NEW ZEALAND CONIFERS

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With one plate

ONE OF THE MOST DISTINCTIVE ELEMENTS in the New Zealand flora is that formed by the native conifers, which are to be found in almost every scrub and forest community from North Cape to Stewart Island. They are no longer to be found, however, on the outlying islands. There are twenty species, all endemic, distributed among three families in five genera. In size they range from the pygmy pine (*Dacrydium laxifolium*), the world's smallest conifer, which may bear cones at a height of eight centimeters (cf. Cheeseman 1925), to giant kauris and podocarps well above thirty metres. A height of nearly sixty metres has been reported for kahihatea (*Podocarpus dacrydioides* — Entrican and Reid, 1949).

A detailed discussion of the taxonomic features of each species would be superfluous here, since a number of adequate descriptions are already available. These are located in the works of Kirk (1889), Cheeseman (1925), Allan (1929), Cockayne and Turner (1939), Laing and Blackwell (1940), and Dallimore and Jackson (1948). Instead, the relevant literature will be briefly reviewed, although this account does not pretend in any way to be an exhaustive one.

An anatomical basis for taxonomic studies has been adopted by several workers. Seward and Ford (1906) and Eames (1913) have contributed to the knowledge of the Araucariaceae in general and of Agathis australis in particular; Eames from a morphological standpoint, the former authors making a broader phylogenetic approach. An early investigation of leaf anatomy of New Zealand conifers was made by Griffin (1907). More recently, a detailed survey of leaf anatomy in Podocarpus has been attempted by Buchholz and Gray (1948), and Gray and Buchholz (1951). These authors place the South Pacific species P. spicatus and P. ferrugineus in a new subsection (Euprumnopitys) of the section Stachycarpus. The new subsection, Euprumnopitys, is distinguished by the absence of idioblasts (i.e. sclerids) in the mesophyll of leaves. Except for Podocarpus dacrydioides in the section Dacrycarpus, the remaining New Zealand species fall into subsection D of Eupodocarpus, based on the absence of accessory transfusion tissue. Geographic distribution of Podocarpus has been studied by Foweraker (1934), and later by Buchholz and Gray (1948). The latter regard the Wegener theory of continental drift as the only feasible solution to distribution problems in this genus. There is some evidence from leaf anatomy that migration between Australia-New Zealand and South-Central America may have taken place in both directions (Buchholz and Gray, op. cit., p. 61). Eupodocarpus is regarded as the most advanced section because of the hypostomatic leaves (stomata confined to the under surface), and the usually prominent accessory transfusion tissue. This feature is lacking, however, in subsection D, which contains the New Zealand species. In the section *Stachycarpus*, *Podocarpus spicatus* has the most primitive known arrangement of female cones.

With a view to practical application, Orman and Reid (1941, 1946) have investigated wood anatomy in the genus *Dacrydium*. These workers have constructed a key for the native *Dacrydium* species, using diagnostic features of wood structure. An informative series of bulletins has been published by the New Zealand Forest Service (Ward and Reid, 1949, Entrican and Reid, 1949) on properties and uses of six of the major timber-producing trees in the country (*Dacrydium cupressinum*, *Podocarpus ferrugineus*, *P. spicatus*, *P. totara*, and *Agathis australis*).

Not the least interesting feature of the New Zealand conifers is the prevalence of distinct juvenile leaf forms (Cockayne, 1932). These occur in all species save a few of the podocarps (*P. totara*, *P. hallii*, *P. nivalis* and *P. acutifolius*). Epharmony, too, may cause plants of the same species to have a very dissimilar appearance when grown under different habitat conditions. For example, *Podocarpus nivalis*, a medium-sized bushy shrub in shade and shelter, is reduced to a prostrate shrub with much smaller leaves in direct sunlight (Cockayne, op. cit.).

Hybrids, although not as common as in angiosperm genera like *Hebe* and *Coprosma*, are known or suspected between the following species:*

Podocarpus acutifolius $ imes$ nivalis	Dacrydium bidwillii $ imes$ laxifolium
Podocarpus hallii $ imes$ nivalis	Dacrydium bidwillii \times biforme?
Podocarpus hallii \times totara (= P.	Dacrydium biforme \times laxifolium?
<i>loderi</i> Cockn.)	Phyllocladus glaucus $ imes$ trichomanoi-
Podocarpus hallii \times acutifolius?	des?
Podocarpus ferrugineus \times totara?	Libocedrus bidwillii × plumosa?
Podocarpus spicatus \times totara?	

Ecological studies are more restricted in number, centering mainly about the kauri (*Agathis australis*). Cranwell and Moore (1936) drew attention to modified growth forms of kauris growing above a height of 660 metres on Te Moehau (Coromandel Peninsula), a refuge of both alpine and subtropical remnants. Further autecological notes have been made by McKinnon (1937, 1940–41), McKinnon and Dumbleton (1935), Harrison-Smith (1938), and Foley (1950). Recently Mirams (1948, 1951, unpubl.) has analysed in detail the environmental factors responsible for growth and regeneration of the kauri. Root nodules of New Zealand conifers were investigated by Yeats (1924).

An important contribution is that of Cranwell (1940), who has described and figured pollen grains of all the New Zealand species, as well as formulating distinctive generic and specific characters according to the peculiarities of each type of pollen grain. Her work indicates that *Dacrydium bidwillii* and probably also *D. biforme* and *D. kirkii* are rightly

* See Cockayne 1932, Cockayne and Allan 1934, Cockayne and Turner 1939.

1954]

placed in a group apart from *Podocarpus*, where Sahni and Mitra (1927) would put them, on the basis of the structure of female cones alone. Cranwell (1938) had previously attempted a partial solution of post-glacial vegetation problems through an analysis of pollen from South Island peat beds. Three main periods are recognised:

1. A grassland period correlated with quite uniformly harsh climatic conditions;

2. A warmer and wetter podocarp period;

3. A mosaic of grassland and beech (*Nothofagus*) forest resulting from local climatic differentiation.

The role played by conifers in New Zealand's past geological time has been clarified still further through the work of Harris, Fergusson and Couper (1951). It appears that a number of extinct species, including at least seven podocarps, dominated forest communities between early Cretaceous and Upper Eocene times. Of the present-day species, *Podocarpus dacrydioides* dates from the Oligocene, and *Phyllocladus* is known even earlier from Upper Cretaceous beds.

CLASSIFICATION

The following is an outline classification of the New Zealand species. A revised key to the species and genera occurring in this country has been published previously (Hay and Dellow, 1952).

Araucariaceae

Agathis Salisb.

Agathis australis Salisb. Kauri

Cupressaceae

Libocedrus Endl.

Libocedrus plumosa (Don) Sargent (= L. doniana Endl.) Kawaka Libocedrus bidwillii Hook. f. Kaikawaka, mountain cedar

Podocarpaceae

Podocarpus L'Hérit.

Section: Stachycarpus Subsection: Euprumnopitys Podocarpus spicatus R. Br. Matai, black-pine Podocarpus ferrugineus D. Don. Miro, brown-pine

Section: Dacrycarpus Podocarpus dacrydioides A. Rich. (FIG. 1). Kahikatea, white-pine
Section: Eupodocarpus
Subsection: D Podocarpus totara D. Don. Totara

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Podocarpus hallii T. Kirk. Hall's totara, thin-bark totara Podocarpus acutifolius T. Kirk Podocarpus nivalis Hook. Alpine totara

Dacrydium Soland.

Dacrydium cupressinum Soland. Rimu, red-pine Dacrydium kirkii F. Muell. Monoao Dacrydium biforme (Hook.) Pilger. Pink-pine Dacrydium bidwillii Hook. f. Bog-pine, mountain pine Dacrydium colensoi Hook. Silver-pine Dacrydium intermedium T. Kirk. Yellow silver-pine Dacrydium laxifolium Hook. f. Pygmy pine

Phyllocladus L. C. Rich.

Phyllocladus trichomanoides Don. Tanekaha Phyllocladus glaucus Carr. Toatoa Phyllocladus alpinus Hook. f. Mountain toatoa

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Wellington, New Zealand.

PLATE I

Podocarpus dacrydioides A. Rich. growing in beech (Nothofagus) forest about 620 metres above sea level, near Lake Waikaremoana, New Zealand.

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PODOCARPUS DACRYDIOIDES A. RICH.



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