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PLANT SUCCESSION ON THE BRAIDED BED OF THE ORONGORONGO RIVER, WELLINGTON, NEW ZEALAND, 1973-1990

Summary: Vegetation on 5 km (*c.* 100 ha) of the braided bed of the Orongorongo River, Wellington, was sampled in March from 1973 to 1990. The riverbed has become aggraded since an earthquake in 1855. Surface water covered little of the riverbed; *Callitriche stagnalis* was the only common vascular aquatic plant. Most grasses and dicot herbs were adventive. The scabweed *Raoulia tenuicaulis* was the commonest dicot. The extent of plant cover was measured on 300 circular plots (radius 1.5 m); it ranged between years from 5% to 22%, depending on the severity of floods. The number of plots with little vegetation varied widely, independently of plant cover. Plots with a sandy substrate had most plant cover. Much wind-blown sand accumulated beneath established vegetation. Patterns of early succession, which relied on available seed, were largely dictated by floods and droughts. If not disturbed for 20-25 years, succession invariably led to a temporary dominance of kanuka (*Kunzea ericoides*), with or without manuka (*Leptospermum scoparium*).

Keywords: Plant succession; Orongorongo Valley; braided riverbed; plant cover; pioneer species; herbs; scrub; rainfall; floods.

Introduction

Braided riverbeds are characteristic of the plains east of the Southern Alps in the South Island of New Zealand; there are others in the North Island. This study of early succession on the braided bed and flats of the Orongorongo River, Wellington, from 1973 to 1990 complemented a study of rabbits (*Oryctolagus cuniculus* L.) living there (Gibb, 1993, and *unpubl.*); it is part of a long-term study of the predominantly forest ecosystem around the Landcare Research Field Station on the east bank of the river, 10 km from the coast (Brockie, 1992).

Study Area

The study area lies near the southern extremity of the Rimutaka Range; the geology is typical of other ranges in central New Zealand (Stevens, 1974). Campbell (1984) described the vegetation of research area in the Rimutaka Forest Park; this is basically a mixed podocarp/hardwood forest.

The Orongorongo Valley here is steep and forested (Fig. 1). The course of the river frequently changes, and the flood plain is bordered by river flats up to 200 m wide. In the study area the river falls from 109 m to 63 m a.s.l. at an average gradient of 1:120; it takes a more circuitous course when in flood than at other times, but rarely covers the entire flood plain.

The rainfall at the Field Station has been recorded since July 1966. The average annual fall in the 24 years 1967-90 was 2370 ± 580 mm (Table 1). Much more fell per month in winter than in summer (mean 269 mm in July, 111 mm in January). The same period included five consecutive dry years 1969-73 (average 1893 mm, range 1448-2301 mm) and six wet years 1974-79 (average 3108 mm, range 2421-3661 mm). These were followed by 11 unexceptional years 1980-90 (average 2177 mm, range 1532-2627 mm) with slightly below average rainfall.

The monthly rainfall at the Field Station was closely correlated ($r = 0.876$, $P < 0.001$) with that at the Wainuiomata Reservoir 9 km to the north, where the average total for the years 1890-1990 inclusive was 1959 mm. Here too the five driest consecutive years were 1969-73 and the five wettest 1976-80. Hence, this study began near the end of an exceptionally dry period and spanned the wet one that followed.

The amount of rain at the Field Station or at any other single site is only a rough guide to the water level of the river because the rain was often concentrated in one or a few catchments (Cunningham and Arnott, 1964).

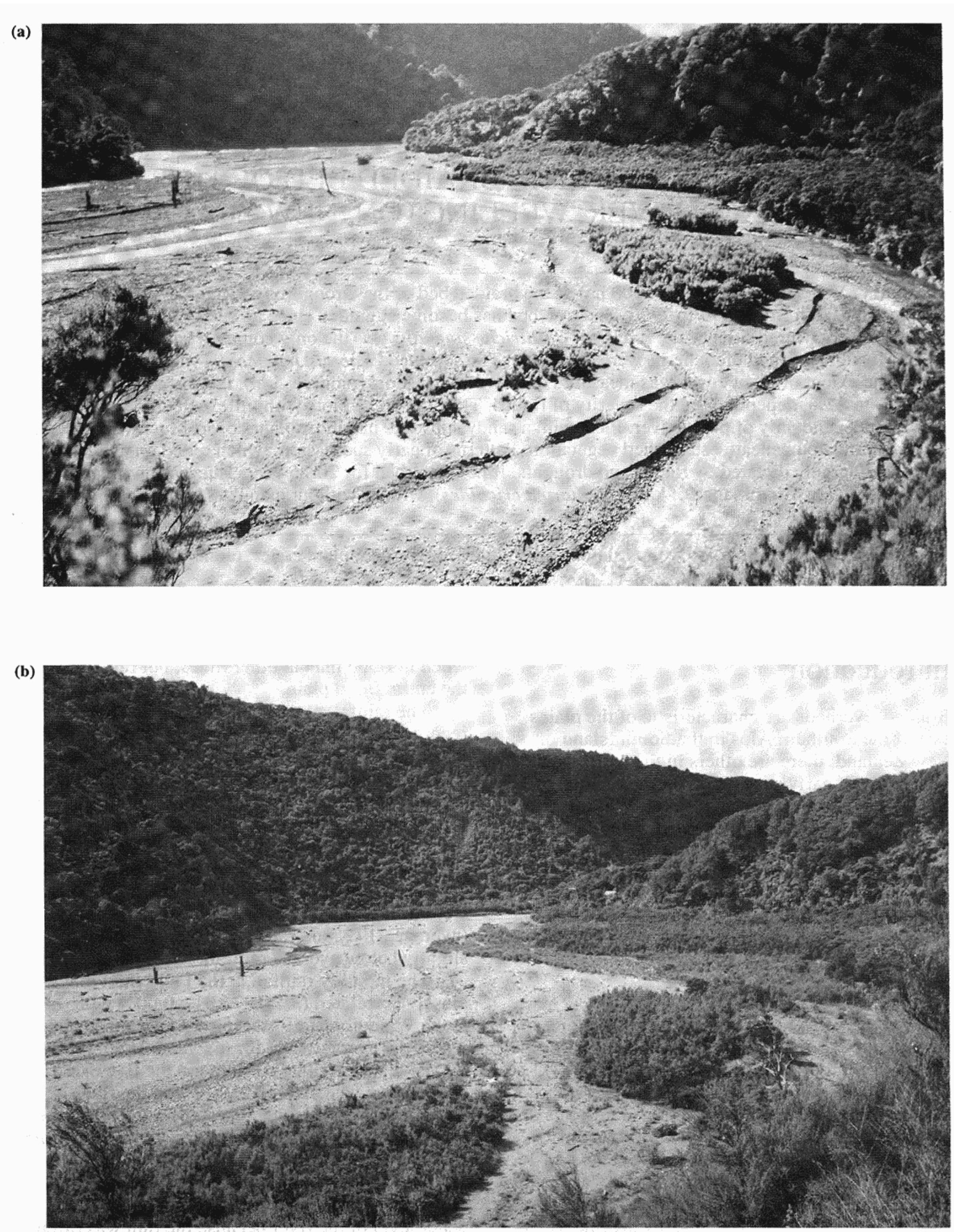

Figure 1. *Photographs of Paua Flat,* c. *1 km downstream from the Field Station, from the east bank facing north (up-river), (a) in July 1982 at the end of the wet period, and (b) in November 1991.*

Table 1: *Annual rainfall (mm) at the Orongorongo Valley Field Station, 1967-1990.*

Year	Rainfall (mm)	Year	Rainfall (mm)
1967	2071	1979	3429
1968	2752	1980	2595
1969	1448	1981	2456
1970	2301	1982	1942
1971	2170	1983	2627
1972	1836	1984	1532
1973	1709	1985	2331
1974	3661	1986	2209
1975	2421	1987	1757
1976	2917	1988	1998
1977	3335	1989	2364
1978	2887	1990	2141

Methods

In about the first week of March each year 1973-90 (excepting 1987), the vegetation in 300 (200 in 1973) sample plots of 1.5 m radius was described. The plots were 55 m apart at intersections of a grid drawn on large scale aerial photographs. No attempt was made to relocate exactly the same plots each year: the same numbered plot was relocated ± 5 m if close to a landmark visible on a photograph, otherwise ± 10 m.

At each plot the total percentage cover by vascular plants was estimated by eye in the classes: Trace, 1-5%, 6-10%, 11-15%, 16-20%, 21-25%, and thereafter ± 5%. Plant taxa present (including mosses and lichens) were listed; some were identified to species, others to genus, and the Juncaceae, Cyperaceae and Poaceae to family. Nomenclature follows Allan (1961), Connor and Edgar (1987), Healy and Edgar (1980), Moore and Edgar (1970), and Webb *et al.* (1988). A record was also made of the nature of the substrate, the extent of surface water, and the presence of mammal sign.

Results

Composition and extent of ground cover

Table 2 lists plant taxa recorded in at least 50 of the 5000 sample plots examined in 1973-90. The scabweed *Raoulia tenuicaulis* was the commonest species; its numbers were boosted by the many seedlings seen in March. Tauhinu (*Cassinia leptophylla*) was the commonest shrub, followed by buddleia (*Buddleja davidii*), kanuka/manuka (*Kunzea ericoides, Leptospermum scoparium*), and gorse (*Ulex europaeus*).

Tauhinu and kanuka/manuka declined similarly in the wet years in the mid-late 1970s; but gorse was barely affected because most of it was above the usual flood level; it was closely grazed by rabbits. Buddleia was in only 20 of the 500 plots examined in 1973 and 1974, but was scarcest in March 1976, in the wet period, when found in only seven of 300 plots. It spread rapidly from 1979 and was the commonest shrub from 1985.

Vascular aquatic plants were concentrated in small streams and backwaters. Starwort (*Callitriche stagnalis*) was the only common aquatic plant; pondweed (*Potamogeton cheesemanii*) and duckweed (*Lemna minor*) were scarce, *Ranunculus trichophyllus* and the water fern (*Azolla filiculoides*) were rare. Beds of emergent watercress (*Rorippa officinale*) clogged some small streams flowing out of the forest; rabbits fed on it along the bank and red deer waded in to get it. *Mimulus guttatus* favoured steep rocky banks with running water; it was also grazed by rabbits. *M. moschata* was scarce, growing solitarily on moist ground.

An index of plant diversity was calculated from the number of different taxa per plot (Table 3). Most of the plants on plots with less than 20% plant cover were seedlings of many taxa from herbs to shrubs. As a result the number of taxa per plot was not correlated with plant cover ($r = 0.49$, $P > 0.05$, N.S.).

The extent of plant cover was reduced by floods. Thus the mean percentage cover was about 21% at the end of the dry period in March 1973-74, but slumped to 5% by March 1982 after the wet period; then, with slightly below average rainfall from 1982 to 1990, plant cover rose to 11-12% (Table 4, Fig. 2).

The extent of ground covered by debris such as logs, broken branches and uprooted shrubs ranged from 0.6% to 2.1% in different years (mean 1.2%, Table 4). Although clearly indicative of upstream erosion aggravated by floods, the amount of stranded debris was only weakly correlated with the total rainfall during the previous six months ($r = 0.449$, N.S.); most floods bring down fresh supplies of debris but remove debris stranded earlier. The extent of surface water obviously varied with recent rainfall, covering 4.4%-17.5% (mean 9.2%, Table 4) of the ground. Short stretches of the river occasionally dried up completely in summer and surfaced again further downstream.

The constituents of the visible substrate of each plot were recorded on a scale of sand to boulders (Table 5). Plots with a sandy substrate had most vegetation: more than 65% of them had more than 60% plant cover. But 21% of the sandy plots, 77% of those with sand + gravel, 78% of those with gravel + stones, and 94% of those with boulders had no more than a trace of cover.

Table 2: *Plant taxa recorded at least 50 times, with the number of plots (max. 5000) in which they occurred.*

Family Principal species	Number of plots in which family recorded (n)	Family rank	Number of plots in which taxon recorded (n)
Mosses and ferns	270		
Juncaceae	152	12	
Cyperaceae	589	10	
Poaceae	2242	2	
Cortaderia fulvida			110
Ranunculaceae	150	14	
Ranunculus repens			150
Brassicaceae	80	18	
Rorippa officinale			80
Caryophyllaceae	1120	4	
Polycarpon tetraphyllum			525
Sagina procumbens			337
Cerastium glomeratum/Stellaria media			258
Polygonaceae	700	7	
Rumex acetosella			527
Polygonum persicaria			173
Onagraceae	897	5	
Epilobium spp.			897
Myrtaceae	657	8	
Kunzea ericoides/Leptospermum scoparium			657
Rosaceae	119	16	
Acaena anserinifolia			119
Fabaceae	2173	3	
Lotus pedunculatus			1085
Ulex europaeus			494
Trifolium repens/T. ornithopodiodes			404
Vicia sativa/V. hirsuta			98
Trifolium dubium			92
Buddlejaceae	862	6	
Buddleja davidii			862
Rubiaceae	85	17	
Coprosma spp.			85
Asteraceae	5817	1	
Raoulia tenuicaulis			1850
Cassinia leptophylla			906
'Flatweeds' (*Crepis, Hypochoeris, Leontodon* spp.)			893
Senecio jacobaea			815
Conyza canadensis			469
Gnaphalium spp.			339
Carduus tenuicaulis/Cirsium vulgare			322
Sonchus asper			158
Raoulia glabra			65
Gentianaceae	50	19	
Centaurium erythrinum			50
Primulaceae	613	9	
Anagallis arvensis			613
Solanaceae	137	15	
Solanum nigrum			137
Scrophulariaceae	534	11	
Digitalis purpurea			160
Prunella vulgaris			152
Parentucellia viscosa			118
Hebe stricta			100

Table 3: *Index of plant diversity (taxa per plot) related to percentage plant cover; bare plots omitted.*

Plant cover (%)	Plots (n)	Taxa per plot (mean ± s.d.)
Trace	1432	4.16 ± 2.88
1-20	596	8.96 ± 3.79
21-60	399	10.24 ± 3.55
61-100	309	11.00 ± 3.35

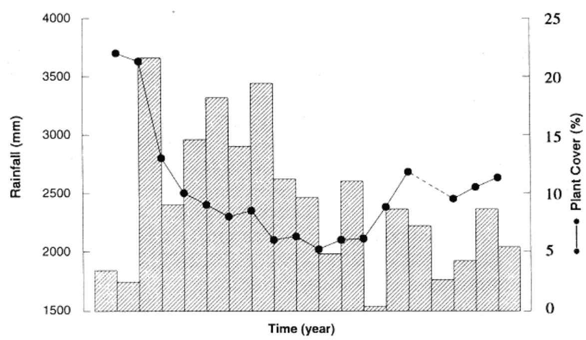

Figure 2. *Annual rainfall (mm, hatched histograms) at the Field Station, with mean plant cover (%) on the riverbed, 1973-90.*

Table 4: *Mean cover by vascular plants, water and debris in March.*

Year	Plants (% ± s.d.)	Water (% ± s.d.)	Debris (% ± s.d.)
1973	21.55 ± 29.37	4.49 ± 23.21	1.17 ± 3.91
1974	21.06 ± 29.72	6.43 ± 20.96	1.80 ± 4.61
1975	13.21 ± 26.95	10.27 ± 26.15	1.87 ± 4.78
1976	10.13 ± 24.46	7.97 ± 24.60	2.07 ± 4.46
1977	8.87 ± 22.85	15.22 ± 33.26	1.89 ± 4.47
1978	7.86 ± 22.92	4.43 ± 16.63	1.34 ± 3.08
1979	8.55 ± 21.33	8.02 ± 24.25	1.50 ± 3.40
1980	5.90 ± 20.18	13.14 ± 30.14	1.30 ± 3.46
1981	6.20 ± 20.68	4.86 ± 18.71	0.97 ± 3.26
1982	5.13 ± 18.04	13.52 ± 31.18	0.95 ± 2.69
1983	5.72 ± 18.79	5.17 ± 20.19	1.31 ± 4.31
1984	5.95 ± 19.53	8.21 ± 25.63	0.66 ± 2.04
1985	8.74 ± 21.65	10.24 ± 29.79	0.57 ± 3.26
1986	11.83 ± 25.13	17.50 ± 36.55	0.65 ± 2.15
1987	Not recorded	Not recorded	Not recorded
1988	9.61 ± 21.93	11.48 ± 29.62	0.87 ± 3.23
1989	10.56 ± 21.21	5.51 ± 20.96	0.97 ± 3.07
1990	11.21 ± 24.09	10.10 ± 28.06	0.70 ± 3.03

Table 5: *Plant cover related to the visible substrate.*

Substrate	Max. particle size (mm)	Mean plant cover (%) 0-trace	5-20	25-60	> 60	Number of plots
Silt + sand	2	20.98	4.90	8.39	64.73	265
Sand + gravel	20	76.82	14.31	6.31	2.56	2963
Gravel + stones	200	78.61	9.36	7.87	4.16	1246
Stones + boulders	> 200	94.01	4.58	0.35	1.66	526

Table 6: *Number of plots per year with mammal sign in March. Notes:*
1. Ungulate droppings were mainly of sheep; eight plots with cattle droppings are included in 1982.
2. Figures for 1973 are multiplied by 3/2 to make them comparable with other years, because only 200 instead of 300 plots were examined in that year.

Year	Number of plots		
	Lagomorph	Possum	Ungulate
1973	112	14	10
1974	101	11	47
1975	44	11	20
1976	22	5	0
1977	19	5	2
1978	26	4	1
1979	26	2	4
1980	29	4	5
1981	40	7	4
1982	30	0	56
1983	35	6	26
1984	29	3	2
1985	46	3	5
1986	67	4	0
1987		Not recorded	
1988	64	2	41
1989	57	2	58
1990	66	7	46

The number of plots with mammal sign is given in Table 6. Besides rabbits, a few hares (*Lepus europaeus* Pallas), possums (*Trichosurus vulpecula* Kerr), and red deer (*Cervus elaphus* L.) fed on the riverbed; small numbers of sheep and occasionally cattle strayed up the river from the farm on the coast. These herbivores had little long-term effect on the extent of vegetation.

Sequence of taxa in succession

Here we consider only those taxa figuring prominently in early succession. The stage of succession reached in each plot was scored crudely by the extent of plant cover of whatever age. Table 7 lists taxa recorded in more than 100 of the 5000 plots examined in 1973-90. The taxa are grouped in three categories: Category 1 for taxa recorded **less often** with increasing plant cover beyond 20%; Category 2 for those recorded most often with varied plant cover; and Category 3 for those recorded **more often** with increasing plant cover beyond 20%. Within each category the taxa are listed in decreasing order of the number of plots in which they occurred.

The commonest pioneers on bare ground were grasses and *Raoulia tenuicaulis* (Category 1), in 68% and 66% respectively of plots with a trace of cover; next were buddleia with 26%, *Epilobium* spp. and lotus each in 22% of the plots. These were followed in descending order by the Cyperaceae, tauhinu, composite flatweeds, *Senecio jacobaea*, *Anagallis*, *Trifolium ornithopodiodes/T. repens, Polycarpon*, *Rumex acetosella* and gorse, all in more than 10% of the Trace plots.

No taxon was in Trace plots as often as in those with more cover, but seven of the 13 taxa in Category 1 plus *Polygonum* in Category 2 were in Trace plots more often than in those with more than 60% cover. The mean percentage of plots in which taxa in Category 1 were present **decreased** from 27.4% in plots with up to 20% cover to 13.2% in those with more than 60% cover; whereas taxa in Category 3 **increased** from 24.3% to 45.0%.

Taxa in Category 1 included the early pioneers on bare ground, notably annual and other short-lived species, and buddleia, a recent adventive. All these were recorded more often in plots with up to 20% cover than in those with more than 60% cover. Some may be poor competitors with other taxa or less able to survive on old compacted beds of shingle or to resist droughts.

The few taxa in Category 2 include lotus, the most widespread herb in summer; its above-ground parts die back in winter. Its creeping shoots were sometimes grazed by rabbits, but not its foliage. Most taxa in Category 3 persisted in more advanced succession: tauhinu, kanuka and manuka, and gorse often made up a closed canopy 10-15 years after first colonisation of the ground. Gorse died out when overshadowed by the others, and the trunks of tauhinu rotted when about 20 years old. Other taxa in Category 3 (except *Parentucellia*) persisted beneath a light shrub canopy.

Several taxa changed rank according to their tolerance or otherwise of plant cover. Any rise in a taxon's rank across the cover classes (Trace to 100%) means that relative to other taxa in the category, it was recorded more often as plant cover increased; and *vice versa* for any fall in rank. In Category 1 *Gnaphalium* spp. rose from rank 9 in Trace plots to rank 2 with more than 60% cover. The pioneering specialists *Polycarpon* and *Sagina* followed parallel courses. The Juncaceae (Category 1) rose from rank 13 (bottom) in Trace plots to rank 7 with more than 60% cover. *Conyza* (Category 2) rose from rank 5 to rank 2. *Kunzea/Leptospermum* rose from rank 6 to rank 2, overtaking tauhinu; and moss rose from rank 10 to rank 6, being shade tolerant; *Ranunculus repens* fell from rank 7 to rank 12. Predictably *Parentucellia*, the only annual in Category 3 and a semi-parasite on other herbs (Wardle, 1991), was almost absent at rank 12 (bottom) in Trace plots, but rose to rank 8 with 25-60% cover.

Table 7: *Sequence of taxa in succession, 1973-1990, expressed as % of plots in which present (n = 5000). Notes:*
1. Includes only taxa present in > 100 plots.
2. The highest percentage occurrence for each taxon is printed in **boldface**.
3. Within each category taxa are ranked in decreasing order of their frequency of occurrence.
4. Two species were under-recorded: Cerastium glomeratum *was a common but not abundant annual, flowering in early spring and dead before March;* T. dubium *was inconspicuous when not flowering, which was mostly over by March.*
5. Trifolium ornitho. *(Cat. 1)* = T. ornithopodiodes. *Poaceae (Cat. 3) excludes* Cortaderia fulvida *(listed separately).*

	Maximum plant cover per plot							
	Trace (n = 1432)		20% (n = 596)		60% (n = 339)		100% (n = 309)	
Taxon	Rank	%	Rank	%	Rank	%	Rank	%
Category 1: Taxa present **less** often as cover increases beyond 20%								
Raoulia tenuicaulis (*n* = 1856)	1	65.92	1	**84.35**	1	77.78	1	44.09
Epilobium spp. (*n* = 897)	3	22.30	2	**56.72**	2	52.34	4	17.89
Buddleja davidii (*n* = 862)	2	26.16	3	**47.94**	3	40.94	3	18.53
Polycarpon tetraphyllum (*n* = 525)	5	11.71	4	**37.56**	4	30.41	9	7.67
Trifolium ornitho./repens (*n* = 404)	4	12.62	7	**18.45**	7	17.25	5	16.93
Gnaphalium spp. (*n* = 339)	9	6.31	6	**19.93**	6	19.59	2	19.49
Sagina procumbens (*n* = 337)	6	8.56	5	**20.92**	5	20.47	11	5.75
Carduus/Cirsium spp. (*n* = 322)	7	8.28	8	**18.45**	8	14.91	6	13.10
Stellaria/Cerastium spp. (*n* = 258)	8	7.57	9	**14.66**	9	11.40	8	7.99
Digitalis purpurea (*n* = 160)	12	2.88	10	**11.04**	12	8.19	11	7.67
Juncaceae (*n* = 152)	13	2.53	11	**9.72**	10	9.06	7	8.31
Sonchus asper (*n* = 138)	11	3.79	12	**8.57**	12	6.43	12	3.20
Solanum nigrum (*n* = 137)	10	4.77	13	**8.24**	13	4.39	13	1.28
Mean % plots occupied		14.11		**27.43**		24.09		13.22
Category 2: Taxa present with varied plant cover								
Lotus pedunculatus (*n* = 1085)	1	21.88	1	51.07	1	**73.39**	1	67.73
Anagallis arvensis (*n* = 613)	3	13.60	2	34.10	2	**41.23**	5	22.68
Cyperaceae (*n* = 589)	2	17.39	4	**28.50**	5	24.27	3	27.16
Rumex acetosella (*n* = 527)	4	11.29	5	24.38	3	**40.64**	4	25.24
Conyza canadensis (*n* = 469)	5	6.52	3	29.16	4	**33.04**	2	27.48
Polygonum persicaria (*n* = 173)	6	5.96	6	7.91	6	**8.48**	7	3.51
Hebe stricta (*n* = 101)	7	1.47	7	**5.77**	7	**5.26**	6	8.31
Mean % plots occupied		11.16		25.84		**32.33**		26.02
Category 3: Taxa present **more** often as cover increases beyond 20%								
Poaceae (*n* = 2132)	1	68.44	1	89.13	1	93.28	1	**94.57**
Cassinia leptophylla (*n* = 906)	2	14.87	2	44.15	3	63.74	4	**66.45**
Composite flatweeds (*n* = 893)	3	13.96	4	40.86	2	66.37	3	**69.97**
Senecio jacobaea (*n* = 815)	4	13.60	3	41.35	4	52.34	5	**61.02**
Kunzea/Leptospermum spp. (*n* = 657)	6	5.54	5	27.84	5	49.12	2	**77.00**
Ulex europaeus (*n* = 494)	5	10.73	6	22.41	6	28.36	7	**34.51**
Moss (*n* = 270)	10	0.28	7	7.25	7	18.42	6	**50.88**
Prunella vulgaris (*n* = 152)	8	1.05	9	4.78	9	11.40	8	**22.05**
Ranunculus repens (*n* = 150)	7	2.45	8	6.43	11	10.82	12	**12.46**
Acaena anserinifolia (*n* = 119)	9	0.35	11	3.30	12	9.94	9	**19.17**
Parentucellia viscosa (*n* = 118)	12	0.14	12	2.97	8	13.16	10	**16.93**
Cortaderia fulvida (*n* = 110)	11	0.28	10	3.86	10	10.53	11	**15.02**
Mean % plots occupied		10.97		24.13		35.62		**45.00**

Discussion

Changes since 1850

The present composition of vegetation on the floor of the Orongorongo Valley is partly a result of its recent history. Clearly, the vegetation has been affected by a rare sequence of perturbations since 1850.

Scree from the ridge-tops, dislodged by the 1855 earthquake, first settled in the headwaters of tributary streams. Since then (perhaps especially in the stormy period of 1870-90; Grant, 1991), much of it has been washed into the main river (Cunningham and Arnott, 1964; Campbell, 1984). As some tributaries descend steeply from the ridges and others more gently, the period of active aggradation has been protracted.

The Orongorongo Valley has been relatively stable since about 1900. Large dead trees still standing on the riverbed far from the present bank (Fig. 1) testify to the river having formerly flowed between forested flats. Kanuka growing at the foot of a large slip east of Paua Flat dates (by ring count) to about 1900 (*pers. obs.*). A live rimu 21 m tall that fell into Green's Stream in 1976 was about 425 years old; it had an adventitious root system then about 70 years old a metre above the main root plate. And an old totara (*Podocarpus totara*) 50 m north of Wootton's Stream and 250 m from the main river (Plate 13 in Brockie, 1992), has its roots buried by at least 1.5 m of debris, presumably from the 1855 earthquake; it is surrounded by kanuka that was 45-50 years old in 1975, and by pole-sized totara somewhat older.

There must have been fewer open river flats and less bare shingle before the earthquake, and the vegetation must have been entirely native. Subsequent aggradation coincided with the introduction of numerous weeds - and mammalian herbivores. Since then, there have been big changes in the surrounding land-use and recently much intensified public use.

The present vegetation

Because the sample plots were not in exactly the same place each year, the progress of succession at any one site cannot be measured. However, plots without or with only a trace of vegetation in March had probably been scoured by the river in the previous six months, and those with much less than 20% cover probably within the previous 12 months. The proportion of plots with no more than a trace of vegetation was exceedingly variable between years, and was not positively correlated (r = -0.65) with overall plant cover (Fig. 3).

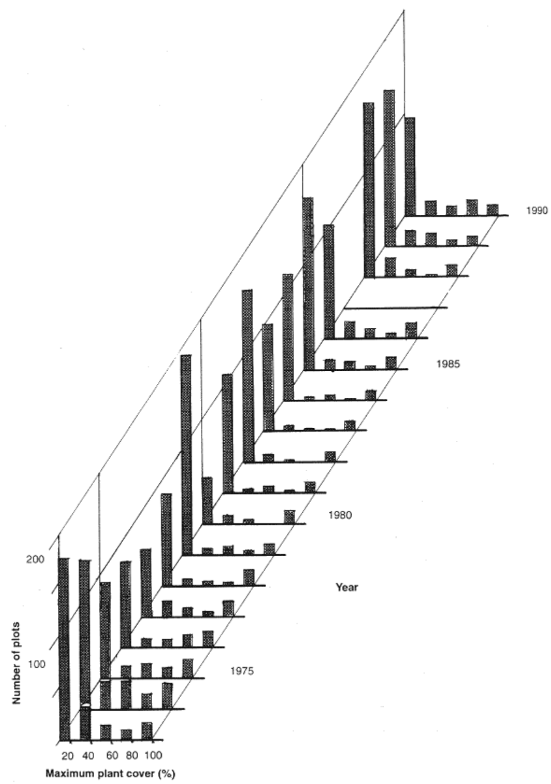

Figure 3. *Number of plots in successive classes of plant cover, 1973-90.*

The proportion of native species in riverbed floras depends on where and when they were sampled. Cockayne (1911) described the then entirely native flora of the upper Rakaia River. With additions by Calder (1961), Burrows (1977) listed 59.7% of the flora as native on the Cass riverbed in Canterbury; and Calder observed that "high-country river-bed communities are some of the few remaining ... not dominated by exotics". By contrast, only 10% of the species beside the Horokiwi Stream, flowing through pastures near Wellington, were native (Croker, 1955). Healy (1973) commented that "Riverbeds are inhospitable habitats ... with a species-poor indigenous flora ... Adventives have, in many localities, provided a more extensive and stable vegetation than did the indigenes"; and Wardle (1991) concluded that "The adventive colonists of recent alluvium far exceed the native in respect of numbers of species, rates of increase, and final height and density ... Excepting urban wasteland, river-beds may be the richest habitat for naturalised plants". Campbell (1984, his Table 1) estimated the proportions of native species in the vascular flora of the research area as 100% of 72 ferns, 89.9% of 59 trees, 84.2% of 19 lianes, 81.8% of 66 shrubs, 75.4% of 118 monocot herbs, and only 42.5% of 167 dicot herbs. On the riverbed alone about 17% of the common dicot herbs are native (*pers. obs.*). The unavoidably coarse identification of some taxa in the present study makes it impossible to give the exact proportion of native species, but among the pioneers they were clearly outnumbered by adventives.

Clouds of wind-blown sand are a feature of braided riverbeds. Sand and silt are deposited in the lee of every obstacle, providing unstable seedbeds for pioneering species. Large stranded logs may become oases of developing vegetation, sometimes lasting for decades. Much of the wind-blown sand drops on the surrounding forest and scrub. Sample plots with a sandy substrate had more vegetation growing on them than had plots with a coarser substrate (Table 5); but the sand may have reached them after the plants became established.

An island of vegetation on Paua Flat (Fig. 1, foreground) first appeared in the late 1960s, when a few logs stranded at the head of what later became an island 50 m long. Other debris accumulated around them. The resulting island was first colonised by scabweed, herbs and seedling shrubs, which in turn attracted more sand. The surface of the ground gradually built up above normal flood level. Mats of scabweed do not catch the wind and their deep roots (McIndoe, 1932) anchor them in times of flood. In the Orongorongo Valley the mats of *R. tenuicaulis* usually became senescent when 4-5 years old. Their centres died after flowering and were not replaced by new growth. The whole mat then slowly turned grey and was liable to be invaded by seedling shrubs, such as tauhinu (see Moore, 1976 for *R. australis* similarly). By the early 1980s, on the island, first the scabweed and then the lotus died beneath the shrubs, then up to 2 m tall. Tauhinu and gorse had mostly disappeared by 1990 and it became possible to walk beneath the canopy.

A fine deposit of wind-blown sand (loess) on the original stony basement of the island was evident by 1984: "by degrees the stony substrate became the subsoil" (Cockayne, 1911). By April 1988 the sand was 400 ± 126 mm deep ($n = 40$ probes); but the rate at which it accumulated could not be measured by probing because the sand compacted. Though the island thus increased in height over the years, its flanks became increasingly eroded. The island survived at least until 1994; but several others that appeared in the same dry period were washed away a few years later.

Since there were fewer plots with kanuka or manuka ($P < 0.05$), tauhinu or gorse ($P < 0.001$), less than 200 mm tall, in 1973 and 1974 than in later years, there was probably some density-dependent restraint on seedling production in the earlier years with more plant cover. Each of the commoner species of shrubs on the riverbed occurred at a different stage in succession (Table 7). Although present up some tributary streams for at least 10 years previously, it was not until 1979 that buddleia spread widely on the main riverbed; where it became the commonest shrub (mainly as seedlings) after 1985. Next in abundance after buddleia were tauhinu, kanuka/manuka, and gorse (Table 2). In the usual mixed stands of scrub, tauhinu grew faster than kanuka for about 10 years; but its trunks began to rot when 15-20 years old and it died back. Buddleia was in only 18.5% of the plots with more than 60% cover, compared with 34.5% for gorse, 66.5% for tauhinu and 77.0% for kanuka/manuka (all differences $P < 0.001$). Most well-grown stands of scrub included both kanuka and manuka. Segregation into more or less pure stands of one or the other species usually took place after they were at least 20 years old - except on very wet sites where manuka alone survived.

The biggest flood between 1966 and 1990 was in May 1981, but its effects were less drastic than were the cumulative ones of the earlier consecutive wet years. From June 1966 to December 1990 inclusive (295 months) the maximum monthly rainfall at the Field Station was 655 mm in April 1968; over 600 mm also fell in April 1974 and July 1983. Of the 58 months with more than 300 mm of rain, 33 were in the wet years 1974-81.

In the summers (December-February) from 1969-70 to 1989-90 there was less than half the average monthly rainfall at the Field Station (129 mm) in 14 of the 63 summer months. Campbell (1984) and Brockie (1992) described the effects of droughts in 1969-70, 1970-71, 1980-81 and 1981-82. In the same period extended to February 1991, January 1989 was the driest month with only 16 mm of rain. By April 1989 more than half the putaputaweta (*Carpodetus serratus*) and three-quarters of the black beech (*Nothofagus solandri* var. *solandri*) in 0.5 ha of the drier scrub on Paua Flat had died; the 34 dead putaputaweta were up to 4 m tall and 13 years old, and the 40 dead beech were up to 4 m tall and 15 years old. Many other shrubs and small trees, sedges and ferns also died.

This short drought thus delayed the transition from shrubs to trees by up to 15 years.

Many of the older stands of scrub on the riverbed, dating back to about 1920, were growing in former 'oxbows' vacated by the river. Many of these still contained sluggish backwaters and swampy ground; and some had small stands of pole-sized kahikatea (*Dacrycarpus dacrydioides*) up to about 80 years old in 1990. Some stands of kanuka 30-50 years old had drowned on recently waterlogged sites. The greater moisture and light penetration produced thickets of *Blechnum* fern and toetoe (*Cortaderia fulvida*), some being replaced by tree ferns (*Cyathea medullaris*), shrubs and small trees. These included pigeonwood (*Hedycarya arborea*), kawakawa (*Macropiper excelsum*), mahoe (*Melicytus ramiflorus*), putaputaweta, kaikomako (*Pennantia corymbosa*), lancewood (*Pseudopanax crassiflorus*), pate (*Schefflera digitata*), and hangehange (*Geniostoma rupestre*). Drier sites included a few rimu (*Dacrydium cupressinum*), totara, horopito (*Pseudowintera axillaris*), beech, more putaputaweta and lancewood, mingimingi (mostly *Leucopogon fasciculatus*, fewer *Cyathodes juniperina*), and rangiora (*Brachyglottis repanda*). Future changes may include such adventives as *Pinus radiata* and *Tradescantia fluminensis* (Campbell, 1984) and pampas (e.g., *Cortaderia jubata*; *pers. obs.*), already recorded on the river flats.

Succession

Describing the headwaters of the Rakaia, Cockayne (1911) commented: "Notwithstanding the extreme variability of river-bed vegetation, a complete cycle of events is always in view ... from the first insecure occupation of the ground to its final conquest by steppe, shrubbery, or forest".

Primary succession begins on sites previously devoid of vegetation, in New Zealand notably volcanic sites and riverbeds. In the Orongorongo Valley suitable sites abound after floods, often with some survivors from earlier stands. Sousa's (1984) description of volcanic White Island as a "shifting mosaic" is appropriate here too.

The earliest pioneers on riverbeds may be regarded as facilitators (Wardle, 1991). Cockayne (1911) listed willowherbs and scabweed as the first pioneers on montane riverbeds; in the Orongorongo Valley *Raoulia tenuicaulis* is much more frequent that *Epilobium* spp. in plots with up to 20% cover ($P < 0.001$), and grasses are slightly more frequent than scabweed ($P < 0.05$) (Table 7). According to Calder (1961), mat plants, notably scabweed, are the first to stabilise subalpine riverbeds; their filling of sand provides a seedbed for other plants, as in the Orongorongo Valley. No site in the Orongorongo Valley followed "the slow 'classical' succession beginning with lichens and mosses" (Clarkson, 1990). Bare ground was colonised promptly by pioneer herbs, scabweed and seedling shrubs; moss came later and lichen much later.

The vegetation that eventually clothes river flats bears some resemblance to that on the surrounding country: subalpine scrub or beech forest in montane catchments (Cockayne, 1911), tussock grassland in Canterbury (Calder, 1961), or rough pasture near Wellington (Croker, 1955). Where the exposed substrate (or seed source) was varied, "all taxonomic groups of plants established more or less concurrently" (Clarkson, 1990), again as in the Orongorongo Valley (Table 3). No amount of research is likely to predict the detailed course of succession in the Orongorongo Valley, because so much depends on the availability of seed after floods and on other chance events.

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