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CHANGES IN THE STRUCTURE OF TALL TUSSOCK GRASSLANDS AND INFESTATION BY SPECIES OF *HIERACIUM* IN THE MACKENZIE COUNTRY, NEW ZEALAND

Summary: A plant sociological survey of tall-tussock grasslands in the Mackenzie country was repeated after an interval of 26-28 years. Changes in physiognomy of the grasslands which have been inferred from earlier studies have been found to be continuing on many sites. A noteworthy feature of most sites has been a reduction in number of indigenous species found. An increase in abundance of *Hieracium pilosella* or *H. praealtum* has occurred at most sites. About 140 species and 9 variables from 53 sites were interrelated in a direct unimodal ordination (canonical correspondence analysis). Ordination results of the 1960s and the 1989 data were compared and interpreted with respect to spread of *Hieracium pilosella* and *H. praealtum*. The dynamics of *Hieracium* infestation was studied within changing community structure. A distinct trend is demonstrated of increasing infestation with increasing grassland degradation.

Keywords: New Zealand; grasslands; indigenous; floristics; degradation; multivariate analysis; *Hieracium*.

Introduction

Since the late 1850s when sheep were first introduced to the Mackenzie country (O'Connor and Kerr, 1978), indigenous grasslands were inferred to have undergone great changes (Connor, 1964). Natural grasslands occurred above timberline. Induced grasslands below timberline resulted from the burning, about 700-1000 years ago during Maori occupation, of lands originally in podocarp and beech forests (Molloy *et al.*, 1963; Connor, 1985). At the time of European occupation tall tussocks of the genus *Chionochloa*[1] dominated large areas of high country.

O'Connor (1986) examined the records of early surveyors and naturalists and found evidence of tall grasslands originally richer in fine grass species than today. Early pastoralists used fire to open the canopy of tough, tall tussocks and scrub; sheep grazed the young shoots of recovering tussocks and the intertussock vegetation. Selective grazing pressure on more palatable and less fire resistant species led to promotion of the typical tussock physiognomy (O'Connor, 1986). Fire and sheep grazing produced finer pastures with smaller tussocks, often of the genus *Festuca*. Depletion of intertussock species and reduction of tall tussock themselves was followed by an increase of short-tussocks. Such transformed short tussock grasslands were observed by Garvie in Otago in the 1850s (O'Connor, 1986) and had already become widespread when Cockayne (1928) first acknowledged that they were the result of modification rather than being a climatically controlled community. Connor (1961, 1964, 1965) provided plant-sociological evidence and ecological explanations for this successional change.

Newly transformed short-tussock grasslands were enriched by indigenous and adventive, mostly palatable inter tussock species. Selective grazing pressure promoted a distinct tussocky appearance, with tufted native grasses of smaller stature (O'Connor, 1986). Cockayne (1928) and his contemporaries believed that the tussock form was naturally best suited to the New Zealand environment and would persist. However, under the influence of fire and grazing, a rosette growth-form seems to be a substitute for the tussock-form in the next step in grassland degradation. Barker (1953) observed native *Celmisia spectabilis* forming a dense cover in disturbed grasslands at higher altitudes. Similar rosette forms were reported from modified, high altitude grasslands by the Tussock Grassland Research Committee (1954), by Wraight (1963), by Connor (1965), by Mark (1965), and Mark and Bliss (1970). In plant sociological records from areas previously affected by sheep and rabbits (Connor and MacRae, 1969; Moore, 1976), the high frequency and increased abundance of species with flat, or small rosettes is apparent. An evidently efficient rosette species,

[1]Binomials used are from Cheeseman (1925), Zotov (1963), Moore and Edgar (1970), Healy and Edgar (1980), Allan (1982), Lambrechsten (1986), and Webb, Sykes and Garnock-Jones (1988) with corrections from Connor and Edgar (1987).

Hieracium pilosella, has spread in areas with deteriorating intertussock vegetation, to eventually form a complete cover over large areas.

The process of deterioration, defined doubtless by Leonard Cockayne for the Commission on Southern Pastoral Lands (1920) as 'a reduction in palatability through the destruction of palatable species', had then already been in progress for 70 years. Since 1920 the process has continued. With the depletion of intertussock vegetation in short tussock grasslands, and its replacement by *Hieracium pilosella,* a notably unpalatable element, further deterioration is evident. The process of transformation of the intertussock vegetation into a cover of *H. pilosella,* although it has taken several decades, largely escaped scientific attention until the 1970s. It has been studied in ecophysiologicaJ experiments using material mainly from the Mackenzie Country plains (Scott, 1975; Makepeace, 1976, 1985a,b). From this perspective *H. pilosella* has been interpreted as an aggressive species that displaces the intertussock vegetation and subsequently also fescue tussocks. Scott (1985) described both *H. pilosella* and *H. praealtum* as species excluding other species and causing reduction of productivity.

In this paper, the invasion of *Hieracium* is interpreted within a wider perspective of a grassland ecosystem represented by a series of stages from little modified tall tussock grasslands to highly modified short tussock grasslands, as described by Connor (1964). Most attention is directed to the changes in community structure in what were, in the 1960s, less modified tall tussock grasslands, still, in 1989, under continuing pastoral use without agronomic amendment.

Methods

In this study the sites of Mackenzie country tall tussock grassland surveyed by Connor (1964) were re-surveyed in 1989. I have fitted the original Mackenzie country data of Connor into a model that reflects structure of grasslands as they were in the late 19605. The same was done for the set of relevés from the repeated survey. The comparison made possible an interpretation of *Hieracium* spread in relation to the dynamics of changing grasslands.

The sites of snow tussock grasslands are located on all the main ranges surrounding the Mackenzie basin (Grampians, Dalgety, Two Thumb, Richmond in the east; and Ben Ohau in the west) over a wide variety of altitudes. The study sites of red tussock grassland are confined to the moraine country near Lake Tekapo within a small altitudinal range. All sites were relocated to within a few metres. The method of recording the vegetation was the same as in the original survey. Each site was 100m^2 and the

abundance of every species present was assessed using the Braun-Blanquet combined scale for abundance and dominance. For later quantification of vegetation parameters for correspondence analysis the Braun-Blanquet scale was rescaled to cover values within the original range of the scale (van der Maarel, 1979):

Braun-Blanquet scale	Transformed scale
r = of erratic occurrence	>0
+ = very sparsely present, cover very small	0.12
1 = plentiful, but of small cover value	0.93
2 = very numerous or covering at least 1/20 of the area	1.78
3 = any number of individuals covering _ to _ of the area	2.73
4 = any number of individuals covering _ to _ of the area	3.77
5 = covering more than _ of the area	5.00

The floristic composition of each site in 1989 is shown in Tables 1 and 2. Species occurring in fewer than two releves are excluded from the correspondence analysis by which Tables 1 and 2 are ordered and from synthesis in Table 3. In all three tables Braun-Blanquet abundance-dominance values are used. Releve numbers are the same as in the original study (Connor, 1964). Data were studied using both correspondence analysis (CA; Hill, 1973) and canonical correspondence analysis (CCA; ter Braak, 1986). Analyses were carried out using the programme CANOCO (ter Braak, 1988).

Canonical correspondence analysis was used to infer the ecological structure of snow and red tussock communities as mutual relationships of environmental variables, all species present and *Hieracium* species in different abundance-dominance classes. As environmental variables reflecting the natural influences I have used measurements of altitude, aspect and slope. As variables reflecting man-induced influences I used vegetation parameters of *Chionochloa* cover (*C. rigida* and *C. macra;* or *C. rubra), Festuca* cover (*F. novae-zelandiae* and *F. matthewsii),* cover of introduced grasses, cover of weeds (introduced plants other than grasses), number of native species, and percentage of bare ground. Environmental variables, and vegetation parameters used as environmental variables, are represented in Figures 1,2,3 and 4 by arrows. Aspect and cover-abundance classes of *Hieracium* were treated as nominal variables and are shown by centroids. Aspects are of true origin: North includes bearing 315-45°, East 45-135°, South 135-225°, and West 225-315°.

Environmental variables in Figures 1-4, when represented by axes (arrows) pointing in similar

Table 1: *Snow tussock grassland releve's and Braun-Blanquet class scores (see text) for the species. Species and relevÈs are arranged* in *order of their CA scores. * = exotic species.*

The following species (rows) are listed in order of their CA scores, each with Braun-Blanquet class scores (+, r, 1, 2, 3, 4, 5) distributed across the relevé columns (relevé numbers given vertically in the header):

- Phyllachne colensoi
- Celmisia viscosa
- Raoulia hookeri
- Colobonthus strictus
- Chionochloa macra
- Leptinella pectinata
- Celmisia lyallii
- Dracophyllum pronum
- Oreobolus peetinatus
- Aciphylla monroi
- Agrostis subulata
- Celmisia sessiliflora
- Celmisia densiflora
- Anisotome flexuosa
- Pentachondro pumila
- Carex colensoi
- Drapetes dieffenbachii
- Acaena saccaticupula
- Gaultheria crassa
- Cassinia fulvida
- Lycopodium fastigiatum
- Dracophyllum uniflorum
- Pimelea travesii
- Racomitrium lanuginosum
- Brachyglottis bellidioides
- Epilobium tenuipes
- Rytidosperma pumila
- Dracophyllum longifolium
- Bulbinella angustifolia
- Gaultheria depressa
- Craspedia lanata
- Cyathodes colensoi
- Scleranthus uniflorus
- Festuca novae-zelandiae
- Vittadina australis
- Deyeuxia avenoides
- Celmisia gracilenta
- Poa colensoi
- Carex breviculmis
- *Rumex aretosella
- Celmisia brevifolia
- Raoulia subsericea
- Helichrysum filicaule
- Aciphylla aurea
- Brachycome sinclairii
- Lachnagrastis filiformis
- Gnaphalium luteoalbum
- Luzula rufa
- *Hieracium pilosella
- Wahlenbergia albomarginata
- Carmichaelia monroi
- Acaena caesiiglauca
- Pimelea sericeo-villosa
- Chionochloa rigida
- *Hypochoeris radicata
- Geranium sessiliflorum
- Polytrichum commune
- Cyathodes fraseri
- Gentiana corymbifera
- Viola cunninghamii
- *Hieracium praealtum
- Pimelea oreophila
- Epilobium alsinoides
- Festuca matthewsii
- Gonocarpus montanus
- Helichrysum bellidioides
- *Crepis capil/aris
- *Holcus lanatus
- Muehlenbeckia axillaris
- Ranunculus multiscapus
- Coprosma petriei
- Blechnum penna-marina
- *Anthoxanthum odoratum
- Discaria toumatou
- Hydrocotyle nova-zelandiae
- Pratia ciliata
- Gnaphalium collinum
- *Agrostis capil/aris
- Agrostis petriei
- Anisotome aromatica
- Oreomyrrhis rigida
- Elymus rectisetus
- Galium perpusillum
- *Trifolium repens
- *Hypericum perforatum
- Carmichaelia petriei
- *Cerastium fontanum
- *Rosa rubiginosa
- Stellaria gracilenta

directions are positively correlated. Axes at right angles indicate near zero correlation, and axes pointing in the opposite directions signify high negative correlation (ter Braak, 1987). The relationship between the axis of an environmental variable and a particular abundance class of *Hieracium* is determined by the junction of a perpendicular drawn from the axis of that chosen variable to the centroid representing that class of *Hieracium* abundance. If a perpendicular meets the axis close to the centre of the ordination space, the relationship is close to zero. If the meeting point is on an axis extended beyond the ordination centre, the relationship is negative. Finally, if a perpendicular from a centroid does not reach a particular axis, the variables represented by a centroid and that axis are mutually independent.

Results

The floristic composition of snow tussock and red tussock grasslands which were resurveyed in 1989 is shown in Tables 1 and 2. Connor (1964) did not originally report grasslands as being dominated by C. *macra,* because that taxon was not described until later (Zotov, 1970). Molloy and Connor (1970) identified *C. macra* stands in the Mackenzie Country as releves 61004, 61005 and 61017 (Table 1). During the re-survey in 1989 one more site (relève 63113) was found to contain *C. macra* together with the more abundant *C. rigida.*

Relèves and species in Tables 1 and 2 are arranged in order of their CA scores. The unimodal response of species to environmental factors is clearly indicated by the elliptical shape oriented on the diagonal from top left to lower right (longman, ter Braak and van Tongeren, 1987). Species in the snow tussock grassland that have their ecological optima in the present community are grouped together in the middle of Table 1. Species shown in the top left corner, mostly of indigenous origin, represent remnants from a previous, less disturbed community. Species in the bottom right corner have their optima in highly modified weed communities. For the red tussock grassland (Table 2), such a diagonal form, reflecting the unimodal response of species to environmental factors, is less obvious. *Chionochloa rubra,* originally dominant, has only a marginal role in this strongly modified community. *Festuca novae-zelandiae,* placed close to the centre of the table, lacks the accompanying suite of species that would form the distinct core of the community. *Hieracium pilosella* links together in the table a number of species, mostly indigenous, which are rosette or mat-forming, often semi-woody or of small stature.

Table 2: *Red tussock grassland relevés and Braun-Blanquet class scores (see text) for the species. Species and relevés are arranged in order of their CA scores. .*= exotic species.*

relevé numbers	63144	63130	63142	63143	61021	63131	61022	61023	63146	63132	63145	63148	63147	63128	63133	63129	63134
Corex coriacea	r	r															
Polytrichum commune	+	2	+			+											
Acaena caesiiglauca		+	+	+													
Chionochloa rubra	3	4	4	r	+	2	r	r	l	r	r		r				
*Agrostis capillaris	2	2	1	1	1	+	1		+								
Geranium sessiliflorum	+	+			+						+						r
*Linum catharticum			+	+	r	1											
Elymus rectisetus			+	+		r	+										
*Hieracium praealtum	3	2			1	2	2	+	1	1	1	+		2	2	1	+
Deyeuxia avenoides		+		+		+	+										
Helichrysum filicaule			r	+		+											
Discaria toumatou				2	3		2	3									
Plantago spathulata		r	1			+	+										
Luzula rufa	+	+	+		+	+	+	+	+	+	+			+	+		
Carex breviculmis		+	r	r	+		+	+			+	+	+	+	r		
Ranunculus multiscapus		1	+	+			+	1		+		+					
Aciphylla aurea			r	r				+									
Festuca novae-zelandiae	2	r	1	3	4	2	3	4	3	2	2	3	2			2	1
Viola cunninghamii		+		+			+	+				+					
*Anthoxanthum odoratum			1	2	+		1	1	+	+	+	+		+		+	
Wahlenbergia albomarginata			+		+		+	+	r					+			
Poa colensoi	+		+	1	+	+	1	1	1	+	+	2	1	+	+		
Carmichaelia petriei			r										r				
*Hypochoeris radicota			+		+		+	+	+			+					+
*Cerastium fontanum			+					+									r
Cyathodes fraseri	+		1	+	+	+	+	1	1	+	1	1	+	1	+	1	
Aciphylla subflabellata				+									r				
Raoulia subsericea			+		1	1	1	1	+	+		+	1	+	+		
Celmisia gracilenta			+	+				+					+				
Gentiana corymbifera			+			+	+			r	+	+					
Pimelea oreaphila		+	+	+	+	1	+	+					+	+	+	+	
Brachyglollis bellidioides			r								+		r				
*Hieracium pilosella	1		1	1	1	2	4	3	2	3	4	4	2	3	3	4	4
*Rumex acetosella		+			+	+		+	1	+	+	+	+		1	1	1
Scleranthus uniflorus					+	+			+						r		+
Rytidosperma pumila			+		+	+	+		+			+	+	+	+	1	1
Gnaphalium collinum			r			r	+	+					+	+	+	+	
Coprosma petriei				+	+	1	1					+	1	1	2		+
Poa lindsayi								+	r								+
Brachycome sinclairii													+		r		
Raoulia hookeri													r		r	+	+
Pyrrhanthera exigua													+		+	+	

Major changes in tall tussock communities

Table 3 presents a summary of major features of change in tall tussock communities arranged by physiognomically important tall tussock species in major altitudinal zones on the Mackenzie Basin. This geographical presentation allows some of the principal changes over three decades to be discerned in different sectors of the grassland communities (O'Connor, 1976).

Reduction in abundance of snow tussocks is not conspicuous in upper subalpine grasslands, whether of *Chionochloa macra* or of *C. rigida*. Reduction in abundance values of tall tussocks throughout the montane zone is widely evident over the three decades depicted in Table 3, both for *C. rubra* and for C. *rigida*. This trend is also evident for *C. rigida* in the eastern sectors of the lower subalpine zone.

Table 3: *Summary of changes from early 1960s (left value in double column) to 1989 (right value in double column) in number of indigenous species, Braun-Blanquet abundance values for principal species of tussocks, introduced grasses, Hieracium and in percentage bare ground for each relevÈ located by map reference, altitude, aspect and slope in five major vegetation zones. CHI = Chionochloa spp., FES = Festuca spp., AGR = Agrostis capillaris, ANT=Anthoxanthum odoratum. Hpil=Hieracium pilosella, Hpra=H. praealtum.*

Relevé	Map reference	Altitude (m)	Aspect (°)	Slope	Indigenous spp. no.	Species abundance changes						Bare ground (%)
						CHI	FES	AGR	ANT	Hpil	Hpra	
A. Snow-tussock grasslands												
1. Upper subalpine *C. macra* grasslands												
61017	S 101 186971	1400	S	22	18-13	3-3	+ -2	0-0	0-0	0-1	0-0	40-40
61004	S 110 213628	1400	S	28	28-20	3-3	+ -2	0-0	0-0	+ -1	0-0	0-40
61005	S 110 210625	1250	S	30	34-19	4-4	3-2	0-0	0-r	r- +	0-0	0-0
63113	S 89 769028	1460	E	26	16-26	4-3	r-2	0-0	0-0	0-0	0- +	20-25
2. Upper subalpine *C. rigida* grasslands												
a. eastern												
61003	S 110 206625	1250	E	27	25-20	3-3	1-2	0-0	0-0	r- +	0- +	60-30
61007	S 110 174610	1280	E	25	28-18	2-3	1-3	0-0	0-0	+ -1	0- +	0-5
61009	S 110 167604	1370	N	23	24-22	3-3	1-1	0-0	0-0	0- +	0- +	60-60
61006	S 110 174613	1270	W	25	21-11	3-3	0-0	0-0	0-0	0-1	0-0	60-60
61018	S 101 190978	1400	N	28	19-11	2-3	2-2	0-0	0-0	0-1	0- +	70-55
61019	S 101 188979	1300	N	28	28-9	4-2	2- +	0-0	0-0	+ - +	0-0	30-55
b. western												
63112	S 89 770027	1450	N	18	28-28	3-3	0-0	0-0	0-0	0-0	+ - +	30-35
63114	S 89 770025	1390	E	35	37-23	3-3	2-2	0-0	0-0	0- +	r-0	10-30
63111	S 89 775032	1200	E	30	40-22	3-3	2-2	0-0	0-0	0-0	r-1	5-5
3. Lower subalpine *C. rigida* grasslands												
a. eastern												
61002	S 110 203624	1160	N	28	34-11	4-3	+ -1	0-0	0- +	r-1	0-0	40-60
61011	S 90 219114	1130	N	32	36-19	4-2	2-3	0-1	0-0	+ - +	0- +	0-10
61015	S 80 406138	1100	W	29	37-30	4-3	2-1	0-2	+ -0	+ -0	0-0	0-20
61014	S 80 409143	1020	W	29	29-23	5-3	1-2	+ -2	+ - +	+ - +	0-0	0-20
61020	S 101 184980	1000	W	30	31-12	3-3	3-2	0-0	+ - +	0-1	0-0	5-20
b. western												
63097	S 108 595673	1040	N	27	26-12	3-3	3-1	0-0	0-0	1-0	+ -1	50-50
63098	S 108 597669	1110	W	36	23-20	3-4	2-2	0- +	0- +	0- +	0-3	40-5
63096	S 108 594673	1000	W	24	33-16	4-4	2-2	0-0	0- +	0-0	1-2	25-30
63095	S 108 595674	950	N	33	33-14	3-3	2-1	0-0	0- +	0-0	+ -2	45-40
63119	S 89 776066	1190	E	33	47-20	3-2	2-2	0-0	0-1	0-2	0- +	25-35
63120	S 89 774069	1110	W	34	38-14	3-3	r-0	0-0	0- +	0- +	r- +	30-30
63121	S 89 772079	1020	E	8	44-17	2-3	3-1	0-0	+ - +	0- +	r- +	0-25
63118	S 89 770071	990	E	31	48-22	3-3	2-3	0-0	+ -1	0- +	0-1	5-0
4. Montane *C. rigida* grasslands												
a. eastern												
61010	S 110 183621	1020	N	26	33-12	3-2	2-3	0- +	+ -1	+ -4	0-0	40-15
61016	S 101 175970	950	W	26	32-11	4-3	2-2	+ -0	1- +	+ -3	0-0	5-30
61001	S 101 235904	760	W	27	40-16	4-3	2-2	+ -1	1-1	1-3	0-0	35-45
63140	S 101 184878	670	S	27	23-15	5-3	+ -1	2-3	+ -1	1-2	r-1	5-5
61013	S 80 324187	820	E	10	25-10	3-0	2-2	r-2	+ -1	0-4	0-0	0-10
b. western												
63116	S 89 782037	950	E	34	34-23	2-2	2-2	3-1	+ -1	0-3	1-1	5-5
63107	S 108 636676	820	S	35	39-17	4-2	2-2	0-0	0-0	0-0	0-3	5-40
63108	S 108 637676	820	S	38	30-13	3-1	3-2	0-0	0-0	0-0	3-3	10-50
63106	S 108 633672	790	E	33	40-13	4-2	2-3	0- +	0-1	0-0	+ -3	35-30
63100	S 101 610652	550	S	36	33-22	3-2	3-3	0- +	+ -1	0-0	1-3	5-5
B. Red-tussock grasslands												
63130	S 89 093032	850	-	0	11-7	5-4	r-r	r-2	0-0	0-0	0-2	0-0
63144	S 100 019988	800	-	0	12-9	5-3	0-2	2-2	0-0	0-1	r-3	0-0
63131	S 89 993032	850	-	0	31-i0	3-2	1-2	0-1	0-0	+ -2	r-2	0-7
63146	S 100 021997	929	S	20	35-13	3-1	3-3	0-0	0- +	0-2	0-1	0-0
63142	S 100 037997	850	S	28	40-19	3-4	2-1	+ -1	r-1	0-1	0-0	5-5
61023	S 89 915015	850	W	11	38-22	3-r	3-4	0-1	r-1	+ -3	0-1	0-0
63128	S 89 997038	850	E	9	42-12	2-0	3-2	0-0	r- +	r-3	0-2	0-15
63021	S 89 916014	820	E	12	42-20	2- +	3-4	0-1	r- +	r-1	0-2	0-0
61022	S 89 916014	820	E	12	38-19	+ -r	4-3	0- +	0-1	+ -4	0- +	0-5
62129	S 89 998038	870	W	5	35-10	+ -0	3-2	0-0	0- +	r-4	r-1	5-20
63133	S 89 991034	850	S	14	37-11	r-0	4-0	0-0	0-0	r-3	+ -2	0-5
63134	S 89 993037	870	W	5	38-10	r-0	4-1	0-0	0-0	r-4	1- +	0-20
63143	S 100 037997	850	E	23	40-12	r-r	4-3	+ -1	+ -2	r-1	r-1	0-0
63145	S 100 013990	820	W	5	33-11	+ -r	3-2	r-0	0- +	r-4	r- +	0-25
63147	S 100 022997	880	S	12	31-15	r-r	3-3	0-0	0-0	0-2	r-0	0-15
63148	S 100 023997	920	W	5	34-10	r-0	3-2	r-0	0- +	r-4	r-0	10-20
63132	S 89 993033	850	-	0	32-10	r-r	2-2	0- +	r- +	r-3	r-1	5-15

In the upper zone of snow tussock grasslands fescue tussocks were still increasing in abundance in 1989. In lower subalpine and montane zone there was no consistent trend. *Festuca novae-zelandiae* or *F. matthewsii* usually did not reach higher abundance than class 3 and rarely declined below class I. In red tussock grasslands *F. novae-zelandiae* was in some instances reduced very drastically, especially on sites that had, in the 19605, already degraded tall tussock cover.

Introduced grasses show comparatively little change in abundance in all zones except the montane, where increase in *Anthoxanthum odoratum* in particular is evident from the notably low occurrence recorded by Connor (1964). *Hieracium* species show general increases in snow tussock grasslands, which are small at high altitudes, and often large for *Hieracium pilosella* in the eastern montane zone, and for *H. praealtum* in the western montane zone and in the western lower subalpine zone. In red tussock grasslands some differentiation is also evident, with increases in *H. praealtum* in more intact grasslands and in *H. pilosella* in the more degraded grasslands.

The most striking and consistent change evident in the snow tussock grassland sites is the almost universal reduction in the number of indigenous species recorded by 1989. This feature is also striking in the red tussock grasslands which have a characteristically smaller number of native species in the more natural condition (Connor, 1964). The dramatic nature of this apparent decline in floristic diversity over a wide range of conditions suggests that in the network of interrelated influences one might govern this trend. To identify such an influence, and express it quantitatively in respect to number of other influences, requires a larger data pool than that at present available in this study. Here interaction of variables related to natural influences and those related to management provides some indications of trends. *Hieracium* increase incorporated into multivariate analysis in the form of abundance-dominance classes shows its relationship to these trends.

Changes in structure in the snow tussock community

The configuration of axes in Figure 1 shows the overall structure of the snow tussock community, and the relationship of classes of *Hieracium* within this structure, as it was in the early 1960s. Most snow tussock sites in Connor's survey (Connor, 1964) were moderately modified snow tussock grasslands, usually with fairly abundant *C. rigida* or *C. macra*. This more or less uniform *Chionochloa* cover was not very influential (short arrow) on the other variables and on the distribution of the species. In natural conditions
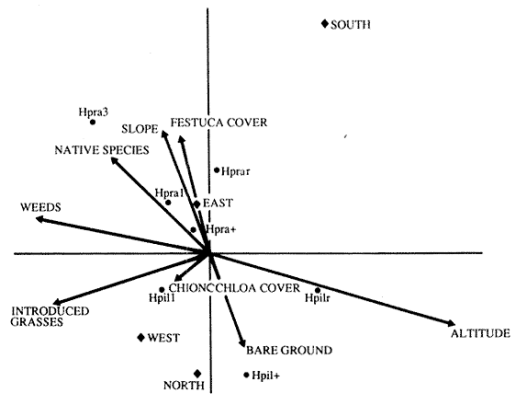
Figure 1: *Snow tussock grasslands in 1961/63. CCA ordination diagram showing abundance classes for Hieracium pilosella and H. praeItum (circles), aspect (diamonds), and axes for environmental variables and vegetation parameters.*

bare ground increases with altitude. This relationship was preserved in the 1960s data set and is shown in Figure 1 by a positive correlation (acute angle) between the axes for bare ground and for altitude. All other variables were negatively correlated with altitude and positively with each other. The negative correlation between altitude and *Chionochloa* cover shows that in the 1960s *Chionochloa* cover decreased with increasing altitude. Altitude, represented by the longest arrow, was a most influential factor. Fescue tussocks substituted for snow tussocks mainly on steeper slopes at lower altitudes. The diversity of native species increased with the growing importance of *Festuca* cover. Introduced grasses occurred in a close positive relationship with *Chionochloa* cover. The relationship between the high influence of weeds and the low influence of altitude is shown by their direct negative correlation. The clear separation of centroids for south and north aspects indicates that an ensemble of species related to the southerly aspect was distinguished from a suite of species associated with northerly conditions.

By the late 1980s the vegetation structure and mutual relationship among variables changed (Fig. 2). The most important of those changes resulted from a reduction in *Chionochloa* cover. Since the snow tussocks survived successfully at higher altitudes, the previously negative correlation between *Chionochloa* cover and altitude changed into a closely positive correlation. The diversity of native species, originally positively correlated with *Festuca* cover, depended, in 1989, more on altitude. The opposite position of the axis for slope to the axes for *Chionochloa* cover and
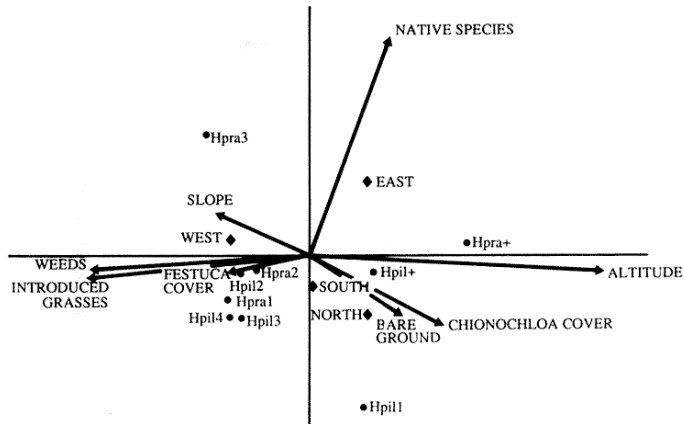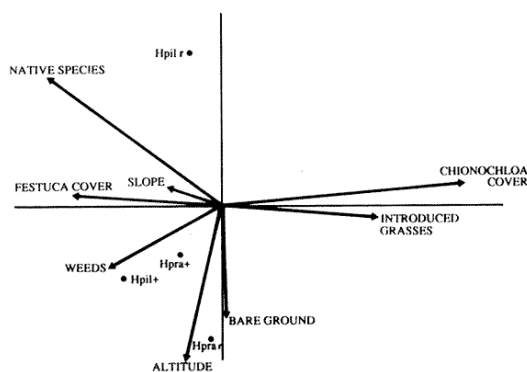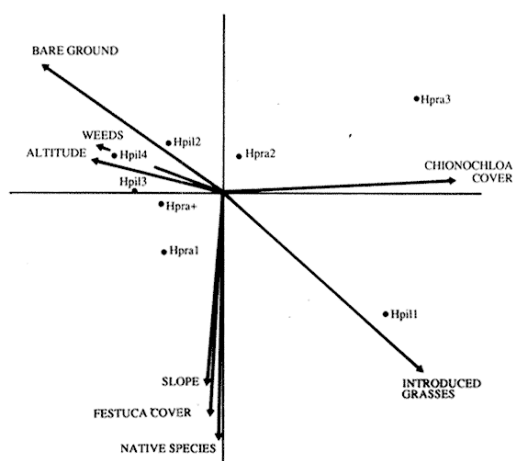
Figure 2: *Snow tussock grasslands in 1989. CCA ordination diagram showing abundance classes for Hieracium pilosella and H. praeltum (circles), aspect (diamonds), and axes for environmental variables and vegetation parameters.*

for altitude demonstrate that snow tussock cover was reduced most on steeper sites at lower altitudes. Continuing degradation greatly reduced the difference between south and north aspects, so that sites of both aspects in 1989 had a more similar vegetation than previously. This homogenization process is also shown by the shortened distance between centroids for north and south aspects. The process of homogenization is closely linked with the process of invasion. Di Castri (1990) postulated that man-induced homogenization rapidly increases susceptibility to invasion.

Relationship of **Hieracium praealtum** *to snow tussock community structure*
In the 1960s *H. praealtum* occurred in grasslands at low 'altitudes and with reduced *Chionochloa* cover (Fig. 1). *Hieracium praealtum* was rare where *Festuca* cover was dense, the slope steep, and where native species were abundant. When *H. praealtum* increased in abundance to class +, its relationship with *Festuca* cover, slope and native species weakened, and it entered a new relationship with weeds. The relationship with weeds intensifies when *H. praealtum* increases in its abundance to class 1. Where *H. praealtum* was in abundance class 3, in the 1960s, it was related to low altitudes, limited *Chionochloa* cover, reduced abundance of introduced grasses, and to weeds at their maximum cover. The strong negative relationship between *H. praealtum* class 3 and bare ground shows that where *H. praealtum* is in a high proportion in these snow tussock grasslands, bare ground is reduced.

In 1989 (Fig. 2) *H. praealtum* in abundance class + was related to *Chionochloa* cover at higher altitudes.

When in increased abundance (classes 1 and 2), it was associated with *Festuca* cover, introduced grasses and weeds. In abundance class 3 *H. praealtum* lessened its relationship with weeds and assumed a positive correlation with *Festuca* cover and with native species.

Relationship of **Hieracium pilosella** *to snow tussock community structure*
In the 1960s (Fig. 1), *H. pilosella* in abundance class r was related to higher altitudes and an increased proportion of bare ground. In abundance class +, *H. pilosella* was related to lower altitude, and showed a tendency towards a relationship with introduced grasses. When *H. pilosella* was in abundance class I, and occurring at still lower altitudes, its relationship with introduced grasses was fully developed as also was its affinity to weeds and bare ground.

In 1989 (Fig. 2), *H. pilosella* in abundance class + was related to reduced *Chionochloa* cover with a minimum of native species, and to a high proportion of bare ground. *Hieracium pilosella* in abundance class 1 was related to *Chionochloa* cover with depleted native species. When *H. pilosella* increased in abundance to class 2 or 3, its relationship to *Chionochloa* cover disappeared and it became related to *Festuca* cover, introduced grasses and weeds. At abundance class 4, *H. pilosella* lost relationship with *Festuca* cover and showed a relationship only with introduced grasses and weeds.

Changes in structure in the red tussock community
Connor's data set (Connor, 1964) contains red tussock sites in a spectrum of stages - from stands with dense tussocks to highly modified grasslands

with *C. rubra* only as remnants. The degree of transformation of red tussock to fescue tussock grassland determined the structure of the community. This process is reflected in the strong negative correlation between *Chionochloa* cover and *Festuca* cover (Fig. 3). A positive correlation between slope and *Festuca* cover shows that, in the area studied, red tussock grasslands are more readily transformed to fescue tussock grasslands on a slope than in a swampy flat. *Chionochloa rubra* was, in the 1960s, in a wide range of abundances which strongly influenced (long arrow) the rest of variables and the distribution of species. There is a close positive relationship between introduced grasses and the abundance of red tussocks. Native species and weeds were both related to the cover of *Festuca*. Nevertheless, the higher rate of change in the diversity of native species influenced community structure more than the changes in the abundance of weeds. The negative relationship between native species and bare ground suggests that in the 1960s bare ground was likely to increase when native species were lost.

By 1989 the transformation of red tussock grasslands was more or less complete and was followed by a reduction in *Festuca* cover. With both red and fescue tussocks losing their role as dominants, their antagonistic relationship also decayed; in Fig. 4 the axes for both parameters are in independent positions. The relationship between native species and bare ground remained similar to the 1960s configuration, but as red tussock sites have been recently further modified, bare ground is more directly related to the amount of introduced grasses. Decline in introduced grasses is associated with increase in bare ground, which is in turn associated with increase in weeds. Those native species that had

Figure 4: *Red tussock grasslands in 1989. CCA ordination diagram showing abundance classes for Hieracium pilosella and H. praeltum (circles), and axes for environmental variables and vegetation parameters.*

not disappeared were closely dependent on the presence of fescue tussock which was more successful on slopes than on the flat.

Relationship of **Hieracium** *species to red tussock community structure*

Figure 3 shows the first occurrences of *H. praealtum* and *H. pilosella* at the original survey of the red tussock grasslands. No class of *Hieracium* is displayed to the right of the ordination centre; that space represents a newly opened, but relatively dense rt:d tussock grassland with intertussock spaces filled by introduced grasses. All classes of hawkweeds are associated with transformed fescue tussock grasslands as shown on the left of the ordination centre. The centroid for *R pilosella* in abundance class r, when transposed on the axes for weeds and bare ground, intersects them close to their end points, representing a maximum influence of those parameters. The axis for *Festuca* cover is reached at a point representing reduced influence of this factor. The axis for native species is reached close to the ordination centre, where the influence of native species is shown to be near to zero. The remaining classes of *Hieracium* (H. pil +, H. pra r, H. pra +) in Figure 3 occur in similar combinations of those factors, suggesting that in 1960s both species of *Hieracium* had already stronger relationships with factors related to a more degraded part of the community.

In 1989 the maximum abundance achieved by *H. praealtum* was class 3 and by *H. pilosella,* class 4. The increase in abundance of *H. pilosella* is reversed in direction to that of *H. praealtum* (Fig. 4). Each species

Figure 3: *Red tussock grasslands in* 1961/63. *CCA ordination diagram showing abundance classes for* Hieracium pilosella *and* H. praeltum *(circles), and axes for environmental variables and vegetation parameters.*

exhibits its maximum cover on opposite sides of the degradation spectrum, represented by maximum *Chionochloa* cover to the right of the ordination centre (with *H. praealtum* class 3), and maximum weed cover and bare ground to the left (with *H. pilosella* classes 2, 3, and 4). *Hieracium praealtum* in abundance class 3 is in close relationship with relatively dense *Chionochloa* cover and with introduced grasses at approximately one-third of their maximum cover. In abundance class 2 *H. praealtum* is weakly associated with *Chionochloa* cover, loses its relationship with introduced grasses, and enters a new one with weeds and bare ground. In abundance class 1 *H. praealtum* exchanges its relationship with *Chionochloa* cover for relationships with *Festuca* cover, weeds and bare ground. *Hieracium praealtum* in abundance class + is associated with negligible *Festuca* cover,. more abundant weeds, and a greater proportion of bare ground.

Discussion

Ecological role of *Hieracium* species in tussock grasslands
The process of infestation by species of *Hieracium,* which was believed to be chaotic and unpredictable, is shown in this paper as a pattern of stages related to the degradation of tussock grasslands. In Connor's relevés of snow tussock grasslands (Connor, 1964), hawkweeds were present at a majority of sites including those in high altitudes. Close examination of high altitude sites, representing enclaves of little modified grasslands, allows the elucidation of conditions under which species of *Hieracium* first enter a community.

In the early stages of modification C. *macra* and C. *rigida* grasslands at high altitudes contained only *H. praealtum*. *Hieracium praealtum* was present, as were many other grassland species, in low abundance. It often even disappeared with them when the diversity of species was reduced. Grasslands in high altitudes containing *H. pilosella* all displayed some signs of degradation. These signs included an increase in *Festuca* cover, reduction of *Chionochloa* cover, an expansion of bare ground, and a reduction in the diversity of alpine and grassland species. The further spread of *H. pilosella* in moderately disturbed high altitude environments was slow. It took *H. pilosella* almost three decades to increase from abundance class r to class +, or to a maximum of 1.

At mid-altitudes, by the 1960s, most sites were already reduced in *Chionochloa* cover, and were often partly transformed to short tussock grassland. Intertussock vegetation was diverse even though sometimes a relatively high proportion of bare ground was exposed. By 1989 the tussocks themselves had not been reduced in number and size at an alarming rate.

The main change, which mostly escaped attention, happened to the intertussock vegetation. Deterioration in the mid-altitude zone was widespread and omnipresent. *Hieracium pilosella,* despite a substantial reduction in diversity and in abundance of intertussock species, rarely exceeded abundance class 1. On rocky sites, *Hypochoeris radicata* was more successful than *H. pilosella*. On sites with more top-soil, introduced grasses substituted for the loss of the original intertussock vegetation. The tussock grasslands on slopes too steep to accommodate patches of *H. pilosella* were invaded by taller, open, and loosely branched *H. praealtum*. On the steeplands, the cover of *H. praealtum* increased to a maximum abundance of class 3 as the community became increasingly degraded. Typically by 1989 the differences between communities on sunny or shaded aspects tended to be reduced or eliminated. Multivariate analyses show a trend towards decreasing influence of natural factors and the increasing influence of parameters related to management.

Montane grasslands of snow tussock origin were, in the 1960s, all highly modified with frequent signs of degradation but some sites were in a reasonable condition. Regardless of that, by 1989 the majority of those grasslands were heavily infested with *H. pilosella*. Stages leading to this condition are preserved in the sites now impoverished of grassland species, but not yet invaded by *H. pilosella*. Usually, the grasslands with depleted intertussock vegetation are occupied by *Agrostis capillaris,* before they are invaded by *H. pilosella*. After a period of continuing defoliation *A. capillaris* gives way to *H. pilosella*. Before there is a complete substitution of *A. capillaris* by *H. pilosella,* the process seems to be reversible.

If *A. capillaris* grows and overshades the already spreading *H. pilosella,* the typical flat leaves of the rosettes of the mouse-eared hawkweed stand upright - resembling more the habit of *H. praealtum* - thus increasing the space for more grass leaves. Cossens, Mitchell and Crossan (1989) also describe the habit of *H. pilosella* becoming more erect as the grass yield increases. Techniques for suppressing *Hieracium* in grassland development were unfolded in Britain as well as New Zealand (Davy and Bishop, 1984; Cossens *et al.,* 1989; Scott, Robertson and Archie, 1990a).

The red tussock grasslands, in the way they were sampled by Connor (1964), are especially informative as a study in succession. Protected from grazing animals by free standing water, some sites began modification only recently after they dried out. These sites were always surrounded by already depleted' grasslands and were under increasing grazing pressure. Successional stages in these grasslands were changing faster and did not reach their maximum manifestation. During the transformation from red

tussock grasslands, the fescue tussocks started declining in abundance before they attained maximum cover. Intertussock species deteriorated before they reached, in newly transformed short tussock grassland, their typical high diversity. The period of an abundance of introduced grasses, which substituted for diverse intertussock vegetation, was shorter. If *Discaria* was present it delayed the depletion by supplying the grasslands with extra nitrogen and other benefits discussed by Daly (1967). However, once grasslands were degraded, the spread of *H. pilosella* and even its depletion progressed quickly.

There is particular opportunity offered by a few red tussock sites in early stages of modification to understand the pattern of succession. After their initial opening, the red tussock stands in the Mackenzie country lack typical red tussock grassland species to fill the intertussock spaces (Connor, 1964). This role was taken by *Agrostis capillaris,* which is often the last source of forage in the surrounding areas of degraded grasslands. *Hieracium praealtum* is the most suitable among the available species to complement *A. capi/laris* affected by defoliation. Under the canopy of red tussocks, and in a sward with *A. capi/laris, H. praealtum* reached abundance class 3. *Hieracium pilosella* does not spread into grasslands of this character, even if it is present in surrounding areas in enormous quantities.

With the depletion of *A. capillaris, H. praealtum* disappears as well, along with the red tussocks. The succeeding short tussock grassland, whose intertussock vegetation is already deteriorating, is soon infested by *H. pilosella* which achieves the same level of high dominance as in degraded *C. rigid a* grasslands of the montane zone. In degraded grasslands of both red and snow tussock origin, the stage with compact cover of *H. pilosella* is not the final. In areas affected by sheep and rabbits, the maximum abundance of *H. pilosella* begins to be reduced. Exposed bare ground is then occupied by *H. praealtum* which, being one of the few remaining palatable species in this type of vegetation, is often defoliated. With reduced grazing pressure it quickly occupies bare ground.

Hieracium praealtum possesses two rather contrary characteristics. It coexists, like other grassland species, in diverse, successionally advanced phases of native grasslands. It is, additionally, an aggressive coloniser, and able to occupy, and re-cover areas stripped of vegetation. It would not be surprising, with the current evidence of its ecological performance, to see this species in the role of initiating the reversal of a successional trend. This potential of *H. praealtum* is demonstrated in the CCA model of the snow tussock grasslands. In the 1960s *H. praealtum* in high abundance was exclusively related to weeds on depleted sites. In the 19805 it shows a

relationship to native species as well. It may well be possible, if the disturbance is adequately reduced, for *H. praealtum* to become just another grassland species in rehabilitated vegetation as it is in moderately modified grasslands.

Some implications of an ecosystematic approach

The Mackenzie Country as a geologically and floristically distinct region (O'Connor, 1976) is especially suited to study changes in native grasslands at the community level. Most stages that have evolved in grasslands ecosystems from the advent of pastoralism until recent times are included in Connor's data collection. The least modified grasslands are the oldest stages; highly modified grasslands are successionally young. Such a data collection represents the time span from the beginning of pastoral use until recent times as well as the area of the Mackenzie Country. My own data collection demonstrates the recent continuation of evolutionary processes of pastoral impact and response.

Dealing with this type of data, inferential statistics are a useful tool for detecting trends and processes. It has been argued by many authors that trends and processes can only be recognised in a 'real' experiment, with controlled conditions. Wiegleb (1989) suggested that in complex situations like ecological systems there is no experiment that can be evaluated without the use of inferential statistics. Therefore, there is no difference in principle between observing a 'natural' and a 'real' experiment. In multivariate methods, like canonical correspondence analysis (CCA; ter Braak, 1986), designed for ecosystematic data, the axes are estimations of controlled conditions of an experiment. In my work the explanatory power of the natural experiment is enhanced by also using data from repeated surveys. This combines the benefits of both approaches.

From a wider perspective of this study, the aggressive and invasive nature of species of *Hieracium* emphasised earlier is only one part of the whole network of influences. The concept of aggressiveness of *Hieracium,* which seemed to be crucial in the isolation of a small subsystem, becomes increasingly inadequate when interdependence with the larger whole is considered.

In the theory of biological invasion, a species-centred approach is only one part of a wider approach based on the information of a species-recipient and a spccies-donating ecosystem (Roy, 1990). The predisposition of the recipient ecosystem to invasion is of high importance especially in an island-like condition of biogeographical isolation (Johnstone, 1986). Results in this paper support the general trend of higher susceptibility to invasion of more disturbed ecosystems than less disturbed ones (di Castri, 1990; Kornas, 1990). The ecosystematic

approach offers an opportunity for an objective assessment to be made of the problem of invasive species. Objectivity increases with increasing complexity which can finally embrace aspects of nature as well as society. Although the model of a part of the grassland ecosystem that I have used provides a perspective of a more inclusive whole, it is only a modest example of what might help to formulate future solutions.

Differences in approach and in the method of analysis have led to different understandings of the ecological role of *H. praealtum* and *H. pilosella* as well as the trends in succession. Severity of infestation by *H. pilosella* is here interpreted as related to degradation of grasslands. The results from investigations of early stages of modification of both snow tussock and red tussock grasslands suggest that a grassland needs to reach a certain degree of degradation before *H. pilosella* becomes troublesome. By protecting the top soil of a depleted grassland with its compact cover, *H. pilosella* delays the next stage of degradation, possibly for a couple of decades.

The interpretation of successional trends, which is proposed here, is in conflict with concepts of vegetation stability advocated by Scott, Dick and Hunter (1988) and Scott, Robertson and Archie (1990b) following studies of both short- and long-term changes and trends in tussock grasslands. From a seven-year trial, Scott *et al*. (1990b) report stability of *Hieracium-dominated* vegetation types on undeveloped paddocks. In their interpretation the composition of grasslands quickly adjusted to a new management of seasonal grazing, and equilibrium is assumed to be reached rapidly. They predict *Hieracium-dominated* types to remain. Scott *et al*. (1988) concluded from a 34 year-long series of trials that an overall proportion of living vegetation and bare ground may have approached a balance with existing conditions and may persist if present conditions prevail. They refer to the relative stability of many of the major elements of the vegetation. Rose (1983) was even more optimistic. He believed that in the absence of any major change in exogenous factors, *Hieracium-dominated* vegetation will persist, with forest and scrub slowly invading it in the long term.

Whether *H. pilosella*-dominated communities remain stable under a wider range of conditions may be revealed by analysis of changes in communities already transformed in the 1960s into short tussock grasslands and weed communities. This is the subject of a further paper.

Recent changes in degradation of tall tussock grasslands

Four major features call for discussion in the central issue of grassland degradation. Historical uphill transformation of tall tussock grasslands to short tussock grasslands is continuing on unimproved terrain, even in the present pastoral conditions. Whether this vegetation trend is caused by present pastoral use or results from conditions set in train by earlier historical events warrants further examination. It appears to be accompanied or followed by *Hieracium* invasion.

The striking feature over all tall tussock grasslands has been the reduction in the number of indigenous species found on resurveyed sites in the present grassland survey in comparison with the early 1960s. O'Connor's (1980, 1982, 1984, 1987) argument that the stability of grassland systems, their conservation, and the sustainability of their pastoral use might properly require attention to be focused on vegetation condition, rather than soil erosion, seems warranted. For this it seems that a better understanding is required of any climatic variations, any changes in soil conditions and any animal grazing factors which might have been affecting vegetation in such a way. The strikingly varied features of this dramatic result about floristic richness suggest that it requires major and multi-dimension research for conservation of biodiversity.

There is evidence in this study after three decades to support the argument propounded by O'Connor over the same three decades (O'Connor, 1960, 1987) that pastoral use of unimproved grasslands is not widely sustainable in the New Zealand high country. Whether the condition of grasslands that have not been agronomically developed has continued to decline elsewhere in New Zealand may be revealed by comparable studies of which I have some to report in further papers.

There is also abundant evidence in the analyses of this study that the processes of grassland degradation and change are by no means stochastic. No matter what remedies are devised for the immediate problems of *Hieracium,* there appears to be powerful linkages between physical and cultural conditions and the conspicuous signs of grassland degradation. Piecemeal remedies will be unavailing. Pastoral systems modification will be essential.

Acknowledgements

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