A LOWLAND VEGETATION SEQUENCE IN SOUTH WESTLAND: PAKIHI BOG TO MIXED BEECH-PODOCARP FOREST
PART 1: THE PRINCIPAL STRATA

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SUMMARY: Six stands of lowland vegetation representing transitions from pakihi bog to mixed beech-podocarp forest are described quantitatively from the coastal plain of the Arawata and Jackson Rivers in South Westland. The sequence depicts progressive changes in canopy height, biomass and floristic richness, and appears to involve, at least in part, a primary succession. Some boundaries have been sharpened by periodic fires but the long-term trend remains unobscured.

Pollen evidence indicates that the pakihi bog began as a lake when the surrounding area was forested by both podocarps and silver beech. The bog seems never to have supported a woody vegetation but in the absence of fire, forest would slowly encroach on it.

With a highway traversing the sequence, its reservation for educational and scientific purposes has been proposed.

INTRODUCTION

A feature of lowland coastal gravel plains and terraces throughout Westland is the occurrence of openings on poorly drained sites in otherwise tall lowland forest (Fig. 1). These forest openings or pakihis have been classed as a soligenous (surface flat or sloping) type of Paludification (blanket) Bog (Cranwell, 1952). They are characteristically underlain either by peat or by highly leached soils associated usually with a loess cap and a strong iron pan formation which seriously impedes drainage.

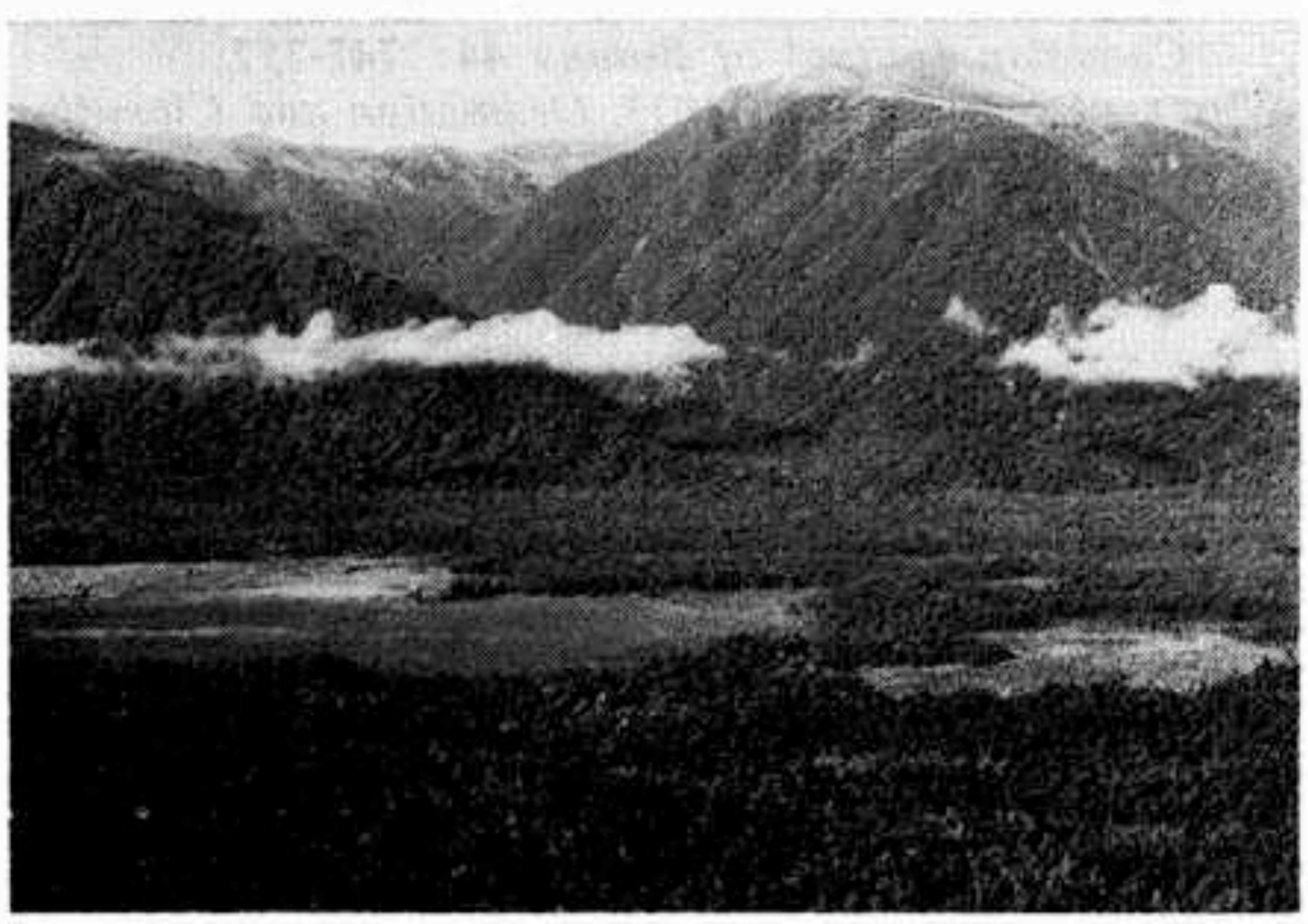


FIGURE 1. *View southeast from the slopes of Mt. McLean showing the lowland forest and pakihi of Dismal Swamp about 2 km northeast of the study area. Hindley Creek drains the valley and crosses the pakihi on the far left. May 1965.*

On pakihis not recently disturbed by fire there is a well defined sequence of vegetation. The open central part of the bog merges into a woody margin via open scrub which gradually thickens and increases in height from low shrubland through woodland, culminating in tall lowland forest (Fig. 2). The concentric pattern of vegetation types representing this sequence is strongly suggestive of a natural plant succession, as indicated by Cockayne (1928, p. 180), Holloway (1954, p. 381) and others (Chavasse, 1962). Indeed, Holloway (p. 381-2), referring to the patchiness of lowland Westland vegetation, suggests that the pakihi succession is part of a more widespread vegetation response to climatic changes occurring some time about the twelfth century A.D. He concedes, however, that the more open pakihis may be stable or at best represent a very slow succession because of recalcitrant soil conditions.

In contrast, there is evidence in some pakihis at least, that they may represent the reverse situation, that is, a forest retrogression associated with soil degradation following a period of apparent steady

FIGURE 2. *Vegetation sequence along pakihi edge in the study area at Dismal Swamp. Open short manuka scrub in the foreground grades into increasingly tall dense manuka woodland, followed by silver pine (dark rounded canopies) with young podocarp forest, especia'ly rimu, silhouetted on the skyline. May 1965.*

state characterised by tall lowland forest. This process, through developing a highly infertile gley podzol with associated iron pan, results in soil conditions inhibitory to the lowland forest and allows the establishment of silver pine *(Dacrydium colensoi)** (Stevens, 1968). Rigg (1962) even claims that pakihis occupying glacial and interglacial terraces in the vicinity of Westport, north Westland, have developed largely from forest due either to soil deterioration under forest or to climatic change, or both. Further, she suggests the possibility of several cycles of succession and retrogression since most of the larger pakihis contain buried timbers. However, she admits that the successional phase is now widespread and has been "for many centuries", although recent burning together with increased waterlogging due to reduced water consumption following logging, have counteracted this tendency at least in the Westport area. This latter claim, however, finds no support from McDonald's (1955) comparison of soil moisture content and other physical properties between forest and adjacent sites reverting to pakihi following logging operations.

The southernmost pakihis may be those on the extensive coastal plain between the Waiatoto and Arawata Rivers which, being south of the Paringa River, are associated with a mixed beech-podocarp forest. This paper describes the typical vegetation sequence in the vicinity of Dismal Swamp, one of the most extensive pakihis on this plain (Fig. 3).

The study began as a University of Otago Science Students' project in 1965 (Smith, 1965) but additional information has been collected subsequently. This paper describes quantitatively the principal strata represented in the vegetation sequence. The epiphytic and ground vegetation, in which bryophytes predominate, is described separately as Part 2 (Scott and Rowley, 1975).

THE STUDY AREA

Physiography

The area studied is underlain by gravel, sand or silt (Mutch and McKellar, 1964). It is situated about 4 km inland and 12 m above sea level. Since the highway immediately north of the Arawata River bridge traverses the entire vegetation sequence, sites for sampling were selected adjacent to it (Fig. 3). The highway not only facilitated access to this low-lying and featureless country but also ensured minimal interference by deer.

A small isolated outcrop of undifferentiated metamorphic rock which the highway crosses about 1 km north of the bridge (Mutch and McKellar, 1964) has somewhat higher relief and was avoided.

Climate

Official Meteorological Service records for two nearby coastal stations, Jackson Bay 11 km to the north-west and Haast, located 29 km northwards along the coast, indicate an annual rainfall somewhat in excess of 3,500 mm fairly evenly spread over about 200 days, and a mean annual air temperature of about 11°C with relatively slight diurnal and seasonal fluctuations. Screen frosts occur on 3 to 9 days between May and October while ground frosts may occur on 53 to 70 days throughout the year. Fog and snow are both uncommon (12 year means of 8.5 and 0.5 days, respectively, for Jackson Bay).

Despite the large number of rain days, sunshine duration (for Haast) is relatively high—1,816 hours annually or 43% of the possible total.

METHODS

Six sites were chosen to represent the vegetation sequence from bog near the centre of the pakihi to fully developed lowland forest close to the Arawata

* Nomenclature follows Allan (1961) for pteridophytes, gymnosperms and dicotyledons, Moore and Edgar (1970) for monocotyledons except for the grasses which follow Cheeseman (1925) or where applicable, Zotov (1963). Otherwise authorities are given in the species list (Appendix, Table I). Voucher specimens of most species listed are deposited in the OTA herbarium.

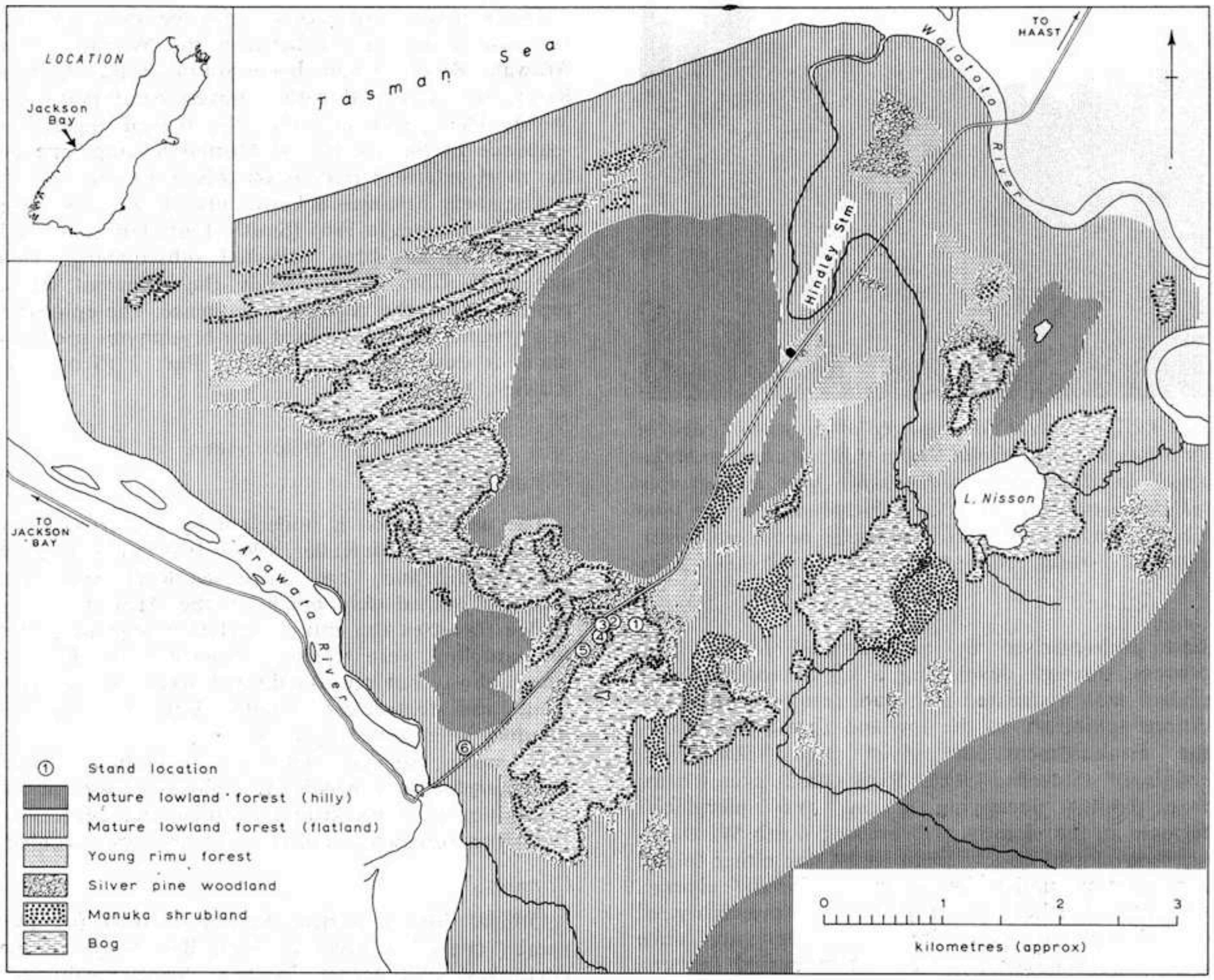


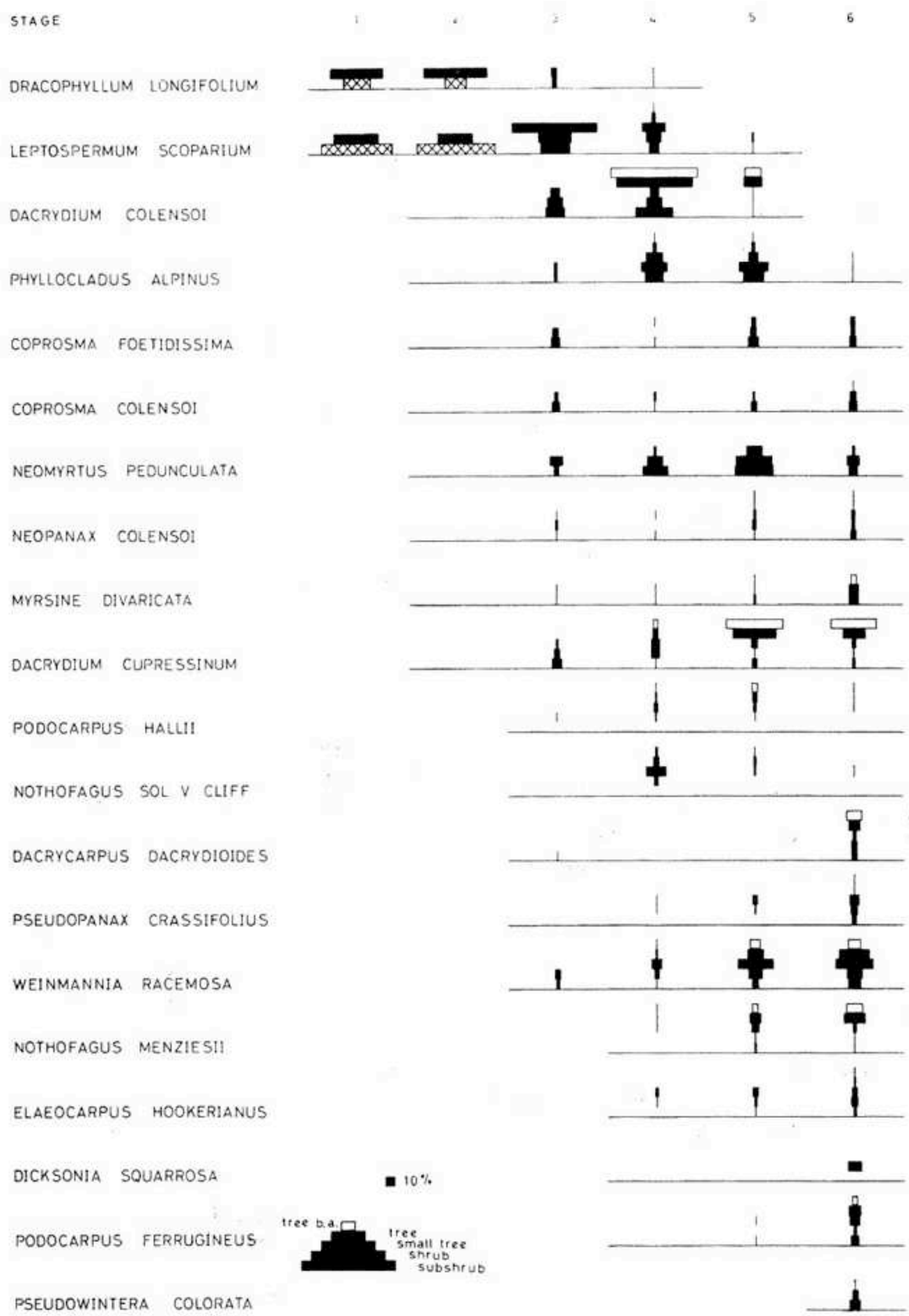
FIGURE 3. *The coastal plain between the Waiatoto and Arawata Rivers, South Westland, showing distribution of the main vegetation types and the approximate location of six stands studied to describe the vegetation sequence. The flatland east of the highway is generally known as Dismal Swamp, that to the west as the Burmeister Morasse. The map was compiled from an enlargement of aerial photograph 3977/11 supplied by N.Z. Aerial Mapping Ltd., Hastings, and with assistance of an unpublished National Forest Survey forest type map supplied by the New Zealand Forest Service.*

River (Fig. 3). For all except the herbaceous plant cover on the pakihi the point-centred quarter method of plotless sampling (Cottam and Curtis, 1956) was used, as for previous studies involving a similar range of vegetation (Mark, *et al.*, 1964).

The categories (and values recorded for each) were:

(i) Trees: woody species > 10 cm d.b.h. (composition, density, basal area);
(ii) Small-trees: woody species < 10 cm d.b.h. but > 5 m tall (composition, density);
(iii) Shrubs: woody species 0.3 to 5 m tall (composition, density);
(iv) Subshrubs: woody species < 0.3 m tall (composition, density);
(v) Herbs: herbaceous species > 15 cm tall (composition, density).

Fifty points were used in all except the mature forest stand where the number was doubled for the small-tree, shrub and subshrub layers to cope with their increased floristic diversity. Points were distri-



CANOPY HEIGHT (m)		0.3	1	4	12	20	30
TOTAL DENSITY (stems / ha.)	Subshrubs	No value	No value	34,500	85,000	34,700	7,100
	Shrubs	6,500	53,400	13,900	22,900	31,400	6,000
	Small-trees	–	–	5,470	4,030	2,800	1,030
	Trees	–	–	–	1,130	1,080	500
TOTAL BASAL AREA – Trees (dm^2 / ha)		–	–	–	4,589	6,559	6,557

FIGURE 4. *Values for relative density of the important woody species (>5% in one or more stands) in four size classes (see key) from six stands of vegetation (Stages 1-6) at Dismal Swamp, South Westland. Values entered for subshrubs in Stages 1 and 2 are relative cover values. Relative basal area of tree species is also included (open blocks) while canopy heights and stand totals for density and basal area are shown at the bottom.*

buted at 20-pace intervals along compass lines of 300°M except for the stands (2-4) where lines were selected so as to remain within the limits of the particular stand. For the herb layer on the pakihi, estimates of percentage cover were more practicable. Here 50 quadrats, each 0.5 m², were distributed as for the quarters.

Values for total and relative basal area and density were calculated as for previous studies (Mark *et al.*, 1964; Wells and Mark, 1966). For practical reasons, any stem of bog dacrydia species emerging from the ground was assumed to be a separate individual and thus eligible for sampling even though it may have been adventitious in origin (Moar, 1955).

Subsequent to completion of our sampling programme the quarter method which we used was found to give abnormally high values for tree basal area (Franklin, 1967), particularly in stands with a wide range of stem diameters (Mark and Esler, 1970). Our absolute values for total basal area may therefore not be reliable but the relative values should be satisfactory.

A soil corer was used to remove samples of peat from two depths (0-20 cm and 180-200 cm) for determining colour, organic matter and pH. The organic content was measured by igniting oven dried samples at 700°C for two hours and acidity with a Macbeth Model 1051 pH meter using 1:1 by volume dilutions with distilled water. The colour of moist soil was checked against Munsell's standard soil colours.

The bog surface was surveyed along a line from near its centre (site 1 in Fig. 3) to the margin with a Watts Autoset level and staff, and a Hiller corer was used to measure depth of peat at intervals along this line and also to obtain a bottom sample from its deepest part for pollen analysis. Location of any buried wood intercepted during the sampling was noted and where possible collected for identification.

The area was revisited in 1972, about five years after an extensive summer fire had swept through the bog and woodland sites previously studied. Several other pakihis more distant from the highway were also visited at this time and brief notes made on their vegetation.

RESULTS

1. The Vegetation Sequence

Quantitative values for the more important species along the vegetation gradient are shown in Figures 4, 5 and 6, while a complete floristic list is given in the Appendix (Table I). Growth ring counts of manuka *(Leptospermum scoparium)*, *Dracophyllum longifolium* and silver pine stems from the four youngest stands are summarised in Table 1.

A brief description of each of the six stages studied is given below:

Stage 1: The Pakihi

The bog surface, although essentially level, consists of a network of minor depressions alternating with low peaty mounds up to 30 cm high and 1 m across. *Calorophus minor* (wire brush) dominates the bog surface, being rooted chiefly on the mounds, but its procumbent habit allows it to partly conceal the depressions. It therefore provides most (90%) of the 58% plant cover in the canopy layer (> 15 cm tall). *Gleichenia circinata* (tangle fern) and the rush *Baumea teretifolia* are both common but, being quite erect in their habit, make only a small contribution

TABLE 1. *Basal diameters (cm) and numbers of growth rings in stems of* Leptospermum scoparium (*manuka*), Dacrydium colensoi (*silver pine*) *and* Dracophyllum longifolium (*inaka*) *from four stands on or near to the pakihi, Dismal Swamp, South Westland. Means of 4 to 7 determinations and their standard errors only, are given.* (*Value without a S.E. is a single determination.*)

Species	*Stand 1 Pakihi*				*Stand 2 Young manuka*				*Stand 3 Old manuka*				*Stand 4 Silver pine*			
	Diam.	S.E.	No. rings	S.E.	Diam.	S.E.	No. rings	S.E.	Diam.	S.E.	No. rings	S.E.	Diam.	S.E.	No. rings	S.E.
Dracophyllum longifolium	1.15	0.11	15.2	1.5	—	—	—	—	—	—	—	—	—	—	—	—
Leptospermum scoparium	0.67	0.01	15.4	1.1	1.26	0.04	18.7	1.0	6.68	0.51	37.9	1.0	—	—	—	—
Dacrydium colensoi	—	—	—	—	—	—	—	—	8.9	—	220	—	25.5	0.8	339.4	9.2

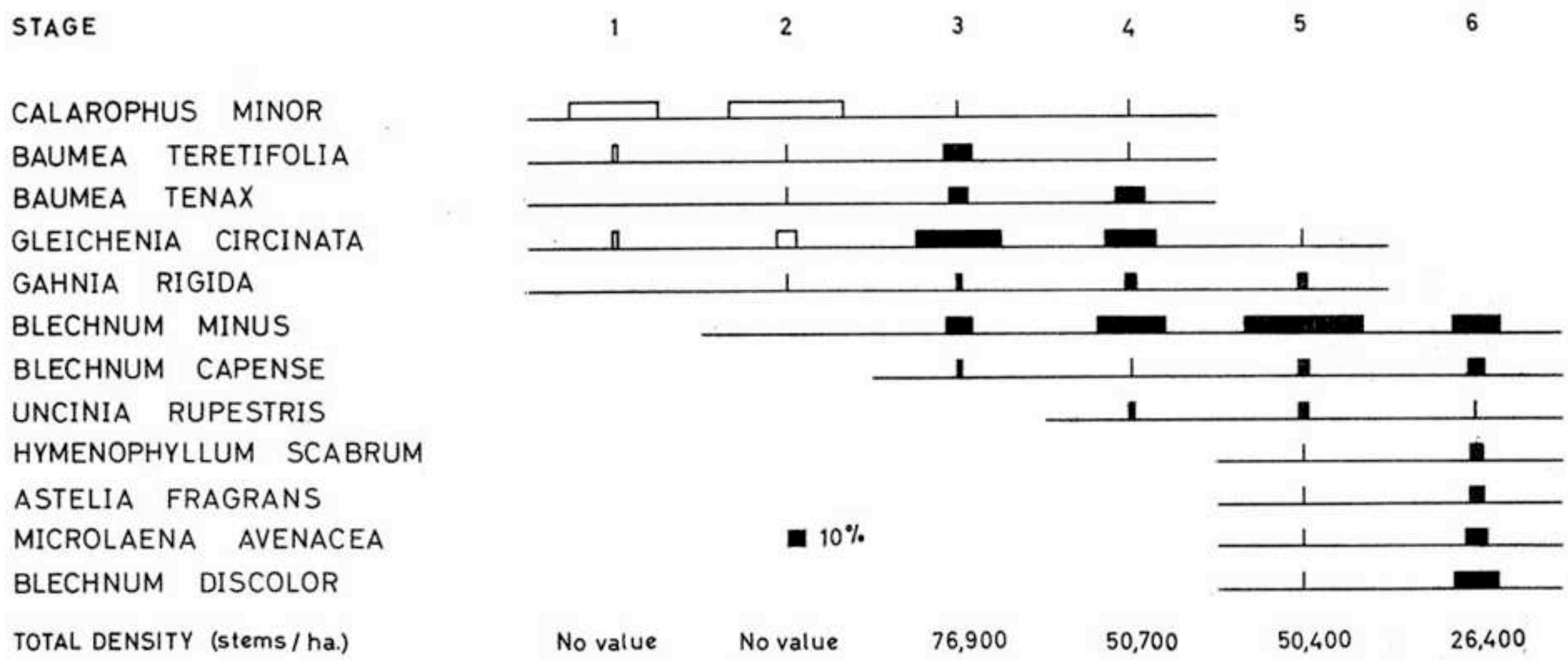


FIGURE 5. *Values for relative density of the important species (>5% in one or more stands) in the herb layer for the same six stands described in Figure 4. Note, values for Stands 1 and 2 are percent cover.*

to the plant cover (Fig. 5).

Co-dominant and emergent shrubs of manuka and *Dracophyllum longifolium* are scattered through most of the bog. Their small size is indicated by their minor cover values (1.3% and 0.5% respectively) provided by about 6,500 shrub-sized plants per hectare (2,950 of manuku and 3,550 of *Dracophyllum*).

Five plants of each species in this stand had similar numbers of growth rings (15) with less variation among the manuka (Table 1). Basal diameter (minus bark) of the manuka stems was less than half that of *Dracophyllum* (Table 1) but on all manuka shrubs examined, the bark at and beneath the soil surface was noticeably inflated. Thus, of the five stems sampled, mean thickness of bark at the ground surface was 1.19 ± 0.19 mm which was 29.2% ± 2.9% of the total stem diameter, compared with 0.29 ± 0.04 mm and 8.6% ± 1.5% for the same stems about 20 cm above ground level.

Most depressions in the bog surface were partly water-filled at the time of study—it contributed 22% to the ground layer—but the peaty surface beneath carried a sparse plant cover. Only the mosses *Dicranoloma billardieri* and *Campylopus introflexus* are generally important in these hollows, contributing together about 66% ground cover but several other species may be locally important or play minor roles, e.g. *Lycopodium ramulosum, Herpoliron novae-zelandiae, Drosera spathulata, D. binata, Nertera depressa, Gaimardia setacea, Liparophyllum gunnii, Thelymitra venosa, Euphrasia disperma* and several bryophytes—for more detail see Scott and Rowley (1975).

Stage 2: Young Manuka on Pakihi Fringe

The most striking change from Stage 1 is an increase in density of manuka shrubs (from *ca* 3,000 to 53,400 per hectare) but their canopies remain sufficiently small and open to allow persistence of a typical pakihi community (Figs. 4 and 5). Only a few minor species have disappeared while others have established (see Table 1 in Appendix), especially on the mounds which here may reach 50 cm high. Large tussocks of *Gahnia rigida* are conspicuous here and there and there are occasional seedlings of silver pine and *Phyllocladus alpinus* established on the drier mounds.

Typical manuka shrubs in this stand contain about 20 growth rings (Table 1) but a few standing dead charred stems of silver pine among the low manuka scrub indicate a history of fire.

Stage 3: Manuka Woodland

This zone, up to 20 m wide, is characterised by a dense canopy, 3-6 m high, of small trees (5,470 stems per hectare), chiefly manuka (Figs. 2 and 4). Several average-sized manuka stems from various parts of the stand contained about 40 growth rings while those of silver pine, which contribute 10% of the small-tree stems and occasionally reach tree size, are much older (Table 1).

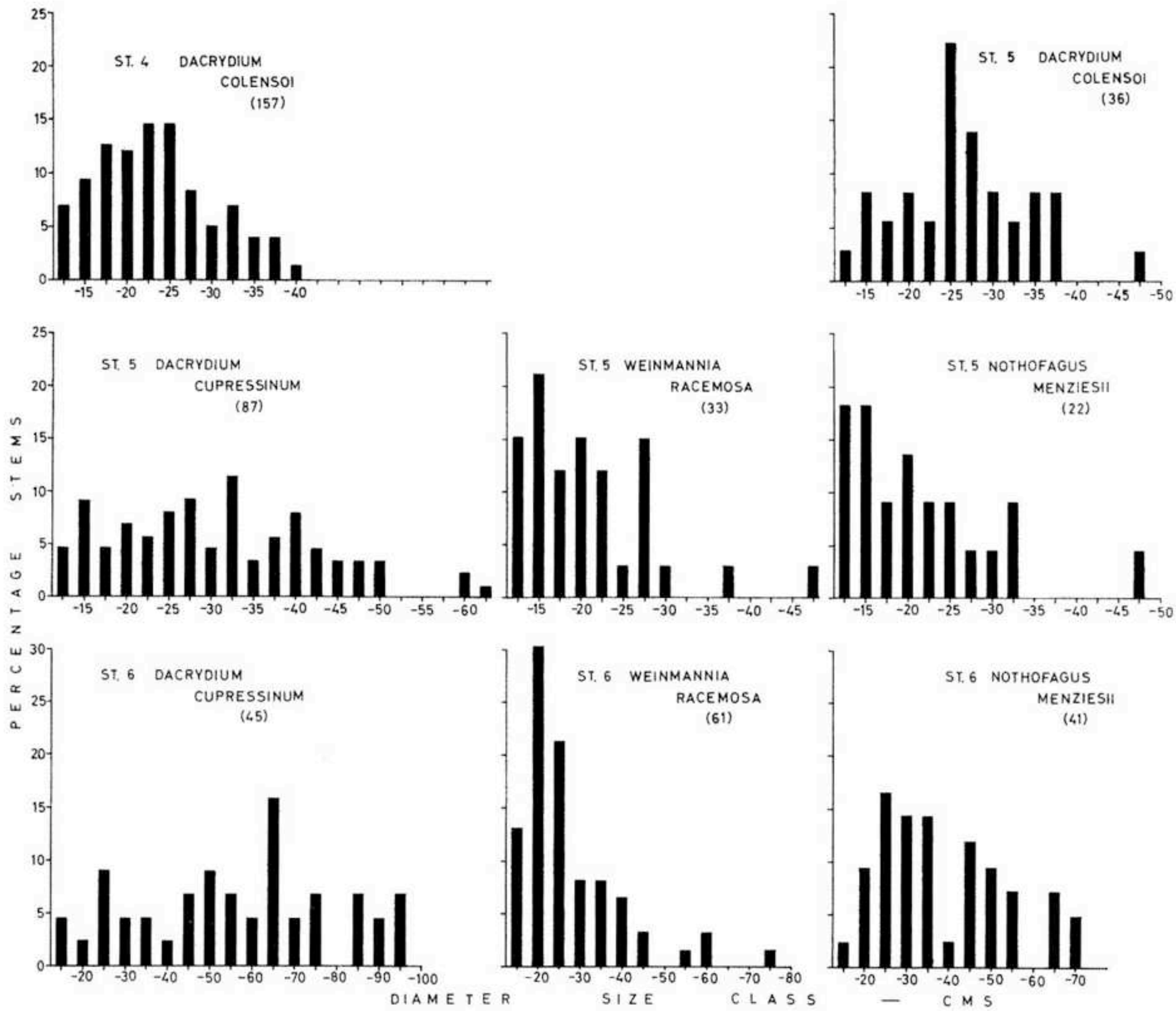


FIGURE 6. *Percentage distribution of diameter size classes for trees (>10 cm diam.) of four species in three stands (St. 4-6). Only species with more than 20 stems measured per stand are included—values in brackets after the species names refer to the number recorded. Note that the size class intervals are 2.5 cm for Stands 4 and 5 and 5 cm for Stand 6.*

Manuka also predominates among the shrub and subshrub layers but small stems of silver pine are plentiful. Several typical forest species have also become established (Fig. 4). Apparently young, vigorous stands of rimu *(Dacrydium cupressinum)* and kamahi *(Weinmannia racemosa)* are common, with fewer of broadleaf *(Griselinia littoralis)*, southern rata (*Metrosideros umbellata*), *Neomyrtus pedunculata, Coprosma foetidissima* and *C. colensoi*. *Dracophyllum longifolium*, however, is reduced to a minor role. *Gleichenia circinata* is the most conspicuous herb with less of *Baumea* spp., while *Calorophus* barely persists. *Blechnum minus* and *B. procerum* enter the sequence at this stage but play only a minor role (Fig. 5).

Stage 4: Silver Pine Woodland

The manuka woodland grades fairly abruptly into a woodland about 12 m tall dominated by tree-size stems with a total density of about 1,130 trees per hectare. Only silver pine is conspicuous in the canopy (78.5 Rel. Den.; 88.8 Rel. Basal Area—Fig. 4) with stems of the most frequent size class (Fig. 6) containing about 340 growth rings (Table 1). Several forest species reach tree size but all have small, apparently young stems (<20 cm d.b.h.) and are of minor importance—they include rimu, mountain beech *(Nothofagus solandri* var. *cliffortioides), Phyllocladus alpinus,* Hall's totara *(Podocarpus hallii)* kamahi and silver beech *(N. menziesii).* Manuka is reduced to a minor role among the trees but overtopped stems persist as the most numerous small-tree species (23.5 Rel. Den.), ahead of establishing stems of mountain beech (20.5%), *Phyllocladus* (17%), kamahi (10.5%) and rimu (8%), and supressed stems of silver pine (9%).

FIGURE 7. *The young rimu stand exposed by the highway close to the area sampled. Dominance of tall thin stems of rimu and a well-stocked understory are apparent. The earlier stages of the sequence are in the background. October 1972.*

In both the shrub and subshrub layers the role of manuka has been superseded by *Phyllocladus, Neomyrtus* and silver pine, while several other typical forest species have become established (Fig. 4).

Blechnum minus predominates among the herbs while *Gleichenia circinata, Baumea gunnii* and *Gahnia rigida* are less conspicuous (Fig. 5).

Distribution of diameter size classes among the silver pine trees in this stand (Fig. 6) indicates a deficiency of smaller stems, suggestive of a decline in regeneration potential.

Stage 5: Young Rimu Stand

The canopy of this stand reaches 20 m and is occupied almost entirely by immature stems of rimu (Figs. 2 and 7), even though it contributes only 44% to the 1,080 tree stems per hectare (Fig. 4). Their trunks, however, comprise almost 60% of the total basal area and moreover show a fairly uniform spread of diameter up to 5 dm (Fig. 6). Stems of silver pine, the second most important tree species, have been overtopped by rimu and it is more poorly represented among the smaller size classes than in the woodland stage (Fig. 6).

Forest tree species continue to increase in density, with predominantly small, vigorous, apparently young stems (see values for kamahi and silver beech in Fig. 6).

Occasional moribund shrubs of manuka persist, but much more numerous are those of typical forest

FIGURE 8. *Interior of the mixed forest stand near the area sampled.* Blechnum discolor *is the prominent fern in the foreground.*

species: *Neomyrtus, Coprosma foetidissima, C. colensoi, Pseudopenax colensoi, Elaeocarpus hookerianus* (pokaka). Among the herbs only *Blechnum minus* is important (Fig. 5).

Stage 6: Mature Lowland Forest

Several lowland podocarp species—rimu, kahikatea *(Podocarpus dacrydioides)*, miro *(Podocarpus ferrugineus)*—reach *ca.* 30 m and emerge above rather separate strata of silver beech and kamahi. The important tree species all show a sufficient range of diameters (Fig. 6) and moreover, appear adequately represented in the subcanopy layers (Fig. 4) to justify designating this impressive forest stand a climax community (Fig. 8). Trunks of rimu were measured up to 90 cm diameter, kahikatea to 85 cm, miro, which enters the sequence relatively late (Fig. 4), to 80 cm, kamahi to 75 cm and silver beech to 70 cm. The relatively large size of the podocarp trees is indicated by their greater percentage contribution to basal area than to density (Fig. 4). The total density of trees (499/ha) is less than half that recorded in either of the other two stands containing trees, but the total basal area (6,557 dm^2/ha) is similar to that recorded in the immature rimu stand (Stage 5) and substantially more than from the silver pine woodland (Stage 4).

Even though density values for the woody subcanopy layers are less than those recorded from any of the other stages, many more species are present (see Appendix) and moreover, none are notably conspicuous. Minimal disturbance by deer is probably a factor here since several palatable species are present *(Coprosma* spp., *Pseudopanax colensoi)*, while pepper tree *(Pseudowintera colorata)* remains insignificant (5.7 Rel. Den. among the shrubs).

Density of herbs is reduced to about half that recorded in any other stand, but among them *Blechnum discolor* has increased to be as abundant as *B. minus*, while *B. capense*, *Microlaena* and *Astelia nervosa* are much less numerous (Fig. 5).

2. Soils

The colour, pH and organic content of soils from the six sites are given in Table 2. Colour showed little variation either among the six sites or between the surface and a depth of 2 m. All samples are fairly uniformly acidic throughout the upper 2 m although that beneath the mature forest is somewhat less so. The organic content exceeds 70% in all but the lower samples of the three latest stages (sites 4-6). In all samples the non-combustible material is mostly coarse sand. Indeed, an almost pure, organically stained sand, presumably of alluvial origin, was found underlying the mature forest at a depth of 1.3 m. Little profile development including gleying, is apparent at this or any other site, within the upper 2 m.

3. Substrate Sampling of Peat Depth, Wood and Pollen

The ground surface along a line at right angles to the pakihi margin extending to Site 1 (Fig. 3), slopes very gently upwards (at *ca.* 0.23°) to an area about

TABLE 2. *Colour, pH and organic matter content (loss on ignition) of soils at two depths from the six sites described in the text and shown in Figure 3. Soil symbols and names follow the Munsell notation.*

Site No	Vegetation	Depth (cm)	pH	% Org. matter	Colour
1	Pakihi	0–20	4.1	96.9	10YR 2/2 Very dark brown
		180–200	4.2	95.6	10YR 2/2 ,,
2	Young Manuka	0–20	4.1	83.9	10YR 2/2 ,,
		180–200	4.2	90.7	10YR 2/2 ,,
3	Manuka Woodland	0–20	3.9	88.2	10YR 2/2 ,,
		180–200	4.1	76.1	10YR 2/2 ,,
4	Silver Pine Woodland	0–20	4.0	71.3	10YR 2/2 ,,
		180–200	3.9	66.4	10YR 2/2 ,,
5	Young Rimu Stand	0–20	3.8	88.6	5YR 2/2 Dark red brown
		180–200	4.1	59.5	5YR 2/2 ,,
6	Mixed Lowland Forest	0–20	4.4	72.0	10YR 2/2 Very dark brown
		130–150	4.5	15.2	10YR 3/2 Very dark gray brown
		180–200	4.6	7.4	2.5YR 3/2 Very dark gray brown

30 m out from the margin. Soundings of peat along this line showed that its depth reaches a maximum (6.1 m) near the centre and becomes somewhat thinner towards the margin (Fig. 9). Roots and buried wood beneath the woody vegetation unfortunately prevented the soundings being extended beyond the bog margin. Where possible, samples of buried wood were collected for identification but all occurrences have been shown on Figure 9.

All but one of the six wood samples encountered in the peat beyond 30 m from the pakihi fringe were fragments and all were deeper than 2.4 m. Of the two fragments identified, one was of silver pine while the other, a small twig, was juvenile wood of kamahi (Fig. 9). It appears likely that all these six specimens would have been carried on to the bog, perhaps during floods, but this explanation becomes less applicable as the incidence of buried wood increases over the remaining 30 m to the existing margin of the bog. At Stations 5 and 6 (see Fig. 9), 30 m and 20 m respectively from the margin, several specimens were intercepted, but only at one or two levels, which again could be the result of periodic deposition by flood waters. At Station 7, however, just 10 m out from the margin and within the zone of young manuka (Stage 2 type), all but one of the ten probes intercepted wood and at a range of depths. Of three specimens identified, one was *Dracophyllum* and the other two were silver pine. This evidence for a previous woody cover on the site is reinforced by the presence of occasional dead charred stems of silver pine, 6-10 cm diameter, still standing among the short open manuka. A similar incidence of buried wood on the existing fringe (Station 8 in Fig. 9) is also indicative of several previous stands of woodland although only manuka wood was identified from this station.

Beneath the tall dense woodland of manuka (Station 9 in Fig. 9) recognition of buried wood was difficult because of the high density of roots but a small specimen with bark still intact from 15 cm depth proved to be silver pine while two specimens of manuka wood were recovered 45 cm down. Along the transition between manuka and silver pine woodlands there was a partly decayed surface log of silver pine, one at 15 cm depth of bog pine *(Dacrydium bidwillii)* and a large log, buried 40 cm, which proved to be yellow-silver pine *(D. intermedium)*. Wood from a depth of 45 cm near the outer edge of the silver pine zone was identified as "probably *Dacrydium cupressinum*" (R. N. Patel, pers. comm.).

Pollen in a sample of basal peat at 6.1 m depth

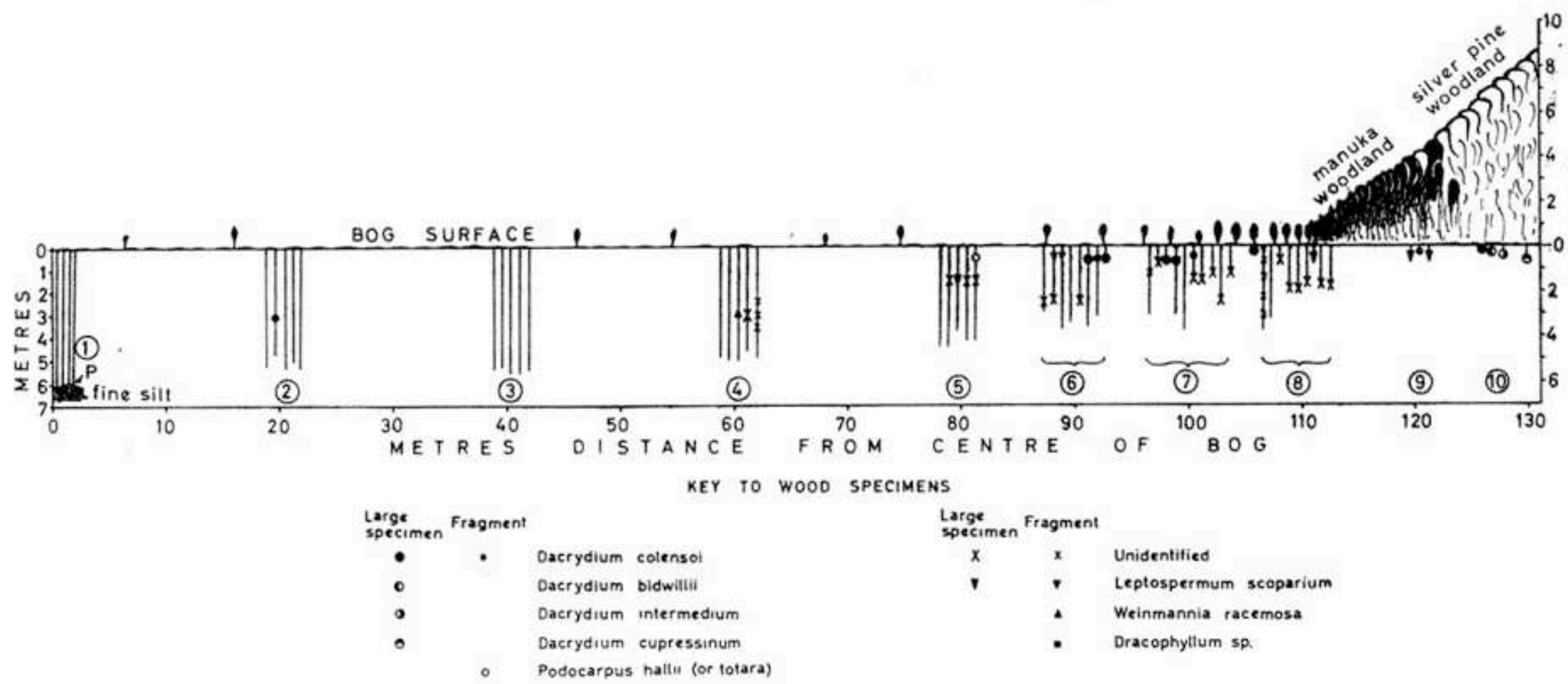


FIGURE 9. *Profile from the silver pine woodland to the centre of the bog (Site 1 in Fig. 3) showing depth of peat and incidence of buried wood at ten sites. Values for each site have been spread out for clarity but are centred on the site numbers (circled). Only peat sample lines shown not ending in a wood specimen indicate the full depth of peat. Material for pollen analyses was taken from the site "P" at Station 1. Note, even though the bog surface is shown as level, it is actually highest at Site 5—from here it falls 30 cm to Site 8 and 55 cm to Site 1.*

near the centre of the pakihi (Station 1 in Fig. 9), as well as that from the fine gray silt immediately underlying it, was analysed by Dr N. T. Moar. The results (Table II in Appendix), as interpreted by Dr Moar (pers. comm.), suggest that the bottom peat is no older than 10,000 years B.P. Moreover, the site of deposition probably was not forested, since pollen of *Phormium, Astelia, Cyperaceae* and *Gramineae* "suggest open, damp conditions, with shrubs, e.g. *Leptospermum*, dotted about. There is little doubt, however, that the region was forested at the time by podocarps, and *Nothofagus menziesii*, judged by the frequency of its pollen in the basal peat, was probably locally abundant. Pollen of the *N. fusca* type could have drifted in from a distance".

DISCUSSION AND CONCLUSIONS

The sequence of vegetation—pakihi bog to mixed beech-podocarp forest—surrounding Dismal Swamp in South Westland, appears at least superfically to represent a genuine primary forest succession. Thus the peat bog occupies a shallow, irregularly and imperfectly drained basin, perhaps an old main or flood channel of the Arawata River and, except near its margins, contains no more buried wood than flood waters might have carried in. Moreover, pollen analysis of its basal peat indicates that the site probably was not forested although the region apparently was (N. T. Moar, pers. comm.). In addition, patterns of size class distribution among the woody species which achieve importance at some stage along the vegetation sequence, consistently imply unidirectional and progressive changes towards the mixed beech-podocarp forest. Small shrubs of manuka and *Dracophyllum longifolium* emerge above the hummocky surface of the bog and towards its margin, manuka in particular becomes more numerous, taller and older. This open scrub merges with a close-canopied manuka thicket which increases in height to about 6 m with distance from the bog margin. Silver pine but not manuka seedlings are numerous beneath the dense manuka canopy and the two species may co-dominate a narrow transition to silver pine woodland containing overtopped and decadent stems of manuka. Rimu and kamahi, already well established beneath the silver pine canopy, eventually overtop it to become the most prominent members of the subclimax forest. Silver pine regeneration fails but many other forest species establish. Eventually a mixed beech-podocarp forest appears to develop. Quantitative data from this mixed forest indicate adequate replacement of all important species and it is therefore interpreted as a climax community.

The vegetation sequence is accompanied by progressive changes both in canopy height and floristic richness, vascular species about trebling in number between the bog (26) and the mixed forest (71). Subshrubs are most abundant in the silver pine woodland while shrubs reach their peak in the young manuka along the fringe of the bog. Density of small-trees and trees, on the other hand, decreases steadily as an index of increasing size of individuals beyond the woodland stages. There is an obvious steady increase in total biomass accompanying the sequence although no attempt was made to measure this. Even though the same values for total tree basal area were obtained for the young rimu forest and mixed forest stands the 10 m increase in canopy height would ensure a greater total biomass in the mixed forest.

Since a pollen analysis from the deepest peat sampled near the centre of the bog indicates a forest vegetation in the vicinity it seems unlikely that the bog was initiated at the close of the last Otiran glacial advance about 14,000 years B.P. (Suggate and Moar, 1970). Dr Moar (pers. comm.) assumes that the basal peat is no older than 10,000 years B.P. and suggests that the post-glacial transition from a regional climax of shrubland to one of forest, well documented at Omoeroa Bluff, coast-wise of Franz Josef Glacier, may have been in the process of completion when the underlying mineral material sampled at Dismal Swamp was deposited.

Although this vegetation sequence *could* represent a genuine hydrarch succession the distinctive soil profile underlying the mixed forest suggests that this stand occupies a sandy rise on the edge of a silt-floored depression. In particular, the relatively shallow organic layer beneath the mixed forest indicates that it did not necessarily develop as the terminal phase of a succession represented by the other five stands. There seems little doubt, however, that Stages 1 to 5 (pakihi bog to young rimu forest) are related developmentally although fire has obviously delayed the early stages of this succession. Even without fire, however, the succession appears to be extremely slow, delayed undoubtedly by unfavourable soil conditions, as suggested for pakihis generally by Holloway (1954), and in particular to a high water table. This is demonstrated both by the rapid establishment and growth of manuka along the embankment of the road traversing one arm of the bog and also by the presence in the manuka from the bog, of inflated but highly porous bark at and below the soil surface. This tissue, which was also reported recently from western Fiordland, may promote aeration of the roots (Wardle, *et al.*, 1973). Growth rings in manuka, assuming they are annual, indicate that plants achieve rapid growth around the bog margin, relative to that of silver pine which eventually succeeds it. Even within the tall manuka woodland, occasional co-dominant stems of silver pine may be five times as old. This age anomaly appears to have resulted from the periodic destruction of woody vegetation along the margin of the bog. High incidence of buried wood of several woodland species and from a wide range of depths down to 3 m, within 20 m of the existing woodland margin, reveals that the bog margin has been subjected to several disturbances in the past. Even without disturbance, however, the very slow growth of silver pine suggests that several generations of manuka would occupy a site while silver pine builds up to dominance. But in the area studied, occasional charred, standing small stems of silver pine among the open manuka in front of the dense woodland and close to the highway, indicates some importance of fire. Information from local residents revealed that these dead stems may have resulted from a fire during the 1930's which apparently was confined to a small area of manuka scrub close to the road. However, the extent which fire can penetrate the woodland was demonstrated during the 1967-68 summer when most of the bog adjoining the highway on the east was swept by a fire apparently lit intentionally to facilitate the hunting of deer. This fire penetrated and destroyed all of the manuka woodland surrounding Dismal Swamp and most of the silver pine woodland as well (Fig. 10). Many of the silver pine trees and all those of manuka perished, but by October 1972 manuka seedlings with up to five growth rings were plentiful throughout the destroyed woodland so that another cycle appears to have been initiated.

The fire also destroyed shrubs of manuka and *Dracophyllum longifolium* throughout the bog. In the initial post-fire period *Baumea teretifolia* made the most rapid recovery but by 1972 both *Calorophus* and *Gleichenia circinata* had regained some of their original importance. Most of the original species were again present on the bog but still less important than before the fire. *Baumea teretifolia* remained the only vascular species to obviously increase in importance.

The general physiogomy of the pakihi is similar to that described by Rigg (1962) near Westport since the more important species are common to both areas. However, 79 of the 101 vascular species, including all eight exotics listed by Rigg, were not recorded at Dismal Swamp. One of the species shared, the small bog eyebright *Euphrasia disperma*, may reach its southern limit on Dismal Swamp.

FIGURE 10. *The area shown in Figure 2 rephotographed about five years after the 1967-68 summer fire. Note destruction of all woody vegetation along the forest margin and its replacement by an herbaceous cover, chiefly* Baumea teretifolia *except for tall tussocks of* Gahnia rigida *in the zone previously occupied by woodland. October 1972.*

The relatively sharp boundaries between the silver pine and manuka woodlands and between the closed and open manuka stands along the margin of the bog probably have resulted from previous fires which penetrated to varying extents. The other four pakihis visited in the Dismal Swamp area were characterised by both an increase in importance of woody species and less abrupt margins than the one studied, suggesting that fires have been less frequent in areas more distant from the highway. Even so, the vegetation pattern is quite variable both within and between the pakihis shown in Figure 1, and a brief study did not clarify the situation. The pakihi crossed by Hindley Creek (see Figs. 1 and 3) obviously has been free from fire for several decades at least. Shrubs of bog pine *(Dacrydium bidwillii) ca* 1 m tall are conspicuous among manuka and *Dracophyllum* near its margin (Fig. 11). Three stems of bog pine with basal diameters of 0.9 to 1.1 cm contained 39 to 42 growth rings. Bog pine persists even near the centre of this pakihi where *Calorophus* provides *ca* 70% of the cover and *Gleichenia, Baumea* spp. and *Lepidosperma australe* are also common. Occasional low shrubs of *Dacrydium intermedium* and stunted stems of *Libocedrus bidwillii* up to 1.5 m tall, throughout much of the bog, also attest to the freedom from fire.

Prevailing moisture conditions could determine the extent of spread of a fire since vulnerability probably decreases from bog via manuka to silver pine wood-

FIGURE 11. *View west towards the southwest corner of the pakihi crossed by Hindley Creek (see Figs. 1 and 3), showing the vegetation pattern within* ca *100 m of its margin. In the foreground shrubs* ca *1 m tall of manuka,* Dacrydium bidwillii *and* Dracophyllum longifolium *with prominent tussocks of* Gahnia rigida *(behind figure) extend above a herb layer of* Calorophus *and* Gleichenia circinata. *With approach to the margin there are, in order, zones of manuka woodland, silver pine woodland and podocarp (mostly* P. dacrydioides) *forest. October 1972.*

land. Only exceptionally, therefore, as with the recent fire, would fire penetrate to the latter. Protracted fluctuations of the water table may also cause extensions and retractions of the woody vegetation along the margin of a bog. The depth of wood remains found suggests that at least some destruction occurred prior to European settlement.

A recommendation to the New Zealand Forest Service and supported by the New Zealand Ecological Society to reserve for educational and scientific purposes, as well as for its aesthetic value, this sequence of South Westland lowland vegetation, has been provisionally approved. The highway not only traverses the sequence but also separates the recently burnt eastern area from the unburnt areas to the west of the highway. Local exploitation of silver pine from areas close to the highway on either side detracts somewhat from its value as a reservation. However, extensive areas of uncut silver pine woodland persist within the proposed reserve and moreover, the cutting licence, which expired in 1972, apparently has not been renewed.

ACKNOWLEDGEMENTS

In addition to those who assisted with the main project (see Smith, 1965) we wish to thank Dr N. T. Moar, Botany Division, DSIR, for analyses and interpretation of pollen; Mr R. N. Patel, Forest Research Institute, N.Z.F.S., for assistance with wood identification; Mr G. A. H. Kidd, Geography Department, University of Otago, for the preparation of the map; Mr J. R. Crush, Botany Department, University of Otago, for field assistance in 1972; the Surveying Department, University of Otago, for loan of surveying equipment; and the N.Z. Meteorological Service for provision of climatological data.

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APPENDIX

TABLE I. *List of vascular plants present in one or more of the six stands representing the vegetation sequence from pakihi bog to lowland mixed beech-podocarp forest at Dismal Swamp, South Westland Symbols denote the tallest layer occupied by the species in each stage as follows: T = tree; St = small-tree; Sh = shrub; Su = subshrub; H = herb; G = ground layer; E = epiphyte; L = liane. An asterisk preceding the species name signifies its occurrence in pakihis of the Westport area (Rigg, 1962).*

	VEGETATION TYPE					
	Bog	*Open Manuka*	*Manuka Woodland*	*Silver Pine Woodland*	*Young Rimu Forest*	*Mixed Forest*
Hemiphues suffocata *var.* novae zelandiae	G	—	—	—	—	—
*Herpolirion novaezelandiae	G	—	—	—	—	—
Lepidosperma australe	H	—	—	—	—	—
*Liparophyllum gunnii	G	—	—	—	—	—
Thelymitra venosa	G	G	—	—	—	—
*Euphrasia disperma	G	—	—	—	—	—
Prasophyllum colensoi	G	—	—	—	—	—
*Drosera binata	G	—	—	—	—	—
Dacrydium laxifolium	G	G	—	—	—	—
Cyathodes empetrifolia	H	H	—	—	—	—
*Schizaea fistulosa	H	H	—	—	—	—
*Drosera spathulata	G	G	—	—	—	—
*Centrolepis ciliata	G	G	—	—	—	—
*Utricularia monanthus	G	G	—	—	—	—
Cassinia fulvida	Sh	Sh	—	—	—	—
Coprosma brunnea	Sh	Sh	—	—	—	—
*Lycopodium ramulosum	G	G	—	—	—	—
*Notodanthonia nigricans	H	H	H	—	—	—
*Calorophus minor	H	H	H	H	—	—
*Baumea teretifolia	H	H	H	H	—	—
Baumea tenax	H	H	H	H	—	—
Dracophyllum longifolium	Sh	Sh	Sh	Sh	—	—
Dacrydium biforme	—	Su	Sh	St	—	—
*Gleichenia circinata	H	H	H	H	H	—
*Leptospermum scoparium	Sh	Sh	T	T	Sh	—
*Dacrydium colensoi	—	Su	T	T	T	—
*Dacrydium intermedium	—	—	Sh	T	—	—
Libertia pulchella	—	—	G	G	G	—
Gahnia rigida	H	H	H	H	H	—
Nertera depressa	G	G	G	G	G	G
*Blechnum minus	—	H	H	H	H	H
Nertera dichondraefolia	—	G	G	G	G	G
*Dacrydium cupressinum	—	Su	St	T	T	T
Neomyrtus pedunculata	—	Su	Sh	St	St	St
Coprosma colensoi	—	Su	Sh	Sh	Sh	St
Pseudopanax colensoi *Philipson var.* ternatus *Wardle*	—	Su	St	St	T	T
Phyllocladus alpinus	—	Su	Sh	T	T	St
Coprosma parviflora	—	Sh	Sh	Sh	Sh	Sh
Coprosma foetidissima	—	Su	Sh	St	St	St
Myrsine divaricata	—	Su	Sh	Sh	St	St
*Phormium tenax	—	—	H	—	—	—
Gaultheria antipoda	—	—	Sh	—	—	—
*Metrosideros umbellata	—	—	T	T	T	—
*Blechnum capense	—	—	H	H	H	H
Griselinia littoralis	—	—	St	St	St	T
Weinmannia racemosa	—	—	T	T	T	T
Cyathodes juniperina	—	—	Sh	Sh	—	—
Podocarpus hallii	—	—	Sh	T	T	T
Dacrycarpus dacrydioides (*Rich.*) *deLaubenfels*	—	—	Su	Sh	Sh	T

Coprosma ciliata	—	—	Su	Sh	Su	Su
Coprosma lucida	—	—	Su	Sh	Sh	St
Clematis paniculata	—	—	L	L	L	L
Earina autumnalis	—	—	EH	E	E	E
Dendrobium cunninghamii	—	—	E	E	—	E
Hymenophyllum multifidum	—	—	G	E	E	E
*Dianella intermedia	—	—	H	—	—	—
Nothofagus solandri *v.* cliffortioides	—	—	Sh	T	T	St
Pseudopanax crassifolius	—	—	Sh	St	St	T
Grammitis heterophylla	—	—	E	E	E	E
Hymenophyllum rarum	—	—	E	E	E	E
Tmesipteris tannensis	—	—	EG	EG	EG	E
Astelia nervosa	—	—	H	H	H	H
Carmichaelia grandiflora	—	—	—	St	—	—
Pseudopanax simplex	—	—	—	Sh	Sh	—
Uncinia rupestris	—	—	—	H	H	H
Gleichenia cunninghamii	—	—	—	H	H	H
Luzuriaga parviflora	—	—	—	EG	EG	—
Libocedrus bidwillii	—	—	—	T	—	—
Nothofagus menziesii	—	—	—	T	T	T
Elaeocarpus hookerianus	—	—	—	St	St	T
Myrsine australis	—	—	—	Sh	Sh	St
Coprosma polymorpha	—	—	—	Sh	Sh	St
Grammitis billardieri	—	—	—	G	G	GE
Asplenium flaccidum	—	—	—	HE	E	E
Dicksonia squarrosa	—	—	—	H	H	St
Trichomanes reniforme	—	—	—	EG	EG	EG
Coprosma parviflora	—	—	—	Sh	Sh	Sh
Podocarpus ferrugineus	—	—	—	St	Sh	T
Lindsaea trichomanoides	—	—	—	H	H	H
Hymenophyllum revolutum	—	—	—	E	E	E
Lycopodium volubile	—	—	—	—	H	—
Histiopteris incisa	—	—	—	—	H	—
Pittosporum crassicaule	—	—	—	—	Sh	—
Hedycarya arborea	—	—	—	—	Su	St
Microlaena avenacea	—	—	—	—	H	H
Blechnum discolor	—	—	—	—	H	H
Ascarina lucida	—	—	—	—	Sh	St
Lycopodium scariosum	—	—	—	—	G	G
Lycopodium billardieri	—	—	—	—	—	E
Pseudopanax edgerleyi	—	—	—	—	—	T
Pseudopanax anomalus	—	—	—	—	—	Sh
Pseudowintera colorata	—	—	—	—	—	St
Carpodetus serratus	—	—	—	—	—	St
Astelia solandri	—	—	—	—	—	E
Earina mucronata	—	—	—	—	—	E
Schefflera digitata	—	—	—	—	—	Sh
Cyathea smithii	—	—	—	—	—	Sh
Hymenophyllum scabrum	—	—	—	—	—	HE
Hymenophyllum flabellatum	—	—	—	—	—	E
Rumohra adiantiformis	—	—	—	—	—	EH
Hymenophyllum sanguinolentum	—	—	—	—	—	E
Hymenophyllum armstrongii	—	—	—	—	—	E
Phymatodes diversifolium	—	—	—	—	—	HE
Freycinetia banksii	—	—	—	—	—	L
Ripogonum scandens	—	—	—	—	—	L
Metrosideros diffusa	—	—	—	—	—	L
Metrosideros fulgens	—	—	—	—	—	L
Metrosideros perforata	—	—	—	—	—	L
Rubus australis	—	—	—	—	—	L
Melicytus ramiflorus	—	—	—	—	—	St
Coprosma rotundifolia	—	—	—	—	—	Sh
Gahnia procera	—	—	—	—	—	H
TOTAL NUMBER	26	31	45	59	57	72

TABLE II. *Pollen analyses of two samples from a pakihi bog, Dismal Swamp, South Westland. Values are percentage figures based on total tree and shrub pollen counted. Analyses by Dr. N. T. Moar.*

	Basal peat *c.* 6.1 m depth	Underlying mineral material
Dacrycarpus dacrydioides	7	5
Podocarpus spp. (incl. *P. ferrugineus*, *P. spicatus* and *P. totara*)	18	17
Dacrydium cupressinum	31	30
D. bidwillii-biforme	1	2
Phyllocladus	2	3
Nothofagus fusca type	3	—
N. menziesii	9	—
Ascarina	3	2
Coprosma	8	19
Coriaria	2	—
Hoheria	1	2
Leguminosae	—	2
Leptospermum scoparium	1	3
Metrosideros	2	—
Myrtaceae	1	2
Myrsine	7	3
Pseudopanax	3	—
Astelia	1	3
Chenopodiaceae	tr.	—
Compositae	1	—
Cyperaceae	33	24
Gramineae	5	19
Gunnera	tr.	16
Haloragis	—	2
Hydrocotyle	tr.	—
Rumex	1	—
Rosaceae	tr.	—
Phormium	6	5
Mondete fern spores	29	92
Phymatodes diversifolium	4	6
Trilete fern spores	2	2
Cyathea colensoi type	41	40
Dicksonia squarrosa	2	—
Gleichenia circinata	15	2
Lycopodium	10	3
Sphagnum	30	50
Total tree and shrub pollen	262	62