

SUCCESSION IN SUBALPINE VEGETATION AT ARTHUR'S PASS, NEW ZEALAND

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SUMMARY: In 1898 Cockayne described succession in subalpine vegetation which had been burnt eight years previously at Arthurs Pass. In 1932 Cockayne and Calder repeated the observations and Calder established ten charted transects, which were re-charted during the summer of 1965–66.

In subalpine scrub, the path of the succession is broadly as follows, although details vary from site to site:

1 year after the fire: appearance of *Marchantia* and ruderal angiosperms.

2–10 years: *Hebe* spp. and *Cassinia fulvida* enter and rise to dominance. Seedlings of climax species also enter, but are relatively slow-growing. Fire-tolerant herbs such as *Hypolepis millefolium* and *Phormium colensoi* may be conspicuous.

40 years: *Senecio bennettii* becomes dominant, *Hebe* almost disappears.

75 years: *Dracophyllum longifolium* and later *Phyllocladus alpinus* regain their original dominance.

Low subalpine forest passes through comparable initial stages, but it is probably about 200 years before the characteristic small trees *Dracophyllum traversii*, *Dacrydium bifforme* and *Libocedrus bidwillii* reach maturity, although their seedlings may appear within 40 years of a fire. In contrast, regeneration of destroyed *Nothofagus solandri* var. *cliffortioides* forest may be rapid, but there is very little tendency for beech to invade scrub and grassland beyond the original forest boundaries. In *Chionochloa* grassland the effect of fire is to allow herb-field species — notably species of *Celmisia* — to achieve at least physiognomic dominance for a few years.

INTRODUCTION

Arthurs Pass is a low (3,020 ft.) saddle across the Southern Alps at latitude 42°55'S., and is crossed by the only road directly linking Canterbury and Westland. It consists of a mile-long stretch of rolling, greywacke moraine between Phipps Peak to the east and Mt. Rolleston to the west (Fig. 1). The climate is marked by very high precipitation (certainly exceeding 200 in. per annum), the possibility of snow falling in any month and lying for some weeks during the winter, and cold winds from the north blowing most of the time — often at gale force. Short spells of dry, warm weather also occur.

The vegetation is predominantly subalpine scrub, which attains its greatest height and density on slopes sheltered from the prevailing wind. There are also areas of tall tussock grassland, herbfield and bog. At the southern (Canterbury) end of the pass there is a steep drop into the beech forest of the Bealey valley dominated by *Nothofagus solandri* var. *cliffortioides* and, at the northern end, an even more precipitous descent into the mixed forest of the Otira valley dominated by *Metrosideros umbellata* and *Weinmannia racemosa*.

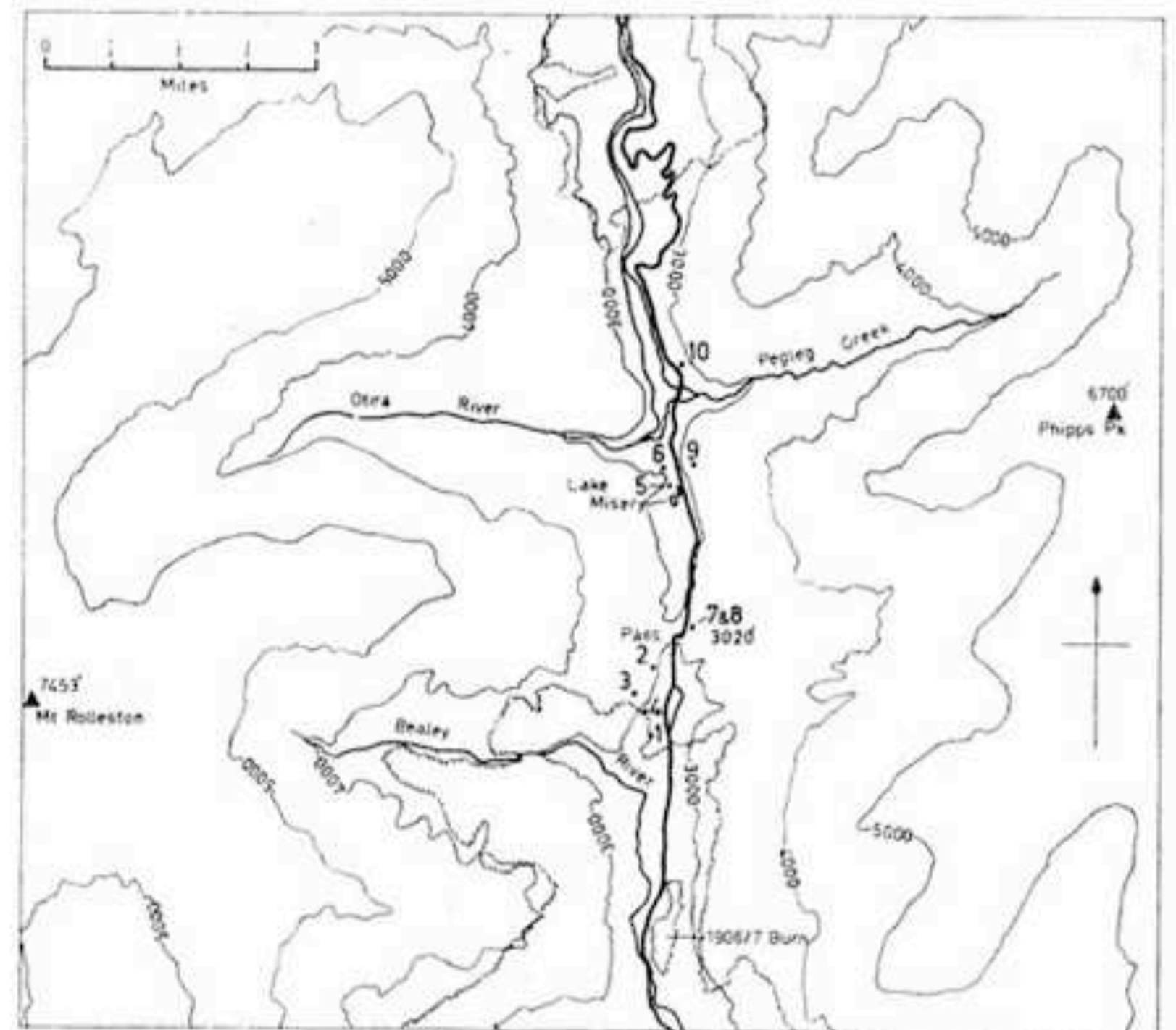


FIGURE 1. Location of transects at Arthurs Pass.

The pass has been an important route since its discovery by Arthur Dobson in 1864 and portions of the vegetation have been burnt from time to time. In 1890, one such fire burnt over the greater

part of the pass, leaving only a few remnants unburnt. Smaller fires have occurred since, but apparently none later than 1933. In the summer of 1897-98, Cockayne compared the developing vegetation of the burnt areas with the original vegetation, basing his reconstruction of the latter both on unburnt remnants and on remains of burnt plants (see Cockayne 1898). In 1932, Cockayne and Calder described the vegetation as it appeared 34 years later, and, during the summers of 1931-32, 1932-33 and 1933-34, Calder mapped 10 permanent belt transects which varied in size from 2½ x 4 ft. to 8 x 66 ft. The present paper is based on a remapping of these transects during the summer of 1965-66 and an inspection of a burnt area within the beech forest, described by Cockayne and Sledge in 1932. Nomenclature has been brought up to date but it is still tentative for a few species, such as *Cassinia fulvida* and *Celmisia discolor*.

METHOD

Position, height and extent of each plant were charted in the field, and areas were measured in the laboratory. The records for 1931-34 and 1965-66 can be compared most readily in respect to canopy areas and heights of shrubs, basal areas of tussock-forming herbs and grasses and areas of mat-forming species. Numbers of plants recorded in 1965-66 are not directly comparable with those

recorded earlier, mainly because of the tendency for vegetative reproduction and clonal division in most species; nevertheless, the fate of individual plants present in 1931-34, and the establishment of new ones can usually be determined confidently.

Only a minimum of statistical information from the transects is given in this paper, but the complete record, including charts, photographs and analyses, is held at the Botany Division, D.S.I.R., Lincoln.

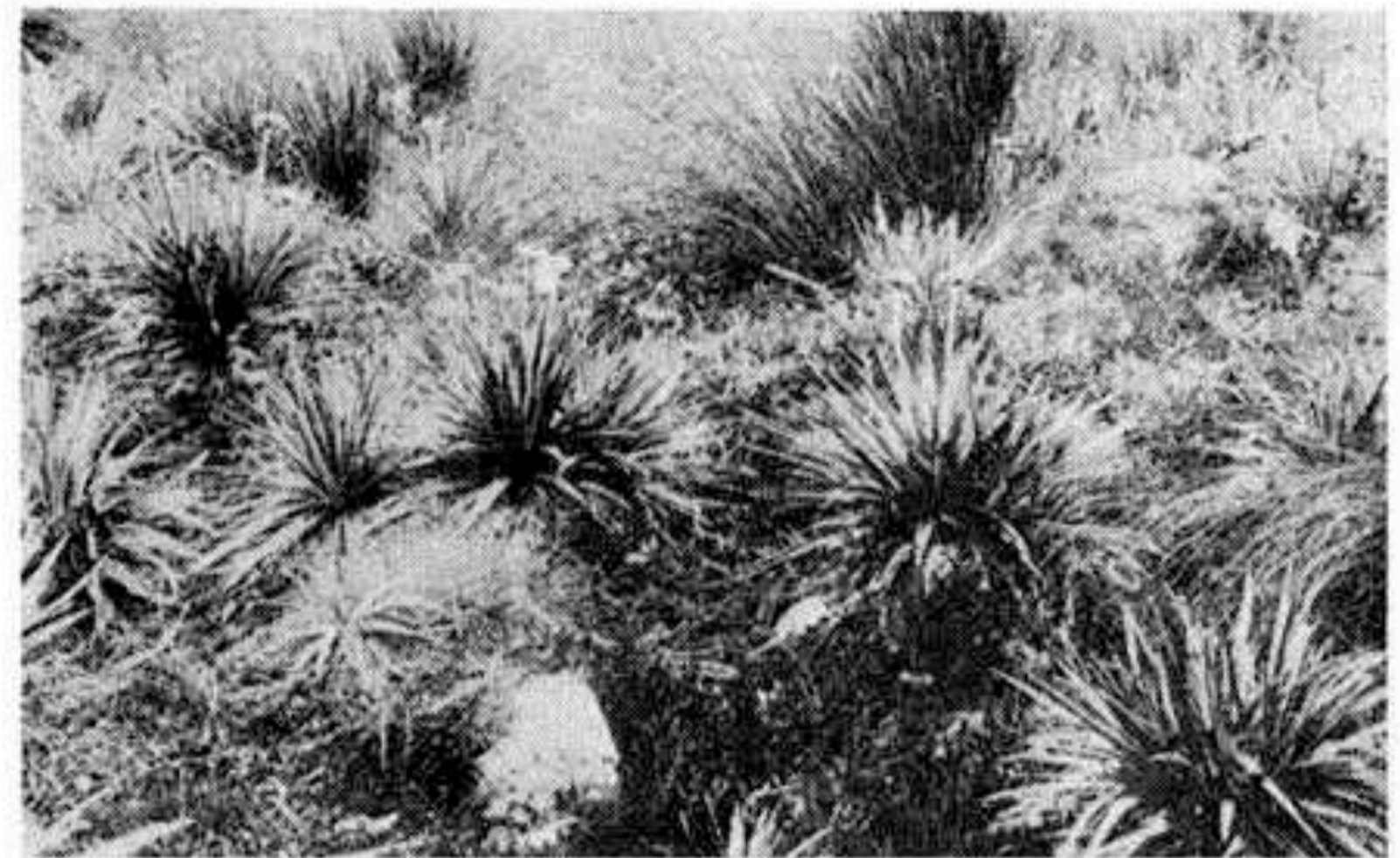


FIGURE 2. Near transect I in 1897-98. Burnt 1890. *Celmisia armstrongii* is the main species. There are also *Chionochloa tussocks*, *Hebe* seedlings (e.g. in foreground), and an extensive colony of *Celmisia discolor*.

Photo, L. Cockayne

TRANSECT I (116 sq. ft. Burnt 1890)

	1931-32	1965-66	1965-66 compared with 1932-33
<i>Dracophyllum uniflorum</i>	22%, 2½'	26%, 4'	Same 5-6 plants
<i>Hebe canterburiensis</i>	4%, 3'	8%, 2½'	Fragments from original 5 plants
<i>Hebe odora</i>	8%, 3½'	5%, 3'	Different plant
<i>Coprosma cheesemanii</i>		31%	
<i>Dacrydium laxifolium</i>	3%	8%	Same 2-3 patches
<i>Celmisia armstrongii</i>	b +	b +	Plants small, different
<i>Chionochloa rubra</i>	b 3%	b 7%	Mostly same (9-11) plants
<i>Chionochloa pallens</i>	b 2%	b 2%	Plants mainly new
<i>Schoenus pauciflorus</i>	b +	b +	One of 2 original plants remaining
<i>Celmisia discolor</i>	11%	2%	One of 2 original colonies remaining
<i>Ranunculus lyallii</i>	+		Still a few reduced plants near transect
Total species	30	30	20 species present both years

Explanation of transect tables

"%" is percentage of the transect covered by a species. This refers to canopies of shrubs (including overhanging branches of shrubs rooted outside the transect, unless otherwise stated), and total areas of spreading and turf-forming herbs. For tussock-forming herbs, it is prefixed with "b", and refers to the basal area only.

"+" and "f" refer to species which cover less than 1% of the transect; "f" is used where individuals are relatively numerous.

Height, in feet or inches, refers to the tallest shrub of each species.

Each table shows only the more important species, but the total number of species is given at the foot.

TUSsock GRASSLAND

Communities dominated by *Chionochloa* (mainly *C. rubra*, but also *C. flavescens* and *C. pallens*) occupy flattish, gently sloping areas. The shrub content, mainly *Dracophyllum uniflorum* and *D. longifolium*, increases on rocky and better-drained terrain. On poorly-drained ground such species as *Carpha alpina* and *Schoenus pauciflorus* are abundant, and these communities grade into bog dominated by cushion plants.

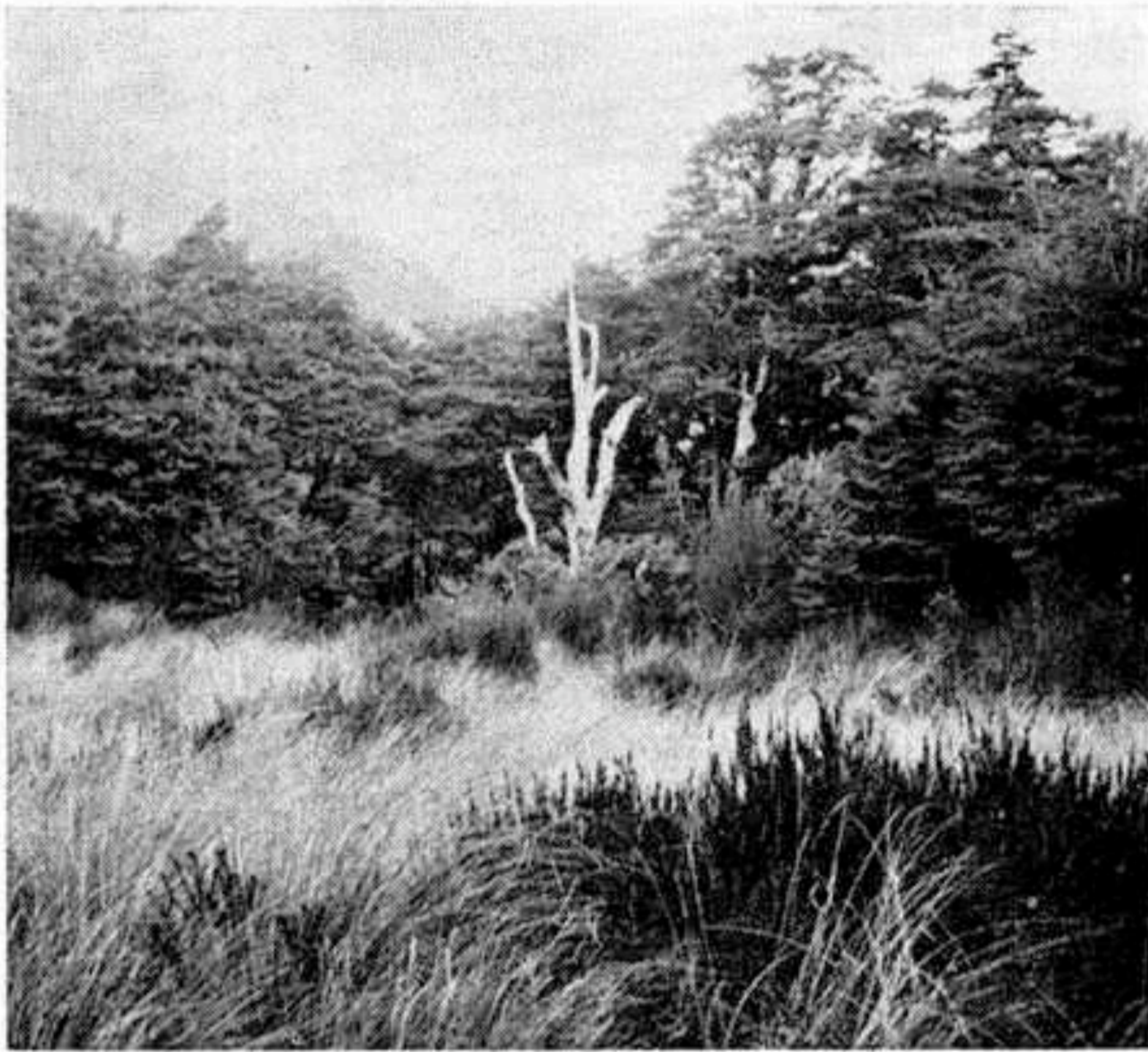


FIGURE 3. The foreground shows the site of Transect I, in February 1965. *Chionochloa* is dominant and the bushes are *Dracophyllum uniflorum*. The tree in the centre of the photograph died in 1933; shrubs of *Dracophyllum longifolium* and *Phyllocladus alpinus* now dominate at this point, whereas to either side young beech trees have overtopped the scrub species.

Photo, J. Somers Cocks

Transect I, which represents the better-drained variant, is on an area burnt in 1890. A photograph taken in the summer of 1897–98 shows that an unburnt fragment consisted of dense *Chionochloa* with small bushes of *Dracophyllum*. The burnt area by that time supported herbfield, with *Celmisia armstrongii* and *Ranunculus lyallii* as the prominent species and only sparse *Chionochloa*. Seedlings of *Hebe* were present (Fig. 2). The surveys in 1932 and 1965 show an increase of *Chionochloa* and entry and increase of *Dracophyllum uniflorum*. Hebes still persist, but in a somewhat reduced state, and the vegetation has in effect regained its original composition (Fig. 3).

Ranunculus lyallii has disappeared almost completely from the vicinity of Transect I, and so has the large colony of this species at the forest margin. This was discussed by Cockayne and Calder (1932). It is possible that it was destroyed by deer, although it was still vigorous in 1931, when deer had been common for at least a decade (Wodzicki 1950).

Transect II is on a poorly-drained area. *Celmisia petiolata* and other herbfield species were much more prominent than *Chionochloa* seven years after the 1890 fire, but by 1931 the latter formed a close cover. A second fire in the autumn of 1932 led to renewed prominence of *Celmisia*, but by 1946 *Chionochloa* was again dominant (Fig. 4). As the transect data suggest, however, *Chionochloa* (mainly *C. rubra*) had been burnt to the ground, but not destroyed; the tussocks present in 1966 were already established before the 1932 fire.

The shrubby component of this boggy area is negligible (apart from the fire-weed *Cassinia*), but on rocky, higher ground just beyond the transect, there was marked re-establishment of *Dracophyllum* after each fire.

TRANSECT II (150 sq. ft. Burnt 1890 and autumn 1932)

	1932–33	1965–66	1965–66 compared with 1932–33
<i>Dracophyllum uniflorum</i>		+, 1'	1 seedling
<i>Dracophyllum longifolium</i>		+, 3'	1 seedling
<i>Cassinia fulvida</i>	+, 2''	3%, 2'	1 resprouted plant, now fragmented
<i>Chionochloa rubra</i>	b 11%	b 14%	Same plants (ca. 27) with division and fusion
<i>Chionochloa flavescens</i>	b 1%	b +	Same plant
<i>Celmisia coriacea</i>	b +	b +	Same 2 plants
<i>Celmisia petiolata</i>	b f	b f	
<i>Carpha alpina</i>	b +	b 10%	
<i>Schoenus pauciflorus</i>	b 6%	b 4%	Original and new plants
Total species	16	35	15 species present both years



FIGURE 4. Site of Transect II, in January 1963, Burnt 1890 and 1932. *Chionochloa*, mainly *C. rubra*, is dominant on poorly drained ground. Compare with Photos 5 and 6 in Cockayne and Calder (1932).

Photo, A. P. Underhill



FIGURE 5. The beech forest margin in January 1963, consisting of young trees. Burnt 1890. Transect III is adjacent to the forest in tall scrub dominated by *Senecio bennettii*. Compare with Photos 1 and 2 in Cockayne and Calder (1932).

Photo, A. P. Underhill

SUBALPINE SCRUB

Before the fire of 1890 a sheltered area at the southern end of the pass, adjacent to the beech forest, supported scrub up to 15 ft. tall, of which *Phyllocladus alpinus* formed quite three-quarters.



FIGURE 6. Transect III in 1933–34, with *Senecio bennettii* dominant among stumps of beech.

Photo, J. W. Calder

Transect III runs along the former forest margin, as shown by trunks of beech which were still standing in 1933–34, but which are now reduced to stumps and rotting logs (Figs. 5 and 6). Transect IV is entirely within the area of the original scrub.

Seven years after the 1890 fire, *Hypolepis millefolium* formed the most striking feature of the new growth, but seedlings of *Senecio bennettii*, *Hebe* spp., and *Coprosma parviflora* were present in considerable numbers and plants of several other species had survived the fire. Photographs taken in 1915 portray scrub 3–4 ft. tall, dominated by *Phormium colensoi* and *Hebe*.

By 1932 the scrub could be described as a mixture of *Senecio bennettii*, *Coprosma parviflora* and *C. pseudocuneata*, although two plants of *Olearia ilicifolia* and two of its hybrids with *O. lacunosa* covered a large percentage of the transects; it is likely that these olearias are old plants which had resprouted from the base after the 1890 fire. By 1966 the areas covered by these species had not changed much, except that *Coprosma pseudocuneata* had shown a 2- to 5-fold increase in its area, both through production of coppice shoots by existing clumps and through establishment of new seedlings.

A very significant trend is the steady gain by the original dominant, *Phyllocladus alpinus*. The taller plants may well have been represented among the very rare and very small seedlings recorded by Cockayne. Subsequent increase has been both by lateral spread and layering and by the infrequent establishment of new seedlings.

		TRANSECT III (518 sq. ft.) and TRANSECT IV (512 sq. ft. Burnt 1890)			
		1897-98	1931-32	1965-66	1965-66 compared with 1931-32
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>			III: +, 3'	6% ^a , 15'	Increased from 1 to 12 plants in III. 2 seedlings in IV
<i>Hebe canterburiensis</i>	Seedlings in quantity, 1'		III: 5%, 4'	f, 2½'	Plants more numerous and dispersed, but smaller
<i>Hebe subalpina</i>	Seedlings abundant, 1'		IV: 6%, 4'	f, 8''	Plants different
<i>Senecio bennettii</i>	Seedlings abundant, 1'		IV: 1%, 3'	+, 1½'	
<i>Coprosma parviflora</i>	Plentiful in places, 2''		III: 31%, 6'	37% ^a , 10'	Plants mainly same, fragmented
<i>Coprosma pseudocuneata</i>	From burnt stump, scarce		IV: 8%, 4'	3%, 4'	Original and new plants
<i>Olearia ilicifolia</i>	Seedlings in small quantity, 4''		III: 3%, 5'	6%, 6'	
<i>Olearia lacunosa</i>			IV: 7%, 5'	12%, 5'	Original and new plants
<i>Olearia lacunosa</i> × <i>ilicifolia</i>			III: 9%, 6'	42%, 8'	
<i>Dracophyllum longifolium</i>			IV: 14%, 5'	27%, 5'	Same 2 plants
<i>Phyllocladus alpinus</i>	Seedlings very rare and very small		III: *, 7'	1%, 8'	
<i>Hoheria glabrata</i>	1 from burnt stump, 1'		IV: 11%, 6'	17%, 12'	Same plant
<i>Aristolelia fruticosa</i>	Seedlings plentiful, 2'		III: +, 3'		Same 2 plants in IV, 1 now moribund
<i>Cassinia fulvida</i>	Seedlings in medium quantity 1'		IV: 13%, 7'	17%, 10'	1 original and new plants
<i>Pseudopanax colensoi</i>	Grown from burnt stump, 2'		IV: +, 3'	7%, 5'	11 original and about 8 new plants
<i>Podocarpus nivalis</i>	A few plants		III: +, 4'	2%, 9'	Plants mainly different and suppressed
<i>Coprosma depressa</i>	Large patches, probably survived fire		IV: 4%, 5'	35%, 8'	Plants suppressed
<i>Myrsine nummularia</i>	In quantity, perhaps little-damaged by fire		III: +, 4'	f, 7'	
<i>Phormium colensoi</i>	In quantity		IV: +, 7'	1%, 11' ^c	2 plants in openings
<i>Astelia nervosa</i>			III: +, 3'	+, 2'	
<i>Chionochloa rubra</i>			IV: 2%, 3'	+, 3'	
<i>Polystichum vestitum</i>			IV: +, 3'	2%, 5'	
<i>Hypolepis millefolium</i>	Main feature		III: +, 4'	+, 7'	Tallest plant the same, others different
<i>Blechnum minus</i>			IV: +, 3'	+, 1½'	Same clone in IV, mainly in opening
			III: 1%	15%	At many points in IV
			III: +	+	At many points in IV.
			IV: b 1%	b 3%	Original plants now mainly small and fragmented
			IV: b 2%	b 1%	Plants now smaller and more dispersed
			III: b +	b +	1 large tussock in opening
			IV: b 1%	b +	
			IV: +	b +	
			III: +	b 1%	
			III: +	+	
			III: +	11%	Rather localised on transects
			IV: +	13%	
Total species (III and IV)	19	24	56	21 species present in 1932 and 1966	

^a % refers only to plants rooted within Transect III. When overhanging canopies are included, values become 16% for *Nothofagus*, and 53% for *Senecio bennettii*.

* Plant outside transect in 1933-43.

^c A plant of *Hoheria glabrata* overhanging the plot is 14 ft. tall.

The other notable trend is the re-establishment of beech. In Transect III the seedling present in 1932-33 is now a young tree with a canopy covering 5% of the transect. Most of the young plants of beech have become established within the original forest boundary indicated by stumps, occurring either where the scrub has been suppressed by the

canopies of taller beech trees or in enclaves of herbfield containing *Chionochloa*, *Phormium colensoi*, *Podocarpus nivalis*, etc. Such enclaves will, of course, be eliminated where overgrown by beech, but if beech does not invade they are remarkably persistent. Pockets and leads of herbaceous vegetation are common even in virgin scrub.

The heights of the main plants of the scrub canopy in Transect IV have been rather static over some 30 years, excepting that *Phyllocladus* has continued to grow steadily. In Transect III, on the

other hand, canopy heights have increased by 2–4 ft., apparently because the shrubs have been “drawn up” under the influence of the encroaching forest.

TRANSECT V (280 sq. ft. Burnt 1890)

	1931–32	1965–66	1965–66 compared with 1931–32
<i>Dracophyllum longifolium</i>	10%, 5'	25%, 6'	Same plants, much fragmented
<i>Dracophyllum traversii</i>	+, 3'	3%, 8'	Same 3 plants
<i>Senecio bennettii</i>	21%, 5'	23%, 6'	Mainly same plants fragmented
<i>Phyllocladus alpinus</i>	1%, 2'	7%, 3½'	Same 4 plants, and 1 new seedling
<i>Olearia colensoi</i>	+, 2'	1%, 3'	Same plant
<i>Hebe subalpina</i>	+, 4'	+, 2'	
<i>Podocarpus nivalis</i>	9%	4%	Original 2 colonies fragmented
<i>Phormium colensoi</i>	b +	b f	Mainly same plants fragmented
<i>Chionochloa flavescens</i>	b +	b +	Same plant
<i>Blechnum minus</i>	3%	33%	Mainly on same part of plot
Total species	21	38	21 species present both years

On spurs, knolls, and rough moraine, *Dracophyllum longifolium* is usually prominent in the scrub. Before the 1890 fire it was apparently co-dominant with *Phyllocladus alpinus* on the south (sheltered) side of the prominent moraine overlooking the Otira Valley, where Transect V is located. Seven years after the fire, *Hebe subalpina* was the most conspicuous plant, but seedlings of *Dracophyllum longifolium* were abundant and *Senecio bennettii* had also re-entered. The *Senecio* had become the most important shrub by 1932, but by 1965 *Dracophyllum longifolium* equalled it. *Phyllocladus* has increased slowly in number and size of plants from the rare seedlings noted in 1897–98, although one shrub which survived the fire has since died. *Dracophyllum traversii* is represented by 3 plants which were 2, 2 and 3 ft. tall in 1932, and 2½, 5 and 8 ft. tall respectively in 1965; the tallest plant is growing in the shelter of a large rock (Fig. 7).

The northern side of the crest of the same moraine, where Transect VI is located, experiences maximum exposure, and the original vegetation was probably low scrub, with tussocks of *Chionochloa*, *Astelia*, *Phormium* and *Celmisia armstrongii*. *Phormium* and *Aciphylla “colensoi”* were present in “large quantities”, but apart from *Coprosma serrulata*, shrubs were reappearing only in sheltered niches such as behind rocks, and *Dracophyllum longifolium* was the commonest. In 1933–



FIGURE 7. Transect V in 1946. *Senecio bennettii* and *Dracophyllum longifolium* are dominant; a sapling of *D. traversii* is at the left. Burnt 1890. Photo, J. W. Calder

34 Transect VI was dominated by low bushes of *Dracophyllum longifolium* and *D. uniflorum* but *Gaultheria rupestris*, *Pentachondra pumila*, *Celmisia armstrongii* and *C. discolor* were also important. The vegetation had evidently attained its full development, for measurement in 1965 showed no important changes, excepting that 24% of the transect had been denuded in the formation of a track.

TRANSECT VI (66 sq. ft. Burnt 1890)

	1933-34	1965-66	1965-66 compared with 1933-35
<i>Dracophyllum longifolium</i>	7%, 1½'	3%, 2'	1 plant fragmented, 3 lost on track*
<i>Dracophyllum uniflorum</i>	6%, 2'	+, 1'	Original plant lost on track, 1 new
<i>Senecio bennettii</i>	+, 1'		Still near transect
<i>Gaultheria rupestris</i>	2%	1%	Same plants
<i>Myrsine nummularia</i>	+	3%	
<i>Coprosma serrulata</i>	+	f	
<i>Pentachondra pumila</i>	2%	+	
<i>Celmisia armstrongii</i>	b 3%	b +	Mostly lost on track
<i>Phormium colensoi</i>	b +	b 4%	Same plants
<i>Schoenus pauciflorus</i>	b 1%	b +	Original and new plants
<i>Chionochloa flavescens</i>	b 1%	b f	9 plants the same, 2 lost on track
<i>Celmisia discolor</i>	12%	13%	Same plants
Total species	18	21	12 species present both years

* A denuded track covered 24% of the transect in 1965.

Effect of a second fire on scrub

An area burnt by the 1890 fire had, by 1930, developed scrub which was dominated by *Senecio bennettii* and *Dracophyllum longifolium* in a flat trough. This vegetation was burnt again in the autumn of 1930. A year later, 16 species were present, among which *Phormium colensoi*, *Astelia nervosa*, *Chionochloa*, *Blechnum procerum*, *Celmisia armstrongii*, *C. discolor*, *Ourisia macrocarpa*, *Anisotome haastii*, *Helichrysum bellidioides*, *Coprosma serrulata* and *Ranunculus lyallii* were re-growing from surviving bases (Fig. 8). On the flat area large thalli of *Marchantia* were common (cf. McQueen's 1951 account of succession after fire in *Nothofagus menziesii* forest). The only woody seedlings recorded were those of *Gaultheria rupestris*, and probably these were really shoots sprouted from rhizomes. Herbaceous seedlings included, among others, the following ruderal species: *Erechtites glabrescens*, *Epilobium* 2 spp., *Gnaphalium luteo-album*, and the exotics *Rumex acetosella*, *Holcus lanatus*, *Agrostis tenuis*, *Stellaria media* and *Cirsium lanceolatum*.

In 1932 Transects VII and VIII, both extending mainly over the flat depression, were mapped. By this time there were small seedlings of *Hebe* and *Cassinia*. Otherwise the area was still dominated by re-sprouted tussocks of *Astelia* and *Phormium*, and by mats of such species as *Blechnum pennamarina*, *Helichrysum bellidioides*, *Myrsine nummularia*, *Viola cunninghamii*, *Wahlenbergia albomarginata*, and *Celmisia gracilentia*.

Photographs taken in 1946 show the flat portion of Transect VII still with *Astelia*, *Phormium* and



FIGURE 8. Near Transect VII in 1931. Burnt 1890 and 1930. The shrubs are dead, but *Phormium colensoi*, *Astelia nervosa*, *Blechnum minus*, *Celmisia armstrongii* and *C. coriacea* are showing re-growth.

Photo, J. W. Calder

the intervening mat; but *Chionochloa* is also obvious and the *Hebe* plants are up to one foot tall. On the moraine, between rocks and clumps of *Phormium*, there is low scrub in which *Senecio bennettii*, *Coprosma pseudocuneata* and *Podocarpus nivalis* are recognisable.

TRANSECT VII (104 sq. ft. Burnt 1890 and autumn 1930)

	1931-32	1965-66	1965-66 compared with 1931-32
<i>Cassinia fulvida</i>		2%, 2½'	Seedlings on Transect VI only in 1932 { Probably same 11-12 } plants 11 plants 4 plants on moraine
<i>Hebe subalpina</i>	{ 11 seedlings } { 3'' }	1%, 2'	
<i>Hebe odora</i>		14%, 3'	
<i>Dracophyllum longifolium</i>		4%, 3½'	
<i>Senecio bennettii</i>		2%, 2'	
<i>Gaultheria rupestris</i>		+	1%
<i>Coprosma serrulata</i>	+	2%	
<i>Phormium colensoi</i>	b 5%	b 2%	Mainly same plants
<i>Astelia nervosa</i>	b 1%	b 2%	Probably same plants
<i>Celmisia armstrongii</i>	b +	b f	Mainly same plants
<i>Chionochloa</i> spp.		b 1%	Includes <i>flavescens</i> and <i>rubra</i>
<i>Blechnum minus</i>		f	Common near transect in 1932
Total species	23	45	15 species present both year

By 1965, *Hebe odora* was the dominant plant on the flat portion of Transect VII but *Astelia*, *Chionochloa* and *Phormium* were still important. The mat-forming species, though mostly still present, were suppressed; whereas the ruderals had disappeared (indeed, *Epilobium* sp., *Cirsium* and *Agrostis tenuis* were the only ruderal species recorded as still present in 1932). Young plants of *Dracophyllum longifolium* were present over the whole transect, but *Senecio bennettii* was only on the morainic portion.

Data for Transect VIII are not presented, because this area is subject to prolonged flooding, so that shrubs do not survive beyond the seedling stage and mat-forming species still dominate.

On the lower slopes of Phipps Peak, above Lake

Misery, there was scrub which, to judge from a remnant which survived the 1890 fire, had *Dracophyllum traversii*, *Pseudopanax colensoi*, *Phyllocladus alpinus*, *Olearia ilicifolia*, *O. nummularifolia*, *Dracophyllum longifolium* and *Coprosma* spp. as the main components on the open face, and *Hoheria glabrata* dominant in a gully. By 1897-98, about 50% of the new growth consisted of *Hebe subalpina*; but *Olearia ilicifolia*, *Senecio bennettii*, *Pseudopanax colensoi*, *Cassinia* and *Hoheria* were present. Later, apparently, *Phormium* became very abundant. By 1921, the shrubby component had increased, *Hebe subalpina* and *Phormium* were still abundant but no longer dominant, and *Aciphylla scott-thomsonii* and *Dracophyllum longifolium* had entered locally.

TRANSECT IX (72 sq. ft. Burnt 1890 and December 1921)

	1933-34	1965-66	1965-66 compared with 1933-34
<i>Coprosma parviflora</i>	+, 3''	1%, 3'	Same plant
<i>Cassinia fulvida</i>	7%, 2'	2%, 1½'	Now moribund fragments
<i>Dracophyllum longifolium</i>	2%, 1¼'	8%, 6'	Same 4 plants
<i>Dracophyllum uniflorum</i>	+, 8''	6%*, 3'	Same 3 plants
<i>Hebe canterburiensis</i>	4%, 2'	+, 2½'	Reduced from 9 plants to 1
<i>Hebe subalpina</i>	10%, 1½'	+, 1½'	Sparse remnants
<i>Olearia ilicifolia</i>	+, 6''		2 seedlings in 1933-34
<i>Senecio bennettii</i>	+, 4''	8%, 3'	Original 4 plants, and 1 new
<i>Coprosma serrulata</i>	+	5%	
<i>Gaultheria rupestris</i>	+	5%	
<i>Phormium colensoi</i>	b 2%	b 2%	Original plant, and 1 new
<i>Celmisia coriacea</i>	b +	b +	Same plant
<i>Astelia nervosa</i>	b 1%	b +	Same 2 plants
<i>Blechnum minus</i>	22%	53%	
<i>Ourisia macrocarpa</i>	6%	f	
Total species	22	21	18 species present both years

* % refers only to plants of *D. uniflorum* rooted within transect.
A plant rooted outside covers 13% of transect.

TRANSECT X (152 sq. ft. Burnt ca. 1878)

	1933-34	1965-66	1965-66 compared with 1933-34
<i>Cassinia fulvida</i>	12%, 5'	1%, 4'	Dying out
<i>Coprosma parviflora</i>	3%, 4'	10%, 6'	Original and new plants
<i>Coprosma pseudocuneata</i>	8%, 5'	7%, 7'	Same plants fragmented
<i>Dracophyllum longifolium</i>	12%, 5'	17%, 5'	Mainly same plants fragmented
<i>Pseudopanax colensoi</i>	+, 2'	6%, 6'	Same plant
<i>Senecio bennettii</i>	10%, 3'	10%, 3½'	Original and new plants
<i>Podocarpus hallii</i>		+, 2'	1 plant
<i>Phyllocladus alpinus</i>		+, 3'	1 plant
<i>Griselinia littoralis</i>		+, 6'	1 plant
<i>Coprosma serrulata</i>	+	4%	
<i>Gaultheria rupestris</i>	+	1%	
<i>Astelia nervosa</i>	b 8%	b 8%	Mainly same plants fragmented
<i>Celmisia armstrongii</i>	b f	b +	Remaining plants are originals
<i>Chionochloa flavescens</i>	b 1%	b 2%	Same 5 plants, and 2 seedlings
<i>Phormium colensoi</i>	b 2%	b 1%	Mainly same plants
<i>Schoenus pauciflorus</i>	b 1%	b +	Probably same 2 plants
<i>Notodanthonia gracilis</i>	+		
<i>Blechnum minus</i>	7%	42%	
Total species	26	27	18 species present both years

The area was burnt again in December 1921, and Transect IX was mapped 11 years later. The transect data and photographs show that, at this time, herbs were still very conspicuous, and that *Cassinia* and *Hebe* were the main shrubs. By 1966, *Dracophyllum longifolium*, *D. uniflorum* and *Senecio bennettii* had become the main shrubs and the scrub had become taller, but *Cassinia* and *Hebe* were much reduced in quantity. The scrub has far to go before it regains its original condition. Thus, it seems that here the second fire strengthened the position of the fire-tolerant herbs, especially *Blechnum minus*, *Phormium* and *Astelia*, and enabled them to form a dense cover resistant to invasion by shrubs.

SUBALPINE LOW FOREST

Transect X is on a terrace which once supported low forest, remnants of which exist in the vicinity. Stumps still remaining show that *Dacrydium biforme** and *Libocedrus bidwillii* were components. Other tall plants would have included *Dracophyllum traversii*, *D. longifolium*, *Phyllocladus alpinus*, *Griselinia littoralis*, *Pseudopanax colensoi*, *P. simplex*, and *Podocarpus hallii*. Such communities are typical of the ecotone between subalpine scrub and the montane *Metrosideros/Weinmannia* forest in Westland.

* Not *D. colensoi*, as stated by Cockayne (1898).

In 1897-98 Cockayne noted only that "*Dracophyllum longifolium* is the leading variety", which suggests that the original vegetation had been burnt considerably before 1890 — perhaps about 1878. *Hebe* spp. were not present in 1933-34, but *Cassinia* was still important and only now does it seem to be disappearing from the community. By 1933-34, the dominant shrubs had nearly reached their present height of 5-7 ft. The main changes on the transect since then have been an increase in density of the scrub (occurring chiefly in the quantity of *Dracophyllum longifolium* and *Coprosma parviflora*), and entry of seedlings of the original forest dominants *Griselinia*, *Phyllocladus*, and *Podocarpus hallii*. Young plants of *Griselinia*, *Dracophyllum traversii* and *Dacrydium biforme* were indeed present on the terrace, but outside the transect, by 1933-34 and seedlings of *Libocedrus* were present in the scrub on neighbouring slopes (Fig. 9).

BEECH FOREST

Cockayne and Sledge (1932) described an open area of about seven acres at 2,800 ft., well within the beech forest. They stated that the site "was originally low subalpine forest, with *Nothofagus cliffortioides* as the sole tree", and that this forest was felled and burnt in 1906-07. In 1931, the ground was occupied by herb-field, scrub and bog; the main communities being those dominated by



FIGURE 9. Site of Transect X in February 1965. The subalpine low forest was burnt, perhaps about 1878, but a *Libocedrus* trunk is still standing. *Dracophyllum longifolium*, *Coprosma parviflora* and *C. pseudocuneata* are now dominant. *Pseudocolensoi* is in the foreground.

Photo, J. Somers Cocks

Chionochoa, *Celmisia*, *Dracophyllum longifolium*, *Cassinia* and *Carpha alpina*. Beech was "rare in the new vegetation, and gives no indication of future re-dominance".

However, examination of nine stumps from the clearing in 1968 showed only one to be beech, three being *Dacrydium bifforme*, and the remainder other dicotyledonous species. Though beech is not a durable wood, it does seem unlikely that many stumps would have rotted completely after 61 years, when they were still quite well preserved on Transect III after 75 years. It seems possible that Cockayne and Sledge were mistaken concerning the original vegetation, and that the site, in fact, supported open scrub with abundant *Phyllocladus alpinus* and *Dacrydium* except in sheltered hollows where there would have been scattered, stunted beech. Such scrub is normal on sites exposed to the prevailing wind, with leached morainic soil. The 1906-07 fire would have destroyed this scrub, and also eaten into the surrounding beech forest.

The vegetation of the open area does not seem to have changed greatly since 1931, and still consists mainly of open scrub dominated by *Dracophyllum longifolium* and boggy grassland dominated by *Chionochoa rubra*. Young plants of *Dacrydium bifforme* and, especially, *Phyllocladus* are common and up to 3½ ft. tall. Establishment of beech is mainly limited to the beech forest margins

(a belt of young beech up to 26 ft. wide now adjoins the marginal trees shown in Cockayne and Sledge's Fig. 2) and to sheltered hollows within the clearing. Post-fire trees are up to 9 in. in diameter.

Where sites which indisputably supported beech forest have been cleared by felling in the Arthur's Pass area, regeneration has occurred and in some places the stands of young beech are very dense.

Concerning undisturbed beech forest, Cockayne and Calder remark that regeneration occurs freely after death of the canopy in places where the trees were originally close enough to suppress the competing undergrowth of shrubs; but where the trees are more widely spaced and stand over a well developed shrub storey (consisting mainly of *Coprosma pseudocuneata*, *C. ciliata*, *C. parviflora*, *Aristotelia fruticosa* and *Phyllocladus alpinus*), no beech seedlings become established. Examination of the particular spot referred to indicates that although the dead trees have now fallen, there is still no young beech among the understorey shrubs. On the other hand, immediately-adjointing scrub is being overtopped by beech saplings, and it seems that on this site, which is at a forest margin, there is "give and take" between the two kinds of vegetation.

DISCUSSION

The most complex succession after fire is that leading towards tall scrub or low forest. By combining the information from several transects, one can see that development is marked by successive dominants with increasing stature and longevity and decreasing growth rate. Within a year of a fire there is an ephemeral appearance of *Marchantia* and ruderal angiosperms and plants which are able to re-sprout from the base. The latter are few in virgin scrub and include mainly herbs and undershrubs with growing points protected by the soil, such as *Hypolepis millefolium*, *Coprosma serrulata* and *Phormium colensoi*. With successive fires such plants become increasingly favoured, and eventually a fire-tolerant community develops which is resistant to invasion by the original dominants. The small tree *Hoheria glabrata* and, probably, *Olearia ilicifolia* can sprout from burnt stumps, but these are not particularly important on the transects, although they are dominant on moist, well-drained sites.

Species of *Hebe*, which are unimportant in virgin scrub, appear as seedlings within two years of a fire, and within 10 years become the dominant feature. *Cassinia* enters at the same time and, unlike *Hebe*, may sprout from the base after a second fire.

Seedlings of *Senecio bennettii*, *Dracophyllum longifolium* and, in very small numbers, *Phyllocladus alpinus* and other species of the climax scrub begin to appear during the first decade. Of these, the *Senecio* is the fastest growing, and by 40 years is usually dominant at the expense of the hebes which from now on play a minor role.

Within 75 years *Senecio*, in its turn, is yielding dominance to the slower-growing *Dracophyllum longifolium* and *Phyllocladus*; but several decades must pass before the latter regains its original status and stature. Even slower recovery is being shown by the slow-growing and long-lived *Dracophyllum traversii* which should require at least another 100 years to reach maturity. *Dacrydium biforme* and *Libocedrus bidwillii*, which are not represented by living plants on the transects, show similar slow recovery.

The decreasing tempo of change culminates in the virtual stagnation of undisturbed tall scrub. In one stand, matching photographs taken in 1931 and 1965 (Fig. 10) show the same trees of *Phyllocladus* and *Dracophyllum traversii*, the latter especially being quite unchanged in appearance. One

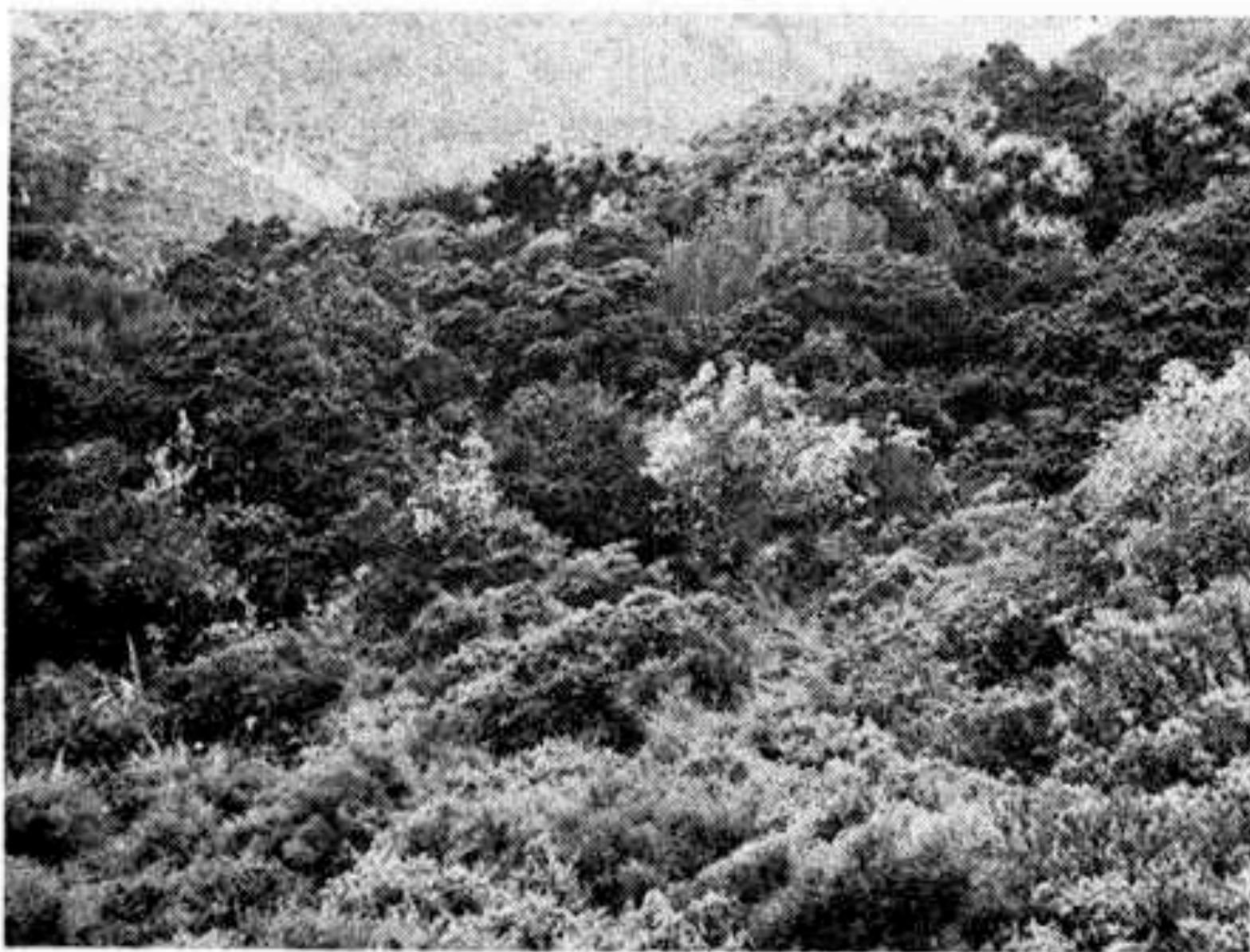


FIGURE 10. *Virgin subalpine low forest* in February 1965, virtually unchanged in 34 years. Compare with Photo 4 in Cockayne and Calder (1932).
Photo, J. Somers Cocks

tree of *Dracophyllum longifolium* has disappeared and so has the only visible plant of *Pseudopanax colensoi*. *Hoheria glabrata* at the margin of this stand is mainly represented by the same clumps, but these do show appreciable changes in size and shape.

The growth rate of *Nothofagus solandri* var. *cliffortioides* is much greater than that of the slow-growing dominants of tall scrub and low forest; and the "turn-over" of individuals in the beech forest is certainly faster. Regeneration of destroyed forest may be rapid but there is very little tendency for beech to invade scrub and grassland beyond the original forest boundaries.

In *Chionochloa* grassland most of the species are able to grow from surviving bases after fire; although in *Chionochloa* itself, the tussocks are weakened and some of them may die. Fire allows herb-field plants — notably species of *Celmisia* — which are normally suppressed by the *Chionochloa* to achieve at least physiognomic dominance for a few years (Fig. 11). The persistence of herbaceous plants is no less remarkable than the longevity of some shrubs, individual plants and colonies of several species being recognisable on the transects over the 32–34 year interval.

When Cockayne described the vegetation of Arthur's Pass in 1897–98, deer had not been introduced, though there may have been some browsing by sheep and cattle. By the nineteen twenties, deer had reached the area but, because of its proximity to habitation, browsing pressure probably has



FIGURE 11. *Celmisia coriacea* in flower in 1897–98 on an area burnt in 1890.
Photo, L. Cockayne

seldom been intense, although deer may have hindered the establishment or persistence of the highly palatable species *Ranunculus lyallii*, *Pseudopanax colensoi* and *Hoheria glabrata* in some transects. Today, such freedom from browsing damage is rare in subalpine vegetation.

It is probably a just claim that the present paper continues one of the longest and best-documented successional studies in New Zealand, if not in the world, and the credit for beginning it belongs to the late Dr. L. Cockayne. As interest in the conservation of native vegetation grows, so should similar transects be mapped in other native plant communities, especially those being modified by introduced mammals and other alien factors.

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