

A Functional Analysis of Podocarp Ecology

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ABSTRACT. Viewed in terms of species diversity, the Southern Hemisphere conifer family Podocarpaceae is equivalent to its northern sister the Pinaceae. However, despite their similar age and common heritage these two families diverge strongly in morphology, physiology, and ecology. Both Pinaceae and Podocarpaceae are successful families of vascular plants, and in both cases this success has been built upon contrasting and rather canalized adaptive differentiation. Pinaceae thrive in virtually all Northern Hemisphere forest environments where freezing limits the success of evergreen angiosperm competitors. In contrast, the Podocarpaceae are most successful in the tropics, where they compete directly with broad-leaved angiosperms, usually in montane rainforest. This chapter discusses some of the key adaptations that have enabled tropical Podocarpaceae to remain competitive during the rise of angiosperms. I also examine the hydraulic “Achilles heel” that limits all members of the Podocarpaceae to a mesic rainfall envelope.

ADAPTATION TO LIFE IN TROPICAL FORESTS

Large, bilaterally flattened leaves are more efficient at harvesting light than spirally arranged needle or scale leaves (Leverenz, 1995; Pickup et al., 2005). This general rule is highly significant when considering the outcome of conifer–angiosperm competition in the period since angiosperm diversification in the Late Cretaceous. With the exception of *Gnetum*, gymnosperms appear to be incapable of producing large laminate leaves, and as such, they cannot benefit from the economic advantages of efficient light harvesting and minimal self-shading that broad leaves offer (Falster and Westoby, 2003). The overwhelming dominance of broad-leaved taxa in most productive regions of the tropics indicates that the benefits of large leaf size reach their peak in this region (Webb, 1968). Warm temperatures and an absence of stresses that could potentially limit leaf size, including cold, soil water deficiency, and abiotic mechanical damage in tropical rainforests, contribute to the predominance of large, flattened leaves. Given the adaptive bias toward large leaves in the tropics and the limited

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capacity in conifers to produce large leaves (Bond, 1989), the modern tropics appear hostile to most conifer families. Remarkably, the Podocarpaceae have evolved multiple anatomies that allow many species to elaborate flattened shoots or broad leaves which appear to be instrumental to the unusual success of the family in the tropics.

MORPHOLOGICAL FLATTENING IN SHORT SHOOTS

The most obvious adaptation in podocarps to affect large, flattened photosynthetic surfaces is the compression of short shoots to form two-dimensional photosynthetic

structures. Some 135 species of extant podocarps from 11 genera exhibit flattened or composite photosynthetic structures (Figure 10.1). Flattening of short shoots is achieved by twisting leaves at the base such that they are oriented parallel to the shoot axis and arranged in a manner typical of the leaflets on angiosperm compound leaves. Flattened shoots are displayed perpendicular to the stem axis, thereby maximizing light collection. Many independent origins of shoot flattening are known (Biffin et al., this volume), leading to an impressive diversity of shoot morphologies in the family. Multiveined “broad leaves” are also found in two genera of Podocarpaceae (*Nageia*

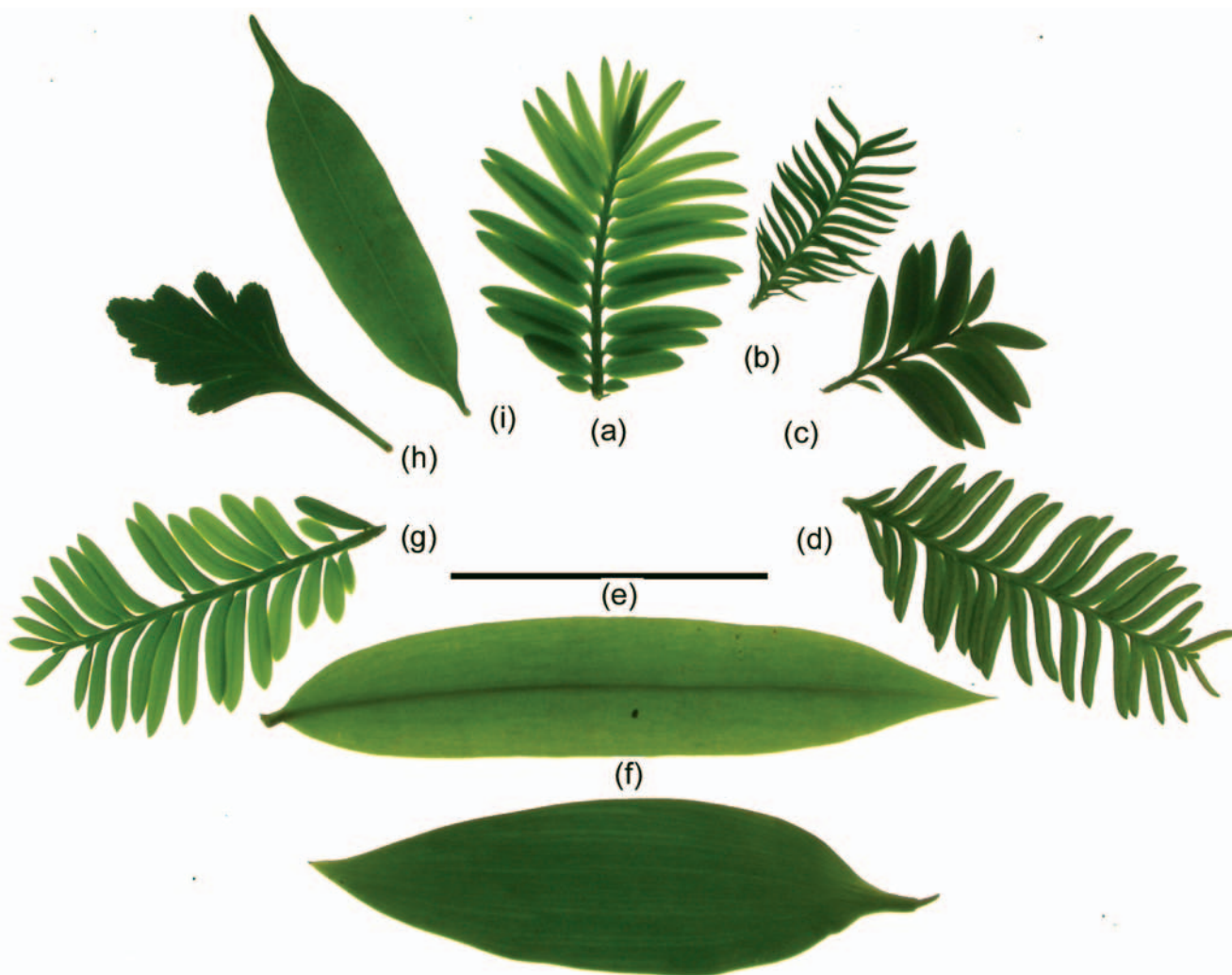


FIGURE 10.1. Some examples of the diversity of shoot flattening in nine genera of Podocarpaceae: (a) *Retrophyllum*, (b) *Dacrycarpus*, (c) *Falcatifolium*, (d) *Acropyle*, (e) *Podocarpus*, (f) *Nageia*, (g) *Prumnopitys*, (h) *Phyllocladus*, and (i) *Sundacarpus*. Along with obvious planation of short shoots (a, b, c, d, g), podocarps have evolved multiveined leaves (f) and phylloclades (h) and internal conducting sclereids (see text). Scale bar is 10 cm.

and *Phyllocladus*), the only genera outside the Araucariaceae with this capability. In *Phyllocladus* whole shoots are flattened into one multiveined lamina, and in the tropical species *P. hypophyllus*, flattened phylloclades are arranged into large structures that resemble the compound leaves of some palms.

The arrangement of leaves in two ranks flattened into a plane is not unique to podocarps, with some Northern Hemisphere conifer taxa such as *Sequoia*, *Metasequoia*, and *Taxodium* also exhibiting bilaterally compressed shoots. However, the Northern Hemisphere is overwhelmingly dominated by needle- and imbricate-leaved conifers, which constitute 96% of its total number of extant conifer species (Welch and Haddow, 1993). Shoots with strong bilateral compression are found only in six species in the Northern Hemisphere, all from the former Taxodiaceae. In marked contrast, about 60% of podocarp species produce distinct bilaterally flattened foliage (Hill and Brodribb, 1999).

ANATOMICAL ADAPTATION IN LEAVES

Most conifer species possess scale or needle leaves, and the absence of large-leaved conifer species can be traced to an apparent inability among extant conifers to form a reticulate plumbing network in the leaf lamina (Bond, 1989). The hydraulic efficiency conferred by vein reticulation is a prerequisite for elaborating large leaves because without an efficient means of distributing water evenly across the lamina, water deficits created by evaporation from the leaf during photosynthesis would lead to cell damage. The evolution of the hydraulic vascular system in plants saw nonliving pipes (xylem) create a “superhighway” for water flow through roots, stems, and leaves, avoiding cell-to-cell transport limitation. However, these pipes terminate within the leaves, at which point water must flow into the living mesophyll tissue, where it encounters a very high resistance to flow as it moves into and between cells. Maximum hydraulic conductance would be achieved if veins of xylem branched such that they contacted all living cells in the leaf, but no plant makes this enormously complex architectural investment. Instead, theory suggests that productive leaves must be internally structured such that evaporating cells are in close proximity to the vein terminals (Brodribb et al., 2007). Through the 400 million years of leaf evolution there have been many experiments with the vascular anatomy and architecture of leaves (Kenrick and Crane, 1991; Boyce and Knoll, 2002), but only two highly convergent patterns emerge as being linked with high productivity: dense

reticulate venation or needle leaves (Brodribb et al., 2007). In conifers, which typically possess a single vein in the leaf, narrowing of the distance from the vein to the leaf margin enables high hydraulic efficiency and photosynthetic rates in needle leaves.

Many members of the Podocarpaceae exhibit a different solution to transporting water through single-veined leaves, allowing them to partially overcome the narrow-leaf-width limitation that applies to most other conifers. In eight genera of Podocarpaceae, hollow sclereids extend radially from the midvein out toward the leaf margins (Figure 10.2). Cumbersomely labeled accessory transfusion tissue (ATT) (Griffith, 1957), these sclereids have been shown to be nonliving water-filled cells analogous to xylem cells, even in their pitted end wall connections (Figure 10.2). In genera such as *Podocarpus* and *Sundacarpus*, accessory transfusion tissue reaches its maximum development, forming a layer of water-conducting cells between the palisade and spongy mesophyll that connect to the midvein through the transfusion tissue. *Podocarpus* species with well-developed ATT are able to attain widths in excess of 30 mm (e.g., *P. dispersmis*). In Podocarpaceae genera such as *Acmopyle*, *Falcatifolium*, and *Sundacarpus* the combination of accessory transfusion tissue and shoot flattening enables species to produce strongly planated shoots that attain a size and shape that falls within the range of associated rainforest angiosperm leaves.

SHOOT FLATTENING AND SHADE

In consideration of the economic advantages of broad leaves it appears likely that shoot flattening in Podocarpaceae is an adaptation that allows species to grow efficiently at low light (Brodribb and Hill, 1997), which may give podocarps the ability to compete with broad-leaved angiosperms in tropical forests. Strong support for this hypothesis was provided by a study of diverse conifer shoot morphologies in the Southern Hemisphere, which revealed that shoot flattening was associated with the light saturation characteristics of leaves (Brodribb and Hill, 1997). Photosynthesis in species with highly flattened leaves became light saturated at low light intensities relative to nonflattened shoots, resulting in an inverse correlation between shoot width and saturating light intensity. The low light requirement of rainforest podocarp leaves combined with the efficient light foraging that comes from shoot planation (Leverenz et al., 2000) makes podocarp foliage highly competitive in rainforest understory.

The unrivalled (among conifers) success of Podocarpaceae in competition with angiosperms in the tropics

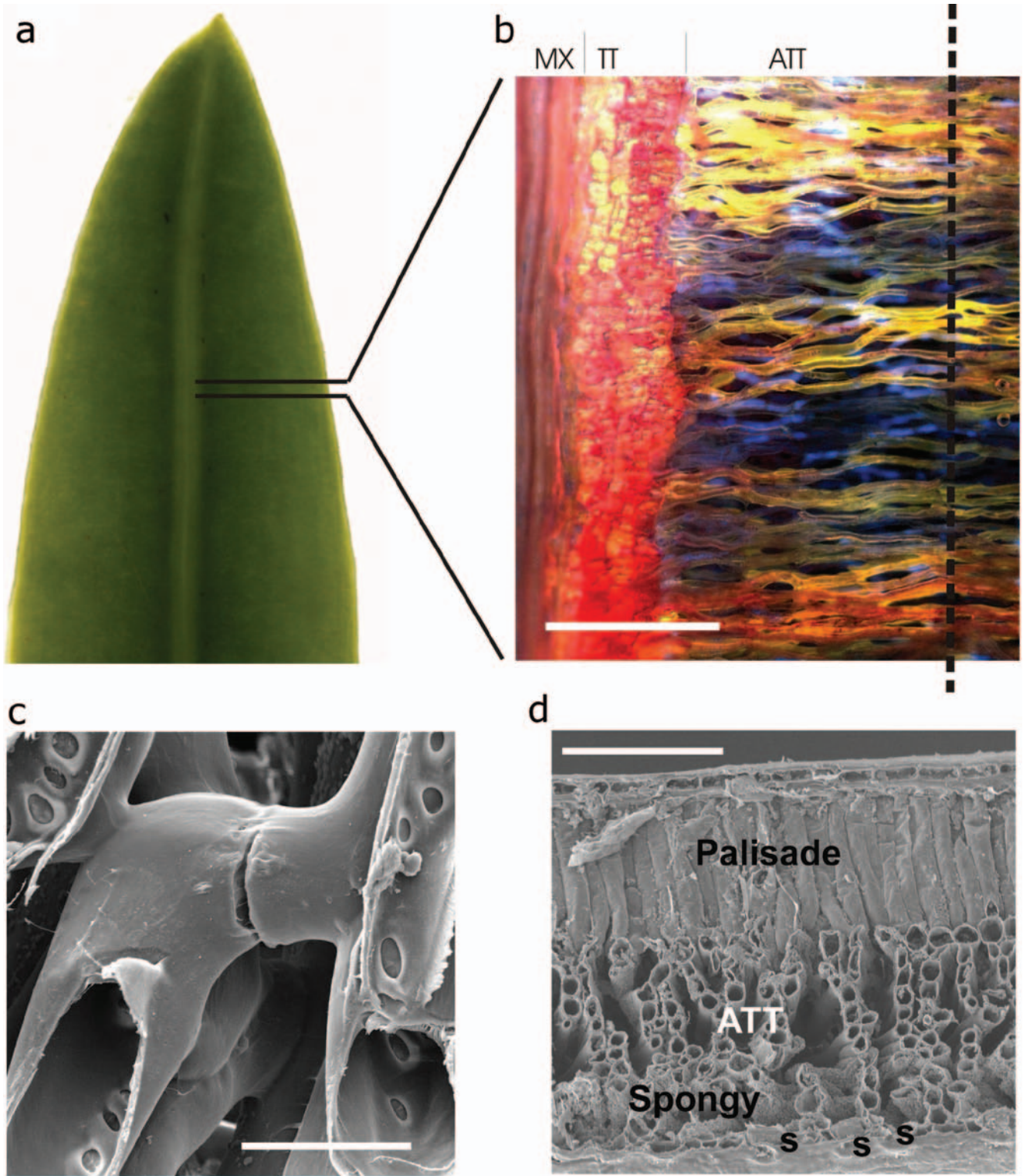


FIGURE 10.2. Anatomical features of the accessory transfusion tissue (ATT) that conducts water radially from the vein (a) toward the margin. Shown in paradermal section (b), these sclereids/tracheids form tubes conducting water away from the midvein (MX). Highly connected ATT cells (c) form a layer between the palisade and spongy mesophyll tissue (d). Scale bars are 200 μ m (b, d) and 20 μ m (c), and stomata are indicated by “s.”

appears to be strongly linked to anatomical and morphological adaptations in the leaf that confer efficient growth in the shade. However, it should be noted that podocarp foliar architecture appears to be bound by functional limits that do not apply to the reticulate-veined broad leaves of angiosperms. It seems probable that ATT is a less efficient means of conducting water than reticulate venation, which may explain why maximum leaf size in podocarps never reaches the extremes seen in angiosperms. This is perhaps also why podocarps do not tend to be abundant in highly productive lowland tropical forests, in which angiosperm leaf size is at its maximum (van Royen, 1979). However, in montane forests, the flattened shoots of tropical Podocarpaceae are well inside the range of leaf sizes found in coexisting angiosperms (de Laubenfels, 1969). Considering the similar vegetative performance of podocarp and angiosperm leaves, it is not surprising that the diversity and success of podocarp species in tropical forests falls within the range of a number of moderately successful angiosperm families.

Podocarpaceae with flattened leaves or shoots first became successful in the early Cenozoic, demonstrating that these species were growing in forests with relatively dark understories (Hill and Brodribb, 1999; Brodribb and Hill, 2003). One possible explanation for the evolution of flattened shoots in podocarp foliage is that angiosperm evolution changed light quality in the conifer regeneration niche. The effect of this would have been either to force conifers into marginal habitats where canopy closure is delayed or incomplete or to favor the convergent evolution of broad leaves, as observed in podocarps.

LEAF ADAPTATION, SHADE TOLERANCE, AND TRANSEQUATORIAL MIGRATION

Podocarps have been successful in crossing the equator from their Southern Hemisphere origin to colonize the low latitudes of the Northern Hemisphere (see Morley, this volume). In contrast, only one species of Pinaceae has colonized south of the equator (*Pinus merkusii* at 2°S, Sumatra). Furthermore, Pinaceae have no fossil record in the Southern Hemisphere (Millar, 1998). An interesting alternative to vicariance as an explanation for the contrasting fortunes of *Pinus* in the Northern and Southern hemispheres is that evergreen tropical forests pose an impenetrable ecological barrier to the southward movement of *Pinus*. In contrast to podocarps, *Pinus* (and Pinaceae in general) have been relatively unadventurous in exploring flattened leaf morphologies, with the probable consequence that virtually all species are shade intolerant and

unable to regenerate beneath a forest canopy (for a review, see Richardson and Rundel, 1998). This conservative leaf morphology may underlie the inability of *Pinus* to penetrate the equatorial zone and into what appears suitable habitat (Grotkopp et al., 2002) in the Southern Hemisphere.

Pinus krempfii is an exception to the rule of Pinaceae exclusion from tropical rainforest. This extraordinary species comes to within a few degrees of the equator and uses specialized flattened leaves that confer the ability to regenerate in the shady forest understory. The leaves of *Pinus krempfii* show striking convergence with the flattened leaves of rainforest Podocarpaceae. Arrays of elongated sclereids in the mesophyll tissue of *Pinus krempfii* are highly reminiscent of those found in most broad-leaved podocarp species (Figure 10.3). According to leaf hydraulic measurements, these sclereids appear to be critical for facilitating radial water transport from the vein toward the leaf margin in broad, single-veined leaves in the same way as Podocarpaceae (Brodribb et al., 2007).

PODOCARPS AND DROUGHT

Considering their impressive ability to compete with angiosperms in the tropics, it is surprising the Podocarpaceae have only enjoyed limited success in temperate latitudes compared with the Pinaceae and Cupressaceae. I argue that the most significant agent preventing podocarp success at the higher latitudes of the Southern Hemisphere today is drought. A major drying trend in the temperate regions of the Southern Hemisphere through the late Tertiary coincides with a period of significant podocarp contraction and extinction in Australia and other southern landmasses (Kershaw et al., 1994). Diminishing rainfall, particularly during glacial periods, has resulted in a situation today whereby the podocarps from midlatitudes are confined to rainforest or wet montane forest and are absent from the dry woodlands that compose a large proportion of the forest cover in temperate Australia, Africa, and South America. The historical explanation for podocarp drought sensitivity most probably lies in the fact that the origins and diversification of the family are associated with cool and wet conditions on the continental margins of Gondwana (Hill and Brodribb, 1999). However the functional explanation seems to be linked to a disproportionately large trade-off in podocarp wood between construction cost and the ability to resist water stress.

Water tension increases in the xylem during soil drying and under extreme stress can become large enough

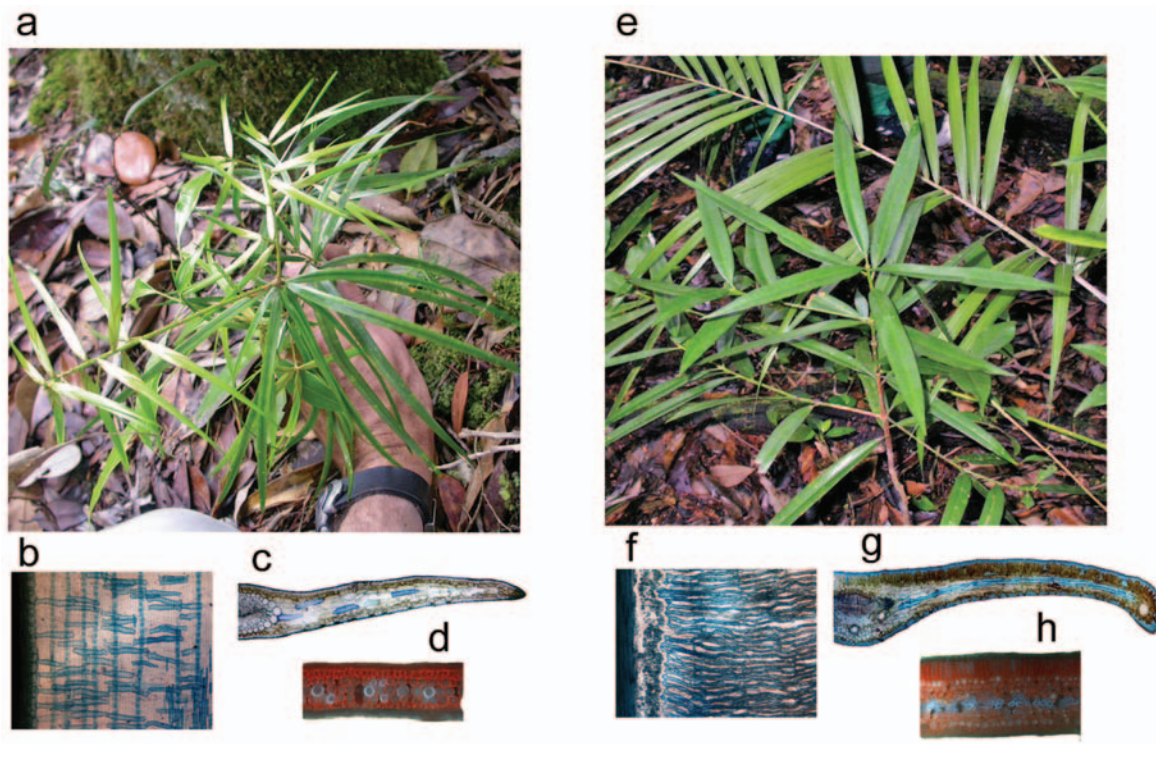


FIGURE 10.3. (a–d) *Pinus krempfii* and (e–h) *Podocarpus neriifolius* growing in the same tropical understory in Vietnam. Along with producing a similar flattened morphology, the *Pinus* leaves exhibit convergent anatomy that sees sclereids (blue) pass radially from the vein to the margin. Light microscope fluorescence images are paradermal (b, f), cross section (c, g), and tangential (d, h).

that air is drawn into the xylem conduits, cavitating the water in the lumen and causing them to cease functioning for water transport (Sperry and Tyree, 1990). The vulnerability of the xylem water column to water-stress-induced cavitation is an important measure of a plant's ability to survive drought (Tyree et al., 2002; Brodribb and Cochard, 2009). In Southern Hemisphere conifers, xylem vulnerability is closely linked to distribution according to the rainfall in the driest quarter (Brodribb and Hill, 1999). Podocarps sampled in this study occupied the wet end of the distribution-vulnerability scale (Figure 10.4). Consequently, drought sensitivity in podocarps has been associated with large extinction and range contractions in Australia since the establishment of the circumpolar current and the onset of glacial drying cycles (Brodribb and Hill, 2003).

Podocarp wood is not especially sensitive to dysfunction under water stress. Surprisingly, the range of hydraulic tensions associated with a 50% loss of xylem function is similar to that of Pinaceae, which appear to be far more tolerant of water stress. The unusual thing about podocarp

wood is its very high density relative to vulnerability. As with most plant groups, there is a clear trade-off in members of the Podocarpaceae between wood density and xylem vulnerability, with cavitation-resistant wood being considerably denser than drought-sensitive wood (Hacke et al., 2001). Strangely, the cost of producing cavitation-resistant wood is much greater in the Podocarpaceae than in either the Pinaceae or Cupressaceae; wood density of podocarp species is about 30% higher than Pinaceae and Cupressaceae species of equivalent cavitation resistance, whereas hydraulic efficiency is substantially lower in the podocarps (Pitterman et al., 2006). Therefore, it is probable that the high cost of drought resistance in podocarp wood is one of the reasons behind the weak competitiveness of podocarps in dry forest.

A second factor likely to limit podocarp success in drier forest is the very same tissue that makes the family so successful in the tropics. The leaf sclereids that allow podocarps to produce broad leaves (see above) are highly susceptible to collapse under water tension because of their unsupported arrangement in the mesophyll (Figure

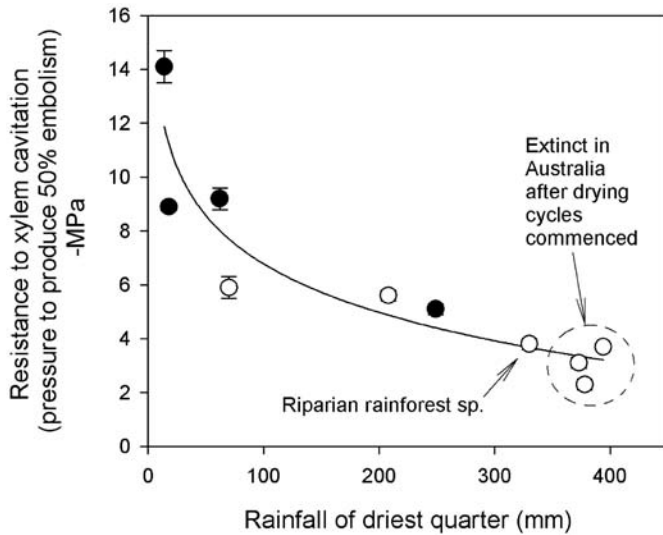


FIGURE 10.4. The relationship between xylem vulnerability to water-stress-induced cavitation and the driest natural range of Southern Hemisphere podocarps (open circles) and Cupressaceae (solid circles). Podocarps are the most vulnerable of the group, and genera at the wet end of the spectrum (within dashed circle) became extinct in Australia during Cenozoic drying. Another species appears to be at its rainfall limit in Australia, growing only on river edges in the wettest parts of Tasmania (*Lagarostrobos franklinii*, indicated by an arrow). Error bars represent standard deviations.

10.5). Despite their thick walls, leaf sclereids were found to collapse at moderate water tensions, causing a loss of hydraulic and photosynthetic function in the leaf (Brodrribb and Holbrook, 2005). One of the most drought-resistant podocarps, *Podocarpus drouynianus*, has very short foliar sclereids and leaves that are almost needles in width, supporting the idea that broad leaves and sclereids tend to limit the drought performance of the family. Shade

and drought tolerance are often considered as antagonistic directions for adaptation, and Podocarpaceae appear to follow such a pattern (Brodrribb and Hill, 2000). Such strong physiological canalization seems to be a characteristic of conifers.

In contrast to podocarps, many Pinaceae are extremely drought resistant, producing tough needle leaves with high photosynthetic rates (Lusk et al., 2003; Brodrribb and Feild, 2008). Once again, however, evolutionary canalization has proved highly limiting because the needle leaves of most Pinaceae are extremely inefficient in the shade, making them uncompetitive in tropical evergreen forests (Richardson and Rundel, 1998).

PINACEAE VERSUS PODOCARPACEAE

Pinaceae-dominated forest covers a significant proportion of the Northern Hemisphere, whereas podocarps constitute a tiny proportion of the Southern Hemisphere forest cover. The high degree of success of Pinaceae relative to Podocarpaceae in temperate latitudes can be largely attributed to the harsh continental climates prevalent in major northern landmasses, which produce strong seasonality and regular freezing that benefit Pinaceae. Freezing is the “great leveler” between conifers and angiosperms because it greatly narrows the hydraulic advantage of angiosperm wood (Feild et al., 2002). When ice forms in the xylem of trees, the probability that air bubbles will form and occlude the xylem upon thawing is related to the size of xylem conduits (Sperry and Sullivan, 1992). The tiny conduits that make up conifer wood are relatively impervious to freeze-thaw embolism, whereas the larger vessels of angiosperms are prone to embolism. In much of the Northern Hemisphere where Pinaceae dominate, major freezing events are common during winter months, resulting in the freeze-induced shutdown of angiosperms at temperate latitudes for much of the year. Northern

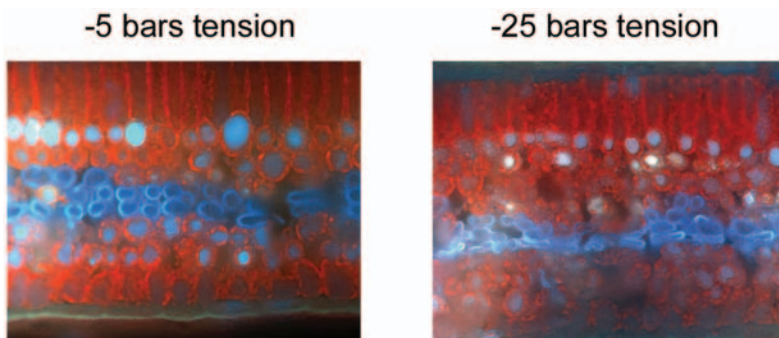


FIGURE 10.5. Tangential sections (cut parallel with the midrib) of a *Podocarpus grayei* leaf, showing accessory transfusion tissue cells (blue due to lignin fluorescence) in hydrated (–5 bars) and mildly water-stressed (–25 bars) leaves. Collapse of the accessory transfusion tissue under moderate water tension may limit podocarp success in drier climates.

Hemisphere conifers benefit greatly from the sensitivity of angiosperms to freezing, and this benefit can be clearly seen in terms of an increasing dominance of conifers moving poleward from the Tropic of Cancer. In contrast, the moderate seasonality experienced in most parts of the Southern Hemisphere means that podocarps do not benefit from the freeze-thaw advantage of its Pinaceae sister except at high latitudes and altitudes. As such, podocarps have a greatly diminished opportunity for the type of biome domination achieved by Pinaceae at higher latitudes in the Northern Hemisphere.

One question that remains is why Podocarpaceae are absent from most of the Northern Hemisphere. Biogeography probably plays a role in driving this pattern, given the relatively recent north–south contacts through Southeast Asia and Central America (Morley, this volume; Dalling et al., this volume). However, considering the demonstrated potential of podocarps for long-distance dispersal (fleshy cones and conspicuous presence on many recent disjunct islands such as Samoa, Fiji, and Cuba), biogeography alone is insufficient to explain the apparent inability of podocarps to colonize seasonal northern habitats. Plant functional limitations also provide a possible insight into the exclusion of podocarps from the Northern Hemisphere. Because of a comparatively warm evolutionary history podocarps appear to have relinquished some of the characteristics that confer freeze tolerance. The water transport characteristics of both wood and leaves of podocarps appear to be poorly adapted to regular sap freezing. Ice formation has a tendency to desiccate the vascular tissue in a similar fashion to drought. Ice has a very low water potential and is able to draw water out of xylem tissue, mimicking the effect of dry soil. As discussed above, podocarps are ill adapted to respond to desiccation stress, and this may contribute to an inefficient response to the types of freezing stresses that regularly occur in the Northern Hemisphere. The other freezing handicap for podocarps is the presence of leaf sclereids, which are likely to form a nucleation center for ice formation in the leaf. In contrast, the Pinaceae appear to have been largely canalized in the opposite direction by diversification in freezing climates, which has culminated in the pines that produce some of the most freeze-tolerant foliage found in any plant group. As such, podocarps are unlikely to be successful in competition with Pinaceae in freezing environments in the Northern Hemisphere. Further work is required to formally quantify the impact of these freezing liabilities for podocarps, but the fact that the podocarps are poorly represented in all but the wettest Southern Hemisphere tree lines suggests that they may not be well suited to the

extended seasonal freezing that characterizes much of the Northern Hemisphere.

CONCLUSIONS

The podocarp capacity to successfully compete with angiosperms in tropical forests is unusual among conifers. The success of the Podocarpaceae can be traced to anatomical and morphological modification of leaves and shoots to produce large foliar units that function similarly to broad leaves in angiosperms. Large foliar units in podocarps probably originated in the Late Cretaceous and may have been a response to angiosperm radiation (Biffin et al., this volume). The economic advantages conferred by the broad leaves and shoots of podocarps are significant in productive tropical forests, but associated limitations appear to prevent podocarps from achieving the degree of success in either the northern or southern temperate latitudes enjoyed by Pinaceae in the Northern Hemisphere.

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