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Kauri forests in the New Hebrides

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A preliminary account is given of lowland tropical rain forest in which *Agathis obtusa* is dominant on basaltic soils. On the islands of Erromanga and Aneityum the shade tolerant *Agathis* seedlings often develop in close proximity to the parent trees, usually in small canopy gaps provided by the death or deterioration of *Calophyllum* and other associated broadleaved trees. There is no accumulation of litter or mor humus beneath *Agathis obtusa* and no evidence of podzolization was found.

Agathis obtusa appears to be one of the most stable components of the lowland primary forest in the New Hebrides and no windthrown trees were found. It is suggested that the emergent *Agathis* could moderate the effect of hurricane-force winds on the broadleaved canopy but that the smaller canopy breaks allow the growth of previously established but stagnating *Agathis* seedlings; similar release of *Agathis* regeneration has resulted from small-scale selective logging on Aneityum.

Introduction

Agathis species are dominant in some of the wetter parts of lowland primary rain forest on a number of islands in the southwest Pacific region. In several island groups these *Agathis* species are popularly known as 'kauri' which is the Maori name for *Agathis australis* in New Zealand, where trees of the genus were first exploited for timber on a large scale.

Many species of *Agathis* appear to be closely related and large mature trees of different species are often similar in habit, though such features as bole length and crown spread may be influenced by site and the height of the associated broadleaved canopy.

At higher altitudes in equatorial forests, and at lower altitudes further south, *Agathis* species are usually associated with one or more species of the Podocarpaceae. Together they form an ancient floristic element in forests of broadleaved (Angiosperm) trees, many of which belong to Malesian genera as far east as Fiji, and as far south as northern New Zealand where there is a humid, warm temperate climate.

While extensive tracts of virgin forest with *Agathis* still exist in lowland forests of West Irian, in Kalimantan and on the smaller islands of Melanesia, logging is rapidly depleting the forests with *Agathis*. There is little evidence that the indigenous Melanesian peoples of the New Hebrides, Santa Cruz Islands, Fiji, and New Caledonia substantially reduced the area of forests containing *Agathis*, at least in recent times, though fire may have damaged the margins.

In New Zealand the kauri forests in the north were thought to extend to a million hectares or more before the arrival of man about 1000 years ago. By the time Europeans arrived two hundred years ago there were considerable areas of heathland where kauri formerly grew, and it seems certain that Polynesian fires destroyed some of the original forest. The bulk of the virgin kauri forest has, however, been destroyed during the past 150 years through land settlement, logging, and uncontrolled fires. Today, the natural forests with stands or scattered trees of mature kauri have been reduced to remnants totalling some 5000 hectares (ha).

On the island of Erromanga in the southern New Hebrides, 14000 ha of forest in the central area contain groups or scattered trees of *Agathis obtusa* (Lindl.) Morrison. This forest was apparently little disturbed by man until 1967, when large-scale logging started to remove all kauri over 60 cm diameter, and *Calophyllum neo-ebudicum* Guill. which is its main broadleaved associate on this island. On the much smaller neighbouring island of Aneityum, kauri and several broadleaved species have been logged on a small scale for 50 years, but virgin stands of kauri remain in the upper part of its altitudinal range near the centre of the island, and over a wider range near the east coast. The central parts of both Erromanga and Aneityum consist of extinct basalt volcanoes. Dr D. G. Mallick (personal communication) has suggested that the Erromangan volcanic cones may be 4 to 5 million years old while those of Aneityum would be younger.

The central Erromanga forests still constitute the most substantial area of lowland primary forest in the New Hebrides and, together with the remnants of virgin kauri forest on Aneityum and the logged forests, provide the opportunity to study the ecology of *Agathis* in a relatively accessible area. These islands, with their marginally tropical climate, are situated at latitudes 18° 40′ to 20° 20′ S, between the more tropical forests with *Agathis* to the north and west and the warm temperate kauri forests of New Zealand. Studies of the structure of their kauri forests, the regeneration pattern of kauri, and its relation to the broadleaved species may contribute to an understanding of the ecological status of *Agathis* in this part of its wide geographical range. This paper gives a preliminary account of the southern New Hebridean kauri forests as the result of a two-week visit in July/August 1971. The author has also visited forests with *Agathis* species in New Zealand, Malaya, Queensland and Brunei and some comparisons are made with the regeneration of *Agathis* species in these countries.

No climatic data has been recorded in the kauri forests of the New Hebrides and those recorded from a few coastal sites are not a reliable indication of climate within inland and more elevated areas where the optimum development of kauri occurs. It may be inferred, however, that kauri is absent from the more seasonally dry areas and that it is generally confined to regions with average annual rainfall of over 2000 mm.

Whitmore (1966*a*) has given an account of *Agathis macrophylla* Mast. on Vanikolo, one of the Santa Cruz islands, and has summarized hypotheses on the ecological status of conifers in the southwest Pacific region. He concluded that *A. macrophylla* on Vanikolo is a normal component of the climax rain forest and does not depend for its survival on wide-scale destruction of the forest. More recently, Havel (1971) concluded that the *Araucaria* species in New Guinea are normal components of certain forest types in which the broadleaved canopy is reduced in height and density through unfavourable climatic or edaphic conditions.

Distribution of Agathis *species in the New Hebrides*

Present information indicates that *Agathis obtusa* is confined to the southern islands of Erromanga and Aneityum, while *A. macrophylla* occurs in the northern island of Espiritu Santo as well as in the Santa Cruz islands. Whitmore (1966*b*) has given a thorough description of *A. macrophylla* from the Santa Cruz group but the few other published descriptions of the two species (e.g. in Dallimore & Jackson 1966) and their distribution give a confused picture. Doubts are raised as to whether they are, in fact, two distinct species or merely geographical forms of one variable species. A definitive study of the taxonomic status of *Agathis* species would assist biogeographical studies. All *Agathis* specimens collected by 1971 Expedition members on Erromanga and Aneityum were identified by D. R. Hunt of Kew as *A. obtusa* (Lindl.) Morrison.

Guillaumin (1948) gives the New Hebridean range of *A. macrophylla* and *A. obtusa* as Santo, Erromanga and Aneityum. In the list of species collected in Espiritu Santo by members of the 1933/34 Oxford University Expedition (Guillaumin 1938) there is reference to a single large specimen of *A. macrophylla*, 30 ft (10 m) in girth, found in rain forest north of Sara on the western side of the Cumberland Peninsula, 'the only one of its kind in the district'. *A. obtusa* is recorded as occurring in the 'Hapuna Valley mountain forest at 2000 ft' (612 m).

G. P. Robinson (unpublished), after a geological survey of northern Espiritu Santo in 1964, reported that stands of kauri were found on westward-facing ridges of the Cumberland Peninsula, commonly around 600 m. Harrisson (1936) referred to large, scattered emergent kauri in elevated forest west of the main range on the Cumberland Peninsula, and other travellers mention rare isolated large trees further eastward in the Big Bay region. Harrisson also mentioned that local inhabitants of the Cumberland Peninsula would sometimes for amusement set fire to resin exudations extending up trees. They used the resin for torches but there is no evidence that kauri in the New Hebrides was ever tapped for resin as in New Zealand and parts of Indonesia.

Kajewski (1930) briefly described the vegetation near Dillon's Bay on the drier western side of Erromanga and mentioned that kauri occurred as occasional scattered emergent trees in elevated rain forest inland from coastal strips of grassland and scrubland.

Most of the kauri on Erromanga is found from 200 to 400 m a.s.l. though trees may be found as low as 100 m on the wetter southeastern side and up to 500 m towards the centre of the island. It is not found on the raised terraces of coral limestone which fringe the island and extend inland for several kilometres in places. These terraces have a cover of secondary forest, open woodland, or grassland, resulting from shifting cultivation and fire in times when there was a much larger Melanesian population which extended inland. Today, there are only a few scattered coastal villages. An account of the depopulation of Erromanga and Aneityum over the past 100 years has been given by McArthur & Yaxley (1968).

On Aneityum, which lacks any substantial area of limestone terraces, kauri must have descended almost to sea level in places, as groves of trees occur at 100 m a.s.l. near the southeast coast above a narrow strip of fire-induced scrub with *Acacia spirorbis*. Small residual trees are found in logged forest at 50 m a.s.l. near Anelcauhat on the south coast in an area of shifting cultivation.

The author found little evidence on either Erromanga or Aneityum that kauri is advancing into fire-induced scrubland in eroded coastal belts or into secondary forests. The upper altitudinal limit of kauri is near the commencement of forest dominated by *Weinmannia* and *Metrosideros* species. On these islands kauri appears to be confined to volcanic soils.

On Espiritu Santo, Expedition members saw only one kauri tree, a large specimen, possibly of planted origin, near the mouth of the Jordan River in Big Bay. It was not possible to visit the Cumberland Peninsula and confirm its apparent relic status there or its presence at altitudes as high as 600 m. There was formerly a substantial Melanesian population practising shifting cultivation in the mountainous regions of Espiritu Santo (Harrisson 1936), and fire may have reduced the numbers of kauri there. While it seems unlikely that fire would carry through undamaged primary forest with scattered kauri in the wetter regions of the New Hebrides, it is known that some secondary forests will carry fire after hurricane damage. Presumably, storm damaged primary forest could carry fire and the fires from piecemeal land clearing associated with shifting cultivation would reduce primary forest with kauri by a process of attrition.

Description of kauri forest on Erromanga and Aneityum

Reference points were established where structure, floristics and environmental factors were recorded as fully as possible, on a proforma suggested by Webb *et al.* (1970) for use where the flora is poorly known. These reference points are listed as Forest Ecology Sites 412, 539, 540 and 541 in the Collection Data Handbook of the Expedition (Lee 1974).

On Erromanga a number of tree species were just beginning to flower in early August but most botanical specimens were sterile and had to await comparison with identified material at Kew or other Herbaria. Tentative determinations of wood specimens have been made by the C.S.I.R.O. Melbourne. In the field most trees were identified only to generic level.

Johnson (1971) reported on the results of a forest inventory of Erromanga. He has provided some general infomation of ecological interest and data on the structure of the forests in the form of tables showing frequency of kauri and broadleaved species in 10 cm diameter classes (see table 1). The maps attached to Johnson's report give a good picture of the distribution of kauri, land forms and broad forest types related to the land forms and degree of forest disturbance. Kauri is not found in any of the disturbed forest types resulting from former cultivation and fire, and subject to more hurricane damage than that which generally occurs in the primary forest.

On Erromanga, kauri is found in groups or as scattered trees on steep, dissected, and gentle terrain on soils derived from basalt. There are no extensive stands of pure kauri, but the massive fan-shaped crowns of the mature trees are most abundant on ridges and upper slopes, and are emergent over a rather low (15–20 m tall), dense, unstratified forest of broadleaved trees, many of which have distorted crowns and short, irregular or leaning boles. The crowns of the broadleaved trees mingle with the lower upwardly-directed branches of the kauri. The kauri have relatively short boles, ranging between 10 and 15 m in length. Total height is usually about 30 m, with a few trees approaching 40 m. Maximum breast height stem diameter is approximately 3 m, but there are few trees over 2 m. Crown diameter may extend to 30 m.

Young kauri trees retain their monopodial habit until they have grown above the broadleaved canopy. The change from a narrow conical to a spreading crown with upward growing branches occurs when stem diameter is between 30 and 50 cm.

The main broadleaved associates of kauri are *Calophyllum neo-ebudicum* Guill. and *Hernandia cordigera* Vieill. After extensive sampling Johnson found that no other large trees were abundant, but of the 20 or so other species with stems that exceeded 60 cm diameter only *Palaquium neo-ebudicum* Guill. was relatively common. His report lists 60 tree species collected in primary rain forest and identified by scientific and Erromangan names.

At reference sites in the author's study the 24 canopy-forming trees nearest to a central reference tree of emergent kauri were identified to generic level when possible. Combining results from two adjacent inland plots (site 412) on a rolling ridge at 200 m, 48 trees were distributed amongst 19 species as shown below. Determinations to specific level were mainly made at Kew.

Agathis obtusa (Lindl.) Morrison	2 trees
Ilex vitiensis A. Gray	9
Hernandia sp. cf. *H. cordigera* Vieill.	6
Palaquium neo-ebudicum Guillaum	5

Planchonella sp. cf. *P. pyrulifera* (A. Gray) H. J. Lam	2 trees
Planchonella linggensis (Burck) Pierre	1
Garcinia sp. cf. *G. vitiensis* Seem.	7
Calophyllum neo-ebudicum Guillaum	2
Syzygium sp.	3
Dysoxylum aneityense Guillaum	2
Spiraeanthemum sp.	1
Geissois sp. cf. *G. denhamii* Seem.	1
Ficus granatum Forst. f. var *minor* Corner	1
Canthium cymigerum (Val.) B. L. Burtt	1
Bleasdalia lutea (Guillaum) A. C. Sm. & J. Haas	1
Linociera cf. *brachystachys* (Schltr.) P. J. Green	1
Elaeocarpus hortensis Guillaum	1
Celtis paniculata (Endl.) Planch.	1
Achronychia simplicifolia (Endl.) McGillivray and Green subsp. *neo-scotica* P. J. Green	1

The understorey consisted of several species of Araliaceae and Rubiaceae, *Myristica*, *Dracaena* and seedlings of Sapindaceae, Sapotaceae, Guttiferae, *Ilex* and *Syzygium*. Climbers included *Epipremnum*, *Calamus*, *Pandanus*, *Freycinetia*, *Uncaria* and *Piper* species. At this site most canopy trees were unbut tressed or had low buttresses. Apart from kauri with its flaking bark, and *Calophyllum* with its fissured bark, most trees had smooth or lenticillate bark. Bark thickness measured with a bark gauge ranged from 15–25 mm for kauri, *Hernandia* and species of Sapotaceae, and from 7–15 mm for other species. Most canopy trees had entire-margined, leathery leaves, falling into mesophyll and notophyll size classes, with a slight proponderance of notophylls. Structurally and physiognomically, the Erromanga kauri forest has many of the features of 'submontane forest' within the Tropical Rainforest Formation as described by Baur (1968).

On Aneityum reference points were established in logged forest at 50 and 260 m altitude (sites 540 and 541) and in an apparently virgin stand near the lower limit of kauri on the south-east side of the island, at 120 m a.s.l. (site 539). At this coastal site, close to the margin of fire-induced scrub, the forest was exposed to the prevailing wind and there was evidence of persistent wind damage with the stems of kauri trees tending to be sinuous. Compared with the inland Erromanga site described above, the kauri were smaller (up to 20 m high and ranging from 21 to 75 cm diameter) and more abundant, with crowns barely emergent from the broadleaved canopy; epiphytes and climbers were fewer, and both the understorey and ground vegetation more sparse. The last two features are characteristic of dense kauri groves. *Calophyllum neo-ebudicum*, so abundant on Erromanga, was not seen near sites described on Aneityum although Guillaumin (1931) recorded that it was a common tree in Anelcauhat Bay in 1928. *Hernandia* was the most common associate of kauri at Site 539 in two adjacent plots centred on kauri reference trees on a moderately steep slope. The 48 canopy trees were distributed among 14 species as follows:

Agathis	19 trees
Hernandia	11
Canarium	2
Lauraceae	2

Myristica	2 trees
Fagraea	1
Dysoxylum	1
Ficus	1
Syzygium	1
Sapotaceae	1
unidentified	7 trees of 4 species

The understorey contained Rubiaceae and *Dracaena* and the ground vegetation consisted mainly of *Selaginella*, a creeping *Freycinetia*, *Schizaea dichotoma*, the root parasite *Balanophora fungosa* and tree seedlings.

On Aneityum the composition of the broadleaved canopy of some 50 species does not appear to vary greatly throughout the kauri forest. In partly logged forest *Alphitonia* is one of the most prominent secondary species, and *Weinmannia* and *Serianthes* commonly form part of the residual canopy. Kauri is well represented in the younger size classes and by small trees that were undersize at the time of logging.

The pattern of kauri regeneration and forest structure

Figure 1 is a plan of a plot at site 412 on Erromanga showing the canopy of the central reference tree in relation to the stems of the nearest 24 canopy-forming trees and to regeneration of kauri. On this particular site several trees of *Calophyllum* have died, leaving the remains of standing and fallen stems. Other *Calophyllum* are moribund and disintegrating, the thinning crowns being loaded with epiphytic ferns and orchids. Kauri regeneration appears to be associated with gaps caused by the death of *Calophyllum*. Small kauri seedlings do occur directly beneath the large kauri crown but larger seedlings and saplings are found mainly towards the periphery of the crown or outside it. Most of the dead and moribund *Calophyllum* had stem diameters of approximately 1 m, probably approaching the maximum size for this site. Other groups of *Calophyllum* near this site were still vigorous but reconnaissance further afield showed a pattern of kauri regeneration similar to that described above. The relation of seedling or sapling groups to canopy gaps, or the remains of dead broadleaved trees, was not always apparent and many young kauri persist in heavy shade. In this situation straight, slender kauri saplings up to 7 m high often showed a habit characteristic of slow growth, having shallow, compressed crowns consisting of a few closely-spaced whorls of long, slender, lax or horizontal branches. In canopy gaps, the lower branches of young trees were starting to thicken when total height was about 15 m and stem diameter from 15 to 20 cm.

Table 1 is an adaptation of one of Johnson's stand tables for a section of the forest where kauri was most abundant. It shows that kauri is well represented in all size classes up to 2 m diameter with 8.8 trees/ha between 10 and 50 cm, representing young trees with a monopodial habit, and 3.4 trees/ha over 50 cm, representing mature trees. Kauri, however, is very unevenly distributed throughout the forest, and trees over 1.5 m diameter may be absent from substantial areas. *Calophyllum*, on the other hand, is abundant throughout the forest; the section of table 1 contains 44.2 trees/ha over 10 cm diameter.

Stems of kauri in the 0–9 cm diameter class would presumably include well-developed saplings as well as small suppressed seedlings which would be difficult to count accurately in continuous 20 m × 50 m plots along belt transects. As kauri seedlings are generally abundant only close to seed-bearing trees, and such trees are unevenly distributed, the table may not give an adequate indication of the regenerative capacity of kauri. Kauri seedlings occurred on 50 % of plots, whereas *Calophyllum* seedlings occurred on 90 % of plots.

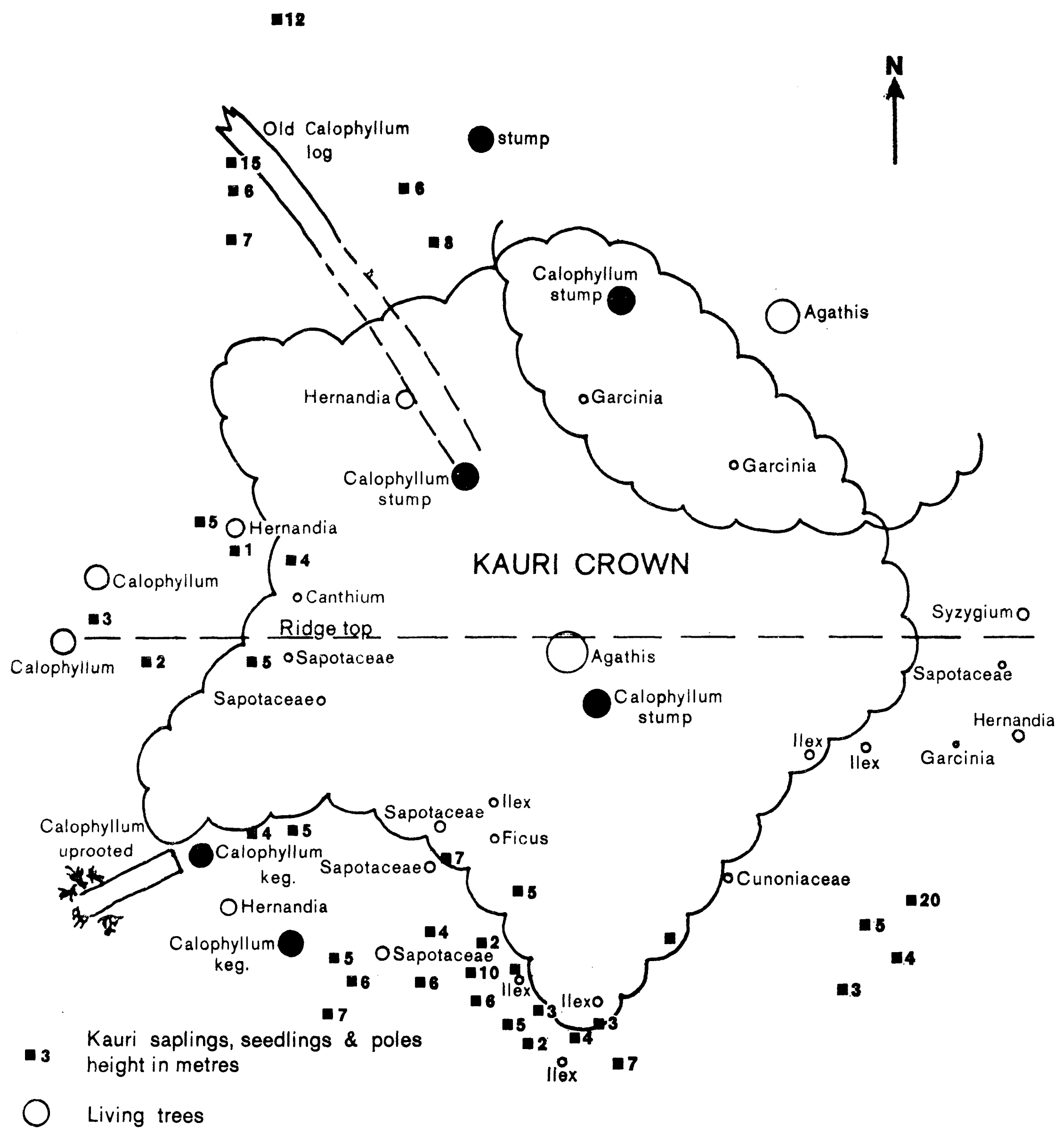

FIGURE 1. Emergent kauri crown in relation to broadleaved canopy trees and kauri regeneration. Site 412, Erromanga. 1 cm = 3 m.

The data in table 1 indicate that the kauri on Erromanga is of all ages. Provided that kauri lives considerably longer than the broadleaved trees, the number of young kauri trees is probably sufficient to replace the old ones. From what is known of *Agathis* growth rates the largest *A. obtusa* are likely to be at least 500 years old. The recruitment of small kauri seedlings near the crowns of parent trees is a continuing process but the further development of these seedlings will depend on the gradual thinning of the broadleaved canopy or the occurrence of breaks in it as illustrated in figure 1. The development of seedling groups could be a continuous process through gradual decay and death of an abundant, well distributed and shorter-lived

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Table 1. Frequency of kauri and broadleaved species in one section of Erromanga forests

(From Johnson 1971.)

diameter class/cm	number of stems per hectare in 10 cm diameter classes: 0–9	10–19	20–29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120–129	130–139	140–149	150–159	no. of stems from 10–49 cm diameter	no. of stems over 49 cm diameter
Agathis	28.335	5.244	1.854	0.949	0.769	0.261	0.230	0.261	0.256	0.246	0.288	0.220	0.173	0.063	0.099	0.110	8.816	3.416
Calophyllum	328.821	11.483	7.505	5.741	5.515	4.099	3.806	2.839	1.725	0.831	0.439	0.146	0.063	0.026	—	—	30.244	13.974
Hernandia	n.a.	2.667	1.175	1.492	1.447	0.837	0.842	0.507	0.314	0.157	0.068	0.047	0.016	0.005	0.005	—	6.781	2.798
all species	n.a.	467.089	177.758	57.775	26.983	8.742	6.682	4.376	2.703	1.443	0.915	0.449	0.273	0.099	0.125	0.115	729.605	26.287

diameter class/cm	160–169	170–179	180–189	190–199	200–209	210–219	220–229	230–239	240–249	250–259	260–269	270–279	280–289	290–299	300–309
Agathis	0.078	0.084	0.058	0.037	0.037	0.010	—	0.016	—	—	0.005	—	0.005	0.010	0.005
all species	0.083	0.084	0.068	0.037	0.037	0.010	0.005	0.016	—	—	0.005	—	0.005	0.010	0.005

Sample area: For trees 10–49 cm diam. – 22.12 ha or 0.45 % of total area sampled (4870 ha).
For trees over 49 cm diam. – 191.25 ha or 3.92 % of total area sampled.

species such as *Calophyllum*, or it could occur intermittently as a result of storm damage reducing the canopy.

During the limited reconnaissance in 1971 no dead, senescent or windthrown kauri were seen, and all the stumps of recently felled kauri examined were sound. There was no evidence of large kauri with stem rot being left by the loggers who normally felled all sound kauri over 60 cm diameter. Johnson does not refer to dead or defective kauri but does record the remarkable fact that he did not find a single windthrown kauri over the 14000 ha of forest sampled by him. Windthrown broadleaved trees, including *Calophyllum*, were common and Johnson records the location of forest areas damaged by a hurricane in 1959 when the wind blew from the northeast. The main kauri areas were sheltered from the full force of this hurricane but there was extensive windthrow and damage of broadleaved trees in exposed areas with sparse kauri. This general lack of dead, decadent and windthrown kauri and the very scattered distribution of trees between 2 and 3 m diameter suggests that mortality of kauri may occur periodically. If there is an accumulation of large, senescent trees over a long stable period, a hurricane could then cause or hasten death of these trees by crown breakage or windthrow, leaving only a few scattered survivors.

In 1971 areas of young secondary forest were examined near Ipotak on the east coast of Erromanga with a 5 to 10 m high canopy of *Macaranga*, *Acalypha* and other Euphorbiaceae, *Kleinhovia*, *Commersonia* and Malvaceae. There were, in places, the rotting remnants of an older secondary forest with stems lying towards the southwest, presumably resulting from hurricane damage. According to local inhabitants, fire spread through much of the forest destroyed by the 1959 hurricane. At the places examined, however, charring was not evident and 'flash' fires may have scorched or consumed mainly leaves, twigs and branches of small dimensions.

Further inland, in areas where kauri is most common, it is probable that the emergent kauri moderates the effect of storms on the smaller broadleaved species and the forest has not been flattened in the manner described above.

It is not suggested that kauri regeneration on Erromanga depends on hurricanes or other catastrophes as it appears to be a continuous process, but strong winds would periodically open up the broadleaved canopy, allowing development of previously established kauri seedlings. Gradual deterioration of the crown of a 'nurse' tree is likely to provide more suitable conditions for the growth of young kauri than the sudden formation of a larger gap through windthrow of dense-crowned trees. In the latter case, small kauri would have to compete with smothering climbers and large-leaved, fast growing species like *Macaranga*; species of *Macaranga* are common in the primary forests, and presumably become established in gaps made by windthrow or on land slips.

Evidence of periodic mortality of the larger kauri on Erromanga needs further examination. Johnson produced 6 stand tables for different parts of the forest and total basal area calculated from his tables for all stems over 10 cm diameter range from 36.2 to 39.7 m^2/ha. These are relatively high figures for rain forests but at present mortality appears to be confined to broadleaved species and the mature kauri may continue to be stable for a long period before declining in vigour.

Impact of logging

Logging on Erromanga has been carried out rapidly and on a large scale but for too short a period to enable a prediction to be made with confidence on the future course of kauri regeneration and the stability of the logged forest. In 1971, only four years after the start of logging, no new kauri seedlings were seen in open areas round kauri stumps or on log extraction tracks, but young kauri had survived in patches of residual forest. Kauri seedlings planted in the open on clearfelled roadside strips, and on loose fill, had grown vigorously and *A. obtusa* from Erromanga has been one of the more promising species in early planting trials on Efaté, even on coral beach deposits similar to those for which a pH of 8.5 has been recorded.

The small-scale logging carried out on Aneityum over a long period has allowed a rapid return to high forest conditions and young kauri are relatively abundant in the logged areas.

With the considerable devastation caused by the more intensive logging on Erromanga there would appear to be danger of greater wind damage to residual vegetation, invasion by creepers, and increase of land slips.

Soils beneath kauri

On Erromanga, soil profiles dug beneath kauri and beneath *Calophyllum* at ecological reference site 412, and described by Lee & Buckerfield (Lee 1974, sites 421 and 422), show some differences in colour and structure of the red-brown clay soils over basalt. All horizons in the root zone are highly acid and presumably strongly leached. There is no appreciable accumulation of mor-type humus beneath the kauri. Chemical analysis (K. E. Lee personal communication) has shown that total Ca^{2+} and Mg^{2+} were lower under the kauri than under *Calophyllum*. While this indicates more intensive leaching under kauri there is no real evidence of podzolization on these Erromanga sites.

Roadside cuttings nearby showed evidence of five successive slumps but the wide-spreading root systems of the mature kauri must give some stability to soils on ridge crests and upper slopes.

Swindale (1957) investigated the characteristics of soils beneath *Agathis australis* developed from rhyolite and from olivine basalt in northern New Zealand. He concluded that kauri vegetation exerted a strong podzolizing effect upon rhyolitic soil parent material with marked profile differentiation. While the soil on strongly weathered olivine basalt did not show much profile differentation, he concluded from a study of the distribution of iron oxides, clay content and minerals that kauri vegetation also has a strong podzolizing effect upon basaltic soil parent material in northern New Zealand. Other writers have concluded that *A. australis* does not podzolize soils derived from basalt owing to its low silica content.

Comparison with Agathis *forests of other countries*

From Whitmore's (1966*a*) account of *Agathis macrophylla* on Vanikolo Island it is obvious that the forests there resemble the *Agathis* forests of the southern New Hebrides in many ways, and that *Agathis* regenerates in a similar manner in each island group through occasional penetration of the broadleaved canopy. Whitmore's description of *Agathis macrophylla* (1966*b*) could generally be applied to *Agathis obtusa* of Erromanga.

Vanikolo is situated some 8° nearer the equator than Erromanga, the climate is non-seasonal, and recorded rainfall on the coast is much higher than that recorded on the west coast of Erromanga. The kauri on Erromanga, however, is confined to the wetter parts of the island and does not occur in the seasonally dry region on the western side.

In the two island groups of the New Hebrides and the Santa Cruz Islands there are resemblances in some general characteristics of the oceanic climates, in the leached soils subject to land slips over weathered basalt, in forest structure and in the flora. Both groups are subject to hurricanes and earthquakes, and in both groups there are islands which previously had a large Melanesian population who practised shifting cultivation further inland than do the few coastal inhabitants today. There is no evidence, however, that shifting cultivation has ever been practised within the present *Agathis* forests.

Although there may be some tendency for mor-type humus to develop on Vanikolo with its very high rainfall, the regeneration pattern of *Agathis* appears to be similar to that on Erromanga; in neither island are there thick layers of litter and raw humus to prevent recruitment of *Agathis* seedlings. Whitmore (1966*a*) did not notice any difference between the soil under kauri and the soil where there was no kauri.

In Malaya, conditions for recruitment of small *Agathis* seedlings are also favourable in the dipterocarp forests where *Agathis dammara* (Lambert) L. G. Rich. occurs in rather restricted areas, often on soils derived from granite and quartzite. It occurs mainly in small groups of two to five trees on ridges and upper slopes at altitudes of 300 to 1200 m. In these taller and relatively stable forests not subject to persistent winds, hurricanes or other catastrophes, the *Agathis* crowns are smaller and not emergent, at least at lower and mid altitudes, while bole length and total tree height are greater than in *Agathis* on the islands of Melanesia. In Malaya seed dispersal of *Agathis* from non-emergent trees could be restricted, though the squalls which occur frequently before thunderstorms could assist in dispersal. *A. dammara* in this part of its wide geographical range does not often have stems over 1.5 m diameter; thus the species may have little competitive advantage over its large broadleaved associates through longevity. P. F. Burgess (personal communication) considers that *A. dammara* gains a competitive advantage through its occurrence on well drained sites where it can withstand conditions of water stress.

In Malaya, saplings and young trees of *A. dammara* are not common in virgin forests but small seedlings occur frequently beneath the crowns of parent trees or in their vicinity. These seedlings are shade tolerant and may persist for some time with little growth, but they quickly resume growth when parent trees are removed in selective logging. *A. dammara* appears to regenerate in a manner similar to that of many of the Dipterocarpaceae. The frequent occurrence of charcoal in soil pits dug beneath *Agathis* in Malaya is an intriguing point for which no explanation has yet been offered as the forests appear to be primary.

In a remnant of virgin *Agathis* forest seen in Brunei, groves of *Agathis* were growing on old raised beaches surrounded by freshwater swamp. A layer of fine *Agathis* feeding roots was situated near the top of 30 cm of raw humus and beneath a few centimetres of undecomposed leaf litter. The raw humus was sharply differentiated from the white sand beneath. *Agathis* trees of all sizes up to 1 m diameter were seen and seedling regeneration was abundant. Death of large trees appeared to follow attack by termites. The *Agathis* in this forest were obviously regenerating *in situ* and seedling regeneration was also prominent within 50 m of seed trees left by partial logging 15 years before.

In northern New Zealand the structure of *Agathis australis* stands in most of the remaining virgin forests, the regeneration pattern of the species, the strong podzolization of some soils beneath kauri and the deep layer of mor-type humus beneath large trees, are in marked contrast to the situation described above for the tropical *Agathis* species.

A. australis grows on a wide range of soils which become leached or podzolized after a period of time, according to the type of parent material (Taylor 1947; Taylor & Sutherland 1954). The soils developed from basalt beneath kauri are brown loams (Taylor, Dixon & Seelye 1950) and become leached over a long period. Kauri is considered to be a species that tolerates low fertility, tending to occur on the less fertile soils and making them even less fertile. Thus the kauri obtains a competitive advantage over broadleaved trees, often producing a mosaic pattern.

A. australis is usually well anchored by vertical 'peg' roots that penetrate deeply in some soils. It has been suggested (J. E. Cox, personal communication) that large kauri may grow on apparently infertile sites by producing feeding roots at depth (evidence found at 3 m) from the 'peg' roots, thus tapping richer sources of nutrients than are available in the podzolized soil above.

In some undisturbed forests, including those on soils derived from basalt, there are few kauri between seedling size and mature trees, all-aged stands being confined to secondary forests resulting from fires and logging. Small kauri seedlings may occur in the proximity of the mature kauri but usually lack vigour and do not persist beneath either kauri, podocarps or broadleaved trees. Mirams (1957) and Bieleski (1959) have carried out autecological studies of kauri near Auckland and have discussed the various hypotheses put forward to explain the ecological status of *A. australis*. Bieleski refers to the importance of soil factors for regeneration. Mor-type humus is subject to drying out and is an unsuitable medium for establishment of kauri seedlings. In one Forest Service experiment removal of ground vegetation, litter and humus to expose mineral soil beneath large kauri resulted in slow seedling recruitment, but over a period of 20 years no seedling persisted for more than a few years, or grew to a height of more than 5 cm.

On some sites *Agathis australis* may start to regenerate directly after removal of the larger trees by logging, but the regeneration period may extend over 50 years or longer through suppression of seedlings during the early seral stages. In one locality a dense cover of sedge initially inhibited regeneration of kauri following selective logging but after 30 years *Leptospermum* and *Weinmannia* had partially suppressed the sedge, allowing development of established seedlings and further recruitment. *Leptospermum* and *Weinmannia* species are the most common nurses for several podocarp species as well as kauri in secondary forest and if they were induced by natural phenomena in the past, new cycles of kauri could have been initiated. Soil scientists have referred to successive podzolized profiles situated one above another, whilst Reed (1964) records that 'gumdiggers' found up to four distinct layers of fossil resin on some sites. A more critical study of forest structure and soils in all the forests with mature *Agathis australis* would probably throw some light on the ways in which kauri groves are initiated. In some forests with skeletal soils various patterns of regeneration may be seen along ridge crests and on steep slopes. In some places it is obvious that podocarps will replace existing kauri. Elsewhere young kauri may grow in groups where podocarps have died, and well established kauri seedlings may be found on recent slips amongst broadleaved shrubs. In valleys the few large kauri are destined to be replaced by broadleaved trees.

On some soils *Agathis australis*, like the Melanesian *Agathis* species, is extremely windfirm up to maturity, and without heart rot or butt rot. Some older trees are hollow, however, and are then subject to collapse or windthrow. There are a few recorded instances of extensive wind throw in New Zealand kauri forests. The latest occurred in 1957 when a cyclonic storm destroyed many trees, both sound and unsound, sometimes in swaths produced by one tree striking the next one (Conway 1959). Most damage was done to a forest partially logged for the larger trees in an operation similar to that on Erromanga. Taylor (1947) has suggested that *A. australis* may become unstable on heavily-podzolized soil with the development of pans and shallow rooting.

There are several sources of catastrophes to explain extensive destruction and probable renewal of New Zealand kauri forest in the distant past and some evidence that sudden destruction did occur, though it is not well documented. Kauri forests, like podocarp/broadleaved forests, have been found buried in swamps with uprooted trees all pointing in one direction (D. S. Preest, personal communication). A pedologist with long experience of North Auckland soils has recorded that 'there is widespread evidence of ancient fires in the form of charcoals in buried soils' (J. E. Cox, personal communication); he suggested that the susceptibility of kauri to fire probably helped to prevent it becoming generally dominant, except on the poorest soils. Northern New Zealand has had a long history of volcanic activity but no recent activity has been recorded north of Auckland.

In the present state of knowledge it is probably fruitless to conjecture further about the long term trends in New Zealand kauri forest and the precise origin of the present kauri stands. In more recent times wind damage and Polynesian fires have been factors in destruction of forest and initiation of new kauri groves.

In summarizing the above account, the *Agathis* species discussed appear to obtain some advantage over their broadleaved competitors by occupying less fertile soils or more freely drained sites, assisted by considerable shade tolerance of seedlings and saplings (less marked with *A. australis*), longevity and stability. *A. australis* appears to be the species that most actively invades secondary forest after substantial destruction of the original kauri forest and it seems that a catastrophic event is required to initiate a new growth cycle in New Zealand. It is possible, however, that ancient fires and shifting cultivation may have had a long-term influence on *Agathis*-bearing sites in tropical forests which now appear to be primary. In the tropical countries referred to above a partial logging generally seems to have stimulated regeneration of *Agathis*, either through growth of small seedlings already present on the ground or through retention of an abundant local seed source.

The association of Agathis *with species of Podocarpaceae*

Throughout the greater part of its range *Agathis* is associated to some extent with podocarps. In Malaya *Agathis dammara* in the upper part of its altitudinal range is associated with species of *Dacrydium* and *Podocarpus* and in particular with two of the most widespread of the podocarps, *Podocarpus imbricatus* Bl. and *Podocarpus neriifolius* D. Don. Other forms of these latter two species are found in the *Agathis* forests of Erromanga and Aneityum but have not been recorded from other islands of the New Hebrides.

In Borneo *Dacrydium* and *Agathis* occur together on the podzolized sands of the heath forests at low altitudes and also in the hill forests. The association of podocarps and *Agathis* continues in the New Guinea highlands and in New Caledonia and Fiji. In the Santa Cruz Islands *Dacrydium elatum* is recorded as an associate of *Agathis macrophylla* (Hadley 1959). In New Zealand most of the forest types containing *Agathis australis* have podocarps as prominent associated species.

Most of the podocarps have seeds with fleshy seed coats, receptacles or arils that are suited for dispersal by birds (Preest 1963). In New Zealand seeds of the taller growing forest podocarps are being efficiently but locally dispersed by the native pigeon (*Hemiphaga novaeseelandiae*) (Beveridge 1964).

The two podocarps of Erromanga and Aneityum could be dispersed to the intervening island of Tanna or to more remote islands of the New Hebrides but they have not been recorded there. One reason for their absence may be the more recent history of volcanicity on a number of these islands.

The small-winged *Agathis* seed has been considered to be poorly adapted for long distance dispersal by wind (Guppy 1906). The bulk of the seed would generally fall near the parent tree but it is possible that on rare occasions rising air currents could catch seed released from cones disintegrating on emergent crowns and carry it for considerable distances. Viability of *Agathis* is rapidly lost in natural conditions, however, and the chances of successful establishment of trees from long distance dispersal of seed are remote; there appears to be no recorded evidence that it occurs. In the southern New Hebrides *Agathis* has not been recorded outside the primary forest. In central Espiritu Santo scattered large trees of *Agathis* have been recorded many kilometres apart, and distant from groups of trees remaining on the Cumberland Peninsula. While these trees could be the result of relatively long distance dispersal, they could equally well be relics of a wider distribution; conceivably some could even have originated from the planting of seedlings by Melanesians.

Conclusions

Agathis obtusa in the southern New Hebrides is maintaining its dominant position in the primary rain forests through longevity, stability, the shade tolerance of its seedlings and saplings, and the ability of these to develop in small gaps occurring in the broadleaved canopy. While the broadleaved trees growing beneath the crowns of large kauri will replace these emergent trees, the kauri have themselves replaced *Calophyllum* and other broadleaved species on the same site. Young kauri become established most commonly in the vicinity of the parent trees. Kauri is thus regenerating cyclically in a mosaic pattern. It provides a relatively stable element in forests which are subject to damage by hurricanes.

The kauri stands appear to be vigorous and relatively young except for a scattering of trees between 2 and 3 m in diameter. It seems probable that there are periods of widespread *Agathis* mortality followed by periods of stability when the mature trees are able to withstand storms and to moderate their impact on the smaller broadleaved trees.

Small-scale selective logging as carried out on Aneityum has left a high forest structure and enabled kauri regeneration to continue. In New Zealand and Malaya selective logging has initiated kauri regeneration, though the regeneration period in New Zealand is a long one and residual kauri are subject to windthrow in severe storms. In the lowland *Agathis* forests of Brunei, growing on podzolized sands, *Agathis* regeneration appears to be a continuing process in both virgin and partially-logged forests.

The wind-distributed seeds of *Agathis* are capable of being dispersed a considerable distance but the different species do not appear to invade secondary forests that lack seed-bearing *Agathis* trees, or they do so only to a very limited extent.

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