

opportunistic and will colonize new areas with some rapidity. Sea level rise remains a problem, however, as mangrove communities in many areas may become squeezed out as sea level rise forces mangrove communities landwards, but human use prevents landward migration.

Protection and Plantation

Despite the massive losses that mangrove communities have gone through in the past decades there have also been concerted efforts to protect them in some areas, and the growing realization of their value has led to widespread efforts to utilize mangroves in a more sustainable manner, and in some places large areas of mangrove plantations have now been established.

Worldwide, there are currently over 1100 protected areas with mangroves managed for conservation purposes spread between 99 countries. These cover some 10% of the global total. Although this is a far higher proportion than for many other forest types, active protection is absent from many of these areas, and the remaining unprotected sites are probably more threatened than many other forest types because of their vulnerability to human exploitation.

Increasing recognition of the various values of mangrove forests is leading to the establishment of mangrove plantation or restoration projects in many countries: for coastal defense, as a source of fuel or timber products, for fisheries enhancement, or often for a combination of these benefits. Plantation and restoration has been most widespread in Asian countries, with over 2300 km² in Bangladesh, Pakistan, and Vietnam.

Although the total area of such plantations remains insignificant when compared to global mangrove losses, they represent an important new development. Active management for direct economic benefits in these and other mangrove areas is growing. The Matang Mangrove Reserve in Malaysia has been managed for 100 years. Studies have shown combined benefits arising from timber and fuelwood products (notably charcoal), but also from the large nearshore fishery (directly or indirectly providing employment for over 4000 people), from aquaculture on the mud flats below the mangroves, and from tourism.

It is rare that such holistic studies have been carried out. Often the human benefits provided by mangrove fall between several sectors of the economy – fisheries, forestry, tourism, and coastal protection – and their combined benefits are not realized. Improved assessment of these benefits will undoubtedly lead to much wider-scale protection and sustainable management for mangroves globally.

Acknowledgement

Adapted with permission from Spalding MD (2001) Mangroves in Steele JH, Turekian KK and Thorpe SA (2001). *Encyclopedia of Ocean Sciences*. Published by Academic Press, London.

See also: **Ecology:** Aquatic Habitats in Forest Ecosystems. **Environment:** Environmental Impacts; Impacts of Elevated CO₂ and Climate Change. **Resource Assessment:** Forest Resources. **Silviculture:** Treatments in Tropical Silviculture. **Sustainable Forest Management:** Causes of Deforestation and Forest Fragmentation. **Tree Physiology:** A Whole Tree Perspective; Root System Physiology; Stress. **Tropical Tree Seed Physiology.** **Tropical Ecosystems:** Bamboos, Palms and Rattans. **Tropical Forests:** Combretaceae; Tropical Moist Forests.

Further Reading

- Field CD (1995) *Journey amongst Mangroves*. Okinawa, Japan: International Society for Mangrove Ecosystems.
- Field CD (ed.) (1996) *Restoration of Mangrove Ecosystems*, p. Okinawa. Japan: International Society for Mangrove Ecosystems.
- Lacerda LD (2002) *Mangrove ecosystems: function and management*. Heidelberg, Germany: Springer-Verlag.
- Robertson AI and Alongi DM (eds) (1992) *Tropical Mangrove Ecosystems*, Coastal and Estuarine Studies no. 41. Washington, DC: American Geophysical Union.
- Saenger P (2003) *Mangrove Ecology, Silviculture and Conservation*. Dordrecht, The Netherlands: Kluwer Academic Publications.
- Saenger P, Hegerl EJ, and Davie JDS (eds) (1983) *Global Status of Mangrove Ecosystems*, IUCN Commission on Ecology Papers no. 3. Gland, Switzerland: IUCN (World Conservation Union).
- Spalding MD (1998) *Biodiversity Patterns in Coral Reefs and Mangrove Forests: Global and Local Scales*. PhD dissertation, University of Cambridge.
- Spalding MD, Blasco F, and Field CD (eds) (1997) *World Mangrove Atlas*, p. Okinawa. Japan: International Society for Mangrove Ecosystems.
- Tomlinson PB (1986) *The Botany of Mangroves*. Cambridge, UK: Cambridge University Press.

Southern Hemisphere Conifers

J C G Banks, Australian National University, Canberra, Australia

© 2004, Elsevier Ltd. All Rights Reserved.

Introduction

The southern hemisphere is home to almost half of the world's conifers including a small number of tropical species that occur in both hemispheres

Table 1 World conifers, by hemispheres, families, genera and species

Taxon	World	Hemisphere		
		North	Both north and south	South
Araucariaceae				
Genera ^a	3	1	1	3
Species	40	8	3	32
Cupressaceae				
Genera ^b	20	10	1	10
Species	117	82	1	39
Pinaceae				
Genera ^c	10	10	1	
Species	192	192	1	
Podocarpaceae				
Genera ^d	11	0	2	9
Species	174	80	32	124
Taxodiaceae				
Genera ^e	11	10		1
Species	15	12		3

^a Southern hemisphere genera: *Araucaria*, *Agathis*, *Wollemia*.

^b Southern hemisphere genera: *Diselma*, *Fitzroya*, *Austrocedrus*.

^c This family is represented by a single species, *Pinus merkusii*, in the southern hemisphere.

^d Southern hemisphere genera: *Podocarpus sensu lato*, *Dacrydium*, *Phyllocladus*, *Lagostrobos*, *Saxegothaea*.

^e The only genus of this family in the southern hemisphere is *Athrotaxis*.

(Table 1). All five conifer families are represented in both hemispheres with 40% of the genera south of the equator. The Cupressaceae is the most cosmopolitan of the families with 10 genera in each hemisphere, but with most species in the north. The Podocarpaceae occurs in all southern continents with significant numbers of species extending north of the equator in Africa, Southeast Asia, Central America, and the Caribbean. The Araucariaceae has a more restricted distribution found in Australasia, and north through the island chain to Malaysia, with one genus in South America. The Pinaceae and Taxodiaceae are centered in the northern hemisphere with only one and three species respectively found south of the equator. Further details on the ecology of the southern conifers is found in the reference texts. Many northern hemisphere conifers are today grown in the southern continents in plantations and/or as ornamental trees and shrubs in city parks and gardens. The major plantation species is *Pinus radiata* originating from California which supports major timber and paper industries, while other species include *P. elliotii*, *P. caribaea*, *P. patula*, and *P. pinaster*. Ecologically, these are pioneer species and when freed from their natural pests and diseases they are fast growing. Numerous ornamental cultivars, mostly from the Cupressaceae, are important components of the urban forests where they are

planted for their decorative features by civic and private landholders.

Taxonomy

The focus here is on the three dominant southern families, Araucariaceae, Cupressaceae, and Podocarpaceae, with minor reference to Pinaceae and Taxodiaceae that are comprehensively covered in the article on the conifers of the northern hemisphere (see **Temperate and Mediterranean Forests: Northern Coniferous Forests**). The structure of the female cone can be used to recognize the southern families. In the Araucariaceae the female cone scales are spirally arranged with only one relatively large seed per cone scale to which it is fused in the genera *Araucaria* and *Agathis*, but free in *Wollemia*. In all three genera the cone disintegrates at maturity to release the seed. In Cupressaceae all the southern genera belong to the subfamily Callitroideae which has only one monospecific genus, *Tetraclinis articulata*, north of the equator. The cones in this subfamily are distinct possessing valvate scales in pairs or whorls of three; at maturity these open to release relatively small-winged seeds. In contrast the seed bearing cones in Podocarpaceae are variously reduced and in the extreme may consist of a single seed atop a fleshy, plumlike receptacle comprising the fused remnants of the cone, or with one or two seeds attached to the central axis of the 'cone.' This origin of this reduced cone was initially misidentified with the family allocated to the Taxaceae, the yews.

Araucariaceae: The Araucarias and Kauri and Wollemi Pines

The Araucariaceae consists of three distinct genera, *Araucaria*, *Agathis*, and *Wollemia*, found in an island arc from Malaysia to New Zealand and including eastern Australia with *Araucaria* extending to South America (Figure 1). Species occur in tropical to warm temperate rainforests in coastal to montane environments. Rainforest species are regarded as postcyclone pioneers possessing rapid growth and apical dominance. They overtop the broadleaf rainforest as emergents with the tallest species *Araucaria klinkii*, klinki pine (Figure 2), reaching 70 m at maturity. It is found in tropical hill rainforests in New Guinea.

Araucaria: The Araucarias

The genus *Araucaria* consists of about 19 species, two in South America and two in eastern Australia with the remainder in Oceania along the island arc from Norfolk Island to New Caledonia where several

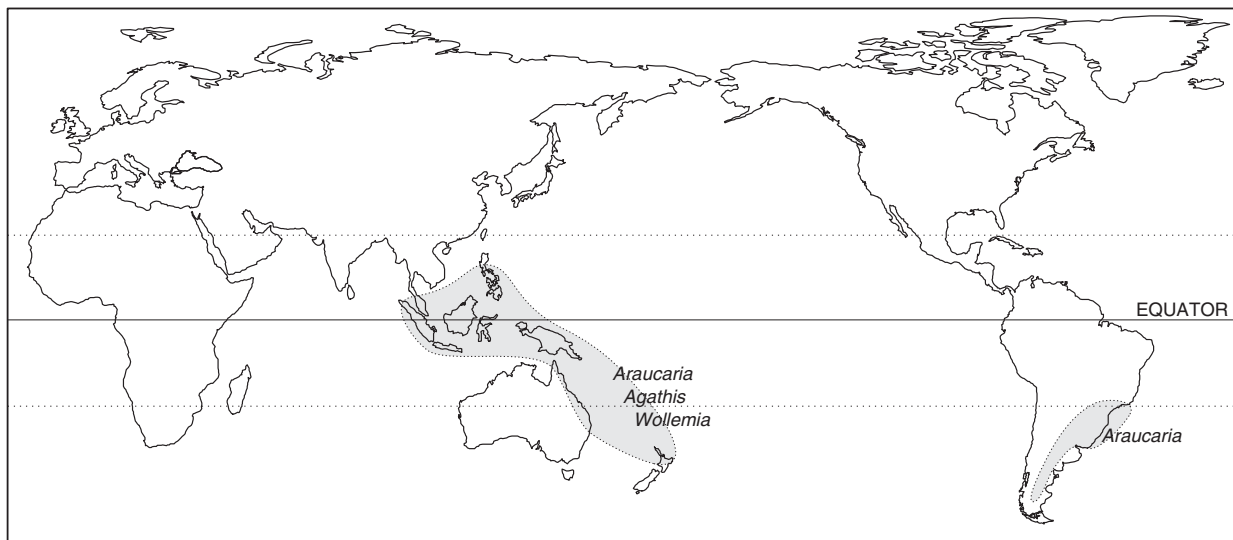


Figure 1 World distribution of Araucariaceae.



Figure 2 Klinki pine, *Araucaria klinkii*, rainforest emergents 70m tall near Bulolo, Papua New Guinea.

species coexist on the Isle of Pines. The majority of species are maritime often occurring in pure coastline forest stands exposed to onshore salt-laden winds. To survive this hostile maritime environment the leaves

are covered in a thick surface wax coat which protects them against salt damage. The significance of this feature was clearly illustrated when in the 1970s *Araucaria heterophylla*, the Norfolk Island pine, long established as a backdrop to Sydney's famous Bondi Beach, went into rapid decline. The primary cause was a new nonbiodegradable detergent that was polluting onshore winds, stripping the wax coat off the foliage and allowing salt to attack the exposed leaves.

A distinctive feature of the araucarias is that species can be readily recognized by their distinctive crown silhouettes. For example the Pacific island species *A. columnaris*, Cook's pine, has the peculiar habit of shedding its lower branches and then regenerating the lower crown from adventitious buds resulting in a dense narrow columnar crown which widens out towards the apex. Another is *A. heterophylla*, which maintains almost perfect crown symmetry with a simple two-order branching system (Figure 3). Similarly, the South American *A. angustifolia*, candelabra pine, and *A. araucana*, Chile pine, which both occur in pure forest stands, possess characteristic silhouettes. *Araucaria bidwillii*, the bunya bunya from eastern Australia, has the distinction of having large football-sized cones weighing 4–5 kg at maturity. *Araucaria cunninghamii*, hoop pine, is the most important araucaria plantation species providing a major softwood resource in southeast Queensland. This species exhibits some genetic variability both within and between geographic occurrences that extend from northern New South Wales to New Guinea. Tree breeding programs that began last century have significantly improved today's breeding stock for plantation use.



Figure 3 Norfolk Island pine, *Araucaria heterophylla*, showing its symmetrical crown trees at Twofold Bay, New South Wales.

Agathis: The Kauri Pines

The kauri pines are majestic trees with examples planted in urban parks in both hemispheres. The genus contains about 19 species that resemble angiosperms by having a wide-spreading crown atop massive primary branches arising from a distinct crown break. The bark is deciduous, a unique feature in the conifers with the exception of *Pinus bungeana*, the lace-bark pine from China. The bole attains massive proportions in old trees and exhibits little or no taper.

The most extensive and greatest kauri forests were in New Zealand where *Agathis australis*, known simply as kauri pine, dominated much of the temperate rainforests in the northern half of North Island. These were first seen by Capt. Cook in 1770 and noted as a potential source of spars with the first trial shipment in 1794. By 1820 timber was being

exported from Whangaroa harbor. Exploitation of these forests in Northland and the Coromandel Peninsula was in full swing by the 1860s reaching its zenith by the turn of the century. Kauri timber is unsurpassed in the conifers. The wood is off-white to red and brown, resinous, straight grained, of great strength and durability and it was available in large sizes. On occasions timber was cut from buried logs, remnants of earlier forests destroyed in past volcanic eruptions. Some of these fossil logs have been dated to 30 000 years old, attesting to the timber's durability. Today only small stands remain, protected in reserves including one in Waipoua which has conserved the stand containing one of the world's largest living conifers, the Tane Mahuta or 'Lord of the Forest,' a 52-m tall tree estimated to be over 2000 years old. In eastern Australia, the three species of kauri pines are minor rainforest trees. Harvesting started in the nineteenth century and followed a similar cycle with the last cutting in the 1960s in the Ingham hinterland. Some kauri timber is still cut in small quantities in Malesia. As a plantation species in Queensland, *A. robusta*, the South Queensland kauri, was unsuccessful as it suffered severe insect defoliation when planted in pure stands.

An unusual commercial product from the kauri forests is the kauri gum, a resin that freely exudes from wounds accumulating on branches and in quantity over time beneath trees more than 1000 years old. Both fossil and fresh resin, called copal or dammar, were harvested in large quantities in New Zealand and Malesia around the end of the nineteenth century. Its principal uses were in varnishes and linoleum. Today small amounts, especially pieces with entrapped insects, are made into jewellery.

Wollemia: The Wollemi Pine

The discovery of this new monospecific genus in 1994 surprised the botanical world, as it had long been assumed that all of the world's conifers had been discovered and the major interest to conifer taxonomists was the ever-increasing number of ornamental cultivars entering horticulture. Its discovery, less than 200 km from Sydney, is described in Woodford's book devoted to the species. The scientific name given to this new taxon is *Wollemia nobilis* (Figure 4). The genus name is that of the national park in which it was found while the specific name alludes to its majestic form. Wollemi pine trees were found in the bottom of a deep sandstone canyon, one of many in this national park. Following intensive searching, only three stands have been located, consisting of fewer than 50 trees in total growing in small remnant stands of warm temperate

rainforest that includes *Ceratopetalum apetalum*, coachwood. The pollen record shows the species to have been once widespread in southern Australia



Figure 4 Wollemi pine, *Wollemia nobilis*, a new conifer genus discovered in 1994 in a deep sandstone gorge in the Wollemi National Park near Sydney. Courtesy of Jaime Plaza, Royal Botanic Gardens and Domain Trust.

with occurrences in Antarctica and South America. Trees exceed 30 m in height and age estimates calculated from annual growth rings on a fallen tree indicates mature trees to be around 400 years old. One very distinctive feature of this new conifer is that it readily regenerates vegetatively from adventitious and basal buds. Only two widely distant conifers exhibit similar features: *Pinus canariensis*, Canary Island pine, and *Sequoia sempervirens*, Californian redwood.

Cupressaceae: The Cypress Pine Family

Most species of the southern Cupressaceae are components of the cool temperate rainforests in South America, New Zealand, and Tasmania with several extending to tropical rainforests in Malesia (Figure 5). Species from four genera have adapted to semi-arid environments comparable to several northern cypresses and junipers, such as *Cupressus arizonica*, the Arizona cypress, and *Juniperus monosperma*, the one-seed juniper from North America's southwest. Compared with their counterparts in the northern hemisphere very few species of the cypress pines are sources of commercial timber and then in only limited quantities, and none has attracted horticultural interest as in *Chamaecyparis*, *Cupressus*, or *Thuja*. Several are monospecific genera representing relic tree genera persisting under present-day environments. One is *Diselma archeri*, known only from a few isolated mountaintops in western and central Tasmania. On Mount Dundas trees of this species reach 11 m in height and 2.0 m in girth with ages in excess of 500 years. Long-lived trees can be used to provide dated tree ring chronologies from which climate signatures can be

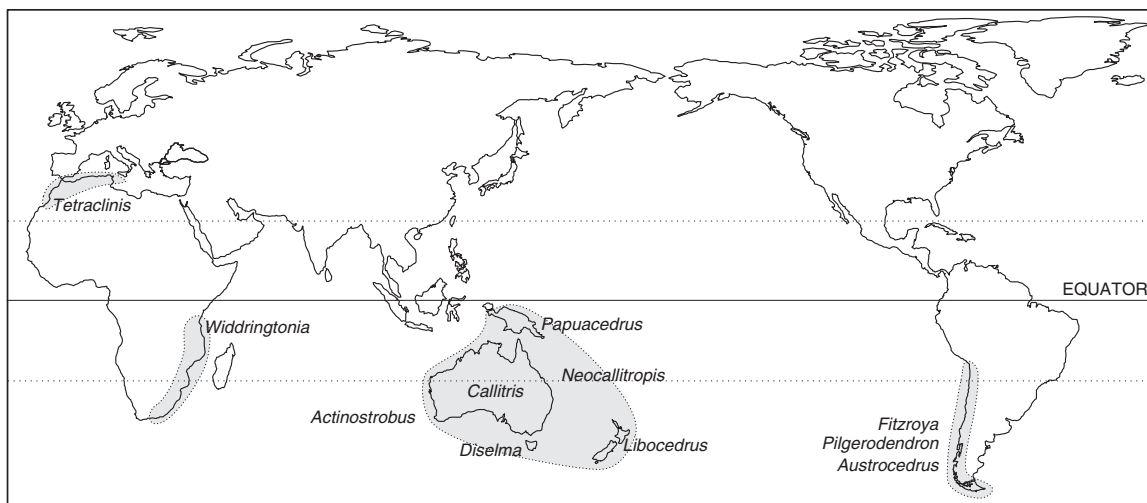


Figure 5 World distribution of Cupressaceae.

extracted for developing past climates. Pines and oaks have been used for this purpose in the northern hemisphere. In the south several Cupressaceae trees, and some from the Podocarpaceae, have proved useful for climate reconstruction. Chronologies of 1500 years have been extracted from *Fitzroya cupressiodes*, the Chilean alerce, trees that can be 50 m tall with a girth of 10 m, and similarly from *Austrocedrus chilensis*, Chilean cedar, a long-lived tree found in pure stands of xeric woodlands near the ecotone with the Patagonian steppe.

Callitris: The Australian Cypress Pines

Callitris and *Actinostrobus* in Australia and *Widdringtonia* in Africa have adapted to dry semi-arid woodlands. The most successful genus, *Callitris*, the Australian cypress pines, has three species in New Caledonia and about 12 in Australia. *Callitris intratropica*, the tropical cypress pine (Figure 6), is a slender tree up to 8 m tall, occasionally found in

small isolated stands in the eucalypt woodlands across the summer rainfall zone of northern Australia. In contrast *C. glaucophylla*, the white cypress pine, is widely dispersed across southern Australia with major occurrences in the southeast where forests lie on the western slopes of New South Wales. It is a small to medium sized tree up to 18 m tall with a conical crown clothed in a variable but usually glaucous foliage. Interestingly, when first discovered, these forests were open woodlands of scattered white cypress pine and eucalypts from the ironbark, box, and red gum groups including *Eucalyptus crebra*, *E. microcarpa*, and *E. dealbata*. Following severe droughts in the late nineteenth century graziers abandoned extensive areas of these woodlands. Dense cypress regrowth then established which is the origin of today's forest stands in the Barrbine and Narrabri and Cobar districts (Figure 7). These are managed for their durable timber, providing about 5% of the State's total timber production.



Figure 6 Tropical cypress pine, *Callitris intratropica*, in the tropical woodlands, Kimberleys, Western Australia.

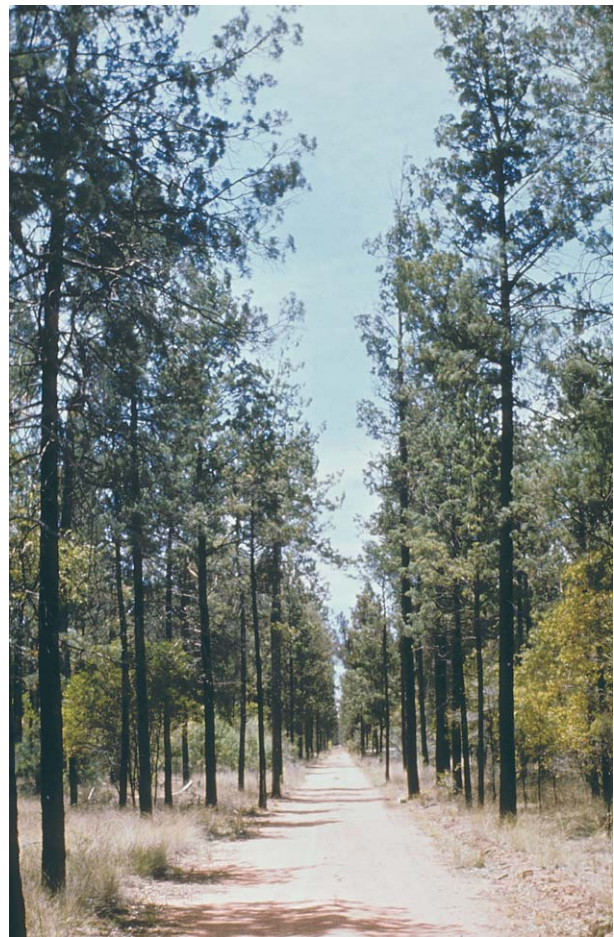


Figure 7 Regrowth forest of white cypress pine, *Callitris glaucophylla*, Pilligra State Forest, Coonabarabran, New South Wales, Australia.

Podocarpaceae: Podocarps, Plum Pines, and Yellow Woods

The Podocarpaceae comprises seven tree and two shrub genera with *Podocarpus* as the largest genus. It is divided into eight sections; these are elevated to generic status by some botanists. All genera are represented in the Australasian–Oceanic region suggesting that the family originated in this area (Figure 8). In total about 130 species are recognized with the majority (70%) in southeast Asia and Australasia, 20% in Central and South America, and 10% in Africa. Almost all are rainforest trees, slow growing and fire-sensitive with tree species producing strong, even-grained, easy-to-work highly valued timbers. The implications of this are that once the slow-growing virgin trees are cut out there will be no secondary timber sources; moreover it is important to conserve areas as examples of the original forest.

Podocarpus

African species of *Podocarpus* belong to the section *Afrocarpus*, most of which are called ‘yellow woods’ on account of the color of the timber. These include *Podocarpus latifolius*, real yellow wood, a tree growing to 30 m in height and 2 m in girth which is widely distributed in southern Africa especially in the southeast. Others are *P. falcatus* called yellow wood, also from southern Africa, and *P. dawie*, a large timber tree up to 30 m tall, from the tropical rainforests in Central Africa. In the Australasian–Oceanic region *Podocarpus* is the most widely distributed genus, with species extending to Asia

including the eastern Himalayas and the southern Japanese islands. *Podocarpus nagi*, one of the most widespread species found from Burma to Fiji, is a slender tree up to 20 m in height that was much sought after as a spar tree in the days of sails. In New Caledonia *P. sylvestris*, the false kauri, has been a valued source of high-quality timber, while *Podocarpus ustus* (a smaller tree) was recognized as late as 1957 to be parasitic on another conifer *Dacrydium taxoides*. This is the only known example of parasitism in the conifers.

In tropical New Guinea the podocarps *Podocarpus archboldii* and *P. papuanus* are found in the cooler tropical environments in high-altitude primary forests between 2000 and 3000 m above sea level. In South America two species, *P. curvifolius* and *P. nubigenus*, are found in the southern Andes. Australian tree species are all rainforest trees and never very common; *P. amarus* and *P. elatus*, the black and brown pines, are large trees up to 30 m tall in lowland rainforests. In New Zealand the podocarps have in the past been important timber trees. *Podocarpus dacrydioides*, the kahitaea, is a buttressed 30 m tree of wet swamp forests, and *P. spicatus*, the matai, of the hill forests at altitudes up to 600 m above sea level. Today temperate rainforests containing residual stands of these conifers are in conservation reserves. Several species have adapted to environments outside the rainforest where they occur as small trees or shrubs. In Australia *P. spinulus* occurs in coastal sand dune woodlands in the southeast, *P. drouynianus* is a shrub in the jarrah forest in the southwest growing on poor laterite soil dominated by *Eucalyptus marginata*, and *P. lawrencei* is a small tree

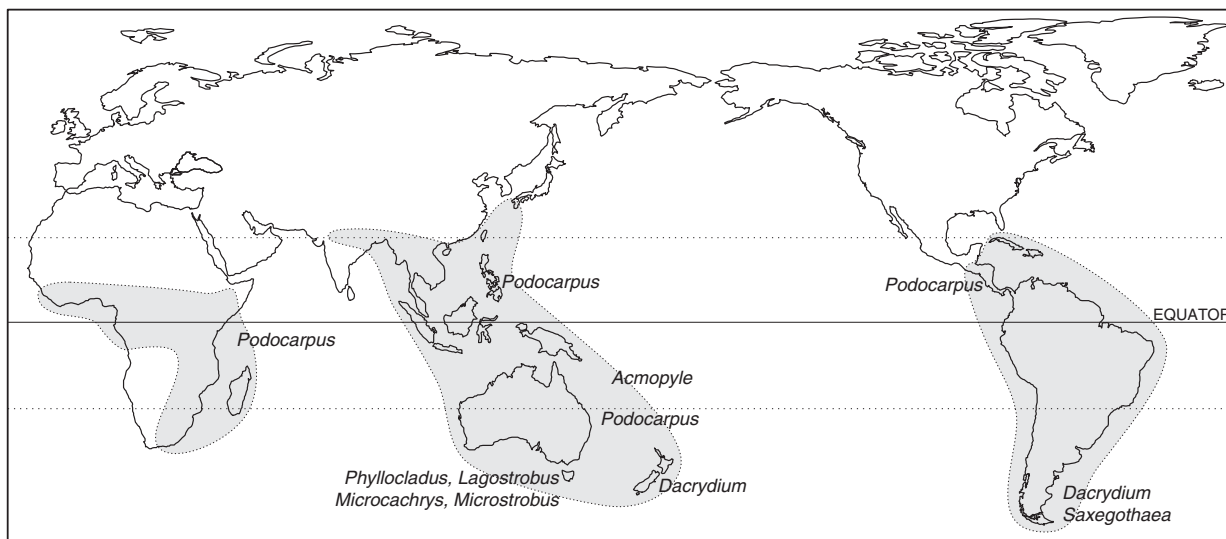


Figure 8 World distribution of Podocarpaceae.

in the subalpine forest and as scramblers in the alpine zone.

Dacrydium*, *Phyllocladus* and *Lagostrobus

Dacrydium, allied to *Podocarpus*, contains 20 species of which five occur in New Zealand, four in New Caledonia, and an equal number in the Indonesian island arc extending as far as Thailand. Two species are also found in New Guinea. The New Zealand species have been important elements in the virgin temperate rainforests with *Dacrydium cupressinum*, the rimu, a major timber species. It has scale leaves similar to those found in the cypress family but differing by being spirally arranged. One small species, *D. fonkii*, is found in Patagonia adding another link to the southern temperate rainforests.

The five species of *Phyllocladus* have one unique feature for the conifers: flattened branchlets, or cladodes, that take over the function of the leaves which are reduced to nonfunctional scales. *Phyllocladus asplenifolius*, the celery top pine, is a long-lived slender tree typically found in the tall wet sclerophyll forests in Tasmania. The cool temperate rainforest species *Lagostrobus franklinii*, the Huon pine, is a very slow growing long-lived species found in valley floors along stream lines and on Mt Read in the north-west. It challenges *Pinus longaeva*, the bristle cone pine, for being the oldest living conifer. The resin rich timber of Huon pine is highly prized for boat-building as it works easily and is durable in salt water.

Saxegothaea

This is a monospecific genus native to southern Patagonia in South America where it occurs in dense cool temperate rainforest. *Saxegothaea conspicua*, the Albert yew, is a small tree 10–12 m tall, and is regarded as a living link between *Araucaria* and *Podocarpus* having foliage resembling the former and wingless pollen and cones of the latter. It was discovered by the plant hunter William Lobb and introduced into cultivation in 1846.

Pinaceae and Taxodiaceae

Only one of the 250+ species in the family Pinaceae extends into the southern hemisphere. This is *Pinus merkusii*, the Tenasserim pine, which has natural occurrences in Burma, Cambodia, Vietnam, the Philippines, and Indonesia extending to the island of Sumatra where it is found in montane forests between 1000 and 1500 m above sea level in the Barsian Range just south of the equator. It grows in small groups of trees in the broadleaf forest and

owes its survival to occasional dry-season spot fires to provide suitable regeneration gaps in the forest.

The genus *Athrotaxis* is an extreme geographic outlier of the redwood family, Taxodiaceae, reminding us that in past times this family was once widespread. Today three species are restricted to the cool montane temperate forests of Tasmania. *Athrotaxis selaginoides*, King William pine, is found in the Western Ranges and around Lake St Claire. It is a slow-growing tree, up to 30 m tall, typically occurring in small isolated stands. It is long-lived, persisting on sites that are rarely burnt by natural wildfires. At higher altitudes the smaller *A. selaginoides* is a component of the treeline forests. The third species, *A. laxifolia*, has intermediate morphology and ecologically lies between the other two species.

See also: **Mensuration:** Tree-Ring Analysis. **Temperate and Mediterranean Forests:** Northern Coniferous Forests; **Temperate and Mediterranean Forests:** Southern Coniferous Forests. **Temperate Ecosystems:** Pines. **Tree Breeding, Practices:** Southern Pine Breeding and Genetic Resources. **Tropical Ecosystems:** Tropical Pine Ecosystems and Genetic Resources.

Further Reading

- Banks JCG (2000) *Interpreting Wollomi Pine Stand Dynamics*. In: Poster Proceedings, International Dendrochronology Conference 2–7 April 2000. Madoza, Argentina.
- Dalimore W and Jackson AB (1966) *A Handbook of Coniferae and Ginkgoaceae*, revd SG Harrison. London: Edward Arnold.
- Dargavel J, Hart D, and Libbis B (eds) (2001) *Perfumed Pineries: Environmental History of Australia's Callitris forests*. Canberra: Centre for Resource and Environmental Studies, The Australian National University.
- Enright NJ and Hill RS (1995) *Ecology of the Southern Conifers*. Melbourne, Victoria: Melbourne University Press.
- Jones WD, Hill KD, and Allen JM (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. *Telopea* 6: 173–176.
- Mirov NT (1967) *The Genus Pinus*. New York: Ronald Press.
- Rolls E (1973) *Running Wild*. Sydney, New South Wales: Angus & Robertson.
- Simpson TE (1973) *Kauri to Radiata: Origin and Expansion of the Timber Industry of New Zealand*. Auckland, New Zealand: Hodder & Stoughton.
- Vidakovic M (1991) *Conifers: Morphology and Variation*, transl. Maja Soljan. Hrvatske, Croatia: Graficki Zavod.
- Woodford J (2000) *The Wollemi Pine: The Incredible Discovery of a Living Fossil from the Age of the Dinosaurs*. Melbourne, Victoria: Text Publishing.