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TROPICAL FORESTRY PAPERS, No. 11

# A FIRST LOOK AT AGATHIS

By T. C. WHITMORE

DEPARTMENT OF FORESTRY  
COMMONWEALTH FORESTRY INSTITUTE  
UNIVERSITY OF OXFORD

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Unit of Tropical Silviculture  
Commonwealth Forestry Institute  
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## Foreword

Foresters in countries where *Agathis* occurs naturally have long been interested in the genus for its many excellent qualities, but attempts at its cultivation in plantations have met with several difficulties. A solution to these problems would be of particular value in countries outside its natural range, where *Agathis* may be considered as a crop.

In 1974, the Ministry of Overseas Development agreed to finance a research scheme for the study of *Agathis* based at the Commonwealth Forestry Institute, to be undertaken by Dr. Whitmore, who had previously investigated *Agathis macrophylla* in the Solomon Islands.

This report summarises the results of a wide ranging survey of the ecological and morphological properties of the genus particularly relevant to its silviculture.

L. LEYTON  
Acting Head  
Forestry Department

## Author's Preface

My interest in conifers was first aroused by A. S. Watt, F.R.S., who used to conduct a memorable course in Cambridge, notable for its originality of approach and insight. Some eight years later I had the chance as forest botanist in the Solomon Islands to investigate the autecology of *Agathis macrophylla* on Vanikolo, both to provide the scientific base for interpreting and developing its silviculture and to attempt to explore some of Dr. Watt's ideas. The 1963 UNESCO Symposium at Kuching on research in humid tropics vegetation passed a resolution that *Agathis* should receive critical study (UNESCO 1965). In 1974, eleven years later, I began this more comprehensive study of the whole genus, based on Oxford, centre in England for tropical forest studies. This monograph emphasizes the practical results likely to be useful to the practising forester.

T. C. Whitmore

## Acknowledgements

This report could not have been written without the generous co-operation of Forest Departments, timber companies and forest scientists throughout the range where *Agathis* grows. To all the very many persons, and to others in Europe, who have given so freely of their time and knowledge, appreciation is expressed.

This work has been carried out as research scheme R2881 of the British Ministry of Overseas Development.



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## A Note on Units

Units are expressed in the *Système International d'Unités* (S.I.) following the recommendations of the Royal Society (1968). Measurements made in Imperial Measure have been converted to metric to a reasonable number of significant figures and, following S.I., we eschew the centimetre, except that, following forester's convention, we use it for tree diameters.

The symbols used for mensuration are those recommended by IUFRO, see *Commonwealth Forestry Handbook* 1974, 193-4.

## Place Names

Conventional, anglicised names are mainly used for geographical localities. Their local equivalents are as follows:

Amboina	Ambon
Bt., Bukit	hill (Malay)
Celebes	Sulawesi
G., Gunung	mountain (Malay)
Java	Djawa
Makassar	Ujung Pandun
Moluccas	Maluku
Malaya	Peninsular Malaysia and Singapore
Papua New Guinea	Until recently this was the Territory of Papua New Guinea
Sg., Sungai	river (Malay)
Solomon Islands	Until recently this nation was the British Solomon Islands Protectorate

Note also that Malesia is the biogeographical region stretching from Sumatra to the Bismarck archipelago and Torres Straits and including the Malay peninsula north to the Kra isthmus, in contrast to Malaysia the political State, which comprises Peninsular Malaysia, Sabah and Sarawak. Melanesia comprises the archipelagos of the south-west Pacific Ocean from the Solomons and Santa Cruz islands through New Caledonia and the New Hebrides to Fiji, Samoa and Tonga.



# 1. Introduction

*Agathis* is a genus of some thirteen species of tall, coniferous, resinous trees, widely known as Kauri or Kauri Pine, from the Maori name of the New Zealand species *A. australis*.

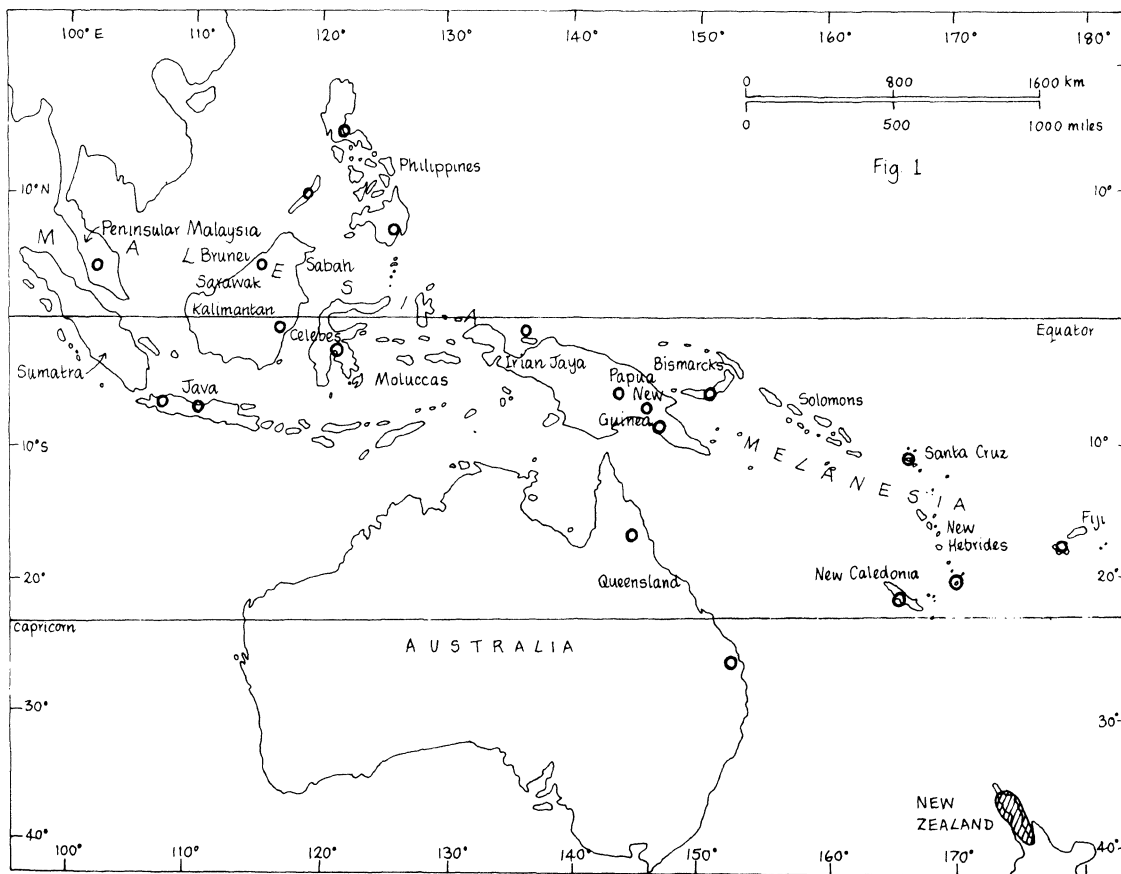
The New Zealand species is the southernmost and occurs beyond the main range of the genus which is the Malay peninsula north to Gunung Jerai, the whole Malay archipelago, and the Bismarck, Santa Cruz, New Hebrides and Fiji archipelagos and New Caledonia in the south west Pacific Ocean. There are also southern outlying species in Queensland.

Besides their considerable geographical range (10° 30'N to 38°S and 96°E to 180°E), which implies existence of forms adapted to both long and short days, *Agathis* have a wide ecological amplitude. Considering solely the tropical species with which this report is principally concerned, most are restricted to perhumid climates (evergreen rain forest) but a few occur in climates with a marked dry season of one to a few months duration (semi-evergreen rain forest). *Agathis* occur up to about 2000-2500 m elevation in lowland, lower montane and upper montane rain forest (forest formations are defined here and throughout as in Whitmore 1975a). In the lowlands they occur on a diversity of rocks and soils including

podzolized sands (in heath forest), ultrabasics, limestone, igneous and sedimentary rocks and either in stands where they are the only top of canopy species or as scattered groves or as scattered individual trees.

Throughout their range *Agathis* are highly prized for the finely grained, pale, uniform timber, which has a good reputation and a ready market at a premium above the price of general rain forest light hardwoods. Resin obtained from the cut bark, which enters commerce as Manila Copal, is an important product in several places. Besides timber *Agathis* have other factors in their favour. These are the intrinsic diversity of a whole genus of wide ecological amplitude; the success already in cultivation of several provenances; and the characteristic tall, narrow, monopodial crown and long fibres of a conifer.

Foresters in many countries have attempted natural regeneration, under-planting and open-planting of *Agathis*, mainly on a small experimental scale but in some places extensively, and in a few places with considerable success. Planting has sometimes been limited by shortage of seed supply. Some experiments have been made on vegetative propagation. In cultivation some *Agathis* grow fast. In Javan plantations volume increments of over 30 m<sup>3</sup>/ha/yr (Table 4.2)



1.1 The Malay and Melanesian archipelagos; sites of detailed study shown.

## 2 Tropical Forestry Papers

have been recorded. There are substantial differences between provenances in the response of young plants to full exposure and in early height growth.

The present survey is based on observations made on selected stands, throughout the natural range, Fig. 1.1, inspection of most plantings and the records of them, discussion and review of the literature. The objectives have been to attempt an assessment of the ecology of *Agathis* and to summarize the experience of foresters. From this the favourable and unfavourable features of *Agathis* are deduced and the next steps in utilization of the genus listed. There has often been the problem with *Agathis* of obtaining adequate planting stock, either seed or ramets, and experi-

ments on seed storage and vegetative propagation are briefly reported.

Knowledge of *Agathis* in cultivation and their response to silvicultural treatment is still fragmentary. This report on a whole genus is therefore much less comprehensive than those previous monographs in this Series which have dealt with single species of which there is far more experience. It is a summary of present knowledge and an indication of future promise; very much, in fact, a first look at a tree which has been described as a 'forester's dream' (in Queensland, J. M. Fielding *pers. comm.*). A subject index is included to give ready reference to all the topics discussed.

## 2. Taxonomy

*Agathis* and *Araucaria* (18 spp.) together form the conifer family Araucariaceae. Technically they differ from each other in the important respect that in *Agathis* the ovuliferous scale is free from the cone scale. Araucariaceae are essentially southern in distribution, though *Agathis* reaches north of the Equator in west Malesia. *Araucaria* is in South America as well as the Asia-south west Pacific region. *Agathis* is restricted to the latter.

*Agathis* are trees, with resin canals in the bark and leaves. Leaves are subopposite to opposite, narrowly to broadly elliptic, leathery, with many more or less parallel nerves (Plate 10a). They are monoecious but dichogamous. Male cones are borne in or slightly above the leaf axils, sessile or nearly so, and cylindrical; cone scales are peltate, numerous, each abaxially with 10-12 pollen sacs. Female cones (Plate 10) are terminal, ovoid to globose, with numerous woody cone scales each bearing a single large ovule abaxially; the cones become massive and woody at maturity; viable seeds form only in the centre of the cone. The seeds are flattened-ovoid with 1 large wing and sometimes a smaller one. Ripe cones shatter on the tree.

The taxonomy of *Agathis* is in a state of considerable confusion. A few regional revisions have been published (sect. 2.1) but no overall study has been made and much herbarium material has never been critically examined. There are numerous species described in Malesia which differ very slightly, if at all, and many names are currently in use which probably have no validity.

No definitive account of *Agathis* is possible without resolution of these problems, but for practical purposes an informal system of provenance nomenclature is introduced here (sect. 2.4) and thirteen species are tentatively recognized which have the following distribution:

New Zealand: *A. australis*;

Fiji: *A. vitiensis*;

New Caledonia: *A. corbassonii*, *A. lanceolata*, *A. montana*, *A. moorei*, *A. ovata*;

Australia, Queensland: *A. atropurpurea*, *A. microstachya*, *A. robusta*;

New Hebrides: *A. obtusa*;

Solomon Islands, Santa Cruz Islands: *A. macrophylla*;

Malesia (from New Britain to Malaya and Sumatra): *A. dammara*, with 3 sub-species.

Overall the range is from Sumatra to Fiji, 96°E to 180°E, and Calayan Island north of Luzon to northern New Zealand, 19° 30'N to 38°S, Figs. 2.1, 2.2. *Agathis* are centred in the tropics but extend to the southern subtropics.

New Zealand has the southernmost and best known species, *A. australis*, restricted to the northern tip of North Island from the Bay of Plenty at 38°S, north as far as 34° 30'S.

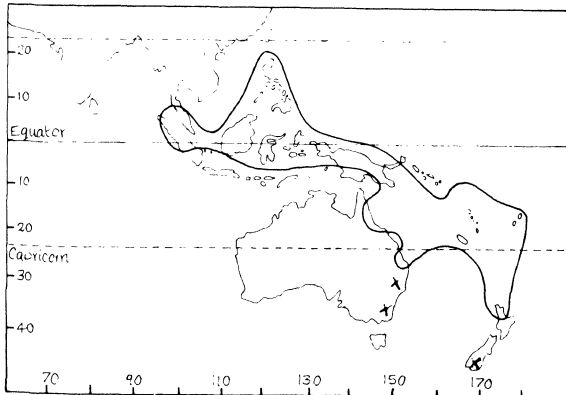
The greatest concentration, five species, is found in New Caledonia. These are restricted to the main island where their geographical ranges and habitats differ (de Laubenfels 1972).

The only other place with more than one species is north Queensland where all three Australian species occur in the rain forest between 15° 30'S and 18° 30'S on the coastal range and to about 100 km inland on the eastern half of the Atherton Tableland west of Cairns. The species occupy slightly different habitats. The best known Australian species, *A. robusta*, has a disjunct distribution as it also occurs in south Queensland on the coast in a small area stretching from Maryborough (26°S, 147°E) south 100 km to Cooroy, inland as far as the coastal range and including Fraser Island. Until recently north Queensland *A. robusta* was called *A. palmerstonii*.

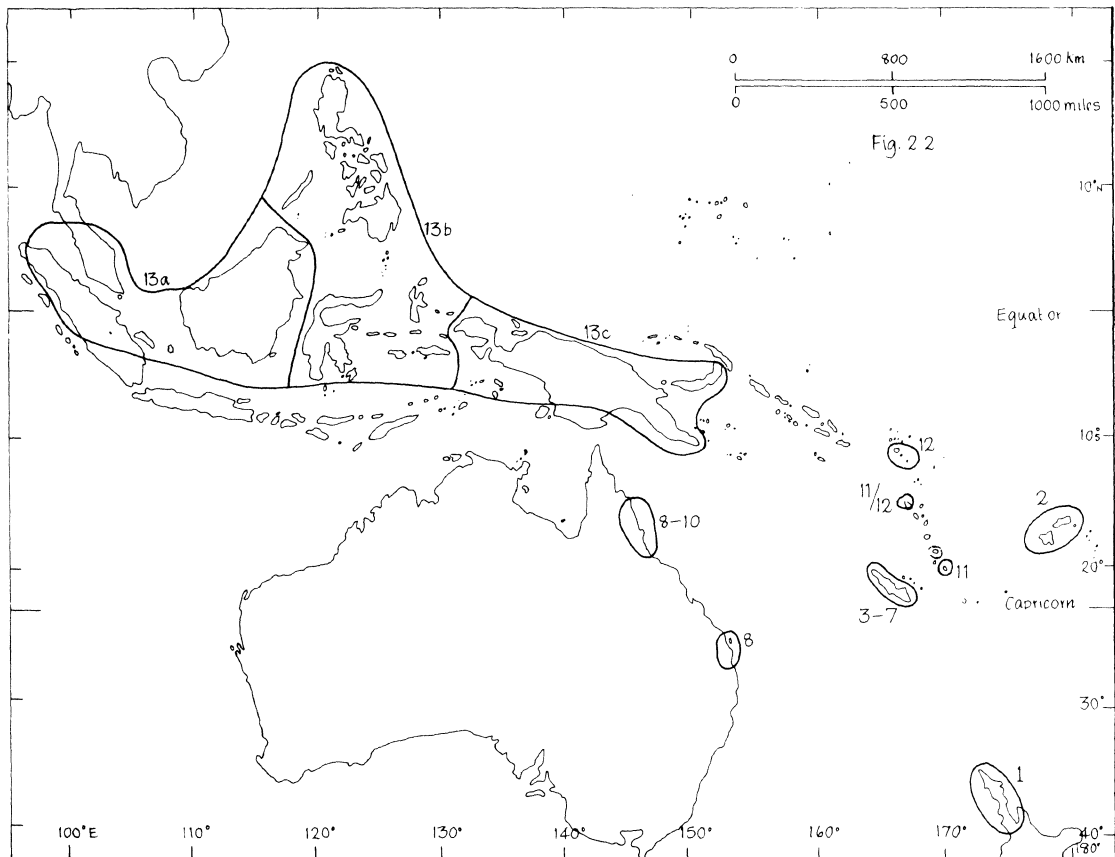
All other species of *Agathis* are allopatric. The various other archipelagoes of the south west Pacific besides New Caledonia each have one. *A. vitiensis* occurs on the principal islands of Fiji. *A. obtusa* occurs in large stands on the islands of Aneityum (170°E, 20°S) and Erromango (169°E, 19°S) in the southern New Hebrides. It also has little-known smaller stands on the western side of the Cumberland peninsula of north west Espiritu Santo (166° 30'E, 15°S) which might be referable to *A. macrophylla*, whose main occurrence is as dense stands on three of the four main islands of the Santa Cruz archipelago, Vanikolo, adjacent Tevai (167°E, 11° 40'S) and Santa Cruz (Ndendö, 166°E, 10° 5'S). The Santa Cruz archipelago is not separated from the New Hebrides by any substantial sea gap, the Banks Islands lie between. It is separated by 400 km of open sea from the Solomons archipelago, although politically it is part of the Solomon Islands nation. *A. macrophylla* and *A. obtusa* are especially similar taxonomically.

The rest of the range of *Agathis*, the whole of Malesia, is occupied by a single species, *A. dammara*. This has three allopatric subspecies which differ in quantitative detail of the male cone. Their ranges are one in New Guinea, some of its offshore islands and New Britain in the Bismarck archipelago (a recent discovery), one in central Malesia (Moluccas, Celebes and Philippines) and one in Borneo, Malaya and Sumatra.

The range and distribution of the different species



2.1 The range of *Agathis*. Fossil occurrences X. (From van Steenis & van Balgooy (1966) and Florin (1951)).



2.2 The ranges of individual *Agathis* species. 1. *A. australis* 2. *A. vitiensis* 3. *A. corbassonii* 4. *A. lanceolata* 5. *A. montana* 6. *A. moorei* 7. *A. ovata* 8. *A. robusta* 9. *A. atropurpurea* 10. *A. microstachya* 11. *A. obtusa* 12. *A. macrophylla* 13. a-c *A. dammara* and its 3 subspecies.

is shown on the map Fig. 2.2. It will be seen that there is a curious gap in the range of the genus, in its complete absence from the Solomon archipelago, approached from the east by *A. macrophylla* in the Santa Cruz Islands, and from the north west by *A. dammara* in New Britain (but not, however, New Ireland east of New Britain despite fairly thorough exploration by New Guinea botanists).

Beyond the present southern limit fossil *Agathis* has been found from the Oligo-Miocene at the south end of South Island New Zealand and from the Oligocene in Australia, in New South Wales and Victoria (Florin 1951, Fig. 2.1).

## 2.1 Principal taxonomic publications

A taxonomic revision of the New Caledonian species has recently been published by de Laubenfels (1972), who added two new species *A. corbassonii* and *A. montana*. The Australian species have also been recently revised (Hyland, *in press*); one new species has been discovered, *A. atropurpurea*. There has never been a taxonomic revision of the Melanesian species and it is possible they are not all distinct. In Malesia there has been great confusion, stemming from the recognition of many species, based on variable and overlapping characters of the cone and

its component parts and on the leaf and its resin canals.

The genus itself dates back to Rumphius, 'the blind seer of Amboina', a naturalist of genius who lived from c. 1623 to 1702, though the name *Agathis* was published in 1807 by Salisbury (*Trans. Linn. Soc.* 8, 311). In 1900 Warburg added seven species, and just before World War 2 the Dutch forester Meijer Drees added a further four (plus two more provisionally identified), based on a revision of material mainly from the Dutch East Indies, present day Indonesia (Meijer Drees 1940, Warburg 1900). The circumscription followed here is due to Danser (1891-1943) who unfortunately died before it was completed. He based his study only on the Leiden and Bogor collections and, like Meijer Drees, only considered the Malesian species. His working typescript has kindly been made available for use by Professor C. G. J. van Steenis. The only consistent differences Danser was able to find in the whole of Malesian *Agathis* were in the male cone. These correlated with geographic distribution which means that sterile or female material can be named if its place of origin is known.

## 2.2 Variation in and with habitat

Danser's treatment of Malesian *Agathis* is a useful

working basis, but formal names cannot yet be given to the three subspecies because the necessary taxonomic study has not been made. Danser gives taxonomic shape to Malesian *Agathis* overall, but does not resolve the problem presented by the existence of extremely different ecotypes. For example, in lowland Borneo *Agathis* occurs on peat, on podzolized sand, on ultrabasics and on sedimentary-derived ultisols. Nor does he resolve the problem of variation with increasing altitude. High mountain *Agathis* is very distinct with small leaves and cones and the trees are small. The name *A. flavescens* has been given to this form from Gunung Tahan in Malaya (an account is given by Keng 1972), and it was discovered by the author in 1972 at similar elevations, around 1800 m, on nearby G. Rabong (collected as specimens FRI 20671, 20632). It has never been proved that this variation is not clinal or phenotypic. The author visited a stand on Bukit Retak in Ulu Temburong, Brunei where half the trees were like this and half with large leaves like lowland *Agathis* (TCW 3056-3060). Kostermans (Kostermans 12820, 12897) has made collections from a similarly polymorphic population at 700 m on Mt. Palimasan in north east Kalimantan.

Another feature correlated with habitat, which might be of considerable importance when considering potential sites for planting *Agathis*, has been revealed by experiments in Java on *A. dammara*. Roots of this, it has been discovered, have a very variable resistance to oxygen deficiency induced by waterlogging, but on average the resistance comes low amongst a total of 373 species tested (Verhoef 1943). This discovery was made in experiments on seedlings. Provenance was not stated. At least some of the variation may be between provenances.

### 2.3 Characters of the living tree

Through the range of *Agathis* there is considerable variation in characters of the living tree. Height may reach 45-60 m and girth 6 m, but some kinds of *Agathis* probably never reach such huge dimensions. The bole (Plate 1) may be cylindrical or may taper (though never strongly) and sometimes has markedly spiral grain. Sometimes there is a tap root, and several big 'sinker' or 'peg' roots may develop. Buttresses do not form, but big swollen superficial roots sometimes occur, and sometimes the butt is swollen to a varying degree. The bark (Plates 4, 5) is scaly, the scales being roundish, sometimes compoundly so as to resemble pieces of a jigsaw puzzle. They vary in number of layers present together and in thickness, and are sometimes scallop-shaped so rendering the surface dippled. Surface colour varies from black to purple through shades of brown to fawn or with a distinctly orange hue. The crown (Plates 2, 3, 7) is monopodial and narrowly conical at first in all *Agathis*. The branches are radial, and may droop or turn up at the ends, and vary in thickness. In some *Agathis* they self-prune (Plates 9d, 11b) to leave a long clean bole which is silviculturally an extremely desirable trait. Ul-

timately the crown broadens, and this can happen in different ways. Some radial limbs thicken and lengthen so that a broad but still monopodial crown develops, and this is sometimes trapezoid in outline. Eventually a truly sympodial structure may develop. The crown branches are sometimes almost as massive as the trunk. The clear bole height and crown depth also vary. Some species have a distinct tendency to develop several trunks. The degree to which this happens, and also the degree of self-pruning and the stage of development and massiveness of the mature crown, can be seen to vary somewhat with environment.

### 2.4 Provenance nomenclature

The taxonomic revision of *Agathis*, when it is complete, will probably be on the lines outlined above and followed in this report. It is unlikely that formal botanical names can be given to all the ecotypes in the lowlands. Variants in the living tree occur between forms which have so far proved indistinguishable in the herbarium. The reasons why formal botanical nomenclature probably cannot be expected to give full resolution to variation in the living tree and the problems raised thereby are discussed in Whitmore (1976). It remains to be ascertained how the variation with elevation will be treated.

For the practising forester, for the purposes of this report, and in order to categorize as much variation in the living tree as possible, different sorts of *Agathis* described will be given a provenance name as well as the botanical one. For example, in Borneo the podzolized sand ecotype is here exemplified by *A. dammara*, *Badas provenance*. To link in with names in current usage which are not followed here, the commoner of these are added in parentheses; for example *A. dammara*, *Javan provenance* (*loranthifolia*). No other attempt is made to provide a list of synonyms. The provenances mentioned are included in the index.

This use of provenance nomenclature amounts to creating a special taxonomy for a particular purpose. It remains to be discovered to what extent, if at all, particular aspects of the living tree, such as facets of its form, its growth rate, its resin composition or its wood properties are heritable. At least the manifestation of these features in wild trees gives some indication of what may be expected.

### 2.5 Chromosome number

We have made counts on root tips of seedlings raised in glasshouses in England of  $2n = 26$  for two provenances of *A. dammara*, *Javan* (*Situgunung*) and *Badas*. Voucher material is preserved at FHO.

# 3. Forests with Agathis and their Exploitation

## 3.1 Forests, climates and soils of the tropical Far East

In 1936 Champion introduced a classification of forest formations for greater India (Champion 1936, Champion & Seth 1968). This was amplified and extended by Burt Davy (1938) and taken up for Malaya by Symington (1943). Recently, a slightly amended scheme with fuller descriptions of the rain forest formations has been introduced for the Eastern tropical rain forests by Whitmore (1975a) and is used here. The recent UNESCO-sponsored scheme (UNESCO 1973) is essentially the same but is fuller than necessary for present purposes and uses less familiar names.

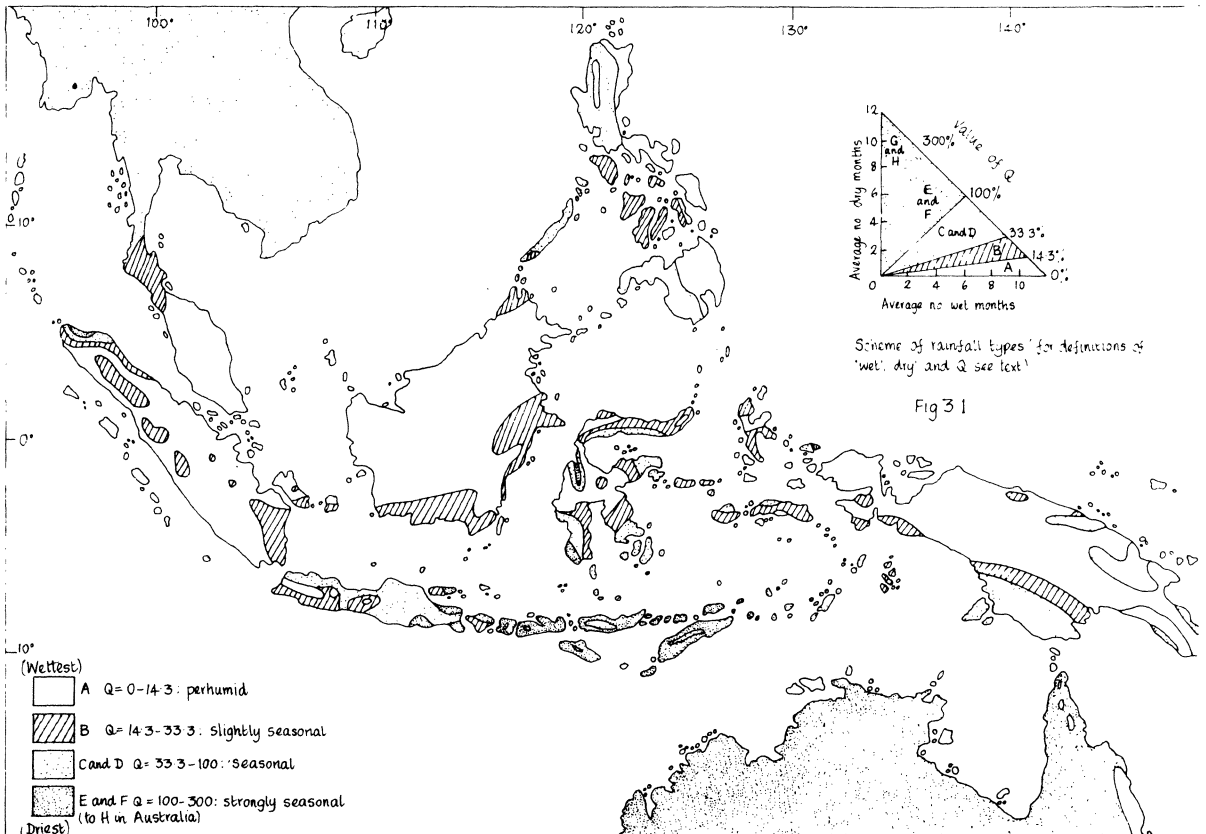
At its latitudinal limits tropical rain forest merges into subtropical rain forest. Webb (1959) and Baur (1964) list structural and physiognomic differences and there are also floristic differences. Baur gives an extended discussion of the broad ecotones of the rain forest formations or their inter-digitation with increasing latitude, and Webb discusses the phenomenon for Australia. The patterns are complex, detailed study is needed to determine them. Most *Agathis* is found in tropical rain forest, but at the

southern end of its range in northern New Zealand it is found in a forest variously described as subtropical or warm temperate. Not much is known about the rain forests of Fiji, New Caledonia and the southern New Hebrides, but these are probably best considered as subtropical not tropical.

Several schemes for describing climate have been proposed. For the region of the Eastern tropical rain forests only the scheme of Schmidt & Ferguson (1951) gives a close correlation between climatic map and forest formation map. A full discussion is given by Whitmore (1975a Chapter 3). In essence, Schmidt & Ferguson define an index Q based on rainfall which is the ratio

$$Q = \frac{\text{dry months}}{\text{wet months}} \times 100$$

A dry month is one with under 60 mm of rain, a wet one has over 100 mm. The value is computed separately for each year and the resulting average used to compute Q. This avoids the problem of other climatic indices which by using long term means obscure important variation. Schmidt and Ferguson then go on to define a number of rainfall types A-H.



3.1 Rainfall types of the tropical Far East based on wet/dry period ratios (Q) of Schmidt & Ferguson (1951). (From Whitmore 1975a, Fig. 3.1, amended for Palawan and its offshore islands.)

from perhumid, with virtually no dry season, to progressively more markedly seasonally dry.

The map, Fig. 3.1, shows the occurrence of these climatic types in the tropical Far East, with the drier types grouped to give greater resolution to the wetter places with which this report is concerned.

In this report, for the sake of convenience, the different rainfall types are given names as follows:

Type A	perhumid climate
Type B	slightly seasonal climate
Type C and D	seasonal climate
Type E and F	strongly seasonal climate

Soil nomenclature follows as far as practicable the current United States Department of Agriculture classification (7th Approximation). The application of this to tropical soils is discussed by Burnham (1975).

### 3.2 Natural *Agathis* and its exploitation

The range of the genus and of its thirteen species has been described in chapter 2 (and Fig. 2.2) starting with the centres of richness in Queensland and New Caledonia. Here, general comment is made on the ecology of *Agathis*, followed by more detailed descriptions island by island, working from west to east and including observations made of selected stands throughout the range. The chapter concludes with a note on conservation (sect. 3.3).

#### General

'*Agathis* has the most tropical distribution of all the genera of Coniferae' (Whitmore 1975a). Comparison of the map of climates (Fig. 3.1) and that of the range of *Agathis* (Figs. 2.1, 2.2) shows that it is mostly restricted to places with a perhumid A climate. It is not native to Java, the Lesser Sunda Islands or the southerly Kai, Tanimbar and Aru groups of the Moluccas. Its absence from the southern bulge of New Guinea is probably because of the zone of dry climates there but its apparent absence from south Sumatra is perhaps due to inadequate exploration. *Agathis* does occur in slightly seasonal B climates, and possibly in a few places in seasonal C/D climates in Sumatra, part of Kalimantan, Palawan, Waigeo and some of the northern Moluccas, principally Ceram and Buru.

It should be noted that, of the other commercially important Malesian conifers, *Araucaria cunninghamii* and *A. hunsteinii* (Hoop and Klinki Pine) occur in slightly drier climates in both evergreen and semi-evergreen rain forest and *Pinus* is restricted to slightly seasonal and seasonal (B and C/D type) climates (Whitmore 1975a).

#### Sumatra

There are no published accounts of *Agathis* in Sumatra. The few herbarium collections are all from the west coast in Sumatra Barat province inland from Padang, around Solok and Painan, except for one collection from Silindoeng, Tapanuli, in Sumatra Utara. The range is 100-1000 m, mostly from over 400 m.

In Sumatra Barat a mixed stand of *Agathis* and

*Pinus merkusii* grows on ridges adjacent to the road from Sungaipenuh to Padang between about km 19 and 32 and at about 750-1000 m elevation (J. D. Dransfield *pers. comm.*). This is part of the only population of the genus *Pinus* south of the equator (Cooling 1968, Whitmore 1975a). *Pinus merkusii* is characteristically a species of seasonally dry climates, and this population of *Agathis* is therefore probably growing in such climate. Inspection of Fig. 3.1 suggests that all the *Agathis* in Sumatra Barat may be growing in a seasonally dry pocket and possibly the Sumatra Utara population too.

#### Malaya

*Agathis* is of sporadic distribution in the mountains in Malaya in the upper part of lowland rain forest and lower part of lower montane. It is abundant on Gunung Jerai (Kedah) and occurs equally as far north in Kelantan near Manek Urai (Sg. Sok) and Kuala Krai (Sg. Lata Tunggul) on the east coast. There are also records from Penang, Perak, Pahang, Selangor and Negri Sembilan (Kenaboi and Berembun). A few trees have been found on Gua Peningat karst tower at c. 200 m elevation by P. F. Burgess. It may occur as isolated trees (as on the north east ridge of Gunung Benom) or in groves (as at Gading, Semangko and Gunung Angsi) and is often associated with *Shorea curtisii*.

A stand visited at Sg. Lallang, Selangor (cmpt. 44, petak finologi 2) is typical. The soil here was coarse, yellow-brown and derived from granite. Thirty-seven *Agathis* trees occurred intermingled with huge *S. curtisii* on the crest and slopes of a broad ridge at 450 m (rather lower than is usual) over an area of about one hectare. The *Agathis* reached 40 m tall and 3 m girth and emerged from the 24-30 m high canopy of the lowland rain forest. Other associates included *Cratogeomys*, *Eugenia*, *Eurycoma*, *Podocarpus neriifolius* and *Swintonia*. The undergrowth included much of the giant, stemless bertam palm *Eugeissona tristis*. The smallest girth *Agathis* was 1 m. There was no regeneration except a very few 2-leaf seedlings.

Differences in Malaya in soil chemical and physical composition under rain forest on hill ridges dominated by different big trees species have been discovered (P. F. Burgess, unpublished figures), but very few ridges with *Agathis* were included in the study for which the significance or otherwise of the findings therefore cannot be assessed. Its association with *S. curtisii* and the other trees mentioned above is indicative of a preference for relatively oligotrophic soil. The G. Jerai stand is growing in very poor, shallow soil over quartzite.

Seedlings which survive selective logging as well as those which establish afterwards survive and grow up. This can be seen at Gading and Semangko forests.

#### Borneo: Brunei, Kalimantan, Sarawak and Sabah

In Borneo *A. dammara* attains its greatest ecological amplitude. It occurs over a great range of elevations, from sea level to about 1000 m and, as noted in sect. 2.2, some high elevation trees have dis-

tinctive small leaves and small cones. In the lowlands it occurs in heath forest, peat swamp forest, on ultisols derived from sedimentary rocks and over ultrabasic rocks. Most of its range is within the area of perhumid climate but near the south and east coasts it occurs in a slightly seasonal B climate (Fig. 3.1).

Throughout Borneo, all the known extensive, dense stands of *Agathis* have been heavily exploited and some have been exhausted. It is likely that all that now remain are scattered small pockets and solitary trees. The exploited stands are around Sampit and Tanahgrogot, Kalimantan; near Tawau, Sabah; and at Badas, Brunei. There has in the past been considerable collection of Manila Copal, especially in Sarawak, but this has now ceased.

The different ecotypes will be considered separately.

*Agathis* occurs in lower montane forest on the slopes of Mt. Kinabalu, Sabah, to about 1500 m. On gentle slopes and plateau sites the soils below it show signs of podzolization, but on eroding slopes and on recent river terraces the soil shows no such signs (Askew 1964). In a sample plot on the south west side 33 trees of mean diameter 45 cm in 1973 (range 18-87 cm) had a mean annual increment of 5 mm over the following three years. There is a good stocking of seedlings. The soil is a clay loam with no signs of podzolization (Sabah Forest Dept. records). Montane *Agathis* has also been recorded in Sabah near Keningau and on G. Trus Madi. It has been collected from most of the high mountains of Sarawak including G. Poi and to 2400 m in the Kelabit highlands where it is fairly common. In Kalimantan Barat it is known from some of the mountains inland from Pontianak and from Kalimantan Timur from the mountains north west of Samarinda but, so far, it has not been recorded from the central spine, the Schwaner and Muller Ranges, or from the Iran Range on the Sarawak border.

During the present survey a stand was examined on the summit ridge of Bukit Retak, 1569 m, in Ulu Temburong, Brunei. The rocks are low grade quartzites and metamorphosed siltstones. On narrow ridges there is a stunted and gnarled 3 m tall upper montane rain forest. *Agathis* occurs on a narrow, gently sloping plateau 40 m wide, with surface undulations of 0.5 m amplitude. In the hollows the soil is a wet, gleyed clay with 30 mm leaf litter; on the hummocks it is similar, but drier and with only 10 mm leaf litter. The forest is lower montane with an even canopy 18-21 m tall and composed of a dense stand of poles 20-30 cm diameter with the *Agathis* larger, 14-70 cm diameter and 21-24 m tall, and slightly emergent or not. *Agathis* is restricted to the hummocks, commonest near the plateau crest and occurs otherwise as solitary trees. Only three seedlings were seen and no saplings or poles. Contrary to Ashton (1964, quoted in Whitmore 1975a) there is no sign of podzolization, although the soils are stable and non-renewing; Ashton's claim that the presence of *Agathis* here on a flattish site indicates the remains of an ancient peneplain near sea level seem unlikely on geological grounds (R. B. Tate *pers. comm.*) and improbable on botanical.

The most extensive and densest *Agathis* forests in the world were those which formerly occurred in the lowlands of Kalimantan Tengah. The greater part of these were around Sampit and had been logged out by the mid 1960s. These forests occurred on ridges of white sand which run through the huge peat swamp forests that occupy the whole of the central south coast of Borneo, reaching over 150 km inland. The total area of the *Agathis* forest pockets was over 30,000 ha with single ones up to 5000 ha (Bakhoven 1942). They occurred in a form of heath forest. *Agathis* also occurs elsewhere in Borneo in heath forest. There is an extensive forest a few kilometres inland at Badas in Brunei, likewise adjacent to peat swamp forest and also with *Agathis* in very dense stands as the commonest big tree. It occurs scattered in heath forest along the Sarawak coast, e.g. around Marudi, around Kuching and at Bako and in inland heath forest e.g. on the Merurong plateau (780 m). In Kalimantan Barat it has been recorded in lowland heath forest at Mandor (Polak 1933). Finally, in Kalimantan Timur, not far inland from Balikpapan, *Agathis* occurs on podzols, derived from Tertiary sandstones or riverine alluvium; in places it forms 75-80 per cent of the big trees, elsewhere it is intimately mixed with *Dipterocarpus* as scattered trees, (G. Dykstra, R. Voss *in litt.*).

The Kalimantan Tengah *Agathis* forests were discovered and explored in the 1930s. From published pre-war accounts (Oedin 1941, Bakhoven 1942) supplemented by more recent ones (Oedin & Achmad 1953, Dilmy 1965) it is possible to construct a fairly detailed picture of their ecology, supplemented by observations made by the author in the Badas forests which appear essentially similar, and in peat swamp forest near Palangkaraya in Kalimantan Tengah.

The climate of south Kalimantan Tengah is slightly seasonal (type B, see Fig. 3.1). At Sampit the annual rainfall totals for 1936-40 were 3213, 3083, 2437, 2178 and 956 mm with 1, 0, 1, 2 and 5 dry months. The peat swamp forest itself lacks *Agathis*. The margins of the sandy ridges which run through it and rise about 7 m above the peat have a forest dominated by *Agathis* over an undergrowth with many broad-leaved species. In one sample *Agathis* occurred at a density of 156-168/ha of 20 cm diameter and over, of which 57-60 per cent were 40 cm and over. The length of clear bole reached about 25 m. The boundary between the *Agathis* forest and the peat swamp forest is sharp, though some tree species grow in both types, and *Agathis* itself occurs scattered in peat swamp forest. The soil is podzolized and the A horizon is yellow-grey, 0.7-1 m thick, with 250 mm of superficial humus. The pan is waterproof and a water table forms above it. Such forests extend right across some ridges but in the centre of most of them there is a shorter, very dense, rather brightly illuminated forest, dominated by pole-sized *Tristania obovata*, which has an indistinct boundary with the *Agathis* forest. Here the humus is only 90-130 mm thick and the A horizon is 630-670 mm thick over the pan and is bleached white sand. Small, pole-sized *Agathis* are abundant in the *Tristania* forest and there are many more stems per

unit area, but there is a much lower timber volume than in the forest of the ridge margins. In one sample there were 213 stems/ha of 20 cm diameter and over but only 23 of 50 cm and over. There were 1049 stems/ha of *Tristania*. This pattern of forest types and their composition on the ridges is maintained by fires which periodically sweep through destroying all or most of the vegetation and burning off the superficial humus. Destruction is greatest and probably most frequent on the ridge crests, which are driest. *Tristania* colonizes the open, burned ground and is able to invade bare white sand, whereas *Agathis* seedlings can only establish themselves where patches of humus remain (cf trial 59 in sect. 4.3). However with time *Agathis* progressively invades the *Tristania* forest as a humus layer redevelops.

In peat swamp forest seedlings of *Agathis* are rare and are restricted to hummocks. They always occur at least 0.2 m above the water table (author obs., Palangkaraya). Within the *Agathis* forest density of regeneration increases inwards from the outer margin with the peat swamp, where the surface becomes drier. Illumination of the ground also increases progressively inwards to the ridge crest and regeneration goes up from 4-13 times the number of trees over 0.2 m diameter to 20 times in the *Tristania* forest. At Badas seedlings and saplings are abundant.

Overall, timber volumes in these forests were ascertained as 100-400 m<sup>3</sup>/ha, or 200 m<sup>3</sup> on average, of trees over 0.35 m diameter. Total volume (for pulping or match making) was 400 m<sup>3</sup> or more. Volume tables have been compiled by Ferguson (1949a). Extraction around Sampit commenced in 1940 and was completed in the mid 1960s. Experiments in the late 1940s showed that if damage at logging could be kept low (as with man-handling and rail extraction) then natural regeneration would grow up, but extraction by tractor caused heavy damage. Properly hardened off, nursery-raised seedlings or wildlings, established into humus containing soil, showed adequate survival and growth (Schrender 1949). In the later years of extraction it is believed little silviculture was carried out.

Dense stands of *Agathis*, though of relatively small extent, also occur in Borneo on ultrabasic rocks. In Sabah there was a stand of 38 ha logged in 1972 on an ultrabasic knoll 600 m high near Sungai Toe, Tawau. *Agathis* was associated with *Eugenia* and *Tristania*. There was a dense seedling stand but no saplings or poles. Two nearby ultrabasic outcrops at Bukit Temuku and Sg. Geminchau are not known to have *Agathis*, but several trees occur on the eastern flanks of Kinabulu on the ultrabasic outcrop of the Mamut copper mine.

Bigger stands occur further down the east coast at about 1° 45'S, 116° 10'E, 50 km north of Tanahgrogot, on the eastern flanks of the Meratus mountains. These were inspected by the author in 1974. The Telaga Mas timber company extracted 50,000 m<sup>3</sup>/year from 1970-73 at about 20 m<sup>3</sup>/ha and the operation continues (1976). The Meratus mountains have a plutonic core and sedimentary flanks. The rocks consist largely of peridotite which is

largely serpentinized (van Bemmelen 1949). The climate is type B, slightly seasonal (Fig. 3.1), probably at least as far inland as the *Agathis* forests. These extend from G. Bolong north to G. Lumut from c. 100-700 m elevation, and lie in a region of jumbled ridges and deep valleys. There are two clearly distinct sorts of rock each bearing a different type of soil and forest. The ultrabasic ridges have 1 m or less of a very coarsely granular, chocolate-brown soil overlying the greasy, grey-green, friable and fragmented rock. There are about 10 mm of humus. These ridges carry a very dense pole forest with a microphyllous, 15 m tall, uniform-topped canopy very reminiscent of upper montane rain forest (Plate 2d). *Casuarina sumatrana*, *Tristania obovata* and *Agathis* are locally abundant and emergent to 15 m above the main canopy; in places each forms a continuous, single-species top layer. Such forest was only seen on ridge crests and sides; valley bottoms have a lush mesophyllous forest with wild banana prominent. The other ridges are composed of shale and have much deeper soil, c. 10 m thick, which is either yellow-brown or red-brown. The boundary with the ultrabasic-derived soils is sharp. The shale ridges carry mesophyllous lowland rain forest of totally different appearance and devoid of *Agathis*, *Casuarina* and *Tristania*. Seedling *Agathis* are abundant near mother trees but absent from wet areas on ridge crests. Bigger saplings and poles are very rare.

After logging, the microphyll forest is replaced by a 1-2 m tall tangle, largely of the sedge *Scleria* and a scrambling bamboo, sometimes with a rattan (cf. *Plectocomiopsis*), all present in the primary forest. The mesophyll forest is replaced by a lush stand of pioneer tree species including *Macaranga aethiadenia*, *M. depressa* agg. *M. gigantifolia*, *Mallotus* sp., *Trema tomentosa*, *Anthocephalus chinensis* (spill slopes) and with the climbers *Mikania* and *Merremia* abundant. *Agathis* seedlings do not survive felling for long due to competition and seem unable to invade the secondary vegetation or open ground.

*Agathis* in lowland rain forest, i.e. on 'normal' or zonal soils, ultisols or oxisols, is reported in Borneo only on the concession of Kayan River Timber Products near Samarinda in Kalimantan Timur.

### Celebes

*Agathis* has been collected from throughout Celebes except from the south east peninsula and offshore islands (Kabaena, Muna, Batung) and from the north-south lying part of the northern limb. All the limbs of Celebes have climates seasonally dry to a differing degree (Fig. 3.1), and all the *Agathis* records from them are from mountains, where probably the climate is wetter and less seasonal than the map shows. Thus, in the south west limb *Agathis* occurs on the slopes of G. Lompobattang east of Makassar and in the Latimodjong range at 1000 m and upwards (Eyma 1938); and in the north east at 500 m upwards around Gorontalo.

The central body of Celebes has mostly a perhumid A type climate. Here *Agathis* occurs from near sea level upwards to c. 2000 m (Eyma 1938). Travellers

reports and the survey by van der Vlies (1940) note its abundance, as discrete but extensive pockets in lowland and lower montane rain forest and also as isolated trees and small groves. Apparently it is the main top-of-canopy big tree in the big stands and van der Vlies speaks of a superabundance of young trees but not all of the same age [size]. Celebes is very mountainous and most *Agathis* stands remain too inaccessible yet to have been logged though concessions are currently being sought. They have traditionally been heavily tapped for resin, though the industry is now much smaller than formerly. When demand from the industrialized world was high during the first few decades of the century substantial damage was done to the trees (Plate 5c) and very many were killed. The Forest Department attempted to introduce controls to prevent this; van der Vlies (1940) gives a full account.

Inland from Malili at the head of the Gulf of Bone is an area containing dense pockets of lowland *Agathis* at c. 2° 45' S, 121° 50' E. This was formerly the basis of a substantial resin collecting industry, the main source of income for the local population. It is currently being logged, though some trees still being tapped are to be preserved. The concession, an undemarcated (1974) 129,000 ha area of *Agathis*-containing forest, dates for 30 years from 1969; yield is about 20 m<sup>3</sup>/ha. *Agathis* here was inspected by the author, including trial plots (Sect. 4.3). A nickel mine has recently been opened in this area. Some, probably most, of the *Agathis* stands occur over ultrabasic rocks. The geology is complex (van Bemmelen 1949). Inland from a narrow coastal plain lie the Verbeek mountains which include Cretaceous limestone chert separated from underlying peridotites by serpentines which form a mylonitic horizon. There are patches of crystalline schists and phyllites and strongly folded imbricated sandstones, shales and limestone. The lowland rain forest has an even canopy of small-crowned trees with much *Casuarina sumatrana* on ridge crests and slopes which give it a fine texture and grey tone. Where the logging road cuts the forest it is seen to lack large trees and to consist of closely placed poles. Much of the soil is a deep chocolate-red colour, containing rock fragments and overlying serpentine. A typical *Agathis* stand was examined at Sg. Pae, a sidestream of the main Sg. Larona, at 150 m elevation. *Agathis*, to 30 m tall and 50-70 cm diameter, occurs as solitary or grouped (3 m apart) trees over a 21-30 m canopy with a dense undergrowth to 6 m containing much scrambling bamboo. The largest *Agathis* are emergent. Butts are badly damaged by tapping scars (Plate 5c). Seedlings occur occasionally, as patches near some mother trees; saplings of healthy appearance are less common. At another site, logged two years previously, no *Agathis* seedlings were seen, either residual or invasive, and pioneer trees had not yet commanded the site.

East of the Verbeek mountains lies an intermontane valley containing the two lakes Danau Towuti and Danau Matano, surrounded by fire-climax (?) grassland, probably with a drier climate than the map (based on coastal records) indicates. Several karst hills of siliceous limestone formerly had

forest dominated by *Agathis* on their summits, growing in deep soil pockets. On Gunung Malindoe, felled five years previously, a lush 3 m tall stand of pioneer trees had since developed. No seedling or sapling *Agathis* was seen.

### Philippines

There are records or herbarium collections of *Agathis* from most islands of this archipelago but extremely little is known about its ecology. The western part of the Philippines has a seasonal climate as it lies in a rain shadow during the months November to April when the north east monsoon is blowing, see Fig. 3.1. There are large areas with seasonally dry C/D climates and others slightly seasonal (type B). *Agathis* has been recorded from several islands in this seasonally dry belt, on Palawan in a C/D climate. Figures in Barrera, Salazar & Simon (1960), show that the western side of Palawan has annual rainfall 2300-3100 mm and the eastern side 1500-2000 mm and there are about four dry months over most of the island. Nowhere else in its entire geographical range is *Agathis* certainly known to grow in a climate more than slightly seasonal (type B), though here as everywhere the mountains are likely to be wetter than the climatic map indicates.

Palawan is a long, narrow island with a central spine of steep, jumbled mountains, many rising to 1000 m, and one to 2084 m (Victoria Peak). The coastal plains and gently sloping foothills are now largely cleared. They are said to have carried forest dominated by several *Dipterocarpus* spp. (apitong) with some *Intsia* and a little of several other species. The lower mountain slopes are still forested. Most of the island is now let out on timber concessions. The steeper slopes and the summits bear a forest with canopy uniform and fine-textured, this reaches down to the foothills in a few places. There are several companies mining manganese, copper, nickel or chromite. In a traverse of the mountains west of Santa Lucia several stretches of road were noted which passed through outcrops of grey-green easily shattered rock, probably a low-grade serpentine. It seems likely that fine-textured forest at low elevations is associated with such ultrabasic outcrops.

It appears likely that *Agathis* occurs as a belt along the central mountains mainly above the heavily stocked *Dipterocarpus* forest. Extensive dense stands are reported from the north facing slopes of the valley which runs down to Bagumbayan, several hours' walk in from the road and from near Brooke's Point in the south east of the island, 4-5 km inland and at 600-700 m elevation. This latter stand contains 250-400 m<sup>3</sup>/ha of *Agathis* mixed with hardwoods. The total volume is 35-40,000 m<sup>3</sup> and individual *Agathis* reach 220 cm diameter. The Infanta Mining Company were in 1975 felling the forest preparatory to mining the copper and nickel ores over which it lay.

A small *Agathis* stand about 0.45 km across and at 330 m elevation was inspected in February 1975, at Bagumbayan which lies 4-5 km from the west coast, c. 40 km from the capital Puerto Princesa, on the main trans-island road of the Palawan Apitong logging

company. It lies on a broad rocky slope with numerous water channels which were dry at the time. The soil is a very firm, dry, brown clay. The forest is lowland rain forest with the canopy 21 m high. The tallest trees, some emergent, are *Dipterocarpus* and *Agathis*. *Casuarina* and *Tristania* are frequent or locally abundant. *Intsia*, *Eugenia*, *Memecylon* and abundant *Orania* occur. The *Agathis* are solitary or as tight clusters and total about 30 trees of diameter 25–90 cm. Only one sapling and four seedlings were seen.

On Luzon island *Agathis* occurs in mixed dipterocarp lowland evergreen rain forest at several places in the Sierra Madre range on the east coast. One stand was examined at Llavac Real (121° 40'E, 14° 30'N), Quezon Province, consisting of a few giant trees left after logging and emergent from the relict forest. The soil is an orange-brown clay over igneous rock. The climate here is probably perhumid. This region is subject to frequent cyclones.

On Mindanao island *Agathis* was inspected in Davao Province at several places on the north east flanks of the extinct volcano Mt. Apo, in lower montane rain forest at 1200–1300 m elevation. Very few seedlings or saplings were seen. In one area the closely structured clay soil was whitish to 0.4 m depth but orange-brown below, suggesting incipient podzolization. The climate of this region is perhumid (figures in Mariano, Lopez & Romero 1953). A relic stand was also seen at 1200 m in lower montane rain forest a few kilometres south of Buda on the provincial boundary, beside the national highway being built from Davao City north to Bukidnon province. The soil was an orange to red-brown blocky clay over a whitish green rock, probably weathered serpentine.

### The Moluccas

There are herbarium collections from all of the northern Moluccas (Morotai, Halmahera, Bacan, Misool, Obi, Buru, Ceram, Amboina) but not from the southern Kai, Aru or Tanimbar groups. There is also no record from the Sula islands. The latter all have a seasonally dry C/D type climate and maize replaces sago as the staple food (Manaputty 1955). Much of the northern Moluccas are also recorded to have a seasonal (C/D) or slightly seasonal (B) climate (Fig. 3.1) though this must be based on extrapolation from a few coastal stations. Nearly all the *Agathis* has been recorded from over 300 m elevation, mostly at 300–500 m but up to 1300 m (G. Hoala, Ceram; Eyma 1938) and these mountain forests may have a wetter and less seasonal climate than the map suggests. There is no published description of forests with *Agathis* in the Moluccas. Formerly resin collection was an important industry with export from Amboina; Ham (1911) gave a lengthy account. The Javan provenance, a land race planted successfully and extensively (sect. 4.1), derives several generations back from Amboina. Plantations (probably for resin production) were established in Dutch times near Lokki on Ceram but it is believed they have now been felled.

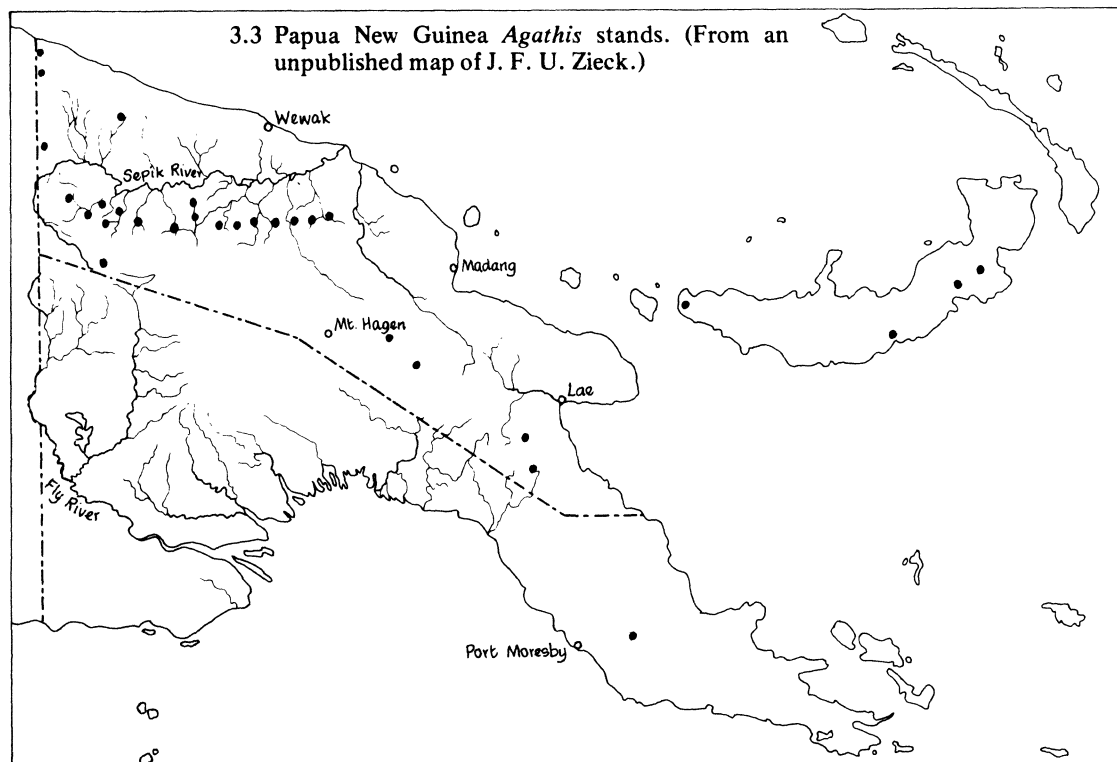
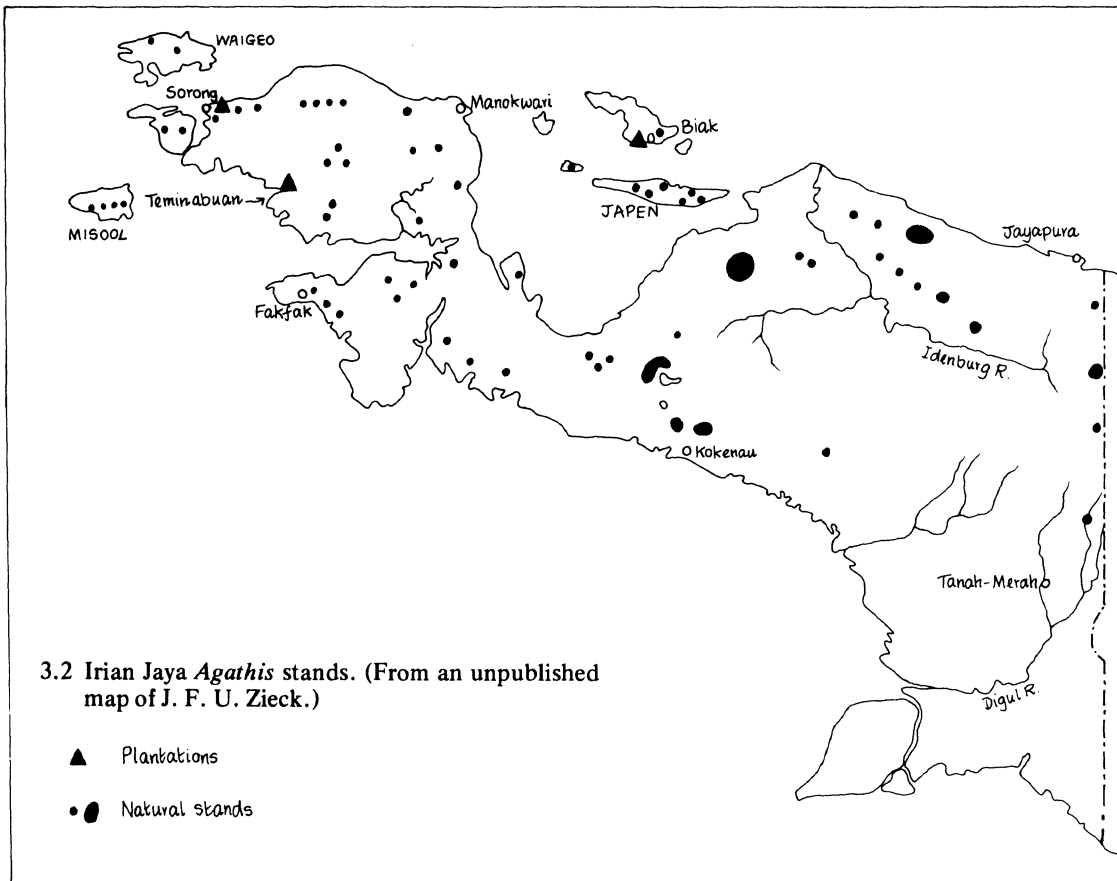
### New Guinea

*Agathis* in New Guinea occurs in scattered stands as giant emergent trees, sometimes reaching 60 m tall. The crowns are roughly cylindrical, with a main bole and with the limbs directed diagonally upwards, in contrast to *Araucaria* spp., also giant emergents, in which the limbs are horizontal. These valuable conifers, which sometimes grow in juxtaposition, are thus easily spotted from a low flying aeroplane or on aerial photographs. Between the years 1946 and 1962 extensive explorations were made in West New Guinea, now Irian Jaya, and since then similar reconnaissance has been undertaken at the eastern end, in Papua New Guinea. Mr. J. F. U. Zieck played the predominant role in these surveys. The maps, Figs 3.2, 3.3 show the occurrence of the main stands so far known. Tiny pockets and isolated trees will have been overlooked, but it is believed that apart from this the maps are a complete record. There is no detailed knowledge of the climate of most of the interior of New Guinea but *Agathis* seems restricted to perhumid or only slightly seasonal climates except perhaps on Waigeo island. It is apparently absent from the dry southern bulge of the island.

In Irian Jaya the importance of *Agathis* lies totally in the production of resin, and in recent years an attempt has begun to develop a similar industry based on the main stands in the Sepik basin of Papua New Guinea. Details are given in sect. 8.2. In Irian Jaya tapping is mainly carried out by the Forest Department itself, and plantations for resin were also established as described in sect. 4.1. There has been little tapping by the indigenous people. Death from over-tapping has been recorded (Salverda 1936/7) as also has the native practice of planting seedling *Agathis* to perpetuate a stand (Becking 1966).

Detailed information on the ecology of *Agathis* in New Guinea is scanty. Observations made during the course of inventory surveys, by botanical explorers and by the pedologist Reynders indicate that it has a wide range of habitats. In Irian Jaya most *Agathis* stands occur in mountainous country and over about 200 m elevation. Reynders (1964) found it in the Star Mountains between 200 and 1700 m on sandy terraces, some with impeded drainage. Salverda (1936/7) recorded it on sandy, freely draining soil, as did Zieck (1960) at several places, including Sjoega south of the MacCluer gulf in the Wagura range, in a microphyllous forest near sea level in which there was abundant regeneration. W. Vink (*pers. comm.*) observed its common association with blackwater streams. All these reports suggest *Agathis* is in heath forest, probably developed on oligotrophic sands podzolized to some degree.

In lowland Irian Jaya *Agathis* stands also occur over ultrabasic rocks, one on Biak island inland from Bosniek (Vink 1960) and several on Japen island (van Dijk 1939). The Biak stand was estimated to contain 21,000 trees over 35 cm diameter of which 18,000 were tappable; it had been tapped for forty years (Bleys 1957). Vink recorded abundant but patchy regeneration of a wide size-range. On Mt. Genofa near Kaimana, in the hinterland of Fak Fak and on



Waigeo island stands have been recorded over limestone, presumably over deep acid peat (Manaputty 1955, van Royen 1963, C. Versteegh *pers. comm.*).

There is a stand on oxisols near sea level at Binsimar river near Biak town. Here a relict lowland rain forest of 2200 ha contains 4600 *Agathis* trees of 70 cm diameter and over. *Agathis* is the tallest tree and attains 40-55 m tall, with clear bole to 35 m and 0.4 m diameter. Seedlings are rare, saplings and poles absent.

In Papua New Guinea, Fig. 3.3, there are numerous extensive stands on nearly all the southern tributaries of the Sepik river in its middle reaches between 45 and 600 m elevation. Small stands contain several thousand trees each at a density of about 24 per hectare, though more often at 4-12. The biggest stands have up to 50,000 mature trees. The total number of tappable trees is estimated to be 200,000 and the total timber volume one million cubic metres. It is believed these stands are associated with ultrabasic outcrops (J. F. U. Zieck *pers. comm.*). South west of Amalab a big stand occurs on a limestone plateau with many pinnacles and sink holes. At Koburi in the Sepik a stand occurs at 800 m in a perched, freshwater swamp, wet enough for the sago palm; regeneration is on hummocks (J. S. Womersley, K. J. White *pers. comm.*).

Only one stand is known in Papua, at Sogeri 30 km east of Port Moresby near the Sirinumu dam, at 147° 30'E, 9° 30'S. The rocks are pyroclastic lavas, and marine and terrestrial clastic sedimentaries (Papua New Guinea Resource Atlas 1974). At the site visited the soil is a friable brown clay loam. The rainfall is about 3500 mm with no month having under 250 mm, i.e. perhumid, type A. *Agathis* occurs in pockets at 10 m spacing, as 27 m tall emergents from a dense lowland rain forest with a 12 m high canopy of slender trees reaching 0.2-0.3 m diameter. The size range of the *Agathis* is 0.13-1 m diameter; seedlings are rare.

In the 1960s *Agathis* was discovered at several locations in lowland rain forest in New Britain. One stand was visited at Fulleborn Harbour. The climate is extremely wet with over 5000 mm/year of rain and no month with less than 140 mm (Brookfield & Hart 1966). The rocks are volcanic, the soil a deep, brick-red clay and above 450 m elevation has 150 mm of superficial humus. Lowland rain forest occurs with a dense, uniform canopy 21-27 m tall. *Agathis* grows as an extensive, diffuse stand 5 km across and at between 5 and 10 km inland, between 300 and 450 m elevation, on ridge crests, slopes and river banks, as single trees at 20 m spacing but never as pure groves. It is the only emergent, and reach 30-40 m tall. Girth is from 1-3 m. In the forest, seedlings are very rare and only one sapling was seen. The logging road was 3-4 years old and passed close to several relict trees of 0.5 m diameter under which were a very few seedlings.

*Agathis* also occurs in lower montane rain forest in both Irian Jaya and Papua New Guinea but the small-leaved variant has never been found (J. S. Womersley *pers. comm.*). In Papua New Guinea the more accessible stands have been decimated by logging and

only a few relict trees persist. One was examined at road 29 Bulolo, 930 m elevation. Thirty trees remain, emergent from grass and shrubs, over lacustrine deposits. The trees reach 30 m tall with massive, columnar boles of 1.4 m diameter. In the Bulolo area diffuse *Agathis* stands not yet logged also occur in the Watut valley in the Paganda logging area, on a hill slope between 750-1500 m intermingled with diffuse *Araucaria cunninghamii*, and also at Gumi Creek. Trees of 2-2.5 m diameter have been extracted, the largest was 3 m. Residual stands were also examined in the Eastern Highlands, at Suwaira (1500 m) and Lufa (Coruka and Hai Toba, 1800 m), occurring as massive trees in patches of depleted forest remaining between agricultural land. The annual rainfall is only about 2000 mm but with no dry month (Brookfield & Hart 1966). Another stand, also partially logged, occurs at 2100 m in the Chimbu gorge, and Ledermann (1919) recorded a stand on Etappenberg in the Sepik at 850 m in montane forest. Brass (1941) recorded *Agathis*, to 45 m tall and 1.5 m diameter, dominant in poorly drained lower montane rain forest on broad ridge crests over grey sand with a peaty surface, in the Snow Mountains of Irian Jaya at 870-950 m. Here *Agathis* reached its upper limit at 1200 m.

### Queensland

In Queensland *Agathis* is a component of various sorts of tropical and subtropical lowland and lower montane rain forest, and does not occur in the sclerophyll forests with which these are interdigitated (Webb 1959, 1968, 1969).

In north Queensland three different species occur in tropical lowland semi-evergreen rain forest and tropical lower montane rain forest over both sedimentary and igneous rocks. They do not occur mixed, each has a slightly different habitat. *A. robusta* occurs where the rainfall is 1250-2000 mm. One of the biggest stands is at about 450 m at Bridle Creek. In this area *A. microstachya* occurs slightly further to the east, higher on the coastal range, where the rainfall is higher. There are other big stands at Kirrima and Windsor Tableland. *A. atropurpurea* is found between 900 and 1500 m over granite in lower montane rain forest. Some of the forests where *Agathis* occurs have been repeatedly selectively logged since about 1910, others since they became accessible in the 1930s. The major Windsor Tableland stand has only recently been opened to logging. In some stands *Agathis* was, or is, the predominant emergent species. After logging it persists as scattered trees. Regeneration is patchy, small seedlings of several sizes are commoner than saplings and poles; it grows faster in heavily disturbed areas (G. C. Stocker *in litt.*).

In south Queensland *A. robusta* ranges from sea level to nearly 900 m (Hall, Johnston & Chippendale 1970). The summers are warm and humid, the winters mild, but with frosts inland (at 600 m there are 20-30 per year). The annual rainfall is 1000-1500 mm with more than half falling between December and March; the driest period is July to September when there is 37

mm/month, seldom less. *Agathis* occupies valleys, flats and coastal ranges on two contrasting soil types. These forests, like those in north Queensland, have been decimated by logging.

In the Kin Kin area, where it was formerly abundant, scattered relic trees remain in patches of forest left when the land was cleared for pasture. The rocks are metamorphics or basalts; over the latter krasnozems soils occur.

On Fraser Island and the adjacent mainland *Agathis* was formerly very abundant in subtropical rain forest over white podzolized sands, a habitat identical with that which supports heath forest in west Malasia. At one site examined small seedlings were abundant, probably resulting from several seasons.

The ecological status of *Agathis* in south Queensland has not been ascertained, but observations of regeneration after logging showed that seedlings responded to increased light (Petrie 1922).

### Solomon Islands, Santa Cruz Islands

This small archipelago is geographically a northern extension of the New Hebrides but politically it forms the eastern part of the Solomon Islands.

The autecology of *A. macrophylla* on Vanikolo island was described in detail by Whitmore (1966). The climate is very wet with no dry season, annual rainfall in the area of the main *Agathis* stands is in excess of 6000 mm a year. The soil is a well-structured clay derived from basalt with no sign of podzolization. Big *Agathis* occur scattered and as groves of trees of mixed size throughout the lowland tropical rain forests of Vanikolo up to c. 480 m elevation, and are slightly commoner on ridge crests. Seedlings are abundant with much mortality at 0.9 m tall. Counts on scattered sample plots led to the suggestion that seedlings are ubiquitous (Whitmore 1966) but subsequent study has revealed they are concentrated up to 40 m from mother trees and are most abundant towards ridge crests (K. D. Marten *pers. comm.*). They appear long-persistent, awaiting development of a canopy gap before growing up to become trees. Recent investigations suggest New Hebridean *Agathis* has similar ecology (see below).

*Agathis* seedlings colonize open ground in abundance. These and survivors in the forest die out in competition with the lush stands of pioneer trees which develop, but they eventually invade secondary forest to form uniform stands.

Vanikolo *Agathis* was almost logged out during the forty years between 1924 and 1964. A small virgin stand remains in the upper part of the Lawrence river valley and another of some 200 ha on adjacent Tevai island.

The *Agathis* on Ndendö (Santa Cruz) island has been logged since 1974. There are two areas, a western one of about 1500 ha and a smaller eastern one. As on Vanikolo, *Agathis* occurs in groves and as scattered trees in lowland tropical rain forest. Here too it is mostly on deep, friable oxisols derived from basalt, though the edges of the stand are on calcareous sandstones and siltstones. After logging, very dense stands of seedlings develop on bare ground but

only patchily. Logging is proceeding eastwards and by mid 1976 was about halfway through the western stand. It is estimated the forests will have been completely logged by about 1980.

### New Hebrides

*Agathis* forests are known in three places. Those of the Cumberland peninsula of Espiritu Santo remain virtually unknown but are believed to be of small extent. Robinson (1969 and *in litt.*) reports that the *Agathis* occur at about 600 m in tall forest in pockets on the western sides of ridges; the eastern sides show evidence of periodic wind damage. He estimates the trees to reach about 50 m tall and 2 m diameter. The soil is well-drained and derived from Miocene basic and intermediate volcanic rocks; annual rainfall is about 4500 mm with a slight but variable dry season mid year. *Agathis* does not occur in the upper montane forest which exists from about 900 m elevation upwards. The *Agathis* forests of the wet, rain relief, eastern side of Erromango were surveyed by Johnson (1971) and together with the third area, on Aneityum, formed the subject of an ecological investigation by Beveridge (1975) who concluded that the ecological status of *A. obtusa* is very similar to that on Vanikolo (above). The climate of the *Agathis* forest areas is per-humid or only slightly seasonal with annual rainfall at coastal stations 2200–2600 mm, and probably more inland (Johnson estimated 5080 mm). The forests occur on well-structured oxisols derived from basalt. Most of the *Agathis* occurs between 200 and 400 m elevation. The upper limit is near to an upper montane rain forest dominated by *Metrosideros* and *Weinmannia*.

These forests are probably best regarded as subtropical rain forest not tropical (sect. 3.1). They are poor in species; Johnson found only 44 tree species with diameter over 60 cm of which only half reach the canopy top. Besides *Agathis*, other common big trees are *Calophyllum neo-ebudicum*, *Hernandia moerenhoutiana* ssp. *samoana* and *Palaquium neo-ebudicum*. Of these the *Calophyllum* is extremely common on Erromango, where its total timber volume was estimated by Johnson as 418,000 m<sup>3</sup> (mean estimate), compared to 118,100 m<sup>3</sup> of *Agathis*. There is a wide range of diameter classes of *Agathis*, and basal areas on Erromango of trees over 10 cm diameter vary between 36.2 and 39.7 m<sup>2</sup>/ha. Seedlings are only abundant close to mother trees. *Agathis* seems very resistant to wind-throw but *Calophyllum* is not, especially in the occasional cyclones experienced. Beveridge (1975) considered the biggest *Agathis* of 3 m diameter to be survivors of cyclones that opened up the canopy and allowed small *Agathis* to grow up.

The forested slopes inland of Anelgahaut Bay on the west coast of Aneityum have been selectively logged, mainly for *Agathis*, for most of this century. Patches of *Agathis* seedlings have developed under the residual stand. They are shade-tolerant and healthy and grow slowly, faster in gaps. There is a wide range of size classes and the species is maintaining itself. The author has seen no other forest anywhere with so

much regeneration of *Agathis* after logging. The evidence clearly points to the conclusion already reached by Beveridge that *Agathis* seedlings are shade-tolerant (and can grow even in deep shade) but grow up mainly in gaps as these occur.

In the four years after logging on Erromango only a few patches of seedlings had developed, colonizing bare earth. In opened areas of the forest some seedlings survived (A. E. Beveridge, R. M. Bennett, *pers. comm.*). One possible reason for the patchiness of seedlings on both Aneityum and Erromango (and also on Santa Cruz) could be the sporadic production of seed, at most only once a year, and the need for there to be a suitable site and weather at the time of seed fall for both germination and seedling survival.

Opinions differ as to whether *Agathis* can invade the secondary forest which fringes the logged primary forest. This is dominated by *Alphitonia zizyphoides*, *Macaranga*, *Serianthes* and *Trichospermum* and develops after cultivation or burning.

The Erromango *Agathis* forests occur in three blocks of total area c. 14,000 ha. The most accessible and densest south east stand was logged between 1967 and 1975. Besides *Agathis* some *Calophyllum* was also removed. *Agathis* has been removed from Aneityum since about 1914, on a small scale except between 1946 and 1955. Operations ceased in late 1976. The logs were carried by road down to the settlement and anchorage at Anelgahaut Bay. Virgin stands remain at some distance inland and of difficult access. In its final years the operation was re-logging forests near the bay.

### New Caledonia

The five species which occur here differ in their distribution and ecology. Two, *A. lanceolata* and *A. ovata*, are restricted to the ultrabasic rocks which comprise about one third of the island and, from the nickel mines on them give New Caledonia its wealth and economic importance. The others occur on schists, sandstones and shales. The forests of New Caledonia are probably best regarded as subtropical rather than tropical (sect. 3.1). The climate is per-humid and annual rainfall 1500-2500 (-3000) mm throughout the area where *Agathis* occurs, i.e. except along the west coast (Brookfield & Hart 1966, Girard & Rignot 1971). The following account is based on discussions and correspondence with Mm. Guinaudeau, McKee, Schmid, Gay and Vernier, a brief visit to a few forests and the account by de Laubenfels (1972). Apparently little is known about the ecology of the different species.

The main timber species is *A. moorei*, a giant tree of lowland rain forest throughout the island on shales, sandstones and schists, up to 1000 m elevation. It attains over 30 m height with clear bole of 18 m, and has been logged out from all the more accessible forests. This species produces seed more frequently and prolifically than the others. Abundant carpets of seedlings sometimes develop, but most are destroyed by introduced mice and rats.

*Agathis lanceolata* is a similar giant tree but is restricted to rain forest on serpentine and peridotite at

low elevations, mainly at 100-300 m, rarely to 900 m, and mainly in the south. Its northern limit is Boulinda. Locally it may be the dominant tree. The tall rain forest it occupies is mainly found in valleys.

*Agathis corbassonii* is a less common giant tree of shales, sandstones and schists which has only recently been recognized as distinct taxonomically from *A. moorei*. It occurs in rain forest on slopes and ridges at 300-700 m, scattered through the island except the southern end.

*Agathis montana*, also recently described, is restricted to upper montane rain forest on the summit plateau of Mt. Panie, and probably adjacent peaks, in the north east beyond Hienghene. It grows to 15-20 m tall, as pure stands, and at 1200-1640 m, on soils overlying mica schists.

Finally, *A. ovata* is restricted to the great ultrabasic block which forms the southern end of the island and up to 800 m elevation. Mostly it occurs in groves on open, sometimes burned, hillsides, emergent from a low maquis, as a short tree to 8 m tall with a massive crown and very short bole (Plate 7b, c); sometimes it is a shrub with no bole at all. Less commonly *A. ovata* is found as a 25 m tall tree with a 12 m trunk in tall, gallery rain forests. It is known to be sensitive to fire and to be light-demanding. This species is unique in the genus in inhabiting open rather than closed forest, in its squat habit and its tolerance of what is probably a periodically hot and dry aerial microclimate and heated soil surface, though it is likely the soil never or seldom desiccates at depth.

### Fiji

*Agathis vitiensis* is an important component of the rain forests, which occupy the wetter parts of Fiji. It is a well-known timber tree and has been logged out of many of the more accessible forests. A forest inventory covering the whole archipelago showed that *Agathis* occurs in a variety of floristic forest types and on a variety of kinds of topography (Berry & Howard 1973). The rain forests of Fiji are probably best regarded as subtropical rather than tropical (sect. 3.1). *Agathis* is commonest in lower montane forest and absent from the wettest climates. The forest canopy is 25 m tall with *Agathis*, *Dacrydium* and *Podocarpus* emergent. *Agathis* reaches 30 m tall and 6 m girth with clear columnar bole to 18 m. Timber volume of trees over 30 cm diameter can reach 100 m<sup>3</sup>/ha. There is an extensive belt of such forest in central Viti Levu at 600-900 m elevation; the climate is slightly seasonal to seasonal, with up to five months with little rain. At one site inspected at 900 m elevation, at Lalavatu east of the Nausori Highlands, the soil was a deep, friable, chocolate-brown clay developed over basalt. The forest was microphyllous in facies with a 9 m tall canopy and scattered 15 m emergents. *Agathis* formed 40 per cent of the timber being extracted followed by *Dacrydium* and *Endospermum*. No seedlings or saplings were seen in unlogged forest, logged forest or along roadsides. This is characteristic. Seedlings do sporadically colonize logging roads and landslides but are commonly killed in competition with a lush forest of pioneer trees

which later develops (M. J. Berry, *pers. comm.*). They do occur rarely in high forest and appear shade-tolerant.

### New Zealand

*Agathis australis* is the most famous species and its Maori vernacular, Kauri, has become the name for the genus in all European languages. It is today restricted to the northern tip of North Island, and at the time of European penetration, about 150 years ago, occurred on over a million hectares, as the biggest tree in a forest of mixed angiosperms and conifers perhaps best described as warm temperate with subtropical affinities. Now only about 7000 ha of virgin forest containing *Agathis* remain (Plates 6, 7). The New Zealand *Agathis* forests have been subject of a great deal of study, more than any others and three bibliographies have been written (Lloyd 1971, Orwin 1974, Anderson 1974), the last two being annotated. There remain considerable differences of opinion on many aspects. A definitive account is in course of preparation by the Forest Research Institute at Rotorua and notes on *Agathis* silviculture have just appeared (Beveridge 1977). The species is anomalous in the genus in its occurrence well south of the tropics and it is considered sufficient for present purposes to give an outline description only, for comparison with tropical *Agathis* and for the sake of completeness, and to refer the reader to the bibliographies and forthcoming treatise for full detail.

The climate of the north peninsula of North Island is more or less permanently humid, rainfall is 1000-2000 mm and well distributed, mean annual temperature is about 13°C and frosts are occasional. Rainfall at the remaining *Agathis* stands is in the higher part of this range. It has been suggested (Bialeski 1959) that the southern limit of *Agathis* is at the latitude where the mean daily temperature during the growing season is below 17°C because below that it is at a competitive disadvantage. Silvicultural observations do not support this hypothesis and cooler Pleistocene climates including more frost may be the determining factor (A. E. Beveridge *in litt.*).

Forests with *Agathis* occur over a variety of rocks, principally basalts, greywackes and sandstones. The soils are often podzolized over the sedimentary rocks which are intrinsically poorer in bases, and occasionally also over other rocks (New Zealand Soil Bureau 1968, Swindale 1957, Plate 6c). Individual *Agathis* sometimes develop a saucer-shaped (so-called 'egg-cup') podzolic pan and occasionally several such pans form superimposed (Gibbs, Cowie & Puller 1968, Reed 1964).

Virgin *Agathis* forests carry a huge amount of timber (2300 tonnes/ha at Trounson, W. Sylvester, *pers. comm.*) and these were formerly the basis of a substantial industry; many towns including Wellington have been built mainly from wood of this species. Resin collection was a second important industry between 1850 and 1920 (Lloyd & Guild 1976), partly by tapping boles and limbs of living trees, but mainly as 'fossil gum' dug up from the ground in pieces weighing up to 50 kg. Some *Agathis*

forests were felled and burned to clear the land for gum digging or for pasture, profligacy matched at the present day in parts of the dipterocarp forests of Malasia being converted to plantation agriculture. Pastures sown over a podzolic pan commonly become waterlogged. Some have been abandoned and are now reverting to scrub.

The only extensive *Agathis* forest remaining is at Waipoua, a Forest Sanctuary of 9000 ha of which some 2600 ha actually contain *Agathis*. There are also scattered small pockets, such as Trounson Kauri Park. In these forests *Agathis* form a top, emergent, canopy 40-50 m tall, in patches of many hectares extent, on plateaux (as at Waipoua and Warawara), ridges and hillsides. Once well-established, *Agathis* can tolerate both drought-stress and a degree of water logging. This tolerance, plus its longevity and regular, abundant seed production can give *Agathis* a competitive advantage on some sites. Frequently a mosaic occurs of *Agathis* on poor sites and broad-leaved species on the better ones (Beveridge 1977). Trees are of vast girth, over 10 m is common, with short clear boles of only 10-12 m, and huge, spreading crowns of massive limbs. These forests are a highly impressive sight, but the huge *Agathis* trees are mostly hollow and many are dying back. Growth is negligible. *Agathis* occur mixed with much smaller and shorter angiosperm trees and a few other conifers (*Dacrydium*, *Podocarpus*, *Libocedrus plumosa*); the total number of species is small by tropical standards. The big trees are believed to be about 500 years old, or occasionally 800, with a few huge trees attaining about 1000 years age; estimates of 2000-4000 years can probably be discounted (Cheeseman 1914, Reed 1964, Beveridge 1977). In fact, age is very difficult to determine because the trees are hollow. The biggest trees have been named individually by the Maoris; Te Matua Ngahere (Father of the Forest) of diameter 5.06 m is stoutest of all. As well as these huge trees there are others of diameter to 1.1 m with taller clear boles and smaller crowns.

Around the butts of the great *Agathis* trees mounds of undecomposed litter accumulate to 3 m thick. Recent study has shown that nearly all the soil nitrogen is immobilized in the litter layer and that the turnover rate is very slow (W. Sylvester *pers. comm.*).

In the region of these forests open, once-forested places are colonized mainly by *Leptospermum scoparium* or *L. ericoides*, reaching 6-9 m and 15-(21) m tall respectively, depending on degree of site degradation. *L. scoparium* is the only species whose roots have been observed to penetrate a podzolic iron pan. Grassland develops on the most degraded sites (Esler & Rumball 1975). *Weinmannia sylvicola*, which has shade-tolerant seedlings, may establish and grow in the very thick sedge litter or on mineral soil. Sometimes *Weinmannia* succeeds *Leptospermum*. Most *Agathis* seeds fall within 20 m of a mother tree, though some reach 100 m distance and freak high winds probably occasionally disperse a few much further. Seedlings may establish before a sedge carpet forms, or before the *Leptospermum* forest. In either case most become suppressed and die, from com-

petition with the pioneers, or in the first dry summer from desiccation, or from insolation in the open. Eventually, *Agathis* seedlings and those of other tree species (including several conifers especially *Dacydium cupressinum* and *Phyllocladus trichomanoides*) establish under the pioneer forest. In a small plot at a typical site in Russell forest (Lloyd 1960) the *Leptospermum* was up to 120 years old, a few *Agathis* trees had established from age 10-20 and many more when it was between 60 and 120 years old. Colonization was facilitated by the gradual opening up of the *Leptospermum* canopy as it aged and by decrease of the initially very thick litter layer. Although *Agathis* regeneration was of mixed age those plants 10-70 years old were all 25-50 mm in diameter, suppressed by competition. Elsewhere more *Agathis* colonizes *Leptospermum* forest in the first few decades (Mirams 1957). Eventually, *Agathis* breaks through the canopy of the pioneer forest and stands of same-height poles (known as 'rickers') with emergent, narrowly conical, monopodial crowns are a common sight throughout its range.

Silviculture has been practised over about 5000 ha in total to shorten the succession by releasing small *Agathis* from suppression, mainly in Russell Forest and on Great Barrier Island. Some areas have been treated several times. The total area of forest with regenerating *Agathis* is estimated to be 74,000 ha of which 20,000 ha are State-owned, but this area is not fully stocked with *Agathis*.

Natural seedlings can grow in height at 0.1 m/year or, on some sites with full overhead light, at 0.25 m/year. Saplings and poles commonly grow 0.3-0.4 m/year with diameter increment 5 mm for uncrowded stems (Beveridge 1977).

Periodic destruction of large swathes of forest is thought to have occurred. Before man came to New Zealand it is believed that both vulcanicity and windthrow were important. Fossilized *Agathis* have been unearthed in swamps, commonly with the trunks snapped off and all lying in the same direction; up-turned root plates have been found. New Zealand today lies beyond the south west Pacific cyclone belt (though that may have been further south in the past (Whitmore 1974)) but occasional cyclones occur and there are records of wind damage to *Agathis* this century (e.g. Conway 1959). The degree to which *A. australis* is wind-firm may depend on its site, trees on strongly podzolized soils only developing shallow root systems being most susceptible. The species has a tap root until about 0.2 m diameter. This is later replaced by vertical peg roots.

Since Maori settlement, a thousand years ago, fire has also probably been a destructive factor. Fire is known to spread into standing green forests on some sites.

Natural catastrophes to high forest, whatever their cause, would have led to regrowth of pioneer forest succeeded in many places by same-size *Agathis* pole stands such as described above. It is most probable that these in turn grew up into the extensive stands of big, overmature trees such as now remain at Waipoua and which to the layman are typical kauri forests. It

seems unlikely that the scattered pockets of smaller girth trees and seedlings seen in these overmature forests are sufficient themselves to develop into extensive stands of giants, though, because of the longevity of individuals and in the absence of age or growth rate estimates, it is impossible to be certain. The smaller girth trees have much longer clear boles than the giants. *Agathis* in pioneer forest starts to form persistent limbs at the level of the canopy top, about 10-12 m. This is about the same as the clear bole length of the giant trees which is powerful circumstantial evidence to corroborate the explanation that extensive stands originate from catastrophes.

Today little resin remains to be collected, and only a few sawmills remain to utilize giant kauri. In the next few decades many pole stands regrown after logging, and containing some trees too small to fell on previous loggings, will reach a size where thinning will probably be necessary both to create a mixed size stand and to stimulate growth.

### 3.3 Ecological status

Observations have been presented in the preceding section on naturally occurring *Agathis*. Many of the details are incomplete or fragmentary. Nevertheless, an attempt is made in this section very briefly to describe in general terms the ecology of *Agathis*, for an overall pattern can be dimly perceived.

*Agathis* in Santa Cruz (*A. macrophylla*) and New Zealand (*A. australis*) can invade the pioneer stands of trees which develop after extensive clearance, and eventually grow up as large stands of uniform age. This is probably the case also in the New Hebrides (*A. obtusa*) but the evidence is less complete. This is the nearest *Agathis* gets to pioneer status (see Whitmore 1975a for a detailed discussion of this ecological 'strategy'). *A. dammara* in Kalimantan invades pioneer *Tristania* forest on white sands. Small plants of *A. macrophylla* are fast growing, given full overhead light, as is *A. obtusa*. The latter also continues to grow fairly fast in shade.

All these species (least so *A. australis*) occur as populations of trees of a wide range of girths, plus seedlings and saplings. This indicates that even in the absence of the catastrophes which cause large sized clearings they are maintaining themselves. Such is also the case on white sand at Badas (Brunei) and Sjoega (Irian Jaya), on ultrabasics at Sg. Toe (Sabah), near Tanahgrogot (Kalimantan) and on Japan island (Irian Jaya), on basalt-derived soils in the Santa Cruz islands and New Hebrides, sedimentary-derived soils in New Caledonia (*A. moorei*) and on unstated soils in central Celebes (*A. dammara*).

By contrast, *A. dammara* occurs only as big trees, scattered or in groves and with small individuals rare or absent, at Sg. Lallang (Malaya), Bt. Retak (Brunei), Mindanao and Palawan (Philippines), Malili (Celebes), Biak-Binsimar (Irian Jaya) and at Sogeri and Fulleborn harbour (Papua New Guinea). In all these cases it is on normal zonal soils, except at Malili where it is over ultrabasics.

Detailed studies have not been made elsewhere, and those summarized above are mostly only on one or a few populations. The generalization which emerges from these fragmentary observations is that *Agathis* populations with a range of size classes i.e. which are apparently self perpetuating are restricted to 'poor' sites throughout Malesia and only in the islands of the south west Pacific do they occur on normal zonal soils. It may be no coincidence that compared to Malesia the rain forests of Santa Cruz, New Hebrides and New Caledonia are poor in species. It remains a mystery how the isolated trees and small groups of large *Agathis* trees on zonal soils in the Malesian rain forests reproduce themselves.

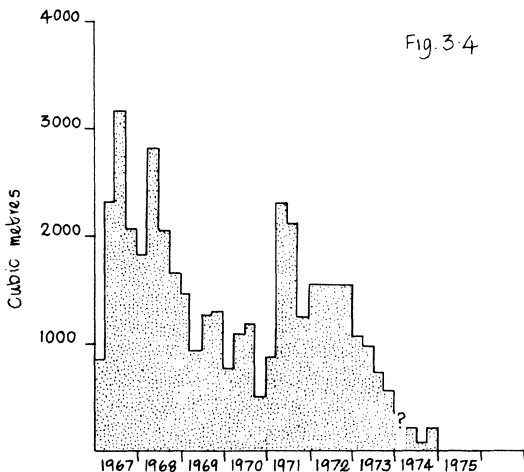
From the forester's viewpoint the species which invade pioneer stands have the greatest number of useful features, as is described further in chapter 5. The forester should also bear in mind the tendency of *Agathis* to podzolize soils, especially oligotrophic ones. Whitmore (1966) should be consulted for an analysis of this phenomenon.

### 3.4 Genetic resource conservation

*Agathis* are distinctive trees, easy to recognise in the forest from their cylindrical, unbuttressed, columnar boles and diphloic to scaly bark. They have specific vernacular names. Moreover, they often occur in groups and occasionally in extensive stands. When it is also remembered that the timber always commands a premium price (sect. 8.1) it is not surprising then to learn that loggers seek *Agathis* out for felling throughout its range.

#### Logging summarized

Export figures from Malaya suggest that the *Agathis* forests are probably diminishing, Fig. 3.4 and



3.4 Sawm timber exports from Peninsular Malaysia. (From *Malaysian Forester*.)

Table 8.2. In Borneo the formerly huge stands in Kalimantan Tengah have been exhausted; extraction is in progress on the east coast in the stands near Tanahgrogot and probably also further north near Balikpapan (International Timber Corporation of Indonesia concession) and Samarinda (Kayan River Timber Products concession). In lowland Sabah a small stand was logged at Sg. Toe in the early 1970s. In Brunei most of the Badas *Agathis* forest was felled during 1958-60. In Celebes the extensive but mainly diffuse lowland stands around Malili are being felled (Zedscoc concession). In Papua New Guinea several small pockets have been logged around Bulolo and Wau, in the Eastern Highlands, and on the south coast of New Britain. In the Santa Cruz islands all the forests on Vanikolo were logged between 1924-64 except for a small area in the Lawrence river valley and on adjacent Tevai island. Operations have recently commenced on Ndendö island and are likely to exhaust the two stands there by about 1980. In the southern New Hebrides the densest, southeastern stand on Erromango was logged in the late 1960s and most of the Anenityum forests have been logged and depleted over many years. In Queensland selective logging since the nineteenth century has removed the big trees from most of the rain forests which once contained *Agathis*. In New Zealand only a few areas of virgin forest remain.

#### Current conservation measures

In Peninsular Malaysia the practice is to leave some areas of *Agathis* unfelled as stands of seed trees, for example at Gading, north Selangor and at Sg. Lallang (cmpt. 44). Also, some trees are sometimes left because below the minimum felling girth of 4.5 ft (0.43 m diameter), as at Semangko.

In Brunei a seed stand has been left at Badas.

In Indonesia the practice is to fell only trees above a certain diameter, 0.4-0.5 m. This ensures that in most stands some trees of mature height persist after logging.

In Sabah the Sg. Toe stand was felled without either of these provisions. Unfortunately an attempt to replant the area failed because the seedlings died.

In the Philippines *Agathis* is totally protected, as a source of resin, but not where it grows on the line of a planned road or track.

In Papua New Guinea standing trees are purchased for felling from their native owners. Scattered *Agathis* have survived logging at Lufa and Suwaira in the Eastern Highlands and probably elsewhere. Recently it has been proposed to conserve unfelled a 40 ha block plus 37 adjacent trees at Gumi Creek. Plantations under high shade of *Castanopsis acuminatissima* at 6 × 6 m have recently been established at Bulolo as conservation stands of Sogeri, Chimbu Gorge, Gumi Creek, Lufa and Suwaira provenances (see trial plots 68, 69, 70 in sect. 4.3).

In the Santa Cruz islands virgin stands of the Vanikolo and the Tevai provenance (which is probably identical) remain unfelled because the concessionaire ceased to operate before reaching them. On Ndendö malformed or damaged great trees are not

felled and also a proportion of smaller trees of full height.

In Queensland and New Zealand felling of *Agathis* has virtually ceased.

#### *Adequacy of current conservation measures*

In most of the areas from which big *Agathis* trees have been removed enough small individuals or seed trees remain eventually to redevelop an *Agathis* forest. This has been done without any precise knowledge of the ecology of the local *Agathis*, especially of its seral status. In fact there is no *Agathis* provenance which can compete with a dense, lush, fast growing stand of pioneer trees. Survival of *Agathis* everywhere probably depends on seedlings invading such stands of pioneers as they grow old and become less dense, plus any small individuals which persist through this pioneer phase.

The practice of retaining seed stands seems to the author to be useful because it conserves population and forest structure including the giant trees which in some provenances are the only ones which produce cones copiously (sect. 6.1). It is shown in Appendix 1 to be likely that the full genetic diversity of an *Agathis* population can only be maintained in perpetuity if a minimum of 5000 trees is conserved and that 10,000 is a safer number.

The retention of mother or seed trees (Indonesian *pohon induk*) appears to be a less secure method of conservation than leaving part of a stand intact. The trees are left isolated in an open forest in a totally unfamiliar microclimate and may be liable to sun-scorch or wind damage. The ground below them is likely to become covered with a dense secondary forest in which small *Agathis* cannot survive or grow.

#### *Genetic erosion*

In summary, *Agathis* is undoubtedly diminishing in diversity as a few stands are removed by logging and others reduced in size. Conservation by retention of mother trees is likely sometimes to lead to a temporary but substantial reduction in numbers as juveniles succumb to competition with secondary forest, and it will be a long time before high forest containing *Agathis* redevelops.

#### *Conservation proposals*

It is advocated that retention of seed stands is preferable to leaving mother trees. In addition, consideration should be given to establishing plantations for conservation. At 3 × 3 m there are 1111 trees/ha, and so full diversity would probably be maintained in stands of 5-10 ha each (Appendix 1). Plantations have the advantage of accessibility. Seed of the Santa Cruz and New Hebridean *Agathis*, which are probably the most valuable for forestry, will be very difficult to harvest once logging operations have ceased. These also are attacked by larvae of the seed-eating moth *Agathiphaga* (sect. 7.1), and seed from plantations outside the natural range would not suffer damage from this cause.

*Agathis* is not yet being logged everywhere in its

range. Land use planning is in progress. One legitimate and rational use of virgin rain forest is to retain samples of it as conservation areas to maintain diversity of flora and fauna and especially the full genetic diversity of actual and potential economic plants. All countries in the region have created or propose to create such conservation areas mainly as National Parks (Whitmore 1975b, Whitmore & Grimwood 1976). These have to compete with other land uses, especially timber production.

As yet plant genetic resources have not been precisely defined. *Agathis* is one example of such a resource, and one moreover of demonstrable value which is currently being depleted. Conservation of selected *Agathis*, based on its occurrence and provenance diversity described in this report, could usefully be incorporated in land use plans. In particular it can be noted that in the following places *Agathis* forests remain in the pristine state or substantially so:

Sumatra,  
Sarawak,  
the central part of Celebes, except around Malili,  
Palawan,  
the Moluccas, of which the Ambon, Buru and  
Ceram populations are the largest,  
Irian Jaya,  
Papua New Guinea, the Sepik and Sogeri  
populations.

In addition there remain parts of the populations of the following provenances where conservation measures need reinforcing or initiating:

Santa Cruz, all three islands: Ndendö, Vanikolo  
and Tevai,  
New Hebrides, Espiritu Santo, Erromango and  
Aneityum.

#### *New Zealand*

There is currently much concern to 'save kauri' but the public which takes an intense interest, confuses the overmature forests of giant *A. australis* trees, where the species is probably dying out or diminishing in abundance (sect. 3.2), with saving the species itself. The very abundant and widespread stands of pole ('ricker') *Agathis*, now emerging from the canopy of secondary forests regrown after clearance of the primary forests many years ago, show that in New Zealand there is no present danger of *Agathis* diminishing in genetic diversity or in abundance.

## 4 Planted *Agathis*

### 4.1 *Agathis* as a plantation tree

Large scale planting of *Agathis* is now confined to Java and Irian Jaya, for timber and resin production respectively. In addition, until the 1950s there were extensive plantations in south Queensland. Open-planting has recently commenced in New Zealand. A few data on height and diameter growth in plantations are presented in Table 5.3 and discussed in chapter 5.

#### *Plantations in Java*

The taxon planted is here described as *A. dammara*, *Java provenance*. The seed source is way-side trees at Cibadak west of Sukabumi in west Java, of which a few were still alive in 1974. These were planted late last century with seed of Moluccan provenance, believed to come from Amboina. Several generations of trees have now been raised in Java. The possibility exists that there has been natural selection, and it is known also that in some seed stands trees with markedly spiral grain have been culled. The *Java provenance* is therefore a land race. It is locally called *A. loranthifolia*.

Trial plots of *Agathis* were established at various places through Java in the 1930s. These were described by de Jong (1938) who gave the following locations:

West Java: Garoet (nr. Bandung), Midden Preanger (Bandung), Tasikmalaja, West Preanger (Sukabumi), Zuid Cheribon.

Central Java: Banjumas (Baturaden), Kedoe, Pekalongan, Probolinggo.

East Java: Banuwangi, Bondowoso, Djember, Oost Brantai (or Malang), Passorean.

In the late 1940s and subsequently planting was concentrated at a few places only, partly because the trials revealed greatest success in the wetter climates and complete failure or poor growth in the dry lowlands of eastern Java.

Extensive plantations exist in five areas, on the mountains north of Sukabumi in western Java and in central Java where the two biggest are on the northern and southern slopes of Gunung Slamet at Pekalongan (Paningaran) and Banjumas Timur (Baturaden) respectively; there are also substantial stands in central Java east of Purworejo and near Magelan. The total areas planted are given in Table 4.1. The plantations

near Sukabumi are now regarded mainly as protection forest in water catchment areas. Planting in central Java is now restricted to the Banjumas Timur area (Plate 9d).

Establishment is usually by taungya (known locally as *tumpang sari*) because to obtain good growth shade is needed for the first few years. In full sun young *Agathis* become chlorotic. Food crops are grown for one or two years and the leguminous treelet *Leucaena leucocophala* is planted to give shade for the first few years, to reduce erosion, to reduce weed growth and to act as a fertilizer (Team Reboisasi 1971, Plate 8b).

The west and central Javan plantations are important because they are at present the only extensive and continuing operation anywhere in the world where *Agathis* is being grown in this way. It is not easy to obtain details of this interesting venture, and therefore notes obtained by the author in Indonesia in 1974 are given here as appendix 2.

Various measures of the growth of the Javan plantations have been published, namely a volume table (Sudarmo 1956b) preliminary stand table (Trijono & Harris 1958), yield tables (Ferguson 1949b, Sudarmo 1956a, the latter more detailed) and a thinning schedule (Ferguson 1949b).

In Table 4.2 details of predicted yield are reproduced from Sudarmo (1956a). He recognized three site classes based on mean height at 25 years age. At thirty years total volume including thinnings is estimated at 702, 831 and 961 m<sup>3</sup>/ha respectively or 23, 27, 32 m<sup>3</sup>/ha/yr. This length of rotation is recommended for pulpwood (Team Reboisasi 1971). For veneer and timber production a 50 year rotation is recommended. Total yields would be 1099; 1245 and 1411 m<sup>3</sup>/ha respectively or 22, 25, 28 m<sup>3</sup>/ha/yr.

#### *Plantations in Irian Jaya*

The taxon planted is the indigenous *Agathis*, described here as *A. dammara Irian Jaya provenance*, which has hitherto usually been called *A. labillardieri*. The total area planted is about 2300 ha, divided between Sorong (km 14 on the road to Klamono) 750 ha, Teminabuan (1000 ha or more) and Biak (over 500 ha), the localities are shown on Fig. 3.2. It is not known if the Sorong and Teminabuan plantations still stand.

One small plantation on Biak was visited, where

Table 4.1 *Agathis* plantations in Java (ha)

West Java*		
Gede Barat	998	
Cicurug	1174	
Lengkong	254	
Rojong Lopang	50	2476
Central Java**		
Banjumas Timur	3477***	
Purworejo	1891	
Magelang	236	
Pekalongan	423	6027
TOTAL		8522

\*From Table 5a in Bagian Kerja Kesatuan Pemangkuan Hutan Sukabumi jangka lima tahun (1 April 1972-31 Maret 1977)

\*\*from Tata Usaha Bagian Produksi, Semarang 16 August 1973

\*\*\*differs from figure given later in text by inclusion of 59 ha recently planted

a few hectares each year are still planted. *Area* 155 ha (1956-7 ha; 1958/60-50 ha; 1964-10 ha; 1961/5-88 ha). *Site*. Raised flattish coralline platform some 15 km from Biak town, 50 m elevation. *Climate*. Perhumid, A type; there are reputedly 15 rainy days every month. Biak is exposed to the Pacific ocean to the north. *Vegetation*. Low secondary forest. *Soil*. Reddish clay over (?) conglomerate at 1 m.

*1964 stand (10 years)*. Canopy open over shrubs. Planted at 10 × 5 m; h 4.5 m, d 15-28 cm, crown depth 3-4 m.

*1961 stand (13 years)*. Sample trees: height 12, 13, 15 m; diameter 20, 24, 29 cm; clear bole 4, 4.5, 5 m; crown width 3 m.

*1958 Araucaria cunninghamii* planted in a line along the track. 18 m tall, 13 cm diameter. Outgrown by *Agathis*, possibly the climate is too hot and wet for it.

*1956 stand (18 years)*. Planted at 10 × 5 m on soil 0.8 m deep. Biggest trees seen 20 m tall, 40 cm diameter. Others 13.5, 18.5, 19.5, 20 m tall and 25, 28, 30, 31, 36, 37, 38, 38 cm diameter. Crowns with numerous branches, 7.3 m diameter. Planted at 10 × 5 m spacing. Soil 0.8 m deep.

### Plantations in southern Queensland

The indigenous south Queensland, *A. robusta*, was planted as extensively as seed supplies permitted

until, in 1959, massive defoliation by the kauri coccid *Coniferiococcus agathidis* caused substantial decrease in growth, and much death (Plate 12a, b). Details are given in sect. 7.1. The species has now been abandoned. Plantations have been largely felled and replaced by other species. The following account is based on Grenning (1957) and Heather & Schaumberg (1966). Table 4.3 gives representative growth figures. 'From the point of view of the production of a high percentage of high quality defect-free timber in plantation on short rotations there could be no species superior to Kauri Pine because of its remarkable capacity at any spacing to prune itself naturally (Plate 11b). Furthermore the method of pruning is such that little or no knotty core is produced'. (Grenning 1957). *Agathis* was capable of producing at least 100 per cent more high quality, defect-free timber than pruned Hoop Pine (*Araucaria cunninghamii*) on a rotation of 50 to 60 years, without any expense of pruning (sect. 4.8). It has been described as 'a forester's dream' (J. M. Fielding *pers. comm.*).

Most of the plantations were in the Mary valley around Imbil, some 50 km inland, separated from the sea by a range of hills. This is 32 km beyond the western margin of the natural range (see sect. 3.2) (though a solitary wild tree was known) and the

Table 4.2 Yield table for *A. dammara* in the Javan plantations

Age	Height (m)	Stems per ha	Main stand		Basal area m <sup>2</sup> /ha	Merchan- table volume m <sup>3</sup> /ha	Merchan- table volume m <sup>3</sup> /ha	Cumula- tive volume m <sup>3</sup> /ha	Total volume (7) + (9) m <sup>3</sup> /ha	m.a.i Volume m <sup>3</sup> /ha	c.a.i. Volume m <sup>3</sup> /ha
			h (m)	d (cm)							
	2	3	4	5	6	7	8	9	10	11	12
SITE CLASS II = SITE INDEX 27 m											
5	5.9	3112	4.6	5.0	6.1	15	10	10	25	5.0	5.0
10	13.9	1183	12.5	13.0	15.7	92	32	42	134	13.4	21.8
15	19.6	742	18.3	20.0	23.3	188	60	102	290	19.3	31.2
20	23.9	552	23.0	26.0	29.3	279	60	162	441	22.0	30.2
25	27.0	445	26.4	31.1	33.8	360	55	217	577	23.1	27.2
30	29.6	372	29.2	35.8	37.5	432	53	270	702	23.4	25.0
35	31.8	325	31.6	40.0	40.8	498	50	320	818	23.4	23.2
40	33.9	290	33.9	43.9	43.9	564	46	366	930	23.2	22.4
45	35.5	265	35.7	47.2	46.3	617	40	406	1023	22.8	18.6
50	36.7	252	37.0	49.8	49.0	658	35	441	1099	22.0	15.2
SITE CLASS III = SITE INDEX 30 m											
5	6.8	2105	5.5	6.6	7.2	21	15	15	37	7.4	7.4
10	16.2	1011	14.4	15.3	18.6	113	51	66	179	17.9	28.4
15	22.2	634	20.5	23.3	27.0	225	70	136	361	24.1	36.4
20	26.7	471	25.3	30.1	33.5	331	70	206	537	26.8	35.2
25	30.0	376	29.0	36.0	38.3	422	60	266	688	27.5	30.2
30	32.8	321	32.1	41.1	42.6	509	55	321	831	27.7	28.6
35	35.3	187	34.8	46.1	46.3	584	50	371	955	27.3	24.8
40	37.4	249	37.2	50.3	49.5	650	46	417	1067	26.7	22.4
45	39.1	228	39.1	54.0	52.2	705	41	458	1163	25.8	19.2
50	40.4	211	40.3	57.1	54.1	750	37	495	1245	24.9	16.4
SITE CLASS IV = SITE INDEX 33 m											
5	7.7	1736	6.6	7.8	8.3	31	15	15	46	9.2	9.2
10	18.5	896	16.5	17.5	21.6	144	60	75	219	21.9	34.6
15	24.8	563	23.0	26.4	30.8	276	80	155	431	28.7	42.4
20	29.5	422	27.9	33.7	37.6	403	75	230	633	31.6	40.4
25	33.0	335	31.7	40.3	42.7	510	65	295	805	32.2	34.4
30	36.2	281	35.0	46.3	47.4	606	60	355	961	32.0	31.2
35	38.8	243	37.9	51.8	51.3	686	56	411	1097	31.3	27.2
40	40.9	217	40.3	56.6	54.5	757	50	41	1218	30.4	24.2
45	42.8	196	42.4	61.1	57.5	823	45	506	1329	29.5	22.2
50	44.1	180	44.0	65.0	59.7	868	37	543	1411	28.2	16.4

All volumes are on timber > 7 cm diameter

Table 4.3 Growth of *A. robusta* south Queensland provenance in plantation

Date	Age	Selected Stems				All Stems		
		Stems/ha	BA/ha	$\bar{d}$	Vol/ha	Stems/ha	Vol/ha	Predom.h
22.9.54	16.9	62	2.04	0.20	12.00	208	35.13	16.9
11.6.58	20.5	62	2.60	0.23	18.02	152	48.22	—
17.7.61	23.7	62	3.02	0.25	22.62	120	57.18	19.5
17.8.63	25.8	62	3.05	0.25	23.18	120	58.31	19.8

Volume in m<sup>3</sup> true under bark, from tables; diameter and height in m  
This is Imbil expt. 338, cmpt. 36 Derrier, plot 7, 0.08 ha

climate is drier with more marked dry seasons.

The species has precise site requirements. It had to be planted on fertile, well-drained soils above the frost line (young stock can be killed by harsh frost though by 2.5 years age only tender young tips get killed (Petrie 1922)).

By March, 1960 769 ha (1923 ac) had been planted, compared with 17, 567 ha (43918 ac) of Hoop Pine and a little Bunya Pine (*Araucaria bidwillii*) and north Queensland *A. robusta* ('palmerstonii') (Anon. 1960). The limited area of *Agathis* planted was due to shortage of seeds, though a successful means of vegetative multiplication of seedlings had been developed (see sect. 6.3).

The average predominant height of the *Agathis* at 25 years was 20.4 m, compared to 23.7 m for Hoop and only 16.5 for Bunya.

At 22 years age, thinned to routine prescription, the following growth figures applied:

	whole stand	selected trees
stocking (stem/ha)	919	
predominant height (20 tallest) (m)		18.9
mean d.b.h. (cm)	20.2	23.8
basal area (m <sup>2</sup> /ha)	35.24	17.27
merchantable vol (u.b. to 0.1 m)	240.7	123.0
m.a.i. (m <sup>3</sup> /ha)	13.79	

### Plantations in New Zealand

Only limited success was achieved in open-planting about 200 ha (Morrison & Lloyd 1972) but recently, following success at Raetea Forest, further planting has commenced. This is costly but is justified by public interest in kauri and hence the official policy to promote its silviculture (Beveridge 1977).

## 4.2 *Agathis* in enrichment planting

In three countries, Peninsular Malaysia, Brunei and the Solomon Islands logged forest is to be enriched by *Agathis* seedlings of the indigenous taxon planted in lines cut through the undergrowth. In addition a small area was replanted after felling in Sabah.

### Malaya

*Agathis dammara* seedlings as wildings, or raised in nurseries from seed obtained locally from natural stands in hilly lowland rain forest, have been planted as part of a big scheme of enrichment planting in

Selangor of logged lowland mixed dipterocarp rain forest, on sites formerly without *Agathis* though within its area (Ismail 1966).

There has been little or no attention paid after planting so most of the seedlings soon become over-shadowed. Survival is good but growth is slow except of the minority of seedlings situated under a canopy gap. The Malayan provenance of *A. dammara* is one of the slowest growing, and grows very slowly in shade.

### Brunei

It was planned to plant up 4,000 ha of heath forest at Badas with nursery raised stock of *A. dammara* Badas provenance over five years from 1975. Failure of the seed crop in 1975 delayed the start by one year. By September 1976 only about 22 ha had been planted. This is a forest in which this taxon naturally occurs, at high density, as described in sect. 3.2. It was logged in 1958-60. In 1974 (*author obs.*) there were a few small stands of sapling *Agathis* of healthy but spindly appearance, and all within 20 m of a relict mother tree. Small seedlings were rare. *Agathis* regeneration has grown slowly under dense shade of regrowth primary forest hardwoods which by 1974 had formed a 9 m high canopy of poles, many as coppicing clumps, including conspicuous *Dipterocarpus borneensis*, *Eugeissona minor*, *Podocarpus neriifolius* and *Whiteodendron moultonianum*.

### Solomon Islands, Santa Cruz Islands

The main *A. macrophylla* stand on Ndendö island has been logged since 1974 (sect. 3.2). It is planned to regenerate a dense stand by replanting naturally occurring seedlings (survivors or new ones) after logging, at 2-3 m spacing in lines 9-10 m apart. This will facilitate periodic removal of overhead regrowth shade. The *Agathis* should grow up together to form continuous lines about 3 m tall in 3 years and 6 m tall in 5 years. If there are not enough wildings supplementary nursery-raised seedlings will be used too. This proposal is based on experience on Vanikolo where natural regeneration was repeatedly released *in situ* (sect. 4.5) which proved very costly and time consuming because the *Agathis* seedlings are scattered irregularly. There would be no market for thinnings on Santa Cruz. The possibility is being considered of interplanting the lines of *Agathis* with mahogany (*Swietenia*) to give a sawn timber crop in 16-20 years. The timber industry is at present, and potentially in the longer term too, the main source of income and

jobs on this very remote island. This is an important factor in Forest Department reasoning (Marten & Watt 1974).

An attempt on Vanikolo to establish seedlings by broadcasting seed on to the surface humus in logged forest failed. It is believed rats and mice, introduced by man, ate them.

*A. macrophylla* line-planted into logged forest in the western Solomons (where it does not grow naturally) grew too slowly, due to overhead shade, to be worthy of consideration (Solomon Islands Forest Dept., unpublished records).

### Sabah

The Sg. Toe stand (sect. 3·2) was totally logged in the early 1970s. Seedlings were raised in a nursery partly from seed collected from unbroken cones on the ground and partly from wildings. They were planted out at 0.1 m tall at about one year old in gaps, under relic canopy or on extraction tracks. After one year 75 percent of planted seedlings and 98 percent natural seedlings were alive, mean height growth had been 50 mm, most death had been from deer browsing. Subsequently, most of the *Agathis* died.

### 4·3 Small trial plots

Species and the localities where they have been tried are summarized in Table 4·4 and a full list is given in Appendix 3. A distinction is made between open-planting and planting under shade, usually into lines cut through secondary or logged forest. For ease of reference all the trials are numbered in a single sequence.

The full data are held in Oxford and are available on request. They have been mostly extracted from unpublished records, and most of the plots have been in-

spected by the author. Discussion of the results of these trials is presented in Chapter 5.

Isolated individuals and small groups of specimen trees are recorded separately, in Appendix 4.

### 4·4 Outside the natural range

Small plots of several kinds of *Agathis* have been planted as exotics. These are summarized in Tables 4·4 and 4·5 and their performance discussed in Chapter 5.

### 4·5 Release of natural regeneration

Treatment to free seedlings and sapling *Agathis* from competition, mainly from overhead light, partly from roots, has been conducted on a small experimental scale with *A. obtusa* in New Hebrides. In Santa Cruz various experiments on Vanikolo have been followed up by treatment of a considerable portion of the forests after logging.

### New Hebrides, *Aneityum*, *A. obtusa*

Nine small (0·1 ha) sample plots were established in forest from which *Agathis* had recently been logged, at 270 m, 4 km inland on a broad slope above Analgeuhat Bay. All residual trees were poisoned on half the area, quarter remained virgin, and quarter was untouched after logging. Four and a half years later (*author obs.*) the poisoned area had a lush 1 m tall regrowth of primary forest species plus a little *Macaranga*, and some 30 m high shade from a few big unpoisoned trees. One edge had been invaded by grass from a track. Neither *Merremia* nor *Mikania* had invaded. The *Agathis* regrowth was vigorous with 150 mm internodes and stood above the competing

Table 4.4 Location and species on small trial plots. (Open planting (o) and underplanting (u))

	<i>A. australis</i>	<i>A. dammara</i>	<i>A. lanceolata</i>	<i>A. macrophylla</i>	<i>A. microstachya</i>	<i>A. moorei</i>	<i>A. obtusa</i>	<i>A. robusta</i>	<i>A. vitensis</i>
Malaya	—	o	—	o	—	—	—	—	—
Sarawak	—	—	—	o/u	—	—	—	—	—
Brunei	—	u	—	—	—	—	—	—	—
Sabah	—	—	—	o	—	—	—	—	—
Java	—	o	—	—	—	—	—	—	—
Celebes	—	o/u	—	—	—	—	—	—	—
Papua New Guinea	—	u	—	o	—	—	—	o	—
Queensland	—	o/u	—	—	—	o/u	—	o/u	—
Solomon Islands	—	o	—	o	—	—	—	o	—
New Hebrides	—	—	—	—	—	—	o/u	—	—
New Caledonia	—	—	o/u	o	—	o/u	u	—	—
Fiji	—	—	—	u	—	—	—	o	—
New Zealand	o	—	—	—	—	—	—	—	o
Outside the natural range (Section 4.4)									
India	—	—	—	—	—	—	—	o	—
Kenya	o	—	—	—	—	—	—	o	—
Mauritius	—	—	—	—	—	—	—	o	—
Puerto Rico	—	—	—	—	—	—	—	o	—
South Africa	—	o	—	—	—	—	—	o	—
Uganda	—	—	—	o	o	—	—	o	—
Zaire	—	o	—	—	—	—	—	—	—

vegetation; the trees had narrow monopodial crowns, a few forked, and some not self-pruning. The logged area had a dense 12-15 m canopy, regrown after logging, and very dense undergrowth. *Alphitonia zizyphoides* was abundant amongst many primary forest species. *Agathis* seedlings appeared healthy, were self-pruning and had internodes of c. 100 mm. The virgin area was similar to the logged but with a 20 m canopy and clearer undergrowth. The *Agathis* were similar but with internodes of only 25-75 mm.

These observations clearly show that this silvicultural treatment has released the *Agathis* regeneration, and that without further treatment a dense stand should develop. Table 4.6 gives measurements which confirm this subjective impression. *A. obtusa* is thus shown to have a marked ability to grow vigorously under slight high shade despite vigorous competition. It appears healthy and to grow, but more slowly, under dense shade.

#### *Santa Cruz Islands, Vanikolo, A. macrophylla*

Logging commenced in 1924. In the late 1950s and 60s several thousand hectares of the forest logged pre-war was treated to release *Agathis* seedlings, saplings and small poles from the dense secondary forest they occupied. The *Agathis* was very patchy in distribution. All or most of it must have resulted from seed blown in because observation has since shown that any juveniles which survive logging or invade bare ground die in competition with the secondary forest which develops (Whitmore 1966). Various combinations of weeding and poisoning were tried. Some areas were treated more than once. A much smaller area of post-war and recently logged forest was also treated, but by 1966, when work ceased and the settlement on the island was abandoned, about a third of the logged area remained untreated. Measurements

and experiments showed that weeding and poisoning both stimulated height growth, the effects are additive and progressively more marked the larger the *Agathis* juvenile. Plants up to 1.2 m tall kept fully weeded and with full overhead light grow 0.9 m/year and plants 1.2-1.8 m tall grow 1.2 m/year. It was ultimately considered that treatment would better have been given soon after logging in order to release both the existing regeneration and new recruits which are in places abundant. Gaps could be planted up with wildings. This treatment would have considerably shortened the time until a new *Agathis* stand developed. Increment measurements (summarized by Marten 1970) showed that relict trees left at logging and recruits can be expected to reach 76 cm diameter in 45-50 years in full overhead light (m.a.i. 16-19 mm). In logged forest without maintenance this would increase to 80-90 years (m.a.i. 8-13 mm) and over 300 m elevation without maintenance as long as 150 years (m.a.i. 8 mm between 30 and 50 cm diameter, otherwise less).

In summary, this experience shows that *A. macrophylla* has the ability to grow fast in full light, especially if root competition is reduced in the early years, and this is most marked at low elevations. Unfortunately in open sites the species has a proclivity to develop heavy persistent branches.

#### 4.6 Two species plantations

In south Queensland the indigenous conifers *Agathis robusta* and *Araucaria bidwillii* and *A. cunninghamii* become chlorotic and stunted and may die if planted in the open on lateritic podzolic soils (ultisols) which naturally carry sclerophyll (*Eucalyptus*-dominated) forest. Their own natural occurrence in this region is in rain forest on more fertile

Table 4.5 *Agathis* plots outside the natural range

*A. australis*: Kenya, Uganda  
*A. dammara*: South Africa, Zaire  
*A. macrophylla*: Uganda  
*A. microstachya* (probably *A. atropurpurea* fide Hyland *in press*): South Africa  
*A. obtusa*: Fiji, Gabon, Samoa, Tonga  
*A. robusta, north Queensland provenance ('palmerstonii')*: India, Dehra Dun, Mauritius, South Africa, Uganda  
*A. robusta, south Queensland provenance*: India, Dehra Dun and Kerala, Kenya, Mauritius, Puerto Rico, Uganda.  
 SOURCES: India, Dehra Dun, Mauritius, South Africa (Zululand at Kwambo), Zaire, Bas Congo, Kinshasa—Lamb (unpublished notes). Gabon—H. F. Maitre (*in litt.*). India, Kerala—Nair (1971). Kenya—Kriek (1970). Puerto Rico—Wadsworth (1960). Uganda—Thogo & Dyson. (1974). Fiji, Samoa, Tonga—M. H. Bennett (*pers. comm.*).  
 Several plots in Ivory Coast are omitted because no details could be obtained and *A. obtusa* growth rates were not ascertained.

Table 4.6 New Hebrides, Aneityum, seedling and sapling release experiment

Plot No.	Number of trees	$\bar{h}$ at start (m)	$\bar{h}$ at end (m)	Interval (yrs)	Mean annual ht growth
<i>Treated</i>					
1	25	2.36	4.43	4.2	0.50
2	4	8.11	3.85	2.7	0.53
3	4	3.4	7.63	2.7	0.39
<i>Logged but untreated</i>					
7	10	1.61	2.33	2.7	0.27
8	9	2.02	2.60	2.7	0.21
9	12	1.37	2.48	2.7	0.41
<i>Virgin forest</i>					
4	21	3.01	3.43	2.7	0.16
5	6	2.55	2.97	2.7	0.16

soils. Full details of the interdigitation of rain and sclerophyll forest have been worked out by Webb and his co-workers (e.g. Webb 1959, 1968, 1969).

It has been discovered (Richards 1961, Richards & Bevege, 1968, Bevege & Richards 1970) that both *Agathis* and *Araucaria* can be successfully established on lateritic podzolic soils if planted under exotic pines (principally *P. elliotii* and *P. taeda*) at least 5-6 years old; the primary factor limiting establishment is nitrogen deficiency, which ceases to occur in the presence of pine. The reasons are complex. In the presence of nitrogen, phosphate increases height growth of small *Agathis* and response to other nutrients has also been detected. Various perennial legumes increased the growth of native conifers in pure, open plantings and over five years, greatly increased the nitrogen content of crop and litter, but depressed growth of exotic conifers (Richards & Bevege 1967).

Destruction wrought by the kauri coccid (sect. 4·1, 7·2) since 1959 has prevented establishment of mixed *Agathis* plantations.

#### 4·7 Wind resistance

Natural *Agathis* has been noted to be resistant to wind-throw in Celebes, a tap root grows deeper than 2·5 m and there are in addition massive laterals extending over 10 m (de Leeuw 1936) *A. obtusa* in the New Hebrides is wind-resistant (sect. 3·2). *A. macrophylla* is probably at least to some extent resistant in the Santa Cruz islands (Whitmore 1966), as are *Agathis* in New Caledonia (several species) and Fiji (*A. vitiensis*). All these four island groups are subject to periodic cyclones. There are several instances known of damage to *A. australis* in New Zealand by cyclonic storms. Wind resistance of this species prob-

ably varies with root system, which is itself dependent on habitat (sect. 3·2).

Plantation grown *A. robusta* in north Queensland around Atherton have been occasionally defoliated by cyclones. On Mauritius old trees of the same species have proved cyclone-resistant but young ones are very vulnerable (A. F. A. Lamb, *obs.*) Young regrowth of *A. macrophylla* on Vanikolo has suffered storm-loss.

#### 4·8 Ability to self-prune

*Agathis robusta* was preferred to Hoop Pine (*Araucaria cunninghamii*) as a plantation tree in Queensland because it naturally sheds its lower branches while still at fairly small girth thus producing knot-free timber good for veneer manufacture (Plate 11b). *South Queensland provenance* is better than *north Queensland* in this respect. The rate of natural pruning is illustrated by a 19 year old stand which had 960 trees/ha, of predominant height 18·6 m, and self-pruned to a mean height of 8·4 m and maximum of 13·3 m.

*Agathis dammara* in the Javan plantations appears to self-prune about as satisfactorily (Plate 9d) as does *A. australis* in New Zealand when grown in dense stands or with a nurse species such as *Podocarpus dactyloides*. The few small plots of *A. obtusa* in the New Hebrides suggest that it too self-prunes. By contrast *A. macrophylla* in open-planting forms persistent rather heavy limbs which showed no sign of self-pruning during the first ten years; it is considered that manual pruning will be necessary to reduce the size of the knotty core (Marten 1970). This species also tends to form several leading shoots in open conditions.

## 5. The Species Compared

Mean annual increment of diameter and height are shown on the scatter diagrams Figs. 5·1, 5·2. These are based on Tables 5·1, 5·2 and 5·3 which themselves are summaries of the plots and plantations listed in sects. 4·1, 4·3 and 4·4 and appendices. Performance is further summarized into broad classes of diameter and height growth in Tables 5·4 and 5·5 respectively. Fig. 5·3 shows growth in height and diameter against age in the Javan plantations. It can be seen that steady growth continues to at least 35 years old, by which time some other extensively grown plantation species would be slowing down.

The observations summarized in these figures and tables are only broadly indicative of the performance of different species in various places. Great caution is necessary in any discussion because of the differences which occur in so many factors including site, elevation, climate, soil, spacing, pruning and thinning. In particular, the Javan plots and plantations

(*A. dammara*) have been selectively thinned, in some cases several times, and the larger trees removed for sale.

Inspection of the scatter diagrams (Figs. 5·1, 5·2) shows that open-planted trees have grown faster than under-planted ones and for *A. dammara*, plantations have, overall, grown best of all. The difference between open and under-planted trees is more marked for diameter growth (see especially *A. macrophylla*), which is known to be a more sensitive indicator than height growth of competition.

The summary, Table 5·4, shows *A. dammara* and *A. macrophylla* have fastest diameter growth, each with several plots showing more than 20 mm annual increment. Closer inspection of *A. dammara* reveals, however, that only some trees in three of the eleven plantations and one Javan plot (18), grows this fast and in this only a few trees persist. Moreover, all the Javan plantings are on andosols, which are more fer-

Table 5.1 Summary of growth in small open-planted trial plots (age—yrs. height and diameter—m diameter increment—mm)

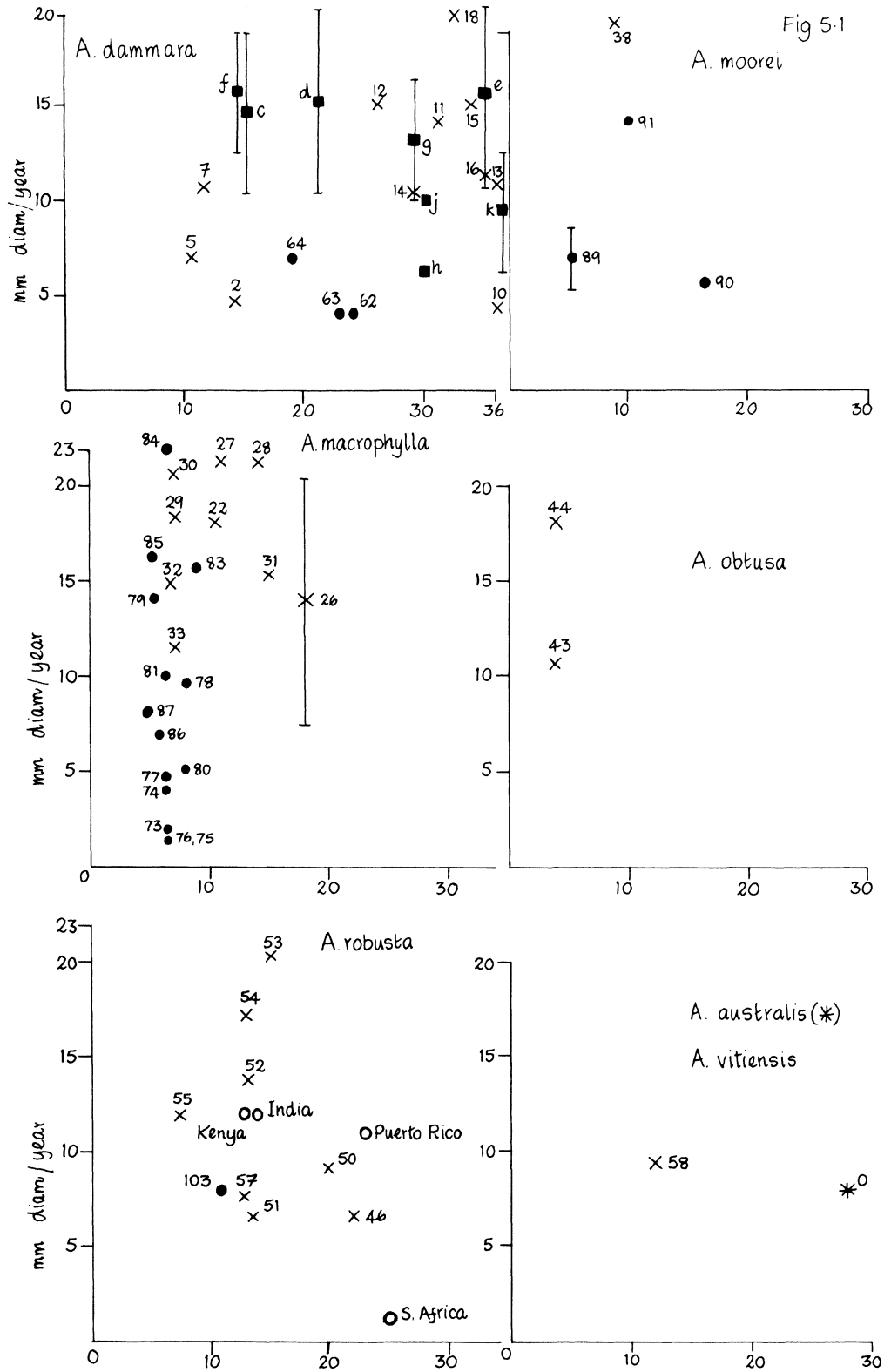
	Trial number	Age	Height		Diameter		Provenance
			Mean	m.a.i.	Mean	m.a.i.	
<i>Agathis australis</i> New Zealand	0	28	8·9	0·3	0·22	8	
<i>Agathis dammara</i> Malaya	2	14·3			0·07	5	Ulu Selangor
	5	10·5			0·07	7	Badas
	7	11·3			0·12	11	Javan
Java	10	36	23·6	0·65	0·51	4	W. Borneo
	11	31	22·8	0·73	0·44	14	W. Borneo
	12	26	22·2	0·85	0·39	15	Minahassa
	13	36	22·5	0·63	0·41	11	Minahassa
	14	29			0·31	11	S. Celebes
	15	34	26·4	0·78	0·50	15	Malili
Celebes	16	35	30	0·86	0·40	11	Malili
Java	18	32·5	36·2	1·11	0·67	21	Lokke
Zaire		20	26	0·77			? Javan
<i>Agathis lanceolata</i> New Caledonia	19	10	2·92	0·24			
<i>Agathis macrophylla</i> Malaya	20	2·7	2·34- 3·02	0·87- 1·12			Vanikolo
	22	10·5			0·19	18	
Sarawak	23	2	1·2	0·45			
Sabah	25	8	7·5-12	0·6- 1·5			
Papua New Guinea	26	18	10-15	0·5- 0·7	0·14- 0·38	8-21	
Solomons	27	11	12	1·1	0·24	22	
	28	14	17	1·2	0·31	22	
	29	7	9·4	1·3	0·13	19	
	30	7	7·4	1·1	0·15	21	
Fiji	31	10	9·8	0·98	0·16	16	
	32	6·5	7·0	1·1	0·1	15	
	33	7	2·2	0·3	0·08	12	
<i>Agathis moorei</i> New Caledonia	35	15	5·25	0·2			
	36	14	3·87	0·15			
	38	9			0·17	19	
<i>Agathis obtusa</i> New Hebrides	42	6	5				
	43	4	3·75	0·93	0·04	11	
	44	4	6·07	1·55	0·07	18	

Table 5.1 (cont)

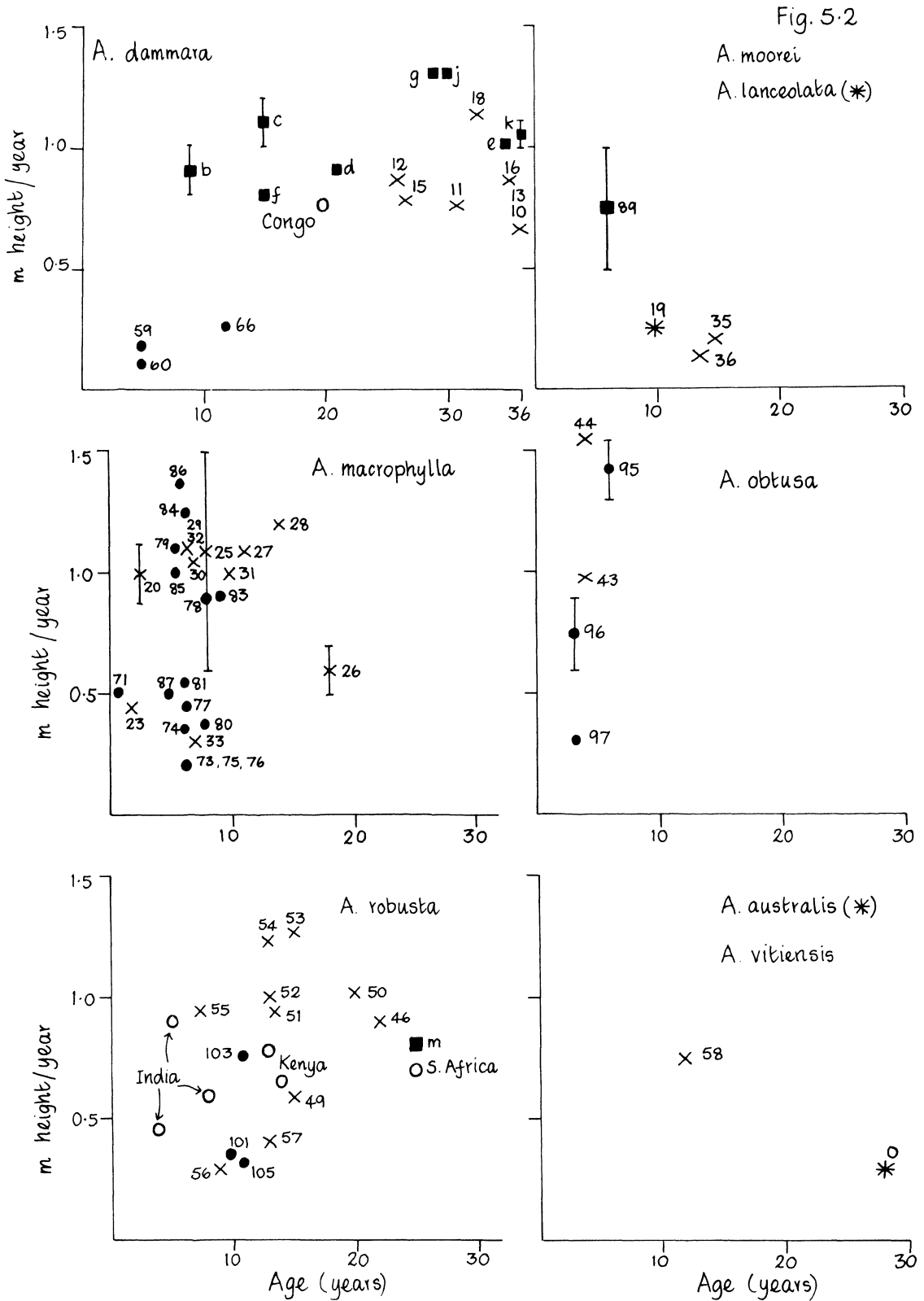
	Trial number	Age	Height		Diameter		Provenance
			Mean	m.a.i.	Mean	m.a.i.	
<i>Agathis robusta</i>							
Papua New Guinea	46	24	21.3	0.89	0.30	7	N. Queensland
Queensland	49	15	9	0.6			N. Queensland
	50	20	20.3	1.0	0.18	9	N. Queensland
	51	13.4	12.8	0.95	0.09	7	N. Queensland
Solomons	52	13	13	1	0.18	14	N. Queensland
	53	15	19	1.27	0.31	21	S. Queensland
	54	13	16	1.23	0.23	17	S. Queensland
	55	7.6	7.3	0.96	0.09	12	S. Queensland
Fiji	56	9	2.77	0.33			S. Queensland
	57	13	5.3	0.41	0.09	7	S. Queensland
South Africa		25	17	0.68	0.37	1	N. Queensland
India, Dehra Dun		4	1.8	0.45			S. Queensland
		8	4.85	0.6			S. Queensland
India, Kerala		5	4.5	0.9			S. Queensland
		14		0.66		12	S. Queensland
Kenya		13		0.79		12	S. Queensland
Puerto Rico		23			0.26	11	S. Queensland
<i>Agathis vitiensis</i>							
Fiji	58	12	9	0.75	0.14	11	S. Queensland

Table 5.2 Summary of growth in small under-planted trial plots (age—yrs, height and diameter—m, diameter increment—mm)

	Trial number	Age	Height		Diameter		Provenance
			Mean	m.a.i.	Mean	m.a.i.	
<i>Agathis dammara</i>							
Brunei	59	5	0.96	0.19			Badas
	60	5	0.63	0.13			
Celebes	62	24			0.1	4	Malili
	63	23			0.1	4	
	64	19			0.13	7	
	66	12	3	0.25			
<i>Agathis macrophylla</i>							Vanikolo
Sarawak	71	1	1.2	0.5			
Fiji	73	6.4	1.42	0.22	0.01	2	
	74	6.4	2.23	0.35	0.03	4	
	75	6.4	1.3	0.2	0.01	1.6	
	76	6.4	1.42	0.2	0.01	1.6	
	77	6.4	2.92	0.46	0.03	5	
	78	8	7.3	0.91	0.08	10	
	79	5.6	6.3	1.1	0.08	14	
	80	8	2.9	0.36	0.04	5	
	81	6.5	3.6	0.55	0.07	10	
	83	9	8.1	0.9	0.14	16	
	84	6.5	8.1	1.25	0.15	23	
	85	5.7	5.5	1.0	0.1	17	
	86	6	8.2	1.37	0.04	7	
	87	5	2.5	0.5	0.04	8	
<i>Agathis moorei</i>							
New Hebrides	89	6	3.6	0.5-1	0.03-0.05	5-8	
New Caledonia	90	16/17			0.11	6	
	91	10			0.14	14	
<i>Agathis obtusa</i>							Erromango
New Hebrides	95	6	8.9	1.3-1.5			
	96	3.3	2.3	0.6-0.9			
	97	3.3	1	0.3			
<i>Agathis robusta</i>							
Queensland	101	10	3.6	0.36			N. Queensland
	103	11	8.2	0.75	0.09	8	
	105	11	3.56	0.32			S. Queensland



5.1 Diameter growth against age. (Small plots—open x; underplanted •; exotic o. Plantations ■.)



5.2 Height growth against age. (Small plots—open x; underplanted •; exotic o. Plantations ■.)

Table 5.3. Summary of growth in plantations. (Most of these plantations have been thinned at least once; (age-yrs: height and diameter—m; diameter increment—mm)

Trial number	Age	Height		Diameter		
		Mean	m.a.i.	Mean	m.a.i.	
<i>Agathis dammara</i> , Javan provenance						
Java, Situgunung	a	56	39	0.7	0.19-0.8	11-14
Java, Pekalongan	b	9	7.5-9	0.8-1		
	c	15	15-18	1.1-2	0.16-0.29	11-19
	d	21	18	0.9	0.22-0.44	11-21
	e	35	36	1	0.38-0.73	11-21
Java, Banjumas Timur	f	15	12	0.8	0.19-0.29	13-19
	g	29	39	1.3	0.29-0.48	10-16
	h	30	—	—	0.19	6
	i	30	40	1.3	0.29	10
	j	30	40	1.3	0.29	10
	k	37	36-40	1.1-1	0.22-0.48	6-13
	l	37	39	1.1	0.67	18
<i>Agathis robusta</i> , south Queensland provenance*						
	m	25	20.4	0.8	—	—

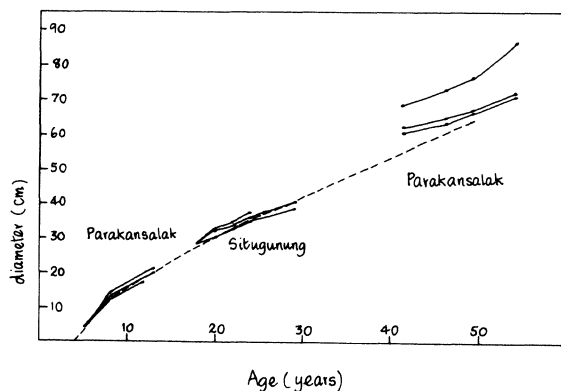
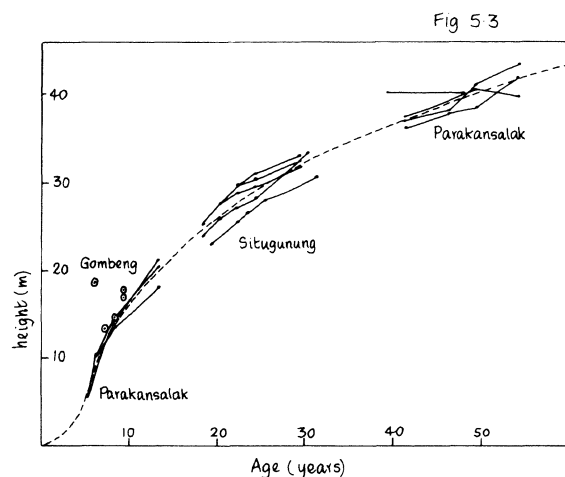
\*The figures in Table 4.3 are similar

tile and better structured than any of the other soils involved, and this can be presumed to enhance growth rate. In fact, outside Java only one Malayan plot (7) shows increment as fast as 10-15 mm/yr (the third growth class); two others in Malaya and three in Celebes are all in the fourth class. With these provisos in mind it can be seen that Table 5.4 and Fig. 5.1 clearly show that *A. macrophylla* has the fastest growth rates with 5 trials out of 23 (including one underplanted) in the fastest class and 6 more in the second class. The only other plot in the top class is no. 53, *A. robusta* in the Solomons (Guadalcanal), with a rainfall regime not very different from its origin, south Queensland. By contrast plot 54 (Solomons Santa Cruz—Vanikolo), the only one in the second growth class, is growing in an extremely wet perhumid climate. These two trials of *A. robusta* are exceptionally good; 6 trials of the total 13 of this species are in the slowest class.

If one turns now to height growth, Table 5.5 and Fig. 5.2, essentially the same picture emerges. *A. macrophylla* is the fastest with 11 trials out of 25 in the top class of 1.0-1.5 m height growth per year and 7 more in class 2 (0.5-1 m). All the *A. dammara* plots in the top two classes are in Java except two. *A. robusta* again has several fast growing plots with 4 out of 19 in the fastest class, three of them in the Solomons. *A. obtusa* shows fast height growth with 2 out of 5 plots in each of the fastest two classes, one of each being an under-planted plot.

In conclusion, it is clear from these trials that *A. macrophylla* stands ahead of the other species. In ecology (sect. 3.2) and taxonomically (chapter 2) it is very similar to *A. obtusa*. The few trials of the latter suggest it might grow equally as fast. Observations of the under-planted trials on Efaté Island, New Hebrides (plots 95, 96, 97) and of an experiment in silviculture after logging described in sect. 4.5 suggest it might be a better species than *A. macrophylla*. Firstly, it does not tend to form persistent limbs when widely spaced and fully illuminated, but has some tendency to self-prune (sect. 4.8).

Secondly, more than any other species including *A. macrophylla*, it appears to remain healthy and vigorous and to continue growth even under quite dense shade. Thirdly, small plots in the New Hebrides, especially trial 42 at Eton, Efaté (Plate 9d), show that it thrives in full light.



5.3 Height and diameter growth in the Javan plantations. (From Ferguson 1949b).

Table 5.4 Diameter growth in broad classes  
(letters refer to plantations, numbers to small plots: open-planted, roman, under-planted, *italic*)

Annual diameter increment	<i>A. dammara</i>	<i>A. macrophylla</i>	<i>A. robusta</i>	<i>A. australis</i>	<i>A. moorei</i>	<i>A. obtusa</i>	<i>A. vitiensis</i>
over 20 mm	18 Java d, e, Java	26 Papua New Guinea 27, 28, 30 Solomons 84 <i>Fiji</i>	53 Solomons				
15-20 mm	d, e, f Java	22 Malaya 26 Papua New Guinea 29 Solomons 31, 32 <i>Fiji</i> 83 <i>Fiji</i>	54 Solomons	0 New Zealand	38 New Caledonia	44 New Hebrides	
10-15 mm	7 Malaya 11, 12, 13, 14, 15 Java 16 Celebes c, d, e, f, g, Java	26 Papua New Guinea 33 <i>Fiji</i> 79, 81, 85 <i>Fiji</i>	52, 55 Solomons Kenya (2) Puerto Rico		91 <i>New Caledonia</i>	43 New Hebrides	58 <i>Fiji</i>
under 10 mm	5 Malaya 10 Java 62, 63, 64 <i>Celebes</i> g, h, j, k Java	73, 74, 75, 76, 77, 78, 80, 86, 87 <i>Fiji</i>	46 Papua New Guinea 50, 51, Queensland 57 <i>Fiji</i> 103 <i>Queensland</i> South Africa		89 <i>New Hebrides</i> 90 <i>New Caledonia</i>		
Total no. trials	23	23	13	1	4	2	1

Table 5.5 Height growth in broad classes  
(letters refer to plantations, numbers to small plots: open-planted roman, under-planted, *italic*)

Annual height increment	<i>A. dammara</i>	<i>A. macrophylla</i>	<i>A. obtusa</i>	<i>A. robusta</i>	<i>A. moorei</i>	<i>A. vitiensis</i>	<i>A. lanceolata</i>
1.0-1.5 m	18 Java c, e, g, h, k, Java	20 Malaya 25 Sabah 27, 28, 30, Solomons 31, 32 <i>Fiji</i> 79, 84, 85, 86 <i>Fiji</i>	44 New Hebrides 95 <i>New Hebrides</i>	50 Queensland 52, 53, 54 Solomons			
0.5-1 m	10, 11, 12, 13, 15 Java 16 Celebes b, f, d Java Zaire	20 Malaya 26 Papua New Guinea 71 <i>Sarawak</i> 78, 81, 83, 87 <i>Fiji</i>	43 New Hebrides 96 <i>New Hebrides</i>	46 Papua New Guinea 49, 51 <i>Queensland</i> 55 Solomons 103 <i>Queensland</i> m <i>Queensland</i> India (2) Kenya (2) South Africa	89 <i>New Hebrides</i>	58 <i>Fiji</i>	
under 0.5 m	59, 60 <i>Brunei</i> 66 <i>Celebes</i>	23 <i>Sarawak</i> 33 <i>Fiji</i> 73, 74, 75, 76, 77, 80 <i>Fiji</i>	97 <i>New Hebrides</i>	56 <i>Fiji</i> 101, 105 <i>Queensland</i> India (1)	35, 36 <i>New Caledonia</i>		19 <i>New Caledonia</i>
Total no. trials	19	25	5	19	3	1	1

## 6. Propagation

### 6.1 Phenology

The development of cones of *Agathis robusta south Queensland provenance* has been described in detail by Nikles (1965). The period for each phase is possibly typical of the whole genus, though the dates differ (for example, *A. microstachya* is pollinated in December).

The sequence of development is:-

- Year 1 February: male cones emerge,  
June-July: female cones emerge,  
August-September: pollination,  
Year 2 September: fertilization,  
Year 3 January: seed fall.

Thus, eighteen months elapse between emergence of the young female cone and its maturation. Except between January and June emerged female cones of two different seasons are present.

Trees are monoecious, but there is such marked dichogamy on any individual that self-pollination is probably impossible, and many crosses will be possible in one direction only. The repeated references in the literature to dioecious *Agathis* probably arise from such dichogamy, though it may also be because young trees often commence production of female cones several years before males are produced.

Araucariaceae are unique amongst conifers in that the pollen is not deposited on the nucellus surface and there is no pollination exudate. Further, the pollen lacks either wings or air sacs. In *Agathis*, pollen grains lodge on the upper surface of the bract scale several millimetres from the micropyle. In *A. robusta* they are receptive from first appearance until 50 mm long though the period for effective pollination may be short. Pollen requires 80 percent relative humidity to germinate and germination is very slow at 25°C. The

ovule is still rudimentary when the cone is 45 mm long. A pollen tube grows over the surface to the nucellus which often protrudes. Pollen tubes are easily visible under the microscope after staining. This gives a simple means of determining the results of experimental pollination treatments within a few weeks of their initiation. The micropyle rarely closes after pollination. *Agathis* is uniovulate. The seed develops slightly embedded in the bract scale and a wing develops on only one side; occasionally a second, rudimentary wing forms.

The age at which female cones first appear has been recorded in plantations as 15 years in Central Java and 20 years in Queensland. In the small trial plots in West Java (nos. 10, 12, 13, 14, 18 in sect. 4.3) ages were 20, 18, 12, 12 and 13 years. In Java it was noted that good germination required that seed came from trees older than 25 years (Team Reboisasi 1971). In most provenances for which we have records ripe female cones are produced regularly once each year at about the same time and over two or three months. Table 6.1 summarises the information available. It is noteworthy that one species in New Caledonia produces seed more regularly and frequently than the two others for which there is information. The size of the ripe cone varies markedly from year to year in *A. australis*, but not, so far as is known, in other species.

The number of cones produced per tree is 200-300 in Java, yielding an average 0.9 kg good seed per tree per year (Team Reboisasi 1971). It has been noticed that both *A. macrophylla* on Ndendö and *A. obtusa* on Aneityum only have large cone crops on big, old trees with massive, spreading crowns. The smaller trees, such as are left behind at logging, bear only light crops.

Table 6.1 The months when female cones mature

	J	F	M	A	M	J	J	A	S	O	N	D
Java — Situngunung, Bogor (1)	—	—	x	*	*	—	—	—	—	—	—	—
— Pekalongan	—	—	—	—	*	*	—	—	—	—	—	—
— Banjumas Timur	—	—	—	—	—	*	*	*	—	—	—	—
Brunei—Badas	—	—	—	—	*	*	*	—	(*)	—	(*)	—
Sabah — Kinabalu	—	*	—	—	—	—	—	—	—	—	—	—
Kalimantan, Balikpapan (2)	—	—	—	—	—	—	—	*	—	—	—	—
Celebes, Poso (3)	*	*	—	—	?	—	—	—	—	?	—	—
Irian Jaya (4)	x	x	x	x	x	x	x	x	x	x	x	x
Queensland — north	—	—	—	—	—	—	—	—	—	—	—	*
— south	—	—	—	—	—	—	—	—	—	—	—	*
Santa Cruz	—	*	*	*	—	—	—	—	—	—	—	—
New Hebrides — Erromango	—	*	—	—	—	—	—	—	—	—	—	—
— Aneityum	*	*	*	—	—	—	—	—	*	*	*	*
New Caledonia (5)	—	*	*	—	—	—	—	—	—	—	—	—
Fiji (6)	*	—	—	—	—	—	—	—	—	—	*	*

? mature cones doubtful

x some mature cones

\* most mature cones

(\*) sometimes

Based on unpublished Forest Department records except as stated below.

(1) some seeds can be found at any time.

(2) G. Dykstra (*pers. comm.*)

(3) van der Vlies (1940) who adds that isolated trees cone all over whereas trees in forest bear few or none.

(4) C. Versteegh (*pers. comm.*)

(5) *A. moorei* produces abundant seed regularly. *A. lanceolata* rarely produces any and *A. ovata* scarcely ever produces seed (M. Corbasson, *pers. comm.*)

(6) occasional years of abundant seed, most years with few.

Table 6.2 Seed moisture content and weight

Species and provenance	Fresh % moisture content*	Seeds/kg at 5% moisture content**
<i>A. australis</i>	14.7	44400
<i>A. robusta</i> , north Queensland	10.2	21400
<i>A. dammara</i> , Badas	64.8	16400
<i>A. dammara</i> , Java	42.7	10300
<i>A. vitiensis</i>	9.6	8600
<i>A. macrophylla</i> , Ndendö	48.9	5900

\*i.e. moisture content on receipt at Kew where the measurements were made.

\*\*determined on a small subsample of 250 seeds or less.

There are records that in several species ripe cones are green and the seed and seed scale brown. In Java immature cones are yellow-green and mature to dark green. The cones shatter on the tree. In Irian Jaya however, ripe cones are reported to be brown and fall entire (C. Versteegh pers. comm.)

Cones are usually harvested by climbers as soon as there are indications that some are mature. In north Queensland the signal is cockatoos destroying the cones, about mid December. In New Zealand, cones are harvested as soon as some seeds are seen on the ground. Harvested intact cones placed in a dry shady place break open in a few days and the seeds fall out. They can also be dried in the sun, as in Java (Team Reboisasi 1971). Seed can be separated from the scales, which are large, through a coarse sieve of mesh about 13 mm. Many seed wings get broken during sieving. 'Empty' seeds need to be removed by hand, they are less plump than good ones.

## 6.2 Seeds and their storage

The ripe cone is ovoid (Plate 10). The fraction of fully formed seeds produced varies, as indicated by the fragmentary information available, from a few in the middle to nearly all. In *A. macrophylla* the ripe cone is about 100 mm diameter and weighs about 1 kg. In this species there are about 70 good seeds per cone. At the other extreme the mature cone of *A. australis* is only about 60 mm diameter and weighs about 0.2 kg, but it also contains a mean number of 70 good seeds, ranging from 42-94 (McKinnon 1937). *A. dammara* Javan provenance has 30-60 good and 10-20 empty seeds per cone (Team Reboisasi 1971). The moisture content of fresh seed is often high and at least in some provenances varies between crops. The fresh moisture content and the weight at 5 percent moisture content of a number of samples is shown in Table 6.2.

Scattered published and unpublished records, available for most species, show that viability drops rapidly in all cases and does not extend beyond a few weeks. It has been extended artificially by drying the seeds before storage. The importance of drying in extending seed life may be illustrated by two examples. In Queensland, seeds are dried on hessian trays under open-walled sheds, and viability is least in years when the weather is wet during the drying period. This is because equilibrium moisture content is higher in such years than others. Secondly, only 75

seeds germinated out of a batch of about 4,000 untreated *A. macrophylla* seed sent to Queensland from the Santa Cruz islands and which had been several weeks in transit.

In its lack of seed storage life *Agathis* resembles other tree species of climax tropical rain forest. The evidence remains very fragmentary but it may prove that, as a class, species of this ecological niche have such seeds and stand in contrast to pioneer tree species of contrasting ecology and whose seeds can be stored (Whitmore 1975a). The very short storage life of seeds makes it very difficult to arrange nurseries or to transport seed and is a major limitation in the use of species with this characteristic in plantation forestry or in the introductory and experimental trials which have to be conducted prior to large-scale planting. This is one reason why plantation forestry has neglected species of climax rain forest.

Experiments, which are still in progress, at the Royal Botanic Gardens, Kew, clearly show that *Agathis* seeds have so-called 'orthodox' behaviour (Roberts 1973), i.e. the viability period can be increased by desiccation, by storage at a low temperature or by storage at reduced oxygen partial pressure. The effects of these three conditions are additive. Roberts (1975) gives a useful review of seed storage problems and reports the discovery, important for long-term storage, that the amount of heritable damage accumulated in stored seed appears to be measured by the amount of viability loss. If the latter can be kept down to 5-10 percent damage is slight.

At Kew it has been discovered that *Agathis* seed reduced to 5 percent moisture content as quickly as possible and without heating and then stored at sub-zero temperatures, or at temperatures as low as possible, have a storage life greatly in excess of the few days of the natural state, possibly years. So far trials have been conducted on *A. australis*, *A. dammara* (3 provenances), *A. macrophylla*, *A. robusta*, and *A. vitiensis*. Full details will be published when the experiments have been completed. A preliminary note is in press (Thompson, Smith & Whitmore 1977).

## 6.3 Vegetative propagation

When *A. robusta* was considered to be the plantation species *sans pareil* in south Queensland it was seed shortage which limited the areas planted each year. This is likely to become a common problem

though improved storage techniques will mitigate it. In Queensland besides increasing the planting stock there was also the desire to propagate superior trees to maximize yield on the small areas of fertile soil available and suitable for *Agathis* plantations. These considerations led to extensive trials on vegetative propagation of *A. robusta* south Queensland provenance which are summarized by Haley (1957).

The most successful means was propagation from root suckers, developed in 1954 after the observation that leafy shoots formed on severed seedling roots left behind in nursery beds, and that ramets of this origin planted in 1939 had grown into good trees.

As finally perfected the technique was as follows. Seedlings are raised in bottomless tubes of c. 50 mm diameter. These are set in open beds with the bottom 75 mm below soil level. The tube wall is raised to bed level to expose the core of soil it contains and this is cut through with a sharp knife to sever the seedling roots within it and leaving their ends exposed at the surface. A trench is made along each side of a row of such severed cores to prevent soil wash from covering the exposed root ends which are thereby left along a ridge of soil. Each root end produces a leafy shoot which is allowed to grow to 150 mm tall and then potted up. If moved sooner the shoots make very slow growth. The original tubed seedling from which the bottom 75 mm has been severed can have the procedure repeated. Up to three such treatments were successfully practiced per seedling with no apparent loss in vigour of the shoots produced. Average figures of shoots produced were first treatment 7, second treatment 12, third treatment 24. The account can be read to imply that the tubed seedlings were rested between liftings.

All present records indicate that lateral branches of *Agathis* are strongly plagiotropic, except that in *A. australis* the branches of the central third of the crown as well as the leading shoot are orthotropic. This renders the sporadic trials made on air-layering and propagation from cuttings of only academic interest as a means of tree multiplication, except for producing trees for seed, unless normal vertical growth can be ensured.

In Queensland (Haley 1957), New Zealand (Dakin & Mearns 1975) and the Philippines (N. Zabala *pers. comm.*) air-layering has met with little success. Stem cuttings struck from young trees have been reasonably successful in Queensland (4 year-old stock, Haley 1957), New Zealand (2½ year-old stock, Dakin & Mearns 1975) and New Britain (lower branches of a 9 year old tree, Papua New Guinea Forest Department, unpublished records).

Recent trials at the Institute of Terrestrial Ecology, Edinburgh (Leakey & Longman 1977) have shown that of five *Agathis* species tested all can be rooted, using the standard mist propagation techniques which allow easy rooting of *Cedrela*, *Chlorophora*, *Cordia*, *Gmelina*, *Terminalia*, *Triplochiton*, and other tropical timber trees (Longman 1976, Bowen *et al.* 1977). The research on *Agathis* is still at a preliminary stage, but already it is clear that small stem cuttings can be used, which therefore increases the rate at

which selected clones may be multiplied. Rooted cuttings were obtained in 4-10 weeks, with up to 80 percent success, and have commenced shoot growth after weaning. *Agathis robusta* (South Queensland provenance) and *A. vitiensis* appeared to be the easiest to root, *A. dammara* (Javan provenance) was moderately easy and *A. macrophylla* (Ndendö provenance) and *A. australis* were more difficult; but this should be regarded merely as a tentative ranking. The ability to root is greatly influenced by the condition of the stockplant, which was far from ideal in this test, and is also affected by the environment of both the stockplant and cutting.

If plagiotropic growth habits can be avoided, the potential for vegetative multiplication in *Agathis* may thus prove to be wider than had been anticipated, both as an alternative to seedling stock and as a direct method of tree improvement. Pending definitive experiments, most success is likely to be obtained by using clones of small, leafy cuttings treated with a commercial rooting powder. Automatic mist and propagating-bed temperature between 25° and 30°C are likely to be the most effective way of rooting cuttings, though in *Triplochiton*, for example, it was found possible to change later to simple, shaded polythene frames, once sufficient experience had been gained. Probably the most important single factor is likely to be the age of the stockplant. Wherever possible the cuttings should be taken from a young seedling, as soon as it has made sufficient shoot growth, as was done in the recent trials. Not only are such cuttings usually much the easiest to root, but they are also most likely to produce orthotropic shoots. Where a larger seedling or established tree is to be propagated, it is important to use the lowest available branches, or, better still, to stimulate coppice shoots from the base of the trunk (Longman *et al.* 1977). In this connection, there are several records of *A. australis* coppicing from cut stumps.

Cleft grafting has been successful in New Zealand where a small seed orchard has been established, New Caledonia (of *A. lanceolata* onto *A. moorei*, Plate 11a) and north Queensland. In south Queensland Nikles (1961) developed a technique, he called bark patch grafting to overcome the plagiotropic problems, which in many forest trees is more pronounced in such grafts made with scions from the crowns of mature trees. It had long been known that *A. robusta* produces secondary leading shoots after loss or removal of the original leader. Nikles found that small patches of bark from near the apex of the leading shoot, side-grafted on to well established seedlings develop orthotropic leafy shoots from invisible, axillary buds and with a high degree of success.

## 6.4 Nursery practice

The experience gained over many years in the large nurseries at Imbil, south Queensland and in Java (Plate 8c) is summarized below, the latter from the published account by Team Reboisasi (1971) which should be consulted for further details. Experience at

Sweetwater, New Zealand, in the Solomon Islands (Marten 1970) and at Sg. Liang, Brunei is also incorporated.

In Java the seed is soaked in cold water for 24 hours to speed germination. It is then sown flat or on its side, wing uppermost, 10 mm deep, at close spacing in drills, or broadcast. Germination is epigeal and occurs mainly between 7 and 14 days from sowing. The testa can be removed to prevent distortion of the hypocotyl. There is no need to inoculate the seed bed with mycorrhizal fungi (see sect. 6.5). The seed beds need to be shaded to prevent scorching of the seedling leaves. This may be by thatch, slats or trees. Too much shade and humidity can lead in Java to infection by the fungus *Gloeosporium* (sect. 7.2). The beds were sprayed in Queensland to prevent attack by fungus and thrips. In New Zealand the seeds are treated with fungicide before planting. In Brunei the rust fungus *Aecidium fragiforme* has to be controlled by weekly spraying. The beds should be watered once or twice a day to keep them continuously moist. The seedlings are potted-on at 70-100 mm tall. They reach 0.25-0.5 m after 1-1.5 years and are then ready to plant out. In the Solomons they are root-pruned every 2-3 weeks from 0.15 m tall onwards and in Queensland were root-wrenched at three and six months age. In Java best success is obtained from planting out potted stock; bare-rooted seedlings 0.3-0.5 m tall had 50 percent mortality. It is preferable to plant out when the terminal bud is dormant and transpiration is reduced by removing some leafy side shoots.

At Baturaden, central Java, nursery-raised seedlings are supplemented by others grown under the mother tree stand. The ground under the mother tree

is cleared and hoed and seeds are allowed to germinate where they fall. A very dense stand develops (Plate 8a) and seedlings are pulled out for planting when they attain about 0.5-0.8 m tall. This cheap method should be tried elsewhere. The seedlings can be potted-up and hardened-off before planting out if this proves necessary.

It has been observed in several places that growth of young *Agathis* is reduced if grass is allowed to grow around them. This is probably because such plants have spreading feeding roots just below the soil surface (Whitmore 1966). An allelopathic interaction might be involved, because with both *Agathis* and *Araucaria* in Queensland poor growth continues even when moisture and nutrients are not limiting (D. I. Bevege *pers. comm.*)

### 6.5 Mycorrhizas

Observations have been made on *A. australis* (Baylis 1969, Morrison & English 1967), *A. obtusa* and *A. robusta* (D. I. Bevege 1968, *pers. comm.*) and *A. dammara* and *A. macrophylla* (Ivory 1975b). These probably apply to all *Agathis*. Vesicular-arbuscular mycorrhizas are formed by the infection of short and long roots by the phycomycete *Endogone*. These fungi are ubiquitous in unsterilized soil which is why, in contrast to *Pinus*, no special steps have ever been found necessary to inoculate *Agathis* seedlings. In *A. australis* the mycorrhizas have been synthesized artificially and demonstrated markedly to stimulate phosphate absorption; small but significant nitrogen fixation was also observed.

## 7. Pests and Diseases

### 7.1 Pests

#### *Seed eating moth, Agathiphaga*

There are two very serious pests, both fortunately of limited geographical range. One of these is a primitive moth *Agathiphaga*, which has been known from Queensland since 1952 (*A. queenslandensis*) (Dumbleton 1952) and also occurs in Fiji and the southern New Hebrides (*A. vitiensis*). In 1976 the second species was discovered by the author also to be present on Ndendö, one of the Santa Cruz islands.

On Aneityum, southern New Hebrides, which is probably typical, the life cycle is as follows (G. S. Robinson, *pers. comm.*). The adult moth emerges and flies about the end of July and lays eggs in the female cones of the local *Agathis obtusa*. The larvae grow within the seed and are fully developed when the cones are mature about December, building a steel-hard larval cell of frass glued with the tree's resin. As they near maturity the larvae make 1-4 holes in the testa. The adults emerge in July. In a sample analysed in March 1976 three quarters of fully sized seeds were infested. The life cycle of the moth is not yet fully known nor is it known how long the female cones of *A. obtusa* take to mature. It may reasonably be conjectured that, like *A. robusta* (sect. 6.1), they take 1.5 years. One may guess that eggs are laid about July within young soft cones (though none were seen in a single cone examined) and do not hatch until the next year, after the seeds have reached mature size. There are no signs that a larva eats more than one seed. Young cones are cylindrical. They gradually become globose as they mature. Infested cones develop into a distorted sphere (Plate 12c) and it may be conjectured that this is because infested seeds and seed scales do not swell in the normal manner. More material needs to be studied to elucidate these points.

Even less is known about the life cycle elsewhere. In Fiji holes are rarely made in the testa so it is virtually impossible to see a difference between good seeds and those containing a chrysalis. Holes have not been found in Queensland seed. In Ndendö infested seeds develop four holes, symmetrically placed at the four corners.

In Fiji the percentage of infested full-sized seed has been found to vary with locality from 8 to 30 percent. In Queensland infestation varies from 2 percent (north) to 50 percent (south) (Dumbleton 1952).

It is unfortunate that this seed-destroying moth parasitizes both *A. macrophylla* and *A. obtusa* which are probably the potentially most important species of *Agathis* for foresters (Chapter 5). It is vitally important that it is not spread to other places where plantations especially might become infested. It was described in sect. 6.2 that storage of *Agathis* seed by desiccation followed by cold storage is likely to be the most practicable technique. *Agathiphaga* is killed by sub-zero temperatures and the developing imago is crippled by low temperatures. Chilling of seed will

therefore probably provide adequate control of this pest. Fumigation is likely to be extremely difficult because the larval case is so hard. Methyl bromide killed a batch of *A. macrophylla* seed (I. A. S. Gibson, *pers. comm.*).

#### *Queensland Kauri Coccid (Plate 12a, b)*

The second serious pest is a coccid which has led to the abandoning of *Agathis* as a plantation tree in Queensland, although it was at one time the most desired species (sect. 4.1). Distrust and lack of confidence following the epidemic were probably more damaging than the coccid itself.

The following notes are based on accounts by Heather & Schaumberg (1966) and Brimblecombe & Heather (1965). The plantations of the local *A. robusta*, were established inland of the main natural range in a drier and more seasonal climate. This emphasizes the biological risk taken, often not apparent from establishment trials, in planting species which naturally occur rather diffusely in pure stands outside their natural area and at their geographic and climatic limit.

In summary, the coccid *Coniferococcus agathidis* attacks young leaves and leads to their abscission. Normally the *Agathis* has an early spring and an autumn flush but defoliation by coccid leads to production of more. The tree is weakened and growth decreases. The first deaths occurred 3-4 years after the initial attack which was in 1959. As vigour declined borers attacked, normally a weevil *Euthyrhinus meditabundus* followed by longicorn beetles.

Susceptibility develops at about four years old. New leaves on older trees or scion wood from older trees is more susceptible than those of younger trees. Hence, grafts from the few resistant trees which were discovered were not themselves resistant.

No biological or chemical control measures have been discovered.

The coccid is indigenous but was unknown until 1959. It is believed to have spread to the plantations from the natural *Agathis* forests. Within two years it had caused serious defoliation of all except very young field stock in the Mary valley plantations. In this case monoculture may have accentuated the problem but cannot have been the cause because the widespread first appearance of the insect indicates that it had gradually spread before the outbreak commenced. Since the early 1960s it has spread to plantations and natural trees within the range of *Agathis* in south Queensland and also to plantations in north Queensland. Big population fluctuations and the appearance of new strains are characteristic of coccids in general (V. H. Eastop, *pers. comm.*)

#### *Queensland Kauri Thrip*

*Oxythrips agathidis* was the major pest of Queensland *Agathis* plantations prior to the coccid epidemic (Heather & Schaumberg 1966). It was first recorded

in 1932 and periodically caused partial or complete defoliation of nursery and field stock, but it did not appear seriously to affect wood production. Like the coccid it too occurs in both north and south Queensland.

### Minor pests

All other pests are of relatively minor importance. **Squirrels** have locally killed plantation *Agathis* by ring-barking the main stem at Kepong and Baloh, Malaya and in Java (Team Reboisasi 1971).

**Parrots and cockatoos** have been variously reported destroying young female cones or eating seed in Celebes (van der Vlies 1940), Queensland and New Zealand. **Rats or mice** have destroyed broadcast seed on Vanikolo, Santa Cruz islands and young seedlings (of *A. moorei*) in New Caledonia. On both islands the rodents are introduced, and may be having a long-term effect on the success of *Agathis* in competition with other non vulnerable trees.

Larvae of two kinds of **beetle** damage female cones and seeds of *Agathis* in central Celebes up to about 1000 m elevation. In 1939 90 percent of the harvest was unsound, in 1940 only 30 percent (van der Vlies 1940). **Crickets** can be a serious nursery pest, destroying young seedlings as in Java (Team Reboisasi 1971) and at Tanahgrogot, Kalimantan Timur.

In Malaya **termites** have been noted on some young trees in small trial plots at Kepong, but at Bahau 5 year old planted *A. macrophylla* appeared much less susceptible to attack than *Araucaria* or *Pinus* of the same age (Tho 1975 and *in litt.*) Wounds made by resin tapping are commonly invaded by termites. The butts of the biggest trees in the Badas-Brunei forest are also termite-infested.

In the dense *Agathis* forest near Sampit, Kalimantan, many trees had their tops broken by **orang utan** during nest building (Ferguson 1949a).

## 7.2 Diseases

### Die-back

Several separate instances are known of die-back often followed by death. In some no pathogen has been found, in others a soil-inhabiting fungus is believed responsible.

In the western Solomons *A. macrophylla* is seriously damaged by bud rot. This has also been seen on the island of origin, Vanikolo. K. D. Marten has made the following observations. Bud rot first appears on young trees about 1 m tall and usually the leading shoot is affected first. It becomes manifest by collapse of the developing shoot. A lateral shoot replaces the leader and itself becomes affected. Eventually a whole series of forks develops. Sometimes the whole tree top dies back and eventually the whole tree. Marten has observed that water collects around the apical bud after heavy rain, trapped by the closely clustered young leaves. He believes that the intensely hot sun which shines through the dust-free and vapour-free atmosphere after a rain storm heats this water and

hence damages the bud. *Araucaria hunsteinii*, which has similarly constructed apices, is also affected. Other *Agathis* spp. do not have such large or such close young leaves, and are not affected. The phenomenon is uncommon outside the western Solomons, but on Guadalcanal heavy rain followed by sun is less frequent, and the Santa Cruz islands, where *A. macrophylla*, originates are cloudier and wetter. It should also be noted that the trial sites in the western Solomons have soils with poor structure and possibly have impeded drainage. Marten believes this might be a contributory factor to bud rot. *A. macrophylla* has shown poor survival and suffered considerable die-back and multiple leader formation at sites in Fiji which have waterlogged soils.

Besides trial 30 (sect. 4.3) at Gizo *A. macrophylla* suffered such severe damage during the first two years in small plots at seven sites through the western Solomons that it was considered to have little potential for open planting though the few survivors grew well. Only one of these plots is described in this report, namely trial 29 in sect. 4.3. Die-back has also been recorded of *A. macrophylla* at Bt. Tapah, Malaya. No pathogen was found (Ivory 1972).

*Agathis dammara* in the Javan plantations sometimes suffers a die-back at 4-5 years old. Trees wilt, leaves turn yellow, die and fall. Eventually the tree dies. The disease is checked by trenching and fumigation of the site, so is attributed to root fungus (Team Reboisasi 1971). Similar symptoms have been recorded on *A. australis* in New Zealand where the fungus *Phytophthora cinnamomi* has been isolated in several cases, but not for example in a site in the Waipoua forest. Podger & Newhook (1971) and Newhook & Podger (1972) give details. Another species, *P. heveae*, was isolated in a thirty year old stand showing similar symptoms (Gadgil 1974). *P. cinnamomi* is a widespread soil-inhabiting fungus whose pathogenicity varies with host and soil conditions. In New Zealand poor soil aeration, such as occurs in an exceptionally wet summer, is thought to precede a serious attack.

Browne (1968) recorded *Fomes annosus* on *A. australis* and *A. vitiensis*. This fungus is a dangerous pathogen in the northern hemisphere but not so where it has occurred in Australia, New Zealand and the Pacific Islands (I. A. S. Gibson, *pers. comm.*)

*A. macrophylla* occurs naturally almost entirely on basalt-derived soils (sect. 3.2), which are by nature well-structured, friable and freely draining. It might be the case that on more closely textured soils the moisture content is higher and the species becomes susceptible to root fungi such as *Phytophthora*. It should be noted that tests on seedling *A. dammara* in Java (sect. 2.2) showed rather low resistance of roots to oxygen deficiency.

### Bark necrosis

At three localities in the western Solomons young trees of *A. macrophylla* have developed necrotic bark, starting at the base of branches. In very severe cases die-back and death has followed. No organisms have been isolated (Marten 1970). Young *A. macrophylla*

in small trial plots in Malaya have developed canker and there have been some deaths (Ivory 1975a), but the species exhibits no significant pathological problems (Ivory 1972).

#### *Corticium salmonicolor*, upas fungus

This is common in the Javan plantations and can cause the death of many trees. The symptoms are that the apex dies and dries out, and the disease spreads down the tree. Wounds resulting from thinning or pruning or caused by squirrels often act as sites of infection (Team Reboisasi 1971). This fungus is a common pathogen of Rubber (*Hevea*) and other plantation trees in the tropics. The sporophore is pink and the disease is commonly called Pink Disease. A description of the disease on Rubber is given by Hilton (1958).

#### *Butt and heart rot*

Marten (1970) reports that old trees of *A. macrophylla* often have a hollow butt. Brown (1968) should be consulted for details of several fungi recorded to cause butt or heart rot.

#### *Queensland leaf cast disease*

In Queensland the fungal pathogen *Hendersonula agathi* causes abscission of mature leaves (Young 1948). It was first recorded in 1936 in north Queensland and later found on plantation and natural *Agathis* in south Queensland (Heather & Schaumberg 1966).

#### *The rust Aecidium*

This is a genus of which two species occur on *Agathis*. Of these *Aecidium balansae* (Plate 12d) is endemic to New Caledonia and the other, *A. fragiforme*, has been recorded from many places elsewhere throughout the range of *Agathis*. Punithalingam & Jones (1971) gave a description of the morphology and Notoatmodjo (1962) a full description of the fungus and disease in Java. The symptoms are orange or brown raised lesions on the leaf surface, bearing pale speckles which themselves bear the pycnia. Large trees often have a few affected leaves but are not damaged. In the nurseries in west and central Java and also at Sg. Liang in Brunei the fungus spreads to petioles and stem tips and can lead to death. In Brunei it is controlled by spraying weekly with 'Agrocide'. In Java removal and burning of infected material is recommended plus location of nurseries at a lower, less humid elevation. Saplings of *A. dammara* *Badas provenance* grown in Brunei on ultisols, rather than the podzols from which the provenance comes, have been severely attacked by *Aecidium* (trial 61, sect. 4·3).

#### *Gloeosporium*

A fungus kills many weak seedlings in the nurseries in Java; dense shade and high humidity render them susceptible. Team Reboisasi (1971) identify this as *Gloeosporium* but *Colletotrichum gloeosporioides* is more probably the causative organism (I. A. S. Gibson, *pers. comm.*).

## 8 Products

### 8.1 Timber

Everywhere it grows *Agathis* timber is highly valued and finds a ready market. It consistently commands a higher price than light tropical hardwoods. The differential varies from 1.2 to 2 or occasionally more.

The timber is straight-grained, with a fine, even, silky texture and lustrous surface. It is pale straw to yellow-brown in colour, uniform, light, strong, knot-free and easily worked. All species are, so far as is known, essentially similar (Anon. 1957). Density at 15 percent moisture content of Malayan samples (*A. dammara*) was 0.47 gm/ml (29.4 lb/cu ft), which is lighter than all other Malayan timbers except pulai (*Alstonia*) and jelutong (*Dyera*) and these are less strong (Lee 1967). The same samples shrank only 1.1 percent radially and 1.7 percent tangentially on drying from green to the air dry state. Their strength is given in Table 8.1. The timber is not durable but it takes preservatives easily. Tests by CSIRO on *A. vitiensis* gave similar results to those reported by Lee (Anon. 1966). It is claimed that in Celebes lowland trees have tough timber, highland ones brittle timber (van der Vlies 1940). *A. australis* timber is denser at 0.61 gm/ml. Compression wood is sometimes present and this can cause veneer to buckle, but this is easily rectified by the application of pressure (J. D. Brazier, *pers. comm.*)

In both New Zealand and in Queensland plantation grown trees have been shown to have timber with similar properties to trees from natural forest, though in Queensland they were about 0.032 gm/ml (2 lb/cu ft) less dense. There is no difference between sapwood and heartwood. In Queensland the central pith is about 10 mm diameter, outside it there is no radial trend of increase in density (Schmidt 1962); this is similar to Hoop Pine, *Araucaria cunninghamii*.

The comment in New Zealand that 'there is no more generally useful softwood' can be applied to all *Agathis*. Uses are legion, including for panelling, cabinet-making, joinery, turnery, mouldings, pattern-

making, battery separators, piano parts and artificial limbs. The wood has no odour and is therefore good for tea-chests and butter boxes. It is highly sought for boat-building and for masts. It makes a good peeled veneer, with an attractive colour and figure for decorative plywood panelling. Investigations in India on 34 years old plantation trees of *A. robusta* have shown it is suitable for wrapping, writing and printing papers and rayon-grade pulps; the fibres were long and thin; mean diameter was 0.0399 mm and lumen diameter 0.0279 mm; mean length was 3.956 mm, 42 percent of fibres were 3-4 mm long and 91 percent 2-6 mm (Guha, Singh *et al.* 1970).

Sawn timber does not cup, spring or bow seriously, though it does sometimes twist. The most serious defect is spiral grain. Sometimes this can be seen while the tree is standing; but at Sampit, Kalimantan, it was only revealed after the bark had been removed, 40 percent of stems were affected (Oedin 1941). Careful study of timber from ten trees of local provenance grown in Wangabel plantation in north Queensland showed the spirality was right-handed and varied significantly between trees and with height, with a minimum between 3 and 6 m and a rapid increase above 6 m. It also varied with radius, being maximal at 8 years age (Schmidt 1962). In Malaya and Java it has been noticed that timber is liable to blue stain and to both shot hole and pin hole borers.

Conspicuous growth rings have been observed in *A. obtusa* on Aneityum (70-80 on a stump 0.6 m diameter), in *A. dammara* in lowland central Celebes (van der Vlies 1940), and at Pekalongan, central Java.

No overall summary of the production of *Agathis* timber is possible. Table 8.2 and Fig. 3.4 give incomplete figures for exports from Peninsular Malaysia and Indonesia. The rarity of *Agathis* is shown by the low percentage of total exports which it comprises. The table suggests that the Malayan *Agathis* forests have probably now been largely logged. In 1972 95 percent of Indonesian production came from Kalimantan, 65 percent from the Kalimantan Tengah

Table 8.1 *Agathis dammara*, physical and mechanical properties (Lee 1957)

Moisture content at test	%	84.0	17.0
Oven-based specific gravity		0.41	0.41
Weight at test	gm/ml	0.75	0.48
<i>Static bending</i>			
fibre stress at maximum load	N/mm <sup>2</sup>	43.34	65.55
modulus of elasticity	N/mm <sup>2</sup>	10538	12062
work to maximum load	mm N/mm <sup>3</sup>	0.034	0.067
total work	mm N/mm <sup>3</sup>	0.068	0.031
<i>Impact bending</i>			
height of drop (22.72 kg hammer)	mm	406	508
<i>Compression parallel to grain</i>			
stress at maximum load	N/mm <sup>2</sup>	21.99	33.65
<i>Hardness</i>			
radial	N	1902	2302
tangential	N	1884	2133
end	N	2493	3369
<i>Shear</i>			
radial	N/mm <sup>2</sup>	8.083	6.931
tangential	N/mm <sup>2</sup>	8.262	6.910
<i>Cleavage</i>			
radial	N/mm width	21.11	19.98
tangential	N/mm width	23.82	23.37

Table 8.2 *Agathis* exports. (In cubic metres. Percentage of total timber exports in parentheses).

	Peninsular Malaysia	Indonesia
1967	8306	
1968	8303	
1969	4401 (0·5%)	
1970	3524	424927 (5·8%)
1971	6449 (2·6%)	309857 (2·3%)
1972	6123 (0·4%)	349203
1973	3245	760915
1974 first 3 quarters	1007	
1975 first 2 quarters	305	

Sources: *Malaysian Forester*: Statistik Pemasaran Hasil Hutan, 1972, Table 25 and Direktorat Pemasaran, Bogor, unpublished figures.

Table 8.3 Summary of *Agathis* timber produced from the Javan plantations (Banjumas Timur) 1967-72, in cubic metres, (export logs length 4·1 m x diam. > 0·23 m; local logs length 1·5 m x diam. > 0·19 m).

Export	47,586
Local	8,478
Total	56,064

heath forest stands (sect. 3·2), then nearing exhaustion. The Telaga Mas concession near Tanahgrogot in Kalimantan Timur alone produced about 50,000 m<sup>3</sup> per year from 1970 to 1973, far more than the whole of Malaya. The Javan plantations have been selectively felled during the last decade or so, and clear felling has now commenced; Table 8·3 gives a summary of the available figures for recent production.

## 8.2 The resin industry

The living inner bark of *Agathis* trees exudes a translucent or clear white resin which slowly hardens on exposure to the air. The amount yielded varies considerably with provenance and species. Resin canals also occur in the leaves but not in the wood. This resin enters world trade as Manila Copal. It is white or yellow to dark brown in colour and hardens with age from kneadable to brittle and fracturable on striking. It is soluble in alcohol and has a melting point between 115 and 135°C. Chemical composition is briefly discussed below in sect. 8·3.

Manila Copal must be distinguished from the other principal resins of the Far Eastern rain forests, though all are often referred to by the Malay vernacular name *damar*. The Dipterocarpaceae are the other main source of resin; in addition Burseraceae produce small amounts.

Before the invention of oil-based synthetics Manila Copal was an important component of many varnishes and, mixed with linseed oil, was extensively utilised in the manufacture of linoleum. There is still a steady demand for specialized uses, sometimes mixed with synthetics, for example in varnishes for certain purposes *e.g.* the labels on food tins and for colour prints, as a component of the compound used to paint lines on roads (Anon. 1968) and for fluxes. Besides production for export there has been a traditional usage of *Agathis* resin nearly everywhere the trees occur.

Before the Second World War Manila Copal was traded through Makassar, Ternate or Singapore, with the former two controlling 80 percent of world production.

In 1926 world production totalled 18,000 tonne of which 88 percent came from the Dutch East Indies, 7 percent from the Philippines and 5 percent from what is now Sabah (van de Koppel 1929). By 1941 production from the Dutch East Indies had increased five fold over the 1931 level (Oedin 1941). In the period 1936-38 world production was 43,396 tonne. By 1957-59 this had dropped 65 percent to 19,830 tonne (Anon. 1968). During 1971-74 Philippines production, mainly exported to Japan and the United States of America, was 709 tonne per year (Bureau of Forest Development unpublished figures). In 1973 Indonesian exports totalled 2,500 tonne. The price in London in Spring 1974 was 60 pence per kg.

Historically, copal from New Zealand was first on the market. This was largely so-called fossil gum, dug out of the ground under the *A. australis* forests of northern North Island (sect. 3·2), some from many metres depth; some also came from coal measures both in this region and in South Island. The industry in New Zealand reached its peak in 1905 when 11,000 tonne were recovered; by 1924 production had declined to 7,000 tonne and by 1950 production had ceased. The 'gum lands' are estimated to have yielded 500,000 tonne in total (Cambie 1971, Thomas 1969). Resin production next commenced in the Philippines, initially by digging it from the ground, whence it spread to Celebes and elsewhere in the Dutch East Indies. Burkill (1935) gives an account. Average annual export through Makassar in the early 1920s was 1,000 tonne, one third from Celebes (van de Koppel 1926).

In Irian Jaya, which is now a principal source in Indonesia, *Agathis* is utilized solely for its resin. Production reached a maximum of 3,200 tonne annually between 1925-29, declined to 1,500 tonne/year by 1941, 200 tonne/yr in 1950 and 800 tonne/year in 1961; nowadays export is through Singapore.

Many kinds of Manila Copal are distinguished in the trade, based on hardness, colour and size of fragment, principally the first. The degree of solubility in ethyl alcohol varies and is inversely proportional to the wax content. The more soluble kinds command a higher price because they are easier to purify. Within the Philippines Luzon and Palawan produce high

Table 8.4 Main types of compound in *Agathis* bole-bark resin (from Thomas 1969, Table 1; figures are approximate percentages of alcohol-soluble resins with their ranking in parentheses.)

	Agathic type	Abietic type	Communic type	Sandaracopimaric type
<i>A. atropurpurea</i>	40(1)	20(2)	20(2)	0
<i>A. australis</i>	35(1)	15(3)	20(2)	10(4)
<i>A. dammara</i>	75(1)	0	+	5(2)
<i>A. lanceolata</i>	35(1)	10(3)		35(1)
<i>A. microstachya</i>	2(3)	40(1)	40(1)	0
<i>A. moorei</i>		+		
<i>A. ovata</i>	0	0	0	0
<i>A. robusta</i>	0	30(2)	45(1)	0
<i>A. vittensis</i>	+	+	+	+

Table 8.5 Diterpene compounds in Queensland *Agathis* resin. (From Carman & Marty (1970). Mean percentage composition, with ranking in parentheses).

	Compound							
	1	2	3	4	5	6	7	8
<i>A. atropurpurea</i>	c.5	? ?		12(3)	15(2)	c.1	8	56(1)
<i>A. microstachya</i>	c.5	? ?		35(2)	49(1)	6	—	3
<i>A. robusta north</i>	c.5	25(3)		39(1)	26(2)	6	—	<1
<i>A. robusta north</i> , grown in south	c.5	15(3)		41(1)	32(2)	7	—	<1
<i>A. robusta south</i>	c.5	1(3)		47(1)	28(2)	10	—	1

Methyl *cis*- and *trans*-communate comprise 50 percent of fresh resin and are not included

1 methyl sandaracopimarate; 2 and 3 not identified; 4 methyl abietate; 5 methyl neoabietate; 6 methyl 15 hydroxydehydroabietate and methyl 15 hydroxyabietate; 7 methyl agathalate; 8 dimethyl agathalate.

grade soluble resin, that from Mindanao is less soluble.

Apart from digging Manila Copal from the ground it is obtained by tapping the tree (Plate 5c), usually the bole, though in Sabah and New Zealand cuts were also formerly made on the limbs so that huge pendulous gobbets of resin developed. Annual yield is usually 10–12 kg per tree and can reach 20 kg. Tapping once a fortnight is adequate. Yield increases for the first six months. It can be stimulated by application of sulphuric acid, liquid or in a paste, as is the case with turpentine production from pines. In the early years of the century there was much destructive tapping and in the Dutch East Indies attempts were made to introduce controls (see *e.g.* van de Koppel 1926, 1929, Salverda 1937). In the 1960s an attempt was made to develop an industry in Papua New Guinea based on the Sepik stands (sect. 3·2). The method of tapping advocated was to make diagonal cuts in the bark 0·2 m long and 0·4 m apart, preferably using a special tool which makes a square-section incision; tapping should be restricted to trees over 0·25 m diameter (J. Zieck 1975 and *pers. comm.*)

### 8.3 Resin chemistry

The resins of *Agathis* are a complex mixture of mono-, di- and sesquiterpenes. Those of *A. australis* have been most thoroughly analysed. Thomas (1969) lists the compounds known at the time he wrote, others have been discovered since (*e.g.* Briggs, Kingsford & White 1974).

Leaf, twig and bole-bark resins differ in composition. Most work has been on the last. The resins are too complex mixtures to be attractive as a source of organic molecules. Their main interest lies in their potential as an aid to taxonomy.

It has been shown in Australia that bole-bark resins

do not differ significantly in composition with season of the year (Carman & Marty 1970). It has also been shown that hardening of this exudate on exposure to air is due to loss of water, of some monoterpenes and of polymerisation.

The first published survey comparing resin composition of different species, by Thomas (1969), showed differences between them, Table 8.4. In addition Thomas reported differences between *A. dammara* from Malaya and a sample of Manila Copal from Indonesia or the Philippines.

A more refined study was made by Marty of the Australian species (Marty 1969, Carman & Marty 1970), based on analysis of the diterpene fraction. Mono- and sesquiterpenes are steam volatile and can undergo complex chemical changes during distillation. Further, it is difficult to achieve identical conditions for each distillation. This inevitably leads to inaccuracies in quantifying the fractions of the distillate and comparing results of different distillations. Hence resin analyses based on steam distillation have limited value for taxonomy. Diterpenes are not steam-volatile and had remained unknown. Marty dissolved them out of the resin and separated and tentatively identified treated samples by gas-liquid chromatography. The identifications were confirmed chemically by separating larger samples by column chromatography and using nuclear magnetic resonance spectroscopy to deduce the structures of the components. Gas chromatography has the extra advantage that only a tiny drop of resin is needed, whereas steam distillation needs about 100 grammes, a point of considerable practical importance. Marty's results are shown in Table 8·5. It can be seen that three chemically different *Agathis* are distinguished. *A. robusta* has the same diterpene composition in north and south Queensland and so does a tree from northern seed grown in the south. This study provided useful additional evidence for the

taxonomic revision of Queensland *Agathis* (Hyland *in press*) including confirmation of foresters' and loggers' suspicions that a third, new, species (*A. atropurpurea*) occurs in north Queensland.

More recently Marty and R. Smith of the University of the South Pacific in collaboration with the present author have extended this study to Melanesian

*Agathis*. The work is still in progress and will be reported later. Suffice it to say that substantial differences between some species have been detected. It is hoped resin analysis will help resolve some of the unsolved taxonomic problems discussed in chapter 2, especially those within the *A. dammara* complex.

## 9. Conclusions

By way of concluding this report on the state of knowledge of *Agathis* its favourable and unfavourable features for forestry use are summarized, in the order in which they have been described in preceding chapters. Plates 1-12 illustrate many of the points mentioned. Finally, various lines for further investigations are suggested.

### 9.1 Favourable features

*Agathis* trees have good form, with a narrow monopodial crown in youth, cylindrical or only slightly tapering bole and no buttresses (sect. 2·3). The branches are radially displayed and are shed naturally in most *Agathis* to leave a clean bole below the crown (sects. 2·3, 4·8).

Taxonomically, *Agathis* is a closely knit genus. All species are allopatric except in New Caledonia and Queensland where they are sympatric but ecologically distinct (chapter 2). They probably all have the same chromosome number (sect. 2·5). These facts suggest that it might be possible to produce interspecific hybrids which would give the possibility of combining desirable features in one tree.

*Agathis* as a genus has a wide geographical range from 19° 30'N to 38°S, so that it grows in both short-day and long-day climates and both in the tropics and the southern subtropics. It has a wide ecological range, from 0-2000 m elevation, from perhumid to seasonally dry climates and on a wide variety of soil types (sect. 3·2). Ecotypes from seasonally dry climates remain untested (e.g. *A. dammara* in Sumatra, Palawan, parts of Kalimantan, Waigeo, and *A. ovata* from open maquis in New Caledonia). The south Queensland provenance of *A. robusta* resists frost.

Some *Agathis* occur naturally as pure or almost pure stands (sect. 3·2) and these presumably have a natural resistance to epidemic pests and diseases.

Experience with *Agathis* in open plantations and under-planted is mostly with small plots (Chapters 4, 5, Appendix 3), of which only a few are outside its natural range. *A. macrophylla*, *A. obtusa* and *A. robusta* seem best but the trial results need to be interpreted with great caution. Seedlings of most species need some shade after planting out from the nursery, and establishment by taungya is successful in Java, but both *A. macrophylla* and *A. obtusa* have succeeded planted in the open. Most species grow slowly or very slowly under dense overhead shade, *A. obtusa*, however, is an exception.

Yields from Javan plantations on andosols (which total 8,500 ha extent) of 700-960m<sup>3</sup>/ha at 30 yrs and 1100-1410 m<sup>3</sup>/ha at 50 years have been predicted (sect. 4·1).

Growth continues at a steady rate up to 35 years age (Fig. 5·3).

In Queensland *A. robusta* can be established on poor soils if mixed with *Pinus* (sect. 4·6).

Most *Agathis* are resistant to wind-throw from cyclones (sect. 4·7).

In most cases seeds are produced regularly once a year (sect. 6·1). Seeds have a natural storage life of only a few weeks but a technique is nearing perfection which extends storage life to several years (sect. 6·2).

Successful techniques for vegetative propagation have been developed (sect. 6·3).

Vesicular-arbuscular mycorrhizas are formed with the phycmycete *Endogone*. This is ubiquitous in soil so no inoculation is needed (sect. 6·5).

In Malaya open-planted small trial plots of *Agathis* proved more resistant to termites than either *Araucaria* or *Pinus* (sect. 7·1), both of which are there growing in a wetter climate than their origin.

The timber of *Agathis* is well-known, in high demand and commands a premium price for a multitude of uses. Density does not vary with radius. Plantation-grown timber has similar properties to that of wild trees but may be slightly less dense. The wood has the typical long fibres of a conifer, (sect. 8·1).

The bark yields a resin, Manila Copal, still in demand at 60<sup>a</sup> pence/kilo, for specialized purposes (sect. 8·2).

There is good sentiment for *Agathis* in all the countries where it occurs, and in most some attempts have been made to cultivate it. Given the newly discovered ability to store seed, the probability that vegetative propagation is feasible and the existence of superior species and provenances, *Agathis* should have a place in managed forest and plantations of the future.

### 9.2 Unfavourable features

There is enormous taxonomic confusion in Malasia (sect. 2·1) but this report gives a clear-cut system of nomenclature based on provenance which should enable foresters to know what they are handling (sect. 2·4).

Some trees have spiral grain (sect. 2·2), some do not naturally shed their lower limbs (sect. 4·8).

Ecologically, *Agathis* are not pioneer species and get eliminated in competition in the secondary forest which develops after modern intensive timber felling. Some invade secondary forest as it becomes moribund (sect. 3·3).

The diversity of *Agathis* is diminishing as loggers seek it out, some provenances are near to extinction or have been seriously depleted (sect. 3·4).

Most *Agathis* grow slowly under overhead shade, especially the well-known Malayan provenances of *A. dammara*, but become chlorotic if planted in full light. Growth is slow during the first few years (Chapters 4, 5).

In some *Agathis* only big trees with spreading crown produce seed copiously (sect. 6·2). Seed is difficult and expensive to collect except in felling areas, especially in large quantity and requires careful handling to preserve viability.

In Fiji, New Hebrides, Santa Cruz and Queensland larvae of a primitive moth (*Agathiphaga*) parasitize a

proportion of the seed (sect. 7·1). Its spread can be controlled by chilling the seed, which is an essential part of the seed storage technique (sect. 6·2). Squirrels can be a pest in plantations (sect. 7·1).

In south Queensland plantations of *A. robusta* established at the climatic and geographical limit of the natural range have been decimated by a coccid. The species is no longer planted in Queensland where it now has a very bad reputation (sects. 4·1, 7·1).

Several species suffer from die-back which might be associated with a root fungus. *A. macrophylla* seems especially susceptible, possibly most so on soils of poor structure (sect. 7·2). This species grows wild mainly on basalt-derived soils of intrinsic good structure. It is noteworthy that the edges of the stands on Ndendö island are on soils of poorer structure (sect. 3·2); trees of this provenance have not yet been tried in plantation. Experiments on *A. dammara* seedlings showed rather low resistance to oxygen deficiency (sect. 2·2).

Uncontrolled tapping for Manila Copal has caused death of many trees in the past (sect. 8·2).

### 9·3 The next steps

The taxonomic confusion remains to be resolved.

Herbarium material, on which conventional taxonomy is in practice based (Whitmore 1976), yields few characters on which to base classification. Investigation of pollen and cuticle by scanning electron microscopy might produce additional characters. Cotyledons differ in size and shape between provenances (N. H. S. Howcroft *pers. comm.*). Work still in progress shows that diterpenes differ between species (sect. 8·3).

Conservation (sect. 3·4) of selected stands of *Agathis* needs to be incorporated into the plans for general forest conservation which are now developing. Thought also needs to be given to establishment of conservation plantations. These would make seed easier to obtain (sect. 6·2) and if several provenances were established in juxtaposition would facilitate breeding. *A. macrophylla* and *A. obtusa* could be established outside the range of the seed infesting moth (sect. 7·1).

There have been no trials of *Agathis* from seasonally dry climates and little trial of ecotypes from 'poor' soils. There have been few trials outside its natural range (sect. 4·4).

The seed storage technique awaits perfection (sect. 6·2), and vegetative propagation needs further trial (sect. 6·3).

## Appendix 1. Population size for conservation

In any discussion of conservation it is vital to know how many individuals of a species need to be conserved to maintain genetic integrity and hence the ability continually to evolve and adapt to secular changes in the environment, and also, one must presume, to changing competition pressures from other species as these too evolve. There is no simple answer to this problem but Dr. D. R. Marshall\* has provided the following argument, which attempts to identify the variables that need to be considered and then to put likely values on them. Depending on the assumptions made the required population size varies from 1,000 to 25,000. The argument runs as follows.

Let us consider a diffusely distributed, outbreeding rain forest tree which we wish to conserve *in situ* to maintain its genetic integrity and hence its ability continually to evolve.

The average heterozygosity detected by electrophoresis of soluble proteins (mainly enzymes) in natural populations of many successful species (mostly animals but some plants) is about 5-15 percent. Since electrophoresis detects only about 1/3 of the possible variants at a locus the real heterozygosity is about 15-45 percent.

To maintain genetic integrity a population size is needed such that this order of average heterozygosity (H) is maintained. In a finite population H is dependent on the mutation rate ( $\mu$ ) and the effective population size ( $N_e$ ) thus:

$$\frac{H = 4 N_e \mu}{4 N_e \mu + 1} \dots (1) \text{ (Crow \& Kimura 1970)}$$

The mutation rate is usually unknown but most estimates for protein variants indicate that it is c.  $10^{-4}$  to  $10^{-5}$  per locus per generation. From (1) and  $\mu = 10^{-4}$  or  $10^{-5}$  we can calculate the population size necessary to maintain any desired level of variation within a species.

On a conservative view one might decide to keep 50 percent average heterozygosity. With  $\mu = 10^{-4}$  we then have:

$$0.50 = \frac{N_e (4 \times 10^{-4})}{N_e (4 \times 10^{-4}) + 1} \quad \text{or } N_e = 2500$$

If  $\mu = 10^{-5}$  and  $H = 0.50$  we have

$$N_e = 25,000$$

On a less conservative view, keeping only 30 percent average heterozygosity,  $N_e = 1070$  and 10,700 when  $\mu = 10^{-4}$  and  $10^{-5}$  respectively.

Hence the range in population size is 1,000-25,000 depending on one's assumptions. Dr. Marshall considers it more likely that  $\mu$  is  $10^{-4}$  than  $10^{-5}$  which implies that a population size of 5,000 would be adequate.

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## Appendix 2. The Javan *Agathis* plantations

### *West Java plantations, general*

The *Agathis* plantations are on the southern slopes of several of the volcanoes in Sukabumi district between 700 and 1,100 m elevation. The locality and ages of the various stands are as follows (details from the same source as Table 4.1):-

Age (yrs)	1	2	3	4	Totals
0-5	435 ha	573 ha	125 ha	10 ha	1143 ha
6-10	175	229	67	—	471
11-15	118	44	62	40	264
16-20	6	10	—	—	16
21-25	68	77	—	—	145
26-30	97	211	—	—	308
31-35	77	30	—	—	107
36-40	—	—	—	—	—
41-45	—	—	—	—	—
46-50	20	—	—	—	20
51-55	2	—	—	—	2
Totals	998	1174	254	50	2476

1. Gede Barat (Bacang, Ciparay (=Situgunung), Cireunden, Pasir Hantap).
2. Cicurug (Cibuntu, Pr. Salak, Kabandungan, Pameungpeuk, Cikadang).
3. Longkong (Hanjuang Barat, H. Tengah, H. Timur, H. Selatan).
4. Bojong Lopang (Pasir Awi, Bojong Jengkol).

### *West Java, Situgunung* (visited by author in 1974)

A small area of plantations at 960 m in Ciparay forest range.

*1970 stand* (4 years). Plate 8b. Steep hillside. Planted by taungya (rice, cabbage, potatoes) as 0.4-0.5 m seedlings in December. Cropping continued for 2 years by when *Agathis* were 1.5 m tall. *Leucaena leucocephala* planted between the rows as a hedge across the contours to reduce erosion. *Agathis* 1.8-2.4 (2.7) m tall (m.a.i. 0.75 m), very healthy and vigorous in appearance. Cleaning is necessary once a year for ten years. By 5 years *Agathis* should be 3.5 m tall. Thereafter growth is faster and by ten years it should be 15 m tall and 0.5-0.8 m girth. In 1974 it more or less equalled in height the dense growth of *Leucaena*, grass and weeds.

The 1974-5 plans for this forest range were: seedlings 0.75 ha; planting 20.00 ha; maintenance 30.00 ha; final felling 39.00 ha; thinning 0 ha. Nearby tea estates were too competitive for labour to make it likely these plans would be realized.

*1918 stand* (56 years) (a on Table 5.3). This oldest stand, 25 ha, is retained as a seed source. Trees are now c. 10 m apart following five thinnings, height c. 39 m, diameter 63-83 cm, about half the boles with conspicuously spiral grains, crowns with no branching. Ferguson (1949b) computed a yield table from this stand. There is said to have been little growth since. The butts and roots of some trees have been attacked and hollowed out by termites.

### Central Java, Pekalongan Timur, Paningaran (visited by author in 1974)

The plantations lie on the north slopes of Gn. Slamet at 690 m elevation. The areas and ages are shown below. No more planting is planned. It is now concentrated in Banjumas Timur.

1939	50 ha	1953	17.2 ha
1940	19.3	1958	9.8
1941	73.7	1959	73.2
1942	23.5	1960	47.7
1943	6.7	1961	119.5
TOTAL AREA		423.00 ha	

**Topography.** Broad ridges and slopes. **Geology.** Recent volcanic. **Climate.** Type B, slightly seasonal, or possibly perhumid, type A. Annual rainfall 2,300 mm, August and September usually dry. **Soil.** Andosol; dark brown to 0.1 m, red-brown below that. Discontinuous leaf litter.

**1965 stand** (9 years, b on Table 5.3). A small area of open hillside near office. No tending. Best trees 9 m, worst 7.5 m tall. All very healthy.

**1959 stand, 30 ha** (15 years, c on Table 5.3). Thinned 1972, 50 percent removed and used for firewood and housing. Trees 15–18 m tall. Diameters 16, 18, 23, 27, 29 cm, variable. Crowns uniformly deep, narrow, conical. Bark quite smooth. These trees are coning. Experimental damar tapping is yielding 3 gm/tree/day.

**1953 stand, 17.2 ha** (21 years, d on Table 5.3). Gentle slope. Planted into relict forest from which big trees had been removed, by taungya, at 2 x 3 m, as 0.5 m tall seedlings and under shade. Seed from the 1939 stands. Taungya ceased at 2 years by which time seedlings were 1.5–2 m tall and no longer needing shade. Thinned at 7 years (should have been 5); the smallest 50 percent removed. Second thinning at 20 years, much too late; the smallest 25 percent removed. Thinnings used for poles.

Nicely formed trees without spiral grain but 30 percent with forked boles. Height 18 m. Diameters 23, 41, 44 cm. A cut stump showed rings 50–100 mm apart. Adjacent plot of *Pinus merkusii* planted 1950 with smaller trees (but tapped for resin since 1960). There are c. 30 seedlings per m<sup>2</sup>. Undergrowth here and all younger plots of low grass and shrubs.

**1939 stand, 20 ha** (35 years, e on Table 5.3). Steep hillside. Three times thinned, most recently 1964. Thinnings used for match splints. Remaining trees widely spaced, sun penetrates to ground layer; as a consequence, several trees now developing heavy limbs in crown.

Height 36 m. Typical diameters 39, 41, 47, 72 cm. Crowns very deep with slender radial limbs. Bark more or less smooth. Undergrowth of shrubs.

### Central Java, Banjumas Timur, Baturaden (visited by author in 1974)

Baturaden lies at 670 m, 14 km from Purwokerto town on the south slopes of Gn. Slamet in Slamet Barat district. There is a forest nursery and rest house. The plantations extend 15 km eastwards to

Serang in Slamet Timur district. This is the main *Agathis* forest on Java and the biggest area of *Agathis* plantations in the world. Driving the 15 km from Baturaden to Serang through the main area, the impression is not of a continuous closed plantation. Gullies have been left unplanted and have much tree fern. Some stands are very open. There has been illicit felling, especially around Serang. The selection felling in 1967–1970 must have also opened up the stands involved. Seen from a higher slope the plantations are most impressive, as close stands of tall narrow, uniform trees covering extensive tracts.

In summary the following areas had been planted up to and including 1972:

age	area	dates
1-5 yrs	117.6 ha	1967-71
6-10	616.6	1962-66
11-15	878.1	1957-61
16-20	932.2	1952-56
21-25	43.3	1947-51
26-30	52.7	1942-46
31-35	293.8	1937-41
Total	3417.6 ha	

By comparison:

<i>Pinus merkusii</i>	8391.3 ha
Teak	3578.4
<i>Altingia</i> and others	2746.2

*Agathis* therefore comes third, and has an area close to that of teak.

**Topography.** Gentle south facing slopes dissected by deep gullies. Reputedly very easily eroded. Plantations lie between 670 and over 1,000 m. **Geology.** Recent volcanic ash over lava. **Climate.** Type A, perhumid, or B, slightly seasonal. Climate stated locally to be 'different from elsewhere' in the absence of a marked dry season and in having almost daily cloud and rain. Average rainfall (mm) and rainy days for 1968, 1969, 1971 and 1972 as follows:

J	F	M	A	M	J	J	A	S	O	N	D	Total
925	566	636	752	464	377	375	404	448	647	970	766	7146
24	21	23	23	19	13	10	11	11	21	24	25	225

**Soil.** Andosol. Brown. Over 6 m deep. **The nursery** employs 12 persons full time. Each year 100,000–150,000 seedlings are raised. The seed source is an adjacent 1.9 ha stand of 750 mother trees (see below) which produces far more seed than are needed. Additional seed could be obtained from the older plantations. **Exploitation.** There was a selection felling for logs for export to Japan about 1968 from the older stands. In 1974 these were being clear-felled in small strips. In addition 0.5/tonne/month copal is produced from some of the oldest trees including the seed tree stand. This is mixed with shellac to make varnish.

**1973 (December) stand** (6 months). An area a few km from Baturaden at 818 m elevation previously vegetated with tree ferns. Seedlings 0.5 m tall, planted out at 3 x 2 m. No shade provided. All have grown one whorl of leaves and look strong and healthy. Old leaves are brown. **Tending.** First year cleaned twice; second and third years once each; by then seedlings will be 1.5 m tall and require no more cleaning. To be thinned to 50 percent at c. 5 years.

1967 stand, 42.3 ha (7 years). 900 m. Planted by taungya at 3 x 2 m under *Leucaena leucocephala*. The crops were *Manihot* once and maize twice. Cleaned thrice. Very healthy 3-5 m tall (m.a.i. 0.4-0.7 m), with very little *Aecidium* emergent from dense *Imperata/Roetboelia/Lantana/Eupatorium pallescens* weed growth and equalling the *Leucaena* in height.

1959 stand (15 years, f on Table 5.3). A very dense plantation which has been thinned once. Trees 12 m tall, 0.6-0.9 m girth.

1945 stand (29 years, g on Table 5.3). Over 39 m tall and 30-50 cm diameter. Height over 39 m (same as 1937 experimental stand below).

1944 stand (30 years), area '20 k' (h on Table 5.3). 900 m. No thinning due to 'troubles'. 1968 selection felling of all stems (20 cm diameter) and up for export to Japan. This removed c. 80 stems/ha. In 1974 strip felling was in progress, the smaller pieces for firewood, the larger for match splints. Felling strip 900 m along by 1,000 m across the contours = 9 ha. This pattern chosen to minimise erosion. Stems being removed at c. 1,100/ha and of 15-50 cm diameter.

In February, 1975 the area was due to be replanted with *Agathis* by taungya on the ridges and by direct labour in the gullies. The felling plan is to remove ç ha/year from 1974 to 1979. One hundred local men are employed on piece work and earn 150-200 rupiahs per day (which is 15-20 pence sterling at the 1974 exchange rate).

The logs are 1.5 m long and are carried out, or the biggest ones are dragged (*kuda kuda*). They are peeled. The fresh timber has a sweet waxy smell. These trees are destined for match splints.

1944 stand (30 years, j on Table 5.3). Trees 40 m tall, 30 cm diameter (m.a.i. 30 mm). Selection felling of best stems in 1968 for export to Japan.

*The mother tree seed stand* (37 years, k on Table 5.3) Planted at 3 x 2 m with seed from the 1918 stand at Situgunung in west Java. First thinned in 1969 (too late). Second thinning 1972; the worst trees were removed, remaining trees of excellent form. Ten percent of boles slightly spiral up to 3 m. Height 36-40 m, diameter 23-50 cm. Crowns very deep and narrow with slender branches (until 1969 trees were very close), but two seen with big limbs in top 5 m.

1937 stand (37 years, l on Table 5.3). An experimental plantation at 670 m. In 1974 trees were over 39 m tall and 70 cm diameter.

### Appendix 3. Small trial plots within the natural range

Fuller details of these plots are held in Oxford and are available on request. Several are discussed in the text. For most there are height and/or growth measurements and these are discussed in Chapter 5. The following publications have been consulted in preparing the plot descriptions: Ash, Wall & Hansell (1974), Berry & Howard (1973), Brookfield & Hart (1966), Chew (1975), Girard & Rignot (1971), Hunting Technical Services (1969), Marten (1972, 1975), Schmidt & Ferguson (1951), Water & Lieth (1960).

### A. Open Planted

#### *A. australis*

0 New Zealand, Cornwall Park

#### *A. dammara*, *Ulu Selangor provenance*

1, 2 Malaya, Kepong

#### *A. dammara*, *Malayan provenance*

3 Malaya, Tapah Hills F. R.

#### *A. dammara*, *Badas provenance*

4 Malaya, Baloh F.R.

5 Malaya, Kepong

#### *A. dammara*, *Borneo white sands provenance*

6 Java, Pasir Awi

#### *A. dammara*, *Javan provenance ('loranthifolia')*

7 Malaya, Kepong

8 S.W. Celebes, west of Makale

9 N. Queensland, Atherton Tableland

#### *A. dammara* *W. Borneo provenance ('beccarii')*

10 Java, Pasir Awi

11 Java, Pasir Hantap

#### *A. dammara*, *Minahassa provenance ('celebica')*

12 Java, Pasir Awi

13 Java, Pasir Hantap

#### *A. dammara*, *S. Celebes provenance ('beckingii')*

14 Java, Pasir Hantap

#### *A. dammara*, *Malili provenance ('hami')*

15 Java, Pasir Awi

16, 17 Celebes, Malili

#### *A. dammara*, *Lokke, Ceram, provenance ('regia')*

18 Java, Pasir Hantap

#### *A. lanceolata*

19 New Caledonia, Ouénarou, Rivière Blanche

#### *A. macrophylla*, *Vanikolo provenance*

20 Malaya, Bahau F.R.

21 Malaya, Baloh F.R.

22 Malaya, Kepong

23 Sarawak, Bintulu, Nyabau F.R.

24 Sarawak, Kuching, mile 12 Penrissen Rd.

25 Sabah, Gum Gum F.R.

26 Papua New Guinea, Bulolo, Anderson's logging area

27 Solomons, Vanikolo

28 Solomons, Guadalcanal, Mt. Austen (Plate 9c)

29 Solomons, Santa Ysabel, Allardyce Harbour

30 Solomons, Gizo

31, 32 Fiji, Viti Levu, Colo i Suva

33 Fiji, Viti Levu, Drasa

#### *A. moorei*

34 N. Queensland, Atherton Tableland, Danbulla F.R.

35, 36 New Caledonia, Ouénarou, Rivière Blanche

37 New Caledonia, Col d'Amieu

38 New Caledonia, Île de Pins, Wameo

39 New Caledonia, Île de Pins, plateau

40 New Caledonia, Paita

#### *A. obtusa*, *Erromango provenance*

41 New Hebrides, Efaté, Lelepa

42 New Hebrides, Efaté, Eton (Plate 9a)

43 New Hebrides, Espiritu Santo, Navota Farm

44 New Hebrides, Espiritu Santo, Mon Bifstek

45 New Hebrides, Tanna

#### *A. robusta*, *north Queensland provenance ('palmerstonii')*

- 46 Papua New Guinea, Wau, Anderson's plantation  
 47, 48 N. Queensland, Atherton Tableland, Wongabel  
 49 N. Queensland, Atherton Tableland, Danbulla F.R.  
 50, 51 N. Queensland, Kuranda  
 52 Solomons, Vanikolo  
*A. robusta, south Queensland provenance*  
 53 Solomons, Guadalcanal, Mt. Austen  
 54 Solomons, Vanikolo  
 55 Solomons, Santa Ysabel, Allardyce Harbour  
 56 Fiji, Viti Levu, Colo i Suva  
 57 Fiji, Viti Levu, Nadarivatu  
*A. vitiensis*  
 58 Fiji, Viti Levu, Colo i Suva

## B. Underplanted

- A. dammara, Badas provenance*  
 59 Brunei, Ulu Badas  
 60 Brunei, Labi Hills F.R.  
 61 Brunei, Andulau F.R.  
*A. dammara, Malili provenance ('A. hami')*  
 62-67 Celebes, Malili  
*A. dammara, Bulolo Rd. 29 (930 m) provenance ('labillardieri')*  
 68 Papua New Guinea, Bulolo  
*A. dammara, Upper Watut provenance ('labillardieri')*  
 69 Papua New Guinea, Bulolo  
*A. dammara, Chimbu Gorge (2100 m) provenance ('labillardieri')*  
 70 Papua New Guinea, Bulolo  
*A. macrophylla, Vanikolo provenance*  
 71 Sarawak, Sibul, Oya Rd.  
 72 Sarawak, Niah  
 73-77 Fiji, Viti Levu, Colo i Suva  
 78, 79 Fiji, Viti Levu, Nacegacega (near Naboutini)  
 83-85 Fiji, Viti Levu, Nukurua  
 86 Fiji, Viti Levu, Nadarivatu  
 87 Fiji, Viti Levu, Kvai  
*A. moorei*  
 88 N. Queensland, Atherton Tableland, Danbulla  
 89 New Hebrides, Efaté, Lelepa  
 90 New Caledonia, La Ouau (Col d'Amieu)  
 91 New Caledonia, Tiakan (Ponerihen)  
*A. obtusa, Erromango provenance*  
 92, 93 New Hebrides, Malekula, Lakatoro  
 94 New Hebrides, Espiritu Santo, Navota Farm  
 95-7 New Hebrides, Efaté, Lelepa  
 98 New Hebrides, Aoba  
 99 New Caledonia, Col d'Amieu  
*A. obtusa, Aneityum provenance*  
 100 New Hebrides, Aneityum  
*A. robusta, north Queensland provenance ('palmerstonii')*  
 101, 102 N. Queensland, Atherton Tableland, Danbulla  
 103, 104 N. Queensland, Kuranda  
*A. robusta, south Queensland provenance*  
 105 N. Queensland, Kuranda

## Appendix 4. Specimen Trees

The following solitary or small groups of *Agathis* planted as ornamentals have come to the author's attention. The main collections are at the Bogor and Lae Botanic Gardens.  
*Argentina. A. robusta* (?) is growing well in Buenos Aires and in the north east.  
*Brazil. A. robusta*(?) is growing well in parks and gardens in Rio de Janeiro and Sao Paulo.  
*Indonesia.* Bogor Botanic Garden. *A. australis*, *A. dammara* various provenances, *A. obtusa*, *A. robusta* several provenances.  
*Papua New Guinea.* Lae Botanic Garden. *A. dammara*, Kuching, Pomio, Sepik, Watut and Wemat provenances. *A. macrophylla*, Vanikolo provenance.  
*Solomon Islands.* Guadalcanal, Mt. Austen. Single trees of *A. obtusa* and *A. vitiensis* are growing well.  
*Sri Lanka.* There are huge trees of *A. dammara* at Peradeniya Botanic Garden also *A. obtusa* but much slower growing. *A. robusta* of good form grows by the road at Combwood Estate on the Colombo to Nuwara Eliya road.  
*Comores. A. obtusa.*

## Appendix 5. Vernacular Names

almaciga	Philippines, general
asong	New Britain, Fulleborn Harbour
baltic	Philippines (Tagbanua)
bamboeng	Kalimantan, Sampit (Dayak)
bengalen	Kalimantan, Sampit
bindang	Brunei; Sarawak
dakua makadre	Fiji
damar malolo	Celebes, Poso, lowland trees
damar minyak	Malaya
damar noenoe (nunu)	Celebes, Poso, highland trees
dure	Vanikolo, Santa Cruz
kaláne	N. W. Ceram
kaori blanc	New Caledonia, <i>A. moorei</i>
kaori de montagne	New Caledonia, <i>A. ovata</i>
kaori rouge	New Caledonia, <i>A. corbassonii</i>
kaori main	New Caledonia, <i>A. ovata</i>
kauri	New Zealand
kèssi	central Ceram
makadre	Fiji, name for Copal
marabete	Santa Cruz
mengilan	Sabah
muwaka	Papua New Guinea, Eastern Highlands, Suwaira
nandu	New Hebrides
neichet	New Hebrides
oeneëla	S. W. Ceram
ogapa	Papua New Guinea, Eastern Highlands, Coruka
oi	New Hebrides
pilau	Kalimantan, Sampit
saleng	Philippines, Negros
tulong	Brunei

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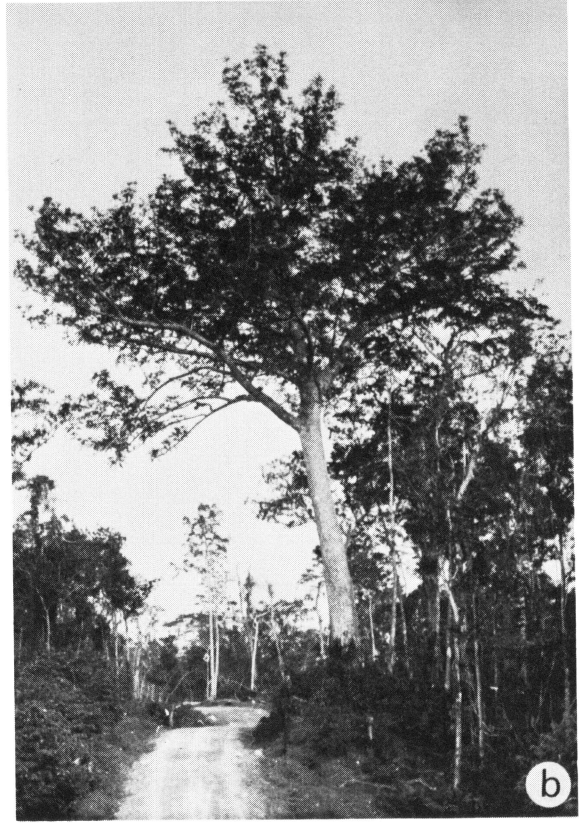
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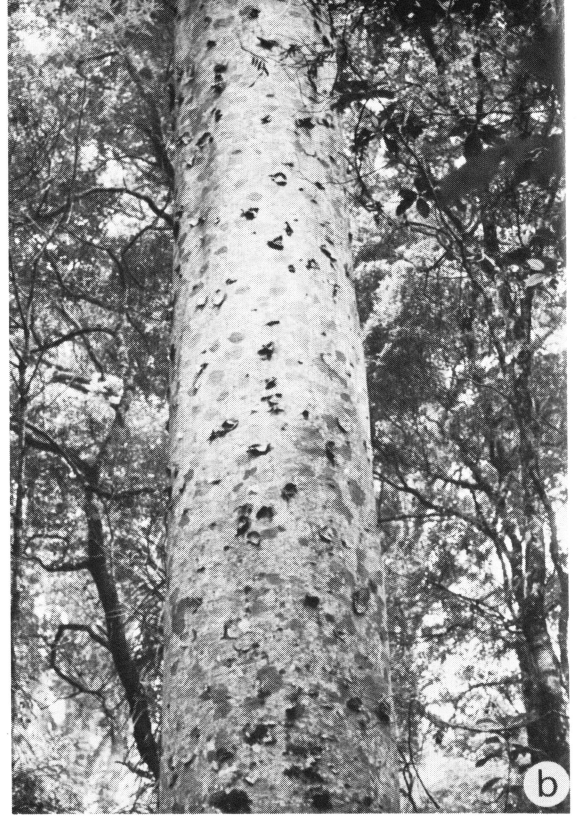
1. Boles, *A. dammara*: **a** Kalimantan, Telaga Mas; **b** Celebes, Malili, **c** Philippines, Palawan; **d** Papua New Guinea, Hai Toba



2. Crowns: **a** *A. atropurpurea*. *A. dammara*: **b** Java, Baturaden seed stand, 37 years old planted tree; **c** Kalimantan, Telaga Mas; **d** Papua New Guinea, Hai Toba.



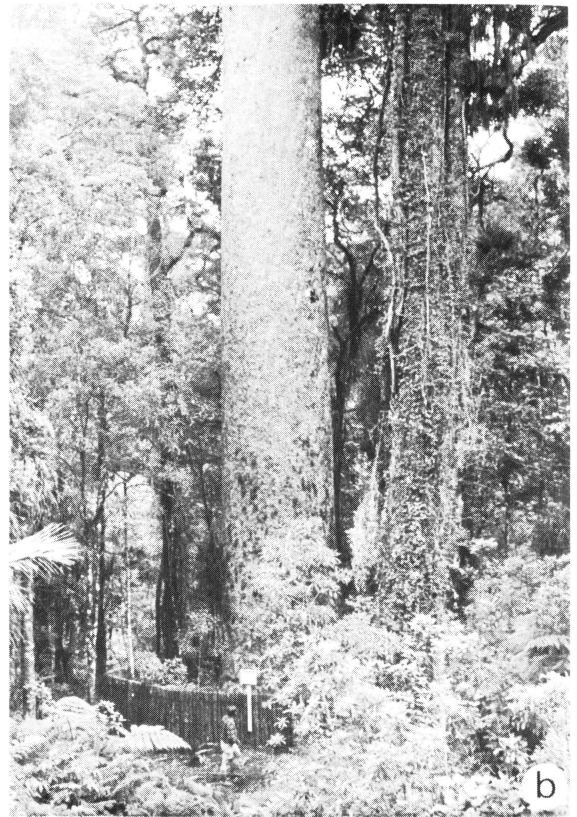
3. Crowns: **a** *A. lanceolata*; **b** *A. macrophylla*; **c** *A. moorei*; **d** *A. obtusa*.



4. Bark: a *A. atropurpurea*; b, c *A. australis* (Trounson); d *A. dammara* (Badas).



5. Bark: **a** *A. moorei*; **b** *A. robusta* (N. Queensland); **c** *A. dammara* showing damage caused by tapping (Celebes, Malili).



6. *A. australis*: **a** the old giant tree Tanemahouta, 4.38 m diameter, at Waipoua; **b** a giant tree at Omahouta; **c** humid podzol in soil derived from interbanded sandstone and mudstone under an *Agathis* tree (Omahouta); **d** stand of giant *Agathis* at Trounson.



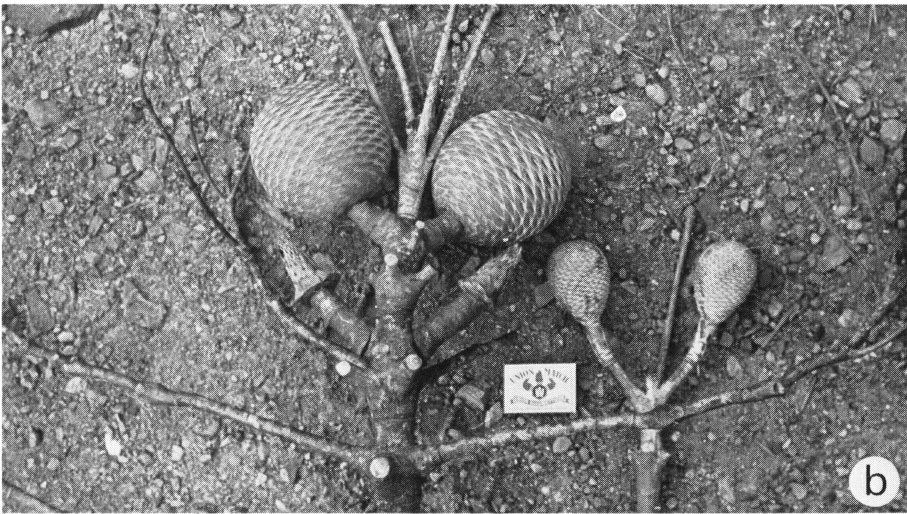
7. **a** *A. australis*, old giant trees at Trounson: **b, c** *A. ovata*.



8. *A. dammara*: **a** seedlings grown below mother tree (Baturaden); **b** plantation at 4 years age, established by taungya (Situgunung); **c** nursery bed; pine needles used to protect soil surface (Baturaden).



9. *A. obtusa*: **a** open-planted at New Hebrides, Efaté, Eton, 6 years age; **b** young specimen tree; **c** *A. macrophylla*, Solomon Islands, Mt. Austen, 16 years age; **d** 30 years old plantation (thinned at 24 years), Java, Baturaden, note scale.



10. Female cones: **a** *A. australis* half mature; **b** *A. moorei*, this season's nearing maturity, next season's and last season's; **c** *A. macrophylla* mature cones awaiting seed extraction, cone scales in background.



11. **a** *A. lanceolata* grafted onto *A. moorei*; **b** self-shed lateral branch of *A. robusta* (Mary Valley, S. Queensland).



12. Pests and diseases: **a, b** coccid attack on *A. robusta*; **c** *A. obtusa* female cones deformed by the larvae of the seed eating moth *Agathiphaga vitiensis* on Aneityum island; **d** the rust *Aecidium balansae* on *A. obtusa* in New Caledonia.



