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## Temperate and Tropical Podocarps: How Ecologically Alike Are They?

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**ABSTRACT.** With few exceptions, podocarps are specialists of nutrient-poor soils within temperate and tropical rainforests. They are locally abundant in some tropical mountains, especially near the tree line, and in the lowland tropics most are confined to heathlands and impoverished habitats, although some can persist in forest understories. The ecology of tropical podocarps is not well understood, so here we draw on literature from temperate regions to help characterize their niches. Temperate podocarps are effective at capturing and retaining nutrients at the expense of competitors. They are universally slow growing, but this is not necessarily an encumbrance on poor soils because competition for light is relatively weak. Temperate podocarps are often outcompeted on richer soils because several factors stack against them: they are ill equipped to compete with angiosperms in the race to occupy canopy gaps, there may be few sites for their establishment on the forest floors, and continuous regeneration by podocarps is seldom found in the forest understory because their growth is severely hampered by shading. We suggest that competition excludes imbricate-leaved podocarps from most lowland tropical forests, whereas broad-leaved species with anastomosing veins (*Nageia* and some *Podocarpus*) are so shade tolerant that they regenerate beneath closed canopies.

### INTRODUCTION

In 1989, Bond revisited an old but unresolved question: why were conifers pushed out of the lowland tropics and mesic temperate regions by angiosperms as they diversified and expanded in range during the Late Cretaceous? Previously, the leading hypothesis was that the evolution of flowers had given angiosperms overwhelming reproductive superiority over conifers: the wasteful process of wind pollination was usurped by directed pollination by animals (Raven, 1977). Bond (1989) and Midgley and Bond (1991) challenged the prevailing view, hypothesizing instead that the physiological traits of conifers made

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them inherently slow growing as seedlings. These traits place them at a competitive disadvantage during the regeneration phase of the life cycle but help them survive in extreme environments, including cold, droughts, nutrient-poor soils, poorly drained soils, and deep shade.

Two decades after Bond's "slow seedling" hypothesis, the latest physiological evidence indicates that podocarps are universally slow growing. Podocarps have long-lived leaves and low specific leaf areas, traits always associated with low photosynthetic capacity per unit leaf mass (Wright et al., 2004). They have lower photosynthetic capacity than angiosperms of comparable specific leaf area (Lusk, this volume). Using a global database of wood densities, we find that podocarps have denser wood than other conifers (Figure 7.1); this trait is associated with podocarps having narrower tracheids (Pittermann et al., 2006a; Lusk, this volume) and results in high hydraulic resistivity and low photosynthetic capacity per unit leaf area (Feild and Brodrribb, 2001). In lowland cool temperate forests, diameter growth of podocarp trees is approximately half that of angiosperm trees under similar conditions (Ogden and Stewart, 1995; Bentley, 2007). In subalpine shrublands, podocarps grow more slowly than several angiosperms (P. Wardle, 1963a). Podocarps are slower growing than other commercially valuable timber species (Bergin, 2000). For example, *Podocarpus totara* seedlings with an initial mean height of 0.85 m reached just 2.9 m after 6 years and 5.5 m after 11 years in a provenance trial on fertile soils under frost-free conditions (Bergin et al., 2008), whereas *Pinus radiata* reaches heights up to 30 m after 17 years (Beets and Kimberley, 1993). Seedlings of *Lagarostrobos franklinii* in Tasmania grow at just 2.3 cm yr<sup>-1</sup>, approximately a third of the rate of the angiosperm tree *Eucryphia milliganii*, which grows in nearby forests (Jennings et al., 2005). Podocarp seedlings are outpaced by angiosperms and even by tree ferns when growing on rich soils in southern New Zealand: height growth under optimal conditions is 3–7 cm yr<sup>-1</sup> versus 11–17 cm yr<sup>-1</sup> for subcanopy angiosperms and ~10 cm yr<sup>-1</sup> for tree ferns (Gaxiola et al., 2008; Coomes et al., 2009). We found no examples of fast-growing podocarps.

The notion that conifers are well equipped to cope with extreme environments remains unchallenged, but the mechanisms by which conifers are competitively disadvantaged in "productive" habitats are still a topic of debate. In the case of podocarps, there is considerable doubt over whether they can even be described as disadvantaged in lowland tropical habitats since a considerable number of shade-tolerant podocarps grow in the shade of tropical forests (e.g., Hill and Brodrribb, 1999). The ~30 species of

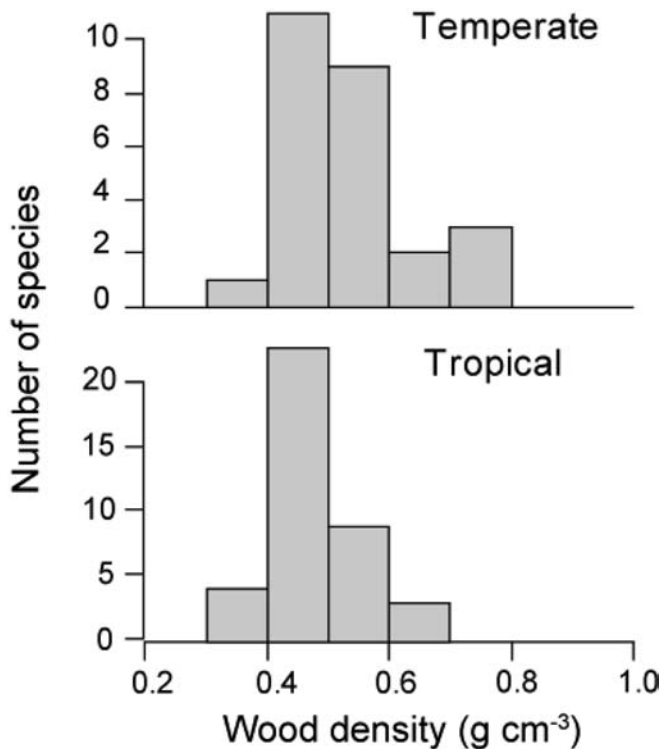


FIGURE 7.1. Wood density (oven-dry mass/fresh volume) of podocarp species from temperate and tropical regions (extracted from a global database; Chave et al., 2009). The Podocarpaceae have a greater mean wood density than six other conifer families ( $0.50 \text{ g cm}^{-3}$  vs. mean of  $0.45 \text{ g cm}^{-3}$ ;  $F_{7,260} = 9.7$ ,  $P < 0.001$ ) and a similar mean density to the Taxaceae ( $0.53 \text{ g cm}^{-3}$ ). Tropical podocarps have a significantly lower wood density than their temperate relatives ( $0.48 \pm 0.01$  vs.  $0.54 \pm 0.02 \text{ g cm}^{-3}$ ;  $t = 2.1$ ,  $P = 0.03$ ).

podocarps found in cool temperate forests have received much more attention from ecologists than the ~150 species of tropical and warm temperate forests. Can our understanding of the ecology of these temperate podocarps inform us about the distribution and dynamics of their tropical cousins? We start by discussing what types of habitats are occupied by temperate podocarps and why they are not observed in the full range of high-stress habitats occupied by conifers as a whole. We then explore the reasons why temperate podocarps often achieve dominance on nutrient-poor soils and why the exceptions prove the rule. We look at the regeneration strategies of temperate podocarps in shaded habitats and how these help explain the presence and persistence of some species in more nutrient-rich forests. These analyses lead us back to

a discussion of the ecology of tropical podocarps and why they are relatively uncommon in the lowlands.

### LIMITS TO GEOGRAPHIC DISTRIBUTION: INTOLERANCE OF COLD AND DROUGHT

Podocarps prevail mostly in climates that are cool and wet. However, they do not tolerate extreme cold as well as Northern Hemisphere conifers: none can withstand temperatures below  $-20^{\circ}\text{C}$ , whereas 88% of 117 Northern Hemisphere conifer species can do so (Figure 7.2; Bannister, 2007). Podocarps seldom form the tree line in temperate mountains but do so in tropical mountains. Instead, *Nothofagus* species often form tree lines in cool temperate South America, New Zealand, and Tasmania; podocarps are present but seldom form significant components of these forests (Wardle, 2008). Some temperate podocarps occur almost exclusively above tree lines as shrubs or prostrate woody plants in alpine ecosystems in New Zealand (Wardle, 1991) and Tasmania (Kirkpatrick, 1997). Perhaps differences in present and past climate have reduced the need and opportunity for the evolution

of traits conferring tolerance of extreme cold. Southern Hemisphere oceans act as vast heat buffers that moderate land temperatures, resulting in milder climates than in the Northern Hemisphere. The Southern Hemisphere was also less extensively glaciated during the Pleistocene (Sakai et al., 1981). Mild climates throughout much of the evolutionary history of the Southern Hemisphere may be responsible for its paucity of cold-tolerant trees: New Zealand's tree lines, at 1,200–1,300 m, are about 500 m lower than continental tree lines at equivalent continental latitudes (Körner and Paulsen, 2004).

Although podocarps are ill equipped to survive in extreme cold, they are relatively well protected against moderate frosts experienced in their current ranges. Frosts in New Zealand's North Island damage the dominant shade-tolerant angiosperm (*Beilschmiedia tawa*) but have no apparent effect on co-occurring podocarps (Kelly, 1987). Pot-grown podocarp seedlings are more tolerant of sub-zero temperatures than angiosperms taken from the same region (Bannister and Lord, 2006). Hardiness of *Podocarpus totara* in New Zealand has a strong genetic basis, with genotypes from the coldest regions being most hardy, suggesting that populations have evolved in response to

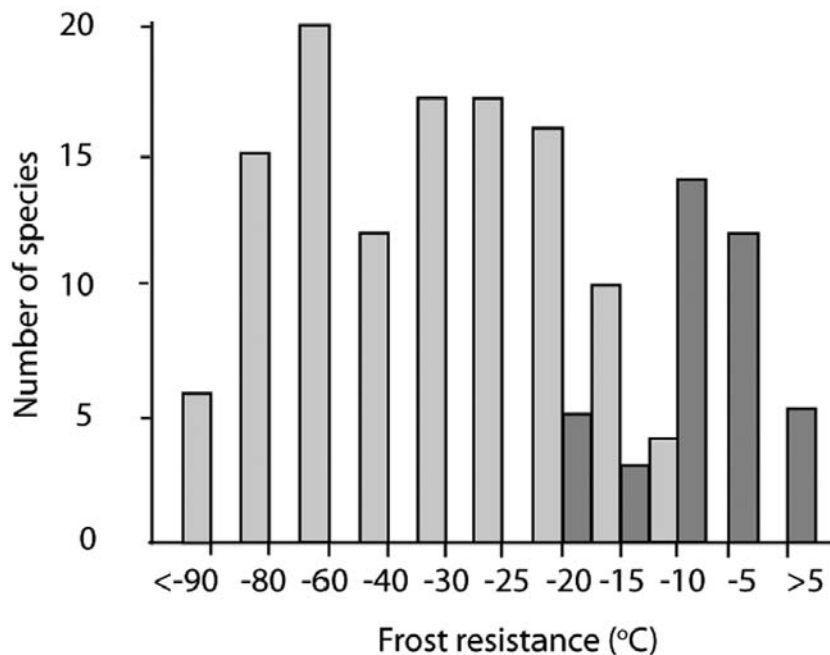


FIGURE 7.2. Frost resistance of conifers from the Northern (light gray) and Southern (dark gray) hemispheres, redrawn from Bannister (2007). Frost resistance was quantified by calculating the temperature at which half of the leaves are damaged by the effects of cold.

environmental pressures (Hawkins et al., 1991). Their frost hardiness appears to come at a cost, in that maximum growth rates of high-latitude genotypes are slower (Bergin et al., 2008). Angiosperms in Tasmanian montane heaths suffer much greater loss in xylem conductivity after being frozen and thawed (17%–83%) than do conifers (<12%), primarily, it seems, because bubbles in the xylem conduits formed during the freeze-thaw cycle are more easily redissolved in the narrow tracheids of conifers than in the wider vessels of angiosperms (Feild and Brodribb, 2001).

Few temperate podocarps grow in dry regions, in contrast to other conifers, and this intolerance can be traced to their vascular systems (see also Brodribb, this volume). Exceptions include *Afrocarpus falcatus* in drier regions of southern Africa (Adie and Lawes, this volume), *Podocarpus drouynianus* in Western Australia (Ladd and Enright, this volume), and *Halocarpus bidwillii*, *Phyllocladus alpinus*, and *Podocarpus hallii* in the dry lowland forests of New Zealand (~400 mm yr<sup>-1</sup>; Bergin, 2000; McGlone, 2001). Drought damages plants if the tension within water columns of the vascular system gets so large (i.e., the water potential gets so low) that cavitation occurs or if conduits implode (Tyree and Sperry, 1989). Plants from dry regions, such as conifers in the Pinaceae and Cupressaceae, withstand high tensions within their vascular systems by having thick tracheid walls that prevent implosion and “plugs” (torus margo) within pit membranes that prevent air bubbles from moving through the vascular system (Pittermann et al., 2006b). However, podocarps are peculiar among conifers in being susceptible to embolism at relatively low tensions, despite having thick tracheid walls (Pittermann et al., 2006b) and having relatively high hydraulic resistance across pit membranes (Pittermann et al., 2006a). It may also be the case that sclereids in podocarp leaves are vulnerable to implosion under tension (Brodribb, this volume). Plants can avoid damage by early closure of stomata, but we found no studies of stomatal responses in podocarps. Podocarps have long-lived leaves, so they are unable to drop all their leaves during dry periods in the way that many drought-deciduous angiosperms do. In one example, *Podocarpus totara* lost many leaves during a drought year, produced shorter leaves, and maintained high internal water potential but fared less well than drought-tolerant angiosperms (Innes and Kelly, 1992).

## TOLERANCE OF NUTRIENT-POOR SOILS

With a few important exceptions, podocarps in the cool temperate regions achieve greatest abundance on the

poorer soils and/or in open habitats. In the coastal range of Chile, two podocarps are most common on shallow mica schists and poorly drained sites (Lusk, 1996), and *Lepidothamnus fonkii* has a dwarf habit and grows in *Sphagnum* bogs (Gardner et al., 2006). In Japan, *Nageia nagi* occurs on thin soils derived from granite on Yakushima (Kohyama and Grubb, 1994), but it is not restricted to poor soils. In southeastern Australia, *Podocarpus lawrencei* occurs on acidic soils on granite and weathered sedimentary rocks, achieving greatest abundance on skeletal soils (Barker, 1991). In New Zealand, podocarps often achieve greatest abundance on poor soils, as shown by investigations on two soil chronosequences: a series of deglaciated terraces near the Franz Josef Glacier and a series of uplifted marine terraces in southern Fiordland. On both chronosequences, plant-available phosphorus becomes depleted on the older sites, and podocarps become increasingly abundant on these impoverished soils, with some species restricted to them (Richardson et al., 2004; Coomes et al., 2005). Bond (1989) proposed that conifers are successful on poor soils because they are almost unrivalled in their tolerance of extreme environments and because competition for resources is neither intense nor important; conifers are stereotyped as “stress tolerators” in the competitor–stress tolerator–ruderal triangle of Grime (1977). Here we argue that podocarps possess traits that allow them not only to tolerate poor soils but also to be successful competitors for belowground resources.

## EFFICIENT CAPTURE OF NUTRIENTS

Fungal hyphae have high area to mass ratios, making them more efficient than roots at foraging for immobile nutrients. Podocarps rely heavily on endomycorrhizal symbionts for nutrient uptake (Baylis, 1969; Russell et al., 2002). Fine roots have low specific root length (Gaxiola et al., 2010) and are heavily infected by mycorrhizal fungi (up to nearly 100% of root length; Dickie and Holdaway, this volume). Podocarps on the Franz Josef chronosequence had lower foliar nitrogen to phosphorus ratios than ferns or angiosperms on the phosphorus-impoverished soils, suggesting that they were better able to extract soil phosphorus (Richardson et al., 2005). Angiosperm species from podocarp-rich forests are also heavily infected by arbuscular mycorrhizas (Hurst et al., 2002), but very little is known about the comparative efficiency of these groups. Slow-growing conifers from the Northern Hemisphere allocate a large proportion of their net primary productivity to roots and ectomycorrhizal fungi, particularly when nutrients are in short supply (Hobbie, 2006). The same may

be true of podocarps: Whitehead et al. (2004) concluded that *Dacrydium cupressinum* in New Zealand swamp forests allocate a high proportion of total carbon belowground, on the basis of the predictions of a process-based simulation model. New Zealand podocarp seedlings have a higher root to shoot ratio than many angiosperm trees, particularly when grown in nutrient-poor soils.

#### INCREASED NUTRIENT RETENTION OF LONG-LIVED LEAVES

Species associated with nutrient-poor soils often have long-lived leaves (Grime, 1977; Chapin, 1980; McGlone et al., 2004) because a long life span reduces the annual rate of mineral nutrient loss via abscission (Monk, 1966). Plants salvage only about 50% of nitrogen and 60% of phosphorus from leaves during abscission (although there is great variability among species), so retaining leaves is strongly advantageous in situations where recapturing nutrients is costly (Aerts, 1995). Podocarp leaves have long life spans compared with angiosperm associates; Gaxiola (2006) observed that four podocarps species from the Waitutu chronosequence in southern New Zealand had a mean leaf life span of 3.1 years, compared with 1.5 years for 11 angiosperm species (nine of which were evergreen). Lusk (2001) measured leaf life spans of several Chilean species, including the following podocarps: *Podocarpus nubigenus* (7.3 years), *Podocarpus salignus* (3.2 years), and *Saxegothaea conspicua* (4.2 years). Podocarp leaves contain significant quantities of terpenes (Brophy et al., 2000), which are known to deter herbivores. However, whether podocarps are better defended than angiosperm is difficult to judge objectively because terpenes are just one of the armory of defenses that plants deploy.

#### LONGEVITY AND NUTRIENT RETENTION

Some temperate conifers, including podocarps, have much longer life spans than co-occurring angiosperm trees (Wardle, 1991; Enright and Ogden, 1995). This is especially the case for some New Zealand podocarps (Lusk and Ogden, 1992; Bentley, 2007) and *Lagarostrobos franklinii* in Tasmania (Gibson and Brown, 1991). However, great longevity is not a feature of podocarps, whereas it is of other conifers in the same forests (e.g., *Cryptomeria japonica* and *Tsuga sieboldii* in Japan, *Fitzroya cupressoides* in Chile, and *Picea balfouriana* in China). A tree releases nutrients back to the soil upon its death, so a long life span is advantageous in situations where regaining those nutrients requires intense competition with neighbors (Ogden and Stewart, 1995; Coomes et al., 2005). A long life span

requires wood that is strong and resistant to boring insects and rot. Podocarps have denser wood than other conifers (Figure 7.1), indicating that the wood is likely to be mechanically strong (Chave et al., 2009). Many podocarp species are prized for their timbers because they are resistant to rot, and powerful antimicrobial chemicals have been isolated from the bark of several *Podocarpus* species (Abdillahi et al., 2008). An array of diterpenoids within bark (Cox et al., 2007), as well as the deposition of phenolics in specialized parenchyma cells (Hudgins et al., 2004), provides robust defense against insects.

#### ECOSYSTEM ENGINEERS THAT STARVE NEIGHBORS OF NUTRIENTS

The tough fibrous leaves of New Zealand's podocarps are slow to decompose (Wardle et al., 2008; Hoorens et al., 2010), resulting in the accumulation of organic matter within soils, an increase in the ratios of carbon to phosphorus and nitrogen to phosphorus in soil, and effects on community structure of soil microflora (Wardle et al., 2008). Nutrients are sequestered within the recalcitrant organic matter. Locking up nutrients in this way is an effective means of competing for nutrients if competitors are relatively intolerant of extreme nutrient shortage or less able to access organic nutrients. In effect, podocarps may engineer their local environment to their own advantage.

#### TOLERATORS OF SOIL ANOXIA

Nutrient-poor soils in high rainfall regions are often poorly drained as a result of subsoil cementation. Species that tolerate low concentrations of soil oxygen and mobilization of toxic ions are advantaged under these conditions. A pot experiment with three New Zealand podocarps showed them to survive well, with much reduced growth, under waterlogged conditions (Gaxiola et al., 2010). The prevalence of conifers in waterlogged sites, both in New Zealand and in other temperate forests, appears to result from various morphological and biochemical adaptations (Crawford, 1987). One New Zealand podocarp, *Manoao colensoi*, produces aerenchyma in its roots that carries air down to submerged fine roots (Molloy, 1995), but no other examples of this in podocarps are known. The reduced stature of podocarps associated with bogs (e.g., *Lepidothamnus intermedius* and *Halocarpus biformis* in New Zealand) may result from a lack of deep anchoring roots in anoxic soils, without which woody plants are unable to grow tall (Crawford et al., 2003).



REDUCED IMPACT FROM ASYMMETRIC  
COMPETITION FOR LIGHT

Podocarps are slow growing, which is not necessarily disadvantageous on poor soils, where resource limitations reduce the potential for fast growth regardless of a species' genetic potential. Forests on nutrient poor and waterlogged soils often have comparatively low leaf area indices and intercept less light (Coomes and Grubb, 2000). For example, 1.5% of incoming photosynthetically active radiation makes its way to the forest floor of phosphorus-rich soils in southern New Zealand, 4.6% gets through on phosphorus-depleted soils, and 16% gets through on even poorer sites (Coomes et al., 2005). The growth of podocarps is hardly influenced by competition from taller neighbors on the poor soils (e.g., Figure 7.3a). As long as competition for light is not intense, podocarps may exclude other plants from nutrient-poor soils through belowground competition (see Coomes and Grubb, 2000).

CANOPY ARCHITECTURE SUITED TO  
GROWTH IN THE OPEN

Genera of podocarps associated with poor soils often have small, scalelike leaves held on upright or pendent stems (*Dacrydium*, *Halocarpus*, *Lepidothamnus*, *Manoao*, *Microcachrys*, and *Microstrobos*) or have whorls of leaves that overlap. Steeply inclined or clustered leaves reduce light interception at the top of the canopy, allowing light to "trickle down" to lower leaves. This increases whole-plant photosynthesis because the uppermost leaves receive near-optimal rather than excessive light levels, while leaves at the bottom of the canopy get a greater share of resources (Horn, 1971). The world's fastest-growing trees (*Betula*, *Casuarina*, and some *Pinus* and *Eucalyptus*) have this canopy architecture, at least once past the seedling stage. However, clumped and pendent leaves are inefficient at scavenging light in deeply shaded understories and ineffective when competing for light against fast-growing neighbors (Leverenz et al.,

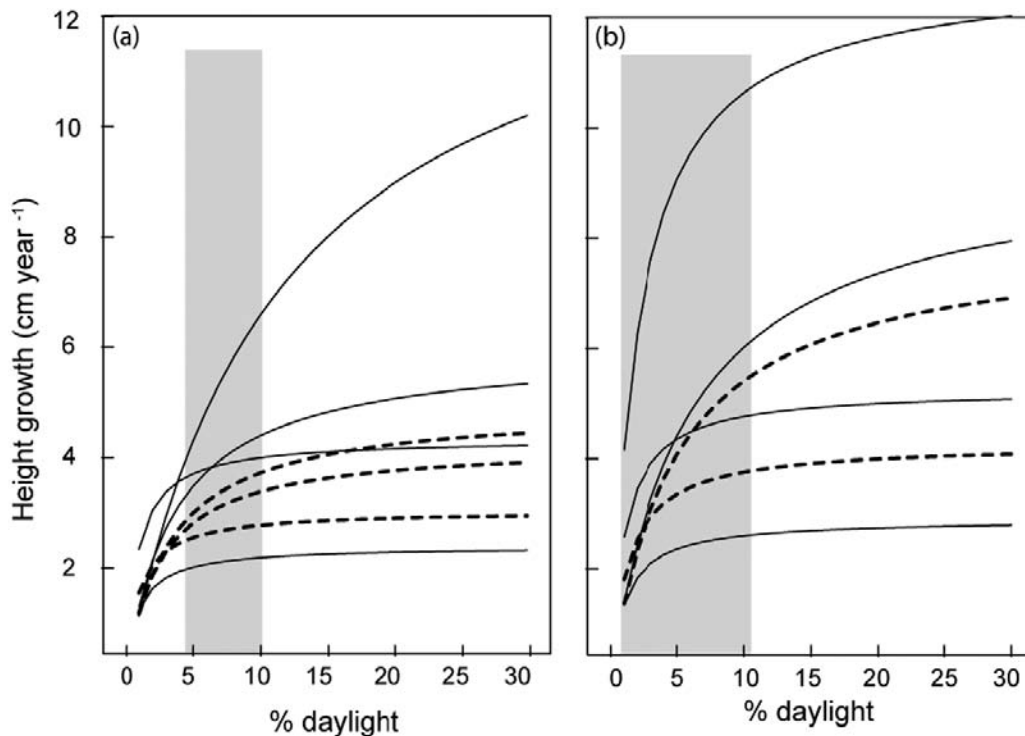


FIGURE 7.3. Height growth of podocarp (dashed line) and angiosperm (solid line) tree seedlings in response to light on (a) phosphorus-depleted terraces versus (b) alluvial terraces in southern New Zealand. The gray bars indicate the percentage daylight typically found at 1.35 m above ground under the canopy, based on the 20th and 80th percentiles of light measurements (redrawn from Coomes et al., 2009).

2000; Pickup et al., 2005). Therefore, these architectures are uncommon in infrequently disturbed communities growing on nutrient-rich soils where competition for light is intense (Horn, 1971).

#### EFFICIENT USE OF LIGHT

The efficient use of whole-canopy light has been investigated in detail for *Dacrydium cupressinum*, which has scalelike leaves positioned on pendent shoots; closed stands have a leaf area index of only  $2.0 \text{ m}^2 \text{ m}^{-2}$  and intercept only 79% of available photosynthetically active radiation when growing on acidic, poorly drained soil (Whitehead et al., 2002). Clumping of leaves within the canopy of *Dacrydium*-dominated forest reduces canopy light interception by 5% but increases canopy photosynthesis by 8% through increased light use efficiency (Walcroft et al., 2005). Even though leaves in the upper crown of *Dacrydium* on poor soils have a maximum rate of carboxylation activity (half-surface leaf area basis) that is only 24% of that of similarly positioned leaves within an oak woodland on nitrogen-enriched soils in summer, the annual carbon uptake rate of the podocarp forest was only 14% lower than that of oak because of its canopy organization (Whitehead et al., 2004). The canopy architecture and evergreen leaves, which continued to take up carbon in winter, contributed to a higher-than-expected carbon uptake rate.

#### SUMMARY

Podocarps are successful on poor soils because they are well adapted to acquiring and retaining nutrients. It may be that podocarps function similarly to slow-growing conifers from the Northern Hemisphere, allocating a large percentage of net primary productivity belowground and thereby enabling their roots systems (and associated mycorrhizas) to forage exhaustively for soil nutrients. In addition, their long-lived leaves, durable wood, and slowly decomposing litter ensure that hard-earned nutrients are not relinquished to competitors. Inherently slow stem growth may not be a serious encumbrance when nutrients are in short supply because asymmetric competition for light is weak, so outgrowing neighbors is not strongly advantageous. Any disadvantages that accrue from slow growth are offset by effective nutrient recovery and retention, longevity, and strength to resist catastrophic disturbance. Scalelike leaves are advantageous in terms of whole-plant photosynthesis in open habitats.

## REGENERATION PROCESSES

### RESPONSES TO FOREST DISTURBANCE

Much attention has been given to the role of disturbances in allowing species with differing regeneration niches to coexist within forests (Poorter and Bongers, 2006). In the context of Southern Hemisphere conifers, Ogden and Stewart (1995) recognized three categories of regeneration response to disturbance: (1) "Catastrophic regeneration" occurs in the aftermath of infrequent massive disturbances (e.g., earthquakes, floods, fires, and cyclones) and is characterized by a pulse of establishment after which no further establishment is possible; at the landscape scale, catastrophic regeneration gives rise to large patches ( $>1,000 \text{ m}^2$ ) of similarly aged trees and strong discontinuities in age structure within and among patches. (2) "Gap-phase regeneration" occurs in smaller gaps ( $<1,000 \text{ m}^2$ ) created by the death a single tree or a few trees; it is characterized by smaller patches and fewer discontinuities in age. (3) "Continuous regeneration" occurs when seedlings and saplings are capable of growing and surviving in the shade of an intact canopy. Typically, these shade-tolerant trees edge slowly upward in the shade, growing more quickly if openings appear in the canopy above them (e.g., Uhl et al., 1988); near-continuous regeneration gives rise to all-aged population structures, composed of many small stems and successively fewer stem in larger age classes.

Temperate podocarps vary greatly in shade tolerance. Some have developed flattened leaves arranged within planes, a shade adaptation that may have arisen in response to changes in light transmissions brought about by the evolution of shade-bearing angiosperms in the early Cenozoic (Hill and Brodribb, 1999; Brodribb and Hill, 2003a, 2003b). Podocarps with shade-tolerant leaf morphology also have shade-tolerant physiology (Brodribb, this volume) and are sometimes capable of continuous regeneration. For example, *Nageia nagi* has large, flattened leaves and regenerates nearly continuously within Japanese warm temperate rainforests (Kohyama, 1986), and *Prumnopitys ferruginea* has shade-tolerant morphology and is quite capable of establishing without multiple-tree gaps in New Zealand (Figure 7.4; Duncan, 1993; Lusk and Smith, 1998; Bentley, 2007). Other species have tiny, scalelike leaves held on upright stems and are unable to tolerate prolonged shade: when adult, *Halocarpus biformis*, a small tree with imbricate scale leaves, is most frequent in open habitats, such as the margins of bogs (Figure 7.4).

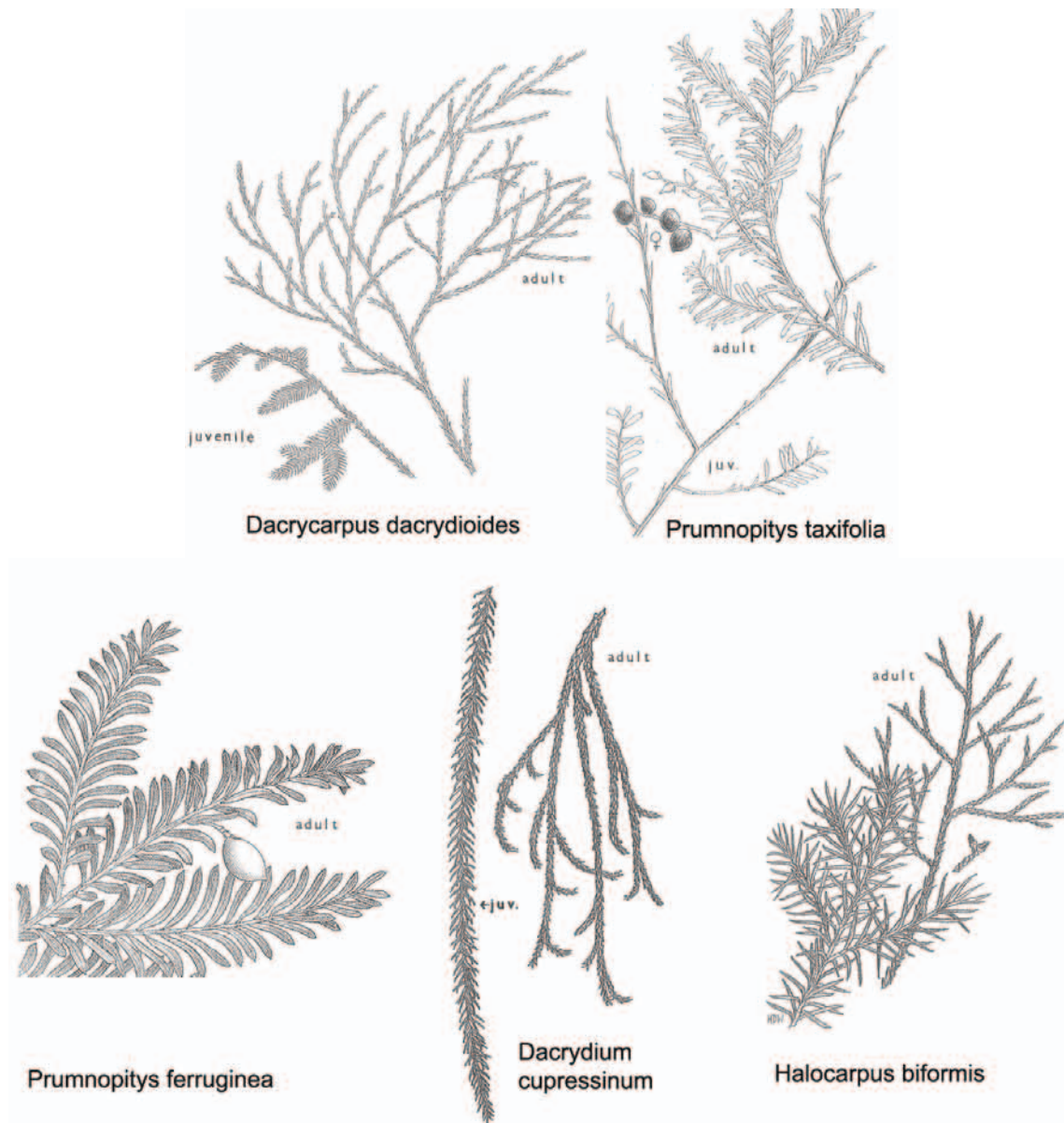


FIGURE 7.4. Juvenile and adult foliage of contrasting podocarps from New Zealand. Drawings modified from Wilson (1982) and reproduced with kind permission of the author and publisher.

#### REGENERATION PROCESSES IN RELATION TO SOIL FERTILITY

Regeneration response depends not only on a species' inherent shade tolerance but also on the light conditions in the understory of the forest. A species capable of regenerating continuously under open forests on poor soils may struggle to regenerate under dense forests on richer soils. For example, two podocarps that grow in the

Chilean coastal range, *Podocarpus nubigenus* and *Sax-egothaea conspicua*, are considered the most shade tolerant of all conifers in temperate South America (Donoso, 1989). They attain greatest abundance on shallow soils (poorly drained sites in the lowlands, ridges, and shallow mica schist at higher altitudes). The main angiosperms at these sites (*Nothofagus nitida* and *Weinmannia trichosperma*) have open canopies under which the podocarps regenerate: there are many seedlings and saplings in the



forest understory, and the tree populations have reverse-J age distributions (Lusk, 1996; Gutiérrez et al., 2004). However, at sites where shade-casting angiosperms such as *Dasyphyllum diacanthoides* and *Laureliopsis philippiana* are common, the podocarps are less abundant and regeneration discontinuous (Lusk, 1996). At sites where shade-tolerant angiosperms are dominant, the podocarps are excluded altogether (e.g., Armesto and Fuentes, 1988). In Tasmania, *Lagarostrobos franklinii* appears to regenerate along rivers that frequently flood but rarely penetrates into closed rainforest (Gibson and Brown, 1991). In South Africa, *Podocarpus latifolius* grows and survives well in the understory of angiosperm-dominated warm temperate forest in the Drakensberg Mountains (5.5% light transmission to forest floor; Adie and Lawes, 2009a) but is unable to regenerate beneath coastal subtropical forest in KwaZulu-Natal, through which only ~1% light is transmitted (Adie and Lawes, 2009b). However, the regeneration success of *P. latifolius* is not simply determined by competition for light: seedlings are unable to establish under mature podocarp forest, even though 7.5% light penetrates to the forest floor, apparently because grasses and/or mature trees exclude seedlings by belowground competition (Adie and Lawes, 2009a). Various other studies indicate that temperate podocarps fail to regenerate beneath parent trees (e.g., Norton, 1991; Cameron, 1960; Ogden and Stewart, 1995).

#### WHY SHADE-TOLERANT PODOCARPS FAIL TO REGENERATE IN THE SHADE

Many podocarps persist in deep shade (e.g., mortality rates in New Zealand lowland forest were just 1% per year; Smale and Kimberley, 1986), but survival counts for little unless accompanied by height growth. Height growth of New Zealand podocarps is strongly suppressed by shading (e.g., Smale and Kimberley, 1986; Ebbett and Ogden, 1998; Coomes et al., 2009; Figure 7.3), limiting opportunities for continuous regeneration in forest understories. For instance, *Podocarpus hallii* seedlings in a cool montane rainforest in New Zealand have an annual mortality rate of just 2.7%, meaning that about 5% of seedlings live for at least 100 years, but height growth is so slow that virtually no individuals get past the seedling stage in the shade; consequently, most regeneration is restricted to landslides (Bellingham and Richardson, 2006). Similarly, *Dacrydium cupressinum* seedlings had an annual mortality rate of 10% and a height growth of 1.5–2.5 cm yr<sup>-1</sup> in a lowland New Zealand forest on highly leached soils, indicating that height growth is insufficient

for seedlings to regenerate continuously in these forests (Coomes et al., 2009; Kunstler et al., 2009). Instead, *Dacrydium cupressinum* requires progressive overstory mortality (Six Dijkstra et al., 1985; Lusk and Ogden, 1992; Lusk and Smith, 1998; Bentley, 2007) or catastrophic disturbance (e.g., Duncan, 1993; Smale et al., 1997) in order to regenerate. Even highly shade-tolerant podocarps such as *Prumnopitys ferruginea* can struggle to get beyond the seedling stage in lowland forests (Smale et al., 1997), and stands of this species have a discontinuous age structure at some sites (e.g., Lusk and Ogden, 1992). The important implication is that shade tolerance assessed from leaf physiology does not necessarily equate with ability to regenerate continuously within a particular habitat. The latter depends upon the degree of shade cast by the forest as well as the physiological shade tolerance of the species and is affected by changes in shade tolerance with size (Kunstler et al., 2009).

#### RELIANCE ON CATASTROPHIC DISTURBANCE IN NUTRIENT-RICH HABITATS

Three species of podocarps dominate the alluvial floodplain forests of New Zealand, apparently contradicting the theory that podocarps are competitively excluded from nutrient-rich sites. *Dacrycarpus dacrydioides* is a dominant tree on poorly drained soils (Smale, 1984; Duncan, 1993; Norton, 1995), and *Prumnopitys taxifolia* and *Podocarpus totara* are dominant on better-drained soils (Esler, 1978; McSweeney, 1982). Establishment opportunities can be limited by near-continuous fern cover at some sites (Coomes et al., 2005), and although smaller-seeded angiosperms are able to take advantage of elevated sites such as fallen trunks and tree fern stems, the larger-seeded podocarps seldom establish in such niches (Lusk, 1995; Christie and Armesto, 2003; Lusk and Kelly, 2003; Gaxiola et al., 2008). Indeed, none of these podocarps can regenerate continuously beneath mature rainforest canopies (e.g., Urlich et al., 2005). Neither is gap-phase regeneration possible because tree fall gaps are colonized rapidly by fast-growing woody angiosperms, ferns, and herbaceous plants, leaving few opportunities for slow-growing trees (Coomes et al., 2005, 2009). Instead, slow-growing podocarps are able to persist in the floodplain forests in western South Island rainforests by regenerating after catastrophic disturbances, such as those resulting from debris triggered by major movements of faults in the Southern Alps and associated floods (Wells et al., 2001; Cullen et al., 2003). The long life span of these podocarps allows them to persist from one rare catastrophic disturbance to

the next (Enright and Ogden, 1995; Veblen et al., 1995; Lusk and Smith, 1998). Currently, regeneration failure and ageing populations are observed over most of their range (Holloway, 1954; Wardle, 1963b), and in some regions this could be because the last major movement of the Alpine fault was nearly 300 years ago (AD 1717; Wells et al., 1999). An event every few hundred years is sufficient to maintain conifers as dominant elements (i.e., a “storage effect” sensu Chesson, 2000). However, catastrophic regeneration of podocarps may be uncommon outside New Zealand. Other species, such as the two Japanese species in typhoon-affected forests, may benefit from disturbance events by being relatively resistant to damage (see Dalling et al., this volume).

Floodplain podocarps grow well in bare mineral soil (e.g., Wardle, 1974) and presumably benefit from reduced competition with angiosperms on fresh alluvium. However, they are not pioneer species, as they arrive after an initial wave of colonization by early successional plants (e.g., Reif and Allen, 1988). Woody plants such as *Aristotelia serrata* and *Melicytus ramiflorus* grow quickly and form an open canopy; birds feed on the pseudo-arils of podocarps and disperse the seeds into these early successional communities (Beveridge, 1964; Wardle, 1991). The podocarps grow up beneath the open-crowned bushes and trees and eventually overtop them (Beveridge, 1973), continuing to colonize sites for many decades after disturbance (e.g., Wells et al., 2001). Interestingly, *Dacrydium dacrydioides* and *Prumnopitys taxifolia* undergo a major switch in leaf morphology at this stage, from having relatively broad leaves held in planes to having small leaves on pendant branches (Atkinson and Greenwood, 1989). These changes may be responses to increased light and exposure once the trees have overtopped the early successional community (McGlone and Webb, 1981). New Zealand has a disproportionate number of long-lived podocarps that rely on flooding, although they are also represented in Tasmania and mainland Australia (Barker, 1991; Gibson and Brown, 1991).

#### INTOLERANCE OF FIRE

Fire disturbance is usually fatal for podocarps, although two Australian podocarps (*Podocarpus drouynianus* and *P. spinulosus*) resist fire by sprouting from belowground reserves (Chalwell and Ladd, 2005; Ladd and Enright, this volume) and *Halocarpus bidwillii* can regenerate after fire in New Zealand heathlands (Wardle, 1991). The increased frequency of fire since the arrival of humans is thought to be the major factor of range contraction of podocarps in Australia (Hill and Brodribb, 1999),

and it all but annihilated forests formerly dominated by podocarps in eastern New Zealand (McGlone, 2001). Podocarps lack traits found in fire-adapted coniferous lineages, such as serotinous cones, an ability to resprout from the roots, and highly flammable leaves and litter. Several *Podocarpus* species have thin bark, suggesting that their vascular cambium could be susceptible to damage during fire. Highly flammable myrtaceous shrubs are the early colonizers of burnt areas in the North Island of New Zealand; the shrublands are soon colonized by podocarps, but fire must be excluded for several decades in order for the trees to overtop the shrubland and form a dense forest (McKelvey, 1963; Ogden and Stewart, 1995; Wilmshurst and McGlone, 1996).

#### RESPROUTING

Tall podocarp species do not, in general, resprout following damage (Martin and Ogden, 2006). For example, in New Zealand forests there was no resprouting of *Dacrydium cupressinum* after logging, and regeneration was dominated by resprouts of the angiosperm tree *Weinmannia racemosa*, to the disadvantage of *D. cupressinum* (Baxter and Norton, 1989). Saplings of *D. cupressinum* were unable to recover after experimental clipping to simulate deer browse because they resprouted poorly (Bee et al., 2007). Typhoon-damaged trees of the podocarp *Nageia nagi* in southern Japan were also ineffective at resprouting, in contrast to many co-occurring angiosperm trees (Bellingham et al., 1996). Resprouting is more apparent for temperate podocarps from poor sites, which are often shrubs or small trees and exhibit multitemmed architecture. These include *Halocarpus bidwillii*, *Lepidothamnus intermedius*, and *Lagarostrobos franklinii*, all of which spread vegetatively in open habitats. By doing so, patches of *L. franklinii* may have persisted for 10,000 years, and trees within remnant populations are genetically homogeneous (Clark and Carbone, 2008). Another tree of open habitats, *Phyllocladus alpinus*, resprouts after wind damage (Martin and Ogden, 2006). A taller podocarp in Chilean rainforests, *Saxegothaea conspicua*, exhibits vegetative regeneration, which is crucial for its maintenance under shade-tolerant angiosperms in undisturbed stands (Veblen et al., 1980; Lusk, 1996).

#### SUMMARY

Podocarps are ill equipped to compete with angiosperms in the race for light in canopy gaps. Some species have evolved to tolerate prolonged shade, and these may regenerate continuously under relatively open-canopied

forest on poorer soils. However, few species can regenerate continuously under forests that are rich in shade-tolerant trees, tree ferns, bamboos, or ground plants because establishment sites are limited in these forests and onward growth is severely hampered. In New Zealand, three podocarp species dominate forests on rich alluvial soils—they do this by escaping competitors when fresh mineral surfaces are created by catastrophic disturbance events. These events may occur every few hundred years, and the long life spans of conifers allow them to persist from one event to the next.

## ECOLOGY OF TROPICAL PODOCARPS

The biogeography of tropical podocarps is dealt with in other chapters but can be summarized as follows: podocarps are dominant elements of forests on a variety of soils in the mountains of Papua New Guinea, Southeast Asia, and subtropical and tropical Africa but are not dominant in the mountains of northern Australia, New Caledonia, and Madagascar and are only locally dominant in South America. There are a few lowland species in Australasia, the Pacific Islands, India, Africa, and the Americas; these can dominate poor soils but are rare in other lowland forest types (P. J. Grubb, University of Cambridge, personal communication; Wade and McVean, 1969; Enright, 1995).

### TOLERANCE OF COLD AND HEAT

Tropical podocarps differ from those in temperate regions in being a major alpine element of tree lines over a wide area (e.g., New Guinea; Grubb and Stevens, 1985), indicating that they are among the least warmth-demanding trees in the tropics. They are also among the most tolerant, forming dense, almost pure stands immediately around frost hollow grassland (Grubb and Stevens, 1985). Like most temperate podocarps, they are excluded from dry regions: although *Afrocarpus falcatus* is common in relatively dry forests of Africa, the overwhelming majority of species are restricted to the wet tropics. Podocarps have easily distinguishable pollen, and the observation that tropical podocarps prevail mostly in climates that are cool and wet is frequently used by palynologists to reconstruct paleoclimates. Thus, the spread of podocarps into lowland Amazonia during Pleistocene glaciations suggests cooler conditions in the basin (Colinvaux et al., 1996), whereas the upward migration of podocarps into the páramo grasslands suggests a period of warmer climate in the Peruvian Andes between 8900 and 3300 BP. As a further example, the waxing and waning

of podocarp-rich rainforests across southeastern Australia during the late Pliocene and Pleistocene (Brodrribb and Hill, 2003b; Sniderman et al., 2007) and the Late Cretaceous (Gallagher et al., 2008) is interpreted in terms of shifts in rainfall patterns driven by Milankovitch cycles (greater summer insolation resulting in warmer tropical seas, bringing greater rainfall to the continent).

### SUCCESS ON POOR SOILS

Many tropical podocarps are restricted to poor soils. In the appendix we provide brief descriptions of 96 species of tropical, subtropical, and warm temperate podocarps, taken mostly from Earle (1997–2009). We categorized each species as either (1) restricted to outstandingly poor soils, (2) restricted to rich soils, or (3) found on both rich and poor soils. “Outstandingly poor soils” included ultramafic soils, podzolized sands, peats, and shallow soils associated with limestone, sandstone, coastal bluffs, and ridgetops. We also included species associated with tree lines in the outstandingly poor soils category, the soils being highly organic and probably with markedly low rates of nitrogen mineralization (P. J. Grubb, pers. comm.). We subdivided their habitats into montane and lowland rainforest species (montane is defined here as >1,000 m elevation in the tropics and >800 m in the subtropics and warm temperate regions).

Most tropical podocarps in Earle’s database are found in mountains (56%), so the majority of the species occupy cool climates. Several of these species (21) are described as locally common, dominant, or forming pure stands at high altitude, on ridges and sometimes in peats. They include *Dacrycarpus* (3), *Dacrydium* (7), and *Podocarpus* (9). Half of the montane species are also found in “normal” montane forests as well as on poor soils, but they are often less common when off the poorest soils: this group includes all seven species of *Dacrycarpus*. Nine species appear to be restricted to “normal” montane forests (i.e., they are not mentioned as growing on poor soils in their ecological descriptions).

In the lowlands, 11 species are restricted to extremely poor soils, 12 are common on poor soils but venture into forest on better soils, and 9 are found in “typical” lowland rainforest. The last group comprises three genera: *Nageia* (3), *Podocarpus* (5), and *Parasitaxus* (1). The *Nageia* species are shade-tolerant trees of warm temperate and subtropical forests (Kohyama, 1986) and are canopy species that are “scattered” and “often common” in the forest understory. The *Podocarpus* species are described as “scattered” and “locally common,” and all are subcanopy (~25 m tall), except *P. spinulosus*, which is a shrub restricted to sheltered coastal sites and gullies. Finally, *Parasitaxus usta* (New

Caledonia) is the only parasitic gymnosperm and never grows taller than 2 m; it persists in shade by virtue of the carbon it gains by parasitism on the roots of *Falcatifolium taxoides*. The 11 species restricted to poor soils are found on peat swamps, kerangas, and ultramafics; they include *Dacrydium* (3), *Falcatifolium* (2), and *Podocarpus* (6). Six of these species are small trees (<12 m tall).

Presumably, podocarps are successful on the poorest tropical soils for the same reasons as in temperate regions. The species restricted to the poorest soils are significantly shorter and have much smaller leaves than species of better soils (e.g., Aiba and Kitayama, 1999), with species associated with both soil types having intermediate height and leaf area (Table 7.1; significance based on analysis of variance). These patterns are observed in both lowland and montane forests. The trend is precisely as anticipated, given that asymmetric competition for light is less intense among plants growing on poor soils, so height growth is not as strongly advantageous, and small leaves held on upright stems are effective for whole-plant photosynthesis within open forest. In lowland and lower montane forests, the heights achieved by podocarps are unremarkable, but at high altitude the species are often emergent. The area of shade leaves (as a ratio of the area of sun leaves) was  $2.4 \pm 0.10$  ( $r^2 = 0.85$ ), with no evidence of variation among forest or soil types (Table 7.1). A shift from big, shade-tolerant juvenile foliage to smaller adult foliage is observed in many tropical podocarps, especially canopy emergents, just as seen in temperate species.

#### SUCCESS IN MOUNTAIN ENVIRONMENTS

It is not surprising that podocarps are prominent in tropical montane forests: these are the environments most similar to temperate environments in which they evolved

as a group (Morley, this volume). Nitrogen and phosphorus are likely to be increasingly limiting in the mountains (Grubb, 1977), to the benefit of podocarps. Podocarps may be particularly effective at photosynthesis in the persistently cloudy conditions often encountered on tropical mountains. Using a physiological modeling approach, Whitehead et al. (2004) found that carbon uptake by *Dacrydium cupressinum* in lowland New Zealand is greater than that of oak trees in the United States when conditions are overcast and the diffuse fraction of incoming radiation is high.

There is little published information on regeneration processes and size structure of tropical montane podocarp populations (but see other chapters in this volume). *Podocarpus urbanii* in Jamaican montane rainforests is most common on less-fertile soils, although not on highly acidic mor soils (Tanner, 1977). It exhibits continuous regeneration in these forests but does not have a reverse-J distribution (Bellingham et al., 1995). Jamaican forests are frequently affected by hurricanes, but *P. urbanii*, like the two podocarp species in typhoon-affected Japanese forests, is resistant to hurricane disturbance (Bellingham et al., 1995). Following hurricanes, the growth rate of *P. urbanii* is faster than that of angiosperm trees, possibly because it survives storms relatively unscathed (Dalling et al., this volume; E. V. J. Tanner, University of Cambridge, personal communication). In addition, abundant seedlings and saplings of podocarps are found in the understory of high-altitude forests in New Guinea (Wade and McVean, 1969), suggesting that the species are sufficiently shade tolerant to regenerate under the canopy. Aiba et al. (2004) compared 42 common species, including four podocarps, in a plot at 1,560 m altitude in Kinabalu Park, Borneo. Two podocarp species were most common on ridges (*Phyllocladus hypophyllus* and *Dacrydium pectinatum*), whereas the other two were less restricted by topography

**TABLE 7.1.** Relationship of mean height and mean leaf area of canopy of leaves to forest and soil type. All data were extracted from descriptions provided by Earle (1997–2009); *N* is the number of species contributing to each mean. Leaf areas were estimated from mean widths and lengths assuming an elliptical shape, and the largest height was used whenever a range was given.

Forest type	Soil	N	Height (m)	Leaf area (cm <sup>2</sup> )	Understory to canopy tree leaf area ratio
Tropical lowland	Poor soils	9	14.9 ± 2.8	4.7 ± 1.7	3.2 ± 0.8
	Mostly poor	11	25.5 ± 5.1	5.1 ± 3.5	3.1 ± 0.8
	Better soils	8	27.5 ± 4.8	9.0 ± 3.4	3.3 ± 1.3
Tropical montane and warm temperate	Poor soils	17	19.2 ± 2.7	1.9 ± 0.8	4.1 ± 0.6
	Mostly poor	14	24.6 ± 3.8	4.7 ± 1.6	2.3 ± 0.3
	Better soils	9	26.2 ± 3.6	4.1 ± 1.5	3.1 ± 1.0
Cool temperate	All soils	25	14.9 ± 2.8	1.1 ± 0.5	4.3 ± 0.9



(*Dacrycarpus imbricatus* and *Falcatifolium falciforme*). All podocarp species except *Falcatifolium falciforme* had a greater proportion of their crowns in exposed positions within the canopy than predicted by chance, suggesting that they were light demanding. In contrast, *Falcatifolium falciforme* had a greater proportion of its crowns in shaded positions and a population structure indicating that the species was shade tolerant (Kitayama et al., this volume).

#### RARITY IN LOWLAND TROPICAL SITES ON BETTER SOILS

Podocarps are absent from much of the lowland tropics, except on poor soils, although they are rare components of Australasian tropical lowland and lower montane forests (Enright, 1995). Two widespread species, *Podocarpus neriifolius* and *Nageia wallichiana*, reach densities of only 1–2 per hectare within the 700–1,500 m elevation band of New Guinean mountains and are usually observed as solitary trees with few seedlings nearby (Enright, 1995). We reason that three factors conspire to exclude podocarps: (1) The high leaf area index of the lowland tropical forests means that the understory is too deeply shaded to allow even the most shade tolerant of podocarps to regenerate, the exception being *Nageia* species, which have large, multiveined leaves (mean for lowland species = 48 cm<sup>2</sup>) similar to those of *Gnetum* (another gymnosperm of rainforest understories). (2) Podocarps are outcompeted in the race for light in tree fall gaps. Tropical podocarps may well grow faster than temperate relatives—their wood contains wider tracheids (Lusk, this volume) and is significantly less dense (Figure 7.1)—but it is inconceivable that they could compete with the growth of light-demanding angiosperms, which can reach upward of 1 m a year (e.g., Richards and Williamson, 1975). For example, a gap-demanding angiosperm, *Toona australis*, was found to have greater stomatal conductance and leaf-specific stem hydraulic conductivity than two tropical podocarps (*Nageia fleuryi* and *Podocarpus grayii*) and grew much more rapidly than the podocarps in full sun (1,300–1,800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Brodrigg et al., 2005). Finally, (3) opportunities for catastrophic regeneration are taken by angiosperms. Among the lowland tropical podocarps, two New Caledonian trees, *Dacrycarpus vieillardii* and *Podocarpus polyspermus*, appear to be exceptions and are maintained by disturbance, colonizing floodplains in a way similar to *D. dacrydioides* and *P. totara* in New Zealand (Jaffré, 1995). For most of the lowland tropics this niche is taken by angiosperm trees, some of which are long-lived (e.g., *Ceiba pentandra*). Other regeneration niches associated with disturbance seem to be taken by angiosperms. For example, the “shade-persistent

pioneer” strategy of the long-lived angiosperm tree *Alseis blackiana* in lowland rainforests in Panama (Dalling et al., 2001) is analogous to some long-lived podocarps (e.g., *Podocarpus totara*) in New Zealand rainforests.

Most tropical podocarp species are intolerant of fire, like their temperate cousins. In the Dominican Republic, fire virtually excludes *Podocarpus aristulatus* from forests above 1,800 m, which are dominated by *Pinus occidentalis*. Fires are prevalent during El Niño droughts in these forests (every seven years or so), and they also have lower temperatures and precipitation than the cloud forests at lower altitude (1,550–1,800 m), which do not support fire and in which *P. aristulatus* is the third commonest tree (Martin and Fahey, 2006; Martin et al., 2007). Similarly, the páramo grasslands of the Andes have spread in response to frequent burning during the last 8,000 years, and podocarps are now restricted to montane forests well away from the grasslands (Niemann and Behling, 2008). Increased fire frequency since the arrival of humans is thought to be the major driver of podocarp extinction in Australia (e.g., *Dacrydium* from tropical north Queensland; Lynch et al., 2007). A few tropical podocarp species are capable of persisting in habitats that burn. *Dacrycarpus compactus*, *Dacrycarpus expansus*, and *Dacrydium novo-guineense* are all locally prominent components of tree fern grasslands and thickets that occur near tree lines on tropical mountains, even though indigenous peoples burn these areas. Corlett (1984) noted that *Dacrycarpus compactus* has thick bark, which might afford it some protection.

## CONCLUDING THOUGHTS

Tropical and temperate podocarps function much as Bond envisaged: they are slow-growing tortoises. Most tropical species are restricted to montane forests with low total leaf area or lowland sites with exceptionally poor soils. Competition for light is less intense in such forests, and podocarps compete effectively by efficient capture and retention of nutrients. In addition, genera with small leaves held on erect/pendent stems may also achieve high rates of whole-plant photosynthesis in open canopied forests that prevail on poor soils. On richer soils in the tropics, slow-growing podocarps are incapable of competing with angiosperms in the battle for light in tree fall gaps. Some species may be capable of tolerating deep shade and surviving for many years in forest understories, but regeneration is not possible unless there is significant height growth, and that is severely hampered by shading. The simplest hypothesis is that the leaf area indices of lowland tropical forests are simply too high to allow regeneration



of imbricate-leaved podocarps, whereas broad-leaved species with anastomosing veins (*Nageia* and some *Podocarpus*) are so shade tolerant that they regenerate beneath closed canopies. Measurement of growth and survival of podocarps in contrasting tropical forest types, in conjunction with demographic models (e.g., Kunstler et al., 2009), would help resolve this issue.

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### APPENDIX: DESCRIPTIVE ACCOUNTS OF PODOCARPS FROM TROPICAL, SUBTROPICAL, AND WARM TEMPERATE REGIONS

Descriptions are taken primarily from Earle (1997–2009), who sourced his data from various primary references, and also from personal communications with P. J. Grubb. Information on Andean and Amazonian species in the last section was sourced from Jorgensen and Leon-Yanez (1999). Tree heights (*H*) are given after each description; where a range of heights for different habitats is published, the largest is quoted.

#### LOWLAND TROPICAL RAINFORESTS

##### *Common on Poor Soils but Not Restricted to Them*

*Dacrycarpus vieillardii*. New Caledonia. Grows throughout the main island on serpentine soils along riverbanks, in moist depressions, and in frequently flooded areas from sea level to 900 m above sea level. Similar in ecology to *D. dacrydioides* of New Zealand. *H* = 25 m.

*Dacrydium balansae*. New Caledonia. Occurs in the drier parts of forests, normally on serpentine soils from sea level to 1,000 m. A few specimens from ombrophilous forest were 20 m tall trees. *H* = 12 m.

*Dacrydium guillauminii*. New Caledonia. Found within a few kilometers along two rivers. *H* = 2 m.

*Dacrydium magnum*. Solomon Islands, Moluccas. Locally common in the canopy of moist tropical forest between 60 and 1,200 m. Often along ridge crests, where it has a somewhat reduced stature. *H* = 30 m.

*Dacrydium nidulum*. Fiji, New Guinea, Moluccas, Celebes, Lesser Sunda Islands. Common in the western parts of New Guinea, but elsewhere populations are mostly rather isolated. A canopy tree of primary and sometimes secondary rainforest from sea level to 1,200 m, but mostly under 600 m. In Fiji it forms open, low-growing, monodominant stands of stunted trees and is also a component of mesic forests (Keppel et al., 2006). *H* = 30 m.

*Dacrydium pectinatum*. Hainan, China, Malesia, Borneo, Philippines. Scattered large individuals are found in primary rainforest other than dipterocarp forest from sea level to 1,500 m, but mostly below 600 m. Dense stands are found in boggy areas, and nearly pure stands of stunted trees occur in shallow sandy soils, especially on degraded heath forests (“padangs”) and on kerangas in heath forest. In Sabah it grows on ultramafic soils; in Brunei it grows in pure stands in the center of peat swamps. *H* = 40 m.

*Nageia maxima*. Borneo (Sarawak). Locally common in the understory of rainforest on ridges in Bako National Park and in the peat swamp forest, from ~0 to 120 m. *H* = 10 m.

*Nageia motleyi*. Southern Thailand, Malesia (Malaya, Sumatra, Borneo). Scattered in primary and secondary rainforest, from very low altitude (15 m) to ~500 m. Occurs not only on slopes and hills on dry soil but also in Borneo in other situations: in Sarawak on deep peat in a mixed ramin-peat swamp, on ridges and hillsides in bindang-dipterocarp forest, and at 1,000 m on podsolic sandy loam. *H* = 54 m.

*Podocarpus confertus*. Malesia. Subdominant in somewhat open and sometimes stunted forest. Found in dense local populations on various poor soils, some or most of which are ultrabasic. *H* = 36 m.

*Podocarpus insularis*. New Hebrides, Solomon Islands, New Britain, New Guinea and adjacent islands. Scattered and locally common in wet rainforest, also in *Nothofagus* forest with undergrowth of *Nastus* from near sea level to 1,680 m, and as smaller trees in low ridge habitats. *H* = 39 m.

*Podocarpus neriifolius*. Nepal, Sikkim, India, Thailand, Vietnam, Malaysia, Indonesia, Philippines, Celebes, Lesser Sunda Islands, Moluccas, New Guinea, New Britain, Solomon and Fiji islands. Scattered and locally common in primary rainforests from near sea level to ~2,100

m. In most areas it appears as an understory tree with occasionally much larger, emergent specimens in the canopy, but in other areas it is normally a canopy tree. Various habitats (often on rocky hilltops, in mossy forest, and swampy forests but rarely riverine) and on various soils (limestone, kerangas in heath forest, sandstone ridges, and laterites, sandy clay, ultrabasic).  $H = 30$  m.

*Retrophyllum minus*. New Caledonia. Southern part of island on ultramafic soils, at elevations of up to 200 m above sea level. A water-dependent plant (rheophyte) inhabiting riparian habitats, in this case lakes and riverbanks in shallow water.  $H = 3$  m.

#### Restricted to Poor Soils or Open Forest

*Dacrydium araucarioides*. New Caledonia. Locally, a dominant species in the vegetation on serpentine soils, from sea level to 1,150 m.  $H = 6$  m.

*Dacrydium elatum*. Vietnam, Laos, Cambodia, Thailand, Malaya, Sumatra, Borneo. Scattered in moist rainforest, from sea level but mostly above several hundred meters to 1,700 m. Grows most abundantly in open situations, indicating a preference for disturbed conditions. It also appears to prosper on difficult soils (sandstone, granite, kerangas). Does not enter into high mountain scrub.  $H = 40$  m.

*Dacrydium nausoriense*. Fiji. In slightly open forest on the leeward sides of the large islands of Fiji and apparently of limited extent.  $H = ?$

*Falcatifolium angustum*. Borneo. Found at 90–240 m on podsolized sands and kerangas.  $H = 20$  m.

*Falcatifolium falciforme*. Malaya, Borneo. Locally common along ridges as a bushy tree or in the subcanopy of primary rainforest, often on podsolitic sands and kerangas, but occasionally on deeper fertile soils. Somewhat emergent forest giant, from 400–2,100 m.  $H = 12$  m?

*Podocarpus beecherae*. Southern New Caledonia. Maquis vegetation on ultrabasic soil (generally toxic to plants and the reason for the stunted plants of the maquis) at low elevation.  $H = 6$  m.

*Podocarpus costalis*. Philippines and other islands between Luzon and Taiwan. On coastal bluffs from sea level to at least 300 m elevation.  $H = 5$  m.

*Podocarpus globulus*. Borneo. Found in primary rainforest or moss forest on ridges and peak at 300–1,500 m elevation in areas where the forest is not dominated by dipterocarps. Adapted to ultramafic soils.  $H = 27$  m.

*Podocarpus micropedunculatus*. Borneo. From 0 to 500 m elevation scattered in *Agathis* forest understory or in thickets at the edges of clearings. Mostly on sandy,

podzolic soils, kerangas, sandstone, humic peaty podzols of raised beaches, and peat swamp forests.  $H = 7$  m.

*Podocarpus polystachyus*. Thailand, Malaysia (Malay Peninsula), Borneo, Philippines, Moluccas, west New Guinea. Mainly at low altitudes in three distinct habitats: (1) sandy beaches, often gregariously bordering the sea at high-tide mark, sandy coastal bluffs and low outcrops, and also sandy ridges in mangroves; (2) on lowland coastal kerangas and sandy pandangs (degraded heath forest) and sandy heath forest; and (3) on limestone hills inland.  $H = 20$  m.

*Podocarpus teysmannii*. Malaysia, Indonesia. An understory tree in primary or secondary rainforest at elevations up to 1,140 m. In Banka it grows on granite sands.  $H = 12$  m.

#### Apparently Associated with Rainforests on Relatively Fertile/Deep Soils (No Mention of Poor Soil in Description)

*Nageia fleuryi*. China (Guangdong, Guangxi, and Yunnan), Cambodia, Laos, Vietnam (mountainous provinces). Occurs sparsely in primary and slightly disturbed evergreen rainforests at elevations of 200–1,000 m. At Cuc Phuong and Cat Ba National Parks, the species occurs in groups and is the main species in some stands. A light-demanding species thriving well on good sites with deep, well-drained soils developed from limestone.  $H = 25$  m.

*Nageia nagi*. Japan, China, Vietnam. Grows in tropical evergreen broad-leaved forest, on hills or mountains below 1,000 m elevation. Neutral, shade-demanding tree when young. When mature, may become a canopy dominant. Associated with ferrallitic, deep and fertile, loamy-sandy soils.  $H = 30$  m.

*Nageia wallichiana*. India (Assam), Burma, Thailand, Indochina, China (Yunnan), Malesia (Sumatra, Malaya, Banka Island, western Java, Lesser Sunda Islands, Borneo, Philippines, north and central Celebes, Moluccas), New Guinea. Scattered and often common (but nowhere reported as gregarious or dominant) in primary rainforests from very low elevation (5 m), ascending occasionally as high as 2,100 m. Widely distributed in southern China, growing on neutral or slightly acidic soils, tolerating shade. One of the tallest trees in the forest, but perhaps barely emergent.  $H = 54$  m.

*Parasitaxus usta*. New Caledonia. Found at 400–1,100 m elevation. This is the only known parasitic gymnosperm.  $H = 1.8$  m.

*Podocarpus ledermannii*. New Guinea, New Britain. Scattered and locally common in the understory of

primary rainforest from low elevation to at least 1,800 m.  $H = 26$  m.

*Podocarpus levis*. Eastern Borneo, Celebes, Moluccas, New Guinea. Scattered and locally common in primary rainforest, from sea level to 1,650 m. In eastern Borneo on limestone.  $H = 25$  m.

*Podocarpus nakaii*. Taiwan. Scattered as a subcanopy tree in broad-leaved forests in the northern and central parts of the island.  $H = ?$

*Podocarpus spathoides*. Solomon Islands, eastern New Guinea, northern Moluccas, Malaya. Scattered and locally common at 1,000–1,200 m in the two western stands and near sea level in the east. Recent field work indicates that "*P. spathoides*" in the Solomon Islands (which occurs at sea level) is sufficiently distinct to be described as a new species (M. Gardner, Royal Botanic Garden Edinburgh, personal communication).  $H = 30$  m.

*Podocarpus spinulosus*. Australia (New South Wales and Queensland). A shrub in sheltered coastal sites and gullies on the adjacent ranges.  $H = 3$  m.

#### MONTANE TROPICAL RAINFORESTS

##### *Common on Poor Soils but Not Restricted to Them*

*Dacrydium cinctus*. Central Celebes, Moluccas, New Guinea. In New Guinea extremely common and often dominant or codominant with *Nothofagus*, *Libocedrus*, *Elaeocarpus*, and *Podocarpus*, in mountain forest and mossy forest. On Mount Binaja in orchard-like pure stands with a mossy ground cover. Rarely in muddy parts of swamps. A canopy tree or sometimes emergent, often thick trunked at 1,800–2,850 m. Occasionally reaches 3,600 m; in Ceram occurs at 1,300–3,000 m.  $H = 33$  m.

*Dacrydium compactus*. New Guinea. In subalpine shrubberies and alpine grasslands, 3,200–3,800 m. Common on the higher peaks near the tree line, sometimes forming pure stands, emerging above a subalpine shrubbery, or scattered in alpine grassland often as isolated specimens and obviously fire resistant. A component of *Podocarpus*–*Libocedrus* forest, rarely on wet peaty soil, at 2,800–3,950 m, but mostly above 3,400 m.  $H = 20$  m.

*Dacrydium beccarii*. Solomon Islands, New Guinea, Moluccas, Philippines, Borneo, Malaya, northern Sumatra. In the eastern part of the range there are only widely separated occurrences, and even in the western part they are somewhat discontinuous. Most common as a shrub or small tree on mossy ridges where it is often dominant, but also found rising above a low, mixed mountain scrub at 600–2,500 m. A variety of soils have been indicated.  $H = ?$

*Dacrydium gibbsiae*. Borneo. Common on the slopes, being codominant on ultrabasic soils in the mountain mossy forest at 1,500–3,600 m.  $H = 12$  m.

*Dacrydium gracile*. Borneo, Sarawak. Rows scattered in the canopy of mountain rainforest. In Sarawak also in heath forest on sandstone. Rare.  $H = 30$  m.

*Dacrydium xanthandrum*. Solomon Islands, New Guinea, Celebes, Philippines, Borneo, northern Sumatra. Locally discontinuous. Locally common or even dominant and shrubby on mossy ridges with peaty soils over clay, sand, granite, sandstone, or dacite. Also scattered as trees in nearby primary forest from (500–)1,000–2,700 m.  $H = ?$

*Falcatifolium taxoides*. New Caledonia. An understory tree in the wet forests on ultramafic soils of the main island.  $H = 15$  m.

*Phyllocladus hypophyllus*. Philippines, Borneo, Celebes, Moluccas, New Guinea. Moist mountain forests sometimes as low as 900 m up to the tree line at 3,200–4,000 m. Scattered in the forest at lower elevation where trees may be quite large. More common but of reduced stature at higher elevations. In New Guinea it is a widespread and common species from the upper lowland forests to the subalpine shrubberies, rarely as a solitary tree in the alpine grasslands (900–3,600 m).  $H = 30$  m.

*Podocarpus laubenfelsii*. Borneo, Sabah, eastern Kalimantan. Scattered in primary rainforest and moss forest, growing as a large emergent on rocky ridges on kerangas. Dominant in heath forests and on waterlogged acid soils of *Agathis* forests.  $H = 35$  m.

*Podocarpus pseudobracteatus*. New Guinea. Scattered and locally common in the understory of mossy *Castanopsis*–*Nothofagus* forest and *Dacrydium* swamp forest, sometimes entering the alpine shrubbery.  $H = 15$  m.

*Podocarpus rotundus*. Eastern Borneo, Philippines. Found in dwarf mossy forest, at about 1,000–2,200 m.  $H = 15$  m.

*Podocarpus rubens*. Sumatra, Celebes, Lesser Sunda Islands, New Guinea. Scattered as a medium-sized tree in primary rainforest, mostly above 1,500 m but as low as 800 m on smaller islands. Otherwise locally common to dominant as a small tree on ridges at 2,000–3,000 m or occasionally higher. Mostly on latosols. In New Guinea in fagaceous mossy forest, rarely in swampy forest on peaty soils with *Dacrydium*.  $H = 30$  m.

*Podocarpus smithii*. Australia (Queensland). Endemic and highly local in montane rainforests on the eastern Atherton Tableland. Usually grows along creeks at mid elevations (900–1,200 m), often on granitic soils.  $H = 30$ .

*Podocarpus urbanii*. Jamaica. Montane rainforests of the Blue Mountains (1,370–2,250 m) across most soil

types, but most abundant on those of low, but not lowest, available nitrogen and phosphorus.  $H = 15$  m.

*Sundacarpus amarus*. Australia (northeastern coastal Queensland), New Guinea, Moluccas, Lesser Sunda Islands, Java, central and southwestern Celebes, Philippines, Borneo, Sumatra. In Queensland primarily in the Atherton Tableland on basaltic soils at 600–1,200 m. Scattered and often common in primary and secondary rainforest. Very common in New Guinea, often in fagaceous forest, sometimes in mossy forest or submontane forest at ~900 m (with *Dysoxylum*, *Macaranga*, and *Ficus*), where it can be emergent as a colossal tree. Often on latosols, rarely on sandy soils or on marshy ground. Occurs from sea level but mainly at 500–2,000(–2,300) m.  $H = 60$  m.

#### Restricted to Poor Soils or Open Forest

*Dacrydium comosum*. Malaya. On exposed ridges as a local dominant in stunted mossy forest at 1,440–2,200 m.  $H = 4$  m.

*Dacrydium ericoides*. Malesia. Locally common in primary forest on exposed mossy ridges at 1,000–1,500 m.  $H = 17$  m.

*Dacrydium lycopodioides*. New Caledonia. At elevations of 900–1,400 m in ombrophilous forests on the southern part of the main island.  $H = 25$  m.

*Dacrydium medium*. Malaya, northern Sumatra. Shrub or small tree rising above and often dominant in low mountain scrub on what appears to be rather poor soils at 960–2,100 m in Malaya and 1,800–2,600 m in Sumatra.  $H = ?$

*Dacrydium novo-guineense*. Celebes, Moluccas, New Guinea. Long, mossy crests and in open areas at 700–3,000 m, but mostly 1,500–2,200 m. Rising above the mid-mountain canopy or a common small tree at higher elevations rising above ferns and other scrub often after fire. Sometimes dominant. On different soil types: clay, stony sand.  $H = 29$  m.

*Falcatifolium gruezoii*. Philippines, Celebes, Moluccas. In exposed locations along ridges or on the borders of open areas. At 1,600–2,200 m in the Philippines, 1,200–1,400 m in Celebes, and 700 m in Obi (Moluccas).  $H = 12$  m.

*Podocarpus archboldii*. New Guinea. Mainly found in upper lowland regions to upper montane areas and occasionally in the subalpine shrubberies (800–3,100 m).  $H = 40$  m.

*Podocarpus brassii*. New Guinea. Usually found in upper montane and subalpine regions, sometimes venturing out into the alpine grasslands. Also as a survivor of burned subalpine shrubberies replaced by grassland.  $H = 15$  m.

*Podocarpus crassigemmii*. New Guinea. Common or subdominant in the canopy of high-mountain mossy forest

or emergent. Often in *Nothofagus* and *Phyllocladus* forest, rarely in secondary forest, and occasionally in grassland.  $H = 38$  m.

*Podocarpus deflexus*. Malaysia (northern Sumatra, Malaya). Rising above and locally dominant in dwarf mountain scrub at 1,500–2,100 m.  $H = 10$  m.

*Podocarpus gibbsiae*. Borneo. At 1,200–2,400 m elevation, typically on moss forest ridges. Mostly or always on ultramafic soils.  $H = 20$  m.

*Podocarpus glaucus*. Solomon Islands, New Guinea, Moluccas, Philippines. A medium-sized tree in the forest or more often dwarfed or even decumbent on mountain crests in stunted mossy forests. Often locally common, (500–)1,000–2,800 m. Recorded from stony, sandy clay and from a limestone ridge associated with *Gymnostoma* and *Rhododendron* on peaty soil.  $H = 15$  m.

*Podocarpus gnidioides*. New Caledonia. Above 600 m elevation on rocky ridges in the mountains.  $H = 2$  m.

*Podocarpus ridleyi*. Malaysia. Localized and more or less dominant on several isolated peaks with poor soils in a somewhat stunted rainforest, at 480–1,300 m. On ridges over sandstone and on granite.  $H = 24$  m.

*Retrophyllum comptonii*. New Caledonia. Ombrophilous forests on ultramafic soils throughout the main island at 750–1,450 m.  $H = 30$  m.

#### Apparently Associated with Rainforests on Relatively Fertile/Deep Soils (No Mention of Poor Soil in Description)

*Dacrydium imbricatus*. Northern Burma, far southern China, Vietnam, Laos, Malaya, Philippines, Sumatra, Borneo, Java, Celebes, Moluccas, Lesser Sunda Islands, New Guinea, New Hebrides, Fiji. Mostly scattered and common in primary and secondary rainforest. In West Java codominant with *Podocarpus neriifolius* and *Altingia noronhae*, on the south slope of Mount Tjeremai volcano characterizing the zone between 2,400–2,700 m, unexplainably without other codominants. In Timor found under more or less seasonal conditions as isolated specimens laden with *Usnea* in grassland after deforestation, mostly at 1,000–2,500 m. In Lombok reported at as low as 200 m, and in Celebes ascending to 3,000 m. Probably exterminated at lower elevations by deforestation. In China in mixed forests or pure stands on slightly acidic yellow earth soils in valleys of montane streams at 400–1,500 m.  $H = 50$  m.

*Dacrydium spathoides*. New Guinea. Growing as a canopy tree at 2,150–2,200 m in moist, mossy mountain rainforest.  $H = 34$  m.



*Falcatifolium papuanum*. New Guinea. Grows in the understory of moist mountain forests at 1,500–2,400 m. Typical associates include *Nothofagus*, Myrtaceae, and other Podocarpaceae.  $H = 22$  m.

*Podocarpus dispermus*. Australia (Atherton Tableland). In rainforest, not plentiful.  $H = 20$  m.

*Podocarpus macrocarpus*. Philippines. Scattered and sometimes common in cloud forests, ~2,000–2,100 m.  $H = 20$  m.

*Podocarpus macrophyllus*. Southern Japan, Burma, China, Taiwan. Virgin broad-leaved forest dominated by over 20 m tall trees of Lauraceae and Fagaceae.  $H = 15$  m.

*Podocarpus magnifolius*. Eastern Venezuela to Bolivia. Widely distributed in cloud forest at 800–1,600 m.  $H = 25$  m.

*Podocarpus neriiifolius*. Vietnam. Occurs as scattered individuals in remaining primary forests in remote areas, growing sparsely along water courses, usually mixed with broad-leaved species, such as *Fokienia hodginsii*, *Celtis australis*, *Altingia siamensis*, *Cinnamomum* spp., *Gironniera subaequalis*, *Mallotus yunnanensis*, *Castanopsis*, and *Lithocarpus* spp. It chiefly appears on humid, fertile, especially sandy soils, but also on clayey-stony soils.  $H = 25$  m.

*Podocarpus rumphii*. Philippines, Taiwan. Scattered in broad-leaved forests at medium altitudes.  $H = 30$  m.

*Prumnopitys ladei*. Australia (Atherton Tableland, Queensland). Rainforests on granite-derived soils at 1,000–1,200 m.  $H = 25$  m.

*Retrophyllum rospigliosii*. Western Venezuela, Eastern Colombia, central Peru. Native to the wet forests of the Andes, it grows best at 500–3,500 m, needing constant humidity and cloudiness. Develops best on gentle slopes, fertile river lowlands, plateaus, and small depressions. Grows in wet, clay or clay-sand, deep, relatively fertile soils with good to slow drainage and acidic pH.  $H = 30$  m.

#### INSUFFICIENT INFORMATION AVAILABLE

*Dacrycarpus cumingii*. Widespread in Philippines, northern Sumatra; rare in Borneo. Locally common at elevations of (1,000–)1,850–2,650(3,314) m in primary moss forest.  $H = 25$  m.

*Dacrycarpus expansus*. Papua New Guinea (Central Highlands). Locally common or even in pure stands or codominant, sometimes emergent. Often in (human) disturbed situations, such as on edges of tree fern grassland, 1,300–2,750 m.  $H = 25$  m.

*Dacrycarpus kinabaluensis*. Borneo. Common, growing in sometimes pure stands in dwarf mountain scrub at

elevations from about 2,700 m to the tree line at about 4,000 m.  $H = 13$  m.

*Dacrycarpus steupii*. Central eastern Borneo, central Celebes, New Guinea. Locally common, particularly in disturbed forests, or in poorly drained areas where it may form nearly pure stands. In boggy grasslands and reed swamps, on sandy clay, once on a rocky riverbank, once on a limestone hillock in mossy forest (Mount Beratus). Elevations of 860–3,420 m, but mostly ~1,500–2,000 m.  $H = 35$  m.

*Dacrydium cornwallianum*. New Guinea. Dominant to nearly pure stands in swamp forests and perhaps also mossy heath forests at 1,450–2,300 m.  $H = 30$  m.

*Dacrydium leptophyllum*. Western New Guinea. Known only from the top of Mount Goliath at 3,000–3,600 m.  $H = ?$

*Prumnopitys standleyi*. Costa Rica. At 2,000–3,200 m, in areas with 2,000–4,000 mm annual rainfall and temperature range of 3°C–25°C.  $H = 25$  m.

*Podocarpus sellowii*. Brazil. Extremely broad and scattered range, occurring in montane vegetation. Typical of montane areas in the tropical coastal range rainforest (Mata Atlántica) and rarely occurs within *Araucaria angustifolia* forests.  $H = ?$ .

*Podocarpus acuminatus*. Brazil.  $H = 4.5$ .

*Podocarpus atjehensis*. Northwestern Sumatra, New Guinea.  $H = 15$  m.

*Podocarpus borneensis*. Borneo. Locally common or even dominant on mossy rocky ridges or scattered in nearby forest, in high kerangas forest and on white, sandy soils. Elevations of 700–2,070 m; one collection from a swamp at 360 m.  $H = 12$  m.

*Podocarpus bracteatus*. Indonesia, Java, Lesser Sunda Islands.  $H = 40$  m.

*Podocarpus brasiliensis*. Brazil, Venezuela. Mountains and in few hectares of wetland in the middle of the massive Cerrado.  $H = 15$  m.

*Podocarpus brevifolius*. Philippines, Indonesia, China (Guangxi and Guangdong), Vietnam. Usually growing on limestone.  $H = 15$  m.

*Podocarpus buchholzii*. Venezuela.  $H = 7$  m.

*Podocarpus glomeratus*. Andes. Elevations of 2,500–4,000 m.  $H = ?$

*Podocarpus ingensis*. Andes. Elevations of 1,000–3,000 m.  $H = ?$

*Podocarpus lambertii*. Argentina, Brazil.  $H = ?$

*Podocarpus lophatus*. Philippines. Mossy forest at 1,800 m elevation.  $H = ?$

*Podocarpus matudae*. Mexico, Guatemala. Large tree.  $H = ?$



*Podocarpus roraimae*. Mountains bordering Venezuela and Guyana. Endemic. Elevations of 1,800–2,400 m.  $H = ?$

*Podocarpus sprucei*. Andes. Elevations of 2,000–4,000 m.  $H = ?$

*Podocarpus steyermarkii*. Venezuela, Guyana.  $H = 25$  m.

*Podocarpus tepuiensis*. Eastern Venezuela. Endemic shrub or small tree.  $H = ?$

*Podocarpus woltzii*. Madagascar.  $H = 20$  m.

*Prumnopitys montana*. Andes. Elevations of 1,500–4,000 m.  $H = ?$

## REFERENCES

- Abdillahi, H. S., G. I. Stafford, J. F. Finnie, and J. Van Staden. 2008. Antimicrobial Activity of South African *Podocarpus* species. *J. Ethnopharmacol.* 119: 191–194.
- Adie, H., and M. J. Lawes. 2009a. Role reversal in the Stand Dynamics of an Angiosperm–Conifer Forest: Colonising Angiosperms Precede a Shade-Tolerant Conifer in Afrotropical Forest. *Forest Ecol. Managem.* 258: 159–168.
- Adie, H., and M. J. Lawes. 2009b. Explaining Conifer Dominance in Afrotropical Forests: Shade Tolerance Favours *Podocarpus latifolius* over Angiosperm Species. *Forest Ecol. Managem.* 259: 176–186.
- Adie, H., and M. J. Lawes. 2011 (this volume). Podocarps in Africa: Temperate Zone Relicts or Rainforest Survivors? In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 79–100. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Aerts, R. 1995. The Advantages of Being Evergreen. *Trends Ecol. Evol.* 10: 402–407.
- Aiba, S., and K. Kitayama. 1999. Structure, Composition and Species Diversity in an Altitude-Substrate Matrix of Rain Forest Tree Communities on Mount Kinabalu, Borneo. *Pl. Ecol.* 140: 139–157.
- Aiba, S., K. Kitayama, and M. Takyu. 2004. Habitat Associations with Topography and Canopy Structure of Tree Species in a Tropical Montane Forest on Mount Kinabalu, Borneo. *Pl. Ecol.* 174: 147–161.
- Armesto, J. J., and E. R. Fuentes. 1988. Tree Species Regeneration in a Mid-elevation, Temperate Rain Forest in Isla de Chiloé, Chile. *Vegetatio* 74: 151–159.
- Atkinson, I. A. E., and R. M. Greenwood. 1989. Relationship between Moas and Plants. *New Zealand J. Ecol.* 12(suppl.): 67–96.
- Bannister, P. 2007. A Touch of Frost? Cold Hardiness of Plants in the Southern Hemisphere. *New Zealand J. Bot.* 45:1–33.
- Bannister, P., and J. M. Lord. 2006. Comparative Winter Frost Resistance of Plant Species from Southern Africa, Australia, New Zealand, and South America Grown in a Common Environment (Dunedin, New Zealand). *New Zealand J. Bot.* 44: 109–119.
- Barker, P. C. J. 1991. *Podocarpus lawrencei* (Hook. f.): Population Structure and Fire History at Goonmirk Rocks, Victoria. *Austral. J. Ecol.* 16: 149–158.
- Baxter, W. A., and D. A. Norton. 1989. Forest Recovery after Logging in Lowland Dense Rimu Forest, Westland, New Zealand. *New Zealand J. Bot.* 27: 391–399.
- Baylis, G. T. S. 1969. Mycorrhizal Nodules and Growth of *Podocarpus* in Nitrogen-Poor Soil. *Nature* 223: 1385–1386.
- Bee, J. N., G. Kunstler, and D. A. Coomes. 2007. Resistance and Resilience of New Zealand Tree Species to Browsing. *J. Ecol.* 95: 1014–1026.
- Beets, P. N., and M. O. Kimberley. 1993. Genotype  $\times$  Stocking Interactions in *Pinus radiata*: Productivity and Yield Implications. In *Management of Structure and Productivity of Boreal and Subalpine Forests*, S. Linder and S. Kellomäki, eds. *Stud. For. Suec.* 191: 11–19.
- Bellingham, P. J., T. Kohyama, and S. Aiba. 1996. The Effects of a Typhoon on Japanese Warm Temperate Rainforests. *Ecol. Res.* 11: 229–247.
- Bellingham, P. J., and S. J. Richardson. 2006. Tree Seedling Growth and Survival over 6 Years across Different Microsites in a Temperate Rain Forest. *Canad. J. Forest Res.* 36: 910–918.
- Bellingham, P. J., E. V. J. Tanner, and J. R. Healey. 1995. Damage and Responsiveness of Jamaican Montane Tree Species after Disturbance by a Hurricane. *Ecology* 76: 2562–2580.
- Bentley, W. A. 2007. Influences of Soils Nutrients, Waterlogging, and Disturbance Factors on Forest Processes along a New Zealand Soil Chronosequence. Ph.D. thesis, University of Cambridge, Cambridge, UK.
- Bergin, D. O. 2000. Current Knowledge Relevant to Management of *Podocarpus totara* for timber. *New Zealand J. Bot.* 38: 343–359.
- Bergin, D. O., M. O. Kimberley, and C. B. Low. 2008. Provenance Variation in *Podocarpus totara* (D. Don): Growth, Tree Form and Wood Density on a Coastal Site in the North of the Natural Range, New Zealand. *Forest Ecol. Managem.* 255: 1367–1378.
- Beveridge, A. E. 1964. Dispersal and Destruction of Seed in Central North Island Podocarp Forests. *Proc. New Zealand Ecol. Soc.* 11: 48–55.
- Beveridge, A. E. 1973. Regeneration of Podocarps in a Central North Island Forest. *New Zealand J. Forest.* 18: 23–35.
- Bond, W. J. 1989. The Tortoise and the Hare—Ecology of Angiosperm Dominance and Gymnosperm Persistence. *Biol. J. Linn. Soc.* 36: 227–249.
- Brodribb, T. J. 2011 (this volume). A Functional Analysis of Podocarp Ecology. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 165–173. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Brodribb, T. J., and R. S. Hill. 2003a. Implications for Leaf and Shoot Physiology in Podocarpaceae. *Acta Hort.* 615: 173–174.
- Brodribb, T. J., and R. S. Hill. 2003b. The Rise and Fall of the Podocarpaceae in Australia—A Physiological Explanation. In *Evolution of Plant Physiology*, A. Hemsley and I. Poole, eds., pp. 381–399. Elsevier Academic Press, London.
- Brodribb, T. J., N. M. Holbrook, and R. S. Hill. 2005. Seedling Growth in Conifers and Angiosperms: Impacts of Contrasting Xylem Structure. *Austral. J. Bot.* 53: 749–755.
- Brophy, J. J., R. J. Goldsack, C. J. R. Fookes, and P. I. Forster. 2000. Essential Oils of Australian Gymnosperms. Part 1. The Leaf Oil of *Sundacarpus amarus* (Blume) C.N. Page (Podocarpaceae). *J. Essential Oil Res.* 12: 421–423.
- Cameron, R. J. 1960. The Indigenous Forests of New Zealand: Intensive and Extensive Management. *Empire Forest. Rev.* 39: 185–194.
- Chalwell, S. T. S., and P. G. Ladd. 2005. Stem Demography and Post Fire Recruitment of *Podocarpus drouynianus*: A Resprouting Non-serotinous Conifer. *Bot. J. Linn. Soc.* 149: 433–449.
- Chapin, F. S., III. 1980. The Mineral Nutrition of Wild Plants. *Annual Rev. Ecol. Syst.* 11: 233–260.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a Worldwide Wood Economics Spectrum. *Ecol. Letters* 12: 351–366; and Dryad Digital Repository. doi:10.5061/dryad.234. <http://hdl.handle.net/10255/dryad.235> (accessed 1 May 2009).
- Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. *Annual Rev. Ecol. Syst.* 31: 343–366.
- Christie, D. A., and J. J. Armesto. 2003. Regeneration Microsites and Tree Species Coexistence in Temperate Rain Forest of Chiloé Island, Chile. *J. Ecol.* 91: 776–784.

- Clark, C. M., and I. Carbone. 2008. Chloroplast DNA Phylogeography in Long-Lived Huon Pine, a Tasmanian Rain Forest Conifer. *Canad. J. Forest Res.* 38: 1576–1589.
- Coomes, D. A., R. B. Allen, W. Bentley, L. E. Burrows, C. D. Canham, L. Fagan, D. M. Forsyth, A. Gaxiola-Alcantar, R. L. Parfitt, W. A. Ruscoe, D. A. Wardle, D. J. Wilson, and E. F. Wright. 2005. The Hare, the Tortoise and the Crocodile: The Ecology of Angiosperm Dominance, Conifer Persistence and Fern Filtering. *J. Ecol.* 93: 918–935.
- Coomes, D. A., and P. J. Grubb. 2000. Impacts of Root Competition in Forests and Woodlands: A Theoretical Framework and Review of Experiments. *Ecol. Monogr.* 70: 171–207.
- Coomes, D. A., G. Kunstler, C. D. Canham, and E. Wright. 2009. A Greater Range of Shade-Tolerance Niches in Nutrient-Rich Forests: An Explanation for Positive Richness–Productivity Relationships? *J. Ecol.* 97: 705–717.
- Corlett, R. T. 1984. Human Impact on the Subalpine Vegetation of Mt Wilhelm, Papua New Guinea. *J. Ecol.* 72: 841–854.
- Colinvaux, P. A., P. E. De Oliveira, J. E. Moreno, M. C. Miller, and M. B. Bush. 1996. A Long Pollen Record from Lowland Amazonia: Forest and Cooling in Glacial Times. *Science* 274: 85–88.
- Cox, R. E., S. Yamamoto, A. Otto, and B. R. T. Simoneit. 2007. Oxygenated Di- and Tricyclic Diterpenoids of Southern Hemisphere Conifers. *Biochem. Syst. Ecol.* 35: 342–362.
- Crawford, R. M. M. 1987. *Studies in Plant Survival*. Blackwell Scientific Publications, Oxford, UK.
- Crawford, R. M. M., C. E. Jeffree, and W. G. Rees. 2003. Paludification and Forest Retreat in Northern Oceanic Environments. *Ann. Bot.* 91: 213–226.
- Cullen, L. E., R. P. Duncan, A. Wells, and G. H. Stewart. 2003. Floodplain and Regional Scale Variation in Earthquake Effects on Forests, Westland, New Zealand. *J. Roy. Soc. New Zealand* 33: 693–701.
- Dalling, J. W., P. Barkan, P. J. Bellingham, J. R. Healey, and E. V. J. Tanner. 2011 (this volume). Ecology and Distribution of Neotropical Podocarpaceae. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 43–56. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Dalling, J. W., K. Winter, J. D. Nason, S. P. Hubbell, D. A. Murawski, and J. L. Hamrick. 2001. The Unusual Life History of *Alseis blackiana*: A Shade-Persistent Pioneer Tree? *Ecology* 82: 933–945.
- Dickie, I. A., and R. J. Holdaway. 2011 (this volume). Podocarp Roots, Mycorrhizas, and Nodules. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 175–187. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Donoso, C. 1989. Antecedentes para la silvicultura del tipo forestal siempreverde. *Bosque* 10: 37–53.
- Duncan, R. P. 1993. Flood Disturbance and the Coexistence of Species in a Lowland Podocarp Forest, South Westland, New Zealand. *J. Ecol.* 81: 403–416.
- Earle, C. J. 1997–2009. Gymnosperm Database. <http://www.conifers.org> (accessed 1 May 2009).
- Ebbett, R. L., and J. Ogden. 1998. Comparative Seedling Growth of Five Endemic New Zealand Podocarp Species under Different Light Regimes. *New Zealand J. Bot.* 36: 189–201.
- Enright, N., 1995. Conifers of Tropical Australasia. In *Ecology of the Southern Conifers*, N. J. Enright and R. S. Hill, eds., pp. 197–222. Melbourne University Press, Carlton, Australia.
- Enright, N., and J. Ogden. 1995. The Southern Conifers—A Synthesis. In *Ecology of the Southern Conifers*, N. J. Enright and R. S. Hill, eds., pp. 271–287. Melbourne University Press, Carlton, Australia.
- Esler, A. E. 1978. *Botany of the Manawatu District, New Zealand*. Government Printer, Wellington, New Zealand.
- Feild, T. S., and T. Brodribb. 2001. Stem Water Transport and Freeze-Thaw Xylem Embolism in Conifers and Angiosperms in a Tasmanian Treeline Heath. *Oecologia* 127: 314–320.
- Gallagher, S. J., B. E. Wagstaff, J. G. Baird, M. W. Wallace, and C. L. Li. 2008. Southern High Latitude Climate Variability in the Late Cretaceous Greenhouse World. *Global Planet. Change* 60: 351–364.
- Gardner, M. F., V. Hechenleitner, P. Thomas, C. Echeverría, B. Escobar, P. Brownless, and A. C. Martínez. 2006. *Threatened Plants of Central and South Chile: Distribution, Conservation and Propagation*. Universidad Austral de Chile, Valdivia, and Royal Botanic Garden Edinburgh, Edinburgh.
- Gaxiola, A. 2006. Limitations to Photosynthesis, Growth and Survival of Plants Associated with a Soil Chronosequence in New Zealand. Ph.D. thesis, University of Cambridge, Cambridge, UK.
- Gaxiola, A., L. E. Burrows, and D. A. Coomes. 2008. Tree Fern Trunks Facilitate Seedling Regeneration in a Productive Lowland Temperate Rain Forest. *Oecologia* 155: 325–335.
- Gaxiola, A., S. M. McNeill, and D. A. Coomes. 2010. What Drives Retrogressive Succession? Plant Strategies to Tolerate Infertile and Poorly Drained Soils. *Funct. Ecol.* 24: 714–722.
- Gibson, N., and M. J. Brown. 1991. The Ecology of *Lagarostrobos franklinii* (Hook. f.) Quinn in Tasmania. 2. Population Structure and Spatial Pattern. *Austral. J. Ecol.* 16: 223–229.
- Grime, J. P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *Amer. Naturalist* 111: 1169–1194.
- Grubb, P. J. 1977. Control of Forest Growth and Distribution on Wet Tropical Mountains with Special Reference to Mineral Nutrition. *Annual Rev. Ecol. Syst.* 8: 83–107.
- Grubb, P. J., and P. F. Stevens. 1985. *The Forests of the Fatima Basin and Mt. Kerigomna, Papua New Guinea, with a Review of Montane and Subalpine Rainforests in Papuasia*. Australian National University, Canberra.
- Gutiérrez, A. G., J. J. Armesto, and J. C. Aravena. 2004. Disturbance and Regeneration Dynamics of an Old-Growth North Patagonian Rain Forest in Chiloé Island, Chile. *J. Ecol.* 92: 598–608.
- Hawkins, B. J., G. B. Sweet, D. H. Greer, and D. O. Bergin. 1991. Genetic Variation in the Frost Hardiness of *Podocarpus totara*. *New Zealand J. Bot.* 29: 455–458.
- Hill, R. S., and T. J. Brodribb. 1999. Southern Conifers in Time and Space. *Austral. J. Bot.* 47: 639–696.
- Hobbie, E. A. 2006. Carbon Allocation to Ectomycorrhizal Fungi Correlates with Belowground Allocation in Culture Studies. *Ecology* 87: 563–569.
- Holloway, J. T. 1954. Forests and Climate in the South Island of New Zealand. *Trans. Roy. Soc. New Zealand* 82: 329–410.
- Hoorens, B., D. Coomes, and R. Aerts. 2010. Neighbour Identity Hardly Affects Litter-Mixture Effects on Decomposition Rates of New Zealand Forest Species. *Oecologia* 162: 479–489.
- Horn, H. S. 1971. *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, N.J.
- Hudgins, J. W., E. Christiansen, and V. R. Franceschi. 2004. Induction of Anatomically Based Defense Responses in Stems of Diverse Conifers by Methyl Jasmonate: A Phylogenetic Perspective. *Tree Physiol.* 24: 251–264.
- Hurst, S. E., M. H. Turnbull, and D. A. Norton. 2002. The Effect of Plant Light Environment on Mycorrhizal Colonisation in Field-Grown Seedlings of Podocarp–Angiosperm Forest Tree Species. *New Zealand J. Bot.* 40: 65–72.
- Innes, K. P. C., and D. Kelly. 1992. Water Potentials in Native Woody Vegetation during and after a Drought in Canterbury. *New Zealand J. Bot.* 30: 81–94.
- Jaffré, T. 1995. Distribution and Ecology of the Conifers of New Caledonia. In *Ecology of the Southern Conifers*, N. J. Enright and R. S.

- Hill, eds., pp. 171–196. Melbourne University Press, Carlton, Australia.
- Jennings, S. M., L. G. Edwards, and J. E. Hickey. 2005. Natural and Planted Regeneration after Harvesting of Huon Pine (*Lagarostrobos franklinii*) at Traveller Creek, Western Tasmania. *Tasforests* 16: 61–70.
- Jorgensen, P. M., and S. Leon-Yanez. 1999. *Catalogue of the Vascular Plants of Ecuador*. Missouri Botanical Gardens Press, St. Louis, Missouri.
- Kelly, D. 1987. Slow Recovery of *Beilschmiedia tawa* after Severe Frosts in Inland Taranaki, New Zealand. *New Zealand J. Ecol.* 10: 137–140.
- Keppel, G., I. H. Rounds, and N. T. Thomas. 2006. The Flora, Vegetation, and Conservation Value of Mesic Forest at Dogotuki, Vanua Levu, Fiji Islands. *New Zealand J. Bot.* 44: 273–292.
- Kirkpatrick, J. 1997. *Alpine Tasmania*. Oxford University Press, Melbourne, Australia.
- Kitayama, K., S. Aiba, M. Ushio, T. Seino, and Y. Fujiki. 2011 (this volume). The Ecology of Podocarps in Tropical Montane Forests of Borneo: Distribution, Population Dynamics, and Soil Nutrient Acquisition. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 101–117. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Kohyama, T. 1986. Tree Size Structure of Stands and Each Species in Primary Warm-Temperate Rain-Forests of Southern Japan. *Bot. Mag. (Tokyo)* 99: 267–279.
- Kohyama, T., and P. J. Grubb. 1994. Below- and Above-Ground Allometries of Shade-Tolerant Seedlings in a Japanese Warm-Temperate Rain Forest. *Funct. Ecol.* 8: 229–236.
- Körner, C., and J. Paulsen. 2004. A World-Wide Study of High Altitude Treeline Temperatures. *J. Biogeogr.* 31: 713–732.
- Kunstler, G., D. A. Coomes, and C. D. Canham. 2009. Size-Dependence of Growth and Mortality Influence the Shade Tolerance of Trees in a Lowland Temperate Rain Forest. *J. Ecol.* 97: 685–695.
- Ladd, P. G., and N. J. Enright. 2011 (this volume). Ecology of Fire-Tolerant Podocarps in Temperate Australian Forests. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 141–155. Smithsonian Institution Scholarly Press, Washington, D.C.
- Leverenz, J. W., D. Whitehead, and G. H. Stewart. 2000. Quantitative Analyses of Shade-Shoot Architecture of Conifers Native to New Zealand. *Trees Struct. Funct.* 15: 42–49.
- Lusk, C. H. 1995. Seed Size, Establishment Sites and Species Coexistence in a Chilean Rain-Forest. *J. Veg. Sci.* 6: 249–256.
- Lusk, C. H. 1996. Stand Dynamics of the Shade-Tolerant Conifers *Podocarpus nubigena* and *Saxegothaea conspicua* in Chilean Temperate Rain Forest. *J. Veg. Sci.* 7: 549–558.
- Lusk, C. H. 2001. Leaf Life Spans of Some Conifers of the Temperate Forests of South America. *Revista Chilena Hist. Nat.* 74: 711–718.
- Lusk, C. H. 2011 (this volume). Conifer-Angiosperm Interactions: Physiological Ecology and Life History. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 157–164. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Lusk, C. H., and C. K. Kelly. 2003. Interspecific Variation in Seed Size and Safe Sites in a Temperate Rain Forest. *New Phytol.* 158: 535–541.
- Lusk, C., and J. Ogden. 1992. Age Structure and Dynamics of a Podocarp Broadleaf Forest in Tongariro National Park, New Zealand. *J. Ecol.* 80: 379–393.
- Lusk, C. H., and B. Smith. 1998. Life History Differences and Tree Species Coexistence in an Old-Growth New Zealand Rain Forest. *Ecology* 79: 795–806.
- Lynch, A. H., J. Beringer, P. Kershaw, A. Marshall, S. Mooney, N. Tapper, C. Turney, and S. Van Der Kaar. 2007. Using the Paleorecord to Evaluate Climate and Fire Interactions in Australia. *Annual Rev. Earth Planet. Sci.* 35: 215–239.
- Martin, P. H., and T. J. Fahey. 2006. Fire History along Environmental Gradients in the Subtropical Pine Forests of the Cordillera Central, Dominican Republic. *J. Trop. Ecol.* 22: 289–302.
- Martin, P. H., R. E. Sherman, and T. J. Fahey. 2007. Tropical Montane Forest Ecotones: Climate Gradients, Natural Disturbance, and Vegetation Zonation in the Cordillera Central, Dominican Republic. *J. Biogeogr.* 34: 1792–1806.
- Martin, T. J., and J. Ogden. 2006. Wind Damage and Response in New Zealand Forests: A Review. *New Zealand J. Ecol.* 30: 295–310.
- McGlone, M. S. 2001. The Origin of the Indigenous Grasslands of Southeastern South Island in Relation to Pre-human Woody Ecosystems. *New Zealand J. Ecol.* 25: 1–15.
- McGlone, M. S., and C. J. Webb. 1981. Selective Forces Influencing the Evolution of Divaricating Plants. *New Zealand J. Ecol.* 4: 20–28.
- McGlone, M. S., R. J. Dungan, G. M. J. Hall, and R. B. Allen. 2004. Winter Leaf Loss in the New Zealand Woody Flora. *New Zealand J. Bot.* 42: 1–19.
- McKelvey, P. J. 1963. The Synecology of the West Taupo Indigenous Forest. *New Zealand Forest Serv. Bull.* 14: 1–127.
- McSweeney, G. D. 1982. Matai/Totara Flood-Plain Forests in South Westland. *New Zealand J. Ecol.* 5: 121–128.
- Middley, J. J., and W. J. Bond. 1991. Ecological Aspects of the Rise of Angiosperms—A Challenge to the Reproductive Superiority Hypotheses. *Biol. J. Linn. Soc.* 44: 81–92.
- Molloy, B. P. J. 1995. *Manoao* (Podocarpaceae), a New Monotypic Conifer Genus Endemic to New Zealand. *New Zealand J. Bot.* 33: 183–201.
- Monk, C. D. 1966. An Ecological Significance of Evergreenness. *Ecology* 47: 504–505.
- Morley, R. J. 2011 (this volume). Dispersal and Paleoecology of Tropical Podocarps. In *Ecology of the Podocarpaceae in Tropical Forests*, B. L. Turner and L. A. Cernusak, eds., pp. 21–41. Smithsonian Contributions to Botany, No. 95. Smithsonian Institution Scholarly Press, Washington, D.C.
- Niemann, H., and H. Behling. 2008. Late Quaternary Vegetation, Climate and Fire Dynamics Inferred from the El Tiro Record in the Southeastern Ecuadorian Andes. *J. Quaternary Sci.* 23: 203–212.
- Norton, D. A. 1991. Seedling and Sapling Distribution Patterns in a Coastal Podocarp Forest, Hokitika Ecological District, New Zealand. *New Zealand J. Bot.* 29: 463–466.
- Norton, D. A. 1995. Forest Structure and Processes. In *Riccarton Bush: Putaringamotu*, B. Molloy, ed., pp. 116–127. Riccarton Bush Trust, Christchurch, New Zealand.
- Ogden, J., and G. H. Stewart. 1995. Community Dynamics of the New Zealand Conifers. In *Ecology of the Southern Conifers*, N. J. Enright and R. S. Hill, eds., pp. 64–80. Melbourne University Press, Carlton, Australia.
- Pickup, M., M. Westoby, and A. Basden. 2005. Dry Mass Costs of Deploying Leaf Area in Relation to Leaf Size. *Funct. Ecol.* 19: 88–97.
- Pittermann, J., J. S. Sperry, U. G. Hacke, J. K. Wheeler, and E. H. Sikkema. 2006a. Inter-tracheid Pitting and the Hydraulic Efficiency of Conifer Wood: The Role of Tracheid Allometry and Cavitation Protection. *Amer. J. Bot.* 93: 1265–1273.
- Pittermann, J., J. S. Sperry, J. K. Wheeler, U. G. Hacke, and E. H. Sikkema. 2006b. Mechanical Reinforcement of Tracheids Compromises the Hydraulic Efficiency of Conifer Xylem. *Pl. Cell Environ.* 29: 1618–1628.
- Poorter, L., and F. Bongers. 2006. Leaf Traits Are Good Predictors of Plant Performance across 53 Rain Forest Species. *Ecology* 87: 1733–1743.
- Raven, P. H. 1977. Suggestion Concerning Cretaceous Rise to Dominance of Angiosperms. *Evolution* 31: 451–452.



- Reif, A., and R. B. Allen. 1988. Plant Communities of the Steepland Conifer-Broadleaved Hardwood Forests of Central Westland, South Island, New Zealand. *Phytocoenologia* 16: 145–224.
- Richards, P., and G. B. Williamson. 1975. Treefalls and Patterns of Understorey Species in a Wet Lowland Tropical Forest. *Ecology* 56: 1226–1229.
- Richardson, S. J., D. A. Peltzer, R. B. Allen, and M. S. McGlone. 2005. Resorption Proficiency along a Chronosequence: Responses among Communities and within Species. *Ecology* 86: 20–25.
- Richardson, S. J., D. A. Peltzer, R. B. Allen, M. S. McGlone, and R. L. Parfitt. 2004. Rapid Development of Phosphorus Limitation in Temperate Rainforest along the Franz Josef Soil Chronosequence. *Oecologia* 139: 267–276.
- Russell, A. J., M. I. Bidartondo, and B. G. Butterfield. 2002. The Root Nodules of Podocarpaceae Harbour Arbuscular Mycorrhizal Fungi. *New Phytol.* 156: 283–295.
- Sakai, A., D. M. Paton, and P. Wardle. 1981. Freezing Resistance of Trees of the South Temperate Zone, Especially Subalpine Species of Australasia. *Ecology* 62: 563–570.
- Six Dijkstra, H. G., D. J. Mead, and I. L. James. 1985. Forest Architecture in Terrace Rimu Forest of Saltwater Forest, South Westland, and Its Implications for Management. *New Zealand J. Forest. Sci.* 15: 3–22.
- Smale, M. C. 1984. White-Pine Bush—An Alluvial Kahikatea (*Dacrycarpus dacrydioides*) Forest Remnant, Eastern Bay of Plenty, New Zealand. *New Zealand J. Bot.* 22: 201–206.
- Smale, M. C., B. R. Burns, P. N. Smale, and P. T. Whaley. 1997. Dynamics of Upland Podocarp/Broadleaved Forest on Mamaku Plateau, Central North Island, New Zealand. *J. Roy. Soc. New Zealand* 27: 513–532.
- Smale, M. C., and M. O. Kimberley. 1986. Growth of Naturally Regenerating *Beilschmiedia* and Podocarps in Unlogged and Selectively Logged Podocarp/Tawa Forest, Pureora. *New Zealand J. Forest. Sci.* 16: 131–141.
- Sniderman, J. M. K., B. Pillans, P. B. O'Sullivan, and A. P. Kershaw. 2007. Climate and Vegetation in Southeastern Australia Respond to Southern Hemisphere Insolation Forcing in the Late Pliocene–Early Pleistocene. *Geology* 35: 41–44.
- Tanner, E. V. J. 1977. Four Montane Rain Forests of Jamaica: A Quantitative Characterization of the Floristics, the Soils and the Foliar Nutrient Levels, and a Discussion of the Interrelations. *J. Ecol.* 65: 883–918.
- Tyree, M. T., and J. S. Sperry. 1989. Vulnerability of Xylem to Cavitation and Embolism. *Annual Rev. Pl. Physiol. Pl. Molec. Biol.* 40: 19–38.
- Uhl, C., K. Clark, N. Dezzeo, and P. Maquirino. 1988. Vegetation Dynamics in Amazonian Treefall Gaps. *Ecology* 69: 751–763.
- Urlich, S. C., G. H. Stewart, R. P. Duncan, and P. C. Almond. 2005. Tree Regeneration in a New Zealand Rain Forest Influenced by Disturbance and Drainage Interactions. *J. Veg. Sci.* 16: 423–432.
- Veblen, T. T., B. R. Burns, T. Kitzberger, A. Lara, and R. Villalba. 1995. The Ecology of the Conifers of Southern South America. In *Ecology of the Southern Conifers*, N. J. Enright and R. S. Hill, eds., pp. 120–155. Melbourne University Press, Carlton, Australia.
- Veblen, T. T., F. M. Schlegel, and B. Escobar R. 1980. Structure and Dynamics of Old-Growth *Nothofagus* Forests in the Valdivian Andes, Chile. *J. Ecol.* 68: 1–31.
- Wade, L. K., and D. N. McVean. 1969. Mt Wilhelm Studies 1. The Alpine and Subalpine Vegetation. *Research School of Pacific Studies, Department of Biogeography and Geomorphology Publication BG/1*. Australian National University Press, Canberra.
- Walcroft, A. S., K. J. Brown, W. S. F. Schuster, D. T. Tissue, M. H. Turnbull, K. L. Griffin, and D. Whitehead. 2005. Radiative Transfer and Carbon Assimilation in Relation to Canopy Architecture, Foliage Area Distribution and Clumping in a Mature Temperate Rainforest Canopy in New Zealand. *Agric. Forest Meteorol.* 135: 326–339.
- Wardle, D. A., S. K. Wiser, R. B. Allen, J. E. Doherty, K. I. Bonner, and W. M. Williamson. 2008. Aboveground and Belowground Effects of Single-Tree Removals in New Zealand Rain Forest. *Ecology* 89: 1232–1245.
- Wardle, P. 1963a. Growth Habits of New Zealand Subalpine Shrubs and Trees. *New Zealand J. Bot.* 1: 18–47.
- Wardle, P. 1963b. Evolution and Distribution of the New Zealand Flora, as Affected by Quaternary Climates. *New Zealand J. Bot.* 1: 3–17.
- Wardle, P. 1974. The Kahikatea (*Dacrycarpus dacrydioides*) Forest of South Westland. *Proc. New Zealand Ecol. Soc.* 21: 62–71.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.
- Wardle, P. 2008. New Zealand Forest to Alpine Transitions in Global Context. *Arctic Antarc. Alpine Res.* 40: 240–249.
- Wells, A., R. P. Duncan, and G. H. Stewart. 2001. Forest Dynamics in Westland, New Zealand: The Importance of Large, Infrequent Earthquake-Induced Disturbance. *J. Ecol.* 89: 1006–1018.
- Wells, A., M. D. Yetton, R. P. Duncan, and G. H. Stewart. 1999. Pre-historic Dates of the Most Recent Alpine Fault Earthquakes, New Zealand. *Geology* 27: 995–998.
- Whitehead, D., G. M. J. Hall, A. S. Walcroft, K. J. Brown, J. J. Landsberg, D. T. Tissue, M. H. Turnbull, K. L. Griffin, W. S. F. Schuster, F. E. Carswell, C. M. Trotter, I. L. James, and D. A. Norton. 2002. Analysis of the Growth of Rimu (*Dacrydium cupressinum*) in South Westland, New Zealand, Using Process-Based Simulation Models. *Int. J. Biometeorol.* 46: 66–75.
- Whitehead, D., A. Walcroft, K. Griffin, D. Tissue, M. Turnbull, V. Engel, K. Brown, and W. Schuster. 2004. Scaling Carbon Uptake from Leaves to Canopies: Insights from Two Forests with Contrasting Properties. In *Forests at the Land–Atmosphere Interface*, M. Mencuccini, J. Grace, J. Moncrieff, and K. G. McNaughton, eds., pp. 231–254. CAB International, Wallingford, UK.
- Wilmshurst, J. M., and M. S. McGlone. 1996. Forest Disturbance in the Central North Island, New Zealand, Following the 1850 BP Taupo Eruption. *Holocene* 6: 399–411.
- Wilson, H. D. 1982. *Field Guide: Stewart Island Plants*. Field Guide Publications, Christchurch, New Zealand.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M. L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The Worldwide Leaf Economics Spectrum. *Nature* 428: 821–827.