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THE DISTRIBUTION AND ABUNDANCE OF *HIERACIUM* SPECIES (HAWKWEEDS) IN THE DRY GRASSLANDS OF CANTERBURY AND OTAGO

Summary: We examined the distribution and abundance of the invasive *Hieracium* species (hawkweeds) in the dry grasslands of the Upper Waitaki Basin (Canterbury) and Otago, using measures of *Hieracium* species frequency and hawkweed cover from 301 vegetation plots. Average hawkweed cover was significantly less in Otago than Canterbury. Hawkweed cover was also lower on drier sites, with hawkweeds having less cover at lower elevation, on more xeric sites and, in Canterbury, on soils with a lower moisture holding capacity. Environmental variables (elevation, moisture index, soil class, and measures of rabbit activity and the amount of recent pasture development) explained 43% of the variation in hawkweed cover in Canterbury, but only 25% in Otago. Furthermore, having controlled for environmental differences among plots, hawkweed cover in Otago was significantly spatially autocorrelated such that plots on the same property had similar hawkweed cover, but tended to differ from plots on other properties. This pattern is consistent with the hypothesis that variation in property management influenced the degree of hawkweed infestation. However, the same pattern was not found in Canterbury.

We propose a general model to explain the observed patterns. The probability that a site will be invaded by hawkweeds is a function of: (1) the suitability of the site for hawkweed establishment (a function of the environment and past management), and (2) the size of the hawkweed propagule rain. The probability of hawkweed invasion is high when one or both of these variables have high values. Following initial invasion, there will be more local propagules coming from newly established plants and hawkweed cover at a site will increase, eventually stabilising at a level predictable from the environmental conditions at the site. This model predicts that the sites most suited for hawkweed establishment would be invaded first and fill the quickest. These susceptible sites would then serve as foci, providing propagules for subsequent hawkweed spread into adjacent, less invasion prone areas. The model predicts that the initial increase in hawkweed cover at a site should be exponential, and that there should be a lag in hawkweed spread whereby less susceptible sites are invaded later or at a slower rate. Both predictions are supported by data from monitoring trials. The model can explain the lower abundance of hawkweeds, the less predictable distribution of hawkweeds in relation to environmental variables, and the significant spatial autocorrelation in hawkweed cover in Otago compared to Canterbury, if hawkweed invasion in Otago is less complete than in Canterbury.

Keywords: invasion, tussock grassland

Introduction

In the last 30 years the tussock grasslands of the eastern South Island, New Zealand, have been extensively invaded by species of *Hieracium* (hawkweeds), especially *H. pilosella*[1], *H. praeltum*, *H. lepidulum* and *H. caespitosum* (Scott, 1985). Hawkweeds were noted in tussock grasslands in the late 1800's, but they began to increase dramatically in abundance in the 1960's and are now the dominant vegetation cover over more than 500 000 ha of the South Island (Hunter, 1991). The most

abundant and widespread species, *H. pilosella*, can form extensive low-growing mats that exclude other species, and that are unproductive for livestock grazing. Consequently, the dominance of *H. pilosella* over large areas threatens the viability of the pastoral industry and the conservation values of tussock grasslands.

There has been considerable debate about whether some management practices facilitate the invasion and spread of hawkweeds in tussock grasslands (Hunter, Mason and Robertson, 1992; Rose, 1992; Rose, Platt and Frampton, 1995). In particular, Treskonova (1991a, b) suggested that hawkweed spread is encouraged by overgrazing and burning, and consequently, destocking, controlling

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[1] Nomenclature follows Webb, Sykes and Garnock-Jones (1988).

rabbit populations, and reducing burning frequency have been suggested as ways of preventing hawkweed invasion (Kerr, 1992). However, few studies have directly tested the hypothesis that management, particularly livestock grazing or burning, is a critical determinant of hawkweed spread. This is probably because of the logistical difficulties in setting up large-scale experiments, or because data are lacking to accurately reconstruct the management history of sites (but see Allan, O'Connor and White, 1992; Allen, Lee and Mark, 1992; Espie and Meurk, 1992; Rose et al., 1995).

If management has influenced hawkweed spread, then the uneven distribution and abundance of hawkweeds across the present landscape could reflect variation in past land-use. For example, areas that now have a high cover of hawkweeds may have been more intensively grazed or burnt in the past than areas where hawkweed cover is low. The alternative is that the present distribution and abundance of hawkweeds bears no relationship to past management, either because management practices have not affected hawkweed spread, or because there has been little variation in past management so that all tussock grasslands were equally predisposed to hawkweed invasion. In the absence of management effects, the present uneven distribution of hawkweeds presumably reflects variation in environmental conditions, or limitations to hawkweed dispersal.

It would be useful to know how much of the spatial variation in hawkweed abundance was attributable to variation in past land-use, and how much was due to present-day environmental variation, for at least two reasons: (1) if much of the present variation in hawkweed abundance is due to variation in past land-use, then it may be possible to identify those management practices that minimise hawkweed invasion and spread, and (2) if some environments are particularly prone to invasion by hawkweeds, then it is important to identify and manage those areas accordingly.

It is usually straightforward to measure environmental variables and to determine how important these are in accounting for variation in species composition. This information could address part 2 above. Gathering data to address part 1 is more problematic because historical events, such as fires or episodes of livestock grazing, are difficult or impossible to measure directly. Nevertheless, we may be able to identify the imprint of past land-use on vegetation pattern because its effect should be evident at a clearly defined spatial scale. The pastorally farmed tussock grasslands of the South Island are divided into properties that are managed independently and that have had stable boundaries

for many decades. Properties almost certainly differ in their historical frequency of burning, stocking rates, the amount of pasture development, and the effort expended on rabbit control (O'Connor and Harris, 1992). If variation in these practices has strongly influenced hawkweed spread, then properties in a similar environment but with a different history of management should differ in their degree of hawkweed infestation. If this is true then, having controlled for any environmental effects, hawkweed abundance should have a nonrandom spatial structure; neighbouring sites on the same property should have similar hawkweed cover, but should differ from sites further away on properties with a different management history.

We use this line of argument to address two questions in this paper: (1) what are the environmental variables that correlate most strongly with hawkweed abundance in the dry grasslands of Otago and Canterbury and how well do these variables explain variation in hawkweed cover, and (2) after accounting for relationships between hawkweed cover and environmental variables, does hawkweed cover have a spatial structure consistent with the pattern expected if past property management were also an important determinant of the degree of hawkweed infestation?

Study Area

The study area is the dry, inland basins and hill slopes of Central Otago and the Upper Waitaki Basin (Canterbury) between 180 m and 1160 m elevation (only five of the 301 vegetation plots in this study were at elevations higher than 1000 m). Vegetation was sampled in twelve ecological districts (McEwen, 1987): Dunstan, Lindis, Maniototo, Mannorburn, Old Man, and Pisa in Otago, and Ahuriri, Benmore, Grampians, Hawkdun, St Mary, Pukaki, and Tekapo in Canterbury.

The study area is isolated from maritime influences by surrounding mountains and the climate is semi-arid. Rainfall is lowest in the basins of Central Otago (344 mm per annum at Alexandra), but increases with altitude, and from east to west approaching the Southern Alps. Annual rainfall is highly variable and the area is subject to droughts. Temperature shows strong seasonal variation with warm summers and cool winters. At Alexandra, the mean daily maximum temperature in July and February is 7.9°C and 22.8°C respectively (Gerlach, 1974).

The study area is in two geologically distinct regions. Sites in Otago are underlain by Mesozoic schists of the Haast Supergroup that have faulted and

lifted to form a characteristic "basin and range" topography (McSaveney and Stirling, 1992). Soils are formed in schist, schist derived loess, or alluvium from various sources. Climate has a major influence on soil properties and the zonal soil types range from brown-grey to yellow-grey to yellow-brown earths along a gradient of increasing precipitation and leaching (Leamy, Ludecke and Blakemore, 1974; Brash and Beecroft, 1987). In Canterbury, the study area is the Pleistocene and Holocene moraine and outwash terraces of the Upper Waitaki Basin, and the lower slopes of the surrounding mountains, underlain mainly by indurated sandstones, mudstones, and conglomerates of the Torlesse Supergroup (greywacke and argillite; Webb, 1992). Soils are formed primarily in greywacke and greywacke derived alluvium or loess. Climate is again a major influence on soil properties and the zonal soil types follow the same sequence with increasing precipitation as in Otago.

The vegetation of the study area has been severely modified by human activity including burning, grazing by livestock and feral animals (especially rabbits), the application of fertiliser, and the introduction of exotic plant species. Descriptions of the vegetation of parts of the study area, and the history of vegetation change in the region, can be found in Zotov (1938), Connor (1964, 1992), Hubbard and Wilson (1988), Wilson, Williams and Lee (1989), and Walker, Mark and Wilson (1995).

Methods

Data collection

This study uses data collected in the summer of 1991/92 for the Rabbit and Land Management Programme (Rabbit and Land Management Taskforce, 1988) to monitor vegetation change on pastoral properties in the dry grasslands of Central Otago and the Upper Waitaki Basin. Vegetation was sampled on 54 pastoral properties, chosen to cover evenly the geographical range of dry grasslands in the study area.

Three hundred and one vegetation plots were located on the 54 pastoral properties. Between 2 and 14 plots were allocated to each property by property size (larger properties having more plots), and to ensure an even coverage of the study area. The plots allocated to a property were located along a previously established rabbit count route that traversed the property along existing tracks. These routes were originally established for monitoring rabbit numbers by night counting and they were marked every kilometre, with their total length

varying from c. 20 - 40 km. Vegetation plots were located equidistantly along these rabbit count routes at a kilometre marker, with the distance between plots determined by the length of the route and the number of plots allocated to the property. When a plot was located at a site unrepresentative of the vegetation of the general area (for example, a small shrub covered gully in grassland), the plot was moved to either the next or previous kilometre marker.

A plot was identified as an area of relatively homogenous vegetation of c. 2 - 4 ha (150 m x 150 m - 200 m x 200 m), adjacent to a kilometre marker. In each plot hawkweed abundance was measured in two ways. First, 100 1 m^2 quadrats were haphazardly located in each plot, and in each quadrat the presence of all *Hieracium* species was recorded. The proportion of quadrats that each species of *Hieracium* was present was used as a measure of species frequency. Second, each plot was traversed with a wheel that placed a spoke on the ground every 1 m. The number of hits, out of 1000 spoke placements, that were recorded as *Hieracium* was used as a measure of hawkweed cover in each plot, expressed as percent cover. Note that the hawkweed cover score sums the cover for all species of *Hieracium* found in each plot; we did not differentiate to species using this method.

At each plot, the following environmental variables were determined: aspect, slope angle, exposure (in four classes from sheltered to open), landform (ridge crest, sideslope, footslope, fan or terrace), and slope shape (concave, convex or straight). Elevation, grid references, and soil set were recorded from topographic and soil maps (New Zealand Soil Bureau, 1964). Soil sets were grouped into one of eight soil classes: recent, brown-grey terrace and fan, brown-grey hill, yellow-grey terrace and fan, yellow-grey hill, yellow-brown terrace and fan, and yellow-brown hill soils. Soils of the yellow-brown Mackenzie set in Canterbury were classed separately. None of the environmental variables that we recorded have a direct influence on plant performance. However, factors that directly influence plant performance, such as temperature, moisture and nutrient availability, vary predictably along elevation, topographic, and soil gradients in the study area (Brash and Beecroft, 1987; Webb, 1992). The environmental variables recorded in this study were therefore used as proxy variables for those factors likely to directly influence vegetation pattern.

In addition, we measured two variables that reflect past management. Each plot was ranked by the amount of recent pasture development (oversowing and fertilising) that appeared to have

taken place, from 0 (no evidence of development) to 3 (recent development), and recent rabbit activity was measured by counting the number of rabbit diggings (burrows and scrapes) in a 100 x 1 m transect laid across each plot. These two measures were included in the set of environmental variables used to characterise each plot.

Data analysis

Topographic position and exposure influence soil moisture regimes through evapotranspiration and water runoff (Birkland, 1984). We constructed an index of relative moisture status for each plot by summing values assigned to each class of the aspect, exposure, slope angle, slope shape, and landform variables (Parker, 1982). Values were assigned to each class according to their perceived influence on site moisture status (Table 1).

Table 1: *Moisture values assigned to each class of the slope angle, exposure, landform, slope shape and aspect descriptors. The values were assigned to each class according to their perceived relative influence on site moisture status. Lower values indicate a lower moisture status. The relative moisture index was obtained by summing the values for each descriptor.*

Descriptor	Class	Moisture value
Slope Angle	0-3°	10
	0-3° + some steeper	9
	4-7°	7
	4-7° + some steeper	6
	8-15°	5
	8-15° + some steeper	3
	16-20°	1
	>21°	0
Exposure	0 (sheltered)	15
	1	10
	2	5
	3 (exposed)	0
Landform	ridge crest	0
	sideslope	7
	footslope	15
	fan	15
	terrace	7
Slope Shape	concave	10
	convex	0
	straight	5
Aspect	N	0
	NE or NW	5
	SE or SW	15
	E or W	10
	S	20
	Open	0

The plots were stratified by region and the data from Canterbury and Otago were analysed separately. There were 155 plots in Canterbury and 146 plots in Otago. In each region, we compared the relationship between *Hieracium* species frequency and hawkweed cover with environmental variables and soil classes using rank correlations and analysis of variance.

Controlling for the effects of environmental variables

We examined the spatial variation in hawkweed cover having accounted for any variation among plots that was attributable to environmental differences. To do this, we constructed a multiple regression model with hawkweed cover as the dependent variable and the environmental variables that accounted for a significant portion of the variation in hawkweed cover as the predictor variables. The residuals from this regression represent the variation in hawkweed cover that was independent of the measured environmental variables. We analysed the spatial distribution of these residuals to test if, having controlled for environmental differences, plots on the same property had a similar cover of hawkweeds but differed from plots on other properties. A variable that exhibits such a non-random spatial structure is said to be spatially autocorrelated.

We used hawkweed cover rather than species frequency as a measure of abundance because cover was better than frequency at differentiating among plots with a lot of *Hieracium* (Figure 1). When hawkweed cover at plots in Canterbury was around 25%, *H. pilosella* was recorded at 80-100% frequency in the quadrats. Subsequent increases in hawkweed cover did not result in a corresponding increase in the frequency of *H. pilosella* because it was already being recorded at, or close to, its maximum frequency. The disadvantage of using hawkweed cover was that it lumped all species of *Hieracium* together and could have obscured differences among species.

We used ordinary least squares regression because methods to analyse spatial autocorrelation in regression residuals have only been developed for least squares methods (Cliff and Ord 1981; Upton and Fingleton 1985). Percent hawkweed cover was arcsine square root transformed prior to analysis. The combination of environmental variables that best explained variation in the transformed cover scores was identified using a forward selection procedure as follows: (1) all environmental variables (including soil class) were tested individually for inclusion in the model and the variable with the
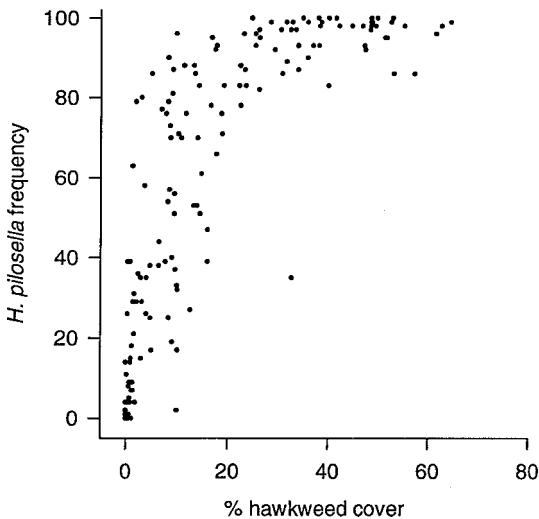
Figure 1: *Percent hawkweed cover plotted against percent* Hieracium pilosella *frequency, for the 155 plots in Canterbury.*

highest significant *F*-ratio was added to the model ($P < 0.05$, the method of significance testing is described below). This procedure was repeated with the remaining environmental variables until no more significant predictors could be added; (2) step 1 was repeated, first using all squared terms, and second using all interaction terms, for the environmental variables included in step 1 of the model construction.

We tested the significance of environmental variables in the regression model using a randomisation test. This was because the presence of spatial autocorrelation in the regression residuals would violate an assumption of least squares regression, that the error terms in the model were independent. This could overinflate the significance of predictor variables when significance was calculated using least squares methods, increasing the chance of a type I error; a variable is included in the model as a significant predictor when in fact it is not (Cliff and Ord, 1981). The randomisation test compared the *F*-ratio of the variable being tested for inclusion in the model with the distribution of *F*-ratios obtained from 500 random assignments of the hawkweed cover scores to the variable of interest (Manly, 1991). A variable was considered a significant predictor if its *F*-ratio exceeded 95% of the *F*-ratios calculated from the 500 random assignments (ie. $P < 0.05$).

Testing for spatial autocorrelation

Having controlled for differences among plots in environmental variables, we tested for spatial autocorrelation in hawkweed cover by analysing the residuals from the regression models. Moran's *I* is a widely used statistic for detecting spatial autocorrelation in sample data (Cliff and Ord, 1981; Upton and Fingleton, 1985; Legendre and Fortin, 1989). However, a modified form of Moran's *I* that controls for the correlation among residuals expected using least squares regression is used when testing for autocorrelation in regression residuals (Cliff and Ord, 1981). This modified test statistic, I_k, is given (in matrix notation) by:

$$I_k = \frac{n}{S_0} \frac{\mathbf{e'} \, \mathbf{W} \mathbf{e}}{\mathbf{e'} \, \mathbf{e}}$$

and

$$S_0 = \sum_{i}^{n} \sum_{j}^{n} W_{ij} \quad \text{where } i \neq j$$

Where *n* is the number of plots, **e** is the (n x 1) vector of regression residuals, **e'** is the transpose of **e**, and **W** is an (n x n) weight matrix constructed in this study as follows: W_{ij} took the value 1 when plots *i* and *j* were on the same property, and 0 otherwise. Constructing the weight matrix to take these values tested the hypothesis that the residuals of plots on the same property were autocorrelated. A positive value of I_k would indicate that plots on the same property had similar hawkweed cover, having controlled for environmental differences.

The significance of I_k was tested using the randomisation procedure described in Cliff and Ord (1981: 206). A 'dummy' vector of regression residuals, with a mean of 0, was constructed using parameters from the regression model and assuming that the random error terms were independently and normally distributed with a mean of 0. The value of I_k calculated from the observed regression residuals was compared with 500 values of I_k calculated by generating the 'dummy' vector of regression residuals 500 times.

Results

Four species of *Hieracium* were recorded in this study and they differed in their regional distribution (Table 2). *H. pilosella* was widespread in both Canterbury and Otago, but occurred at more locations and at higher frequency in Canterbury, *H. praeltum* was widespread in Canterbury but rare in Otago,

Table 2: *The percent of plots on which the four species of* Hieracium *occurred in Canterbury and Otago, and their mean % local frequency ± 1 standard deviation (calculated from quadrat data on plots where they were present). Also shown is the mean percent hawkweed cover (± 1 standard deviation) in each region, averaged over all plots. In Canterbury there were 155 plots and in Otago there were 146.*

| | Canterbury | | Otago | |
	% of plots	Mean frequency (%) ± 1 SD	% of plots	Mean frequency (%) ± 1 SD
H. pilosella	95	63 ± 34	54	20 ± 27
H. praeltum	82	28 ± 28	8	4 ± 6
H. lepidulum	3	4 ± 4	32	15 ± 27
H. caespitosum	1	1		
Mean hawkweed cover (%)		19 ± 18		4 ± 11

H. lepidulum was rare in Canterbury and common in Otago, while *H. caespitosum* was recorded only once. Average hawkweed cover was significantly greater in Canterbury than in Otago (t-test, $P < 0.001$).

Relationship between *Hieracium* frequency, hawkweed cover, and environmental variables

Elevation was the variable that most strongly correlated with *Hieracium* frequency and hawkweed cover (Table 3). In both Canterbury and Otago, all species of *Hieracium* were more abundant at higher elevations. *Hieracium* frequency and hawkweed cover were also correlated with rabbit activity and development although the direction of correlations differed between regions.

Controlling for the effects of elevation by partial correlation changed some of these relationships. Moisture index, which was previously not significantly correlated with any of the abundance measures, was positively correlated with hawkweed cover in both regions, and with *H. pilosella* frequency in Otago. After controlling for elevation, the correlations between *Hieracium* frequency, hawkweed cover, rabbit activity, and development were weakened in Otago, though most remained significant, while correlations between *H. pilosella* frequency, hawkweed cover, and development in Canterbury were strengthened.

Relationship between *Hieracium* frequency, hawkweed cover, and soil type

Hieracium frequency and hawkweed cover were strongly correlated with elevation so it was not surprising that both measures differed significantly among soil classes as these separate along an elevation gradient (Table 4, not shown for Otago). The higher elevation yellow-brown soils generally had a greater frequency and cover of hawkweeds than lower elevation yellow-grey and brown-grey soils, in both Canterbury and Otago. We investigated

Table 3: *Spearman rank correlation coefficients of* Hieracium *species frequency and hawkweed cover with environmental variables in Canterbury and Otago. Also shown are the partial correlation coefficients, controlling for the effects of elevation, between environmental variables and* Hieracium *species frequency and hawkweed cover (indicated by variable$_{elevation}$).* * $P < 0.05$, ** $P < 0.01$; *for Canterbury n = 155, for Otago n = 146.*

| | Canterbury | | | Otago | | |
| | *Hieracium* species frequency | | Hawkweed cover | *Hieracium* species frequency | | Hawkweed cover |
	H. pilosella	*H. praeltum*		*H. pilosella*	*H. lepidulum*	
Elevation	0.40**	0.36**	0.44**	0.40**	0.51**	0.49**
Rabbit activity	0.39**	0.01	0.35**	-0.23**	-0.16	-0.24**
Moisture Index	-0.01	-0.01	0.12	0.09	-0.07	0.03
Development	-0.20*	-0.01	-0.07	0.28**	0.35**	0.35**
Rabbit activity$_{elevation}$	0.38**	-0.02	0.34**	-0.17*	-0.08	-0.18*
Moisture Index$_{elevation}$	0.06	0.05	0.22**	0.23**	0.08	0.20*
Development$_{elevation}$	-0.30**	-0.08	-0.17*	0.14	0.17*	0.19*

Table 4: *Mean hawkweed cover (± 1 standard deviation), and the residuals of hawkweed cover and* Hieracium *species frequency after linear regression on elevation, by soil class, in Canterbury. Soil classes with the same letter do not differ significantly in the residuals of mean* Hieracium *frequency or cover (*P < 0.05, *Duncan's multiple range test for ANOVA). The full names of the soil classes and the soil sets (New Zealand Soil Bureau, 1964) included in each class are: YBEh (= yellow-brown earth hill soils: Benmore, Cass, Kaikoura, Tekapo); YBEtf (= yellow-brown earth terrace and fan soils: Acheron, Pukaki); BGEh (= brown-grey earth hill soils: Otematata, Waitaki); YGEh (= yellow-grey earth hill soils: Omarama, Meyer); YBEm (= yellow-brown earth soil: Mackenzie); BGEtf (= brown-grey earth terrace and fan soil: Grampians); REC (= recent soils: Eweburn, Tasman).*

Soil class class	Number of plots	Mean hawkweed cover (%) ± 1 SD	Residuals of mean hawkweed cover		Residuals of mean *H. pilosella* frequency		Residuals of mean *H.praeltum* frequency	
YBEh	30	34 ± 18	0.124	*a*	0.179	*a*	-0.062	*b*
YBEtf	37	23 ± 18	0.072	*a*	0.166	*a*	0.243	*a*
BGEh	22	18 ± 21	0.015	*ab*	-0.075	*abc*	-0.149	*b*
YBEm	33	9 ± 9	-0.039	*ab*	0.091	*ab*	-0.052	*b*
BGEtf	14	7 ± 8	-0.101	*b*	-0.295	*c*	-0.177	*b*
YGEh	13	14 ± 15	-0.111	*b*	-0.199	*bc*	-0.028	*b*
REC	6	5 ± 5	-0.127	*b*	-0.338	*c*	-0.115	*b*

if soil class influenced hawkweed abundance independently of elevation. We controlled for elevation by calculating the residuals from the linear regression of *Hieracium* frequency and hawkweed cover on elevation (cover and frequency scores were arcsine square root transformed prior to analysis). We then tested for significant differences in the mean residual scores among soil classes using analysis of variance. In Otago, having controlled for elevation, there were no significant differences among soil class in mean *Hieracium* frequency or cover. In Canterbury, however, soil class was a highly significant predictor after controlling for elevation (Table 4). Hawkweed cover and *H. pilosella* frequency were greatest on yellow-brown hill, terrace, and fan soils, and *H. praeltum* frequency was higher on yellow-brown earth terrace and fan soils, than on other soil types.

Spatial structure of the regression residuals

In Canterbury, the significant environmental predictors explained 43% of the variation in hawkweed cover (Table 5). The residuals from this regression did not show significant within-property autocorrelation ($I_k = 0.44$, $P = 0.166$ from 500 randomisations). Thus, having controlled for environmental variation among plots, there was no evidence that an unmeasured spatially structured process, such as variation among properties in past management, was important in influencing hawkweed cover.

In Otago, the same environmental variables explained only 25% of the variation in hawkweed cover, but here the regression residuals were significantly autocorrelated ($I_k = 2.66$, $P = 0.002$

from 500 randomisations). Having accounted for environmental variation, hawkweed cover in Otago had a highly significant spatial structure; plots on the same property had a similar cover of hawkweeds, but differed from plots on other properties.

In Otago, rank correlations showed that *Hieracium* frequency and hawkweed cover were higher in developed pastures and declined with greater rabbit activity, the opposite results to Canterbury (Table 3). However, in Otago rabbit activity and development were confounded with other environmental variables so that neither were significant predictors of hawkweed cover after controlling for elevation, moisture index, and soil class (Table 5).

Table 5: P *values and total* r^2 *for the significant predictors (*P < 0.05*) in the multiple regression models between hawkweed cover and environmental variables in Canterbury and Otago. The* P *value for each environmental variable was estimated by comparing the observed regression F-ratio when that variable was included in the regression model, with the F-ratios from 500 random assignments of the hawkweed cover scores to the variable of interest.*

	Canterbury	Otago
elevation	0.002	0.002
elevation^2	0.040	
moisture index	0.002	0.028
elevation x moisture index	0.030	0.036
rabbit activity	0.002	
development	0.012	
YBEh	0.002	
YBEtf	0.010	
BGEh		0.012
r^2	42.8	25.0

Discussion

Relationship between hawkweed cover and environmental variables

Hawkweed cover was generally lower on drier sites. Thus, the decline in hawkweed cover at progressively lower elevations parallels a decrease in moisture availability due to lower precipitation and higher evapotranspiration (Mark, 1965; Maunder, 1965). In addition, having controlled for elevation, hawkweed cover was lower on more xeric sites (lower moisture index), and the significant interaction between elevation and moisture index (Table 5) indicated that hawkweeds were least abundant at low elevations on sites with a low moisture index. In Canterbury, some of the variation in hawkweed cover with soil class most likely reflects differences in moisture availability due to differences in soil texture. Hawkweed cover was highest on yellow-brown hill, terrace, and fan soils formed in fine-textured loess, that have a high moisture holding capacity. Hawkweed cover was lower on adjacent outwash soils of the yellow-brown Mackenzie set, that are stony and highly drought-prone (Table 4). This decrease in hawkweed cover, moving from loess to nearby outwash soils, parallels a decrease in total vegetative cover (Dymond et al., 1992) that has similarly been attributed to a reduction in soil moisture availability. The mechanism resulting in lower hawkweed cover at lower elevation, on more xeric sites, and on soils with lower moisture holding capacity, may be a requirement for adequate moisture to ensure successful hawkweed germination (Makepeace, 1985).

In Canterbury, though not in Otago, development and rabbit activity were also significant predictors of hawkweed cover. Recently developed grassland had less hawkweed cover than undeveloped grassland, consistent with studies showing that oversowing and fertilising encourage a dense sward of exotic grass and clovers that appear to outcompete species of *Hieracium* (Scott and Covacevich, 1987; Scott, Robertson and Archie, 1990; Cossens, 1992; Svavarsdóttir, 1995). The greater hawkweed cover on sites with higher rabbit activity could have resulted from intensive grazing and modification of the previous vegetation by rabbits, favouring hawkweed spread. Alternatively, it could reflect rabbits' habitat preference for low-growing, open vegetation, with rabbits favouring sites already invaded by hawkweeds.

Above 1000 m, hawkweed abundance apparently declines with elevation (Treskonova, 1991a; Cuff, 1992). Hence, there appears to be an intermediate elevation band in which hawkweed abundance peaks (Rose, 1992). While we suggest that lack of moisture may limit hawkweed spread at lower elevations and on droughty soils, it is not clear what limits hawkweed spread at higher elevations. Certainly a peak in hawkweed abundance at intermediate elevations could reflect optimum environmental conditions for hawkweed growth and spread (see Makepeace, 1985). However, higher elevation tussock grasslands have also been less modified by human activities and may possess a mix of species or vegetation structure that presently resists hawkweed invasion. We suspect that the greatest opportunity to identify attributes of undeveloped tussock grassland vegetation that confer resistance to hawkweed invasion are in these less modified, higher rainfall areas over 1000 m elevation.

Explaining the general patterns in hawkweed cover

The most likely cause of spatial autocorrelation in the Otago residuals is the omission from the regression model of one or more variables that, at the property scale, have a spatially-structured effect on hawkweed cover. Variables that reflect differences among properties in past management not measured in the present study, such as historical grazing intensity or burning frequency, are strong possibilities. An alternative is that one or more unmeasured, spatially structured environmental variables were key determinants of hawkweed cover in Otago. While this is plausible, we do not know what the environmental variable(s) might be. They would have to be independent of the variables already included in this study, and exhibit patchiness at the property scale (thousands of hectares). Apart from the clumping reflecting within-property autocorrelation, a map of the Otago regression residuals showed no patterns consistent with any obvious, large-scale environmental gradients that we might have failed to measure (for example an east-west rainfall gradient).

While the addition of management or environmental variables might account for the spatial autocorrelation in the Otago data, this does not explain why similar spatial autocorrelation was absent in Canterbury (why, for example, would past management influence present hawkweed cover in Otago but not Canterbury?), or why hawkweed cover is less predictable from environmental variables in Otago than Canterbury. Thus, our analysis has uncovered patterns that cannot be readily explained in terms of simple management or environmental gradients. We propose a model of hawkweed spread that can account for all of the

above patterns if, as we suggest, hawkweed invasion in Otago is less complete than in Canterbury. First we outline the model, second we indicate how the model would generate the patterns found in the present study, and third we show that two predictions of the model are supported by data from other studies.

In order for any species to invade a locality, that species propagules (either seed or vegetative parts) must arrive at the site and the site must be a 'safe site' for the species to establish and grow (Johnstone, 1986; Eriksson and Ehrlén, 1992). Different localities almost certainly differ in their 'suitability' for hawkweed establishment, which we could describe as a probability; a single hawkweed propagule has a certain probability of successfully establishing at a site, the higher the probability the more suitable the site is. Hence, the probability that hawkweeds will invade a locality is a function of two variables: (1) the suitability of the site for hawkweed establishment (its susceptibility to invasion), and (2) the size of the hawkweed propagule rain (the strength of the invasion effort). High values of one or both of these variables increase the likelihood of hawkweed invasion. Our results suggest that the suitability of a site for hawkweed establishment is a function of both the environment and past management. Furthermore, following initial invasion, more local propagules will be available at a site and hawkweed cover should increase. However, we propose that hawkweed cover will eventually stabilise at a level predictable from the environmental conditions at a site.

The above model predicts that the sites combining suitable environment and management practices favouring hawkweed establishment would be invaded first (see also Cossens, 1992). The probability that hawkweeds will establish at a site is partly a function of the local environment, so hawkweed cover should be predictable from environmental variables. However, the relationship between hawkweed cover and local environment may be weak in the early stages of invasion, or because of the overriding influence of past management. Hawkweeds may be absent, or occur at low abundance, at sites where hawkweed propagules have had insufficient time to spread, or where management practices prevent or slow successful establishment.

Having invaded a site, the increase in local propagules from newly established plants would increase the likelihood of further local establishment and hawkweed cover would increase, eventually stabilising at a level predictable from the environmental conditions at the site. Areas more prone to invasion because of a combination of environmental conditions and particular management practices would act as initial foci, increasing the number of propagules arriving in surrounding areas, and increasing the likelihood that hawkweeds would invade adjacent sites where management practices may have produced conditions less favourable to invasion. Eventually the propagule rain may be sufficient that areas managed in ways that initially prevented or slowed invasion would end up with high hawkweed cover. Hence, hawkweed cover would become more predictable from environmental variables as the invasion of a region progressed, and sites that initially resisted invasion as a consequence of their past management were swamped by the high propagule rain.

This pattern of spread could explain why hawkweed cover was less predictable from environmental variables in Otago compared to Canterbury, if, as we suggest, hawkweed invasion is less complete in Otago. More sites in Otago may lack their potential cover of hawkweeds, either because hawkweeds have had insufficient time to spread across the landscape, or because management practices have initially slowed the spread into some favourable sites, or both. Furthermore, if property management influenced invasion susceptibility, so that some properties acted as invasion foci, then hawkweed cover should have a spatial structure in the early stages of invasion, similar to that found in Otago. Having controlled for environmental differences, hawkweed cover would be high in the neighbouring plots on susceptible properties that served as foci, and lower in plots on other properties. As hawkweeds spread from these foci the spatial patchiness would disappear; the stage we suggest the Upper Waitaki Basin has reached.

This model could produce complex patterns in hawkweed spread across the landscape because the probability of invasion depends on the availability of hawkweed propagules, in addition to interactions between management and environment. However, in addition to accounting for the patterns in hawkweed cover found in the present study, the model makes two testable predictions. First, if the probability of hawkweed establishment is a function of the number of propagules arriving at a site, then we would expect invading hawkweed populations to show an initial exponential increase in size. Uncolonised areas that were distant from source populations would have a low propagule rain and a low rate of hawkweed establishment. An increase in the number of hawkweeds at a site would lead to more local propagules and a progressively higher rate of establishment, with the population eventually

stabilising at a size determined by the environmental conditions at the site. An analysis of 35 years of permanent quadrat data from the Waimakariri Basin (Scott, 1993) shows an initial exponential increase in hawkweed cover, with the population stabilising at about 34% cover, consistent with predictions. Second, we would expect a lag in hawkweed spread whereby sites less suitable for hawkweed establishment would be colonised later, or at a slower rate. We find it compelling that such a lag is evident in a 25 year record (1965-1990) of vegetation change in short-tussock grasslands in the Harper-Avoca catchment (Rose et al., 1995). For the first 10 years (1965-1975) the rate of spread of *Hieracium pilosella* and *H. lepidulum* in areas retired from grazing (a treatment hypothesised to reduce the likelihood of hawkweed establishment) was less than the rate of spread in grazed areas, although the difference was statistically significant only for *H. lepidulum*. After 1975 the rate of spread increased in the retired areas, such that by 1990 average *H. pilosella* frequency was slightly higher in the retired than the grazed blocks. Nevertheless, there is an alternative explanation for this pattern that is equally consistent with the model predictions; the same pattern of spread could have resulted from hawkweed propagules taking longer to reach the retired areas because they were further from source populations (A. Rose, *pers comm*). Finally, at a larger scale, we are suggesting that there is a lag in the rate at which Otago has been colonised by hawkweeds, compared to Canterbury, a lag that could reflect differences in the geology and soils of the two regions, or a different history of hawkweed introductions.

Previous workers have sought to explain patterns in hawkweed invasion as a consequence of past management (Treskonova, 1991a,b), or the suitability of the tussock grassland environment for hawkweed establishment and spread (Scott, 1985, 1993; see Rose et al., 1995). Our model incorporates both of these viewpoints, and we agree with Rose et al., (1995) that single-factor explanations are unlikely to explain the complex dynamics of tussock grasslands. However, we stress that our model is a tentative, provisional attempt to account for the patterns in hawkweed cover in parts of Canterbury and Otago below 1000 m elevation. We present it as a general hypothesis that also predicts the likely spatial and temporal patterns of hawkweed spread. Our hope is that this will stimulate further discussion and research aimed at testing and refining the model outlined in this paper, and in developing additional models to explain the complex patterns in hawkweed invasion. Progress in understanding tussock grassland dynamics, and ultimately in developing strategies for sustainable management of tussock grasslands, rests on developing, testing, and refining conceptual models of how the system functions.

Acknowledgements

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