

# FOREST COMPOSITION ACROSS GLACIAL TERRACES DIFFERING IN AGE IN SALTWATER FOREST, SOUTH WESTLAND

HOWARD M. ROGERS\*

School of Forestry, University of Canterbury,  
Private Bag 4800, Christchurch, New Zealand

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## ABSTRACT

Plant communities across three different-aged glacial terraces in a south Westland lowland podocarp forest were classified on the basis of floristic composition from 90 vegetation descriptions. Five forest communities were identified, differing in relative abundance of the main tree species and in species richness. One community was dominant on each terrace. Comparisons with other studies in the same forest suggested that differences in stage of soil development could explain floristic differences. The association of different forest communities with particular terraces suggests that species composition will shift over millennia towards a community dominated by *Dacrydium cupressinum* Lamb. and *Manoao colensoi* (Hook.) Molloy. These findings have implications for the sustainable management of south Westland's lowland podocarp forests.

**Keywords:** forest pattern; lowland podocarp forest; ordination; terrace age; soil development.

## INTRODUCTION

In south Westland, where forests vary along catenas of drainage and fertility, forest composition is related to landforms and soils (Chavasse 1962, 1971; Duncan *et al.* 1990; Norton & Leathwick 1990; Smith & Lee 1984; Sowden 1987). Plant community distributions commonly reflect a complex of landform characteristics such as slope, soil drainage, parent material, and landform stability. Studies of the vegetation composition in south Westland have generally investigated forest composition across a range of broadly defined landforms, and between similar landforms of different origin. Comparisons between different landform types have compared vegetation on recent alluvial surfaces, old glacial surfaces, and moraine hills (Norton & Leathwick 1990), and vegetation on alluvial fans, river gravels, beach deposits, and swamp deposits (Duncan *et al.* 1990), reflecting variation associated with a complex of soil-related environmental variables. Where studies have compared similar landforms of the same origin, successional mechanisms have been invoked to explain vegetation differences (Smith & Lee 1984; Sowden 1987). In Saltwater Forest the vegetation

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\* Present address: Forestry Department, Papua New Guinea University of Technology, Private Mail Bag, Lae, Papua New Guinea

composition of different landform types has been investigated (Norton & Leathwick 1990); however, the effect of age-differences between landforms of one type on forest composition in Saltwater Forest has not been considered previously. Sustainable forest management of the terraces in Saltwater Forest will be simplified by an ability to identify distinct floristic communities, and to understand the associated environmental factors. For the ecologically sustainable management of indigenous forests it is important to know whether or not one landform type can be regarded as a relatively homogeneous forest community. The study reported here investigated the influence of landform age on forest composition amongst three relatively old (>14 000 years) glacial terraces, and provided the last opportunity to investigate the vegetation distribution on the remaining unmodified glacial terraces in Saltwater Forest prior to selective logging.

## STUDY SITES

This study was conducted in Saltwater Forest on the West Coast of New Zealand's South Island. The study sites were situated at approximately lat. 43°08'S, long. 170°25'E, 10 km west of Harihari in the Whataroa Ecological Region and the Harihari Ecological District. The sites were located in lowland terrace rimu forest on terrace landforms (up to 60 m a.s.l) reflecting three discrete periods of glacial advance (Almond 1996) (Fig. 1).

## Vegetation

Low-altitude tall forest (below 400 m) in Westland has been broadly classified between forest types on mature soils on the fluvioglacial terraces, and those on recent alluvial surfaces (Wardle 1977). On the flats and terraces dense podocarps form the main canopy reaching over 30 m, above a subcanopy of angiosperms. *Dacrydium cupressinum*\* (rimu) is the dominant conifer of the lowland terrace forest, and stands are often described on the basis of their *Dacrydium* element (McKelvey 1984; Six Dijkstra *et al.* 1985).

The terrace forest of Saltwater Forest intergrades with pakihi wetlands and associated vegetation in Saltwater Ecological Area to the north-west (Norton & Leathwick 1990). To the south-east is conifer/angiosperm forest of Mt Hercules Scenic Reserve/Poerua State Forest. Kahikatea (*Dacrycarpus dacrydioides* (A.Rich.) de Laub.) forest occurs close to the Poerua River, on the recent alluvial surfaces along the northern margin of the forest (Norton & Leathwick 1990).

## Climate

Rainfall in Westland is frequent and long dry spells (15 days or more without rain) are rare. The Southern Alps act as a barrier to the prevailing westerly airflow, and create orographic rainfall which is often heavy and prolonged resulting in a high leaching environment. Rainfall is relatively evenly distributed through the year, but is slightly higher in spring. Annual rainfall in Saltwater Forest is likely to be similar to that at Harihari (3742 mm, New Zealand Meteorological Service 1983). Sunshine averages in coastal south Westland are reasonably high (e.g., 1882 h/yr at Hokitika) and comparable with the east coast of the South

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\* Nomenclature follows Allan (1961), Moore & Edgar (1970), Brownsley (1985), and recent taxonomic changes listed by Conner & Edgar (1987) unless otherwise indicated.

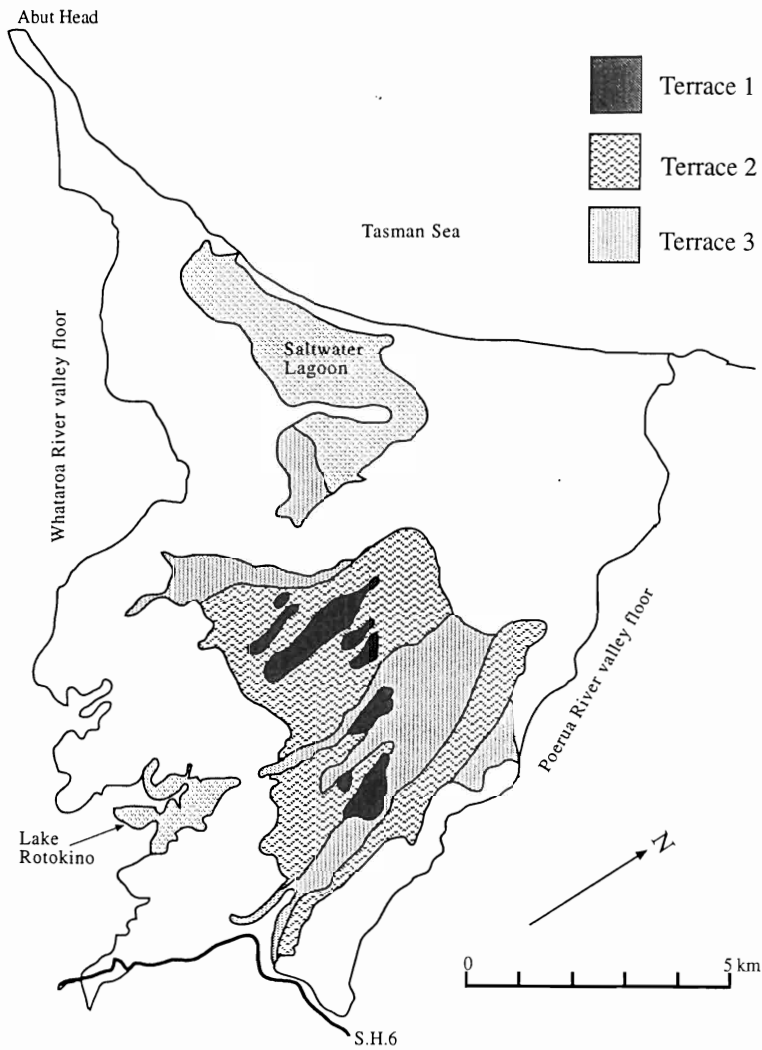


FIG. 1—Location of the glacial terraces in Saltwater Forest (redrawn from Almond 1996).

Island (1974 h/yr at Christchurch). The mean annual temperature at the study area has been calculated at 11.7°C, with a summer mean of 15.8°C and winter mean 7.2°C (Norton 1985).

### Geomorphology

Landforms in Saltwater Forest were formed largely by late Pleistocene glaciation, including both valley glaciers and piedmont ice sheets (Suggate 1965). The glaciers originated in the Southern Alps and during the Pleistocene extended beyond the alpine valleys out on to the piedmont, at times in some areas as far as the Tasman Sea (Almond 1996). The till and outwash gravels comprise Palaeozoic sedimentary, metamorphic, and igneous rocks (greywacke and argillite), of the Haast Schist and Tahua groups (granite) (P.Almond unpubl. data).

Much of Saltwater Forest consists of planar or gently undulating outwash terraces which decrease in elevation and slope towards the coast. The outwash surface has been dissected by late glacial and post-glacial fluvial action, resulting in an undulating landscape of terrace remnants, mounds, small rivers, and streams which generally run from south to north. In the past, the landscape was shaped by a fluvial system that was more active than at present (Almond unpubl. data). Present-day streams are isolated in narrow, stable channels (incised up to 7 m below the level of the dissected surface) and rarely, if ever, overtop their banks.

At least three discrete periods of glacial advance resulted in a complex system of different-aged terraces (Fig. 1) (Almond 1996). The oldest and major advance (Terrace 1) has been dated at greater than 22 600 years B.P. through the presence of Aokautere ash in loess deposits in soils on this terrace. Terrace 1 exists as finger-like remnants of a previously extensive terrace that was dissected by meltwaters from the advance associated with Terrace 2. The second advance (Terrace 2) deposited material over Terrace 1 in some places, but cut through in others. Terraces 1 and 2 are aggradational surfaces, but Terrace 3 comprises degradational terraces and relict channels formed when meltwater rivers incised into older till and outwash gravels. Terrace 3 is gently undulating in some places, which reflects the channels and sand bars of the meltwater river system. Almond (pers. comm.) has suggested that Terrace 2 is c. 18 000 years old and Terrace 3 is 14 000–16 000 years old.

## METHODS

Vegetation data were collected in unbounded plots (generally 400–500 m<sup>2</sup>) in the winters of 1991 and 1994 using a variation of the reconnaissance survey method of Allen (1992). Thirty plots were located on each terrace at 100-m intervals along randomly located transects, selected from a grid overlaid on to aerial photographs. The first plot on each transect was located at a random distance from the start of the transect. Distances were measured with a hip-chain. Across Terrace 1, some of the plots fell in heavily logged areas. When this occurred the plot was located in the next intact area of forest at least 30 m from the boundary of the logged area.

For each plot up to six physiognomic strata of variable height were recognised (ground, shrub, understorey, subcanopy, canopy, and emergent). For each stratum, all vascular species were recorded and their foliage cover was visually estimated and assigned to a cover class (<1, 1–5, 6–10, 11–25, 26–50, 51–75, 76–100%). At each sampling point, slope, aspect, and elevation were recorded. Drainage was not assessed for each plot because the subjective classification commonly used (Allen 1992) is unsuitable when all sites appear poorly drained and are relatively flat.

## Data Analysis

Vegetation data were classified to determine if terraces of different age were compositionally distinct, and ordinated to determine underlying compositional gradients. Species-abundance data were transformed using the programme RECINT (Hall 1992) which quantifies the ecological importance of the species observations by constructing a table of species importance values. Importance values act as mathematical weights, whose relative sizes measure how similar or dissimilar one plot may be to another (Hall 1992). Equal weight was given to each forest tier for this calculation. Classification of the plots was undertaken

based on their floristic composition using the RECINT output. Classification was performed using indicator species analysis (Hill *et al.* 1975) as implemented in TWINSpan (Hill 1979a). Default pseudospecies settings of 0, 2, 5, 10, and 20 were used.

Communities were identified from the TWINSpan dendrogram output and were named using a hierarchical approach similar to that of Atkinson (1985) with the following modifications: no parentheses or brackets around species indicates >10% cover, parentheses ( ) indicates 5–10% cover, and square brackets [ ] indicates <5% cover.

To interpret the vegetation pattern, indirect ordination of all plots was performed using detrended correspondence analysis (Hill & Gauch 1980) with the DECORANA program (Hill 1979b). The impact of rare species on the ordination was down-weighted (the default setting). A rare species is any species whose occurrence is less than 20% of the most common species. Ordination results were interpreted by comparing the four axes produced that summarise different amounts of floristic variation. An eigenvalue is associated with each axis. Generally, the higher the eigenvalue the more significant the axis is in depicting variation in the data (Hall 1992). However, if eigenvalues are relatively low, a significant drop in the eigenvalue from one axis to the next also suggests that the axis associated with the higher value models much of the floristic variation. In addition, the four axes were plotted against each other to visually assess how interpretable the gradients were.

## RESULTS

Altitudes of the plots ranged between 30 and 60 m a.s.l., with no measurable slope across the unbounded plot areas.

### Community Classification

Five communities were identified from the dendrogram (Fig. 2). The mean percentage cover summed over all strata of 62 species was used to summarise the vegetation differences between the communities (Table 1). In all communities *Dacrydium cupressinum* was the physiognomic dominant and generally dominated the canopy, while the understorey was dominated by the angiosperms *Weinmannia racemosa* L.f. and *Quintinia acutifolia* Kirk. However, cover of the conifers *Manoao colensoi*\*, *Prumnopitys ferruginea* (D. Don) de Laub., and *Phyllocladus* sp. aff. *alpinus* Hook.f. varied considerably amongst communities. High abundance of *Prumnopitys ferruginea* generally occurred with low abundance of *Manoao colensoi* and vice versa. Differences between the communities were also apparent in the cover of *Q. acutifolia*, the tree fern *Dicksonia squarrosa* (Forst.f.) Swartz, the small trees *Hedycarya arborea* J.R. et G. Forst. and *Myrsine australis* (A. Rich.) Allan, the ferns *Blechnum discolor* (Forst.f.) Keys and *Grammitis billardieri* Willd., and the climbing rata *Metrosideros diffusa* (Forst.f.) W.R.B. Oliver. The communities also differed in the number of species they contained—in particular, divaricating shrubs. On each terrace, a particular community was dominant (Table 2) reflecting floristic variation between terraces. A brief description of the communities follows based on the classification (Table 1) and field descriptions.

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\* *Manoao colensoi* sensu Molloy (1995)

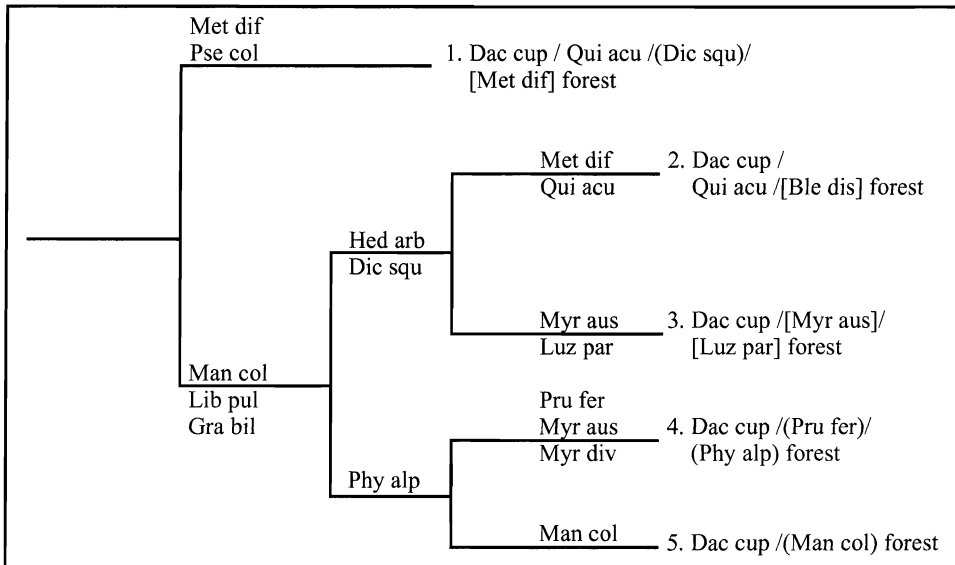


FIG. 2—Dendrogram showing indicator species and the relationship between the five plant communities. No parentheses or brackets around species indicates >10% cover, parentheses ( ) indicate 5–10% cover, and square brackets [ ] indicate <5% cover. Abbreviations of plant names use the first three letters of the generic name followed by the first three letters of the specific name. Full names are given in Table 1.

TABLE 1—Mean percentage cover abundance matrix for all species present in each of the five communities. + indicates species <1% cover. Boxes around numbers indicate >80% frequency in that community. Community names are given in the text.

Species	Community				
	1	2	3	4	5
<i>Coprosma ciliata</i>			+		
<i>Asplenium bulbiferum</i>		+	+		+
<i>Carex</i> sp.			+		
<i>Hymenophyllum</i> sp.			+	+	+
<i>Hymenophyllum scabrum</i>					+
<i>Lindsaea trichomanoides</i>				+	
<i>Manoao colensoi</i>	+	3	2	2	8
<i>Luzuriaga parviflora</i>	+	+	+	+	+
<i>Podocarpus hallii</i>		+		+	
<i>Grammitis billardieri</i>	+	+	+	+	1
<i>Coprosma lucida</i>	+		+	+	+
<i>Sticherus cunninghamii</i>	+	1	+	+	+
<i>Uncinia</i> sp.	+	1	+	+	1
<i>Libertia pulchella</i>	+	1	+	+	+
<i>Trichomanes reniforme</i>	+	+	+	+	+
<i>Phyllocladus alpinus</i>	+	1	2	8	+
<i>Coprosma colensoi</i>	+	+	+	+	+
<i>Elaeocarpus hookerianus</i>	3	5	3	3	5

TABLE 1—cont.

Species	Community				
	1	2	3	4	5
<i>Griselinia littoralis</i>	4	3	3	3	3
<i>Coprosma foetidissima</i>	2	3	3	3	3
<i>Blechnum procerum</i>	+	2	+	2	2
<i>Blechnum</i> sp. 1. "kiokio"	+	+	+	+	+
<i>Dacrydium cupressinum</i>	10	10	10	11	12
<i>Prumnopitys ferruginea</i>	6	7	3	9	3
<i>Weinmannia racemosa</i>	16	17	15	14	13
<i>Quintinia acutifolia</i>	15	16	9	8	11
<i>Pseudopanax colensoi</i>	2	4	2	2	2
<i>Pseudopanax crassifolius</i>	3	3	3	3	3
<i>Neomyrtus pedunculata</i>	3	4	5	5	5
<i>Nertera villosa</i>	1	2	+	+	+
<i>Astelia fragrans</i>	+	+	+	+	+
<i>Myrsine divaricata</i>	+	+	+	+	+
<i>Coprosma parviflora</i>	+	+	+	+	+
<i>Dicksonia squarrosa</i>	7	3	3	2	+
<i>Blechnum discolor</i>	2	2	+	+	+
<i>Ripogonum scandens</i>	+	+	+	+	+
<i>Nertera depressa</i>	1	+	+	+	+
<i>Hedycarya arborea</i>	+	2	2	+	
<i>Asplenium flaccidum</i>	+	+	+	+	
<i>Cyathea smithii</i>		+	+	+	
<i>Phymatosorus diversifolius</i>			+		
<i>Ascarina lucida</i>	+	+	+		
<i>Myrsine australis</i>	2	+	2	+	+
<i>Hymenophyllum demissum</i>	+	+	+	+	+
<i>Dacrycarpus dacrydioides</i>	+	+		+	
<i>Metrosideros diffusa</i>	+	+	+	+	
<i>Leptopteris superba</i>	+	+	+	+	
<i>Blechnum fluviatile</i>	+	+	+	+	
<i>Corybas rivularis</i>	+		+	+	
<i>Pseudowintera colorata</i>	+	+	+	+	
<i>Rubus cissoides</i>	+				
<i>Coprosma</i> sp.	+	+			
<i>Aristotelia serrata</i>	+			+	
<i>Elaeocarpus dentatus</i>	+				
<i>Schefflera digitata</i>	+				
<i>Carpodetus serratus</i>	+		+	+	
<i>Melicytus ramiflorus</i>	+				
<i>Coprosma rotundifolia</i>	+				
<i>Coprosma rhamnoides</i>	+			+	+
<i>Microlaena avenacea</i>	+			+	
<i>Rubus australis</i>	+				
<i>Melicytus lanceolatus</i>	+				

TABLE 2—The number of plots on each terrace in the five plant communities. Plant communities are described in the text.

	Community				
	1	2	3	4	5
Terrace 1	1	9	5	3	12
Terrace 2	15	1	1	8	5
Terrace 3	4	0	8	16	2
Total	20	10	14	27	19

(1) *Dacrydium cupressinum*/*Quintinia acutifolia*/*Dicksonia squarrosa*/[*Metrosideros diffusa*] forest (20 plots)

This community possessed 85% of all species recorded and was dominant on Terrace 2. *Dacrydium cupressinum* occurred as scattered tall emergents and was occasionally present throughout the other strata. *Quintinia acutifolia* was abundant in the understorey and occasionally present in the subcanopy together with *Prumnopitys ferruginea*. The shrub layer contained a diverse range of small tree species, in particular pepperwood (*Pseudowintera colorata* (Raoul) Dandy) and divaricating shrubs such as *Myrsine divaricata* A. Cunn. The tree fern *Dicksonia squarrosa* had its highest mean cover in this community and was present as conspicuous and tall specimens (2–3 m). The fern *Blechnum discolor* and the climbing rata *Metrosideros diffusa* were common on the forest floor.

(2) *Dacrydium cupressinum*/*Quintinia acutifolia*/[*Blechnum discolor*] forest (10 plots)

This community occurred more frequently on Terrace 1 than on the other terraces and contained 71% of all species recorded. The canopy was dominated by stands of *Dacrydium cupressinum* of similar height, with *Manoao colensoi* and *Prumnopitys ferruginea* and conspicuous tall *Quintinia acutifolia* stems in the subcanopy, but less evident in the understorey where *Weinmannia racemosa* dominated. *Hedycarya arborea* was common as a small tree up to 2 m.

(3) *Dacrydium cupressinum*/[*Myrsine australis*]/[*Luzuriaga parviflora* (Hook. f.) Kunth.] forest (14 plots)

This community occurred more frequently on Terrace 3 than on the other terraces, and contained 76% of all species recorded. The canopy was dominated by large and heavily branched *Dacrydium cupressinum*. The conifers *Prumnopitys ferruginea* and *Manoao colensoi* had their lowest mean cover in this community. The understorey and shrub layers were dominated by small stems of *Weinmannia racemosa*. *Myrsine australis* and *Hedycarya arborea* were common in the shrub layer. The kidney fern *Trichomanes reniforme* Forst. f. was common on fallen trees and rotting large branches.

(4) *Dacrydium cupressinum*/(*Prumnopitys ferruginea*)/(*Phyllocladus* sp. aff. *alpinus*) forest (27 plots)

This community was the most common and was dominant on Terrace 3, frequent on Terrace 2, and rare on Terrace 1. The community contained 76% of all species. It was characterised by scattered, large, heavily branched *Dacrydium cupressinum*. The conifers



*Prumnopitys ferruginea* and *Phyllocladus* sp. aff. *alpinus* had their highest mean cover in this community. *Prumnopitys ferruginea* occurred as large subcanopy trees with occasional stems present in the understorey and shrub layers, while *Phyllocladus* sp. aff. *alpinus* occurred mainly in the shrub layer, and in the understorey in gaps with *Weinmannia racemosa*. *Quintinia acutifolia* had its lowest mean cover in this community. *Astelia fragrans* Col. occurred as large individuals on the forest floor, mainly in the plots on Terrace 3. *Libertia pulchella* (R.Br.) Spreng. and *Grammitis billardieri* were common on the forest floor.

(5) *Dacrydium cupressinum*/(*Manoao colensoi*) forest (19 plots)

This community occurred most frequently on Terrace 1 and contained the least (58%) species. Stands were the most uniform consisting of dense poles of *Dacrydium cupressinum* and *Manoao colensoi* in the canopy and subcanopy. *Manoao colensoi* occasionally dominated; it had its highest mean cover in this community. Stems of *Weinmannia racemosa* and *Quintinia acutifolia* were sparse in the understorey, with occasional tall stems of *Quintinia acutifolia* in the subcanopy. The tree fern *Dicksonia squarrosa* had its lowest mean cover in this community, and the less common ferns (e.g., *Blechnum fluviatile* (R.Br.) Salom.), divaricating shrubs (e.g., *Coprosma rotundifolia* A.Cunn.), and small tree species were generally absent.

### Plot and Species Ordination

Axes 1 and 2 were used to summarise the floristic gradients. Other combinations of axes could not be interpreted, and the relatively large drop in eigenvalue from Axis 1 to Axis 2 suggests that Axis 1 modelled much of the variation (Fig. 3 and 4). The distribution of plots

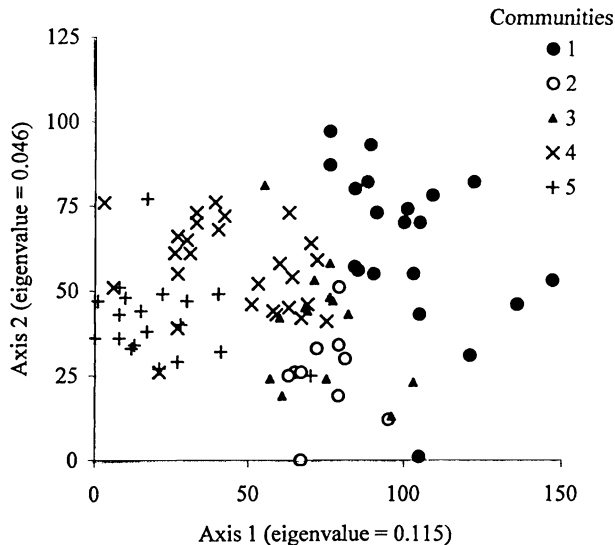


FIG. 3—Scatter diagram of Axis 1 and Axis 2 of the plot ordination obtained from the DCA output, with ISA communities superimposed. Community names are given in the text. Axis scales are in units of average standard deviation of species turnover ( $\times 100$ ).

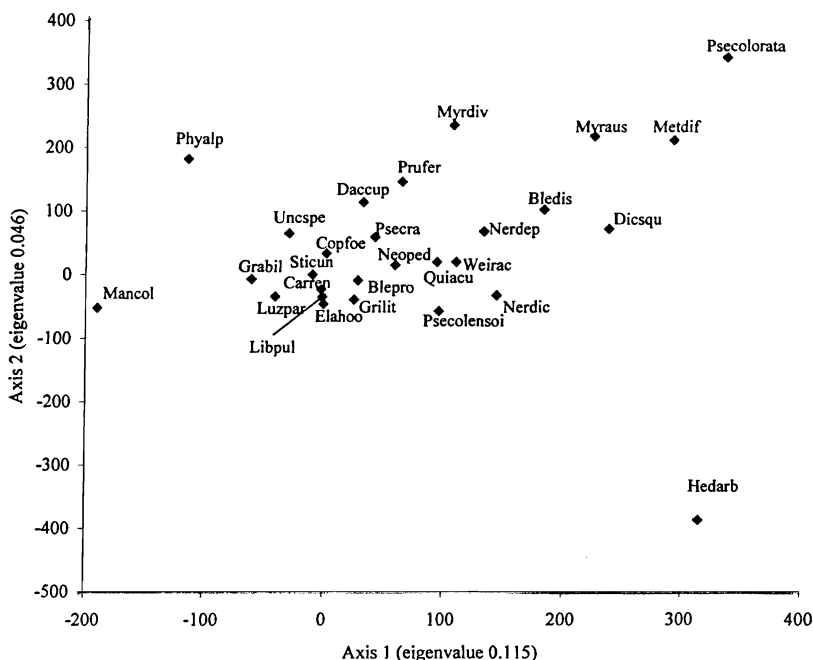


FIG. 4—Scatter diagram of Axis 1 and Axis 2 of the species scores from the DCA output. Only species that occur with a frequency of >80% in a particular community (Table 1) and indicator species are plotted. Full names are given in Table 1. Axis scales are in units of average standard deviation of species turnover ( $\times 100$ ).

in the ordination diagram in relation to the TWINSpan communities (Fig. 3) suggested a gradient along Axis 1 from Community 5 (associated with low scores and characterised by dense stands of *Dacrydium cupressinum*, the highest abundance of *Manoao colensoi*, and the lowest abundance of *Prumnopitys ferruginea*) to Community 1 (associated with high scores and characterised by scattered large emergent *Dacrydium cupressinum* and the lowest abundance of *Manoao colensoi*). Along Axis 2 the main separation of communities was between Community 2, mainly associated with low scores, and Community 4 associated with high scores. Community 2 was characterised by dense stands of *Dacrydium cupressinum* of even height while Community 4 was characterised by large scattered *Dacrydium cupressinum* and the highest abundance of *Prumnopitys ferruginea* and *Phyllocladus* sp. aff. *alpinus*.

The species ordination indicates a compositional gradient from low scores on Axis 1 (species more commonly associated with communities on Terrace 1, e.g., *Manoao colensoi*, and Terrace 3, e.g., *Phyllocladus* sp. aff. *alpinus*) to high scores on Axis 1 (species more commonly associated with Terrace 2, e.g., *Myrsine australis*, *Dicksonia squarrosa*, and *Metrosideros diffusa*) (Fig. 4).

## DISCUSSION

The distribution of plant species along environmental gradients has been documented in south Westland between different landform types (Norton & Leathwick 1990; Duncan *et al.*

1990; Norton 1994). In this study, however, floristic differences occurred within one landform type, outwash terraces, suggesting the influence of terrace age. Others have attributed changes in species composition across terraces in Saltwater Forest to stand age (Six Dijkstra *et al.* 1985) and to small changes in topography (Cornere 1992). Small changes in topography are more likely to account for smaller scale compositional changes. Although stand age will affect the species complement in a regenerating patch, the stands sampled here had reached canopy closure. For stands that have reached canopy closure, differences in stand structure and disturbance history are considered to have more influence on stand composition in south Westland's podocarp forests (Duncan 1993; Rogers 1995). The influence of stand structure on composition is supported by the separation of Communities 2 and 4 along Axis 2 of the plot ordination, reflecting differences between a dense stand of *Dacrydium cupressinum* of similar height and a less dense stand of large heavily branched *Dacrydium cupressinum* and large *Prumnopitys ferruginea*.

For such uniform terraces where age is the main variable, difference in stage of soil development is likely to be an important factor in compositional trends. As terrace soils age they become impoverished through deteriorating drainage and declining fertility, reflecting soil development. However, for such old terraces in Saltwater Forest differences in soil fertility have not been detected (P. Almond pers. comm.), but both soil drainage, as inferred from soil aerobic depth, and soil depth vary substantially from deep, extremely poorly drained soils on Terrace 1 to more shallow and less poorly drained soils on the younger Terrace 2 and Terrace 3 (Rogers 1995).

Differences in community composition described in the present study are similar to those described for Saltwater Ecological Area (Norton & Leathwick 1990) which were associated with a drainage gradient. Community 5 (*Dacrydium cupressinum*/*Manoao colensoi*) forest dominant on Terrace 1 is similar to their (*Dacrydium cupressinum*)/*Manoao colensoi*/*Phyllocladus* sp. aff. *alpinus* forest that occurred on poorly drained sites. Community 1 (dominant on Terrace 2) is similar to their *Dacrydium cupressinum*/*Quintinia acutifolia* forest that occurred on moderately drained sites. Community 4, dominant on Terrace 3, where *Prumnopitys ferruginea* was most common was not recognised in Saltwater Ecological Area; however, a forest community with *Prumnopitys ferruginea* was common on well-drained sloping sites (Norton & Leathwick 1990). These comparisons imply that the association of the dominant communities with differently aged terraces in part reflects soil drainage differences associated with soil development. Consequently, the uniform *Dacrydium cupressinum*, *Manoao colensoi* forest type (Community 5) dominant on Terrace 1 may reflect a community most suited to impoverished soil conditions associated with an advanced stage of soil development, while the *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Phyllocladus* sp. aff. *alpinus* forest type dominant on Terrace 3 may reflect a community best suited to less well-developed, and less impoverished younger soils.

In addition to floristic variation amongst terraces, there was variation in community composition within terraces, which cannot be explained in terms of a secular trend in soil development. However, changes in soil characteristics such as poor drainage can arise as a result of factors other than soil age (Smith & Lee 1984). The meltwaters of the glacial advances forming the terraces would have created a system of deep channels and raised sandbars similar to those present in the nearby Poerua River. Over time, organic matter would accumulate in the channels cut by the meltwater, promoting ponding and the

formation of very poorly drained organic soils. A similar explanation accounted for the floristic variation around mire-forest ecotones in the adjacent Saltwater Ecological Area (Norton 1989), and may in part account for the complex of *Dacrydium cupressinum*-dominated forest communities found within individual terraces.

The floristic gradient of the species ordination could be interpreted as reflecting a soil drainage gradient. *Phyllocladus* sp. aff. *alpinus* and *Manoao colensoi*, associated with low scores on Axis 1, are associated with poorly drained older surfaces (Norton & Leathwick 1990). In addition *Blechnum procerum* (Forst.f.) Swartz, also associated with low scores on Axis 1, favours poorly drained landforms while *Blechnum discolor*, associated with high scores on Axis 1, is associated with well-drained sites (Norton 1989). However, the distribution of *Manoao colensoi* has also been related to stage of forest development and disturbance pattern. Six Dijkstra *et al.* (1985) suggested that *Manoao colensoi* is generally outclassed by *Dacrydium cupressinum* trees as a stand matures, but Rogers (1995) and Ogden & Stewart (1995) suggested *Manoao colensoi* persists primarily on sites that are wet and have also been catastrophically disturbed. In the present study the position of *Manoao colensoi* on the ordination axes, associated with low scores on Axis 1, presumably reflected a combination of these factors.

Species richness also varied with stand characteristics. Stands with a relatively uniform canopy height had the lowest number of species (Community 5, dominant on Terrace 1) while the highest number of species occurred where canopy height was more varied and broken (Community 1, dominant on Terrace 2). A more varied stand structure would create a heterogeneous environment which allowed opportunities for species with greater niche differentiation than in a uniform stand (Whittaker 1975). This idea is consistent with the dominant disturbance histories on each of these terraces. Rogers (1995) suggested that infrequent catastrophic disturbance on Terrace 1 has resulted in homogeneous even-aged stands where *Dacrydium cupressinum* dominates associated species, but on Terrace 2 intermittent smaller-scale disturbances have resulted in a more heterogeneous environment.

Because of the uniformity in altitude, slope, and landform origin, changes in vegetation composition across the three terraces appear in part to reflect factors associated primarily with terrace age, which implies that the composition of the terrace forest will shift over millennia towards the Community 5-type forest dominant on the oldest terrace. However, the factors controlling the vegetation composition can only be inferred. Differences in stage of soil development, soil drainage, stand structure, and disturbance histories have been indicated as factors influencing the forest composition. Further investigation of the relative importance of these factors on each terrace in relation to the dominant communities described is required.

### Forest Management Implications

The dominance of one community on each terrace suggests a degree of floristic distinction between terraces. If forest management of indigenous forests is to be ecologically sustainable, efforts should be made to maintain the natural diversity and composition of each terrace, which may require different silvicultural treatments for each terrace. However, before this can be achieved criteria by which the dominant communities can be recognised in the field are required, together with further study of the dynamic processes that underlie the dominant communities.

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