Principes, 36(1), 1992, pp. 7-17

Ecology and Distribution of Nibung (Oncosperma tigillarium within the Krakatau Islands, Indonesia

T. PARTOMIHARDJO, E. MIRMANTO, S. RISWAN AND R. J. WHITTAKER[1]

"Herbarium Bogoriense," Research and Development Centre for Biology, Indonesian Institute of Sciences, Jalan Ir. H. Juanda 22-24, Bogor 16122, Indonesia and School of Geography,[1] University of Oxford, Mansfield Road, Oxford, OX1 3TB, UK

ABSTRACT

A study of the distribution and ecology of *Oncosperma tigillarium* (Jack) Ridl. (nibung) within the Krakatau Islands, Indonesia, was conducted to gain an understanding of factors controlling location and dynamics of populations. The history of its colonization and that of other palm species is also briefly examined. Four plots were established at different sites on the three main islands.

Reconnaissance throughout the islands between 1979 and 1989 revealed that nibung grows in the lowlands below 150 m altitude, but away from the immediate vicinity of the sea. Populations were studied within a number of different forest types (as described by Whittaker, Bush and Richards 1989), and it was concluded that the palm appears to be relatively insensitive to community characteristics and to between-island differences in disturbance histories.

Examination of seed, seedling and sapling densities in relation to parent trees revealed a large number of propagules failing to disperse, and in consequence tendencies toward clumped distributions. The seedlings tend to grow best in hollow and/or moister sites. The Krakatau islands remain poor in palm species (eight) and numbers of individuals, however, the evidence from this study, exemplified by nibung, is of a slow but steady increase in their presence.

Nibung (*Oncosperma tigillarium* (Jack) Ridl.), is one of eight palm species known from the Krakatau Islands (below). The tree is tall, clustering and spiny with distinct crown shafts and pinnately divided leaves. Nibung may reach in excess of 25 m in height and clusters may have up to 10 major stems. Based on the collections at Herbarium Bogoriense and other available information (e.g., Seeman 1856, Ethelbert Blatter 1926), nibung is widely distributed throughout Sumatra, Kalimantan, Peninsular Malaysia, and Java. The species is generally confined to forest below 50 m above sea level, in near-costal localities (Steenis 1935, Backer and van den Brink 1968, House 1984).

Recently this palm tree has become threatened in many places, especially near the coast, due to utilization for "bagang" poles. Stems of nibung are also used as a major building component, the leaf sheaths in basket making and the heart or cabbage is eaten raw or cooked in a coconut sauce (Dransfield 1976, House 1983). Seeman (1856) quotes Low as stating it to be "the most esteemed of all the excellent vegetables of Borneo," with a very sweet nutty flavor. According to local fishermen, it currently sells in Lampung for about 20,000 rupiahs per stem. Despite the economic value of the plant, little is known about the ecology and distribution of this palm. By studying it in a habitat protected from marked human disturbance, we hope to be able to make a small contribution to an understanding of the autoecology of the species.

The Krakatau islands provide a classic site for the study of primary colonization and ecosystem regeneration in the humid tropics, a context in which palms are a relatively neglected component. In focusing on the history and dynamics of nibung within these islands it is intended to provide a simple case study, hopefully provoking further interest in the subject.

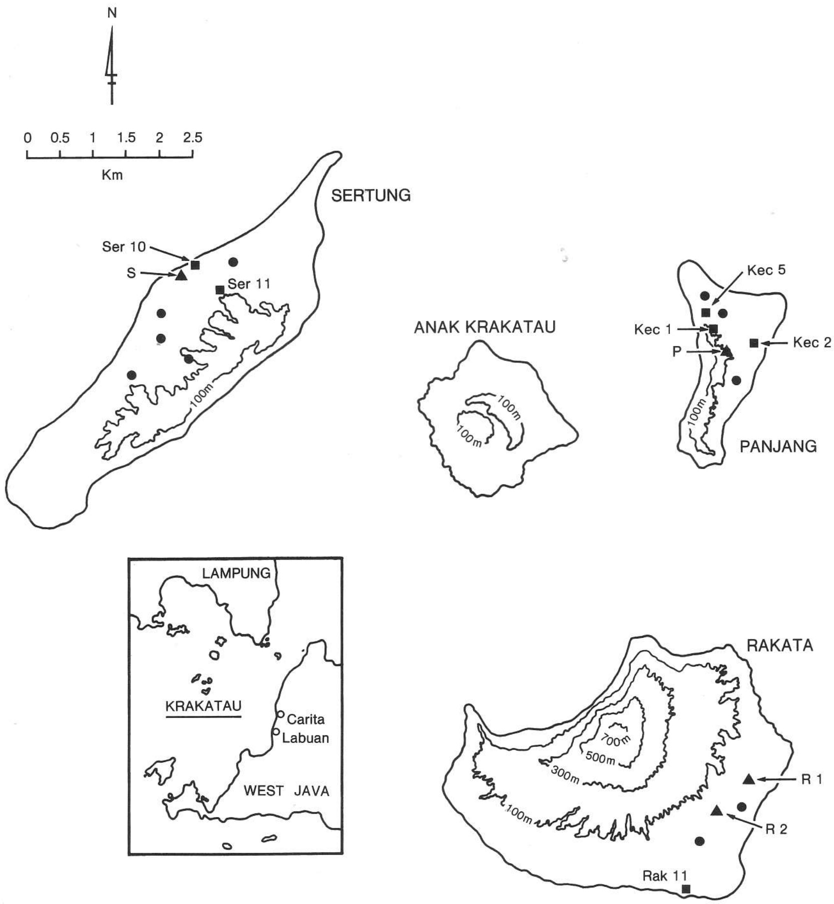
Study Area and Methods

The Krakatau Islands are situated approximately in the middle of the Sunda Straits, between West Java and South Sumatra (Fig. 1). The group consists of four small islands: Rakata or Krakatau Besar, Sertung or Verlaten, Panjang or Lang (Rakata Kecil), and Anak Krakatau (the smallest island with an active crater). The Islands are mostly forest-covered with the exception of Anak Krakatau, the majority of which still consists of open bare areas of black ash. The group was completely sterilized in the eruptions of 1883, but now supports a variety of secondary forest communities. The history of recovery and current forest types are described by Whittaker, Bush, and Richards (1989).

The soils of Rakata have developed on top of a thick layer of white volcanic ash produced by the 1883 eruptions, but those of Sertung and Panjang are developed from complex series of mainly post-1930 ejecta (RJW, work in progress). These were produced by Anak Krakatau, which emerged in the center of the group over the period 1927 to 1930, and which has been intermittently active since. Particularly severe eruptions occurred in 1930, 1932, 1934/5, 1952/3, 1961 and around 1970; in each of these cases (and doubtless others) Sertung and/or Panjang has been affected (reviewed in Whittaker et al. 1989). It appears that little, if any, of either island has escaped from serious damage at one time or another. The forests of both islands are consequently ecologically immature and species-poor in comparison to Rakata. In addition, their soils are less developed and the surface horizons are coarser textured, being typically 80–90% sand fraction (Newsome 1986, M. Saunter, unpubl. data). Erosion by fluvial action has produced pronounced ridge and gully systems, particularly on Rakata, with most major gully-forming activity probably taking place in the initial unvegetated period. The shorelines of the three older islands have also been eroded by wave action, such that the majority of the coastline consists of steep ash walls with many hanging valleys (Bird and Rosengren 1984). The coastline is quite dynamic and although the major process has always been erosion, areas of accretion (and hence colonization of thalassochorous species) exist on each island. On Sertung there is a quite pronounced spit, fed by longshore drift from the eroding cliffs (see Fig. 1). In short, inland parts of Rakata have been relatively stable since very shortly after the eruptions of 1883, but the vegetation of Panjang and Sertung has experienced significant disturbance by volcanic events in the past sixty years. Coastal and near-coastal populations have also been variously affected by geomorphic change.

Reconnaissance was undertaken to determine the nibung distribution within each island. The data presented in Table 1 were then collected using a plot based method. Three plots of 10 × 100 m and one of 10 × 120 m were set up under selected parent nibung trees. Two plots were established on Rakata and one plot each on Sertung and Panjang. All trees with trunks of >10 cm dbh and saplings of 2 cm diameter at 1 m above ground level were measured. Data recorded were diameter, total height and bole height in all sub-plots of 10 × 10 m. Ground cover was sampled from further subplots of 2 × 2 m, which were set up systematically within each 10 × 10 m sub-plot. Voucher specimens were collected for identification of all taxa present. The fallen seeds of nibung under the selected parent nibung trees were counted systematically, within concentric contours.

Prior to the analyses of these data, we first review the historical data for the colonization of the islands by Nibung and other palms. Surveys of the islands have not been



1. Known distribution of *Oncosperma tigillarium* in the Krakatau Islands, Indonesia. NB. Site locations are approximate. ■ 1983/4 plots in which *O. tigillarium* was recorded (after Whittaker et al. 1989); ▲ 1989 study sites; ● other locations in which *O. tigillarium* was recorded in 1989.

particularly systematic and have been of varying frequency and intensity through time. Whittaker et al. (1989) group the survey data into the following "collection periods," which broadly indicates the pattern: 1886, 1897, 1908, 1920, 1922, 1924, 1929, 1932, 1934, 1951, 1979, 1982, 1983. In addition, we report previously unpublished finds of 1989.

Results and Discussion

History of palm colonization of the Krakatau Islands. Nibung is one of seven palm species recorded for the Krakatau Islands post-1883 by Whittaker et al. (1989). One of these, *Nypa fruticans* Wurmb has been observed only as a seedling on Anak Krakatau in the early 1930s, and did not survive the eruptions of that period. The remaining species are *Calamus unifarius* Bl., *Calamus viminalis* Willd., *Cocos nucifera* L., *Corypha utan* Lam., and *Licuala spinosa* Thunb., all of which have been recorded during the surveys of 1979–1989. However, specimens collected in 1989 and provisionally identified as *Licuala spinosa*, were later found

Table 1. Sample plot data recorded in 1989.

	R1		R2		S		P	
	No.	I.V.	No.	I.V.	No.	I.V.	No.	I.V.
Tree Layer								
Neonauclea calycina	10	58.29	21	108.03	2	12.15	9	80.49
Terminalia catappa	6	55.82	3	21.64	7	50.72	—	—
Ficus fistulosa	8	49.65	3	22.06	—	—	—	—
Timonius compressicaulis	5	29.65	—	—	31	118.83	18	122.83
Villebrunea rubescens	3	15.75	—	—	—	—	—	—
Macaranga tanarius	2	13.19	—	—	—	—	1	8.09
Ficus fulva	2	12.69	—	—	—	—	1	8.09
Ficus ampelas	2	11.78	—	—	—	—	—	—
Ficus septica	2	11.36	2	15.82	—	—	—	—
Dysoxylum guadichaudianum	1	6.41	—	—	—	—	4	36.32
Ficus tinctoria	1	6.33	2	15.04	—	—	—	—
Oncosperma tigillarium	7	6.31	21	83.48	8	26.55	5	28.02
Arthrophyllum javanicum	1	5.82	—	—	—	—	—	—
Bridelia monoica	1	5.70	1	7.85	—	—	—	—
Glochidion borneense	1	5.63	—	—	—	—	—	—
Antidesma montanum	1	5.62	—	—	—	—	—	—
Pipturus argenteus	—	—	5	18.99	—	—	1	8.00
Tarenna fragrans	—	—	1	7.09	—	—	—	—
Gnetum gnemon	—	—	—	—	7	40.37	—	—
Hernandia peltata	—	—	—	—	6	26.98	—	—
Morinda citrifolia	—	—	—	—	3	18.33	—	—
Artocarpus elasticus	—	—	—	—	1	6.07	1	8.16
Shrub/Sapling								
Leea sambucina	64	54.83	82	87.85	1	2.65	18	29.65
Ficus fistulosa	30	34.34	12	20.68	4	7.05	7	23.20
Antidesma montanum	38	33.29	22	31.48	—	—	20	37.47
Timonius compressicaulis	26	27.73	1	2.25	11	28.86	1	3.41
Dysoxylum gaudichaudianum	12	25.32	—	—	4	6.70	37	51.06
Neonauclea calycina	18	24.50	19	32.55	2	7.77	6	16.26
Leucosyke capitellata	18	22.63	12	17.70	—	—	—	—
Arthrophyllum javanicum	15	15.78	4	8.52	—	—	3	7.56
Tarenna fragrans	8	11.01	6	14.09	—	—	—	—
Villebrunea rubescens	5	7.32	5	7.53	—	—	1	2.98
Ficus ampelas	6	7.14	10	14.38	1	2.64	6	12.38
Buchanania arborescens	4	6.26	4	8.68	—	—	18	27.33
Ficus septica	3	5.08	6	8.91	—	—	—	—
Ficus tinctoria	3	4.45	4	8.07	—	—	7	26.09
Bridelia monoica	3	4.36	2	4.26	—	—	—	—
Ficus fulva	3	3.95	5	7.04	6	13.63	4	8.24
Morinda citrifolia	2	3.72	—	—	1	2.81	1	2.28
Calophyllum inophyllum	2	3.03	—	—	3	8.56	—	—
Mussaenda frondosa	1	1.82	—	—	—	—	—	—
Ardisia humilis	1	1.57	—	—	1	2.79	—	—
Ficus pubinervis	1	1.47	—	—	—	—	1	2.73
Macaranga tanarius	—	—	3	3.81	1	2.90	2	3.69
Pipturus argenteus	—	—	2	2.79	—	—	3	8.44
Syzygium polyanthum	—	—	1	2.23	—	—	3	7.09
Litsea sp.	—	—	1	2.04	—	—	—	—
Glochidion borneense	—	—	1	2.04	—	—	—	—
Melastoma malabathricum	—	—	1	2.01	—	—	—	—
Gnetum gnemon	—	—	—	—	202	167.73	4	8.20

Table 1. Continued.

	R1		R2		S		P	
	No.	I.V.	No.	I.V.	No.	I.V.	No.	I.V.
Hernandia peltata	—	—	—	—	6	24.87	—	—
Oncosperma tigillarium	—	—	—	—	8	14.40	6	13.54
Artocarpus elasticus	—	—	—	—	1	2.64	—	—
Terminalia catappa	—	—	—	—	—	—	2	5.00
Mangifera indica	—	—	—	—	—	—	2	3.40
Seedling and Herb								
Neonauclea calycina	129	91.41	3	3.78	—	—	—	—
Mussaenda frondosa	25	28.96	—	—	—	—	—	—
Antidesma montanum	29	26.61	10	20.17	—	—	3	9.09
Syzyzium polyanthum	14	23.25	—	—	—	—	—	—
Macaranga tanarius	13	19.26	—	—	—	—	1	3.24
Nephrolepis hirsutula	11	11.30	—	—	—	—	—	—
Bridelia monoica	6	11.00	1	2.77	—	—	—	—
Angiopteris evecta	6	9.35	—	—	—	—	3	41.09
Tetrastigma lanceolarium	5	8.10	51	68.72	1	5.84	1	3.24
Terminalia catappa	5	7.77	3	3.98	1	5.84	—	—
Flagellaria indica	4	7.21	1	2.77	—	—	—	—
Hoya diversifolia	11	7.05	—	—	—	—	—	—
Ficus tinctoria	7	6.56	1	12.63	—	—	—	—
Ficus fistulosa	2	6.51	2	3.17	1	7.23	—	—
Tylophora asthmatica	3	3.83	1	2.77	8	21.90	9	20.89
Leea indica	3	3.83	4	10.76	—	—	17	19.61
Oncosperma tigillarium	1	3.82	12	13.24	4	7.86	3	13.29
Smilax zeylanica	2	3.48	2	3.17	—	—	—	—
Drynaria quercifolia	2	3.36	—	—	—	—	—	—
Tectaria melanocaula	3	2.72	—	—	—	—	—	—
Dysoxylum gaudichaudianum	2	2.14	1	2.57	1	5.84	46	53.05
Lygodium flexuosum	1	2.02	27	54.51	—	—	2	6.62
Ficus septica	1	2.02	—	—	1	5.84	—	—
Buchanania arborescens	1	1.79	2	3.78	—	—	3	8.78
Nephrolepis biserrata	—	—	20	28.88	1	5.84	—	—
Tectaria dissecta	—	—	7	10.21	—	—	1	3.39
Glochidion borneense	—	—	1	6.47	—	—	—	—
Microsorium punctatum	—	—	2	5.95	—	—	27	56.15
Ficus fulva	—	—	2	5.95	—	—	—	—
Arhtrophyllum javanicum	—	—	2	5.54	—	—	1	4.64
Tacca palmata	—	—	2	5.01	—	—	—	—
Tarenna fragrans	—	—	1	4.41	—	—	—	—
Mycetia javanica	—	—	1	4.41	—	—	—	—
Pteris vittata	—	—	2	3.37	—	—	—	—
Cayratia trifolia	—	—	1	2.77	—	—	—	—
Leucosyke capitellata	—	—	1	2.57	—	—	—	—
Ficus ampelas	—	—	1	2.57	—	—	—	—
Calophyllum inophyllum	—	—	1	2.57	1	5.84	1	3.39
Hernandia peltata	—	—	—	—	80	149.52	—	—
Gnetum gnemon	—	—	—	—	8	26.86	—	—
Stenochlaena palustris	—	—	—	—	3	23.66	—	—
Ardisia humilis	—	—	—	—	3	20.09	3	8.78
Dicranopteris linearis	—	—	—	—	1	5.84	—	—
Elaeagnus latifolia	—	—	—	—	10	32.21	—	—
Microsorium nigrescens	—	—	—	—	1	9.30	—	—
Artocarpus elasticus	—	—	—	—	1	3.24	—	—

Table 1. Continued.

Total number of *Oncosperma tigillarium* seedlings recorded within study plots: Plot R1 = 130, R2 = 215, S = 11, P = 47.

Site details			
Site	R1	Locality	S.E. Rakata
Plot size (m^2)	1200	Slope (°)	20
Altitude (m)	10	Vegetation	*Terminalia-Neonauclea*
Site	R2	Locality	S.E. Rakata
Plot size (m^2)	1000	Slope (°)	30
Altitude (m)	50	Vegetation	*Neonauclea*
Site	S	Locality	N.W. Sertung
Plot size (m^2)	1000	Slope (°)	15
Altitude (m)	20	Vegetation	*Timonius-Terminalia*
Site	P	Locality	Central Panjang
Plot size (m^2)	1000	Slope (°)	10
Altitude (m)	120	Vegetation	*Timonius-Neonauclea*

No. = number of individuals.
I.V. = importance value (Relative dominance + relative density + relative frequency. For seedlings, dominance was calculated from cover values.)

to belong to *Corypha utan* (J. Dransfield, pers. comm.). It is thought most parsimonious that the only previous record of *L. spinosa*, in 1982, was also a misidentification of *C. utan*. In the 1989 survey a further species, *Salacca zalacca* (Gaertn.) Voss, has been provisionally identified from Rakata and a confirmed identification of another *Calamus* has also been made, *C. polystachys* Becc. (J. Dransfield, pers. comm.). Thus, excluding the *Licuala*, there are eight palm species known from the Krakatau Islands, of which seven may be regarded as successful colonists.

The first palm species recorded on the group was *Cocos nucifera* L., found in 1897 on Rakata and Panjang. The next record is for nibung in 1920, by Docters van Leeuwen. He found a very young specimen growing in a "wilderness" of *Hibiscus tiliaceus* L. on the sandy spit at the northern end of Sertung. It was mentioned that the soil there was moist but not salty (Docters van Leeuwen 1936). Given his frequent visits to Rakata and occasional visits to Sertung during the 1920s, it is unlikely that it colonized the former, or spread markedly in the latter during this period, as he would typically have recorded such events. The next record of this species is not until 1932, when he found it at two places on Panjang. He did not observe it in his first brief visits to Panjang in 1928/29, but in 1932 he found three young specimens in a mixed wood in the northeast of the island, behind the strandbank and about 10 m from the coast. He also observed some specimens in one of the highest ravines on the south-east side of the island, about 90 m above sea level. The specimens were well-developed and rose with their leaves above the surrounding vegetation, but were not yet flowering (Docters van Leeuwen 1936). The other palms present at this time in the group, *Cocos nucifera* and *Corypha utan*, were respectively slightly more common and slightly less common than nibung. The history of the first fifty years of ecosystem recovery on Krakatau is thus one of an extreme poverty of palms, both in numbers of species (three) and in numbers of individuals (e.g., contrast with House 1984).

Borssum Waalkes (1960) failed to record *Oncosperma tigillarium* during his botanical observations on the Krakatau Islands in 1951 and 1952, but it should be noted that he spent only a few hours on Panjang and Sertung, in comparison to about 9 days on Rakata. In the more intensive sampling efforts of 1979–1989, the palm has been recorded on each of the three main islands but it has not yet been found on Anak Krakatau (Whittaker et al. 1989: appendix 1 and 2*).

Present Distribution of Nibung

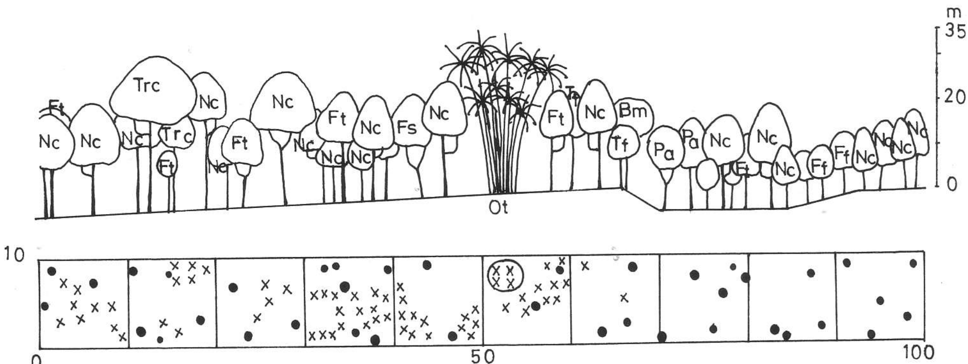
Of 35 vegetation sites (average size approximately 900 m^2) enumerated by the Krakatoa Centenary Expedition in 1979 and 1983/84, nibung was recorded in six (Bush and Whittaker 1986), as follows. Their Rakata site 11 was located at 15 m altitude, in near-coastal *Neonauclea calycina–Terminalia catappa* ecotone forest on the south side of the island. The palm was large enough to be recorded as part of the tree layer, with 2.7% csa (cross-sectional area). On Sertung, it was found in sites Ser 10 (2.63% csa) and Ser 11 (present but <30 cm girth), respectively at 35 m and 80 m altitude. The former site was in the *Terminalia catappa–Timonius compressicaulis* forest, the latter in *Timonius compressicaulis* forest. Both sites were at the northern end of the main part of Sertung. In Panjang, nibung was present in sites Kec 1 (Kecil = Panjang), Kec 2, Kec 5, each as individuals of less than 30 cm girth, and respectively at altitudes of 90 m, 115 m, and 90 m, in the northern half of the island (Fig. 1).

During the 1982 and 1983 Kagoshima/Bogor expeditions, the first author (TP), also observed several clusters of flowering and fruiting nibung on Panjang, Sertung and Rakata. In 1989 particular attention was paid to this species, and patches of seedlings and trees were observed scattered within the three islands (Fig. 1). Four additional sites were selected for detailed study (above). In these plots (R1, R2, S, and P), 34 arboreal species were recorded, belonging to 28 genera and 17 families (Table 1).

The two Rakata plots, R1 and R2, were located on the gentle slope of south-east Rakata at altitudes of 10 m and 50 m above sea level. The vegetation of both sites was dominated by *Terminalia catappa* and *Neonauclea calycina* (Fig. 2 and Table 1), with the former providing the tallest trees, of about 35 m height. The second layer consisted of a mixture, principally of *Timonius compressicaulis, N. calycina, Dysoxylum gaudichaudianum* and nibung itself. The data in Table 1 are entirely compatible with the coastal and near-coastal vegetation types described for Rakata by Whittaker et al. (1989). The nibung clusters consisted of about 7 stems in the first plot and 21 stems in the second plot. Most of the nibung trees were flowering and fruiting. In the third layer, there were several shrub species, such as *Antidesma montanum, Leea indica, Leucosyke capitellata* and *Villebrunea rubescens.* The ground vegetation layer was characterized by *Tetrastigma lanceolarium, Nephrolepis biserrata, Lygodium flexuosum* and nibung. The latter occurred as seedlings in both sites, most numerously in R2, in which the species was clearly better established (Table 1).

Plot S was placed within the *Timonius compressicaulis* forest on the west side of Sertung island (Fig. 1, Table 1). The emergent trees consisted of *Terminalia catappa* and *Hernandia peltata,* reaching heights up to about 30 m (Fig. 3). The main canopy was characterized by *T. compressi-*

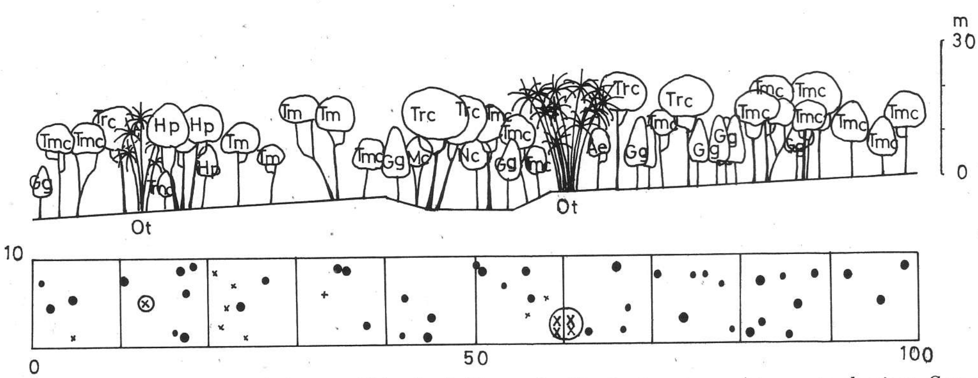
* See for taxonomic authorities of species mentioned in this paper, unless given here.



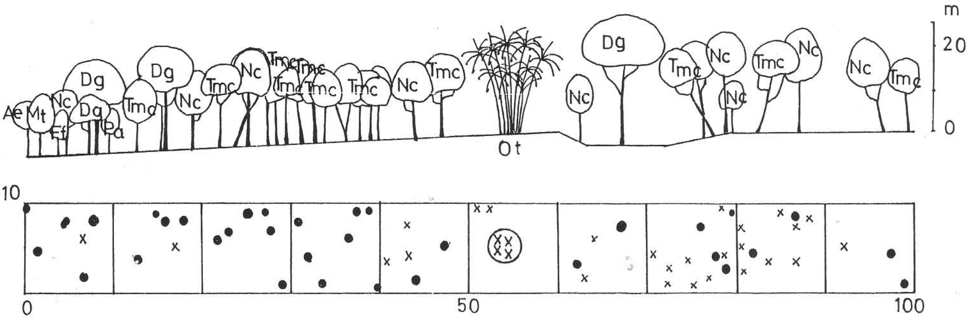
2. Profile diagram and map of trees within plot R2. x = seedling of nibung. Ot = parent tree. • = other tree species Bm = *Bridelia monoica*, Fs = *Ficus septica*, Ft = *Ficus tinctoria*, Nc = *Neonauclea calycina*, Pa = *Pipturus argenteus*, Ff = *Ficus fistulosa*, Trc = *Terminalia catappa*, Tf = *Tarenna fragrans*.

caulis and, to a lesser extent, *Neonauclea calycina*. In this less mature forest nibung grew as an emergent tree, in a cluster of 8 stems. There were some saplings of nibung in the second layer, but it was dominated by *Gnetum gnemon* (common at this end of Sertung). In general the ground vegetation was sparse, due to the relatively dense arboreal cover. However, a small number of nibung seedlings were observed in hollow sites near to the parent trees (Table 1).

The last plot (site P) was established on the central ridge of Panjang, which supported a *Timonius compressicaulis* community unusually rich (for Panjang) in *Neonauclea calycina*, such that it might be termed a patch of *Timonius–Neonauclea* forest. The shrub/sapling data (Table 1) indicate this site to be transitional to *Dysoxylum gaudichaudianum* forest, a pathway described by Whittaker et al. (1989). As in plot S, the forest had a relatively thin, broken canopy (Fig. 4), typical of *T. compressicaulis*, allowing healthy growth of the nibung, the crowns of which were an important component of the main forest canopy layer. Although requiring shade in the early stages of growth, *Oncosperma tigillarium* is known as a facultative light demanding species when approaching reproductive maturity;



3. Profile diagram and map of trees within plot S. Key as for Fig. 2, plus: Ae = *Artocarpus elasticus*, Gg = *Gnetum gnemon*, Hp = *Hernandia peltata*, Mc = *Morinda citrifolia*, Tmc = *Timonius compressicaulis*.



4. Profile diagram and map of trees within plot P. Key as for Figure 3, plus: Dg = *Dysoxylum gaudichaudianum*, Ff = *Ficus fulva*, Mt = *Macaranga tanarius*.

however, exposure is needed gradually for its development into the mature tree (House 1984). This was reflected by the occurrence of several small clusters of nibung under quite dense forest canopies (e.g., see Fig. 2). The data presented here are interpreted as showing nibung to be insensitive to community type within these near-coastal forests and to have no obvious association with other plant species.

Distribution of Nibung in Relation to Environment

In mainland Java, Sumatra and Kalimantan, nibung is generally known from brackish swampy areas or behind the tidal forests (Steenis 1935). Backer and van den Brink (1968) mention that nibung can be found at altitudes between 1 and 50 m above sea level, extensively associated with near-coastal localities, salt water swamps and "denudated rocks." Interestingly, Hommel (1987) describes an *Oncosperma tigillarium–Salacca edulis* (=*S. zalacca*) vegetation community from a low-land fluvio-alluvial plain within Ujung Kulon (west Java). It is described as secondary in status and is near-coastal in location, but its distribution explicitly does *not* include the coastal plains, swamps and beaches. It is not stated, however, whether *O. tigillarium* itself is similarly restricted. In the relatively aseasonal climate of Siberut (140 km west of Sumatra) another member of the genus, *Oncosperma horridum* (Griff.) Scheff., occurs commonly in the interior, but is replaced by *O. tigillarium* near the coast on sandy beach-derived deposits and along the tidal stretches of large rivers (House 1984). House found on Siberut that both species show a preference for coarse-textured, well-drained soils, of low fertility, and that these conditions were more often met with on slopes rather than in hollows. On Krakatau, such conditions are more or less ubiquitous and indeed drought conditions in the dry season are more likely to be limiting than is water-logging.

Within Krakatau, nibung has been found in Rakata, Sertung and Panjang at altitudes between 2 and 150 m above sea level. Although the young plants of *Oncosperma tigillarium* are reported to tolerate saline conditions (Koebernik 1966), no seedlings were recorded close to the shore line during the present study. The closest individual of nibung to the shore was about 10 m from an eroding coast. We conclude therefore that at least in the Sunda Straits area, it behaves as a near-coastal but not strand-line species.

Dispersal and Regeneration

The fruits of nibung are globular and about 12 mm in diameter. At first they are dark green but they turn black-purple on ripening (Backer and van der Brink

1968). Docters van Leeuwen (1936) was of the view that they had been brought to the islands by birds, probably the pigeon *Myristicivora bicolor*, which occurred at that time in large numbers. In support of this he cites observations of Ridley (1930) that the fruits are taken by other pigeons and, the facts that the young plants stood together in groups within woodland some distance from the beach.

The maximum distance that seeds were found from the parent trees within the study plots was about 10 m. A detailed count of the number of seeds in the vicinity of selected parent trees is shown in Table 2. House (1984) states that the closely related *Oncosperma horridum* does not germinate in open, sunny conditions but that the shade requirement for establishment and early growth is gradually lost as the palm grows into the main tree canopy. Nibung may well have a similar autoecology, requiring shady, humid conditions in the early stages. This is supported by our field observations that seedlings of nibung tended to be found in largest numbers in the moister sites within the study plots examined. In addition to seed production, nibung clumps also increase by the production of new buds at the base of the trunks of mature plants.

The distribution and population dynamics of nibung on the Krakatau Islands may be influenced by many factors. Strong winds, unconsolidated substrates and heavy rain all contribute to tree-fall. This means that canopy structures are relatively unstable. As important, the forests of Panjang and Sertung have been significantly disturbed by volcanic action on several occasions (above). It is hard to judge the impact on the nibung populations of these processes. The populations have spread as well on the more disturbed islands Panjang and Sertung as on Rakata, on which, however, it arrived most recently. The known distribution of the species within the islands suggests that most seed falls close to the parent trees, but that populations on each island have gradually spread from the initial colonization point, presumably aided by occasional animal-dispersal of seeds into suitable sites. Although nibung is not known as a true gap exploiter, it needs canopy space for successful flowering and fruiting. The seed falling very close to the parent trees is effectively "wasted," as the effects of continuous shading from the dense array of palm crowns, the damage caused by falling palm fronds and competition with parent plants leads to poor prospects of survival. The apparent ineffectiveness of dispersal agencies (Table 2) may thus be a limiting factor on the spread of the species, although the proportion of seed production involved is unknown. On the other hand, the buds shooting from the base of the trunk will generally be protected from the fallen palm leaves since nibung stems (especially the outer side of the clusters) tend to be a bit bent. As the palm, when full grown, is often taller than the surrounding trees, particular clumps may thus persist well. It may be that the main factor limiting the spread of nibung is low levels of soil moisture, particularly in the dry season. Comparison of data in Tables 1 and 2 indicates better initial germination and establishment rates in the deeper shade and more mature forests of Rakata;

Table 2. Densities of nibung seeds per m^2 on the study plots.

Distance from parent tree (m)	Nibung seeds				
	Plot				
	R1	R2	S	P	Average
0–1	6	11	1	2	5 (±4.6)
1–2	8	14	1	1	6 (±6.8)
2–3	8	17	6	1	8 (±6.7)
3–4	2	6	4	1	3.3 (±2.3)
4–5	7	5	3	1	4 (±2.6)
5–6	1	0	1	0	0.5 (±0.6)
6–7	0	0	2	0	0.5 (±1.0)
7–8	0	0	1	0	0.3 (±0.5)
8–9	0	0	0	0	0 (±0.0)
9–10	0	0	0	0	0 (±0.0)

although this remains something of a matter for speculation. It was also noted, however, that the development of the nibung population appears to be threatened by illegal cutting on each island.

Conclusions

1. In the first fifty years of recovery following sterilization in 1883 only three palms species were recorded on Krakatau, *Oncosperma tigillarium* being one of them.

2. After 106 years, eight palm species are known, all but one of these having established a continued presence. Nibung has now established a scattered distribution in near-coastal vegetation, below 150 m altitude and away from the strand-line.

3. Nibung appears from our data to be relatively insensitive to the between-island differences in vegetation, soil development and disturbance histories within the Krakatau islands.

4. Its spread appears to be limited by the effectiveness of local dispersal agencies and quite possibly by soil moisture conditions. Nonetheless it forms an occasional canopy component in all three original islands of the group.

5. We hope that this paper, although leaving many unanswered questions, may serve to awaken further interest in the ecology of palm colonization within tropical forest successions.

Acknowledgments

This paper is Krakatau Research Project Publication No. 34. We thank all those who participated in the project, and who helped the project in any way, financial or otherwise. The major part of the field work was conducted on the joint Oxford University, Ohio State University, and Herbarium Bogoriense 1989 expedition to Krakatau. Major financial support was provided by The Royal Society of London, The British Ecological Society, The Royal Geographical Society, The Percy Sladen Fund, Meyer International PLC., Smee Timber Importers (UK), Oxford University, and BP.

Literature Cited

BACKER, C. A. AND R. C. BAKHUIZEN VAN DEN BRINK, JR. 1968. Flora of Java. Vol. III. N.V.P. Noordhoff, Groningen.

BIRD, E. C. F. & N. J. ROSENGREN. 1984. The changing coastline of the Krakatau Islands, Indonesia. Zeitschrift fur Geomorphologie N.F. 28: 347–366.

BORSSUM WALLKES, J. VAN. 1960. Botanical observations on the Krakatau Islands in 1951 and 1952. Annales Bogoriensis 4: 1–64.

BUSH, M. B. AND R. J. WHITTAKER. 1986. The vegetation communities of Sertung, Rakata Kecil and Rakata. Chapter 3. *In:* M. B. Bush, P. Jones, and K. Richards (eds.). The Krakatoa Centenary Expedition: 1983 final report. Miscellaneous Series No. 33, Department of Geography, University of Hull, pp. 14–49.

DOCTERS VAN LEEUWEN, W. M. 1936. Krakatau 1883–1933. Annales du Jardin Botanique de Buitenzorg 46–47.

DRANSFIELD, J. 1976. Palms in the everyday life of West Indonesia. Principes, 20(2): 39–47.

ETHELBERT BLATTER, S. J. 1926. The palms of British India and Ceylon. OUP: London.

HOMMEL, P. W. F. M. 1987. Landscape-ecology of Ujung Kulon (West Java, Indonesia). 206 pp. Published by the author, Wageningen.

HOUSE, A. P. N. 1983. The use of palms by man on Siberut island, Indonesia. Principes 27(1): 12–17.

———. 1984. The ecology of *Oncosperma horridum* on Siberut Island, Indonesia. Principes 28(2): 85–89.

KOEBERNIK, J. 1966. Salt tolerance in young palms. *Principes* 10(4): 130–132.

NEWSOME, D. 1986. Aspects of soil surface characteristics on Rakata and Anak Krakatau. Chapter 9. *In:* M. B. Bush, P. Jones, and K. Richards (eds.). The Krakatoa Centenary Expedition: 1983 final report. Miscellaneous Series No. 33, Department of Geography, University of Hull, pp. 134–156.

RIDLEY, H. N. 1930. The dispersal of plants throughout the world. Reeve, Ashford, England.

SEEMAN, B. 1856. Popular history of the palms. London, Lovell Reeve.

STEENIS, C. G. G. J. VAN. 1935. Maleische Vegetatieschetsen. Tijdschr. Kon. Aardrijksk. Genootschap. Serie II vol. LII.

WHITTAKER, R. J., K. RICHARDS, AND M. B. BUSH. 1989. Plant recolonization and vegetation succession on the Krakatau Islands, Indonesia. Ecol. Monogr. 59: 59–123.