonius compressicaulis* was abundant in the interior of R. Kecil, but unimportant on the other islands. Thus, chance or

uneven distribution of favored points of landfall for the avifauna may have been leading to some inter-island differences. Variations in the rate of successional development were also evident. In particular, the vegetation of west and northeast Rakata, and of R. Kecil and Sertung, appears to have been discernibly slower to develop towards forest than in south and south-east Rakata (Docters van Leeuwen 1936:166). Moreover, by 1931, the destruction wrought on Sertung had, at least temporarily, introduced greater variation. Subsequent eruptive episodes, for example in 1952–1953, were known to have hit both Sertung and R. Kecil. These eruptive influences have almost certainly had a significant impact on the course of succession.

FIELD METHODS AND ANALYSIS OF 1979–1984 SURVEY DATA

Field methods

The major vegetation surveys in this period were in 1979 and 1983 by the Hull University expeditions (Flenley and Richards 1982, Bush et al. 1986a) and in 1982 by the Kagoshima University expeditions (Tagawa 1984). The vegetation analyses reported are based on the work of the Hull expeditions and additional observations by Bush in 1984, although all survey data are incorporated in the floral analyses.

The expeditions of 1979, 1983, and 1984 enumerated the vegetation communities of the main islands by means of quadrats in which tree cover was quantified and the diversity of the ground flora recorded. Two factors ultimately restricted plot size: time and terrain. Species–area curves indicated that plots as small as 400 m² provided an adequate local representation of the vegetation of Rakata (Whittaker 1982). Most vegetation plots were larger than this, the norm being 900 m², and the maximum 2500 m². The sample was stratified, with the aim of representing the full range of habitats within the group while minimizing sampling effort (Fig. 7). Plot locations were chosen on the criterion of suitable topographic conditions. Girth at breast height (gbh) was recorded by species, for each tree that exceeded 30 cm gbh. (Diameter at breast height can be obtained from girth by dividing by π .) In all, 67 species were recorded on this basis, from 19 plots on Rakata, 13 on Sertung, and 5 on R. Kecil (see Fig. 7 legend for plot sizes). Within each plot the composition and relative abundance of the ground flora, epiphytes, and climbers were also recorded. On Anak Krakatau, where the stands of consistent physiognomic type were small, and generally aligned parallel to the coast, the quadrat sizes were also smaller (250 m²). Percentage cover estimates were made for all species of higher plants (reported in Bush et al. 1986a).

General plant collecting was carried out by each expedition, with the aim of making as complete a survey of each island's flora as was practicable, given the difficult nature of the terrain. These data together with

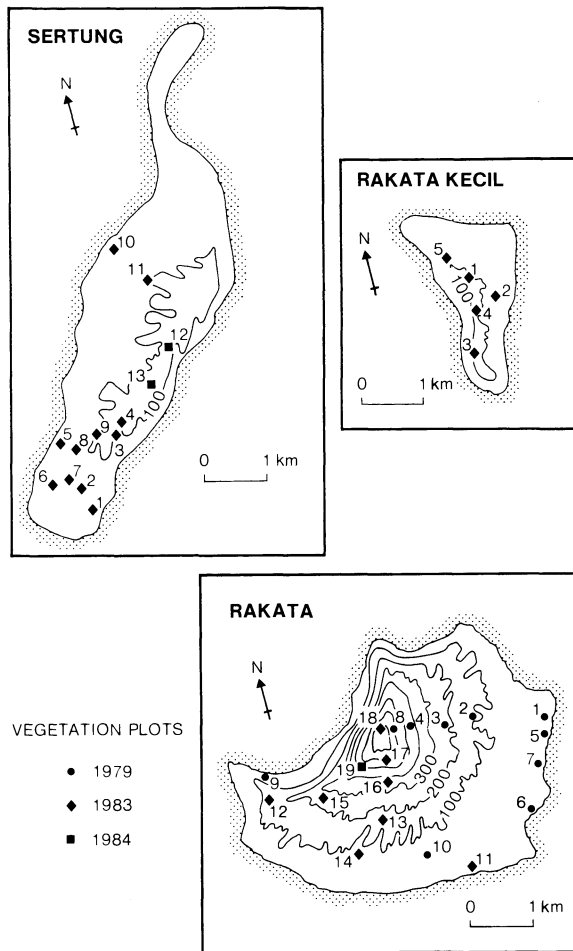


FIG. 7. Location of vegetation plots sampled in 1979, 1983, and 1984 on Rakata, Sertung and Rakata Kecil. Site altitudes (in metres) and areas (in square metres) are as follows: Rakata (1)10, 2500; (2)110, 1250; (3)260, 400; (4)420, 1250; (5):1 (i.e., beach-edge), 1250; (6)1, 1800; (7)1, 625; (8)670, 400; (9)1, 900; (10)40, 625; (11)15, 500; (12)150, 1600; (13)170, 400; (14)85, 625; (15)250, 1000; (16)400, 750; (17)530, 625; (18)730, 400; (19)500, 625; Sertung (1)5, 2500; (2)70, 400; (3)5, 540; (4)35, 500; (5)3, 500; (6)45, 400; (7)70, 600; (8)70, 450; (9)100, 900; (10)35, 900; (11)80, 900; (12)170, 900; (13)160, 900, R. Kecil (1)90, 900; (2)115, 750; (3)135, 1050; (4)125, 900; (5)90, 900.

the revised plant lists for all earlier surveys are recorded in Appendix I (Rakata, Sertung, and R. Kecil) and Appendix II (Anak Krakatau). Provisional identifications were made at the Herbarium Bogoriense. Duplicate specimens were sent to the Rijksherbarium, Leiden, and to Hull University (1979, 1983, and 1984 collections), and Kagoshima University (1982 collection).

Numerical analysis of the vegetation data

The tree girth data recorded in 1979, 1983, and 1984 were converted to cross-sectional area (i.e., basal area or "ba") and standardized by site (Jones 1986a). Analysis was performed by means of Detrended Corre-

spondence Analysis (DCA; Hill 1979a), and Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979b; see Fig. 8). Additional information on the composition of a selection of the sites is provided in Fig. 9. DCA is an eigenvector ordination analysis that produces results similar to principal components analysis, but which is more effective at displaying strong floristic gradients (Hill and Gauch 1980, Gauch 1982).

TWINSPAN is a polythetic, divisive classification technique (Hill 1979b). This form of classification uses a maximum of information and provides a hierarchy, i.e., relationships between groups are discerned (Gauch 1982). The technique operates on a semi-quantitative level, employing "pseudospecies cut-levels," which divide species into crude abundance scales. The optimal cut-levels and weightings are determined empirically and, in this case, the most intelligible results were obtained with pseudospecies cut-levels of 0, 2, 5, 10, 20, 40, and 70% ba and weightings of 1, 1, 1, 2, 2, 3, 4, respectively (Bush and Whittaker 1986). In practical terms this means that, for example, twice as much weight is attached to values of 10–39% ba than to values of <9.9% ba. Given the range of values in the data, these appeared to be sensible levels, utilizing a maximum of the information present in the data and attaching greater importance to the forest dominants than to the rare occurrences or understory species. The stopping rule used was that groups of less than five sites should not be subdivided any further. The pseudospecies preferentials at levels 6 and 7 (Hill 1979b) were utilized to annotate the hierarchy. Essentially they indicate species that accounted for ba in excess of 40%, and which were preferential to the sites on one side of a division. They thus provide an objective label for the forest types separated at each division. For further explanation of this technique, see Gauch (1982).

DESCRIPTION OF THE VEGETATION COMMUNITIES OF 1979–1984

Introduction: The TWINSPAN classification and DCA ordination—a framework for description

Hierarchical classification by TWINSPAN was utilized to provide an objective framework for the full description of the current vegetation communities of the three main islands (Fig. 8A). The first level of the classification distinguished between the *Neonauclea calycina*–*Ficus pubinervis* forests of inland Rakata and the forests of R. Kecil, Sertung, and coastal Rakata (*Timonius compressicaulis* present). Subsequent levels on the right of the analysis separated the inland forests of Rakata in a pattern generally related to the distributions of *Neonauclea calycina* and various *Ficus* spp. On the left side of the hierarchy, the second level of the analysis divided five of the seven coastal/near-coastal Rakata plots (*Terminalia catappa*, *Casuarina equisetifolia*, and *Barringtonia asiatica*-rich) from the

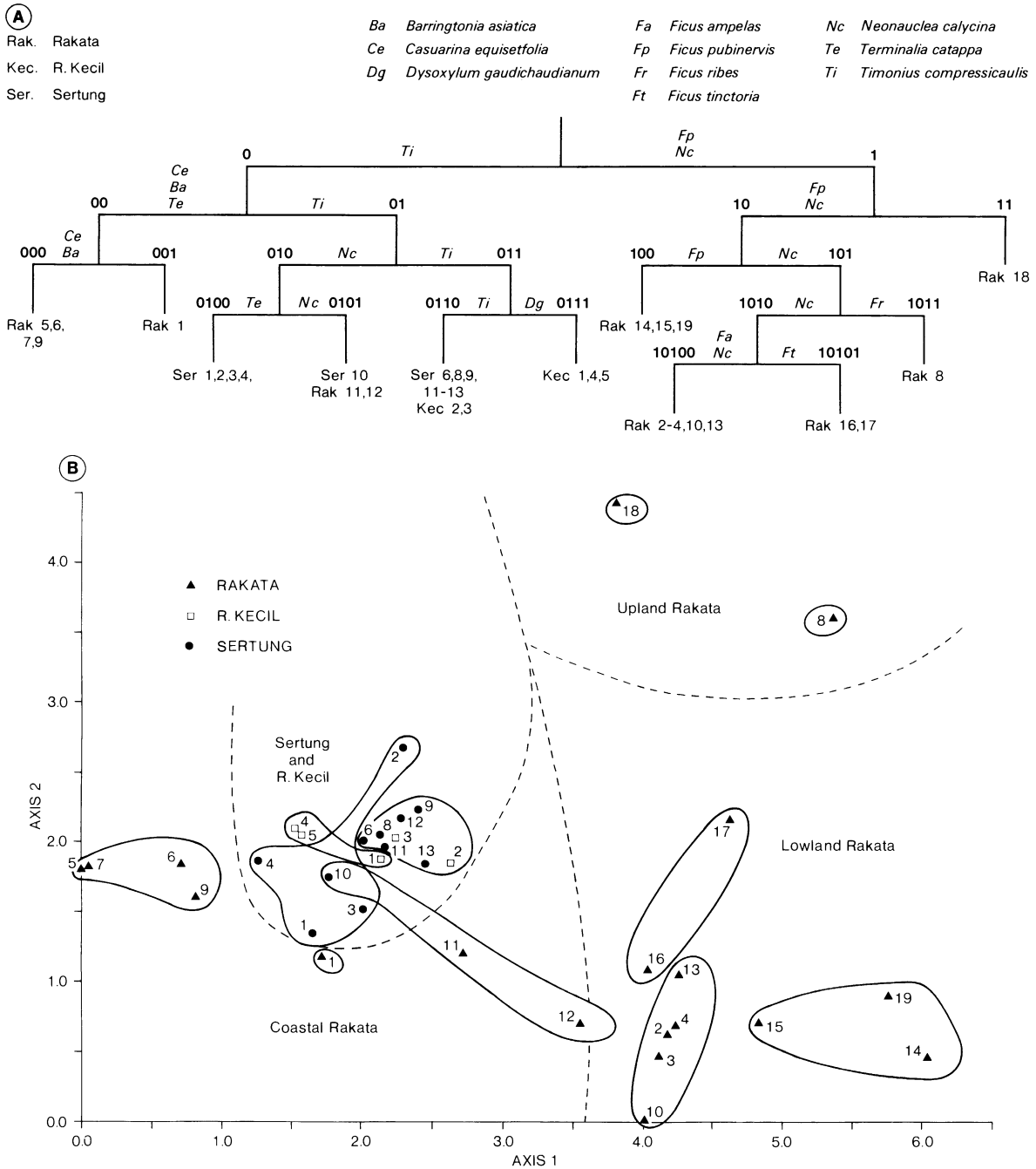


FIG. 8. (A) TWINSpan classification of the vegetation plots sampled in 1979–1984 on Rakata, Sertung, and R. Kecil. Basal area data standardized by site, of the arboreal component of >30 cm gbh. The hierarchy has been annotated with the strongest preferentials (6th and/or 7th cut-levels occurring on only one side of a division). Cut-levels 0, 2, 5, 10, 20, 40, and 70%, weightings 1, 1, 1, 2, 2, 3, and 4. After Bush and Whittaker 1986. (B) DCA axes 1 and 2 of the vegetation plots sampled in 1979–1984 on Rakata, Sertung, and R. Kecil, annotated with the TWINSpan groupings from Fig. 5A (solid lines). Axis units are average standard deviations of species turnover (Hill 1979a).

generally *Timonius compressicaulis*-rich Sertung and R. Kecil plots and the two remaining near-coastal Rakata plots. Within the latter group, further divisions appeared to distinguish between *Neonauclea calycina* (Rakata), *T. catappa*, *T. compressicaulis*, and *Dysoxy-*

lum gaudichaudianum-rich forest types (Sertung and R. Kecil).

One of the features of Detrended Correspondence Analysis (DCA) is that the ordination axes are scaled consistently (Hill 1979a); thus the axis units can be

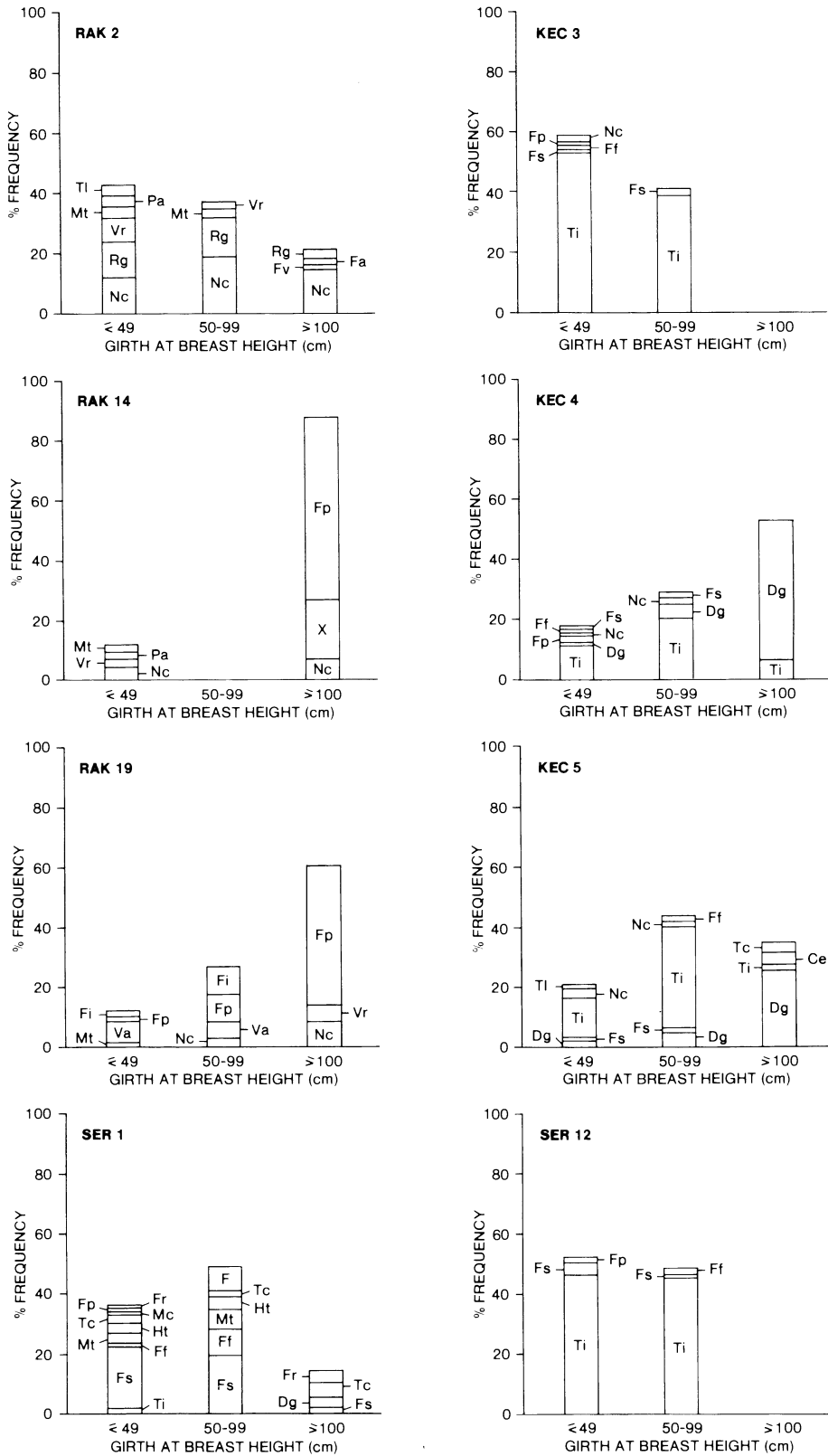


FIG. 9. Tree-size histograms for a selection of the vegetation plots sampled on Rakata, Sertung, and R. Kecil in 1979-1984. Species codes: Ce = *Casuarina equisetifolia*; Dg = *Dysoxylum gaudichaudianum*; F = *Ficus* sp.; Fa = *Ficus ampelas*; Ff = *Ficus fulva*; Fi = *Ficus ribes*; Fp = *Ficus pubinervis*; Fr = *Ficus retusa*; Fs = *Ficus septica*; Fv = *Ficus variegata*; Ht =

TABLE 1. Range of SD scores on DCA site axes, occupied by Rakata, Sertung and R. Kecil plots.* The values are standard deviations of species turnover at the individual sites (Hill 1979a), and provide an indication of the variability accounted for by the vegetation sampled on each island.

| Island | n | Axis 1 | | Axis 2 | | Axis 3 | | Axis 4 | |
|-----------|----|---------|------|---------|------|---------|------|---------|------|
| | | Range | Span | Range | Span | Range | Span | Range | Span |
| Rakata† | | | | | | | | | |
| Coastal | 5 | 0.0–1.7 | 1.72 | 1.2–1.8 | 0.64 | 0.0–1.6 | 1.55 | 0.0–1.1 | 1.12 |
| Inland | 14 | 2.7–6.0 | 3.33 | 0.0–4.5 | 4.49 | 0.9–1.8 | 0.99 | 0.3–2.2 | 1.89 |
| All | 19 | 0.0–6.0 | 6.04 | 0.0–4.5 | 4.49 | 0.0–1.8 | 1.84 | 0.0–2.2 | 2.15 |
| Sertung | 11 | 1.3–2.5 | 1.20 | 1.4–2.7 | 1.34 | 0.0–1.5 | 1.54 | 0.7–2.3 | 1.53 |
| R. Kecil | 5 | 1.5–2.6 | 1.12 | 1.8–2.1 | 0.34 | 1.5–2.7 | 1.20 | 0.8–1.2 | 0.40 |
| S and K‡ | 16 | 1.3–2.6 | 1.37 | 1.4–2.7 | 1.34 | 0.0–2.7 | 2.69 | 0.7–2.3 | 1.53 |
| All sites | 35 | | 6.04 | | 4.49 | | 2.70 | | 2.26 |

n = number of sites in each group.

† The location split for Rakata is sites 1, 5, 6, 7, 9 = coastal, sites 2–4, 8, 10–19 = inland.

‡ S and K = Sertung and R. Kecil combined.

* The eigenvalues for axes 1 to 4 are 0.832, 0.490, 0.313, 0.189, respectively. Axes 1 and 2 are displayed in Fig. 8B.

used as a measure of the amount of variation in vegetational composition accounted for by the sites from each island within each axis. The DCA ordination produced a first axis similar to the overall layout of plots in the TWINSpan analysis (Fig. 8B), with Rakata coastal and inland plots occupying the extremes of the axis, a span of 6.04 SD units in total (Table 1). The second axis split the inland Rakata forest group into upland stands at the positive extreme of the axis and lowland stands at the negative extreme. Neither axis accomplished any significant separation of the forests of Sertung and R. Kecil, leaving them as a compact, centrally located group. The third axis did not provide an unequivocal pattern, perhaps due to the fairly large proportion of zero entries in the data matrix, but at its extremes did appear to separate *Dysoxylum gaudichaudianum*-rich stands (Kec 1, 4, 5) from *Terminalia catappa*-rich stands (e.g., Rak 7, 9, and Ser 2, 4). Only on this axis do the Sertung and R. Kecil stands combined provide as much variation as the inland plots of Rakata, and even in this axis the five coastal Rakata plots contain greater variation than those of each when taken separately (Table 1). The fourth axis was not interpretable ecologically. These analyses clearly show that of the forests sampled from the three islands, by far the most varied were the Rakata stands, with Sertung intermediate and R. Kecil the least varied.

Rakata

The first level of the TWINSpan analysis and the first axis of the DCA separated the coastal and near-coastal sites of Rakata from the inland forests (Fig. 8).

Coastal vegetation communities.—Eroding coastlines along much of the Krakatau islands offer poor habitats for plant colonization. Trunks fallen from the

cliff above often litter the intertidal zone, e.g., on the southern shores of Rakata. The forest at the cliff edge may contain one or two light-demanding shrub and herb species (e.g., *Lantana camara* and *Eupatorium odoratum*), but often it is essentially a low-altitude secondary forest community that has been exposed by the cliff retreat (Bush 1986a).

In less extreme beach environments, coastal trees and shrubs, e.g., *Morinda citrifolia*, *Pandanus tectorius*, and *Premna corymbosa*, may establish on the cliff-top and even at the base of the cliff. These individuals seldom reach maturity before they are uprooted by further erosive action. The canopy of the lowland forest is broken at the cliff-edge, allowing the inland migration of the coastal fringe community. The latter remains a narrow belt as the outer edge is continually pared by the action of the sea. Rakata also has areas of gently shelving sandy beaches supporting *Pes-caprae* backed by stands of *Barringtonia asiatica* and other species of the coastal woodland fringe (Fig. 10).

1. *Pes-caprae formation.*—*Pes-caprae* formations are recorded from low-energy beach environments throughout the Indo-Pacific (Whitmore 1984). This formation of low-growing herbs and creepers commonly includes *Ipomoea pes-caprae*, *Canavalia maritima*, *Vigna marina*, *Spinifex littoreus*, and *Wedelia biflora*. Coastal erosion ensures the expanse of *Pes-caprae* on Rakata has never been great at any stage after 1883. Being a formation of herbs and creepers, it is not represented in the TWINSpan analysis.

2. *Terminalia forest (Barringtonia formation).*—The large fruits produced by *Barringtonia asiatica* are exclusively sea-dispersed (Docters van Leeuwen 1936); thus, unlike many other constituents of the coastal vegetation, *B. asiatica* is restricted to coastal sites. Al-

←
Hibiscus tiliaceus; Mc = *Morinda citrifolia*; Mt = *Macaranga tanarius*; Nc = *Neonauclea calycina*; Pa = *Pipturus argenteus*; Rg = *Radermachera glandulosa*; Tc = *Terminalia catappa*; Ti = *Timonius compressicaulis*; Tl = *Tetrastigma lanceolarium*; Va = *Vernonia arborea*; Vr = *Villebrunea rubescens*; X = Unknown.

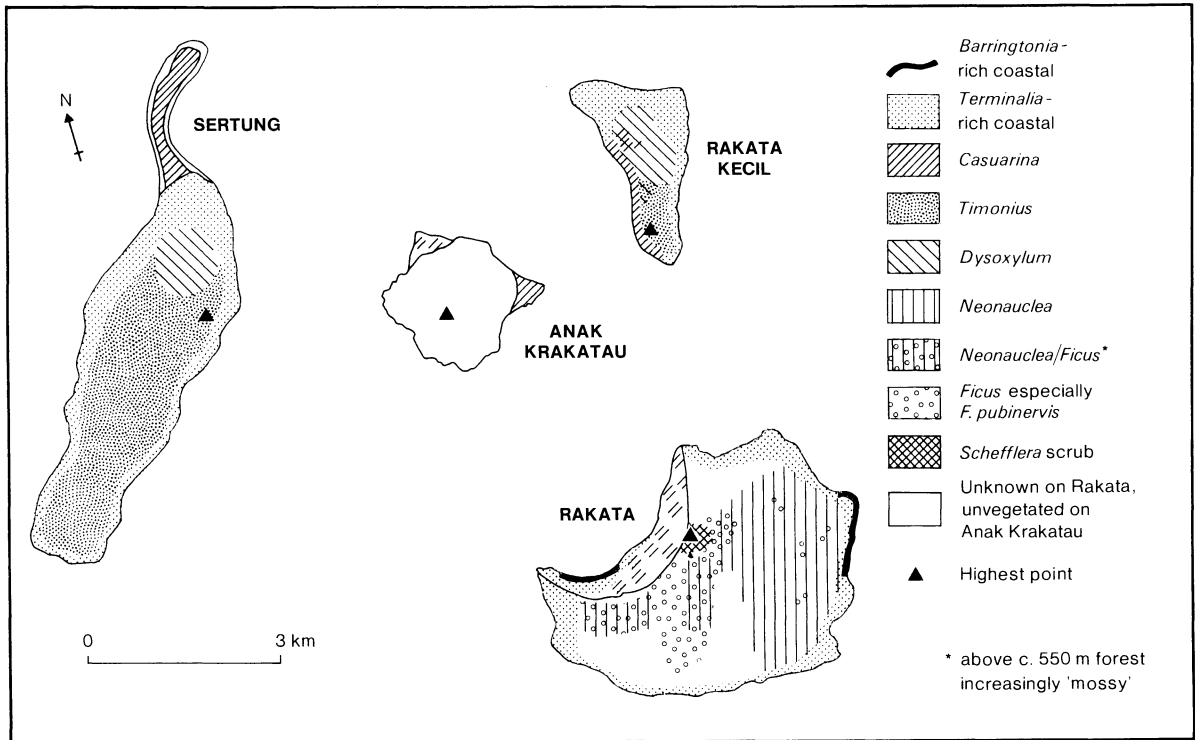


FIG. 10. Principal vegetation types of the Krakatau Islands. Generalized map derived from field survey between 1979 and 1984. Large areas of the islands were covered by communities dominated by single species, e.g., the lowland *Neonauclea* forest of southeast Rakata, and extensive areas of early regrowth *Timonius* forest on Sertung and R. Kecil. In parts, however, the canopy composition was less monotonous. Mostly transitions were not sharp edged, but rather gradations between forest types (e.g., between *Timonius* and *Terminalia* forests on much of Sertung). Exceptions appeared to relate to sharp boundaries in topography, or to recent environmental disturbances.

though "*Barringtonia* formation" is the classical name for the coastal communities, it is often not the dominant canopy tree. On Krakatau, as shown by the TWINSPAN results (Fig. 8), the canopy is dominated principally by *Terminalia catappa*. It is therefore fitting to call these communities "*Terminalia* forests" (cf. Tagawa et al. 1985).

Terminalia catappa is a common component of the Indo-Pacific strand flora (Whitmore 1984) but, although primarily sea-dispersed, the fruits may be spread locally by rats. Dispersal by rats probably explains this species' presence some 450 m inland at an altitude of 40 m (in Rak 10; Fig. 7). The seaward margin of *Terminalia* forest was often composed of a fringe of the thick, irregular trunks of *Barringtonia asiatica* that had been undercut by the sea (e.g., in Rak 5 and 7). Shrubs and small trees growing in this fringing forest included *Hibiscus tiliaceus*, *Pandanus tectorius*, and *Morinda citrifolia*, but immediately inland of this fringe *Terminalia catappa* was the dominant species. The canopy of these forests was formed by understory trees 9–11 m in height with the larger emergent species, e.g., *T. catappa* and *Erythrina orientalis*, rising to 13–15 m. On moving away from the fringe, there was a change

in the understory species, as predominantly coastal species were joined by species such as *Ficus fulva*, *F. septica*, and *Macaranga tanarius*. Other characteristic species were *Hernandia peltata*, *Calophyllum inophyllum*, *Desmodium umbellatum*, and, in the case of Rak 6, a stand of *Casuarina equisetifolia*, a remnant of the once abundant coastal distribution described by Docters van Leeuwen (1936).

In Rak 1 there were 17 species/800 m² compared with a maximum of 10 species in an equivalent area of the other coastal plots (Rak 5, 6, 7, and 9). Many of the additional species (e.g., *Neonauclea calycina*) are characteristic of the inland forest, indicating that this plot was located in the ecotone between the coastal and inland forests. This difference in floristic composition was reflected at the third level of the TWINSPAN analysis, where Rak 1 was separated from the *Barringtonia asiatica*- and *Casuarina equisetifolia*-dominated coastal sites (Fig. 8).

3. *Casuarina* forest.—*Casuarina equisetifolia* is a characteristic tree of disturbed or unstable habitats, and a pioneer in coastal habitats. Although once a major component of the pioneer vegetation on Rakata, by 1979 it was found to have become restricted to one

or two spots on the south coast (e.g., Rak 6), and to the precipitous north face of the island, where a normal forest cover could not establish.

Inland forests.—The coastal forest was found to grade into the inland forests, forming a continuum. This is exemplified by the positions of Rak 1, 11, and 12 (all near-coastal) in the DCA and TWINSpan analyses (Fig. 8A and B). Rak 11 was ≈ 50 m inland and Rak 12 was located on the promontory above Zwarte Hoek. Although a high proportion of the basal area (44 and 62% ba, respectively) was attributable to *Neonauclea calycina*, the presence of *Terminalia catappa* and *Timonius compressicaulis* in both sites was sufficient to place them on the left of the initial division of the TWINSpan analysis. The right side of the classification contained only inland Rakata sites, divided into four groups. The separation of the two highest plots, Rak 8 and 18, from each other is viewed as an artefact of the sampling, as the most abundant arboreal species in both was *Schefflera polybotrya*, which had too small a girth to be represented adequately in the data set. These two plots were sufficiently similar for us to override the structure suggested by TWINSpan and to treat these stands as belonging to one vegetation type. The remaining sites did not segregate in a clear altitudinal pattern but rather their placing was related to the abundances of *N. calycina*, *Ficus pubinervis*, and *F. tinctoria*.

1. *Neonauclea forest.*—*Neonauclea calycina* was found to be the dominant canopy tree over most of the interior of Rakata, from 40 to >550 m elevation (Fig. 10). Within this altitudinal range there are variations in the associated species very similar to those described in 1951–1952 by Borssum Waalkes (1960). Thus, *Vernonia arborea* was found mainly at higher altitudes, whereas *Pipturus argenteus* and *Macaranga tanarius* were recorded only in the low-altitude plots. In addition, there are variations within the forest that may be ascribed to topography; for example, the shrub *Cyrtandra sulcata* is particularly common in the ravines (Tagawa et al. 1984).

Within the plots of the *Neonauclea* forest (Rak 2, 3, 4, 10, and 13), *N. calycina* varied from 52 to 89% total ba, with individuals generally in the range 60 to 100 cm gbh (maximum 220 cm) (Bush and Whittaker 1986). This was a relatively open forest, with the canopy at 11–15 m and with distinct ground and shrub layers. In addition some large specimens of other species were found, e.g., *Ficus* spp. and *Timonius compressicaulis*. The understory of the *Neonauclea* forests included *Clidemia hirta*, *Leucosyke capitellata*, *Leea sambucina*, *Ardisia humilis*, and *Macaranga tanarius*. The creepers *Smilax zeylanica* and *Mussaenda frondosa* and ferns such as *Nephrolepis biserrata* and *Davallia denticulata* were common constituents of the ground flora, and the forests also included climbers such as *Tetrastigma lanceolarium*, *Flagellaria indica*, and various Asclepi-

daceae. With increasing altitude a gradual increase in the cover of moisture-loving epiphytes was observed, especially of bryophytes, although they did not achieve the dense cover found within the upland *Ficus* and *Schefflera* communities. Forster (1982) reported a similar altitudinal trend in bryophytes, which he attributed to the humidity gradient.

2. *Neonauclea/Ficus forest.*—The explorations of 1979–1984 revealed some patches within and above the *Neonauclea* forest, with a high *Ficus* spp. content in the canopy (Fig. 10). Where *Neonauclea calycina* (up to 134 cm gbh and 15 m tall) and *F. tinctoria* (up to 262 cm gbh and 16 m tall) shared the dominance of the canopy (Rak 16 and 17; 420 and 550 m altitude, respectively), the forest was generally composed of larger trees than in the *Neonauclea* forest, with the canopy at 12–14 m and emergents attaining heights of up to 18 m. Among the canopy trees was the largest specimen of *Timonius compressicaulis* (2.0 m gbh and 13 m tall) recorded from any site on the islands. In Rak 17, the canopy was merged with a dense understory so that there was a tangle of branches from the forest floor to ≈ 10 m. Emergents rose above this layer, e.g., a specimen of *Vernonia arborea* of 176 cm gbh and 17 m height. Understory species included *Medinilla* spp., *Leea sambucina* in Rak 16, and *Medinilla* spp., *Cyrtandra sulcata*, and *Schefflera polybotrya* in Rak 17. In this latter plot the growth of these shrubs was so dense that it was necessary to crawl on the forest floor. The branches of these shrubs carried an epiphytic flora, poorly developed at Rak 16, but more luxuriant at the higher Rak 17, and which included *Asplenium nidus*, *Dendrobium crumenatum*, *Pyrrosia* spp., and *Selaginella* spp. The ground flora contained *Smilax zeylanica*, *Costus speciosus*, *Davallia* spp., and *Nephrolepis* spp.

3. *Ficus forest.*—Rak 14, 15, and 19 comprise a group at the third level of the TWINSpan analysis, characterized by low scores for *Neonauclea calycina* and high scores for *Ficus pubinervis*. Rak 14 (70 m altitude) was particularly interesting, being dominated by a specimen of *F. pubinervis* (girth 495 cm, above the buttress) and an unidentified emergent (girth 300 cm, height 24 m) (Fig. 9 and 11). Of all the forests on the islands, this small patch had the openness and size of trees most closely approaching that of mature lowland forest. The understory included *Villebrunea rubescens*, *Pipturus argenteus*, *Macaranga tanarius*, with a ground flora of *Smilax zeylanica*, *Costus speciosus*, *Lygodium circinnatum*, and *Selaginella* sp. Rak 15 (400 m altitude) contained three principal canopy species, *F. pubinervis* (48%), *N. calycina* (35%), and *Timonius compressicaulis* (11%). Both plots Rak 15 and Rak 19 (520 m altitude) were located in areas of deeply dissected topography, with almost all trees growing on narrow ridges between steep-sided gullies. The canopy of Rak 19 was dominated by *F. pubinervis*, which accounted



FIG. 11. *Ficus pubinervis* forest on Rakata. A very large specimen of *F. pubinervis* (495 cm girth) recorded in Rak 14. Note person at lower right for scale (M. Bush 1984).

for 85% ba, largely due to one very large individual. Other sizeable trees included *N. calycina*, *Vernonia arborea*, *Villebrunea rubescens*, and other *Ficus* species (Fig. 9). The canopy formed at 8 m, with some specimens reaching 13–16 m. Understory and ground flora included *Medinilla speciosa*, *Cyrtandra sulcata*, *Cyclosorus* cf. *interruptus*, *Tectaria melanocaula*, *Piper blumei*, and *Begonia isoptera*.

The two highest vegetation plots, Rak 8 and 18 (670 and 730 m altitude) were located in the near permanently wet cloud forest. At these altitudes the covering of mosses was even more luxuriant than in Rak 17 (580 m), covering virtually all branches. The forest was low growing, with branching beginning at ground level. The shrubs *Schefflera polybotrya* and *Leucosyke capitellata* were the most abundant species in this layer. The dense growth of the multiple-trunked *S. polybotrya* characterized both these plots. Although this was by far the most common arboreal species present in the plots, the trunk girth seldom exceeded the minimum size criterion for data collection; consequently this species was seriously under-represented in the data set. The two plots are thus viewed as part of the same vegetation type, despite being separated within the TWINSpan hierarchy (Fig. 8A). Occasional *Ficus ribes* (in Rak 8), *Villebrunea rubescens*, and *Saurauia nu-*

diflora (in Rak 18) protruded above this low canopy. *Neonauclea calycina* was virtually absent from this forest (3 and 0% ba, respectively, in Rak 8 and 18) (Bush and Whittaker 1986). The low canopy produced a shaded and species-poor ground flora.

4. *Summit vegetation*.—Below the summit region, *Cyrtandra sulcata* remained an important but mainly understory component of the 1983 forest. Nearer the summit, *Schefflera polybotrya* provided most cover, with only a broken canopy of trees above. The summit ridge was covered by the pioneer grass *Saccharum spontaneum*, with *Eupatorium odoratum* and *Lantana camara*. The occurrence of “pioneer” species at the summit edge may be attributed to frequent disturbance events such as lightning strikes, rockfalls, and landslips.

Sertung

The vegetation plots recorded from Sertung and R. Kecil were placed between the extremes of Rakata’s coastal and inland forest types in the TWINSpan analysis and by the first two DCA axes (Fig. 8). They also contained less variation in vegetation composition than Rakata’s forests (Table 1). The inland forests of both Sertung and R. Kecil were predominantly made up of two communities absent from Rakata, dominated by *Dysoxylum gaudichaudianum* (formerly *D.*

amooroides) and *Timonius compressicaulis* (Figs. 9 and 10). A third, coastal-edge community, in which *Ficus fulva*, *F. septica*, and *Terminalia catappa* were co-dominants, was also without close parallel on Rakata. The *Neonauclea calycina*- and *Ficus pubinervis*-dominated forests of Rakata were absent from these islands (Tagawa et al. 1985, Bush and Whittaker 1986). The vegetation of these elongated, low-lying islands does not escape the coastal environmental influences to the degree reached on Rakata. This is reflected in Fig. 8, and in the occurrence of coastal species, e.g., *Calophyllum inophyllum*, in the interior.

Coastal and near-coastal communities.—The basic constituents of the coastal communities of Sertung were found to be similar to those described from Rakata, although the importance of particular species differed. Those Sertung plots placed in the coastal/near-coastal group at the third level of the TWINSpan hierarchy (Fig. 8) were Ser 1, 2, 3, 4, and 10. The foreshore plot, Ser 5, did not feature in these analyses, as it contained no trees > 30 cm gbh (Bush and Whittaker 1986).

1. *Pes-caprae formation.*—The best example of this formation was on the eastern, accreting side of the spit. It differs little from that described above (see also Partomihardjo 1985), with the exception of seedling *Casuarina equisetifolia* that were encroaching on the upper portions of the accreting beach. Elsewhere on Sertung, the lack of suitable beaches explains the absence or poor development of this vegetation type.

2. *Terminalia forest.*—In 1982–1984 *Barringtonia asiatica* was found on Sertung and R. Kecil only as isolated specimens in a few very sheltered locations; for instance, none was found on the spit of Sertung. These coastlines are dynamic and rapid erosion has led to the development of a forest type best described as near-coastal. This forest extends inland, with *Terminalia catappa* widespread and often dominant in the canopy. Most of the coastal species of Rakata were observed on Sertung within *T. catappa* forest. It was not until the third divisive level that the near-coastal plots (group 010 in Fig. 8A) were separated from the “inland” *Timonius compressicaulis* forest sites (e.g., see Ser 12 in Fig. 9). *Terminalia catappa* shared the dominance of near-coastal plots with *Ficus septica*, *F. fulva*, and *Timonius compressicaulis*. In addition, *Calophyllum inophyllum*, *Hernandia peltata*, *Pandanus tectorius*, *Hibiscus tiliaceus*, *Melastoma affine*, and *Leucosyke capitellata* were all abundant. Although most trees in this forest were 30–60 cm gbh, forming a canopy at 10–12 m, there were some larger individuals, e.g., specimens of *Ficus retusa* (202 cm gbh; 19 m tall) and *Dysoxylum gaudichaudianum* (194 cm gbh; 18 m tall) recorded in Ser 1 (Fig. 9 and Bush and Whittaker 1986). The ground layer was composed of *Nephrolepis biserrata*, *Stenochlaena palustris*, *Davallia denticulata*, *Tacca leontopetaloides*, and *Eupatorium odoratum*. There were generally few epiphytes, but the canopy of Ser 4 was festooned with the climber *Cayratia trifolia*.

At the northern end of the island, another near-coastal plot, Ser 10 (900 m² area, Fig. 7), dominated by *Terminalia catappa* and *Timonius compressicaulis*, provided a more diverse forest than that encountered at the southern end. It contained 33 species, compared with fewer than 20 in each of Ser 3 and 4 (both 900 m²) and Ser 1 (2500 m²). Ser 10 also included some species common in the north but absent from the south, e.g., *Gnetum gnemon* and *Oncosperma tigillarum*. The relatively low values for *Ficus fulva* and *F. septica* from this plot, and the dominance of *T. catappa*, were sufficient for it to be placed with the near-coastal forests of Rak 11 and 12 within the TWINSpan hierarchy (Fig. 8).

3. *Casuarina forest.*—*Casuarina equisetifolia* covered the length of the spit (Fig. 10) in a woodland of varying density. Where it cast a dense shade, the undergrowth was very sparse, but where the canopy was broken, a poor grassland and herb association dominated by *Ischaemum muticum* could be found. The trees were often festooned by the climber *Flagellaria indica*, and on the sheltered eastern side of the spit the edges of the woodland were bordered by *Caesalpinia bonduc* and *Pes-caprae*. This noticeable tree was elsewhere found only on a few steep slopes on the eastern side.

Inland forests.—Two main types of inland forest were found on Sertung, dominated respectively by *Dysoxylum gaudichaudianum* and *Timonius compressicaulis* (Fig. 10). This distinction was reflected in the fourth level of the TWINSpan analysis, by which R. Kecil plots 1, 4, 5 (rich in *D. gaudichaudianum*) were separated from sites rich in *T. compressicaulis* (Fig. 8A). The *D. gaudichaudianum* forests of Sertung, as described by Tagawa et al. (1985) in 1982, were found at the northern end of the island. In 1983–1984 (to avoid unnecessary duplication) inland forest plots were measured only in the south and middle of Sertung. These were all found subsequently to be of the *T. compressicaulis* type (group 0110) so that the *Dysoxylum* forests of Sertung were not represented in Fig. 8A (group 0111).

1. *Timonius forest.*—Only on R. Kecil and Sertung does *Timonius compressicaulis* constitute a community dominant. TWINSpan grouped Ser 6, 8, 9, and 11–13 as similar *T. compressicaulis* stands. Almost pure stands of young, apparently even-aged individuals covered substantial areas of inland Sertung, and along the central ridge and eastern flank there were large areas where it suddenly gave way to dense stands of the pioneer grass *Saccharum spontaneum*, e.g., in Ser 7 (Fig. 7). Ser 12 (900 m²) is an example of an almost monotypic stand; of the 120 trees enumerated, 112 were *Timonius compressicaulis* (Fig. 9). The trees of this woodland were remarkably uniform in size, forming a canopy at 10–12 m. The only other canopy species were *Ficus septica* and *F. fulva*. In the understory were a variety of shrubs and sapling trees, perhaps the most

important of which were the saplings of *Dysoxylum gaudichaudianum*. These were commonly 7 m tall with a girth of between 17 and 23 cm, and may be expected to overtop the *T. compressicaulis* canopy. Also present in the understory were *Ardisia humilis*, *Leucosyke capitellata*, *Macaranga tanarius*, *Melastoma affine*, and *Piper aduncum*. The ground flora was dominated by *Stenochlaena palustris* and *Nephrolepis* spp.

At Ser 13, *Saccharum spontaneum* grew in dense, almost impenetrable stands, with individual flower spikes reaching heights of 3 m. These openings were fringed by a greater diversity of trees and shrubs than found in the adjacent forest. Species recorded in these plots included *Ficus fulva*, *F. retusa*, *F. septica*, *Leucosyke capitellata*, *Morinda citrifolia*, and *Neonauclea calycina*. Ser 7 was not included in the TWINSPAN analysis, but included a large patch of *S. spontaneum*, among which grew saplings of <30 cm gbh. The charred stumps of trees larger than any found in the quadrat suggest that this area is in an early stage of regeneration following disturbance by fire. That sizeable areas of central Sertung bear this *Saccharum/Timonius* mix is indicative of recent and quite destructive disturbance over considerable areas of the island.

2. *Dysoxylum forest*.—Specimens collected in 1979 and 1983 and initially identified at Bogor as *Dysoxylum parasiticum* (*D. caulostachyum*) have subsequently been re-attributed to *D. gaudichaudianum* (*D. amooroides*) (*D. Mabberley personal communication* 1986), which was the first member of the genus observed, being found on R. Kecil in 1932. We consider it highly probable that the material collected in 1982 (Tagawa 1984, Tagawa et al. 1985), and also determined at Bogor, will be found to belong to this species, and have assumed this throughout.

The *Dysoxylum gaudichaudianum*-rich forest on Sertung, described by means of a quantitative survey in 1982 by Tagawa (1984, Tagawa et al. 1985), covered the main ridge and east-facing slopes, commencing ≈ 0.5 km south of the spit. This forest type extended 0.5 km farther south (Fig. 10) and was bounded to the west by a deeply incised gully. Individuals of *D. gaudichaudianum* in this forest achieved quite large sizes, ranging up to 25 m tall with a girth of 210 cm. Beneath the *D. gaudichaudianum* canopy, *Gnetum gnemon* was the most abundant tree, with an understory of *Ficus fulva*, *F. septica*, *Leucosyke capitellata*, *Macaranga tanarius*, and occasional *Timonius compressicaulis*. Tagawa et al. (1985) suggest that approaching the coast, *Terminalia catappa* was mixing as a co-dominant with *Dysoxylum*, in the manner of the *T. catappa* and *T. compressicaulis* mix described above. The ground flora of this forest was found to be denser than in the equivalent forest on R. Kecil, with a tangled growth of *Stenochlaena palustris* and *Nephrolepis hirsutula*.

Gnetum gnemon is commonly associated with people (its fruits are edible) and was planted in Handl's garden on Rakata (Docters van Leeuwen 1936). Lim-

ited cultivation was practiced on Sertung for a while prior to the 1952 eruption, and it is possible that it may have been introduced to the island at that time.

R. Kecil

Examination of the coastal vegetation of R. Kecil in 1983 revealed communities consistent with those of Sertung, and it was therefore felt unnecessary to quantify them. This explains their absence from Fig. 8. The true coastal communities are far less extensive than on either of the larger islands. Conversely, as was found on Sertung, the inland forests of this small, elongated island do not entirely escape the influences of coastal conditions. The plots enumerated on R. Kecil in 1983 were of two types, *Timonius* forest (group 0110 in Fig. 8A) and *Dysoxylum* forest (group 0111). The third DCA axis (not illustrated) may have been a reflection of a *Dysoxylum* to *Terminalia* axis, i.e., "inland" to "coastal" forests of R. Kecil and Sertung, but due to the peculiarities of sampling described, both extremes were not recorded from either island. Thus, whereas Ser 4 and 10 (*Terminalia*-rich) appeared at the negative end of the axis, Kec 1, 4, and 5 (*Dysoxylum*-rich) were placed at the positive end. This interpretation does indicate, albeit tentatively, a third important gradient of vegetational structure.

Coastal and near-coastal communities.—Most of R. Kecil is fringed by ash cliffs and lacks a well-developed beach vegetation, a situation that has changed little in the last 50 yr. Extensive growth of *Pes-caprae* seems to be restricted to the gently shelving northern beach. Behind this, a fringing forest included the common coastal elements *Terminalia catappa*, *Pandanus tectorius*, *Premna corymbosa*, and *Hibiscus tiliaceus*. *Barringtonia asiatica* was extremely scarce in the areas examined, although Soeriatmaadja et al. (1985) recorded it as common from an unspecified location on the island. They also recorded *Hernandia peltata*, as forming "consocieties," including *B. asiatica*, *T. catappa*, *Ficus fulva*, and *H. tiliaceus*, which are broadly consistent with the *Terminalia* forests of Rakata and Sertung, apart from the dominant role ascribed to *H. peltata*. This is of interest, as such a stand-type was not recorded in the 1982 or 1983 surveys, and the coastal fringe areas of the northern half of the island explored in 1983 bore *Terminalia catappa* forest similar to that described from Sertung.

1. *Casuarina stands*.—All three main islands of the Krakatau group are more precipitous on the side facing the interior of the prehistoric caldera. In the case of R. Kecil, the inward slope also faces the predominant wave direction. It is steep and rocky and remains clad in *Casuarina equisetifolia*. In addition, remnant stands of old trees were noted from within a mixed forest of *Timonius compressicaulis*, *Neonauclea calycina*, and *Dysoxylum gaudichaudianum* in the north of the island (Fig. 10).



FIG. 12. *Timonius compressicaulis* forest on R. Kecil. Note the even-age structure of this young forest (T. Richards 1983).

Inland forests.—The high scores of *Timonius compressicaulis* in the R. Kecil plots caused them to remain as a single group (011 in Fig. 8A) until the fourth level of the TWINSpan classification. The two subsequent groups were characterized respectively by high scores of *T. compressicaulis* (Kec 2, 3) and *Dysoxylum gaudichaudianum* (Kec 1, 4, 5).

1. *Timonius forest.*—The almost pure stands of *Timonius compressicaulis* on Sertung were matched on R. Kecil, where it was a dominant on high ground in the south (Fig. 12). This forest was represented by two very similar plots, Kec 2 and 3 (Fig. 7). In a 1225-m² plot at Kec 3, 153 of the 163 stems (constituting 93% of the basal area) were *T. compressicaulis* (Fig. 9). A forest of many small-stemmed trees (the largest was only 89 cm gbh, and the great majority were between 35 and 50 cm gbh), it had the smallest stature of all those described from the three islands (Bush and Whitaker 1986). It was clearly an immature forest at an early stage of development. The only species that broke the dominance of *T. compressicaulis* in the canopy were the invasive (and in these islands common coastal) figs *Ficus fulva* and *F. septica*. The understory was characterized by a greater variety of shrubs and sapling trees, e.g., *Ardisia humilis*, *Leucosyke capitellata*, *Ma-*

caranga tanarius, *Melastoma affine*, *Piper aduncum*, and perhaps the most important, *Dysoxylum gaudichaudianum*. The latter were commonly ≈ 7 m tall, with a girth of 17–23 cm, and were thriving beneath the *T. compressicaulis* canopy. The ground flora was dominated by *Stenochlaena palustris* and *Nephrolepis* spp.

The creeper *Elaeagnus latifolia* was also common in the *Timonius compressicaulis* forests of R. Kecil, providing a dense, thorny ground cover and also, in parts, matting the canopy. Interestingly, it is not common on Rakata and Sertung, where *Smilax zeylanica*, and to a lesser extent *Flagellaria indica*, respectively, appeared to fill similar niches.

2. *Dysoxylum forest.*—Three plots were located in *Dysoxylum gaudichaudianum* forest, Kec 1, 4, and 5, in the central and northern parts of the island, near the main ridge at altitudes of ≈ 100 m. They were separated from the other R. Kecil stands at the fourth TWINSpan level (Fig. 8A). The ba values for *D. gaudichaudianum* ranged from 22% in Kec 1 and 51% in Kec 5 to 76% in Kec 4. Kec 1 contained just two specimens of *D. gaudichaudianum*. Both were very large trees (162 and 254 cm gbh), and their presence accounts for the location of the plot within the TWINSpan

framework. Nevertheless, that stand was somewhat different from Kec 4 and 5, in that it was otherwise composed entirely of *Timonius compressicaulis* (54.3%) and *Neonauclea calycina* (12.6%). This plot may represent an intermediate stage between the *Timonius-Neonauclea*-dominated community described by Tagawa et al. (1985) and the *D. gaudichaudianum*-dominated forest of Kec 4 and 5.

Kec 4 and 5 had the highest total ba-to-quadrat-area ratios of the R. Kecil and Sertung plots (Bush and Whittaker 1986: Fig. 3.2), indicative of the greater stature of this forest type, which was comparable in this respect to the inland forests of Rakata. *Dysoxylum gaudichaudianum* achieved a dominance in the canopy, with *T. compressicaulis* the most important understory species (Fig. 9). Few *N. calycina* were recorded from these plots. In Kec 4, only 16 of the 58 trees measured in the 900-m² plot were *D. gaudichaudianum*, yet they accounted for 76% of the ba. This compares with 33 specimens of *T. compressicaulis*, constituting only 21 % of the ba. The ranges in girth of the two species differ in line with these figures, with many of the *D. gaudichaudianum* exceeding a gbh of 2.0 m, but the maximum gbh of *T. compressicaulis* only 101 cm. Similarly, *D. gaudichaudianum* achieved greater heights, mostly exceeding 20 m, with the tallest measured reaching 33 m. Beneath these specimens, *T. compressicaulis*, *Ficus montana*, and *F. tinctoria* formed a canopy at 10–12 m. This forest was relatively open in the understory, with saplings of *Buchanania arborescens*, *F. fulva*, *F. septica* and *Macaranga tanarius*, in addition to the common *T. compressicaulis* and *D. gaudichaudianum*. In total, 34 species of higher plants were recorded in Kec 4 (900 m²), including 10 pteridophytes, which made up most of the ground cover. In particular, *Stenochlaena palustris* was an important terrestrial component in all three *D. gaudichaudianum*-rich plots.

VEGETATION COMMUNITIES OF ANAK KRAKATAU, PAST AND PRESENT

Anak Krakatau IV appeared in the center of the prehistoric caldera on 12 August 1930. Seedlings of typical coastal species were described in 1932, but this vegetation was destroyed by eruptions later in 1932–1933, and in April 1934 only five species were found (Docters van Leeuwen 1936). Further eruptions in July 1939 totally buried the island's vegetation (Dammerman 1948, Borssum Waalkes 1960), but the next botanical observations were not made until June 1949, when a beach vegetation on the northern part of the island was examined. This consisted of young specimens of herbs and ligneous plants, such as *Barringtonia asiatica*, *Calophyllum inophyllum*, *Cyperus pennatus*, *Erythrina* sp., *Ipomoea pes-caprae*, *Pandanus tectorius*, and some 6 m high *Casuarina equisetifolia*. Further inland, some scattered clumps of *Saccharum spontaneum* were seen (Pijl 1949, Borssum Waalkes 1960).

In 1951, the vegetated area remained mostly limited to the flat strip behind the beach on the east and north sides of the island. The oldest part of this vegetation was sampled by Borssum Waalkes (1960) and found to be dominated by *Spinifex littoreus*, with *Ipomoea pes-caprae* and *Canavalia maritima*. Scattered bushes and clumps of *Saccharum spontaneum* occurred within this vegetation and the older *Casuarina equisetifolia* specimens were by then 10 m in height. There were other small patches of slightly differing composition, and on the slopes a vegetation of scattered tussocks of *S. spontaneum* persisted to an altitude of 25 m, and to 50 m in the erosion gullies. A species of moss and several small ferns (e.g., *Nephrolepis* sp.) were also found within these gullies. Between late August and 10 October 1952, eruptive activity covered this vegetation in several metres of black ash. Only the skeletons of the young *C. equisetifolia* trees rose above it, and Borssum Waalkes (1960) concluded that all life on the island may well have been killed. Vegetation development has subsequently been affected by volcanic action, for example in 1953, 1960–1961, 1972 and 1979–1982, but mostly without direct observation. The only recent botanical surveys have been in 1979, 1982, and 1983 (Barker and Richards 1982, 1986, Tagawa et al. 1985).

In 1979, the vegetated areas of Anak Krakatau amounted to a few small patches around the eastern coast and one large area covering the coastal foreland on the eastern side. Barker and Richards (1982) examined a transect extending from the beach into the interior. The first 25 m was covered in *Pes-caprae*, including species such as *Ipomoea pes-caprae*, *Cassytha filiformis*, and *Canavalia maritima*, and with some *Casuarina equisetifolia* seedlings. There were some young *Barringtonia asiatica* at the top of the beach, but *C. equisetifolia* dominated the next zone inland in almost pure stands. *C. equisetifolia* is a light-demanding species and in the more mature areas of woodland its seedlings were absent, although there were young specimens of, for example, *Terminalia catappa*, *Calophyllum inophyllum*, *Hibiscus tiliaceus*, and *Radermachera glandulosa*. The transect next crossed a (possibly disturbed) patch of open grassland dominated by *Ischaemum muticum*, in which some secondary forest species were found, e.g., *Dalbergia junghuhnii*, *Ficus fulva*, *F. septica*, *Morinda citrifolia*, and *Neonauclea calycina*. Inland, as the marine deposits gave way to volcanic deposits, the vegetation cover fell from nearly 100% to <5%, consisting of scattered *Saccharum spontaneum* and *C. equisetifolia* with some typical beach plants and, on the sides of the erosion gullies, *Eupatorium odoratum*, *Imperata cylindrica*, *Melastoma affine*, *Nephrolepis hirsutula*, and *Pogonatherum panicum* (Fig. 13). There appears to be a sharp physical and/or chemical boundary between the beach and the volcanic deposits on Anak Krakatau, such that a dense vegetation cover has never been recorded on the latter



FIG. 13. Pioneer vegetation in a gully on Anak Krakatau (T. Richards 1983).

(Fig. 14 and Barker and Richards 1986). From ≈ 130 m inland, the only vegetation consisted of scattered clumps of *S. spontaneum*.

By 1983, some diversification of the forested area was noted, with several new forest tree species, including *Timonius compressicaulis*. There had also been a visible increase in the area of closed *Casuarina equisetifolia* canopy (Barker and Richards 1986). Several lava flows dating from between 1963 and 1979 were examined by Tagawa (1984) in 1982 and were found to be mostly devoid of plant life. Nevertheless, where some volcanic ash had mixed with the 1973 lava flow, *Pityrogramma calomelanos*, *Nephrolepis* sp., *Im-*

perata cylindrica, *Saccharum spontaneum*, *Melastoma affine*, and *Ficus fulva* were found. A similar but younger vegetation, of the two ferns only, was reported from comparable areas of the 1975 lava flow.

DISCUSSION OF SUCCESSIONAL PATHWAYS, VEGETATION DYNAMICS AND ENVIRONMENTAL INTERACTIONS

Vegetation and environmental gradients

A clear gradient in arboreal communities with increasing altitude has been established for Rakata. This pattern was paralleled by a similar gradient in bryophyte communities, and by temperature, humidity,

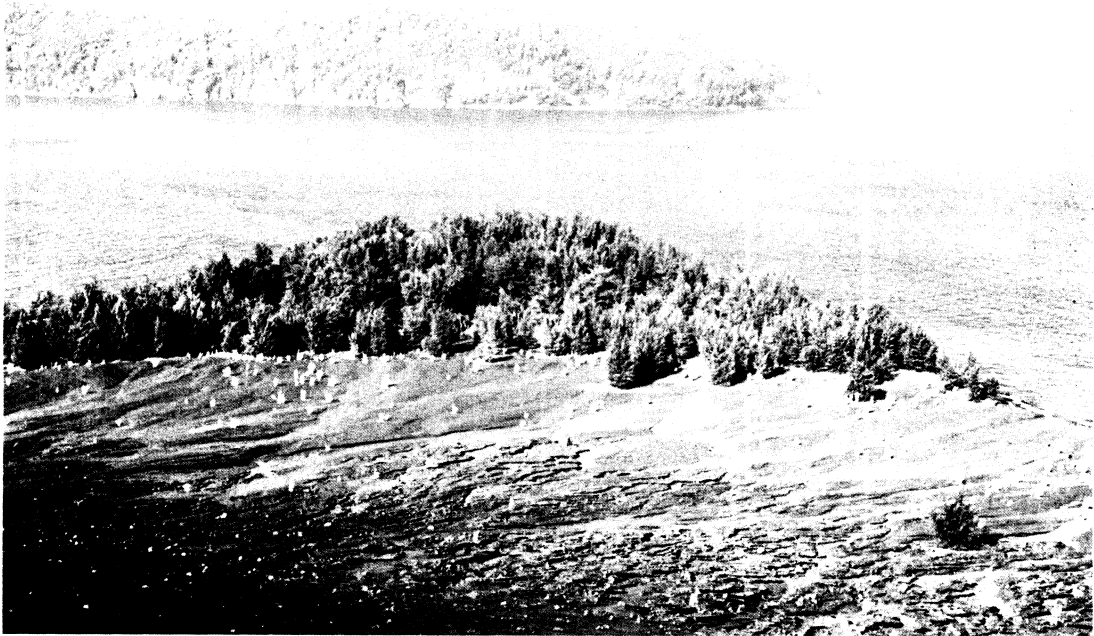


FIG. 14. The closed canopy of *Casuarina equisetifolia* forest on the south-eastern promontory of Anak Krakatau in 1983. This photograph represents the most advanced vegetation yet recorded on this active volcano. Note that the vegetated area is almost entirely restricted to the accreting coastal deposits, with only scattered clumps occurring inland. The island in the background is R. Kecil (N. Barker 1983).

and soil properties (Fig. 2 and Forster 1982, Newsome 1982, 1986). The epiphytic cover of the uplands was much more luxuriant and differed in composition from the lowlands (e.g., see Appendix III, Jones 1986b). The change in tree species composition was less dramatic than the alteration in structural appearance and epiphytic cover, although the sudden rise of *Schefflera polybotrya* as a dominant in the shrub layer was equally notable. The main structural features were the squat form of the trees and the merging of the ground, shrub, and tree layers. Newsome (1982, 1986) and Shinagawa et al. (1985) found no significant differences between the lowland and upland soils in the levels of K, Na, Al, Mg, Ca, P, and N. Despite an increased depth of humus in the mossy forest (12 cm compared with 0–3 cm in the lowland forests; Newsome 1982), Bush (1986a) concluded that edaphic factors were not the cause of stunting. Similar vegetation patterns on the coastal Mount Victory in Papua New Guinea were described by Taylor (1957) who reported an altitudinal contraction of zones, with a change to dwarfed montane (moss-covered) thicket at 900 m. The uppermost 100 m of Rakata is frequently shrouded in cloud, and the gradients described in vegetation and environment together suggest a transition to submontane or montane mossy forest at ≈ 550 –600 m, a much lower altitude than the norm. Taylor (1957) suggests 2000 m for the vegetational transition in the interior of Papua New Guinea, while Whitmore (1984) observes that

clouds normally form around tropical peaks in excess of 1200 m, but that this altitude limit is reduced on offshore islands. The cause of these effects is probably best ascribed to coastal (i.e., oceanic) contraction of certain environmental gradients. The plentiful atmospheric moisture, high humidity, and the cooling influence of the tropical seas result in the near permanent presence of cloud in the upper parts, further lowering temperatures. Wind conditions near the summit may also be important, especially with regard to the stunted appearance of trees.

The influence of geological variation on the vegetation of the islands has not emerged as significant, apart from its role in the differing initial colonization patterns described on Anak Krakatau (Tagawa et al. 1985, Barker and Richards 1986, Newsome 1986). These variations have more to do with the physical than with the chemical properties of the substrate, and indicate considerable differences in the rate of ecosystem development between scoria, ash, lava, and pumice substrates.

Vegetation dynamics and environmental dynamics

The islands of the Krakatau group provide a set of long-running tropical successions. These began as primary successions but now include various subseres or secondary successional elements. The detailed surveys of the 1979–1984 period enable an update of the de-

scriptive summary schema of Richards (1952), Whittaker et al. (1984), and Tagawa et al. (1985).

Successional schema.—Tagawa et al. (1985) proposed a summary scheme, relating to the entire island group, which incorporates the vegetation communities of Anak Krakatau as pioneer stages leading to mid-successional stages as found on the main islands in the early part of the century. It is argued here that Anak Krakatau is in several significant ways a poor analogue for the early successions on the other islands. The alternative schemata presented in Fig. 15 are intended principally as historical summaries. We have chosen to deal separately with the successions on Rakata, and on R. Kecil and Sertung, because of the markedly different course of post-1883 events. We have ignored, for these purposes, the impact of coastal erosion and deposition, which may lead to the lateral migration of vegetation communities and ecotones. It is perhaps paradoxical that the coastal succession is illustrated as the simplest and most quickly realized of all the islands' seres, whereas the coastal fringe is actually one of the more dynamic environments. Fig. 15 reflects the essential stability of the composition of the coastal communities. The characteristic taxa became established early and, despite the unstable nature of the coastlines, relatively few have become extinct.

Tagawa et al. (1985) have proposed that *Dysoxylum* forest is the most advanced community of the Krakatau islands, and that both *Timonius compressicaulis* and *Neonauclea calycina* forest will be dominated by *D. gaudichaudianum* in time. They suggest that the order and timing of arrival on each island of these three dominants can account for the broad differences in vegetation between the islands. In examining these hypotheses, three aspects are of particular importance: first, the spatial extent of sampling has now been extended, providing new data on each island; second, the status of the *Dysoxylum* forest may be less advanced than previously thought; and third, the role of ash-falls from Anak Krakatau may have differed significantly between islands.

1. *Successional pathways on Rakata.*—We have made a distinction between the lowland, near-coastal secondary forest of southeast Rakata, dominated by *Neonauclea calycina* and a much less extensive submontane secondary forest (*Ficus ribes*, etc.) near the peak (Fig. 15A). The gradation between lowland and upland forest was identified as early as the 1920s (Docters van Leeuwen 1929), as well as in the surveys of 1951 and 1979 (Whittaker 1982). While no sharp boundaries were evident in these surveys, an attempt has been made to show the approximate distributions of the main forest types in Fig. 10. Up to 1932 the western parts of Rakata, from which the *Ficus pubinervis*-rich forest was sampled in 1983, were apparently slower to develop a forest cover than the eastern (*N. calycina*-rich) areas (Docters van Leeuwen 1936). The post-1883 environmental histories of these areas do

not appear to have differed, apart perhaps from the 1919 fire, and the areas burned do not correspond to all areas supporting *Ficus*-rich stands (compare Fig. 3 and Fig. 10). Alternatively, there may be an environmental reason (e.g., aspect controlled climatic variation) for the slower forest closure and subsequent successional changes. Patchy seed dispersal of *F. pubinervis*, perhaps related to roost sites, may also be important and, whatever the cause, it is apparent that a number of different successional pathways are being followed on Rakata (Fig. 15A).

2. *Dysoxylum forest dominance?*—The proposed role of *Dysoxylum parasiticum* as the next forest dominant throughout the main islands (Tagawa et al. 1985) must be viewed in the light of its emended specific determination to *D. gaudichaudianum* (see Description of the Vegetation Communities of 1979–1984: Sertung: Inland Forests: *Dysoxylum* Forests, above). *D. parasiticum* is apparently a canopy component of mature forest (Kartawinata 1977, cf. Whitmore 1984), whereas *D. gaudichaudianum* is a widely dispersed, early or intermediate seral species (Mabberley, *personal communication*). With the possible exception of *Planchonella duclitan*, this re-identification removes the only "primary forest" tree (cf. Whittaker et al. 1984) from the floral list of Krakatau (T. C. Whitmore, *personal communication*).

Despite the success of *Dysoxylum gaudichaudianum* on Sertung and R. Kecil, it is still a comparatively rare tree on Rakata, where it appeared to be principally near-coastal in its distribution. Even as a seedling it was only recorded from Rak 1, 9, 10, 11, 12 and 15. Of these only Rak 15 (250 m) was at an altitude > 40 m. This site lay close to the northwestern bluff of Rakata, and was therefore more exposed to coastal influences than a site of corresponding altitude on the eastern side of the island. The only sites where *D. gaudichaudianum* was recorded as being larger than a sapling were Rak 1 (2.7% ba), Rak 10 (0.3% ba), and Rak 11 (1.1% ba). There seems little evidence to suggest that *D. gaudichaudianum* is in the process of invading the higher altitude or *Ficus*-rich forests of Rakata.

3. *Sequence of arrival of forest dominants.*—Part of the reason for suggesting that *Dysoxylum*-dominated forest would be a natural successor to the existing forests of Rakata was the inferred pattern of succession on R. Kecil and Sertung and the sequence of arrival of potentially dominant species on each island (Tagawa et al. 1985). In support of this view, *Neonauclea calycina* was first recorded on Rakata in 1905, the only island on which it is widespread as a forest dominant, but was not found on Sertung until 1920, nor on R. Kecil until 1929 (Appendix I). *Timonius compressicaulis* was first found in 1929 in a single gully on Rakata, and in the same year on R. Kecil, where it was noted to be already common in the interior (Docters van Leeuwen 1936). Nevertheless, it is improbable that these differences in the timing of initial establishment

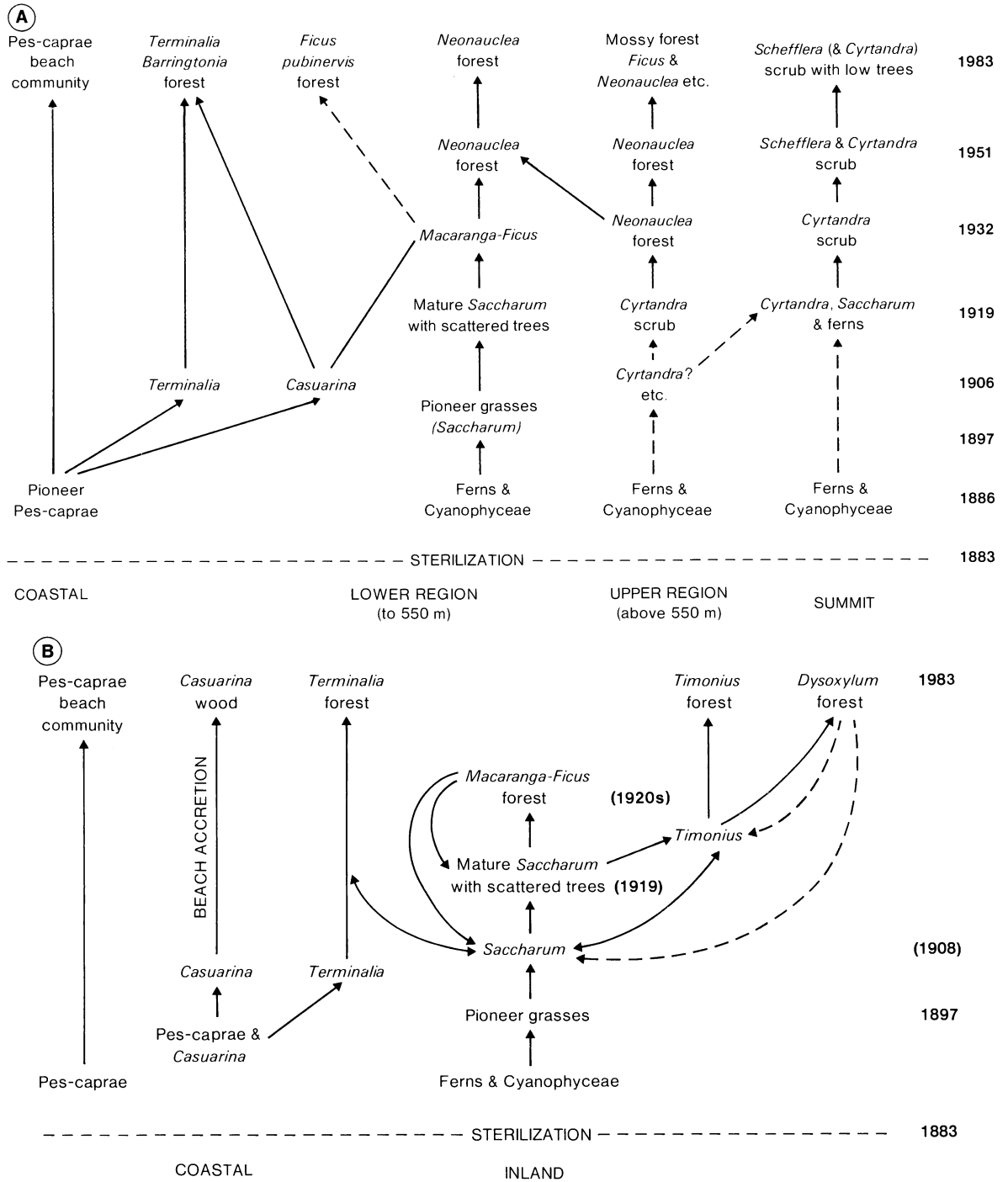


FIG. 15. Principal successional pathways on (A) Rakata and (B) Sertung and R. Kecil. (A) Rakata has experienced 100 yr of ecosystem development, apparently uninterrupted by the volcanic disturbance that has hit the other islands. In 1979–1983 the inland forests consisted of a mosaic of stands in which *Neonauclea calycina*, *Ficus pubinervis*, and *F. tinctoria* were dominant, either singly or in varying combinations, with a transition to a submontane mossy forest (*F. ribes*, *Saurauia nudiflora*, *Villebrunea rubescens*) at about 550–600 m altitude. Adapted from Whittaker et al. 1984. (B) Eruptive activity of Anak Krakatau has interrupted forest development on Sertung and R. Kecil on several occasions since 1930. The more severe events caused a return to open grassland communities dominated by *Saccharum spontaneum* (as indicated by downward pointing arrows). It is postulated that such disturbance induced a deflection from the *Macaranga-Ficus* pathway, to *Timonius* followed by *Dysoxylum* forest types, although damage has presumably not been completely evenly spread (see Fig. 3). Dates indicate the time at which vegetation types were first recorded.

are wholly responsible for the absence of *N. calycina* forest on R. Kecil, and of *T. compressicaulis* forest on Rakata. Rather the available evidence (small stature of much of the *T. compressicaulis* forest, etc.) supports a disturbance-related explanation for the presence of the *T. compressicaulis* forest (as Fig. 15B). This applies not only to R. Kecil, but also to Sertung, on which it was first recorded as late as 1982. In the case of *D. gaudichaudianum*, the recorded order of arrival within the group is clearly unrelated to the distribution of forests it dominates, as it is dominant on R. Kecil and Sertung, but not on Rakata, and the order of "arrival" was R. Kecil 1932, Rakata 1979, and Sertung 1982.

Critical to this debate is that survey intervals, extents, and efficiencies have varied greatly among the islands (Table 2 and Whittaker and Richards 1986). For example, with regard to the arrival times of *N. calycina* (above), between 1897 and 1929 collecting was undertaken on R. Kecil on only two separate days. Thus, dates on which particular species have first been recorded on each island cannot be assumed to mirror accurately the order of their arrival. The unequivocal evidence can be summarized as follows: *T. compressicaulis* was established in substantial numbers on R. Kecil earlier than on Rakata; *N. calycina* was well established on Rakata by the time *T. compressicaulis* was first found on that island; and *Dysoxylum gaudichaudianum* was the last found on all three islands (Appendix I). These observations thus do not provide unequivocal support for an explanation for inter-island differences based on arrival times of the three dominants.

4. *Importance of continued volcanism.*—The distribution of these forest dominants may also be explained by different autecological requirements. Tagawa et al. (1985) reported that *Dysoxylum gaudichaudianum* occupied predominantly flat areas, east-facing slopes and ravines, which were sites of a relatively high soil moisture content. *Timonius compressicaulis* forest was reported to occupy relatively drier sites on west- and north-facing slopes. In our survey in 1983 and 1984, however, extensive areas along the spines of Sertung and R. Kecil were recorded as supporting a virtually monospecific canopy of *T. compressicaulis* forest, in which *D. gaudichaudianum* were present as understory saplings. The slightly moister soils reported by Tagawa et al. (1985) from beneath the *D. gaudichaudianum* forest may well reflect an increased soil maturity, perhaps the result of a longer period of uninterrupted forest development and pedogenesis, than below the *T. compressicaulis* forest. In short, the patchy distribution of *D. gaudichaudianum* as a mature forest dominant, combined with its widespread occurrence as a sapling, would be more consistent with a response to past environmental events (cf. Shinagawa et al. 1984), rather than to time-independent edaphic limitations. On several occasions (e.g., 1930, 1932, 1934, 1935, 1952, 1953) since the 1883 "sterilization," Anak Krakatau

has caused the partial destruction of areas of forest on both Sertung and R. Kecil, but apparently not on Rakata (see Physical Environment: Volcanic and Tectonic Activity since 1883, above; Fig. 3). Parts of both islands have received a significant fall of ash on five or six separate occasions (Shinagawa et al. 1984). It is suggested here that volcanism is the key factor in understanding the present distribution of *Dysoxylum gaudichaudianum* and *Timonius compressicaulis* forest on Sertung and R. Kecil, and that *T. compressicaulis* has acted as a "nursery crop," modifying the environment and enabling the establishment of the later successional *D. gaudichaudianum* (Fig. 15B).

5. *Successional deflection.*—The damage caused to the vegetation of Sertung and R. Kecil by the eruptions of Anak Krakatau has been varied. Docters van Leeuwen (1936) and Borssum Waalkes (1960) regarded the damage they observed as not comparable to the sterilization of 1883. Both considered that "recovery" would only take a few years, providing no further disturbance took place, although in fact further damage did occur shortly after both visits. The potential of this environment to support the recovery of a vegetative cover following disturbance should not be underestimated. For instance, Docters van Leeuwen (1936) described a stand of *Casuarina equisetifolia* trees ≈ 1 yr old and 3 m tall, which developed in 4 yr into a woodland with trees > 20 m tall. Similarly, in July 1924, 5–6 m high *Macaranga tanarius* were found in an area that had been cleared for a campsite in January 1922. Yet if the null hypothesis that volcanic activity has not caused mid- or long-term alteration to vegetation development were to stand, why should the forests of Sertung and R. Kecil not have reached a stature equivalent to those of Rakata? Although some stands in the *Dysoxylum gaudichaudianum*-dominated parts contain some large trees, none is as massive as those recorded from the southern side of Rakata. Moreover, *Timonius compressicaulis* specimens of 200 cm gbh were recorded from Rakata, while the largest recorded from the surveys of Sertung and R. Kecil was only 120 cm gbh. There was also a marked difference in the stature of this species between differing patches of forest on R. Kecil and Sertung. In the near-monotypic *T. compressicaulis* forest of Kec 3, the largest trunk was 89 cm gbh, and only 4 out of 143 specimens were of > 70 cm gbh. Similar data were recorded from Sertung plots Ser 12 and 13. In contrast, the *D. gaudichaudianum* forest, as exemplified by Kec 4, contained fewer individuals of *T. compressicaulis*, but 30% were > 70 cm gbh, with a maximum of 120 cm gbh. These patches must represent populations of differing ages. The stature of some of the *T. compressicaulis* patches described would suggest that it may have seeded in as late as the early 1970s. It is ideally suited to the rapid invasion of bare ground, its seeds are bird dispersed, it grows rapidly, and can flower when only 1 m tall (Corner 1952). The presence of patches of *Saccharum spon-*

taneum within some parts of the *T. compressicaulis* forest (e.g., Ser 7), in which young seedlings of *T. compressicaulis* were observed, suggests that disruption is still taking place, and that the *S. spontaneum* patches represent the first stages of recovery. This model is supported by soils data that reveal several new starts to pedogenesis (Shinagawa et al. 1984). Moreover, in some areas at least, the "disturbance" horizons were very recent (cf. Simkin and Fiske 1983:359).

The presence of stands of *D. gaudichaudianum* may also relate to volcanic disturbance. It is a relatively recent arrival on the islands, is capable of rapid growth in the right circumstances, is characteristic of disturbed sites, and certainly was not an important constituent of the forests prior to the eruptions of the 1930s. We suggest that the disruption of the forest communities of Sertung and R. Kecil enabled a more rapid spread of this species. Furthermore, the well-defined edge to the present *D. gaudichaudianum* forests suggests that they may be the remnants of a more extensive forest, which was destroyed by one or other of the eruptive episodes. Instead of Sertung and R. Kecil having the ecologically most mature forests of the islands (Tagawa et al. 1985), they have, compared to Rakata, very young forests.

The importance of variations in seed availability should not, however, be dismissed; the current dominants have only achieved that status by having a sufficient seed supply and transport to enable invasion when the opportunity became available. In addition to the species discussed, there have clearly been many others that have shown uneven patterns of arrival both between and within islands (Docters van Leeuwen 1936). For example, *Ficus pubinervis*, now a "dominant" in areas on Rakata, appears to owe its position to chance early arrival by bird/bat transport in that area. Similarly, there was a patch of forest in northern Sertung (Ser 10 and 11), in which the otherwise uncommon *Gnetum gnemon* was the principal understory species. This species may well owe its distribution to introduction by humans. The forest creeper *Smilax zeylanica*, a late arrival but now common on Rakata, has not been recorded on Sertung or R. Kecil (Appendix I). On Sertung, *Cayratia trifolia*, *Flagellaria indica*, and *Hoya diversifolia* fill a similar role to *S. zeylanica*. In the case of R. Kecil, another late arrival, *Elaeagnus latifolia*, achieves an importance it lacks on the other islands, and in places (e.g., Kec 3) can be so abundant as almost to obscure the foliage of the trees.

Although the extent of ash-fall and forest damage has been incompletely documented, different-aged forests occurring in well-defined areas of the island indicate a clear causal link between volcanic events and the current patterns of vegetation type. Further corroborative data emerge from analyses of the floral data, in which the overall richnesses of the R. Kecil and Sertung assemblages do not appear to have increased since the 1920s, in contrast to the pattern for Rakata,

which has continued to rise (Non-cumulative species totals, below). The disturbances have clearly varied in intensity, distribution, and interval, but their combined impact has been not only to slow the progression towards richer mature forest, but also to deflect the main successional pathways of the communities of the interior (Fig. 8B).

The stature attained by *Dysoxylum gaudichaudianum* on Sertung and R. Kecil suggests that this species may become an important component in the near-coastal forest of Rakata. However, as there is no sign of this tree spreading in the forests at higher altitudes, or among the *Ficus pubinervis* and *F. tinctoria* forests, it would be rash to assume that it is the natural successor as the forest dominant over the greater part of Rakata. Rather it is anticipated that it will contribute to an increased forest diversification and that the period of large areas of monotonous forest numerically dominated by single species may give way to a more patchy mosaic.

Comparison of the early successions on old and new Krakatau islands.—It has been proposed that Anak Krakatau provides an analogue for the post-1883 period on the main islands, which might fill gaps in the early years of study, in particular of the fauna (Dammerman 1948, Thornton 1984). It is our contention, however, that there are such major environmental and ecological differences that the new island offers only a poor representation of the early habitats on the other islands.

The importance of ferns in the earliest stages of the succession on Rakata was such that 11 of the 24 species of higher plants found by Treub in 1886 were pteridophytes. More important, they were responsible for the majority of the vegetation cover of the interior. The "soil surface" was principally of little-altered ash, and the ferns and the few other plants of the interior were species typical of minimally developed soils and exposed localities (Appendix I, Docters van Leeuwen 1936). In contrast, only six species of ferns have been recorded from Anak Krakatau (Appendix II), and they have never been an important constituent of the vegetation cover. One of the critical factors differentiating the immediate post-1883 successions of the main islands and the post-1930 succession of Anak Krakatau is the presence of nearby sources of propagules and some of the animal agents of their dispersal. Thus the rain of propagules reaching Anak Krakatau is likely to differ both qualitatively and quantitatively from the post-1883 period. Nearly all of the species found on Anak Krakatau are known elsewhere in the group (below, Appendices I and II). A further major difference is the volcanic activity of Anak Krakatau. It has been both regularly noxious and spasmodically violent, and has caused repeated disruption of the developing vegetation cover, on occasions, such as in 1952, amounting to the virtual elimination of the vegetation (Borssum Waalkes 1960). This history of disruption, in which no

fixed starting date can be identified, contrasts with the quiescent period between 1883 and 1927, the early years of ecosystem development on Rakata, Sertung, and R. Kecil.

Active gas vents were seen in 1984 near the crest of the outer ridge of the volcano, and in view of the extremely slow upslope spread of vegetation, gas release could be one of the factors inhibiting vegetation development. Pyroclastic fallout was also observed over large parts of the interior in 1979. Perhaps a key factor, however, in the remarkably poor colonization away from the spit is the nature of the soil material, in particular the structure of the surface (Newsome 1986). Borssum Waalkes (1960) suggested that the hard ash of Anak Krakatau in 1951–1952 would be relatively impermeable to water and to penetration by the roots of seedlings, while the indurated crust observed on the surface of the outer cone in 1979–1983 contrasts with the friable ash cover recorded post-1883 by Verbeek (1885) and Treub (1888). Mineralogical differences between the 1883 ashes and those from Anak Krakatau (Shinagawa et al. 1984) are of unknown importance.

The two cusped forelands where the vast majority of the island's vegetation and resident fauna occur are principally marine deposits, and are therefore atypical of the rest of the island and of the majority of the Krakatau island group. The very slow spread of vegetation inland from these marine deposits, because of substrate and/or disturbance, has no parallel in either the post-1883 period, nor the more recent events on Sertung and R. Kecil. For these reasons, it is considered inappropriate to promote Anak Krakatau as an analogue for the early post-1883 period, and attempts to incorporate the two together in successional schema may be misleading.

THE DEVELOPING FLORAS OF KRAKATAU

Introduction

There is a long tradition of ecological and biogeographical interest in island biotas, much of it concerned with the nature and stability of island assemblages (e.g., see Gorman 1979, Williamson 1981). Krakatau provides a "natural experiment" of known starting point in the colonization of insular areas by both plants and animals. The early plant and bird data for the group as a whole were examined by MacArthur and Wilson (1967) in the context of their "Equilibrium Theory of Island Biogeography"; by 1934 there was no sign of a decline in the rate of plant colonization, as predicted by their theory in its simplest form (MacArthur and Wilson 1967:48). Furthermore, the apparent levelling of numbers of bird species now appears to have been a temporary feature of the data, as successional changes in the vegetation led to the loss of bird species of open habitat during the 1920s and 1930s, followed by the gain of more forest species (see Hoogerwerf 1953, Thornton 1984). Surveys in 1951–1952, 1979, and 1982–1984 provide new data for analysis of the ac-

cumulation and turnover of plant species over a uniquely long time scale and enable a fresh look at the relevance of island biogeographic theory.

The first question is whether there has been a significant trend toward dynamic equilibrium of the form predicted by MacArthur and Wilson (1967)? A second facet of their model is also of interest: the hypothesis that species number should be dependent on island area, which they employed in part as a surrogate for habitat diversity. Recent literature, as exemplified by Buckley's (1982, 1985) "habitat-unit" model of island biogeography, has indicated that the possession of particular identifiable habitat types may be critical, rather than a more general measure of habitat diversity. On the same theme, Bush (1986*b*) has noted that the butterfly species richness of the Krakatau islands is more closely related to the presence and extent of specific vegetation communities, than to island size or overall habitat diversity. It may thus be an opportune point to revive the analyses initiated by Ernst (1908) and Docters van Leeuwen (1936) of the roles of habitat type and dispersal mechanism in the floral recolonization. There is no *a priori* reason, however, to suppose equivalent controls on the faunal and floral elements. The broadly differing life history characteristics of fauna and flora (cf. Sauer 1969, Whittaker and Flenley 1982), and the manner in which they interact, may inhibit the successful incorporation of both into a single unifying framework for island biogeographical analysis.

There are a number of constraints regarding the analysis of the Krakatau data and the derivation of rates of immigration, extinction, and turnover. First, there is the matter of the definition of immigration and extinction events, which may differ among taxa, especially when comparing faunal and floral data. Second, data quality is a serious and for some purposes unquantifiable problem. Third, survey intervals have varied greatly during the study period 1883–1983, and have differed among islands. Fourth, Anak Krakatau has added new habitats within the group and has disrupted and deflected the progress of succession on R. Kecil and Sertung. This means that there are now substantial differences in the ages and complexities of communities within the group, and, with the exception of Rakata, there can no longer be assumed to be a fixed starting point to re-colonization (Richards 1986*a*). Perhaps the most fundamental consideration, clearly established by the foregoing sections, is the key role of successional processes in the floral history.

It is thus necessary to establish the nature and quality of the available data, a problem hindered by the emotive tone of some of the Krakatau literature (see Backer 1929, 1930, Docters van Leeuwen 1936). The weight of evidence presented by Docters van Leeuwen (1936) is convincing for the complete or near-complete sterilization of the islands, for the long-distance transport of propagules to the islands, and for the processes of

TABLE 2. Plant collecting on the Krakatau islands. Principal sources: Docters van Leeuwen (1936), Boedijn (1940), van Borssum Waalkes (1960), Whittaker and Flenley (1982), Tagawa et al. (1984).

| Collection period | Principal collector* | Year | Rakata | Sertung | R. Kecil | Anak Krakatau |
|-------------------|----------------------|--------|--------|---------------------------------|----------|---------------|
| | | | | Time spent by collector (days†) | | |
| No plants seen | (Verbeek) | 1883 | + | | | |
| 1886 | (Cotteau) | 1884 | <2 | 0.5 | 0.5 | |
| 1897 | Treub | 1886 | 3 or 4 | | | |
| | Boerlage | 1896 | | | 1 | |
| | Penzig | 1897 | 0.5 | <1 | 2 | |
| 1908 | Ernst | 1905 | + | | | |
| | Ernst | 1906 | 1 | 1h | | |
| | Backer | 1908 | 2 | <1 | 1 | |
| 1920 | DvL | 1919 | 5.5 | 3 | | |
| | DvL | 1920 | | 7 | | |
| 1922 | DvL | 1921 | | <1 | | |
| | DvL | 1922 | 7 | | | |
| 1924 | DvL | 1924 | 7 | | | |
| 1929 | DvL | 1928 | 9 | 2 | 1 | |
| | DvL | 1929 | 3 | 1 | 2 | |
| 1932 | DvL | 1931 | 2 | 1 | | |
| | DvL | 1932 | | | 3 | 1h |
| 1934 | Boedijn | 1933/4 | + | + | + | 1h |
| 1951 | vBW | 1951 | 9 | 2h | 0.4h | 1h |
| | vBW | 1952 | | 2h | | 1h |
| 1979 | Hull 1 | 1979 | 16 | | | 3 |
| 1982 | Tagawa | 1982 | 7 | <11 | <7 | <5 |
| 1983 | Hull 2 | 1983 | 6 | 9 | 3 | 7 |
| | Bush | 1984 | + | + | | |

* DvL = Docters van Leeuwen. In 1932–1934 Boedijn made six visits to the group, each of 5 or 6 d, but collected principally lower plants. vBW = van Borssum Waalkes. Bush collected a few species as part of the 1984 La Trobe Expedition; these have been included in the 1983 survey.

† Units are days unless marked “h” (hour) or “+” (short but unspecified time).

vegetation succession described above; however, he clearly set out to support the worth of the botanical studies, and to argue the various surveys to be as complete as the evidence would allow. The general quality of the evidence presented appears from a retrospective viewpoint to be commendable, but the account and interpretations are perhaps colored by the vitriolic attack made by Backer (1929) (see review by Hill 1930). We therefore paid considerable attention to the extents and efficacies of the floral surveys.

Floral surveys 1883–1984

The number of collectors, their experience, the time spent on each island, and the area covered have not been uniform. Given the nature of the terrain it would be difficult to achieve controlled survey conditions were that aim rigorously pursued, but for many surveys it is difficult to establish even the number of days spent collecting (Whittaker and Richards 1986).

Rakata.—Verbeek, who reached the summit in October 1883, and Cotteau, in May 1884, found no evidence of plant life (Verbeek 1885, Docters van Leeuwen 1936). Treub collected the first plants from Zwarte Hoek beach and the lower parts of the interior in 1886 (Table 2). The early savanna vegetation was extremely difficult to penetrate: Ernst (1908) reached only 50 m altitude in his 1906 survey, while Backer (1909) extended the trail up to 400 m in 1908.

Docters van Leeuwen (1936) visited the island sev-

eral times between 1919 and 1931 (Table 2), spending most effort on the southeast side. On each trip but his last he made an ascent to the summit and, except in 1929, collected from both beach and interior floras. His last visit to the southeast was on 1 March 1931, when he reached 300 m altitude. He did not camp on the north side, but landed several times at Zwarte Hoek, where he collected from the beach and the interior. He also penetrated into west and northeast Rakata from the landing points on the southeast side and from Zwarte Hoek, but is not specific as to when and for how long (Docters van Leeuwen 1936).

Boedijn (1940) collected mainly lower plants in six visits to the islands between 1932 and 1934. On each occasion he visited both the southeast side of Rakata and Zwarte Hoek. The next botanical study was not until 1951, when Borssum Waalkes (1960) made several excursions along the shore and into the interior, including the summit area. The first phase of the Hull University–Kratatoa Centenary Expedition spent 16 d on the south side of Rakata in 1979, collecting being carried out by up to three separate groups throughout the period (Flenley 1980). A visit was also made to Zwarte Hoek and to an area of shoreline on the northeast side. Tagawa's 1982 expedition spent 7 d in various research work, including plant collection (Tagawa 1984). The second phase of the Hull Expedition camped at Zwarte Hoek, and examined mostly those areas not investigated in 1979 and 1982.

Sertung.—Cotteau landed on Sertung on 26 May 1884 and found no plant life. The expeditions of Penzig, Ernst, and Backer each landed for less than a day on Sertung. Ernst (1908:37) actually specifies his collection of 42 species to have been made by "... two of us during a visit of barely one hour. . . ." Docters van Leeuwen (1936) principally collected from the northern end of the island, exploring the beach and part of the interior. His main collecting effort was made in 1920, when he traversed about one-third of the length of the island, reaching an altitude of ≈ 150 m. His only exploration of the south was made in 1929. Borssum Waalkes' (1954, 1960) two brief visits were both to the northern end, the second after the vegetation was severely damaged by volcanic eruptions. Tagawa's (1984) expedition spent ≈ 11 d in various studies on the island, and appears to have collected exclusively from the northern end of the island. The second phase of the Hull Expedition (Bush et al. 1986a) extended the area studied by Tagawa to include the southern end of the island.

R. Kecil.—Cotteau landed briefly and again recorded no plant life (Table 2). The collection of Boerlage in 1896 was made in a single day, during which he reached the highest point of the island. He duplicated among his collection all the species collected by Nolthenius (a nonbotanist) during a longer period in the same year. Penzig, in 1897, collected from the beach and from the north end, as did Backer in the following year. Docters van Leeuwen's visits spanned 1928 to 1932, and van der Pijl and Boedijn also visited the island in the 1932–1934 period, finding a few additional species (Docters van Leeuwen 1936, Boedijn 1940). Tagawa's group spent about 7 d in various investigations on the island in 1982, apparently collecting mainly from the northeast and central southwest (Tagawa 1984). The subsequent phase of the Hull Expedition concentrated on extending the 1982 survey. An additional survey of *R. Kecil* was made by Soeriaatmajda et al. (1985) in 1982; however, their species determinations contain significant anomalies of taxonomy from the rest of the literature, and, in view of the need for confirmation, their reported taxa have not been incorporated into Appendix I.

Anak Krakatau.—The first botanical records from Anak Krakatau are from 1932, when three separate but brief collecting trips were made. Eruptions subsequently wiped out the seedling flora, and only two species were found by Boedijn in 1933. This interrupted pattern continued, and the flora sampled in 1949 and 1951 by van der Pijl (1949) and Borssum Waalkes (1960) was wiped out in 1952. Barker (University of Hull) spent 3 d in vegetational survey and plant collecting in September 1979. This visit was followed by 5 days of investigation by the Kagoshima group in 1982, and a further 7 d by Barker in July 1983. The 1979 to 1983 studies constitute a virtually complete floristic survey.

Survey efficiency

Although it is regrettable that the floral surveys have not been conducted on a standardized basis, it is also clear that in the early years the vegetation was indeed very species-poor and monotonous. Thus, although Treub (1888) explored only a small part of the interior of Rakata in 1886, this deficiency is balanced by the obvious species-poverty of the vegetation he described (Docters van Leeuwen 1936). Similarly, he collected from only one beach, a sheltered bay at Zwarte Hoek, but there were very few such reasonably stable beach environments at the time, all other areas being narrow strips fronting perpendicular tuff-walls (Docters van Leeuwen 1936). Thus his total of 24–26 species is probably a reasonable indication of the diversity of the flora at the time.

Very little of the interior of Rakata was explored in 1906 (Ernst 1908), yet on extending the trail from the 50 m altitude reached by Ernst up to 400 m altitude in 1908, Backer (1909) found only 10 new species. Docters van Leeuwen (1936) interpreted this as evidence of the continued poverty of the flora, which remained a feature when he first visited the islands in 1919.

Up to 1919 and even later it was a striking fact that the vegetation was very monotonous. One could wander for hours through the ravines and over the ridges without finding a new species, after having collected everything at the beginning of the excursion. . . . (Docters van Leeuwen 1936:86)

Nonetheless, poor though the flora may have been, the species totals for the early years cannot be argued to be complete. While Docters van Leeuwen's surveys were much more thorough, even his treatment was not standardized. For example, the majority of the survey effort on Sertung was carried out in 1919–1920, whereas he did not visit *R. Kecil* until 1928 (Table 2). Also, the central section of Sertung appears not to have been explored botanically at all, due to the extreme difficulty of the terrain, until penetrated by Bush in 1984. His observations provide no reason to suggest a radically different flora in the central section of the island, but effectively only a reduced area of the island has been involved in sampling. Only on the much smaller (but disrupted) Anak Krakatau can we assume that a thorough investigation of the entire vegetated area of an island was carried out. Each census on the main islands must be considered as only a sample of the total species present. It is clear from the quantitative sampling (Bush and Whittaker 1986) that many tree species occur as rare individuals scattered in a matrix of a few common species. It is likely that some will always be missed. If each survey were then to sample only ≈ 80 – 90% of the total flora of an island (cf. Nilsson and Nilsson 1985), the resulting "pseudo-turnover" among the less common species could account for a high proportion of the

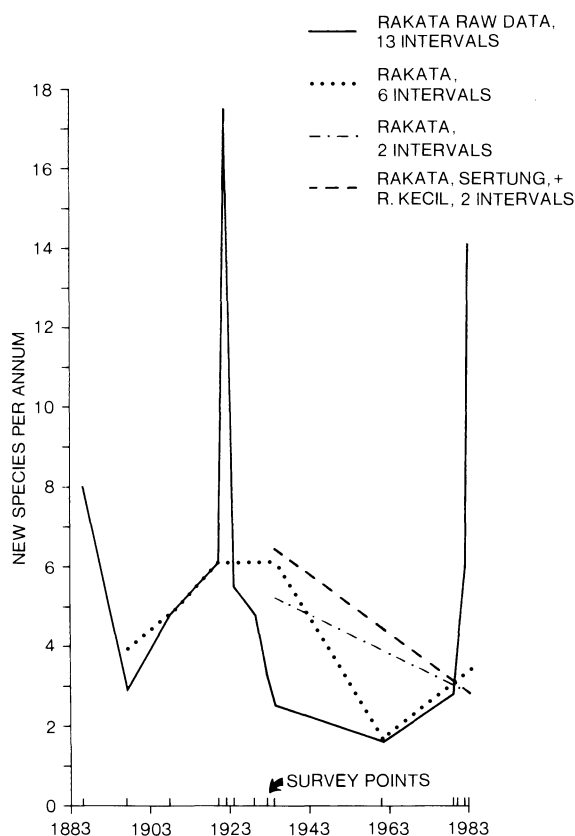


FIG. 16. Numbers of new species of higher plants recorded over a variety of intervals, expressed as an annual rate. These figures exclude re-invasions. Data from Table 3.

expected real turnover at "equilibrium." This is in itself another clear argument against attempting to use floral data to test island biogeographic theories without very careful assessment of data quality. In addition to these problems, taxonomic uncertainties (Appendix I, Bush et al. 1986a:214–216) have resulted in a range of possible values for species number calculations. The nature of the data necessitates a cautious approach to their analysis: there is much that is interpretative rather than sound statistics.

Survey interval

The number of surveys in a given period may clearly influence the efficiency of the sampling. When the surveys have been very close together there is often a strong case for combining them. They have tended to overlap in personnel, who have concentrated during later excursions on searching out new areas and species not found on their previous visit (Whittaker and Richards 1986). Conversely, they may ignore areas searched, or species known to have been collected, on their previous visit; indeed it is probably more difficult to assess the true pattern of species losses than gains. Thus by considering such surveys as independent, species turnover may be artificially increased, while if the data are

combined, the efficiency of the combined surveys is much improved. If we first examine data for each separate survey, following the approach of Whittaker and Flenley (1982), the smoothing effect of subsequently calculating immigration rates over greater intervals, ignoring intervening data, can be seen (Fig. 16). Interestingly the immigration peak of the 1920s remains, despite the removal of adjacent survey data. This peak is therefore not simply the product of increased frequency of surveys, but is likely to reflect an important phase of the recovery process. Despite thorough survey efforts of the 1979–1983 period, the number of new species found is lower over the last 50 yr than over the first 50 yr, a pattern repeated when data from the whole island group (Rakata, Sertung, and R. Kecil) are considered. This simple form of analysis can be improved by the use of combined survey data for 1979–1983, as developed in analyses below.

Definition of immigration and extinction events

In studies of island biogeography various criteria have been proposed to define immigration and extinction events (reviewed in Williamson 1981), but in this study the data take the most basic form, viz., simple lists of plant species that have been collected and identified in a particular year (Appendices I and II). Such a list takes no note of the abundance of a species, and can include a seedling colonist not yet independent of its parental resources, or can exclude a forest giant that could not be climbed for the necessary specimen material.

The term "extinction" is used throughout in the local, island biogeographical sense of the loss of a species from an island. Whittaker and Flenley (1982), Whittaker et al. (1984) and Richards (1986a, b) calculated extinction on the basis of the lack of positive evidence for the presence of a species in a particular survey. For most plant species, extinction events can rarely be proven for areas of the size of the Krakatau islands, and artefactual species losses may lead to overestimates of extinction and thus of turnover. In this paper we make use of an alternative model, assuming minimal turnover, i.e., in calculating "extinction" a species is only counted as having gone extinct if not found in any survey subsequent to the survey in question. This assumes that species simply went unrecorded rather than becoming extinct and re-invading. Although a small proportion of species, e.g., coastal ephemerals, may indeed have been lost and then re-invaded, this assumption probably fits the great majority of cases. In particular, this can be argued for species of the interior forests of Rakata, such as *Ficus hispida* and *Smilax zeylanica*, which, given their autecology and current numbers, are highly unlikely to have gone extinct since their initial recorded establishment, despite the lack of a positive record in every survey. It should be noted, however, that this approach is dependent on the further

assumption that the 1979–1983 sample is a relatively efficient and unbiased sample.

Floral assemblages and the cumulative curve of colonization

The data in Appendices I and II provide a complete revised account of the higher plant floras of the Krakatau islands. Summary data are given in Table 3. Lists are also available for the mycetozoa, fungi, and lichens, from collections made by Docters van Leeuwen (1936) and by Boedijn (1940). Summary data in comparable form of both lower and higher plants are given in Table 4. Given the difficulty of making a thorough collection, especially of certain groups of lower plants, the values for mycetozoa and fungi are clearly low estimates. Apart from the higher parts of Rakata (>400 m), where Docters van Leeuwen was the sole collector of lower plants, the survey effort in the three islands was of similar intensity (Boedijn 1940). The inter-island comparisons are thus of greater interest than the absolute values. It is nonetheless remarkable how impoverished the lichen flora was up to 1934. None was collected on the first post-1883 excursions, nor by Boedijn in 1932–1934 on the new volcano. The species that were found in this period were all epiphytic on higher plants (Boedijn 1940).

There is a consistent ranking in the number of species in each taxonomic group in Table 4, with Rakata having the largest flora, followed by Sertung and then R. Kecil; however, the numbers are not proportional to island area. Sertung generally had fewer species up to 1934 than might be predicted on the basis of area alone, but in contrast, also held a high number of species of fungi not found on the other islands. This pattern is not repeated in the higher plants, of which Rakata had far more “unique” species up to 1934 than Sertung and R. Kecil. By 1983, the 13-km² area of Sertung might be expected to have collected a higher cumulative vascular plant species total in comparison to R. Kecil’s 3 km²; the numbers were 238–246 and 202–203 species, respectively (Table 4). The variations in survey thoroughness and timing may be partially responsible for this, although the similar proportions of the 1982–1983 floras of these two islands (Table 3) suggests that this relationship is a genuine feature.

Larger islands provide not only more opportunity for establishment but also a generally more diversified nature (Boedijn 1940). R. Kecil and Sertung are both long, thin, low islands, with a very similar range of habitats. The major apparent differences between them are (1) the lagoons once found on Sertung, which enabled only one or two additional species to colonize (e.g., *Lumnitzera racemosa* and *Halophila ovalis*), and (2) in the proportions of particular coastal habitats. In contrast, Rakata is a rounded island, with a large expanse of upland, providing habitats of environmental characteristics very different from those of the other islands. Many species have been recorded only in these

higher parts of Rakata, e.g., *Acriopsis javanica*, *Agrostophyllum bicuspidatum*, *Crepidomanes bipunctatum*, *C. humilis*, and *Schefflera polybotrya* (see also Docters van Leeuwen 1936). The family that fits this pattern most clearly is the Orchidaceae; of 51 species known from the group, 33 have been found only on Rakata (Appendices I and II). These observations support the view that the occurrence of major habitat types is of overriding importance in determining the number of species on these islands (cf. Buckley 1982, 1985, Bush 1986b). The low numbers of lichen species recorded from Sertung and R. Kecil and the low numbers of fungi on the latter cannot be explained on the basis of constraints of area. Habitat differences, or environmental history (such as volcanic emissions from Anak Krakatau) may be the key, but data are insufficient to resolve this question.

In general, the inter-island patterns shown by the cumulative totals for 1883–1983 are similar to the 1883–1934 figures (Table 4). There have, however, been a disproportionately large number of new species of Pteridophyta found in the last 50 yr as compared to the first, particularly so in the case of R. Kecil, although the actual numbers involved with Rakata are much larger. The cumulative curve for the whole group of islands remains steep (Fig. 17A), with the gap between spermatophyte and pteridophyte totals continuing to increase, albeit at a lesser rate. The most similar pattern to this is shown by the Rakata data (compare Figs. 17A–D), with the 1983 cumulative total representing 87% of the total for the group of islands, compared to 52 and 44% for Sertung and R. Kecil, respectively. The latter two islands did not receive a proper survey in 1951, nor a 1979 data point, and thus have a flatter curve between 1934 and 1982 than Rakata. Nonetheless, the rate of increase in the flora is clearly less than for Rakata in the post-1934 period (cf. Table 3). These figures are paralleled by the pattern in species found on only one of the islands, for both the 1883–1934 and 1883–1983 collations (Table 4). A substantial proportion of the Rakata flora has not been found on Sertung or R. Kecil, amounting to 45% (of which half were ferns), compared to totals of 17 and 8% for the equivalent portions of the Sertung and R. Kecil floras. This pattern is argued to be substantially based upon “habitat,” rather than “area.”

Noncumulative species totals

Rakata. — Although the comparability of the various surveys is not directly quantifiable, the broad pattern of the change in species number present on Rakata remains of interest. The precise form varies, depending on the initial assumptions made (compare Table 3, Figs. 17, 18, 19), but the underlying pattern is one of a continually increasing flora in which the gap between cumulative and noncumulative totals has continued to rise over the last 50 yr. We present two means of estimating noncumulative totals for Rakata: (1) the num-

TABLE 3. Higher plant species numbers of the Krakatau islands. Nrec is the number of species recorded in each survey as given in Appendices I and II. The numbers in parentheses are species introduced to the islands by people. A range in the data is indicated by two figures separated by a hyphen; this allows for uncertain taxonomy.

| Date* | Pteridophyta | | Spermatophyta | | P + S total | |
|--|--------------|------------|---------------|------------|-------------|--------------|
| | Nrec | Cumulative | Nrec | Cumulative | Nrec | Cumulative |
| a. Rakata | | | | | | |
| 1886 | 11 | 11 | 13-15 | 13-15 | 24-26 | 24-26 |
| 1897 | 13 | 14 | 38 | 42 | 51 | 56 |
| 1908 | 11-12 | 18 | 88 | 91 | 99-100 | 109 |
| 1920 | 40-42 | 43-45 | 116-120 (18) | 139 | 156-162 | 182-184 |
| 1922 | 40-42 | 53 | 112-117 (8) | 166 | 152-159 | 219 |
| 1924 | 37-39 | 53 | 116-133 (5) | 177 | 153-172 | 230 |
| 1929 | 40-43 | 56 | 140-156 (5) | 198 | 180-199 | 254 |
| 1932 | 32-39 | 58 | 115-140 (4) | 206 | 147-179 | 264 |
| 1934 | ... | 58 | 20-21 (0) | 211-212 | 20-21 | 269-270 |
| 1951 | 30 | 69-71 | 105-107 (1) | 227-230 | 135-137 | 296-301 |
| 1979 | 43-44 | 86-89 | 157 (3) | 283-292 | 200-201 | 369-381 |
| 1982 | 36-39 | 92-98 | 108 (1) | 291-303 | 144-147 | 383-401 |
| 1983 | 32-34 | 96-102 | 125-126 (0) | 301-314 | 157-160 | 397-416 |
| 29 + 32 | 42-45 | | 154-168 (5) | | 196-213 | |
| 29 to 34 | 42-45 | | 160-175 (5) | | 202-220 | |
| 79 to 83 | 64-67 | | 198-205 (3) | | 262-273 | |
| b. Sertung | | | | | | |
| 1897 | 1 | 1 | 11 | 11 | 12 | 12 |
| 1908 | 4 | 5 | 68-69 | 71-72 | 72-73 | 76-77 |
| 1920 | 25 | 25 | 118-121 | 130-133 | 143-146 | 155-158 |
| 1929 | 7-19 | 25 | 71-107 | 135-139 | 78-126 | 160-164 |
| 1932 | 7-19 | 25 | 71-113 | 143-145 | 78-132 | 168-170 |
| 1934 | ... | 25 | 14 (1) | 148-150 | 14 | 173-175 |
| 1951 | 2 | 25 | 42 (8) | 156-158 | 44 | 181-183 |
| 1982 | 15 | 31 | 83 | 182-185 | 98 | 213-216 |
| 1983 | 23 | 42 | 89-92 | 196-204 | 112-115 | 238-246 |
| 20 + 29 | 25 | | 119-124 | | 144-149 | |
| 20 to 32 | 25 | | 133-136 | | 158-161 | |
| 20 to 34 | 25 | | 138-141 (1) | | 163-166 | |
| 29 + 32 | 19 | | 114-116 (0) | | 133-135 | |
| 29 to 34 | 19 | | 119-121 (1) | | 138-140 | |
| 82 + 83 | 30 | | 118-121 | | 148-151 | |
| c. Rakata Kecil | | | | | | |
| 1897 | 5 | 5 | 46 | 46 | 51 | 51 |
| 1908 | 3 | 6 | 54 | 65 | 57 | 71 |
| 1929 | 10-16 | 12-17 | 71-85 (4) | 94-101 | 81-101 | 106-118 |
| 1932 | 15-18 | 18 | 91-107 (7) | 127 | 106-125 | 145 |
| 1951 | 3 | 19 | 33 | 128 | 36 | 147 |
| 1982 | 13 | 27 | 58 | 152 | 71 | 179 |
| 1983 | 24 | 40 | 73-74 | 162-163 | 97-98 | 202-203 |
| 29 + 32 | 18 | | 114 (9) | | 132 | |
| 82 + 83 | 31 | | 89-90 | | 120-121 | |
| d. Anak Krakatau | | | | | | |
| 1934 | 0 | 0 | 17-20 | 17-20 | 17-20 | 17-20 |
| 1949 | 1 | 1 | 11-12 | 22-25 | 11-13 | 23-26 |
| 1951 | 2 | 2 | 20 | 31-34 | 22 | 33-36 |
| 1979 | 3 | 3 | 42-43 | 49-54 | 45-46 | 52-57 |
| 1982 | 4 | 5 | 31 | 56-62 | 35 | 61-67 |
| 1983 | 3 | 6 | 63 | 80-87 | 66 | 86-93 |
| 79 to 83 | 6 | | 74-77 | | 80-83 | |
| e. Cumulative totals for Rakata, Sertung, and R. Kecil combined | | | | | | |
| Date | Pteridophyta | | Spermatophyta | | Total | Total - (I)† |
| 1886 | 11 | | 13-15 | | 24-26 | 24-26 |
| 1897 | 14 | | 55 | | 69 | 69 |
| 1908 | 19 | | 111 | | 130 | 130 |
| 1920 | 50 | | 184 (18) | | 234 | 216 |
| 1922 | 58 | | 205 (18) | | 263 | 245 |
| 1924 | 58 | | 215 (18) | | 273 | 255 |
| 1929 | 59 | | 234 (22) | | 293 | 271 |
| 1932 | 61 | | 257 (27) | | 318 | 291 |

TABLE 3. Continued.

| Date | Pteridophyta | Spermatophyta | Total | Total - (I)† |
|------|--------------|---------------|---------|--------------|
| 1934 | 61 | 264-265 (28) | 325-326 | 297-298 |
| 1951 | 72-74 | 280-283 (32) | 352-357 | 320-325 |
| 1979 | 89-92 | 328-339 (32) | 417-431 | 385-399 |
| 1982 | 99-105 | 334-360 (32) | 433-465 | 401-433 |
| 1983 | 104-110 | 351-378 (32) | 455-488 | 423-456 |

* Combinations of different surveys are given as: '29 + 32' = 1929 and 1932, '29 to 34' = 1929, 1932 and 1934.

† Total - (I) is total higher plants minus introduced species. In addition to the species found on the main islands, 8 or 9 species have been found only on Anak Krakatau, 3 or 4 of these as seedlings in 1932-1934, 1 in 1979, 1 in 1982 and 3 in 1983 (Appendix II). Two of the species in the 'I' category have subsequently been found on a second island without necessarily having been introduced by people.

ber of species actually recorded as present in a particular survey or combination of surveys (=Nrec); (2) the number of species present on the assumption of minimum turnover, i.e., Nrec plus species found both previously and since (=Nmt). The Nrec model (Fig. 18) smooths the data, suggesting a gradual increase in the size of the flora, rather than the fluctuations indicated by the raw survey data (Table 3, Fig. 16). The 1979 data revealed apparent stabilization in the number of pteridophyte species present on Rakata since 1920; however, 64-71 species of pteridophytes are now known for the 1979-1983 period, indicating a clear increase

from the 40-42 species known from 1920. Thus both pteridophyte and spermatophyte components have continued to increase through the study period (Fig. 18).

The noncumulative total may also be estimated using Nmt (Fig. 19A). By this "minimum turnover" model it is assumed that species simply went unrecorded rather than going extinct and re-invading (above). By this model, it is apparent that the noncumulative total is underestimated in the 1920s by Nrec (see Fig. 19B). These analyses suggest that it would be unwise to attempt to make a precise estimate of the rate of increase

TABLE 4. Cumulative species totals. Two figures separated by a dash indicate a range due to uncertain taxonomy. Numbers in parentheses indicate species introduced by people. R + S + K indicates combined data for all three islands. Data are from Appendix I (higher plants), and Boedijn 1940 (lower plants).

| Subject | Area Altitude | Rakata | Sertung | R. Kecil | R + S + K |
|--------------------------------------|------------------|---------------------------------|-----------------------------|----------------------------|--------------|
| | | 17 km ² 735-813 m | 13 km ² 182 m | 3 km ² 147 m | |
| A. For period 1883 to 1934 inclusive | | | | | |
| HIGHER PLANTS | | | | | |
| Pteridophyta | | 58 | 25 | 18 | 61 |
| Spermatophyta | | 211-212 (18) | 148-150 (1) | 127 (9) | 264-265 (28) |
| Total | | 269-270 | 173-175 | 145 | 325-326 |
| Species recorded on that island only | | | | | |
| Pteridophyta | | 36 | 3 | 0 | |
| Spermatophyta | | 85-86 (18) | 27 (1) | 20 (9) | |
| Total | | 121-122 | 30 | 20 | |
| LOWER PLANTS | | | | | |
| Mycetozoa | | 26 | 9 | 0 | 28 |
| Fungi | | 206 | 135 | 23 | 282 |
| Lichens | | 13 | 0 | 1 | 13 |
| Total | | 245 | 144 | 24 | 323 |
| Species recorded on that island only | | | | | |
| | | 153 | 70 | 6 | |
| B. For period 1883 to 1983 inclusive | | | | | |
| HIGHER PLANTS | | | | | |
| Pteridophyta | | 96-102 | 42 | 40 | 104-110 |
| Spermatophyta | | 301-315 (18) | 196-204 (8) | 162-163 (9) | 351-378 (32) |
| Total | | 397-416 | 238-246 | 202-203 | 455-488 |
| Species recorded on that island only | | | | | |
| Pteridophyta | | 53 | 5 | 1 | |
| Spermatophyta | | 124-126 (15) | 36 (5) | 16 (9) | |
| Total | | 177-179 | 41 | 17 | |

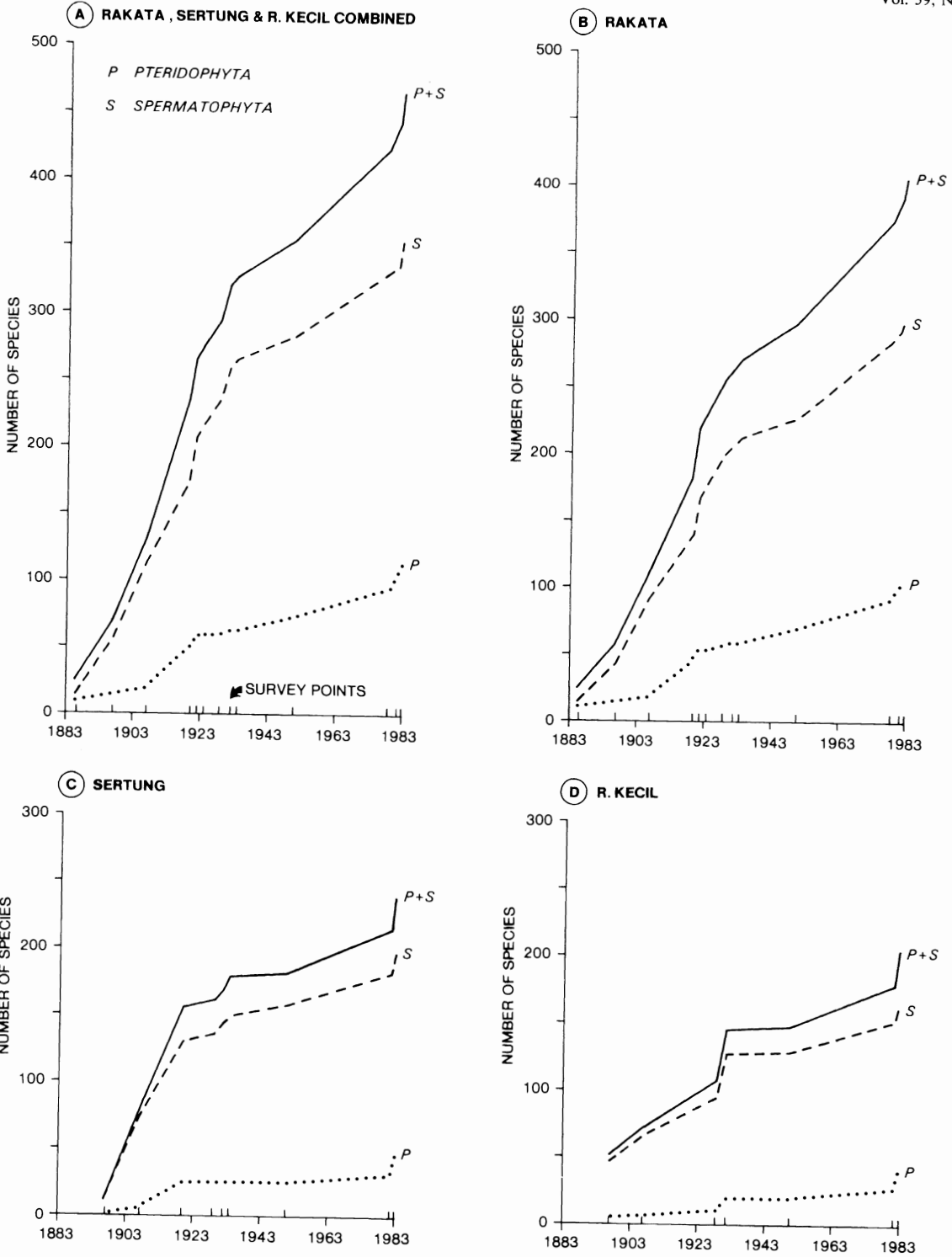


FIG. 17A-D. Cumulative species totals over time for Pteridophyta (*P*), Spermatophyta (*S*), and all higher plants (*P* + *S*) for the three older Krakatau Islands. Data from Table 3; where a range is given in Table 3, only the minimum value has been plotted.

in noncumulative totals on Rakata on the basis of the raw survey data. Clearly the minimum-turnover calculations (Nmt) are dependent on thorough surveys at the end of the study period, and hence the later data points are not reliable; 1951 was a poor sample, and 1979 was not independent of the 1982–1983 data; therefore they both underrepresent the flora of the last 50 yr. Apart from the early portion of this curve, the main interest in calculating the minimum-turnover values is in the pattern of persistence of the early assemblages, discussed below (see Rate of Loss of Early Rakata Assemblages).

R. Kecil and Sertung.—Despite an intensive survey effort, in which some parts were explored for the first time, the 1982–1983 species total for Sertung is no greater than the 1920 total (Fig. 18B). In the case of *R. Kecil*, the number of spermatophytes has fallen dramatically compared to the 1929–1932 total (Fig. 18C). In spite of a near doubling in the number of pteridophytes (in line with the cumulative pattern), the combined total for all higher plants on *R. Kecil* also falls compared to 1929–1932. This pattern can be seen equally well in comparisons of single survey points in Table 3. A rise in extinction rate due simply to successional driven habitat loss could not provide an adequate explanation for this pattern given that no such fall has occurred on Rakata, and given that most of *R. Kecil* had experienced forest canopy closure by the time Docters van Leeuwen (1936) commenced his study there. Species numbers on *R. Kecil* are remarkably low, with Spermatophyta totals comparable to those on Anak Krakatau, with its relatively tiny vegetated area (Table 3c, d). Although Anak Krakatau has undoubtedly been more thoroughly surveyed, this pattern clearly is evidence of an impoverished flora on the larger island. Both islands have been subject to disruption, Anak Krakatau more so than *R. Kecil*; thus the low species number on the latter may reflect an impoverishment of habitats caused by disturbance events so timed (and of the right magnitude) to enable a few opportunistic tree species, principally *Timonius compressicaulis*, to form the monotonous and species-poor forest described above (pages 79–80). We interpret these data as being incompatible with the application of an equilibrium model, rather the patterns described are the outcome of the partial destruction of the Sertung and *R. Kecil* floras by volcanic action and the subsequent vegetational response to the disturbances.

Between-island comparisons.—Krakatau provides an opportunity to examine not only the relationships between area, habitat, and species number, but also the extent to which different islands sample different subsets of the overall species pool. The number of species found only on one island showed a consistent ranking from Rakata to *R. Kecil* in the cumulative data (above, Table 4). This pattern is repeated within the 1979–

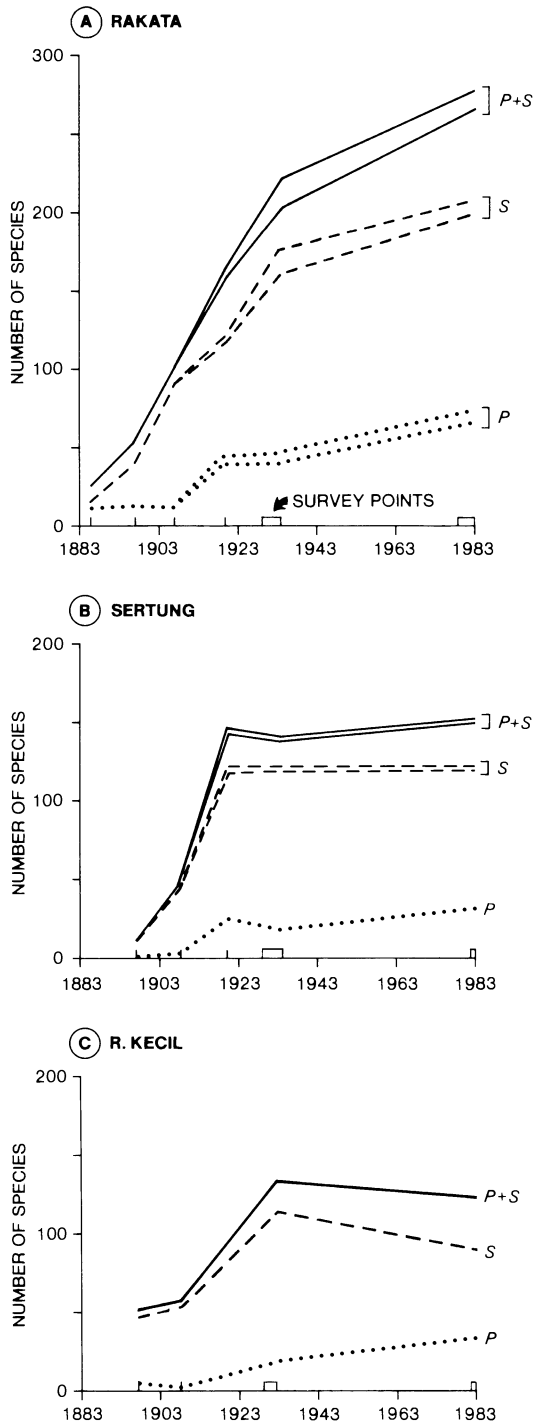


FIG. 18A–C. Species recorded as present in particular survey periods (Nrec) for Pteridophyta (P), Spermatophyta (S), and all higher plants (P + S) for the three older Krakatau Islands. The ranges indicate uncertain identifications in Appendix I. Collations are as marked above the horizontal axis of each graph (e.g., 5th data point on [A] is for 1929–1934). Data derived from Table 3.

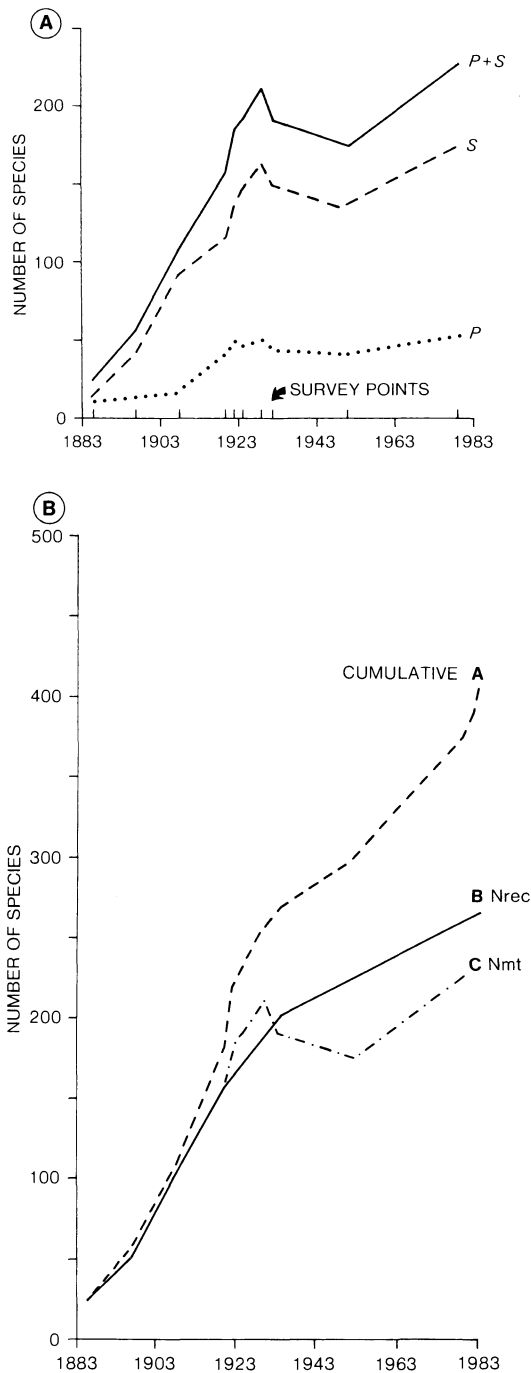


FIG. 19. (A) Species present on Rakata for given survey dates, calculated on the assumption of minimum turnover (Nmt), i.e., cumulative totals minus species losses that were permanent within the study period (i.e., up to 1979–1983). Data from Appendix I. (B) Rakata flora build-up according to three differing models, for all higher plants. From Figs. 17B, 18A, and 19A. The difference between curves A and B, and A and C, is equal to the species extinction curve for each method of calculation. Comparison of B and C suggest that each method underestimates the number of species present on the island at some points in time (see *The Developing Floras of Krakatau: Noncumulative Species Totals: Rakata*, pages 91–95).

1983 survey data, both for simple totals and as proportions of each island's flora (Table 5). Relatively few species occur in two-island combinations, especially between Sertung and R. Kecil, whereas >50% of the Sertung and R. Kecil floras are shared by all three islands. Examination of Appendix I and Tables 4 and 5 indicates a core of shared species, presumably related to the possession of common habitat types, with Rakata effectively sampling a separate pool of upland taxa.

Similar proportions of the 1883–1934 floras of each island have been re-recorded in the 1979–1983 period (Table 6), ranging from 54% for Rakata to 49% for R. Kecil; however, the early pteridophyte floras have persisted better on R. Kecil than on the other two islands. This may be hypothesized to be due to the reprieve of early light-demanding pteridophytes on R. Kecil due to recent volcanic disturbance and the consequent interruption of successional processes (see Appendix I). Particularly in the case of R. Kecil, however, the numbers involved are small and the apparently high 'persistence' of this flora could be a reflection of a low initial sample. The pattern displayed by the spermatophyte flora is of more interest, and displays an improving trend of persistence from R. Kecil to Sertung to Rakata, which is supportive of the disturbance explanation outlined above, and of a variable response rate to environmental change by the pteridophyte and spermatophyte floras (see discussion of dispersal mechanisms, below).

Rate of loss of early Rakata assemblages

Of the 24 species identified from Rakata in 1886, 50% were found on the island in the 1979–1983 surveys (Table 7). Most of the species loss is accounted for by pteridophytes, only 3 of the 11 species being found in 1979–1983. Of the 108 species of the 1908 assemblage, 59% are still present on Rakata, with the pteridophytes again accounting for the greatest proportionate loss, only 40% of their number remaining. Table 8 provides a summary of the fate of each Rakata assemblage, and the overall shapes of the decay curves are given in Fig. 20. The percentage of each pteridophyte assemblage that remained in the 1979–1983 period steadily increases up to the 1922 datum, with a particularly clear increase from the 41% for the 1908 assemblage, to 61% for the 1920 assemblage. This is probably a result of the colonization by 1920 of forest fern species, a group whose habitat has remained undisturbed throughout the remainder of the study period. The high persistence of the early spermatophytes, especially of the 1897 assemblage, may be habitat-controlled in that a species-stable beach community constituted a large part of the earliest assemblages (Table 8 and below). The persistence of each of the 1920s spermatophyte assemblages is very similar, with a marked increase in the figure for the 1932 and 1951 assemblages. Interestingly, if these data are converted to an overall rate of species lost per year, the highest rate of loss is from the 1929 assem-

blage, declining thereafter (Table 8). Fig. 20 also suggests a continual increase in the steepness of the decay curves for each assemblage up to the 1929 starting point, while the less thorough survey of 1951 has a shallower slope. This pattern probably relates to the completion of forest canopy closure in the late 1920s, and thus to an increase in successional "turnover."

Habitat and species-turnover

From data presented in Treub (1888) and Ernst (1908) it is possible to follow the fate of the beach and inland components of the early assemblages of Rakata (Table 7). It is evident that the 1886, 1897, and 1908 assemblages show a greater loss from the inland flora than from the beach flora (Table 7). These data indicate that the earliest beach floras have persisted well and have been little affected by "turnover." The floras of the interior have shown a much greater rate of loss, with a disproportionately high number of these being of the pioneering species of pteridophytes. Two hypotheses may be constructed: first, that there may have been some under-sampling of the interior compared to the beaches in 1979–1983, leading to artefactual differences in extinction rates; and second, that the differing natures of successional processes in the "inland" and "coastal" habitats have resulted in more species turnover in the inland flora. Neither hypothesis can be rejected on the available evidence. Coastal floras may have been more thoroughly surveyed, as it is difficult to investigate the interior as systematically, but the nature of the species lost also fits with a habitat-determined explanation, in which much of the turnover inland has been successional in nature, as fern and grass savanna gave way to shrubland and forest, while the coastal vegetation communities have changed little (Fig. 15). This pattern is clearest in the 1886 and 1897 assemblages in which, respectively, 80 and 84% of the beach assemblages were found in 1979–1983, compared to 29 and 47% of the inland assemblages. The data for 1908 indicate a weakening of the pattern, with

TABLE 5. Species found on Rakata (R), Sertung (S), and Rakata Kecil (K) in the period 1979–1983. P = Pteridophyta, S = Spermatophyta. The percentage calculations are for each cell as a proportion of the total species number for each island (R, S, or K) for the indicated period. Data derived from Appendix I.

| Species present on | P | S | Total | % of R | % of S | % of K |
|---------------------|----|-----|-------|--------------|--------------|--------------|
| R only | 36 | 93 | 129 | 49 | | |
| S only | 6 | 25 | 31 | | 22 | |
| K only | 3 | 4 | 7 | | | 6 |
| R and S (but not K) | 3 | 27 | 30 | 11 | 21 | |
| R and K (but not S) | 8 | 21 | 29 | 11 | | 25 |
| S and K (but not R) | 3 | 3 | 6 | | 5 | 5 |
| R and S and K | 17 | 59 | 76 | 29 | 53 | 64 |
| Overall total | 76 | 232 | 308 | | | |

TABLE 6. Fates of the species found within the first 50 yr on Rakata, Sertung and R. Kecil, i.e., of the cumulative assemblage of the period shown. P1, S1, and Tot1 are the numbers of species of pteridophytes, spermatophytes, and their sum, respectively. P2, S2, and Tot2 are the percentage of each of these floras found within the period 1979–1983.*

| | P1 | P2 | S1 | S2 | Tot1 | Tot2 |
|--------------------|----|-----|-----|-----|------|------|
| Rakata 1886–1934 | 58 | 53% | 194 | 55% | 252 | 54% |
| Sertung 1897–1934 | 25 | 52% | 148 | 52% | 173 | 52% |
| R. Kecil 1897–1932 | 18 | 67% | 118 | 46% | 136 | 49% |

* The introduced species (I in Appendix I) have been excluded from these calculations, as they show a disproportionately high rate of loss (as shown in Table 3).

an increased susceptibility of the beach flora and a continued improvement in the persistence of the inland flora. Overall, these data support the view that the characteristic strand-line taxa of these islands established early and have been little affected by "turnover" sensu MacArthur and Wilson (1967). The data presented by Docters van Leeuwen (1936:77) indicate that the size of the beach flora for all three islands combined increased from 68 in 1920 to only 75 in 1934, despite the fairly comprehensive surveys of the period, indicating a divergence from the pattern for the flora as a whole, which has continued to rise throughout.

Means of arrival of the Krakatau floras

Using the characteristics given by Ridley (1930), Docters van Leeuwen (1936), and Backer and Backhuizen van den Brink (1968), data for those plants recorded on the islands (excluding Anak Krakatau) between 1979 and 1983 have been added to the data for dispersal mechanism given by Docters van Leeuwen (1936:240) (Fig. 21). The cumulative totals for spermatophytes in each dispersal category for the entire 1883–1983 period are wind = 99, sea = 103, animal = 123, humans = 32 species (compare with Fig. 21). Clearly it is difficult to prove that a given species has arrived by any one particular dispersal agent, but the general pattern is probably fairly reliable. In a few cases, it was not possible to decide between two alternative mechanisms and a score of 0.5 was then assigned to both categories.

The wind-dispersed component.—The first colonizers recorded in the interior of Krakatau after 1883 were principally blue-green algae and pteridophytes, with only a few flowering plants. The large production and small size of cyanophyte and pteridophyte propagules pre-dispose these groups to long-distance wind dispersal. In the pioneering species, these features are combined with the ability to tolerate the extreme climatic and edaphic conditions on the islands. The initial vegetation cover of the interior was dominated (in terms of both cover and species number) by pteridophytes, a situation that had changed by 1897. The early wind-borne flora changed the nature of the soil and microclimate, thereby improving the conditions for other

TABLE 7. Fates of early floral assemblages of Rakata, assuming minimum turnover. Each dated assemblage is made up of the cumulative species total to the year given, minus those species not found in either that or any subsequent survey.*

| | | Census date | | | | | | 1979– 1983 | % persisting‡ |
|---------------------------|---------------|-------------|------|------|------|------|---------------|--------------------|--------------------|
| Habitat† | Order | 1886 | 1908 | 1920 | 1929 | 1951 | | | |
| Beach | Pteridophyta | 1 | 1 | 1 | 1 | 0 | 0 | Total Beach = 80% | |
| Beach | Spermatophyta | 9 | 9 | 9 | 9 | 8 | 8 | | |
| Inland | Pteridophyta | 10 | 9 | 8 | 6 | 3 | 3 | Total Inland = 29% | |
| Inland | Spermatophyta | 4 | 4 | 4 | 3 | 1 | 1 | | |
| Combined total | | 24 | 23 | 22 | 19 | 12 | 12 | = 50% | |
| b. The 1897 assemblage | | | | | | | | | |
| Habitat† | | 1897 | 1908 | 1920 | 1929 | 1932 | 1951 | 1979– 1983 | % persisting‡ |
| Beach | Pteridophyta | 2 | 2 | 2 | 2 | 2 | 1 | 1 | Total Beach = 84% |
| Beach | Spermatophyta | 23 | 23 | 23 | 23 | 22 | 21 | 20 | |
| Inland | Pteridophyta | 11 | 11 | 10 | 8 | 7 | 3 | 3 | Total Inland = 47% |
| Inland | Spermatophyta | 19 | 19 | 17 | 15 | 13 | 11 | 11 | |
| Combined total | | 55 | 55 | 52 | 48 | 44 | 36 | 35 | = 64% |
| c. The 1908 assemblage | | | | | | | | | |
| Habitat† | | 1908 | 1920 | 1929 | 1932 | 1951 | 1979– 1983 | % persisting‡ | |
| Beach | Pteridophyta | 2 | 2 | 2 | 2 | 1 | 1 | Total Beach = 70% | |
| Beach | Spermatophyta | 38 | 36 | 34 | 32 | 29 | 27 | | |
| Inland | Pteridophyta | 15 | 14 | 12 | 11 | 7 | 6 | Total Inland = 53% | |
| Inland | Spermatophyta | 53 | 49 | 46 | 40 | 32 | 30 | | |
| Combined total | | 108 | 101 | 94 | 85 | 69 | 64 | = 59% | |
| d. The 1920 assemblage | | | | | | | | | |
| Species group | | 1920 | 1922 | 1924 | 1929 | 1932 | 1951 | 1979–1983 | |
| All Pteridophyta | | 41 | 40 | 40 | 40 | 36 | 27 | 25 | |
| All Spermatophyta | | 133 | 118 | 112 | 112 | 104 | 83 | 75 | |
| Combined total | | 174 | 158 | 152 | 152 | 138 | 110 | 100 | |
| Introductions | | 18 | 9 | 6 | 6 | 5 | 4 | 3 | |
| Total minus Introductions | | 156 | 149 | 146 | 146 | 133 | 106 | 97 | |
| e. The 1922 assemblage | | | | | | | | | |
| | | 1922 | 1924 | 1929 | 1932 | 1951 | 1979–1983 | | |
| All Pteridophyta | | 48 | 47 | 47 | 42 | 32 | 30 | | |
| All Spermatophyta | | 145 | 141 | 137 | 124 | 99 | 91 | | |
| Combined total | | 193 | 188 | 184 | 166 | 131 | 121 | | |
| Total minus Introductions | | 184 | 182 | 178 | 178 | 127 | 118 | | |

* As an illustration, in part c, 8 (inland) species of the "1908 assemblage" were not collected in 1905–1908, but were found both earlier and later, and have therefore been included in the starting figure of 108 species. Subsequent cells to the right give the number of species remaining on the island on the assumption of minimum turnover (i.e., extinctions are counted only if permanent up to 1979–1983 inclusive).

† The breakdown into beach and inland components follows Ernst (1908) and Docters van Leeuwen (1936) and reflects the habitat in which each species was first found. Species of uncertain taxonomy have not been included unless known to be the only member of the genus found. Data from Appendix 1.

‡ The percentage figures are the proportion of the starting total found in 1979–1983.

nonxerophytes. We cannot necessarily assume that the wind-borne seed/spore bank has remained constant through the period since the 1883 eruption, but doubtless propagules of many species arrived several times

prior to their eventual colonization yet failed to establish due to unsuitable environmental conditions. Eleven of the initial 16 anemochorous species were pteridophytes (Fig. 21), but as the succession proceeded the

early dominance of this group declined, and in 1908 only 12 of 32 anemochorous species were pteridophytes. The proportion of Pteridophyta fell from 42% of the total vascular plant flora in 1886 to 10% in 1908.

During this period, a *Ficus-Macaranga* forest had begun to develop on the lower slopes of Rakata and the upper areas had a cover of *Saccharum* grassland. As the forest of the low to middle altitudes developed, new habitats became available for colonization. This was evidenced by a substantial increase in the number of pteridophytes, especially forest species, between 1908 and 1920 (Fig. 21). The forest cover was not complete at this time, resulting in a mixed flora of shade-tolerant and heliophilous species. Almost all of the pteridophytes that colonized during this period were epiphytic or shade/moisture demanding species (e.g., *Asplenium nidus*, *Davallia denticulata*, and *Lygodium* spp.) (Appendix I). There then followed an increase in the rate of arrival of anemochorous flowering plants, as they colonized this new habitat. There appears to have been a slight lag (up to 12 yr) between the upturn in pteridophyte and spermatophyte colonization (Fig. 21). The number of pteridophytes on the islands continued to increase over the period 1934–1983, and accounts for the majority of the net increase in the anemochorous flora. Approximately 45 species of pteridophytes and 37 anemochorous spermatophytes were recorded for the first time in 1979–1983, with only 50% of the 1883–1934 anemochorous spermatophytes persisting (Table 9). There has been a slightly higher proportion of pteridophytes lost of the 1883–1934 Rakata flora than of the equivalent R. Kecil flora (Table 6), and the wind-dispersed spermatophytes found only on Rakata in 1883–1934 also show a poor degree of persistence (Ta-

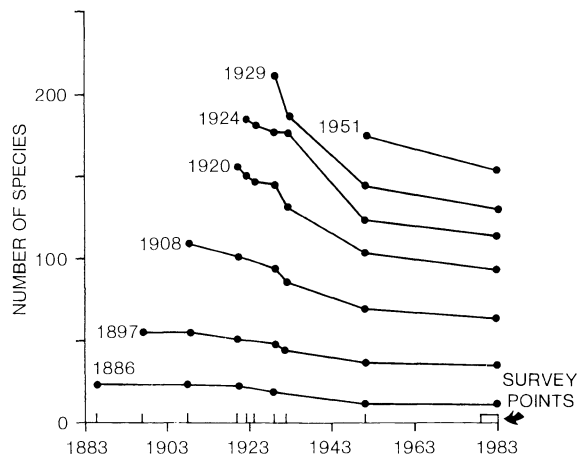


FIG. 20. Decay of Rakata floral assemblages (all higher plants) calculated on the assumption of minimum turnover. The dates indicate the starting point of each assemblage (see The Developing Floras of Krakatau: Rate of Loss of Early Rakata assemblages, page 96). Data from Appendix I.

TABLE 8. Overall fates of Rakata floral assemblages. Each assemblage is made up of the species counted as present in the respective year (time1) on the assumption of minimum turnover. P1, S1, and Tot1 are the numbers of Pteridophyta, Spermatophyta, and their sum, respectively. P2, S2, and Tot2 are the percentage of these floras found within the period 1979–1983 inclusive (time2).

| Assemblage | P1 | P2 | S1 | S2 | Tot1 | Tot2 | Annual loss rate* |
|------------|----|-----|-----|-----|------|------|-------------------|
| 1886 | 11 | 27% | 13 | 69% | 24 | 50% | 0.52% |
| 1897 | 13 | 31% | 42 | 74% | 55 | 64% | 0.42% |
| 1908 | 17 | 41% | 91 | 63% | 108 | 59% | 0.55% |
| 1920† | 41 | 61% | 115 | 63% | 156 | 62% | 0.60% |
| 1922† | 48 | 63% | 136 | 65% | 184 | 64% | 0.59% |
| 1924† | 49 | 61% | 146 | 64% | 193 | 64% | 0.61% |
| 1929† | 50 | 60% | 163 | 64% | 213 | 63% | 0.69% |
| 1932† | 44 | 71% | 149 | 71% | 193 | 71% | 0.57% |
| 1951† | 44 | 91% | 134 | 88% | 178 | 89% | 0.34% |
| 1979† | 50 | | 174 | | 224 | | |

* The proportion of Tot1 lost between time1 and time2 expressed as an annual rate.

† The Introductions noted in Appendix I have been excluded from these calculations, as they show a disproportionately high rate of loss (see Table 7).

ble 9). As those species lost were very often the most strongly heliophilous members of the early savanna vegetation (Appendix I), these results support the interpretation of turnover as in large part successional in nature.

The sea-dispersed component.—The early importance of the thalassochorous plants reached a peak of >50% of the total flora 25 yr after the eruption. Since then the net curve for sea-dispersed taxa has levelled off, and over the last 50 yr has fallen slightly. This is in part because relatively few new sea-dispersed species have been recorded in 1979–1983, the figures for sea-, animal-, and wind-dispersed components being 16, 39, and 37 respectively. Small losses from the 1886, 1897, and 1908 assemblages of Rakata suggest that the early beach assemblages (broadly equivalent to the sea-dispersed species) formed a species-stable community. In contrast, only 53% of the 1883–1934 sea-dispersed flora (of the three islands) was recorded in 1979–1983, which is almost as low as for the wind-dispersed flora (50%), and considerably lower than for the animal-dispersed flora (71%) (data in Table 9). This indicates a considerable increase in turnover among sea-dispersed species colonizing in the 1920s and 1930s.

Several factors may be important in explaining this apparent contradiction. First, there are few accreting beach environments on Krakatau; coastal erosion has been the dominant process throughout the post-1883 period. Thus certain coastal habitats have been non-continuous or restricted in their extent, and the loss of some sea-dispersed species can be directly attributed to the disappearance of their habitat (e.g., the brackish lake on Sertung). These species include: *Centella asiatica*, *Halophila ovalis*, *Lumnitzera racemosa*, and *Xylocarpus granatum*. Species on the spit of Sertung may have been lost because of either coastal change or erup-

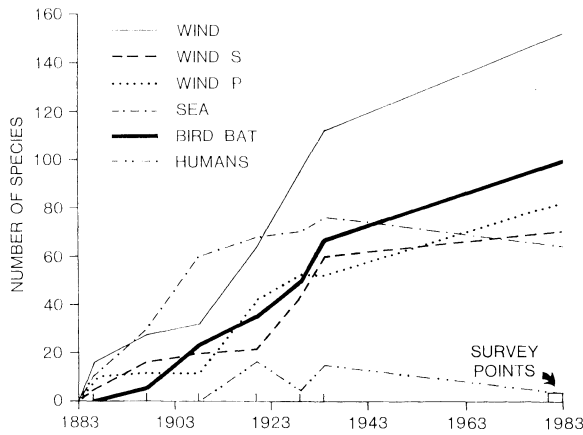


FIG. 21. Means of dispersal of the Krakatau flora: all higher plants and for all islands (combined) except Anak Krakatau. Data from Docters van Leeuwen (1936) for all points except 1979–1983, data from Appendix I, with dispersal characteristics culled from Ridley (1930), Docters van Leeuwen (1936), and Backer and Bakhuizen van den Brink (1968). The totals are for collations, rather than only the dates indicated. WIND/S and WIND/P = wind-dispersed Spermatophyta and Pteridophyta, respectively.

tions: of 15 sea-dispersed species recorded only on Sertung in the 1883–1934 period, only 1 was found within the group in 1979–1983. Some of the other apparent losses leading to the decline in this component of the flora were of species that never really colonized successfully, being collected (largely in the 1920s and 1930s) in juvenile form from the strand-line. An example of this “over-sampling” is the mangrove *Avicennia alba*, recorded on Rakata; the largest specimen had only 6–10 leaves (Docters van Leeuwen 1936:413), and the island clearly lacks the necessary habitat for successful mangrove establishment. Other examples of such juveniles or “ephemerals” include: *Aeschynomene in-*

dica, *Crotolaria striata*, *Messerschmidia argentea*, *Opuntia elatior*, and *Spondias mangifera*. It would be difficult to be consistent in removing such ephemerals from the data, we therefore retained them for the calculations. These factors provide a partial explanation for the apparent increase in turnover in the 1920s (see Rate of Loss of Early Rakata Assemblages, above).

We have few data on the frequency of particular species in the strand-line flora; however, a crude indication of the commonness of groups of species can be derived from the number of islands on which they have been found through time (Appendix I). Table 9 shows the dispersal mechanism compared to the island combinations on which each species was found in 1883–1934. Species found on only one island display the poorest persistence, and those occurring on all three islands the best persistence. This pattern is shown in each of the dispersal categories taken separately, but is strongest in the sea-dispersed category, in which 42 of the 47 species persisting in 1979–1983 were found on all three islands in 1883–1934 (Table 9). This corroborates the suggestion that most losses have been of species of restricted distributions (e.g., many of the “ephemerals”) and few, if any, of the characteristic species of the early strand flora have been lost (above).

The animal-dispersed component.—Six zoochorous taxa, probably all bird-sown, were recorded in 1897 (Docters van Leeuwen 1936). The zoochorous component has increased steadily to a total of ≈ 99 in 1983, showing the highest rate of increase from 1934 totals of the four spermatophyte components (Fig. 21). The continued increase in this component may be related to a positive feedback in which more fruiting trees attract greater numbers of visiting birds and bats. These visitors drop more seeds, introducing more zoochorous species (Thornton 1984). There are now four species of frugivorous bats and 11 species of frugivorous birds on the islands (Thornton 1986, Tidemann and Zann

TABLE 9. Fates of 1883–1934 floras by dispersal mechanism. The combined 1883–1934 floras of Rakata, Sertung, and R. Kecil (R, S, and K respectively) are broken down into island vs. dispersal mechanism combinations.*

| Island | Persisting in 1979–1983 | | | | Absent in 1979–1983 | | | |
|-----------|-------------------------|------|--------|------------|---------------------|-----|--------|------------|
| | Wind | Sea | Animal | Row totals | Wind | Sea | Animal | Row totals |
| R | 11 | 1 | 16 | 28 | 17.5 | 9.5 | 11.5 | 38.5 |
| S | 1 | 1 | 3 | 5 | 1 | 14 | 4.5 | 19.5 |
| K | 2 | 0.5 | 3.5 | 6 | 0 | 4 | 1 | 5 |
| RS | 3 | 0 | 10 | 13 | 5 | 7 | 1 | 13 |
| RK | 3 | 2 | 1 | 6 | 2 | 0 | 1 | 3 |
| SK | 0 | 0 | 4 | 4 | 1 | 0 | 1 | 2 |
| RSK | 12.5 | 42 | 20.5 | 75 | 6 | 6.5 | 3.5 | 16 |
| Col. tots | 32.5 | 46.5 | 58 | 137 | 32.5 | 41 | 23.5 | 97 |

* To be counted as “persisting” in 1979–1983 a species had to be recorded on any combination of R, S, and K, e.g., ten animal-dispersed species were found on both R and S (but not K) in the 1883–1934 period and on one or more of the three islands in 1979–1983. The numbers of species of 1883–1934 which were not found in 1979–1983 are given in the right half of the table, as “Absent” (e.g., for the same case = 1). In a few cases it was not possible to decide between two possible mechanisms and a value of 0.5 was entered.

1986, Thornton et al. 1988). Of the main inland forest types of Krakatau (*Dysoxylum*, *Ficus*, *Neonauclea* and *Timonius* forests), all except the *Neonauclea* forest are dominated by zoochorous species. The zoochorous component shows both a comparable number of new species to the anemochorous component (above) and a significantly lower proportion of losses from the 1883–1934 flora (Table 9). The implications of these findings are discussed below.

Introduced flora.—In Appendix I, 32 species are recorded as having been introduced to the islands by humans. Of these, only 3 (i.e., only 9%) were found in the 1979–1983 period. They have thus sustained a remarkably high proportion of losses compared with all other groups of species. It is instructive to consider the details involving each island.

1. *Rakata.*—Docters van Leeuwen (1936) lists 17 species of weeds and cultivated plants found around Handl's cottage in 1919, to which can be added a specimen of *Citrus* sp. found at \approx 400-m altitude, and probably introduced by visitors. Most of these species were shaded out shortly after the abandonment of the site. In 1931, only *Gnetum gnemon*, *Mangifera indica*, *Antigonon leptopus*, and *Boesenbergia pandurata* could be found, and only 3 of the 18 were found in 1979–1983. *Cocos nucifera* has been planted on all of the islands at various times, but since there is every reason to believe it to be a natural colonist as well (Docters van Leeuwen 1936) it has been excluded from the I category in Appendix I.

2. *Sertung.*—Borssum Waalkes (1960) observed a cottage garden on Sertung in 1951, containing crop and weed species, 8 of which were new to the island (Table 3). Three other "garden" species had been found earlier and could have been introduced by earlier temporary inhabitants (cf. Ernst 1908). All were destroyed as a result of the 1952 eruption of Anak Krakatau, and none has been found since. *Gnetum gnemon*, found for the first time in 1982, may also have been introduced by humans (above), although it could have been animal transported, and has also been found on R. Kecil, where it is far less likely to have been introduced by humans.

3. *R. Kecil.*—Nine species of weeds were recorded by Docters van Leeuwen (1936) in the period 1928–1934 as having been introduced near the Volcanological Service camp (species marked I in Appendix I). None has been found since, and it is probable that they were shaded out very shortly after the post was abandoned.

Dispersal mechanisms and families.—Certain plant families have been particularly important in shaping the dispersal curves. For instance, the Orchidaceae accounts for half of the wind-dispersed spermatophytes both for 1883–1983, and for 1979–1983 (respectively 52 out of 99 and 35 out of 69). Anemochorous Asclepiadaceae (13 species), Compositae (17 species) and Orchidaceae account for 82 of the 99 wind-dispersed

species of 1883–1983. The wind-dispersed component is thus mainly made up of nonarboreal species, including many epiphytes. A third of the 103 sea-dispersed species of 1883–1983 have been Leguminosae, but this component of the flora is otherwise fairly diverse in its composition. Animal-dispersed species provide the largest group of spermatophytes, with 123 species between 1883 and 1983. The two largest family groups within this are the Euphorbiaceae, 14 of which are zoochorous (10 found in 1979–1983), and the Moraceae, with 22 figs and one other zoochorous species (19 found in 1979–1983, Appendix I). Apart from these families, the animal-dispersed component is also a diverse group. It will be noted that this group is the most important in supplying inland forest tree species. Only the *Neonauclea calycina* forests of Rakata are dominated by a wind-dispersed species, and the trend evident in these data is a continued diversification of the inland forest, in which species attractive to birds and bats (e.g., *Ficus* spp., *Dysoxylum* spp., etc.) are anticipated to play an important role.

The floras of Anak Krakatau

The repeated interruptions to the colonization of Anak Krakatau have resulted in a flora that may well post-date the 1972 eruption. Disruptions to the processes of recolonization and vegetation development may have occurred at many points, and certainly occurred where major eruptions are noted, e.g., 1932–1933, 1952–1953, 1960–1961, 1972, 1979–1982. Thus there is no known starting point for the colonization, and rates of immigration or extinction cannot be calculated. The present stature of the *Casuarina equisetifolia* forest, its rate of expansion, and the pace of the 1979–1983 increases in the flora (Appendix II, Table 3d) would be consistent with a post-1972 revegetation of the island. The 1979–1983 surveys recorded a combined total of 80–83 species of higher plants, a considerable increase on previous totals. If the diversity of the flora is an accurate guide, it would suggest that this period represents the longest period of relatively undisturbed colonization in the island's history. Not only has diversity increased, but the composition of the flora has changed (Appendix II). Prior to 1979 only one animal-dispersed species and three wind-dispersed species had been found, and while the majority of the cumulative spermatophyte flora (Table 3) are sea-dispersed species ($n = 45$), both wind-dispersed species ($n = 17$) and animal-dispersed species ($n = 14$) have increased in importance (the remaining four species were of unknown dispersal mechanism). In particular the recent surveys have revealed that a few species typical of forest habitats elsewhere in the Krakatau group have begun to colonize, e.g., *Dysoxylum gaudichaudianum*, *Ficus* spp. and *Timonius compressicaulis* (Appendix II). The low count in 1982 (Table 3d) is probably attributable to collecting efficiency, but the

minor eruptions of the period cannot be totally disregarded in their possible effect on this assemblage (Barker and Richards 1986).

The species found on Anak Krakatau since 1930 are essentially a subset of those found on the main islands. Although 8–9 species have been found only on Anak Krakatau (Appendix II), 3–4 of these were as seedlings in 1932–1933 and can be viewed as ephemerals, with the remaining five being found within the 1979–1983 period. These figures support the importance of the local seed source, in particular for species such as *Dysoxylum gaudichaudianum*, which has probably been introduced from within the group by birds. There has been some debate within island biogeography as to the extent to which stochastic vs. deterministic rules operate, and in this context it is interesting to note that all but one of the 23 species of the 1949–1951 vegetation, destroyed in the 1952–1953 eruptions (Borssum Waalkes 1960), have been found subsequently. This demonstrates a strong deterministic element, presumably controlled jointly by habitat and dispersal opportunities. Anak Krakatau remains remarkably poor in Pteridophyta compared to the other islands, and whereas, in the cases of some early surveys of R. Kecil or Sertung, this might be attributed to survey efficiency, Anak Krakatau has been very thoroughly surveyed, and its impoverishment must be due to the unfavorable and disruptive environmental conditions operating.

DISCUSSION: SPECIES BUILD-UP AND THE COMPONENTS OF TURNOVER

The unique facet of this study has been the analysis of re-colonization of an insular locality in terms of both successional ecology and island biogeography. To understand the factors controlling the pattern of species turnover and the shape of the colonization curve it is clearly important to examine the relationships between community dynamics and floristic dynamics. In 1983, >50 yr after forest closure, the Krakatau islands remained characterized by large tracts of species-poor forest, with a few dominant canopy species, all of which were typical early seral species. Of the lowland forest communities, those of Rakata were the most mature. Large areas of Sertung and R. Kecil were covered in very young forests of *Timonius compressicaulis*, an early stage in recovery from disturbance. Not only were the vegetation communities and soils of these islands significantly less mature than those of Rakata, but the floral data also followed a clearly different pattern, with Rakata the only island showing continued increase in species richness.

Perhaps the major factor explaining the inter-island differences in vegetation and in the curves of species colonization has been the intermittent disturbances, of varying severities, which have originated from Anak Krakatau. On Rakata, there has not been opportunity for *Timonius compressicaulis* and *Dysoxylum gaudichaudianum* to invade large tracts of disturbed vege-

tation in which the canopy has been broken or destroyed. In the absence of such disturbance it is unclear if *D. gaudichaudianum* will play a major role in the forests of the main island, on which its distribution in 1983 was principally near the coast. The explanation for the relatively low species numbers recorded on Sertung and R. Kecil in 1982–1983 is probably linked in some way to the disturbances, but demands further field studies. It may be that insufficient time had elapsed since disturbance-induced losses, or it may be that the renewed space was occupied so rapidly by the few common species (especially *T. compressicaulis* and *D. gaudichaudianum*), that they have delayed the colonization of further species. It is anticipated that in the absence of major disturbances the dominance of the canopy of all the islands will become increasingly shared and that species number will undergo further increases.

On Anak Krakatau, frequent volcanic disturbance, inhibition of vegetational spread away from the accreting coastal deposits, and the short distance from large local seed sources (i.e., the other islands), make the island a poor analogue for the early post-1883 period. The major dispersal group has been the sea-dispersed species and the flora contains a deterministic core which re-colonized following disturbance. The flora of Anak Krakatau has increased in recent years, its composition indicating that it has been strongly influenced by the surrounding islands: recent colonizers include the commonest tree species of the inland forests of the other islands.

Analyses of the floral data by habitat and by dispersal mechanism have revealed an underlying pattern to the accumulation of species number and species turnover on the main islands of the group. The relationships revealed are interesting for several reasons. First, the coastal environments of the Krakatau islands are clearly very dynamic, yet the early colonists of the strand-line of Rakata have been subject to a very low proportion of losses, relative to the flora of the interior. This trend decreases as the starting point is shifted from 1886, through 1897 to 1908, and later sea-dispersed species arriving on the group have undergone a relatively high rate of losses compared to the animal-dispersed species. This is at least partly because of habitat losses (due to coastal change rather than autogenic processes), and oversampling of ephemerals in the 1920s.

Wind-dispersed species appear to have colonized in two phases, providing the bulk of the primary colonizers inland, and then after a period of little change (possibly a reflection of low sampling intensity) a steep increase in numbers as forest habitats became available. In both phases, the pteridophytes were faster to colonize than the anemochorous spermatophytes. Underlying the curve for anemochorous spermatophytes has been a relatively high rate of turnover, much of which has been due to succession (cf. Docters van Leeuwen 1936). The animal-dispersed component was the slowest to colonize, as would be expected, but has since

shown the most consistent pattern of increase in numbers, suffering a very low rate of losses. Only 29% of the 1883–1934 animal-dispersed flora was not found in 1979–1983, compared to values of $\approx 50\%$ for the other components. Tree species turnover has probably been unimportant (especially so for animal-dispersed species), among those species that once established a viable population, with most real “turnover” being of the nonarboreal species of the open successional phase. Large arboreal species have continued to arrive on the Krakatau islands, although few if any that could be termed characteristic “primary” forest species. The animal-dispersed species may nonetheless be viewed as the most advanced seral group, forming a second species-stable component (along with the early beach species). We expect that the majority of further arrivals of forest tree species on these islands will also be as a result of the migratory movements of birds and bats (cf. Thornton 1984). The anthropogenic impact on both the course of succession and the composition of the floras of the group remains remarkably slight. Those species known to have been introduced by humans have shown a disproportionately high rate of loss. While those on Sertung were destroyed by eruptions in 1952, those introduced to Rakata and R. Kecil were shaded out by the forest.

Floral diversity appears to be only loosely related to island area, but is a function of ecosystem maturity and habitat diversity. Much of the pattern within the curves of species number through time, and in the loss of species, can be explained with reference to habitat-based successional changes. Furthermore, the possession of definable habitat types (e.g., eroding and accreting coastal habitats, lowland and submontane habitats) appears important in determining the size and composition of the floras of these islands (cf. Whitehead and Jones 1969, Buckley 1982, 1985). Of the species found in 1979–1983, 129 were found only on Rakata (50% of that island's total), the only island with upland, with the next largest island combination being Rakata, Sertung, and R. Kecil with 76 species. Only 44 species were found on Sertung and/or R. Kecil but not on Rakata. The common core of each successive “new” flora on Anak Krakatau, and the similarities and differences established among the floras of the main islands, indicate clear differences in the probabilities of dispersal and establishment within the overall species pool. Nevertheless, the composition of the forests of Rakata shows a gradual variation with altitude (rather than a boundary at which lowland switches to upland conditions), illustrating that the “habitat model” is also a simplification.

In conclusion, the status of Krakatau as both a classic case study of tropical forest succession (Richards 1952) and of island biogeography (MacArthur and Wilson 1967) demands review. While a primary successional framework may be applied to Rakata, the other islands now include substantial secondary successional ele-

ments. This may be viewed as adding to the value of this “natural experiment,” rather than detracting from it. The deflection of succession on R. Kecil and Sertung exemplifies this, showing unpredictable transition probabilities between different successional paths.

In examining the Krakatau floral data from an island biogeographical perspective we conclude that the rigorous data required for a testing of “equilibrium theory” are impracticable to obtain for islands of this size and geocological character, and that there are also several strong reasons for rejecting the model as being fundamentally inappropriate. The one island of the group where an uninterrupted history is available is Rakata, and its flora has continued to increase in diversity. Furthermore, far from species turnover being a random process, it is apparent that: (1) certain groups of species do not contribute to “turnover,” (2) the species of differing habitats may behave differently in this respect, and (3) much of the apparent turnover involves “ephemerals,” species lost due to habitat destruction, and species introduced by humans. Of the rest, much can be attributed to the processes of vegetation succession (i.e., it is “successional turnover”) and accompanying environmental and zoogeographical changes. Neither the pattern of change in the flora, nor that for some groups of fauna, e.g., the birds and butterflies (Hoogerwerf 1953, Thornton 1984, Bush 1986*b*) can be understood without reference to vegetation succession and the key period in the 1920s when the savanna vegetation of the interiors gave way to forest. Attempts to calculate simple immigration and extinction rates for the total species population are for these reasons inappropriate to an understanding of the Krakatau data. Instead, a successional model of island recolonization is required, involving evaluation of habitat and dispersal mechanisms.

It is important to emphasize, finally, that the forests remain of an early seral character, and that the timescale of seral progression will become increasingly slower, if for no other reason than the lengthening generation times of the succeeding canopy species. Despite the protected status of the islands, the influence of humans may be expected to become increasingly significant, indirectly, in removing the source pool of potential further colonists on Java and Sumatra.

ACKNOWLEDGMENTS

We thank all those who contributed to the two Hull University: Krakatoa Centenary Expeditions, in particular John Flenley and Peter Jones for encouragement and comments. Provisional identifications were carried out at the Herbarium Bogoriense, Bogor, and where appropriate were checked by staff of the Reijksherbarium, Leiden and the Royal Botanic Gardens, Kew. We are indebted to the following for the supply of information and/or for comments on text: G. A. De Neve, J. Dransfield, D. Mabberley, D. Newsome, the late C. G. G. J. van Steenis, I. W. B. Thornton, and T. C. Whitmore. We thank J. J. Ewel, E. G. Leigh, Jr., F. E. Putz and W. H. Schlesinger, for their valuable suggestions in respect to an earlier version of the manuscript. This work could not have

been carried out without the cooperation of L.I.P.I. (the Indonesian Institute of Sciences). The Herbarium Bogoriense provided invaluable support and expertise, and we are particularly indebted to Dr. Kuswata Kartawinata, Gregori Hambali, Harry Wiriadinata, Mohammed Amir, and Ramlanto. Major financial assistance was provided by The National Geographic Society (U.S.), P.T. BAT Indonesia, The Royal Society, The British Ecological Society, and The University of Hull. M. B. Bush thanks the La Trobe 1984 Krakatau Expedition for funding to participate in that project, and Mark Walker, Mark Harvey, and Pat Vaughan for being staunch field allies. We thank the Geography Departments of Hull University, Birkbeck College and Oxford University, and the Oxford University Computing Service, for technical assistance and computing facilities. Figures were drawn by Angela Newman and Sarah Rhodes.

LITERATURE CITED

- Baas, P. 1982. Identity of the carbonised wood sample from Krakatau. Pages 181–183 in J. R. Flenley and K. Richards, editors. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Backer, C. A. 1909. De flora van het eiland Krakatau. In De opnemng van de Krakatau-Groep in Mei 1908. Jarr-verslag van den Topographiscen dienst in Nederlandsch-Indie over 1908, 4:189–191.
- . 1929. The problem of Krakatao as seen by a botanist (translation (from Dutch) by A. Fitz). Published by the author, Surabaya.
- . 1930. De vermeende sterilizatie van Krakatau in 1883. *Vakblad voor Biologen* 12:157.
- Backer, C. A., and R. C. Bakhuizen van den Brink, Jr. 1963–1968. Flora of Java. Three volumes. N.V.P. Noordhoff, Groningen, The Netherlands.
- Baren, J. van. 1931. Properties and constitution of a volcanic soil, built in 50 years in the East-Indian Archipelago. *Mededeelingen van de Landbouwhoogeschool te Wageningen*, 35(6):1–29.
- Barker, N., and K. Richards. 1982. The vegetation of Anak Krakatau. Pages 143–164 in J. R. Flenley and K. Richards, editors. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Barker, N., and K. Richards. 1986. Notes on the plant ecology and biogeography of Anak Krakatau. Pages 167–181 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Berg, N. P. van den. 1884. Vroegere Berichten Omtrent Krakatau. De uitbarsting van 1680. *Tijdschrift voor Indische Taal-Land-, en Volkenkunde, (Batavia)* 29:208–228. (English translation. Pages 283–291 in T. Simkin and R. S. Fiske (1983). *Krakatau 1883: the volcanic eruption and its effects*. Smithsonian Institution Press, Washington, D.C., USA.)
- Bird, E. C. F., and N. J. Rosengren. 1984. The changing coastline of the Krakatau Islands, Indonesia. *Zeitschrift für Geomorphologie N.F.* 28(3):347–366.
- Boedijn, K. B. 1940. The Mycetozoa, fungi and lichens of the Krakatau Group. *Bulletin du Jardin Botanique de Buitenzorg (iii)* 16:358–429.
- Borssum Waalkes, J. van. 1954. The Krakatau Islands after the eruption of October 1952. *Penggemar Alam* 34:97–104.
- . 1960. Botanical observations on the Krakatau Islands in 1951 and 1952. *Annales Bogorienses* 4:1–64.
- Buckley, R. C. 1982. The habitat-unit model of island biogeography. *Journal of Biogeography* 9:339–344.
- . 1985. Distinguishing the effects of area and habitat type on island plant species richness by separating floristic elements and substrate types and controlling for island isolation. *Journal of Biogeography* 12:527–535.
- Bush, M. 1986a. Some effects of physical processes on the redevelopment of the forests of Krakatau. Pages 57–76 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- . 1986b. A biogeographical appraisal of the butterflies of Krakatau. Pages 97–112 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Bush, M., P. Jones, and K. Richards, editors. 1986a. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Bush, M., P. Jones, and K. Richards. 1986b. Conservation of Krakatau. Pages 157–166 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Bush, M., and R. J. Whittaker. 1986. The vegetation communities of Sertung, Rakata Kecil and Rakata. Pages 14–55 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Camus, G., and P. M. Vincent. 1983. Discussion of a new hypothesis for the Krakatau eruption in 1883. *Journal of Volcanology and Geothermal Research* 19:167–173.
- Corner, E. J. H. 1952. *Wayside trees of Malaya*. Two volumes. Government Printer, Singapore.
- Dammerman, K. W. 1948. The fauna of Krakatau 1883–1933. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde (Tweede Sectie)* 44:1–594.
- De Neve, G. A. 1953a. Krakatoa and Anak Krakatoa, with a communication on the latest investigation in October 1953. Pages 6–7 in 8th Pacific Science Congress and 4th Far Eastern Prehistory Congress (Manila, Philippines, November 1953). National Research Council of the Philippines, Quezon City. Abstracts of papers, supplement.
- . 1953b. Rapport concernant l'activité volcanique en Indonésie pendant la première trimestre de l'année 1953. *Berita Geologi (Bulletin of the Volcanological Survey of Indonesia) (Bandung)* 1(3–4):3–16.
- . 1982. The Krakatau group and Anak Krakatau's eruptivity. Snapshot of 1981. *Berita Geologi/Geosurvey Newsletter* 14(23):195–211.
- . 1985. Geovolcanology of the Krakatau group in the Sunda Strait Region—review of a hundred years development (1883–1983). Pages 20–34 in *Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding*. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Docters van Leeuwen, W. M. 1921. The flora and the fauna of the islands of the Krakatau group in 1919. *Annales du Jardin Botanique de Buitenzorg* 31:103–140.
- . 1923. On the present state of the vegetation of the Islands of the Krakatau Group and of the Island of Sebesy. Pages 313–318 in *Proceedings of the Second Pan Pacific Science Congress*. Australian National Research Council, Melbourne, Australia. Volume 1.
- . 1929. Krakatau's new flora. Pages 56–79 in *Proceedings of the Fourth Pacific Science Congress*. (Batavia), Part 2. (Reprinted as pages 424–430 in T. Simkin and R. S. Fiske (1983). *Krakatau 1883—the volcanic eruption and its effects*. Smithsonian Institution Press, Washington, D.C., USA.)

- . 1936. Krakatau 1883–1933. *Annales du Jardin Botanique de Buitenzorg* 46:47.
- Ernst, A. 1908. The new flora of the volcanic island of Krakatau. Translation by A. C. Seward. Cambridge University Press, Cambridge, England.
- Flenley, J. R., editor. 1980. The Krakatoa Centenary Expedition interim report. Miscellaneous Series Number 24, Department of Geography, University of Hull, Hull, England.
- Flenley, J. R., and K. Richards, editors. 1982. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Forster, M. 1982. A study of spatial distribution of Bryophytes on Rakata. Pages 103–126 in J. R. Flenley and K. Richards, editors. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Gauch, H. G., Jr. 1982. Multivariate analysis in community ecology. Cambridge Studies in Ecology 1. Cambridge University Press, Cambridge, England.
- Genolagani, J. M. G. 1985. Assessment of conservation and management needs of the Krakatau volcano islands, Indonesia. Pages 346–371 in Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Gorman, M. L. 1979. Island ecology. Chapman and Hall, London, England.
- Hardjosoestastro, R., and J. Dai. 1985. Pumiceous tuff from the eruption of Krakatau in 1883 on Rakata Island and its development. Pages 72–83 in Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Hill, A. W. 1930. Botanical exploration of Krakatau. *Nature* 125:627.
- Hill, M. O. 1979a. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, Ithaca, New York, USA.
- . 1979b. TWINSPLAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Section of Ecology and Systematics, Cornell University, Ithaca, New York, USA.
- Hill, M. O., and H. G. Gauch, Jr. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42:47–58.
- Hoogerwerf, A. 1953. Notes on the vertebrate fauna of the Krakatau Islands, with special reference to the birds. *Treubia* 22:319–348.
- Jones, P. A. 1986a. Field and analytical methods for the vegetation survey. Pages 6–13 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- . 1986b. The bryophytes of the Krakatau Islands. Pages 77–86 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Kartawinata, K. 1977. Structure and composition of forests in some nature reserves in West Java, Indonesia. Pages 59–68 in Papers presented at the 13th Pacific Science Congress, Vancouver, Canada, August 1975, LIPI (Indonesian Institute of Sciences).
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Mohr, E. C. J., and F. A. van Baren. 1954. Tropical soils: a critical study of soil genesis as related to climate, rock and vegetation. N. V. Uitgeverij, W. van Hoeve, The Hague, The Netherlands.
- Newsome, D. 1982. Soil development on Rakata. Pages 83–102 in J. R. Flenley and K. Richards, editors. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- . 1986. Aspects of soil surface characteristics on Rakata and Anak Krakatau. Pages 134–156 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Nilsson, I. N., and S. G. Nilsson. 1985. Experimental estimates of census efficiency and pseudo-turnover on islands: error trend and between-observer variation when recording vascular plants. *Journal of Ecology* 73:65–70.
- Ninkovich, E. 1979. Distribution, age and chemical composition of tephra layers in deep-sea sediments of western Indonesia. *Journal of Volcanological and Geothermal Research* 5:67–86.
- Partomihardjo, T., S. Riswan, and R. Abdulhadi. 1985. Plant communities on the Anak Krakatau. Pages 411–416 in Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Penzig, O. 1902. Die fortschritte der flora des Krakatau. *Annales du Jardin Botanique de Buitenzorg* 18:92–113.
- Pijl, L. van der. 1949. Botanische notities over een bezoek aan Anak Krakatau in Augustus 1949. *Chronica Naturae* 105(11):283–285.
- Richards, K. 1982. Notes on the geomorphology of Krakatau. Pages 184–187 in J. R. Flenley and K. Richards, editors. The Krakatoa Centenary Expedition: final report. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- . 1986a. The flora of the Krakatau islands: a case study in island biogeography. Pages 113–133 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- . 1986b. Equations used in the calculation of biogeographical rates. Pages 222–224 in M. Bush, P. Jones, and K. Richards, editors. The Krakatoa Centenary Expedition 1983: final report. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Richards, P. W. 1952. The tropical rain forest: an ecological study. Cambridge University Press, Cambridge, England.
- Ridley, H. N. 1930. The dispersal of plants throughout the world. Reeve, Ashford, England.
- Rosengren, N. J. 1985. The changing outlines of Sertung, Krakatau Islands, Indonesia. *Zeitschrift für Geomorphologie N.F.* 57:105–119.
- Sauer, J. D. 1969. Oceanic islands and biogeographic theory. *Geographical Review* 59:582–593.
- Schroter, C. 1929. Das Pflanzenleben der Alpen. Verlag von Albert Raustein, Zurich, Switzerland.
- Shinagawa, A., N. Miyauchi, T. Higashi, R. Djuwansah, and A. Sule. 1984. The soils on the Krakatau Islands. Pages 1–43 in H. Tagawa, editor. Interim report of Grant-in-aid for overseas research in 1982 and 1983. Researches in the ecological succession and the formation process of volcanic ash soils on the Krakatau Islands. Kagoshima University, Kagoshima, Japan.
- Simkin, T., and R. S. Fiske. 1983. Krakatau 1883—the volcanic eruption and its effects. Smithsonian Institution Press, Washington, D.C., USA.
- Soeriaatmadja, R. E., editor. 1985. Vegetation analysis of

- plant communities at the Rakata Kecil Island. Pages 437–447 in *Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding*. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Steenis, C. G. G. J. van. 1930. Gezichtspunten over het ontstaan van de nieuwe flora van Krakatau na 1883. *Vakblad voor Biologen* 12:57.
- . 1931. De nieuwe flora van Krakatau na 1883. *Vakblad voor Biologen* 13:64.
- . 1938. *Nepenthes op Krakatau*. *Tropische Natuur* 27:131.
- . 1972. *The mountain flora of Java*. E. J. Brill, Leiden, The Netherlands.
- Stehn, Ch. E. 1929. The geology and volcanism of the Krakatau Group. Pages 1–55 in *Proceedings of the Fourth Pacific Science Congress (Batavia)*. (Reprinted as Pages 311–340 in T. Simkin and R. S. Fiske (1983). *Krakatau 1883—the volcanic eruption and its effects*. Smithsonian Institution Press, Washington, D.C., USA.)
- Subagio, H., and H. van Reuler. 1985. Some characteristics of brown soils on Rakata Island developed in material originating prior to the 1883 Krakatau eruption. Pages 288–295 in *Proceedings of the Symposium on 100 years development of Krakatau and its Surrounding*. Volume 1. Jakarta, 23–27 August 1983, LIPI (Indonesian Institute of Sciences).
- Sudrajat, S. A. The morphological development of Anak Krakatau Volcano, Sunda Strait. *Geologi Indonesia* 9(1): 1–11. (Reprinted as Pages 359–367 in T. Simkin and R. S. Fiske (1983). *Krakatau 1883—the volcanic eruption and its effects*. Smithsonian Institution Press, Washington, D.C., USA.)
- Switsur, V. R. 1982. A carbonised wood sample from Rakata and its radiocarbon assay. Pages 177–180 in J. R. Flenley and K. Richards, editors. *The Krakatoa Centenary Expedition: final report*. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Tagawa, H., editor. 1984. Interim report of Grant-in-aid for overseas research in 1982 and 1983. Researches on the ecological succession and the formation process of volcanic ash soils on the Krakatau Islands. Kagoshima University, Kagoshima, Japan.
- Tagawa, H., E. Suzuki, T. Partomihardjo, and A. Suriadarma. 1985. Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio* 60:131–145.
- Tagawa, H., E. Suzuki, and T. Partomihardjo. 1986. A list of plant species collected from the Krakatau Islands and adjacent areas, Indonesia. *Memoirs of the Kagoshima University Research Center for the South Pacific* 7:1–21.
- Taylor, B. W. 1957. Plant succession on recent volcanoes in Papua. *Journal of Ecology* 45:233–243.
- Thornton, I. W. B. 1984. Krakatau—the development and repair of a tropical ecosystem. *Ambio* 13:217–225.
- , editor. 1986. 1985 Zoological Expedition to the Krakataus: preliminary report. Miscellaneous Series Number 2, Department of Zoology, La Trobe University, Melbourne, Australia.
- Thornton, I. W. B., R. A. Zann, P. A. Rawlinson, C. R. Tideman, A. S. Adikerana, and A. H. T. Widjaya. 1988. Colonization of the Krakatau Islands by vertebrates: equilibrium, succession, and possible delayed extinction. *Proceedings of the National Academy of Sciences (USA)* 85: 515–518.
- Treub, M. 1888. Notice sur la nouvelle flore de Krakatau. *Annales du Jardin Botanique de Buitenzorg* 7:213–223.
- Verbeek, R. D. M. 1885. *Krakatau, Batavia, Java*. (Original in Dutch, but see partial translation to English in T. Simkin and R. S. Fiske (1983). *Krakatau 1883—the volcanic eruption and its effects*. Smithsonian Institution Press, Washington, D.C., USA.)
- Whitehead, D. R., and C. E. Jones. 1969. Small islands and the equilibrium theory of insular biogeography. *Evolution* 23:171–179.
- Whitmore, T. C. 1984. *Tropical rain forests of the Far East*. Second edition. Clarendon, Oxford, England.
- Whittaker, R. J. 1982. Aspects of the vegetation of Rakata. Pages 54–82 in J. R. Flenley and K. Richards, editors. *The Krakatoa Centenary Expedition: final report*. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Whittaker, R. J., and J. R. Flenley. 1982. The flora of Krakatau. Pages 9–53 in J. R. Flenley and K. Richards, editors. *The Krakatoa Centenary Expedition: final report*. Miscellaneous Series Number 25, Department of Geography, University of Hull, Hull, England.
- Whittaker, R. J., and K. Richards. 1986. Floral surveys on the Krakatau islands: their duration and efficiency. Pages 182–186 in M. Bush, P. Jones, and K. Richards, editors. *The Krakatoa Centenary Expedition 1983: final report*. Miscellaneous Series Number 33, Department of Geography, University of Hull, Hull, England.
- Whittaker, R. J., K. Richards, H. Wiriadinata, and J. R. Flenley. 1984. Krakatau 1883 to 1983: a biogeographical assessment. *Progress in Physical Geography*, 8(1):61–81.
- Williamson, M. 1981. *Island populations*. Oxford University Press, Oxford, England.

APPENDIX I.

THE COMPLETE PLANT LIST FOR RAKATA,
SERTUNG, AND R. KECIL 1883-1983.

Survey data are combined as shown by the collection periods in Table 2. Upper case R, S, and K indicate species recorded from Rakata, Sertung, and R. Kecil respectively. Lower case r, s, and k indicate species recorded, but with some ambiguity in Docters van Leeuwen (1936) as to the year. "?" = uncertain identification. "*" = identification to genus only, when other species in the same genus have been found. "I" species recorded as having been introduced by humans. ?, *, and I are placed in the column of the island on which they were recorded. Names in parentheses indicate synonyms, and in square brackets, either varieties or grouped species. Further taxonomic notes are given at end of table.

Sources: Ernst 1908, Docters van Leeuwen 1923, 1929, 1936, Steenis 1938, Boedijn 1940, Borssum Waalkes 1960, Whittaker and Flenley 1982, Tagawa 1984, Tagawa et al. 1986, Bush et al. 1986a.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|------|------|------|------|------|------|---------|
| P T E R I D O P H Y T A | | | | | | | | | | | | | |
| ANGIOPTERIDACEAE | | | | | | | | | | | | | |
| <i>Angiopteris evecta</i> (Forst.) Hoffm. | | | | R | R | R | R | R | | | R | | R |
| <i>Angiopteris lancifoliata</i> v. A. v. R. | | | | | | | | | | | R | | |
| <i>Angiopteris palmiformis</i> (Cav.) C. Chr. | | | | | | | | | | | | R | |
| ASPLENIACEAE | | | | | | | | | | | | | |
| <i>Asplenium longissimum</i> Bl. | | | | | R | R | R | R | | | | | |
| <i>Asplenium macrophyllum</i> Sw. | | | | | | | | | | | R | R | R |
| <i>Asplenium nidus</i> L. | | | | RS | R | R | Rs | RsK | | R | R | R | RSK |
| <i>Asplenium thunbergii</i> Kunze (<i>Asplenium decorum</i> G. Kuntze) (<i>Asplenium belangeri</i> O.K. sensu auct. - - jav.) | | | | | R | | R | r | | R | R | R | R |
| BLECHNACEAE | | | | | | | | | | | | | |
| <i>Blechnum orientale</i> L. | | R | R | | R | | | | | | | | |
| <i>Stenochlaena palustris</i> (Burm.f.) Bedd. | | R | R | | RS | R | R | RSK | RSK | | RSK | R | RSK RSK |
| CYATHEACEAE | | | | | | | | | | | | | |
| <i>Cyathea contaminans</i> (Hook.) Copel. (<i>Alsophila glauca</i> J.Sm.) | | | | R | R | R | R | R | | | R | | |
| <i>Cyathea</i> sp. | | | | | | | | | | | | * | * |
| Genus ignota | | | | | | | | R | | | | | |
| CRYPTOGRAMMACEAE | | | | | | | | | | | | | |
| <i>Onychium siliculosum</i> C. Chr. | | R | R | R | | | | | | | | | |
| DAVALLIACEAE | | | | | | | | | | | | | |
| <i>Davallia denticulata</i> (Burm.f.) Mett. | | | | | RS | R | R | Rs k | RSK | | R | R | RSK |
| <i>Davallia solida</i> (Forst.) Sw. | | | | | | | | | | | R | R | |
| <i>Davallia trichomanoides</i> Bl. (<i>Davallia dissecta</i> J.Sm.) | | | | | | | | | | | | | SK |
| <i>Humata heterophylla</i> (Sm.) Desv. | | | | | R | R | R | R | | | R | R | R |
| <i>Humata repens</i> (L.f.) Diels | | | | | | | | | | | R | R | K |
| <i>Scyphularia pentaphylla</i> F'ee | | | | | | | | | | | R | R | |
| DENNSTAEDTIACEAE | | | | | | | | | | | | | |
| <i>Lindsaea repens</i> (Barry) Thwaites (<i>Lindsaea pectinata</i> Bl.) | | | | | | R | | | | | | | |
| <i>Pteridium aquilinum</i> (L.) Kuhn (<i>Eupteris aquilina</i> Newm.) | | R | R | | | R | R | R | R | | | | |
| <i>Microlepia speluncae</i> (L.) Moore | | | | | S | | | | | | | S | R K |
| <i>Sphenomeris chinensis</i> (L.) Maxon (<i>Stenolama chusanum</i> Chun.) | | | | | R | R | R | R | | | | | |
| DRYOPTERIDACEAE | | | | | | | | | | | | | |
| <i>Diplazium polypodioides</i> Bl. | | | | | R | | | | | | R | R | ? |
| <i>Pleocnemia conjugata</i> (Bl.) Pr. | | | | | | | | | | | R | R | K RS |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|------|------|------|------|------|------|------|
| <i>Pleocnemia cf. hemiteliiformis</i> (Racib) Holtt. | | | | | | | | | | | R | | RSK |
| <i>Pleocnemia irregularis</i> (Pr.) Holtt. (<i>Arcypteris irregularis</i> (Pr.) Holtt.) | | | | | | | | | | R | | R | |
| <i>Stenosemia aurita</i> (Sw.) Pr. | | rS | r | R | Rs | Rs | | | | | R | S | |
| <i>Tectaria dissecta</i> (Forst.) Lellinger (<i>Ctenitis dissecta</i> (Forst.) Ching) | | | | | | | | | R | R | R | K | K |
| <i>Tectaria herpetocaulos</i> Holtt. | | | | | | | | | | | | R | K |
| <i>Tectaria melanocaula</i> Copel. (<i>Aspidium melanocaulon</i> Bl.) | | R | R | R | R | R | | | | R | R | R | |
| <i>Tectaria siifolia</i> (<i>Tectaria polymorpha</i> Wall. Copel.) | | | | | | | | | | R | | | K |
| <i>Tectaria</i> sp. | | | | | | | | | | | | * | |
| EQUISETACEAE | | | | | | | | | | | | | |
| <i>Equisetum debile</i> Roxb. | | | R | R | R | R | R | | | | | | |
| GLEICHENIACEAE | | | | | | | | | | | | | |
| <i>Dicranopteris currani</i> Copel. | | | | | | | | | | | R | R | |
| <i>Dicranopteris linearis</i> (Burm. f.) Underw. | | | | | | | | | | | | S | |
| GRAMMITIDACEAE | | | | | | | | | | | | | |
| <i>Ctenopteris alata</i> (Bl.) Holtt. (<i>Prosaptia alata</i> Christ.) | | | | | | | | | | | R | R | R |
| <i>Ctenopteris blechnoides</i> (Grev.) Wagner - + Grether (<i>Ctenopteris moultoni</i> (Copel.) Adelbert) (<i>Polypodium moultoni</i> Copel.) | | | | | | | | | | R | | | |
| <i>Grammitis cervicornis</i> (v.A.v.R.) Adelbert | | | | | | | | | | R | | | |
| HYMENOPHYLLACEAE | | | | | | | | | | | | | |
| <i>Crepidomanes bipunctatum</i> (Poir.) Copel. (<i>Trichomanes bipunctatum</i> Poir.) | | | | R | R | R | | | | R | | R | |
| <i>Reediella humilis</i> (Fasd.) Pic. Ser. (<i>Crepidopteris humilis</i> (Forst.) Copel.) (<i>Trichomanes humile</i> Forst.) | | R | R | R | R | R | R | | | R | | R | |
| <i>Hymenophyllum cf. javanicum</i> | | | | | | | | | | | | | R |
| LYCOPODIACEAE | | | | | | | | | | | | | |
| <i>Lycopodium carinatum</i> Desv. | | | | | | | | | | | R | R | |
| <i>Lycopodium cernuum</i> L. | | R | R | R | R | R | R | R | | | | | |
| <i>Lycopodium nummularifolium</i> | | | | | | | | | | | | | R |
| <i>Lycopodium squarrosum</i> Forst. | | | R | R | | | R | | | | | | |
| OLEANDRACEAE | | | | | | | | | | | | | |
| <i>Nephrolepis acuminata</i> (Houtt.) Kuhn | | | | | | | | | | | R | | |
| <i>Nephrolepis biserrata</i> (Sw.) Schott (<i>Nephrolepis exaltata</i> (Sw.) Schott) | R | R | K | RSK | RS | R | R | RSK | RSK | R | R | SK | RSK |
| <i>Nephrolepis hirsutula</i> (Forst.) Pr. | | | | R | | | | | | | R | SK | RS |
| OPHIOGLOSSACEAE | | | | | | | | | | | | | |
| <i>Ophioglossum pendulum</i> L. | | | | | R | R | | | | | R | | |
| <i>Ophioglossum reticulatum</i> L. | | R | | RS | R | R | Rs k | Rs k | | | | | |
| <i>Ophioglossum</i> sp. | | | | | | | | | | * | | | |
| POLYPODIACEAE | | | | | | | | | | | | | |
| <i>Aglaomorpha heraclea</i> (Kze) Copel. (<i>Polypodium heracleum</i> Kze) | | | | R | R | | R | | | | R | | R |
| <i>Belvisia callifolia</i> (Chr.) Copel. (<i>Hymenolepis callifolia</i> Chr.) | | | | | R | R | R | R | R | | | | |
| <i>Belvisia revoluta</i> (Bl.) Copel. (<i>Hymenolepis revoluta</i> Bl.) | | | | R | R | R | R | R | | | R | | |
| <i>Belvisia</i> sp. | | | | | | | | | | * | | | |
| <i>Crypsinus trilobus</i> (Houtt.) Copel. | | | | | | | | | | | R | R | R |
| <i>Drymoglossum piloselloides</i> (L.) Pr. | | | | R | R | R | | | | | R | R | SK |
| <i>Drynaria quercifolia</i> (L.) J. Sm. [+ <i>Drynaria sparsisora</i> (Desv.) Moore] | R | R | RS | R | R | R | RSK | RsK | | RS | R | RSK | RSK |
| <i>Lecanopteris sinuosa</i> (Wall. ex Hooker) Copel. (<i>Phymatodes sinuosa</i> (Wall.) J. Sm.) (<i>Polypodium sinuosum</i> Wall.) | | | | | | | | R | | | | | RS |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|------|------|------|------|------|------|------|
| <i>Cyclosorus cf. interruptus</i> (Willd.) Ito | | | | | | | | | | | | | S |
| <i>Macrothelypteris polypodioides</i> (Hook.) Ching | | | | | | | | | | | | R K | |
| <i>Macrothelypteris setigera</i> (Bl.) Ching (<i>Thelypteris setigera</i>) | | | | | | | | | | | R | | |
| <i>Macrothelypteris torresiana</i> (Gaud.) Ching (<i>Dryopteris uliginosa</i> C. Chr.) | R | R | R | RS | | | | K | K | | | | |
| <i>Metathelypteris flaccida</i> (Bl.) Holttum (<i>Dryopteris flaccida</i> O.K.) | | | | RS | R | R | Rs | Rs | | | | | |
| <i>Pneumatopteris truncata</i> (Poir.) Holttum (<i>Cyclosorus truncatus</i> (Poir.) Farw.) | | | | | | | | | | | R | | K |
| <i>Sphaerostephanos penniger</i> (Hook.) Holttum (<i>Cyclosorus megaphyllus</i> (Mett.) Ching) (<i>Dryopteris megaphylla</i> C. Chr.) (<i>Thelypteris megaphylla</i> (Mett.) K. Iwats.) | | | | R | R | R | R | R | | | R | R | |
| <i>Sphaerostephanos polycarpus</i> (Bl.) Copel. (<i>Mesochlaena polycarpa</i> Bedd.) | | | | S | | | | | | | | | |
| <i>Sphaerostephanos unitus</i> (L.) Holttum (<i>Dryopteris unita</i> O.K.) | R | R K | RS | RS | R | R | RSK | rSK | | | | | |
| VITTARIACEAE | | | | | | | | | | | | | |
| <i>Antrophyum reticulatum</i> (Forst.) Kaulf. [+ <i>Antrophyum callifolium</i> Bl.] | | | | R | | r | R | r | | R | R | R | RSK |
| <i>Vittaria angustifolia</i> Bl. | | | | | | | | | | | | | K |
| <i>Vittaria elongata</i> Sw. | | | | | | | | | | | R | | RSK |
| <i>Vittaria ensiformis</i> Sw. | | | | | | | | | | R | | R | |
| <i>Vittaria zosterifolia</i> Willd. | | | | | R | R | r | r | | | | | |
| SPERMATOPHYTA | | | | | | | | | | | | | |
| AIZOACEAE | | | | | | | | | | | | | |
| <i>Sesuvium portulacastrum</i> (L.) L. | | | S | S | | | s | s | | | | | |
| AMARANTHACEAE | | | | | | | | | | | | | |
| <i>Amaranthus spinosus</i> L. | | | | | | | | | | I | | | |
| <i>Cyathula prostrata</i> (L.) Bl. | | | | I | | | | | | R | | | |
| AMARYLLIDACEAE | | | | | | | | | | | | | |
| <i>Crinum asiaticum</i> L. | | | K | S | | | RS | RS | | R K | R | R | R |
| ANACARDIACEAE | | | | | | | | | | | | | |
| <i>Buchanania arborescens</i> (Bl.) Bl. | | | | | | | | | | | R | RSK | RSK |
| <i>Gluta renghas</i> L. | | | SK | | | | S | Rs | | | | | |
| <i>Mangifera indica</i> L. | | | | I | I | I | I | I | | | R | R | K |
| <i>Spondias mombin</i> L. (<i>Spondias lutea</i> L.) | | | | S | | | | S | | | | | |
| <i>Spondias pinnata</i> (L.F.) Kurz (<i>Spondias mangifera</i> Willd.) | | | S | | | | | | | | | | |
| APOCYNACEAE | | | | | | | | | | | | | |
| <i>Alstonia scholaris</i> (L.) R. Br. | | | | | | | | | | | R | RS | R |
| <i>Cerbera manghas</i> L. | R | R K | RS | RS | R | r | rsk | rsk | | | | S | R |
| <i>Ochrosia oppositifolia</i> (Lmk) K. Schum. (<i>Ochrosia salubris</i> Bl.) | | | | S | | | | | | | | | |
| ARACEAE | | | | | | | | | | | | | |
| <i>Alocasia longiloba</i> Miq. | | | | | R | R | R | R | | | | | |
| ARALIACEAE | | | | | | | | | | | | | |
| <i>Arthropphyllum javanicum</i> Bl. | | | | | | | | | | | R | RSK | R |
| <i>Polyscias nodosa</i> (Bl.) Seem. | | | | S | | | RsK | | | RSK | | | |
| <i>Schefflera polybotrya</i> (Miq.) Vig. | | | | | | | | | | R | R | R | R |
| ARISTOLOCHIACEAE | | | | | | | | | | | | | |
| <i>Aristolochia tagala</i> Cham. | | | | RS | R | R | RSK | RSK | | | | | RSK |
| ASCLEPIADACEAE | | | | | | | | | | | | | |
| <i>Ceropegia curviflora</i> Hassk. | | | | S | | | | | | | | | |
| <i>Cynanchum ovalifolium</i> Wight (<i>Cynanchum laeve</i> (Bl.) K. Schum.) | | | | | R | R | Rs | RsK | | R | | SK | RSK |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|------|------|------|------|------|------|------|
| <i>Emilia sonchifolia</i> (L.)DC. ex Wight (<i>Senecio sonchifolius</i> (L.)Moench) | | | | | | | | | | | R | | R |
| <i>Erechtites hieracifolia</i> (L.)Rafin. ex DC. | | | | RS | RS | | | R | | | | S | |
| <i>Erechtites valerianifolia</i> (Wolf)DC. | | | | | R | | r | R | | | | | |
| <i>Erigeron linifolius</i> Willd. | ? | R | K | R | | | | | | | | | |
| <i>Erigeron</i> sp. | | | | | | | | | | | | | * |
| <i>Eupatorium odoratum</i> L. | | | | | | | | | | | R | RSK | RSK |
| <i>Gynura procumbens</i> (Lour.)Merr. | | | | R | R | r | r | k | r | k | R | R | S |
| <i>Mikania cordata</i> (Burm.f.)B.L.Robinson | | | | RS | S | R | r | Rs | r | sK | R | K | R |
| <i>Pluchea indica</i> (L.)Less. | ? | R | K | RSK | RS | R | R | RSK | RSK | R | R | RSK | R |
| <i>Porophyllum ruderale</i> (Jacq.)Cass. | | | | | | | | | | | | R | R |
| <i>Synedrella nodiflora</i> (L.)Gaertn. | | | | I | | | | | | | | | |
| <i>Vernonia arborea</i> Buch.-Ham. | | | | | R | r | R | r | | | R | | R |
| <i>Vernonia cinerea</i> (L.)Less. | | R | K | R | K | RS | R | R | RSK | RSK | R | R | RS |
| <i>Wedelia biflora</i> (L.)DC. | R | R | K | RSK | RS | R | R | RSK | RSK | RSK | R | RS | RSK |
| CONVOLVULACEAE | | | | | | | | | | | | | |
| <i>Ipomoea alba</i> L. | | | | | | | | | | | | | S |
| <i>Ipomoea digitata</i> L. | | | | S | | | | S | S | | | | |
| <i>Ipomoea glaberrima</i> Boj. | | | | RSK | RS | R | R | RSK | RSK | | | | |
| <i>Ipomoea gracilis</i> R.Br. | | | | RSK | RS | R | R | RSK | RSK | RSK | | K | K |
| <i>Ipomoea pes-caprae</i> (L.)R.Br. | R | R | K | RSK | RS | R | R | RSK | RSK | RSK | R | RSK | RSK |
| <i>Ipomoea stolonifera</i> (Cyr.)Gmel. | | | | | | | | | | | | | R |
| <i>Ipomoea tuba</i> (Schlechtend.)G.Don | | | | | | | | | | | R | R | |
| <i>Merremia peltata</i> (L.)Merr. | | | | | | | | | | | R | | R |
| <i>Operculina</i> sp. | | | | | R | R | R | R | | | | | |
| CRASSULACEAE | | | | | | | | | | | | | |
| <i>Kalanchoe pinnata</i> (Lmk)Pers. | | | | I | | | | | | | | | |
| CUCURBITACEAE | | | | | | | | | | | | | |
| <i>Bryonopsis laciniosa</i> (L.)Naud. | | | | | R | | | | | | R | | |
| <i>Coccinia grandis</i> (L.)Voigt (<i>Coccinia cordifolia</i> Auct. non Cogn.) | | | | | | | | | | | R | R | K |
| <i>Luffa cylindrica</i> Roem. | | | R | RS | | | | s | | | | | |
| <i>Luffa</i> sp. | | | | | | | | | | | * | | |
| <i>Melothria</i> sp. | | | | | | | | | | | R | | |
| <i>Trichosanthes bracteata</i> (Lmk)Voigt | | | | RSK | RS | | r | r | s | k | r | s | k |
| CYCADACEAE | | | | | | | | | | | | | |
| <i>Cycas rumphii</i> Miq. | | | R | K | RS | R | R | RSK | RSK | S | R | R | R |
| CYPERACEAE | | | | | | | | | | | | | |
| <i>Cyperus cylindrostachys</i> Boeck. | | | | | R | | | | | | | | |
| <i>Cyperus javanicus</i> Hoult. (<i>Cyperus pennatus</i> Lamk) | R | RSK | RSK | RS | R | R | RSK | RSK | | K | R | | |
| <i>Cyperus kyllingia</i> Endl. (<i>Kyllinga monocephala</i> Rottb.) | | | | | I | | | | | | | | |
| <i>Cyperus odoratus</i> L. | | | | | | | | | R | | | | |
| <i>Cyperus pedunculatus</i> (R.Br.)Kern (<i>Remirea maritima</i> Aubl.) | | R | R | RS | | | | SK | Rs | k | | | RS |
| <i>Cyperus uncinatus</i> Poir. | | | | | | R | | | | | | | |
| <i>Fimbristylis cymosa</i> R. Br. (<i>Fimbristylis spathacea</i> Roth.) | R | R | K | RS | RS | R | R | RSK | RSK | R | R | | RS |
| <i>Fimbristylis</i> sp. | | | | | | | | | | | | | * |
| <i>Scleria ciliaris</i> Nees | | | | | | | | | | | | S | |
| DIOSCOREACEAE | | | | | | | | | | | | | |
| <i>Dioscorea bulbifera</i> L. | | | | | | | | | S | | | | |
| <i>Dioscorea nummularia</i> Lamk (<i>Dioscorea oppositifolia</i> L.) | | | | S | | | R | | | | | | |
| <i>Dioscorea</i> spp. | | | | | | | | | | | * | ** | |
| ELAEAGNACEAE | | | | | | | | | | | | | |
| <i>Elaeagnus latifolia</i> L. | | | | | | | | | | | R | K | K |
| ELAEOCARPACEAE | | | | | | | | | | | | | |
| <i>Elaeocarpus glaber</i> Bl. | | | | | | | | | | | R | | |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|------|------|------|------|------|------|---------|
| EUPHORBIACEAE | | | | | | | | | | | | | |
| <i>Acalypha indica</i> L. | | | I | I | | | | | | | | | |
| <i>Antidesma bunius</i> (L.) Spreng. | | | | | | | R | | | | | | |
| <i>Antidesma ghaesembilla</i> Gaertn. | | | | | | | | | | | R | | |
| <i>Antidesma montanum</i> Bl. | | | | | | | | | | | R | RSK | RSK |
| <i>Breynia cernua</i> (Poir.) M.A. | | | S | | | | s | s | | | | SK | |
| <i>Bridelia monoica</i> (Lour.) Merr. (<i>Bridelia tomentosa</i> Bl.) | | | S | | | | Rs | rs | | R | R | R | K RSK |
| <i>Bridelia stipularis</i> (L.) Bl. cf. <i>Bridelia</i> sp. (not <i>B. monoica</i>) | | | | | | R | Rs | RsK | | | | S | ** |
| <i>Claoxylon polot</i> (Burm.f.) Merr. | | | | | R | R | rS | rs | | | | | |
| <i>Euphorbia atoto</i> Forst.f. | R | K | RSK | R | R | R | RSK | RSK | | S | | S | |
| <i>Euphorbia hirta</i> L. | | | | | | | | I | | | | | |
| <i>Euphorbia thymifolia</i> L. | | | | | | | | I | | | | | |
| <i>Excoecaria agallocha</i> L. | | K | SK | S | R | R | RS | s | | | | | |
| <i>Glochidion borneense</i> (M.A.) Boerl. | | | | | | | | | | | R | | |
| <i>Glochidion</i> sp. | | | | | | | | | | | * | * | * |
| <i>Homalanthus populneus</i> Pax | | | R | R | | R | R | R | | R | R | R | R |
| <i>Macaranga tanarius</i> (L.) M.A. | K | RSK | RS | R | R | R | RSK | RSK | | RSK | R | RSK | RSK |
| <i>Mallotus multiglandulosa</i> (Bl.) Rchb.f. & Zoll. (<i>Mallotus moluccanus</i> M.A.) | | | S | S | | | s | sK | | | | | |
| <i>Mallotus</i> sp. | | | | | | | | | | | | | * |
| <i>Manihot esculenta</i> Crantz (<i>Manihot utilisima</i> Pohl) | | | | I | | | | | | I | | | |
| <i>Phyllanthus indicus</i> (Dalz.) M.A. | | | | | | | | | | | R | | |
| <i>Phyllanthus microcarpus</i> (Benth.) M.A. cf. <i>Phyllanthus</i> sp. | | | | | | | | | | | R | | * |
| <i>Ricinus communis</i> L. | | | | I | | | | | | | | | |
| FLAGELLARIACEAE | | | | | | | | | | | | | |
| <i>Flagellaria indica</i> L. | | | | | | R | RS | RSK | R | R | R | RSK | RSK |
| GESNERIACEAE | | | | | | | | | | | | | |
| <i>Aeschynanthus longiflorus</i> (Bl.) DC. (<i>Trichosporum longiflorus</i>) | | | | | | | | | | | R | | |
| <i>Aeschynanthus pulchrum</i> Bl. (<i>Trichosporum pulchrum</i> Bl.) | | | | R | | | R | | | | | | |
| <i>Aeschynanthus radicans</i> Jack var <i>pulcher</i> - - (Bl.) G. Don | | | | | | | | | K | | R | R | R |
| <i>Aeschynanthus volubilis</i> Jack (<i>Trichosporum volubile</i> Nees) | | | | R | R | R | R | | | R | | | |
| <i>Cyrtandra sulcata</i> Bl. [+ <i>Cyrtandra sandei</i> De Vr.] | | R | RS | R | R | R | Rs | Rs | | R | R | R | R |
| <i>Didymocarpus barbata</i> Jack <i>Didymocarpus</i> sp. | | | | | | | | | R | | | * | |
| GNETACEAE | | | | | | | | | | | | | |
| <i>Gnetum gnemon</i> L. | | | | I | I | I | I | I | | | R | SK | SK |
| GOODENIACEAE | | | | | | | | | | | | | |
| <i>Scaevola taccada</i> (Gaertn.) Roxb. (<i>Scaevola frutescens</i> Krause) (<i>Scaevola sericea</i> Vahl) (<i>Scaevola koenigii</i> Vahl) | R | RSK | RSK | RS | R | R | RSK | RSK | | R | K | R | RSK RSK |
| GRAMINEAE | | | | | | | | | | | | | |
| <i>Cyrtococcum oxyphyllum</i> (Hochst. ex - - Steud.) Stapf (<i>Panicum pilipes</i> Nees & Arn.) | | | | | | | R | | | | | | |
| <i>Cyrtococcum patens</i> (L.) A. Camus (<i>Panicum trigonum</i> Retz.) | | | | | | | R | r | | | R | | |
| <i>Dactyloctenium aegyptium</i> (L.) Richt. | | | | | | | | I | | | | | |
| <i>Digitaria rhopalotricha</i> Buse. | | | | | | | | R | | | | | |
| <i>Eleusine indica</i> (L.) Gaertn. | | | | I | I | I | I | | | I | | | |
| <i>Eragrostis amabilis</i> O.K. | | | | | | | | I | | | | | |
| <i>Eriochloa proceva</i> (Retz.) C.E. Hubb. (<i>Eriochloa ramosa</i> (Retz.) O.K.) | | | | I | | | | | | | | | |
| <i>Imperata cylindrica</i> (L.) Beauv. | R | K | R | K | RS | R | R | RSK | RSK | R | R | S | RSK |
| <i>Ischaemum muticum</i> L. | R | K | RSK | RS | R | R | R | RSK | RSK | RSK | | R | RSK |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|------|-------|-------|------|------|------|------|
| <i>Lepturus repens</i> (Forst.f.)R.Br. (<i>Monerma repens</i> (Forst.f.)Beauv.) | | | | S | | | | s | s | | | | |
| <i>Neyraudia madagascariensis</i> Hook.f. [var. <i>zollingeri</i> Hook.f.] | R | RSK | | rS | r | R | | r s k | r s k | | | | |
| <i>Oplismenus compositus</i> (L.)Beauv. (<i>Hoplismenus compositus</i>) | | | | RS | R | R | | RsK | RsK | | R | R K | RSK |
| <i>Oplismenus undulatifolius</i> (Ard.)Beauv. | | | | | | | | | | | | S | |
| <i>Paspalum conjugatum</i> Berg. | | | | | | | | R | R K | | | | R |
| <i>Paspalum vaginatum</i> Swartz | | | | S | | | | | | | | | |
| <i>Pennisetum macrostachyum</i> (Brog.)Trin. | R | R K | RSK | | | | | R | S | | | | |
| <i>Pogonatherum paniceum</i> (Lamk)Hack. | | R K | RSK | RS | R | R | | RSK | RSK | R | R | S | RS |
| <i>Saccharum officinarum</i> L. | | | | | | | | | | I | | | |
| <i>Saccharum spontaneum</i> L. | | R K | RSK | RS | R | R | | RSK | RSK | R | RSK | R | RS |
| <i>Spinifex littoreus</i> (Burm.f.)Merr. | | R K | RSK | RS | R | R | | RSK | RSK | | RS | | S |
| <i>Sporobolus berteroi</i> Hitche. | | | | I | | | | | | | | | S |
| <i>Thuarea involuta</i> (Forst.f.)R.& S. | | | | RS | | | | S | s | | RSK | | |
| GUTTIFERAE | | | | | | | | | | | | | |
| <i>Calophyllum inophyllum</i> L. | R | SK | RSK | RS | R | R | | RSK | RSK | | RSK | R | RSK |
| HERNANDIACEAE | | | | | | | | | | | | | |
| <i>Hernandia peltata</i> Meissn. [+ <i>Hernandia sonora</i> L.] | R | | RSK | RS | | R | | RSK | RSK | | RSK | R | K |
| HYDROCHARITACEAE | | | | | | | | | | | | | |
| <i>Halophila ovalis</i> (R.Br.)Hook.f. | | | | S | | | | S | s | | | | |
| LABIATAE | | | | | | | | | | | | | |
| <i>Hyptis brevipes</i> Poit. | | | R | r | r | | | R | | | | | |
| LAURACEAE | | | | | | | | | | | | | |
| <i>Cassytha filiformis</i> L. | | | RSK | RSK | RS | R | R | RSK | RSK | | R K | R | RS |
| LECYTHIDACEAE | | | | | | | | | | | | | |
| <i>Barringtonia asiatica</i> (L.)Kurz | | R K | RSK | RS | R | R | | RSK | RSK | RS | RSK | R | RS |
| <i>Planchonia valida</i> (Bl.)Bl. | | | | | | | | | | | | | S |
| LEGUMINOSAE | | | | | | | | | | | | | |
| <i>Adenanthera pavonina</i> L. | | | | | | | | | | | | | S |
| <i>Aeschynomene indica</i> L. | | | | S | | | | | | | | | |
| <i>Albizia chinensis</i> (Os.)Merr. | R | | | | | | | R | | | | | |
| <i>Albizia lebbek</i> (L.)Bth. | | | | | | | | | R K | | R | R | K |
| <i>Albizia retusa</i> Bth. | | | R | r | r | | | | | | RS | | |
| <i>Caesalpinia bonduca</i> (L.)Roxb. (<i>Caesalpinia bonducella</i> Flem.) [+ <i>Caesalpinia crista</i> L.] | | | S | S | R | R | | RSk | RSK | | RS | R | RS |
| <i>Canavalia maritima</i> (Aubl.)Urb. | | RSK | RSK | RS | R | R | | RSK | RSK | RS | RS | | RSK |
| <i>Canavalia microcarpa</i> (DC.)Piper (<i>Canavalia obtusifolia</i> Auct. non DC.) | | | | | | | | | | | | R | R K |
| <i>Cassia siamea</i> Lmk | | | R | | R | | | | | | | | |
| <i>Crotolaria mucronata</i> Desv. (<i>Crotolaria striata</i> DC.) | | | | S | | | | | | | | | |
| <i>Dalbergia candenatensis</i> (Dennst.)Prain | | K | K | | R | R | | | | | | S | S |
| <i>Derris elliptica</i> (Roxb.)Bth. | | | | | | | | | | | R | | |
| <i>Derris heterophylla</i> (Willd.)Back. | | | RSK | RS | R | R | | Rs k | Rs k | | R | | |
| <i>Derris scandens</i> (Roxb.)Bth. | | | | K | | | | | | | | | |
| <i>Derris trifoliata</i> Lour. | | | | | | | | | | | | R | |
| <i>Desmodium triflorum</i> (L.)DC. | | | | | | | | | I | | | | |
| <i>Desmodium umbellatum</i> (L.)DC. | | | K | RSK | RS | R | R | RSK | RSK | S | RSK | R | R K |
| <i>Dolichos</i> sp. | | | | | | | | | | | R | | |
| <i>Entada phaseoloides</i> (L.)Merr. | | S | K | S | | R | | RSK | RSK | | R | R | K |
| <i>Erythrina fusca</i> Lour. | | | K | RS | | | | | K | | | | |
| <i>Erythrina orientalis</i> (L.)Murr. (<i>Erythrina variegata</i> L. var. - - <i>orientalis</i> Merr.) | R | | K | RSK | RS | R | R | r s | r s K | | RS | R | R |
| <i>Indigofera zollingeriana</i> Miq. | | | | RSK | | | | R | R | | | | |
| <i>Intsia amboinensis</i> Thou. | | | | K | | | | | | | | | |
| <i>Leucaena leucocephala</i> (Lmk)De Wit | | | | | | | | | | | | | SK |
| <i>Mucuna acuminata</i> DC. | | | R | | R | R | R | R | R | | | | S |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 | |
|---|------|------|------|------|------|-------|-------|-------|------|------|------|------|------|-----|
| <i>Mucuna gigantea</i> (Willd.) DC. | | | | RS | R | R | | RSK | RSK | R | K | R | RS | RSK |
| <i>Mucuna pruriens</i> (L.) DC. | | | S | | | | | | | | | | | |
| <i>Mucuna</i> sp. | | | | | | | | | | | | | | * |
| <i>Phaseolus adenanthus</i> G.F. May. | | | | | | R | RS | RSK | | | | | | |
| <i>Pithecellobium umbellatum</i> (Vahl) Bth. (<i>Pithecolobium umbellatum</i> Bth.) | | | RS | RS | | | | R | K | S | | R | | |
| <i>Pongamia pinnata</i> (L.) Pierre | | K | RSK | RS | | r | r s k | R s k | | RSK | R | R | RS | |
| <i>Serianthus grandiflora</i> Bth. | | | | S | | | S | S | | | | | | |
| <i>Sophora tomentosa</i> L. | | K | RSK | S | | | s k | s k | | | | R | | |
| <i>Vigna marina</i> (Burm.f.) Merr. | R | K | RSK | RS | R | R | RSK | RSK | R | R | | R | K | RSK |
| LILIACEAE | | | | | | | | | | | | | | |
| <i>Pleomele elliptica</i> (Thunb.) N.E. Br. | | | | | R | R | r | r | | | R | | | |
| <i>Smilax zeylanica</i> L. | | | | | R | R | R | | | R | R | R | R | |
| MALPIGHIACEAE | | | | | | | | | | | | | | |
| <i>Tristellateia australasiae</i> A. Rich. | | | | | | | | | K | | | | | |
| MALVACEAE | | | | | | | | | | | | | | |
| <i>Hibiscus tiliaceus</i> L. | R | K | RSK | RS | R | R | RSK | RSK | RS | RSK | R | RSK | RSK | |
| <i>Thespesia populnea</i> (L.) Soland. ex Correa | | | R | S | R | r | r s | r s | | | | | | |
| MELASTOMATACEAE | | | | | | | | | | | | | | |
| <i>Clidemia hirta</i> (L.) D. Don | | | | S | | | S | S | | R | R | R | R | |
| <i>Medinilla eximia</i> | | | | | | | | | | | R | R | R | |
| <i>Medinilla cf. pterocaula</i> Bl. | | | | | | R | R | | | | | | | |
| <i>Medinilla speciosa</i> (Reinw. ex Bl.) Bl. | | | | | | | | | | R | | | RS | |
| <i>Melastoma affine</i> D. Don (<i>Melastoma polyanthum</i> Bl.) | S | RSK | RS | R | R | RSK | RSK | | | R | K | R | S | S |
| MELIACEAE | | | | | | | | | | | | | | |
| <i>Dysoxylum arborescens</i> (Bl.) Miq. | | | | | | | | | | | R | | | |
| <i>Dysoxylum gaudichaudianum</i> (A. Juss.) Miq. (<i>Dysoxylum amoorooides</i> Miq.) | | | | | | | | K | | | R | RSK | RSK | |
| <i>Melia azederach</i> L. | | | | | | | | SK | | | R | | | K |
| <i>Xylocarpus granatum</i> Koen. | | R | | | | | | | | | | | | K |
| <i>Xylocarpus moluccensis</i> Roem. | | | | | | | | S | | | | | | |
| MENISPERMACEAE | | | | | | | | | | | | | | |
| <i>Cyclea barbata</i> Miers | | | | | | | R | r | K | RS | | R | K | R |
| <i>Pericampylus glaucus</i> Miers | | | | | R | R | R | R | | | | | | |
| <i>Stephania japonica</i> (Thunb. ex Murr.) Miers [var. <i>discolor</i> (Miq.) Forman] | | | | | | | | | | | R | | | |
| <i>Tinospora glabra</i> (Burm.f.) Merr. (<i>Tinospora coriacea</i> (Bl.) Beumee) (<i>Tinospora crispa</i> (L.) Diels) | | | RS | R | R | RSK | RSK | R | R | R | | | RS | |
| MORACEAE | | | | | | | | | | | | | | |
| <i>Artocarpus elasticus</i> Reinw. ex Bl. | | S | S | | | | s k | s k | | | | | RSK | SK |
| <i>Artocarpus incisa</i> (Thunb.) L.f. | | | | | | | | | | I | | | | |
| <i>Ficus ampelas</i> Burm.f. | | | RS | R | R | RS | RS | R | R | R | R | RSK | SK | |
| <i>Ficus annulata</i> Bl. | | | | | | | | | | R | R | | R | |
| <i>Ficus asperiuscula</i> Kunth & Bouche (<i>Ficus leptorhyncha</i> Val.) | | | S | | | | | | | | | | | |
| <i>Ficus callosa</i> Willd. | | | S | | | Rs | s | | | | | S | | |
| <i>Ficus elastica</i> Roxb. | | | | | | | | | | R | | | | |
| <i>Ficus fistulosa</i> Reinw. ex Bl. | | R | K | RS | R | R | RSK | RSK | | R | R | RSK | RSK | |
| <i>Ficus fulva</i> Reinw. ex Bl. | R | K | R | K | RS | R | RSK | RSK | R | R | R | RSK | RSK | |
| <i>Ficus glomerata</i> Roxb. | | | | | | | | | | | | R | | |
| <i>Ficus heterophylla</i> L.f. | | | | | | | | | | | R | | | |
| <i>Ficus hirta</i> Vahl | | RS | | | | | | | R | | | | | |
| <i>Ficus hispida</i> L.f. | | K | RS | | R | r s k | R s k | | | R | R | S | K | |
| <i>Ficus lepigarpa</i> Bl. | | | | | | | | | | | | R | K | |
| <i>Ficus montana</i> Burm.f. (<i>Ficus quercifolia</i> Roxb.) | | | R | R | R | R | R | R | | R | R | R | R | K |
| <i>Ficus padana</i> Burm.f. (<i>Ficus toxicaria</i> L.) | R | K | Rs | Rs | R | r | r | r | | | | | | |
| <i>Ficus pubinervis</i> Bl. | | | | R | R | R | R | R | | R | R | RSK | RSK | |
| <i>Ficus retusa</i> L. | | | | R | R | R | | | | R | | | S | |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|------|------|------|------|------|------|-------|
| <i>Ficus ribes</i> Reinw. ex Bl. | | | | R | R | R | R | R | | | R | R | RS |
| <i>Ficus septica</i> Burm.f. | | K | SK | RS | R | R | RSK | RSK | R | RS | R | RS | RSK |
| <i>Ficus subulata</i> Bl. | | | | | R | R | R | R | | | R | | |
| <i>Ficus sumatrana</i> Miq. | | | | | | | | | | | | S | |
| <i>Ficus tinctoria</i> L.f. ssp. <i>gibbosa</i> - (Bl.) Corner (<i>Ficus gibbosa</i> Bl.) | | | | S | | | sk | sk | | R | R | RSK | RSK |
| <i>Ficus variegata</i> Bl. | | | | R | R | r | R | R | | R | R | R | K RSK |
| MUSACEAE | | | | | | | | | | | | | |
| <i>Musa acuminata</i> Colla (<i>Musa zebrina</i> Van Houtte ex Planch.) | | | | | | | R | | | R | R | R | R |
| <i>Musa paradisiaca</i> L. | | | | | | | | | I | I | | | |
| MYRSINACEAE | | | | | | | | | | | | | |
| <i>Ardisia humilis</i> Vahl [+ <i>Ardisia elliptica</i> Thunb.] | | | | | | | | RSK | | R | R | R | RSK |
| MYRTACEAE | | | | | | | | | | | | | |
| <i>Syzygium polyanthum</i> (Wight) Walp. (<i>Eugenia polyantha</i> Wight) | | | | | | | | | | | R | R | K R |
| NEPENTHACEAE | | | | | | | | | | | | | |
| <i>Nepenthes</i> sp. | | | | | | | | | R | | | | |
| NYCTAGINACEAE | | | | | | | | | | | | | |
| <i>Boerhavia erecta</i> L. | | | | | | | | | I | | | | |
| OLACACEAE | | | | | | | | | | | | | |
| <i>Ximenesia americana</i> L. | | | RS | S | | | RsK | rs | | | | | |
| ORCHIDACEAE | | | | | | | | | | | | | |
| <i>Acanthephippium parviflorum</i> Hassk. | | | | | | | | R | | | | | |
| <i>Acriopsis javanica</i> Reinw. | | | | | R | R | | | | | R | R | |
| <i>Agrostophyllum bicuspidatum</i> J.J.S. | | | | | R | R | R | R | | | | | |
| <i>Agrostophyllum denbergeri</i> J.J.S. | | | | | R | r | | | | R | R | R | R |
| <i>Appendicula reflexa</i> Bl. | | | | | | | | | | R | R | R | |
| <i>Arundina graminifolia</i> (D. Don) Hochr. (<i>Arundina speciosa</i> Bl.) | | R | K | R | K | RS | R | R | RSK | RS | | | S |
| <i>Bulbophyllum purpurascens</i> T. & B. | | | | | | | | R | R | | | | |
| <i>Bulbophyllum unguiculatum</i> Rchb.f. | | | | | | | | | | ? | | | |
| <i>Bulbophyllum</i> sp. | | | | | | | | | | | * | | |
| <i>Calanthe angustifolia</i> (Bl.) Lindl. | | | | | | | | | | | | | K |
| <i>Calanthe</i> sp. | | | | | | | | | | | * | | |
| <i>Coelogyne longifolia</i> Lindl. | | | | | | | | | | | | R | |
| <i>Coelogyne rochussenii</i> De Vr. | | | | | | | | | | | R | | R |
| <i>Cymbidium finlaysonianum</i> Lindl. | | K | R | | rs | r | r | r | | | | | R |
| <i>Cymbidium pubescens</i> Lindl. | | | | | S | | | R | | | | | |
| <i>Cymbidium simulans</i> Rolfe | | | | | | | | | | | R | | |
| <i>Dendrobium acuminatissimum</i> (Bl.) Lindl. | | | | | | | | | | | | R | |
| <i>Dendrobium crumenatum</i> Swartz | | | | | | R | r | R | R | ? | | RS | RS |
| <i>Dendrobium mutabile</i> (Bl.) Lindl. | | | | | | R | R | R | R | R | | R | R |
| <i>Dendrobium secundum</i> (Bl.) Lindl. | | | | | | R | R | R | R | | | R | |
| <i>Dendrobium</i> sp. (or spp.) | | | | | | | | | | | * | | |
| <i>Eria annulata</i> (Bl.) Bl. | | | | | | | | | | | | R | |
| <i>Eria obliterata</i> (Bl.) Rchb.f. | | | | | | | | | | | | | R |
| <i>Eria retusa</i> (Bl.) Rchb.f. | | | | | | | | | | | | | R |
| <i>Eulophia graminea</i> Lindl. | | | RS | | | | | | | | | S | |
| <i>Eulophia macrostachya</i> Lindl. | | | RS | R | R | | RSK | RSK | | | | | |
| <i>Eulophia squalida</i> Lindl. | | | | | | R | R | K | K | R | | R | |
| <i>Eulophia zollingeri</i> (Rchb.f.) J.J.S. | | | | | | | | | | R | | | |
| <i>Galeola kuhlii</i> (Rchb.f.) Rchb.f. | | | | | | | | | | | | | |
| <i>Geodorum purpureum</i> R.Br. | | | | | | | R | K | | R | | S | K |
| <i>Goodyera colorata</i> (Bl.) Bl. | | | | | | | | | | | | | R |
| <i>Goodyera cf. repens</i> | | | | | | | | | | | | R | |
| <i>Goodyera</i> sp. | | | | | | | | | | | * | | |
| <i>Grammatophyllum speciosum</i> Bl. | | | | S | | | | | | | | | |
| <i>Habenaria</i> sp. | | | | R | | | | | | | | | |
| <i>Liparis viridiflora</i> (Bl.) Lindl. | | | | R | R | R | R | R | | | | | |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|-------|-------|------|------|------|------|------|
| <i>Liparis wrayi</i> Hook.f. | | | | RS | R | R | Rs | Rs | | | | | |
| <i>Liparis</i> sp. | | | | | | | | | | | | | * |
| <i>Macodes petola</i> Lindl. | | | | | | | | | | | | | R |
| <i>Malaxis latifolia</i> J.E.Smith (<i>Microstylis latifolia</i> (J.E.Smith)J.J.S.) | | | | S | R | R | R | R | | | | | |
| <i>Nervilia aragoana</i> Gaudich. | | | R | RS | R | R | RsK | RsK | | R | | RS | RS |
| <i>Nervilia punctata</i> (Bl.)Schlect. | | | | | | | | | R | R | | | |
| <i>Oberonia monstrosa</i> (Bl.)Lindl. | | | | | R | R | R | R | | | | | R |
| <i>Oberonia</i> sp. (not <i>O. monstrosa</i>) | | | | R | | | | | | | | | |
| <i>Peristylus goodyeroides</i> (D.Don)Lindl. | | | | | | R | | | | R | | | RS |
| <i>Peristylus gracilis</i> Bl. | | | | RS | | R | R | R | | | | | |
| <i>Peristylus grandis</i> Bl. | | | | | | | | | | | R | | |
| <i>Phaius tankervilleae</i> (W.Ait.)Bl. | RS | R | | S | | R | R | R | | | | | R |
| <i>Phaius</i> sp. | | | | | | | | | | | | | ** |
| <i>Pholidota imbricata</i> Lindl. | | | | | | | | | | | R | | R |
| <i>Podochilus bancanus</i> | | | | | | | | | | | R | | |
| <i>Spathoglottis plicata</i> Bl. | R | K | RSK | RS | R | R | RS | RSK | | R | | S | RS |
| <i>Taeniophyllum</i> sp. | | | | | | | | R | | | | | |
| <i>Thrixspermum comans</i> J.J.S. | | | | | R | R | R | R | | | | | |
| <i>Thrixspermum</i> sp.1 (not <i>T. comans</i>) | | | | R | | | | | | | | | * |
| <i>Thrixspermum</i> sp.2 | | | | | | | | | | | * | | * |
| <i>Tropidia curculigoides</i> Lindl. | | | | | | | | | | | R | | |
| <i>Vrydagzynea albida</i> Bl. | | | | | | | | | | | R | | R |
| <i>Vrydagzynea</i> sp. | | | | S | R | r | r s k | r s k | | | | | R |
| <i>Zeuzine gracilis</i> Bl. | | | | R | | | | R | | | | | |
| PALMAE | | | | | | | | | | | | | |
| <i>Calamus unifarius</i> Bl. | | | | | | | | | | | R | | |
| <i>Calamus viminalis</i> Willd. | | | | | | | | | | | R | | R |
| <i>Calamus</i> sp. | | | | | | | | | | | | | * |
| <i>Cocos nucifera</i> L. | R | K | RS | RS | R | R | RSK | RSK | S | RSK | R | S | RSK |
| <i>Corypha utan</i> Lamk | | | | | | | R | K | S | R | R | | K |
| <i>Licuala spinosa</i> Thunb. | | | | | | | | | | | | S | |
| <i>Oncosperma tigillarum</i> (Jack)Ridl. (<i>Oncosperma filamentosum</i> Bl.) | | | | S | | | | K | | | R | RSK | RSK |
| PANDANACEAE | | | | | | | | | | | | | |
| <i>Freycinetia</i> sp. | | | | | | | | | | | R | | |
| <i>Pandanus tectorius</i> Soland. ex Park. | R | K | RS | RS | R | R | RSK | RSK | | RSK | R | RS | RSK |
| PASSIFLORACEAE | | | | | | | | | | | | | |
| <i>Passiflora foetida</i> L. | | | | | | | R | | S | RS | | S | |
| PIPERACEAE | | | | | | | | | | | | | |
| <i>Piper aduncum</i> L. | | | | | | | | | | | R | RS | RSK |
| <i>Piper blumei</i> (Miq.)Back. (<i>Piper malamiris</i> (non L.)Bl.) | | | | | R | R | R | r | | R | R | R | R |
| <i>Pothomorphe subpeltata</i> (Willd.)Miq. (<i>Heckeria umbellata</i> (L.)Kth. var. - - <i>subpeltata</i> DC.) | | | R | RS | | R | Rs | r s | | | | | R |
| POLYGONACEAE | | | | | | | | | | | | | |
| <i>Antigonon leptopus</i> Hook. & Arn. | | | | I | I | I | I | I | | | R | | |
| PORTULACACEAE | | | | | | | | | | | | | |
| <i>Portulaca oleracea</i> L. | | | | | | | | I | I | | | | |
| RANUNCULACEAE | | | | | | | | | | | | | |
| <i>Clematis smilacifolia</i> Wall. | | | | | | | | | | | R | R | R |
| RHAMNACEAE | | | | | | | | | | | | | |
| <i>Colubrina asiatica</i> (L.)Brogn. | | | S | S | | | RSk | s k | | R | K | R | RS |
| ROSACEAE | | | | | | | | | | | | | |
| <i>Maranthes corymbosum</i> (<i>Parinari corymbosum</i> (Bl.)Miq.) | | | | | | | | | | | R | | |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|------|------|------|------|------|------|------|
| RUBIACEAE | | | | | | | | | | | | | |
| <i>Guettarda speciosa</i> L. | | | RSK | RS | R | R | RSK | RSK | | RSK | R | RSK | RSK |
| <i>Hedyotis diffusa</i> Willd. (<i>Oldenlandia diffusa</i> (Willd.)Roxb.) | | | R | R | | | | R | | | | | |
| <i>Morinda citrifolia</i> L. | R | K | RSK | RS | R | R | RSK | RSK | S | RSK | R | RSK | RSK |
| <i>Mussaenda frondosa</i> L. | | | | R | R | R | | | | R | R | R | RS |
| <i>Mycetia javanica</i> (Bl.)Reinw. ex Korth. | | | | | | | | | | | R | R | |
| <i>Nauclea excelsa</i> (Bl.) Merr. | | | | | | | | | ? | | | | |
| <i>Neonauclea calycina</i> (Bartl. ex DC.)Merr. (<i>Nauclea purpurascens</i> Korth.) | | | R | RS | R | R | RSK | RSK | | R | R | RSK | RSK |
| <i>Tarenna dasyphylla</i> (Miq.)Valet. ex Steen. | | | | | | | | | | | | R | |
| <i>Tarenna fragrans</i> (Bl.)Koord. et Valet. | | | | | | | | | | R | R | R | |
| <i>Timonius compressicaulis</i> (Miq.)Boerl. | | | | | | | R | K | r | K | R | R | RSK |
| <i>Uncaria ferrea</i> (Bl.)DC. | R | | S | R | | | Rs | Rs | | | | | |
| RUTACEAE | | | | | | | | | | | | | |
| <i>Citrus</i> sp. | | | I | I | | | | | | | | | |
| SAPINDACEAE | | | | | | | | | | | | | |
| <i>Allophylus cobbe</i> (L.)Raeusch. | | | | | | | | | S | | | S | S |
| <i>Dodonaea viscosa</i> Jacq. | R | K | S | | | | s | s | | | | S | |
| <i>Erioglossum rubiginosum</i> (Roxb.)Bl. (<i>Erioglossum edule</i> Bl.) | | | | | | R | r | r | | | | | |
| SAPOTACEAE | | | | | | | | | | | | | |
| <i>Planchonella duclitan</i> (Blanco)Bakh.f. (<i>Planchonella nitida</i> Dub.) | | | | | | | | | | R | R | K | |
| SAURAUICEAE | | | | | | | | | | | | | |
| <i>Saurauia nudiflora</i> DC. | | | S | | | | Rs | Rs | | R | R | R | K |
| SCROPHULARIACEAE | | | | | | | | | | | | | |
| <i>Lindernia crustacea</i> (L.) F.v.M. | | | | | | | | | I | | | | |
| <i>Stemodia verticillata</i> (Mill.)Bold. | | | I | | | | | | | | | | |
| SOLANACEAE | | | | | | | | | | | | | |
| <i>Capsicum frutescens</i> L. | | | RS | | r | rsk | rsk | | | S | R | R | R |
| <i>Lycianthes laevis</i> (Dunal)Bitt. (<i>Solanum blumii</i> Nees ex Bl.) | | | R | R | R | R | R | | | | | | |
| <i>Lycopersicon lycopersicum</i> (L.) Karsten (<i>Solanum lycopersicum</i> L.) | | | | | | | | | | I | | | |
| <i>Solanum melongena</i> L. | | | | | | | | | | | R | | |
| <i>Solanum torvum</i> Swartz | | | | | | | K | K | | R | | | R |
| <i>Solanum verbascifolium</i> L. | | | | | | | K | K | | | | | |
| STERCULIACEAE | | | | | | | | | | | | | |
| <i>Melochia umbellata</i> (Houtt.)Stapf | R | RS | RS | R | R | RSK | RSK | | | RSK | R | RSK | SK |
| <i>Sterculia foetida</i> L. | | | | | | | | K | | | | S | |
| <i>Sterculia urceolata</i> J.E.Smith | | | | | | | | | | | R | | |
| TACCACEAE | | | | | | | | | | | | | |
| <i>Tacca leontopetaloides</i> (L.)O.K. | | | | | | | | | | S | | S | S |
| <i>Tacca palmata</i> Bl. | | | | | | | | | | R | R | R | R |
| ULMACEAE | | | | | | | | | | | | | |
| <i>Trema orientalis</i> (L.)Bl. | | R | RS | R | R | RSK | RSk | | | | | | RS |
| UMBELLIFERAE | | | | | | | | | | | | | |
| <i>Centella asiatica</i> (L.) Urb. | | | S | | | | | | | | | | |
| URTICACEAE | | | | | | | | | | | | | |
| <i>Debregeasia longifolia</i> (Burm.f.)Wedd. - - var. <i>affinis</i> | | | | | | | | | | | R | | |
| <i>Leucosyke capitellata</i> (Poir.)Wedd. (<i>Missiessya capitellata</i> (Poir.)Bakh.f.) | | R | RS | R | R | RSK | RSK | | | R | K | R | RSK |
| <i>Pipturus argenteus</i> (Forst.f.)Wedd. (<i>Pipturus incanus</i> (Bl.)Wedd.) | | RSK | RS | R | R | RSK | RSK | | | R | R | RS | SK |
| <i>Pouzolzia zeylanica</i> (L.)Benn. | R | | R | | | | | R | | | | | |

APPENDIX I. Continued.

| | 1886 | 1897 | 1908 | 1920 | 1922 | 1924 | 1929 | 1932 | 1934 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|-------|------|------|------|------|------|------|-------|
| <i>Villebrunea rubescens</i> (Bl.)Bl. (<i>Oreocnide rubescens</i> (Bl.)Miq.) | | | | R | R | R | R | R | | R | R | R | RSK |
| VERBENACEAE | | | | | | | | | | | | | |
| <i>Avicennia alba</i> Bl. (<i>Avicennia marina</i> (Forsk.)Vierh. [var. <i>alba</i> (Bl.)Bakh.]) | | | | | | | | R | | | | | |
| <i>Clerodendrum disparifolium</i> Bl. | | | | | R | R | R | R | | | | | |
| <i>Clerodendrum inerme</i> (L.)Gaertn. | RS | RS | r | r | RSK | r s k | | | | | | | |
| <i>Lantana camara</i> L. | RS | RS | R | R | RSK | RSK | | | RSK | R | | RSK | RSK |
| <i>Premna corymbosa</i> (Burm.f.)Rottl. & Willd. (<i>Premna integrifolia</i> L.) [+ <i>Premna obtusifolia</i>] | RSK | RS | | | R | RSK | RSK | | RSK | R | | R | K RSK |
| <i>Stachytarpheta indica</i> (L.)Vahl | | S | | | | | | | | | | | |
| <i>Vitex glabrata</i> R.Br. | | | | | | | | | | | | | R |
| <i>Vitex paniculata</i> Lamk | RS | RS | | | R | RS | r s | | | | | | |
| VITACEAE | | | | | | | | | | | | | |
| <i>Cayratia trifolia</i> (L.)Domin (<i>Columella trifolia</i> Merr.) (<i>Vitis trifolia</i> L.) | RS | RS | R | R | RSK | RSK | | | R | R | | RSK | RSK |
| <i>Leea aequata</i> L. | R | R? | R | R | R K | R K R | | | | | | | |
| <i>Leea sambucina</i> (L.)Willd. (<i>Leea indica</i> (Burm.f.)Merr.) | | S | R | R | RSK | RSK R | | | R | R | | RSK | RSK |
| <i>Leea</i> sp. | | | | | | | | | | | | | * |
| <i>Tetrastigma lanceolarium</i> (Roxb.)Planch. | | RS | R | r | r s | r s | | | R | R | | S | RSK |
| ZINGIBERACEAE | | | | | | | | | | | | | |
| <i>Boesenbergia pandurata</i> (Roxb.)Schlect. (<i>Gastrochilus panduratus</i> Ridl.) | | | I | I | I | I | I | | | | | | |
| <i>Costus speciosus</i> (Koen.)J.E.Smith (<i>Costus sericeus</i> Bl.) | R | RS | R | R | R | R | | | R | R | | R | R |

Notes: 1. *Lumnitzera racemosa*, *Excoecaria agallocha*, *Crotalaria mucronata* and *Casuarina equisetifolia* were recorded on Sertung in 1921, but have been placed in the 1920 column for simplicity. Only *Crotalaria mucronata* had not previously been recorded. 2. Specimens of *Dysoxylum* collected in 1982 were attributed to *D. caulostachyum* (Tagawa 1984) but have been assigned here to *D. gaudichaudianum* (for details see page 20). 3. It has sometimes been necessary to re-combine certain taxa in the table as compared to earlier authors (e.g., we treat *Nephrolepis biserrata* as synonymous with *N. exaltata*, although some authors have split them). For a complete list of such taxonomic revisions and problems see Whittaker and Flenley (1982:25-29) and Bush et al. (1986a:214-216).

APPENDIX II.

The complete plant list for Anak Krakatau 1930–1983.

| | 1934 | 1949 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|
| P T E R I D O P H Y T A | | | | | | |
| BLECHNACEAE | | | | | | |
| <i>Stenochlaena palustris</i> (Burm.f.)Bedd. | | | | | | A |
| OLEANDRACEAE | | | | | | |
| <i>Nephrolepis cf. cordifolia</i> (L.)Pr. | | | | | a | |
| <i>Nephrolepis hirsutula</i> (Forst.)Pr. | | A | A | A | A | A |
| PTERIDACEAE | | | | | | |
| <i>Pityrogramma calomelanos</i> (L.)Link | | | A | A | A | A |
| SCHIZAEACEAE | | | | | | |
| <i>Lygodium circinnatum</i> (Burm.)Sw. | | | | A | | |
| <i>Lygodium flexuosum</i> (L.)Sw. | | | | | A | |
| S P E R M A T O P H Y T A | | | | | | |
| AMARYLLIDACEAE | | | | | | |
| <i>Crinum asiaticum</i> L. | | | | | | A |
| APOCYNACEAE | | | | | | |
| <i>Cerbera manghas</i> L. | A | | | A | | |
| ARISTOLOCHIACEAE | | | | | | |
| <i>Aristolochia tagala</i> Cham. | | | | | | A |
| ASCLEPIADACEAE | | | | | | |
| <i>Cynanchum ovalifolium</i> Wight. | | | | | A | A |
| <i>Tylophora asthmatica</i> (Roxb.)W. & A. | | | | | A | |
| <i>Tylophora cf. tenuis</i> Bl. | | | | | | A |
| <i>Tylophora</i> sp. | | | | * | | |
| BIGNONIACEAE | | | | | | |
| <i>Radermachera glandulosa</i> (Bl.)Miq. | | | | A | | |
| CARICACEAE | | | | | | |
| <i>Carica papaya</i> L. | | | | | | A |
| CASUARINACEAE | | | | | | |
| <i>Casuarina equisetifolia</i> J.R. & G.Forst. | | A | A | A | A | A |
| COMBRETACEAE | | | | | | |
| <i>Terminalia catappa</i> L. | A | | A | A | A | A |
| COMPOSITAE | | | | | | |
| <i>Crassocephalum crepidioides</i> (Benth.)- [- S. Moore] | | | | | | a |
| <i>Eclipta prostrata</i> (L.)L. | | | | | | A |
| <i>Erechtites</i> sp. | | | | | | A |
| <i>Erigeron linifolius</i> Willd. | | | | | | A |
| <i>Eupatorium odoratum</i> L. | | | | A | A | A |
| <i>Mikania cordata</i> (Burm.f.)B.L.Robinson | | | | A | | A |
| <i>Porophyllum ruderale</i> (Jacq.)Cass. | | | | A | | A |
| <i>Wedelia biflora</i> (L.)DC. | | | | | | A |
| CONVOLVULACEAE | | | | | | |
| <i>Ipomoea gracilis</i> R.Br. | | | | | A | |
| <i>Ipomoea pes-caprae</i> (L.)R.Br. | A | A | A | A | A | A |
| <i>Ipomoea stolonifera</i> (Cyr.)Gmel. | | | | | | A |

APPENDIX II. Continued.

| | 1934 | 1949 | 1951 | 1979 | 1982 | 1983 |
|---|------|------|------|------|------|------|
| <i>Ipomoea tuba</i> (Schlechtend)G.Don | | | | | | A |
| CUCURBITACEAE | | | | | | |
| <i>Coccinia grandis</i> (L.)Voigt | | | | | A | |
| CYCADACEAE | | | | | | |
| <i>Cycas rumphii</i> Miq. | | | A | A | | A |
| CYPERACEAE | | | | | | |
| <i>Cyperus javanicus</i> Houtt. | | A | A | | | |
| <i>Cyperus pedunculatus</i> (R.Br.)Kern | | | | A | | A |
| EUPHORBIACEAE | | | | | | |
| <i>Antidesma ghaesembilla</i> Gaertn. | | | | A | | |
| <i>Antidesma</i> sp. | * | | | | | |
| <i>Macaranga tanarius</i> (L.)M.A. | | | | | | A |
| GOODENIACEAE | | | | | | |
| <i>Scaevola taccada</i> (Gaertn.)Roxb. | | A | A | A | A | A |
| GRAMINEAE | | | | | | |
| <i>Chloris barbata</i> (L.) Swartz. | | | | | | a |
| <i>Imperata cylindrica</i> (L.)Beauv. | | | A | A | A | A |
| <i>Ischaemum muticum</i> L. | | | A | A | A | A |
| <i>Panicum</i> sp. | | | | A | | |
| <i>Pogonatherum paniceum</i> (Lamk) Hack. | | | | A | A | A |
| <i>Saccharum spontaneum</i> L. | | A | A | A | A | A |
| <i>Spinifex littoreus</i> (Burm.f.)Merr. | | A | A | A | | A |
| <i>Thuarea involuta</i> (Forst.f.)R.& S. | | | A | | | A |
| GUTTIFERAE | | | | | | |
| <i>Calophyllum inophyllum</i> L. | A | A | A | A | | A |
| HERNANDIACEAE | | | | | | |
| <i>Hernandia peltata</i> Meissn. | | | A | A | | A |
| [+ <i>Hernandia sonora</i> L.] | | | | | | |
| LAURACEAE | | | | | | |
| <i>Cassytha filiformis</i> L. | | | A | A | A | A |
| LECYTHIDACEAE | | | | | | |
| <i>Barringtonia asiatica</i> (L.)Kurz. | A | A | | A | A | A |
| LEGUMINOSAE | | | | | | |
| <i>Albizia retusa</i> Bth. | | | | | | A |
| <i>Caesalpinia bonduc</i> (L.)Roxb. | | | | | | A |
| <i>Canavalia maritima</i> (Aubl.)Urb. | A | A | A | A | A | A |
| <i>Dalbergia junghuhnii</i> Bth. | | | | a | | |
| <i>Dalbergia</i> sp. | | | | * | | |
| <i>Derris trifoliata</i> Lour. | ? | | | | | |
| <i>Desmodium umbellatum</i> (L.)DC. | | | A | A | A | A |
| <i>Erythrina orientalis</i> (L.)Murr. | A | ? | | A | A | A |
| <i>Mimosa pigra</i> L. | | | | | | a |
| <i>Mucuna gigantea</i> (Willd.)DC. | | | | A | | A |
| <i>Phaseolus</i> sp. | ? | | | | | |
| <i>Pithecellobium umbellatum</i> (Vahl)Bth. | | | | A | | A |
| <i>Pongamia pinnata</i> (L.)Pierre | A | | | A | | A |
| <i>Sophora tomentosa</i> L. | | | | | | A |
| <i>Vigna marina</i> (Burm.f.)Merr. | A | | | A | | A |
| MALVACEAE | | | | | | |
| <i>Hibiscus tiliaceus</i> L. | | | | A | A | A |
| <i>Thespesia populnea</i> (L.)Soland. ex Correa | | | | | | A |

APPENDIX II. Continued.

| | 1934 | 1949 | 1951 | 1979 | 1982 | 1983 |
|--|------|------|------|------|------|------|
| MELASTOMATACEAE | | | | | | |
| <i>Melastoma affine</i> D. Don | | | | A | A | A |
| MELIACEAE | | | | | | |
| <i>Dysoxylum gaudichaudianum</i> (A. Juss.) Miq. | | | | | | A |
| <i>Xylocarpus granatum</i> Koen. | A | | | | | |
| MORACEAE | | | | | | |
| <i>Ficus fulva</i> Reinw. ex Bl. | | | | A | A | A |
| <i>Ficus septica</i> Burm. f. | | | | A | A | A |
| MUSACEAE | | | | | | |
| <i>Musa paradisiaca</i> L. | A | | | | | |
| ORCHIDACEAE | | | | | | |
| <i>Calanthe</i> sp. | | | | A | | |
| <i>Dendrobium crumenatum</i> Swartz | | | | | | A |
| <i>Dendrobium</i> sp. | | | | * | | |
| <i>Eulophia graminea</i> Lindl. | | | | | A | A |
| <i>Spathoglottis plicata</i> Bl. | | | | | | A |
| PALMAE | | | | | | |
| <i>Cocos nucifera</i> L. | A | A | A | A | A | A |
| <i>Nypa fruticans</i> Wurmb | a | | | | | |
| PANDANACEAE | | | | | | |
| <i>Pandanus tectorius</i> Soland. ex Park. | A | A | A | A | A | A |
| PASSIFLORACEAE | | | | | | |
| <i>Passiflora foetida</i> | | | | | A | |
| RHAMNACEAE | | | | | | |
| <i>Colubrina asiatica</i> (L.) Brogn. | | | | | | A |
| RHIZOPHORACEAE | | | | | | |
| <i>Rhizophora stylosa</i> Griff. | a | | | | | |
| RUBIACEAE | | | | | | |
| <i>Morinda citrifolia</i> L. | | | A | A | A | A |
| <i>Neonauclea calycina</i> (Bartl. ex DC.) Merr. | | | A | A | A | A |
| <i>Timonius compressicaulis</i> (Miq.) Boerl. | | | | | A | A |
| RUTACEAE | | | | | | |
| <i>Murraya exotica</i> L. | a | | | | | |
| SAPINDACEAE | | | | | | |
| <i>Allophylus cobbe</i> (L.) Raeusch. | | | | | | A |
| STERCULIACEAE | | | | | | |
| <i>Melochia umbellata</i> (Houtt.) Stapf | | | | | A | |
| URTICACEAE | | | | | | |
| <i>Pipturus argenteus</i> (Forst. f.) Wedd. | | | | | | A |
| VERBENACEAE | | | | | | |
| <i>Premna corymbosa</i> (Burm. f.) Rottl. & Willd. | | | | A | A | A |
| VITACEAE | | | | | | |
| <i>Cayratia trifolia</i> (L.) Domin | | | | | | A |
| <i>Cissus repens</i> Lamk ? | a | | | | | |

1934 = collections in 1932, 1933 and 1934, all being 'seedling' floras. 1949 = collections by Petroschevsky and van der Pijl. A = species recorded on Anak Krakatau. a = species recorded only on Anak Krakatau, ? = uncertain identification. * = identification to genus only, when other species in the same genus have been found. Names in square brackets indicate either varieties or grouped species. For synonyms see Appendix I.

Sources: Docters van Leeuwen 1936, van der Pijl 1949, Borssum Waalkes 1960, Whittaker and Flenley 1982, Tagawa 1984, Tagawa et al. 1986, Bush et al. 1986a.

APPENDIX III

THE BRYOPHYTES OF KRAKATAU

Two species of unidentified mosses were found on Rakata as early as 1886, but the first identifications were of *Bryum coronatum* and *Philonotis secunda*, collected in 1906 (Ernst 1908). Between 1919 and 1932, Docters van Leeuwen (1936) recorded over 33 species of mosses. The difficulty of collecting and identifying these taxa has prevented a comparable collation for the 1979–1983 period (Jones 1986b). At least nine taxa recorded in the 1920s are still present on the islands: *Floribundaria floribunda* (abundant in upland Rakata), *Aerobryopsis longissima* (ditto), *Pelekium velatum*, *Taxithelium nepalense*, *Vesicularia reticulata*, *Ectropothecium* sp., *Calymperes* cf. *tenerum*, *Leucophanes* sp., *Fissidens* sp.

Mosses, commonly *Fissidens* sp., were often found on the bare, unconsolidated ash at low altitudes. They were also found along termite trails, on the few rocks to be found, and on dead wood and tree trunks. In the upper reaches of Rakata, the covering of bryophytes was more ubiquitous and differed in composition (Docters van Leeuwen 1936, Forster 1982).

The lack of a similar altitudinal range on Sertung and R. Kecil is reflected in a less diverse moss flora, from which those species characteristic of the cloud or "mossy" forest of Rakata are largely absent (Jones 1986b). One genus, *Calymperes*, has been recorded from Anak Krakatau in 1982 (Tagawa et al. 1986).

Data for the Hepaticae are poor. Only one species was found prior to 1919, but during the 1920s Docters van Leeuwen (1936) recorded 38 taxa, mostly from Rakata alone. The canopy habitat of much of this flora makes undersampling particularly likely for this group. Of the recent surveys, only Tagawa et al. (1986) have produced any identifications (six taxa), these to a generic level. On Anak Krakatau in 1982, Jones (1986b) recorded a hepatic, tentatively identified as *Marchantia* sp., growing as a pioneer on the side of the island remote from the vegetated areas. Further work on the collected bryophyte material is in progress (Jones, *personal communication*).

NOTE ADDED IN PROOF

We are grateful to Dr. Barbara Parris (Royal Botanic Gardens, Kew) for revisions of the fern taxonomy received subsequent to acceptance of this paper. These revisions were incorporated into the text (including tables and appendices) but arrived too late for revision of the figures. In consequence some graphs of species number against time contain minor inaccuracies. However, these errors do not exceed eight species on any island in any single year, and in most cases the error is zero, one, or two species. Such changes would be barely perceptible on the graphs.