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Abstract

Severe road-making disturbance of a New Zealand high-alpine cushionfield initiated a secondary succession which has been assessed against the adjacent undisturbed community with permanent transects over 24 yrs. The succession has recently (yrs 11–24) accelerated as areas of bare soil-stone pavement continue to be colonized. Total plant cover has increased on the disturbed sites over this period (from 36 to 48%) and is now within the range of that in the intact cushionfield (48–59%), while the early dominant graminoids, particularly *Poa colensoi*, are now declining as other species establish. Floristic richness in the recovering system (33 species) now exceeds that of the intact cushionfield (21–27 species) with establishment of nine apparently seral species plus several mainly cushion species characteristic of the undisturbed cushionfield. Transition probabilities among seven recognized cover states for the most recent period (1986–1999) further clarify the succession by showing the "other species" category increasing in importance at the expense of the other six states. This contrasts with the relative stability of the intact cushionfield where autotransitions predominate over the same period. The severe high-alpine environment rather than physical differences between the disturbed and undisturbed sites appears to be limiting the rate of succession toward the undisturbed state. Despite establishment of several characteristic cushionfield species, the still minor role of its dominant, *Dracophyllum muscoides* (1% vs. 26–32% cover), indicates that the succession remains far from complete. Among the various succession models, autosuccession is untenable given the establishment of nine apparently seral species; only the inhibition and intermediate disturbance hypotheses could be entertained with the results to date.

Introduction

Roxburgh et al. (1988) described the first 11 yrs of a secondary succession following extensive blading of high-alpine cushionfield on a ca. 20 m strip on either side of a road, re-constructed in 1974, along the crest of the Old Man Range (1695 m), Central Otago Ecological Region (McEwen, 1987) in south-central New Zealand (Fig. 1). The adjacent undisturbed cushionfield was used as the basis for assessing the degree of recovery which, after 11 yrs, was still well short of the pre-disturbed state in terms of both its plant composition and much more limited cover.

The succession or rate of recovery following disturbance depends largely on its severity and the prevailing environment (Crawley, 1997; Sarmiento et al., 2003). Plant species diversity is usually linked to the paradigm which views a community as a mosaic of patches in various stages of recovery from a previous disturbance (Griggs, 1956; Horn, 1975; Connell, 1978; Pickett, 1980). The post-disturbance stage at which plant diversity peaks is controversial and the basis of competing successional models.

Long-term successional data sets for the alpine zone, along with predictions as to successional trajectories and rates of recovery, are relatively few but predicted to be slow, with little involvement of ruderal and competitive species (Grime, 1979). Consistent with this view are documented cases which indicate that many vascular species that are relatively important colonizers can also be components of mature alpine communities, confirming that such successions are condensed or telescoped because the relatively few species that can tolerate such extreme environments are already present (Ebersole, 2002), as in some arctic and desert systems (Whittaker, 1974; MacMahon, 1980).

Such cases would be referred to as an autosuccession (Muller, 1952) or demographic succession (Urbanska, 1997b), based on an initial floristics paradigm (Egler, 1954). The intermediate disturbance hypothesis of succession (Connell, 1978) is based on species richness peaking at an intermediate intensity of disturbance and at an intermediate time span following the disturbance. By contrast, Egler's (1954) initial floristic model asserts that species in both the early and late stages of the sequence are present immediately following the disturbance, such that the succession can be considered a function of differential growth rates and survivorship among the early and late successional species (Pickett et al., 1987). With this latter model, species richness would be highest early in the successional process and lowest late in the sequence. The notion of initial floristic composition is also incorporated into the tolerance and inhibition models of Connell and Slatyer (1977). The former requires that environmental modifications by earlier colonists do not affect later establishing species: delayed success of certain species is attributed to their later arrival and/or slower growth. Alternatively, the inhibition model requires that the earlier colonists suppress the establishment or growth of later colonists and the latter succeed only if they have sufficient resources, or resources are released through damage or death of previous occupants, to give them competitive superiority. Longer-lived species generally prevail. The relay floristics (facilitation or autogenic) model, based on Clements (1916), demands that only certain pioneering species may colonize a newly disturbed site and that these early seral species progressively modify the environment, so creating conditions more suitable for establishment of later successional species.

Roxburgh et al. (1988) used the Markovian approach in an attempt to forecast successional changes based on trends over the first
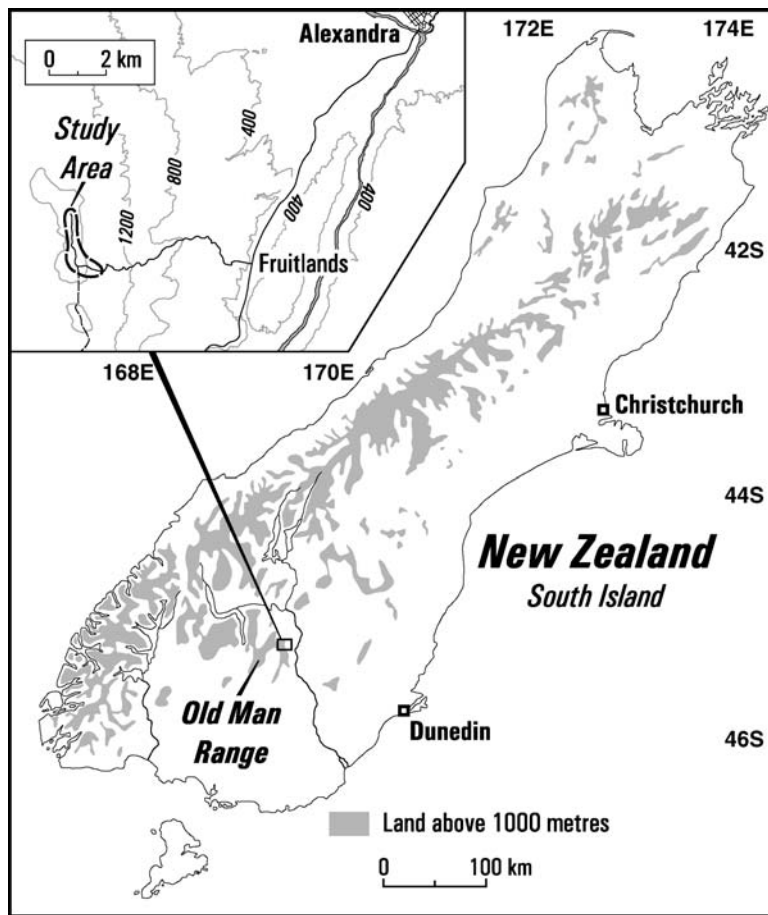
FIGURE 1. Map showing the approximate location of the study area on the summit of the Old Man Range, south-central South Island, New Zealand.

11 yrs in the disturbed cushionfield community on the Old Man Range. The Markov model is concerned with the temporal movement of one identifiable community state to another, particularly the predominant direction and the rate of change, as discussed by van Hulst (1979) and Usher (1981). The Markov model is based on the Markov process which Bartlett (1955) defined as "a stochastic process for which the values of X_r at any set of times t_r ($r = 1, 2 \ldots n$) depend on the values of X_s at any set of previous times t_s ($s = 0, -1 \ldots -j$) only through the last available value X_o." Therefore, the Markovian process is only dependent on the single and last value X_o and consideration of the plant community history is irrelevant when predicting future vegetation states. Indeed, basing a Markov model on a single transition matrix of cover change data results in a stationary or homogenous model. Usher (1981) reports several disadvantages with Markov models: (1) states that are to be used in the model can be difficult to define; (2) vegetation history is irrelevant as the model has only a single dependence (X_o); (3) transition probabilities can vary through time; and (4) introduction of new arrivals cannot be included. Additional problems with the model include its tendency to be conservative for long-term changes, as reported by Hobbs (1983) and Lough et al. (1987), and determination of an "ergodic property" (Usher, 1979), i.e., convergence toward a limiting probability distribution among the states of the system, irrespective of the starting state of the system.

The objectives of our study were, first, to quantify the plant community composition and structure, including species richness and diversity, as well as their evenness, i.e., the homogeneity of their relative abundances on the disturbed sites in relation to the adjacent intact cushionfield community 24 yrs after disturbance. This comparison was also to be made in relation to the earlier seral stages as described by Roxburgh et al. (1988). Second, we planned to use a Markovian model on the 1988–1999 transition matrix to predict future trends in the

succession on the disturbed sites, as was done for the earlier records by Roxburgh et al. (1988). Thirdly, we planned to assess the various successional models, briefly described above, in relation to the records to date, in this high-alpine cushionfield community.

Methods

THE STUDY AREA

The Old Man Range (45°15′S; 169°9′E) is one of the more accessible of the distinctive block-faulted mountains in the basin-and-range region of Central Otago that reach the high-alpine zone. The highly exposed upper slopes and summit plateau are dominated by extremely dwarfed cushionfield vegetation, generally less than 2 cm tall and sometimes referred to as alpine tundra (Billings and Mark, 1961) or tundra-like (Mark and Bliss, 1970; Bliss and Mark, 1974; Mark and Dickinson, 1997), with scattered plants and small patches of slim snow tussock grass, *Chionochloa macra*. These tussocks are remnants of a once more widespread tussock grass cover that was eliminated, probably during the early decades of pastoral farming in the late 1800s, associated with European settlement (Mark, 1994b; Mark et al., 2003, Figs. 24 and 28).

The landscape is dotted with shaft tors, block-like outcrops of chlorite schist bedrock, up to 10 m or more high. The basement rock is mantled with acidic, highly leached eldefulvic (alpine podzolized yellow-brown) soils (Mark, 1994a; Mark and Dickinson, 1997) derived from schist colluvium and loess, of variable depth depending largely on exposure.

The high-alpine zone is characterized by a range of patterned ground (soil stripes and hummocks, and solifluction terraces) and a periglacial environment, with a mean annual air temperature close to

0°C (Mark, 1994a). Monthly means range from ca. 5°C in mid-summer to −7°C in mid-winter, while freeze-thaw cycles occur on about 179 d (49%) a year, with 113 d (31%) remaining below freezing and the remaining 73 d (20%) being frost-free. The longest frost-free period over five summers varied from only 8 to 13 d, while the degree days (0°C base) here amount to about 986 annually. The soil at 10 cm depth remains unfrozen for the warmest four months and is continuously frozen to at least 20 cm for about five months (Mark, 1994a). The predominantly westerly winds are an important abrading agent (Mark and Dickinson, 1997), being usually very strong and with little seasonal variation: values at 1.25 m above ground level averaged 5.7 m s⁻¹ over a 2-yr period. Fog is not uncommon on the upper slopes of the range where annual precipitation is about 1600 mm, far exceeding potential evapotranspiration, so that soil moisture remains close to field capacity throughout the snow-free period of about 180 d. Snow, however, melts completely on the Old Man Range only about 1 year in 10 (Mark, 1994a).

THE DISTURBANCE

The last 3 km of roading to the summit of the Old Man Range traversed cushionfield in the high-alpine zone. Subsoil, mixed with a limited amount of topsoil, persisted on the road verges following the disturbance in December 1974 (see Roxburgh et al., 1988, Fig. 1). This situation, together with the relatively severe climatic conditions, would have been important factors in determining the initial rate of recovery.

Nine permanently marked 20 m transect pairs were established in February 1975, within two months of the initial disturbance. They were resampled early in 1999, as for the previous five recording periods (Roxburgh et al., 1988). Point intercepts at 20 cm intervals provided 100 records along each transect (except for Disturbed Transects 5 and 9, which provided only 90 and 80 points, respectively). Aside from species richness, the same five cover categories were recorded as previously: dead attached plants, litter, bare soil, loose stone pavement, and immovable rock. Records of an additional resampling by Roxburgh, in April 1990, were also made available (Stephen Roxburgh, personal communication, 2004) for inclusion in the results but not in the Markov analysis. The full set of records has been deposited in both electronic form and hard copy, in the University of Otago Botany Department's archives and also in the New Zealand National Vegetation Survey Databank (NVS) (http://nvs.landcareresearch.co.nz).

Above- and below-ground (to 20 cm depth) plant biomass was also sampled, in January 1999, in single randomly placed 10 cm × 10 cm plots, close to (but >60 cm from) the center of each transect line. The above-ground samples were separated into live and dead components, while below-ground samples were washed through a 2 mm sieve to separate roots before all three components were oven-dried (65°C until weight remained constant) and weighed (Kalra and Maynard, 1991).

To characterize the environment at the study site, a Campbell Scientific CR10X datalogger and sensors were located adjacent to Transect 7 for six months from mid-November 1998. This logger monitored air (+15 cm), and soil (−10 cm) temperatures from six microsites: four disturbed (*Poa* tussock; *Poa* intertussock area; *Celmisia brevifolia* clump; bare ground) and two undisturbed (cushion hummock; cushion depression). Type-T (copper constantan) 24 ga. thermocouples were mounted on wooden dowling and placed within radiation shields (white plastic tubing 10 cm × 3.5 cm diameter, vented from the bottom and ends). One 3-cup (MetOne model 014) anemometer was placed 25 cm above ground level on the undisturbed cushionfield site to record windspeed. To establish volumetric soil moisture, a probe (Time Domain Reflectometry method) was inserted from the walls of two soil pits (one in the disturbed and the other in the undisturbed site), parallel with the surface at 10 cm depth. The soil block was then replaced. Probe calibration was not required since the soils had <30% clay content (Campbell Scientific, 1996) and were also low in organic matter and quartz. The moisture probes were set to record hourly and all other sensors at 1-min intervals. Output included daily maximum, minimum, and mean values.

Soil of the rooting zone was sampled in February 1999 to determine a range of physical and chemical properties in the disturbed and undisturbed sites adjacent to each transect. Profiles were described from soil pits dug following removal of the samples. Undisturbed cores, 6.9 cm diameter, were taken with a sharpened steel tube 12.8 cm long, double bagged in plastic, and transferred to the laboratory within two days for determination of color, bulk density, volumetric water content, texture, organic content, pH, and several macro-nutrients (total N and P, extractable K, NO_3, and NH_4). Bulk density and water content were determined from oven-dry weights, color using a Munsell soil chart, the >2 mm fraction by sieving, the <2 mm fraction of sand, silt, and clay by the Bouyoucos hydrometer method (Kalra and Maynard, 1991), and organic matter by loss-on-ignition. Total N and P were determined by the standard Kjeldhal digestion method (McGill and Figueiredo, 1993), K with atomic absorption, while a KCl extraction and Technicon Autoanalyzer II were used to determine extractable NO_3 and NH_4 values (Kalra and Maynard, 1991).

ANALYSES

The cover data were used, as previously (Roxburgh et al., 1988), to construct Markovian models for determining both direction and rate of change in surface cover for both the disturbed and undisturbed sites. For the disturbed sites, the dominant plant species, *Poa colensoi*, the only one to have a mean cover of >5% in any one sampling period, was treated as a separate state from the "other species." Similarly, for the undisturbed sites, the dominant species here, *Dracophyllum muscoides*, and the only one to exceed 5% mean cover in any of the seven samples, was treated as a separate state from that of the "other species."

To determine the frequency and type of transition which occurred during the period 1986 to 1999, cover values from the 1999 data collection were compared with those for the 1986 record and tally matrices of cover state change for both the disturbed and undisturbed sites were created. A transition represents a change in cover state during the interval while autotransitions represent no change. Tally matrices were converted into transition matrices by dividing the number of times cover state A changed to state B, etc., by the number of times A was observed at the earlier sampling time. Transition matrices were used to calculate transition probabilities (*P*): the probability that any cover state will change to another state or remain the same from one sampling period to another (Collins, 1975). Cover characteristics at discrete time intervals can be predicted (Collins, 1975) and, in our case, it was the last 13 yrs between the 1986 and 1999 samples.

The species cover and site data for the 1999 samples were also analyzed using Detrended Correspondence Analysis (DCA). Species richness was expressed as the total number of plant species recorded at any one time in all of the nine transects on the disturbed and the undisturbed sites. Species diversity was expressed by the Shannon-Wiener diversity (H′) index, using the point intercept data. Evenness (J′) was expressed using the diversity data as a proportion of the maximum possible diversity as recommended by Zar (1999, p. 42), with cover values by species, as recorded (Table 1); a value of 0.1% was assigned to those with <1% mean cover.

Results

TEMPORAL PATTERNS IN THE FLORA AND VEGETATION

The total flora recorded over the 24-yr period on the undisturbed sites has fluctuated (21 to 27 species), without any clear temporal trend

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TABLE 1

Mean cover values of undisturbed and disturbed sites during seven sampling periods and corresponding values for species richness, diversity, and evenness. Mean cover values for dead plants, litter, bare soil, stone pavement, and rock are also included. Cover is based on 1000 and 870 point intercepts for the undisturbed and disturbed sites, respectively. Cover values of <1% are indicated with a +. Nomenclature is according to the Allan Herbarium (2000). The one exotic species is indicated with an astetrisk preceding its name.

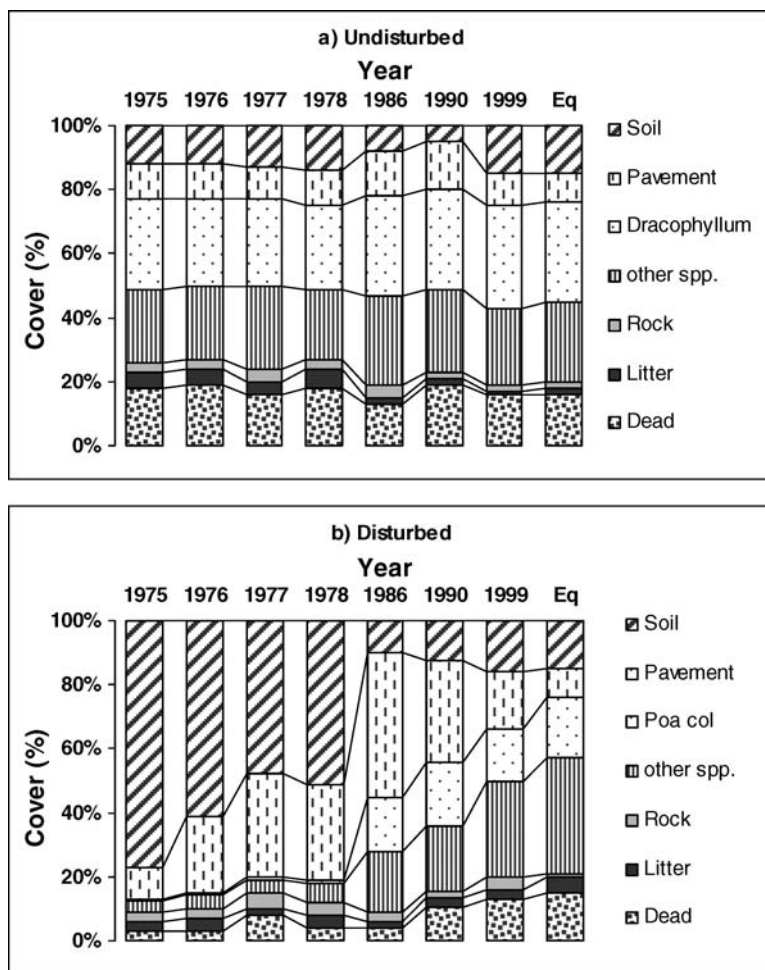| Species	Undisturbed							Disturbed						
	1975	1976	1977	1978	1986	1990	1999	1975	1976	1977	1978	1986	1990	1999
Dicotyledons														
Abrotanella inconspicua	+	1	5	+	+	+	+					+		+
Anisotome imbricata				+										
Anisotome lanuginosa	+		+	+	1	+								
Celmisia brevifolia	+	+	+	+	1	+	+					+	+	4
Celmisia laricifolia	1	+	1	+		+		+						+
Celmisia sessiliflora	+	+	+	+	1	+	+					+	+	+
Celmisia viscosa	2	2	2	2	3	1	4					+	+	+
Chionohebe densifolia			+											
Chionohebe thomsonii	+	+			+	+								
Colobanthus buchananii	+	+	+	+		+						+	3	+
Coprosma perpusilla													+	
Dracophyllum muscoides	28	27	27	26	31	31	32	+	1	+	+	1	1	1
Epilobium alsinoides												4	4	+
Euphrasia zelandica	+													
Gentianella bellidifolia					+								+	
Hebe hectorii						+								+
Hectorella caespitosa	+	1	1	1	1	1	1	+				1	1	+
Kelleria childii	1	1	1	1	1	1	2	+					+	+
Leptinella goyenii	1	+	1	+	+			5						+
Myosotis pulvinaris	+	+	+	+	+	+	+						+	+
Neopaxia sessiliflora														+
Phyllachne rubra	+	1	+	1	1	+	+	+	+			+	+	
Ranunculus enysii														+
Raoulia grandiflora	+	+	1	+		+							+	
Raoulia hectorii	3	2	2	3	5	4	4					+	+	2
Raoulia subsericea												+	+	+
Rumex acetosella														+
Viola cunninghamii														+
Wahlenbergia albomarginata														+
Monocotyledons														
Agrostis muelleriana	1	+	+	2	2	+	1				+	+		2
Carex pterocarpa	+	+		+								+	+	+
Luzula pumila	1	+	1	1	1	1	2	+	+	+	+	4	2	3
Poa colensoi	2	2	3	1	3	4	2	+	+	1	1	17	21	16
Poa lindsayi												+		
Rytidosperma pumilum							+							3
Trisetum spicatum		+					+					+		1
Pteridophyte														
Lycopodium fastigiatum	1	+	+	+	1	+								+
Bryophyte														
Psilopilum australe	+	1	1	+	1	+	+					2	2	1
Other bryophytes														+
Lichens														
Alectoria nigricans	2	3	1	1	2	4	2					+	+	1
Cetraria islandica	4	4	5	4	1		3							3
Cladina sp.							+							
Hypogymnia lugubris	+	+		+	+									
Siphula sp.	+	1	+	1	+	+	+							+
Thamnolia vermicularis	3	3	3	3	3	3	2				+	+	+	1
Total plant cover (%)	51	50	53	48	59	55	56	4	5	5	7	36	42	48
Species richness	28	27	25	27	24	24	21	8	4	3	4	20	21	33
Species diversity H′	0.82	0.82	0.88	0.82	0.86	0.68	0.75	0.85	0.34	0.25	0.43	0.66	0.62	1.00
Evenness J′	0.56	0.57	0.63	0.57	0.63	0.49	0.57	1.00	0.57	0.52	0.62	0.51	0.48	0.70
Dead plants	18	19	16	18	13	19	16	3	3	8	4	4	11	13
Litter	5	5	4	6	2	2	1	3	4	2	4	2	3	3
Soil	12	12	13	14	8	5	15	77	61	48	51	10	13	16
Pavement	11	11	10	11	14	17	10	10	24	32	30	45	33	18
Rock	3	3	4	3	4	2	3	3	3	5	4	3	2	4

FIGURE 2. Percentage cover of seven components at each of seven recording times and Markov predictions for the eventual stable equilibrium (Eq) of the undisturbed (a) and disturbed (b) sites.

in comparison to that on the disturbed sites where species number have increased from 3 to 33 (Table 1). Two months following the disturbance, eight species were recorded, reduced to four the following year, but subsequently there was a marked increase between yrs 3 and 11 (1978–1986) and then a steady increase to yr 24 (1999), when 33 species were recorded, which exceeds the maximum number documented on the undisturbed sites (28; see Table 1). Of the initial eight species on the disturbed site, three (*Dracophyllum muscoides*, *Luzula pumila*, *Poa colensoi*), reported by Roxburgh et al. (1988), have persisted, but five others (*Celmisia laricifolia*, *Hectorella caespitosa*, *Kelleria childii*, *Leptinella goyenii*, and *Phyllachne rubra*) did not persist beyond two years, the first four for less than a year. However, all five species had re-established by yrs 11–24, together with another 28, nine of which (*Coprosma perpusilla*; *Epilobium alsinoides*; *Neopaxia sessiliflora*; *Ranunculus enysii*; *Raoulia subsericea*; *Viola cunninghamii*; *Wahlenbergia albomarginata*; *Poa lindsayi*; and the only exotic, *Rumex acetosella*) were not recorded in the undisturbed cushionfield. Conversely, seven of the species present in the intact cushionfield (*Anisotome imbricata*; *A. lanuginosa*; *Chionohebe densifolia*; *C. thomsonii*; the only annual, *Euphrasia zelandica*; and two lichens, *Hypogymnia lugubris* and *Cladina* sp.), were not recorded from the disturbed sites.

Total plant cover in the undisturbed cushionfield has remained relatively stable at 48–59%, with *Dracophyllum muscoides* dominating throughout (mean cover 28%; Table 1, Fig. 2a). The other six cover types recognized were relatively stable in the undisturbed cushionfield (Fig. 2a), with "other species" contributing about 24%, the organic components of dead plants and litter accounting for about 17 and 4%, respectively, while the other three (bare soil,

pavement, rock) contributed another 26% (12%, 11%, and 3%, respectively).

The disturbed site, by contrast, showed obvious temporal changes, particularly as the initially predominant cover of bare soil (77%) was steadily replaced, largely by stone pavement through wind erosion over the first 11 yrs following disturbance (Fig. 2b). The total plant cover at yr 24 (48%) equals the lowest value recorded over the 24-yr period on the adjacent intact cushionfield. The cover of rock and plant litter have remained small and stable (1–6%), whereas the extent of dead plants increased substantially, particularly following 1986, largely reflecting the partial or complete mortality of the older and larger plants of *Poa colensoi*. These plants had developed into prominent small tussocks, associated with the accumulation of wind-blown soil (loess) in their bases, and their cover amounted to 17% on these sites in 1986, as reported by Roxburgh et al. (1988). Subsequently, the larger tussocks of *P. colensoi* were eroded on their windward sides and began to disintegrate. This process continued while the total cover provided by *P. colensoi* increased over the next four years to 21% in 1990. However, by 1999 its cover had decreased by 5% (Fig. 2b) through decimation of the older and larger tussocks by wind abrasion and senescence.

Both diversity and evenness of species remained relatively stable over the 24-yr study period on the intact cushionfield but varied considerably on the disturbed sites, with larger values being recorded for both indices during the initial and later periods (Table 1). Cover values of the seven classes used for the Markov projections, based on the 1977–1986 transition matrix (Roxburgh et al., 1988), also varied little on the undisturbed sites. The values recorded in 1999 were generally close to those predicted, as were the equilibrium values predicted for periods ranging from 2012 to 2077 (Fig. 2a). The

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a) undisturbed

Frequency
— 0.1 - 0.29
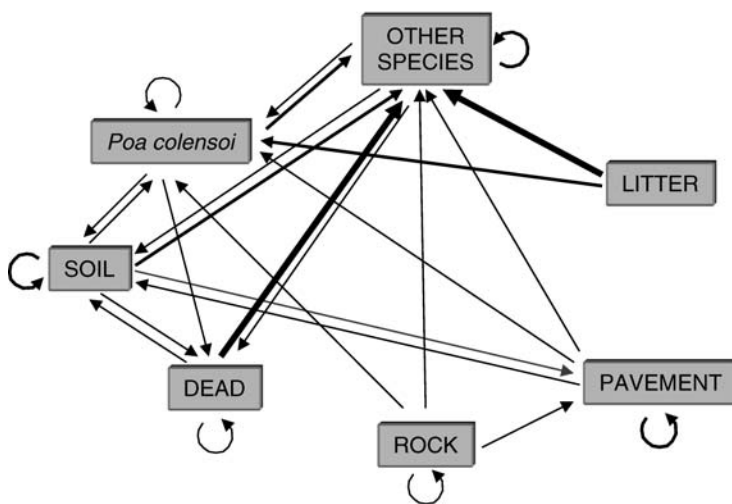— 0.3 – 0.49
— 0.5 – 0.55
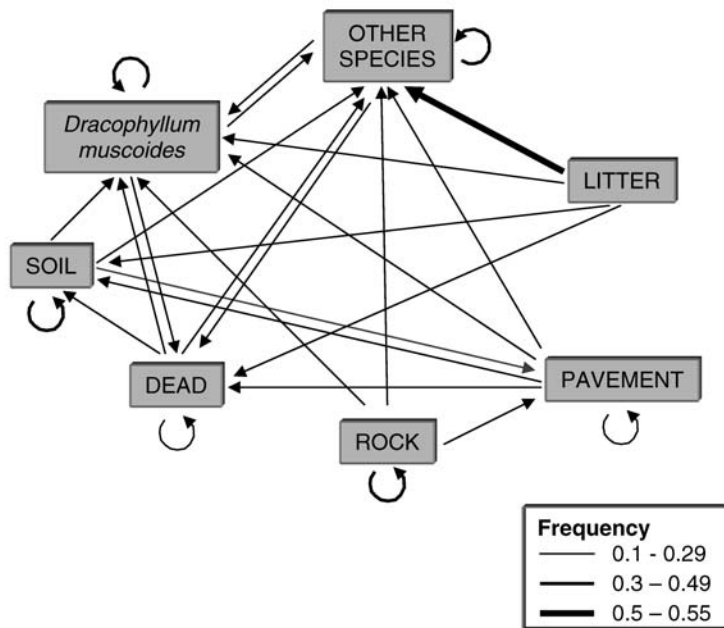
b) disturbed

FIGURE 3. Transition probabilities from 1986 to 1999 among the seven cover classes on both the undisturbed (a) and disturbed (b) sites. Only transitions with a frequency of ≥0.1 are shown, as indicated.

equilibrium predicted is for the cover of *Dracophyllum* to remain close to 32% with the "other species" class contributing another 25%, soil and dead plants each about 15%, with smaller amounts of pavement (8.5%), and litter (1.5%). The relative stability of cover in the intact cushionfield, and the absence of any obvious temporal trend over the 24-yr study period, means that the transitional probabilities for the seven cover classes at these sites over the more recent period (1986–1999) can be classed as autotransitions (Fig. 3a). The only exception, the increased probability of the litter to "other species" transition, resulted from half of the transitions from litter being in this direction, though its mean cover was a mere 2–3% over this time.

Despite the obvious temporal changes in several cover classes on the disturbed sites, the Markov predictions for these sites, based on the 1977–1986 transition matrix (Roxburgh et al., 1988), were generally close to the actual values recorded in 1999, although they were somewhat high for *Poa colensoi* and low for the "other species" category (Fig. 2b). Predictions for all five non-plant classes were within

1% of their actual values. Predictions for the equilibrium condition on these disturbed sites, based on the 1986–1999 transition matrix, show increased values for "other species" (up 8% to ca. 36%), and *Poa colensoi* (up 1.1% to 18.5%), with more minor increases in dead plants (to 14.5%) and litter (to 5.3%). There were concurrent small decreases in the cover of soil (to 14.8%), pavement (to 9%), and rock (to 1.5%). The transition probabilities for the disturbed sites over the most recent period of monitoring (1986–1999) had fewer autotransitions than for the undisturbed sites (but more than indicated by Roxburgh et al. (1988) for the 1977–1986 period), and most of the trends were toward increasing importance of *Poa colensoi*, "other species," and dead plants (Fig. 3b), as expected from the relevant Markov projections.

FLORISTICS AND SPECIES GROUPINGS

Detrended Correspondence Analysis of the plant cover data from the nine transects from each of the disturbed and undisturbed sites in

1999 indicates that the disturbed and undisturbed communities were distinct. Such distinction was absent, however, among the 36 species involved (data not shown), though certain species were associated with particular sites. The undisturbed cushionfield was dominated by *Dracophyllum muscoides* (32% cover), in association with much smaller amounts (to 5% cover) of several other cushion species: *Raoulia hectorii*, *Hectorella caespitosa*, *Phyllachne rubra*, *Myosotis pulvinaris*, *Abrotanella inconspicua*, *Kelleria childii*, *Celmisia sessiliflora*, and some small herbs: *Celmisia viscosa*, *Poa colensoi*, *Agrostis muelleriana*, *Luzula pumila*, *Trisetum spicatum*, and *Rytidosperma pumilum* among the vascular species, and *Thamnolia vermicularis*, *Cetraria islandica*, *Alectoria nigricans*, *Cladina* sp., and *Siphula* sp. among the lichens (Table 1). The disturbed sites, by contrast, were dominated by *Poa colensoi* (16% cover) with the equivalent associates occupying a comparable area on the ordination diagram being *Celmisia brevifolia*, *Epilobium alsinoides*, and *Leptinella goyenii* (data not shown).

BIOMASS

Using Students *T*-test there were no significant differences ($p > 0.05$) between above-ground biomass values for either live or dead plant material in the intact cushionfield (live, 2603 ± 2134 g m^{-2}; dead, 1141 ± 786 g m^{-2}: SD), and those from the disturbed sites (live, 1701 ± 1525 g m^{-2}; dead, 899 ± 783 g m^{-2}). Neither were they significant for the below-ground biomass where the values were greater but the difference much less (undisturbed = 3118 ± 1511 g m^{-2}; disturbed = 3447 ± 3535 g m^{-2}).

MICROCLIMATE

Only temperature records for air ($+15$ cm) and soil (-10 cm) are presented here for the 6-month period, 19 November 1998–18 May 1999, based on daily values. Mean and minimum air temperatures did not differ significantly (ANOVA; $p > 0.05$), but maxima were significantly higher ($p < 0.05$) above the *Poa colensoi* intertussock site (mean = $23.8 \pm 2.7°$C) than above the *Poa* tussock ($19.7 \pm 2.5°$C), *Celmisia brevifolia* clump ($19.2 \pm 2.5°$C), bare ground ($18.0 \pm 2.5°$C), or cushion hummock ($21.6 \pm 2.9°$C). Air maxima above the cushion hollow were significantly warmer (mean = $22.3 \pm 2.9°$C) than above the bare ground. Mean soil temperatures did not vary significantly between the six sites, but maxima were significantly higher under bare soil (mean = $14.7 \pm 2.3°$C) than any of the vegetated sites: *Poa* tussock ($12.1 \pm 2.0°$C), *Poa* intertussock spaces ($11.1 \pm 2.0°$C), *Celmisia* ($11.0 \pm 1.9°$C), cushion hollow ($9.5 \pm 1.8°$C), and cushion hummock ($8.8 \pm 2.0°$C). Minima were also significantly lower under the bare soil (mean = $5.4 \pm 1.8°$C) than any other location (range = $6.5–7.9°$C) except the cushion hummock ($6.1 \pm 1.9°$C). Thus, bare soil had the greatest temperature range of all six sites. The magnitude of diurnal temperature ranges increased from December to February at all six sites and decreased rapidly from March to May when mean values dropped close to or below freezing at all six sites.

Mean daily wind speed at 15 cm height varied from ca. 2 to 10 m s^{-1} over the mid-November to mid-May period of measurement, with daily maxima mostly in the range of 3–10 m s^{-1} but peaking at 23 m s^{-1}.

SOIL FACTORS

Soil disturbance had only minor effects on its physical properties after 25 yrs. Bulk density was not significantly higher on the disturbed than the undisturbed sites (1.206 ± 0.148 vs. 1.136 ± 0.216), while moisture content was only slightly lower. The stone fraction was almost 10% lower on the disturbed sites (20.8% vs. 29.2%), but neither this nor the three components of the mineral fraction were significantly different (both sites were sandy loams). Organic content, however, was significantly lower in soil from the disturbed sites (6.3% vs. 9.6%) while only pH and NO$_3$-N of the chemical factors measured were significantly different ($p < 0.05$) between the two sites, both being higher in soil on the disturbed sites (pH: 4.94 vs. 4.69 and NO$_3$-N: 0.98 vs. 0.28 ppm).

Discussion and Conclusions

Secondary succession in the Central Otago high-alpine cushionfield has been slow, a situation mirrored by comparable situations in other parts of the world (Willard and Marr, 1971; Bayfield, 1980; Chambers, 1993; Bridle, et al., 2001; Ebersole, 2002; Kershaw, 2003). This reflects the general environmental severity of the alpine zone and the Central Otago high-alpine zone in particular (Billings and Mark, 1961; Mark and Bliss, 1970; Mark, 1994a), despite the relatively long (~5 mo) growing season here (Bliss and Mark, 1974).

Plant cover generally continued to increase over the first 24 yrs, but only very slowly in the first four years, following the gross disturbance associated with intermittent blading of a dwarfed cushionfield community either side of a reconstructed road along the crest of the Old Man Range in 1974. Of the microclimatic and soil factors recorded, the few significant differences between the disturbed and undisturbed sites appeared more likely to be the effects rather than the causes of the associated differences in surface cover and microtopographic patterns. Among the several physical and chemical soil factors compared between the disturbed and undisturbed sites, only organic content, pH, and nitrate nitrogen were significantly different, the former being lower and the latter two higher on the disturbed sites. Soil bulk density, organic matter, and pH were all within the ranges obtained by Mark (1994a) for the subsurface soil associated with nearby vegetated soil stripes and thus are unlikely, in themselves, to have affected the pattern of succession.

Disturbances in extreme alpine environments can result in higher resource availability, particularly in terms of soil nutrients, but the general climatic severity may outweigh such potential gains (Urbanska and Schütz, 1986). The early stages of the secondary succession on the Old Man Range, which involved a very sparse cover of *Poa colensoi*, *Luzula pumila*, and *Dracophyllum muscoides*, appeared to reflect very limited survival and negligible seedling establishment, despite the proximity of the adjacent intact cushionfield. The later predominance of *Poa* confirms its greater ability to establish seedlings and tolerate this severe environment, in terms of both its growth (Roxburgh et al., 1988) and annual seeding. This is also consistent with its dominance on lightly used vehicle tracks in the high-alpine zone in the region, often to the exclusion of the remaining cushionfield flora. It is also consistent with the observations of Spence (1990a) that *Poa colensoi* was among the most abundant species represented in the rain of viable seed of alpine plant communities on the Craigieburn Range of inland Canterbury, 350 km to the north, where most of it fell within 50 cm of the nearest source. Like *Poa colensoi*, the remaining seven graminoids recorded in our study were also more important on the disturbed sites where they comprised ~46% of the cover at yr 24, compared with only 9% on the adjacent intact cushionfield. Removal of vegetation and disturbance of the organic soil horizon has been found to favor graminoids in a range of cold environments, largely through increased nutrient availability coupled with the absence of competitors (Bliss and Wein, 1972; Chapin and Chapin, 1980; Chapin and Shaver, 1981; May and Webber, 1982; Shaver and Chapin, 1986; Chambers, 1993; McDougall, 2001).

The total plant cover has continued to increase on the Old Man Range and after 24 yrs is within the range recorded in the intact cushionfield. In terms of individual species, however, the cover

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provided by the dominant, *Dracophyllum muscoides*, is still minor (1%) in relation to its contribution to the intact cushionfield (26–32%) so that the succession obviously remains far from the comparative undisturbed state. The early seral stages were characterized by dominance of bare soil and stone pavement, and a slowly increasing cover of the perennial native grass *Poa colensoi*. As reported by Roxburgh et al. (1988), the *Poa* attained 17% cover 11 yrs following disturbance and by yr-16 had peaked at 21%. Over this period the larger tussocks, which had become increasingly prominent through accumulation of wind-blown soil among their central tillers, were collapsing through wind abrasion. This situation contrasts with the very minor role of this species in the intact cushionfield, where its cover ranged from 1 to 3% as a low sward, consistent with the height of the dominant cushion plants. This mortality in *Poa*, which has been previously reported for the leading edges of cushion plants on the more exposed sites on the Old Man Range by Billings and Mark (1961), was continuing on the remaining larger plants of *Poa colensoi* on the disturbed sites after 24 yrs. We predict that this species will continue to decline on the disturbed sites, possibly down to the minor role it plays on the adjacent intact cushionfield. The early dominance of *Poa* and the elevated tussocks it produced on the disturbed sites could have been significant in increasing the surface roughness and thus also the boundary layer (Oke, 1987) of the often severe winds in the area. This effect may have facilitated seedling establishment of many of the species which have colonized the disturbed sites over the two most recent sampling intervals (1987–1990 and 1990–1999). In this context, the *Poa* clumps may have had an important nurse effect by trapping propagules and also providing a suitable substrate of dead plant material, litter, or soil derived from the collapsed plants, for establishment of a range of other species, as described by Arroyo et al. (2003) for cushions of *Azorella monantha* under severe alpine conditions in the Patagonian Andes.

Plant species have continued to establish on the disturbed sites on the Old Man Range, with more recorded at yr-24 (33) than in any of the samples of the adjacent intact cushionfield (21–28) over the same period. Of the initial eight species on the disturbed site only three persisted, the original dominant *Dracophyllum muscoides* and two graminoids, *Poa colensoi* and *Luzula pumila*. The other five (*Celmisia laricifolia*, *Hectorella caespitosa*, *Kelleria childii*, *Leptinella goyenii*, and *Phyllachne rubra*) were probably plants which survived the disturbance but could not tolerate the greatly altered conditions. Of the 33 species recorded with most recent sampling (yr-24), nine are exclusive to the disturbed sites and five of these (*Neopaxia sessiliflora*; *Poa lindsayi*; *Raoulia subsericea*; *Epilobium alsinoides*; and the only exotic recorded, *Rumex acetosella*) are generally characteristic of open habitats on the Old Man Range. The latter three are only common at lower elevations and thus, by implication, have established from more distant seed sources. These species should probably be considered as being of mid-to-late seral status, and their fate will be an important aspect of the continued succession to assess with future monitoring. None of these five species were recorded within the first four years following disturbance and so should not be classed as pioneers in the sense that *Poa colensoi*, *Luzula pumila*, and even the cushionfield dominant *Dracophyllum muscoides* might be considered, since these three have been present throughout. *Poa colensoi*, however, was the only one of the three to subsequently assert itself but not before yrs 4–11. This pattern is consistent with a stress-tolerant competitor as described by Grime (1979). The *Dracophyllum*, by contrast, has maintained a very minor role (~1% cover) up to yr-24, yet achieves dominance (26–32% cover) in the intact cushionfield, and so is consistent with Grime's description of a stress-tolerant competitor. The future trend of *Dracophyllum* cover on the disturbed sites will thus be important to follow, along with that of the nine cushion species (*Raoulia hectorii*, *Hectorella caespitosa*, *Celmisia sessiliflora*, *Colobanthus buchananii*, *Abrotanella inconspicua*, *Leptinella goyenii*,

Myosotis pulvinaris, *Phyllachne rubra*, and *Kelleria childii*), several small herbs, four lichens (*Thamnolia vermicularis*, *Cetraria islandica*, *Alectoria nigricans*, and *Siphula* sp.), and the moss *Psilopilum australe*, all present in the intact cushionfield, which have now established on the disturbed sites. Although the only annual recorded in the cushionfield, *Euphrasia zelandica*, has not yet been recorded on the disturbed sites, the marked increase in floristic richness, now evident, signals a major development in the successional process. Moreover, only two of the species, *Dracophyllum muscoides* and *Poa colensoi*, now have cover here that is notably different from that in the intact cushionfield. The slowness of the *Dracophyllum* to dominate is paralleled by the cushion *D. minimum* in Tasmania, where it was amongst the slowest to establish in an exposed alpine cushion heath succession despite being a dominant in the adjacent closed community (Gibson and Kirkpatrick, 1992). Most of the non-vascular species have been slow to establish, as has been reported by Urbanska (1997a) for degraded alpine ski runs in the Swiss Alps.

Disturbance may facilitate encroachment of invasive species but on the Old Man Range, only one exotic, *Rumex acetosella*, was recorded and had a minor presence only on the disturbed sites at yr-24. *R. acetosella* is prominent in the succession on stabilized road verges in Australian alpine areas (McDougall, 2001), and it also dominates among several exotics during the early stages of secondary succession associated with long-term fallowing in the similarly severe alpine environments of the tropical high Andes (Sarmiento et al., 2003).

The above- and below-ground biomass values at yr-24, the first recorded for both disturbed and undisturbed sites, were not significantly different between sites. The above-ground values were close to those of the dominants, *Poa colensoi* and *Dracophyllum muscoides*, in similar high-alpine vegetation on the nearby Rock and Pillar Range (Bliss and Mark, 1974). However, the below-ground values for both sites on the Old Man Range were higher than those for either cushionfield or herbfield on the Rock and Pillar Range.

PREDICTIONS

Predictions of the changes in the eight cover classes recognized from the disturbed and undisturbed sites on the Old Man Range, based on analyses using a Markov model, confirmed the nature of the secondary succession in the high-alpine cushionfield. Probabilities based on the 1978–1986 transition matrix were generally validated by the results of the latest (1999) sampling for both sites. However, predictions for the future of the disturbed sites, plus a likely equilibrium state, based on the 1986–1999 transition matrix, although trending closer, did not yet approach comparable values for the adjacent intact cushionfield. This discrepancy between the predicted equilibrium for the disturbed sites and the predicted (and actual) situation on the undisturbed sites may be because the model has only two states of plant cover (*Poa colensoi* and "other species"; *Dracophyllum muscoides* and "other species," respectively) for each of these sites. Since *Dracophyllum* comprises only a very minor component (~1%) of the cover provided by the "other species" on the disturbed sites, it cannot be separately included in the Markov model until it increases sufficiently to provide for a separate projection, and similarly for *Poa* in the intact cushionfield. Such is a major limitation of the Markov model, as discussed by Usher (1981).

Transition frequencies for the most recent period (1986–1999), among the seven cover classes recognized for each of the undisturbed and disturbed sites, confirm the relatively steady state of the former and the dynamic state of the latter. Autotransitions (no change in the cover type over the period) predominate in the intact cushionfield, reflecting persistence or tenacity among the cushions, as also reported recently for cushions in a low-alpine mixed cushion/turf/snow tussock/shrub community in southeastern New Zealand (Mark and Wilson, 2005).

The minor litter in the cushionfield was the only cover state where autotransitions were absent. This was also the case for the 1977–1986 period (Roxburgh et al., 1988), and contrasts with the transition frequencies for the disturbed sites where autotransitions remain generally insignificant. Transitions from bare soil and rock to pavement, and from dead plants to *Poa colensoi*, which characterized the first period (1977–1986) on the disturbed sites, were no longer conspicuous in the most recent period (1986–1999). Rather, the recent transitions were predominantly to "other species" from the six other cover classes. This trend clearly reflects the increased species richness and plant cover over this period, as the succession proceeds. The transition from *Poa* to dead plants only became significant in this most recent period and reflects the partial or total mortality associated with its destruction by wind abrasion.

The irregular periods between the samples, up to the most recent one at yr-24, annually for the first four years, followed by an eight year gap, then four and nine year intervals to the latest monitoring, have impaired our ability to critically assess variation in the succession trajectory. In terms of diversity and cover of the cushion and other dwarfed species, typical of the intact cushionfield, the rate of succession appears to be increasing. Continued monitoring of the transects will be needed to further clarify the situation and perhaps record the return of a typical cushionfield community dominated by *Dracophyllum muscoides* within the foreseeable future. Although this species has established on the disturbed sites, its cover (~1%) remains far short of its contribution to the adjacent intact cushionfield (26–32%). An eventual return of an inferred, earlier structural dominant *Chionochloa macra* (slim snow tussock), remains a much more remote possibility. However, recent cessation of grazing by domestic stock, associated with the transfer to conservation status of much of the study area in the late 1990s, may increase the likelihood. That said, seedling establishment of *C. macra* has been minor in the cushionfield to date, which may reflect its relatively low seed set and viability in the area (Mark, 1965). Spence (1990b) also recorded very limited success in seedling establishment of this species in low-alpine grassland on the Craigieburn Range, mid-Canterbury, associated with rapid decline in seed viability, grazing damage to seedlings, and high early mortality of seedlings, particularly in a *Poa colensoi* turf. Continued light grazing of the conservation area by European hare (*Lepus europaeus*), however, might retard recovery of slim snow tussock despite the recent removal of domestic stock.

SUCCESSION CONCEPTS

In relation to the various concepts of succession, their dynamics in extreme environments such as arctic (and alpine) tundra, where few adaptive strategies are possible, may be characterized by changes in species abundance through progressive colonization by climax species rather than species replacement (Grime, 1979; Ebersole, 2002). Such a pattern would be consistent with an autosuccession (Muller, 1952; Wilson and Lee, 2000) or demographic succession (Urbanska, 1997b). The absence of obvious pioneer species in this secondary succession, together with the severe environment, could imply an autosuccession, as Wilson and Lee (2000) indicated, based on the results for the first 11 yrs presented by Roxburgh et al. (1988). However, the more recent establishment of several species, which are apparently confined to the disturbed sites, would appear to discount this concept. Egler's (1954) initial floristic model also appears inappropriate, given the delay of at least four years associated with the first appearance of many apparently initiating species. The intermediate disturbance hypothesis of Connell (1978) is consistent with the observed pattern of species richness apparently peaking at an intermediate time span, yr-24, but continuation of the study will be needed to confirm this. The tolerance model of Connell and Slatyer (1977) gains no support from the outcome of

this study to date since several of the earlier colonists are not present in the intact cushionfield and so appear unlikely to persist. Their inhibition model, however, is more tenable through embracing the successful establishment and growth of later colonists with competitive superiority in terms of dependence on resources released through damage or death of previous occupants of the site. The role of *Poa colensoi* in the 11- to 24-yr period of this succession is certainly closer to this concept than to the relay floristics (facilitation or autogenic) model of Clements (1916), in relation to the lack of an obvious sequence of pioneering and mid- to late-seral species on the disturbed sites. By contrast, Gibson and Kirkpatrick (1992) rejected the inhibition model in their interpretation of alpine cushion heath dynamics in Tasmania, on the basis of continuous fragmentation and coalescence of cushions associated with the relatively rapid changes they recorded. Continued study of this succession is recommended to clarify the several unresolved issues.

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