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8 Distribution and Ecology of the Conifers of New Caledonia

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DESPITE ITS small area (19 000 km^2) New Caledonia possesses a rich and distinctive flora, totalling 3000 species of phanerogams of which 75 to 80 per cent are endemic. Among these are 43 conifers (all endemic) belonging to four families: Taxaceae (one sp.), Podocarpaceae (18 spp.), Araucariaceae (18 spp.), Cupressaceae (six spp.).

The sole species of the family Taxaceae belongs to the endemic genus *Austrotaxus*. The Podocarpaceae is divided among eight genera: *Podocarpus* (seven spp.), *Dacrydium* (four spp.), *Retrophyllum* (two spp.), *Falcatifolium*, *Dacrycarpus*, *Acmopyle*, *Prumnopitys* and *Parasitaxus* (one sp. each), the last being endemic to New Caledonia (Page 1988). The Araucariaceae comprises two genera, *Araucaria* (13 spp.) and *Agathis* (five spp.), and the Cupressaceae the genera *Libocedrus* (three spp.), *Callitris* (two spp.), and the monotypic and endemic *Neocallitropsis* (de Laubenfels 1972). No other region of the world with such a small area possesses such a rich and distinctive conifer flora.

Growth forms

The majority of New Caledonian conifers are tall trees but there are also small trees and shrubs. The Araucariaceae, all arborescent, includes nine species exploited for their timber (*Agathis corbassonii*, *A. lanceolata*, *A. moorei*, *A. ovata*, *Araucaria columnaris*, *A. bernieri*, *A. laubenfelsii*, *A. luxurians*, *A. subulata*).

The *Agathis* species are among the most massive forest trees; some individuals of the tallest species, *Agathis lanceolata*, have trunks more than 2.5 m in diameter and attain a height of 30–40 m. *A. corbassonii* and *A. moorei* are often 25 m high and exceed 30 m in the most favourable sites, while *A. montana* reaches 15 to 20 m. *A. ovata* is generally shorter (10–20 m) but can exceed 25 m in sheltered forests.

The araucarias have smaller diameters but several species (*Araucaria bernieri*, *A. laubenfelsii*, *A. subulata*, *A. columnaris*) reach a height of 50 m. Individuals of *A. columnaris* more than 60 m high have been recorded in the Loyalty Islands and

on the Isle of Pines. Unlike the other Araucariaceae, *A. humboldtensis* and *A. scopulorum* are small trees, not exceeding 15 m.

The Podocarpaceae includes shrubs, small trees and trees, with certain species often exhibiting a variety of adult states. Only *Retrophyllum comptonii*, occasionally exploited for timber, reaches a height of 30 m. Individuals 20–25 m high have been observed for *Dacrydium lycopodioides* and less often for *Dacrycarpus vieillardii*, *Acmopyle pancheri*, *Prumnopitys ferruginoides* and *Podocarpus longefoliolatus*. *Dacrydium balansae*, *Falcatifolium taxoides*, *Podocarpus polyspermus* and *P. lucienii* reach 10–15 m; *Dacrydium guillauminii* and *Retrophyllum minor* 1–6 m. This last species has a very distinctive bottle-shaped trunk and very light wood, which led to the local name 'cork wood'. *Podocarpus novaecaledoniae*, *P. gnidioides*, *P. decumbens* and *Parasitaxus ustus* do not exceed 2 m in height (Fig. 8.1). The last is remarkable in being the only known parasitic conifer in the world. It is easily recognised by its dark wine colour and it is always associated with *F. taxoides*, from which it obtains nourishment by means of haustoria penetrating the base of the trunk or the roots (Köpke *et al.* 1981). *Podocarpus decumbens* is also noteworthy, tending to be lianescent, while *P. gnidioides*, has a prostrate, more-or-less creeping habit when growing in exposed sites.

The Cupressaceae are usually trees or small trees, *Libocedrus austrocaledonica* and *L. chevalieri* not exceeding 2 and 5 m respectively, while *Callitris sulcata* and *Libocedrus yateensis* are often up to 12 m high. Existing populations of *Neocallitropsis pancheri* and *Callitris neocaledonica* (Figs 8.2 and 8.3) comprise individuals not exceeding 6 to 8 m, but some isolated specimens of large stature (20 m high and 0.6 m diameter for *N. pancheri*, 15 m high and 1 m diameter for *C. neocaledonica*) can be found (H. Mackee pers. comm.) These are remnants of ancient populations decimated by fire, timber exploitation and, in the case of *N. pancheri*, by the filling of the Yaté dam. The latter species, the wood of which contains an essential oil used as perfume fixative (Jaffré *et al.* 1987a), was the object of exploitation, destructive for the largest specimens, during the first half of the century.

Austrotaxus spicata (Taxaceae), like many forest Podocarpaceae, is very polymorphic, the height of adult individuals varying from 5 to 20 m.

The conifers within the various vegetation types

Thirty-six species of conifers belong primarily to the dense evergreen rainforest with 24 species strictly confined thereto (Table 8.1). Seventeen species occur in the maquis (shrubland) on ultramafic rocks known as 'maquis minier' (the maquis where nickel is mined), but only five are restricted to this vegetation, the other 12 being also found in dense rainforest. Two species are restricted to light-demanding vegetation along river margins. No conifer has been recorded in sclerophyll or dry forests which essentially develop in regions where the annual mean rainfall is below 1300 mm.

Fig. 8.1 The parasitic conifer, *Parasitaxus ustus* (Podocarpaceae), growing at the base of its specific host, *Falcatifolium taxoides* (Podocarpaceae), in forest on Mt Dzumac (850 m a.s.l.)

Fig. 8.2 Remnant *Neocallitropsis pancheri* (Cupressaceae) on Montagne des Sources (850 m a.s.l.)

Dense evergreen rainforest

On the 'Grande Terre' (Main Island), dense evergreen rainforest (defined and described by Morat *et al.* 1981) occupies the flanks of hills and mountains, their summits, and steep slopes, particularly at the heads of valleys. The forest generally starts at 300 m above sea-level (a.s.l.), but occurs at lower altitude in some favourable areas exposed to trade winds which maintain an annual mean rainfall above 1500 mm. From about 300 to 1000 m a.s.l. (i.e. in the zone receiving between 1500 and 3500 mm rain annually) the 'dense evergreen rainforest of low to middle altitude' comprises trees of rather modest size (20–25 m high and less than a metre in average diameter). The forest is significantly shorter on ultramafic rocks than on sedimentary or metamorphic rocks. It is rich in species: 131 species of phanerogams in 1.25 hectares on slopes (Jaffré and Veillon 1990) including the majority of Araucariaceae exploited for timber, and various dicotyledonous trees such as Araliaceae (*Schefflera*), Cunoniaceae (*Cunonia*, *Geissois*, *Pancheria*), Guttiferae (*Calophyllum*, *Garcinia*, *Montrouziera*), Myrtaceae (*Carpolepis*, *Metrosideros*, *Syzygium*), Proteaceae (*Kermadecia*, *Macadamia*, *Sleumerodendron*), Sapoteaceae (*Bureavella*, *Pycnandra*). This forest is generally rich in palms and tree-ferns (*Cyathea*, *Dicksonia*). It has a dense and floristically varied undergrowth in which shrubby conifers have a patchy distribution. There are also arborescent conifers that only rarely occur singly in the forest. They form populations of a few to several

Fig. 8.3 *Callitris neocaledonica* (Cupressaceae), Montagne des Sources (950 m a.s.l.)

hundred individuals in the case of *Araucaria* and always form part of the canopy (*Agathis*, *Dacrydium*, *Retrophyllum*) or are emergent above it (*Agathis*, *Araucaria*). The emergent and gregarious behaviour of the Araucariaceae transforms the physiognomy of the forest, giving it a very distinctive character.

Table 8.1 Species distribution in different types of vegetation.

Rainforest	Maquis (shrub)	Maquis/rainforest	River bank vegetation
Araucariaceae	Cupressaceae	Araucariaceae	Podocarpaceae
Agathis corbassonii	*Libocedrus chevalieri*	*Agathis ovata*	*Dacrydium guillauminii*
A. montana		*Araucaria humboldtensis*	*Retrophyllum minor*
A. moorei	Podocarpaceae	*A. laubenfelsii*	
A. lanceolata	*Dacrydium araucarioides*	*A. luxurians*	
Araucaria bernieri	*Podocarpus decumbens*	*A. montana*	
A. biramulata	*P. gnidioides*	*A. muelleri*	
A. columnaris	*P. novaecaledoniae*	*A. rulei*	
A. nemorosa		*A. scopulorum*	
A. schmidii			
A. subulata		Cupressaceae	
		Callitris neocaledonica	
Cupressaceae		*C. sulcata*	
Libocedrus austrocaledonica		*Neocallitropsis pancheri*	
L. yateensis			
		Podocarpaceae	
Podocarpaceae		*Dacrydium balansae*	
Acmopyle pancheri			
Dacrycarpus vieillardii			
Dacrydium lycopodioides			
Falcatifolium taxoides			
Parasitaxus ustus			
Podocarpus longefolioliatus			
P. lucienii			
P. polyspermus			
P. sylvestris			
Prumnopitys ferruginoides			
Retrophyllum comptonii			
Taxaceae			
Austrotaxus spicatus			

Above 1000 m where annual rainfall exceeds 3500 mm and where the vegetation is often under a blanket of cloud, the lower altitude forest is replaced by the 'dense evergreen rainforest of higher altitudes' (Morat *et al.* 1981). It is distinctly shorter and the upper stratum is made up of small, tortuous trees with poorly developed trunks, 3–8 m high. The flora is less rich in angiosperms, while mosses, pteridophytes and lichens become more abundant. Families with primitive features (Sphenostemonaceae, Trimeniaceae, Winteraceae) are well represented as are the Cunoniaceae (*Cunonia*, *Weinmannia*), Myrtaceae (*Metrosideros*), Saxifragaceae (*Quintinia*) and the endemic families (Paracryphiaceae, Phellinaceae, Strasburgeriaceae). Conifers are always abundant in an undergrowth that is relatively dense and often illuminated through light-gaps in the low and discontinuous canopy. Among the understorey species are *Austrotaxus spicata* (Taxaceae), *Libocedrus austrocaledonica* (Cupressaceae), and the majority of the Podocarpaceae. The species contributing to the canopy of the forest, or more often standing above it, are all the Araucariaceae, *Callitris*, *Retrophyllum comptonii* and *Dacrydium lycopodioides* (Podocarpaceae).

The distribution of species according to altitude (Fig. 8.4) shows that six species are restricted to higher altitudes and establish only, or mostly, in evergreen rainforest above 1000 m: *Agathis montana* constitutes the monospecific tree stratum of the summit forests of Mt Panié and the neighbouring Mt Colnett and Mt Ignambi (Nasi 1982), and *Araucaria schmidii* is only found as an emergent above a low forest on the escarpment slopes bordering the summit plateau of the Mt Panié range. *Dacrydium lycopodioides* is confined to exposed summits, while the more widespread *Retrophyllum comptonii* occupies a variety of sites. The extremely rare *Podocarpus longefoliolatus* (recorded from only three localities on crests) and *Libocedrus austrocaledonica* are the only conifers exclusive to the undergrowth of higher altitude forests.

A total of 11 species are found principally at altitudes between 150 and 1000 m. Of these, seven species (*Acmopyle pancheri*, *Austrotaxus spicata*, *Falcatifolium taxoides*, *Parasitaxus ustus*, *Podocarpus lucienii*, *P. sylvestris* and *Prumnopitys ferruginoides*) have a wide altitudinal distribution and extend beyond 1000 m elevation. A single canopy species, *Araucaria biramulata*, which always overtops low forests on crests, rocky ridges and very steep slopes, has an altitudinal range exceeding 1000 m.

The species restricted to evergreen rainforest of low altitudes comprise two Podocarpaceae and seven Araucariaceae. Among the former, *Dacrycarpus vieillardii* is very often restricted to gallery forests where it occupies alluvium subject to flooding, while *Podocarpus polyspermus* (of limited distribution) is found mostly on slopes above 600 m, but has been observed in gallery forest at 50 m a.s.l. The low-altitude Araucariaceae comprise three *Agathis* and four *Araucaria* species. *Agathis corbassonii*, *A. moorei* and *A. lanceolata* (the last exceptionally exceeding 1000 m a.s.l.) are most often found as small clusters or groups of individuals but, sometimes, in more extensive populations individuals are dispersed within the forests without any obvious ecological explanation. These species seem completely at home

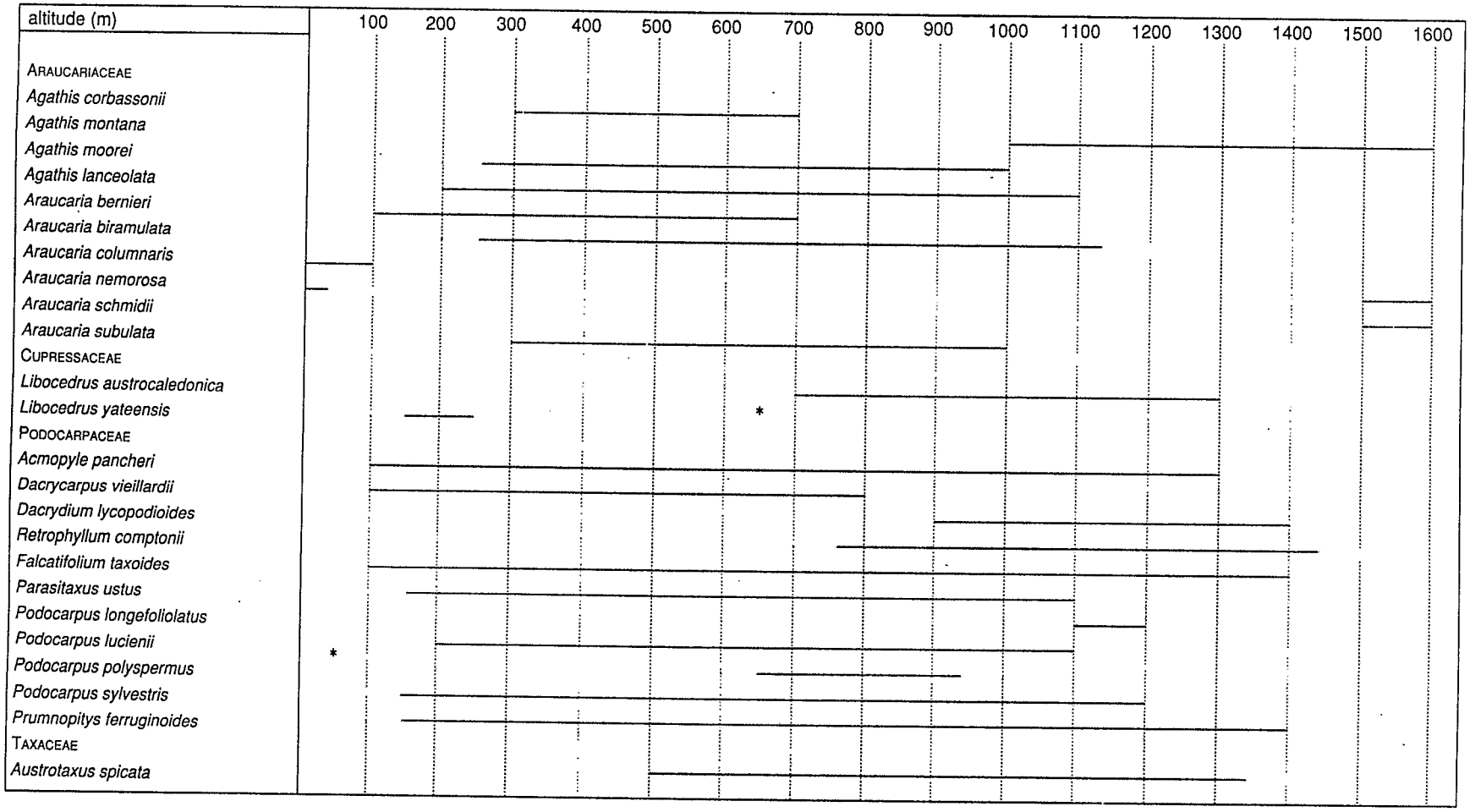

Fig. 8.4 Altitudinal distribution of forest conifers. Asterisks indicate altitudinal outliers.

in this type of forest where, unlike many arborescent conifers, they never occupy marginal sites.

Araucaria bernieri (Fig. 8.5) and *A. subulata* generally occupy steep slopes and debris slips in deep valleys and gullies. *A. bernieri* is also often associated with *Agathis lanceolata* in the southern massif.

Araucaria columnaris is entirely different. It has its maximum growth and abundance at the edge of the sea within an edaphic, and undoubtedly climatic, variant of the dense rainforest of low and middle altitudes: the 'dense evergreen forest on calcareous rock' that grows on the ancient raised coral reefs of the Loyalty Islands and the Isle of Pines (Morat *et al.* 1981). It forms dense, monospecific, arborescent populations that stand above a stunted forest on cliffs exposed to the prevailing winds. These populations of *A. columnaris*, which mostly form narrow strips a few dozen metres wide, are among the most spectacular plant formations of New Caledonia. On the Grande Terre *A. columnaris* also occupies certain sites totally lacking a shrub stratum on littoral cliffs exposed to the prevailing winds (Fig. 8.6).

Araucaria nemorosa, known only from a single population of several dozen individuals, is associated with *A. columnaris* in the Bay of Port Boisé at the extreme south of the Grande Terre.

Although there are few published studies on the forests of New Caledonia (CTFT 1975, Nasi 1982, Jaffré and Veillon 1989), the importance of the Araucariaceae within the dense rainforests is readily demonstrated (Table 8.2; reproduced from the Forest Inventory of New Caledonia, CTFT 1975). *Agathis* and *Araucaria* constitute a substantial proportion of the exploitable timber (more than 10 per cent of the timber trees more than 40 cm in diameter in the case of the Dzumac forest on ultramafic rocks at about 100–900 m a.s.l.), but do not constitute populations sufficiently dense and extensive to form veritable 'conifer forests'. These stands often have a strong representation of angiosperms, in contrast to the observations of Whitmore and Page (1980).

The high number of individuals and basal area by diameter classes of *Agathis lanceolata* (Table 8.3) and *A. bernieri* (Table 8.4) in the forest on ultramafic rocks at the Rivière Bleue Park (Jaffré and Veillon 1990) show the importance of these two species in the tree stratum of the forest. Of trees with diameters above 40 cm they contribute 9.9 per cent of the individuals and 12.3 per cent of the basal areas. Furthermore, the distribution of diameter classes indicates good regeneration of *A. lanceolata*. In fact this appears to be the case for the majority of the forest conifers with young plants often abundant in the undergrowth and in forest openings.

These observations agree with those of Havel (1971) and Enright (1982a, d, e) on the regeneration of *Araucaria hunsteinii* and *A. cunninghami* in New Guinea and with those of Whitmore (1975) on the regeneration of *Agathis macrophylla* on Santa Cruz. Thus the Araucariaceae appears to be a stable component of many dense forests regardless of the extent of floristic domination by broad-leafed species. For example, even though 300 species of angiosperms and only seven conifers have been recorded in 2.8 ha of forest on slopes at the Rivière Bleue, the Araucariaceae contributes one of the principal components of the tree stratum.

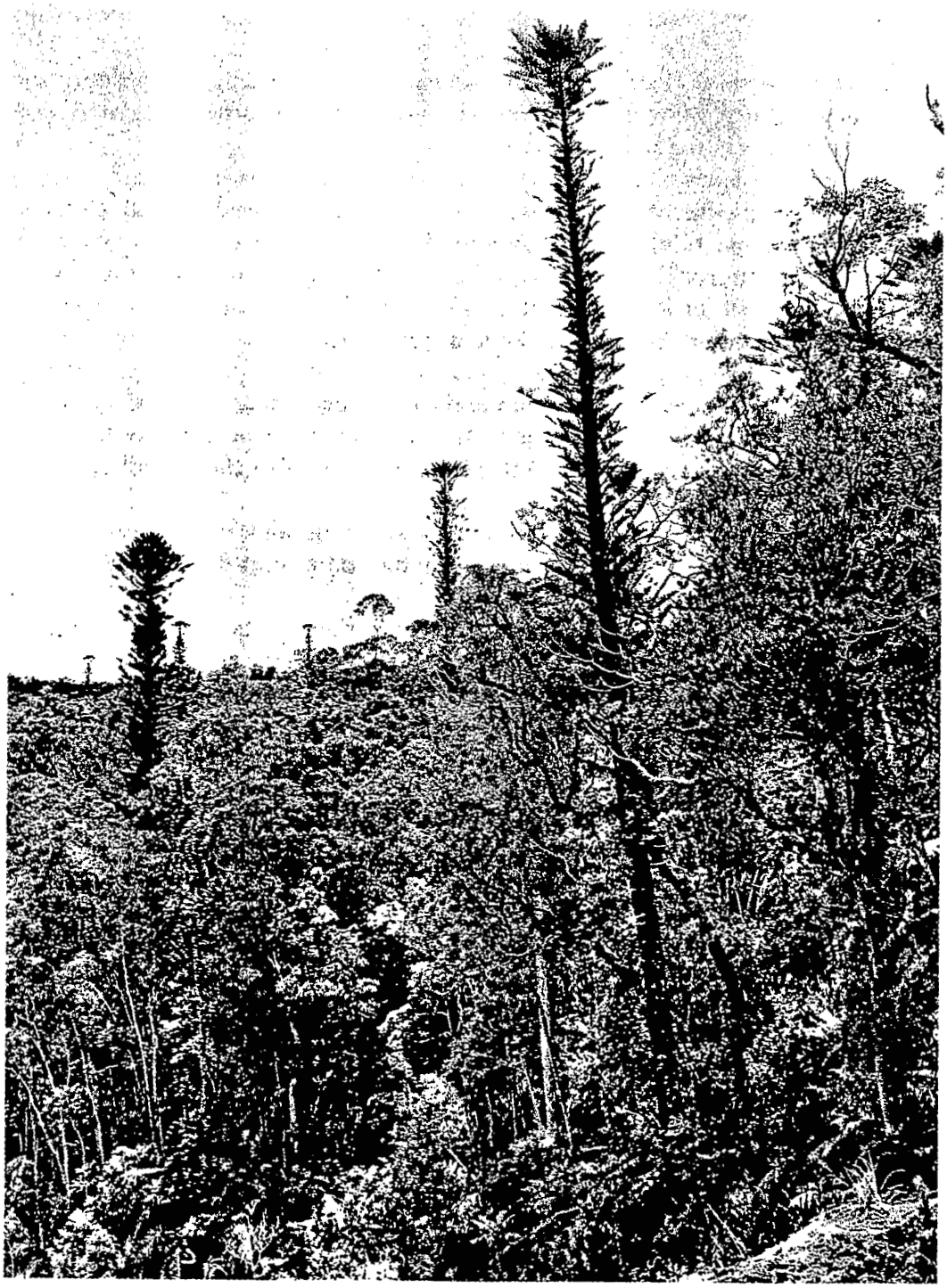

Fig. 8.5 Emergent *Araucaria bernieri* (Araucariaceae) in rainforest at Mt Dzumac (750 m a.s.l.)

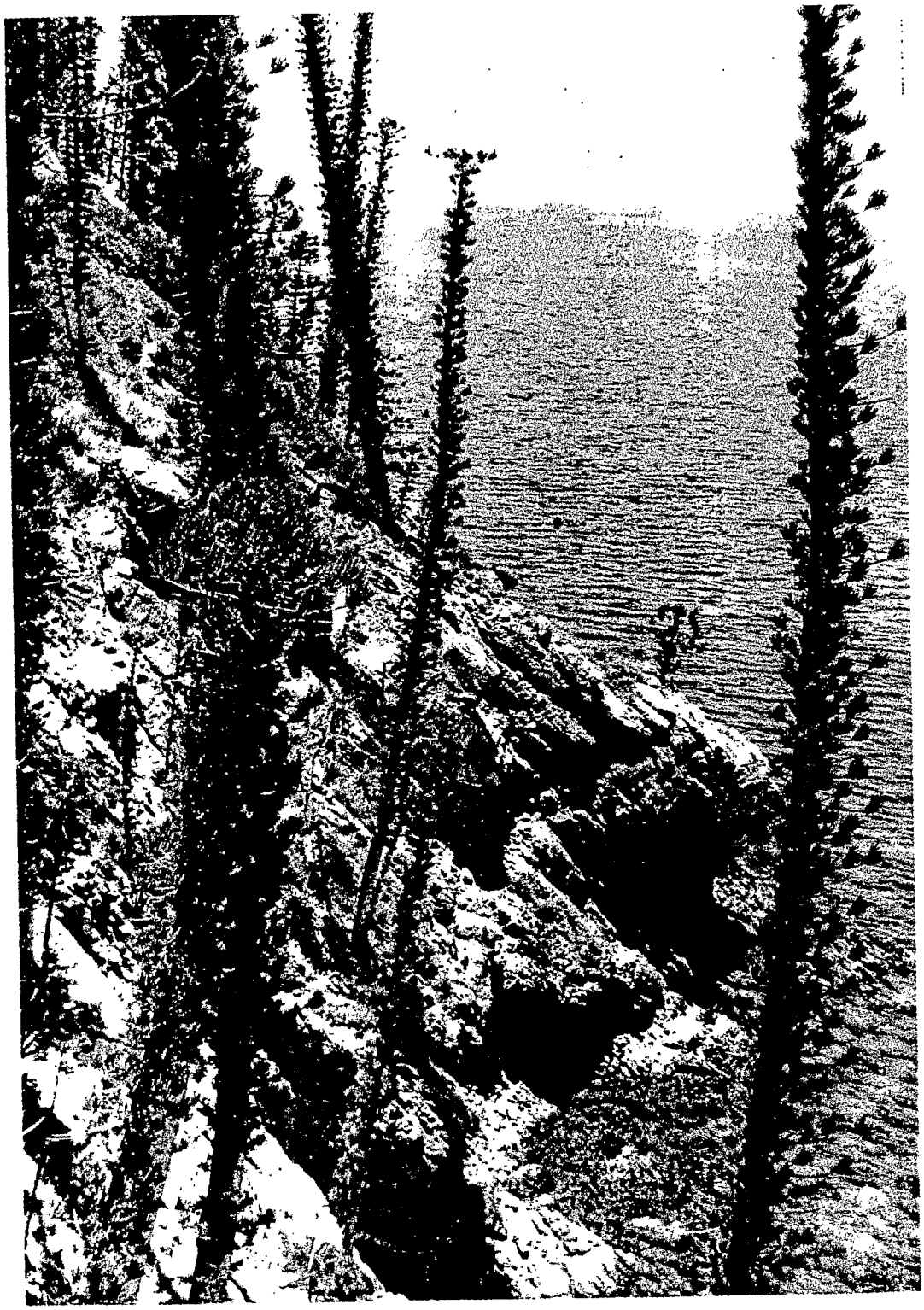

Fig. 8.6 *Araucaria columnaris* (Araucariaceae) on coastal cliffs, îlot Porc Epic

Table 8.2 Numbers of *Agathis* spp. and *Araucaria* spp. ha^{-1} compared with the numbers of all trees for different dbh classes

Region	Species	20–30	30–40	40–50	50–60	60–70	70–80	80–95	> 95	> 40	> 40 (%)
Région Est	*Agathis*	0.31	0.21	0.13	0.09	0.10	0.05	0.02	0.03	0.42	0.98
(138.4 ha)	*Araucaria*	—	—	0.01	0.01	0	0	0	0	0.02	0.05
	all trees	—	—	18.8	11.4	6.12	3.37	1.8	1.4	42.90	
Région Centre	*Agathis*	0.23	0.14	0.10	0.08	0.06	0.06	0.02	0.03	0.34	0.66
(119.4 ha)	*Araucaria*	—	—	0.04	0.01	0.01	0.01	0	0	0.07	0.14
	all trees	—	—	22.6	13.6	7.40	4.15	2.17	1.19	51.18	
Mont Mandjélia	*Agathis*	2.55	0.41	0.16	0.41	0.33	0.41	0.66	0.16	2.13	4.44
(4.5 ha)	*Araucaria*	—	—	0	0	0	0	0	0	0	0
	all trees	—	—	15.67	10.65	11.84	5.19	3.37	1.39	48.22	
Touho Tiwaka	*Agathis*	0.40	0.32	0	0.16	0	0.16	0.08	0	0.40	0.85
(12.7 ha)	*Araucaria*	—	—	0	0	0	0	0	0	0	0
	all trees	—	—	23.43	11.85	7.20	3.21	1.02	0.24	46.95	
Mont Dzumac	*Agathis*	0.56	0.70	0.82	0.25	0.18	0.19	0.12	0.26	1.86	4.39
(15.04 ha)	*Araucaria*	—	—	1.01	1.36	0.13	0.25	0	0.13	2.82	6.66
	all trees	—	—	24.76	9.90	4.56	1.83	0.69	0.58	42.33	

Source: CTFT 1975

Table 8.3 Density of trees and basal area of *Agathis lanceolata* for different dbh classes in rainforest on a mid-slope site

dbh CLASS (cm)	DENSITY OF TREES (ha^{-1})	TOTAL DENSITY (%)	BASAL AREA ($cm^2\ ha^{-1}$)	TOTAL BASAL AREA (%)
2–5	44.0	0.75	423	0.89
5–10	10.40	0.39	325	0.31
10–20	6.81	0.60	1 213	0.73
20–30	3.22	1.34	1 637	1.47
30–40	2.86	3.10	2 820	3.25
40–50	1.07	2.63	1 839	2.88
50–60	2.15	13.33	5 550	14.55
60–70	1.07	23.07	3 429	23.03
70–80	0.35	16.66	1 697	17.82
> 40	4.64	7.19	12 515	9.56

Source: Jaffré and Veillon 1990

Table 8.4 Density of trees and basal area of *Araucaria bernieri* for different dbh classes in rainforest on a mid-slope site

dbh CLASS (cm)	DENSITY OF TREES (ha^{-1})	TOTAL DENSITY (%)	BASAL AREA ($cm^2\ ha^{-1}$)	TOTAL BASAL AREA (%)
10–20	2.15	0.19	263	0.16
20–30	0.71	0.30	387	0.35
30–40	1.43	1.55	1424	1.64
40–50	1.43	3.51	2353	3.69
50–60	0		0	
60–70	0.35	7.69	1258	8.45
> 40	1.79	2.78	3611	2.76

Source: Jaffré and Veillon 1990

The results of studies on the growth of *Agathis moorei* and *A. lanceolata* (Nasi 1982), although still fragmentary, indicate that natural populations of these two conifers (of great silvicultural interest) have growth rates very similar to those of the majority of African and Asian commercial timber trees. However, the mean annual increase in diameter of mature individuals more than 90 years old is higher for *A. moorei* on sedimentary substrates (0.38–0.66 cm) than for *A. lanceolata* on ultramafic substrates (0.14–0.28 cm), reflecting the great poverty in nutritive elements of the latter.

'Maquis minier' (ultramafic maquis)

According to Jaffré (1980) and Morat *et al.* (1986), the term 'maquis minier' is peculiar to New Caledonia. It is applied to evergreen, sclerophyllous, light-

demanding formations associated with ultramafic rocks and comprising either bushy shrubs or a woody–herbaceous combination with a dense layer of sedges that may be locally dominated by an arborescent stratum of *Araucaria* spp. or *Agathis ovata* (Fig. 8.7). One of the common features of all maquis, unlike the dense forests, is that they are composed almost entirely of light-demanding species. Open formations with an arborescent stratum (more than 150 trees per hectare) classed as 'open forest' by Nasi (1982), are here classified as maquis since their floristic composition is similar to that of neighbouring maquis without arborescent araucarias.

At low and middle altitudes it is only the secondary maquis that has conifers. At higher altitudes one finds them both in the secondary maquis, distinguished by a discontinuous shrubby layer, and often a sedge layer, and also in the climax maquis (Jaffré 1980), which is characterised by a dense shrub layer below 2.5 m, overtopped by arborescent conifers up to 7–8 m high. These maquis are strongly light-demanding, but nevertheless grow close to higher altitude, dense rainforest. They replace these forests on sites exposed to the wind (Nasi 1982).

The species exclusive to the ultramafic maquis generally have their maximum development at altitudes above 600 m and, with the exception of *Podocarpus novaecaledoniae* which often grows along streams, do not grow in regions receiving less than 2000 mm of mean rainfall per year (Fig. 8.8).

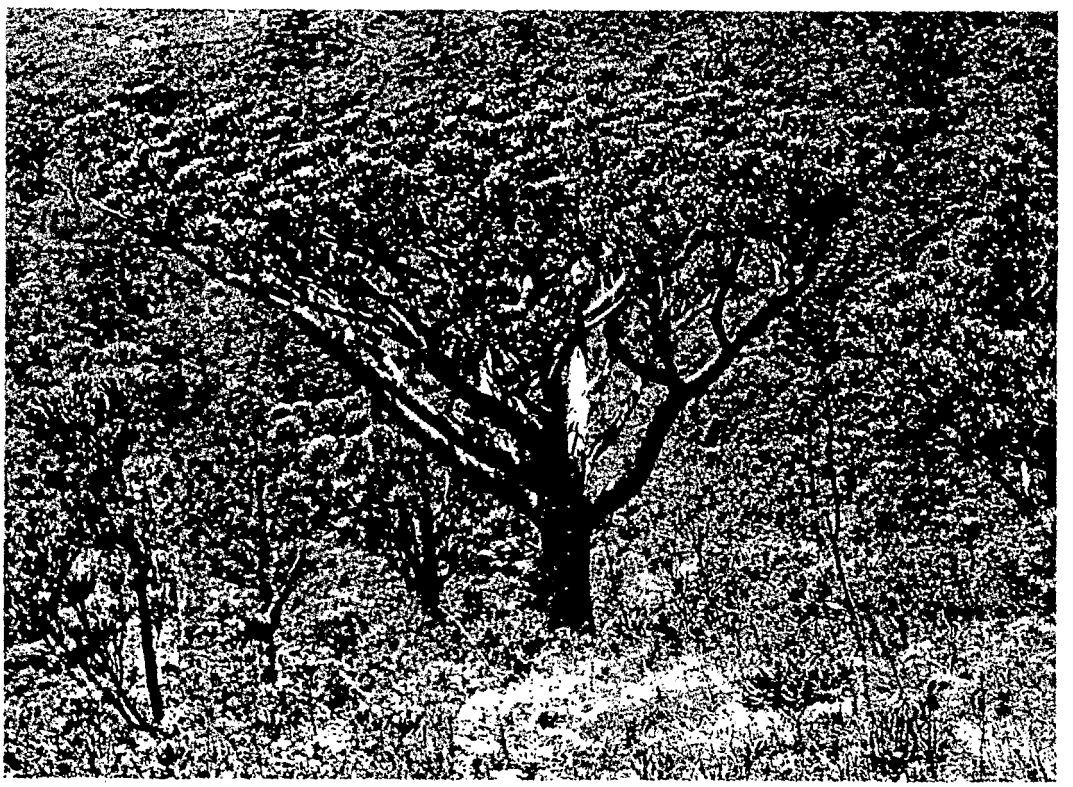

Fig. 8.7 *Agathis ovata* (Araucariaceae) in maquis at Mt Dzumac (750 m a.s.l.)

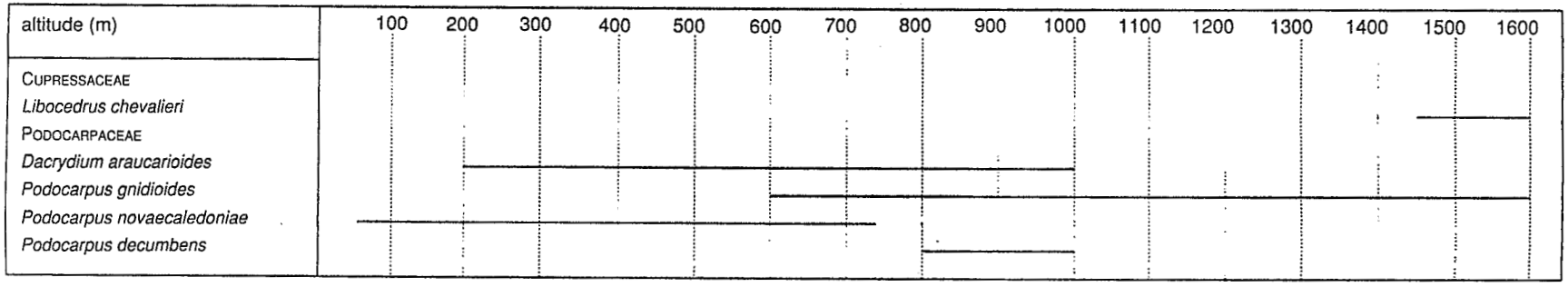

Fig. 8.8 Altitudinal distribution of maquis conifers

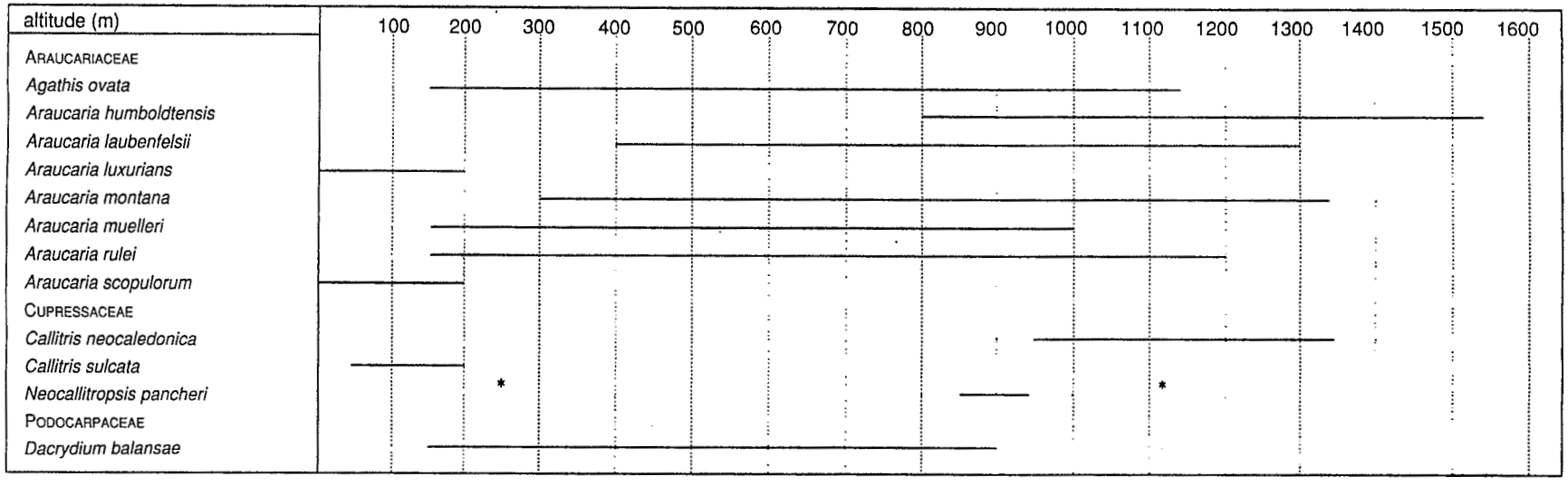

Fig. 8.9 Altitudinal distribution of conifers that grow in both rainforest and maquis

Libocedrus chevalieri and *Podocarpus decumbens* are rare, gregarious species restricted to localities on the summits of Mts Humboldt and Kouakoué, and on the summit of the Montagne des Sources, respectively. They belong exclusively to the climax maquis of higher altitudes. *Dacrydium araucarioides* is a common species mainly found in shrubby secondary maquis on gently sloping sites often dominated by *Gymnostoma deplancheanum* (Casuarinaceae) and sometimes by *Neocallitropsis pancheri* (Cupressaceae). It is a pioneer species favouring open sites and disappears when the vegetation cover is re-established. *Podocarpus novaecaledoniae* and *P. gnidioides* occur in ligno-herbaceous (sedge) maquis which, although secondary, appears to be relatively stable on the human time-scale. Although *P. novaecaledoniae* is common in dense or open populations in a variety of ecological situations, including moist banks, *P. gnidioides* is restricted to a few localised populations on rocky or lateritic crests.

Dense rainforest and 'maquis miniers'

These are all light-demanding species that can tolerate moderate shade in the juvenile stage. As adults they emerge over the other species of the forest or maquis. Emergent species of the maquis are mostly secondary except in the case of certain higher altitude versions dominated by *Araucaria humboldtensis* (800 to 1600 m a.s.l.) or by *Callitris neocaledonica* (900 to 1300 m a.s.l.). The presence of the latter at 135 m a.s.l., as noted in the flora of New Caledonia (de Laubenfels 1972), is doubtful. It is probable that the higher altitude maquis with *Neocallitropsis pancheri* (only known to form forest in a population on a crest in the Paéoua massif; Jaffré *et al.* 1987b) is primary. It is likely also that certain populations of *Neocallitropsis pancheri*, such as that on the plateau of the Montagne des Sources, are climax formations, probably partly degraded by human action. They are not the result of a secondary succession, nor are stands developing towards forest.

Of the conifers common to dense forest and maquis, six have broad and overlapping ranges between 500 and 1000 m a.s.l. (Fig. 8.9). The Araucariaceae (*Agathis ovata*, *Araucaria laubenfelsii*, *A. montana*, *A. muelleri* and *A. rulei*) grow in very similar ecological sites occupying rocky slopes, plateaux with lateritic duricrusts or nodules, and sheltered basins. However, *A. montana* mostly occurs on summit crests and plateaux while *A. rulei* and *Agathis ovata* (Virot 1956) prefer intermediate plateaux and terraces that here and there interrupt the steepness of the foothills. *Dacrydium balansae* forms open populations of a few individuals most often in degraded vegetation on slopes.

Only four species (*Callitris sulcata*, *Araucaria nemorosa*, *A. scopulorum* and *A. luxurians*) are found at altitudes below 200 m. The last two, as well as *Dacrydium balansae* when it grows at low altitude, occur in regions receiving less than 2000 mm mean annual rainfall. *A. scopulorum* and *A. luxurians* that overtop maquis or low, degraded forest, always occupy windswept sea cliffs. *Callitris sulcata*, scattered or in thickets, occurs mostly in gallery forests or in maquis on slopes along certain rivers within the Mt Humboldt massif.

Most of the conifers represented in the maquis are strongly gregarious, especially in the case of *Neocallitropsis pancheri*. The floristic richness of two surveyed populations of 0.1 ha at the Chute de la Madeleine (Table 8.5) remains high despite the dominance of *Neocallitropsis* and associated *Dacrydium araucarioides*. These two conifers do not significantly impoverish the flora as is generally the case with dominant gregarious species. This same phenomenon has also been observed in the case of maquis dominated by *Araucaria rulei* on the Boulinda massif, where the very distintive flora described for the lateritic plateaux between 700 and 900 m (Jaffré 1980) remains the same whether the tree stratum of *Araucaria* is present or not (Fig. 8.10).

Table 8.5 Density of stems (0.1 ha^{-1}) and cover of conifers in two stands of *Neocallitropsis pancheri*

	La Chute	Montagne des Sources
Total number of woody species	58	53
Total density of stems	3269	3043
Neocallitropsis pancheri	99	747
Density (%)	3.03	25.55
Cover (%)	55	85
Dacrydium araucarioides	223	2
Density (%)	6.82	0.06
Cover (%)	20	< 1
Agathis ovata	0	2
Density (%)	0	0.06
Cover (%)	0	< 1

These observations recall those made by Enright (1982b), who showed that *Araucaria hunsteinii* in New Guinea behaves a little like an element superimposed on the forest. It seems as if certain conifers do not enter directly into competition with other tree species in the main vegetation layer which they overtop. The different Araucariaceae common to forest and maquis regenerate perfectly and very often abundantly in both situations.

Observations on the Mt Do massif, which has not been subject to fire since 1981, show that the forest is clearly expanding at the expense of maquis as the result of marginal spread of *Araucaria laubenfelsii*. This species is also multiplying abundantly in the heart of the maquis, where the density of differently sized individuals is such in places that we can clearly observe the beginning of the return of forest. This secondary succession is quite unusual in that the arborescent species of the upper canopy establish first, creating the conditions that favour the implantation of more shade-loving species without the intermediate stage of short-lived shrubby pioneers as is generally the case. This phenomenon warrants further study to explain the role of certain conifers in the developmental processes of the forest.

Fig. 8.10 *Araucaria rulei* (Araucariaceae) in maquis on the Massif du Boulinda (750 m a.s.l.)

Riversides and marshes

The steep relief, the rarity of plains, and the short, often torrential rivers result in few river margins or wet plains of any significant extent in New Caledonia (Morat *et al.* 1981). The swampy forests of the north of the island and some degraded coastal sites are dominated by *Melaleuca quinquenervia* (Myrtaceae) and are without conifers. The only species strictly confined to river margins and marshes occur in the southern ultramafic massif of the Grande Terre, notably in the Plain of Lakes region. These are *Dacrydium guillauminii* and *Retrophyllum minor* (Podocarpaceae). The former is limited to just four localities scattered along several kilometres on the margins of the Rivière des Lacs and at the edge of the Lac en Huit. The latter species, which is also endemic to the southern massif, grows at the margins of several watercourses and more rarely on lateritic duricrust in shallow depressions, flooded from time to time. Both species form populations of a few to several dozen individuals.

These relict populations are shrinking at the present time as a result of fire and human depredations. Although reproduction is abundant—notably in the case of *Retrophyllum minor*, the seeds of which germinate readily—scarcely any seedlings establish beyond the perimeter of the parent populations. The long-term decline of *R. minor* populations has been confirmed by G. Hope (pers. comm.), who has recorded fossil wood of *R. minor* in certain Plain of Lakes sediments.

Three species already considered in other formations, *Dacrycarpus vieillardii*, *Podocarpus novaecaledoniae* and, to a lesser degree, *Callitris sulcata* also grow along stream-sides and appear perfectly adjusted to temporary inundation.

The conifers and their substrates

Twenty-seven of the 39 species recorded on ultramafic rocks are restricted to these substrates. Only four species–three Araucariaceae (*Agathis corbassonii*, *A. montana*, *Araucaria schmidii*) and the sole Taxaceae (*Austrotaxus spicata*)–have not been recorded on this rock type.

Soils derived from ultramafic rocks are characterised by deficiencies in nitrogen, phosphorus, potassium and calcium. They also have highly variable, and sometimes excessive, amounts of magnesium, nickel and manganese (Jaffré 1980). The distribution of conifer species relative to the major soil categories on ultramafic rocks is shown in Table 8.6.

Only three species (*Araucaria bernieri*, *A. luxurians* and *Dacrydium balansae*) are able to grow on brown hypermagnesian soils in which the effects of a deficit in exchangeable calcium (less than 2 milli-equivalents 100 g^{-1}) is considerably accentuated by the antagonistic action of magnesium (Jaffré 1976). The concentration of the latter sometimes exceeds 25 milli-equivalents 100 g^{-1}. On the other hand many conifers grow on colluvial or eroded soils characterised by a less marked or non-existent Ca/Mg disequilibrium and by more elevated concentrations of nickel (> 0.5 per cent). On humic soils at higher altitudes and on duricrusts the plants must be adapted to the acidity of the substrate (pH < 3.5) and to high levels of manganese (> 1 per cent) that is all the more toxic when the soils are desaturated.

Few species are restricted to a single soil type, although *Dacrydium araucarioides* rarely departs from desaturated lateritic soils of duricrust or nodules, and *Libocedrus austrocaledonica* and *L. chevalieri* from strongly humic and very acid soils. No matter what the chemical nature of the substrate, the conifers often grow on skeletal soils covering outcrops of rock or rubble.

A comparison of average proportions of mineral elements in chlorophyllous tissues for different genera, species or families of conifers growing on ultramafic rocks with those of dicotyledons of forest and maquis (Table 8.7) shows that the conifers are adapted to the peculiar conditions of the substrate. Their mineral composition reveals limited requirements for nitrogen, phosphorus and potassium as well as a capacity to selectively absorb calcium from the soil and to limit the absorption of manganese and nickel. These two elements nevertheless occur at higher concentrations than currently observed in plants on 'normal' soils.

The distribution of the conifers on different types of substrate compared with that of the representative angiosperm families (or groups of families) shows that their distribution accords less with the archaic angiosperms than with the more advanced angiosperms (Table 8.8). Admittedly, the latter includes a majority of light-demanding species well represented on ultramafic rocks.

Table 8.6 Conifer distribution in relation to ultramafic soils

	Type of soil					
Species	Humic	Oxydic indured	Oxydic colluvial	Oxydic eroded	Alluvial	Brown hypermagnesien
Araucariaceae						
Agathis lanceolata			**	***	**	
A. moorei			**	**		
A. ovata		***	**	*		
Araucaria bernieri			**	***		**
A. biramulata				**		
A. columnaris		*				
A. humboldtensis			**	**		
A. laubenfelsii		**	**	**		
A. luxurians				**		**
A. montana		***	*	**		
A. muelleri		**	*	*		
A. nemorosa		*				
A. rulei		**		*		
A. scopulorum		**		***		
A. subulata			**	**		
Cupressaceae						
Callitris neocaledonica		**	**			
C. sulcata			**	**	**	
Libocedrus austro-caledonica	***			**		
L. chevalieri				**		
L. yateensis				**	**	
Neocallitropsis pancheri		***	**	**		
Podocarpaceae						
Acmopyle pancheri				**		
Dacrycarpus vieillardii			*	*	**	
D. araucarioides		***				
D. balansae			*	**	*	**
D. guillauminii					*	
D. lycopodioides			**	**		
Falcatifolium taxoides	**	**	**			
Parasitaxus ustus	**		**			
Podocarpus decumbens	***	**		**		
P. gnidioides		**	**	**		
P. longifoliolatus	**					
P. lucienii				**	**	
P. novaecaledoniae				***	**	
P. polyspermus	**		**	***		
P. sylvestris			**	**		
Prumnopitys ferruginoides	**		**	**	**	
Retrophyllum comptonii	*		**			
R. minor		**			**	

***high abundance **medium abundance *low abundance

Table 8.7 Mineral composition of green parts of maquis and forest conifers on ultramafic rocks compared with the mineral composition of dicotyledons

	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	Na (%)	Mn (ppm)	Ni (ppm)
Forest								
Podocarpaceae	0.73	0.030	0.47	1.61	0.13	0.15	900	80
Cupressaceae	0.72	0.029	0.39	0.81	0.12	0.04	870	30
Dicotyledons	1.34	0.044	0.86	1.55	0.38	0.25	280	120
Maquis								
Araucaria spp.	0.51	0.023	0.42	1.86	0.25	0.26	172	22
Agathis ovata	0.77	0.032	0.55	0.75	0.09	0.09	1360	6
Podocarpaceae	0.59	0.025	0.57	1.03	0.19	0.05	695	27
Cupressaceae	0.51	0.018	0.52	1.47	0.17	0.14	870	11
Dicotyledons	1.01	0.031	0.72	1.10	0.49	0.19	720	175

Table 8.8 Distribution of plant species on different substrates by family or other taxonomic grouping

Taxon	Ultramafic only	Ultramafic and other	Other only
Conifers	27	13	4
Primitive Families*	13	18	25
Myrtaceae	116	62	51
Rubiaceae	91	40	87
Euphorbiaceae	103	41	64
Orchidaceae	44	124	24
Gramineae	8	49	67
Araliaceae	46	15	28
Cyperaceae	25	28	32
Cunoniaceae	49	19	13
Rutaceae	45	24	20
Sapotaceae	51	14	17
Sapindaceae	18	28	17
Myrsinaceae	14	15	25
Palmae	12	7	14
Pandanaceae	10	14	15

* Vessels absent or primitive. Families: Amborellaceae, Annonaceae, Atherospermataceae, Chloranthaceae, Menispermaceae, Monimiaceae, Piperaceae, Trimeniaceae, Winteraceae

Geographic distribution

New Caledonia can be divided into five phytogeographic regions as in an earlier study devoted to the palms (Jaffré and Veillon 1989) (Fig. 8.11). The distribution of the conifers according to these regions is given in Table 8.9. Almost 84 per cent of the total (36 species) are concentrated in the Great Southern Ultramafic Massif and

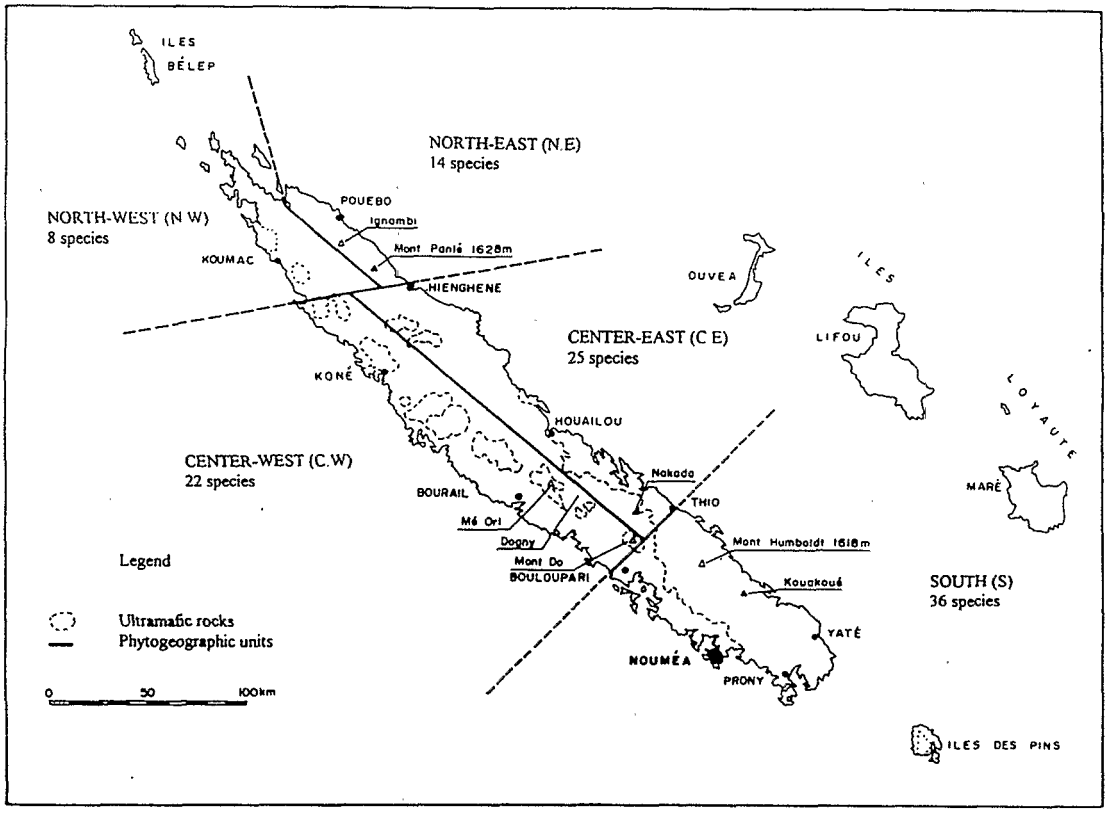

Fig. 8.11 Phytogeographic regions of New Caledonia and the distribution of conifer species

12 of these are local endemics. The Centre-East and Centre-West regions, with a variety of geological substrates, have, respectively, 25 and 22 species.

The North-East region comprises the metamorphic chain of Mt Panié that rises, as does Mt Humboldt in the south, to more than 1600 m. Here there are 14 species, of which *Araucaria schmidii* and *Agathis montana* are regional endemics. The North-West region includes a variety of substrates but, with the lower rainfall, there are only eight conifer species, all associated with outcrops of ultramafic rocks except *Podocarpus polyspermus*, which is recorded on schists at 50 m a.s.l. to the north of Koumac.

The Southern Massif, which combines important areas of ultramafic rocks, high altitudes, high rainfall (more than 4000 mm annually on the summits) and a variety of vegetation formations from open maquis to dense rainforest, is by far the richest region for conifers. This general richness also applies to individual sites. For example, there are six different conifer genera (*Araucaria*, *Agathis*, *Dacrydium*, *Neocallitropsis*, *Podocarpus*, *Retrophyllum*) in an area of about ten hectares within the botanical reserve of the Chute de la Madeleine. This locality on the Plain of Lakes at 200 m a.s.l. receives more than 2000 mm of rainfall yearly, and includes both river margin and maquis formations.

The greatest concentration of conifers is found in the Kouakoué massif where, as has already been reported (Jaffré *et al.* 1987b), there are six and ten co-occurring species between 800 and 1000 m and above 1000 m a.s.l. respectively.

Table 8.9 Geographic distribution of New Caledonian conifers (see also Fig. 8.11)

	S	CE	CW	NE	NW
ARAUCARICEAE					
Agathis corbassonii		*	*	*	
A. lanceolata	*	*	*		
A. montana				*	
A. moorei		*	*	*	
A. ovata	*	*			
Araucaria bernieri	*	*			*
A. biramulata	*	*	*		*
A. columnaris	*		*		
A. humboldtensis	*				
A. laubenfelsii	*		*		
A. luxurians	*	*	*		*
A. montana	*	*	*	*	*
A. muelleri	*				
A. nemorosa	*				
A. rulei	*	*	*		*
A. schmidii				*	
A. scopulorum		*			*
A. subulata	*	*			
CUPRESSACEAE					
Callitris neocaledonica	*				
C. sulcata	*				
Libocedrus austrocaledonica	*		*		
L. chevalieri	*				
L. yateensis	*	*		*	
Neocallitropsis pancheri	*	*			
PODOCARPACEAE					
Acmopyle pancheri	*		*	*	
Dacrycarpus vieillardii	*	*	*		
Dacrydium araucarioides	*	*			
D. balansae	*	*	*		*
D. guillauminii	*				
D. lycopodioides	*				
Falcatifolium taxoides	*	*	*	*	
Parasitaxus ustus	*	*	*	*	
Podocarpus decumbens	*				
P. gnidioides	*				
P. longefoliolatus	*	*	*		
P. lucienii	*	*	*	*	
P. novaecaledoniae	*				
P. polyspermus		*	*		*
P. sylvestris	*	*	*	*	
Prumnopitys ferruginoides	*	*	*	*	
Retrophyllum comptonii	*	*	*	*	
R. minor	*				
TAXACEAE					
Austrotaxus spicata		*	*	*	

It is perhaps surprising that there are relatively few conifers in the North-East region, which is so rich in palms (Jaffré and Veillon 1990) and other primitive groups (Morat *et al.* 1984). The difference from the southern massif largely results from the absence of open maquis vegetation such as on ultramafic rocks and river banks. This prevents the establishment of light-demanding shrubby or small arborescent species, but differences in the structure of the forests, due to the nature of the substrate, could also play a role.

Significance and role of the conifers in the flora

The conifers belong to the Gondwanan floristic element in New Caledonia, a land isolated perhaps since the Triassic and certainly since the end of the Jurassic (Raven and Axelrod 1974, Paris 1981). If the evolution of tropical floras has been marked, as Aubréville (1973) suggested, by the progressive expansion of angiosperms to supplant the conifers, then in New Caledonia the emplacement of peridotites at the end of the Eocene has favoured the survival and even the expansion of groups, including the conifers, most tolerant of the development of particularly difficult habitat conditions.

The conifers, because of the number of species and the abundance of some of them in dense rainforest and ultramafic maquis, are a highly visible and distinctive floristic element in the vegetation of New Caledonia. They are mostly found in very wet conditions (in dense rainforest, at higher altitudes and at the margins of watercourses) and on ultramafic rocks. They are usually light-demanding, overtopping dense rainforests or contributing to the dominant stratum of the maquis. They are also adapted to a much wider range of habitats than the other archaic groups, which are largely confined to dense rainforest.

The affinity of the conifers for ultramafic rocks probably results from their pre-adaptation to infertile soils, their apparent tolerance of sometimes toxic concentrations of nickel and manganese, and their light-demanding nature and preference for rocky sites. On ultramafic rocks the vegetation is less vigorous than on normal soils and the forest is lower, permitting the arborescent conifers to penetrate the canopy easily. In the climax maquis of higher altitudes, as in secondary maquis elsewhere, the shrubby or low arborescent conifers also find satisfactory light-conditions and less severe interspecific competition. This is because the nature of the substrate limits the growth of angiosperms and prevents the establishment of rapidly growing species with their high demands for nitrogen and phosphorus.

The shade intolerance of conifers, noted by Aubréville (1965), explains their abundance on ridges and on steep slopes where the ecological conditions, and notably the action of wind, reduce the size of the angiosperms. The tall, narrow shape of the araucarias as well as their strong root systems (Veillon 1980) make them particularly resistant to wind and so able to tolerate exposed situations.

The conifers of New Caledonia are adapted to extreme habitat conditions with the exception of aridity. Intolerance of aridity is equally true for other archaic

groups such as the palms, Winteraceae, Balanopsidaceae, Trimeniaceae and Sphenostemonaceae, which are also absent from sclerophyll forests of the dry regions (Jaffré *et al.* 1993).

The rarest conifers are found in limited populations (*Dacrydium guillauminii*, *Podocarpus decumbens*, *Retrophyllum minor*, *Libocedrus chevalieri*, *P. longefoliolatus*) that are sometimes discontinuous (*Neocallitropsis pancheri*, *Callitris neocaledonica*, *P. lucienii*). This is explained by the decline of these species which undoubtedly formerly occupied much larger areas and are restricted today to special sites (margins of watercourses, exposed ridges) which have provided them with a refuge. Although most of these populations are in botanical reserves, they are not protected from fires which have accelerated their decline since the arrival of humans. The most threatened species is undoubtedly *D. guillauminii* whose few, small populations are confined to a very accessible locality on the Plain of Lakes. Here tourism is developing without adequate controls and the survival of the species is threatened.

Certain conifers common in dense rainforest, such as *Falcatifolium taxoides*, *Prumnopitys ferruginoides*, *Retrophyllum comptonii*, as well as some less common species with a wide distribution (e.g. *Parasitaxus ustus*, *Acmopyle pancheri*) show no evidence of decline within the broad-leafed forests. On the other hand, they could be seen as the present-day representatives of genera more strongly represented in the ancestral flora.

The Araucariaceae, and particularly the genus *Araucaria*, are regarded as a relictual group that had a wider distribution in both hemispheres during the Mesozoic. As there are a large number of species in New Caledonia (13 araucarias of the 19 known in the world) it is suggested that there was a differentiation of new species post-Eocene after the emplacement of the peridotites. The dynamism exhibited by most of the Araucariaceae in their preferred habitats makes them less vulnerable than the species of a relictual character for which the reconquest of lost territory is always problematic.

Nevertheless repeated fires, mining and forest exploitation destroy entire populations of Araucariaceae, imperilling the genetic potential of the species. This is particularly the case for *Agathis lanceolata*, over-exploited for resin production at the beginning of the century and now exploited for timber. Nasi (1982) advocated the protection of as many sites as possible in order to preserve the remaining genetic diversity in this species. Protection is also needed for *Araucaria rulei* which generally occupies sites containing nickel ore, extraction of which necessitates the removal of the soil. *A. nemorosa*, known from only one locality, as well as *A. luxurians* and *A. scopulorum* are local in maquis and forests sensitive to fire. They require stricter protection measures than the other Araucariaceae which are better protected in moister forests and in less accessible sites.

Representatives of an ancestral flora, the conifers of New Caledonia constitute, by reason of their uniqueness and diversity, a heritage of exceptional value. Apart from the economic value of their timbers, and perhaps unknown potential uses, they have an undeniable scientific interest. Their further study will add to understanding

of the evolution of floras through time and of the dynamics of flora and vegetation submitted to particular edaphic and climatic constraints. Analyses of the way natural populations of conifers function in New Caledonia would assist in the development of models for management and conservation of relict species that lack dynamism and are threatened with extinction. It will also assist with the formulation of models for silvicultural production or protection in regions of extreme ecological conditions requiring a specialised plant cover.

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