

Podocarpaceae in Tropical Forests: A Synthesis

Lucas A. Cernusak, Hylton Adie, Peter J. Bellingham, Edward Biffin, Timothy J. Brodribb, David A. Coomes, James W. Dalling, Ian A. Dickie, Neal J. Enright, Kanehiro Kitayama, Philip G. Ladd, Hans Lambers, Michael J. Lawes, Christopher H. Lusk, Robert J. Morley, and Benjamin L. Turner

Lucas A. Cernusak, The Australian National University, Canberra, Australia. *Hylton Adie*, University of KwaZulu–Natal, Scottsville, South Africa. *Peter J. Bellingham* and *Ian A. Dickie*, Landcare Research, Lincoln, New Zealand. *Edward Biffin*, The University of Adelaide, Adelaide, South Australia, Australia. *Timothy J. Brodribb*, University of Tasmania, Hobart, Tasmania, Australia. *David A. Coomes*, University of Cambridge, Cambridge, UK. *James W. Dalling*, University of Illinois at Urbana-Champaign, Urbana, Illinois, USA. *Neal J. Enright* and *Philip G. Ladd*, Murdoch University, Murdoch, Western Australia, Australia. *Kanehiro Kitayama*, Kyoto University, Kyoto, Japan. *Hans Lambers*, The University of Western Australia, Crawley, Western Australia, Australia. *Michael J. Lawes*, School for Environmental Research, Charles Darwin University, Darwin, Northern Territory, Australia. *Christopher H. Lusk*, Macquarie University, Sydney, New South Wales, Australia. *Robert J. Morley*, Palynova Limited, Littleport, UK, and University of London, Egham, UK. *Benjamin L. Turner*, Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panama. **Correspondence:** L. Cernusak, Lucas.Cernusak@anu.edu.au.

Expanded author information precedes the References section. Manuscript received 13 April 2010; accepted 9 July 2010.

The Podocarpaceae comprises 18 genera and about 173 species of evergreen, coniferous trees and shrubs. It is the most successful gymnosperm family in angiosperm-dominated tropical forests (Brodribb, this volume). Podocarps are distributed mainly in the Southern Hemisphere, with populations also extending as far north as China and Japan and to Mexico and the Caribbean in the neotropics (Dalling et al., this volume; Enright and Jaffré, this volume; Adie and Lawes, this volume).

Molecular and fossil evidence suggests that the Podocarpaceae originated during the Triassic–Jurassic in Gondwana (Biffin et al., this volume; Morley, this volume). Currently, the greatest generic diversity of the Podocarpaceae is in Malesia (Enright and Jaffré, this volume). Podocarps did not migrate into tropical latitudes until later in their evolutionary history, appearing for the first time in Southeast Asia during the late Eocene, probably dispersing via the Indian Plate (Morley, this volume). Thus, the present latitudinal distributions have emerged in Asia and Africa over the last 40 million years. Although extinction rates in general appear to have been high within the family, a major shift in diversification rate is estimated to have taken place in the mid- to Late Cretaceous and Paleocene, with most extant genera becoming established in Gondwana

during this period. This shift could reflect reduced extinction and/or increased speciation in response to the expansion of angiosperm-dominated tropical forests (Biffin et al., this volume). An alternative explanation for the Late Cretaceous and Paleocene diversification could be the onset of wetter and warmer climatic conditions associated with the opening of the Southern Ocean (Morley, this volume).

Some podocarp taxa show widespread and/or disjunct distributions. In the absence of molecular data, it is difficult to infer migration patterns or the potential for gene flow among these disjunct populations. Patterns of relatedness among populations in tropical forests could help reveal whether current populations are relicts of cooler tropical climates associated with the Last Glacial Maximum or the consequence of postglacial occupancy of suitable habitat.

Tropical podocarps are most abundant in mid- to high-elevation forests, suggesting that the habitat requirements of temperate ancestors have been retained as podocarps radiated into the tropics. Podocarps also occur occasionally in lowland tropical rainforest, but this is the exception, rather than the rule (Dalling et al., this volume; Enright and Jaffré, this volume; Adie and Lawes, this volume; Coomes and Bellingham, this volume). One such exception is their prominence in lowland heath forests (kerangas) on Borneo (Enright and Jaffré, this volume). Thus, in Asia, podocarp taxa have apparently dispersed through both lowland and montane habitats. For example, the dispersal pathway for *Dacrydium* appears to have been via India through kerangas, i.e., heath forests growing on acidic, sandy soils that are low in nutrients, during the Paleogene. On the other hand, *Dacrycarpus* and *Phyllocladus* appear to have jumped between islands of montane/alpine habitat via New Guinea at the time of Plio–Pleistocene global cooling (Morley, this volume; Enright and Jaffré, this volume). A similar pattern of distributions can also be found in the neotropics, where podocarps are mainly montane, but with notable lowland exceptions (Dalling et al., this volume). There, podocarps are absent from most of the Amazon lowlands, except for the white sands around Iquitos, Peru, and nutrient-poor soils of the Guyana Shield. However, podocarps do occur at sea level on islands off both the Pacific and Atlantic coasts of Central America. It should also be noted that podocarp pollen was relatively common in lake sediments from the Amazon lowlands during the Last Glacial Maximum approximately 18,000 years ago but decreased to trace amounts during the Holocene, presumably as a result of climate warming (Colinvaux et al., 1996).

Given that podocarps in lowland tropical forests appear to achieve their highest abundance on low-fertility soils (Dalling et al., this volume; Enright and Jaffré, this volume; Coomes and Bellingham, this volume), do they have high nutrient use efficiency and/or unique mechanisms for acquiring nutrients? Nutrient use efficiency can be defined as the product of nutrient productivity and mean nutrient residence time (Berendse and Aerts, 1987; Aerts and Chapin, 2000). Nutrient productivity is a rate variable, expressed as carbon uptake per unit of nutrient per unit time. Mean nutrient residence time is the average amount of time that a unit of nutrient spends in the plant between acquisition from the environment and loss through above- and below-ground litter production. Leaf-level measurements suggest that podocarps do not have nutrient productivities that can match those of tropical angiosperms. In a comparison of conifer and angiosperm seedlings grown in Panama, *Podocarpus guatemalensis* had photosynthetic nitrogen productivity of $38 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$, whereas mean values were 64 and $162 \mu\text{mol CO}_2 \text{ mol}^{-1} \text{ N s}^{-1}$ for three other conifer species and 11 angiosperm species, respectively (Cernusak et al., 2008). Mean values for photosynthetic phosphorus productivity were 0.5, 0.7, and $2.5 \text{ mmol CO}_2 \text{ mol}^{-1} \text{ P s}^{-1}$ for *P. guatemalensis*, three other conifer species, and 11 angiosperm species, respectively. In general, podocarps have low photosynthetic rates per unit leaf mass compared to angiosperms, in common with other conifer taxa (Lusk, this volume). Low mass-based photosynthetic rates contribute to low leaf-level nutrient productivities (Aerts and Chapin, 2000).

It seems likely, therefore, that any advantage that tropical podocarps have in terms of nutrient use efficiency should derive from mean nutrient residence time, rather than from nutrient productivity. Mean nutrient residence time can vary as a function of leaf and root life spans, tissue nutrient concentrations, and the efficiency of nutrient resorption from senescing tissues. In common with other conifers, podocarps do tend to have long leaf life spans compared to angiosperms (Lusk, this volume). Podocarps can also have lower leaf nutrient concentrations than angiosperms: *P. guatemalensis* had leaf nitrogen and phosphorus concentrations of 1.5% and 2.5‰, respectively, compared with values of 1.2% and 2.9‰ for three other conifer species and 1.7% and 3.1‰ for 11 angiosperm species grown under similar soil conditions in Panama (Cernusak et al., 2008). Similarly, *Podocarpus urbanii* also had lower leaf nitrogen and phosphorus concentrations than co-occurring angiosperms in Jamaica (Dalling et al., this volume), but on Mount Kinabalu in Borneo nitrogen and

phosphorus concentrations in the phyllodes of *Phyllocladus hypophyllus* were not different from those in leaves of co-occurring angiosperms (Kitayama et al., 2004). More data are therefore needed to determine whether leaf nutrient concentrations in tropical podocarps tend, in general, to be lower than in co-occurring angiosperm trees. There are no data that we are aware of for nutrient resorption efficiency from senescent leaves of tropical podocarps. Nor are we aware of data for root life spans, root nutrient concentrations, or resorption efficiency from senescing roots. Thus, although it is likely that tropical podocarps will have longer mean nutrient residence times than tropical angiosperms, the evidence currently available is insufficient to demonstrate this conclusively.

In response to the second part of the question posed above, podocarps do not appear to possess any unique mechanism for acquiring nutrients. They do have conspicuous nodules on their roots that grow in the absence of fungi or bacteria; their function remains unclear, although they appear to play no significant role in atmospheric nitrogen fixation. Podocarp roots show very high rates of infection by arbuscular mycorrhizal fungi in both long and short nodular roots (Dickie and Holdaway, this volume). Thus, the nodules may simply serve to increase root volume for interaction with symbiotic mycorrhizal fungi. Dickie and Holdaway (this volume) argue that the nodules could minimize root construction and turnover costs while maximizing the root volume available to support mycorrhizal associations. On the basis of measurements on Mount Kinabalu, Borneo, Kitayama et al. (this volume) further suggest that podocarps may form loose symbiotic associations with soil microbial communities.

In summary, there does not appear to be a single, outstanding feature that can explain why podocarps are relatively most successful on infertile soils in lowland tropical forests. The explanation may rather lie in a suite of traits that combine to enable podocarps to compete successfully when the productivity advantage of angiosperms is diminished by nutrient poverty (Brodribb and Feild, 2010). Some possible examples of such traits are long mean nutrient residence times associated with long leaf and root life spans and low tissue nutrient concentrations, efficient manipulation of mycorrhizal symbioses, and some degree of control over the composition of soil microbial communities by root exudates and the quality and quantity of leaf litter (Kitayama et al., this volume).

Despite the frequent association of tropical podocarps with low-nutrient soils, it would be incorrect to assume that they are strictly confined to those soils. Broad-leaved podocarps, in particular, can also occur on more

productive sites. This may be because broad leaves are important for light interception efficiency and competitiveness with co-occurring angiosperms at nutrient-rich sites, where dense canopies cast a pronounced shadow over regenerating seedlings (Adie and Lawes, this volume). Broad-leaved podocarps tend to be faster growing and shorter lived and have shorter leaf longevity and higher leaf litter quality than imbricate-leaved genera (Enright and Jaffré, this volume). These traits in broad-leaved podocarps may approach those of co-occurring angiosperms. Under African forest conditions, superior shade tolerance by broad-leaved podocarps allows them to dominate competing angiosperms over a range of soil nutrient conditions (Adie and Lawes, 2009). Phylogenetic analyses suggest that the broad-leaved podocarps may have a higher diversification rate than genera with imbricate leaves (Biffin et al., this volume), possibly linked to differences between the two groups in metabolic rates.

The ability to produce flattened, plagiotrophic leaves and shoots is fundamental to the success of podocarps in competition for light with angiosperms. Leaf flattening is a prominent feature within the Podocarpaceae and distinguishes the broad-leaved podocarps from most other conifer taxa. Flattened leaves are likely to be a key factor enabling shade tolerance of podocarps (Brodribb, this volume). The flattened leaves contain sclereids, which increase water transport from the leaf midvein to the sites of evaporation in the leaf lamina. Freed from the temperate-zone constraint of freezing, tropical broad-leaved podocarps can increase leaf size and thus have converged upon a strategy of leaf architecture that resembles that of co-occurring angiosperms. Whereas temperate podocarps tend to have lower leaf area ratios than co-occurring angiosperms, tropical podocarps may be more able to emulate shade-tolerant tropical angiosperms and intercept sunlight with a similar efficiency.

In general, podocarps do not tolerate drought. This may be because they possess wood that is vulnerable to embolism by water stress and are unable to refill embolized tracheids (Brodribb, this volume). Additionally, the vascular system associated with homoxylous conifer wood may be insufficient to supply water to the relatively large leaf area carried by broad-leaved podocarps under conditions of high evaporative demand and/or low soil water potential. This may lead to excessively low leaf water potentials and sharply curtailed photosynthetic rates under such conditions. An extreme exception to the general intolerance to drought among podocarps occurs in the Mediterranean-type climate of southwest Australia. There, *Podocarpus drouynianus* forms a lignotuber that allows it

to resprout following shoot dieback caused by fire and/or drought (Ladd and Enright, this volume). Kerangas forests are also subject to occasional drought, and species growing in them, including podocarps, show an array of leaf traits, in combination with reduced plant size, that reduce water loss (Enright and Jaffré, this volume).

Podocarps are long-lived in the temperate zone, and there is evidence that they also have a longevity advantage over competing angiosperms in the tropics (Kitayama et al., this volume). They are often subcanopy components and not emergent in tropical forests, unlike many New Zealand podocarps (Coomes and Bellingham, this volume). Landscape-scale disturbance is probably not necessary for regeneration of tropical podocarps, even though many species occur in areas where disturbances such as cyclones and landslides are common. Tropical podocarps are fire intolerant. In general, podocarp seedlings show low abundance. Thus, in many cases, slow growth and high persistence likely facilitate their ultimate recruitment to the canopy. Little is known about herbivory in tropical podocarps or their defenses against herbivores. Similarly, pollination and seed dispersal in tropical podocarps have been little studied.

CONSERVATION, MANAGEMENT, AND GLOBAL CHANGE

In common with most tropical trees, the immediate threat to tropical podocarps is deforestation associated with timber extraction, mining, and other modern anthropogenic activities, including drainage of peat swamps and expansion of agricultural activities onto poor soils. Several podocarps are local montane endemics, and these may be further threatened by shifting climatic zones associated with global climate change and deforestation (Walther, 2004; Jump et al., 2009). These species could become increasingly rare within narrowing altitudinal bands, particularly on islands and mountains. Tropical podocarps are fire and drought intolerant, so they will be particularly adversely affected wherever climate change leads to hotter, drier conditions with more frequent fires.

Although podocarp timber has many uses for human activities, their slow growth rates make their exploitation ecologically unsustainable. Therefore, continued harvesting of existing individuals from natural stands threatens populations (Lawes et al., 2007).

Habitat specialization restricts the potential area of suitable sites for podocarps, which requires broad-scale habitat conservation to capture potential conservation sites. The association with unusually infertile soils is also

significant with regard to podocarp conservation. International Union for Conservation of Nature (IUCN) assessments of species conservation status are effectively determined by range sizes, in the absence of data on population number or population change. Many podocarps have large ranges (i.e., thousands of square kilometers) but probably only occupy a fraction of that area. Thus, if podocarps really are restricted to unusual habitats, then they may be more endangered than current assessments suggest. Additionally, if conservation priorities are defined by phylogenetic diversity, podocarps have a high conservation value because their nearest living sister taxa are separated by about 250 million years (Biffin et al., this volume).

A summary of tropical podocarp species that are threatened based on assessments in the 2009 IUCN Red List of Threatened Species (IUCN, 2009) is provided in Table 12.1. In addition to these species, a number of taxa are also considered “near threatened” or “data deficient.” Thus, Table 12.1 likely represents a conservative estimate of the true number of tropical podocarp species currently under threat of extinction. Taking this conservative estimate, roughly one-fourth of tropical podocarp species are threatened, with five species considered critically endangered, 18 species endangered, and 16 species vulnerable (Table 12.1). Many of the species in Table 12.1 are island endemics, including four species from Madagascar, six species from New Caledonia, and seven species from Borneo. In addition, there are a number of species endemic to islands in the Western Pacific and the Caribbean.

Because podocarp-dominated forests are often associated with ecosystems that have poor drainage and large accumulations of organic material on the forest floor, they play an important role in carbon storage. Leaf and litter characteristics of podocarps generally result in slow decomposition rates, leading to an accumulation of carbon in the litter layer and in the soil. This carbon can be rapidly lost when podocarp-dominated forests are cleared for other land uses (Freier et al., 2010). Thus, the UN global initiative to reduce emissions from tropical deforestation and degradation should place a high value on podocarp-dominated forests.

RECOMMENDATIONS FOR FUTURE RESEARCH

Podocarps are potentially good indicators of environmental change over their 250 million year history. Important aspects of the phylogeny of Podocarpaceae remain to

TABLE 12.1. Conservation status of threatened tropical species of the Podocarpaceae (IUCN, 2009). Abbreviations: CR, critically endangered; EN, endangered; VU, vulnerable.

Species	Status	Location	Habitat
<i>Acmopyle sahniana</i>	CR	Fiji	Montane forest
<i>Afrocarpus mannii</i>	VU	São Tomé, Gulf of Guinea	Montane forest
<i>A. usambarensis</i>	VU	East African highlands	Montane forest
<i>Dacrydium comosum</i>	EN	Malay Peninsula	Montane Forest
<i>D. ericoides</i>	VU	Sarawak, Borneo	Hill forest, ultrabasic
<i>D. gracile</i>	VU	Sabah, Borneo	Montane forest
<i>D. guillauminii</i>	CR	New Caledonia	Riparian
<i>D. leptophyllum</i>	VU	Irian Jaya	Montane heath forest
<i>D. nausoriense</i>	EN	Fiji	Montane rainforest
<i>Falcatifolium angustum</i>	VU	Sarawak, Borneo	Lowland rainforest
<i>Nageia maxima</i>	VU	Sarawak, Borneo	Peat swamp forest
<i>Parasitaxus usta</i>	VU	New Caledonia	Montane rainforest understory
<i>Podocarpus affinis</i>	VU	Fiji	Montane rainforest
<i>P. angustifolius</i>	EN	Cuba	Montane rainforest
<i>P. aristulatus</i>	VU	Cuba, Hispaniola	Montane forest
<i>P. beecherae</i>	EN	New Caledonia	Wet maquis
<i>P. brevifolius</i>	VU	Sabah, Mount Kinabalu	Montane forest
<i>P. capuronii</i>	EN	Madagascar	Montane forest
<i>P. costalis</i>	EN	Philippines, Taiwan	Montane forest
<i>P. costaricensis</i>	VU	Costa Rica	Lowland to montane forest
<i>P. decumbens</i>	CR	New Caledonia	Montane stunted forest
<i>P. deflexus</i>	EN	Malay Peninsula, Sumatra	Montane forest
<i>P. gibbsii</i>	VU	Sabah, Mount Kinabalu	Montane forest
<i>P. globulus</i>	EN	Sabah, Borneo	Lowland to montane forest
<i>P. hispaniolensis</i>	EN	Dominican Republic	Montane forest
<i>P. humbertii</i>	EN	Madagascar	Montane forest, heath
<i>P. laubenfelsii</i>	EN	Sarawak, Borneo	Kerangas, montane heath
<i>P. longifoliolatus</i>	EN	New Caledonia	Montane rainforest understory
<i>P. lophatus</i>	VU	Philippines	Montane forest
<i>P. nakaii</i>	EN	Taiwan	Subtropical forest
<i>P. palawanensis</i>	CR	Philippines	Lowland rainforest
<i>P. pallidus</i>	VU	Tonga	Montane forest
<i>P. pendulifolius</i>	EN	Venezuela	Montane rainforest
<i>P. perrieri</i>	CR	Madagascar	Montane forest
<i>P. polyspermus</i>	EN	New Caledonia	Montane forest
<i>P. purdieanus</i>	EN	Jamaica	Montane forest
<i>P. rostratus</i>	EN	Madagascar	Montane forest
<i>Retrophyllum minus</i>	EN	New Caledonia	Riparian
<i>R. rospigliosi</i>	VU	Venezuela, Colombia, Peru	Montane forest

be resolved, and more and better information would aid their use as environmental indicators. A phylogeographic perspective could help in understanding population connectivity under changing climate in the Holocene.

Dispersal and recruitment dynamics of infrequent lowland tropical podocarps are largely unknown. As

podocarps are mostly dispersed by large-bodied animals, local extinction of dispersers may particularly impact upon podocarp regeneration and recruitment and genetic diversity, especially on islands. Population genetic data could effectively address issues of pollen and seed dispersal, genetic diversity, and relatedness.

Podocarps colonize second-growth forests in some temperate regions. The potential for podocarps to colonize second-growth tropical forests, which are increasing in area in some tropical regions, is unknown. Physiological and growth responses of podocarps to variation in atmospheric CO₂ concentration are unknown but could have important implications for their use as indicators of environmental change.

Understanding why tropical podocarps are mostly restricted to wet, infertile environments requires information about their ecophysiology. For example, seedling leaf area ratios of temperate podocarps are generally low relative to co-occurring angiosperms, but virtually nothing is known of leaf area ratios of large-leaved lowland tropical podocarps. More information about physiological mechanisms of drought sensitivity, including stomatal function and susceptibility to cavitation, is key to understanding current podocarp distributions. The physiological adaptations allowing podocarp success on infertile soils, potentially including conspicuous root nodules, mycorrhizal symbioses, and nutrient retention strategies, are key areas for further research. A better understanding of podocarp ecophysiology is likely to be achieved through integrated, whole-plant studies, rather than by addressing nutrient, carbon, and water relations independently of each other.

Finally, podocarps are poorly represented in permanent census plots in tropical forests, which limits knowledge of demography and habitat associations. Important demographic factors and environmental drivers are likely to be longevity, relative shade tolerance, and edaphic properties. Permanent plot data could provide an opportunity to collate such information. Results could provide a framework to inform decisions about silviculture and forest management of podocarps.

EXPANDED AUTHOR INFORMATION

Lucas A. Cernusak, Research School of Biology, The Australian National University, Canberra, ACT 0200, Australia; Lucas.Cernusak@anu.edu.au. **Hylton Adie**, School of Biological and Conservation Sciences, Forest Biodiversity Research Unit, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, South Africa. **Peter J. Bellingham** and **Ian A. Dickie**, Landcare Research, PO Box 40, Lincoln 7640, New Zealand. **Edward Biffin**, Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Science, The University of Adelaide, Adelaide, South Australia 5005, Australia. **Timothy J. Brodribb**, School of Plant Science, University of Tasmania, Hobart, Tasmania 7001,

Australia. **David A. Coomes**, Forest Conservation and Ecology Group, Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK. **James W. Dalting**, Department of Plant Biology, University of Illinois at Urbana-Champaign, 265 Morrill Hall, 505 S. Goodwin Avenue, Urbana, Illinois 61081, USA. **Neal J. Enright** and **Philip G. Ladd**, School of Environmental Science, Murdoch University, Murdoch, Western Australia 6150, Australia. **Kanehiro Kitayama**, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan. **Hans Lambers**, School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia. **Michael J. Lawes**, School for Environmental Research, Charles Darwin University, Darwin, Northern Territory 0909, Australia. **Christopher H. Lusk**, Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia. **Robert J. Morley**, Palynova Limited, 1 Mow Fen Road, Littleport CB6 1PY, UK, and Department of Earth Sciences, Royal Holloway, University of London, Egham TW20 0EX, UK. **Benjamin L. Turner**, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Republic of Panama.

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