

## Vegetation change after artificial disturbance in an alpine *Chionochloa pallens* grassland in New Zealand

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**Abstract:** We describe the colonisation of artificially created gaps in an alpine grassland dominated by *Chionochloa pallens*. Twelve years after their creation, the 50 cm × 50 cm gaps supported a distinctive vegetation composed of a mixture of perennial forbs, grasses and mosses. Three species (*Bryum* sp., *Epilobium alsinoides* and *Plantago novae-zelandiae*) were recorded only in the gaps. *Plantago novae-zelandiae* and *Polytrichum juniperinum* had their highest frequency in the centres of the gaps, while *Celmisia gracilenta* and *Geranium microphyllum* were most frequent at the edges. The distinctive species composition of the gap plots indicates that they are still in an early stage of succession, assuming an eventual reversion to the surrounding 'climax' grassland.

**Keywords:** alpine grassland; disturbance; gaps; seed dispersal; succession.

### Introduction

The response of vegetation to disturbance in alpine habitats in New Zealand is poorly documented. The studies by Lough *et al.* (1987) and Roxburgh *et al.* (1988) on successional processes in high alpine cushionfield communities, and by Wardle (1972) and Rogers and Leathwick (1994) on montane vegetation, appear to be the only published investigations of vegetation change at higher altitudes in New Zealand. In this paper we report on the colonisation of artificially created bare-soil gaps in an alpine tussock grassland dominated by *Chionochloa pallens*.

Frequent disturbance is characteristic of high altitude environments in southern New Zealand. The Southern Alps mountain chain has been formed by tectonic uplift along the Alpine Fault over the last five million years. A moist westerly wind-drift at right angles to this alpine chain causes high rainfall (> 2000 mm yr<sup>-1</sup>), which induces frequent disturbance through agents such as surface water flow, landslide and avalanche. In addition, smaller scale disturbance may occur by frost heave or mortality of individual plants. Recurrent disturbance is a crucial factor for the maintenance of relatively fertile soils in the alpine zone, as a result of regular input of fresh rock material through alluvial and colluvial processes. The consequent diversity of alpine habitats may be the cause of species radiations occurring in many different groups (Raven and Raven, 1976). It would seem likely that some of these species would have evolved to

exploit short-lived disturbance patches, although Roxburgh *et al.* (1988) were able to identify only one such species.

The importance of disturbance for the maintenance of ecological processes is widely appreciated. By creating competition-free space, disturbance may be a key factor allowing coexistence of species at the community scale (Wilson, 1990), or play an essential role in regeneration (Veblen and Stewart, 1982; Lusk and Ogden, 1992; Duncan, 1993). Some species appear to have quite specific preferences in terms of gap size, quality or timing for regeneration (e.g., Stewart, 1989), but in most communities many species show qualitatively similar establishment responses to gaps (Bullock, 2000).

Research on the response of vegetation to disturbance in New Zealand is dominated by studies below the natural treeline (e.g. Calder *et al.*, 1992; Gibb, 1994; Rogers and Leathwick, 1994). There are two reasons why successional processes may differ in the alpine zone. Rates of succession will almost certainly be slower, because of limitations to productivity caused by the harsher environment at higher elevations. These rates have rarely been quantified. Colonisation processes may also differ, due to differences in dispersal mode between lowland and alpine habitats. In New Zealand, wind dispersal and vegetative expansion seem likely to be the most important factors at high altitudes, due to the low diversity of animal dispersers at such altitudes. Although seed rain has been recorded in alpine vegetation in New Zealand (Spence, 1990a),

little is known about the microsite requirements of early-colonising plants in these habitats. Seedling establishment may be hindered by factors such as frost heave and freezing conditions, favouring vegetative expansion as an alternative strategy for invading newly created gaps.

In 1998 an opportunity arose to examine vegetation change in an alpine *Chionochloa pallens* tussock grassland in the Murchison Mountains of southwest New Zealand. A number of gaps had been artificially created in 1986. These gaps originally consisted of bare ground resulting from excavation of all vegetation, and were part of an experiment started in 1977 to determine the response of *C. pallens* to clipping and fertiliser treatments (Lee *et al.*, 1988). The plant community that developed in the 12 years following gap creation appeared to represent a successional stage in a sere whose 'climax' is the surrounding vegetation dominated by *C. pallens*.

We consider the following questions: (1) What species act as primary colonisers in this habitat and what is their likely means of dispersal? (2) What are the implications of this scale of disturbance for coexistence at the community level? (3) What length of time is required for this alpine grassland to recover from this type of disturbance?

## Methods

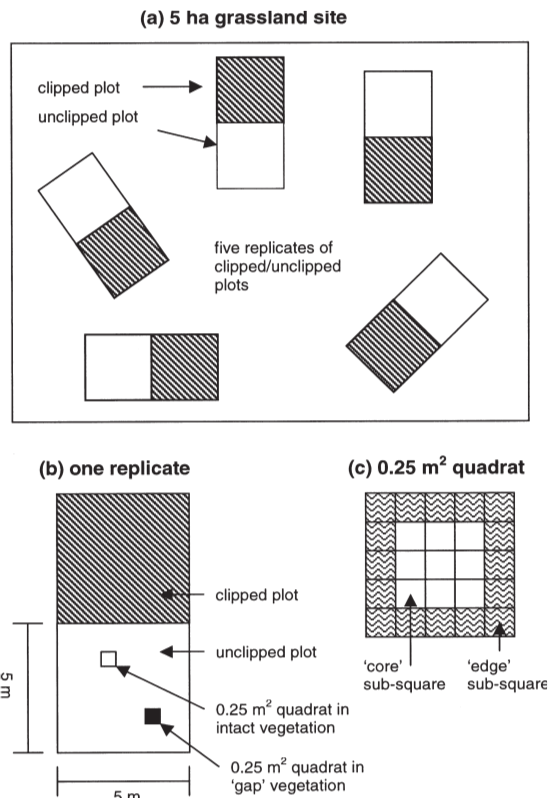
### Study site

The study area lies in eastern Fiordland, South Island, New Zealand, where in the Murchison Mountains rainfall is approximately 2000 mm per annum. Mixed low-alpine scrubland and grassland above the treeline experience a mean monthly temperature of 10°C in January and less than 0°C in July. Two species of southern beech (*Nothofagus menziesii* and *N. solandri* var. *cliffortioides*) form forest that occupies the valley sides and lower mountain slopes in the montane zone, ending abruptly in a distinct treeline at approximately 1050 m. Above this lie extensive tussock grasslands where several species of *Chionochloa* form the dominant plant cover, the species segregating according to soil and aspect (Williams *et al.*, 1976).

*Chionochloa pallens* typically occupies well-drained fertile sites associated with colluvial fans, flood plains and crush zones in the low alpine zone (Lee *et al.*, 1988). At the study site in Dana Basin (latitude 45° 13'18.55" S, longitude 167° 37'44.83" E) approximately 5 ha of grassland, in which *C. pallens* is the physiognomic dominant, occupies gently sloping alluvium on the floor of an alpine basin at 1120 m altitude. Full details of the site are given in Lee *et al.* (1988; 2000).

### Treatments

In November 1977, all *Chionochloa* plants in five plots (5 m × 5 m) were clipped at the blade-sheath junction, approximately 10 cm above the ground, to simulate severe deer grazing. All cut material was removed from the plots. Five adjacent unclipped plots were set aside as controls (Fig. 1a). After 8.5 years (in April 1986), all *Chionochloa pallens* material was removed from one randomly located 0.5 m × 0.5 m quadrat within each of the clipped and unclipped treatments of the five replicated plots (Fig. 1b). In these ten 0.25-m<sup>2</sup> quadrats, soil was also excavated to a depth of 10 cm. The treatments thus created a number of square bare-soil gaps in an otherwise continuous vegetation. We define the 1977 treatment as 'clipping' and the 1986 treatment as 'gap creation'. Both are forms of disturbance, but gap creation appeared to have had the most severe effect on the vegetation and examining this effect was our primary objective.



**Figure 1.** Schematic diagram of experimental layout, showing (a) plots within the site, (b) quadrats within plots and (c) 'edge' and 'core' sub-squares within quadrats. Diagram is not to scale.

## Vegetation sampling

The clipped and unclipped  $5 \times 5$  m plots were relocated in 1998. Within each of these plots, the  $0.5 \times 0.5$  m quadrats from which all vegetation had been removed in 1986 were located exactly, and paired with quadrats of the same size in adjacent (non-gap) vegetation. The latter were located randomly within the plot, avoiding the gap quadrat. The presence of all vascular plant and moss species was recorded in twenty five  $0.01 \text{ m}^2$  sub-squares within each  $0.5 \times 0.5$  m quadrat. In addition to calculating overall frequencies, species frequencies in the 16 'edge' and 9 'core' sub-squares (Fig. 1c) were calculated, to examine the role of colonisation by vegetative spread v. establishment from propagules.

## Statistical analysis

We tested for the effects of both types of disturbance, clipping and gap creation, in our statistical analyses. Detrended Correspondence Analysis (DCA) was carried out on the species/quadrat data, excluding species that occurred only once, to examine the effects of clipping and gap creation on the vegetation pattern. Analysis of variance (ANOVA) was used to examine the effects of gap creation and clipping on species richness and species distributions between quadrats. These analyses of variance used a split-plot design, with clipping at the level of the  $5 \times 5$  m plots, and gap creation at the quadrat level, nested within the clipping treatments. Chi-squared tests were used to test for differences in species distributions within quadrats (i.e. 'core' v. 'edge' sub-squares), although our use of the Chi-squared statistic is indicative only because it is unlikely that sub-squares within quadrats represent independent statistical units.

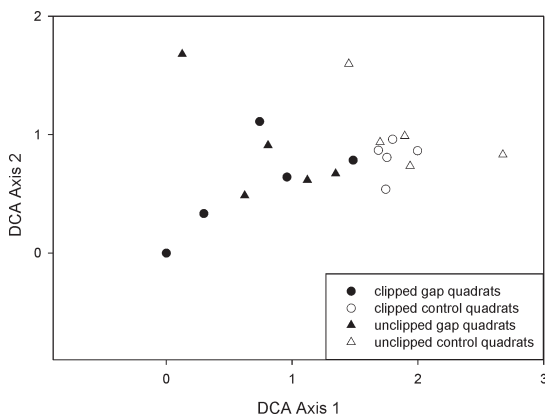
## Results

### Effects of gap creation

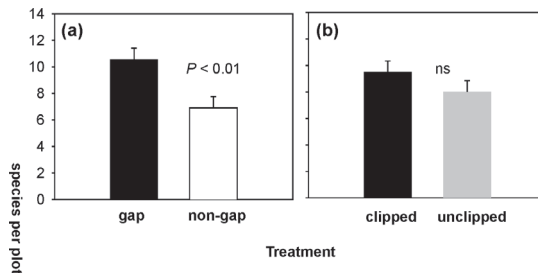
Twelve years after the creation of the gaps, there were still marked differences in vegetation composition between the gap quadrats and control quadrats, which are largely separated by axis one of the DCA ordination (Fig. 2). The quadrats from which the vegetation had been removed in 1986 showed greater variation in species composition than intact (control) quadrats, which apart from two outliers are tightly associated on the ordination diagram. Mean species richness was greater in gap quadrats than in the control quadrats (10.6 v. 6.9 species per  $0.25 \text{ m}^2$ , respectively), (ANOVA:  $F_{1,8} = 15.3$ ,  $P < 0.01$ ) (Fig. 3).

Several species differed in their distribution between the gap quadrats and control quadrats. Of the

species that occurred in at least five quadrats, *Agrostis dyeri*, *Anisotome aromatica*, *Celmisia verbascifolia*, *Epilobium alsinoides* and *Plantago novae-zelandiae* were significantly more frequent in gap quadrats, while *Chionochloa pallens* was significantly more frequent in control quadrats (Table 1). *Bryum* sp. and *Polytrichum juniperinum* were more frequent in gap quadrats, but not significantly so at  $\alpha = 0.05$ . Of the 16 species that occurred in less than five quadrats, 8 were found only in gap quadrats. No species were restricted to control quadrats, and no exotic species were observed.



**Figure 2.** Ordination of quadrats by Detrended Correspondence Analysis, showing gap creation and clipping treatments.



**Figure 3.** Effects of gap creation and clipping on mean species richness. In (a) solid bar = gap quadrats, open bar = non-gap quadrats; in (b) solid bar = clipped quadrats, grey bar = unclipped quadrats. For gap creation,  $n = 10$  and for clipping treatments,  $n = 5$ . Significance was tested by analysis of variance, ns = non-significant. The standard error of the mean is represented by error bars.

**Table 1.** Species frequencies between gap quadrats and control quadrats. Only species that occurred in at least five quadrats are used in the statistical comparison. *P*-values are derived from analysis of variance of mean frequencies within the 25 sub-squares of each quadrat. ns = not significant.

	Mean frequency (%)		<i>P</i> -value
	Gap plots	Control plots	
<b>Species in &gt; 5 quadrats</b>			
<i>Agrostis dyeri</i>	43.6	30.8	< 0.05
<i>Anisotome aromatica</i>	75.2	9.2	< 0.001
<i>Bryum</i> sp.	19.6	0	< 0.1
<i>Celmisia verbascifolia</i>	22.0	5.2	< 0.05
<i>Chionochloa pallens</i>	30.8	82.4	< 0.01
<i>Epilobium alsinoides</i>	11.6	0	< 0.05
<i>Geranium microphyllum</i>	7.6	12.0	ns
<i>Geum leiospermum</i>	5.2	4.4	ns
<i>Plantago novae-zelandiae</i>	35.2	0	< 0.01
<i>Poa hesperia</i>	76.8	90.4	ns
<i>Polytrichum juniperinum</i>	17.6	3.2	< 0.1
<b>Species in &lt; 5 quadrats</b>			
<i>Anisotome haastii</i>	2.8	0	
<i>Carex brevifolia</i>	2.4	2.0	
<i>Carex</i> sp.	1.2	3.2	
<i>Celmisia gracilentia</i>	4.8	4.8	
<i>Celmisia petriei</i>	3.6	7.2	
<i>Colobanthus strictus</i>	6.8	0	
<i>Dicranoloma robustum</i>	0.8	3.2	
<i>Ditrichum difficile</i>	0.8	3.2	
<i>Euphrasia petriei</i>	1.2	0	
<i>Gaultheria depressa</i>	4.4	0	
<i>Hebe hectorii</i>	0.8	0	
<i>Helichrysum bellidioides</i>	3.6	0	
<i>Luzula pumila</i>	2.4	0	
<i>Oreomyrrhis colensoi</i>	4.4	7.6	
<i>Ranunculus cheesemanii</i>	2.4	0.4	
<i>Schoenus pauciflorus</i>	4.0	0	

### Effects of clipping

The 1977 clipping of the *Chionochloa pallens* tussocks had no detectable effect on the species composition of the vegetation in either the gap or control quadrats. The DCA ordination (Fig. 1) shows no separation of quadrats from the clipped v. unclipped plots, in contrast to the separation of gap v. control quadrats. Neither did clipping in 1977 have any significant effect on species richness in 1998 (ANOVA:  $F_{1,4} = 0.93$ ,  $P = 0.38$ ; 9.5 v. 8.0 species per 0.25 m<sup>2</sup> for clipped and unclipped quadrats respectively; Fig. 3).

### Edge versus core effects

In gap quadrats, only three of the species that occurred in more than five quadrats had distributions that differed significantly between edge and core sub-squares (Table 2). *Plantago novae-zelandiae* and *Polytrichum*

*juniperinum* were both more frequent in core sub-squares ( $\chi^2$ , d.f. = 1:  $P < 0.01$ ), while *Geranium microphyllum* was more frequent in edge sub-squares ( $\chi^2$ , d.f. = 1:  $P < 0.05$ ). *Celmisia gracilentia* was also more frequent in edge sub-squares ( $\chi^2$ , d.f. = 1:  $P < 0.05$ ) but only occurred in two quadrats. In control plots, species distributions did not differ significantly between edge and core subplots.

**Table 2.** Species frequencies between edge and core sub-plots within the gap quadrats. *P*-values are derived from Chi-squared tests of frequencies between the core and edge sub-squares of quadrats in which the species were present. ns = not significant. Only species occurring in at least five quadrats are listed here.

Species	Frequency (%)		$\chi^2$ statistic	<i>P</i> -value
	Edge	Core		
<i>Agrostis dyeri</i>	48	46	0.03	ns
<i>Anisotome aromatica</i>	73	80	0.43	ns
<i>Bryum</i> sp.	22	38	3.58	< 0.1
<i>Celmisia gracilentia</i>	34	6	3.99	< 0.05
<i>Celmisia verbascifolia</i>	30	22	1.14	ns
<i>Chionochloa pallens</i>	38	33	0.25	ns
<i>Epilobium alsinoides</i>	17	24	0.98	ns
<i>Geranium microphyllum</i>	14	3	5.87	< 0.05
<i>Plantago novae-zelandiae</i>	45	83	8.75	< 0.01
<i>Poa hesperia</i>	90	79	0.68	ns
<i>Polytrichum juniperinum</i>	20	46	8.28	< 0.01

## Discussion

The vegetation that colonised the gaps in this alpine grassland formed a distinctive community of forbs, grasses and mosses of small stature (mostly < 10 cm). Many of these small plants appeared to have regenerated from seeds or spores rather than by vegetative means. As in any newly colonised habitat in a secondary succession, the propagules could either have been already in the soil at the time of the disturbance, or could have subsequently arrived as seed rain. In the present study the seedbank was probably of limited importance as the top 10 cm of soil (which usually contains most of the seedbank) had been removed. Studies in other alpine grasslands have shown seedbank contributions that range from negligible (Spence, 1990b; Urbanska and Fattorini, 1998) to high (Diemer and Prock, 1993; Chambers, 1993; Semenova and Onipchenko, 1996). The seed rain in alpine environments is known to be very variable in space and time (Spence, 1990a; Molau and Larsson, 2000). None of the colonising species here has any specialised means of dispersal, but small seeds might be dispersed by wind or surface water flow. Spence (1990a) investigated the seed rain of various New Zealand



alpine communities and found that for most species, seeds were dispersed within 50 cm of their source.

*Bryum* sp., *Epilobium alsinoides*, *Plantago novae-zelandiae* and half of the minor species were present in gap plots but completely absent from the mature community and may thus be gap-dependent. Other species show a much higher frequency in the gaps than in the intact vegetation, notably *Anisotome aromatica*. It appears likely that vegetation gaps formed by small disturbances are critical to the persistence of many species in this tall grassland community. The microhabitats within these gaps may favour individual species differentially. The central area of a gap is probably subjected to much greater fluctuations of temperature, light and moisture than the edges, resulting in the establishment of different species in the two microsites. Although we collected no environmental data, a reduced ability to establish in the conditions of the gap centres might explain the tendency for *Celmisia gracilentia* and *Geranium microphyllum* to occur more frequently at the edges. Competition for light is likely to be lower away from the gap edges, consistent with the greater frequency in gap centres of low-growing species such as *Plantago novae-zelandiae* and *Polytrichum juniperinum*, which also lack capacity for vegetative spread. Twelve years after gap creation, the dominant grass species are approaching equivalence in abundance across gap edges and centres, although they still tended to be less frequent in gap centres, consistent with colonisation through vegetative expansion from the edges. Core v. edge effects have also been found in gaps in old-field vegetation (Davis and Cantlon, 1969), heathland (Miles, 1974) and low-altitude grassland (Kotanan, 1997).

Natural gaps in *Chionochloa pallens* vegetation probably range from minor disturbances caused by frost heave and local surface runoff to large-scale events such as landslides and alluvial deposition. The artificially created gaps were representative of the smaller end of this scale, but were big enough to allow the establishment of distinct patches of vegetation. The persistence, even after 12 years, of a distinctive species composition in the gaps suggests a return to the dominant surrounding vegetation is unlikely for some years. This is consistent with observations of succession in other alpine vegetation types where recovery from disturbance is found to be consistently slow. For example, Roxburgh *et al.* (1988) found that areas disturbed by road making in an alpine New Zealand cushion-field community had attained only 58% of the cover of the control areas after 11 years. Urbanska and Fattorini (1998) found very poor recovery on an unrestored ski-run in the Swiss Alps even after 27 years. Clearly, in these harsh environments vegetation recovery from any perturbation is slow. This can include recovery from grazing. Tiller biomass of the

*Chionochloa* tussocks in this experiment had not fully recovered from the clipping treatments (simulating deer grazing) applied 20 years previously (Lee *et al.*, 2000). In the gap plots, *Chionochloa pallens* had attained a frequency of 30.8%, showing that the likely eventual dominant has already established a considerable foothold. However, only future monitoring of this experiment will indicate whether the gap vegetation does in fact reach the same species composition of the mature vegetation, or whether an alternative state is maintained.

## Acknowledgements

Funding for this study was provided by the Miss E.L. Hellaby Indigenous Grasslands Research Trust and the Foundation for Research, Science and Technology (KML contract LRCX0003; WGL contract CO9X0004). Comments from Peter Bellingham and Ian Payton improved the manuscript.

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