A LOWLAND VEGETATION SEQUENCE IN SOUTH WESTLAND: PAKIHI BOG TO MIXED BEECH-PODOCARP FOREST
PART 2: GROUND AND EPIPHYTIC VEGETATION

G. A. M. SCOTT[1] AND JENNIFER A. ROWLEY[2]

Botany Department, University of Otago, Dunedin

SUMMARY: The quantitative composition of ground and epiphytic vegetation, consisting predominantly of bryophytes, is recorded from a lowland stand of climax beech-podocarp forest at Jacksons Bay, South Westland, together with briefer accounts from five pre-climax transitional stands. A survey of epiphylls, indicators of very high humidity, is included and comparisons are made with stands on Secretary Island and Stewart Island.

INTRODUCTION

In Part 1 (Mark and Smith, 1975) an account has been given of six stands of vegetation considered to represent a sequence, possibly a primary succession, from bog to climax forest on the flood plain of the Arawata and Jackson Rivers in South Westland. The ground strata (< 15 cm in height) and epiphytes, which present particular sampling problems because of the great predominance of bryophytes, are here treated separately as Part 2. The data presented in this part were collected in May 1965 at the same time and in the same stands as those described in Part 1. They are summarised in Tables 1-8. Because of the great cryptogamic richness of climax mixed beech-podocarp forest (Stage 6) most of the time available was spent sampling it, quantitatively, as extensively as possible and the other stages, 1-5, were more cursorily investigated and described:

1. Pakihi bog.
2. Young *Leptospermum scoparium* (manuka) on the fringe of the bog.
3. *Leptospermum* woodland.
4. *Dacrydium colensoi* (silver pine) woodland.
5. Young *Dacrydium cupressinum* (rimu) forest.

As explained in Part 1 the term "pakihi" is a Maori name applied to the bogs in poorly drained forest openings on lowland coastal gravel plains in Westland. Evidence is there presented that this particular bog started in the post-glacial period, 10000 years ago or less, the slowness of the succession being attributed to a combination of unfavourable soil conditions and periodic fires.

METHODS

The methods of recording are similar to those used in previous studies (Scott and Armstrong, 1966; Scott, 1970). In the climax forest, epiphytes were recorded on a basal 2 m of trunk on all trees (>10 cm d.b.h.) up to a limit of 10 trees of each species, encountered in a traverse through the stand. On each tree (phorophyte) the abundance of each species of epiphyte was estimated and these abundance estimates were later converted to approximate mean cover values on a conversion scale which has proved to be reasonably constant in practice (Scott, 1966): dominant = 80%, abundant = 40%, frequent = 15%, occasional = 5%, rare = 1%, present = 0.1%. Ground vegetation in the climax forest was recorded as local frequency (out of 25) in a 5 x 5 grid of contiguous one dm^2 quadrats. This grid was staggered alternately to either side, 200 times, along a rough transect line through the stand. The percentage cover of vegetation and of standing water at the time of sampling were also recorded using the 36 points of intersection of the grid as point quadrats. To fill in the picture of forest cryptogams, collections were taken of epiphylls on the evergreen leaves of those species most prone to

1 Present address: Botany Department, Monash University, Clayton, Victoria, Australia.
2. Present address: Plant Physiology Division, DSIR, Palmerston North.

bear them (Scott, 1971), *Pseudowintera colorata, Pseudopanax crassifolius,* and a few collections of epiphytes were made from minor trees (Table 8).

Provisional names were given to all species and voucher specimens taken for later identification; samples of these are in the OTA Herbarium. The data were transferred to punch cards and processed on Monash University's Burroughs B6700 computer. Mean abundance figures and 95% Confidence Intervals for each species on the ground and on each species of phorophyte were then calculated. The accuracy of the confidence limits is questionable (Scott, 1970) but they do give an idea of the degree of precision of the mean and have been tabulated instead of the mean wherever they appear to be meaningful and therefore useful. This limit of usefulness is arbitrarily fixed at the level where the lower confidence interval is not less than 0. When the confidence limits are wider than this, the mean has been expressed only in broad terms, in four categories (c.f. Scott and Armstrong, 1966). The number phorophytes on which each species of epiphyte occurs is also recorded where appropriate.

Once again, as in previous surveys, no attempt was made to sample the epiphytes of small shrubs or fallen branches, or of trees and branches above 2 m, all of which present severe problems (Scott, 1971).

In Stages 3-5 only estimates of the relative abundances of the commonest species were made. In Stages 1 and 2 the vegetation was sampled by the party responsible for the sampling of the principal strata (Mark and Smith, 1975), using 5000 point quadrats arranged in 50 blocks of 100 points.

TAXONOMY

Nomenclature follows Sainsbury (1955) for mosses, except where otherwise stated, and Hamlin (1972) for liverworts, Allan (1961) for vascular plants. Authorities for lichen names are in the tables. Where the nomenclature conflicts with names used in previous papers on New Zealand forest cryptogams (Scott and Armstrong, 1966; Scott, 1970) the names used in earlier papers have been given in brackets as cross references. As always, certain groups of species are particularly prone to misidentification and confusion in the field, and data for these may have to be pooled or at least the differences between them treated with scepticism. These groups are particularly: *Metzgeria* spp., *Plagiochila deltoidea* and *sinclairii, Macromitrium* spp., *Chiloscyphus* spp. especially *coalitus* and *cuneistipulus, Telaranea tetradactyla* and *gottscheana.*

In the genus *Riccardia,* where the New Zealand species are not yet properly understood, accurate species names have been beyond us and we have had to resort to mere statements of affinity and file specimens for later references.

RESULTS

Stage 1. Pakihi bog

Despite the dense mat of *Calorophus* dominating much of the bog surface (52% cover) and even though 22% of the bog surface lay under water at the time of sampling, the masaic of vegetation is sufficiently varied for a considerable range of other plants to develop. Especially abundant is *Dicranoloma billardieri* which is almost everywhere (66% cover). A similar form of this polymorphic species or species-aggregate is found elsewhere in semi-aquatic or boggy habitats, e.g. in alpine cushion bogs.

Stage 2. Young Leptospermum

The slightly increased stability and maturity round the edge of the bog allows the development of much more *Sphagnum falcatulum* (28.5%) and a wider range of vascular plants. *Dicranoloma billardieri* was correspondingly greatly reduced.

Stage 3. Leptospermum *woodland*

The ground cover here is very fragmentary and confined to small gaps in the dense carpet of *Gleichenia* fronds and *Leptospermum* twigs, mainly where there are pools with *Sphagnum* and associated species. The epiphytes too are very sparse, partly because of the crowding of the trees and partly because the *Leptospermum* bark sloughs off continually. Only *Radula physoloba* seems able to cope with the ecological problems of epiphytic growth in these conditions and even it is almost confined to a zone halfway up the trunks. Below that, the older bark of the tree-base flakes off too much for even the tightly spreading fingers of *Radula* to hold in position; above it, the trunks are too concealed from both light and rain to be readily colonised.

Stage 4. Dacrydium colensoi *woodland*

The much more open and less exclusive woodland of this stage permits a quite different although still restricted ground flora to develop, characterised especially by *Lycopodium ramulosum* and by the advent of the large hepatics and mosses which are a striking feature of later stages: *Lepidozia microphylla, Hypnodendron* spp., *Ptychomnion aciculare,* etc. The bark of *Dacrydium* is a long-lasting stable habitat which supports a much richer flora of epiphytes than on *Leptospermum*, including several filmy ferns. The clasping growth form of *Radula*, so necessary for *Leptospermum* bark, is here a rarity.

Stage 5. Young Dacrydium cupressinum *forest*

The tendencies apparent in the previous stage become much more prominent in this stage: large mosses and liverworts, mostly of an erect growth form, predominate on the forest floor, especially *Lepidozia microphylla, Plagiochila gigantea, Hypopterygium novae-zelandiae*, and mosses of dendroid growth form which are abundant in the climax forest. The forest is still open enough and young enough for *Sphagnum* to be abundant.

On the *Dacrydium* trunks the epiphytes too are greatly increased in diversity and abundance and are rather similar to those in the climax forest. The abundance of *Plagiochila annotina, Lepidozia microphylla*, and *Trichomanes reniforme* and *Hymenophyllum multifidum* are distinctive features.

Stage 6. Climax forest

As can be seen from Tables 5-8, this is a very rich and varied forest floristically, with a greatly increased species list but with a strong general similarity to the preceding stage. At a casual glance the ground flora differs in the abundance of *Hypnodendron* spp., the replacement of *Sphagnum* by *H. marginatum* in the innumerable pools over the forest floor, and the still further increase in the preponderance of large erect bryophytes such as *Schistochila, Pterygophyllum, Tylimanthus*, etc. The hanging fish-bone fronds of *Mastigophora flagellifera* are a striking feature of the epiphytic vegetation and *Trichocolea mollissima* and *Lepidolaena clavigera*, which have rather similar growth forms too, are much more abundant than in earlier stages, while *Lepidozia microphylla* ceases to be an abundant epiphyte. A curious feature is the switch from *Hymenophyllum multifidum* to *H. sanguinolentum* as the predominant filmy fern. A further and most noticeable feature of this stand of forest is the abundance of epiphylls (Table 7), i.e. epiphytes on the leaves of various species, notably the long-lived *Pseudowintera colorata* and *Pseudopanax crassifolius*.

In this dense, perpetually humid forest of high and consistent rainfall the differences between epiphytes and ground flora are minimal and a striking feature of the ground flora is the commonness of species which, elsewhere, are obligate epiphytes, such as *Goebeliella cornigera, Mastigophora flagellifera, Marsupidium knightii*. This may be explained mainly by the provision of suitably moist habitats for the long-term persistence of epiphytes which fall to the forest floor.

Physiognomically, too, the forest at this stage is much more varied and shows several of the classic features diagnostic of rain forest: abundance of lianes (e.g. *Metrosideros* spp., filmy ferns *(Hymenophyllum* and *Trichomanes)* and epiphylls (Table 7).

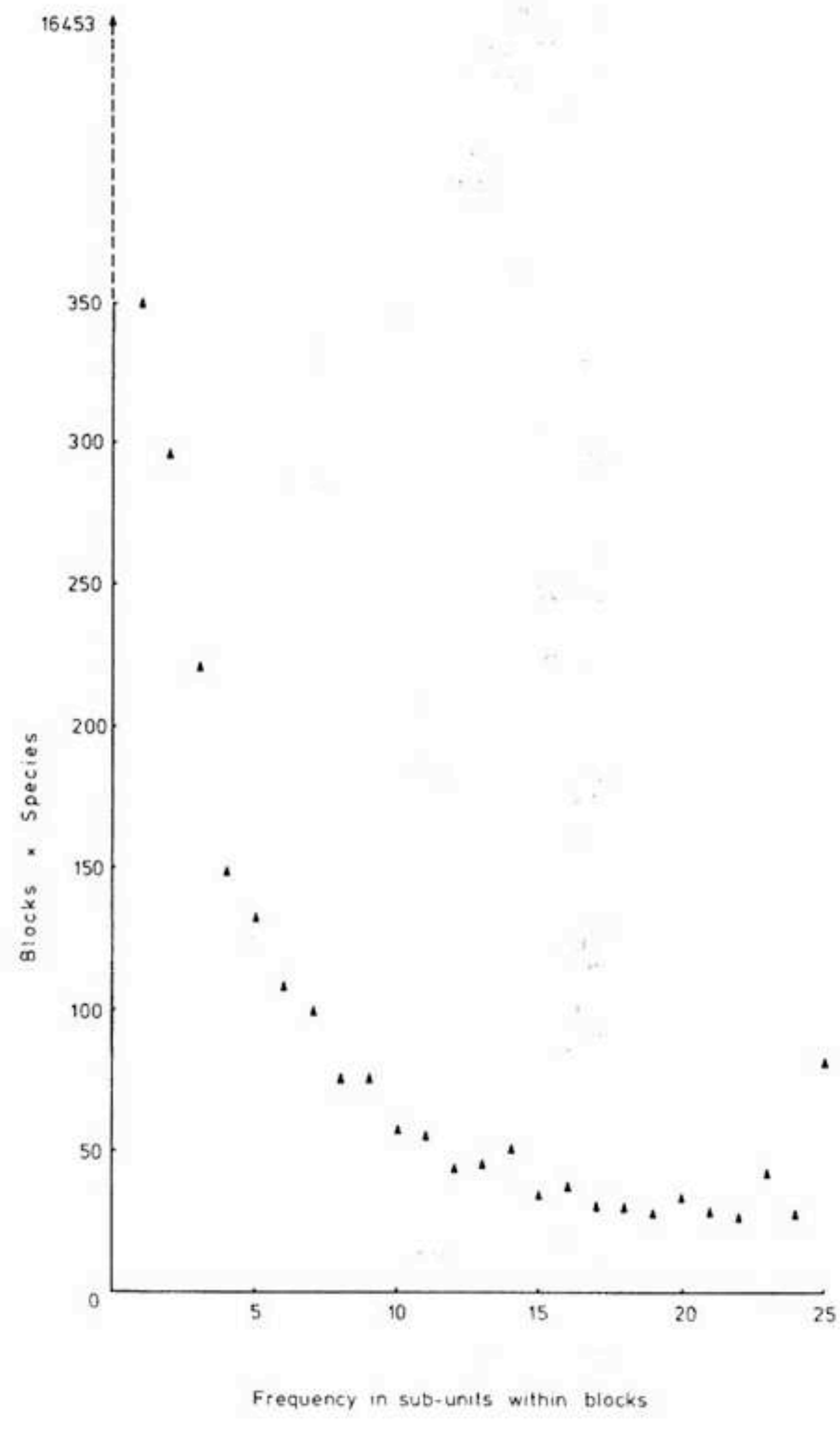

FIGURE 1. *Frequency distribution of scores out of 25 subunits for 99 species over 200 blocks (see text).*

TABLE 1. *Principal ground species of 5 stages in the transition from pakihi bog to climax forest at Jackson Bay, South Westland; May 1965. The 5 stages (columns) are:— 1: open pakihi bog. 2: young colonising* Leptospermum. *3:* Leptospermum *woodland. 4:* Dacrydium colensoi *woodland. 5: Young* Dacrydium cupressinum *forest. Species which are also found in the climax forest, either on the ground or as epiphytes, are marked accordingly in column 6.*

Figures are for cover values; those in columns 1 and 2 are based on 5000 points; the others are visual estimates in the classes: dominant, very abundant, abundant, frequent, occasional, rare, just present (+). Where species are also found as epiphytes they are marked "e" in the appropriate column.

Vascular Plants	*1*	*2*	*3*	*4*	*5*	*6*
Lycopodium ramulosum	1	0.5		a		
Nertera dichondraefolia	+	+			f	GE
Blechnum minus		+	r	o	f	GE
Hypolaena sp.		a				
Hymenophyllum multifidum			r	(e)	f(e)	GE
Libertia pulchella				o	f(e)	GE
Trichomanes reniforme					o(e)	GE
Lycopodium scariosum					o	
Mosses						
Dicranoloma billardieri	65.9	12.9	r	f	(e)	GE
Sphagnum falcatulum	3.1	28.5				
S. cristatum		0.7	f	a	a	
Wijkia (Acanthocladium) extenuata (*Brid.*) *Crum.*			r		(e)	GE
Hypnodendron (Mniodendron) comosum (*Labill.*) *Mitt.*				o	f(e)	GE
H. (Sciadocladus) menziesii (*Hook.*) *Par.*					f(e)	GE
Pterygophyllum quadrifarium					f	GE
Ptychomnion aciculare				f(e)	va(e)	GE
Hypopterygium novae-seelandiae					o	GE
Liverworts						
Riccardia ?striolata	1.0	1.3				
R. ?alcicornis	0.4	4.2				
Kurzia hippuroides	+		o			
Zoopsis caledonica		2.5				E
Lepidozia glaucophylla		1.6				
Telaranea gottscheana		0.1	f			GE
Lepidozia kirkii		+	o	+		E
Tetracymbaliella decipiens		+	o	o		
Chiloscyphus billardieri		+	+	+(e)	o(e)	GE
Bazzania novae-zelandiae				o		
Riccardia oppositifolia			f	(e)	+	G
Lepidozia pendulina			o	f	a	GE
Trichocolea mollissima			+	o	o(e)	GE
Tylimanthus saccatus					f	GE
Lepidozia microphylla				a(e)	d(e)	GE
Schistochila nobilis				o(e)	a(e)	GE
S. glaucescens				o	o	GE
Lepicolea scolopendra				+(e)	(e)	GE
Plagiochila gigantea					f	GE

TABLE 2. *Principal epiphytic species of 5 stages in the transition from pakihi bog to climax forest at Jackson Bay, South Westland; May 1965. Details as in Table 1. Species also found in ground vegetation are marked "g" in the appropriate column.*

Vascular Plants	*1*	*2*	*3*	*4*	*5*	*6*
Hymenophyllum multifidum			(g)	a(g)	f–a	GE
H. rarum			(g)	o	r	
H. armstrongii			(g)	f	o	E
Trichomanes reniforme				r	a	GE
Grammitis billardieri				+	o	GE
Lycopodium billardieri					f	GE
Hymenophyllum revolutum					o	GE
Tmesipteris tannensis					o(e)	E
Hymenophyllum scabrum					o	GE
Mosses						
Macromitrium longipes				o		E
Ptychomnion aciculare				+(g)	g(g)	GE
Dicranoloma menziesii				+	f	E
D. billardieri	(g)	(g)	(g)	(g)	o	GE
Hypnodendron comosum (*Labill.*) *Mitt.*				(g)	o	GE
H. menziesii (*Hook.*) *Par.*					o(g)	GE
Wijkia extenuata (*Brid.*) *Crum.*				r	o	GE
Hypopterygium novae-seelandiae					f(g)	GE
Weymouthia cochlearifolia			(g)		f	GE
Zygodon hookeri + intermedius					o	GE
Liverworts						
Radula physoloba			f	+		
Lepicolea scolopendra				a	f	GE
Schistochila tuloides				f	o	E
Riccardia oppositifolia				o		G
Lepidozia microphylla				o(g)	f–a(g)	GE
Chiloscyphus billardieri		(g)	(g)	+(g)	o(g)	GE
Trichocolea mollissima			(g)	(g)	f(g)	GE
Bazzania adnexa				+	f	GE
Schistochila nobilis				(g)	o(g)	GE
Radula caespitosa?				+	o	GE
Chiloscyphus chlorophyllus				+	o	E
Plagiochila pleurata				+	o	GE
Acrobolbus lophocoleoides				+	o	E
Plagiochila annotina					va	
Schistochila pinnatifolia					o	E
Mastigophora flagellifera					o	GE
Lichens						
Sticta glabra *Hook. f. & Tayl.*					o	G
Sphaerophorus melanocarpus *DC.*				f	o	E

TABLE 3. *Minor ground species in transitional forest at Jackson Bay, South Westland; May 1965. Details as in Table 1.*

Vascular Plants	*1*	*2*	*3*	*4*	*5*	*6*
Herpolirion novae-zelandiae	r					
Liparophyllum gunnii	r					
Gaimardia ciliata	r	r	r			
Nertera depressa	r	r	r			GE
Drosera spathulata	r	r				
Utricularia sp.	r	+				
Thelymitra longifolia	+	+				
Coprosma foetidissima		+				GE
Dacrydium colensoi		+				
Schizaea fistulosa		+				
Dacrydium cupressinum		+				E
Neomyrtus pedunculata		+				GE
Coprosma colensoi		+				GE
Pseudopanax colensoi		+				GE
Phyllocladus alpinus		+				GE
Hymenophyllum rarum			+	(e)	(e)	
H. armstrongii			+	(e)	(e)	E
Luzuriaga parviflora				r	r	GE
Mosses						
Hypnum cupressiforme	+		(e)			GE
Campylopus introflexus	+	+				
Dicranoloma fasciatum			+			
Distichophyllum pulchellum					+(e)	GE
Liverworts						
Kurzia allisonii	+					
Pallavicinia tenuinervis	r	+				
Temnoma corrugatum	+	r				
Saccogynidium australe	+	r				
Telaranea spinosissima		r				G
Lepidozia concinna		r				G
Bazzania adnexa			+			GE
Telaranea tetradactyla			+			G
Geocalyx novae-zelandiae			+			

TABLE 4. *Minor epiphytic species in transitional forest at Jackson Bay, South Westland. Details as in Table 2.*

Vascular Plants	*1*	*2*	*3*	*4*	*5*	*6*
Libertia pulchella				(g)	r	GE
Asplenium flaccidum					r	GE
Lycopodium volubile					+	GE
Mosses						
Hypnum cupressiforme	(g)		+			GE
Sematophyllum subcylindricum				r	+	GE
Holomitrium perichaetiale				+		E
Dicnemon calycinum				+		GE
Campylopus clavatus				+		
Distichophyllum pulchellum					r	GE
Cyathophorum bulbosum					r(g)	GE
Liverworts						
Harpalejeunea colensoi			+	+		
Lopholejeunea colensoi			+			
Metzgeria saccata			+			
Diplasiolejeunea lyratifolia			+			
Frullania aterrima + rostrata			+	+		
F. adeplanata			+			
Lejeunea sp.			+	+	+	
Goebeliella cornigera			+	+		G
Marsupidium knightii				r		G
Herberta alpina				r	r	E
Lepidozia kirkii		(g)	(g)	+(g)		E
Acromastigum anisostomum				+	+	
A. integrifolium				+		
Frullania ptychantha				+		E
Lepidolaena ?palpebrifolia				+		
Radula multiamentula				+		
Tetracymbaliella cymbalifera				+		
Radula uvifera				+		E
Acrochila biserialis				+		E
Leptoscyphus australis				+		
Adelanthus falcatus				+		E
Acromastigum cavifolium				+		
Cuspidatula monodon				+		G
Metzgeria ?hamata					+	GE
Radula buccinifera					+	
Lepidolaena clavigera					+	GE
Chiloscyphus hastatus					+	
Blepharidophyllum xiphophyllum					+	
Lichens						
Sphaerophorus tener *Laur.*				+		E
Stereocaulon sp.				+		
Sticta sp.					r	

TABLE 5. *Abnudance of main species of epiphytes and ground vegetation in climax beech-podocarp forest at Jackson Bay, South Westland; May 1965. Abundance figures for epiphytes, on 5 species of phorophyte, are mean estimated % cover in three classes (√ = % cover, * = 1.1–5%, * * = 5.1–25%) together with the number of phorophyte trunks on which recorded. Where the 95% confidence limits of mean cover rates are sufficiently narrow (see text) they are given* (**bold type**) *instead of abundance classes. Abundance figures for ground species are % frequency in 10 × 10 cm quadrats, in 200 half metre square blocks of 25 (see text). Symbols are for epiphytes, together with the number of blocks in which each species was present.*

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
No. of trunks/quadrats sampled	10		10		10		10		5		200	
Total no. of species Tables [5, 6]	91		101		59		44		33		118	
Mean no. moss spp./tree [5, 6]	9.0		6.0		6.0		1.7		1.2		2.7	
Mean no. liverwort spp./tree [5, 6]	10.2		10.4		5.8		5.6		6.6		4.8	
Mean no. all spp./tree [5, 6]	28.8		28.0		20.1		12.4		12.6		11.7	
Phanerogams												
Coprosma colensoi	√	1	√	2	√	1					**0.3–1.4**	15
Dacrycarpus dacrydioides			√	2							**0.1–0.5**	10
Eleocarpus hookerianus			√	1							**0.1–0.8**	99
Libertia pulchella			√	2			√	2			**0.9–2.5**	21
Luzuriaga parviflora	√	4	√	3							**0.6–1.8**	17
Metrosideros diffusa											**4.3–7.5**	63
M. hypericifolia	**0.4–1.0**	7	**0.1–0.9**	5	**1.0–1.0**	10	**0.2–1.0**	6				
M. scandens	**0.4–1.0**	7	**0.1–0.9**	5	√	1	**0.2–1.0**	6	√	2	**1.1–3.1**	28
Neomyrtus pedunculata			√	1			√	1			**1.2–3.2**	24
Nertera depressa	√	2									**4.1–8.2**	53
N. dichondraefolia	√	4	√	2	**0.4–1.0**	7					**16.3–22.8**	121
Phyllocladus alpinus			√	1							**0.1–0.6**	8
Podocarpus ferrugineus	√	2	√	3	√	1	√	1			**0.2–0.8**	17
Pseudopanax anomalum											√	2
P. colensoi	√	2	√	2							**0.1–0.6**	10
Ripogonum scandens			√	1	√	3	√	1	√	1	**1.4–2.6**	48
Uncinia rupestris											**2.1–4.4**	37
Ferns												
Asplenium flaccidum	√	1	*	3	*	5	√	1			√	1
Blechnum capense					√	2					**0.3–1.6**	13
B. minus	*	3	√	1	*	5	√	1			**3.0–5.8**	56
Grammitis billardieri	*	7	**1.0–7.4**	8			**1.6–9.4**	7	√	2	**0.3–1.1**	14
Hymenophyllum armstrongii			√	1					*	3		
H. multifidum	√	2	√	4							**0.3–1.6**	13
H. revolutum	* *	6	**3.0–5.4**	10	√	1	**6.5–29.5**	9	* *	4	**0.2–0.9**	13
H. sanguinolentum	*	4	**3.0–12.4**	9	**1.3–4.9**	7	* *	4	*	2	**8.1–12.8**	93
H. scabrum	* *	2	√	1	* *	6			*	1	√	1
Rumohra adiantiformis	* *	5	√	2	*	3					√	1
Trichomanes reniforme	**17.1–41.9**	8	* *	7	* *	7			*	3	**0.4–2.2**	14

TABLE 5. (*Cont.*)

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
Mosses												
Cyathophorum bulbosum	√	2	*	4	*	3	√	1	√	1	√	66
Dicranoloma menziesii	**0.6–4.0**	7	**0.5–3.5**	8	√	2	*	3	√	2		
D. platycaulon	√	1	*	3							√	1
Distichophyllum pulchellum	√	3	*	4	√	1					√	4
Fissidens tenellus	√	3			*	3						
Hypnodendron (Mniodendron) comosum (*Labill.*) *Mitt.*	*	4			√	2					√	6
H. marginatum											**4.5–9.9**	36
H. menziesii (*Hook.*) *Par.*	√	1									**12.5–19.2**	88
Hypnum cupressiforme	√	1	√	1							√	1
Hypopterygium novae-seelandiae	**2.5–9.7**	9	*	6	**3.6–11.4**	9	√	1			**14.0–21.0**	99
Leucobryum candidum	√	4	*	4			*	3			√	3
Lopidium concinnum	*	9	√	2	**1.7–7.7**	9			√	1		
Plagiothecium denticulatum	√	1			*	3						
Pterygophyllum quadrifarium	√	3	√	1	√	1					**13.1–19.1**	115
Ptychomnion aciculare	*	5	*	4	*	4	*	3	√	1	**28.5–38.6**	120
Rhacopilum strumiferum					*	6						
Sematophyllum amoenum	√	1									**0.1–0.3**	8
Thuidium furfurosum v. sparsum	√	3	√	1	**0.8–4.4**	6					**0.8–2.7**	20
Weymouthia cochlearifolia	**1.9–7.7**	10	*	4	**0.6–4.0**	7	√	1	√	1	√	2
Wijkia (Acanthocladium) extenuata (*Brid.*) *Crum.*	*	3	*	4	√	1	*	4			√	11
Zygodon intermedius	**1.1–4.5**	8	√	1	√	2						
Liverworts												
Acrobolbus lophocoleoides	√	3	√	1			*	3	√	1		
Acrochila biserialis			√	1			*	1	*	1		
Bazzania adnexa	√	5	**2.4–7.8**	9			*	4	*	3	√	4
Chiloscyphus chlorophyllus	*	3	√	1					√	1		
C. coalitus			√	1							**4.6–8.2**	74
C. cuneistipules			√	1							**0.3–0.9**	16
C. lyallii											*	12
Lepicolea scolopendra	* *	3	* *	3			*	1			√	5
Lepidolaena clavigera	**15.8–34.2**	10	* *	7	**8.0–41.0**	10					√	2
Lepidozia kirkii			*	1								
L. microphylla	*	4	√	2	√	1	√	1			**46.3–57.2**	160
L. pendulina	√	1	*	6	√	1	√	2			**31.3–41.7**	133
L. procera							*	5	* *	4	√	2
Mastigophora flagellifera	**5.1–37.9**	9	**6.5–42.5**	9	*	4	*	3	*	2	√	1
Metzgeria hamata	*	7	√	4	**7.7–26.3**	10					√	1
Plagiochila annotina	**1.2–9.4**	7	* *	8	**2.0–11.0**	7					√	1
P. deltoidea	*	1			*	1	√	1			√	6
P. gigantea			*	1							**8.8–16.1**	60

TABLE 5. (*Cont.*)

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
P. pleurata	√	1	√	1			**3.6–13.6**	8	**2.2–15.8**	5	√	5
P. retrospectans											*	10
P. sinclairii	*	2	*	1							√	6
P. stephensoniana					**6.5–42.5**	9					√	3
Podomitrium phyllanthus							*	1				
Radula caespitosa	*	4	√	3	√	2			**	2	√	1
R. levieri	*	4			√	2						
Schistochila appendiculata											**0.3–1.7**	14
S. nobilis	√	4	√	3							**16.7–23.0**	123
S. pinnatifolia	√	1	*	5			√	2	*	4		
S. tuloides	√	3	*	4			√	1	*	5		
Symphyogyna hymenophyllum			√	1			*	1				
Telaranea gottscheana							*	1			√	3
Trichocolea mollissima	**4.5–13.7**	9	**4.3–13.7**	8	*	4	**4.4–24.8**	10	**	2	**5.2–9.1**	81
Tylimanthus saccatus			√	2							**24.2–33.3**	127
T. tenellus	√	3					**1.8–5.2**	7	√	1	**0.3–1.1**	15
Zoopsis argentea	√	1	*	4							√	4
Lichens												
Brown Psoroma	*	6	√	1	√	1						
Sticta filix *Nyl.*	**0.8–4.0**	8	*	5	√	5	*	4	√	1	√	8
S. fragillima *Bab.*	√	1	√	1	*	3						
S. glabra *Hook. f. & Tayl.*	*	3	**2.2–5.2**	9	√	1	*	2	√	1		

TABLE 6. *Minor species of epiphytes and ground vegetation in climax beech-podocarp forest at Jackson Bay, South Westland; May 1965. Figures refer to the numbers of phorophytes or blocks of 25 quadrats for which each species was recorded, as in Table 5.*

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
Phanerogams												
Ascarina lucida											√	1
Astelia nervosa											√	5
Coprosma ciliata					√	1					√	2
C. foetidissima			√	1							√	1
C. lucida			√	1								
Dacrydium cupressinum			√	2			√	2				
Dendrobium cunninghamii	√	1	√	2					√	1		
Dianella intermedia											√	1
Griselinia litoralis			√	2							√	6
Hedycarya arborea					√	2					√	1
Microlaena avenacea					√	1						
Myrsine australis	√	1			√	2						
M. divaricata											√	3
Nothofagus menziesii	√	1	√	2								
Pseudopanax crassifolius	√	1	√	3	√	2						
Weinmannia racemosa	√	1					√	2			√	11
Ferns											√	3
Asplenium bulbiferum					√	2					√	10
Blechnum discolor	√	1			√	1					√	5
Dicksonia squarrosa	√	1										
Gleichenia cunninghamii	√	1	√	1	√	1					√	1
Grammitis heterophylla			√	1							√	1
Lindsaea trichomanoides			√	1								
Lycopodium billardieri											√	1
L. volubile	√	1			√	2					√	1
Phymatodes diversifolium											√	1
Polystichum richardii											√	1
Pyrrosia serpens	√	1	√	2			√	2	√	1		
Tmesipteris tannensis												
Mosses	√	1									√	1
Bryum billardieri	√	1										
Catagonium politum	√	1									√	2
Cladomnion ericoides			√	1							√	2
Dicnemon calycinum												
Dicranoloma billardieri &	√	2	√	1							√	1
robustum			√	3								
Holomitrium perichaetiale	√	2										
Macromitrium erosulum			√	1								
M. longipes			√	1								

TABLE 6. (*Cont.*)

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
M. prorepens			√	2							√	2
Papillaria flavo-limbata											√	1
Rhacocarpus humboldtii		√	√	2								
Rhizogonium novae-hollandiae											√	1
Rhynchostegium tenuifolium	√	2										
Trachyloma planifolium	√	3	√	2	√	1	√	1			√	2
Weymouthia mollis												
Liverworts												
Acrobolbus cinerascens	√	3	√	1								
Acromastigum colensoanum			√	1							√	1
Adelanthus falcatus			√	2								
Archilejeunea olivacea					√	2						
Bazzania convexa			√	1			√	2			√	2
Chiloscyphus billardieri			√	2							√	9
C. multispinus	√	1	√	1								
C. triacanthus	√	2	√	1	√	2						
Cololejeunea laevigata											√	1
Cuspidatula monodon											√	1
Frullania ptychantha			√	1								
Goebeliella cornigera											√	1
Herberta alpina	√	2										
Hymenophyton flabellatum					√	1						
Lepidolaena palpebrifolia											√	2
L. reticulata			√	1							√	2
L. taylorii											√	7
Lepidozia concinna											√	1
Lophocolea cf. helmsiana	√	1										
L. muricata											√	2
Marsupidium epiphytum			√	1								
M. knightii											√	4
M. setulosum									√	1		
Megaceros sp.											√	2
Metzgeria atrichoneura											√	3
M. colensoi	√	1										
Plagiochila circumdentata	√	1										
P. fasciculata	√	1			√	1					√	2
P. ramosissima	√	1										
Plagiochilion conjugatum			√	2								
Porella elegantula	√	1									√	2
Psiloclada clandestina	√	1										
Ptychanthus securifolius			√	1								
Radula buccinifera					√	1						

TABLE 6. (*Cont.*)

Phorophyte:	Dacrydium cupressinum	No. of trunks	Nothofagus menziesii	No. of trunks	Dacrycarpus dacrydioides	No. of trunks	Dicksonia squarrosa	No. of trunks	Weinmannia racemosa	No. of trunks	Ground	No. of blocks
R. uvifera & physoloba									√	1		
Riccardia cf. lobulata											√	3
R. cf. oppositifolia											√	6
R. cf. pinguis											√	3
Schistochila glaucescens											√	4
Symphyogyna subsimplex							√	1				
Telaranea longiscypha	√	1					√	1			√	3
T. spinosissima											√	1
T. tetradactyla											√	7
Temnoma pulchellum											√	6
Thysananthus anguiformis			√	1								
Zoopsis caledonica	√	1	√	1								
Lichens												
Sphaerophorus melanocarpus *DC*			√	4					√	1		
S. tener *Laur.*			√	2					√	1		

TABLE 7. *Epiphylls on leaves of* Pseudopanax crassifolius *and* Pseudowintera colorata *in climax forest at Jackson Bay, South Westland.*

Mosses	*Pseudopanax*	*Pseudowintera*	
Camptochaete ?ramulosa	1	—	—
Daltonia angustifolia	1	—	—
Glyphothecium sciuroides	1	—	—
Hampeela alaris	3	—	—
Macromitrium ?erosulum	2	—	—
Papillaria ?nitens	1	—	—
P. ?flavolimbata	—	—	1
Sematophyllum ?amoenum	4	5	1
Trachyloma planifolium	—	1	—
Wijkia extenuata	—	1	—
Liverworts			
Cololejeunea cucullifolia	1	—	—
C. laevigata	81	54	21
Diplasiolejeunea lyratifolia	12	—	—
Frullania aterrima	17	2	—
Harpalejeunea colensoi	5	1	—
Goebeliella cornigera	1	1	—
Lejeunea sp.	—	1	—
Lepidolaena clavigera	—	—	1
L. taylorii	—	5	1
Lopholejeunea colensoi	2	—	—
Metzgeria ?hamata	1	—	—
M. colensoi	1	—	—
Microlejeunea cucullata	1	1	—
Plagiochila pleurata	4	4	3
Radula physoloba	2	—	—
Radula sp.	1	4	—
Strepsilejeunea tereticalyx	1	—	—
Lichens			
Bacidia apiahica (*Muell. Arg.*) *Zahlbr.*	2	—	—
Parmelia c.f. thysanota (*Stirt.*) *Zahlbr.*	1	—	—
Pseudocyphellaria sp.	1	—	—
P. glabra (*Hook. f. & Tayl.*) *Dodge*	3	—	—
Psoroma sphinctrinum (*Mont.*) *Nyl.*	1	—	6
Psoroma sp. (*025258*)	—	—	2
Sticta episticta *Nyl.*	—	—	1
Strigula elegans (*Fee*) *Muell. Arg.*	20	—	—
Fungi (*Ascomycetes*)			
Trichopeltheca asiatica *Bar. Costa & Cif.* (*det. R. R. McNabb*)	81	29	—

DISCUSSION

Distribution Curves

Experience has shown (Scott, 1966) that, in the dark, wet conditions of New Zealand rain forest, recording accurate cover values of individual species using point quadrats may often be beyond the physical limitations of human eyesight. There is therefore no alternative to frequency as a measure of cryptogam performance in such cases. Local frequency, in sub-units of a divided sampling unit, gives a more sensitive measure which converges on the actual cover values as the size of the sub-unit decreases. The data, however, are statistically intractable since, far from being even approximately normal, they form almost the inverse of a normal distribution. The ground samples in Stage 6 are sufficiently numerous to show this very clearly. From each of 99 species recorded in the field (i.e. excluding those added to the records by laboratory examination of voucher specimens) there are 200 scores, each out of 25 quadrat sub-units. The actual figures recorded are plotted in Figure 1, where the curve is smoothed by pooling and averaging adjacent values; this shows a clearly J-shaped curve. The rise in the tail of the curve is caused by the accumulation in the last few categories, 23, 24, 25, of a whole range of possible plant densities from 1 individual per sub-unit to many hundreds, i.e. all these high levels of distribution have been telescoped into the upper few categories (Greig-Smith, 1964). Because of the long species list and the large number of rather rare species there is an enormous preponderance of zeros in which two quite separate categories are confounded (Pielou, 1969): those that are ecologically significant (i.e. where the space is uninhabitable because the plant is excluded for some good ecological reason) and those that are irrelevant (i.e. where the space is habitable and the plant is absent merely by chance). Most zeros of rare species of low frequency must fall into the latter category, and at least some zeros of abundant species must fall into the former. There is no way of separating them. The distribution is closer to a Poisson than a Normal but is sufficiently remote from either to make statistical tests of dubious validity, and no amount of transformation will normalise it. The statistics of J-shaped distributions might well repay further work since it is evident that much ecological data will be of this type.

Substrate

Analysis of the data in Tables 5 and 6 show, as might be expected, that it is the commoner species

TABLE 8. *Epiphytes on sub-canopy trees in climax mixed forest stand at Jackson Bay, South Westland; May 1965. Presence/absence data from varying numbers of individuals.*

Phorophyte:	*Ripogonum scandens*	*Neomyrtus pedunculata*	*Myrsine divaricata*	*Elaeocarpus hookerianus*
Ferns				
Grammitis billardieri	*	*		
Hymenophyllum armstrongii			*	*
H. minimum		*		
Mosses				
Cladomnion ericoides			*	
Dicnemon calycinum		*	*	*
D. semicryptum				*
Dicranoloma menziesii		*		*
Glyphothecium sciuroides	*			
Holomitrium perichaetiale		*		
Macromitrium longipes			*	*
M. prorepens		*		
Papillaria flavo-limbata		*		
Sematophyllum amoenum	*		*	*
Weymouthia cochlearifolia	*			
W. mollis		*		
Wijkia extenuata (*Brid.*) *Crum.*	*			
Liverworts				
Bazzania adnexa			*	
Chiloscyphus chlorophyllus			*	*
Cololejeunea laevigata			*	*
Cuspidatula monodon		*		*
Frullania rostrata		*	*	*
Harpalejeunea colensoi				*
Lepicolea scolopendra	*	*	*	*
Lepidolaena clavigera	*			
L. taylorii	*		*	*
Marsupidium knightii		*		*
Mastigophora flagellifera	*			
Metzgeria hamata	*			
Plagiochila annotina				*
P. deltoidea	*			
P. pleurata	*	*	*	*
Porella elegantula		*		
Ptychocoleus securifolius		*		
Radula physoloba		*	*	*
Schistochila tuloides	*	*	*	*
Thysananthus anguiformis			*	
Trichocolea mollissima			*	
Lichens				
Brown Psoroma (*024918*)	*	*	*	*
Sticta sp. (*024939*)	*	*	*	*

which tend to be more tolerant ecologically and to occur both on the ground and as epiphytes. Thus 61/68 of the ground species in Table 5 (common species) are found also as epiphytes, but only 23/50 of those in Table 6 (rarer species). The biggest difference between the two tables in this respect is with the liverworts, of which only 7 out of 46 rarer species are found both as epiphytes and on the ground. No doubt this difference in ecological amplitude is at least partly a reflection of the less open conditions on the forest floor providing fewer habitats for rarer and less dominant species. The mean ground cover of bryophytes in the climax forest is 61% (95% C.I. 56-66) and that of standing water 22% (95% C.I. 19-25), which leaves only 17% available for vascular plants and any open ground. Evidently this is a closed community into which rarer species might find it particularly hard to gain entrance.

The data do not permit conclusions on the restrictions of species to separate niches on the forest floor, with one exception. There is an evident correlation in the field between standing water at the time of this survey and the distribution of *Hypnodendron marginatum*. Since the cover of water was recorded for each quadrat, a correlation between that and abundance of *Hypnodendron* can be calculated. The linear regression of *Hypnodendron* frequency on water cover is highly significant at the 0.01% level and there is no doubt, from field evidence too, that this is a characteristic species of small wet hollows within the forest, although no measure is available of the pattern of persistence of water in these hollows.

Phorophytes

The restriction of individual species of epiphytes to particular species of phorophytes is not at all evident in Table 5. Fourteen of the species in Table 5 which are restricted to a single phorophyte are also found on the ground and have therefore no claim to specificity in their substrate, and there are only 3 other species, solely epiphytic on one kind of phorophyte, in this stand of forest: *Rhacopilum strumiferum*, *Lepidozia kirkii*, and *Podomitrium phyllanthus*. Only the last of these has any claim to be considered host-specific (Scott, 1970 p. 41). Among the rarer species (Table 6) of course such specificity is a commonplace, shown by 43 out of 64 species, but it must be considered a function of their rarity rather than of their exclusiveness. Therefore, as on Secretary Island (Scott, 1970 Table 8) species restriction to a single phorophyte form by far the largest class and there is some evidence that species which occur both on the ground and as epiphytes are those of wider tolerance which are capable of colonising a wider range of phorophytes. Only 15% of purely epiphytic species occur on 4 or more phorophytes, compared with 27% of ground/epiphytic species. Differences between species of phorophyte in their epiphyte floras are not striking. Of the 60 epiphytes restricted to one species of phorophyte, *Nothofagus menziesii* has 29 (48%) and *Dacrydium cupressinum* 16 (27%). Of the 32 species found on 2 phorophytes, *N. menziesii* has 8 (25%), *D. cupressinum* 23 (72%). Of the 42 species found on 3 or 4 phorophytes, *N. menziesii* and *D. cupressinum* both have 40 (95%). These two species of tree must be considered the most favoured habitats for epiphytes in this stand of forest, presumably from a combination of longevity and persistent bark.

Comparison with other areas

Comparisons of bryophyte floras are now possible (Table 9) with Stewart Island (Scott and Armstrong, 1966) and Secretary Island (Scott, 1970) which have themselves already been compared (Scott, 1970). The simple floristic comparison of Table 9, based on bryophytes alone, produces the ranking in terms of similarity: J.B./Sec.Is. > Sec.Is./St.Is. > J.B./St.Is. This coincides with the geographical separation of these localities and raises the possibility of a continued and detectable floristic gradient throughout New Zealand. Further comparable data would be required to establish such a floristic continuum. The species already noted as being abundant on the ground in both Secretary Island and Stewart Island (Scott, 1970 p. 44) comprise: *Ptychomnion aciculare*, *Hypnodendron (Sciadocladus) menziesii*, *Plagiochila gigantea*, *Schistochila nobilis*, which also predominate at Jackson Bay and *Leucobryum candidum*, *Dicranoloma menziesii*, *Bazzania adnexa*, *B. novae-zelandiae*, *Plagiochila ramosissima*, *Schistochila appendiculata* and *Zoopsis argentea* which are absent or much less abundant at Jackson Bay. The major epiphytes, common to Secretary Island and Stewart Island, likewise comprise: *Dicranoloma menziesii*, *Weymouthia cochlearifolia*, *Bazzania adnexa*, *Lepidolaena clavigera* and *Plagiochila pleurata* which also predominate at Jackson Bay, and *Chiloscyphus chlorophyllus*, *Frullania aterrima*, *F. ptychantha* and *Plagiochila ramosissima* which are absent or less prominent. *Lopidium concinnum* and *Plagiochila annotina* are two further epiphytes which are particularly abundant on both Secretary Island and Jackson Bay but not on Stewart Island.

The most distinctive characteristics of the Jackson Bay ground bryophyte flora, compared with the other

TABLE 9. *Numbers of bryophyte species found in climax lowland forest at Jackson Bay, with the numbers of species (bracketed) found in comparable forest in Stewart Island and Secretary Island, and a similar comparison between Jackson Bay and Secretary Island.*

	Mosses	Liverworts	Total
JACB/SECISD	36(25)/49(25)	82(48)/90(48)	118(73)/139(73)
JACB/STEWISD	36(18)/33(18)	82(35)/70(35)	118(53)/103(53)
SECISD/STEWISD	49(22)/33(22)	90(40)/70(40)	139(62)/103(62)

two localities, are the presence of *Hypnodendron marginatum* and the abundance of *Lepidozia microphylla, Pterygophyllum quadrifarium* and *Tylimanthus saccatus.* Among the epiphytes *Mastigophora flagellifera* and *Trichocolea mollissima* are similarly distinctive. The hepatic/moss ratio of the ground and epiphytic species lists in the climax forest, from Tables 5 and 6, is 2.2, which is precisely that of Stand B in the lowland forest on Secretary Island (Scott, 1970 p. 48), and is typical of wet New Zealand forest.

Humidity

The actual humidity regime within the Jackson Bay forest is unknown but, from the abundance and variety of the epiphylls (Table 9) it is evident that high humidity prevails. Since the epiphyllous flora is considerably richer than that of Precipice Cove in Doubtful Sound (Scott, 1970 Table 11) it is reasonable to infer that the humidity is either higher or more consistently high at Jackson Bay, within the confines of the forest. In more open communities, as in the earlier stages of the succession, epiphylls are either absent or very rare whereas those at Precipice Cove were growing in light open scrub fully exposed to whatever atmospheric desiccation there might be. Evidently the microclimate within the Jackson Bay climax forest, no doubt assisted by the abundant standing water within the forest, attains a humidity regime far wetter than the prevailing external macroclimate would suggest, equivalent, in terms of conditions for plant growth, to a much wetter macroclimate with a rainfall of the order of perhaps 5000 mm or more. But it is impracticable at present, lacking data on actual temperature, rainfall and humidity conditions, to correlate humidity levels with epiphyte floristics and hence there is still no way of diagnosing humidity regimes, except in very broad terms, from the vegetation that they support.

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