Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990–2000

Colin D. Meurk[1], Susan Walker,[2,*] Roger S. Gibson[3,5] and Peter Espie[4]
[1] Landcare Research, P.O. Box 69, Lincoln, New Zealand
[2] Landcare Research, Private Bag 1930, Dunedin, New Zealand
[3] Landcare Research, P.O. Box 282, Alexandra, New Zealand
[4] AgResearch, Private Bag 50 034, Mosgiel, New Zealand
[5] Present address: Swann Rd, R.D. Cromwell, New Zealand
[*] Corresponding author (E-mail: walkers@LandcareResearch.co.nz)

Abstract: Changes in vegetation from 1990 to 2000 were examined at 10 high country localities, representing four grassland types: fescue tussock (*Festuca novae-zelandiae*), snow tussock (*Chionochloa rigida*), red tussock (*C. rubra*), and silver tussock (*Poa cita*). At each locality, three treatments were established: ambient sheep+rabbit grazing, rabbit grazing only, and no grazing. The mutivariate methods of classification and ordination were used on individual-quadrat cover data to define vegetation states and to examine transitions between them over time. Vegetation states in quadrats already dominated by *Hieracium pilosella* (> 50% cover) in 1990 showed little change in species composition regardless of grassland type and grazing treatment. In fescue tussock grassland, *H. pilosella* increased regardless of grazing treatment in states with low initial *H. pilosella* cover (< 5%), while the cover of *Carex colensoi*, *Aira caryophyllea* and *Rumex acetosella* decreased. In the single silver tussock locality, *Poa cita* decreased markedly in the ungrazed treatment as adventive species such as *Dactylis glomerata* and *Echium vulgare* increased. However, *Poa cita* also decreased, probably due to drought, in the grazed treatment. Snow tussock and red tussock grassland states were more stable than those in short tussock grasslands, but there was also a general trend towards increasing *H. pilosella* cover in intertussock vegetation regardless of treatment. However, at one snow tussock locality, transitions from *H. pilosella*-dominated to *C. rigida*-dominated states occurred in ungrazed quadrats, while the reverse occurred in grazed vegetation. Implications for the management of tussock grasslands for conservation are discussed.

Keywords: grazing effects; *Hieracium*; New Zealand vegetation states and transitions; rabbits; sheep; tussock grasslands.

Introduction

Many mechanisms exist that may prevent an altered plant community from returning to its original composition once the disturbances that initiated the changes have been removed (Westoby *et al.*, 1989; Laycock, 1991; Friedel, 1991). Once disturbances such as grazing are removed from a system, communities may make a transition and move toward an entirely new state, often because of invasion by other species.

Substantial vegetation-composition changes have taken place in New Zealand high country tussock grasslands over the last 150 years, as a consequence of burning, grazing, addition of fertiliser, and introductions of exotic species (e.g. Treskonova, 1991). These changes have resulted in highly modified system dynamics. In recent decades, there has been a rapid invasion of several species of the genus *Hieracium* (Asteraceae) into these tussock grasslands. Some of these species (most notably *H. pilosella*, *H. praealtum*, *H. lepidulum* and *H. caespitosum*) have the potential to significantly alter the invaded plant community, and are perceived to be threats to both biodiversity conservation and pastoral production (Rose *et al.*, 1995; Wiser *et al.*, 1998). Biological control measures are being investigated (Morin and Syrett, 1996).

Causes and processes of ongoing changes in New Zealand tussock grasslands are well described (e.g. O'Connor, 1982). However, relatively few studies have investigated what happens to modified New

Zealand grassland communities once grazing disturbance is removed (e.g. Meurk *et al.*, 1989; Lord, 1990; Allen *et al.*, 1995; Rose *et al.*, 1995; Walker, 1997; Walker and Lee, 2000). This study analyses data collected from different tussock grassland types over 10 years, to examine changes in vegetation states, and particularly in *Hieracium* cover, following partial and complete exclusion of both feral and domestic grazing disturbance. We discuss the implications of our results for management of tussock grasslands for conservation.

Study area and methods

The study sites were situated at 10 localities representing different grassland communities within the intermontane Mackenzie Basin in eastern South Island, New Zealand (Table 1). In 1989, three contiguous treatment blocks (75 m × 75 m) were established at each locality: ambient sheep+rabbit grazing, rabbit-grazing (standard 7-wire sheep fence), and ungrazed (standard 7-wire sheep fence with rabbit netting). Fences were checked annually. Grazing intensity fluctuated in the control and rabbit-grazing treatments, but was low compared with historical levels, due to reduced stocking and poison operations conducted under the Rabbit and Land Management Programme (RLMP) shortly after the trials were established, and the introduction of RHD (rabbit haemorrhagic disease) in winter 1997. Weather conditions varied across the study period. Particularly low-rainfall summers were experienced from 1990 to 1992, and from 1997 to 1999. The percentage cover of all plant species was visually estimated within eight, randomly positioned 0.25-m^2 quadrats in each treatment. In this paper, we consider data from two sampling dates: 1990 and 2000.

Cluster analysis (city-block difference measure, flexible sorting strategy, β = –0.25; Clifford and Stephenson, 1975) was used to identify grassland types within the 10 localities at the initial sampling date (1990). From this analysis, we identified four

Table 1. Characteristics of study sites in the Mackenzie Ecological Region.

Study site	Soil series[1]	Elev. (m)	Slope (°)	Aspect (°)	Temp. (°C)	Pptn (mm)	Init. Hawkweed	Init. Tussock	Init. Bare+Rock	RAP[3]	Vegetation[3]
Fescue tussock grassland											
Ben Ohau	Mackenzie	487	0	0	20.8	640	2.8	5.9	40.1	Pukaki 8	Fescue-scabweed
Maryburn	Pukaki-Holbrook	548	0	15	20	600	16.6	8.1	8.6	Pukaki 14	Fescue-matagouri
Richmond	Sawdon	755	10	90	16.6	800	37.8	12.6	1.2	Tekapo 30	Fescue-dwarf shrub
Sawdon	Fork fluvioglacial	670	5	15	18.9	550	48.9	2.5	31.7	Pukaki 16	Fescue-hawkweed
Simons Hill	Mackenzie	423	0	135	18.5	480	0.2	6.3	30.3	Pukaki 9	Fescue-sorrel-scabweed
Snow tussock grassland											
Lindis	Nevis	944	15	45	15.9	1150	7.1	7.9	13.9	Ahuriri 14	Snow tussock
Omahau	Craigieburn	609	10	135	16.8	800	6.8	5.3	33.0	Pukaki 7	Snow tussock-manuka
Red tussock grassland											
Balmoral	Tekapo hill	944	20	135	13.9	700	11.9	43.2	0.8	Tekapo 11	Red/fescue grassland
Pukaki Downs	Bendhu-Cox	700	5	100	16.9	900	7.7	7.0	9.7	Pukaki 3	Red/fescue bog
Silver tussock grassland											
Rostriever	Omarama steepland	548	25	45	18.9	550	0.0	5.9	63.0	Benmore 9	Silver tussock-scabweed

Elev. = elevation above sea level, Temp. = mean January temperature, Pptn = annual rainfall, Init. = initial, Hawkweed = cover of all *Hieracium* species, Tussock = cover of native *Chionochloa, Festuca* and *Poa* species, Bare/Rock = cover of bare soil plus cover of bare rock

[1] T.J. Webb (1992; *pers. comm.*)

[2] Belton and Ledgard (1984)

[3] Recommended Area for Protection designations and vegetation types (from Espie *et al.*, 1984)

Table 2. The number of quadrats at each locality in 1990 and 2000 within the four vegetation states identified by classification for each grassland type.

Grassland type		States			
Fescue tussock grassland		**A**	**B**	**C**	**D**
Ben Ohau	1990	24	0	0	0
	2000	0	0	11	13
Maryburn	1990	0	21	0	2
	2000	0	0	0	24
Richmond	1990	0	12	0	12
	2000	0	1	0	23
Sawdon	1990	0	0	17	7
	2000	1	1	14	8
Simons Hill	1990	24	0	0	0
	2000	4	0	17	3
Snow tussock grassland		**A**	**B**	**C**	**D**
Lindis	1990	9	0	15	0
	2000	8	0	16	0
Omahau	1990	4	4	13	3
	2000	4	5	13	2
Red tussock grassland		**A**	**B**	**C**	**D**
Balmoral	1990	14	6	0	4
	2000	12	3	0	9
Pukaki Downs	1990	3	19	2	0
	2000	1	19	4	0
Silver tussock grassland		**A**	**B**	**C**	**D**
Rostriever	1990	15	7	2	0
	2000	9	4	8	3

groups of localities, namely, fescue tussock (*Festuca novae-zelandiae*, five localities), snow tussock (*Chionochloa rigida*, two localities), red tussock (*Chionochloa rubra*, two localities), and silver tussock (*Poa cita*, one locality) grassland types (Table 2). Data from each of these four grassland types were thereafter analysed separately, as follows.

Within each grassland type, we used a second cluster analysis to objectively assign quadrats in the joint (1990 + 2000) datasets to communities (hereafter called vegetation states). Each analysis was terminated at the arbitrary level of four states (A to D); average city-block dissimilarities between states at the lowest (i.e. third) level of division ranged from 2.7 to 3.2. If a quadrat was assigned by cluster analysis to different vegetation states in different years, this was interpreted as a transition between states. Chi-squared tests were used to seek evidence for non-independent distributions, among treatments and localities, of quadrats in vegetation states in 1990, and of quadrats that had undergone transitions between states by 2000. Columns of the chi-squared contingency tables were states, rows were localities or treatments, and cell entries were numbers of quadrats. If vegetation transitions were independent of treatment, this would support the null hypothesis that changes in species composition were unrelated to current grazing treatments.

To display these results, the positions of species and individual quadrats (in both 1990 and 2000), were plotted on the first two principal gradients of vegetation composition in each grassland type, which were identified by Principal Components Analysis (PCA; Goodall, 1954). The domains of the four vegetation states were outlined on the ordination plot, and state changes were displayed using arrows representing the trajectories of quadrats between sampling dates. We chose PCA over other ordination methods for this display because it best separated the states along the short vegetation gradients within the grassland types.

Results

Grassland types

The fescue tussock grassland type, identified by the initial cluster analysis of data from the 10 localities, was represented by five localities (Ben Ohau, Maryburn, Richmond, Sawdon, Simons Hill; Table 2). Snow tussock grassland was represented by two localities (Lindis and Omahau), red tussock by two localities (Balmoral and Pukaki Downs), and silver tussock by one locality (Rostriever).

The results that follow were obtained from separate analyses of each grassland type. Figures 1, 2, 3 and 4 show the states and transitions for the grassland types.

Fescue tussock grasslands

The four fescue tussock vegetation states (A to D) were unequally divided among localities in 1990 ($P < 0.05$ by chi-squared test), but were relatively evenly distributed among the treatments being applied. Most quadrats at Maryburn, and half of the quadrats at Richmond, were classified as State B (Table 2). This vegetation had a moderately high cover of *H. pilosella* (18%), but retained several native species, including *F. novae-zelandiae* (10%), *Discaria toumatou* (5%), *Coprosma petriei*, *Pyrrhanthera exigua*, *Rytidosperma pumilum*, *Carex breviculmis*, *C. colensoi*, *Leucopogon fraseri*, *L. muscosa* and *Craspedia lanata*, as well as the exotic grass *Anthoxanthum odoratum*. State A comprised all of the quadrats at the Ben Ohau and Simons Hill localities in 1990. It was dominated by *Rumex acetosella*, *Festuca novae-zelandiae*, *Carex colensoi*, *Aira caryophyllea* and *Raoulia australis*, with low (*c.* 1.5%) cover of *H. pilosella* and much bare ground (32%). States C and D were dominated by *H. pilosella* (35% and > 50% average cover respectively). State C contained few other species, and little *F. novae-zelandiae* (< 1%), and in 1990 was represented by most quadrats at Sawdon. The remaining Sawdon and Richmond quadrats, and a few quadrats at Maryburn, were classified as State D in 1990. Although *H. pilosella* cover was greater, quadrats in this state retained higher cover of native species, such as *F. novae-zelandiae*, *Pyrrhanthera exigua* and *Coprosma petriei*, than those in State C.

Over the decade, the number of quadrats showing transitions to different states was independent of grazing treatment, but differed significantly among localities, as might be expected given their different initial compositions. Most quadrats in States C and D (i.e. those already dominated by *H. pilosella* in 1990), remained in these states (Fig. 1). However, by 2000, many quadrats that were formerly classified within States A and B had undergone transitions to one of the two *H. pilosella*-dominated states (Fig. 1): State C made a net gain of 24 quadrats, while State D made a net gain of 50 quadrats (together representing 62% of quadrats). As *H. pilosella* increased over time, *F. novae-zelandiae*, *Coprosma petriei*, *Pyrrhanthera exigua*, *Discaria toumatou, Rytidosperma pumilum*, *Carex breviculmis*, *C. colensoi* and the exotic annual grass *Aira caryophyllea* decreased in those quadrats previously in State B (at Maryburn and Richmond localities), while bare ground and the cover of *Rumex acetosella*, *Aira caryophyllea* and *Raoulia australis* decreased in quadrats previously in State A (at Ben Ohau and Simons Hill localities).

At Sawdon, single quadrats underwent transitions from State C to States A and B, in the ambient sheep+rabbit grazing, and rabbit-grazing treatments, respectively. We interpret these atypical changes as local recovery of native species, despite relatively high *H. pilosella* cover, as a consequence of reduced grazing intensity across all treatments after 1990. Our observations also suggest that the 1999 drought may have locally reduced the cover and competitiveness of *H. pilosella* at this extremely arid site.

Snow tussock grasslands

The four vegetation states identified by cluster analysis in the snow tussock grassland type were distributed relatively equally among treatments and localities in 1990. Nine quadrats at Lindis and four quadrats at Omahau were in State A (dominated by *Chionochloa rigida* at 27% cover, with 6% *H. praealtum*, 4% *H. pilosella* and 3% *F. novae-zelandiae*). Four quadrats at Omahau represented State B, which was dominated by *Leptospermum scoparium* (43% cover), with *H. praealtum* and *Anthoxanthum odoratum* (both 5% cover), and 4% *C. rigida*. Most quadrats at both snow tussock localities were classified within State C in 1990 (Table 2). Here, *C. rigida* tussocks were widely spaced (average cover 3%) and intertussock vegetation comprised *H. pilosella* (12% cover) and *H. praealtum* (6%), together with *A. odoratum*, *Agrostis capillaris*

Figures 1, 2, 3 & 4. Results for the four grassland types: a) Relative positions of vegetation states (A to D, bold type), individual quadrats in 1990 and 2000, and c) major species (×, inset graphs) on the first two axes of the PCA ordinations for the four grassland types; and b) the number of quadrats showing transitions between states from 1990 to 2000 (indicated by arrows, with the number of quadrats appended). Divergent arrows indicate that quadrats were initially similar, but underwent transitions to different vegetation states over time, parallel or convergent arrows indicate changes to similar states, and circular arrows indicate no change in state.

Key to common species on the inset graphs:

Abbreviation	Species
AGRCAP	*Agrostis capillaris*
AIRCAR	*Aira caryophyllea*
ANTODO	*Anthoxanthum odoratum*
CARBRE	*Carex breviculmis*
CARCOL	*Carex colensoi*
CELGRA	*Celmisia gracilenta*
CHIRIG	*Chionochloa rigida*
CHIRUB	*Chionochloa rubra*
COPPET	*Coprosma petriei*
DACGLO	*Dactylis glomerata*
DEYAVE	*Deyeuxia avenoides*
DICCRI	*Dichelachne crinita*
DISTOU	*Discaria toumatou*
ECHVUL	*Echium vulgare*
FESNOV	*Festuca novae-zelandiae*
HIEPIL	*Hieracium pilosella*

Abbreviation	Species
HIEPRA	*Hieracium praealtum*
HYPRAD	*Hypochaeris radicata*
LEPSCO	*Leptospermum scoparium*
LEUFRA	*Leucopogon fraseri*
LEUMUS	*Leucopogon muscosa*
LUZRUF	*Luzula rufa*
OXAEXI	*Oxalis exilis*
PENPUM	*Pentachondra pumila*
POACIT	*Poa cita*
POACOL	*Poa colensoi*
PYREXI	*Pyrrhanthera exigua*
RAOAUS	*Raoulia australis*
RAOSUB	*Raoulia subsericea*
RUMACE	*Rumex acetosella*
RYTUNA	*Rytidosperma unarede*
TRIARV	*Trifolium arvense*

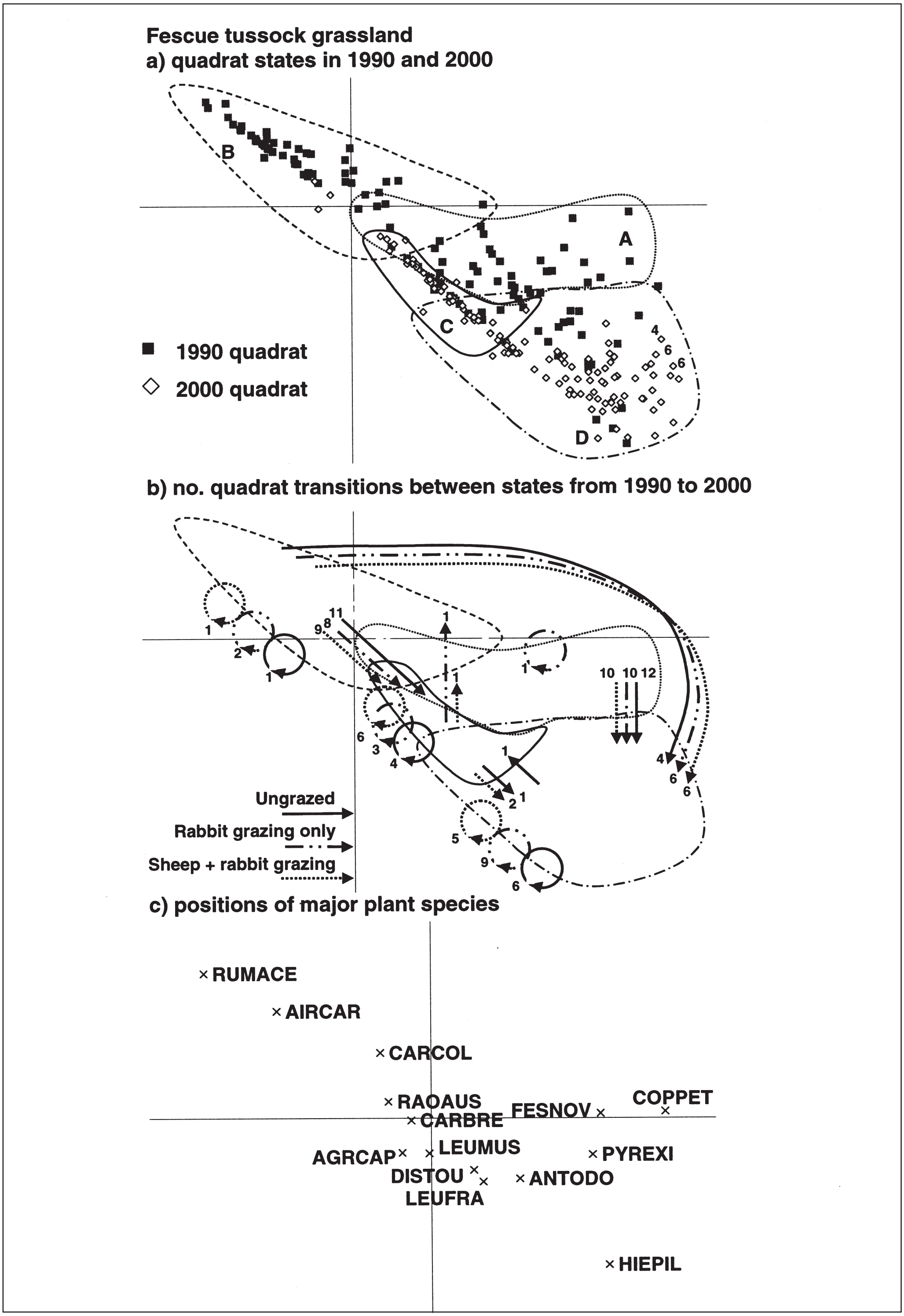

Figure 1. Fescue tussock grassland.

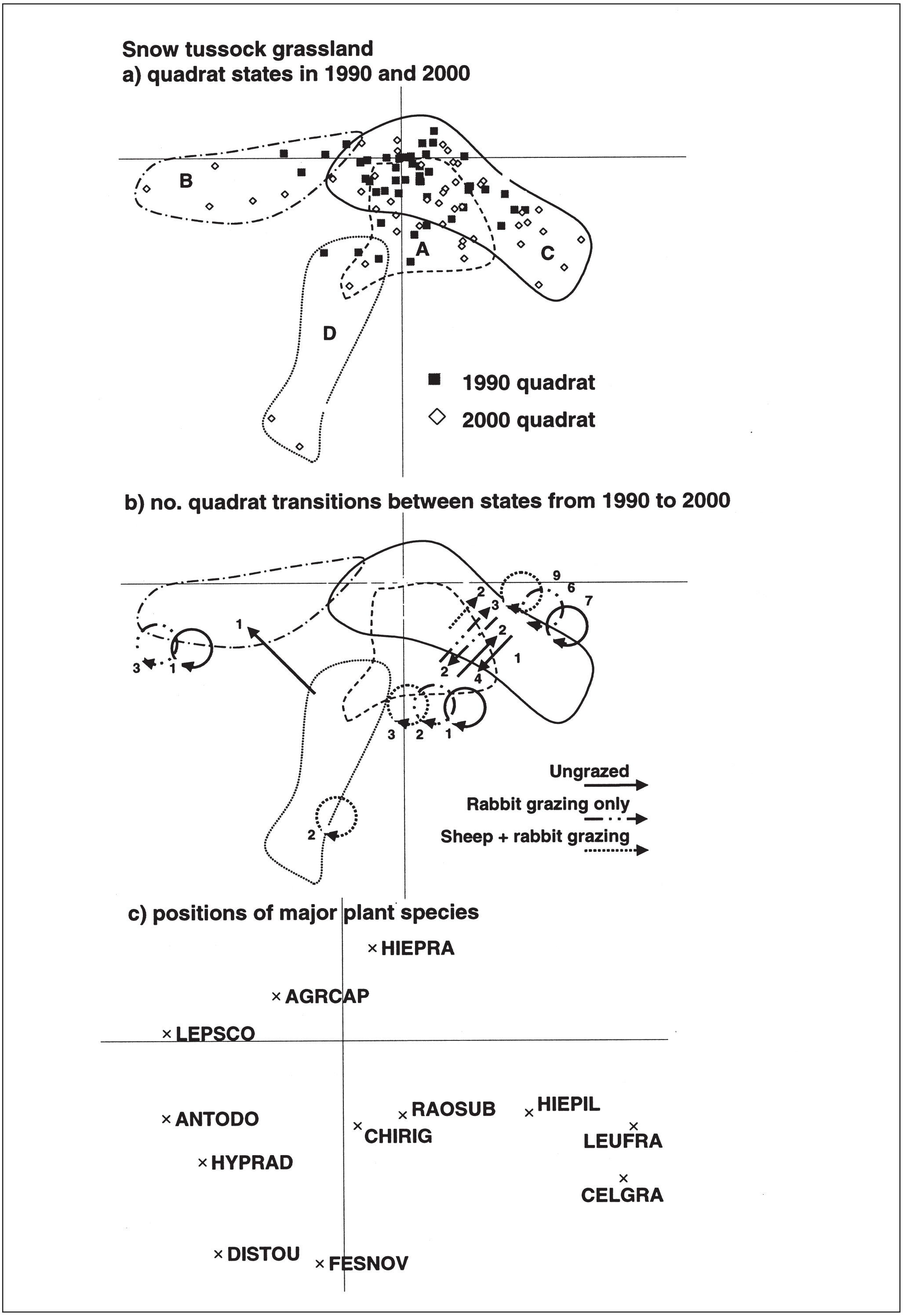

Figure 2. Snow tussock grassland. See page 98 for caption.

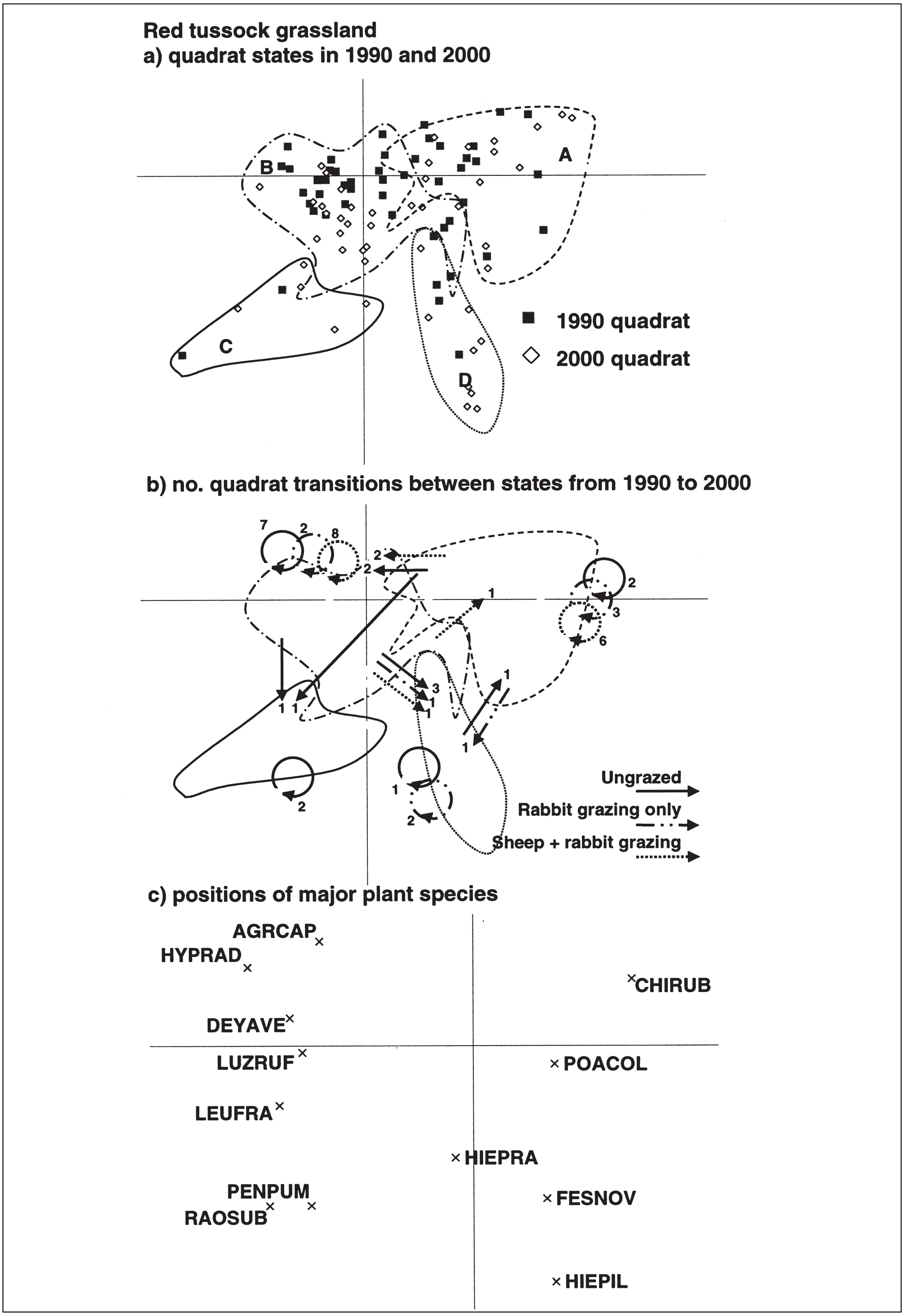

Figure 3. Red tussock grassland. See page 98 for caption.

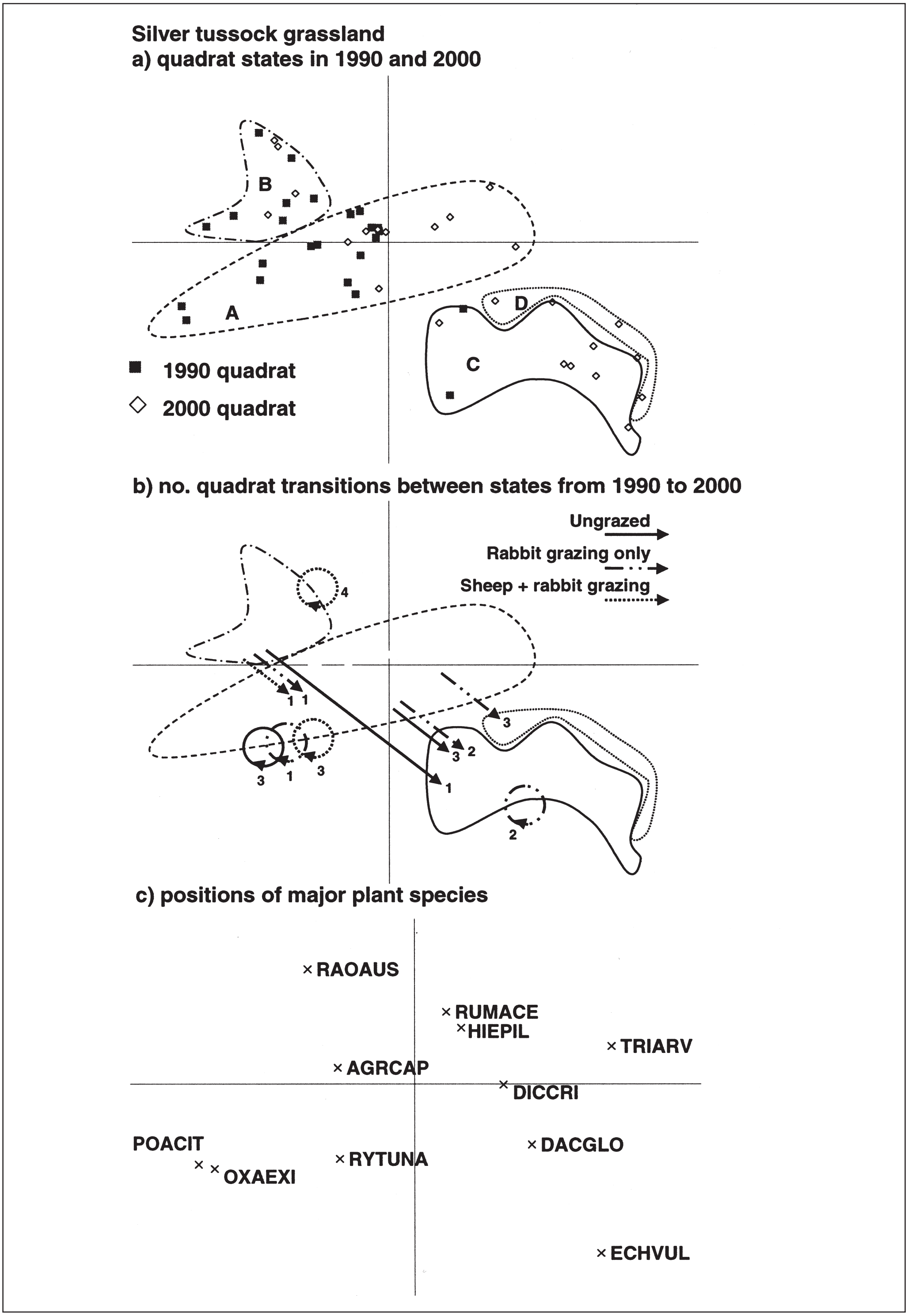

Figure 4. Silver tussock grassland. See page 98 for caption.

and *Leucopogon fraseri*. Three quadrats at Omahau were in State D, which was dominated by *Discaria toumatou* (33% cover) and *F. novae-zelandiae* (8%) with *A. odoratum*, *H. pilosella,* and *H. praealtum* (all 6%), and 3% *C. rigida* cover.

At Omahau, only three quadrats (13%) changed state over the 10 years, whereas 11 quadrats (46%) changed state at Lindis (Fig. 2). The direction of state changes differed between treatments at Lindis: in the ungrazed treatment, four quadrats recovered from State C (*H. pilosella*-dominated) to State A (*C. rigida*-dominated). The opposite trend was recorded in one ungrazed quadrat, two quadrats in the ambient sheep+rabbit grazing treatment, and three quadrats in the rabbit-grazing treatment. At Omahau, one quadrat in the rabbit-grazing treatment changed from State C to State A, while transitions from State D to State B (i.e. increased *L. scoparium* cover) and from State A to State C (i.e. increased *H. pilosella* cover) occurred in one quadrat each in the ungrazed treatment.

Thus, fewer state changes were seen in snow tussock grasslands than in fescue tussock grasslands. At Lindis, we observed relatively consistent gradual recovery of *C. rigida* stature, and consequent suppression of *H. pilosella*, with removal of grazing, while reduction of *C. rigida* cover and invasion by *H. pilosella* continued under sheep+rabbit grazing. However, at the second locality (Omahau), with lower, more patchy *C. rigida* cover, transitions were few and inconsistent.

Red tussock grasslands

In 1990, the red tussock grassland vegetation states were divided unequally between the two localities, and between treatments within those localities (both $P <$ 0.05 by chi-squared test). Vegetation states differed principally in the abundance of *Chionochloa rubra*, *H. pilosella* and the subshrub *Pentachondra pumila*; all contained the native species *F. novae-zelandiae*, *Poa colensoi*, *Deyeuxia avenoides*, *Rytidosperma pumilum*, *Luzula rufa* and *Leucopogon fraseri*. The exotic species *Agrostis capillaris*, *Anthoxanthum odoratum*, *H. praealtum* and *Hypochaeris radicata*, were present at low cover values. In 1990, State A vegetation comprised 3 and 14 quadrats from the Pukaki Downs and Balmoral localities, respectively, which were dominated by *C. rubra* (> 50% cover), and had moderate *H. pilosella* cover (average 8%). Most (19) quadrats at Pukaki Downs, and 6 quadrats at Balmoral, were classified within State B, which comprised somewhat higher *H. pilosella* cover (13%) and widely-spaced tussocks of *C. rubra* (average 7% cover). Two quadrats at Pukaki Downs were classified as State C, in which *Pentachondra pumila* (29%) and *H. pilosella* (19%) were abundant. Four quadrats from Balmoral were dominated by *H. pilosella* (at > 50%), and contained 11% *C. rubra*, and were classified as State D.

Fewer transitions were observed at Pukaki Downs (3 quadrats) than at Balmoral (11 quadrats; Fig. 3), and fewer state changes were seen in sheep+rabbit grazing treatments than in rabbit-grazing and ungrazed treatments (2, 4 and 8 transitions, respectively). Transitions from State B to State D (reflecting increased *H. pilosella* dominance between the sparse tussocks) were recorded in one or more quadrats in all treatments at Balmoral. Transitions from State A to States B, C and D (reflecting increased *H. pilosella* dominance and a decrease in *C. rubra* cover) were seen in a few quadrats in both ungrazed and rabbit-grazed treatments at both localities. However, the opposite trend, i.e. transitions to State A (*C. rubra* dominance), was also recorded in quadrats in ungrazed and sheep+rabbit grazing treatments at Balmoral.

As in snow tussock grasslands, red tussock grassland states appeared to be relatively stable. Despite an overall trend towards increased *H. pilosella*, average *C. rubra* cover remained similar after 10 years at both localities. The observed changes in state could not be attributed to particular grazing treatments.

Silver tussock grassland

Three of the four vegetation states recognised at the silver tussock locality were present in 1990. At that time, vegetation in most quadrats comprised scattered tussocks of *Poa cita* (average cover *c*. 4%, with 63% bare soil and rock) and a sparse sward of *Rytidosperma unarede*, *Dichelachne crinita, Raoulia australis* and the exotic forbs *Rumex acetosella, Trifolium arvense* and *Echium vulgare* (State A). Six quadrats in each of the ungrazed and rabbit-grazing treatments, and three quadrats in the sheep+rabbit grazing treatment, were classified within this state (i.e. 68% of quadrats in 1990). Remaining quadrats in the ungrazed treatment (2 quadrats), and in the sheep+rabbit grazing treatment (5 quadrats), were classified within State B. Here, mats of *Raoulia australis* (*c*. 20% cover) were prominent between *Poa cita* tussocks. Two quadrats in the rabbit-grazing treatment were characterised by *Echium vulgare* (23% cover), with *Poa cita*, *Dactylis glomerata*, *Dichelachne crinita* and *Trifolium arvense* as minor components (State C).

By 2000, four ungrazed quadrats and two quadrats in the rabbit-grazed treatment had undergone transitions from States A or B to State C (Fig. 4). These transitions reflect substantial increases in the cover of *Echium vulgare*, and smaller increases in *Dactylis glomerata*, *Trifolium arvense*, and the native grasses *Dichelachne crinita* and *Rytidosperma unarede*. The average cover of *Poa cita* decreased significantly in these quadrats. In the other three rabbit-grazed quadrats, we recorded transitions to a new state (D), which was dominated by *Dactylis glomerata* (29–39% cover) and *Echium* *vulgare*. Here, *Poa cita* decreased from 24, 12 and 7% cover in 1990, to absence in all three quadrats in 2000. Sheep+rabbit grazed quadrats remained within States A and B between 1990 and 2000. However, cover of *Poa cita* decreased here too, from *c.* 6% in both states in 1990, to < 1% in State A, and *c.* 3% in State B, in 2000.

Thus, *Poa cita* decreased in all treatments over the 10 years of the study. The most striking changes were recorded where *Dactylis glomerata* and *Echium vulgare* invaded quadrats with previously high cover of *Poa cita* in rabbit-grazed treatments. However, substantial decreases in *Poa cita* were also recorded where *Echium vulgare* invaded both grazed and ungrazed quadrats. The latter appeared to be a consequence of whole tussock death caused by drought, rather than by grazing, as rabbit numbers were low over the observation period. We attribute the dramatic increase in forbs following reduced grazing to high natural fertility enhanced by topdressing.

Discussion

Of the four grassland vegetation types monitored in the Mackenzie Basin, short fescue and silver tussock grasslands showed the most striking changes in species composition over the first 10 years of this trial.

In fescue tussock grasslands, invasion of *H. pilosella* and the loss of intertussock herbs and, in some cases, fescue tussock, has occurred regardless of whether sheep and/or rabbits were excluded. Rose *et al.* (1995) recorded similar changes in fescue tussock grasslands in the Harper and Avoca valleys in Canterbury, following the cessation of sheep grazing. Rapid invasion of *H. pilosella* into similar tussock grassland communities, with abundances reaching > 50% cover, have also been reported in the eastern South Island, especially in Otago (Duncan *et al.*, 1997; Johnstone *et al.*, 1999). All of these studies suggest that transitions to *H. pilosella*-dominated states are likely to continue to occur in fescue tussock grasslands regardless of grazing management.

Rose and Frampton (1999) suggested that where oversowing and topdressing was not feasible or desirable, e.g. on land managed for conservation, the best strategy for combating the invasion of *Hieracium* was to encourage and maintain tall, dense tussock canopies and litter layers. However, at our fescue tussock study sites, tussock canopies had increased very little following the removal of sheep and rabbit grazing for 10 years. The low (average *c.* 6%) cover of short tussocks may be below the density threshold required for recovery and *H. pilosella* suppression. Nevertheless, we did observe early signs of recovery of certain native shrubs, e.g. scattered *Carmichaelia petriei* and *C. vexillata* shrubs increased in stature in ungrazed treatments. Moreover, *Discaria toumatou* (matagouri) seedlings were seen establishing in *H. pilosella* mats in sites throughout the study period, presumably in response to generally reduced levels of grazing since 1990. We conclude that the removal of grazing in fescue tussock grasslands may not lead to rapid recovery of tussocks, but will encourage very slow succession to canopy-forming native shrublands and woodlands. This would produce communities that would have natural character and high conservation value, and environments less conducive to *H. pilosella* invasion than the present, open, short-tussock states.

We found no evidence of prolific establishment of palatable adventive species in response to reduced grazing, except at the one silver tussock locality. Options for conserving silver tussock grasslands on naturally fertile sites in the long term appear to be few: in this trial *Poa cita* cover decreased substantially where there was competition from exotic species following grazing-removal. Similar transitions to exotic-dominated states were recorded in silver tussock grasslands on the Port Hills, Canterbury, in response to grazing-removal (Meurk *et al.*, 1989; Lord, 1990). However, in our sheep plus rabbit grazing treatments, whole tussocks died, apparently from drought, without replacement by younger cohorts or by seedling recruitment**.** Intensive weeding to remove aggressive adventive grasses and forbs, in the absence of grazing, might be an option to both maintain *Poa cita* cover and enable seedling recruitment, but this would be feasible only within small areas.

Grassland states dominated by tall (red and snow) tussocks were more stable than short (fescue and silver) tussock grasslands, although *Hieracium* spp. increased in intertussock patches. This result suggests that the practice of opening up and transforming tall tussock to short tussock through burning and grazing has reduced the stability of the plant communities. Our results support the conclusion of Rose and Frampton (1999) that large tussocks and associated thick litter layers confer the greatest resistance to the invasion of *Hieracium* spp. in tussock grasslands. At one snow tussock locality, there was evidence that grazing had exacerbated the loss of tussock cover and facilitated invasion and transition to a *H. pilosella*-dominated state, while grazing-removal reversed this process. Moreover, some *Chionochloa* seedlings were observed within ungrazed snow tussock grasslands, despite the presence of *Hieracium* spp. These results are consistent with other studies showing the recovery of snow tussock following the removal of grazing (Rose and Platt, 1992; Lee *et al.*, 1993; Duncan *et al.*, 2001). Vegetation at the other red and snow tussock grassland localities appeared to have reached more stable states, and showed relatively small and inconsistent responses to grazing treatments.

Our data suggest that fescue (*F. novae-zelandiae*) tussock, snow (*C. rigida*) tussock, and probably also red (*C. rubra*) tussock grasslands, will require different conservation management practices from those for silver tussock (*Poa cita*) grasslands. In fescue, snow or red tussock grassland study sites, where there was no evidence that grazing removal led to increased weed invasion, we suggest that the removal of both sheep and rabbit grazing will provide the best opportunities for the establishment of later-successional life forms such as native shrubs, for the regeneration and extension of tussock canopies, and for the build-up of litter to combat *H. pilosella* invasion. However, in the absence of grazing it will probably be necessary to control forest-forming woody weed species that were not well represented at our study localities (e.g. *Pinus* spp.).

Our experiment has not so far demonstrated any practical options for managing induced tussock grasslands for the maintenance of diverse indigenous intertussock floras. Intertussock species richness appears to be declining in grasslands across the eastern South Island, irrespective of current levels of grazing and burning (e.g. Duncan *et al*., 2001). The weak effects of grazing treatment in this experiment may be due to relatively small differences between them, as a consequence of low ambient stock-grazing intensities and good feral rabbit control over the decade. However, other studies also suggest that the effects of manipulated grazing levels on intertussock biodiversity is inconsistent between sites (e.g. Allen *et al.*, 1995; Walker and Lee, 2000). Duncan *et al*. (2001) suggest that a causal link between *H. pilosella* and declining intertussock species richness has been difficult to demonstrate. Nevertheless, in our study, *H. pilosella* increased and native low growing species have decreased simultaneously. We therefore suggest that successful biological control of *H. pilosella* may present new opportunities and options for maintaining intertussock native biodiversity by altering the present competitive balance, and these should continue to be explored.

Conclusions

H. pilosella has invaded *F. novae-zelandiae* grasslands regardless of grazing treatment. *H. pilosella* cover may be approaching a plateau in some areas. Cessation of grazing is unlikely to lead to the rapid recovery of short-tussock cover in these grasslands. However, slow succession to native shrubland may be possible, with appropriate woody weed control, over time periods of several decades. Dense red and snow tussock grasslands of *Chionochloa* spp. have been more stable than fescue grasslands, and more resistant to invasion by *Hieracium* spp., perhaps due to the effects of shading and deeper litter layers. In one snow tussock grassland locality, *C. rigida* tussocks recovered and *H. pilosella* cover decreased with complete grazing removal, but continued grazing by sheep and/or rabbits perpetuated decreases in *C. rigida* cover and increases in *H. pilosella*. It is too early to determine the effects of grazing treatments on red tussock grasslands. *Hieracium* biological control initiatives may give rise to more options for managing induced tussock grasslands for the maintenance of indigenous intertussock floras. To successfully conserve silver tussock grasslands over the long term, intensive management may be needed to control competing exotic species and to enable silver tussock seedling recruitment.

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