

The New Zealand Rain Forest: A Comparison with Tropical Rain Forest¹

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ABSTRACT: The structure of and growth forms and habits exhibited by the New Zealand rain forest are described and compared with those of lowland tropical rain forest. Theories relating to the frequent regeneration failure of the forest dominants are outlined. The floristic affinities of the forest type are discussed and it is suggested that two main elements can be recognized—lowland tropical and montane tropical. It is concluded that the New Zealand rain forest is comparable to lowland tropical rain forest in structure and in range of special growth forms and habits. It chiefly differs in its lower stature, fewer species, and smaller leaves. The floristic similarity between the present forest and forest floras of the Tertiary in New Zealand suggest that the former may be a floristically reduced derivative of the latter.

PART 1 OF THIS PAPER describes the structure and growth forms of the New Zealand rain forest as exemplified by a forest in the far north. In Part 2, theories relating to the regeneration of the dominant trees in the New Zealand rain forest generally are reviewed briefly, and their relevance to the situation in the study forest is considered. Reference is also made to possible parallel situations in lowland tropical rain forests. Part 3 considers the floristic affinities of the New Zealand rain forest.

Before human occupation, rain forests probably occupied a greater area of New Zealand than any other type of vegetation. In the North Island, rain forests were particularly extensive, but they also occurred in more localized areas, mostly near the coasts, to the far south of the South Island and in Stewart Island (Fig. 1).

¹In the senior author's concept of "rain forest," lowland tropical rain forest is regarded as the basic example. The New Zealand forests, excluding those dominated by species of *Nothofagus*, are included in this category because they agree with lowland tropical rain forest in structure and in range of special growth habits and forms. The term "rain forest" has often been applied much more widely to any forests of high rainfall areas, e.g., the *Nothofagus* forests of Tasmania and the coastal coniferous forests of the northwestern United States. As this could lead to the largely unwarranted assumption that such forests agree with lowland tropical rain forest in more than just raininess of climate, this wide definition is not favored.

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The approximate number of species of seed plants in these forests is 240. From north to south there is an overall decrease in number of species. At about 38°S a number of species, mostly trees and shrubs, drop out or become restricted to coastal sites, but it is not until about 42°S, in the South Island, that many of the conspicuous epiphytes and lianes begin to disappear together with additional trees and shrubs.

It is now very difficult to find any area of rain forest in New Zealand which has not been much modified by man or the animals he has introduced. The example forming the basis of this paper, however, is less disturbed than some in New Zealand and has the further advantage of being situated in the far north where the forest type is best developed.

1. STRUCTURE AND GROWTH FORMS

The study forest is at 35°10'S in the far north of New Zealand (Fig. 1) and covers the Maungataniwha Ranges not far from the town of Kaitaia. The forest has not been milled or burnt, except marginally in European times, and, unlike the majority of New Zealand forests, neither deer nor opossums are present. There has been some penetration by cattle from surrounding farmland, and wild pigs, causing localized soil disturbance, are also present.

The Ranges have a maximum height of 2,463 feet (750 meters) and are composed of basalt,

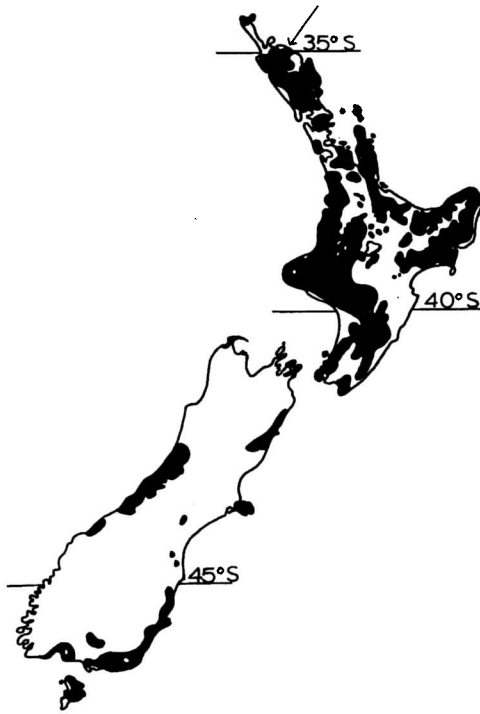


FIG. 1. Map of New Zealand showing in black the approximate extent of rain forest in pre-European times. Study forest indicated by arrow.

which weathers to a deep red, moderately fertile soil. There are no weather records for the Ranges themselves, but nearby at Kaitaia the mean annual rainfall is 54 inches (1372 mm) with a lowest monthly mean of 2.8 inches (71 mm); the mean annual temperature is 59.6°F (15.3°C) with a mean temperature for the three warmest months of 66.1°F (18.9°C) and a mean temperature for the three coolest months of 53.3°F (11.8°C). Kaitaia has an average of 2.2 light frosts per year.

There are some changes in the composition of the forest with altitude, but the detailed studies were carried out at about 600 feet (183 meters) and can be regarded as typical of the lowland forest zone.

Stratification of the Forest

On the basis of a profile diagram (Fig. 4) and observations of the forest as a whole, it is possible to recognize several horizontal layers.³

³ In the following account the species lists are based

The highest, from about 90 to 110 feet (28 to 34 meters), comprises the emergents (Fig. 2). These tend to be concentrated on the ridge crests and are predominantly *Dacrydium cupressinum* and the initially epiphytic *Metrosideros robusta* (Myrt.). On the same sites there may be occasional emergent trees of *Knightia excelsa* (Prot.), and in one place a few trees of *Agathis australis* were also seen, but this species is much more abundant on poorer soils than on those derived from basalt.⁴ In the moister valley bottoms there are fewer emergents, and these are mostly *Podocarpus dacrydioides* and *Laurelia novae-zelandiae* (Monim.). On the valley sides emergents are generally very scattered.

The main canopy at about 60 to 70 feet (18 to 21 meters) is dominated by *Beilschmiedia tarairi* (Laur.) with smaller representation of *B. tawa*, *Elaeocarpus dentatus* (Elaeo.), *Vitex lucens* (Verb.), *Nestegis cunninghamii* (Olea.), and *Podocarpus ferrugineus*.

Where the main canopy is well developed, the subcanopy layer at 40 to 50 feet (12 to 15 meters) is dominated by *Dysoxylum spectabile* (Mel.), while in openings *Weinmannia silvicola* (Cunon.) and some *Cyathea medullaris* are the main species. Rare *Corynocarpus laevigatus* (Coryn.) has also been recorded and presumably contributes to this layer.

A small tree layer at 30 to 40 feet (9 to 12 meters), best developed in canopy gaps, includes *Meliclytus ramiflorus* (Viol.) and *Hedycarya arborea* (Monim.) (the two most shade tolerant species), and *Ackama rosaefolia* (Cunon.), *Pseudopanax arboreum* (Aral.), *P. edgerleyi*, *P. crassifolium*, *Hoheria populnea* (Malv.), *Rhopalostylis sapida* (Palm.), *Cyathea dealbata*, *Pittosporum tenuifolium*, *Aristotelia serrata* (Til.), *Pennantia corymbosa* (Icac.), *Carpodetus serratus* (Esc.), *Alectryon excelsum* (Sap.), *Quintinia serrata* (Esc.), *Ixerba brexioides* (Esc.), and *Litsea calicaris* (Laur.).

in part on McKelvey and Nicholls (1959) and Carse (1911). The lists are probably not complete.

⁴ The forests in which the kauri (*Agathis australis*) dominates, especially those on old sand dunes, may be similar to the tropical heath forests described by Richards (1952:244). In the Malesian tropics these heath forests also are often dominated by species of *Agathis*.



FIG. 2. Exterior view of Maungataniwha forest including sample depicted in the profile diagram (Fig. 4). Ridge crest stand with emergent *Dacrydium cupressinum* and *Metrosideros robusta* above a main canopy mosaic dominated by *Beilschmiedia tarairi* and *Weinmannia sylvicola*. 35°S. (Photograph by B. V. Sneddon.)

Eugenia maire (Myrt.) occurs in swampy situations, and *Fuchsia excorticata* (Onag.) and *Sophora tetraptera* (Leg.) are often found alongside streams.

The shrubs, up to about 20 feet (7 meters), are also most abundant in canopy gaps and include *Coprosoma australis* (Rub.), *Macropiper excelsum* (Pip.), *Geniostoma ligustrifolium* (Log.), *Pseudowintera axillaris* (Wint.), *Myrsine salicina* (Myrs.), *M. australis*, *Mida salicifolia* (Sant.), *Alseuosmia macrophylla* (Capr.), *A. quercifolia*, *A. banksii*, *Olearia rani* (Comp.), *Lophomyrtus bullata* (Myrt.), *Brachyglottis repanda* (Comp.), *Rhabdothamnus solandri* (Gesn.), *Schefflera digitata* (Aral.), *Cyathea dealbata*, and *Dicksonia squarrosa*.

The herbaceous ground layer includes *Elatostema rugosum* (Urt.), *Pratia physaloides* (Camp.), *Nertera* (Rub.) spp., *Microlaena avenacea* (Gram.), and many ferns belonging to the genera *Marattia*, *Asplenium*, *Blechnum*, *Adiantum*, *Todea*, *Pellaea*, *Pteris*, *Hymenophyllum*, *Trichomanes*, and several others.

When an opening in the canopy is made by a falling emergent, the space becomes occupied by some or all of the small tree and shrub species listed above (as shown in Fig. 4, on the right). A number of the more shade tolerant of these may persist after the canopy re-forms, but where the latter is dense the small tree and shrub layers may be virtually absent.

If the mature heights of the species in the Maungataniwha forest are drawn in order of decreasing height no stratification in the forest appears to exist. However, if only the dominant species are considered, the strata outlined above can be recognized.

Special Growth Habits

This section is concerned mainly with vascular epiphytes⁵ and lianes which are particu-

⁵ The epiphytes described here, although primarily adapted to an epiphytic role, may occur terrestrially in well lit, sometimes rocky situations. However, this is probably true of all epiphytes, even the most specialized tropical forms.



FIG. 3. Interior view of Maungataniwha forest. Large trunk at center is of *Metrosideros robusta* (emergent). Smaller trunks to left bearing epiphytic *Astelia solandri* are *Beilschmiedia tarairi* (main canopy). Branch at top of photo belongs to *Dysoxylum spectabile* (sub-canopy). Left foreground, the root climber *Freycinetia banksii*; right foreground, *Macropiper excelsum*; center foreground, young plants of the palm *Rhopalostylis sapida* with an older specimen on the right-hand side of the photo. Shrub layer in the middle distance comprises mostly young plants of *Dysoxylum spectabile* with some *Geniostoma ligustrifolium*, *Hedycarya arborea*, and *Meliclytus ramiflorus*. (Photograph by B. V. Sneddon.)

larly conspicuous in this forest, as they are in all North Island rain forests.

LOW CLIMBERS: These do not reach the forest canopy and comprise one twining fern (*Lygo-*

dium articulatum) and several root-climbing ferns. Notable among the latter is *Blechnum filiforme* in which the leaves undergo a remarkable increase in size as they ascend the tree trunks. Some of the aroids of tropical forests



FIG. 4. Profile diagram of a ridge crest sample (115 by 25 feet) of the Maungataniwha forest. The smaller trees on the right hand side of the diagram have grown up in a canopy gap. AF, *Asplenium falcatum*; AR, *Ackama rosaefolia*; AS, *Astelia solandri*; Bt, *Beilschmiedia tawa*; BT, *Beilschmiedia tarairi*; CA, *Coprosma australis*; CD, *Cyathea dealbata*; CH, *Collospermum hastatum*; DC, *Dacrydium cupressinum*; DS, *Dysoxylum spectabile*; ED, *Elaeocarpus dentatus*; FB, *Freycinetia banksii*; GI, *Geniostoma ligustrifolium*; GL, *Griselinia lucida*; HA, *Hedycarya arborea*; Mm, *Mida salicifolia* var. *myrtifolia*; MP, *Metrosideros perforata*; MR, *Metrosideros robusta*; MS, *Mida salicifolia* var. *salicifolia*; OR, *Olearia rani*; PA, *Pseudopanax arboreum*; RA, *Rubus australis*; RS, *Rhopalostylis sapida*; VL, *Vitex lucens*; WS, *Weinmannia silvicola*.

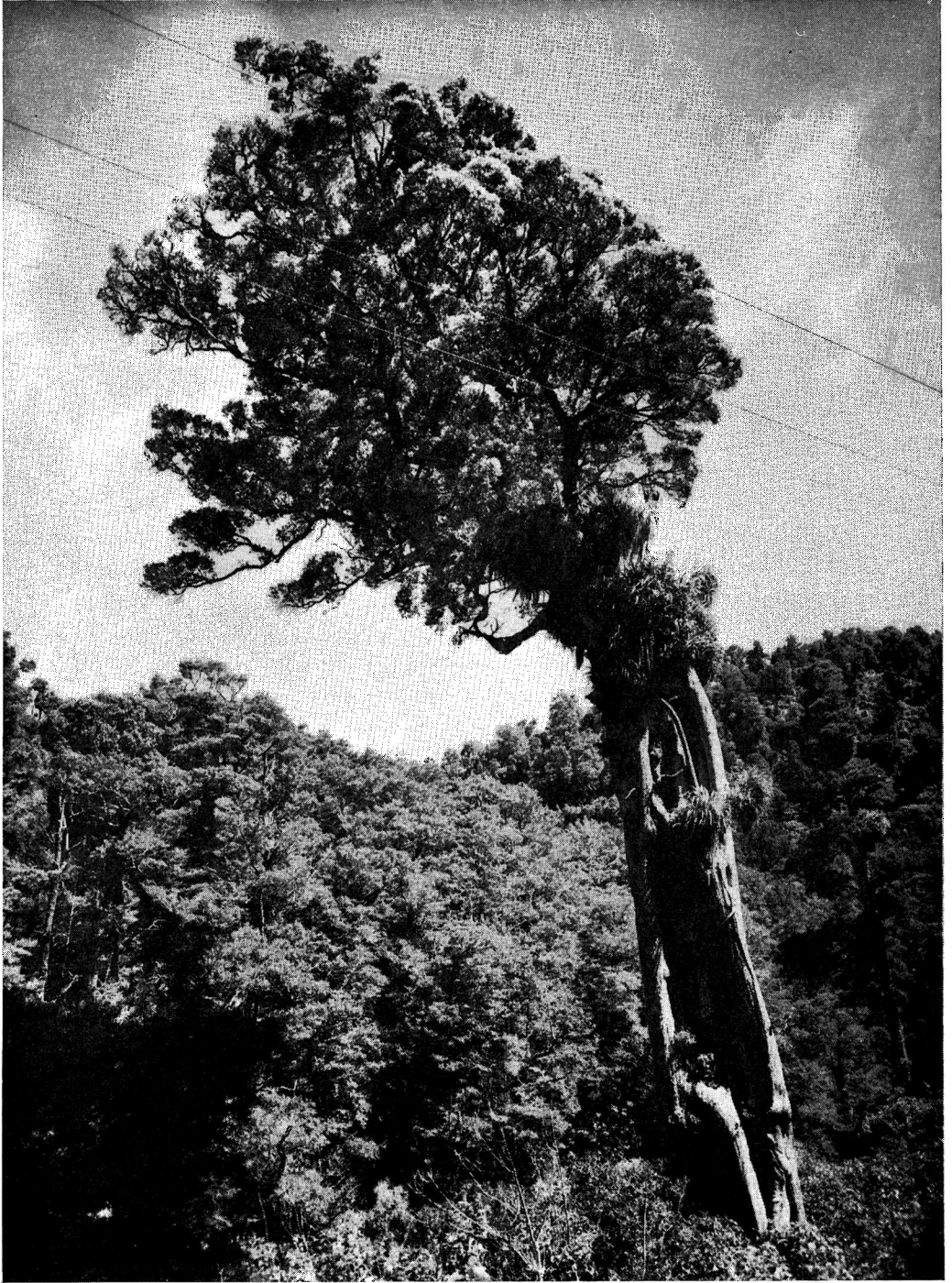


FIG. 5. The "strangling" epiphyte *Metrosideros robusta*. The pseudo-trunk formed by coalesced roots still encloses the dead trunk of the supporting tree. Kaitoke, near Wellington, 41°S. (Photograph by M. D. King.)

exhibit a similar phenomenon. Other root-climbing ferns in the forest are *Phymatodes scandens*, *P. diversifolium*, *Artbropteris tenella*, and *Rumobra adiantiformis*.

HIGH CLIMBERS (LIANES): These extend into the canopy and usually flower only in full light. As in rain forests generally, the lianes are most abundant in regenerating forest in canopy gaps and similar situations, and so to a large extent they can be regarded as growing up with the trees. This is not always the case with *Freycinetia banksii* (Pand.) and the liane species of *Metrosideros* (Myrt.), which can often be seen growing up the trunks of large emergent trees.

The modes of climbing are various. *Freycinetia banksii* and the five liane species of *Metrosideros* climb by adventitious roots, *Tetrapathaea tetrandra* (Pass.) by branch tendrils, *Clematis paniculata* (Ranunc.) by twining petioles, *Muehlenbeckia australis* (Polygon.), *Parsonsia heterophylla* (Apoc.), and *Rhipogonum scandens* (Liliac.) by twining stems, and *Rubus cissoides* (Ros.), *R. australis*, and *R. schmidelioides* by recurved prickles on the stems and leaves.

A number of the species have large cable-like stems when mature. In *Metrosideros perforata* (Fig. 7), *M. fulgens*, *Tetrapathaea tetrandra*, and *Rubus cissoides*, for example, the stems may attain a diameter of more than 6 inches (15 cm).

TUFTED HERBACEOUS EPIPHYTES: These belong to two genera of the Liliaceae—*Astelia* and *Collospermum*. The epiphytic species are *Astelia solandri*, *Collospermum hastatum* (Fig. 6), and *C. microspermum*. The *Collospermums* require full light and are most abundant on the taller trees while *Astelia* is less light demanding and ranges to lower levels in the forest. The *Collospermums* are also the more specialized as epiphytes. They build up large amounts of humus largely by the decay of their own old roots and leaves, and in time develop into massive clumps which look like huge bird nests in the tree branches. They can also be classified as "tank," as well as humus, epiphytes. Their leaves, arranged fan-wise, have broad, markedly concave bases separated by spaces which contain considerable quantities of water—sufficient, in

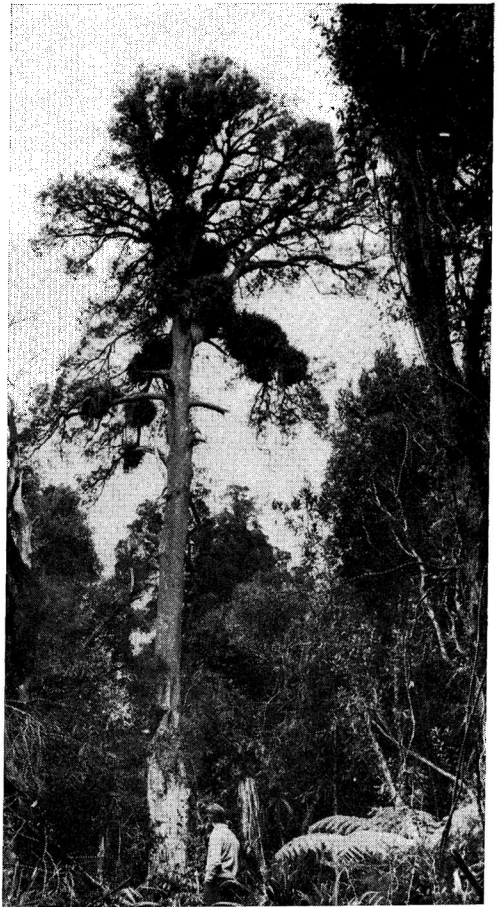


FIG. 6. An emergent *Podocarpus dacrydioides* with abundant "nests" of the epiphyte *Collospermum hastatum*. Te Marua, near Wellington, 41°S. (Photograph by M. D. King.)

fact, to provide a shower bath for the unwary when a fallen clump is picked up and tilted.

The ability to store water makes the species of *Collospermum* comparable to the bromeliad tank epiphytes of the American tropics, and it has even been suggested (Oliver, 1930:37) that they agree also in having special water absorbing structures in the leaf bases. Later work has shown that these are the persistent bases of scales (Oliver, 1930:39), and it has not yet been demonstrated that they absorb water as do the leaf scales of the bromeliads.

The bromeliad epiphytes provide a habitat for a number of species of frogs and mosquitos. Recently in New Zealand a new species of

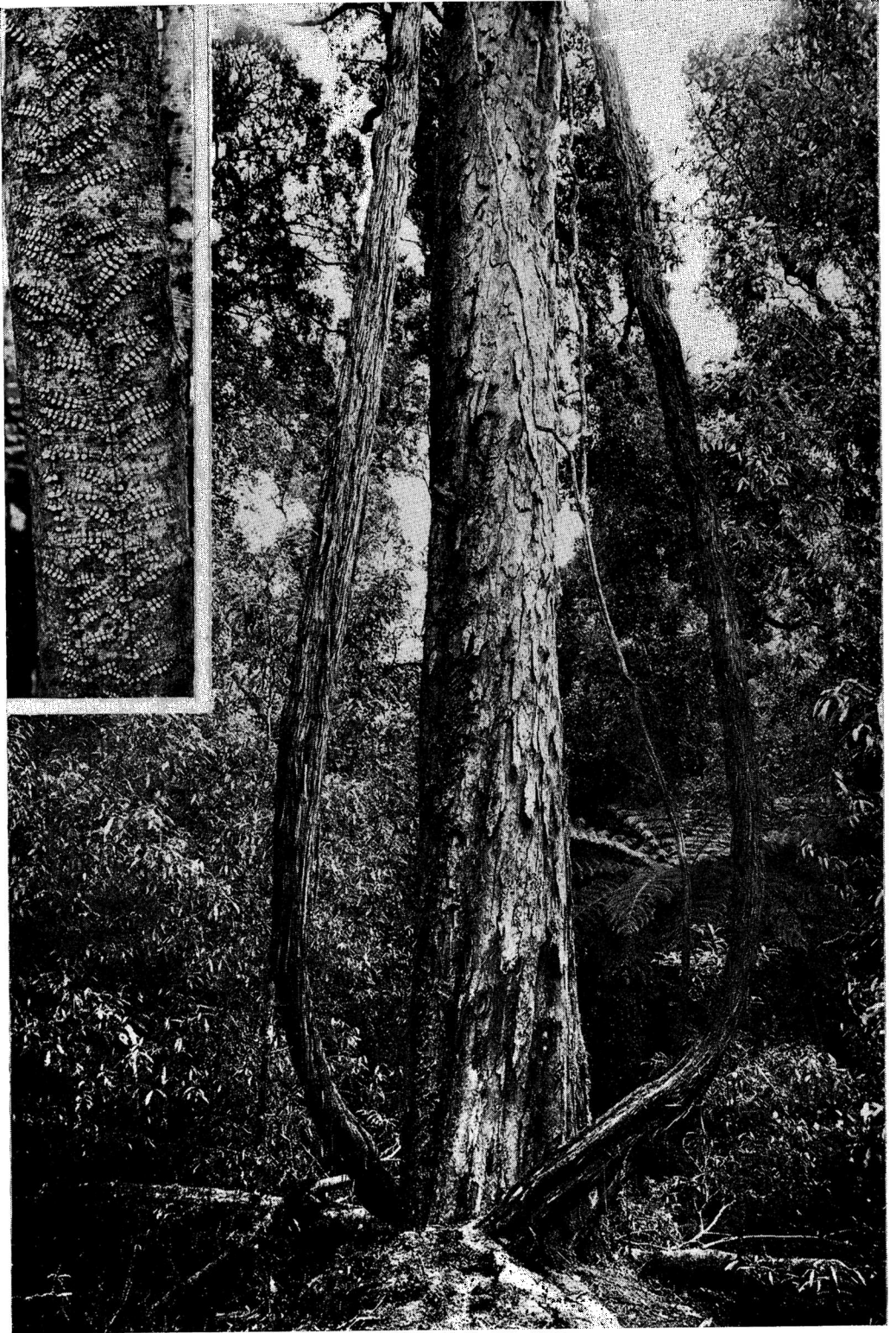


FIG. 7. Cable-like stems of the root-climbing liane *Metrosideros perforata*. The supporting tree is *Dacrydium cupressinum*. Inset: Leaf mosaic of a young plant. Kaitoke, near Wellington, 41°S. (Photograph by M. D. King.)

mosquito has been found which breeds in the water reservoirs of *Collospermum* (Belkin, 1968).

PENDENT HERBACEOUS EPIPHYTES: These are often rooted in *Collospermum* clumps and hang below them. *Asplenium falcatum*, *A. flacidum*, and the swaying tassels of *Lycopodium billardieri* are common in this situation, but a *Tmesipteris* may also be found, which is thought by some to be a species distinct from the smaller *T. tannensis* commonly occurring on tree fern trunks.

The orchids *Dendrobium cunninghamii*, *Earina mucronata*, and *E. autumnalis* may grow with *Collospermum* clumps or hang from mossy branches.

HERBACEOUS EPIPHYTES ATTACHED DIRECTLY TO TRUNKS OR BRANCHES: The thick-leaved creeping fern *Pyrosia serpens* is often abundant in full light on higher branches. The orchid *Sarcophilus adversus* occurs in a more scattered fashion on branches or even trunks and is attached by widely spreading roots. Two other orchids, *Bulbophyllum pygmaeum* and *B. tuberculatum*, form mosslike patches in similar situations.

Peperomia urvilleana (Pip.) was not seen in the study area, but it occurs elsewhere in the Northland region as a low trunk epiphyte. A number of ferns also occur as low trunk epiphytes, particularly on tree ferns. These include many species of *Hymenophyllum*, *Trichomanes*, *Grammitis heterophylla*, and *Anarthropteris lanceolata*. *Lycopodium novae-zelandicum* and *Tmesipteris tannensis* favor similar situations.

SHRUB EPIPHYTES: *Pittosporum cornifolium*, *P. kirkii*, *Senecio kirkii*, and *Coprosma lucida*⁶ are small shrubs usually rooting in the soil of *Collospermum* clumps. In this situation they probably never send roots to the ground.

Griselinia lucida (Corn.?) becomes a much larger shrub and, although also often beginning its life in association with *Collospermum*, eventually sends roots to the ground (Dawson, 1966). It does not, however, become entirely self-supporting.

⁶ Better known as a terrestrial shrub in pioneer communities.

"STRANGLING" EPIPHYTES: The most important and conspicuous example in this category is *Metrosideros robusta* (Fig. 5). The young plants become established in a tree crown, most frequently of the emergent *Dacrydium cupressinum*, but little is known of the precise situations in which they occur since the great height of the supporting trees makes observations difficult. Probably they often establish in *Collospermum* clumps, but in one case a young plant was seen attached directly to the bark of the supporting tree.

Beddie (1953:2) has reported root tubers in young plants of *Metrosideros robusta* which he suggests may be similar to the fire surviving lignotubers of *Eucalyptus* or may be water storing organs.

The one to several roots of *Metrosideros robusta* which descend to the ground are usually attached to the supporting tree in the early stages by horizontal girdling roots. The root system enlarges greatly and on death of the supporting tree the *Metrosideros* becomes self-supporting. The conflicting views on the relationship between *M. robusta* and the supporting tree are reviewed by Dawson (1967).

The second relatively frequent strangling epiphyte—*Pseudopanax arboreum*—is a much smaller plant. As an epiphyte, it occurs only on tree ferns in the secondary communities occupying canopy gaps and similar situations. The seedling establishes just below the crown of the tree fern (Pope, 1926:92, 94) and usually develops at least one girdling root as well as the many roots descending to the ground. *P. arboreum* also frequently establishes directly on the ground in seral communities.

Coprosma australis and *Pseudopanax edgerleyi* may also occur as tree fern epiphytes, but appear to be less specialized than *P. arboreum*.

Weinmannia silvicola and *Ackama rosaefolia* often begin their lives as low epiphytes on tree ferns, but they can hardly be regarded as strangling epiphytes. The species of *Weinmannia* further south, *W. racemosa*, has a similar habit to that of *Pseudopanax arboreum*.

EPIPHYLLAE: These are small non-vascular plants—leafy liverworts, lichens, and filamentous algae—which grow on the upper surfaces of leaves and are often abundant in tropical rain

forests. A similar range of epiphyllous species occurs in New Zealand, but they are only locally abundant (Zahlbruckner, Keissler, and Allan, 1928).

PARASITES: *Mida salicifolia* and the variety *myrtifolia* are root hemi-parasites. Branch hemi-parasites are probably uncommon in the study forest, although the family Loranthaceae is represented by four genera and eight species in New Zealand. The latter appear to be more common in shrubby vegetation and *Nothofagus* forest than in rain forest proper. The fleshy complete root parasite *Dactylanthus taylori* (Balan.) probably occurs in the area studied as it has been recorded from a nearby locality.

SAPROPHYTES (ANGIOSPERM): These are uncommon. *Thismia rodwayii* (Burm.) and the orchids *Gastrodia sesamoides*, *G. cunninghamii*, and *Corybas saprophyticus* have been recorded from Northland.

BIOLOGICAL SPECTRUM

According to Raunkiaer's life form definitions (Raunkiaer, 1934), the species so far recorded from the study forest can be classified as follows:

| | | |
|-------------------------|-------------|----|
| (a) ALL VASCULAR PLANTS | (total 174) | |
| Phanerophytes | | 91 |
| Trees | | 61 |
| Conifers | 5 | |
| Dicotyledons | 50 | |
| Monocotyledons | 2 | |
| Tree ferns | 4 | |
| Shrubs | | 10 |
| Herbs | | 1 |
| Climbers | | 19 |
| Lianes | 13 | |
| Subcanopy | 6 | |
| Chamaephytes | | 45 |
| Angiosperms | | 7 |
| Ferns | | 38 |
| Geophytes (orchids) | | 3 |
| Epiphytes | | 35 |
| High | | 19 |
| Shrubs | 5 | |
| Herbs | 14 | |
| Monocot. | 9 | |
| Pterid. | 5 | |
| Low | | 16 |
| Dicotyledons | 1 | |
| Pteridophytes | 15 | |

Biological Spectrum: Epiphytes 20%; Phanerophytes 52%; Chamaephytes 26%; Geophytes 2%

(b) FLOWERING PLANTS ONLY

Biological Spectrum: Epiphytes 15%; Phanerophytes 75%; Chamaephytes 7%; Geophytes 3%

The last is similar to the biological spectra for tropical rain forests. The biological spectrum for the tropical rain forest at Moraballi Creek, British Guiana (Richards, 1952:8) is as follows: Epiphytes 22%; Phanerophytes 66%; Chamaephytes 12%.

Special Growth Features

Special types of growth are relatively common in tropical rain forests, but are less well developed in the New Zealand rain forest. In this and later sections, to make the record complete, some examples are referred to which are not found in the study forest.

PLANK BUTTRESSES: These are commonly developed only by *Laurelia novae-zelandiae*, a species which favors swampy situations. *Dysoxylum spectabile* may also occasionally develop narrow flanges at the base of the trunk.

PNEUMATOPHORES: The "loop" type of pneumatophore, which is formed by a root growing up into the air then down into the soil again, is well developed in *Laurelia novae-zelandiae* (Fig. 8), when it is growing in swampy situations. These "loop" pneumatophores have prominent lenticles and often enlarge to become flat and platelike by eccentric secondary growth from their upper sides.

Eugenia maire, often associated with *Laurelia novae-zelandiae* in swampy situations, has pneumatophores formed from special upwardly growing root tips. These are very similar to those of the sole mangrove species in New Zealand—*Avicennia resinifera*.

The root-climbing *Freycinetia banksii*, also often associated with *Laurelia novae-zelandiae*, develops a very distinctive pneumatophore (Fig. 8) when it is growing terrestrially in swampy situations. Thick widespreading roots grow horizontally just beneath the swamp surface, and from them, branch-roots modified to act as pneumatophores grow into the air. The pneumatophores have a series of rings of lenticel tissue which gives them a very distinctive appearance.



FIG. 8. Pneumatophore of *Laurelia novae-zelandiae*. At the bottom left of the pneumatophore is an aerial root of *Freycinetia banksii* showing the distinctive rings of lenticel tissue. Kaitoke, near Wellington, 41°S. (Photograph by M. D. King.)

PROP ROOTS: A young tree of *Eugenia maire* in the study forest had three slender, downwardly arching roots arising from the trunk at about 18 inches (45 cm) above ground level. *Metrosideros excelsa*, a common coastal tree in Northland, often produces aerial roots very freely and these may enter the ground to form props for some of the usually several trunks. This species does not, however, occur in the study forest.

CAULIFLORY AND RAMIFLORY: *Dysoxylum spectabile* is cauliflorous, producing inflorescences on the larger branches and sometimes directly on the trunk. The same is often true of *Fuchsia excorticata*. *Planchonella novae-zelandica* (Sapot.), found in coastal forests in the northern parts of the North Island, is described as occasionally cauliflorous (Allan, 1961:539). *Tecomathe speciosa* (Bign.), restricted to the Three Kings Islands off the northern tip of New Zealand, is also cauliflorous.

Ramiflory, or the production of flowers on the

slender woody branchlets just below the leaves, is more common in the New Zealand rain forest. It is exhibited in species of *Melicytus* and *Myrsine* as well as in the liane *Metrosideros diffusa*.

PULVINI: These are spongy, more or less elastic swellings at the base of the petiole or sometimes where the petiole joins the lamina. They are not common in the New Zealand rain forest.

The species of *Nestegis* have dark-colored pulvini at the petiole bases. Juvenile leaves of *Elaeocarpus dentatus* have pulvini at both ends of the petiole. *Dysoxylum spectabile*, *Alectryon excelsus*, and *Marattia salicina* may have pulvini where the petiolules of the leaflets join the rachis.

DRIP TIPS: These are narrowly drawn out points of leaves. They are neither strongly developed nor very common in New Zealand, and in some species they are formed only when the plants are growing under sheltered shady conditions.

Drip tips have been observed in *Melicytus ramiflorus*, *M. macrophyllus*, *Coprosma lucida*, *Hoheria populnea*, *Geniostoma ligustrifolium*, *Mida salicifolia* var. *myrtifolia*, *Beilschmiedia tawa*, *Elaeocarpus dentatus*, *Rhipogonum scandens*, *Parsonsia heterophylla*, and *Muehlenbeckia australis*.

Leaf Sizes

In lowland tropical rain forests, angiosperm species with large leaves are in the majority. In an example cited by Richards (1952:83) from the Philippine Islands, which he analyzed according to Raunkiaer's leaf size categories, 86 per cent of the woody species had leaves of mesophyll size (area between 2,025 and 18,225 mm²), 10 per cent of macrophyll size (area between 18,225 and 164,025 mm²), and only 4 per cent of microphyll size (area between 225 and 2,025 mm²).

In the study forest the approximate areas of leaves or leaflets of woody angiosperm species were calculated as two-thirds of the length times the breadth of the lamina. Of the species studied 6 per cent were nanophyllous (leaf area between 25 and 225 mm²), 68 per cent

microphyllous, 25 per cent mesophyllous, 1 per cent macrophyllous (*Brachyglottis repanda*). A second macrophyllous species, *Meryta sinclairii* (Aral.), is restricted to two groups of small islands off the Northland coast.

Leaf Forms

In tropical rain forests the commonest type of leaf is simple and entire; compound and toothed leaves are quite rare. In a Nigerian forest, for example, 80 per cent of the species had simple, entire leaves (Richards, 1952:82).

In the study forest, of the same group of species considered in the last section, 53 per cent had simple entire leaves, 29 per cent simple toothed leaves, 11 per cent compound leaves with toothed leaflets, and 7 per cent compound leaves with entire leaflets.

Bud Protection

In north temperate areas, trees having specialized bud scales which serve to protect stem apices during the winter are quite common. In tropical rain forests, where there is no unfavorable season and growth is more or less continuous, bud scales are very uncommon. Richards (1952:77), however, points out that the buds of tropical trees are not always as unprotected as has been thought. In some cases the young leaves are protected by stipules or sheaths of older leaves or by a few fleshy scales. Even when there are no special protective organs the young leaves may be protected by pubescence or by gummy or mucilaginous secretions.

The majority of New Zealand rain forest species are comparable to those of the tropical rain forest in modes of bud protection. In the study forest 34 per cent of the woody flowering species and 48 per cent of the genera have no special bud protective structures, although in most cases the young leaves are pubescent. The genera are *Alectryon*, *Beilschmiedia*, *Brachyglottis*, *Carpodetus*, *Clematis*, *Dysoxylum*, *Eugenia*, *Hedycarya*, *Ixerba*, *Knighitia*, *Laurelia*, *Litsea*, *Lophomyrtus*, *Melicope* (Rut.), *Olearia*, *Parsonsia*, *Pennantia*, *Pseudowintera*, *Quintinia*, *Rhabdodhammus*, *Senecio*, *Tetrapatahaea*, *Vitex*.

In 18 per cent of the species and 10 per cent of the genera, the first leaves of a developing bud are often much smaller than the later leaves,

but they usually become green and separated by internodes, so that, although they serve for bud protection, they are relatively unspecialized—*Alseuosmia*, *Metrosideros* (liane spp.), *Mida*, *Mrysiine*, *Nestegis*.

In 3 per cent of the species and 4 per cent of the genera, a few specialized but fleshy bud scales are found, which are essentially sheathing leaf bases bearing vestigial laminae—*Corynocarpus*, *Griselinia*, *Meryta*.

Thin, often numerous bud scales (and consequently buds similar to those of many temperate trees) occur in 7 per cent of the species and 6 per cent of the genera—*Metrosideros robusta*, *Pittosporum* (modified leaves), *Aristolelia*, *Fuchsia* (modified stipules).

In 19 per cent of the species and 17 per cent of the genera, at least some protection is provided by the stipules of mature leaves—*Ascarina*, *Elaeocarpus*, *Hoheria*, *Melicytus*, *Muehlenbeckia*, *Paratophis*, *Rubus*.

Interpetiolar stipules occur in 12 per cent of the species and 9 per cent of the genera—*Acakama*, *Coprosma*, *Geniostoma*, *Weinmannia*.

There are sheathing leaf bases in 7 per cent of the species and 6 per cent of the genera—*Macropiper*, *Pseudopanax*, *Schefflera*.

The Deciduous Habit

In north temperate forests many trees and shrubs are leafless during the winter, and in tropical forests growing in areas where there is a distinct dry season, some species may be leafless during the unfavorable period. In the New Zealand rain forest, which grows in parts of the country where there is no well marked dry season and winters are relatively mild, the deciduous habit is uncommon.

The following New Zealand rain forest species are partially or completely leafless during the winter: *Aristolelia serrata*, *Fuchsia excorticata*, *Muehlenbeckia australis*, *Plagianthus betulinus*, *Sophora microphylla*. However, at least with *Fuchsia* and *Aristolelia*, leaf fall is determined by temperature rather than day length, which is the determining factor for most northern hemisphere deciduous trees (Bussel, 1968:74). Cockayne (1928:146) reported that both species lose their leaves in cold localities but not in warm ones.

2. REGENERATION PROBLEMS

In any forest, if the old individuals of the various species are replaced as they die by more or less equal numbers of younger individuals of the same species, then the forest can be regarded as being in a state of equilibrium. This does not appear to be the case in the study forest nor in most rain forest stands elsewhere in New Zealand.

In the study forest the commonest conifer emergents, *Dacrydium cupressinum* and *Podocarpus dacrydioides*, appear to be mature to old trees with younger plants extremely rare. The dominant main canopy species, *Beilschmiedia tarairi*, appears to be evenly old with many trees exhibiting some dead or unhealthy looking branches. Again, despite the reputation of this species for shade tolerance, younger individuals and seedlings are very rare. In this case, however, pigs may be partly responsible, as Beveridge (personal communication) reports that pigs eat quantities of *B. tawa* seeds in forests elsewhere.

Even in canopy gaps, the pioneer small trees and shrubs seem to give way not to *Beilschmiedia* but to *Weinmannia silvicola*, so that the forest canopy can be regarded as a mosaic of aging *Beilschmiedia tarairi* and younger, more vigorous *Weinmannia silvicola*. The only other species that is regenerating well is the sub-canopy *Dysoxylum spectabile*, and in places its seedlings and saplings are abundant (Fig. 3).

This regeneration failure of the emergent conifers and some of the main canopy angiosperm species is not peculiar to the study forest but has been noted in similar forests throughout New Zealand. A number of theories which have been advanced to explain the lack of regeneration of the emergent podocarps in particular will now be considered briefly.

(1) Cockayne (1928:153) suggested that because the dominant podocarps are light-demanding in varying degrees they cannot regenerate when the main canopy is fully established. In his view the podocarps can regenerate only in the better lit seral communities leading to rain forest, but persist to a late stage in the sequence presumably by virtue of their height and long life span. Eventually they give way to climax dominated by *Beilschmiedia tarairi* in

the far north, *B. tawa* further south, and beyond its range, *Weinmannia racemosa*.

According to this theory, then, the study forest, with its aging and dwindling emergents, would be nearing a climax condition. However, the lack of regeneration of the main canopy dominant, *Beilschmiedia tarairi*, is not in accordance with this view.

(2) Cameron (1954) postulated a regeneration cycle to explain forest patterns in a central North Island locality. He envisaged the emergents, mostly podocarps, giving way to *Beilschmiedia tawa*, which in turn would give way to *Weinmannia racemosa*. Under the latter, the podocarps would regenerate to complete the cycle.

Beveridge and Franklin (personal communication) have recently discovered actual examples of a similar cycle on volcanic soils in the central North Island. In this case, tree fern communities develop in canopy gaps and are then suppressed by epiphytic *Weinmannia racemosa*, which is followed by the establishment of podocarp seedlings.

In the study area, the type of cycle envisaged by Cameron would involve replacement of the emergents mostly by *Beilschmiedia tarairi*, which appears to be replaced by *Weinmannia silvicola*. However, no evidence was seen of emergent species regenerating under the latter.

(3) Holloway (1954) proposed a "Climate Change Hypothesis," based on a study of certain South Island rain forests. According to this theory the failure of podocarps to regenerate is due to a change in climate to cooler and possibly drier conditions after the present aging podocarp emergents became established. This means that the change would have begun about 1200 A.D.

In the study forest, this theory might be used to explain the present status of the emergents. It might also provide an explanation for the similar condition of the main canopy dominant, *Beilschmiedia tarairi*, which, in view of its restriction to the far north in contrast with the New Zealand-wide range of the podocarps, might be expected to be even more susceptible to cold weather. However, the life span of the *Beilschmiedia* is much shorter than those of the emergent species, which would indicate a more recent date for the change in climate. Wardle

(1963), on the basis of studies of podocarps in South Island forests, has already proposed that the climate change was several centuries later than the date suggested by Holloway. However, even if Wardle's view were correct, it would still be necessary to explain why there are no medium-aged as well as old podocarp emergents, and why *Dysoxylum spectabile* is regenerating even though its present distribution indicates that it is less cold tolerant than the podocarps.

(4) In his "Broadleaf Forest Dominance Hypothesis," Robbins (1962) ascribes the decline of the podocarps to competition between a gymnosperm forest climax, which they comprise, and an angiosperm forest climax. He suggests that the former traces its ancestry to the early Mesozoic when it is believed angiosperms did not exist. Following establishment of the angiosperm forest climax in New Zealand, Robbins envisages a long drawn out state of competition between the two climaxes, with the more highly evolved and aggressive angiosperms inevitably gaining the ascendancy, or, in his own words, "There is a slow and gradual rise to dominance of one forest type over another; a struggle into which one may still read something of the story of the rise to supremacy of angiosperms over gymnosperms." Natural calamities such as glaciations or volcanic eruptions may grant the species of the gymnosperm climax a reprieve since, unlike the angiosperms, they are able to tolerate immature soils. As edaphic conditions improve, Robbins suggests, the angiosperm dominants enter. In the face of their competition, successive gymnosperm generations become sparser and less vigorous and eventually are entirely eliminated. Viewed in the light of this theory, the conifers of the study forest presumably belong to the last of a series of generations initiated at some time after the last glaciation.

Two questions arise, however. First, if the "angiosperm forest climax" dominated by *Beilschmiedia tarairi* is now the victor, one would expect that the dominant species would be regenerating successfully and would be represented by individuals of all ages. But in fact there appears to be little or no regeneration of *Beilschmiedia tarairi* and there is a predominance of old trees. However, as mentioned earlier, this may be at least partly the result of the destruction of seeds by pigs.

Second, since the far north is thought to have been a forest refuge during the last glaciation, it seems unlikely that the podocarps would have had new sites to colonize, at least not at the low altitudes at which the forest was studied. Robbins does suggest, however, that generally throughout the North Island the podocarps may have replaced *Nothofagus* forest, which usually occurs on poor soils.

The controversial problem of the role of the emergents in the New Zealand rain forest is still far from being solved. This type of problem is not peculiar to New Zealand, however; it has been recognized also in tropical rain forests, although here the emergents are exclusively angiosperms in most places.

In Nigeria, Jones (1956) reported inadequate regeneration of many of the angiosperm emergents and suggested that many of them, particularly the more light-demanding, may be sub-climax. This is very similar to Cockayne's interpretation of the role of the podocarp emergents in New Zealand.

There have been a number of reports also from the Southeast Asian tropics of a lack or inadequacy of regeneration of some of the emergent dipterocarps (Cousens, 1965).

The apparently similar ecological behavior of the predominantly coniferous emergents in the New Zealand forests and some of the predominantly angiospermous emergents of lowland tropical forests suggests that it might be profitable to compare the regeneration problems in the two forest types. If, as a result, the New Zealand emergents can be shown to be truly ecologically equivalent to the lowland tropical emergents, then Robbins' interpretation of the conifers among the former as relicts will need to be reconsidered.

3. FLORISTIC CONSIDERATIONS

A number of genera in the New Zealand rain forest, admittedly represented by only one or two species, are restricted in Australia often to much lower latitudes. In the following list these genera are grouped according to their approximate southern limits in Queensland or New South Wales, with the approximate southern

limits in New Zealand for each genus shown in parentheses.

15°S in Queensland: *Corynocarpus* (44°), *Geniostoma* (41°). Both genera also occur in New Caledonia to about 21°S.

22°S in Queensland: *Freycinetia* (45°), *Schefflera* (47°), *Tecomathe* (34°).

30°S in New South Wales: *Ackama* (36°), *Alectryon* (44°), *Beilschmiedia* (42°), *Dysoxylum* (42°), *Litsea* (38°), *Melicope* (46°), *Peperomia* (41°), *Vitex* (39°).

33°S in New South Wales: *Elatostema* (41°), *Macropiper* (44°), *Pennantia* (46°).

Certain other genera shared with New Zealand a range in eastern Australia from the tropics to Victoria or Tasmania, that is, into New Zealand latitudes: *Bulbophyllum* (44°), *Dendrobium* (47°), *Elaeocarpus* (47°), *Eugenia* (41°), *Hedyocarya* (45°), *Heimerliodendron* (38°), *Myrsine* (50°), *Parsonsia* (47°), *Quintinia* (44°), *Rhipogonum* (47°), *Sarcochilus* (47°).

Most of the genera in the preceding lists can probably be regarded as lowland tropical in origin, although the majority include some montane tropical species.

Other New Zealand rain forest genera appear to be predominantly montane in the tropics, and consequently their origins are more difficult to determine. Did they originate in lowland New Zealand and/or other regions of similar latitude and later migrate to the tropical mountains, or was the reverse the case? Some of the genera in this category are *Aristotelia*, *Ascarina*, *Astelia*, *Carpodetus*, *Collospermum*, *Coprosma*, *Clematis*, *Dacrydium*, *Fuchsia* sect., *Skinnera*, *Melicytus*, *Metrosideros*, *Muehlenbeckia*, *Nertera*, *Phyllocladus*, *Podocarpus*, *Rubus*, and *Weinmannia*.

In this group are included many of the liane and epiphyte species, which are of particular interest because they represent ecological parallels to those of the lowland tropical forests. In forests of the latter type north of New Zealand, for example, the genus *Ficus* provides most of the strangling epiphytes and some of the lianes, while several species of ferns are common as specialized "bird's nest" epiphytes. In New Zealand, and to some extent in montane forests in New Caledonia, Fiji, Hawaii and other high

Pacific Islands, *Metrosideros* takes the place of *Ficus* (Dawson, 1968), and the liliaceous genera *Collospermum* or *Astelia* the places of the "bird's nest" ferns.

The mostly conifer emergents in New Zealand and the abundant tree ferns might also be regarded as parallels to the mostly angiosperm emergents and the palms of the tropical lowlands.

The foregoing can only be regarded as a preliminary review of the situation, and much remains to be learned taxonomically about many of the genera as well as about the details of their latitudinal and altitudinal distribution. The same can be said with greater emphasis for the New Zealand rain forest genera which are not listed, and which include those thought to be endemic and others of probable South American origin.

Fossil evidence suggests that present New Zealand rain forests are very similar floristically to those existing under warmer climatic conditions in the Tertiary. Couper (1952) described the pollen and spore flora of fossil beds at Mangonui, a coastal locality very close to the study forest. These beds are thought to be Miocene in age and are notable for the presence of small fruits of an extinct species of *Cocos*. The latter, together with evidence from a number of marine groups, has led to the belief that the Miocene was a warm period in the New Zealand Tertiary, possibly near tropical, and so one would hardly expect the forests at that time to be similar to those of the present day. Couper, however, records the following forest species: *Podocarpus* sp., *Laurelia novae-zelandiae*, *Macropiper excelsum*, *Dysoxylum spectabile*, *Metrosideros* sp., *Aristotelia* sp., *Weinmannia* sp., *Griselinia* sp., *Alectryon* cf. *excelsum*, *Pseudopanax arboreum?*, *Rhopalostylis sapida*, *Rhipogonum scandens*, *Muehlenbeckia* sp., as well as an extinct species of *Nothofagus*, two extinct proteaceous species, and a number of ferns and lycopods.

The evidence suggests a forest flora in the Miocene very similar to forests in the same region today. This is a very different situation from those of other Tertiary floras with tropical affinities, such as those in Oregon and southern England, which differ greatly from the present day temperate floras in the same regions.

CONCLUSIONS

Ecologically, the New Zealand rain forest is comparable to lowland tropical rain forest in stratification and in range of special growth forms. It differs chiefly in having a lower stature than most lowland tropical rain forests, many fewer species, and a smaller average leaf size.

Floristically, there appear to be two main elements, lowland tropical and montane tropical, the latter including the majority of both the emergent species and the lianes and epiphytes.

It is suggested that the New Zealand rain forest has survived, with floristic reduction, from similar forests in the Tertiary, while other middle latitude rain forests have become extinct (North America and Europe) or have suffered greater reduction than those of New Zealand (Chile, southeast Australia, southeast Africa).

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