4

Ecology and Distribution of the Malesian Podocarps

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ABSTRACT. Podocarp species and genus richness is higher in the Malesian region than anywhere else on earth, with maximum genus richness in New Guinea and New Caledonia and maximum species richness in New Guinea and Borneo. Members of the Podocarpaceae occur across the whole geographic and altitudinal range occupied by forests and shrublands in the region. There is a strong tendency for podocarp dominance of vegetation to be restricted either to high-altitude sites close to the limit of tree growth or to other sites that might restrict plant growth in terms of water relations and nutrient supply (e.g., skeletal soils on steep slopes and ridges, heath forests, ultramafic parent material). Although some species are widespread in lowland forests, they are generally present at very low density, raising questions concerning their regeneration ecology and competitive ability relative to co-occurring angiosperm tree species. A number of species in the region are narrowly distributed, being restricted to single islands or mountain tops, and are of conservation concern. Our current understanding of the distribution and ecology of Malesian podocarps is reviewed in this chapter, and areas for further research are identified.

INTRODUCTION

The Malesian region has the highest diversity of southern conifers (i.e., Podocarpaceae and Araucariaceae) in the world (Enright and Hill, 1995). It is a large and heterogeneous area, circumscribing tropical and subtropical lowland to montane forest (and some shrubland) assemblages, extending from Tonga in the east to India in the west and from the subtropical forests of eastern Australia in the south to Taiwan and Nepal in the north (Figure 4.1). As a natural entity, the region is best defined by the distribution of closed forests with tropical affinity (Webb and Tracey, 1981; Whitmore, 1984). The Podocarpaceae is the largest conifer family in the region in terms of genera and species, and the genus *Podocarpus* is both the most numerous and widespread (Table 4.1, Appendix).

The taxonomy of the Podocarpaceae in this region has been extensively described by de Laubenfels (1969, 1985, 1987, 1988), who continues to add
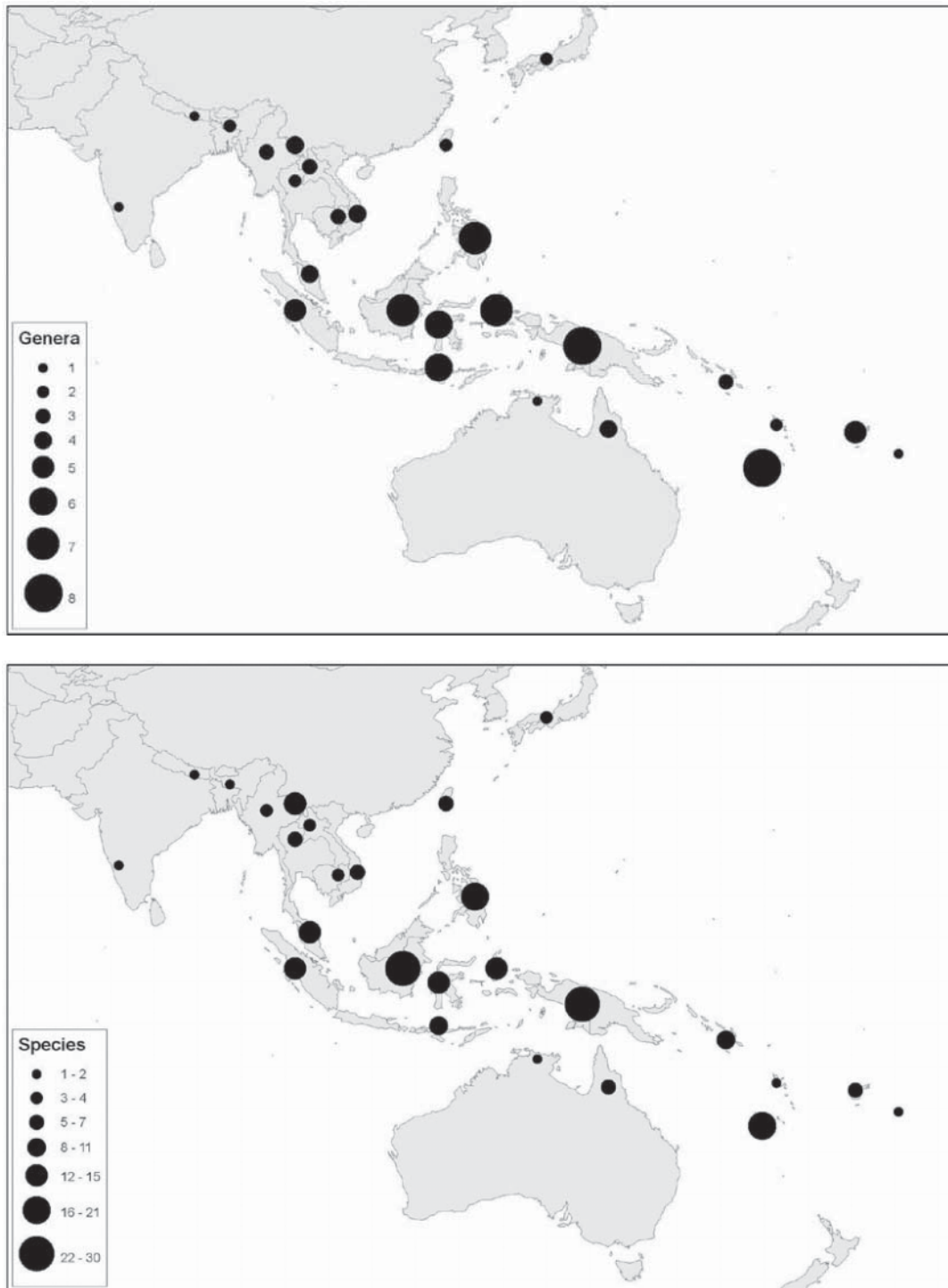
FIGURE 4.1. Malesian distribution of (top) genera and (bottom) species in the family Podocarpaceae, showing nodes of maximum genus diversity in New Caledonia and New Guinea, high levels in eastern Indonesia to the Philippines, and nodes of maximum species diversity in New Guinea and Borneo. Information for southern Australia and New Zealand is not shown. Although outside the region discussed here, data are shown for Japan to indicate the northern range limit for Podocarpaceae globally. (Figure prepared by H. Kobryn.)

TABLE 4.1. Malesian distribution of genera and species in the family Podocarpaceae, showing the total species in each genus and the percentage of the global total occurring within the region. Data were compiled from de Laubenfels (1969, 1985, 1987, 1988, 2003, 2005), Silba (1986, 1987), Enright and Hill (1995), Farjon (1998, 2008), and the Gymnosperm Database (http://www.conifers.org/index .html).

Distribution	*Acmopyle*	*Dacrycarpus*	*Dacrydium*	*Falcatifolium*	*Nageia*	*Parasitaxus*	*Phyllocladus*	*Podocarpus*	*Prumnopitys*	*Retrophyllum*	*Sundacarpus*	Total
Tonga	0	0	0	0	0	0	0	1	0	0	0	1
Fiji	1	1	2	0	0	0	0	2	0	1	0	7
New Caledonia	1	1	4	1	0	1	0	9	1	2	0	20
Vanuatu	0	1	0	0	0	0	0	1	0	0	0	2
Solomon Islands	0	1	4	0	0	0	0	6	0	0	0	11
NE Australia	0	0	0	0	0	0	0	4	1	0	1	6
New Guinea	0	5	7	1	1	0	1	14	0	1	1	31
Moluccas	0	2	3	0	1	0	1	6	0	1	1	15
Sulawesi	0	3	4	0	1	0	1	5	0	0	1	15
Sunda Islands	0	1	1	1	1	0	0	3	0	0	1	8
Borneo	0	4	7	2	3	0	1	12	0	0	1	30
Sumatra	0	2	4	0	2	0	0	7	0	0	1	16
Malaya	0	1	5	0	2	0	0	6	0	0	0	14
Vietnam	0	1	1	0	2	0	0	3	0	0	0	7
Laos	0	1	1	0	1	0	0	0	0	0	0	3
Thailand	0	0	0	0	2	0	0	3	0	0	0	5
Cambodia	0	0	1	0	1	0	0	1	0	0	0	3
Assam	0	0	0	0	1	0	0	1	0	0	0	2
India	0	0	0	0	1	0	0	0	0	0	0	1
Nepal	0	0	0	0	0	0	0	1	0	0	0	1
China	0	1	1	0	3	0	0	7	0	0	0	12
Philippines	0	2	3	1	1	0	1	11	0	0	1	20
Taiwan	0	0	0	0	1	0	0	5	0	0	0	6
Burma	0	1	0	0	1	0	0	2	0	0	0	4
TOTAL SPECIES	2	8	20	5	6	1	1	55	2	3	1	104
GLOBAL SPECIES	2	9	21	5	6	1	5	106	9	5	1	195
PERCENT MALESIAN	100	89	95	100	100	100	20	52	22	60	100	54

new species to the group (de Laubenfels, 2003, 2005). New Guinea (31 species), Borneo (30 species), and New Caledonia (20 species), followed by the Philippines and Peninsular Malaysia, show the highest levels of species diversity in the region (Figure 4.1, bottom). Tropical eastern Australia is notable for its lower diversity of podocarps (six species, four genera) relative to tropical regions to

the north and east and New Zealand and Tasmania to the temperate south. Even Fiji has higher diversity at the genus level (five genera). Lowest diversity is associated with extreme isolation, with one species each in Tonga in the southeast and India in the west. Low podocarp diversity in the Australian tropics may reflect species losses due to the impacts of Pleistocene climate change associated with

glacial–interglacial cycles and the increased occurrence of fire, which has relegated closed forests to fire-protected moist gullies in many areas (Webb and Tracey, 1981; Kershaw, 1988). In India, low podocarp diversity is likely to be associated with plate tectonic and climate history since the Late Cretaceous, whereas in some tropical islands (e.g., Vanuatu) it is associated with recent geological formation (Enright and Gosden, 1992). Local radiation of species appears to be the major source of species diversity in areas characterized by high numbers of endemic species (e.g., New Caledonia, Borneo), especially within the genus *Podocarpus*.

Conifers are often characterized by great longevity and a low potential rate of population increase relative to angiosperm competitors (Loehle, 1988), which may place them at a competitive disadvantage under either low-stress or high-disturbance regimes (Grime, 1979). Bond (1989), Midgley and Bond (1989), and Midgley (1991) emphasized functional constraints on growth rate in their analyses of the reasons for the decline of conifers relative to angiosperms at the evolutionary timescale. They argued that conifers have a less-efficient vascular system than angiosperm trees since their tracheids are generally more resistant to solute flow than are angiosperm vessels and their leaves are not as fully vascularized. This has limited the range of possible leaf sizes and shapes in conifers and, they argued, helps to explain why conifers are rarely prominent in shaded habitats. Subsequent experimental studies and reviews by Brodribb and colleagues (Brodribb and Hill, 1998, 1999, 2004; Brodribb et al., 2005), Becker (2000), and others (Pammenter et al., 2004; Coomes et al., 2005) support this contention, illustrating that conifers generally have lower hydraulic efficiency and so are disadvantaged under high potential productivity conditions (see Brodribb, this volume). However, under low-light conditions this competitive disadvantage relative to angiosperms declines (but is not eliminated), and under a combination of low-light and low-nutrient conditions, such as in some tropical forests, the disadvantage may disappear altogether (Becker, 2000; Pammenter et al., 2004). Given these constraints, the Podocarpaceae are undoubtedly the most successful of all conifers, with a large number of species showing a broad range of leaf adaptations, facilitating persistence in a range of tropical (and temperate) forests from sea level to altitudinal tree line and beyond.

Population size structures for conifers in both tropical and southern temperate forests are frequently discontinuous, with regeneration gaps evident in the sapling and small tree stages (Clayton-Greene, 1977; Veblen and Stewart, 1982; Veblen and Lorenz, 1987; Stewart and Rose, 1989; Burns, 1991; Lara, 1991; Lusk and Ogden, 1992). Demographic studies have generally shown that such discontinuities in stage structures are typically local in extent and can be explained by differential response to disturbances at local to landscape scale, with the conifers often characterized as long-lived colonizers (e.g., Ogden, 1985; Enright, 1995; Enright et al., 1999). Although this may be true for podocarp species that dominate high-altitude forests in parts of tropical Malesia, the population dynamics of many species present at lower density in angiosperm-dominated lowland and lower montane tropical forests is less well understood.

There have been few major ecological studies that focused on podocarp species in the Malesian region. The limited information presented here is obtained from a variety of published and unpublished sources, and it deals mostly with forest composition and structure in general or focuses on how our knowledge of podocarp ecology in temperate forests or of other tropical plant groups with some shared attributes (e.g., rarity) informs a growing understanding of their ecology.

DISTRIBUTION AND ECOLOGY OF MALESIAN PODOCARPS

Podocarps are typically infrequent components of lowland and lower montane tropical forests, but may strongly dominate in upper montane forests, alpine shrublands, and some swamp forest associations at both low and high elevations (Paijmans, 1976; Enright and Hill, 1995). Species of *Podocarpus*, *Nageia*, *Prumnopitys*, and *Sundacarpus* (with generally flattened, broad leaves) are most common in lowland and lower montane forests in Australia, New Guinea, and Southeast Asia, whereas those of *Dacrydium*, *Dacrycarpus*, and *Falcatifolium* (with generally imbricate/small leaves) are most common in higher-elevation forests of New Guinea and the Indonesian and Philippine islands. *Podocarpus* and *Dacrydium* species are also locally common in lowland peat and heath forests in Sarawak and Borneo (Whitmore, 1984; Nishimua et al., 2007). New Caledonia represents such a unique set of circumstances in terms of its isolation history, ultramafic geology, and associated vegetation assemblages (Jaffré, 1993) that its rich and wholly endemic podocarp flora is treated separately here.

WIDESPREAD AND COMMON SPECIES

Three species stand out in terms of their distributions, both geographically and altitudinally, through the

Malesian region: *Dacrycarpus imbricatus* is widespread in montane forests (500–3,000 m) from Fiji to northern Myanmar, *Podocarpus neriifolius* occurs in lowland to montane forests from Fiji to Nepal, and *Nageia wallichiana* occurs from India to New Guinea and the Philippines, mostly in lower montane and montane forests, but occasionally also in lowland stands close to sea level (Kuang et al., 2006; Thomas et al., 2007; see Appendix, Table 4.A1). *Podocarpus neriifolius* is exploited for timber and has been depleted in some regions, especially in low- and middle-altitude forests. Other species with wide geographic distributions include *Sundacarpus amarus* (northeastern Australia to the Philippines), *Podocarpus pilgeri* (Solomon Islands to southern China), and *Dacrydium beccarii* and *D. xanthandrum* (Solomon Islands to the Philippines). Although not necessarily widespread, some podocarps may be abundant within their geographic ranges, dominating the forest stands in which they occur. For example, *Dacrycarpus compactus* occurs only in New Guinea but is the principal tree line species there. It is present on almost all mountains of the central mountain chain, often as the tree line dominant. However, it is virtually absent from sandstone mountains (e.g., Mount Jaya) where *Papuacedrus papuana* (Cupressaceae) and *Phyllocladus hypophyllus* dominate (Hope, 1976). A range of podocarps is locally abundant on poor soils associated with ultramafic geology (e.g., *Podocarpus gibbsiae* and *P. confertus* in Borneo) and other resource-limiting substrates (e.g., *Dacrydium cornwallianum* in montane swamp forests in New Guinea and *D. pectinatum* in lowland heath and peat forests on acid sands in Borneo).

Rare and Restricted Species

Among 85 species from 10 genera in the Malesian region outside of New Caledonia, 45 show geographic ranges restricted to a single country or island (Appendix). There are at least six endangered podocarps, and a further seven species are known from only one or a few collection sites. In Fiji, a number of narrow endemic taxa, including *Acmopyle sahniana* (critically endangered), *Dacrydium nausoriense* (endangered), and *Podocarpus affinis*, occur in small stands in cloud forest on ridgetops at 375–900 m. *Acmopyle sahniana* is restricted to three small stands at Namosi, Viti Levu. Populations are declining, seed production is poor, and there is no recent evidence of germination and recruitment of seedlings. In Tonga, the endemic *P. pallidus* occurs on steep slopes in *Calophyllum*- and *Garcinia*-dominated montane forest at 190–300 m on 'Eua, one of the oldest (Eocene) and largest limestone

islands in the Tongan island chain (Drake, 1996). These isolated island species are threatened by logging and associated erosion, and little detailed information is available about the ecology of the podocarps growing there.

Other endangered species include *Dacrydium comosum* in Peninsular Malaysia, *Nageia fleuryi* in mainland Southeast Asia, *Podocarpus costalis* in the Philippines and Taiwan, and *P. nakaii* in Taiwan (Appendix). A number of local endemics are restricted to one or a few localities in northern Borneo on or near Mount Kinabalu, including *Dacrycarpus kinabaluensis*, *Podocarpus gibbsiae*, *P. globulus*, and *Falcatifolium angustum* (Sarawak), or to single mountains in New Guinea (*Dacrydium leptophyllum*, *D. spathoides*) or the Philippines (*Podocarpus lophatus*).

Altitudinal Zonation and High-Altitude Stands

Johns (1982) describes a generalized altitudinal forest zonation for New Guinea, with *Podocarpus* species often present at low density in angiosperm-dominated lowland (0–700 m) and lower montane rainforest (700–1,800 m), *Podocarpus* and *Dacrydium* present in *Nothofagus*-dominated mid-montane forests (1,800–3,000 m), and *Dacrycarpus* (with *Papuacedrus*; Cupressaceae) dominant near the tree line at altitudes of 3,000–3,900 m. Similar sequences can be described for other parts of Malesia, although mountain forest zones and altitudinal tree lines tend to occur at lower altitudes on smaller land masses and mountain ranges (the mass elevation effect), so that it is difficult to compare directly species' altitudinal ranges among species and locations. Several podocarp species also occur above the tree line as shrubs in alpine scrub, including *Dacrycarpus kinabaluensis* on Borneo, *Dacrydium medium* in Sumatra, *Podocarpus spathoides* in Peninsular Malaysia, and *Dacrycarpus imbricatus* and *Podocarpus pilgeri* in central Irian Jaya (west New Guinea), where they form dense thickets 1–2 m high on infertile sandstone sites at 3,000 m (G. Hope, Australian National University, Canberra, Australia, personal communication).

Wade and McVean (1969) describe the high mountain forests of Mount Wilhelm, the highest peak in Papua New Guinea (4,510 m above sea level (asl)), in some detail: *Dacrycarpus cinctus* is prominent in *Nothofagus*-dominated montane forests at 2,400–2,800 m, reaching a diameter at breast height (dbh) of >100 cm. In mountain "cloud" forest at 3,100–3,350 m emergent podocarps (*Dacrycarpus compactus* and *Podocarpus pilgeri*) form an open canopy at around 25 m over a diverse angiosperm tree canopy (containing at least 44 species) at about 18 m. Seedlings and saplings of the tree species are abundant

in the understory, which is draped in bryophytes and filmy ferns. Associated species are primarily derived from groups with tropical affinity. However, with increasing altitude, a greater number of the forest species show affinity with either southern or northern temperate-latitude taxa.

Lower subalpine forest extends upward to about 3,600 m (Wade and McVean, 1969). These forests are lower (9–15 m) and structurally and floristically less complex (~35 tree species). Trees are often crooked, and few exceed 20 cm dbh, apart from the emergent *Dacrycarpus compactus*. *Gleichenia bolanica* and bryophytes may form thickets that exclude woody plants from the forest floor. The upper subalpine (tree line) forests on Mount Wilhelm occasionally reach 3,900 m, interfingered with alpine grasslands. *Dacrycarpus compactus* and *Rapanea vaccinioides* are emergent above a low tree canopy (6–12 m) containing a total of only 15 tree species. Woody shrubs from the Ericaceae are abundant in the understory.

Kitayama (1992) and Aiba and Kitayama (1999) describe altitudinal zonation of vegetation on Mount Kinabalu, Borneo, with patterns differing between ultramafic and nonultramafic substrates. In general, Kitayama (1992) identified four forest zones: lowland forests to 1,200 m, montane forests to 2,000 m, upper montane forests to 2,850 m, and subalpine forests to the tree line at 3,400 m. *Dacrycarpus imbricatus*, *Dacrydium pectinatum*, and *Falcatifolium falciforme* are prominent components of montane forest (at 1,560 m) on Tertiary sedimentary substrates, with densities of 20–50 trees >10 cm dbh per hectare (Aiba et al., 2004). *Falcatifolium falciforme* shows moderate abundance of small trees and saplings in the shaded understory, but juveniles of *Dacrycarpus* and *Dacrydium* are infrequent and appear to be associated with canopy openings. Forest structure and composition diverge markedly in the upper montane forest zone: forests on ultramafic substrate are of smaller stature and are dominated by *Dacrycarpus kinabaluensis* and the ultramafic endemic *Dacrydium gibbsiae*, whereas forests on nonultramafic substrate are dominated by angiosperm tree species. Podocarps (particularly *D. kinabaluensis*) become more prominent in subalpine forest on nonultramafic substrate, whereas they decline in abundance on ultramafic sites and are replaced there by dense, low (to 6 m) stands of *Leptospermum recurvum* (Myrtaceae). See Kitayama et al. (this volume) for more detailed coverage of the altitudinal vegetation sequence and factors affecting the distribution of podocarps on Mount Kinabalu. Detailed analyses of forest structure and composition in relation to altitude are lacking for many other parts of the region.

LOWLAND RAINFOREST

Podocarps are rare in the tropical lowlands. *Podocarpus neriifolius*, *Nageia wallichiana*, *N. motleyi* (Malaysia), *N. fleuryi* (Vietnam), and *Sundacarpus amarus* (northeastern Australia) are large trees (to 40 m height and >100 cm dbh) that tend to occur as solitary canopy trees in angiosperm-dominated lowland and lower montane forests. Seedlings and saplings are infrequent. Extensive prelogging surveys of lower montane (700–1,500 m asl) rainforests in the Bulolo and Jimmi Valleys of Papua New Guinea conducted in the 1940s and 1950s reported densities of 0–2 canopy trees >50 cm dbh per hectare for *P. neriifolius* and *S. amarus* (Papua New Guinea Department of Forests, unpublished reports). In a sample of 32 half-hectare plots in lower montane forest enumerated in the 1970s near Bulolo, Papua New Guinea, and dominated by either *Araucaria*, *Castanopsis*, or *Lithocarpus* (Fagaceae) species, podocarps were present in 10, mostly at densities of 2–4 individuals >10 cm dbh per hectare (N. Enright and R. Johns, Bulolo Forestry College, Papua New Guinea, unpublished data). A single outlier plot contained 16 individuals (32 ha^{-1}), evenly split between *P. neriifolius* and *S. amarus*, comprising ~12.5% of stand density and basal area. Although densities are too low to allow spatial analysis, the two species appear to occupy separate regions of the sample space and are not well mixed.

In a large rainforest census plot in the Pasoh Forest Reserve, Peninsular Malaysia (80 m asl), 27 trees of *N. motleyi* >1 cm dbh were recorded in a 50 ha plot containing >300,000 trees, and in a plot in Lambir Hills National Park, Sarawak, three trees were recorded in a sample of about 350,000 individuals in the forest overall at 100–200 m asl (http://www.ctfs.si.edu). *Podocarpus neriifolius* is also listed as a "frequent" canopy tree in rainforest on sandstones of the McHenry Uplands of Cape York Peninsula (11°S–12°S) in far northern Queensland, Australia (Adam, 1992). These species have among the largest leaves of any podocarp, along with *P. dispermum*, a geographically restricted species growing in the understory of wet forests in northeast Queensland between 16°30'S and 17°50'S.

HEATH AND SWAMP FORESTS

Heath (kerangas) and peat (kerapah) forests form on low-nutrient acidic sands and wet peaty soils, respectively, most commonly at low altitude in Borneo, Sumatra, and Malaya (Bruenig, 1990). They are characterized by

at least seasonal waterlogging and low levels of mineral nutrient availability and support high stem densities of small-diameter trees (typically <20 cm dbh) with smaller leaf size and markedly different floristic composition than lowland dipterocarp rainforest on nearby red-yellow clay soils (Oxisols and Ultisols) (Whitmore, 1984; Newbery et al., 1986). Drought stress is thought to be a major driver of forest structure and composition, with shallow root systems (a response to seasonal waterlogging) leading to increased vulnerability during dry periods. Miyamoto et al. (2007) reported a marked decrease in stand productivity during the El Niño drought of 1997–1998, followed by rapid return to much higher rates of biomass production, with overall rates similar to lowland dipterocarp forests. They concluded that a combination of high leaf mass allocation, small specific leaf area (as well as low leaf stomatal density and thicker/multiple palisade layers; Cao, 2000), and long leaf life span relative to adjacent lowland dipterocarp forest stands on more-fertile soils facilitated the maintenance of moderate levels of stand productivity under conditions of recurrent drought stress. Tyree et al. (1998) found no evidence of increased resistance to xylem cavitation/embolism among heath forest tree species, so that adaptation to drought appears primarily through leaf attributes. Nutrient deficiency, antiherbivore defenses, and heat load have also been suggested as factors that may interact with drought to explain the structure and dynamics of these forest types (Whitmore, 1984; Miyamoto et al., 2007). Riswan and Kartawinata (1991) reported much higher levels of recovery through vegetative resprouting (rather than seedling recruitment) following canopy disturbance relative to nearby dipterocarp forest, which may also be linked to water- and nutrient-related stress tolerance attributes of heath forest species.

Given these attributes, conifers might be expected to be generally more abundant in heath and swamp forests than in dipterocarp forest, and this is, indeed, the case. *Agathis borneensis* (Araucariaceae) is widespread and often dominant, and some of the highest-density stands of podocarps in the region also occur in heath forests. For example, Newbery (1991) recorded 40–72 *Podocarpus neriifolius* trees >7.6 cm dbh ha^{-1} (but low basal area of 0.12–0.40 m^2 ha^{-1}) in heath forests in Sarawak and Brunei codominated by the dipterocarps *Shorea ovata* and *S. revoluta*, and Nishimua et al. (2007) reported 20 trees >5 cm dbh (but relative basal area of only 0.19%) for *N. wallichiana* in a 1 ha heath forest plot near Palangkaraya, Kalimantan. Although there are no data on recruitment or mortality rates, stem diameter growth rate over two years

was similar to or greater than that for most co-occurring angiosperm tree species (Nishimua et al., 2007). A number of other podocarps occur in heath and peat swamp forests in Borneo, including *Dacrydium pectinatum*, *Nageia maxima*, *Podocarpus laubenfelsii*, and *Sundacarpus amarus*. The higher-than-expected colonization of roots by arbuscular mycorrhizal fungi (relative to ectomycorrhizal fungi) in the surface organic soils of heath and swamp forests compared with mixed dipterocarp forest (Moyersoen et al., 2001) may be linked to the higher density of conifers, all of which have arbuscular mycorrhizal symbionts.

Podocarp dominance in swamp forest stands also occurs at some mid-montane elevations (1,400–2,300 m) in New Guinea. Several *Dacrydium* species (especially *D. nidulum*, but also *D. cornwallianum*) occur in almost pure stands (>95% of all trees) on swampy land in the Western and Southern Highlands. Associated species there include *Nothofagus grandis* and *Pandanus* sp. (Johns, 1976).

Members of the Podocarpaceae cover the whole geographic and altitudinal range occupied by forests in the Malesian region. Nevertheless, there is a strong tendency for dominance to be restricted either to high-altitude sites close to the limit of tree growth or to other sites that might restrict plant growth in terms of water relations or nutrient supply (e.g., steep slopes and ridges, heath and swamp forest formations, ultramafic geology, limestone hills, other infertile parent material, and skeletal soils). There is surprisingly little specific ecological information available for podocarps in lowland forest, probably because the extremely low density of trees makes field studies of demographic behavior difficult and unrewarding relative to the opportunities afforded by the many more abundant co-occurring (and sometimes commercially important) tree species.

DISTRIBUTION AND ECOLOGY OF NEW CALEDONIAN PODOCARPS

New Caledonia is distinctive in its podocarp flora, sharing no species with any other part of the region and with most species restricted to ultramafic substrates with unusual chemical properties. The Podocarpaceae of New Caledonia comprises 20 species in 8 genera: *Podocarpus* (9 spp.), *Dacrydium* (4 spp.), *Retrophyllum* (2 spp.), *Prumnopitys*, *Falcatifolium*, *Dacrycarpus*, *Acmopyle*, and *Parasitaxus* (Table 4.1). All species and one genus (*Parasitaxus*) are endemic (Appendix). They include shrubs, small trees, and trees (Figure 4.2). *Retrophyllum comptonii* reaches a
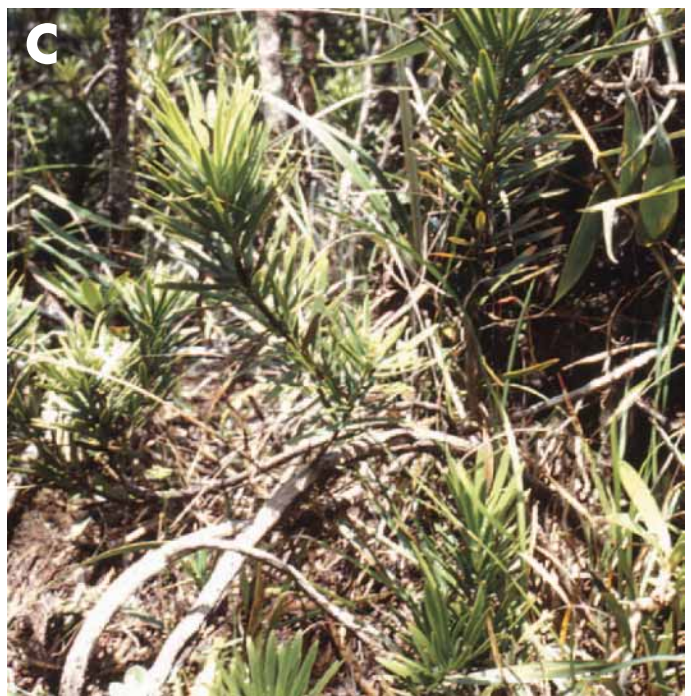
FIGURE 4.2. Examples of podocarps endemic to New Caledonia. *Facing page*: (A) *Parasitaxus usta*, the only known parasitic gymnosperm; (B) *Retrophyllum minus*, an endangered species restricted to permanent and ephemeral stream banks in the south of the Grand Terre; (C) *Podocarpus decumbens*, a critically endangered, sometimes lianescent, species restricted to high-altitude maquis on the summit of the Montagne des Sources in the south of the Grand Terre. *Above*: (D) *Acmopyle pancheri*, a widely distributed tree species of forests from 150 to 1000 m asl; (E) *Podocarpus novae-caledoniae*, a shrub species of low-altitude (0–700 m asl) ligno-herbaceous maquis in the south of the Grand Terre; (F) *Dacrydium guillauminii*, a critically endangered species restricted to a few streambank locations in the Plain of Lakes region in the south of the Grand Terre.

height of 30 m, and individuals 20–25 m high have been observed for *Dacrydium lycopodioides*, both species occurring in the canopy layer of dense evergreen rainforest. *Acmopyle pancheri*, *Dacrycarpus vieillardii*, *Dacrydium balansae*, *Falcatifolium taxoides*, *Podocarpus longefoliolatus*, *P. polyspermus*, *P. lucienii,* and *Prumnopitys ferruginoides* may reach 10–15 m but are usually shorter. Most occur in stunted montane rainforest at altitudes >1,000 m, except *D. vieillardii* (100–800 m), *D. balansae* (150–900 m), and *Podocarpus polyspermus* (650–950 m). *Dacrydium guillauminii* and *Retrophyllum minus*, reaching heights of 1–6 m, are restricted to river and lake edges in the south of the main island on ultramafic substrates. *Podocarpus novae-caledoniae*, *P. gnidioides*, *P. decumbens*, and *Parasitaxus usta* do not exceed 2 m in height. *Podocarpus decumbens* tends to be lianescent, whereas *P. gnidioides* has a prostrate habit when growing in exposed sites (Jaffré, 1995).

The overall distribution of podocarps in New Caledonia accords less with the archaic angiosperms than with the more advanced angiosperms. Grandcolas et al. (2008) reviewed recent geological and phylogenetic work on New Caledonian plants and animals and concluded that many groups, including the podocarps, most likely arrived by long-distance dispersal after 37 MYA, following up to 20 million years of total submersion of the main land mass, with little chance of survival in situ for Gondwanan stock. Low gene sequence divergence rates within the New Caledonian species of *Retrophyllum* reported by Herbert et al. (2002) support this view. Further, most new, locally endemic species within this (and other) taxa appear to have arisen over the last few million years, primarily in response to the major climatic fluctuations associated with glacial-interglacial cycles.

VEGETATION TYPES AND SPECIES DISTRIBUTIONS

Although only reaching a maximum elevation of about 1,600 m asl, the mountains of New Caledonia are characterized by montane cloud forest above 900 m similar in structure to forests at higher altitude (typically >2,000 m) on larger land masses such as New Guinea (Nasi et al., 2002). Annual rainfall exceeds 3,500 mm, and the vegetation is distinctly shorter than at lower altitudes, comprising a broken canopy layer of small trees with poorly developed trunks to 8 m high. The flora is less rich in angiosperms, although several species of the genera *Metrosideros* (Myrtaceae), *Cunonia*, and *Pancheria* (Cunoniaceae) are prominent, and genera with primitive features (*Nemuaron*, *Paracryphia*, *Quintinia*, *Sphenostemon*,

Trimenia, *Zygogynum*) are well represented, including the endemic family Phellinaceae. Podocarps are frequent in and beneath the low and discontinuous canopy, although many have fragmented distributions. *Retrophyllum comptonii* and *Dacrydium lycopodioides* contribute to the canopy of the forest or are emergent above it. *Dacrydium lycopodioides* is confined to exposed summits, whereas the more widespread *Retrophyllum comptonii* occupies a variety of sites. The extremely rare *Podocarpus longefoliolatus* (recorded from six localities on crests) is confined exclusively to the undergrowth of higher-altitude forests. *Acmopyle pancheri*, *Falcatifolium taxoides*, *Parasitaxus usta*, *Podocarpus lucienii*, *P. sylvestris*, and *Prumnopitys ferruginoides* have a wide altitudinal distribution between 150 and >1,000 m asl. Two podocarps are restricted to evergreen rainforest of low altitudes, *Dacrycarpus vieillardii* to gallery forests on alluvium subject to flooding and *Podocarpus polyspermus* on slopes mostly above 600 m and, less frequently, in gallery forest at 50 m asl. *Podocarpus novae-caledoniae* and *P. gnidioides* occur in lignoherbaceous (sedge) maquis, the latter restricted to a few localized populations on rocky or lateritic crests.

Podocarps are rarely dominant, but *Dacrydium balansae* forms an almost pure canopy layer in forest on the massif of Koniambo between 400 and 600 m (perhaps suggesting cohort recruitment after landscape-scale disturbance), and *D. araucarioides* is an abundant species in shrubby secondary maquis often codominated by *Gymnostoma deplancheanum* (Casuarinaceae). *Dacrydium araucarioides* is a fire-killed, small tree to 20 cm dbh in low-altitude (mostly 100–400 m asl, but also in one locality at 900 m at Montagne des Sources), open-maquis vegetation on shallow soils and lateritic boulder fields (cuirasse ferralitique) derived from ultramafic parent material. McCoy (1998) and McCoy et al. (1999) found that growth rings were clear and probably annual, with counts suggesting ages of up to 125 years for individuals approaching 20 cm dbh. *Dacrydium araucarioides* may recruit continuously in dry, open forests with *G. deplancheanum* prominent, but recruitment declines in more-mesic sites as rainforest tree species form a closed canopy, with disturbance (e.g., by fire) needed for recruitment to resume.

Dacrydium guillauminii and *Retrophyllum minus* are confined to river margins and marshes in the southern ultramafic massif of the Grande Terre, in the Plain of Lakes region. The former is limited to four localities on the margins of the Rivière des Lacs and at the edge of the Lac en Huit. The latter grows at the margins of some other watercourses and, more rarely, on lateritic duricrust in shallow, periodically flooded depressions. Both species form

populations of a few to several dozen individuals, which are shrinking as a result of increased fire frequency and other human impacts, with population size of *R. minus* < 2,500 (Farjon and Page, 1999; Herbert et al., 2002) and considerably smaller for *D. guillauminii*. Although seed production and germination is good, seedling establishment beyond the perimeter of existing parent populations is very rare. Two other species, *Dacrycarpus vieillardii* and *Podocarpus novae-caledoniae,* also grow along stream banks and tolerate temporary inundation.

Parasitaxus usta is the only known parasitic conifer. Its foliage is red-purple, and it is always associated with *Falcatifolium taxoides*, from which it obtains nourishment by means of haustoria penetrating the base of the trunk or the roots (Köpke et al., 1981). Feild and Brodribb (2005) recently demonstrated that *P. usta* does not photosynthesize, has a strong connection of tracheids between its roots and those of *F. taxoides,* and is mycoheterotrophic—in combination, a unique solution to the parasitic life-form. It occurs around 1,000 m asl in mixed-angiosperm montane forests to 20 m high, with occasional emergent *Araucaria* to 30 m (and at a few locations in forests below 300 m in the south of the Grande Terre). Seeds are produced, but there has been little success in ex situ germination, and seedlings are infrequent. There are no data on stem growth rates or estimates of longevity, but on average, longevity must be less than that of its host plant *F. taxoides,* so perhaps up to 200 years.

ENVIRONMENTAL CONTROLS

All of the New Caledonian podocarps are either restricted to ultramafic substrates (which cover about one-third of the Grand Terre, mostly in the south) or occur on both ultramafic and nonultramafic (mostly metamorphic) parent materials. Soils derived from ultramafic rocks are characterized by low concentrations of nitrogen, phosphorus, potassium, and calcium. Only *Dacrydium balansae* is able to grow on hypermagnesium soils, in which a deficit in exchangeable calcium (<2 meq 100 g^{-1}) is accentuated by the antagonistic action of magnesium (Jaffré, 1980). On the other hand, many conifers grow on colluvial or eroded soils (often covered with a thick organic horizon at higher altitudes) characterized by a less-marked calcium/magnesium disequilibrium and greater concentrations of available nickel (>0.5%) and manganese in acidic soils. Analysis of mineral elements in chlorophyll tissues reveals a limited requirement for nitrogen, phosphorus, and potassium, as well as a capacity to selectively absorb calcium while limiting the absorption of manganese and nickel.

Root nodules are present, but no research has been conducted into their form for New Caledonian species or the role that they might play in mediating (or restricting) element uptake from soil.

The podocarps are mostly found in very wet environments (in dense rainforest, at higher altitudes, and at the margins of watercourses) and on ultramafic geology. They are usually light demanding, overtopping dense rainforests, or contributing to the dominant stratum of the maquis. They are also adapted to a wide range of habitats. Their affinity for ultramafic rocks probably results from their preadaptation to infertile soils and rocky sites, their apparent tolerance of sometimes toxic concentrations of nickel and manganese, and their light-demanding nature. In addition, the ultramafic substrate may limit the growth of some angiosperm groups, preventing the establishment of more rapidly growing species that have a high demand for nitrogen and phosphorus.

CONSERVATION AND THREATS

The rarest podocarps undoubtedly formerly occupied much larger areas but are now restricted to sites in wet montane forest on ridges (*Podocarpus decumbens*, critically endangered, and *P. longefolaliatus,* endangered) or along the margins of watercourses (*Dacrydium guillauminii*, *Retrophyllum minus*), which have provided them with a refuge from fire. The main populations of *Dacrydium guillauminii* (critically endangered) and *Retrophyllum minus* (endangered) are now protected within botanical reserves. However, mining activities in the region, leading to possible dewatering of soil profiles near intermittent watercourses, continue to be a potential threat to the survival of some populations (Pascal et al., 2008).

Perhaps among the most threatened species are the recently described *Podocarpus beecherae* (critically endangered, closely related to *P. novae-caledoniae*) from hilltop maquis in the south of the Grand Terre (de Laubenfels, 2003) and *P. colliculatus* (endangered) from a single locality in moist forest on ultramafic substrate at Pic N'ga, Île des Pins, where tourism is developing without adequate control (de Laubenfels, 2005). However, the taxonomic status of *P. colliculatus* remains to be officially confirmed, and this collection may be synonymous with *P. sylvestris* (T. Jaffré, personal observations). In contrast, conifers common in dense rainforest, such as *Falcatifolium taxoides, Prumnopitys ferruginoides*, and *Retrophyllum comptonii*, as well as some less-common species with a wide distribution (e.g., *Acmopyle pancheri*) show less evidence of decline within the broad-leaved forests, although

post-European settlement fragmentation, logging, fire, and road construction (including many mining exploration and recreational tracks) have certainly had some impact; *A. pancheri* has been revised recently to nearly threatened. Now listed as vulnerable, *Parasitaxus usta*, the only known parasitic conifer, also seems to be disappearing from some formerly occupied sites. The potentially deleterious genetic consequences of fragmentation and population contraction in New Caledonian conifers have been illustrated for the rare *Araucaria nemorosa*, with genetic diversity lower in recent recruits than in parents and inbreeding becoming more common (Kettle et al., 2007). For the species of high-altitude, wet montane forests, global warming also poses a real threat that could cause the disappearance of their very specific ecological requirements (Nasi et al., 2002).

LIFE HISTORY ATTRIBUTES AND POPULATION ECOLOGY

Insights into the ecology of the Malesian podocarps may be gleaned from a consideration of their morphological and physiological attributes and comparison with those of co-occurring angiosperm tree species. For the majority of attributes little detail is known for these tropical podocarps relative to their temperate relatives. Nevertheless, some generalizations can be made and areas for fruitful future investigation identified.

ECOPHYSIOLOGY

Brodribb and Hill (1998, 1999, 2004) and Brodribb et al. (2005) have established a detailed understanding of the ecophysiological responses of podocarp seedlings for a mix of both temperate and tropical taxa that informs our understanding of their growth and survival in the understory of lowland mixed angiosperm–conifer forests. Most species have evolved bilaterally flattened leaves that mimic angiosperm leaves in shape and are efficient in the low-light environment of the forest understory. However, other than in the genus *Nageia*, podocarp leaves are single-veined, and this may set limits to leaf size and hydraulic conductivity that place them at a disadvantage relative to angiosperm tree species. On the basis of a broad survey of podocarp distributions in relation to climate and water availability, Brodribb and Hill (1998) concluded that podocarps were more constrained by seasonal drought than by overall patterns of rainfall, so that species were largely confined to moist, aseasonal or weakly seasonal climates. Brodribb et al. (2005) showed that seedlings of two tropical Malesian understory podocarps (*N. fleuryi* and *P. grayae*) had sixfold lower growth than comparison angiosperms under high-light conditions (1,300–1,800 mmol s^{-1}), whereas at low light levels (30 mmol s^{-1}) growth rates were more similar but still significantly lower. The podocarps consistently had lower leaf to stem ratios (i.e., were constrained to support more nonphotosynthetic tissue) and were slower to respond to increases in light. Ultimately, the authors concluded that these tropical podocarps had lower rates of gas exchange and less-efficient production of leaf area than angiosperms and were best able to compete with angiosperms as stress tolerators under low light, where their disadvantage was at a minimum. Despite multiple veins per leaf, species of (the more recently evolved) *Nageia* are not clearly more successful than other forest podocarps.

Similar results were reported by Rundel et al. (2001), who found very low rates of net photosynthesis in *N. wallichiana* under high-light conditions in Thailand, and by Pammenter et al. (2004) in relation to hydraulic properties of angiosperms and conifers, including *Podocarpus latifolius*, in southern Africa. Pammenter et al. (2004) further concluded that the competitive advantage to angiosperms was maximized under high-productivity circumstances, with conifer competitiveness less impacted under low-soil-nutrient (e.g. see Becker, 2000) and low-light conditions, such as in cloud forest, where both canopy and atmospheric factors contribute to low light availability.

POPULATION ECOLOGY

Many podocarps, especially in the genus *Podocarpus,* are dioecious, and all have wind-dispersed pollen, traits that may lead to the generally low tree densities reported for them in lowland tropical forests. Pollen dispersed by wind must fortuitously find its way from male to female plants across a landscape filled with competing species, whereas seeds (and seedlings recruited from them) can only be produced and dispersed from female adults, so that sex ratios and spatial distributions of adults also become important components of the species dynamics. Indeed, Haig and Westoby (1991) and Regal (1977) argued that the cost of rarity in angiosperms was lower than that in conifers because of the advantages of efficient insect and bird pollination relative to inefficient wind pollination. To what extent the combination of dioecy and wind pollination occurs in rainforest tree floras is unknown, but it may be infrequent; for example, Behling et al. (1997) reported that *Podocarpus lambertii* was the only wind-pollinated

species among 97 tree species in a 1 ha plot in southern Atlantic rainforest in Brazil. Nanami et al. (2005) investigated the sex ratio in the Japanese podocarp *Nageia nagi*, finding a bias in the number of males, faster growth rate in males, and spatial segregation between male and female adults. Female trees were also more heavily impacted by neighbor competition. No similar studies have been conducted for podocarps in tropical forests.

Podocarp seeds are dispersed by birds, and perhaps some small mammals, which are attracted by the typically single-seeded fleshy fruit and/or swollen bract. Fruiting structures range from green to red or purple in color. Seed production varies considerably among species, being recorded as infrequent or even rare in some cases (e.g., *P. neriifolius* in Vietnam). Germination of tropical podocarp species is usually rapid, ranging from 20 to 60 days for *Dacrycarpus imbricatus*, *Nageia fleuryi*, and *P. neriifolius*, with seeds then losing viability so that there is no persistent soil-stored seed bank. Baskin and Baskin (2001) noted that the widespread and common *Dacrycarpus imbricatus* and *Podocarpus neriifolius* exhibit morphological dormancy (underdeveloped embryos at time of dispersal) but that germination can occur within four weeks of dispersal, whereas the rare and endangered *Dacrydium comosum* exhibits morphophysiological dormancy, requiring both growth of the embryo to critical size and breakdown of physiological dormancy, thus slowing germination. Delayed seed germination, sometimes exceeding one year (Enright and Cameron, 1988; Geldenhuys, 1993), and a requirement for cold stratification have been reported for a number of temperate podocarps (Fountain and Outred, 1991) but are unlikely for tropical species. Seed germination ex situ has proven difficult in some other tropical species; for example, Doust et al. (2006) were unable to germinate cleaned seeds of *Sundacarpus amarus* in a study of rainforest restoration procedures in northeast Australia. This species is thought to be dispersed by the flightless cassowary, a tropical forest bird species now in significant decline due to forest fragmentation, logging, and other human impacts (Westcott et al., 2005). Cassowaries are considered to be important in the dispersal of >100 species of rainforest trees in northeast Australia and New Guinea, and their loss as a dispersal vector may seriously impact the future abundance and genetic structure of such species (Stocker and Irvine, 1983; Mack, 2006). Cordiero and Howe (2002) documented significantly lower rates of seedling recruitment in plant species dependent upon fruit-eating animals for seed dispersal (relative to wind and gravity dispersal species) in small versus large forest fragments for a tropical submontane forest in Tanzania, with primate and bird counts confirming frugivore species decline with decreasing fragment size.

Masting has been well documented for many temperate podocarps and is also likely among tropical species, especially given its occurrence in other tropical conifer taxa, such as *Araucaria*. Chalwell and Ladd (2005) suggested that synchronized high cone and pollen production years may be beneficial to dioecious understory plants (such as *Podocarpus drouynianus* in southwestern Australia; see Ladd and Enright, this volume), which are dependent upon wind dispersal of pollen in a low-wind environment. Although the tropical podocarps may be canopy trees, their low density provides a similar context within which one might argue that mast strobili and coning years would best ensure pollination of low-abundance, coning trees. However, parentage could be asymmetrical; female trees of both canopy and subcanopy size may receive pollen, but only canopy males may successfully disperse pollen to them if pollen dispersal in subcanopy males is limited by reduced atmospheric turbulence. Over what distances predominantly understory podocarps of closed forests successfully disperse pollen is unknown. Behling et al. (1987) measured pollen rain in traps distributed systematically through a 1 ha Atlantic rainforest plot in Brazil containing four *Podocarpus lambertii* trees. Pollen influx for the podocarps was generally low but highly variable across the plot, with distinctly higher values at two pollen trap sites (presumably close to pollen-producing trees). They concluded that pollen transport among rainforest trees can often be very limited and short distance.

In the absence of a persistent soil seed bank, potential recruits to the subcanopy, and eventually the canopy, of the forest must accumulate and persist in a seedling bank in the low-light environment of the forest understory. Data for size frequency distributions of podocarps in tropical forests are as infrequent as the species themselves and are generally restricted to individuals >5 cm dbh, so that there are no data for seedlings and small saplings. Aiba et al. (2004) reported size distributions (>5 cm dbh) for *Dacrycarpus imbricatus* and *Falcatifolium falciforme* in tropical montane forest at Mount Kinabalu, and in both cases the numbers in the smallest size class were smaller than those in some larger classes, suggesting relatively poor rates of recruitment in undisturbed forest. Elsewhere, Tesfaye et al. (2002) reported "hampered" regeneration in *Afrocarpus falcatus* in montane forests in Ethiopia based on size distribution studies, and Arriaga (2000) recorded *P. matudae* as a gap-phase species dependent upon disturbance for recruitment in tropical montane cloud forest at Tamaulipas, Mexico.

PERSISTENCE AND COEXISTENCE

Given the low density of many podocarp species in lowland rainforests, it is uncertain how they can persist with the large number of co-occurring tree species, many of which show higher levels of fecundity and faster growth rates under both high- and low-light conditions. This conundrum also applies to rare or infrequent angiosperm species. Rosetto and Kooyman (2005) found that persistence of the paleoendemic rainforest tree *Eidothea hardeniana* (Proteaceae) in a subtropical forest in northern New South Wales, Australia, was best explained by a combination of large and unpalatable fruits, on the one hand, and tolerance facilitated by basal resprouting, on the other. On the basis of a life history trait analysis of 258 local taxa, they concluded that these traits might explain the restricted distribution and rarity of a number of other locally endemic rainforest species.

Wright (2002) reviewed mechanisms for coexistence in tropical forests, identifying the lack of competition between suppressed understory plants as potentially important, and Russo et al. (2005) reported lower growth and mortality rates among trees on infertile soils in lowland Bornean rainforest, with increased cost of herbivory on resource-poor sites perhaps selecting for better-defended and slower-growing taxa, such as conifers. Indeed, among lowland forest sites, podocarps achieve their highest densities in low-nutrient swamp and heath forests. These findings suggest that podocarp populations in angiosperm-dominated rainforests are best viewed as stress tolerators, characterized by slow growth rate and low mortality rate (but also low levels of herbivore damage), largely avoiding competition with faster-growing species through their location on low-nutrient sites and in deep shade, where angiosperm competitiveness is reduced most strongly.

Although the development of dense podocarp and other conifer species stands in montane forests may be associated with large-scale disturbance by storms and fire (e.g., see Enright et al., 1999, on araucarian forest stand dynamics in the Southwest Pacific region), the ultimate growth of low-abundance podocarps to the canopy layer in lowland tropical forests most likely depends upon canopy gaps caused by the death of individual trees. However, ecophysiological evidence suggests that angiosperm competitors should be greatly advantaged by any sudden increase in light availability (e.g., Brodribb et al., 2005) and would preempt such gaps. Thus, it may take several cycles of gap formation at a single location before the subcanopy podocarps are able to capture a canopy space, implying the need for markedly greater longevity than in co-occurring angiosperm species.

Indeed, longevity is one of the most obvious differences in life history traits between conifers and comparable angiosperm woody perennial species at a global scale. Loehle (1988) compiled typical and maximum life spans, time to reproduction, growth rate, and shade tolerance for a sample of 44 conifer and 76 angiosperm tree species from North America. These data revealed a median longevity of 250 years for angiosperms and 400 years for conifers. A list compiled for Southern Hemisphere conifers by Enright and Ogden (1995) revealed a strikingly similar distribution of maximum longevities but a higher median for conifers of 525 years, although some arid-zone conifers (e.g., *Callitris* species of semiarid woodlands in Australia) with longevities in the 100- to 300-year range were excluded from consideration. Little additional information of relevance has been published since this analysis. Data on stem diameter growth rate and maximum recorded tree size for three tropical podocarps from Mount Kinabalu (*Dacrycarpus imbricatus* and *Falcatifolium falciforme*; Aiba et al., 2004) and Kalimantan (*Nageia wallichiana*; Nishimua et al., 2007) suggest life spans of 400 years or more. Co-occurring angiosperm tree species growth rates and tree sizes suggest longevities ranging from less than 200 years to more than 400 years, so that although most angiosperm trees were shorter-lived, at least some were likely equally long-lived. Overall, data for forest podocarps suggest that tropical podocarp species of lowland and lower montane forests might have longevities in the 400- to 600-year range (Table 4.2).

Southern Hemisphere conifers also show very high nutrient use efficiency for nitrogen and phosphorus relative to most (but not all) angiosperm tree types (Enright and Ogden, 1995), although there is little specific evidence for podocarps. The ability to photosynthesize over a longer time period per unit of nutrient use (i.e., greater leaf longevity) and lower mean leaf nitrogen concentration may be the primary mechanism of increased use efficiency (Chapin, 1980; Enright and Ogden, 1987; Sprugel, 1989; Becker, 2000). Although very long leaf longevities have been shown for araucarians and some other conifer groups, little information is available on leaf longevity and nutrient levels for tropical podocarps relative to co-occurring angiosperm trees.

Another question relevant to the dynamics of some sparse, lower montane and lowland podocarp populations is the extent to which long-distance dispersal of seeds and pollen might operate to maintain (or rescue) populations that may otherwise decline and disappear. Some podocarp species of lowland forests are broadly distributed and are characterized by much greater population sizes

TABLE 4.2. Selected life history properties of Southern Hemisphere podocarps (modified from Enright and Ogden, 1995). Data are from Palmer and Pitman (1972), Ogden (1978,) Veblen et al. (1981), Ash (1985), Norton et al. (1988), Lusk and Ogden (1992), Enright et al. (1995), McCoy (1998), Aiba et al. (2004), and Nishimua et al. (2007).

Species	Location	Longevity (years)	Growth rate [a]	Shade tolerance [b]
Afrocarpus falcatus	South Africa	700	2	3
Dacrycarpus dacrydioides	New Zealand	600	1	2
D. imbricatus	Borneo	400 [c]	2	2
Dacrydium araucarioides	New Caledonia	200	1	1
D. cupressinum	New Zealand	1,160	2	3
D. nidulum	New Guinea	363	3	3
Falcatifolium falciforme	Borneo	400 [c]	1	3
Nageia wallichiana	Borneo	400 [c]	2	3
Podocarpus hallii	New Zealand	555	2	2
P. latifolius	South Africa	500	2	4
P. lawrencei	SE Australia	460	1	2
P. nubigenus	South America	400	3	3
P. totara	New Zealand	890	2	2
Prumnopitys ferruginea	New Zealand	771	1	4
P. ladei	SE Australia	600	2	3
P. taxifolia	New Zealand	1,013	1	2
Saxegothaea conspicua	South America	400	3	4

[a] Scale: 1 = <1 mm year^{-1}, 2 = 1–2 mm year^{-1}, 3 = 2–3 mm year^{-1}.
[b] Scale: 1 = intolerant (full light) to 4 = tolerant.
[c] Longevities based on growth rate and stem diameter data.

and densities at higher altitudes or under specific habitat conditions (e.g., *Podocarpus neriifolius* occurs from sea level to 2,100 m, typically as scattered trees in lowland forests, but at increasing density at higher altitudes on dry ridgetops, on infertile soils), and it is not clear to what extent the dynamics of sparse lowland populations might be supported by inputs from higher-elevation populations or might rely upon local dynamics. The "rescue" hypothesis is supported by evidence from Behling et al. (1997), who reported pollination of a single individual of *Araucaria angustifolia* in Atlantic rainforest in Brazil from long-distance-transported pollen grains that must have come from a highland population at least 25 km away. This question could readily be addressed by using genetic methods to identify both mother (from nuclear microsatellite markers) and father (from chloroplast microsatellite markers) plants for each seedling/sapling/small tree encountered, so that the distribution of individuals in relation to pollen and seed dispersal could be analyzed. Such analyses would reveal dispersal distances and the extent to which pollen and seed is derived within local populations (e.g., see Godoy and Jordano, 2001; Dick et al., 2003).

SYNTHESIS

The ecology of podocarps in tropical forests of New Caledonia and the Malesian region is massively understudied relative to that for their temperate counterparts in New Zealand, Tasmania, South Africa, and South America. This is particularly true for species present in low-density populations of lowland and lower montane angiosperm-dominated forests and reflects both the significant problems of studying low-abundance species in situ and the demand for scientific attention from the many competing (including more abundant and more economically important) species in these high-diversity ecosystems. Field studies of low-abundance tree species are difficult; trees are hard to locate (and to relocate), sample sizes are small, and study sites are large (and therefore often highly

heterogeneous), complicating data collection, analysis, and interpretation in relation to basic questions concerning their ecology and demography. Although some components of these species' life histories might be explored ex situ, including seed viability and germination and seedling growth/ecophysiology in relation to key environmental gradients (light, nutrients), and other information might be obtained from analyses of wood and leaf properties, most parts of their life histories (particularly pollen and seed dispersal, recruitment, growth and survivorship) must be examined in situ if we are to understand how and why they are able to persist at low density in angiosperm-dominated stands.

In this review we have sought to detail what is known about the distribution and ecology of podocarps in tropical and subtropical vegetation types of the Malesian region and why podocarp species are distributed in this way. A lack of data from field-based investigations means that conclusions about drivers of population dynamics often must be inferred using data from ex situ experiments on seeds and seedlings and in situ studies for other (better studied) conifers and some angiosperm tree species characterized by (analogous) low density in tropical forests. Our conclusions largely support the hypotheses proposed by Midgley and Bond (1989) and Wright (2002) and the conclusions of experimental studies of seedling physiology by Brodribb and colleagues (Brodribb and Hill, 1998, 1999, 2004; Brodribb et al., 2005). Podocarps are often most abundant at sites where the growth of competing species is limited. However, their high species diversity in the Malesian region and the broad range of vegetation types and environments in which they are found suggest that they are a highly successful plant group that has adapted to a remarkably broad range of environmental conditions. Nevertheless, detailed field investigations of species demographies (including genetic marker studies of pollen and seed dispersal) are required urgently in order to establish a sound understanding of tropical podocarp ecology and to explain their population dynamics and the circumstances facilitating their recruitment and persistence.

APPENDIX

TABLE 4.A1. Podocarp species of the tropical and subtropical Malesian region. Data were compiled from de Laubenfels (1969, 1985, 1987, 1988, 2003, 2005), Silba (1986, 1987), Enright and Hill (1995), Farjon (2008), and the Gymnosperm Database, http://www.conifers.org/index.html.

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
Acmopyle Pilg.																								
A. pancheri	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. sahniana Buchh. & Gray	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dacrycarpus (Endl.) de Laub.																								
D. cinctus (Pilg.) de Laub.	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. compactus (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. cumingii (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	1	-	-
D. expansus de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. imbricatus (Blume) de Laub.	-	1	-	1	1	-	1	1	1	1	1	1	1	1	1	-	-	-	-	-	1	1	-	1
D. kinabaluensis (Wassch.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
D. steupii (Wassch.) de Laub.	-	-	-	-	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
D. vieillardii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dacrydium Soland.																								
D. araucarioides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. balansae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(continued)

TABLE 4.A1. (*Continued*)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
D. beccarii Parl.	-	-	-	-	1	-	1	1	1	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-
D. comosum Corner	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
D. cornwallianum de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. elatum (Roxb.) Wallich	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	-	1	-	-	-	-	-	-	-
D. ericoides	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
D. gibbsiae Stapf.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
D. gracile de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
D. guillauminii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. leptophyllum (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. lycopodioides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. magnum de Laub.	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. medium de Laub.	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-
D. nausoriense de Laub.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. nidulum de Laub.	-	1	-	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. novo-guineense Gibbs.	-	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. pectinatum de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	-	-
D. spathoides de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. xanthandrum Pilg.	-	-	-	-	1	-	1	-	1	-	1	1	1	-	-	-	-	-	-	-	-	1	-	-
Falcatifolium de Laub.																								
F. angustum de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
F. falciforme (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
F. gruezoi de Laub.	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
F. papuanum de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F. taxoides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nageia Gaert.																								
N. fleuryi (Hickel) de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	1	-	-	-
N. formosensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
N. maxima (de Laub.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
N. motleyi (Parl.) de Laub.	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-	-	1	-	-	-	-	-	-	-
N. nagi (Thunb.) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
N. wallichiana (Presl.) O. Kuntze	-	-	-	-	-	-	1	1	1	1	1	1	1	-	-	1	-	1	1	-	1	1	-	1
Parasitaxus (Veillard)																								
P. usta	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllocladus L. C. et A. Rich																								
P. hypophyllus	-	-	-	-	1	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
Podocarpus L. Herit. ex Pers.																								
P. affinis Seeman	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. annamiensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
P. archiboldii Gray	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. atjehensis (Wassch.) de Laub.	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
P. beecherae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(*continued*)

TABLE 4.A1. (*Continued*)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
P. borneensis de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. bracteatus Blume	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
P. brassii Pilg.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. brevifolius (Stapf.) Foxw.	-	-	-	-	-	-	-	-	1	1	1	1	-	1	-	-	-	-	-	-	1	1	-	-
P. chinensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
P. chingianus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
P. colliculatus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. confertus de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. costalis C. Presl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
P. crassigemmis de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. decumbens	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. deflexus Ridley	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-
P. degeneri (Gray) de Laub.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. dispermus White	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. elatus R. Brown ex Endl.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. fasciculus de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
P. gibbsiae Gray	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. glaucus Foxw.	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
P. globulus de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. gnidioides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. grayae de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. insularis de Laub.	-	-	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. laubenfelsii Tiong	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. ledermannii Pilg.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. levis de Laub.	-	-	-	-	-	-	1	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. longefoliolatus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. lophatus de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
P. lucienii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. macrocarpus de Laub.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
P. macrophyllus (Thunb.) Sweet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1
P. micropedunculatus de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
P. nakaii Hayata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
P. neriifolius Don ex Lamb.	-	1	-	-	1	-	1	1	1	-	1	1	1	1	-	1	-	1	-	1	-	1	-	-
P. novae-caledoniae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. palawanensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
P. pallidus Gray	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. pilgeri Foxw.	-	-	-	-	1	-	1	1	1	-	1	-	-	-	-	1	1	-	-	-	1	1	-	-
P. polyspermus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. polystachyus R. Brown ex Endl.	-	-	-	-	-	-	1	1	-	-	1	-	1	-	-	1	-	-	-	-	-	1	-	-
P. pseudobracteatus de Laub.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. ridleyi (Wassch.) Gray	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-

(*continued*)

TABLE 4.A1. (*Continued*)

Genus and species	Tonga	Fiji	New Caledonia	Vanuatu	Solomon Islands	NE Australia	New Guinea	Moluccas	Sulawesi	Sunda Islands	Borneo	Sumatra	Malaya	Vietnam	Laos	Thailand	Cambodia	Assam	India	Nepal	China	Philippines	Taiwan	Burma
P. rotundus de Laub.	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
P. rubens de Laub	-	-	-	-	-	-	1	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
P. rumphii Blume	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-
P. salomoniensis Wassch.	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. smithii de Laub.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. spathoides	-	-	-	-	1	-	1	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
P. subtropicalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
P. sylvestris	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. teysmannii Miquel	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-
Prumnopitys Philippi																								
P. ferruginoides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
P. ladei (Bailey) de Laub.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Retrophyllum C. N. Page																								
R. comptonii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R. minus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R. vitiense (Seem.) C. N. Page	-	1	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sundacarpus (Buchh. & Gray) C. N. Page																								
S. amarus (Blume) C. N. Page	-	-	-	-	-	1	1	1	1	1	1	1	-	-	-	-	-	-	-	-	-	1	-	-
TOTAL SPECIES	1	8	20	2	11	6	31	15	15	8	30	16	14	7	3	5	3	2	1	1	12	20	6	4
TOTAL GENERA	1	5	8	2	3	4	8	7	6	6	7	5	4	4	3	2	3	2	1	1	4	7	2	3

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