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Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 1: The vegetation and soil patterns

A. F. Mark,¹ G. Grealish,² C. M. Ward³ and J. B. Wilson¹

This paper presents quantitative descriptions of the vegetation plus associated vascular flora and soils on a sequence of ten marine terraces that extend from a Holocene raised beach a few metres above sea level to a terrace remnant at an elevation of 630 m some 12 km inland. From the floristically rich coastal turf and scrub that occupies the most recent terrace there is a distinct sequence of vegetation. Tall mixed silver beech-podocarp-broadleaved forest on the lower altitude terraces (Terraces 2 to 4, <150 m elevation) grades via mixed mountain beech-podocarp-manuka woodland through shrubland to open bog on the five terraces above 250 m.

A postulated long-term, uninterrupted soil-vegetation chronosequence has not been confirmed. Soil development has been strongly affected by devegetation and surface deflation under periglacial conditions, and differential accumulation of loess during Pleistocene glacial periods. It is concluded that the vegetation pattern is related to a range of soil factors, particularly gradients in profile wetness that are associated with the increasing elevation between terraces and minor differences in topography within terraces.

The sequence provides an extensive, essentially unmodified and valuable soilvegetation complex representative of marine terrace ecosystems formerly of widespread distribution nationally, which justifies formal reservation.

Keywords: Vegetation sequence, Waitutu Ecological District, southern New Zealand, forest, woodland, shrubland, bog, soil, climosequence, chronosequence.

INTRODUCTION

Study area

One of the most distinctive geomorphological and ecological features of the Waitutu Ecological District (Simpson, 1982), on Fiordland's south-eastern margin, is the flight of some ten marine terraces which extends inland from the present coastline west of Sand Hill Point for up to 12 km and rises progressively to c. 630 m (Ward 1988).⁴

Description

The extensive terraced area is of generally low relief but is bordered on the west, north and east by mountain ranges that rise above the regional treeline. However, because it is open to the ocean on its southern edge, the area is exposed to the frequent southwesterly storms that sweep along the southern coast, and it is generally wetter and

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⁴ In the companion paper (Ward 1988) at least 13 marine terraces extending to 1040 m elevation are described. The highest "terraces", however, are eroded remnants now seen only as rounded near-level ridge crests. This paper concerns essentially *planar* terrace surfaces, of which the highest is a portion of Terrace 10 of Ward (1988) at 630 m altitude (*c.f.* inferred "shoreline" altitude of 660 m for that terrace).

cooler than the forests to the east. Although no climatological records are available from the District, rainfall is estimated at 1600-2400 mm annually near the coast, increasing inland to over 4000 mm (N.Z. Meteorological Service, 1973).

The extensive terrace surfaces are mostly underlain by a veneer of gravels derived from gneiss, granite and greywacke with a variable cover of loess that, according to Bruce (1984), tends to be thicker in coastal areas and on the eastern side of major waterways. The gravels overlie soft Tertiary sediments that are usually exposed by the deeply incised southward-flowing streams and rivers, the larger of which have their own series of alluvial terraces (Wood, 1969).

The extensive forest of the District has been described and mapped in general terms, largely by the National Forest Survey, whose primary aim was to assess the commercial timber resource (Holloway, 1952; Nicholls, 1976; Gover, 1978). Five broad forest classes were recognised, and within these, 31 forest and two shrubland types. Less than half of the area was sampled, and forest ranked as unmerchantable received little attention. General ecological information was obtained, and some has been published. Indeed, Holloway (1954) developed his climatic change hypothesis of forest instability in part from the forests of this District. Nicholls' (1976) account outlines the five broad forest classes and their distribution in the District. Podocarp forest, often very dense and, for western Southland, floristically rich, is extensive on the lower marine terraces in the east but only locally inland. Podocarp-beech forest, with various admixtures of podocarps, beeches and other hardwoods, characterises the alluvial terraces and the marine terraces of moderate elevation; increased stunting and changing composition may be seen in the stands "approaching an altitude of 300 m a.s.l." Beech-podocarp forest, characterised by abundant silver and mountain beech (Nothofagus menziesii and N. solandri var. cliffortioides), or either alone, with only very scattered podocarps, extends to about 450 m altitude on hill country and upper flood plains. Silver beech is more widespread with "mountain beech occurring consistently only at higher altitudes". Beech forest is widespread on hill slopes above the altitudinal limit of podocarps. Hardwood forest and shrubland characterise respectively areas adjacent to the coastal cliffs and above treeline on Hump Ridge to the east.

A generally representative series of the District's soils, apart from those on the higher terraces, has been surveyed, mapped and described at a reconnaisance level by Bruce (1984), following an earlier survey by Wright (1951). A recent wildlife survey of much of the District has rated the avifauna as relatively rich (Elliot and Ogle, 1985).

The present study, carried out during 12-19 May 1985, was aimed at compiling a comprehensive description and understanding of the inter-relationships between one of the Waitutu District's most important and distinctive landforms, the sequence of marine terraces west of Sand Hill Point (Ward, 1988), and its soil-plant-animal components. In particular, there was to be a critical assessment of the suggestion that the terrace sequence might contain a soil-vegetation chronosequence that not only predates the Pleistocene glaciation, but moreover, may have avoided much of its influence and still persist, relatively unmodified by European impacts. In this context it could resemble the classic chronosequence of ecosystems of Mendocino County, California, the so-called "pygmy forest ecological staircase" as described by Jenny (1980) and others (Jenny *et al.*, 1969; Westman, 1975). Their striking similarity in both physiography and physiognomy was stressed by Dr David Bellamy during a brief visit to the area with two members of the team (C.M.W. and A.F.M.) in September 1984. The only modification expected to the Waitutu terraces was by introduced mammals, particularly to the forest understorey by red deer and locally by pigs (Nicholls, 1976; Ross and Cuddihy, 1979).

Study transect and site selection

The terrace sequence east of the Angus Burn includes by far the largest remnant of the mid-altitude Terrace 6 and the only surviving essentially planar remnants of the higher Terraces 7, 8 and 10 (Fig. 1; *c.f.* Ward 1988, fig. 2). This dictated the choice of the study transect down the terrace sequence. However, privately-owned land extends about 2 km inland in this segment of the terrace sequence, and was not made available for study.



Fig. 1 - Map of part of Waitutu Ecological District showing the locations of the 16 sites studied in relation to the sequence of marine terraces (numbered 1 to 10 as for the study sites) and the limits of the last (Otiran) glaciation. Map based on Ward (1988).

This meant that the two lowest forested terraces (3 and 2) had to be sampled immediately to the west of the Angus Burn.

On each of the terrace surfaces, study sites were selected on the ground with the aid of colour vertical aerial photographs of approximately 1:15,000 scale. Sites were selected to represent as far as possible the interior of terrace remnants remote from the terrace edges and dissecting valleys, where there is a more or less obvious gradation of the vegetation towards that of the adjacent slopes (Fig. 2). On the more extensive Terraces 10, 6 and 4, three or four sites were selected to represent the range of vegetation visible in aerial photographs, whereas on the other terraces only one site was sampled (Fig. 1).

Chiefly because some of the terrace remnants are rather small, some sites are less than ideal in that they do not represent genuinely planar terrace surfaces remote from edge effects. The physical characters of the sites in relation to their terraces are described below in the order of sampling.

Sites 10A and 10B represent the 25 ha planar remnant of Terrace 10 at c. 630 m altitude. The estimated age of this terrace is c. 600,000 years (Ward, 1988). Site 10A is considered typical, whereas 10B is based on the wettest portion at the highest part of the terrace remnant, with some ponded water. Site 10C represents a seaward remnant of the same terrace, but reduced to a somewhat broadened, roughly planar ridge crest about 100 m wide, at which width edge effects are unavoidable. Site 9 is clearly not ideal,

but none better is available as this terrace remnant consists only of a broadly rounded ridge crest, gently sloping to seaward.

Terrace 8 is several hundred metres wide but the surface is gently undulating with local relief up to 5 m. This unevenness appears to have little influence on the vegetation, and the site is centred on the terrace remnant, mainly on a small-scale ridge. Terrace 7, though of much greater overall size, is sharply incised by several watercourses which create discernible edge effects. Site 7 is in the centre of one of the broader interfluves.

Terrace 6 is a very extensive (c. 600 ha) almost flat planar surface, which supports a wide range of vegetation types (Fig. 2). Four study sites were chosen to represent open bog-shrubland (Sites 6B and 6D), more uniform denser shrubland (Site 6A), and short forest or woodland occupying the northern 60 ha (Site 6C). Ward (1988) estimates the age of this terrace to be about 300,000 years. Terrace 5 remnants in the vicinity of the chosen transect are narrow ridge crests, or small shelves on which the soils are likely to be influenced by wash from the steep slopes behind them. Consequently, no attempt was made to sample this terrace. The only essential planar remnant of reasonable size is some 5 km distant, east of Crombie Stream.



Fig. 2–Vegetation pattern near the northeastern margin of the large Terrace 6 segment between Angus Burn and Crombie Stream. A mosaic of open bog and shrubland predominates, with a sharp gradation through dense woodland to tall beech forest at the edge of the large incised gully. Dense woodland is also extensive at upper right and upper left, while a band of low forest is associated with a sinuous watercourse near the lower edge of the photograph. The lower edge of the photograph spans c. 500 m.

Terrace 4 is very extensive and well preserved, but is divided into segments by sharply incised streams. Fans of alluvial silt derived from the eroded former sea cliff at the inland margin of this terrace have been deposited on the terrace surface. Widely spaced study sites were positioned seaward of this influence and remote from terrace edges. Not all the forest-type variation on this terrace could be sampled.

The only area of Terrace 3 available for study is dissected and the most suitable site present is on an interfluve no more than 200 m wide. Edge effects are possible but could

neither be assessed on the ground, nor avoided. Terrace 2 is more extensive and the site selected, although within 100 m of a terrace edge, appeared to be unaffected by it. Ward (1988) identifies Terraces 2, 3 and 4 to be of Last Interglacial age (80,000-120,000 years).

Terrace 1 is markedly different from the older and higher terraces. It is a mid-Holocene raised beach a few metres above sea level, and where it was sampled east of the Angus Burn, it extends inland from a low bank above the modern storm beach for about 30 m. No attempt was made to avoid edge effects in choosing a study site here.

Methods

Each study site measured 100 m \times 20 m. Three sample quadrats, each 20 m \times 10 m were selected at random within each site. Strata were recognised according to instructions given by Allen and McLennan (1983), except that emergent trees (tier 1) were virtually absent and so were not recorded separately. Cover values were estimated for each species in up to five categories, which were usually but not always recognisably distinct strata, as follows: trees (>12 m tall), small trees (5-12 m), large shrubs (2-5 m), shrubs (0.3-2 m), herbs (herbaceous species 0.3-2 m tall), ground layer (vascular plants <0.3 m tall). Lianes and epiphytes were merely listed by species for each plot, while diameters of all tree-sized stems (>10 cm d.b.h. or, in stands with low-branched stems, diameter at ground level) were measured. Canopy height was measured for each site, using an abney level for trees above 5 m. Bryophytes, which were a prominent feature of the vegetation at most sites, were recorded separately (Tangney, 1988). For details of nomenclature of flora, see Table 2.

Wood cores were extracted at breast height from usually five tree-sized stems of beech (mountain and/or silver beech), spread over the three quadrats in all except the coastal terrace, and one of the four sites (6B) on the large terrace at c. 300 m. Beech cores were also taken from one non-terrace site at 390 m in which both species were co-dominant. Diameters, heights and species of all stems were recorded and the cores stored in plastic drinking straws prior to mounting and polishing. The radial extent of the first and second groups of 10 growth rings from the trunk perimeters were later measured with a micrometer eyepiece at $\times 30$ with a binocular microscope.

Data for each of the three quadrats per site were pooled to obtain values for total and relative basal area and density of trees, as well as mean cover for each tier by species and mean total cover for each tier. Distribution records for vascular species in each of the three quadrats per site were independently subjected to classification and ordination. Twodimensional ordinations were calculated for the 106 vascular species (plus three lichens that were locally important on bogs and a liverwort on the coastal turf) recorded from the 48 quadrats using Detrended Correspondence Analysis (Hill and Gauch, 1980). In addition, an Inverse Cluster Analysis using the City-block distance measure and flexible sorting stategy (beta = -0.25) grouped the species according to their distribution patterns, and a Normal Cluster Analysis using City-block distance and average sorting strategy grouped the quadrats according to their species composition. For details of these methods see Sneath and Sokal (1973). The dendrograms were truncated at an arbitrary 8-group level.

The objective for soil sampling was to typify the soils within each study site rather than to select areas independently where soil development on the particular terrace might be expected to best represent the terrace. Auger holes were used to investigate the soils at each study site and a representative soil for the site was then selected, exposed and its profile described according to Taylor and Pohlen (1979), with horizon designations according to FAO/UNESCO (FAO, 1974). Samples were collected for subsequent analyses of pH (ratio of 1 g soil to 25 ml distilled water after pretreatment with hydrogen peroxide and sodium dithionite), total carbon and texture (Thomas, 1973), the last two using the <2 mm fraction. For analyses of total carbon, 0.05-0.35 g of air-dried, 2 mm sieved samples were weighed into crucibles, Sn, Cn and Fe metal accelerators were added and the samples ignited in a stream of oxygen for 3 minutes. Blanks and standards (CaCO₃) were also run. The CO₂ evolved on combustion in a Leco induction furnace was collected in a bottle containing "Ascarite" and the amount of CO₂ was determined by the weight difference.

RESULTS

Vegetation and flora

Details of the various analyses will be considered before describing the flora and vegetation at the various sites. The data from Terrace 1 were notably different from the rest, and had a substantial effect on all analyses. Nevertheless the ordinations of both quadrats and species based on Detrended Correspondence Analyses achieved satisfactory separations using the first and third axes (Figs 3 and 4). The two-way table arranges the species and quadrats in the groups from the Inverse and Normal classifications, respectively, and appears to show meaningful community and species groups (Fig. 5).

The distinctiveness of the flora of the coastal terrace (Site 1) is clear from the results of all the analyses. In the ordination (Fig. 3) the three quadrats from Site 1 are isolated on the extreme left of Axis 1. The species of the left-hand extreme of Axis 1 (Fig. 4) are correspondingly those found almost exclusively on this terrace. The classification (Fig. 5) shows the three Site 1 quadrats isolated at the 3-group level; species characteristic



Fig. 3-Two-dimensional ordination of the 48 quadrats from 16 sites on the Waitutu marine terraces, based on the first and third axes of a Detrended Correspondence Analysis of their floras.



Fig. 4 – Two-dimensional ordination of 110 plant species (3 lichens, 1 brophyte, and 106 vascular plants) recorded from the 48 quadrats at 16 sites on the Waitutu marine terraces, based on the first and third axes of a Detrended Correspondence Analysis. Plant names are abbreviated to the first three letters of the genus and species (full names appear in Table 2). Congestion on the left of Axis 1 has prevented 38 species being shown separately. Centred around Point 1 are: *Carex virgata, Elaeocharis acuta, Epilobium pedunculare, Galium propinquum, Holcus lanatus, Juncus pauciflorus, Montia fontana, Plantago triandra, Polystichum vestitum, Ranunculus foliosus and Trifolium repens. Around Point 2 are: Brachyglottis rotundifolia, Coprosma ciliata, Cotula dioica, Epilobium chionanthum, Marchantia berteroana, Muehlenbeckia australis. Around Point 3 are: Blechnum minus, Cardamine debilis, Colobanthus muelleri, Epilobium nerteroides, Fuchsia excorticata, Gunnera dentata, Hebe elliptica, Helichrysum bellidioides, Hydrocotyle novae-zelandiae, H. heteromeria, Hymenophyllum minimum, Isolepis cernua, I. reticularis, Juncus bufonius, J. gregiflorus, J. planifolius, Poa annua, P. pusilla, Pratia angulata, Rubus australis and Senecio minimus.*

of Terrace 1 (Species Groups 7 and 8) remained separate from all other species until the final fusion. The discontinuity is readily apparent in Figure 5: there is little overlap between the flora of Site 1 and those of the other sites.

The relatively tall forest stands of the three terraces below 150 m (Sites 2, 3 and 4A-C) are also fairly distinct; all 15 quadrats were classified together as Group D. In all of them, the 31 species of Group 5 were nearly always present, plus some of those from Groups 6 and 1 (Fig. 5).

Another major community comprises the mixed woodland on the better drained sites of the terraces above 250 m (Sites 6C, 7, 8, 9, 10C); all but one of the quadrats from these sites were classified together as Group E. Figure 5 emphasises the transitional character of this community. In addition to the species of Group 5 (which are shared with the tall forest below 150 m), these sites contain many of the species of Groups 1 and 3



Fig. 5-Two way nodal table for the 110 plant species and 48 quadrats at 16 sites sampled on the Waitutu marine terraces. The species have been grouped using an Inverse Cluster Analysis and the quadrats with a Normal Cluster Analysis (see text for details).

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Fig. 6-Quantitative information for the 31 more important species (at least 5% contribution to one stratum) from 16 sites studied on the Waitutu marine terraces. Sites are arranged, as in Table 1, according to their general vegetational similarity. The key (upper left) shows the order of presentation (relative tree basal area, relative tree density and percentage cover for each of five strata). Absolute values for strata are given in Table 1.

shared with the more poorly drained sites of the upper terraces, in particular pink pine (Halocarpus biformis), yellow-silver pine (Lepidothamnus intermedius), Cyathodes juniperina and Dracophyllum longifolium.

The relatively open stands of shrubland-bog that characterise the sites of poorer drainage



Fig. 7—Soil types associated with each of the 16 study sites on the Waitutu marine terraces. Sites are arranged on the same two-dimensional ordination as in Fig. 3, based on the flora of the quadrat in which the soil was sampled.

on the terraces above 250 m are clearly separated from the forest and woodland communities, and themselves separate into two communities (Groups F and G; Fig. 5). At the three shrubland-bog sites from the large mid-altitude terrace at 290-320 m (Sites 5A, 6B and 6D) most species from Groups 1 and 2 were recorded but relatively few of Group 3 species, whereas the two sites on the uppermost terrace above 600 m (Sites 10A and 10B) had most of the species from Groups 1 and 3 but relatively few from Group 2 (Fig. 5). This distinction between the mid- and higher-altitude terraces is also revealed in the ordination of the quadrats (Fig. 3). The quadrats of Sites 10A and 10B are quite distinct from Sites 6A, 6B and 6D on Axis 3, although not on Axis 1.

Results of the above analyses have been used as a basis for the one-dimensional ordering of the 16 sites to present the quantitative information (Fig. 6 and Table 1). Table 1 shows the reduction in tree basal area and canopy height from the forest on the lower terraces to that of the dwarfed open bog-shrubland communities of the higher terraces. Tree density (but not basal area) is markedly higher in the woodland of the upper terraces than in the tall lowland forest of Terraces 2, 3 and 4. There is no consistent trend in species richness.

Distribution patterns and performance of the more important species along the vegetation sequences are shown in Fig. 6. The low-growing species of permanently wet open sites are largely restricted to the more open areas of the dwarfed woodland and shrubland above 250 m. Among these, Oreobolus strictus, Donatia novae-zelandiae, Centrolepis ciliata, Lepidothamnus laxifolius and Gleichenia dicarpa are generally important, while several others are minor though characteristic, e.g. Gaimardia setacea, Drosera spp. and Gentianella lineata, together with several lichens, particularly Cladia retipora, C. sullivanii and Siphula decumbens. Mosses, especially Sphagnum cristatum, which are also usually important, were assessed separately (see Tangney, 1988). Water ponds of varying size also characterise the wettest sites, *e.g.* Site 10B (where they occupied 20% of the ground area) on the highest terrace and Sites 6B and 6D on the large mid-altitude terrace (3% and 8% water, respectively). On these sites Leptospermum scoparium (manuka), 3 to 5 m tall (decreasing with altitude) provides most of the open woody cover, but mountain beech, pink pine, yellow-silver pine, Dracophyllum longifolium and Cyathodes juniperina are usually also prominent here. The density and basal area of tree-sized stems, as measured at ground level, is very low (Table 1).

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utum ee stratum (>12m)* –	۔ ص	31	31	37	36	22	19	41	I	Ι	I	I	Ι	Ι	Ι	I
nall tree ratum (5-12m) —	-	9	15	23	23	22	15	19	32	12	l	1	ł	I	I	I
rge shrub ratum (2-5m) 1	1	3	8	6	7	15	21	16	22	26	28	69	28	14	9	ω
rub stratum $(0.3-2m)$ 15	7	9	4	2	3	11	14	15	17	37	77	49	42	65	31	21
erb stratum (0.3-2m) 24	5 1	6	10	4	2	1	0	0	0	0	0	0	0	0	0	0
cound stratum <0.3m) 7(3	12	39	21	14	31	31	18	17	28	73	44	45	83	89	59
mber vascular spp. 58	3 4	ł2	39	36	40	39	38	34	29	35	31	28	43	30	26	46
ter table depth (cm) 7^{t}	5 7	15	10	95	60	10	45	75	32	100	40	30	10	20	0	0-55

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With improved drainage on these two terraces (Sites 10A, 10C, 6A), as well as on Terrace 8 (Site 8), there is an increase in cover, height and diversity of the woody species. Southern rata (*Metrosideros umbellata*) and pokaka (*Elaeocarpus hookerianus*) are notable additions, although many of the typical bog speices persist on the relatively well-lit floor, *e.g. Cyathodes empetrifolia, Centrolepis ciliata, Pentachondra pumila, Oreobolus strictus, Empodisma minus, Lycopodium ramulosum*. Tree basal area increases to 23-35 m² ha⁻¹ and density to over 1000 stems per hectare, but the number of vascular species is not appreciably different from the wetter more open sites (Table 1).

Further increases in vegetation height and canopy cover associated with improved drainage (Site 9) plus decreased altitude (6C and 7) are characterised by the absence of typical bog species, a substantial increase in tree basal area (to 61-75 m² ha⁻¹) and high values for tree density (1430 to 2390 stems ha⁻¹). Total numbers of vascular species, however, remain unchanged at 29 to 38 (Table 1). A distinct herb layer is absent on the mid- and higher-altitude terraces, though numerous small plants of *Blechnum procerum* provide up to 20% of the ground cover.

However, all the forest stands below the extensive Terrace 6 at c. 300 m have a herb layer dominated by *Blechnum discolor* (crown fern). Another feature of these forests is a codominance of podocarps, mostly rimu (*Dacrydium cupressinum*), together with silver beech, only occasionally in association with mountain beech (Site 4C). Kamahi (*Weinmannia racemosa*) is usually prominent in these lower altitude forests, particularly as a subcanopy component, while miro (*Prumnopitys ferruginea*), *Neomyrtus pedunculata* and the tree fern *Dicksonia squarrosa* are also characteristic members of the community. The five stands studied on the three lower forested terraces (Sites 2, 3, 4A, 4B and 4C) all had canopy heights of 20 m or more and, as well, had generally similar values for densities (833 to 983 stems ha⁻¹) and basal areas (63 to 92 m² ha⁻¹) of trees (Table 1). The highest values for both canopy height and tree basal area, however, were recorded on the lowest of these terraces (Site 2).

Terrace 1 was sampled across most of its width where it is relatively well developed immediately east of the Angus Burn mouth (Fig. 1) at an elevation of c. 5 m above mean sea level. Here a zone of dense turf, 2-5 cm tall and of variable width up to c. 15 m, extends from a low bank above a boulder beach to a zone of dense coastal scrub containing dead emergent stems of southern rata and kamahi. There is an intermittent zone of ferns and low shrubs up to 10 m wide separating the zones of turf and coastal scrub. The relatively high species diversity recorded from the three plots on this site (58 species) reflects the heterogeneity of vegetation types sampled. The areas of turf are dominated by, in order of importance, Schizeilema nitens (15% cover), Poa pusilla (15%), Gunnera dentata (12%), G. monoica (8%), Cotula dioica (8%), Isolepis cernua (7%), Hydrocotyle novae-zelandiae var. montana (7%), and Marchantia berteroana (4%). Occasional tufts of Juncus gregiflorus, Carex virgata, C. appressa and C. coriacea are present both in the area of turf and in the fern zone that is dominated by Histiopteris incisa (20% cover), Blechnum discolor (5%), Coprosma ciliata (4%), C. rhamnoides (3%), with numerous sprawling plants of Muehlenbeckia australis, Rubus australis, R. schmidelioides, R. cissoides and some hybrids. Persistent and fallen dead tree trunks support a range of epiphytes (Table 2). The zone of coastal scrub, 3-4 m tall, at the rear of the terrace is dominated by Brachyglottis rotundifolia with minor amounts of Dracophyllum longifolium and Hebe elliptica.

Modification to the vegetation by red deer was evident throughout, while damage by pigs was confined to forested areas immediately below the large Terrace 6 at c. 300 m. Deer pellets were noted in most plots throughout the area; tracks were common; browse damage to broadleaf (*Griselinia littoralis*), kamahi, *Dicksonia squarrosa* and most *Coprosma* species was obvious, with some localised bark rubbing on stems of yellow-silver pine, rimu and *Neomyrtus pedunculata*. Also, the virtual absence of other than seedlings of three finger (*Pseudopanax colensoi*), of accessible foliage of broadleaf and of accessible plants of *Coprosma lucida* (only a few epiphytic specimens were seen in the study area) was in striking contrast with the numerous robust adult specimens of all three species in inaccessible stands on bluffs along the lower reaches of the Wairaurahiri River c. 8 km to the east (Fig. 1). In view of the presence of a well established deer population, the rarity of the

	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
LICHENS																
Cladia retipora								х		х				х	х	
C. sullivanii															х	
Eladonia alpestroides								х		х				х	х	
Siphula decumbens								х		х						
PTERIDOPHYTES																
Lycopodium ramulosum							х	х		х		x		х	х	х
Ľ. varium		х		х	х						x	x				
L. volubile											x					
Psilopsida																
Tmesipteris elongata	х															
T. tannensis	х	х	+			х			+							
Filicopsida																
Asplenium flaccidum		х	х	х	х	х			х							
Blechnum discolor	х	х	х	х	х	х										
B. minus	х															
B. procerum	х	х	х	х	х	х			х		х		х	х		х
Ctenitis heterophylla		х	х	х	х	х	х		х	х	х	х	+			
Cyathea smithii					х											
Dicksonia squarrosa	х	х	х	х	х	х										
Gleichenia dicarpa							х	х		х	х					
Grammitis billardieri		х	х	х	х	х			х		х	х	х			х
G. magellanica								х	х	х	х	х	х	х		х
Histiopleris incisa	х	х			x											
Hymenophylium armsirongii H dilatatum					х		х		х			х				
H Habellatum		x	X	••		•••			•••							
H Inglin		х	х	X	х	x			л		х	v	л			
H minimum	v			л												
H multifidum	Λ	v	v	v	v	v	v	v	v	v	v	v	v	v	v	v
H rarum		x	x	x	x	x	x	л	x	~	x	x	~	~	л	~
H. revolutum	x	x	x	x	x	x			~							
H. sanguinolentum		x	x	x	x	x				x					х	x
H. scabrum				х	х											
Polystichum vestitum	x															
Pyrrosia serpens			+													
Rumohra adiantiformis		х	х		х											
Schizaea fistulosa							х	х		х				х	х	х
Trichomanes reniforme						х										
GYMNOSPERMS																
Podocarpaceae																
Dacrydium cupressinum	х	х	х	х	х	х			х		х					
Halocarpus biformis				х			х	х	х	х	х	х	х	х	х	х
Lepidothamnus intermedius				х			х	х	х	х	х	х	х		х	
L. laxifolius								х		х						
$L.$ laxifolius \times intermedius										х						
Phyllocladus asplenufolius v.																
alpinus													х	х	х	
Podocarpus hallii	х	х	х	х	х	х	х		х		х		х			
Frumnopitys jerruginea		х	х	х	х	х					х					
ANGIOSPERMS DICTYLEDONS																
Apiaceae																
Actinotus novae-zelandiae							х	х						х	х	
Hydrocotyle heteromeria	x															
~ -														(co	ntin	ued)
														,00		

Table 2–List of vascular species¹ and important terrestrial lichens from sixteen study sites in Waitutu Ecological District. Species adjacent to study sites have also been noted (+).

Table 2 – Continued.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
H. novae-zelandiae v. montana Schizeilema nitens	x x															
Araliaceae Pseudopanax colensoi y																
ternatum	х	х	x	х	х	х	х		х		x	х	x	x	х	x
P. crassifolius		х	х	х	х	х			х		х					
P. linearis									х		х		х	х	х	х
P. simplex		х	х	х		х			х		х	х	х	х	х	
Asteraceae																
Brachyglottis buchananii Brachyglottis	v														+	
Cotula dioica	x															
Helichrysum bellidioides	x															
Lagenifera petiolata	х															
Olearia arborescens	х															
O. avicenniaefolia	х															
Senecio minimus	x												х			
Carvonhyllaceae	~															
Colobanthus muelleri	x															
Stellaria parviflora	x															
Cornaceae																
Griselinia littoralis		х	х	х	х	х	x		х		х	х			x	
Cruciferae																
Cardamine debilis	х															
Cunoniaceae																
Weinmannia racemosa		х	х	х	х	х			х		х		х			
Donatiaceae																
Donatia novae-zelandiae								х		х				х	х	
Droseraceae																
Drosera arcturi															x	
D. spathulata							х			х		х		х	х	
D. stenopetala														х	х	х
Elaeocarpaceae																
Elaeocarpus hookerianus		х		х	х	х	х		х		х		х			
Epacridaceae																
Archeria traversii Cwathodes empetrifolia		+		+			v	v		x		x		v	v	v
C, iuniperina			+	x		x	x	x	x	x	x	x	x	x	x	x
Dracophyllum longifolium				~			x	x	x	x	x	x	x	x	x	x
D. politum															х	
D. pronum															х	
D. uniflorum Pentachandra humila														x	x	
							х	х		х		х		х	х	
* Trifolium repens	v															
Frances	Λ															
ragaceae Nothofagus menziesii		v	v	v	v	v							v		v	
N. solandri var. cliffortioides		Λ	л	x	А	x	x	x	х	x	x	х	x	х	x	x
Gentianaceae																
Gentianella lineata										x						
G. montana								x		x					х	
Haloragaceae																
Gunnera dentata	х															
G. monoica	х															
Lobeliaceae																
Pratia angulata	х															
														(co	ntin	ued)

Table 2 – Continued.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10 B	10C
Loranthaceae																
Alepis flavida Peraxilla colensoi		x	x		x		х	х		x	х	х		х	х	х
Myrsinaceae																
Myrsine australis	х	х				х										
M. divaricata		х							х		х		х			
M. nummularia														х	х	
Myrtaceae																
Leptospermum scoparium Metrosideros umbellata	x	v	v	v	v	v	х	x	v	х	v	x	x	x	х	x
Necrostaeros ambenana Necmortus pedunculata	~	x	x	x	x	x			x		л	л	л	~		^
Onagraceae																
Epilobium chionanthum	x															
\tilde{E} . nerteroides	x															
E. pedunculare	х															
Fuchsia excorticata	х															
Plantaginaceae																
Plantago triandra	х															
Polygonaceae																
Meuhlenbeckia australis	х															
Portulacaceae																
Montia fontana	х															
Ranunculaceae																
Clematis paniculata			х													
Kanunculus foliosus	х															
Rosaceae																
Rubus australis	х				х											
R. cissoides R schmidelioides	x +															
R. schmaenonaes	•															
Cobrosma cuneata													v	v		
C. ciliata	x												Α	А		
C. colensoi		x	х	x		х	х		x		х	х	х	х	х	х
C. crenulata														х	х	
C. foetidissima	х	х	х	х	x	х	х		х		х	х	x	x	x	x
C. pseudocuneata C. rhamnoides		x	v			v							х	х	х	x
Galium propinguum	x	~	~			4										
Nertera depressa	х		х			х										
N. cf. dichondraefolia		х	х	х	х	х										
Scrophulariaceae																
Hebe elliptica	x															
Stylidiaceae Forstera tenella														v		
Thumalaaaaaa														л		
Pimelea gnidia														x		
Winteraceae																
Pseudowintera colorata				+												
MONOCOTYLEDONS																
Centrolepidaceae																
Centrolepis ciliata Gaimardia setacea							х	X		x		х		X	x	x
								х		х				X	х	
Carer abbressa	v															
C. coriacea	x															
														(00	ntin	hau

Table 2 – Continued.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
C. flagellifera	+															
C. virgata	х															
Carpha alpina							х	х		х					х	
Elaeocharis acuta	х															
Gahnia procera												х		х	х	х
Isolepis aucklandica							х			х		х		х	х	х
1. cernua	х															
I. reticularis	х															
Oreobolus impar														х	х	
O. strictus							х	х		х		х		х	х	
Uncinia rupestris		х	х	х												
Iridaceae																
Libertia pulchella		х	х	x	x	x			х		х		х			x
Juncaceae																
* Juncus hufenius	v															
Juncus Dujonius I gregiflorus	×															
J. gregijiorus I. bauciflorus	v															
J. paucifiorus I. planifolius	л У															
J. planijolius	л															
Liliaceae																
Astelia nervosa																х
Herpolirion novae-zelandiae								х								
Luzuriaga parviflora		х	х	х	х	х			х		х		х	х	х	х
Orchidaceae																
Aporostylis bifolia							х		х			x	х	х	х	х
Ćorybas oblongus											х					
C. trilobus				+		х					х					
Earina autumnalis		x	х	х	х	х			х	х	х					
E. mucronata		х	х	х	x	х					х	х	х			
Dendrobium cunninghamii		х	х	х	х	х					x	х				
Thelymitra venosa							х	х							х	
Pozceze																
Agrostic muscosa	v															
Chionochlog acicularis	л												v	<u>ــــــــــــــــــــــــــــــــــــ</u>		
* Holeus lanotus													x	т		
*Pog annug	X															
P pusilla	X															
1. pasitia	х															
Restionaceae																
Empodisma minus							х	х		х		х		х	х	
Smilaceae																
Ripogonum scandens		х														

Nomenclature follows Galloway (1985) for lichens and Allan (1961), Moore and Edgar (1970) for indigenous vascular species, as appropriate except where subsequent revisions have been made (Brownsey *et al.* 1985, Connor and Edgar 1987), and Keble Martin (1982) for adventives (indicated with an asterisk preceding their names).

unpalatable pepper tree (*Pseudowintera colorata*) on the marine terraces is surprising, although it is prominent on the flood plain of Crombie Stream and other alluvial sites.

Information on diameter growth rates of beech trees at 14 of the 16 study sites is summarised in Table 3, where sites are arranged according to these rates. In about half of the sites between Terraces 4 and 10, one of the five cores showed growth rings insufficiently distinct to be usable. Analysis of variance of the growth rate values revealed a highly significant difference between sites, but none between the two decades measured (1966-75 and 1976-85), and no significant interaction, so that the results for the last two decades have been pooled (Table 3). On the one site where both beech species were present (4C) the mean ring width in mountain beech trees (0.53 mm) was only 62% of that in silver beech (0.85 mm) whereas in a steep hill slope forest stand near Terrace 6 at c. 360 m, where both species were codominant (canopy height c. 20 m) the differences were

Table 3– Values for mea marine terraces. Values included. Cores and diame	n widths are based ster measu	of growth on the ou trements w	rings from tter 20 gr vere taken	n trees of owth ring from brea	two beec s on usua st height f	h specie dly five or trees e	s at 14 s trees per	ites (onl r site. N g 5 m tal	y one si Aean dia Il, and at	te, 4C, uneters t 50 cm	containe and hei for trees	ed both ghts of with me	species) the sterr an heigh	on the ¹ is measu its less th	Naitutu ıred are an 5 m.
Site Number Altitude (m)	4A 135	4B 125	3	4C 125	2 50	7 355	4C 125	6C 315	6A 310	8 460	6D 300	9 570	10B 630	10C 600	10A 625
Species ¹ Species ¹ Mean ring width (mm) ²	N. men 1.25	N. men 1.22	N. men 1.00	N. men 0.85	N. men 0.82	N. sol 0.65	N. sol 0.53	N. sol 0.52	N. sol 0.52	N. sol 0.45	N. sol 0.42	N. sol 0.42	N. sol 0.34	N. sol 0.26	N. sol 0.19
Significant differences ³															
Mean tree diameter (cm) ⁴	65.0 ±5.7	63.6 ±7.5	55.6 ± 12.3	29.0 ±3.7	42.3 ± 10.4	24.8 土2.3	45.5 ±5.4	24.2 ±1.9	14.2 ± 2.5	$\begin{array}{c} 16.0 \\ \pm 1.1 \end{array}$	16.7 ± 3.7	24.6 ±4.0	15.4 ± 2.6	14.8 ±1.8	11.4 ±0.6
Mean tree height (m) ⁴	22.8 ±1.1	23.0 ± 1.0	21.2 ±1.2	$\begin{array}{c} 20.4 \\ \pm 1.2 \end{array}$	22.5 ± 0.6	11.6 ± 0.5	± 1.5	13.4 ± 0.5	4.4 ±0.4	4.9 ±1.0	$^{4.2}_{\pm 0.1}$	4.6 ±1.4	± 0.2	3.4 ± 1.0	2.4 ± 0.2
 N. men = Nothofagus n Values are geometric The lines join values ⁴ ± Standard error. 	<i>tenziestii</i> ; h means. not signif	I. sol = N. icantly dif	solandri v fferent (P	ar. <i>cliffor</i> = 0.05) b	<i>tioides.</i> ased on I)uncan's	New M	fultiple	Range '	Test.					

reversed; the mean ring width for silver beech (0.62 mm) was only 76% of that for mountain beech (0.82 mm). An analysis based on the growth rates of the two species at the two sites where both were present (Site 4C plus the hill slope stand), showed a significant (P < 0.01) species × site interaction. The variation in diameter growth rates of beech trees between study sites conforms in general with the pattern of the plant communities; growth rates tend to decrease in those towards the right and/or top of the axes in Fig. 3.

Soils

The soils of the 16 sites are classified into broad groups in Table 4. Values for pH, texture and carbon content for some representative horizon samples are given in Table 5. Water table depths at the time of the study are included in Table 1. Detailed profile descriptions according to Taylor and Pohlen (1979) with FAO/UNESCO horizon designations, are given in Appendix 1.

There is a general correlation between the plant community patterns and the broad soil groups (Fig. 7). Yellow-brown earths and podzols are associated with the forestwoodland communities (Sites 2, 3, 4A, 4B and 4C, 6C, 7 and 9) that have a moderate rating on Axis 1 of the ordination (Fig. 3). These soils have a very soft, humic silt loam to sandy loam topsoil, over a humic eluviated horizon with a gritty silty texture, containing clean quartz grains, on a firm, massive, sandy loam gleyed horizon and/or gravels. Gleyed podzols are associated with the communities that fall somewhat higher on this axis of the ordination (Sites 8 and 10C). These gleyed soils have a peaty horizon over a soft, humic silt loam, structureless horizon on a firm, massive, reduced horizon with a texture

Terrace Site No.	New Zealand Classification	U.S.D.A. Classification
1	Organic soil	Medihemist
2	Podzolised YBE	Haplaquod
3	Podzolised YBE	Sideraguod (or Haplaguod)
4A	Gleyed YBE (Podzolised)	Sideraquod (or Haplaquod)
4B	Gleyed YBE (Podzolised)	Sideraquod (or Haplaquod)
4C	Gleyed YBE (Podzolised)	Sideraquod (or Haplaquod)
6A	Organic soil	Medihemist
6B	Organic soil	Luvifibrist
6C	Podzolised YBE	Sideraquod (or Halplaquod)
6D	Organic soil	Medihemist
7	Podzol	Placaquod
8	Gley Podzol	Haplaquod (or Sideraquod)
9	Podzolised YBE	Haplaquod (or Sideraquod)
10A	Gley	Humaquept
10 B	Organic soil	Luvifibrist
10C	Gley Podzol	Haplaquod (or Sideraquod)

Table 4-Classification of the Waitutu marine terrace soils according to both the New Zealand classification (Taylor and Pohlen 1979) and the U.S.D.A. classification.

ranging from silty clay loam to gritty sandy loam, on gravels. A gley is associated with the community located in the upper right corner of the ordination (Site 10A) while organic soils characterise those located towards the lower right (Sites 6A, 6B, 6D and 10B) and also at Site 1 on the Holocene raised beach that is subject to excessive salt spray. These organic soils have a thick (>40 cm), dark reddish brown, very moist, soft, peaty horizon over a sandy reduced horizon and/or gravels.

Rooting depth in all soils only rarely exceeds 60 cm. Common barriers to roots are the firm, massive, reduced horizons or compacted gravels. The soils are generally very poorly to poorly drained—most had a high water table at the time of our visit in mid-May 1985 (range 0 to 100 cm—see Table 1 and Appendix 1).

An attempt has been made to classify the Waitutu soils according to the American Soil Taxonomy (Table 4), but in the absence of detailed chemical and physical analyses this must remain tentative. While classification of the Histosols are relatively

				-	Fexture	2	
Site No.	Horizon	pH^1	%C	% Sand	% Silt	%Clay	Textural Class ³
1	Om ₁	4.5 (5.0)	13.17				
2	Ah	~ /		60.1	28.0	11.9	Sandy loam
2	$\mathbf{C}\mathbf{g}$			46.3	31.6	22.1	Silt loam
4A	Aň	4.3					
4A	Brg			47.7	34.1	18.2	Silt loam
4C	Cg			63.8	24.1	12.1	Sandy loam
6A	OF_1	(4.2)	17.65				,
6A	OF ₂	(4.0)	22.41				
6A	AL	~ /	11.59	52.2	30.1	17.7	Silt loam
6A	В		4.99	48.6	26.0	25.4	Silt loam
6A	С			69.6	17.8	12.6	Sandy loam
6C	Bw			49.8	27.1	23.1	Silt loam
6C	$\mathbf{C}\mathbf{g}$			53.1	22.9	24.0	Silt loam
6D	Om	(3.8)	41.47				
6D	Oh	4.6 (4.4)	41.48				
7	$\mathbf{A}\mathbf{h}$	4.5 (4.6)					
7	Eh		3.42	77.0	12.9	10.1	Sandy loam
10C	Ah	4.4 (4.6)	4.34	75.9	15.5	8.5	Sandy loam

Table 5 - Values for pH, percentage carbon and texture for some representative soils and horizons from nine sites on the Waitutu marine terraces.

Values in brackets are for soil which previously had been air dried.

² Method according to Thomas (1973); values expressed on an organic- and iron-free basis.
 ³ Based on Taylor and Pohlen (1979).

straightforward (Luvifibrists and Medihemists) and the remaining soils are clearly in an aquic soil moisture regime, the distinction between Aquods and Aquepts is less clear since it is based on the presence or absence of a spodic horizon. In most cases the spodic horizon was recognised on macroscopic criteria, but where these were equivocal and detailed chemical indices are necessary that were not determined in this study, then only tentative identification was possible. Although spodic horizons were not unequivocally determined they were assumed to be present in most places.

DISCUSSION

The main sequence of communities is expressed well by Axis 1 (Fig. 3). This axis might appear at first to be primarily a reflection of altitude. However, it is more likely that the discrimination of the shrubland-bog communities on Axis 3 is principally due to altitude: Axis 1 instead might reflect reductions in soil fertility, as a function primarily of terrace age and only secondarily of elevation, *i.e.* a chronosequence. Alternatively wetness (rainfall/drainage) might be the main environmental gradient expressed by Axis 1.

The vegetation pattern both between and within the terraces is influenced by edaphic factors such as rooting depth, wetness and fertility. The very poorly-drained organic soils above c. 300 m are associated with a mosaic of open areas of bog with dense thickets of woodland and/or scrub. The characteristic species of the bogs include the cushions Donatia novae-zelandiae, Centrolepis ciliata, Oreobolus pectinatus; the trailing shrubs Cyathodes empetrifolia, Pentachondra pumila, Lepidothamnus laxifolius; plus Empodisma minus, Lycopodium ramulosum, the lichens Cladia retipora, C. sullivanii, Siphula decumbens, Cladonia alpestroides, and sphagnum moss (Sphagnum cristatum). The scrub component, up to 5 m tall, is dominated by manuka, pink pine, mountain beech and also usually yellow-silver pine. Density and basal area of tree-sized stems are both relatively small. The scrub component of the mosaic grades into dense woodland of similar composition that is associated with gleys and gley podzols. These are coarse-textured soils that are only slightly better drained than those associated with the bog-shrubland areas. Tree basal area remains small at 26-35 m² ha⁻¹ but tree density is relatively high at 1240-1540 stems per ha.

Somewhat better-drained podzolised or gleyed yellow-brown earths support forest

16-28 m tall, dominated by mountain beech on the terraces above c. 300 m and by silver beech in association with rimu and kamahi at lower altitudes. Below 300 m there is a dense herb layer of *Blechnum discolor*. The basal area of trees in these forests is generally in the range of 63-90 m² ha⁻¹, while tree density varies from 830 to 980 stems per ha.

Diameter growth rates of the two beech species in general reflect the variation in site conditions; values for mean ring width of the outer 20 growth rings range from 0.19 to 1.25 mm. Values for rings of silver beech in the taller forest stands on the terraces below c. 150 m are substantially wider (range 0.82-1.25 mm) than those for mountain beech that characterises the woodland-shrubland stands under 15 m tall that are located above this altitude (range 0.19-0.65 mm). These differences are greater than can be accounted for by altitude alone (Wardle 1984, fig. 10.7) and undoubtedly reflect the wide variation in site conditions.

The soils of the wooded sites on the terraces below 400 m appear to be Spodosols with an aquic moisture regime, and are either Sideraquods or Haplaquods. Haplaquods are low in free iron whereas Sideraquods have a high content due to some external source. The four soils described from the Mendocino terrace sequence in California (Westman, 1975) are also Spodosols, two Sideraquods and two Haplorthods (Orthods are more or less freely drained Spodosols).

By contrast, the higher altitude terraces and those other sites with cushion bog-shrubland mosaics are Histosols characterised by the accumulation and persistence of organic matter in response to the persistently high water table plus relatively low temperatures and pH. An aquic soil moisture regime indicates reducing conditions, with the water perched above the spodic horizon and/or tightly compacted gravel beneath.

The broad range of plant communities represented along the sequence of ten marine terraces described here from the Waitutu Ecological District—from tall mixed silver beechpodocarp-broadleaved forest on the lower forested terraces through mountain beechpodocarp woodland at mid-altitudes to mosaics of dwarfed, manuka-mountain beechpodocarp shrubland and cushion bog on the higher and older terraces—at first glance suggests a soil-vegetation chronosequence. This wide range of vegetation appears to conform with the geomorphological evidence for both the substantial time range involved in the origin and development of the terrace sequence—up to c. 600,000 years for Terrace 10—plus the absence of direct influence of glacial ice on the area during the Pleistocene (Ward, 1988).

However, the soil profiles of the higher terraces contain feldspar grains, as well as granite and amphibolite pebbles, that are only slightly or moderately weathered, implying no great age for these soils. Presumably they are much younger than the inferred terrace ages of 300,000 to 600,000 years (Ward, 1988). A well-defined pebble layer is present at several sites on the highest terraces, immediately underlying the solum and overlying slightly pebbly silt or sandy loams probably derived from late Tertiary marine sediments. The pebble layer is interpreted as lag gravel formed mainly by wind deflation during glacial periods, the late Otiran in particular, when the upper terraces probably had a severe alpine or periglacial climate.

Conversely, the parent material of the soils of Terraces 2-4 is for the most part loess (of presumed late Otiran age), as previously observed by Bruce (1984), who noted loess overlying peat on Terrace 2 west of the Waitutu River. Again, the soils are clearly younger than the ages of the terraces on which they have formed (80,000-120,000 years for Terraces 2-4, according to Ward, 1988). The consequence of wind deflation of the higher terraces combined with loess accumulation on the lower ones is a strong tendency for all the marine terrace soils to be "reset" at an age corresponding to the end of the last (Otiran) glaciation, that is, about 14,000 years B.P.

Some residual effect of the pre-Holocene history of soil development may persist in the modern soils of the higher terraces. However, it is likely that edaphic factors other than soil age, especially drainage, are more significant in explaining the vegetation differences between the lower and higher terraces.

Striking variations in the vegetation within single terraces may be attributed to the

influence of drainage. For example, on Terrace 6, scrub like that at Site 6A typically occupies an intermediate zone between bog-shrubland (Sites 6B and 6D) and a sharp ecotone to tall beech forest within 10-30 m of the edge of incised gullies or the outer terrace edge (Fig. 2), as well as dominating the entire western half of the large Terrace 6 remnant. Similarly, on Terrace 4 there are several 10-20 ha patches of very poorly drained organic soils (Aan soils of Bruce, 1984, and Wright, 1951) that closely resemble those of Sites 6A, 6B and 6D, which support an open woodland community of yellow-silver pine, pink pine, unthrifty rimu and mountain beech, and locally manuka over Dracophyllum longifolium and Cyathodes juniperina. This community, while analogous to the bog-shrubland of Terrace 6, is perhaps intermediate in character to the woodland communities of Sites 6C, 7 and 8. This vegetation type, described by Holloway (1954) and mapped as Type Y in the National Forest Survey (Gover, 1978; Nichols, 1976), is conspicuous on airphotos but was not available for study within Waitutu State Forest in the vicinity of the Angus Burn. There are small patches of it on Terrace 4 in the forest east of Crombie Stream, and an extensive area of similar vegetation on Terrace 2 west of the Waitutu River. The "Y" patches appear to be sites of abnormally low gradient or shallow hollows on Terrace 4, which has an average slope of about 1°. Terrace 2, immediately west of the Waitutu River, has an average gradient of 0.4° (0.007) and this lower gradient, combined with the increased rainfall to the west, is probably responsible for the poorer drainage, the development of an organic soil and the formation of a yellow-silver pine bog forest.

The large Terrace 6 remnant traversed in this study has an average gradient of about $0.006 (<0.5^{\circ})$. The apparent degradation of the vegetation of Terrace 6 compared with the typical forest of Terrace 4 is probably a result mainly of excess soil moisture (poorer drainage) on Terrace 6 due to lower gradient combined with higher rainfall and lower temperatures, and hence lower evapotranspiration and biological productivity.

CONCLUSIONS

We infer that increasing wetness is the principal environmental gradient reflected by Axis 1 of Fig. 3, and is the factor most responsible for the vegetation sequence up the marine terraces. This wetness gradient results from a combination of rainfall, drainage quality (slope and degree of dissection of the terraces) and the indirect effects of altitude. It appears that the extreme position of Site 1 quadrats in Fig. 3 can be rationalised as a response to the salinity of this coastal site which reduces the effective moisture availability and also retards decomposition of organic matter.

We reject an alternative interpretation, that progressive soil degradation, as a consequence of greater soil age with increasing terrace age, is responsible for the vegetation sequence on the Waitutu marine terraces. This conclusion is consistent with those of investigations of alluvial terrace sequences in Westland (Stevens, 1968; Ross *et al.*, 1977; Smith and Lee, 1984), under generally similar conditions of high rainfall and relatively low temperatures, that vegetation and soils on terrace gravels may develop to a severely degraded condition over a period substantially less than the age of all but the youngest marine terraces at Waitutu.

Although further study of the variation in soils and vegetation both between and within the terraces is desirable, it is clear from the present study that the wide range of soils and the diversity of vegetation types are closely interrelated. The changes in physiognomy and several of the floristic features of the vegetation sequence on the Waitutu terraces resemble those described by Wardle (1980) for the later stages of primary succession in Westland National Park, in particular the deterioration from "climax" forest to heathland and pakihi that is associated with soil changes to gley podzols with impervious iron pans. Beech, however, is conspicuously absent from the central Westland region; and the mosaic pattern of bog-shrubland at Waitutu is unknown in Westland pakihi bogs, most of which have a zonation pattern of vegetation and have been strongly influenced by fire in recent centuries (Holloway, 1954; Rigg, 1962; Mark and Smith, 1975). Apart from some modification by red deer and locally by feral pigs, the extensive Waitutu terrace system is in an unmodified state and notably free from the effects of fire.

Marine terraces or their remnants are widespread features of the New Zealand coastal

zones (New Zealand Geological Survey, 1983), but coastal flatlands have long been the focus of human activity. There are very few fragments of original vegetation surviving on marine terraces in New Zealand, except on the South Island's West Coast and in Fiordland. The few marine terraces on the West Coast that still retain their original vegetation are very small relative to the Waitutu terraces; hence soil-vegetation patterns there may be dominated by edge effects. Moreover, they belong to sequences of few terraces of far lesser age range than at Waitutu. The western continuation of the Waitutu terraces in Fiordland National Park includes very limited areas of terraces in the lowland zone (Bishop, 1985; Ward, 1988) and these support woodland or short forest communities probably similar to those of Sites 7 and 8 of this study. Lowland marine terraces are extensive in the West Cape area of Fiordland, but these surfaces support shrub-tussockland rather than tall forest (Wardle *et al.*, 1970).

Consequently, we believe that formal protection of the sequence of marine terrace ecosystems at Waitutu is justified on the grounds that the sequence is representative of a once widespread and significant component of New Zealand's indigenous ecosystems and natural landscapes and, moreover, it is superior to all other surviving examples.

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APPENDIX 1. Descriptions of soil profiles from 16 sampling sites on nine marine terraces, Waitutu Ecological District.

TERRACE/SITE 1	
Classification:	Organic soil
Grid reference:	S174/319160
Altitude (a.m.s.l.):	5 m
Topography:	Site on herbfield; on terrace 3 m above storm beach. Beach covered with granite, quartz, mudstone cobbles and boulders.
Profile drainage:	Very poor
Depth to watertable:	75 cm
Vegetation:	Coastal herbfield:back part of terrace-shrubland and rushland
Parent material:	Peat on gravels
Om ₁ 0-65 cm	Dark reddish brown (5YR 2/2) sandy peat; very moist slightly sticky; clean quartz grains; upper 20 cm abundant very fine roots forming a thick root mat, below common fine roots; structureless.
$Om_2 65-90 + cm$	Dark reddish brown (5YR 2/2) peaty sand; very moist common fine roots (dead?); common, subrounded, unweathered granite cobbles.
TERRACE/SITE 2	
Classification:	Podzolised yellow-brown earth
Grid reference:	S174/314168
Altitude:	50 m
Topography:	Slope 3° to SE; 20 m from terrace edge; hummocky
Profile drainage:	Poor
Depth to watertable:	
Vegetation:	Forest: silver beech, some rimu, over kamahi, over 50% litter, moss and ferns
Parent material:	loess
F 2-0 cm	Root mat and moss
Ah 0-20 cm	Brown (10YR 4/3) humic sandy loam; many, medium distinct dark brown (7.5YR 4/3) mottles; moist, soft, structureless; abundant roots
Eh 20-60 cm	Dark brown (7.5YR 4/3) silt loam; common clean quartz grains; structureless
Bg 60-85 cm	Light yellowish brown (2.5Y 6/4) silt loam; common, fine, distinct strong brown (7.5YR 5/8) mottles associated with cracks; moist; massive; few roots
Cg 85-100 + cm	Light yellowish brown (2.5Y 6/4) silt loam; many, medium, distinct strong brown (7.5YR 5.8) mottles.
TERRACE/SITE 3	
Classification:	Podzolised yellow-brown earth – best example
Grid reference:	S174/313172
Altitude:	80 m
Topography:	Hummocky

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Profile drainage:	Very poor
Depth to watertable:	10 cm
Vegetation:	Forest, canopy 20-25 m: rimu, some silver beech, rata, over kamahi; over moss and ferns
Parent material:	loess on sand
Of 3-0 cm	Root mat: black (7.5YR 2/1)
Ah 0-15 cm	Dark brown (7.5YR 3/2) humic fine sandy loam; very moist; soft; structureless; abundant roots; indistinct boundary
Eh 15-37 cm	Brown (7.5YR 4/3) find sandy loam; wet; firm; massive; abundant fine and few coarse roots; many clean quartz grains
Bh 37-57 cm	Dull reddish brown (5YR 4/3) sandy loam; very moist; firm; massive; many medium roots; few clean quartz grains
Bg 57-85 cm	Light olive brown (2.5Y 5/4) clayey sand; many, distinct, medium dark reddish brown (5YR 3/3) mottles; very moist; massive; very compact: no roots
Cu 85-100 + cm	Light olive brown (2.5Y 5/4) sand; very compact.
TERRACE/SITE 4A	
Classification:	Gleyed yellow-brown earth—best example
Grid reference:	S174/330191
Altitude:	135 m
Topography:	Hummocky; drainage channel 20 m to the east
Profile drainage:	Poor
Depth to watertable:	60 cm
Vegetation:	Forest, canopy 18-20 m: silver beech, rimu, miro over kamahi understorey, over moss and ferns
Parent material:	loess
L 2-0 cm	Moss layer and litter
Ah 0-28 cm	Dark reddish brown (5YR 3/2) humic silt loam; very moist; structureless; soft; abundant fine and medium roots; indistinct irregular boundary
ABg 28-45 cm	Dark brown (7.5YR 4/2) silt loam; many, medium distinct dark reddish brown (5YR 2/3) mottles; very moist; massive; soft; many fine and common coarse roots: distinct irregular boundary
Brg 45-100 cm	Pale olive (5Y 6/3) silt loam; many, coarse, distinct strong brown (7.5YR 5/8) mottles; very moist; firm; massive; low medium roots: distinct smooth boundary
Cr 100-130 + cm	Olive grey (5GY 6/1) clayey sandy loam; sand grains consist of quartz, feldspar and mica; very moist; compact; massive; no roots.

TERRACE/SITE 4B

Classification:	Gleyed yellow-brown earth
Grid reference:	S174/314187
Altitude:	125 m
Topography:	Forest dimpled
Profile drainage:	Poor
Depth to watertable:	95 cm
Vegetation:	Forest, canopy 20-26 m: silver beech, kamahi, over mosses and
	ferns
Parent material:	Loess
L 2-0 cm	Moss, twigs, bark and leaves, weakly decomposed
Ah 0-12 cm	Dark brown (7.5YR 3/2) humic fine sandy loam; very moist; soft;
	structureless; many fine-coarse roots
AB 13-63 cm	Pale olive (5Y 6/3) sandy loam; many, coarse, distinct light olive
	brown (2.5Y 5/6) mottles; moist; massive; firm; few fine roots
BC 63-73 cm	Pale olive (5Y 6/3) sandy loam; few, coarse distinct light olive
	brown (2.5Y 5/6) mottles; moist; massive; firm

C 73-100 + cm	Olive (5Y 5/3) sandy loam; sand consists of mica, quartz and feldspar grains; moist; massive; compact.
TERRACE/SITE 4C	
Classification:	Gleyed yellow-brown earth
Grid reference:	S174/307183
Altitude:	125 m
Topography:	Forest dimpled
Profile drainage:	Very poor
Depth to watertable:	10 cm
Vegetation:	Forest, canopy 22 m: rimu, mountain beech, over kamahi understorey, over moss and ferns
Parent material:	loess
L 2-0 cm	Twigs, leaves and bark weakly decomposed
Of 0-8 cm	Very dusky red (2.5YR 2/3) silty peat; very moist; moderately decomposed plant fibres
Ah 8-30 cm	Dark brown (7.5YR 4/3) silt loam; very moist; massive; soft; common fine to coarse roots
Bh 30-60 cm	Dark brown (7.5YR 3/3) humic silt loam; abundant fine and medium, faint dark reddish brown (5YR 2/2) mottles; massive; very compact: common fine roots
BCg 60-80 cm	Colours mixture of above and below; silt loam; common, distinct, medium dark reddish brown (2.5YR 4/3) mottles; moist; massive
Cg 80-100 cm	Greyish olive (5Y 5/3) silt loam; few, fine, distinct dark reddish brown (2.5YR 4/3) mottles; moist; sticky; massive.
TERRACE/SITE 6A	

Classification: Organic soil-typical example Grid reference: S174/333227 Altitude: 310 m Topography: Hummocky, amplitude 30 cm, site in hollow Profile drainage: Very poor Depth to watertable: 40 cm Vegetation: Woodland, canopy 1.5 m: yellow-silver pine, manuka over Lycopodium Parent material: Peat over gravels and sand Of₁ 0-39 cm Dark brown (7.5YR 3/4) sandy peat; wet; soft abundant fine and medium roots; base of horizon dead conifer wood; distinct sharp boundary Of₂ 39-43 cm Very dark brown (7.5YR 2/2) plant fibres, very fine roots, bits of bark, no mineral material; peat wet; soft; distinct sharp boundary Ah 43-53 cm Dark brown (7.5YR 3/2) humic silt loam; moist; massive; firm; abundant fine roots Bu 53-65 cm Olive brown (2.5YR 4/4) silt loam with quartz pebbles; moist; massive; firm; common fine roots Cu 65-75 cm Olive (5Y 4/4) coarse sandy loam, very moist; soft to firm; massive; no roots or stones. On stones.

TERRACE/SITE 6B

Classification:	Organic soil
Grid reference:	S174/333228
Altitude:	310 m
Topography:	Site in a hollow; amplitude 30 cm
Profile drainage:	Very poor
Depth to watertable:	At surface

S174/328234

Forest dimpled

315 m

Poor

75 cm

Vegetation:	Open bog, herbfield with some shrubs: 10% manuka, over moss and ferns
Parent material:	Peat on loess and stones
Of 0-50 cm	Dark reddish brown (5YR 3/3) fibric peat; wet; soft; abundant fine roots and other plant material
Ah ₁ 50-70 cm	Very dark grey (5YR 3/1) peaty silt loam; wet; soft; many medium, fine roots
Ah ₂ 70-80 cm	Dark reddish brown (5YR 2/2) peaty silt loam; very moist; massive: few very fine dead roots
С	stones.
TERRACE/SITE 6C	
Classification:	Podzolised vellow-brown earth

silver pine, over bryophytes and ferns

Pebbly mudstone, siltstone.

of granite and quartz

quartz and feldspar pebbles

Forest, canopy 14-16 m: pink pine, mountain beech, over yellow-

Dark brown (7.5YR 3/2) humic fine sandy loam; wet; massive; slightly sticky; firm; abundant fine, few medium and coarse roots

Dark brown (10YR 3/3) silt loam; common medium, faint dark reddish brown (5YR 3/3) mottles; very moist; massive; slightly sticky; common fine roots; few unweathered subrounded cobbles

Olive grey (5GY 6/1) silt loam; few, fine distinct yellowish red

(5YR 4/8) mottles; massive; very compact; very plastic; contains

Grid reference: Altitude: Topography: Profile drainage: Depth to watertable: Vegetation:

Parent material: Ah 0-35 cm

Bw 35-70 cm

Cg 65-100 + cm

TERRACE/SITE 6D

IERRAUE/SITE OD	
Classification:	Organic soil
Grid reference:	S174/333216
Altitude:	300 m
Topography:	Hummocky, site on a hump, amplitude 45 cm
Profile drainage:	Very poor
Depth to watertable:	20 cm
Vegetation:	Open bog, shrubland plus herbfield: canopy 0-4 m, manuka, yellow-silver pine over moss and ferns, with dwarf pink pine, manuka, and numerous bog plants
Parent material:	Peat on sand
Of 0-3 cm	Very dusky red (2.5YR 2/2) peat; very moist; abundant fine plant fibres and roots
Om 3-55 cm	Dark reddish brown (5YR 2/4) hemic peat; wet; common fine roots and few large decomposed roots
Oh 55-80 cm	Dark reddish brown (5YR 2/2) sapric peat; wet; no plant fibres
C 80-100 + cm	Greyish brown (2.5Y 5/2) coarse sand; very moist; common, medium, faint dark brown (7.5YR 4/3) mottles.

TERRACE/SITE 7

Classification:IGrid reference:SAltitude:STopography:IProfile drainage:IDepth to watertable:S

Podzol S174/344235 355 m Forest dimpled Poor 45 cm

Vegetation:	Forest, canopy 5->15 m: mountain beech, over kamahi, pink nine over forms and broophytes
Parent material	Gravels and sands derived from granite amphibolite quartz
I 3-0 cm	Leaves twigs plant material plus root mat
Ab 0-12 cm	Dark reddish brown (5VR 3/3) humic silt loam: very moist:
	structureless: soft: many roots: distinct irregular boundary
Eh 12-21 cm	Brown (7 5YR 5/2) coarse sandy loam: many medium distinct
	dark reddish brown (5YR 3/3) mottles: very moist: massive:
	slightly sticky: firm: common medium and few large roots: clean
	quartz and feldspar grains: NaF -ve: distinct wavy boundary
Bhs 21-32 cm	Dark reddish brown (5YR 2/3) few strongly weathered stones.
	incipient iron/humus pan: slightly cemented: NaF + ve: distinct
	wavy boundary
Bh 32-57 + cm	Brownish vellow (10YR 6/6) abundant gravels and stones of
	granite, amphibolite and quartz in a sand matrix; humus
	accumulation around some stones; common, medium, distinct
	dark brown (7.5YR 7/4) mottles; no roots; NaF -ve.
TERRACE/SITE 8	
Classification:	Gley podzol
Grid reference:	\$1/4/350250
Altitude:	
l opography:	Slope 4° to SE; hummocky amplitude 20 cm
Profile drainage:	100
Depth to watertable:	Fourte constant of the second state in the second state is the second state in the second state is the sec
vegetation:	Forest, canopy 2-5.5 m: pink pine, mountain beech over yellow-
Parant motorials	Silver pille over bryophytes
Of 0.30 cm	Vors dualay red (2.5VD 2/2) fibric post, wet soft, abundant fina
OI 0-50 Cm	and common medium roots; indistinct boundary
Fb 30-48 cm	Dark reddishish brown (5VR 3/2) sandy loam; wet: massive:
	common fine roots: clean grains of quartz and feldspar: at hase
	few unweathered granite stones (diameter about 6 cm): distinct
	irregular boundary
Brg 48-90 cm	Olive grey $(2.5 \text{GY} 5/1)$ coarse sandy loam: common fine distinct
0	dark yellowish brown (10YR 4/4) mottles (associated with cracks
	and channels); very moist; massive; compact; no roots; common
	unweathered pebbles plus grains of quartz, feldspar and mica
Cr 90-110 + cm	Greenish grey (10GY 6/1) coarse sandy loam; very moist;
	common, strongly weathered feldspar and quartz gravels.
TEDDACE/SITE O	
Cleasification	Deductional willow known conth
Crist references	Podzonsed yellow-brown earth
Altitude:	5174/551204
Topography:	570 m Forest dimpled
Profile draine gou	Poor
Depth to watertable	20 am
Vegetation:	Forest comprise 7.5 m; mountain basch nink ning over mingi
vegetation.	mingi pink pine over mosses
Parent material	Sand gravels and boulders (?conglomerate)
F 2-0 cm	Moderately decomposed leaves twigs and plant material
Ah 0-10 cm	Dark brown (7.5YR 3/4) humic sandy loam: very moist
	structureless; slightly sticky; soft: abundant fine roots: indistinct
	boundary
Bwh 10-40 cm	Dark brown (7.5YR 3/2) gritty sandy loam; wet; massive; firm;
	common fine roots; few unweathered cobbles

 \mathbf{C}

Many granite boulders, unweathered (diameter up to 70 cm) in a coarse sand matrix (contains quartz, feldspar and mica grains).

TERRACE/SITE 10A

Classification:	Gley soil
Grid reference:	\$1/4/35/284
Altitude:	625 m
Topography:	Hummocky; site in a hollow, clear of tall vegetation; on the humps
Profile drainage	Vor noon
Profile utalitage.	
V metation	10 cm Statistical and the second state with size
Vegetation:	Shrubland: manuka, mountain beech, pink pine
Parent material:	Peat over peoply mudstone
Oh 0-30 cm	Dark reddish brown (5YR 3/2) fibric peat; wet; very soft; abundant fine and few medium roots; at base of horizon common quartz and granite cobbles unweathered; distinct sharp boundary
Br 30-75 cm	Yellowish grey (2.5YR 6/1) silt loam; very moist; massive; slightly sticky; plastic; firm; common fine quartz and feldspar pebble sized
Cr 75-100 + cm	Olive grey (5GY 6/1) silt loam; very moist; massive; firm; very compact; common fine unweathered quartz and feldspar pebble
	sized fragments; no roots.
TERRACE/SITE 10R	
Classification.	Organia soil
Child references	S174/255994
Altitude	620 m
Tonographu	Uummaaluu aita an a humn amnlituda 50 am
Profile drainage	Poor
Depth to wetertable	55 am
Vagetation:	Uarbfield with some shrubs: manuke over nink nine, hog plants
vegetation:	manuka
Parent material:	Peat on loess and gravels (?conglomerate)
Of ₁ 0-65 cm	Very dusky red (2.5YR 2/2) fibric peat; wet; very soft; abundant
	fine and common coarse roots; no coarse fragments; indistinct
Of 65.00 am	Doundary $(7.5 \text{VP} 4/4)$ loomy post wat slightly sticky
012 03-90 cm	soft: abundant fine roots:
Ab 00 100 am	Soft, abundant lifte roots, Vani dank brown (7 5VD 2/2), party silt, wate structural assess of t
All 50-100 cm	to firm; common fine roots; distinct wavy boundary
Br 100-105 + cm	Yellowish grey (2.5Y 6/1); gravelly fine sandy loam; very moist;
	firm; massive; many quartz and feldspar grains; no roots. On stones.
TERRACE/SITE 10C	
Classification:	Gley podzol
Grid reference:	S174/353271
Altitude:	600 m
Topography:	Hummocky; large granite boulders on 5-10% of surface
Profile drainage:	Very poor
Depth to watertable:	30 cm
Vegetation:	Shrubland, canopy height 1.5-6 m; pink pine, manuka, mountain
3	beech, over pink pine, manuka and low bog plants
Parent material:	Loess and gravels (? conglomerate)
Ah 0-25 cm	Dark reddish brown (5YR 3/2); humic loamy sand: wet very soft:
	structureless; abundant roots
Eh 25-50 cm	Brown (7.5YR 5/2); gritty silt loam: wet: soft: structureless: many
	clean quartz grains; many roots
Br 50-60 + cm	Light brownish grey (2.5Y 6/2); gravelly silt loam; very moist;
	massive; quartz and feldspar fragments; no roots.
	On stones and gravels.

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