

APPLIED ECOLOGICAL STUDIES OF SHORELINE VEGETATION AT LAKES MANAPOURI AND TE ANAU, FIORDLAND

PART 1: VEGETATION OF LAKE MANAPOURI SHORELINE

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SUMMARY: Transects at right angles to the shoreline are used to describe seven herbaceous, two scrub and four forest communities of the lake edge. Composition, structure, site preference and relation to lake level are given for these communities. The effect of browsing mammals on the flora and structure of mountain beech forest is shown by comparison of forest on Bun-crana Island with that on the adjacent mainland. Shoreline vegetation is compared with that recorded from other areas in Fiordland.

INTRODUCTION

Apart from a broad account of the forests by Holloway (1954) there is no published information on the vegetation surrounding Lake Manapouri. Kelly (1968) undertook a botanical reconnaissance of the shoreline—particularly on the smaller islands. This present work, carried out from November 1969 to January 1971, was aimed at gaining detailed information on the lake-edge communities and their relationship to lake levels and to document the vegetation which would be disturbed or lost if the lake was raised above its natural levels. It concentrates on the smaller islands which are largely free of browsing mammals and thus offer a rare opportunity to study near-virgin vegetation.

CLIMATE, GEOLOGY AND TOPOGRAPHY

Mean annual rainfall increases, according to New Zealand Meteorological Service records, from 1157mm at Manapouri township to 3786mm at West Arm over a distance of only 27km. Mean annual temperature is about 10°C and sunshine duration about 1600 hours per year (McLintock 1960).

Mountains to the north, west and south, mostly Paleozoic gneisses, rise steeply to about 1500m, hold thin soils and are studded with landslide scars from tree line to lake edge. Granite forms Pomona Island and with epidiorite occurs on the

mainland shores directly north-east and south-east, at the Beehive and Stockyard Cove respectively (Fig. 1). Pomona Island and the Beehive are great round-topped hills, again with steep sides. An outcrop of schist occurs halfway down the eastern side of the lake, where it forms a shore of moderate slope. Tertiary sandstones, mudstones and conglomerates along the eastern flank of the main ranges form low hills and gentle to steep shorelines. Quaternary outwash moraines and gravels form the moderately-sloping eastern shores and recent alluvium fills the floors of the main valleys running into the lake (Wood 1966).

Soils of the eastern shoreline are mostly yellow-brown loams classified as Dunton (New Zealand Soil Bureau 1968). Elsewhere yellow-brown earths and podzols of the Titiraurangi series predominate.

Beaches are best developed on the Tertiary and Quaternary deposits in the east where they may be of fine sand, gravel or loose rocks. Further west beaches occur regularly in the bay heads, where they tend to be of fine gravel, and on stream deltas which hold coarser gravels. The length of the shoreline, including that of the islands, is approximately 190km.

The countryside everywhere shows signs of glaciation, with U-shaped valleys, cirques, lakes and partially truncated spurs such as that forming the Mahara and Holmwood Islands (Speight 1921). Many of the islands show a *roche mou-*

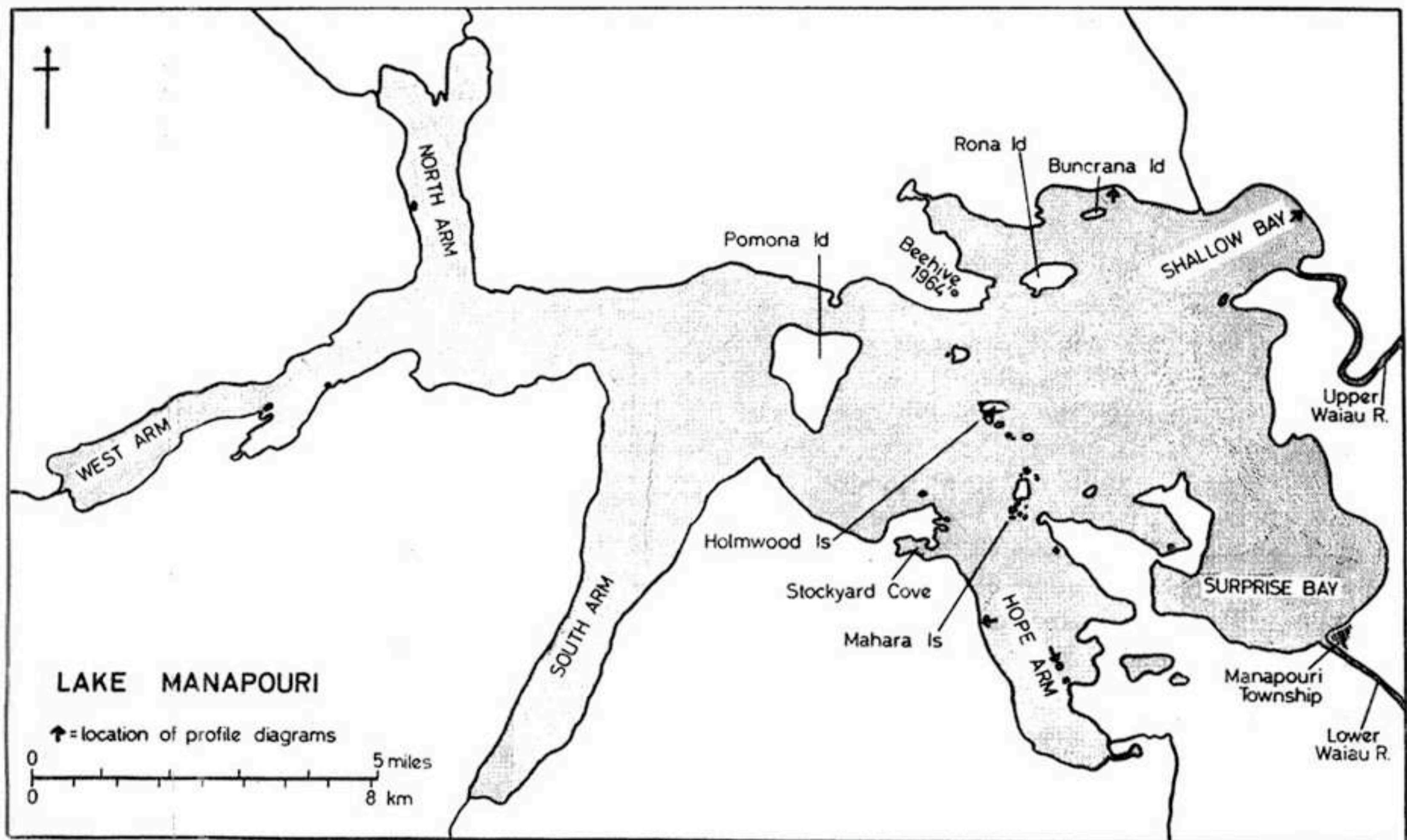


FIGURE 1. Map of Lake Manapouri showing places mentioned in text.

tonnée form with a gentle, smooth scour side and a steep, ragged pluck side. There are 31 islands which support forest or scrub and another two which support herbs only. This number varies with the level of the lake; during a period of high water, a few of the smaller islands are submerged or divided and when the lake is low some are joined to the mainland. Pomona Island, rising 340m above the lake, is the largest with an area of 260ha and Rona Island next at 55ha. The other islands are smaller, 18ha or less, and 17 of them would be completely drowned if the lake was at its proposed raised level of 610ft (185.9m). Lake level data are given in Part 2 of this series (Johnson 1972 p120.).

INTRODUCED ANIMALS

Wodzicki (1950) records that red deer (*Cervus elaphus*) were liberated near the head of Hope Arm in 1901. He shows little spread to the north and west by 1924 but records medium to heavy

infestation throughout the Manapouri basin by 1947. The opossum (*Trichosurus vulpecula*) was liberated at Te Anau in 1890.

Deer have been seen on many of the islands (Mr B. Murrell pers. comm.) but their visits to the smaller ones are probably infrequent and of short duration. Only on Pomona Island and possibly also Rona Island are deer likely to be found regularly. No sign of opossums was seen on any of the islands though they were evident on the mainland, at least around the eastern part of the lake. Mice (*Mus musculus*) were seen quite commonly on the mainland and on two islands. A few mustelids were seen on the mainland at Shallow Bay.

METHODS

At sites selected to cover the wide range of topography and vegetation, transects were laid out at right angles to the shoreline and extending to about 15m (50ft) vertically above the lake.

Plant categories recorded were:

trees	over 4in (102mm) diameter at breast height.
small-trees	under 4in (102mm) d.b.h. but over 15ft (4.6m) high.
shrubs	1 to 15ft (0.3 to 4.6m) high.
herbs and sub-shrubs	0.5 to 1ft (15 to 30cm) high.
ground	less than 0.5ft (15cm) high.

Diameter at breast height and density were recorded for trees and small-trees in adjacent 4×4m quadrats along the transect, density of shrubs in adjacent 2×2m quadrats, cover of herbs and sub-shrubs in alternate 1×1m quadrats and ground cover in alternate 0.5×0.5m quadrats using a wooden frame gridded into 25 squares to facilitate visual estimation of cover. All quadrats were nested. Total area sampled varied from one transect to another, but the average area for the six forest stands presented is 720m².

Survey of each transect with an abney level and a staff graduated in feet, together with the lake level recorded for the day, enabled precise heights to be given to points along the transect. Twenty eight transects were completed, three in West Arm and the rest in the eastern half of the lake.

The podocarp stand at the head of Hope Arm was sampled by ten alternate quadrats arranged in a line. For trees 10×10m quadrats were used, small-trees were recorded with shrubs in 4×4m quadrats, herbs and sub-shrubs in 2×2m quadrats, both nested in one corner of the large quadrats. Ten ground cover quadrats were laid out along one side of each of the large quadrats.

Mean depth of bryophytes on Buncrana Island and the nearby mainland was calculated from 200 measurements taken 2m apart along a line for each site. An aluminium staff graduated in inches was pushed into the bryophytes until resistance was met in the form of gravel, soil or roots.

A few bryophytes, unfortunately among the most common genera, are difficult to separate precisely in the field and have been combined as follows in the quantitative data. All *Chiloscyphus* species are treated together, '*Plagiochila* spp.' em-

braces all except *P. stephensoniana*, '*Lepidolaena* spp.' embraces *L. taylorii*, *L. palpebrifolia* and *L. clavigera* and *Dicranoloma robustum* may include some *D. billardieri* and *D. cylindropyxis*. Similar combination and caution applies here to those lake-edge herbs listed in Part 2 (Johnson 1972, p.130), wherein nomenclatural authorities are also given (p.129).

RESULTS

Thirteen plant communities have been recognised which are described as follows.

Aquatic Vegetation

On shores of gentle to moderate slopes *Isoetes alpinus*, *Myriophyllum elatinoides* and, in places, *Elodea canadensis* form a dense carpet, up to 30cm thick, extending about 20ft (6m) below the mean lake level of 583ft (177.7m). Scattered plants of *Chara corallina*, *C. fibrosa* and *Nitella* sp. occur within this carpet while in shallower water *Potamogeton cheesemanii* then *Myriophyllum propinquum* become important. Three feet (1m) below mean level plants of *Isoetes* and *M. elatinoides* are smaller and more scattered and are joined by sub-aquatic herbs of the lake-edge turf.

Lake-Edge Turf

Lake-edge turf is confined to a narrow vertical range between the upper limit of aquatic vegetation at about 580ft (176.8m) and either open rock or communities of *Leptocarpus similis* or manuka (*Leptospermum scoparium*) which replace the turf at or below 586ft (178.6m). The turf occupies a substrate of soil accumulated over a gentle to moderate slope usually of gravel. It is most extensive in sheltered bay heads, but can occur as isolated patches.

This community is made up of some 45 species of tightly matted, mostly creeping herbs, only a few of which (e.g. *Eleocharis acuta*) exceed an inch in height. Table 1 shows the mean percentage ground cover on six transects at three elevations—below, around and above mean lake level. Just below mean level the vegetation is dominated by *Isoetes* (18% cover) and *Myriophyllum*



FIGURE 2. Mainland near Mahara Islands with low lake level (580.0ft) or 176.8) showing extensive lake-edge turf dominated by *Myriophyllum propinquum*, manuka scrub and mountain beech forest behind.

propinquum (8%). The latter is more important (12%) around mean level (Fig. 2) where it shares dominance with *Selliera radicans* (8%) and *Centrolepis pallida* (7%) over a wider range of minor species. Above mean level dominance shifts to *Eleocharis acuta* (11%) and *Carex gaudichaudiana* (8%).

In addition to variation with elevation, composition varies with the type of soil. Some species, such as *Centrolepis* and *Myriophyllum propinquum*, predominate on deep soft clay or fine silt while others like *Eleocharis acuta* and *Ptilularia novae-zelandiae* are more important in gravelly areas. Succession may be taking place in the turf following deposition of silt and clay or exposure of a fresh surface by wave action. Minute *Centrolepis* plants colonise these bare areas. Presumably they grow to form the coalesc-

ing cushions 10cm deep that dominate parts of the lake edge. In places however, the *Centrolepis* looks over-mature with the cushions broken up by wave action. There are no young plants of *Centrolepis* between these cushions and it is possible this species is giving way to others such as *Selliera radicans*.

Carex Sward

On very gentle slopes, notably at the head of Hope Arm and at Shallow Bay, *Carex gaudichaudiana* sward forms a belt up to 50m wide from 584-7ft (178.0-178.9m), usually between a narrow zone of lake-edge turf and one of either *Leptocarpus* or manuka. At Shallow Bay (Table 1 and Fig. 3) *C. gaudichaudiana* forms a dense sward (47% cover) up to 25cm tall on deep, poorly drained soil. *Hydrocotyle tripartita*

TABLE 1. *Percentage Ground Cover in Four Lake-Edge Communities**.

	Lake edge turf			<i>Carex</i> sward	<i>Leptocarpus</i> community	Manuka scrub
	580-2'	582-4'	584-6'			
Rock	21	3	2	—	—	—
Clay	19	16	12	—	4	—
Gravel	7	8	28	9	8	—
Drift & Litter	—	3	—	1	16	44
<i>Isoetes alpinus</i>	18	4	p	—	p	—
<i>Potamogeton cheesemanii</i>	4	p	—	—	—	—
<i>Myriophyllum elatinoides</i>	3	p	—	—	—	—
<i>Tridontium tasmanicum</i>	2	p	p	—	—	—
<i>Centrolepis pallida</i>	2	7	p	—	—	—
<i>Pilularia novae-zelandiae</i>	5	6	2	—	—	—
<i>Scirpus aucklandicus</i>	2	6	3	—	—	—
<i>Myriophyllum propinquum</i>	8	12	3	—	p	—
<i>Limosella lineata</i>	p	1	—	—	p	—
<i>Callitriche ?petriei</i>	p	p	6	—	1	—
<i>Juncus pusillus</i>	2	2	p	—	2	—
<i>Gratiola ?nana</i>	p	2	p	p	p	—
<i>Selliera radicans</i>	3	8	2	p	p	—
<i>Plantago triandra</i>	p	1	4	p	p	—
<i>Hydrocotyle tripartita</i>	p	2	2	8	p	p
<i>Tillaea sinclairii</i>	—	p	p	2	—	—
<i>Epilobium komarovianum</i>	—	p	1	p	—	—
<i>Fissidens asplenioides</i>	—	p	p	—	2	—
<i>Eleocharis acuta</i>	—	3	11	2	p	—
<i>Cotula perpusilla</i>	—	3	3	2	p	—
<i>Hypsela rivalis</i>	—	p	p	2	6	—
<i>Schizeilema cockaynei</i>	—	p	1	p	p	—
<i>Gunnera dentata</i>	—	p	p	4	p	—
<i>Carex gaudichaudiana</i>	—	p	8	47	5	p
<i>Leptocarpus similis</i>	—	3	p	p	51	p
<i>Viola lyallii</i>	—	p	p	1	—	p
<i>Pratia angulata</i>	—	p	p	1	—	1
<i>Centella uniflora</i>	—	p	p	5	1	3
<i>Leptospermum scoparium</i>	—	p	p	—	p	3
<i>Breutelia pendula</i>	—	p	p	—	p	17
<i>Juncus gregiflorus</i>	—	p	—	2	p	p
<i>Potentilla anserinoides</i>	—	—	p	3	—	—
<i>Lachnagrostis striata</i>	—	—	p	1	—	—
<i>Lachnagrostis filiformis</i>	—	—	p	2	—	p
<i>Coprosma propinqua</i>	—	—	p	p	p	1
<i>Chiloscyphus</i> spp.	—	—	—	—	2	3
<i>Ptychomnion aciculare</i>	—	—	—	—	—	9
<i>Rhizogonium mnioides</i>	—	—	—	—	—	1
<i>Plagiochila</i> spp.	—	—	—	—	—	1
<i>Blechnum penna-marina</i>	—	—	—	—	—	6
<i>Nothofagus</i> s. var. <i>cliffortioides</i>	—	—	—	—	—	1
<i>Pseudowintera colorata</i>	—	—	—	—	—	1
<i>Neomyrtus pedunculata</i>	—	—	—	—	—	1
<i>Uncinia uncinata</i>	—	—	—	—	—	2

* Lake-edge turf is shown at three intervals of elevation. Only those species which form at least one percent cover in one community are included; p indicates lesser values in other communities.

(8% cover), *Centella uniflora* (5%), *Gunnera dentata* (4%) and *Potentilla anserinoides* (3%) are the important associated herbs. Tufts of *Juncus gregiflorus* and small clumps of manuka up to 2.5m high grow within the sward. Runnels of water are bordered by *Ranunculus rivularis*, *R. flammula* and *Myosotis caespitosa*. Around the edge of the sheltered Hope Arm lagoon, *Carex berggrenii* and *Juncus bufonius* join *C. gaudichaudiana* and impart a red colour to the community.

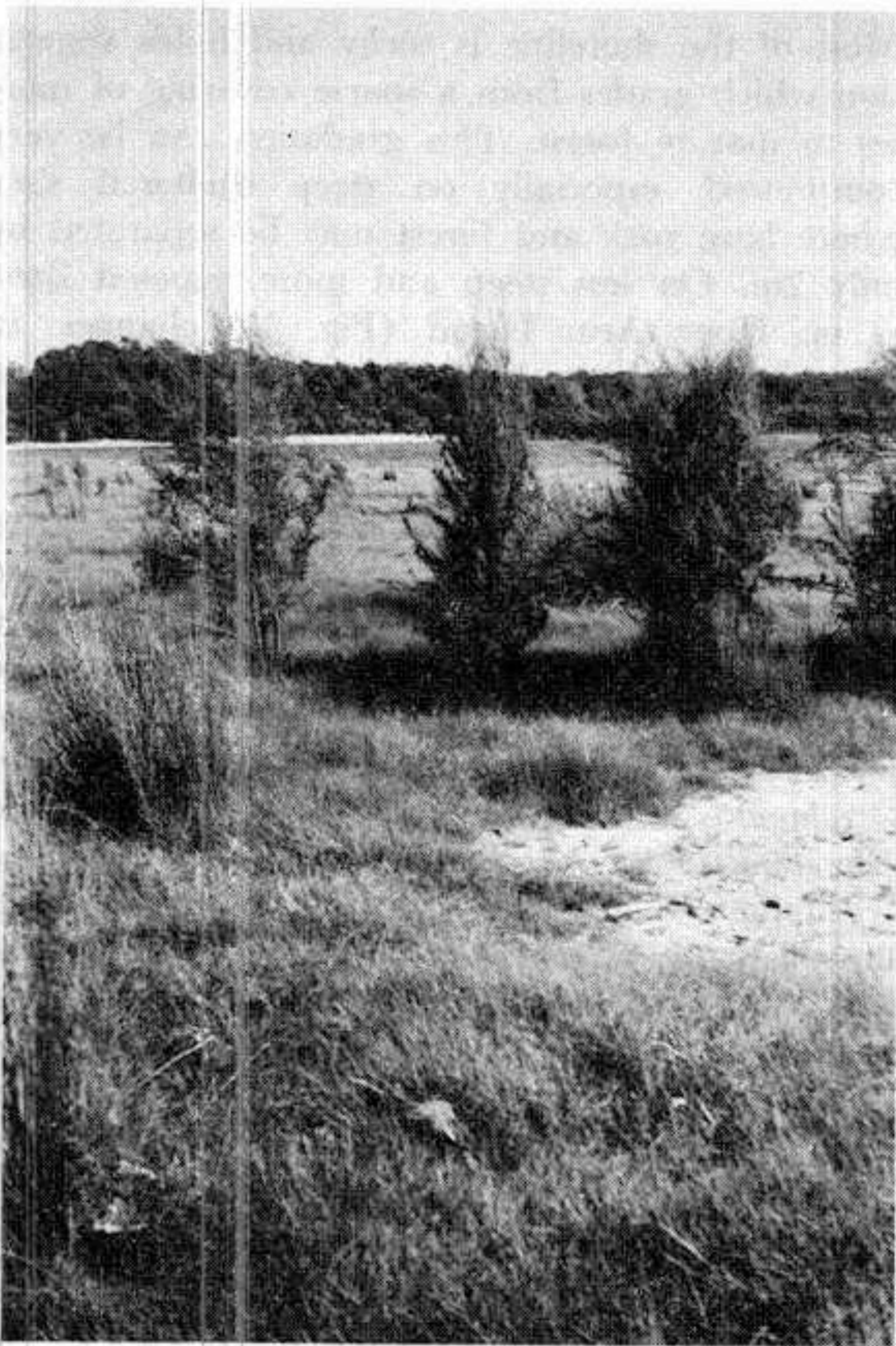


FIGURE 3. *Carex gaudichaudiana* sward with scattered manuka and *Juncus gregiflorus* forming a wide belt at Shallow Bay. Lake level 584.2ft (178.1m).

Leptocarpus Community

Leptocarpus similis up to 1m high forms dense stands which are conspicuous as a brown fringe on gentle shores between manuka scrub and one

or more of the above communities; like them, it is best developed around the eastern shores as at Surprise Bay (Fig. 4). *Leptocarpus* often extends under manuka but here it thins out, giving way to some extent to the smaller sedges *Schoenus pauciflorus* and *Lepidosperma australe*. All the ground species, as shown in Table 1 for two transects at 583-585ft (177.7-178.3m), are found also either in the lake-edge turf or under manuka. *Leptocarpus* usually grows on a deep, often gravelly soil but also on thin soils on rock terraces.

Manuka Scrub

On both sheltered and exposed gentle slopes manuka dominates a narrow belt of scrub between one or more of the communities just described and forest (Figs. 2 and 4). At the head of Hope Arm this belt is about 7m wide with a total density of 31,100 stems/ha. The canopy is 5m high near the lake, rising to 8m against mountain beech forest. Manuka has a relative density of 60%, the other important shrubs being *Pseudowintera colorata* (15%), *Neomyrtus pedunculata* (10%) and *Coprosma parviflora* (10%). The herb layer is sparse (13% cover), mostly woody seedlings but with some *Uncinia uncinata* (2%) and a little *Leptocarpus* and *Lepidosperma*. The flora associated with manuka dominance is large and variable, probably because of the wide tolerance of manuka itself. Thus many of the associated ground species (Table 1) are found also in the forest and in the communities already described. Nevertheless a few plants such as *Blechnum penna-marina* are almost restricted to manuka communities and others such as the mosses *Breutelia pendula* and *Rhizogonium mnioides* are most important here.

More commonly manuka forms a belt only a few plants thick on the forest edge. On gravelly sites it shares dominance with *Dracophyllum longifolium* and *Coprosma propinqua*. *Schoenus pauciflorus* and *Lepidosperma australe* are important in the herb layer, and the common ground plants are *Haloragis micrantha*, *Lagenophora petiolata*, *Polytrichum commune* and *Breutelia pendula*.

Frequently the manuka community has the appearance of a seral stage towards forest, old and

even-aged manuka overtopping saplings of forest species, particularly rimu (*Dacrydium cupressinum*). Succession here could be of two types. Firstly, disturbance of manuka stands by Maoris and more certainly by Europeans, who cut manuka for fuel for steam-driven boats, and perhaps by manuka blight (Hoy 1964), would be expected to result in regeneration of manuka. This could be taken to explain the even-aged, old manuka at some sites, while the saplings of forest trees could be interpreted as part of a climax determined by frequency of flooding. Secondly, there could be a general extension of manuka infilling of the lake shore, or downwards through a gradual long term lowering of lake level.

Infilling by streams like the Garnock Burn at the head of Hope Arm is likely to result in outward movement of the lake edge and a succession from lake-edge communities, via manuka, to forest.

On the isthmus of the peninsula facing the Mahara Islands, infilling by wave-carried silt and organic matter may be taking place. Manuka on deep soil here is 4m high at its outer edge, with old scattered specimens rising to 12m over young and vigorous kahikatea (*Dacrycarpus dacrydioides*) against the abrupt edge of mountain beech forest. An increase in soil depth with a resulting rise in soil surface relative to the lake is a likely cause for replacement of manuka by kahikatea. But on the other side of this isthmus similar manuka and kahikatea stands grow directly on rock. Any succession here could only be a result of a gradual lowering of mean lake level over a long period perhaps because of deepening of the Waiau bed or by a long term decrease in precipitation.

The lake shore vegetation can be expected to respond to such changes and the forests to do so with considerable time lag, so that evidence of this could indicate a change that commenced centuries ago. The possibility should not be overlooked that a relationship may exist between the present lake shore vegetation and past lake levels, similar to that suggested by Holloway (1954) to exist between present forests in the South Island and past climates.

Willow (*Salix* sp.) has partly usurped manuka along the north side of Buncrana Island, at two small sites on the nearby mainland and at Shallow Bay near the mouth of the Waiau River. These trees were planted at the end of last century (Mr B. Murrell pers. comm.). There is also a mature willow on one of the Mahara Islands and small cuttings are not uncommon within about 1km of the parents.

Rocky Shore Communities

Most of the shoreline is rocky and holds vegetation which grades from a sparse covering of mosses to mature forest. This gradation can be very compressed, especially on steep sheltered sites where bare rock and forest may be separated by only 2m. On less steep and more exposed sites, as on Hope Arm Island (Fig. 4), changes in the vegetation can be more readily seen and a division made into an open rock community and one of rupestral scrub.

Just above mean water level mosses such as *Dicranum aucklandicum*, *Weissia controversa*, *Bryum laevigatum* and *B. dichotomum* form a sparse cover of up to 5% on the rock. These are progressively replaced by other mosses, especially *Grimmia apocarpa*, *Campylopus bicolor*, *C. clavatus*, *C. introflexus*, *Ceratodon purpureus*, *Rhacomitrium crispulum*, *Hedwigia ciliata*, *H. integrifolia*, *Rhacocarpus humboldtii*, and simultaneously by lichens, firstly species of *Parmelia* and *Placopsis*, then *Stereocaulon colensoi*, *Cladia aggregata* and *Cladonia leptoclada*. Like the mosses these increase in cover further from the lake. The grasses *Notodanthonia setifolia*, *N. gracilis* and *Lachnagrostis filiformis* appear, then small scattered shrubs—mainly *Cassinia vauvilliersii* and manuka.

The rupestral scrub increases in number of species, density and height towards the forest edge where it is up to 5m high and dominated by manuka, southern rata (*Metrosideros umbellata*), mingimingi (*Cyathodes juniperina*) and *Dracophyllum longifolium* with some *Pseudopanax lineare*, *P. crassifolium* and *P. colensoi*. Among the smaller shrubs, *Dendrobium cunninghamii*, *Cassinia*, and *Gaultheria rupestris* are the most com-

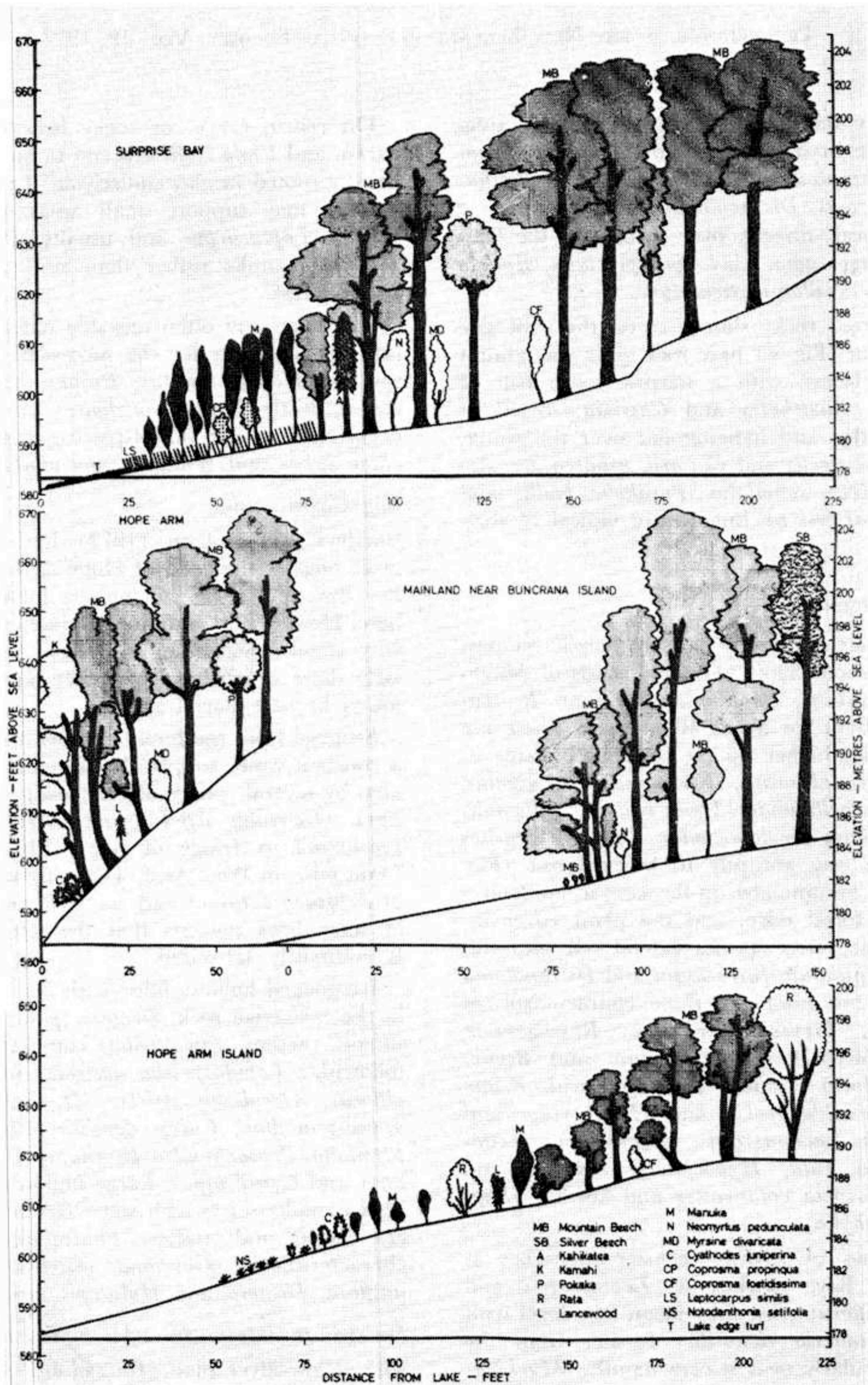


FIGURE 4. Profile diagrams, showing all trees and shrubs recorded in 2m wide transects—on a gently sloping shore where soil has accumulated to lake level (top), above a beach (right), on a sheltered rocky shore (left) and an exposed rocky shore (below). The base line represents mean lake level in each profile.

mon. Under the shrubs, and in the open areas between, the bryophytes *Rhacomitrium lanuginosum*, *Eucamptodon inflatus*, *Chandonanthus squarrosus*, and *Dicranoloma robustum* form a complete cover, directly over rock, with the lichens *Cladia aggregata*, *Cladonia leptoclada*, *Siphula* sp. and *Stereocaulon corticatulum*.

On sheltered rocky shores, as on the west side of Hope Arm (Fig. 4) bare rock gives way almost directly to forest, with a narrow scrub belt of mingimingi, *Gaultheria* and *Cassinia*, rooted at the forest edge and hanging out over the water. *Olearia arborescens* and *Coriaria arborea* are also common, *Hebe salicifolia*, *Parahebe lyallii* and *P. catarractae* less so, but all are typical of sheltered sites.

Beach Communities

Sandy beaches are mostly bare in their lower part but, above about 590ft (179.8m), mats of *Muehlenbeckia axillaris*, *Raoulia hookeri* and *R. tenuicaulis* account for about 10% cover. These are joined a little higher up by occasional plants of *Lachnagrostis filiformis*, *Notodanthonia gracilis*, *Helichrysum bellidioides*, *Viola lyallii*, *V. filicaulis* and *Epilobium melanocaulon*. Sandy beaches usually give way abruptly to beech forest (Fig. 4) but litter accumulates on the sand a few metres outside the forest edge, and the plant cover increases. Some forest species extend out into this strip (e.g. *Thuidium furfurosum* and *Dicranoloma robustum*), but most are those characteristic of forest edge. *Breutelia pendula*, *Rhizogonium mnioides*, *Polytrichum juniperinum* and *Bryum truncorum* form cushions interlaced with *Pratia angulata*, *Muehlenbeckia* and *Helichrysum* and studded with *Lachnagrostis*, *Lagenophora petiolata*, *Luzula rufa*, *Hypochaeris radicata* and shrubs of *Corokia cotoneaster* and kowhai (*Sophora microphylla*).

On beaches of slightly coarser material, as at Shallow Bay, patches of *Leptocarpus* and *Juncus gregiflorus* grow near mean lake level with toetoe (*Cortaderia richardii*) further from the water, particularly near stream mouths. *Muehlenbeckia* is again important, along with *Epilobium cinereum*, *E. melanocaulon* and *E. atriplicifolium*.

On coarse gravel or rocky beaches, *Muehlenbeckia* and *Viola lyallii* descend to mean lake level, usually rooted in clay underlying the gravel. Such beaches may support small areas of lake-edge turf or *Leptocarpus* and usually give way to a zone of manuka rather than run directly under beech forest.

The open and often unstable nature of beaches probably accounts for the success of exotic plants such as *Holcus lanatus*, *Rumex acetosella* and scotch thistle (*Cirsium vulgare*) and the chance occurrence of such out-of-place species as *Chionochloa rubra* and *Wahlenbergia albomarginata*.

Bog Communities

Burrows and Dobson (1972) have studied the large bogs at the head of Hope Arm and at Shallow Bay, and these will not be further described here. However, in addition to these extensive bogs, very small ones occur on rocky shores, particularly those which have been left smooth and hollowed by past glacial action.

Seepage from the forest supplies some bogs with a constant water supply. These tend to be dominated by several species of *Campylopus* and *Sphagnum*, *Oreobolus strictus* and invariably *Drosera spathulata*. A fringe of bog is the rule at the forest edge in West Arm. The constant occurrence of *Schizaea fistulosa* and the rich bryophyte flora of these bogs suggests that the soil in this area is constantly saturated.

Ice-gouged hollows filled with peat are common in the lake-edge rock. *Drosera spathulata* is again usually present with various combinations of the following: *Lepidosperma australe*, *Schoenus pauciflorus*, *Oreobolus strictus*, *O. impar*, *Juncus novae-zelandiae*, *Carex demissa*, *Cyathodes empetrifolia*, *Pentachondra pumila*, species of *Sphagnum* and *Campylopus*. Large hollows and troughs hold manuka scrub with some *Dracophyllum*, several sedges and rushes, *Phormium tenax* and characteristically *Gentiana grisebachii*, *Centella uniflora*, *Drosera* and *Haloragis micrantha*.

Dacrydium intermedium-Mountain Beech Forest

The yellow-silver pine (*Dacrydium intermedium*) is found in isolated patches on thin soils as far east as the mainland near the Mahara Islands. At

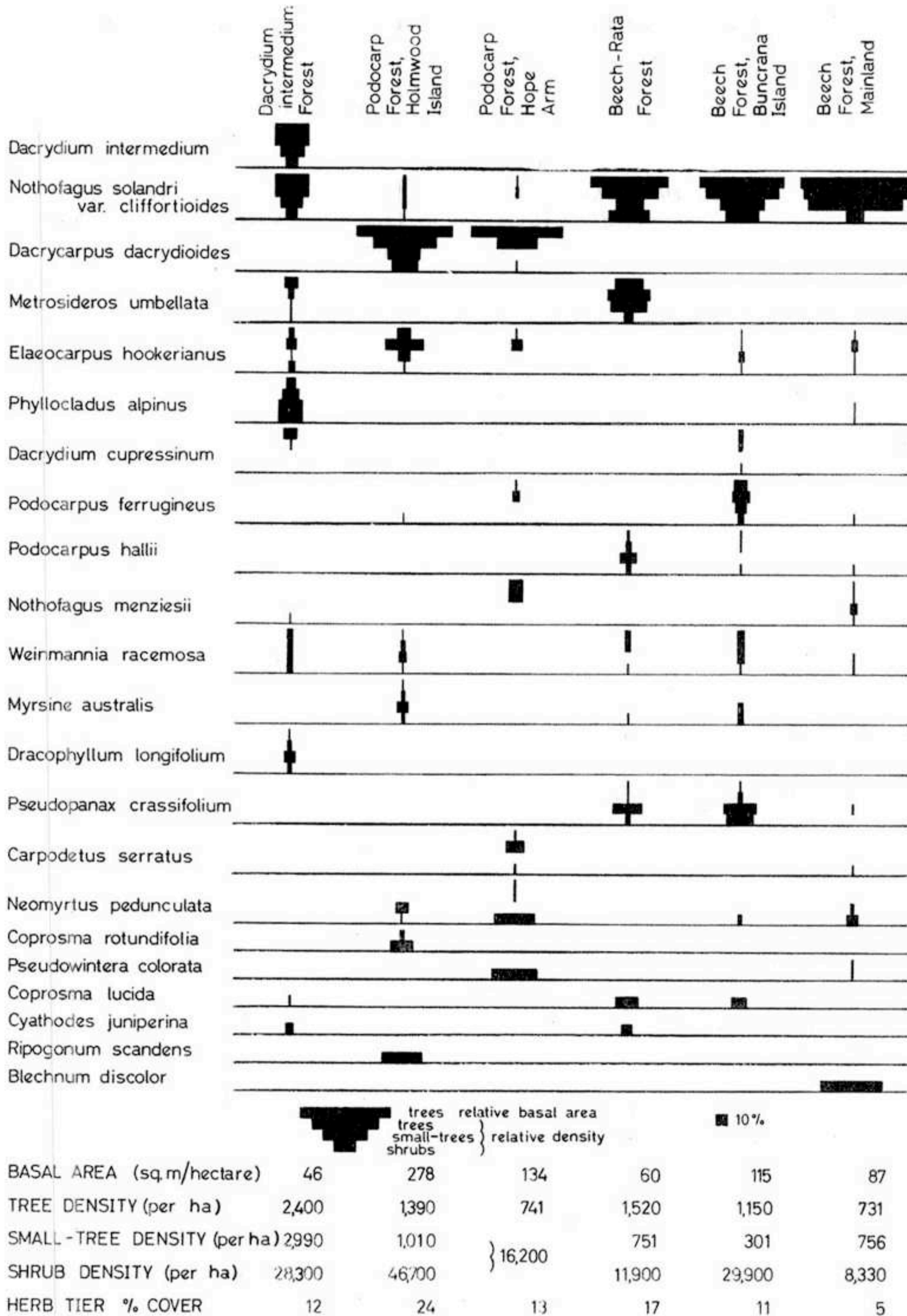


FIGURE 5. Relative basal area and relative density of the important species (10% or more in at least one stand) in three size classes from six forest stands at Lake Manapouri. Total basal areas and densities are shown, together with total cover of the herb tier. Small-trees are included with shrubs in the Hope Arm stand.

TABLE 2. *Percentage Ground Cover in Six Forest Communities**.

	<i>Dacrydium</i> <i>intermedium</i> forest	Podocarp forest Holmwood Id	Podocarp forest Hope Arm	Beech/rata forest	Beech forest Bunscrana Id	Beech forest mainland
<i>Nothofagus s. var. cliffortioides</i>	p	—	p	2	3	4
<i>Elaeocarpus hookerianus</i>	p	1	p	p	p	p
<i>Dacrycarpus dacrydioides</i>	—	7	9	—	—	—
<i>Coprosma rotundifolia</i>	—	1	1	—	—	—
<i>Ripogonum scandens</i>	—	4	p	—	p	—
<i>Parsonsia heterophylla</i>	—	1	1	—	—	—
<i>Earina autumnalis</i>	—	—	—	16	—	—
<i>Nertera dichondraefolia</i>	—	—	3	—	p	—
<i>Polystichum vestitum</i>	—	p	1	—	—	—
<i>Hymenophyllum multifidum</i>	4	—	p	2	p	p
<i>Trichomanes reniforme</i>	19	—	—	—	—	—
<i>Aneura ?lobata</i>	1	—	—	—	p	p
<i>Bazzania adnexa</i>	2	—	—	2	—	—
<i>B. novae-zelandiae</i>	2	—	—	2	p	4
<i>Camptochaete pulvinata</i>	—	2	p	—	p	—
<i>C. ramulosa</i>	—	—	2	—	—	—
<i>Chandonanthus squarrosus</i>	2	—	—	1	—	—
<i>Chiloscyphus</i> spp.	4	1	1	2	2	3
<i>Dicranoloma robustum</i>	3	—	—	3	p	1
<i>Hymenophyton flabellatum</i>	—	p	2	—	—	—
<i>Hypnodendron arcuatum</i>	—	p	3	—	p	p
<i>H. marginatum</i>	—	8	3	—	—	—
<i>Hypnum cupressiforme</i>	1	—	p	p	p	p
<i>Hypopterygium setigerum</i>	—	6	2	—	—	—
<i>Lepicolea scolopendra</i>	1	—	—	—	—	—
<i>Lepidolaena hodgsoniae</i>	p	—	—	p	5	7
<i>L. spp.</i>	p	p	p	7	2	p
<i>Lepidozia pendulina</i>	p	—	—	—	p	16
<i>Lophocolea leucophylla</i>	—	—	—	—	1	2
<i>Plagiochila stephensoniana</i>	—	—	9	—	—	—
<i>P. spp.</i>	—	p	4	10	28	11
<i>Ptychomnion aciculare</i>	9	—	p	1	p	1
<i>Trichocolea mollissima</i>	5	—	1	4	p	4
<i>Thuidium furfurosus</i>	—	—	—	p	p	1
litter	36	72	47	43	51	37
mud	—	—	8	—	—	—
Total woody species	3	15	6	2	3	4
Total herbs and ferns	24	1	8	19	1	2
Total bryophytes	37	12	31	36	45	57

* Only species with at least one percent cover in one community are shown; p indicates lesser values in other communities.

the mouth of West Arm yellow-silver pine abruptly joins mountain beech and co-dominates with it under high rainfall on the steep slopes in West and North Arms. Figure 5 and Table 2 show the structure and composition (from three transects, one on Koinga Island in West Arm and two on the adjacent mainland). The canopy rarely exceeds 12m in height though there are occasional emergent rimu. Total basal area is smaller (46m²/ha) and tree density higher (2400/ha) than in the other forest types. Yellow-silver pine (28% Relative Density) and mountain beech (28%) dominate *Phyllocladus alpinus* (15%), pokaka (*Elaeocarpus hookerianus*) (9%), *Dracophyllum longifolium* (4%) and southern rata (7%). Mountain beech (20%), yellow-silver pine (22%) and *Phyllocladus* (19%) are important small-trees, while the shrub layer is dominated by *Phyllocladus* (20% RD) with yellow-silver pine (10%) and mountain beech (10%) still prominent though sharing this tier with many other species—particularly kamahi (*Weinmannia racemosa*) (7%), mingimingi (7%), pokaka (5%), *Archeria traversii* (7%), *Pseudopanax simplex* (8%) and *P. lineare* (6%).

Woody seedlings account for half the 12% cover of the herb and sub-shrub tier though *Gahnia procera* and *Blechnum minus* each contribute 2% cover. On the ground, herbs and ferns (24% cover) are much more conspicuous than in the forest further east. Kidney fern (*Trichomanes reniforme*) makes up most of this, along with filmy ferns. The bryophytes form deep cushions with *Trichocolea mollissima* and *Ptychomnion aciculare* dominating. Yellow-silver pine frequently has a prostrate trunk with branches arising vertically so that apparently separate specimens are linked by a half-buried trunk.

In addition to the covering of bryophytes on trunks and branches, kidney fern, filmy ferns and the two species of *Earina* are common epiphytes.

Swamp Podocarp Forests

At the head of Hope Arm, at Shallow Bay, and on Holmwood Island are impressive stands of forest dominated by kahikatea.

The largest of the Holmwood Islands has a broad, poorly drained trough rising to 590ft

(179.8m) running across its south-eastern corner. This trough was once the site of a Maori eel weir so it is possible that the kahikatea forest it now supports is a late stage of succession after disturbance. Mature trees rise to 27m with d.b.h. up to 1140mm. Young trees are frequent and in places saplings up to 3m high have a density of 9/m², and seedlings form up to 60% cover in a 0.25m² quadrat. The total basal area recorded (278m²/ha) is very high but may have been over-estimated because of the small size and the long narrow shape of the area sampled. Nevertheless, high basal area is to be expected in this type of forest. Kahikatea accounts for 85% of the basal area with pokaka (11%) and a little mountain beech, kamahi and *Myrsine australis*. Kahikatea has a relative density of 56% and pokaka 33%. Kahikatea (28% RD) is also the most abundant small-tree and still has 23% RD in the shrub tier which it shares with supplejack (*Ripogonum scandens*) (36%) and *Coprosma rotundifolia* (19%). Supplejack grows up the kahikateas to about 15m and its inclusion for measurement among the shrubs helps account for the high density recorded here (46,700/ha). The lianes, *Rubus australis* and *R. schmidelioides* are less common but *Parsonsia heterophylla* sprawls over most of the shrubs.

Sub-shrubs, particularly kahikatea (5% cover), supplejack (5%) and *Coprosma rotundifolia* (3%), plus the ferns *Asplenium bulbiferum* (4%) and *Blechnum capense* (5%), account for most of the dense herb tier (24%). Most of the ground cover is litter (72%) though woody seedlings are numerous (15%). Bryophyte cover is small but is dominated by the umbrella mosses *Hypnodendron marginatum* and *Hypoterygium setigerum*.

At the head of Hope Arm is a low-lying area of about 500ha which holds a mosaic of lakes, bogs and swamp forests. Kahikatea forest (Fig. 5 and Table 2) is the commonest of these, with trees rising to 36m, a density of 741/ha and a basal area of 134m²/ha.

Kahikatea dominates the trees (79% relative basal area and 36% RD) though there are quite a few *Carpodetus serratus* (15% RD) pokaka (10%) silver beech (*Nothofagus menziesii*) (12%) and miro (*Podocarpus ferrugineus*)

(6%). Kahikatea is of little importance among the shrub, herb and ground tiers. *Neomyrtus pedunculata* (37% RD) and *Pseudowintera colorata* (40%) dominate the shrubs. Herbs and subshrubs (13% cover) are less dense than on Holmwood Id, being mostly *Pseudowintera* (3%), *Parsonsia* (2%) and the ferns *Polystichum vestitum* (2%) and *Blechnum discolor* (1%). The ground bryophytes are dominated by the hepatics *Plagiochila stephensoniana* (9% cover), other *Plagiochila* spp. (4%) and by the umbrella mosses *Hypopterygium setigerum*, *Hypnodendron arcuatum* and *H. marginatum*. The soil here is very wet. Pare mud makes up 8% of the ground cover and the water table must be very near the surface. Uprooted trees characteristically leave puddles behind them, and these are colonised by *Scirpus habrus*, *Juncus articulatus* and *Callitriche ?petriei*.

At Shallow Bay on the alluvial fan at the mouth of the Waiau River is a stand of forest in which matai (*Podocarpus spicatus*) co-dominates with kahikatea. The trees are all very big, up to 1780mm in diameter and 36m high, and except for occasional seedlings there are no matai or kahikatea stems below tree size.

On granite at Stockyard Cove is a stand of hill forest dominated by large and rather scattered emergent matai, miro and rimu. Mountain beech, silver beech and kamahi form an uneven canopy above the small-trees *Fuchsia excorticata*, *Melicytus ramiflorus*, *Pennantia corymbosa*, *Lophomyrtus obcordata*, the tree ferns *Dicksonia squarrosa* and *Cyathea smithii* and the ground ferns *Blechnum discolor* and *Polystichum vestitum*.

Mountain Beech-Southern Rata Forest.

Mountain beech dominates by far the majority of the shoreline forests—alone in flat sheltered areas and with yellow-silver pine in the west or southern rata on the steep slopes and thin soils that characterise most of the shoreline. On the smaller islands, like the largest in Hope Arm and the third largest of the Holmwoods, this vegetation is in an undamaged state. Tree density is fairly high (1520/ha) with mountain beech (51% RD) and southern rata (38%) about 12m high co-dominant over Hall's totara (*Podocarpus*

hallii) (5%) and kamahi (6%). Total basal area is small (60m²/ha) with mountain beech accounting for 68% and southern rata 24%. Mountain beech (26% RD) is much less important among the small trees. Lancewood (*Pseudopanax crassifolium*) (26%) and Hall's totara (14%) are more conspicuous here. Shrub density is 11,900/ha with mountain beech (37% RD) the commonest shrub, followed by *Coprosma lucida* (17%), *Dendrobium cunninghamii* (12%), mingingi (10%) and southern rata (8%). The herb layer is quite dense (17%), being predominantly *Earina autumnalis* which carpets the ground on islands such as these, especially near the forest edge. *Earina* accounts for 16% of the total ground cover, but this figure rises to ca. 80% around the forest edge. Bryophytes form a deep carpet on the ground, dominated by hepatics, species of *Plagiochila*, *Chiloscyphus* and *Lepidolaena*, *Trichocolea mollissima* and the moss *Dicranoloma robustum*. Epiphytes are few in this forest, bryophytes forming only thin epiphytic cushions and ferns such as *Asplenium flaccidum* and *Grammitis heterophylla* occurring infrequently. The mistletoes, *Elytranthe tetrapetala*, *E. flavida* and, to a lesser extent, *Loranthus micranthus* are common on the beech trees.

The beech forests of the islands and mainland are by no means uniform, but vary with slope, soil, exposure and interference by browsing mammals. The beech-rata forest described above is typical of moderate to steep slopes with thin soils on exposed parts of shoreline. Small islands hold beech-rata forest on their sides and tops while slightly larger islands have flat tops where deeper soil supports more beech and less rata (with a canopy at about 18m), fewer orchids beneath, a slightly thinner bryophyte carpet and more litter. On the second largest of the Mahara Islands for example, basal area is still low (51m²/ha) with beech 83% and rata 16% of this. Tree density (979/ha) is lower, probably reflecting the smaller number of multi-leadered trees in the tall forest, while shrub density (15,600/ha) is higher.

Bellevue Island, at the mouth of Circle Cove, supports mountain beech and a few rata which rise only to 5m and in places are very scattered.

This island held only bryophytes and scattered shrubs comparatively recently (Mr B. Murrell, pers. comm.) and it has probably been burnt at some stage. Similar disturbed forest can be seen between Circle Cove and Surprise Bay where an area of about four hectares, up to about 60m above the lake, holds dense manuka scrub. Occasional emergent mountain beech and an abrupt boundary between manuka and beech forest suggest that the manuka is part of a succession back to forest following fire.

Slopes of the largest islands such as Pomona, Rona, and the largest of the Holmwood and Mahara groups hold tall beech with occasional rata, miro, Hall's totara and rimu, with a canopy height and luxuriance approaching that of the beech forest on Buncrana Island, described below.

Podocarps such as rimu, Hall's totara and miro occur throughout the beech forests but they seldom form a major component of the forest. On the eastern shores of Hope Arm, rimu occurs regularly as emergent trees and parts of this forest could be considered as beech-rimu forest. At the eastern mouth of Hope Arm rimu achieves a density of 47/ha but makes up only 4% of the total density of 1250 trees/ha and 15% of the total basal area of 115m²/ha. Kamahi is an important tree here with a relative density of 31% and a relative basal area of 11%.

Precipitous slopes support scattered, stunted mountain beech rooted in crevices or on small terraces, interspersed with shrubs of rata, mingimingi, *Gaultheria rupestris*, and especially *Dendrobium*, and by large mats of *Notodanthonia setifolia*, *Earina autumnalis*, *Phymatodes diversifolium*, *Pyrrosia serpens* and to a lesser extent *Earina mucronata*. The north side of Holmwood Island, which has a slope of ca. 50°, supports mountain beech trees 6-8m high, with a density of 1360/ha but a basal area of only 42m²/ha. Such sites in the wetter, western half of the lake are clothed in colourful bryophyte cushions—red-brown *Chandonanthus squarrosus*, brown and green *Dicranoloma* spp. and the bright yellow *Eucamptodon inflatus*.

Mountain Beech Forest

Buncrana Island rises to 610ft (185.9m), has an area of 5.3ha and is the only island of its type

in Lake Manapouri, being almost flat and composed of morainic outwash. In the absence of browsing animals it supports virgin mountain beech forest (Figs. 5, 6 and Table 2).

Mountain beech trees, rising to 27m, dominate the canopy and form 76% of the total basal area of 115m²/ha. Relative density of mountain beech trees is 66% compared with miro (17%), kamahi (7%), rimu (4%) and lancewood (3%). Small-trees are sparse (301/ha) but again mountain beech (39% RD) dominates lancewood (29%), miro (10%) and several other species, especially kamahi, pokaka and *Myrsine australis*. The dense shrub layer (29,900/ha) is mostly of mountain beech (31% RD), lancewood (23%), *Coprosma lucida* (12%) and bracken, *Pteridium aquilinum* v. *esculentum* (10%). The occurrence of bracken in the beech forests of the islands is rather surprising. Scattered stems arise singly from the deep bryophyte carpet, even under moderately dense canopies and are frequently 4m long.

The herb and sub-shrub tier forms a cover of 11%, most of this being woody, particularly mountain beech (4%), miro (1%) and lancewood (1%). *Phymatodes diversifolium* (2%) is the only conspicuous herb. On the ground mountain beech accounts for almost all of the 3% cover of woody seedlings. Herbs and ferns account for only 1% cover but bryophytes dominated by *Plagiochila* spp. (28%), *Lepidolaena hodgsoniae* (5%), *Lepidolaena* spp. (2%) and *Chiloscyphus* spp. (2%) form coalescing cushions up to 66cm deep.

Mountain beech forest on the mainland adjacent to Buncrana Island is strikingly different (Figs. 5, 7 and Table 2). Mountain beech is almost the sole dominant of the tree and small-tree layers, forming a forest with a canopy again at 27m, with a lower basal area (87m²/ha) and tree density (731/ha) but a higher small-tree density (756/ha).

Density of the shrub layer is strikingly low (8330/ha compared with 29,900/ha on the island). The accompanying floristic change is more startling. Thus on the island, lancewood with a shrub density of 6780/ha, *Coprosma lucida* (3550), bracken (2960), *Myrsine australis*



FIGURE 6. Mountain beech forest on Buncrana Island. The dense shrub layer dominated by beech, lancewood and *Coprosma lucida* indicates little disturbance by browsing animals.

(1240), *Pittosporum tenuifolium* (823), *Pseudopanax colensoi* (735) and *Griselinia littoralis* (295) together account for 55% of the shrubs yet are quite absent from the mainland. Conversely, on the mainland, *Blechnum discolor* (4620/ha), *Histiopteris incisa* (265), *Pseudowintera* (168) and *Myrsine divaricata* (95) account here for 62% of the stems in the shrub layer and are quite absent from the island. Miro shows a decrease in shrub density from island to mainland from 1620 to 48/ha, pokaka and *Pseudopanax simplex* both from 353 to 28/ha, mountain beech 9180 to 1440/ha, *Coprosma foetidissima* 323 to 48/ha and *C. polymorpha* 413



FIGURE 7. Mountain beech forest on the mainland near Buncrana Island. The understory is sparse except for the unpalatable fern, *Blechnum discolor*.

to 120/ha. *Neomyrtus pedunculata* has a similar density on both the island (955/ha) and mainland (843/ha) while *Coprosma propinqua* is more common on the mainland (240/ha compared with 103/ha).

Cover in the herb and sub-shrub tier (5%) is low on the mainland with *Blechnum discolor* contributing most. On the ground the cover of litter (37%) is less than on the island (51%) with the result that the apparent cover of bryophytes is greater (57% compared to 45%). Depth of ground bryophytes averages 18.0cm on the mainland, just half that on the island (36.7cm). *Plagiochila* spp., which form deep cushions, are

less important on the mainland (11% cover against 28%) while *Lepidozia pendulina*, *Trichocolea mollissima* and *Bazzania novae-zelandiae* are more common, these three hepatics tending to interlace cushions of other bryophytes on the island but forming low carpets of their own on the mainland.

Other areas of mainland mountain beech forest have a similar structure. The mainland near Bellevue Island supports forest with a total basal area of 33m²/ha, a tree density of 1380/ha and a shrub density of 14,300/ha—higher than that on the mainland near Buncrana Island but still much lower than that on the island itself. At Surprise Bay mountain beech forest has a total basal area of 93m²/ha, a tree density of 1530/ha and a low shrub density of 6130/ha.

Silver beech occurs rarely throughout the shoreline forests, achieving its greatest importance in riparian stands at the head of Hope Arm. It may be important also at the mouths of the Spey River in West Arm, Awe and Freeman Burns in North Arm—areas that were not studied. Red beech (*Nothofagus fusca*) is absent though a few red x mountain beech hybrids were seen on the mainland near Buncrana Island.

EFFECTS OF INTRODUCED ANIMALS

Most of the above differences between the mountain beech forest of Buncrana Island and the adjacent mainland can be ascribed to browsing mammals, particularly red deer. The floristic change follows the same trend as noted by Holloway (1950) in the forests of western Southland, browsing reducing or eliminating palatable species such as *Coprosma lucida* and favouring an increase in unpalatable ones like *Blechnum discolor*. However there is no evidence that *Coprosma lucida* is less susceptible to reduction by deer than *Neomyrtus* or *Pseudowintera* in the lowland Manapouri forests as inferred by Wardle *et al.* (1971) (from relative tier frequencies) to be the case in the forests of northern Fiordland.

Trampling rather than browsing may be in part responsible for the floristic changes. The ground cover of *Earina* and *Dendrobium* on rocky islands has no counterpart on accessible parts of the main-

land and it is likely that these orchids are sensitive to disturbance of the deep bryophyte cushions in which they usually grow. The floristic differences in ground bryophytes between Buncrana Island and the mainland are undoubtedly related less to browsing than to trampling and an increase in the amount of light reaching the forest floor. Differences in bryophyte depth are certainly a result of trampling. The effectiveness of ungulate hoofs in compacting ground vegetation can be readily appreciated by the longevity—at least six weeks—of human footprints in the bryophytes of Buncrana Island.

The structural differences between island and mainland forests are similar to those recorded by James and Wallis (1969) in a similar situation in a North Island *Nothofagus* forest. They also note less dense shrub and herb layers and a more dense small-tree layer in disturbed mainland forest. The markedly higher small-tree density on the Lake Manapouri mainland may have resulted from release of these small-trees from competition for nutrients or moisture from the dense shrub layer to be seen on the island. However, some cause other than browsing ungulates must be sought for the island to mainland decrease in tree density and basal area.

Beech forest free of deer at 620ft (189m) on Secretary Island (Mark 1963) has a shrub density of 9580 per acre (23,700/ha) which, like that of Buncrana Island, is comparatively high. In contrast, deer-infested beech forest above Lake Thomson at 700ft (213m) (Mark *et al.* 1964) and at the same altitude near Lake Hankinson (Scott *et al.* 1964) have low densities of this same shrub tier, viz. 600 per acre (1480/ha) and 1656 per acre (4090/ha) respectively—similar to those in the mainland forest at Lake Manapouri.

Plant communities other than forest and scrub show no obvious difference between mainland and islands, and would therefore seem less susceptible to modification by browsing mammals. However, during periods of low water, deer feed extensively on *Isoetes* (Mr J. Murrell pers. comm.). Poole (1951) records heavy browse on *Carex gaudichaudiana* where it dominates river valley bogs in the Caswell and George Sounds district. Similar

browse was noted by the author at Lake Te Anau in May 1971 but no grazed plants were seen at Lake Manapouri in the 1969-70 summer.

DISCUSSION

The lack of published information on lake-edge vegetation elsewhere makes evaluation of that at Lake Manapouri difficult. Aquatic vegetation dominated by *Isoetes alpinus* and *Myriophyllum elatinoides* is probably a feature of all the large southern lakes, occurring also at least in Lakes Te Anau, Wakatipu and Wanaka. *Elodea canadensis* has been previously recorded from Lake Manapouri by Mason (1960) but she does not show it as present in any other southern lakes.

Lake-edge turf, *Carex* sward and *Leptocarpus* communities very similar to those at Lake Manapouri occur also at Lake Te Anau but were not seen in the lower third of Lake Monowai by the author in April 1970. This lake, ca. 35km south of Lake Manapouri, was raised about 3.5m in 1925 for hydro-electric purposes. Gentle parts of shoreline there have an early successional appearance with only scattered plants, mainly *Juncus articulatus*, but a dense zone of *J. gregiflorus* behind.

The lake-edge communities have certain affinities with coastal ones and some lake-edge species such as *Leptocarpus* are notable for their disjunct coastal and inland distribution (Burrows 1964).

The forest types of Lake Manapouri have been recorded elsewhere in Fiordland. Near Lake Monowai, Wardle (1953) records mountain-silver beech forest with a canopy at 60 to 70ft (18 to 21m) on terraces and 45ft (14m) on dry exposed lower slopes. He recognises a beech-kamahi forest on less exposed lower slopes with scattered podocarps plus tree ferns. As at Lake Manapouri, the western end of Lake Monowai is floristically richer and Wardle notes *Dacrydium intermedium* here. Poole (1951) records *Dacrydium intermedium*-mountain beech bog forest on a steep spur in the Caswell Sound area. Similar forest, described by Wardle *et al.* (1971) as class M3, occupies shallow, low-fertility soils over a wide altitudinal range in north-west Fiordland and at the heads of Middle and South Fiords of Lake Te Anau.

The mountain beech-southern rata and mountain beech forests at Lake Manapouri most closely resemble class E1 of Wardle *et al.*, this forest occupying the lower slopes on the eastern side of northern Fiordland. The main difference is that the Manapouri shoreline forests contain virtually no silver beech. The dominance of mountain beech may be assisted by low rainfall in the east and by the shallow soils of the steep western slopes.

Holloway (1954, p.401) suggests that the Fiordland forests reflect, both in type and in condition, mainly present environmental conditions. However this does not appear to be so for the areas of swamp-podocarp forest at Shallow Bay and Hope Arm and particularly the hill podocarp stand at Stockyard Cove. In these stands the dominant matai and kahikatea are overmature, there is almost no regeneration of either species, and the associated species include *Pennantia corymbosa* and *Lophomyrtus obcordata*. All these features accord with Holloway's description of relict stands which are out of phase with present climate.

There is no detailed information on the islands of other Fiordland lakes though Kelly (1968), who briefly visited the Dome group in South Fiord, Lake Te Anau, records "a general impression of similarity" and "some of the same phenomena and species" but "failed to find an island which compared in degree with the islands to be lost in Manapouri" (with particular reference to lack of deer damage).

CONCLUSIONS

The locations with respect to natural lake levels of the plant communities described are such that if the lake was held 27.5ft (8.4m) above its natural mean level the herbaceous and almost all the scrub communities would be totally submerged. At this level the lake would be up to 20ft (6.1m) above the present forest edge. Because of the intolerance of most forest species to submergence (Johnson 1972) death of these submerged forests is expected to be fairly rapid. Death of forests for varying distances above a raised lake level is expected also—as a result of raised

water tables and of those factors which have resulted in the present forest edge being considerably above the lake on exposed shores.

Regardless of provisions to clear the lake shore forests the new lake-edge habitat would differ from the natural one in two important respects. Firstly, the lake would be held at its high level for long periods but there would nevertheless be periods of draw-down to the present minimum level. Secondly, the new lake edge would lie on forest soils. Under these conditions re-establishment of the lake-edge communities as they are now is doubtful. Seral species such as wineberry (*Aristotelia serrata*), *Fuchsia excorticata* and water-fern (*Histiopteris incisa*) may become more important for a time. Woody species like manuka and *Coprosma propinqua*, which tolerate long periods of submergence, might increase in importance under a large lake level fluctuation. Aggressive exotic species might establish readily. Finally, many species of the herbaceous lake-edge communities indicate by their local distribution and the small areas over which they grow throughout New Zealand that their ecological requirements are very precise. These species are unlikely to survive a much altered lake level regime.

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