Post-pastoral changes in composition and guilds in a semi-arid conservation area, Central Otago, New Zealand

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Abstract: Changes in the vegetation of Flat Top Hill, a highly modified conservation area in semi-arid Central Otago, New Zealand, are described four years after the cessation of sheep and rabbit grazing. Unusually moist weather conditions coincide with the four-year period of change in response to the cessation of grazing. Between 1993 and 1997, the average richness and diversity (*H'*) of species increased, and the average proportion of native species decreased significantly. The vegetation was significantly richer in exotic annual and perennial grass species, exotic perennial forbs, exotic woody species and native tussock grasses in 1997 than in 1993. Eight response guilds of species are identified. Most "remnant" native shrubs and forbs were stable, in that they remained restricted to local refugia and showed little change in local frequency. However, taller native grass species increased, some locally, and others over wide environmental ranges. Rare native annual forbs and several native perennial species from "induced" xeric communities decreased, and this may be a consequence of competition from exotic perennial grasses in the absence of grazing. The invasive exotic herb *Sedum acre* decreased in abundance between 1993 and 1997, but several other prominent exotic species increased substantially in range and local frequency over a wide range of sites. Exotic woody species, and dense, sward-forming grasses are identified as potential threats to native vegetation recovery.

Keywords: semi-arid, grassland, shrubland, post-pastoral succession, Response Guild, invasion, exotic species, conservation management

Introduction

Lowland Central Otago was considerably disturbed by mining and pastoral land-use following European settlement in the 1850s (Petrie, 1912; Cockayne, 1919; Zotov, 1938). Until the late 1980s, this highly-modified semi-arid region was generally thought to retain little of value for biological conservation, and the native flora and vegetation of the region was largely overlooked (Wilson, 1989). However, recent botanical and zoological investigations have revealed that it contains important native faunal and floral remnants (e.g. Johnson and Hewitt, 1991; Patrick, 1994).

Restoration of lowland Central Otago vegetation is seen as being problematic. Most of the region is so highly modified that it probably cannot be restored to a state approximating the pre-human condition by any change in management. Recent evidence (Clark *et al.*, 1996) suggests that the pre-human vegetation included podocarp forest patches, and was generally more woody than the frost- and fire-maintained shrubland-grassland mosaic previously envisaged (e.g. McGlone, 1989). The arrival of Polynesians from *c.* 800 years B.P. saw the transformation of the vegetation to seral grassland and shrubland and the elimination of a rich native avifauna. Further degradation of the vegetation cover, through frequent burning and overgrazing by European pastoralists from the 1850s, was exacerbated by plagues of rabbits after *c.* 1870, leading to still greater losses of palatable and/or fire-sensitive plant species (Wardle, 1985). Over large areas, topsoil stripping by wind and water erosion has reduced soil depth and organic content over the last 150 years, and the associated reduction in moisture-holding capacity has exacerbated the aridity of the region (Gibbs, 1980; Hewitt, 1996). These soil changes are, at best, only very slowly reversible.

Central Otago's semi-arid lowlands have been especially prone to invasions of exotic fauna and flora (Petrie, 1883; Williams, 1980; Wilson, 1989; Wilson *et al.*, 1989) and exotic plants present a major problem for the restoration of the native vegetation. In less-modified and more mesic New Zealand ecosystems, the removal of exotic herbivores and predators and the control of exotic plant species can result in succession towards native-dominated communities (e.g. Meurk, 1982; Rose and Platt, 1987). However, in semi-arid areas, the exotic flora dominates the majority of the land area, and the further spread of many exotic species may actually be held in check by simultaneously introduced mammalian herbivores such as rabbits and sheep. Cessation of grazing in some lowland short tussock grasslands has led to dominance by a few of the more vigorous exotic species and to reductions in native and total species richness (e.g. Meurk *et al.*, 1989; Lord, 1990).

In 1992, the Department of Conservation acquired Flat Top Hill, an 820 ha area of highly modified semi-arid grassland/shrubland in Central Otago, near to the driest point in New Zealand, in order to protect its natural values (Johnson and Hewitt, 1991; Figure 1). In 1993, vegetation surveys of the area were carried out and permanent monitoring sites were established (Walker *et al.*, 1995). Three categories of native species were recognised (Walker, 1994):

Type 1. Restricted "remnant" mid- to late-successional species that were probably more abundant and widespread in Central Otago in pre-European times (e.g. shrubs such as *Sophora*[1], *Aristotelia*, *Carmichaelia, Coprosma*, *Kunzea, Olearia* and *Ozothamnus* spp., and short tussock grasses including *Festuca novae-zelandiae* and *Elymus*, *Poa* and *Rytidosperma* spp.).

Type 2. Widespread species of native-rich, xerophytic communities, including *Stellaria gracilenta*, dwarf native grasses (*Poa* and *Rytidosperma* spp.) and mat-forming *Raoulia* and *Colobanthus* spp. These are thought to be early-successional species that, in pre-human times, were restricted to frequently-disturbed and periodically dry places such as braided riverbeds. Their spread may have been "induced" (*sensu* Cockayne, 1928) by the maintenance of open expanses of short vegetation and bare soil in Central Otago by grazing.

Type 3. Native spring annual species which are present as plants only for a few weeks a year, in the early spring, in a few xeric sites on Flat Top Hill. Their pre-human origin and habitat is not known, but it has been suggested that they occupied local areas of periodically dry saline or shallow soils which were unable to support taller vegetation (Walker, 1994).

Type 1 (remnant) species and Type 3 (annual) species are ascribed high conservation values. The latter are representatives of the few annuals in the New Zealand flora, and are known from only a small number localities in Southern New Zealand. Widespread exotic species dominated the vegetation of Flat Top Hill in 1993 and had a greater influence on community structure than native species (Walker *et al.*, 1995). As successful invader species, they share the ability to disperse and persist at low abundance in unfavourable environments, and to rapidly increase and invade spaces when there are short periods of favourable conditions (Wardle, 1985; Jackson & Roy, 1986; Wilson, 1989).

In 1992, sheep grazing on Flat Top Hill Conservation Area ceased, and control operations were undertaken which eliminated feral goats and considerably reduced rabbit numbers. No previous studies showed the effects of release from grazing under such low rainfall, or across the range of plant communities present on Flat Top Hill, and the long-term effects of the new management regime on the vegetation were therefore difficult to predict. In particular, it was not known whether native remnant species (Type 1, above) would be able to recover and spread, whether natural cycles of aridity would be sufficient in the absence of grazing to maintain open, disturbed habitats occupied by high-conservation-value (Type 3) native annual species, whether these, and more widespread native xerophytic species (Type 2), would persist, and whether exotic species would increase to pose a threat to native species and reduce the natural values of the Conservation Area.

A resurvey of permanent vegetation monitoring sites on Flat Top Hill was undertaken in Spring 1997, and changes in the vegetation from Spring 1993 are described in this paper. Classification is used to simplify the description and interpretation of this change. Groups of sites showing similar changes (Site Groups) are identified by classification of changes in composition between 1993 and 1997 (i.e. rather than classification of composition *per se*), and the environmental characteristics of, and differences between, Site Groups is investigated. Species are grouped into "Response Guilds" (*sensu* Szaro, 1986), which are functionally related groups of species that showed similar changes in the Site Groups over the four-year sampling interval. The implications of the initial vegetation changes for long-term trends, and for the management of the Flat Top Hill for conservation, are discussed.

Methods

Study area

Flat Top Hill is an elongated, flat-crested hill extending from Lake Roxburgh (140 m a.s.l.) in the east, rising to 545 m on the crest, and falling to 300 m in the west (Figure 1). It experiences a mean annual rainfall of *c.* 350 mm, which results in a growing-season water

[1]Nomenclature follows Cheeseman (1925), Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), Connor and Edgar (1987), Brownsey and Smith-Dodsworth (1989) and Edgar and Connor (1999) for native species, and Webb, Sykes and Garnock-Jones (1988) and Stace (1991) for exotic species.

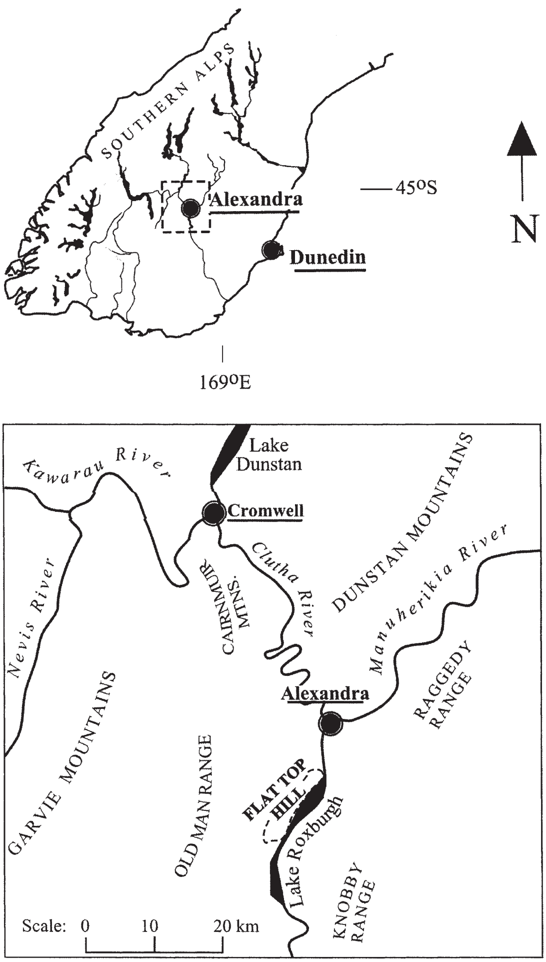

Figure 1. Map showing the position of Central Otago in South Island, New Zealand, and the position of Flat Top Hill in relation to the main local landscape features.

deficit of *c*. 400 mm. Average summer daily maxima (December to February) are between 25 and 35°C and average daily winter minima (June to August) are from -3 to 1°C (New Zealand Meteorological Service, 1983). Annual variability in precipitation and temperature is high (Garnier, 1951; Maunder, 1965), frosts are frequent and extreme in winter, and light frosts may occur in any month.

Available soil moisture was the primary determinant of the vegetation pattern of Flat Top Hill in 1993. North- and west-facing slopes and the ridge crest of Flat Top Hill typically have shallow (<0.3 m), coarse textured, brown-grey earth soils (Conroy shallow sandy loams and hill soils; Hewitt, 1995) and are subject to extreme and protracted seasonal soil water deficits in most years. Here, *Thymus vulgaris*, *Sedum acre* and *Raoulia australis* were the most prominent species in 1993, and there were large amounts of bare soil due to previously high rabbit numbers (Walker *et al.*, 1995). Annual soil water deficits are less extreme on shady east and south-facing slopes which are sheltered from drying northwesterly winds and exposed to rain-bearing southerly winds. Here, soils grade into deeper yellow-grey earths (Cairnside and Roxburgh soils), which in 1993 supported taller and more species-rich vegetation, characterised by the presence of the exotic species *Anthoxanthum odoratum*, *Festuca rubra*, *Hypochaeris radicata* and *Crepis capillaris*.

Sampling

In order to represent as fully as possible the range of environmental and vegetation variation on Flat Top Hill, 118 permanently marked study sites were positioned using restricted randomisation (Greig-Smith, 1983) in Autumn (April) 1993 (Walker *et al.*, 1995). Vegetation at each of the sites was sampled in Autumn and Spring 1993, and Summer 1994, and fourteen plant communities (Communities A to N) were described. In Spring 1997, eighty-eight of the sites were re-sampled, omitting three restricted communities of low natural value (Communities L, M and N; Walker *et al.*, 1995), and selecting the sites to resample at random in proportion to the number of sites in each remaining community in Spring 1993 (A to D and F to K; Walker *et al.*, 1995). Sampling coincided with the appearance of native spring annual species in both 1993 and 1997, with the phenological state of the spring flora matched as closely as possible.

Sampling methods were designed to record the predominantly fine-textured, low-growing vegetation present on Flat Top Hill in 1993 (Walker *et al.* 1995). Each site comprises a permanently-marked 4 m × 0.5 m plot, with the long axis parallel to the contour. Four 0.5 m × 0.5 m quadrats are positioned at equal intervals within the plot, with their centres at 0.5, 1.5, 2.5 and 3.5 m, respectively, on the long axis. Estimates of local frequency are obtained by recording the shoot presence of each vascular plant species within twenty-five 1 cm × 1 cm subquadrats, projected perpendicular to the soil surface, on a 10 cm × 10 cm grid, in each of the four quadrats (i.e. 100 subquadrats in all). Presences are summed to produce a percentage local frequency score for each species, and any species present within the site, but not within any of the 1 cm × 1 cm subquadrats, are also recorded and assigned an arbitrary small local frequency value of 0.5%. Environmental data recorded at each site include altitude, aspect, slope, topsoil (A horizon) depth, and total soil depth to bedrock (A + B horizon).

Data analysis

Analyses compare vegetation in the 88 sites sampled in Spring 1993 with that in Spring 1997. Species recorded in one sample and in one year only were excluded, leaving 96 (53 native and 43 exotic) vascular species. Changes were calculated in the number of sites occupied (hereafter referred to as distributional range or simply range) and in average local frequency between 1993 and 1997.

Paired *t*-tests were used to identify significant (P<0.05) differences between 1993 and 1997 in (i) the local frequency of each individual species and (ii) vegetation characteristics: i.e., species-richness, diversity (*H'*; Shannon and Weaver, 1949) and community evenness (*E'*; Camargo, 1993), and (iii) proportions of 14 *a priori* guilds of species, based on origin and morphology. These tests use the 88 sites as replicates, extracting the variation due to differences between replicates and using the treatment × replicate interaction as error. Because it was necessary to perform multiple tests, a significant (i.e. P<0.05) difference in any one species, vegetation characteristic or guild must be regarded as indicative only.

The multivariate method "cluster analysis" (Clifford and Stephenson, 1975) was used to group study sites (normal classification) and species (inverse classification) that showed similar changes in composition, rather than composition *per se*. To give equal emphasis to rare and abundant species, the data used were the relative, rather than the absolute, change in the local frequency of each of the 96 vascular plant species in each of the 88 resampled study sites, calculated as:

$$x_i = \frac{2(i_b - i_a)}{i_a + i_b}$$

where x_i is the relative change for species i, i_a is the local frequency of species i in 1993, and i_b is its local frequency in 1997. Differences between sites were represented by the city-block distance, the flexible sorting strategy was used to cluster sites and species, and β was set to -0.5 to weight the classification towards even-sized groups. Following inspection of classification dendrograms, the analysis was terminated at the 6-group level for sites, and the 8-group level for species, which were considered optimal in resolving major site and species groups while minimising the number of single-site or single-species groups.

A posteriori tests were used to determine which environmental characteristics were related to vegetation changes. Significant differences in altitude, slope, aspect (degrees east and north), topsoil depth, soil profile depth to bedrock, and potential annual solar radiation (PASR, calculated from latitude, slope and aspect) were identified for the two sides of each division of the normal classification using *t*-tests. Aspect and slope were examined as well as PASR, because although the latter is estimated from latitude, slope and aspect, it does not incorporate differential exposure to drying north-westerly winds, and to moisture-bearing southerly winds, which are important additional influences on plant growth in Central Otago (Walker, 1994).

To compare the magnitude of vegetation change that had occurred between Site Groups, Percentage Difference (*PD*) was calculated for each site:

$$PD = 100 \times \left[\frac{2\sum_{i=1}^{n} min\{x_i, y_i\}}{\sum_{i=1}^{n} (x_i + y_i)} \right]$$

where x_i is the percentage local frequency of species i at time x (i.e. 1993), y_i is the percentage local frequency of species i at time y (i.e. 1997), and n is the number of species (i.e. 96). This index reflects dissimilarity in both the presence and the local frequency of species (Podani, 1994). Testing for significance of differences was performed using *t*-tests, with regard to average *PD*, species richness, diversity (*H'*), evenness (*E'*) and native percentage, on either side of each classification division. Again, because several factors were examined, multiple *t*-tests were performed, and significant differences between Site Groups are interpreted with caution.

Vegetation change at any site may be determined by initial vegetation composition, most notably by the functional characteristics of the dominant species, as well as by environmental characteristics (Diaz *et al.* 1992). In 1993, 48% of the 88 resampled sites on Flat Top Hill were dominated, in terms of local frequency, by *Sedum acre*, 18% by *Anthoxanthum odoratum* and 11% by *Thymus vulgaris*. Chi-squared tests were used to determine whether the distribution of sites on either side of the first three divisions of the classification was independent of the dominant species in 1993. Columns were the two sides of each classification split, dominance and non-dominance by that species were rows, and entries in the table were the number of sites in each category.

The eight species groups of the inverse classification are 'Response Guilds', i.e. groups of species which show similarities in their changes in local frequency. Chi-squared tests were used to determine whether the categories of Response Guilds were independent of *a priori* guilds at each of the first four divisions of the Response Guild classification (i.e. those divisions for which site numbers were sufficient to perform the test); rows in the contingency tables were *a priori* guilds, columns were Response Guild categories and entries in cells were the number of species in the *a priori*-Response Guild combination. For each of the Site Groups of the site classification, paired *t*-tests were performed to indicate whether average distributional range of each Response Guild (i.e. the number of sites occupied, using member species of the Response Guilds as replicates) and the local frequency of each Response Guild (using sites and species as replicates) differed significantly between 1993 and 1997. For each Response Guild, changes within each Site Group in the distributional range of individual member species were examined, and *t*-tests were used to identify species that showed notable changes in local frequency from 1993 to 1997. Because of the large number of tests required to examine Response Guild and individual species changes, *t*-test results are regarded with caution, as indicative only.

Results

Overall vegetation change

Average per-site species richness and species diversity (*H'*) increased significantly on Flat Top Hill over the four years (Table 1). This was largely a consequence of an increase in exotic species richness: highly significant increases in species richness per site were seen in all morphological groups of exotic species with the exception of annual forbs. There was no significant change in the per-site richness of native species, but a significant decrease in the proportion of native species contributing to the total richness. However, the average number of native tussock grasses per site increased significantly over the four years. Those species showing the largest changes in range and local frequency were all exotic species (Table 3). *Hypochaeris radicata* and *Crepis capillaris* showed the greatest increases in distributional range, and the annual *Anagallis arvensis* showed the greatest decrease. *Anthoxanthum odoratum* showed the greatest increase in total local frequency, while *Sedum acre* showed the greatest decrease.

Site Groups

The site classification produced groups that are similar in the way that species composition changed over the four years (Table 2). The primary division of the site classification divides mesic, shady, south and east-facing sites with deep topsoils and deep soil profiles, situated east of the main ridge of Flat Top Hill (Site Group F), from more gently-sloping, north and west-facing sites on the sunny western slopes, with higher PASR (Site Groups A to E). Mesic Group F sites were dominated by the exotic grasses *Anthoxanthum odoratum* or *Festuca rubra*, or the native fern *Blechnum penna-marina* in 1993, and showed relatively small

Table 1. Average vegetation characteristics, and the average number of species in a priori origin and morphology guilds, over the 88 resampled study sites on Flat Top Hill, in 1993 and 1997. The probability of no difference between the two sampling dates, by individual t-tests, is indicated: * = P<0.05, ** = P<0.01, *** = P<0.001. When the conservative Bonferroni correction for multiple tests is applied, only those tests for which P<0.001 are significant.

All species	1993	1997
Species richness	12.7	15.1**
Diversity (*H'*)	1.5	1.8***
Evenness (*E'*)	0.3	0.3
Native percentage	39.7	31.3**
Native species		
All	5.5	5.2
All grasses	1.5	1.8
Tussock grasses	0.5	0.7*
Non-tussock perennial grasses	1.1	1.1
Other perennial monocots	0.2	0.3
Annual forbs	0.1	0.1
Perennial forbs	3.6	3.1
Woody	0.1	0.1
Exotic species		
All	7.2	9.9***
Annual grasses	0.0	0.4***
Perennial grasses	1.2	2.3***
Annual forbs	2.2	2.3
Perennial forbs	3.8	5.0***
Woody dicots	0.5	0.9***

average decreases in species richness, diversity (*H'*), evenness (*E'*), and percentage native species. In contrast, in the five xeric Site Groups, average species richness, diversity (*H'*) and evenness (*E'*) increased, while percentage native species decreased (Table 2).

The second classification division separates Site Groups A and B, which receive the highest PASR, and which were dominated by *Thymus vulgaris* and *Sedum acre* in 1993, from the somewhat less sunny Site Groups C, D and E (Table 2). Site Groups A and B showed a larger increase in species richness and diversity (*H'*), but overall vegetation change (*PD*) was less than in Site Groups C, D and E. Site Group A comprises sites at the xeric extreme in the reserve; soils are shallow, and the vegetation was dominated in 1993 by *T. vulgaris*, *S. acre* or *Raoulia australis*. Group B sites, on deeper loessial soils of gently-sloping mid-altitude "bench" landforms on the western face of Flat Top Hill, were dominated exclusively by *S. acre* in 1993, and the decrease in the percentage native species was greater here than in any other Site Group. Site Group C comprises seven sites at mid-altitudes on both the eastern and western slopes of Flat Top Hill, five of which were dominated by *S. acre* and two by

Table 2. Classification of vegetation change on Flat Top Hill: average environmental characteristics, number of sites dominated in 1993 by prominent species, and changes between 1993 and 1997, at Divisions 1 to 5 of the Site Groups A to F (Figure 2). *n* = Number of sites, asterisks indicate probability of no difference (for environmental factors, by *t*-tests), and of non-independence (for sites dominated by individual species, by χ^2 tests), respectively, between the two sampling dates: + = 0.10<*P*<0.05, * = *P*<0.05, ** = *P*<0.01, *** = *P*<0.001. When the Bonferroni correction for multiple tests is applied, only those tests for which *P*<0.01 are significant.

	Division 1		Division 2		Division 3		Division 4		Division 5	
Site Groups compared	A-E	F	A,B	C-E	C,D	E	C	D	A	B
N	63	25	37	26	21	5	7	14	28	9
Average										
Altitude (m a.s.l.)	429	431	427	432	447	368 *	419	461	432	411
Slope (°)	15	20 *	15	14	14	14	13	15	14	16
North aspect (°N)	101	73 *	102	99	101	89	108	97	106	89
East aspect (°E)	87	111 +	95	75	80	50	89	76	102	73
Topsoil depth (cm)	1	6 ***	1	2	1	3	2	1	0	1
Profile depth (cm)	27	35 *	27	28	30	21	27	32	24	43 ***
Solar radiation (kcal per cm^2 per annum)	6499	6036 *	6722	6182 **	6169	6237	6406	6051	6819	6421
No. of sites dominated (in 1993)										
Sedum acre	39	3 ***	27	12 *	10	2	5	5 *	18	9 *
Anthoxanthum odoratum	4	12 ***	0	4 *	4	0	0	4	0	0
Thymus vulgaris	8	2	7	1	1	0	0	1	7	0
Festuca rubra	0	3	0	0	0	0	0	0	0	0
Raoulia australis	3	0	1	2	2	0	2	0	1	0
Blechnum penna-marina	0	2	0	0	0	0	0	0	0	0
Changes (1993 to 1997)										
Species richness	3.65	-0.76 ***	4.49	2.46	1.90	4.80	2.86	1.43	4.39	4.78
Diversity (*H'*)	0.52	-0.12 ***	0.64	0.36 *	0.36	0.35	0.47	0.30	0.67	0.54
Evenness (*E'*)	0.03	-0.02	0.04	0.02	0.04	-0.07 +	0.06	0.03	0.04	0.02
Native percentage	-9.75	-5.13	-10.11	-9.23	-10.21	-5.11	-11.48	-9.58	-8.42	-15.37
Percentage Difference	70	67	67	75 *	74	77	77	73	66	70

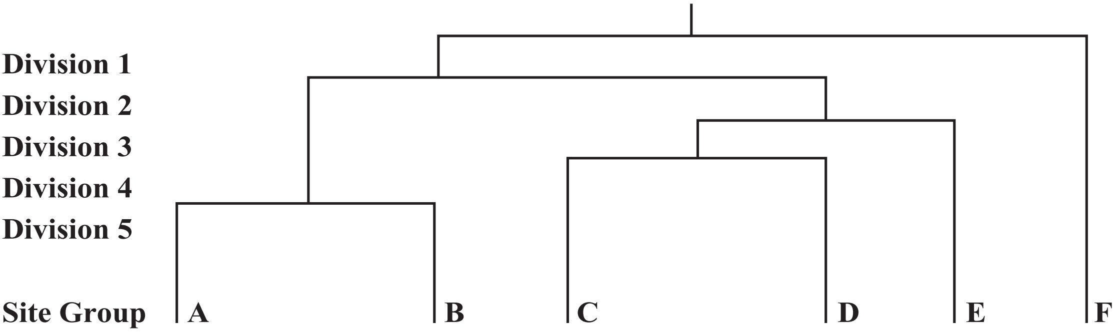

Figure 2. Dendrogram showing the five levels of division of the classification of vegetation change on Flat Top Hill, forming Site Groups A to F.

Table 3. Number of study sites occupied (out of 88), total local frequency (out of 8800 possible observations), and changes between Spring 1993 and Spring 1997, in native and exotic species of the eight Response Guilds. Probability, by individual *t*-tests, of no difference in local frequency between the two sampling dates, is indicated: + = 0.05<*P*<0.10, * = *P*<0.05, * = *P*<0.01, *** = *P*<0.001. When the Bonferroni correction for multiple tests is applied, only those tests for which *P*<0.001 are significant.

	No. sites			Local frequency				No. sites			Local frequency		
NATIVE SPECIES	1993	1997	change	1993	1997	change	EXOTIC SPECIES	1993	1997	change	1993	1997	change
Response Guild I - Stable species													
Acaena caesiiglauca	2	2	0	2	2	1	*Bromus tectorum*	0	2	2	0	1	1
Aciphylla aurea	1	1	0	1	1	1	*Euphorbia peplus*	2	3	1	1	2	1
Asplenium flabellifolium	3	0	-3	2	0	-2	*Hieracium pilosella*	3	3	0	2	6	5
Celmisia gracilenta	1	3	2	1	6	5	*Lolium perenne*	2	2	0	12	15	3
Ceratocephalus pungens	3	0	-3	2	0	-2	*Myosotis discolor*	17	17	0	16	13	-3
Colobanthus strictus	1	3	2	1	2	1	*Rytidosperma racemosa*	7	5	-2	28	115	87
Coprosma propinqua	3	2	-1	2	8	6	*Trifolium dubium*	0	4	4	0	4	4
Elymus falcis	0	2	2	0	61	61	*Urtica urens*	2	0	-2	1	0	-1
Epilobium alsinoides	2	0	-2	2	0	-2	*Vulpia bromioides*	0	3	3	0	20	20
Helichrysum filicaule	6	7	1	24	28	5							
Hydrocotyle novae-zelandiae	4	0	-4	10	0	-10							
Lachnagrostis filiformis	2	0	-2	15	0	-15							
Lagenifera cuneata	2	0	-2	3	0	-3							
Leucopogon fraseri	1	1	0	1	51	50							
Melicytus alpinus	3	4	1	18	20	2							
Microtis unifolia	0	4	4	0	4	4							
Myosotis pygmaea var *minutiflora*	6	5	-1	8	6	-3							
Oreomyrrhis ramosa	3	1	-2	6	1	-5							
Ozothamnus leptophyllus	1	1	0	1	2	2							
Poa "tiny"	0	4	4	0	10	10							
Poa cita	0	5	5	0	53	53 +							
Raoulia subsericea	3	4	1	22	29	7							
Rytidosperma buchananii	5	0	-5	7	0	-7							
Rytidosperma thomsonii	3	0	-3	2	0	-2							
Rytidosperma unarede	3	1	-2	23	1	-22							
Thelymitra sp.	1	3	2	1	6	6							
Uncinia elegans	2	0	-2	14	0	-14							
Response Guild II - Local increasers and decreasers													
Acaena buchananii	13	6	-7	28	9	-19	*Acaena agnipila*	8	10	2	24	34	10
Blechnum penna-marina	2	2	0	7	53	47	*Agrostis capillaris*	7	14	7	71	170	99
Carex breviculmis	18	14	-4	22	25	4	*Cerastium fontanum*	4	10	6	6	12	6
Colobanthus brevisepalus	19	13	-6	29	36	7	*Cirsium arvense*	14	4	-10	55	7	-48 +
Elymus solandri	0	6	6	0	36	36 *	*Cirsium vulgare*	15	13	-2	14	31	17
Festuca novae-zelandiae	12	16	4	94	148	54	*Dactylis glomerata*	0	8	8	0	91	91 *
Gnaphalium ruahinicum	11	5	-6	7	4	-3	*Echium vulgare*	9	5	-4	21	4	-17
Oreomyrrhis rigida	5	7	2	3	9	6	*Erophila verna*	3	5	2	4	6	2
Oxalis exilis	17	7	-10	22	7	-15 +	*Marrubium vulgare*	10	8	-2	42	8	-34
Poa colensoi	22	14	-8	34	37	3	*Myosotis stricta*	34	28	-6	108	49	-60
Poa lindsayi	16	2	-14	22	5	-17 +	*Reseda luteola*	18	0	-18	24	0	-24 *
Rytidosperma clavatum	27	43	16	264	545	281 *	*Taraxacum officinale*	0	8	8	0	7	7
							Trifolium repens	9	16	7	58	56	-2
							Verbascum thapsus	5	6	1	4	33	29
							Verbascum virgatum	8	11	3	8	20	13
							Veronica verna	0	6	6	0	29	29
							Vicia sativa	1	19	18	1	71	70 +
							Vittadinia gracilis	5	16	11	3	29	27 **
Response Guild III - Xerophytic decreasers													
Myosurus minimus ssp. *Novae-zelandiae*	2	0	-2	1	0	-1	*Anagallis arvensis*	41	18	-23	52	40	-13
Poa maniototo	38	17	-21	187	39	-148 **	*Erodium cicutarium*	33	15	-18	96	20	-76 *
Raoulia australis	45	38	-7	538	412	-127							
Raoulia beauvardii	19	14	-5	90	91	1							
Stellaria gracilenta	32	33	1	150	193	44							
Vittadinia australis	25	22	-3	34	30	-4							

Table 3 cont.

	No. sites			Local frequency					No. sites			Local frequency			
NATIVE SPECIES	1993	1997	change	1993	1997	change		EXOTIC SPECIES	1993	1997	change	1993	1997	change	
Response Guild IV - *Sedum acre*															
								Sedum acre	71	66	-5	2782	1607	-1175	**
Response Guild V - *Trifolium arvense*															
								Trifolium arvense	41	62	21	275	1281	1007	***
Response Guild VI - *Anthoxanthum odoratum*															
								Anthoxanthum odoratum	50	77	27	1178	2905	1727	***
Response Guild VII - Rapid increasers															
Acaena novae-zelandiae	32	36	4	58	170	112	*	*Aira caryophyllea*	0	27	27	0	256	256	***
Dichelachne crinita	0	17	17	0	119	119	**	*Aphanes arvensis*	21	24	3	30	51	21	
Elymus tenuis	6	19	13	17	173	156	*	*Festuca rubra*	25	38	13	413	882	469	+
Epilobium hectorii	22	31	9	24	61	38	+	*Holcus lanatus*	14	31	17	88	333	245	*
Geranium sessiliflorum	38	32	-6	43	42	-1		*Hypericum perforatum*	9	27	18	11	79	68	*
Rytidosperma cf *maculatum*	1	9	8	1	68	67	*	*Poa pratensis*	3	23	20	44	222	17	+
								Rosa rubiginosa	11	34	23	8	48	40	***
								Rumex acetosella	45	41	-4	190	187	-3	
								Thymus vulgaris	31	44	13	607	1117	511	*
Response Guild VIII - Mesic increasers															
								Crepis capillaris	33	63	30	123	431	308	**
								Hypocharis radicata	25	56	31	61	224	163	***

R. australis in 1993, while Site Group D encompasses a range of habitats, mostly close to the crest of Flat Top Hill, including sunny and shady tor-side sites, which were variously dominated by *S. acre*, *Anthoxanthum odoratum*, *T. vulgaris*, *Poa pratensis*, *Rytidosperma clavatum*, *Holcus lanatus* and *Raoulia beauverdii* in 1993. Site Group E comprises five sites on relatively shallow soils at low altitude on the western faces of Flat Top Hill which were dominated in 1993 by *Myosotis stricta, R. beauverdii, Agrostis capillaris* and *S. acre*. Here, species richness increased, and community evenness (*E'*) decreased (i.e. dominance increased), more than in any other Site Group.

Response guild classification

Highly uneven-sized species groups were formed in the classification despite weighting towards even-sized groups and the use of relative rather than absolute local frequency changes (Table 3). The primary division separates a large number of less-abundant species which showed little change, or which showed some local frequency change but remained restricted to a few sites (Response Guilds, I and II, accounting for 71% of species), from those that showed more substantial increases or decreases in local frequency or distributional range (Response Guilds III to VIII). A higher proportion of the former are native species, while the latter, which dominated vegetation changes on Flat Top Hill between 1993 and 1997, are predominantly exotic species (χ^2 = 9.99, P=0.0016).

Response Guild I **– Stable species**

Native species predominate in this Response Guild, accounting for *c.* 76% of the 38 species (Table 3). Most stable species had very narrow distributions in 1993 and either did not reoccur in sampling sites, or remained restricted in distribution on Flat Top Hill in 1997, showing only small or insignificant *in situ* changes in local frequency (Figure 3a).

Response Guild II **– Local increasers and decreasers**

Response Guild II contains a higher proportion of exotic species (17 out of 30) than the stable species Response Guild I (χ^2 = 10.12, P = 0.0014; Table 3). Although local increasers and decreasers tended to show greater *in situ* changes in local frequency than stable species (Figure 3b), most had restricted distributional ranges on Flat Top Hill in 1993, and few showed a tendency to invade new sites. Two individual species (*Taraxacum officinale* and *Vicia sativa*) increased substantially in local frequency in Site Group A, *Cirsium arvense*, *Cirsium vulgare*, *Aphanes arvensis* and *Dactylis glomerata* increased in Site Group D, whereas *Reseda luteola* decreased in Groups A and D (all P<0.05 by individual t-test). Of the few individual species that showed notable changes in distributional range, *Cerastium fontanum, T. officinale* and *V. sativa* increased in Site Group A, while in the mesic Site Group F, *D. glomerata*, *V. sativa* and *Vittadinia gracilis* increased, and the native xerophytes *Poa lindsayi* and *Colobanthus brevisepalus* decreased (all P<0.05 by individual t-test).

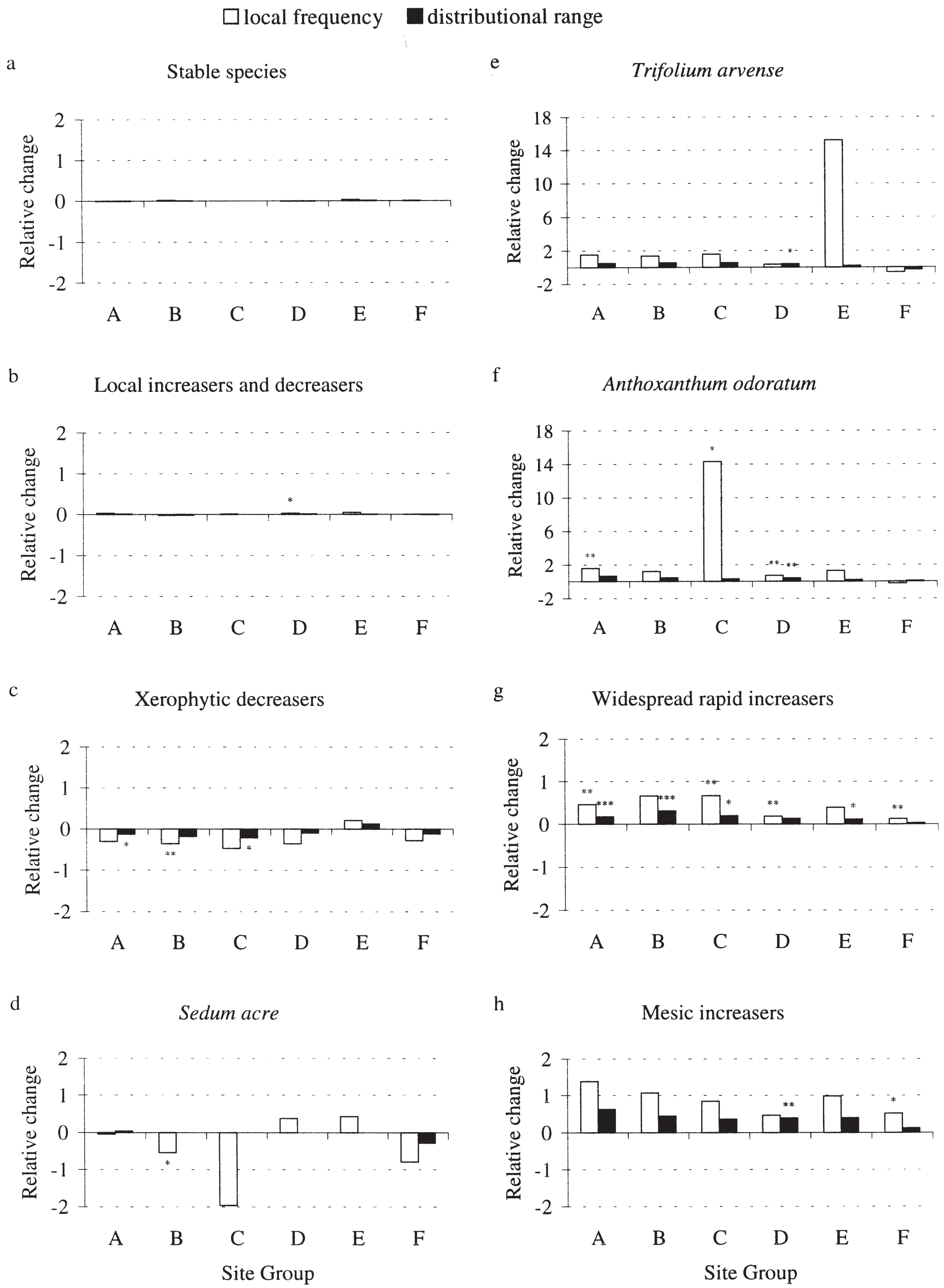

Figure 3. Average relative changes in local frequency, and in distributional range, (percentage occupied in 1997-percentage occupies in 1993)/100, in the six Site Groups (A to F), for each of the eight Response Guilds (a to h). Note the change in scale for the abundant species *Trifolium arvense* and *Anthoxanthum odoratum*. The probability of no significant change in absolute local frequency, and in distributional range, by *t*-tests, is shown: * = P<0.05, ** = P<0.01, *** = P<0.001.

***Response Guild III* – Xerophytic decreasers**

As a group, these eight species decreased in local frequency and/or distributional range in the xeric Site Groups, most notably in Site Groups A, B and C (Table 3; Figure 3c). Individual species also decreased in more mesic sites. *Stellaria gracilenta* decreased in local frequency, and *Erodium cicutarium* and *Poa maniototo* decreased in range in Site Group D, while *Anagallis arvensis*, *E. cicutarium*, *P. maniototo* and *Raoulia australis* decreased in range in the mesic Site Group F (all $P<0.05$ by individual *t*-test).

***Response Guild IV* – Sedum acre**

Sedum acre was the most widespread species on Flat Top Hill in 1993 (Table 3). It is distinguished xerophytic decreaser species (Response Guild III) by greater decreases in local frequency across a wider environmental range, and by its comparatively small change in distributional range (it occupied 66% of the 88 sites in 1997 and 71% in 1993; Table 3; Figure 3d). Its most notable decreases in local frequency were in Site Group B, where it was most abundant in 1993, and in the mesic Site Group F (both $P<0.05$ by *t*-test), but large relative decreases in local frequency were seen in Site Group C (where it was replaced by *Anthoxanthum odoratum*, *Thymus vulgaris* and *Hypochaeris radicata*) and in Site Group F.

***Response Guild V* – Trifolium arvense**

Distributional range and average local frequency of the exotic annual forb *T. arvense* increased in the five xeric Site Groups, most notably in Site Groups D and E (Figure 3e), but not in the mesic Site Group F, where it was uncommon in 1993.

***Response Guild VI* – Anthoxanthum odoratum**

Anthoxanthum odoratum replaced *Sedum acre* as the most abundant species on Flat Top Hill between 1993 and 1997 (Table 3; Figure 3f). Its local frequency increased relative to 1993 in the xeric Site Groups, most notably in Site Groups A (previously thyme-dominated sites with shallow soils and high PASR), C (mid-altitude previously dominated by *S. acre* or *Raoulia australis*), and D (xeric high-altitude and tor-side sites), while its range in the five xeric Site Groups also increased markedly from *c.* 46% in 1993 to *c.* 86% in 1997. Moreover, in the mesic Group F sites, where it was most widespread, and already abundant, in 1993, *A. odoratum* invaded two more sites, so that it occupied 92% of all resampled sites by 1997.

***Response Guild VII* – Widespread rapid increasers**

These fifteen species increased in distributional range and local frequency in Site Groups across the whole xeric:mesic gradient (Table 3; Figure 3g). Several individual species in this Response Guild showed notable changes ($P<0.05$ by individual *t*-test unless otherwise noted). Three of the six native species are perennial grasses, of which *Dichelachne crinita* increased in range and local frequency in Site Group A ($P<0.01$), *D. crinita* and *Rytidosperma clavatum* increased in local frequency in Site Group D, and *D. crinita, Elymus tenuis* and *R. clavatum* each increased in range in the mesic Site Group F. Among the exotic species, the shrub *Rosa rubiginosa* increased in average local frequency and range in Site Groups A and F (all $P<0.01$), and in local frequency in Site Group D, while the sub-shrub *Thymus vulgaris* increased in local frequency in Site Groups A ($P<0.01$), D, and F ($P<0.01$), and had invaded most of the five low-altitude Site Group C sites, where it was not previously recorded, by 1997. Both woody species spread rapidly: the range of *R. rubiginosa* increased from 13 to 39% of all study sites, and that of *T. vulgaris* increased from 35 to 50%, between 1993 and 1997 (Table 3). Of the herbaceous exotic species, *Aira caryophyllea* increased in local frequency and range ($P<0.001$), and *Poa pratensis* increased in range, in the xeric Site Group A, and both increased in range Site Group F. *Holcus lanatus* increased in range in Site Group B and in average local frequency in Site Group D. *Festuca rubra* increased in local frequency, and the exotic forb *Hypericum perforatum* increased in range and local frequency in Site Group F.

***Response Guild VIII* – Mesic increasers**

These two exotic rosette forbs (*Crepis capillaris* and *Hypochaeris radicata*) increased in relative local frequency and in distributional range in all Site Groups from 1993 to 1997 (Table 3; Figure 3h). Their increase in range in Site Group D, and in local frequency in the mesic Site Group F, was particularly notable.

Discussion

Initial vegetation changes

Between 1993 and 1997, growing-season rainfall was higher, and temperatures were lower than the 80-year averages in Central Otago, and these abnormally favourable weather conditions for plant growth may have obscured the initial effects of release from grazing to some extent on Flat Top Hill. However, short-term vegetation responses to the cessation of grazing and to release from moisture stress tend to be similar, and additive, in Central Otago plant communities. For example, Walker (1997a) described vegetation changes in continually-grazed plant communities comparable to those on Flat Top Hill (i.e. increases in perennial and tall annual grasses, and decreases in some ephemeral species) between 1993 and 1997 in three long-term study sites on Earnscleugh Station with a climatic range approximating that on Flat Top Hill. Similar, but greater, vegetation changes were seen within adjacent grazing-exclosures at these sites over the same period.

Most studies of New Zealand short tussock grassland following stock removal show that annual and short-lived species have decreased and that vegetation has become dominated by a few tall exotic perennial species over time (e.g. Meurk *et al*., 1989; Lord, 1990; Allen *et al*., 1995; Walker, 1997b). This is the trend predicted by the "range succession" model of Heady (1975), based on Clements' (1916) concept of succession to climax. The initial vegetation changes on Flat Top Hill from 1993 to 1997 do not entirely fit this pattern; despite a rapid increase in exotic perennial species, on average, sites had not become more dominated by a few competitive species by 1997. In fact, mean species richness increased significantly, and there was no significant change in community evenness (i.e. the inverse of dominance) across all sites. Moreover, annual species (e.g. *Trifolium arvense*, *Aira caryophyllea* and *Aphanes arvensis*) increased as well as perennial species, particularly in xeric sites, and tall native grasses increased, rather than decreased. However, these changes might represent an early stage of succession, as in the 'competitive-sorting' succession model of Peet (1992) and the 'three-phase' model of Gitay and Wilson (1995), in which an early invasion of numerous species precedes competitive-sorting and exclusion of those species from some sites later in succession (see also O'Connor and Aarssen, 1987).

Differences in vegetation change between study sites on Flat Top Hill was related to their initial (i.e. 1992) vegetation composition, which was strongly determined by the pattern of available soil moisture. Mesic and xeric communities on Flat Top Hill may continue to show different types of vegetation change, as has been shown in mesic and xeric study sites on Earnscleugh Station over 14 years following stock and rabbit exclusion (Walker, 1997a; S. Walker and J. B. Wilson, *unpubl. data*). For example, competitive-sorting been demonstrated on a shady (therefore mesic) slope on Earnscleugh Station, in which early increasers such as *Cerastium fontanum*, *Vicia sativa* (both Response Guild II on Flat Top Hill), *Trifolium arvense* (V) *Anthoxanthum odoratum* (VI), *Aira caryophyllea, Holcus lanatus*, *Poa pratensis, Hypericum perforatum* (VII), and *Crepis capillaris* (VIII) were later replaced by the longer-lived, more competitive species *Dactylis glomerata* (Response Guild II), *Festuca rubra*, *Rosa rubiginosa* (VII) and *Hypochaeris radicata* (VIII). Initial changes in mesic (Site Group F) communities on Flat Top Hill include increases in all of the "late" successional species on Earnscleugh Station, and might anticipate similar successional trends over time.

At the dry extreme of the xeric-mesic climate gradient on Flat Top Hill, changes observed from 1993 to 1997 may be temporary, reversible, weather-induced fluctuations, rather than the initiation of a long-term successional trend. Short-term "successional" changes following high rainfall periods have been reversed in low rainfall years at two long-term study sites on Earnscleugh Station, so that the vegetation retains a large component of annual, ruderal species, even after 14 years of grazing-exclosure (Walker, 1997a; S. Walker and J. B. Wilson, *unpubl. data*). Fluctuation, rather than succession, has also been recorded in semi-arid grasslands overseas; where rainfall is too low and variable to drive continuous vegetation change, and where pastoralism has caused persistent soil degradation, successional changes do not necessarily follow the cessation of grazing, even after several decades (e.g. Rice and Westoby, 1978). This may been seen as evidence that vegetation has reached a stable or persistent state, as described in the model of multiple stable states (e.g. Walker *et al*., 1981) and the State and Transition framework of Westoby *et al*., (1989). These may prove more appropriate than succession models for describing the dynamics of post-pastoral vegetation change in the driest short tussock grasslands of Central Otago, including parts Flat Top Hill (Walker, 1997b).

Response guilds

The classification of groups of plant species, such as life-form types (Raunkiær, 1907), functional types and guilds (Wilson, 1999), seeks to identify more simple patterns in complex, species-rich ecosystems. A fundamental motivation for the identification of functional types (e.g. McIntyre *et al*., 1999; Landsberg *et al*., 1999) is that groups of species exhibiting similar strategies and traits are likely to show similar responses to an environmental change, i.e. these groups will be "Response Guilds". Moreover, it is thought that recognising shared strategies or traits will enable the prediction of responses of groups of species to environmental conditions in future (e.g. Diaz and Cabido, 1997; Pausas, 1999). Species within Response Guilds on Flat Top Hill tend to share geographical origins or evolutionary histories, with implications for future trends in, and management strategies for, the different native and exotic elements of the flora of the Conservation Area .

By far the largest group of native species are the 29 classified into Response Guild I. Most are fire- and/or grazing-sensitive "remnant" shrubs, forbs and grasses (Type 1 of Walker, 1994) that remain too poorly represented in the sampling sites for statistically significant change to be demonstrated. Several species remain restricted to tor-side habitats in 1997, e.g. *Acaena caesiiglauca*, *Asplenium flabellifolium,* *Celmisia gracilenta*, *Epilobium alsinoides, Oreomyrrhis ramosa*, *Raoulia subsericea*, *Rytidosperma unarede*, *Thelymitra longifolia* and *Uncinia elegans* in shady tor-side sites, *Luzula banksiana* on sheltered tor-ledges, and *Poa cita*, *Aciphylla aurea* and *Oreomyrrhis ramosa* in sunny tor-side positions. The native grass *Elymus falcis* is not associated with rock tors, and is present only on deep loessial soils and gentle slopes. Because sources of propagules are few and widely scattered, future dispersal and establishment is predicted to be slow, and the extent to which future increases in native remnants will be inhibited by competition from other, principally exotic, species, remains unknown. However, any recovery of native shrubs seems unlikely if grazing or browsing is resumed.

Response Guild I also contains rare native annual species (*Ceratocephala pungens* and *Myosotis pygmaea var. minutiflora* —Type 3 of Walker, 1994) and dwarf xerophytic grasses (*Rytidosperma buchananii* and *R. thomsonii*) and which were minor, apparently habitat-specialist species, confined to a small number of xeric sites in "induced" habitat that was heavily rabbit-grazed until 1992. These, and the slightly more widespread native annual *Myosurus minimus* ssp. *novae-zelandiae* (Response Guild III; Garnock-Jones, 1986), were recorded less frequently in 1997 than in 1993; and the most rare (*C. pungens* Garnock-Jones, 1984; de Lange *et al*., 1999), was not found on Flat Top Hill in 1997, despite a thorough search of locations in which it was known to have occurred previously. The reduced abundance of restricted native species in 1997 may have been a consequence of competition from perennial grasses, particularly *Agrostis capillaris* (Response Guild II) and *Poa pratensis* (Response Guild VII), which formed a short, dense sward at the previously sparsely vegetated sites. If so, the persistence of restricted xerophytic native species on Flat Top Hill will depend on whether increases in exotic grasses represent a long-term change or merely a temporary fluctuation, i.e. whether periodic droughts and sequences of low-rainfall years will maintain sufficient suitable, sparsely vegetated habitat in the absence of grazing. *C. pungens* plants were observed to be present again on Flat Top Hill in Spring 1998 (Mr. J. Barkla, Department of Conservation, Dunedin, N.Z., *pers. comm.*).

Thus, the two groups of native species with high priority for conservation on Flat Top Hill are too restricted for change to be detected with confidence at the resolution of the present sampling regime, and additional, specific monitoring of populations of these species will be necessary to determine their trends. The paradox for the management of the Conservation Area is that native remnant and native annual species may require different management strategies for persistence and/or recovery.

The few exotic species classified in Response Guild I may be recent invaders (e.g. *Hieracium pilosella*), or specialist species in relatively rare habitats, or those for which Flat Top Hill is a marginal environment.

Response Guild II contains several sub-groups of species which had restricted distributions in 1992. Native species comprise grazing-sensitive remnants (e.g. the three tussock grasses *Elymus solandri*, *Festuca novae-zelandiae* and *Poa colensoi*) and those confined to a few xeric sites (e.g. the annual *Myosotis stricta*, the mat species *Colobanthus brevisepalus*, the sedge *Carex breviculmis* and dwarf grasses *Poa lindsayi* and *Rytidosperma* cf *maculatum*), while exotic species may be habitat-specialists (e.g. *Cirsium arvense* was confined to deep, loessial soils on sunny faces, and *Marrubium vulgare* occurred on high-fertility stock camps), recently-arrived invaders, or grazing-sensitive species able to persist only at low abundance under the previous grazing regime. Species of Response Guild II may also be divided into those that decreased between 1993 and 1997, and those that increased. Local decreasers (including the exotic species *M. stricta* and *Erophila verna*, *C. arvense*, *Echium vulgare* and *Reseda luteola*, several low-growing xerophytic natives and the remnant tussock grass *P. colensoi*) may be poor competitors. Should grazing intensity remain low, local decreasers are less likely to spread in the future than local increasers, whose ability to increase when rare suggests competitive traits and/or fecundity. Most local increasers are exotic (e.g. *Agrostis capillaris*, *Dactylis glomerata* and *Trifolium repens*), but two native tussock grasses (*F. novae-zelandiae* and *E. solandri*) and one dwarf native grass (*R.* cf *maculatum*) are included in this category.

Response Guild III includes the native annual *Myosotis minimus* ssp. *novae-zelandiae* and five perennial native species (*Poa maniototo*, *Raoulia australis, R. beauverdii, Stellaria gracilenta* and *Vittadinia australis*) which became widespread, prominent components of "induced" xeric vegetation in Central Otago after 1850 (Petrie,1883, 1912) . These species possess traits that have enabled them to avoid grazing (e.g. temporal avoidance in the native annual flora, structural defense in the low-growing, tightly-packed *Raoulia* mat species and sclerophyllous dwarf grasses such as *P. maniototo*). *Sedum acre*, a recent but successful and widespread invader on Flat Top Hill (Response Guild IV), has grazing-deterrent secondary compounds. Grazing-avoidance traits are correlated with the ability to survive water stress, but are also related to slow relative growth rates and poor competitive ability (e.g. Milchunas *et al*., 1988), and these species had been displaced in 1997 by

Anthoxanthum odoratum (Response Guild VI) and exotic species of Response Guild VII, including *Trifolium arvense*, *Aira caryophyllea*, *Aphanes arvensis*, *Rumex acetosella*, *Poa pratensis*, *Agrostis capillaris* and *Thymus vulgaris*. In the future, sequences of low-rainfall years may favour species of the xerophytic decreaser guild and *S. acre* over some of these competitors, but a continued decrease in the range of Response Guilds III and IV seems likely should grazing intensity remain low.

Twice as many exotic species as native species are classified in the four Response Guilds (V to VIII) which showed the greatest increases on Flat Top Hill from 1993 to 1997. Most of these species are too widespread for chemical or mechanical weed-control to be feasible, and some may pose a threat to the recovery of a native-dominated grassland and shrubland vegetation in the medium and long term.

The spread of the rapidly-increasing woody exotic species *Thymus vulgaris* and *Rosa rubiginosa* (Response Guild VII) in both xeric and mesic habitats will have long-term consequences for native vegetation recovery on Flat Top Hill. *T. vulgaris* changes the physiognomic character of the vegetation it invades from grassland to dominance by long-lived sub-shrubs. Although taller woody vegetation may succeed *T. vulgaris* in the long-term (e.g. reproducing clumps of the taller, native *Ozothamnus leptophyllus* shrubs are present within *T. vulgaris* shrubland) most native shrub species remain scattered and poorly represented in the study sites, and so far show little evidence of regeneration (e.g. the Response Guild I species *Coprosma propinqua*, *Melicytus alpinus*, *Muehlenbeckia complexa* and occasional specimens of *Kunzea ericoides, Olearia bullata* and *O. odorata*). The deciduous *R. rubiginosa* has a high growth rate, rapid seed production, efficient seed dispersal aided by animals, and has the potential to form dense shrubland and significantly alter the vegetation physiognomy over much of Flat Top Hill if not controlled. Little is known of its potential effects on ecosystem function and native species recruitment.

Swards of increasing exotic grasses may be inimical to the establishment and the persistence of native species. For example, *Poa pratensis* (Response Guild VIII) and *Agrostis capillaris* swards might displace rare native species in xeric sites. Although *Anthoxanthum odoratum* (Response Guild VI) forms a comparatively sparse, short sward, it has increased dramatically relative to Response Guild III on Flat Top Hill. The replacement of a diverse, low-growing, “induced” native flora by a species-poor *A. odoratum* sward has been recorded at Luggate, in the north of Central Otago in response to high rainfall and grazing-exclosure (Walker 1997a; S. Walker and J. B. Wilson, *unpubl. data*). This change was not reversed, either in low-rainfall years or after grazing was resumed for four years. However, taller native tussock grasses (e.g. *Festuca novae-zelandiae*, *Poa colensoi*, *Elymus tenuis*) and *A. odoratum* increased simultaneously in the absence of grazing at Luggate, as they have so far on Flat Top Hill.

On shady slopes on Flat Top Hill (Site Group F), native tussock grasses may be excluded, and vegetation succession to shrubland may be slowed or impeded, by grassland comprising *Festuca rubra* (Response Guild VII), and *Dactylis glomerata* (Response Guild II). Elsewhere in New Zealand, decreases in native short tussock grasses have been attributed to the establishment of a tall, dense, competitive sward of *D. glomerata* following the cessation of grazing (Meurk *et al*., 1989; Lord, 1990). In Central Otago, all native species were excluded from a short annual grassland on Earnscleugh Station by the development of a tall *D. glomerata*-*F. rubra* sward in response to high rainfall and the cessation of grazing (Walker 1997a), while on Galloway Station, *D. glomerata* has increased at the expense of the native *Festuca novae-zelandiae* over 14 years since grazing-exclosure.

So far, however, seven out of eight “tall” native grasses increased in both xeric and mesic sites under the conditions of high rainfall and grazing-release on Flat Top Hill, and there is little evidence of their exclusion in competitive-sorting and successional processes. Only *Poa colensoi* decreased in range; it was not recorded in 8 of the 22 sites in which it was present at low abundance in 1993. Scattered remnants of *Poa cita*, *Elymus falcis* (Response Guild I), *E. solandri* and *Festuca novae-zelandiae* (Response Guild II) increased *in situ*, and three more widespread native grasses are included in the rapid-increaser Response Guild (VII). Of these, *Rytidosperma clavatum* had formed a short continuous tussock sward between and amongst patches of thyme west of the main ridge, *Dichelachne crinita* had increased both in *Thymus vulgaris* canopies at xeric sites, and in *Anthoxanthum odoratum* and *Festuca rubra* swards in mesic communities, and *Elymus tenuis* had increased in a diverse range of environments. At present, control of rabbits and mammalian browsers, and the absence of stock appears the best management option to ensure the continued recovery of remnant native tussock grassland on Flat Top Hill.

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