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VEGETATION CHANGE OVER 25 YEARS IN A NEW ZEALAND SHORT-TUSSOCK GRASSLAND: EFFECTS OF SHEEP GRAZING AND EXOTIC INVASIONS

Summary: Vegetation changes were investigated on 27 transects in agriculturally unimproved short tussock grasslands dominated by *Festuca novae-zelandiae* in the Harper-Avoca catchment, Canterbury. These were remeasured at 5 or 10 year intervals between 1965 and 1990. Change was widespread. It was characterised by invasions by exotic species, declines in native species (including *F. novae-zelandiae*), and a trend towards vegetation dominated by the flatweeds *Hieracium lepidulum* and *H. pilosella*, and the grass *Agrostis capillaris*. The effects of different histories of sheep-grazing were examined on the transects and on 174 quadrats established in 1988. Although prolonged grazing generally promoted decline in native species and invasion by exotic species, including *H. lepidulum*, these trends also developed on sites protected from grazing for 22 or 35 years. There was no evidence that the rate or extent of invasion by *Hieracium pilosella* was enhanced by continued sheep grazing, or that removal of grazing prevented invasion. Two common hypotheses seek to explain *Hieracium* success as either a symptom of ecosystem depletion or an example of an aggressive invader. However, neither hypothesis alone adequately accounts for the observed patterns of *Hieracium* invasion. Such single-factor explanations fail to account for interactions between the many mechanisms that affect plant populations at different spatial and temporal scales. Similarly, single-factor prescriptions for preventing or controlling *Hieracium* invasion, such as the removal of grazing, may not provide widespread success.

Keywords: Tussock grassland; vegetation change; vegetation analysis; *Hieracium*; grazing; Canterbury.

Introduction

The original beech (*Nothofagus*[1]) and podocarp (Podocarpaceae) forests of the eastern South Island high country were extensively burnt by Polynesian immigrants between 1000 and 500 B.P. (Molloy *et al.*, 1963; Molloy, 1977). By the time of European settlement about 150 years ago, tall-tussock (*Chionochloa*) grasslands and shrublands had become established over large areas. As exploitative pastoralism based on sheep (*Ovis aries* L.) wool production became the dominant land use, the pre-European grassland communities were extensively and regularly burnt to promote palatable regrowth. Stock numbers increased rapidly. For many areas, historical botanical accounts indicate that, within

only 20 years of settlement, pastoralism probably caused a major reduction in grassland stature and density as short tussocks replaced the less resilient snow tussocks and intertussock vegetation became depleted or was invaded by exotic plants (O'Connor, 1982, 1986). By the 1950s, sheep numbers had fallen by 30-90% from the peak levels attained around the turn of the century, reflecting declining overall grassland condition and rabbit (*Oryctolagus cuniculus* L.) plagues in the driest areas (O'Connor, 1981). The resulting semi-natural short tussock grasslands now occupy about 1.1 million ha of New Zealand's land area (Newsome, 1987). Typically dominated by endemic *Festuca* tussocks, they form a major ecosystem in the semi-arid to humid montane-subalpine zone of the eastern South Island. Although the frequency of burning has declined and stock have been removed from many eroded high-elevation areas, the past 40 years have seen continued structural and compositional changes in the short tussock grasslands. These include further vegetation depletion (particularly in semi-arid rabbit-prone areas), natural invasions by herbaceous and woody species, and restoration and agricultural

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[1] Botanical nomenclature follows Connor (1991) for *Chionochloa* species and Cheeseman (1925) for other indigenous grasses; Allan (1961) and Connor and Edgar (1987) for other indigenous species; Edgar and Forde (1991) for *Agrostis* and Lambrechtsen (1992) for other adventive grasses; and Webb, Sykes and Garnock-Jones (1988) for adventive dicotyledons.

improvement of large areas by oversowing with exotic pasture species and addition of fertiliser.

The most recent and widespread threat to both pastoralism and conservation in the short-tussock grasslands is invasion by species of *Hieracium* (hawkweeds), in particular *H. pilosella*, *H. praealtum*, *H. caespitosum*, and *H. lepidulum*. Inadvertently introduced in the late 19th century, these hawkweeds have spread dramatically in the last 2 decades and are now dominant in more than 500 000 ha of the South Island (Hunter, 1991). Concern at the spread of hawkweeds has generated several recent reviews (Scott, 1985; McKendry and O'Connor, 1990; McMillan, 1991; Parliamentary Commissioner for the Environment, 1991; Hunter, Mason and Robertson, 1992). At present, one of the only means of combating hawkweeds is oversowing with more vigorous pasture species. However, maintenance of such species usually requires continual inputs of fertiliser and an adequate soil moisture regime (e.g., Scott, Robertson and Archie, 1990). For the large areas where pasture improvement is not viable, de-stocking and severe control of feral animal populations (particularly rabbits), have been suggested as likely ways of enhancing vegetation vigour and resisting hawkweed invasion (e.g., Parliamentary Commissioner for the Environment, 1991; Kerr, 1992).

Although it is recognised that the "unimproved" short-tussock grasslands are undergoing extensive changes, there are few quantitative studies of long-term trends on which to develop conceptual models for the wide range of grassland communities, environments, and disturbance regimes (e.g., Moore, 1976; Rose, 1983; Scott, Dick and Hunter, 1988; Treskonova, 1991; White, 1991; Connor, 1992). In this study, we summarise the dominant pathways of vegetation change between 1965 and 1990 on permanent transects in the unimproved grasslands of the Harper-Avoca catchment, Canterbury. These are compared with earlier trends that were based on remeasurements made up to 1980 (Rose, 1983). In addition, by comparing sites with different grazing histories we address current ideas on hawkweed success and the hypothesis that removal of sheep grazing can prevent or arrest *Hieracium* invasion.
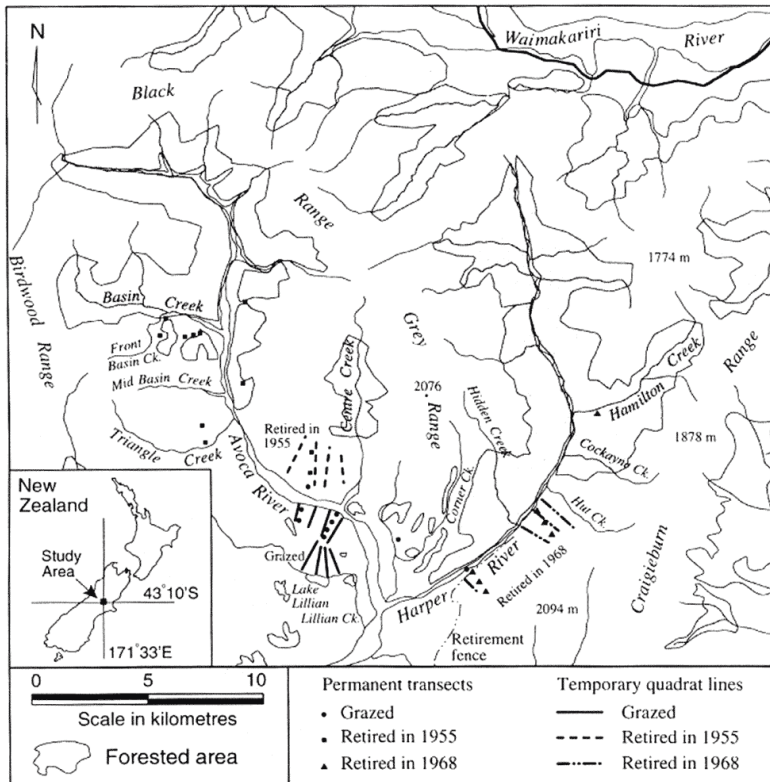

Figure 1: *Study area location showing the position of the permanent transects established in 1965 and the temporary quadrat lines established in 1988.*

Methods

Study area

The study area (Fig. 1) comprises the montane-subalpine hillslopes of the lower Avoca and Harper River valleys, Canterbury (43°10'S, 171°33'E). The predominant soils are relatively infertile yellow-brown earths or podzolised yellow-brown earths (mean topsoil pH = 5.2; A.B. Rose, *unpubl. data*). These originally developed under mountain beech forest (*Nothofagus solandri* var. *cliffortioides*), on highly indurated sandstone and argillite colluvium. Long-term records from nearby indicate annual rainfall is about 1200 mm in the lower valleys but may rise to 1500 mm further up the valleys (see Mosley, 1979; Harris and O'Connor, 1980).

The short or fescue-tussock (*Festuca novae-zelandiae*) grasslands extend from the valley floors (700 m a.s.l) to the former treeline (1350 m). The first recorded forest fire was in 1860, and by about 1910 most of the lower-valley beech forest had been burnt (Packard, 1947; R.J. Brown, *pers. comm.*). The subsequent history of burning is unclear, but the grasslands have not been burnt for at least the last 40 years.

Sheep and feral animal history

Since sheep were first introduced in 1858 (Packard, 1947), the area has been used for extensive grazing during summer, but detailed records are lacking. In 1955-56, much of the area was retired from sheep grazing for gazetting as State Forest. In 1968, further areas were also retired because of perceived high rates of erosion in the alpine zone. For areas that are still grazed, present stocking rates are lower than before the 1960s and grazing management is generally more intensive. For example, restricted areas are grazed in early summer to prevent seeding of *Hieracium*, and other areas are grazed during winter (R.J. Brown, *pers. comm.*). Despite the lower stocking rates, a few sheep or cattle sometimes get past the fences, rivers, and bluff systems that protect the retired areas. However, such grazing is mainly restricted to the river flats for periods of about 2 - 20 days (R.J. Brown, *pers. comm.*).

The grasslands have also been browsed by introduced red deer (*Cervus elaphus* L.) and chamois (*Rupicapra rupicapra* L.) for over 50 years. The history of red deer, the main feral browsers in the area, is well documented (see Hickling, 1986) and that of chamois is broadly similar. Deer spread into the catchment in about 1910, and chamois in the late 1920s. Subsequent increases in numbers prompted sporadic control operations between 1936 and 1953 (the effects of these operations on animal numbers are not recorded). An intensive campaign between 1955

and 1961 reduced deer numbers by about 75% in the alpine (*Chionochloa*) grasslands (their preferred habitat), and by about 40% in the forests, scrub, and fescue tussock grasslands. Hunting was then prohibited and deer numbers began to rise, reaching about 50% of pre-1955 densities by the early 1970s. Because of increasing levels of illegal hunting, the population was again declining by the late 1970s. By the mid 1980s, numbers were only about 35% of those attained in the late 1970s (Hickling, 1986). With hunting again permitted, the population has declined to even lower levels (*pers. obs.*).

Low populations of rabbits and moderate populations of European hares (*Lepus europaeus* Pallas) are also present. Rabbits appear to have been mainly restricted to the valley floors where for at least the last 25 years the small isolated pockets have required only sporadic control (R.J. Brown, *pers. comm.*). Browsing by hares appears to be light overall in the hillslope fescue tussock grasslands, where obvious browsing damage to fescue tussocks is rare (A.B. Rose, *unpubl. data*). In the areas retired from sheep grazing, only 2-13% of tall tussock plants present in mixed tall tussock - fescue tussock stands show evidence of browsing damage, and this has not prevented seedling recruitment (Rose and Platt, 1992). Favoured sites adjacent to forest margins are more heavily browsed.

Overall changes on permanent transects

Between November 1965 and January 1966, 27 permanently marked transects were established to monitor changes in species composition and proportion of bare ground. They were remeasured during a similar period in 1975-76, and then at 5 year intervals up to 1990-91. Most transects are 40 m long. Their origins are set at 100-300 m elevational intervals along lines located to broadly represent the grassland communities in the area. The transects sample grasslands that are still grazed by sheep and those retired in either 1955 or 1968 (Fig. 1). All transects run directly upslope and are marked with steel pegs at 20 m intervals. For each transect, the percentage frequency of all vascular species was determined from their presence within 15 cm diameter, circular subplots spaced at 40 cm intervals. The frequency of bare ground (exposed soil, colluvium and bedrock) was calculated from point intercepts also spaced at 40 cm intervals (at the centre of each subplot) (Allen, Rose and Evans, 1983).

Effects of grazing history on vegetation composition

The effects of different grazing histories on species composition were examined by comparing the

vegetation of management blocks present in the study area that are either still grazed, or were retired in 1968 or in 1955 (Fig. 1). Two types of data were used: changes in species frequencies since 1965 on a subset of the original transects, and the cover of dominant species present on temporary quadrats established in 1988.

The effects of two different grazing histories were examined on 16 of the original 27 permanent transects located in the lower valleys. In 1965, the 16 transects were all grazed by sheep. Nine transects (in the lower Avoca valley) are still grazed, and seven (in the lower Harper valley) were retired from grazing in 1968. Because the blocks are spatially separated, such comparisons can risk confounding the effects of management and environment (Walters and Holling, 1990). However, such spatial separation is inevitable in the unimproved tussock grasslands, where management blocks comprise thousands of hectares and grazing management is extensive rather than intensive. Therefore, we ensured that the transects used in the comparison occurred over a similar range of rainfall, aspect, elevation, and soils. The 16 transects are located predominantly on north-facing hillslopes with similar annual rainfall (estimated at 1200 mm). Mean elevation of the transects in each block is also similar (grazed = 924 m; retired = 950 m). Soil samples collected at stratified random points along the 16 transects in 1990 (0-10 cm depth, 8 bulked samples per transect) indicated that soil fertility was similar between blocks, with no significant differences in mean pH, total C and N, exchangeable bases (Na, Ca, Mg, K), $CaCl_2$-extractable Al, Olsen P, or phosphate-extractable SO_4 (analysis of variance, $P > 0.05$; A.B. Rose, *unpubl. data*). No soils data were collected in earlier years.

Other grazing comparisons using permanent transects were precluded because of low sample size or environmental constraints. Therefore, in December 1988 the effects of contrasting grazing histories were further investigated by surveying vegetation cover on 174 temporary quadrats located in four management blocks in the lower valleys (Fig. 1). This allowed two comparisons: (1) between north-aspect grasslands that are still grazed or were retired in 1968 (the same two blocks sampled by the 16 permanent transects); and (2) between south-aspect grasslands that are still grazed or were retired in 1955. For each block, 40-48 quadrats (4 m^2) were spaced at 100 m intervals along four representative grassland lines located from aerial photographs to avoid screes and patches of woody vegetation (Fig. 1). The lines ran on a predetermined compass bearing from the base of the hillslope directly to the upper limit of the fescue tussock grasslands. For

each quadrat, the vegetative cover of all species with greater than 5% cover was estimated in four classes (6-25; 26-50; 51-75; 76-100%). Site factors were recorded (altitude, aspect, slope, landform) and ground cover was estimated to the nearest 5% for each of seven categories (vegetation, litter, subsoil, topsoil, erosion pavement, broken rock, bedrock).

Analysis

For the permanent transects, serial changes in mean percent frequency of the most abundant species and bare ground were first analysed for all 27 transects. The effects of two contrasting grazing histories were then examined by analysing changes on the subset of 16 lower-valley transects located on blocks that were either still grazed or had been retired from grazing in 1968. Although some species differed in initial (1965) mean frequency between the blocks, the two grazing histories were regarded as different treatments with unequal pseudoreplication.

For each species independently, the effects of time and grazing history were assessed. The consistent effects of grazing history were compared using one-way analysis of variance (ANOVA) for unbalanced designs. This effectively compares the mean transect frequencies between the different grazing histories over all time periods. Because of unequal sampling intervals, two different techniques were used to analyse serial effects and interactions between time and grazing history. For 1965-75 comparisons, ANOVA was used because the standard assumptions of this test are met when there are only two serial measurements. For the 5 yearly 1975-90 comparisons, multivariate repeated measures ANOVA was used, with grazing history as a between-transects effect (Morrison, 1967). Although this technique has relatively low power, it is not dependent on a restrictive set of assumptions. Changes from 1975 to 1990 were also tested for significant linear and higher-order trends using the standard decomposition of the serial sums of squares. When significant serial effects were detected, individual time points were compared using the LSD test.

For the temporary quadrats, different grazing histories were again regarded as different treatments with unequal pseudoreplication. Only species with greater than 5% estimated cover were recorded in the field. For each quadrat, such species were assigned percentage cover values corresponding to the midpoints of the cover classes listed above; in addition, all other species recorded on other quadrats were assumed to be present and were assigned 1% cover. The cover of the most abundant species (> 5% mean cover) was then compared between grazed and

retired blocks using ANOVA and the Mann-Whitney U-Test. Initial ANOVA results indicated significant effects of aspect, elevation and grazing history for most species analysed. The Mann-Whitney U-Test was then used to compare the cover of abundant species and percentage bare ground between grazed and retired blocks of equivalent aspect, in two elevational zones (< 1000m, $\geq$ 1000). These zones were selected because they reflected major differences in the cover of dominant species and each zone contained about half the quadrats per block.

Table 1: *Changes in mean frequency (%) of the most abundant species and bare ground on permanent transects established in 1965 in the Harper-Avoca catchment. Mean frequencies were calculated for the total number of transects (n) on which a species has been recorded. Species with > 5% frequency recorded on at least 14 transects are presented. Significance levels are based on ANOVA (1965-75) or multivariate repeated measures ANOVA (1975-90): * = P < 0.05; ** = P < 0.01; *** = P < 0.001. Significant linear (L) or quadratic (Q) trends between 1975 and 1990 are indicated. Within each group, species are arranged in order of decreasing overall mean frequency.*

	Mean frequency (%)					Trend		n
	1965	1975	1980	1985	1990	1965-75	1975-90	
(a) Increasing species								
Hieracium pilosella	3	13	22	34	41	*	*** L	24
Hieracium lepidulum	14	20	22	26	28	*	*** L	27
Agrostis capillaris	2	13	14	23	35	*	*** L Q	25
Linum catharticum	3	2	8	10	10	ns	** L Q	24
Hieracium caespitosum	2	2	5	4	7	ns	** L	23
(b) Decreasing species								
Festuca novae-zelandiae	36	26	28	21	22	**	** L	27
Hypochoeris radicata	31	23	21	21	15	*	*** L	27
Raoulia subsericea	24	20	18	16	16	*	ns L	18
Poa cita	16	13	14	10	8	*	* Q	22
Rumex acetosella	18	22	9	8	4	ns	*** L Q	26
Holcus lanatus	21	9	12	8	5	***	** L Q	27
Crepis capillaris	18	6	9	7	3	***	*** L Q	25
Acaena spp.	11	8	7	6	6	**	ns	26
Viola cunninghamii	11	7	5	8	7	***	ns	26
Epilobium alsinoides	12	6	5	4	4	**	ns	24
Luzula spp.	8	3	5	4	4	*	ns	22
Uncinia/Carex spp.	9	6	3	3	3	ns	** L Q	24
Cerastium fontanum	7	5	5	3	1	ns	*** L Q	27
Ranunculus foliosus	10	3	2	3	2	**	ns	16
Dichelachne crinita	7	2	1	0	1	*	ns	18
(c) Others								
Anthoxanthum odoratum	39	45	56	52	30	ns	*** L Q	27
Wahlenbergia albomarginata	33	30	27	34	30	ns	*	27
Leucopogon fraseri	26	20	27	30	33	*	* L	20
Trifolium repens	20	14	16	15	9	ns	ns Q	24
Poa colensoi	15	12	17	15	14	ns	ns Q	26
Blechnum penna-marina	13	13	13	14	15	ns	ns	16
Elymus rectisetus	10	18	12	15	12	*	ns	27
Helichrysum spp.	12	9	12	14	11	ns	ns	25
Rytidosperma setifolium	18	7	8	12	12	***	*** L	27
Hydrocotyle novae-zelandiae	13	5	9	14	8	***	*** L Q	25
Muehlenbeckia axillaris	11	9	9	11	9	ns	ns	20
Rytidosperma gracile	5	5	6	2	7	ns	**	24
Brachyglottis bellidioides	6	5	3	4	4	ns	ns	14
Geranium microphyllum	6	5	4	5	2	ns	*	25
Deyeuxia avenoides	5	2	2	5	7	ns	** L	24
Trifolium dubium	10	+	4	2	+	ns	*	15
(d) Bare ground	30	27	26	26	25	*	ns	27

Results

Overall vegetation changes on the permanent transects

Of the 167 species recorded on the 27 permanent transects, only 12 attained at least 20% mean frequency in any one remeasurement period (Table 1). These included fescue tussock (*Festuca novae-zelandiae*), native herbs and subshrubs (*Raoulia subsericea*, *Wahlenbergia albomarginata*, *Leucopogon fraseri*), and exotic herbs and grasses (e.g., *Hieracium pilosella*, *H. lepidulum*, *Hypochoeris radicata*, *Agrostis capillaris*, *Anthoxanthum odoratum*).

Marked changes in mean frequency for many of the most frequent species revealed three different trends between 1965 and 1990 (Table 1). A group of exotic species increased significantly over this period ($P < 0.05$), notably *Hieracium pilosella* (from 3 to 41% mean frequency), *Agrostis capillaris* (2-35%), and *Hieracium lepidulum* (14-28%). A group of native and exotic species declined ($P < 0.05$), e.g., *Festuca novae-zelandiae* (36-22%), *Hypochoeris radicata* (31-15%), *Holcus lanatus* (21-5%), *Rumex acetosella* (18-4%), and *Crepis capillaris* (18-3%). A third group showed non-significant trends or wide fluctuations in frequency.

For example, *Anthoxanthum odoratum* increased markedly between 1965 and 1980 (39-56%), but had decreased again by 1990 (30%). Despite such widespread changes in composition, all species in the three groups were present in both 1965 and 1990 and the mean number of species present on the transects remained remarkably similar (32.5 ± 5.82 in 1965 and 33.4 ± 8.64 in 1990, mean ± S.D). The proportion of bare ground (exposed soil, colluvium and bedrock) showed a non-significant downward trend, from 30% to 25% of total ground cover.

Effects of grazing history on vegetation composition

Changes on the permanent transects

Many of the common species that showed marked overall changes in frequency also showed such temporal changes on the subset of 16 permanent north-facing transects with different grazing histories (i.e., still grazed or retired from grazing in 1968; Table 2). Although *Hieracium pilosella* was uncommon in 1965 (*c*. 5% mean frequency), it increased rapidly on both the grazed and retired north-facing blocks (Fig. 2; Table 2). Despite an apparent lag on the retired block between 1965 and 1975, the rate of increase was similar for both blocks

Table 2: *Significance of changes in frequency of the most frequent species on predominantly north-facing, lower-valley transects that are either still grazed or were retired from grazing in 1968. Species with more than 20% mean frequency in at least one year are presented. Temporal trends for several species are shown in Fig. 2. n = 16 except for* Hieracium pilosella *(n = 15). L = significant linear trend. G = grazing history; T = time; TxG = time x grazing history interaction. * = P < 0.05; ** = P < 0.01; *** = P < 0.001.*

|	1965-75			1975-90		
	G	T	T x G	G	T	T x G
(a) Increasing species						
Hieracium pilosella	ns	*	ns	ns	*** L	ns
Agrostis capillaris	*	*	ns	**	*** L	*
Hieracium lepidulum	*	*	*	*	*** L	ns
(b) Decreasing species						
Festuca novae-zelandiae	*	***	***	ns	*	ns
Hypochoeris radicata	ns	*	***	ns	*** L	**
Holcus lanatus	ns	***	ns	ns	* L	ns
Rumex acetosella	ns	ns	*	ns	*** L	ns
Crepis capillaris	ns	**	ns	ns	** L	ns
Epilobium spp.	*	*	ns	**	ns	**
(c) Others						
Anthoxanthum odoratum	ns	ns	*	**	*** L	ns
Elymus rectisetus	ns	ns	ns	**	ns	ns
Poa colensoi	**	ns	ns	**	ns	ns
Leucopogon fraseri	*	**	ns	ns	*	ns
Trifolium repens	ns	ns	ns	ns	ns	ns
(d) Bare ground	ns	*	ns	ns	*	ns
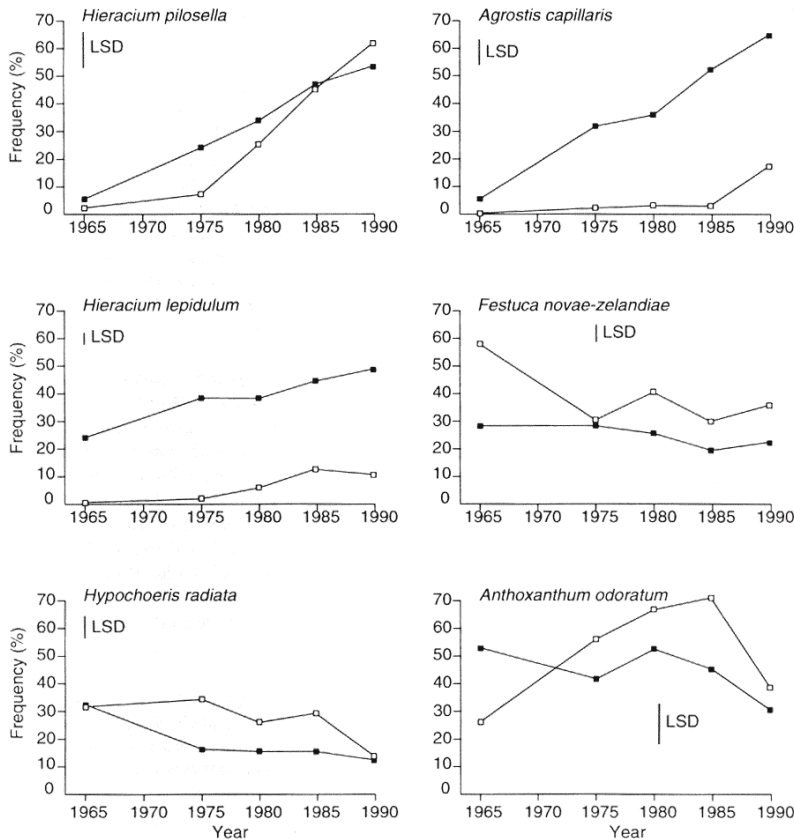
Figure 2: *Temporal changes in mean frequency of representative species (> 20% mean frequency) on lower valley, predominantly north-facing permanent transects that are either still grazed (solid squares) or were retired from grazing in 1968 (open squares). n = 16, except for* Hieracium pilosella *(n = 15). For each species, error bars represent the 95% LSD for 1975-90 measurements.*

(non-significant time x grazing history interaction, Table 2). By 1990, this species had reached 52% mean frequency on the grazed block and 60% on the retired block.

Agrostis capillaris and *Hieracium lepidulum* also increased significantly over the 25 years. However, for these species, both the extent and rate of invasion differed between blocks (Table 2). Between 1965 and 1990, *A. capillaris* increased from 4 to 64% on the grazed block (Fig. 2). In contrast, on the retired block this species remained at less than 5% frequency until 1985, and by 1990 had reached only 17%. In 1965, *H. lepidulum* was already well established on the grazed block, where

it increased and remained more frequent than on the retired block over the study period. However, between 1975 and 1990 the rate of invasion was similar on both blocks (Fig. 2; Table 2).

Festuca novae-zelandiae, *Hypochoeris radicata*, *Holcus lanatus*, *Rumex acetosella*, *Crepis capillaris*, and *Epilobium* spp. (predominantly *E. alsinoides*) declined on both blocks (Table 2). Although their initial frequencies and the rate and timing of declines often differed between blocks, by 1990 most had declined to reach similar frequencies on both blocks. The range of responses was typified by *Festuca* and *Hypochoeris*, the most frequent species in this group (Fig. 2).

In 1965, *Festuca novae-zelandiae* was more than twice as frequent on the block that was subsequently retired (58% mean frequency) than on the block that remained grazed (28%). However, by 1975 it had declined markedly on the retired block, so that frequencies were now very similar on both blocks (Fig. 2). Between 1975 and 1990, this species tended to be more frequent on the retired block, but this was not statistically significant (Table 2). *Holcus lanatus*, *Rumex acetosella*, and *Epilobium* spp. were also initially more frequent on the retired block. Between 1965 and 1990, *Holcus* declined from 37% to 8% frequency on the retired block and from 18% to 3% on the grazed block; *Rumex* declined from 35% to 7% (retired) and from 11% to 5% (grazed); and *Epilobium* spp. declined from 22% to 9% (retired) and from 9% to 1% (grazed). Between 1975 and 1990, differences between blocks were significant only for *Epilobium* spp. (Table 2).

For *Hypochoeris radicata*, both the initial and 1990 mean frequencies were similar on both blocks (Fig. 2). The most marked period of decline was earlier on the grazed block (1965-75) than on the retired block (1975-90) (Table 2). *Crepis capillaris* showed a similar overall trend, declining from 22% frequency on both blocks in 1965 to 3% on the

retired block and 1% on the grazed block in 1990. For this species, the rate of decline was similar on both blocks (Table 2).

Among other frequent species (Table 2), *Anthoxanthum odoratum* showed contrasting trends between 1965 and 1975, increasing on the retired block but decreasing under continued grazing. Between 1975 and 1990 this species was more frequent overall on the retired block (Fig. 2), but by 1990 there was no significant difference between the two blocks. Despite some fluctuation, *Elymus rectisetus*, *Poa colensoi*, and *Leucopogon fraseri* were more frequent overall on the retired block over the study period.

Comparative vegetative cover on the quadrats

Cover data from the 174 temporary quadrats confirmed that exotic grasses and *Hieracium* species had become well established throughout the retired and grazed blocks by 1988 (Table 3). At low elevation (< 1000 m), such species dominated the vegetation, irrespective of aspect and grazing history (total exotic cover 48 - 80%, total native cover 12 - 31%). With increasing elevation, total cover of exotic species generally declined and native cover and bare ground increased. Total exotic cover was

Table 3: *Estimated mean % cover and % bare ground in two altitudinal zones in December 1988 for areas still grazed (G) or retired from sheep grazing in either 1955 (R55) or 1968 (R68). Species with > 5% mean cover are presented. n = number of 4 m^2 quadrats. + indicates $\leq$ 5% cover for all quadrats (see Methods). For each species, significance levels are for cover comparisons between retired and grazed blocks of equivalent aspect and elevational zone using the Mann-Whitney U-Test; blank = not significant; * = P < 0.05; ** = P < 0.01.*

	North aspect								South aspect							
	<1000 m				≥1000 m				<1000 m				≥1000 m			
	R68		G		R68		G		R55		G		R55		G	
n	22		22		26		22		23		21		19		19	
(a) Exotic species																
Agrostis capillaris	+	**	27		+	**	10		12		6		5		2	
Hieracium lepidulum	+	**	17		+	**	9		29	**	55		19		25	
Hieracium caespitosum	+	*	6		+	**	4		6		4		1		2	
Anthoxanthum odoratum	19		22		3	*	7		4		4		1		4	
Hieracium pilosella	26	**	8		6	**	27		1		1		1		1	
Total	48	**	80		12	**	57		52	**	70		27		34	
(b) Native species																
Festuca novae-zelandiae	17	**	9		17	**	7		8	**	2		7		4	
Poa colensoi	6	**	+		10	**	+		4	*	+		11		6	
Cyathodes colensoi	2		+		6	**	+		+		+		+		+	
Chionochloa flavescens	+		+		4	*	+		+		+		+		+	
Gaultheria depressa	2		+		8	**	+		12	**	3		7	**	+	
Rytidosperma setifolium	+		+		+		+		+		+		11	**	+	
Chionochloa macra	+		+		1		+		+		+		11	**	1	
Celmisia spectabilis	+		+		+		+		+		2		11		18	
Total	31	**	16		48	**	14		29	**	12		60	**	33	
(c) Bare ground	5		6		29		26		4	**	13		5	**	20	

greater on the grazed than on the retired blocks of equivalent aspect and elevation (significant for all except south aspects at high elevation). Total native cover showed a converse pattern. However, native species dominated only the retired blocks at high elevation (Table 3).

The effects of grazing history on individual species varied with both aspect and elevation. On the north-facing blocks, mean cover of *Agrostis capillaris*, *Hieracium lepidulum*, and the less abundant *H. caespitosum* strongly reflected grazing history (Table 3), reinforcing the trends recorded for the permanent transects (e.g., Fig. 2). On the grazed block these species totalled 50% cover at low elevation and 23% at high elevation. In contrast, on the block retired in 1968, they totalled less than 5% cover in both elevational zones. On the south-facing blocks, the effects of grazing history on *A. capillaris*, *H. lepidulum*, and *H. caespitosum* were less distinct. *H. lepidulum*, the most abundant of these species on this aspect, attained high cover values on both the grazed block and the block retired in 1955, but was most abundant on the grazed block at low elevation (55% mean cover). However, the effect of grazing history on cover was not significant for *H. lepidulum* at high elevation, or for *A. capillaris* or *H. caespitosum* at either elevation. Both *Anthoxanthum odoratum* and *Hieracium pilosella* were uncommon on the south-facing blocks. On the north-facing blocks there was little evidence that grazing history had had a major impact on their overall cover (Table 3). This was most marked for *H. pilosella*, which attained similar mean cover on the retired and grazed blocks. However, this species showed contrasting elevational distributions, achieving greatest abundance on the retired block at low elevation and on the grazed block at high elevation (26% and 27%, respectively). Reasons for this converse pattern are unclear; at low elevation on the grazed block, perhaps early dominance by *Agrostis capillaris* and *H. lepidulum* (as suggested by the permanent transects; Fig. 2) restricted the ability of *H. pilosella* to invade. *Anthoxanthum odoratum* was most prevalent at low elevation on both blocks (*c.* 20% cover).

Most of the eight common native species on the quadrats were significantly more abundant on retired than on grazed blocks of equivalent aspect and elevation (Table 3). For example, *Festuca novae-zelandiae* (see also Fig. 2) and the tall tussock *Chionochloa flavescens* ssp. *brevis* were most abundant on the retired north-facing block, and *C. macra* and the short tussock *Rytidosperma setifolium* were most abundant on the retired south-facing block. The main exceptions to this pattern occurred on the south-facing blocks at high elevation, where

there was no significant effect of grazing history on mean cover of *Celmisia spectabilis*, *Festuca novae-zelandiae*, or *Poa colensoi*. However, none of these attained greater cover on grazed sites.

Discussion

Dominant pathway of vegetation change

The composition of the Harper-Avoca fescue tussock grasslands has changed markedly over the study period. The most consistent features include a series of invasions by exotic species, corresponding declines in native species, and a resulting widespread trend away from tussock grassland towards vegetation dominated by exotic grasses and flatweeds. This trend probably began before 1955, was present in 1965, and was well advanced by 1980 (Rose, 1983). Qualitatively similar long-term changes have been documented for the adjacent Waimakariri catchment short-tussock grasslands (Scott *et al.*, 1988; White, 1991).

In 1965, the tussock grasslands already contained abundant exotic grasses (*Anthoxanthum odoratum* and *Holcus lanatus*) and weeds (e.g., *Hieracium lepidulum*, *Hypochoeris radicata*, *Crepis capillaris*, and *Rumex acetosella*). Between 1965 and 1990, hawkweeds (*Hieracium lepidulum* and *H. pilosella*) and the grass *Agrostis capillaris* increased in abundance and distribution. As these exotic species increased, *Festuca novae-zelandiae*, many other native species, and previously abundant exotic species such as *Hypochoeris radicata* declined. Although *Anthoxanthum odoratum* increased and spread through the study area between 1965 and 1980, its frequency had almost halved by 1990 as other exotic species increased.

During the study period the proportion of bare ground did not decline significantly and bare patches larger than *c.* 1 m^2 typically remained unvegetated (*pers. obs.*), suggesting that *Hieracium* species and *A. capillaris* invaded only small gaps or vegetated sites at the expense of formerly abundant species (see also Rose, 1983). Rapid expansion of *H. pilosella* patches into existing vegetation may reflect their ability to take up nutrients from the area beyond the patch margins (McIntosh, Loeseke and Bechler, 1995).

Factors influencing *Hieracium* invasion

The different management blocks varied in initial (1965) vegetation composition, e.g., on north-facing slopes *Festuca novae-zelandiae* was less abundant, and *Hieracium lepidulum* and *Anthoxanthum odoratum* were more abundant on the block that

remained grazed than on that retired in 1968 (Fig. 2). The greater abundance of tussocks combined with similar levels of bare ground in 1965 indicates that the retired grasslands were actually in better "condition" in 1965. However, this had little effect on the direction of vegetation change and the trend towards *Hieracium* dominance over the 25 years. Such findings suggest two likely interpretations: either that *Hieracium* is an aggressively invasive weed, or that the magnitude of grassland depletion resulting from grazing/burning before 1965 was sufficient to predispose all management blocks to *Hieracium* invasion.

Explanations for the dramatic spread of hawkweeds in South Island tussock grasslands have centred on two such interpretations. The "invasive weed" hypothesis (e.g., Scott, 1985) implies that hawkweeds aggressively invade because they are ideally suited to the tussock grassland environment. By contrast, the "symptom of depletion" hypothesis (e.g., Treskonova, 1991) contends that hawkweeds invade because management (principally burning/overgrazing) has depleted the vegetation and possibly the soils. Although neither hypothesis has been exclusively validated, they have generated considerable debate in which they are often perceived as mutually exclusive. The spread of *Hieracium* in the Harper-Avoca is inadequately explained by either hypothesis alone. The depletion hypothesis predicts that *Hieracium* invasion should be most pronounced on sites with a history of prolonged grazing. In general, a history of continued grazing did promote exotic species and disadvantage native species in the study area. However, the trend towards hawkweed dominance also occurred on sites protected from grazing for 22 or 35 years. For *H. pilosella* on predominantly north-facing sites, we found no evidence that 22 years of protection from grazing had prevented invasion or that continued grazing had promoted invasion over the study period. For *H. lepidulum*, grazing appeared to promote invasion as this species was most abundant on grazed sites in 1990. However removal of grazing still did not prevent substantial invasion, as *H. lepidulum* was also dominant on south-facing sites retired for 35 years and had increased over the last decade on north-facing sites retired for 22 years. The invasive weed hypothesis predicts that environment or past management would have had no impact on *Hieracium* invasion, which should be uniform in the study area. Clearly this hypothesis also inadequately explains the distribution and abundance of *H. pilosella* and *H. lepidulum*.

The premise that all tussock grasslands are uniformly susceptible to invasion is not restricted to the invasive weed hypothesis. Although the invasion

hypothesis attributes susceptibility to characteristics of the weeds, the depletion hypothesis attributes it to characteristics of the grasslands and soils induced by past and present management (an assumption that is untestable in the absence of any stands unaffected by burning and grazing disturbances in the culturally induced short-tussock grasslands). Single-factor explanations seldom adequately explain the causes of vegetation change (Glenn-Lewin, Peet and Veblen, 1992). It is hardly surprising, therefore, that neither hypothesis explains adequately the causes for *Hieracium* invasion and short tussock grassland change. Successions result from a multiplicity of interacting factors (Pickett, Collins and Armesto, 1987; Glenn-Lewin, Peet and Veblen, 1992) that affect the population dynamics of the constituent plant species (Peet and Christensen, 1980). Explanations for change in the tussock grasslands must take account of mechanisms of vegetation change such as: colonisation abilities of different species, initial vegetation composition and its effects on resistance to invasion, competition, species' life history attributes, herbivory, and changes in environment, and how such factors act at different spatial and temporal scales, and their hierarchical relationships to the three general causes of succession - site availability, differential species availability, and differential species performance (Pickett *et al.*, 1987).

Although the two predominant hypotheses for *Hieracium* invasion provide useful concepts for evaluating research and management experience, it is unlikely that real progress will be made in understanding the causes of *Hieracium* success until the mechanisms of species replacements along environmental, disturbance, and compositional gradients are quantitatively established.

Future trends

In the study area, widespread recovery of fescue tussock grassland seems improbable, and *H. pilosella*, *H. lepidulum*, and *Agrostis capillaris* are likely to increase further. Although it is unknown whether grasslands dominated by hawkweeds and *A. capillaris* will persist in the long term, even in the absence of these species the grasslands would probably continue to change as native woody vegetation and snow tussocks (*Chionochloa* spp.) gradually increase (Rose, 1983, 1992; Rose and Platt, 1992).

Although the demise of culturally induced short-tussock grasslands may be hastened by the effects of prolonged grazing, our study indicates that it may not be reversed by the removal of grazing. As with understanding causes, single-factor prescriptions for preventing or controlling

Hieracium invasion are unlikely to provide widespread success. The challenge is to accept the inevitability of vegetation change, identify the proximate causes, establish feasible and sustainable management goals, and monitor management outcomes to gauge management success.

Acknowledgements

References

Allan, H.H. 1961. *Flora of New Zealand, Volume I.* Government Printer, Wellington, N.Z. 1085 pp.

Allen, R.B.; Rose, A.B.; Evans, G.R. 1983. *Grassland survey manual: A permanent plot method.* FRI Bulletin No 43, New Zealand Forest Service, Forest Research Institute, Christchurch, N.Z. 71 pp.

Cheeseman, T.F. 1925. *Manual of the New Zealand flora.* Government Printer, Wellington, N.Z. 1163 pp.

Connor, H.E. 1991. *Chionochloa* Zotov (Gramineae) in New Zealand. *New Zealand Journal of Botany 29*: 219-282.

Connor, H.E. 1992. The botany of change in tussock grasslands in the Mackenzie Country, South Canterbury, New Zealand. *New Zealand Mountain Lands Institute Review 49*: 1-31.

Connor, H.E.; Edgar, E. 1987. Name changes in the indigenous New Zealand flora, 1960-1986 and *Nomina Nova* IV, 1983-1986. *New Zealand Journal of Botany 25*: 115-170.

Edgar, E.; Forde, M.B. 1991. *Agrostis* L. in New Zealand. *New Zealand Journal of Botany 29*: 139-161.

Glenn-Lewin, D.; Peet, R.K.; Veblen, T.T. 1992. *Plant succession: Theory and prediction.* Chapman and Hall, London, England. 352 pp.

Harris, P.S.; O'Connor, K.F. 1980. The grazing behaviour of sheep (*Ovis aries*) on a high-country summer range in Canterbury, New Zealand. *New Zealand Journal of Ecology 3*: 85-96.

Hickling, G.J. 1986. *Red deer population surveys in the Harper - Avoca catchment (1956 - 1983).* FRI Bulletin No. 107, New Zealand Forest Service, Forest Research Institute, Christchurch, N.Z. 10 pp.

Hunter, G.G. 1991. The distribution of hawkweeds (*Hieracium)* in the South Island, indicating problem status. *New Zealand Mountain Lands Institute Review 48*: 21-31.

Hunter, G.G.; Mason, C.R.; Robertson, D.M. (Editors) 1992. *Vegetation change in tussock grasslands, with emphasis on hawkweeds.* New Zealand Ecological Society Occasional Publication No. 2, New Zealand Ecological Society, Christchurch, N.Z. 105 pp.

Kerr, I.G.C 1992. The high country in transition - some implications for occupiers and administrators. *New Zealand Mountain Lands Institute Review 49*: 32-50.

Lambrechtsen, N.C. 1992. *What grass is that?* New Zealand Department of Scientific and Industrial Research Information Series No. 87, GP Publications Limited, Wellington, N.Z. 150 pp.

McIntosh, P.D.; Loeseke, M.; Bechler, K. 1995: Soil changes under mouse-ear hawkweed (*Hieracium pilosella*). *New Zealand Journal of Ecology 19*: 29-34.

McKendry, P.J.; O'Connor, K.F. 1990 (unpublished). *The ecology of tussock grasslands for production and protection.* Centre for Resource Management, Lincoln University and University of Canterbury, Christchurch, N.Z. 161 pp.

McMillan, G. 1991. Hawkweed report. *New Zealand Mountain Lands Institute Review 48*: 8-19.

Molloy, B.P.J. 1977. The fire history. *In:* Burrows, C.J. (Editor), *Cass,* pp. 157-170. University of Canterbury, Christchurch, N.Z. 418 pp.

Molloy, B.P.J.; Burrows, C.J.; Cox, J.E.; Johnston, J.A.; Wardle, P. 1963. Distribution of subfossil forest remains, eastern South Island, New Zealand. *New Zealand Journal of Botany 1*: 68-77.

Moore, L.B. 1976. *The changing vegetation of Molesworth Station, New Zealand.* New Zealand. Department of Scientific and Industrial Research Bulletin No. 217, Department of Scientific and Industrial Research, Wellington, N.Z. 118 pp.

Morrison, D. 1967. *Multivariate statistical methods.* McGraw - Hill, New York, U.S.A. 338 pp.

Mosley, M.P. 1979. *Sediment sources in the Harper-Avoca catchment.* New Zealand Forest Service, Forest Research Institute Technical Paper No. 68, Christchurch, N.Z. 33 pp.

Newsome, P.F.J. 1987. *The vegetative cover of New Zealand*. Water and Soil Miscellaneous Publication No. 112, Ministry of Works and Development, Palmerston North, N.Z. 153 pp.

O'Connor, K.F. 1981. Changes in the tussock grasslands and mountain lands. *Tussock Grasslands and Mountain Lands Institute Review 40*: 47-63.

O'Connor, K.F. 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology 5*: 97-107.

O'Connor, K.F. 1986. The influence of science on the use of tussock grasslands. *Tussock Grasslands and Mountain Lands Institute Review 43*: 15-78.

Packard, W.P. 1947. Lake Coleridge catchment: a geographic survey of its problems. *New Zealand Geographer 3*: 19-40.

Parliamentary Commissioner for the Environment 1991 (unpublished). *Sustainable land use for the dry tussock grasslands in the South Island*. Office of the Parliamentary Commissioner for the Environment, Wellington, N.Z. 80 pp.

Peet, R.K.; Christensen, N.L. 1980. Succession: a population process. *Vegetatio 43*: 131-140.

Pickett, S.T.A.; Collins, S.L.; Armesto, J.J. 1987. Models, mechanisms and pathways of succession. *Botanical Review 53*: 335-371.

Rose, A.B. 1983. *Succession in fescue (*Festuca novae-zelandiae*) grasslands of the Harper-Avoca catchment, Canterbury, New Zealand*. FRI Bulletin No. 16, New Zealand Forest Service, Forest Research Institute, Christchurch, N.Z. 35 pp.

Rose, A.B. 1992. A general model of past and likely future vegetation changes in grazed and retired tussock grasslands of the Harper-Avoca catchment, 700-1400m altitude, 1200-1500 mm annual rainfall. *In*: Hunter, G.G.; Mason, C.R.; Robertson, D.M. (Editors), *Vegetation change in tussock grasslands, with emphasis on hawkweeds*, p. 18. New Zealand Ecological Society Occasional Publication No. 2, New Zealand Ecological Society, Christchurch, N.Z. 105 pp.

Rose, A.B.; Platt, K.H. 1992. Snow tussock (*Chionochloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand. *New Zealand Journal of Botany 30*: 373-382.

Scott, D. 1985. Hawkweeds in run country. *Tussock Grasslands and Mountain Lands Institute Review 42*: 33-48.

Scott, D.; Dick, R.D.; Hunter, G. G. 1988. Changes in the tussock grasslands in the central Waimakariri River basin, Canterbury, New Zealand, 1947 - 1981. *New Zealand Journal of Botany 26*: 197-222.

Scott, D.; Robertson, J.S.; Archie, W.J. 1990. Plant dynamics of New Zealand tussock grassland infested with *Hieracium pilosella*. I: Effects of seasonal grazing, fertilizer and overdrilling. *Journal of Applied Ecology 27*: 224-234.

Treskonova, M. 1991. Changes in the structure of tall-tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. *New Zealand Journal of Ecology 15*: 65-78.

Walters, C.J.; Holling, C.S. 1990. Large-scale management experiments and learning by doing. *Ecology 71*: 2060-2068.

Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988. *Flora of New Zealand, Volume IV*. Botany Division, Department of Scientific and Industrial Research, Christchurch, N.Z.

White, E.G. 1991. The changing abundance of moths in a tussock grassland, 1962-1989, and 50- to 70-year trends. *New Zealand Journal of Ecology 15*: 5-22.