Recovery of short tussock and woody species guilds in ungrazed *Festuca novae-zelandiae* short tussock grassland with fertiliser or irrigation

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Abstract: In a *Festuca novae-zelandiae* short tussock grassland in South Island, New Zealand, we tested the propositions (1) that present regional trends in vascular plant species-richness in tussock grasslands are independent of current pastoral management, and (2) that grazing retards the invasion and dominance of non-native species, particularly where soil resources are not limiting. Sheep and rabbit-grazed, ungrazed, ungrazed+fertilised and ungrazed+irrigated treatments were applied in a replicated experiment that was sampled annually from 1988 to 2000. Native species richness and native forb cover decreased, and exotic grasses increased in all treatments, with no significant differences between grazed and ungrazed treatments in either trends or final cover. Exotic species richness decreased in the ungrazed, ungrazed+fertilised and ungrazed+irrigated treatments but showed no trend in grazed vegetation. Cover of native tussock grasses and the tall shrub *Carmichaelia petriei* decreased in the grazed treatment, remained steady in the ungrazed treatment and increased in the ungrazed+fertilised and ungrazed+irrigated treatments. Native subshrubs decreased in the grazed, ungrazed+fertilised and ungrazed+irrigated treatments but not in the ungrazed treatment. The invasive forb *Hieracium pilosella* increased with time in grazed, ungrazed, and ungrazed+irrigated treatments, but after 10 years it decreased in the ungrazed+fertilised treatment and its cover was negligible there after 12 years. Grazing appeared to reduce the cover of tussocks and certain woody species, and we conclude that current management affected vegetation trends. Grazing did not decrease the dominance of exotic species, or maintain native species richness at a higher level than in ungrazed vegetation. There was limited recovery of taller native species with grazing removal alone. However, grazing removal plus 12 years of resource enrichment promoted the growth of native tall shrubs and tussocks and did not result in physiognomic dominance by exotic species. Succession towards taller native tussock-shrubland communities may be an appropriate goal for conservation management of short tussock grasslands, and nutrient enrichment in the absence of grazing may be an appropriate management device in some circumstances.

Keywords: grazing; *Hieracium pilosella*; irrigation; long-term change; nutrient; recovery; short tussock grassland.

Introduction

Short tussock grasslands dominated by *Festuca novae-zelandiae* (fescue tussock or hard tussock) occupy *c.* 1 million ha of montane to subalpine land in eastern South Island, New Zealand (Rose *et al*., 1998). In prehuman times, these grasslands were probably restricted to shallow or drought-prone soils on the floors of the driest basins east of the Southern Alps (Connor, 1964; McGlone, 2001) and to areas of frequent natural disturbances (e.g. river valleys; Walker and Lee, 2000; 2002). Most prehuman forests and woodlands of inland eastern South Island were cleared by Polynesian fires after *c.* 800 yr BP (Molloy *et al*., 1963; Connor, 1965; Mark, 1992; McGlone, 2001; Wardle, 2001) and the resulting seral scrub and tall tussock grassland communities were further modified by frequent burning, overstocking, and high feral rabbit numbers in the decades following the arrival of European pastoralists (Buchanan, 1868; Petrie, 1883; O'Connor, 1982). Therefore, most of today's *F. novae-zelandiae* short tussock grasslands are induced communities that have undergone profound historical changes in structure and composition.

Further changes have been reported in lowland and montane eastern South Island short tussock grasslands in recent decades. The stature and density of the native tussocks has declined, native intertussock species (particularly low-growing herbs) have decreased in cover and number, and a stoloniferous forb, *Hieracium pilosella* (Asteraceae) has invaded (e.g. Scott *et al*., 1988; Treskonova, 1991; Rose *et al*., 1995; Duncan *et al*., 1997; Johnstone *et al*., 1999; Duncan *et al*., 2001). Some authors have attributed these trends to current pastoral management practices (e.g. Treskonova, 1991), while other studies suggest that they may be largely independent of recent grazing and burning (e.g. Duncan *et al*., 2001).

There is a growing awareness of the need to protect and restore a wider range of New Zealand ecosystems and biodiversity, particularly at low elevations (Department of Conservation 2000; McGlone, 2001; Rogers and Walker, 2002). The short tussock grassland biome is under-represented in public conservation lands (Leathwick *et al*., 2002) due to the high economic value of lowland grasslands for pastoralism and previous emphasis on conserving less modified vegetation types such as forest (O'Connor, 1982; McGlone, 2001).

The role of domestic stock grazing in retarding or facilitating weed invasion and dominance in short tussock grasslands has been discussed in recent years (Meurk *et al*., 1989; Lord, 1990; Walker 2000). Removal of grazing (sometimes referred to as passive management) has been seen as counter-productive for conserving native species in some short tussock grasslands. Meurk *et al*. (1989) and Lord (1990) suggested that the cessation of grazing in short tussock grassland generally resulted in dominance by a small number of exotic species (mainly grasses) and in the demise of native grasses and forbs, especially where exotic species growth rates were not limited by factors such as drought or cold. These conclusions were largely based on studies in high-fertility silver tussock (*Poa cita*) grasslands on the Port Hills, and in *Rytidosperma* grasslands among kanuka remnants near the Canterbury coast.

In *Festuca novae-zelandiae* short tussock grasslands, comparisons of exclosures adjacent to grazed plots have shown relative increases in exotic species with grazing removal in some sites, but not in others (e.g. Walker, 1997; Meurk *et al*., 2002). Vegetation recovery toward states dominated by native species following the cessation of grazing has been slow and limited, where it has occurred at all (e.g. Rose, 1983; Rose *et al*., 1995; Allen *et al*., 1995; McIntosh and Allen, 1998; Walker, 2000; Walker and Lee, 2000; 2002; Meurk *et al*., 2002).

In this paper, we compare the responses of different plant guilds at a single *F. novae-zelandiae* short tussock grassland site to different experimental manipulations comprising sheep- and rabbit-grazed, ungrazed (exclosure), ungrazed+fertilised and ungrazed+irrigated treatments. We test the propositions that trends in tussock grasslands may be independent of current pastoral management, and that grazing retards the invasion and dominance of non-native species in short tussock grassland, especially where soil resources (e.g. water, nutrients) do not limit growth. We discuss the implications of our results for the conservation management of *F. novae-zelandiae* short tussock grasslands in south-eastern New Zealand.

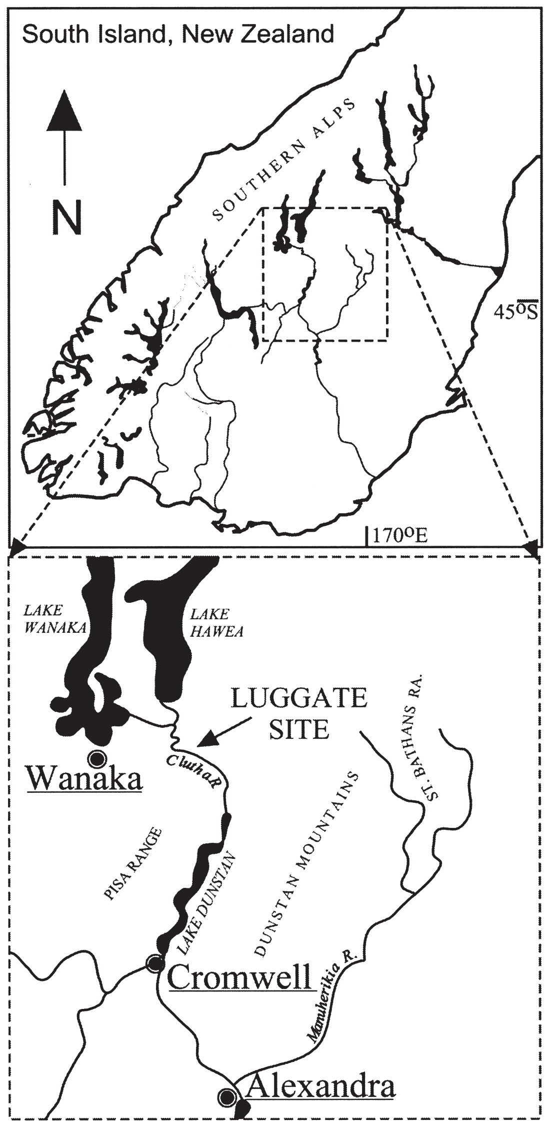

Figure 1. Position of the Luggate study site in Central Otago, southern New Zealand, in relation to major towns (underlined), mountain ranges, rivers and lakes.

Study area

The Luggate long-term experiment is situated on an outwash terrace of the Hawea Glacial Advance (14 to 24 million yr BP), in the north-west of central Otago (Ward *et al*., 1994; Fig. 1). Rainfall is between 600 and 700 mm yr^{-1} (New Zealand Meteorological Service, 1983). The experiment was established in 1988 to study the interactions of native and exotic species under different resource additions (King, 1995). At that time, the short, finely-textured vegetation comprised a mixture of native grasses (e.g. *Festuca novae-zelandiae*, *Poa colensoi*, *Dichelachne crinita*, *Elymus solandri, Rytidosperma unarede*), tall shrubs (mainly *Carmichaelia petriei* and *Discaria toumatou* which had been coppiced by grazing and browsing to <10cm height, but also widely-spaced *Kunzea ericoides* shrubs), subshrubs (e.g. *Coprosma petriei*, *Pimelea pulvinaris*), and forbs (e.g. *Luzula ulophylla*, *Carex breviculmis, Leptinella pectinata*, *Wahlenbergia albomarginata*). Exotic species included grasses (e.g. *Anthoxanthum odoratum*, *Agrostis capillaris*), forbs (e.g. *Crepis capillaris*, *Hypochaeris radicata*), and widely-spaced shrubs of *Rosa rubiginosa*. The cover of *Hieracium pilosella* was low (average at the site <0.5%). In the subsequent 12-year study period, poisoning operations twice reduced feral rabbit numbers to low levels (prior to sampling in 1989 and 1996), and sheep stocking rates were consistently low.

Methods

Four separate replicate blocks (5 m × 20 m) were established in September 1988 (Replicates 1 to 4; King, 1995). Each block has four plots of 5 m × 5 m, to which treatments were assigned in a randomised block design. Three plots in each block were fenced to exclude sheep and rabbits, and the fourth was left unfenced as the grazed treatment. One fenced plot was fertilised (ungrazed+fertilised), another was irrigated (ungrazed+irrigated), and the third was the ungrazed treatment. Fertiliser was applied annually over the entire area of each fertilised plot, at a rate equivalent to 20 kg ha^{-1}, yielding 0.56 g m^{-2} of sulphur (0.2 g m^{-2} immediately available sulphate plus 0.36 g m^{-2} elemental sulphur), 0.14 g m^{-2} of phosphorus (as phosphate), and 0.40 mg m^{-2} of molybdenum. Each year, from October to April, the irrigated treatment received supplementary water once per week, equivalent to 20 mm of rainfall.

The sampled area of each plot originally comprised two half plots, each 1 m × 2 m in size, separated by a 1-m buffer zone for sampling access, but the plots were split in 1994 and treatments continued in one of the original half plot pair, for which we present data here. All treatments were sampled annually in spring (September), a total of 13 times from 1988 until 2000. Cover was recorded for each vascular plant species using 50 points per half plot on a grid of 20 cm × 20 cm, using a 50-μ-diameter pin. From 1994 to 2000, data were collected at 200 points per half plot on a grid of 5 cm × 20 cm, and species richness was estimated using rarefaction (i.e. repeated random sampling of a subset of 50 points per half plot) to ensure equivalence with 1988–1993 point sampling density. The number of recorded hits for each species was expressed as a percentage of the number of sampled points in the quadrat, i.e. percentage cover (hereafter simply 'cover'), which has an upper bound of 100%. Plant species were categorised into the following life form groups or guilds: tall native grasses and sedges >20cm (hereafter 'native tussock grasses'), other native grasses, native tall shrubs, native subshrubs, native mat forbs, native erect forbs, exotic grasses, *H. pilosella*, and other exotic forbs. Percentage cover was summed across all species in each guild.

We compared temporal changes and final values in the richness (i.e. number) of native and exotic species per half plot, and in the cover of common individual plant species (i.e. those averaging >1% cover over the whole experiment) and plant guilds between the experimental treatments. We identified significant linear trends with time using regression, and compared these between treatments with the test for differences between slopes (Snedecor and Cochran, 1980). Where trends were non-linear, we used analysis of variance to detect treatment differences in richness or cover changes between average initial (the average for 1988 and 1989, to smooth over inter-annual fluctuations) and final (average for 1999 and 2000) values. We also compared final (average for 1999 and 2000) species richness and cover values between treatments using analysis of covariance (initial richness or cover was the covariate in each case). Bonferroni corrections for multiple tests of significance were applied to probability values.

Point quadrat sampling is suitable to quantify species abundances in short-statured species. However, the method is less appropriate for emergent tall shrubs, which grew to >1 m height in resource-addition treatments after *c*. 1994. Therefore, to better quantify the tall shrub guild, we measured each tall shrub rooted in the 1 × 2 m half-plots in Autumn 2002, recording maximum canopy height, and canopy radius in two directions (north-south and east-west). Plant volume (calculated as for a cone, since most shrubs were of this shape, with a narrow base at ground level) was used as an estimate of plant size, and compared between treatments using analysis of variance.

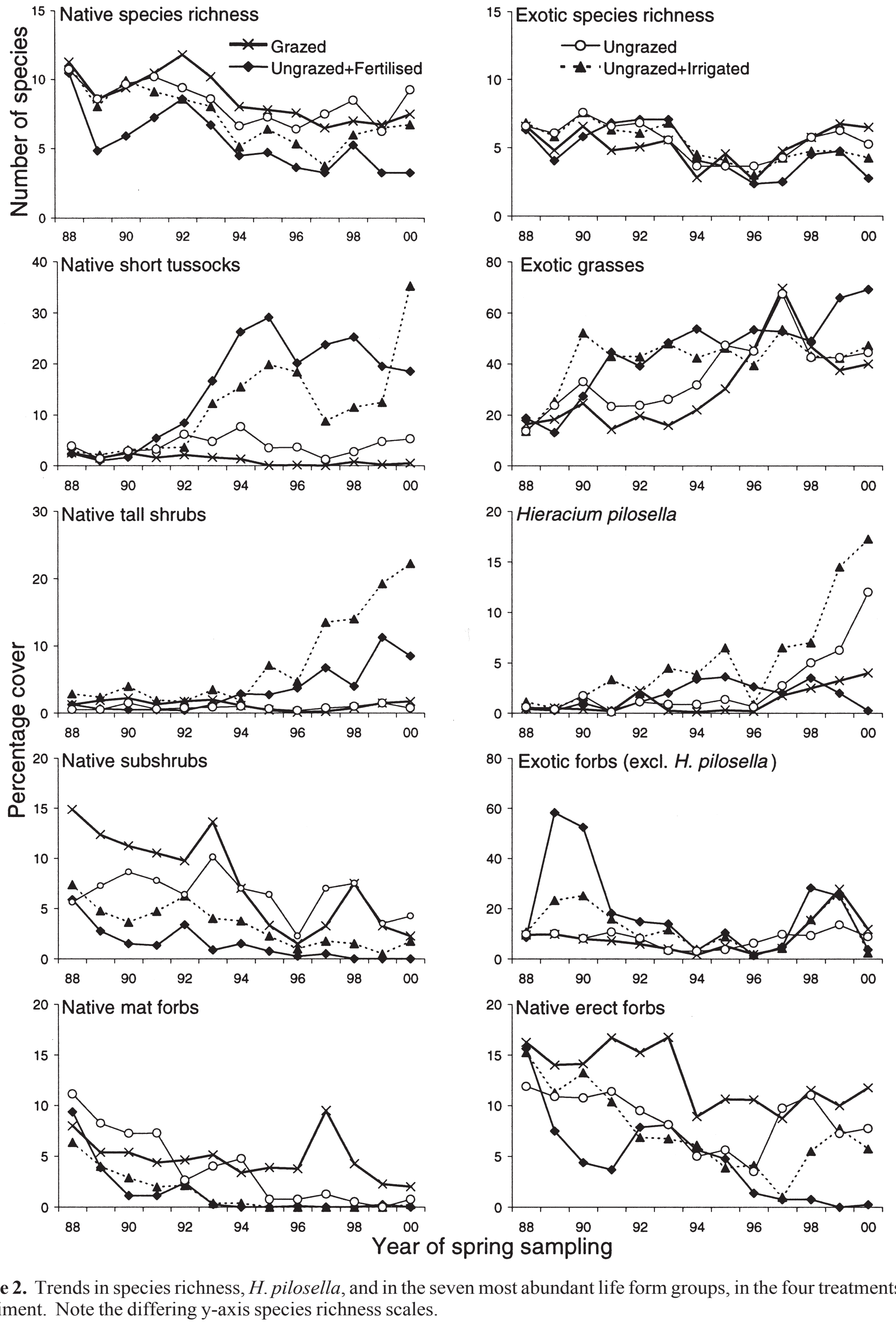

Figure 2. Trends in species richness, *H. pilosella*, and in the seven most abundant life form groups, in the four treatments of the experiment. Note the differing y-axis species richness scales.

Table 1. (a) Slopes of significant linear trends on time in native and exotic species richness, and (b) number of species in spring 2000.

	(a) Slope of richness on time[1]						(b) Number of species in 2000[2]			
	Grazed	Ungrazed	Ungrazed + fertilised	Ungrazed + irrigated	Diff slopes	Treat. × time	Grazed	Ungrazed	Ungrazed + fertilised	Ungrazed + irrigated
Native species richness	–0.31	–0.20	–0.41	–0.37	NS	NS	7.50[a]	8.75[a]	3.25[b]	6.75[a]
Exotic species richness		–0.17	–0.28	–0.27	*	NS	6.50[a]	5.25[ab]	2.75[c]	4.25[bc]

[1] NS indicates where slopes (Diff. slopes) or changes in cover (Treat × time) do not differ significantly between treatments, and * indicates a significant difference at $P > 0.05$.
[2] Within each row, numbers followed by the same letter do not differ significantly at $P > 0.05$.

Results

In continually grazed plots, native species richness and the cover of native tussock grasses and sedges, subshrubs, and erect and mat forbs decreased over the 12-year study period (all $P < 0.05$ by regression; Fig. 2; Table 1). Native tussock grasses and sedges, erect forbs, mat forbs and subshrub guilds, the individual tall shrub species *Carmichaelia petriei,* the tussocks *Festuca novae-zelandiae* and *Poa colensoi*, the erect forbs *Luzula ulophylla*, *Carex breviculmis* and *Leucopogon fraseri*, the mat forb *Raoulia parkii*, and the subshrubs *Coprosma petriei* and *Pimelea pulvinaris* all decreased (all $P < 0.05$ by regression). Some native tussock and shrub species decreased to the extent that they were no longer recorded in some half plots: by 2000, *F. novae-zelandiae*, *Poa colensoi* and *Carmichaelia petriei* were recorded in only one of the three or four half plots which they occupied in 1988, and *C. petriei* was not present in any grazed half plots when shrub volumes were measured in autumn 2002. The cover of exotic grasses (especially *Anthoxanthum odoratum*), and of the exotic forbs *Hieracium pilosella* and *Crepis capillaris*, increased with time (all $P < 0.001$; Fig. 2; Table 1).

In the ungrazed treatment (U), the cover of native tussock grasses, tall shrubs and subshrubs showed no significant overall trends or changes in cover between 1988 and 2000 (Fig. 2; Table 1). In 2000, native tussocks and the tall shrub *Carmichaelia petriei* remained present in all of the ungrazed half plots in which they were recorded in 1988. Changes in native tussock cover (from 2.6 to 5.0% in ungrazed half plots) were not quite significantly different from those in grazed half plots (from 2.0 to 0.4%; treatment × sampling time interaction $P = 0.079$). However, decreases in the tall shrub *Carmichaelia petriei* and in the native subshrub guild were significantly slower than in grazed vegetation ($P < 0.05$ by test for difference between slopes; Fig. 2), and the final volume of *C. petriei* shrubs was greater in the ungrazed than in the grazed treatment by the end of the study period ($P < 0.05$; Table 1). Native and exotic species richness, and the cover of the native mat forb guild decreased, and the cover of exotic grasses increased from 1988 to 2000 (all $P < 0.05$); these trends were not significantly different to those in grazed vegetation. However, *H. pilosella* increased more rapidly in ungrazed than in grazed vegetation, and final cover of the native grass *Rytidosperma unarede* and the forb *Luzula ulophylla* were lower in ungrazed than in grazed half plots (all $P < 0.05$ by analysis of covariance; Fig. 2; Table 1).

In the ungrazed+fertilised treatment, native and exotic species richness decreased to significantly lower levels than in the grazed and ungrazed treatments, and the cover of native tussock grasses, tall shrubs and exotic grasses increased from 1988 to 2000 (all $P < 0.05$; Fig. 2; Table 1). Native tussocks and tall shrubs, and *Poa colensoi* and *Carmichaelia petriei* individually, showed more rapid increases and had greater final cover (and volume, in the case of tall shrubs) than in the grazed and ungrazed treatments (all $P < 0.05$). Final exotic grass cover was also greater than in the grazed treatment ($P < 0.05$). Plant guilds differed in the time taken to respond to the treatment: exotic grass cover increased after the first year, native tussock grasses increased after 3 years, and increases in tall shrubs were recorded after 6 years. The cover of native subshrubs, erect and mat forbs and non-tussock grasses decreased with time ($P < 0.05$ by regression). Although their trends and changes in cover were not significantly different to those in the grazed treatment, non-tussock native grasses and native erect and mat forbs were not recorded in most ungrazed+fertilised half plots by 2000. *Hieracium pilosella* increased to *c*. 4% cover in 1998, but thereafter it decreased, and was absent in three of the four half plots by 2000. Other exotic forbs also decreased in cover overall following a short-lived initial increase, chiefly in the annual legume *Trifolium arvense* (Fig. 2; Table 1).

In the ungrazed+irrigated treatment, both native and exotic species richness decreased, while native tussock grasses, tall shrubs (particularly *Discaria*

Table 2. (a) Slopes of significant linear trends on time in the cover of plant guilds, and in common individual species (significant changes in percentage cover from 1988/99 to 1999/2000 are shown in parentheses where the trend is non-linear), and (b) average percentage cover (and, for tall shrubs only, volume in parentheses) in spring 2000.

	(a) Slope of percentage cover on time[1] (or difference final - initial percentage cover)						(b) Percentage cover in 2000[2]			
	Grazed	Ungrazed	Ungrazed + fertilised	Ungrazed + irrigated	Diff slopes	Treat. × time	Grazed	Ungrazed	Ungrazed + fertilised	Ungrazed + irrigated
Native tall shrubs			0.75	1.55	**	**	1.75^{b}	0.75^{b}	8.50^{a}	22.25^{a}
(volume in m^3 per m^2)							(0.52^{c})	(1.86^{bc})	(5.46^{ab})	(6.82^{a})
Carmichaelia petriei	–0.13		0.74	0.42	**	*	0.25^{b}	0.75^{b}	8.50^{a}	7.00^{ab}
(volume in m^3 per m^2)							(0.00^{c})	(1.4^{b})	(4.26^{a})	(2.87^{ab})
Discaria toumatou				1.15	**	**	1.50^{b}	0.00^{b}	0.00^{b}	15.25^{a}
(volume in m^3 per m^2)							(0.52)	(0.46)	(1.20)	(3.72)
Native tussocks & sedges	–0.22		2.04	1.80	**	*	0.50^{b}	4.75^{b}	18.5^{a}	35.25^{a}
Festuca novae-zelandiae	–0.11				NS	NS	0.25	2.25	4.00	9.00
Poa colensoi	–0.08		0.61		**	*	0.00^{b}	0.75^{b}	6.00^{a}	4.00^{ab}
Carex colensoi			0.89	0.87	*	NS		0.25	7.50	13.00
Other native grasses			–0.30	–0.21	NS	NS	3.00^{a}	1.50^{ab}	0.00^{b}	0.00^{b}
Rytidosperma unarede			–0.27	–0.2	NS	NS	3.00^{a}	0.50^{b}	0.00^{b}	0.00^{b}
Native erect forbs	–0.56		–0.97	–0.81	NS	NS	11.75^{a}	7.75^{a}	0.25^{b}	5.75^{a}
Luzula ulophylla	(–3.3%)	–0.24	–0.27	–0.45	NS	NS	2.50^{a}	0.00^{b}	0.00^{b}	0.50^{ab}
Carex breviculmis	–0.23	–0.12	–0.21		NS	NS	1.25	1.50		0.50
Leucopogon fraseri	–0.26	–0.14	–0.17		NS	NS	3.00	2.25		3.00
Native mat forbs	(–4.8%)	–0.87	–0.50	–0.46	NS	NS	2.00	0.75		0.25
Raoulia parkii	–0.26	–0.63	–0.39	–0.26	NS	NS				
Native subshrubs	–1.04		–0.36	–0.49	*	NS	2.25	4.25		1.75
Coprosma petriei	–0.79		–0.35		NS	NS	2.00	3.5		1.75
Exotic grasses	3.06	2.81	3.85	(+24.8%)	NS	NS	40.00^{b}	44.50^{ab}	69.25^{a}	47.25^{ab}
Anthoxanthum odoratum	3.19	2.72	4.32	1.83	NS	NS	36.50^{ab}	32.50^{b}	68.25^{a}	45.00^{ab}
Hieracium pilosella	0.24	0.63		1.07	**	**	4.00^{ab}	12.00^{ab}	0.25^{b}	17.25^{a}
Other exotic forbs			–2.01		**	*	11.75^{a}	8.75^{ab}	3.75^{ab}	2.50^{b}
Trifolium arvense			–2.13		**	*	2.00			
Crepis capillaris	0.4	0.42	–0.12	–0.24	*	**	7.00^{a}	7.75^{a}	0.25^{b}	0.75^{b}

[1] NS indicates where slopes (Diff. slopes) or changes in cover (Treat × time) do not differ significantly between treatments, and * indicates a significant difference at $P > 0.05$.
[2] Within each row, numbers followed by the same letter do not differ significantly at $P > 0.05$.

toumatou, but also *Carmichaelia petriei*) and exotic grasses (largely *Anthoxanthum odoratum*) increased in cover ($P < 0.05$; Fig. 2, Table 1). Final exotic species richness was significantly lower than in the grazed treatment ($P < 0.05$), but native species richness was not. Final cover of native tall shrub and native tussock guilds was higher in the ungrazed+irrigated treatment than in all other treatments ($P < 0.01$ by analysis of covariance). However, final exotic grass cover was not significantly greater than in grazed and ungrazed treatments. *Hieracium pilosella* increased more rapidly than in other treatments, to 17% cover in 2000 ($P < 0.01$ by linear regression). Its final cover was greater than in the ungrazed+fertilised treatment (*c.* 0.25% cover, $P < 0.05$ by analysis of covariance), but not significantly different to those in ungrazed and grazed treatments (12% and 4% cover, respectively; Fig. 2; Table 1).

Discussion

Current trends in short tussock grasslands

Relatively high native species richness in the *Festuca novae-zelandiae* short tussock grasslands on the Luggate terraces was recognised in the late 1980s, and the area was recommended for protection in the Protected Natural Areas survey report (Ward *et al.*, 1994). Since that time, directional vegetation changes have taken place under a management regime of low-intensity grazing by sheep and feral rabbits. There have been significant decreases in total native species richness, and in the cover of native tussock grasses (which were at very low levels at the time the experiments were established), native erect and mat forbs and subshrubs, while exotic grasses and forbs (including *Hieracium pilosella*) have increased. These trends are broadly similar to those reported elsewhere in South Island short-tussock grasslands in recent decades (e.g. Treskonova, 1991; Rose *et al*., 1995; Duncan *et al*., 1997).

From analyses of transect data from a wide range of Otago and Canterbury tall and short tussock grasslands, Duncan *et al*. (2001) concluded that decreases in species richness and in the cover of small herbs has occurred regardless of conservation or pastoral management practices since the mid-1980s. Native species richness and the cover of native forbs decreased in all of the four treatments (grazed, ungrazed, ungrazed+irrigated, ungrazed+fertilised) in the Luggate experiment, which spans a similar time period. However, we found significant differences between treatments in the trends or changes in most other plant guilds: i.e. in the number of exotic species, and in the cover of native tall shrubs, tussock grasses and sedges, subshrubs, exotic grasses, *H. pilosella* and other exotic forbs. These results suggest that current management practices may significantly affect physiognomic and compositional trends, at least in this short tussock grassland.

Effects of grazing and grazing-removal

The cover of tall shrubs and tussocks was very low when the experiment was initiated in 1988, and differences in these guilds between grazed and ungrazed treatments were therefore subtle. Subshrubs and the tall shrub *Carmichaelia petriei* showed little change in ungrazed vegetation, but these trends were significantly different from the decreases recorded in adjacent grazed vegetation. Trends in native tussocks were not quite significantly different between ungrazed and grazed vegetation, although tussocks decreased with grazing to the extent that *Festuca novae-zelandiae* and *Poa colensoi* were no longer recorded in most grazed half plots by 2000, whereas they remained present, and their cover did not decline in ungrazed half plots. Given their low initial cover, and their subsequent absence from most grazed half-plots, our conclusion is that the taller species that are the potential physiognomic dominants of the community are declining due to current grazing management. This contrasts with the conclusions of Meurk *et al*. (1989) and Lord (1990), who recommended that moderate or low intensity grazing might be the best short-term option to retain a short tussock grassland physiognomy in highly modified grasslands, having observed competitive suppression of remaining native grasses *Poa cita* and *Rytidosperma* spp. in exclosures and retired sites in coastal Canterbury. At least in this *F. novae-zelandiae* grassland, it seems unlikely that continued low-intensity grazing will retain the short tussock grassland physiognomy.

Fan and Harris (1996) proposed a mechanism whereby the native tussock *F. novae-zelandiae* would be displaced by *H. pilosella* under grazing, due to the native tussock's slower recovery from defoliation. Our study did not provide direct evidence for this process, but reciprocal trends in grazed vegetation (increases in *H. pilosella* and exotic grasses, and decreases in subshrubs and the taller species *Carmichaelia petriei*, *F. novae-zelandiae* and *P. colensoi*) are compatible with these native species being slower to recover from defoliation by grazing than *H. pilosella* and exotic grasses.

We expected that grazing would benefit short-statured native species that avoid herbivory, and which are better adapted to the open canopies and high light intensities associated with frequent disturbance (cf. British chalk grasslands; Wells, 1969). Indeed, at least two short-statured native species (the grass *Rytidosperma unarede* and the rush *Luzula ulophylla*) had lower final cover in ungrazed than grazed vegetation in our study. However, trends and changes in the total cover of both erect and mat native forb guilds were not significantly different between grazed and ungrazed treatments. Although correlations do not imply cause, simultaneous increases in exotic grasses and *H. pilosella* are consistent with competitive exclusion of native forbs by these exotic species in both treatments.

Taken together, our results suggest that grazing may have slowed the decrease in certain shorter, herbaceous elements of the native flora, but that it did not maintain native species richness because the gradual demise of tussocks and certain native woody plants continued under grazing. We suggest the latter changes have considerable implications for the survival of some native physiognomic dominants, and hence the potential for long-term vegetation recovery in this short tussock grassland. Competition from exotic species in ungrazed vegetation did not appear to suppress native tussocks, subshrubs or *Carmichaelia petriei* to the same extent as grazing. Our study comprises a single site, but nevertheless highlights the need for recommendations for conservation management to distinguish between environments and short tussock grassland types.

Once a disturbance such as grazing is removed from a grassland, ecological changes (e.g. changes in soil nutrients, introduction of competitive exotic species) and barriers to recovery (loss of seed sources or vegetative stock) may be only slowly reversed (e.g. Westoby *et al*., 1989; Basher and Lynn, 1996; McIntosh and Allen, 1998). There is so far little evidence that the cessation of grazing alone may lead to the recovery of native species in *F. novae-zelandiae* short tussock grasslands. For example, in Canterbury, Rose *et al*. (1995) found little evidence to suggest that the cessation of sheep grazing for 25–35 years led to tussock recovery. Sixteen years of freedom from grazing in the Upper Waitaki district resulted in increased total biomass but no increase in native species dominance (McIntosh and Allen, 1998). Where *H. pilosella* initially dominated *F. novae-zelandiae* grasslands in the Mackenzie Basin, vegetation states changed little in 10 years, while elsewhere *H. pilosella* increased, and short tussocks showed little change, regardless of treatment (Meurk *et al*., 2002). Our study also found no significant changes in native shrub and tussock cover after 12 years of sheep and rabbit exclosure in *F. novae-zelandiae* grasslands, while *H. pilosella* increased and native species richness decreased. Our results support the conclusion of McIntosh and Allen (1998), that grazing removal alone may not be a realistic option for native vegetation rehabilitation in short tussock grasslands in the short and medium term.

Effects of fertiliser and irrigation in the absence of grazing

It has been suggested that the potential for invasion and dominance of exotic species in short tussock grasslands is greater in resource-rich sites, especially those with high fertility. Meurk *et al*. (1989) and Lord (1990) observed that native species were most disadvantaged by grazing removal in sites with higher natural fertility or rainfall regimes, because exotic species were more vigorous. This has led to recommendations to withhold fertiliser additions from short tussock grasslands managed for conservation (e.g. Davis and Meurk, 2001, p 28.).

Relatively few studies have examined the effects of resource additions (i.e. fertiliser or irrigation) together with grazing-removal in short tussock grasslands. However, Scott (2000) applied different levels of superphosphate and nitrogen fertiliser treatments to ungrazed *Festuca novae-zelandiae* grasslands near Tekapo in the Mackenzie Basin over an initial, 18-month period, and monitored changes for 9 years. Tall shrubs were not recorded at Tekapo, but *F. novae-zelandiae* tussocks showed conspicuous height increases in response to fertiliser treatments, despite increased cover of exotic guilds, while shorter native forbs and subshrubs decreased in relative abundance rank over the study period.

At Luggate, exotic forbs and grasses increased initially with resource additions, and native species richness, and forb and subshrub cover declined rapidly. However, annual fertiliser and irrigation treatments enhanced the growth of taller native species in the longer term, so that by 2000, native shrubs and tussocks overtopped exotic grass swards in both ungrazed+irrigated and ungrazed+fertilised treatments. Whereas Scott's (2000) study focused on the rejuvenation of native *F. novae-zelandiae* tussocks following a short period of fertilisation, our results further suggest that where tall shrub remnants remain in *F. novae-zelandiae* grasslands, it may be possible to initiate succession to more woody seral states by elevating the soil nutrient or moisture status over an extended period.

After 10 years of annual fertiliser inputs, the exotic forb *H. pilosella* was almost entirely excluded from the ungrazed+fertilised plant community by a dense sward of native tall shrubs and tussocks and exotic grasses. *H. pilosella* continued to increase in other treatments where canopy closure was less complete by 2000, including the ungrazed+irrigated treatment. This outcome supports the proposition that vegetation structure may be a factor in the vulnerability of tussock grassland communities to invasion by *H. pilosella* (e.g. Rose and Frampton 1999).

A suggested goal for native biodiversity conservation in short tussock grasslands

Evidence is accumulating to suggest that species richness is currently decreasing in eastern South Island tussock grasslands, especially at low elevation sites where *F. novae-zelandiae* short tussock grasslands are most common (Duncan *et al*., 2001). The greatest decreases have been in the number of small herbs, but larger herbaceous species have also become less numerous, whereas woody species richness has remained relatively constant. Duncan *et al*. (2001) concluded that these were directional trends rather than short-term fluctuations, but could not identify their causes at a regional scale. In our study, changes in grazed vegetation differed from those reported for the whole region in some details: e.g. native richness declined, but exotic richness did not, and subshrubs decreased significantly. Furthermore, we suggest grazing was a factor in the declining richness of taller species at our study site, and we could not eliminate exotic species competition as a possible cause of the decrease in short-statured native forbs, irrespective of treatment.

It has long been known that most of today's eastern South Island *F. novae-zelandiae* short tussock grasslands are induced, i.e. they were previously woodlands and shrublands, or mixtures of tall tussocks and shrubs, including *Carmichaelia*, *Coprosma*, *Discaria*, *Halocarpus*, *Kunzea*, *Melicytus*, *Olearia*, *Ozothamnus*, *Phyllocladus*, *Pimelea*, *Podocarpus* and *Sophora* spp., which were removed, or which retreated to fire refugia, following the arrival of humans (Molloy *et al*., 1963; Connor, 1964). These woody communities are among New Zealand's most reduced, modified and threatened vegetation types (McGlone, 2001; Leathwick *et al*., 2002). The details of prehuman vegetation compositions remain uncertain, and the reconstitution of any precisely defined prior state is unlikely to be feasible. Nevertheless, there is a strong case for the restoration of some form of climax native woody vegetation in the environments that presently support short tussock grasslands, in order to re-establish some of the prehuman ecological processes, habitats and biodiversity (e.g. Atkinson, 2001). We therefore suggest that an appropriate goal for conservation management of induced short tussock grasslands would be to increase the biomass and stature of native vegetation, i.e. to encourage succession towards native climatic climax communities which include native woodlands, shrublands and mixtures of shrubs and tussock grasses. This goal would change the focus of short tussock grassland conservation management from the maintenance of present, predominantly herbaceous non-equilibrium seral states, to promoting successional change and in particular, the restoration of native woody communities.

Previous studies in *F. novae-zelandiae* short tussock grasslands have shown that the recovery of native species dominance and other ecosystem properties may occur very slowly, if at all, following the removal of herbivores. Our results, and those of Scott (2000), indicate that it may be possible to increase the growth rates of native shrubs or tussocks, and to promote succession, by elevating soil resources in some grasslands. Fertiliser applications seem an appropriate management tool to assist native vegetation restoration in environments that now support *F. novae-zelandiae* short tussock grasslands, since soil nutrient levels were probably considerably higher prior to the advent of pastoralism (McIntosh, 1997). However, alternative methods and techniques to promote succession may be found.

Short-statured, light-demanding, early-seral native herbs, which typically account for high proportions of native species richness in *F. novae-zelandiae* short tussock grasslands, would be likely to decrease with succession to taller, more woody states (Walker, 2000). However, there may be few measures that will maintain high numbers of small native herbs in today's non-equilibrium grasslands: in our experiment they decreased in cover regardless of treatment, while at a regional scale they appear to have decreased in number irrespective of management (Duncan *et al*., 2001). Labour-intensive, artificial disturbance (e.g. hand weeding) may be justified at small scales to ensure the survival of critically endangered seral plant species that were previously dependent on localised, naturally disturbed habitats (e.g. cliffs, braided riverbeds, or inland salt pans), but such efforts might not be warranted for the more common seral herbs of extensive short tussock grasslands.

The restoration of taller, woody vegetation offers a means to maintain and increase the extent of native-dominated vegetation in those environments that now support seral short tussock grasslands within public conservation lands. However, the feasibility of and the potential for the restoration of taller, more woody native vegetation will vary greatly with differences in species composition, environment and disturbance history. Where succession is feasible, it seems likely that time scales of change will be slow, trajectories of change will remain relatively uncertain, many exotic species will persist, and long-term protection from fire and feral herbivores will be needed. Because experience is so limited, field research will be essential to explore methods to reintroduce seed sources and enable the recruitment of native woody species, to control competition from exotic grasses and woody weeds, and to optimise resource inputs to maximise benefits to native species.

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