Podocarpaceae in Tropical Forests: A Synthesis


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 μmol CO₂ mol⁻¹ N s⁻¹, whereas mean values were 64 and 162 μmol CO₂ mol⁻¹ 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 mmol CO₂ mol⁻¹ 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 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 Field, 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 homoxyloous 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 grow-
ing 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 Zea-
land podocarps (Coomes and Bellingham, this volume).
Landscape-scale disturbance is probably not necessary for
regeneration of tropical podocarps, even though many spe-
cies occur in areas where disturbances such as cyclones and
landslides are common. Tropical podocarps are fire intoler-
ant. 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 anthro-
pogenic 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 in-
creasingly rare within narrowing altitudinal bands, par-
ticularly 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 harvest-
ing 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. Interna-
tional Union for Conservation of Nature (IUCN) as-
seSSments of species conservation status are effectively
determined by range sizes, in the absence of data on pop-
ulation 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 conser-
vation 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 esti-
mate, roughly one-fourth of tropical podocarp species are
threatened, with five species considered critically endan-
gered, 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 Bor-
neo. In addition, there are a number of species endemic to
islands in the Western Pacific and the Caribbean.

Because podocarp-dominated forests are often associ-
ated 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 de-
composition rates, leading to an accumulation of carbon
in the litter layer and in the soil. This carbon can be rap-
idly 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 environ-
mental change over their 250 million year history. Impor-
tant aspects of the phylogeny of Podocarpaceae remain to
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.


<table>
<thead>
<tr>
<th>Species</th>
<th>Status</th>
<th>Location</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acmopyle salicina</td>
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</tr>
<tr>
<td>Afrocarpus mannii</td>
<td>VU</td>
<td>São Tomé, Gulf of Guinea</td>
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<td>A. usambarensis</td>
<td>VU</td>
<td>East African highlands</td>
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<td>Dacrydium comosum</td>
<td>EN</td>
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<td>VU</td>
<td>Sarawak, Borneo</td>
<td>Hill forest, ultrabasic</td>
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<td>D. gracile</td>
<td>VU</td>
<td>Sabah, Borneo</td>
<td>Montane forest</td>
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<tr>
<td>D. guillauminii</td>
<td>CR</td>
<td>New Caledonia</td>
<td>Riparian</td>
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<td>D. leptophyllum</td>
<td>VU</td>
<td>Irian Jaya</td>
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<td>Podocarpus affinis</td>
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<td>P. angustifolius</td>
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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 $CO_2$ 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.

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**References**


