SUSAN WALKER, ALAN F. MARK and J. BASTOW WILSON

Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.

THE VEGETATION OF FLAT TOP HILL: AN AREA OF SEMI-ARID GRASSLAND/SHRUBLAND IN CENTRAL OTAGO, NEW ZEALAND

Summary: An account is given of the vegetation of Flat Top Hill, in the driest part of semi-arid lowland Central Otago, New Zealand. Although highly modified, the area was acquired for conservation in 1992, following almost 150 years of pastoral use. The vegetation was sampled in a composite scheme using permanent monitoring sites placed to include the majority of habitats and communities present. A number of environmental factors were measured in each sample.

Native species comprise 53% of the vascular flora of the area (211 species). From multivariate analyses of the data collected over three seasons, fourteen 'communities' are recognised. Although there are few constant or faithful species, strong relationships are shown with certain environmental parameters. Moisture stress is the major environmental influence on the vegetation; soil depth and past disturbance are secondary determinants. The communities differ by a factor of 10 in vascular species richness; the richest communities, and those with the greatest native component, are those around rock tors.

Many of the communities present have not been reported from other vegetation surveys in Central Otago. Moisture stress at xeric sites in the dry core of the region has excluded some exotic species, and allowed the survival of the native component, including three tiny spring ephemerals.

Near elimination of grazing, as a result of reservation, will probably lead to an increase in the cover of taller, palatable exotic grasses and *Thymus vulgaris*, which may threaten the survival of some native species. Optimum management, for recovery or persistence of native species, may comprise exclusion of grazers in some areas, but continuity of grazing in others.

Keywords: Central Otago; environmental correlations; exotic species; grazing; management; New Zealand; semi-arid.

Introduction

Semi-arid grasslands are highly variable ecosystems, showing strong temporal variation, and spatial patchiness that is often difficult to relate to the current environment (Friedel, Bastin and Griffin, 1988). They are susceptible to overgrazing and fire, and contain some of the worst examples of land degradation by humans (Walker and Noy-Meir, 1982). Semi-arid areas are also susceptible to invasion by exotic species, especially those species that are able to persist through environmental fluctuations (Dasti and Agnew, 1994).

In eastern South Island, New Zealand, the rainshadow of the Southern Alps creates a semi-arid climate, as defined by the Thornthwaite (1948) moisture index, which is based on temperature and rainfall (Hubbard and Wilson, 1988). This aridity is most pronounced in the intermontane basin of Central Otago. The region experiences an almost 'continental' climate, with maximum and minimum temperatures among the most extreme recorded in New Zealand (Maunder, 1965).

The Central Otago region has a complex history of disturbance. Post-glacial forest may never have extended to the drier basins of Central Otago, and the establishment of grassland, possibly through natural fires, preceded human settlement by several centuries (Wardle, 1985; McGlone, 1989; McGlone, Mark and Bell, 1995). Human impact since Polynesian times has led to changes in soils and vegetation. Those changes brought about by pastoral use of the land since European settlement may be traced from early (e.g., Buchanan, 1868; Petrie, 1895, 1912; Zotov, 1938), and recent descriptive accounts (e.g., Mark, 1965). The induced vegetation has been widely described as "desert", "steppe" or "semi-desert". There are few endemic species, and the region has been particularly vulnerable to invasion by exotic species (Wardle, 1963, 1985). Degradation has often been blamed on the rabbit pest (*Oryctolagus cuniculus* L.), which has intermittently reached plague proportions, although burning, and overgrazing by sheep (*Ovies aries* L.) and feral goats (*Capra hircus* L.) have also contributed.

Recent studies of semi-arid plant communities in Central Otago have examined the relationships between the vegetation and environmental factors. Hubbard and Wilson (1988) described the lowland vegetation of the Upper Clutha basin; a more detailed study (Wilson, Williams and Lee, 1989) examined the vegetation of an area in the north of the region, near Luggate, including agricultural sites. Partridge *et al.* (1991) described the vegetation of the Kawarau Gorge, in the northwest of Central Otago.

In 1992, 820 ha at the northern end of Flat Top Hill (Fig. 1), a prominent and easily accessible landscape feature in lowland Central Otago, was set aside for conservation after some 150 years of pastoral use. In 1993 and 1994, an intensive rabbit-control program was carried out within the reserved area, dramatically reducing rabbit numbers. At the same time, domestic sheep were removed. The reserve therefore provides an opportunity to monitor the recovery of flora, fauna and soils immediately following the near-elimination of exotic mammalian herbivores.

The aim of this study was to use the Flat Top Hill reserve to document the vegetation patchiness found in the semi-arid lands of lowland Central Otago, and to establish its environmental correlations at a more detailed scale than has been attempted in previous surveys. Flat Top Hill provides an opportunity to do this in an area that has retained a relatively high proportion of native plant species, and which is close to the most arid part of the region. This record of soils and vegetation will provide a basis for long-term monitoring under conditions of conservation management.

The study area

The reserve, situated 10 km south of Alexandra, lies in the north east corner of the Old Man Ecological District within the Central Otago Ecological Region (McEwan, 1987) between the latitudes 45° 19' S and 45° 17' S and longitudes 169° 18' 30" E and 169° 21' 30" E. Flat Top Hill is an elongated, flat-crested, lowland foothill of the Old Man Range (Fig. 1). It extends from Lake Roxburgh (140 m a.s.l.) in the east, rises to 545 m on the crest, and drops to 320 - 300 m in the west. Periglacial weathering has left schist tors along its summit (Fig. 2), and alluvial outwash terraces and fans at lower altitudes; all are distinctive features of the lowland Central Otago landscape (Molloy, 1988).

The position of Central Otago in the most inland part of South Island is reflected in high daily maximum temperatures in summer (25 to 35°C) and low temperature minima in winter (-3 to 1°C) (New Zealand Meteorological Service, 1983). The region is subject not only to extremes of temperature and low precipitation, but also to high annual variability in these factors (Garnier, 1951; Maunder, 1965). Frosts are frequent and extreme in winter, while light frosts may occur in any month. Mean annual rainfall is *c.* 350 mm, and water deficit is *c.* 400 mm over the growing season. Such incidence of frost and moisture deficit probably excluded forest from low altitudes during the Holocene (Mark, 1965; Wardle, 1985).

Temperature and wind direction measurements were made on the crest of Flat Top Hill between 20 July 1993 and 20 January 1994. Over this period the diurnal temperature range (shielded sensor at 140 cm above ground level) was on average 3.5°C lower than the official screen temperature at Alexandra (140 m), with summer daily maxima 4°C lower. Winter daily minima were on average 2.5°C higher than at Alexandra. Northeasterly and northwesterly winds predominate on the crest of Flat Top Hill, which is sheltered from winds from the northeast and east.

Soils on the reserve are mainly brown-grey earths (Conroy shallow sandy loams and hill soils) but grade into yellow-grey earths (Cairnside and Roxburgh soils) on the east face and towards the southern boundary (Johnson and Hewitt, 1991). Profiles are shallow, having been stripped of their topsoil, following depletion of vegetation cover since European settlement. Although available Ca, Mg and K in these soils are relatively high, N is low, and S is deficient for agricultural crops (Gibbs, 1980). The carbon content of soils is well below 2% of dry weight, and therefore classified as very low (Blakemore, Searle and Daly, 1987).

Fossil soils (palaeosols formed a minimum of 20 to 25 million years ago) have been exposed by sluicing beside Butchers Dam (Fig. 1), and areas of exposed white weathered schist of Tertiary age are found scattered along footslopes (Johnson and Hewitt, 1991). 'Alkaline' or 'solonetzic' soils (Gibbs, 1980; Molloy, 1988) are found in depressions on the crest, and along the toes of fans on the western face.

Human disturbance

Human disturbance of the area has been significant. Over most of the reserve, the vegetation cover is sparse, topsoils are shallow or absent, and exotic species dominate the plant communities. Pastoral occupation of the interior grasslands of the South Island by European settlers was completed by the 1950s. A combination of frequent fires and grazing is thought to have very soon reduced the component of finer, palatable species, and forced the pastoralists

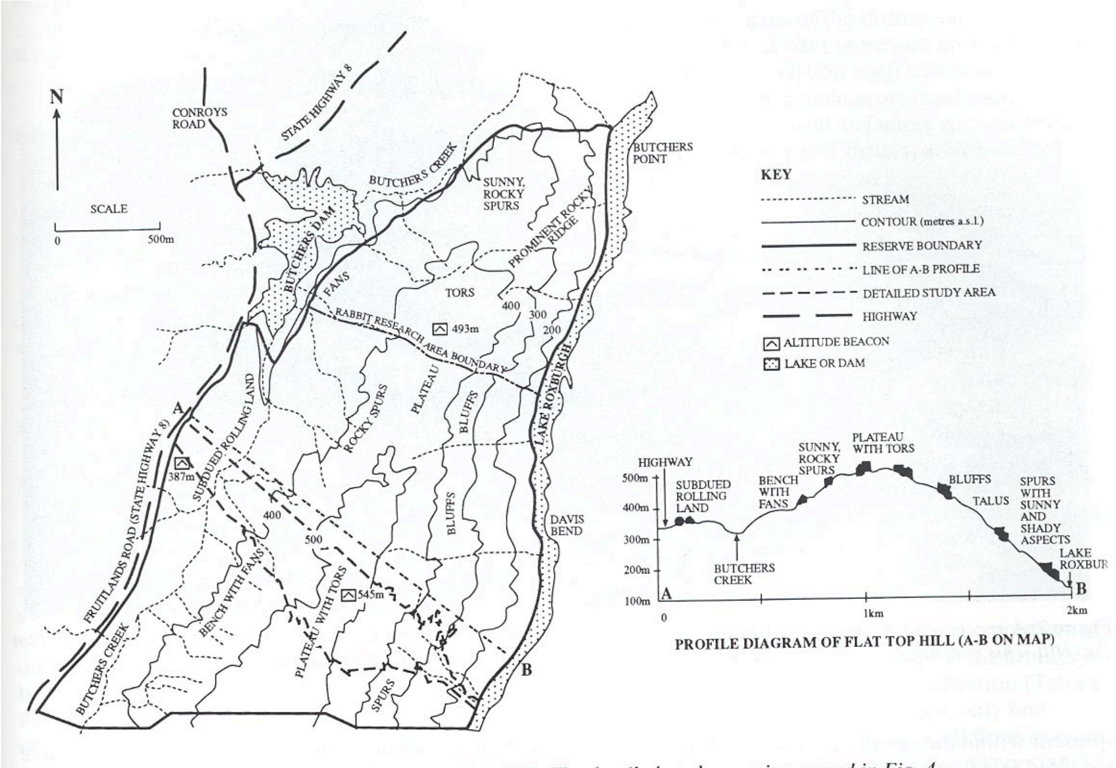

Figure 1: *The main topographical features of Flat Top Hill. The detailed study area is mapped in Fig. 4.*

into the practice of frequent burning to maintain palatability (Buchanan, 1868; O'Connor, 1986). In 1870, rabbits were introduced to New Zealand. They rapidly increased in numbers and compounded the effects of pastoralism, particularly in semi-arid regions (Petrie, 1883).

Petrie (1912) estimated that by 1911, about a million hectares of Central Otago were left "desert-like". This land was colonised by "semi-desert" vegetation dominated by *Raoulia* species. (Cockayne, 1910; Cockayne, 1919; Zotov, 1938). The desertification of Central Otago has been described as one of the most dramatic examples of land degradation to have resulted from European expansion overseas during the nineteenth century (Mather, 1982).

Methods

Vegetation data

In autumn (March) 1993, 116 study sites on Flat Top Hill were established and permanently marked for sampling. Of these, 91 sites were placed using a 'restricted random' sampling scheme within a detailed study area, which includes the full range of altitude and aspect (Figs. 1, 3). A further nine sites were placed along the crest plateau, and 16 in additional habitats and communities of special interest that are too rare within the reserve to be detected by random sampling. The latter comprise trans-fenceline comparisons, vegetation adjacent to tors on contrasting aspects, a debris fan including a saline soil, a community dominated by *Festuca novae-zelandiae* (rare within the reserve), an ephemeral pool, and an area of exposed tertiary sediment.

Each study site comprises four 0.5 x 0.5 m quadrats, placed 0.5 m apart along the contour, and is permanently marked using aluminium angle stakes at either end, 4 m apart. The shoot presence of all vascular plant species, plus lichens and bryophytes, was recorded in each of 100, 1 x 1 cm subquadrats placed at the intersections of a 10 x 10 cm grid within each quadrat. Presence values for each species in the 100 subquadrats were summed in each sample to produce a local frequency score as an approximation for cover. Minor species

Figure 2: *A species-rich herbaceous plant community is found in the moist southern lee of a schist tor on the summit of Flat Top Hill. This community contrasts with the surrounding species-poor* Thymus vulgaris *dominated vegetation.*

(present within the sampling frames, but not recorded in any of the 1 x 1 cm subquadrats) were assigned an arbitrary frequency value of 0.5. Maximum height of vegetation and mean canopy height were estimated for each site. Botanical nomenclature follows Cheeseman (1925), Allan (1961), Moore and Edgar (1970), Healy and Edgar (1980), Galloway (1985), Connor and Edgar (1987) and Brownsey and Smith-Dodsworth (1989) for native species, and Webb, Sykes and Garnock-Jones (1988) and Stace (1991) for exotic species. Only the most conspicuous mosses and lichens were identified and recorded.

Sampling was repeated in both spring (October 1993) and summer (January 1994), to include seasonal variation in the vegetation. Two additional study sites were placed inside 5 x 5 m permanently-fenced, rabbit-proof exclosures, that were erected in December 1993. These sites were included in the summer sampling.

The vegetation data for all sites in the three seasons were classified together by Indicator Species Analysis using the program TWINSPAN (Hill, Bunce and Shaw, 1975), and ordination of data was performed by Detrended Correspondence Analysis (DCA) with the program DECORANA (Hill and Gauch, 1980). Program defaults were used in both analyses. Four vegetation parameters (factors): total and native species richness, the percentage of native species, and the Shannon-Weaver (1949) measure of alpha species diversity, were calculated for each site.

Environmental data

Aspect (converted to north and east aspect components), slope, and the number of rabbit faeces were recorded at each site. Presence of plant litter, rock (fragments >20 mm diam.), gravel (fragments < 20 mm and >2 mm diam.), and the occurrence of bare soil within the 100 subquadrats were also recorded, where these could be seen through the plant cover across each of the 1 x 1 cm subquadrats. The following soil characteristics were obtained for the study sites:

i) mean soil profile depth (cm), measured using a screw auger, to rock, of five random points within a 1 m margin around the study site;
ii) topsoil depth (cm), by measurement of the A horizon at five random points adjacent to the site;
iii) soil moisture content (% dry weight; loss of moisture at 105°C for 24 hours), at three sampling times: in the winter, and during the spring and summer sampling periods;
iv) organic matter content (% dry weight; loss of weight on ignition at 500°C for 2 hours);

v) pH (with 1:2.5 volume dilution in deionised water);
vi) conductivity (i.e. soluble salts) (microsiemens g^{-1} of dry soil, with 1:1 volume dilution in distilled water);
vii) exchangeable potassium (me. 100 g^{-1}; extracted with 1 M ammonium acetate and determined by spectrophotometry; Blakemore, Searle and Daly, 1987);
viii) exchangeable sodium (me. 100 g^{-1}; extracted with 1 M ammonium acetate and determined by spectrophotometry);
ix) exchangeable K:exchangeable Na ratio;
x) carbon content (% dry weight; by potassium dichromate digestion - Blakemore *et al.*, 1987) (on a sub-sample of 25 soils);
xi) bulk density (g cm^{-3} of dry soil from 15 undisturbed cores collected at each site);
xii) texture (% dry soil of gravel (2.0 - 20.0 mm), sand (0.02 - 1.99 mm), silt (0.002 - 0.020 mm) and clay (<0.002 mm); by the hydrometer method of Thomas, 1973).

Analyses iv-xii were performed on soil samples collected during the spring vegetation survey.

T-tests were used to identify significant differences in environmental and vegetation factors between samples on the two sides of each division of the vegetation classification, to the fourth level of division. Where a site was classified into the same community in more than one season, factors which remained constant (e.g., altitude, aspect, slope and all soil factors with the exception of soil moisture) were used only once in performing the '*t*-tests'.

Multiple regression equations were calculated for the first four axes of the ordination, with ordination scores of sites regressed on environmental factors. Simple correlation coefficients were calculated between sample scores and each vegetation factor, as well as factors such as plant litter, gravel and bare soil factors, which are not independent of the vegetation.

Results

The total recorded flora of Flat Top Hill is 232 plant species (28 woody dicotyledons, 118 dicotyledon herbs, 52 monocotyledons, 13 ferns, with 7 conspicuous mosses and 14 lichens). Native species make up 57% of those species recorded (53% excluding non-vascular plants). Of the 163 plant species recorded within the 116 sampling sites, 96 (59%) are native species and 67 (41%) are exotic. All sites contained exotic species in all seasons, while at one site in spring no native species were recorded.

The communities

Fourteen communities (sample groups, represented by the letters A to N) were defined at the arbitrary fourth division of the normal classification (Tables 1, 2; Fig. 3). Of these communities, only one (Community E) was not present in all three seasons. Although species show low fidelity and constancy within communities (Table 2), many environmental and vegetation factors differentiate groups of samples at the early levels of division (Fig. 3).

Table 1: *Mean values of selected environmental and vegetation factors in the 14 communities. Soil moisture values are the mean of three winter, spring and summer measurements. The total number of samples in each community (over three seasons) is shown. Percentage native species is per sample.*

	Community													
Variate	A	B	C	D	E	F	G	H	I	J	K	L	M	N
No. samples (3 seasons)	*4*	*82*	*83*	*24*	*1*	*8*	*14*	*36*	*37*	*37*	*9*	*3*	*8*	*3*
Altitude (m)	375	419	408	425	371	403	328	468	418	426	483	310	333	310
North aspect (°, N = 180)	62	94	110	111	178	124	110	85	62	56	48	42	63	0
East aspect (°, E = 180)	122	82	92	111	92	107	156	133	101	99	100	48	63	0
Slope (°)	15	9	17	14	18	20	26	15	18	22	26	26	33	0
Profile depth (cm)	50	28	34	16	37	19	12	39	34	38	50	14	30	2
Topsoil depth (cm)	4	1	3	4	1	0	0	3	7	5	0	14	15	2
Gravel (%)	5	8	6	8	12	11	13	3	8	7	6	3	11	2
Sand (%)	40	41	38	37	46	39	36	36	37	39	41	36	58	23
Silt (%)	50	47	48	51	35	43	45	57	49	50	49	53	51	43
Clay (%)	6	6	6	4	6	7	6	4	6	4	4	8	9	2
Moisture (%)	16	17	20	18	17	17	12	27	30	30	34	3	31	34
Organic matter (%)	2.4	2.0	3.8	4.8	3.5	4.5	3.2	5.4	5.8	5.8	4.3	6.8	5.1	5.0
pH	6.45	6.54	6.58	6.64	6.64	6.87	6.68	6.55	6.45	6.36	6.14	6.09	6.30	6.92
Potassium (%)	1.06	1.09	1.15	1.10	0.70	1.04	0.73	1.29	1.27	1.34	1.38	0.57	0.77	-
Species richness	8.0	16.4	15.7	10.9	15.0	17.5	6.8	12.6	16.0	20.0	20.4	23.3	12.5	16.3
Native species (%)	9	62	48	51	33	58	74	34	46	53	59	39	35	12

Table 2: *Percentage frequency of occurrence in samples of the 50 most abundant plant species within the 14 communities (A to N) delimited at the fourth level of division of the normal classification of the data from the autumn, spring and summer vegetation surveys. Asterisks indicate exotic species. Six-letter abbreviations refer to those used in Figure 6.*

Species Group	Species (50 most abundant)		Community A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	*Poa maniototo*	POA MAN	25	80	49	50				28	3					
	Raoulia beauvardii	RAO BEA		50	6	25						8				
	Stellaria gracilenta	STE GRA		78	20	21		13		8	19	3				
	Epilobium hectorii	EPI HEC		43	31	4		25			5	8				
	Poa lindsayi	POA LIN		22	34					14		11				
	* *Reseda luteola*	RES LUT	25	22	29	13				19						
	Rytidosperma clavatum	RYT CLA		6	25					6	3	3				
	* *Anagallis arvensis*	ANA ARV		49	81	29		88		17	3	30			13	
	Candelariella vitellina	CAN VIT		18	30	46		75	43			8				
2	*Colobanthus brevisepalus*	COL BRE		46	6	8		13				8	33			
	Raoulia australis	RAO AUS		91	51	29		13		22	51	49				
	Rytidosperma buchananii	RYT BUC		28	14	8					22	3				
	* *Cirsium vulgare*	CIR ARV		10	35					8		14	33			
	* *Erodium cicutarium*	ERO CIC	75	26	19	13	100			8	8	3				
	Oxalis exilis	OXA EXI		15	37	4		13		11	11	8	11			
	* *Cirsium arvense*	CIR ARV		7	49					58	14	8				
	Vittadinia australis	VIT AUS		40	47		100	38		6	11	19	22			
3	* *Poa pratensis*	POA PRA		11	7	8				11				67	13	
	* *Sedum acre*	SED ACR	25	90	99	88	100	100	36	92	43	62	56	33	13	
	Xanthoparmelia molliuscula	XAN MOL		62	23	29		13	57	17	16	14				
4	* *Thymus vulgaris*	THY VUL		34	35	100	100	88	100	39		16				
5	*Parmelia signifera*	PAR SIG		51	33	42		50	93	11	32	24	11			
	Xanthoparmelia cf. *conspersa*	XAN CON		32	18			100	36	8	27	11	11		25	
	Buellia sp.	BUE SP.		27	36	63		63	57	3	16	22	67	100		
	* *Myosotis stricta*	MYO STR	50	16	14	21		25		3	16	8				
6	*Acaena novae-zelandiae*	ACA NOV		27	54					31	27	65	67	67		33
	Geranium sessiliflorum	GER SES		40	46	8		25		36	27	43	11			
	* *Hypericum perforatum*	HYP PER		27	16	4		38		6		30				100
	* *Rumex acetosella*	RUM ACE	25	48	59	13	100	75		36	41	49	33	33		
	Chondropsis semiviridens	CHR SEM	50	49	39	46		25	43	53	70	27				
7	*Rhizocarpon geographicum*	RHI GEO		44	19	21		88	86	8	41	41	67			
8	*Rytidosperma racemosum*	RYT RAC		2	23	8	100	88	7	11	14	62	11			
9	*Carex breviculmis*	CAR BRE		23	17			38			3	27	33			
10	* *Rosa rubiginosa*	ROS RUB		4	29	17		13	21	8	43	35		33	50	67
	Grimmia pulvinaris	GRI PUL		10	14	29		25	14	25	32	5		33		
11	* *Aira caryophyllea*	AIR CAR		18	14	8		25		25	43	35			13	
	* *Trifolium arvense*	TRI ARV	100	55	46	33		38		83	89	51	44	67	63	
12	* *Agrostis capillaris*	AGR CAP		12	1				7		49	22		100	100	100
13	* *Anthoxanthum odoratum*	ANT ODO		30	45	58	100	38		100	100	100	100	100	100	100
	Elymus solandri	ELY SOL		5	1	21	100	38	7	6	43	19	22	33	25	
	* *Crepis capillaris*	CRE CAP		9	31	13		25		69	51	76	89	100	38	
	Acaena buchananii	ACA BUC		11	8					25	24	16	33			
	Poa colensoi	POA COL		18	14	13		88	11	38	51	67		13		
14	* *Festuca rubra*	FES RUB		1	12	13				78	78	68	56	67	88	
	* *Hypochaeris radicata*	HYP RAD		6	12	4		13		61	65	84	100	100	63	
	Hypnum cupressiforme	HYP CUP		6	5	8		25		31	43	70	33	67	88	
	* *Trifolium repens*	TRI REP			4					8	27	41	100	100	63	100
	* *Dactylis glomerata*	DAC GLO			2	13				6	8	8	22	100	100	67
15	*Festuca novae-zelandiae*	FES NOV			1					6	32	57	67		38	
	* *Holcus lanatus*	HOL LAN		6	8			13		3	32	73	100	67	38	

Seven ‘xeric’ (A to G) and seven ‘mesic’ (H to N) communities are separated by the primary division of the classification (Fig. 3). The species *Sedum acre*, *Poa maniototo* and *Anagallis arvensis* are characteristic of the xeric group, which occur on north- and west-facing slopes and shallow (<30 cm), coarse textured, brown-grey earths, at the northern end of the study area and on the crest of the hill (Fig. 4), where relatively extreme and protracted seasonal soil water deficits occur in most years. Rabbit numbers have been high, and there are large amounts of bare soil. However, there are higher proportions of native species than in the mesic communities (55 cf. 44%).

Communities A to C are present on gentle, sunny slopes (footslopes, ‘bench’ features, ridge crests) which are strongly preferred by rabbits, while the more shallow (16 *cf.* 31 cm), coarse-textured, alkaline (pH *c.* 6.7) soils of steep, gravely slopes have been most vulnerable to invasion by *Thymus vulgaris* sub-shrubs, which dominate communities D to G (Table 2).

The mesic group (Communities H to N) is characterised by the presence of the exotics *Anthoxanthum odoratum*, *Festuca rubra*, *Hypochaeris radicata* and *Crepis capillaris*. They occupy steeper, south- and east-facing slopes above Lake Roxburgh and west of Butchers Creek (Fig. 4), with deeper (>30 cm), finer, less alkaline soils (pH 6.4 *cf.* 6.6 in xeric communities) grading from brown-grey earths to yellow-grey earths, with higher organic matter (5.6 *cf.* 3.9% in xeric communities) and potassium (1.2 *cf.* 1.1% in xeric communities). On the east- and south-facing slopes where this vegetation occurs, soil water deficits are less severe than in other parts of the reserve. The vegetation is taller, and species richness is higher than in the xeric communities (17 *cf.* 15 spp.).

The more native species-rich communities H to K (45% native species) are found at high elevations on the shady Lake Roxburgh face, on relatively potassium-rich soils (1.3 *cf.* 0.7% in communities L to N). South aspect, slope, surface rock and gravel, soil moisture, potassium, total species richness and

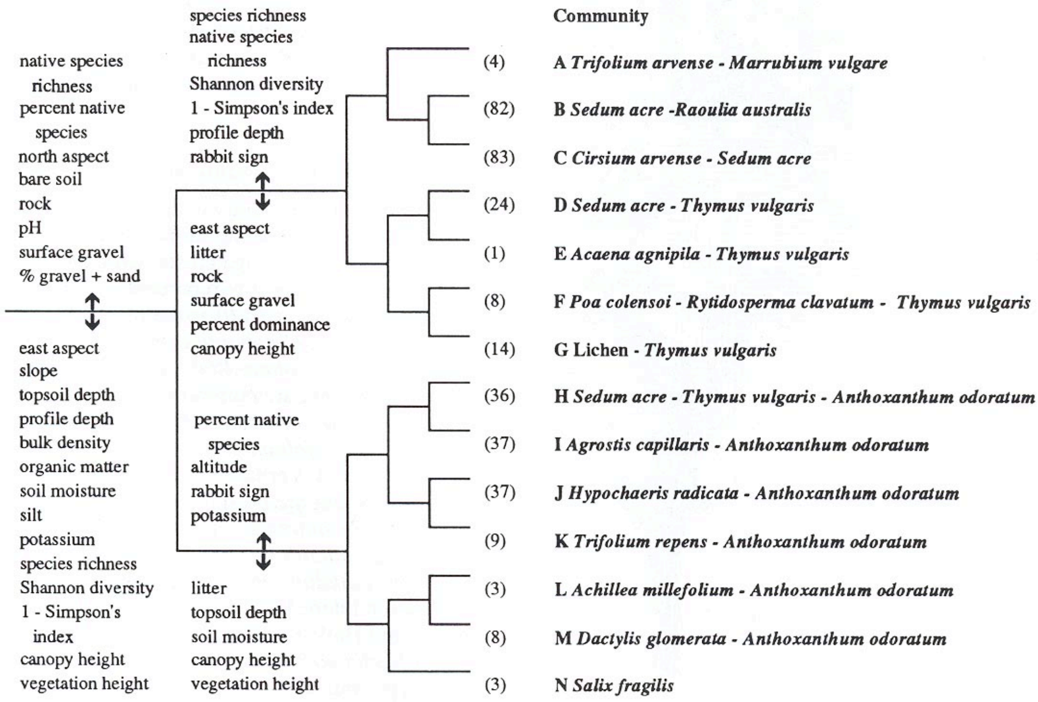

Figure 3: *Classification of sites on the combined data from three seasons (autumn, spring and summer) to the fourth level of division, showing environmental factors separating the vegetation types at the primary and secondary levels of division (*P<0.05 by t*-tests, arrows indicate the direction of the difference), no. of samples, in brackets, and names of plant communities recognised.*

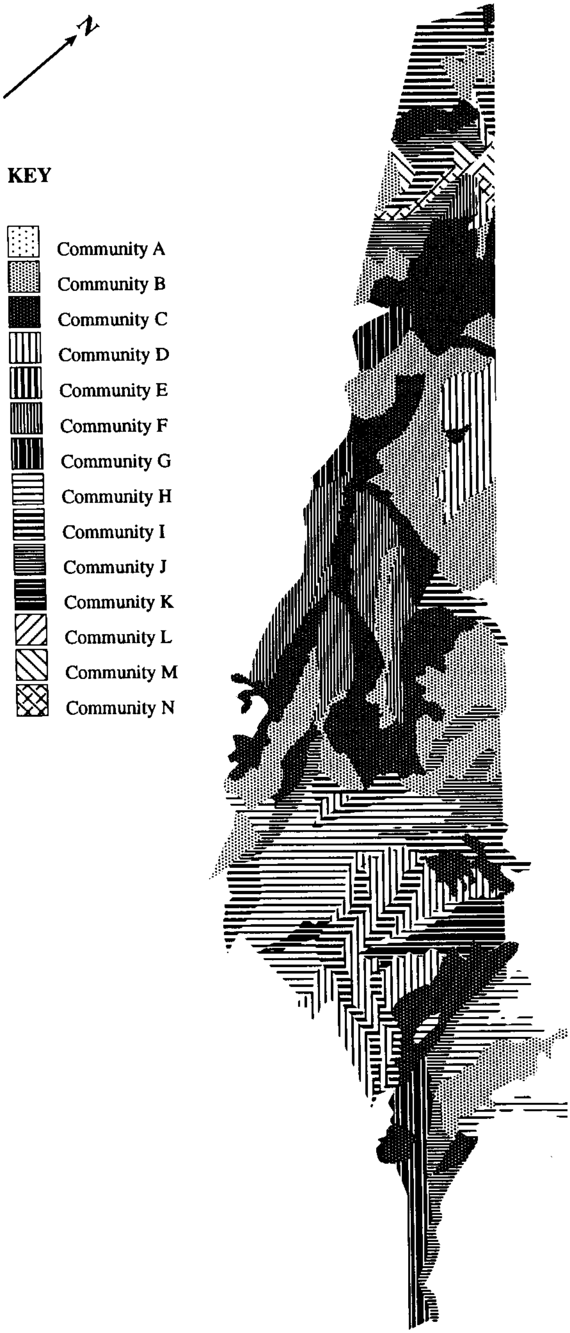

Figure 4: *Distribution of the 14 communities from the classification of vegetation data, within the 91 land units of the detailed study area on Flat Top Hill, in the spring (October) of 1993.*

diversity, native species richness and percentage native species increase across communities H to K, while bare soil, number of rabbit faeces and soil pH decrease. Communities L to N are associated with well-shaded slopes and gullies with consistently high soil moisture, deep topsoils, low rabbit presence, the accumulation of plant litter and a low proportion (31%) of native species. Soils of communities L and M have relatively large clay fractions (9 *cf.* 5% over all other sites). A shrub or tree layer is characteristic.

A. Trifolium arvense - Marrubium vulgare *community*

Soil carbon content is significantly higher than in other communities (although still very low; <0.2%), but these patches of vegetation show no other distinguishing environmental features. It is suggested that they are former stock 'camps' which were subject to excessive manuring. Vegetation cover is extremely sparse, native species are virtually absent and species richness is low (*c.* 8 spp.). *Echium vulgare*, *Lolium perenne*, *Marrubium vulgare* and *Trifolium arvense* are present throughout the year, while exotic annuals contribute to the flora in different seasons: *Aphanes arvensis*, *Erodium cicutarium*, *Myosotis stricta* and *M. discolor* in spring, and *Gypsophila australis* and *Veronica verna* in summer. *L. perenne* is presently uncommon elsewhere in the reserve.

B. Raoulia australis - Sedum acre *community*

This widespread community occupies flat, west-facing locations, such as the saline toeslopes of fans, and shallow, denuded ridge crests, which are highly utilised by rabbits. Sixty-two percent of the species are native. *Raoulia australis* is the most abundant native species, and *Colobanthus brevisepalus*, the tiny grass *Poa maniototo, Raoulia beauverdii* and *Stellaria gracilenta* are common, while the exotic species *Anagallis arvensis*, *Sedum acre*, *Rumex acetosella* and *Trifolium arvense* occur at low abundance (>5%). Vernal mosses and a range of ephemeral species are present in spring. Three native ephemerals, *Ceratocephalus pungens*, *Myosotis pygmaea* var. *minutiflora* and *Myosurus minimus* ssp. *novae-zelandiae*, are of particular botanical and conservation interest (Garnock-Jones, 1984, 1986; Johnson and Hewitt, 1991). The occurrence of *Atriplex buchananii* and *Puccinellia* cf. *stricta* indicates periodically high salinity at some sites.

C. Cirsium arvense - Sedum acre *community*

Sedum acre forms an almost continuous cover on relatively deep (*c.* 34 cm), silty soils and shady aspects of the western face of Flat Top Hill. *Cirsium arvense*, *Cirsium vulgare*, *Raoulia australis*, *Reseda luteola*, *Rumex acetosella* and *Trifolium arvense* are also abundant, while the exotic grasses *Anthoxanthum odoratum* and *Rytidosperma racemosum*, the native *Rytidosperma clavatum*, and shrubs and seedlings of *Rosa rubiginosa* and *Thymus vulgaris* are less common. Small native grasses (e.g., *Poa maniototo* and *Poa lindsayi*) and herbs (e.g., *Acaena novae-zelandiae*, *Epilobium hectorii*, *Geranium sessiliflorum*, *Oxalis exilis*) and the exotic species *Anagallis arvensis* and *Crepis capillaris* are minor species.

D. Sedum acre - Thymus vulgaris *community*

Community D extends to higher altitudes and occupies more gentle slopes and siltier, more fertile soils (*c*. 1.1% potassium) than other *Thymus vulgaris* dominated communities. The vegetation is species-poor and ranges from a mosaic of young *Thymus vulgaris* shrubs and *Sedum acre* to a dominant, tall canopy of *T. vulgaris* with a variable understorey of *S. acre* and low herbs. Low-growing native species such as *Poa maniototo* and *Rytidosperma buchananii* occur where *T. vulgaris* shrubs are scattered, while taller grasses (e.g., *Arrhenatherum elatius*, *Dactylis glomerata*, *Elymus solandri*, *Festuca rubra* and *Poa annua*) are common within a dense *T. vulgaris* canopy. There is a diverse lichen component (9 conspicuous spp. recorded).

E. Acaena agnipila - Thymus vulgaris *community*

This community is found only on the sandy north-facing slopes west of Butchers Creek. The native grass *Rytidosperma clavatum* and the exotic species *Acaena agnipila*, *Rumex acetosella*, *Trifolium arvense* and *Marrubium vulgare* form a *c*. 35 cm tall canopy. Sub-shrubs of *Vittadinia australis*, *V. gracilis* and *Thymus vulgaris*, and the summer ephemeral *Gypsophila australis* are present, while lichens are absent.

F. Poa colensoi - Rytidosperma clavatum - Thymus vulgaris *community*

Thymus vulgaris forms an open canopy, with occasional plants of *Anthoxanthum odoratum*, *Hypericum perforatum*, *Verbascum thapsus* and *Vittadinia australis* on sunny, rocky slopes, where the surface of the shallow soil is paved with gravel. The sparse ground cover includes *Anagallis arvensis*, *Carex breviculmis*, *Sedum acre*, *Trifolium arvense* and the tiny native grass *Rytidosperma thomsonii*, which is uncommon elsewhere in the reserve. Taller native grasses (e.g., *Elymus solandri*, *Poa colensoi*, *Rytidosperma clavatum*) occur about the bases of rocky outcrops.

G. Lichen - Thymus vulgaris *community*

This community is supported by the most dry, shallow, coarse textured, relatively alkaline (pH *c*. 6.9) and potassium-poor soils (*c*. 0.7%) in the reserve. Native mosses and lichens account for most of the species present (*c*. 7 spp. per sample), but contribute little to cover in the impoverished, *Thymus vulgaris*-dominated vegetation. The few vascular plants species include infrequent shrubs of *Rosa rubiginosa*, native grasses such as *Elymus solandri* and *Rytidosperma clavatum* around rock outcrops, and occasionally a sparse ground cover of *Sedum acre*.

H. Sedum acre - Thymus vulgaris - Anthoxanthum odoratum *community*

The driest of the ‘mesic’ communities, this sparse, species-poor mixed grassland community occurs on gentle, north- and east-facing slopes, which are favoured by rabbits. *Anthoxanthum odoratum* is the only species consistently present. *Cirsium arvense*, *Poa maniototo*, *Raoulia australis*, *Reseda luteola* and *Sedum acre* are present on the somewhat gentler slopes, while *Thymus vulgaris* occurs on the steeper gradients and shallower, gravely soils. Exotic forbs (*Crepis capillaris*, *Hypochaeris radicata*, *Rumex acetosella* and *Trifolium arvense*) are found at low (<5%) frequency at most sites, while *Acaena novae-zelandiae* and *Geranium sessiliflorum* are the most abundant native species.

I. Agrostis capillaris - Anthoxanthum odoratum *community*

This short grassland occupies steeper, more gravely, rocky and south-facing slopes than Community H. Soils are moist, loamy silts, usually with relatively intact (7 cm) topsoils. The flora is more diverse (16 *cf.* 13 spp.), and richer in native species (46 *cf.* 34%), than that of Community H. *Agrostis capillaris*, *Anthoxanthum odoratum* and *Festuca rubra* account for most of the vegetation cover; *Raoulia australis* and *Sedum acre* are frequent subordinate species, and shrubs of *Rosa rubiginosa* are common. *Elymus solandri* and *Poa colensoi* are present on sunny slopes, while *Festuca novae-zelandiae*, *Holcus lanatus* and *Trifolium repens* are found on cooler aspects.

J. Hypochaeris radicata - Anthoxanthum odoratum *community*

This variable community is found at a range of altitudes and aspects on steep, rocky slopes or beside rock tors. *Anthoxanthum odoratum*, *Festuca rubra* and *Rytidosperma clavatum* form a short sward, with interstitial forbs such as *Acaena novae-zelandiae*, *Crepis capillaris*, *Holcus lanatus*, *Hypochaeris radicata* and *Sedum acre*. Tussocks of *Festuca novae-zelandiae* and shrubs of *Rosa rubiginosa* are common. The community is relatively rich in native species (*c*. 11 spp.), and includes the grasses *Elymus solandri*, *Poa colensoi* and *Rytidosperma unarede*, the herbs *Helichrysum filicaule*, *Oreomyrrhis ramosa*, *Pseudognaphalium luteoalbum* and *Wahlenbergia albomarginata*, the orchids *Microtis unifolia* and *Thelymitra longifolia*, and the ferns *Asplenium flabellifolium* and *Blechnum penna-marina*.

K. Trifolium repens - Blechnum penna-marina *community*

The relatively acidic soils (pH *c*. 6.1) in the southern lee of rock tors and bluffs support the most floristically diverse (*c*. 20 spp.) and native species-rich (*c*. 13 spp.) community in the reserve. Exotic species dominate the sward in terms of cover, particularly in summer, when *Anthoxanthum odoratum*, *Festuca rubra*, *Holcus lanatus*, *Hypochaeris radicata* and *Trifolium repens* are most abundant. The native herbs *Gnaphalium audax*, *Lachnagrostis filiformis*, *Rytidosperma unarede* and *Uncinia elegans* are restricted to these habitats, and *Acaena caesiiglauca*, *Colobanthus strictus*, *Festuca novae-zelandiae*, *Hydrocotyle novae-zelandiae*, *Luzula banksiana* var. *rhadina*, *Melicytus alpinus*, *Poa colensoi* and *Oreomyrrhis ramosa* are characteristic species.

L. Achillea millefolium - Anthoxanthum odoratum *community*

Moist, clay soils of steep, low-altitude slopes beside Butchers Creek support a shrub canopy dominated by the natives *Discaria toumatou* and *Coprosma propinqua*, with a minor contribution by the exotic *Rosa rubiginosa*. The dense understorey sward of the exotic species *Agrostis capillaris*, *Anthoxanthum odoratum* and *Dactylis glomerata* has the forbs *Achillea millefolium*, *Hypochaeris radicata* and *Trifolium repens* as common subordinate species. The principal native species are *Acaena novae-zelandiae*, *Elymus solandri*, *Muehlenbeckia complexa*, *Oreomyrrhis ramosa*, *Rytidosperma unarede* and *Uncinia elegans*.

M. Agrostis capillaris - Anthoxanthum odoratum *community*

Community M is found on steep, rocky slopes and bluffs, and in moist gullies west of Butchers Creek. Soils have a large clay fraction and topsoils are deep (*c*. 14 cm) and intact. The flora is dominated by exotic species; the few remaining native species contribute little to the plant cover. *Agrostis capillaris*, *Anthoxanthum odoratum* and *Dactylis glomerata* are constant and abundant, and *Festuca rubra* is common. Tussocks of *Festuca novae-zelandiae*, shrubs of *Rosa rubiginosa*, and the scrambling native *Muehlenbeckia complexa* are present. *Acaena agnipila*, *Holcus lanatus*, *Hypochaeris radicata*, *Trifolium arvense* and *T. repens* are prominent exotic herbs.

N. Salix fragilis *community*

The narrow, sandy, periodically inundated alluvial terrace beside Butchers Creek is shaded by a tall canopy of *Salix fragilis* and *S. babylonica*, and adjoined at its upper limit by a dense thicket of *Cytisus scoparius*, *Ribes uva-crispa* and *Ulex europaeus*. The short understorey sward is dominated by *Anthoxanthum odoratum*, *Cerastium fontanum*, *Dactylis glomerata* and *Trifolium repens*, together with *Achillea millefolium*, *Conium maculatum*, *Galium aparine*, *Leucanthemum vulgare*, *Poa annua*, *Prunella vulgaris*, *Senecio jacobaea* and seedlings of *Cytisus scoparius* in different seasons. *Muehlenbeckia complexa* is present in the understorey and as a climber in the lower branches of the trees.

The vegetation gradients

Eigenvalues for the first four axes of the ordination are 0.642, 0.489, 0.424 and 0.306 respectively. Multiple regression showed that environmental factors explain a total of 63.3% of the variation on the first ordination axis, but a relatively small proportion of variation on subsequent axes (30.3, 32.2 and 21.5% on Axes 2, 3 and 4, respectively). Simple correlations showed that several site and vegetation factors are also significantly correlated with the axes of the ordination (Table 3).

The first ordination axis clearly reflects a soil moisture gradient. High soil moisture content, soil profile depth, steep slope, high altitude, and deep and well developed topsoils are positively correlated with Axis 1; all indicate a less extreme soil moisture deficit in the summer months (Fig. 5a). North aspect, bare soil and surface rock are negatively correlated with the first axis (Table 3). In the species ordination (Fig. 6a), species of exposed tertiary soils and silty benches (e.g., *Sisymbrium polyceratum*, *Verbascum thapsus*), those of steep, rocky slopes (e.g., *Thymus vulgaris*, lichen species), and low-growing, native species of dry, alkaline soils (e.g., *Poa maniototo*,

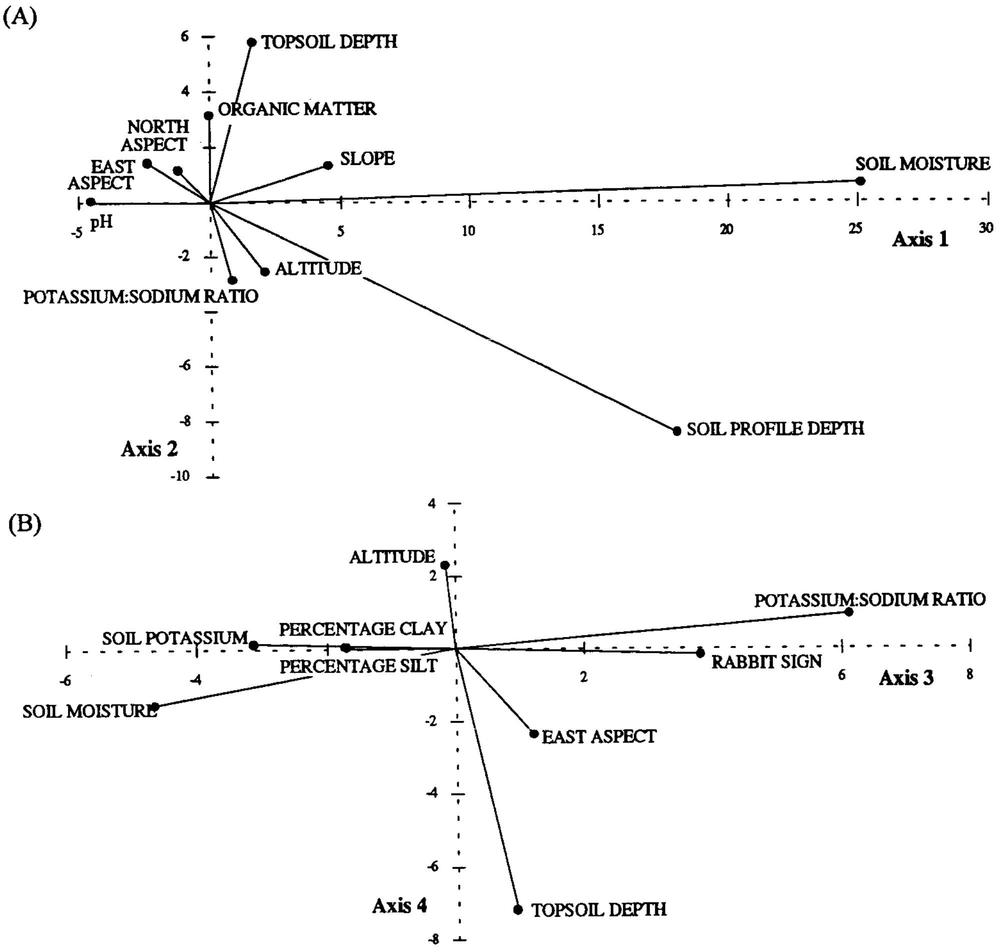

Figure 5: *Vector diagrams of significant (*P*<0.05) environmental factors contributing to the overall multiple regression equation of the first four axes of the ordination of vegetation data on the factors. Vector length is proportional to the total explained variance on the two axes, and direction indicates the proportional contribution to the two axes.*

Table 3: *Correlation coefficients (*R*) between site and vegetation factors and the four axes of the ordination. These factors were not included in the multiple regression in order to avoid circularity. Significant correlations (Sig) are indicated: * =* P*<0.05; ** =* P*<0.01; *** =* P*<0.001.*

Factor	Axis 1		Axis 2		Axis 3		Axis 4	
	R	Sig	R	Sig	R	Sig	R	Sig
Bare soil	-0.30	***	-0.14	**	0.23	***	0.11	*
Litter	0.14	*	0.14	**	0.12	*	0.11	*
Rock	-0.15	**	0.14	*	-0.07	ns	-0.13	*
Vegetation height	0.26	***	0.21	***	-0.00	ns	0.22	***
Canopy height	0.28	***	0.56	***	0.20	***	-0.47	***
Species richness	0.21	***	-0.15	**	-0.34	***	0.19	***
Native species richness	-0.07	ns	-0.21	***	-0.33	***	0.17	**
% Native species	-0.36	***	-0.07	ns	-0.17	**	0.01	ns
Shannon-Weaver Diversity	0.45	***	-0.06	ns	-0.15	**	0.18	***

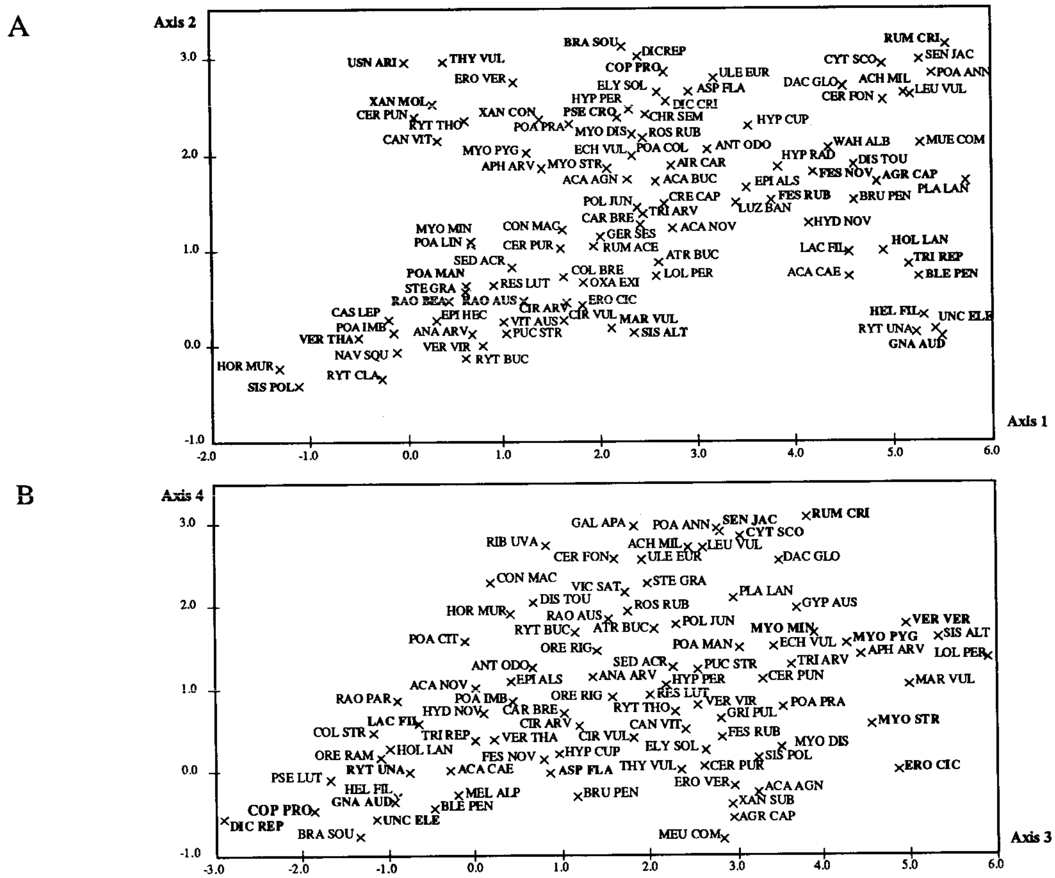

Figure 6: *Distribution of species on (A) the first and second and (B) the third and fourth axes of the ordination of the autumn, spring and summer vegetation data. Axis units represent standard deviations. Species mentioned in the text are in bold type. The full species list for the reserve is given in Walker (1994). Abbreviations not shown in Table 2: ACA AGN*=Acaena agnipila *var.* aequispina; *ACA BUC*=Acaena buchananii; *ACA CAE*=Acaena caesiiglauca; *ACH MIL*=Achillea millefolium; *AGR CAP*=Agrostis capillaris; *APH ARV*=Aphanes arvensis; *ATR BUC*=Atriplex buchananii; *ASP FLA*=Asplenium flabellifolium; *BLE PEN*=Blechnum penna-marina; *BRA SOU*=Brachyglottis southlandicus; *BRU PEN*=Breutelia pendula; *CAS LEP*=Cassinia leptophylla; *CEL GRA*=Celmisia gracilenta; *CER FON*=Cerastium fontanum; *CER PUN*=Ceratocephalus pungens; *CER PUR*=Ceratodon purpureus; *COL STR*=Colobanthus strictus; *CON MAC*=Conium maculatum; *COP PRO*=Coprosma propinqua; *CRE CAP*=Crepis capillaris; *CYT SCO*=Cytisus scoparius; *DIC CRI*=Dichelachne crinita; *DIC REP*=Dichondra repens; *DIS TOU*=Discaria toumatou; *ELY SOL*=Elymus solandri*; EPI ALS*=Epilobium alsinoides *var.* atriplicifolium; *ERO CIC*=Erodium cicutarium; *ERO VER*=Erophila verna; *FES RUB*=Festuca rubra *var.* commutata; *GAL APA*=Galium aparine; *GER MIC*=Geranium microphyllum; *GNA AUD*=Gnaphalium audax*; GYP AUS*=Gypsophila australis; *HEL FIL*=Helichrysum filicaule; *HOR MUR*=Hordeum murinum; *HYD NOV*=Hydrocotyle novae-zelandiae *var.* montana; *HYP CUP*=Hypnum cupressiforme; *HYP RAD*=Hypochaeris radicata; *LAC FIL*=Lachnagrostis filiformis; *LEU VUL*=Leucanthenum vulgare; *LOL PER*=Lolium perenne; *LUZ BAN*=Luzula banksiana *var.* rhadina; *MAR VUL*=Marrubium vulgare; *MEL ALP*=Melicytus alpinus; *MEU COM*=Muehlenbeckia complexa; *MYO ARV*=Myosotis arvensis; *MYO PYG*=Myosotis pygmaea *var.* minutiflora; *MYO MIN*=Myosurus minimus *ssp.* novae-zelandiae; *NAV SQU*=Navarettia squarrosa; *ORE RAM*=Oreomyrrhis ramosa; *ORE RIG*=Oreomyrrhis rigida; *OXA EXI*=Oxalis exilis; *PLA LAN*=Plantago lanceolata; *POA ANN*=Poa annua; *POA CIT*=Poa cita; *POA COL*=Poa colensoi; *POA IMB*=Poa imbecilla; *POL JUN*=Polytrichum juniperinum; *PRU VUL*=Prunella vulgaris; *PSE CRO*=Pseudocyphellaria crocata; *PSE LUT*=Pseudognaphalium luteoalbum; *PTE ESC*=Pteridium esculentum; *PUC STR*=Puccinellia *cf.* stricta; *RAO PAR*=Raoulia parkii; *RIB UVA*=Ribes uva-crispa; *RUM CRI*=Rumex crispus; *RYT THO*=Rytidosperma thomsonii; *RYT UNA*=Rytidosperma unarede; *SIS ALT*=Sisymbrium altissimum; *SIS POL*=Sisymbrium polyceratium; *ULE EUR*=Ulex europaeus; *UNC ELE*=Uncinia elegans; *USN ARI*=Usnea arida; *VER THA*=Verbascum thapsus; *VER VIR*=Verbascum virgatum; *VER VER*=Veronica verna; *VIC SAT*=Vicia sativa; *VIT GRA*=Vittadinia gracilis; *WAL ALB*=Wahlenbergia albomarginata; *XAN SUB*=Xanthoparmelia subnuda; *XAN TAS*=Xanthoparmelia tasmanica;

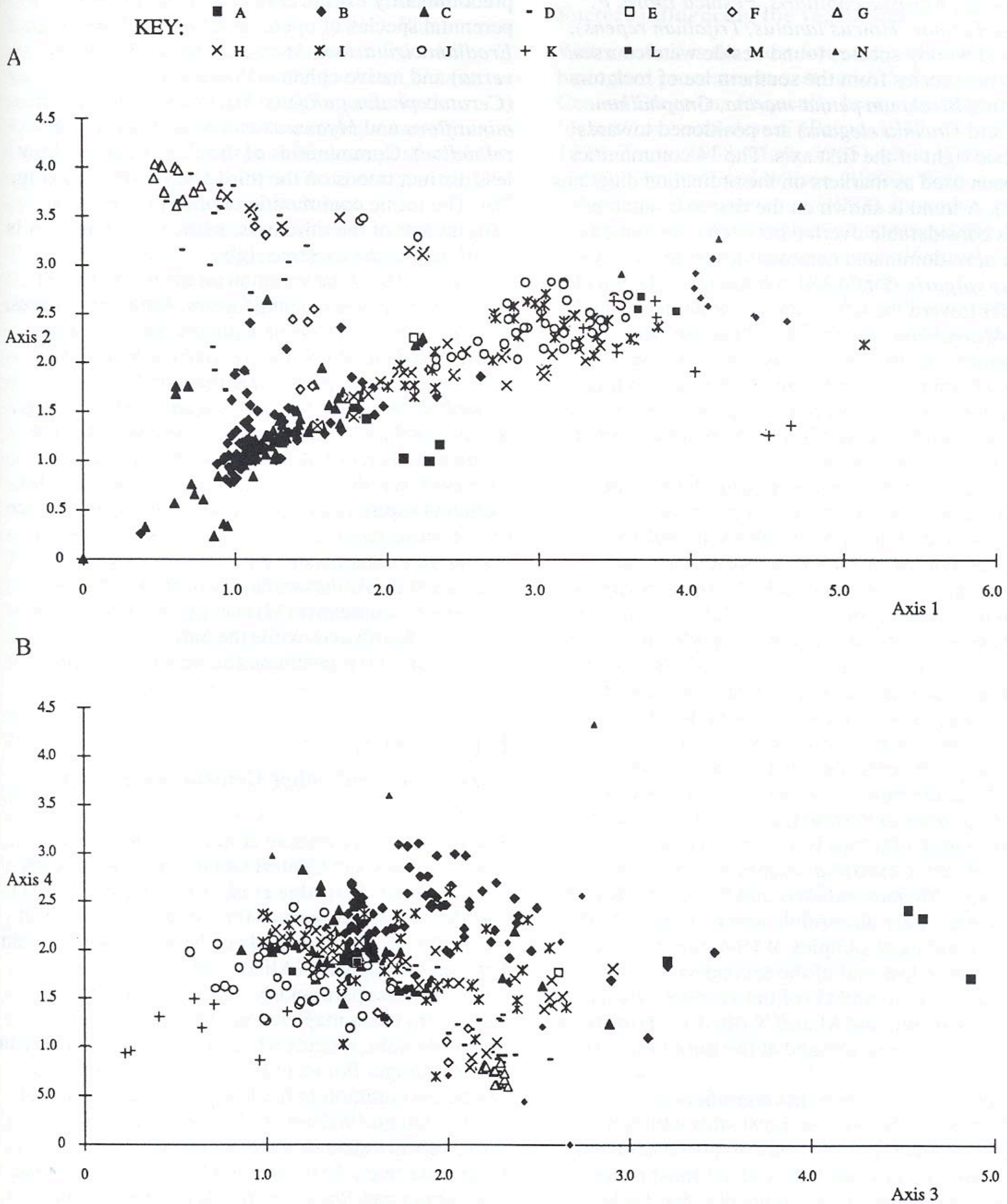

Figure 7: *Distribution of the samples of the 14 communities (A-N) from the classification on* (A) *the first and second and* (B) *the third and fourth axes of the joint ordination of the autumn, spring and summer vegetation data. Axis units represent standard deviations.*

Raoulia australis, *R. beauverdii* and spring ephemerals), are positioned towards the moisture-stressed left of the first axis. Species of steep, shady slopes (e.g., *Agrostis capillaris*, *Festuca rubra*, *F. novae-zelandiae*, *Holcus lanatus*, *Trifolium repens*), forbs and woody species found beside watercourses, and native species from the southern lee of rock tors (including *Blechnum penna-marina*, *Gnaphalium audax* and *Uncinia elegans*) are positioned towards the mesic right of the first axis. The 14 communities have been used as markers on the ordination diagrams (Fig. 7). A trend is shown on the first axis, although there is considerable overlap between communities. *Sedum acre*-dominated communities (B and C), and *Thymus vulgaris*-dominated communities (D, F and G) occur toward the left, while Communities A and E, the *Marrubium vulgare* - *Trifolium arvense* Community and the *Thymus vulgaris* - *Acaena agnipila* Community, are found to the right of these. Communities H, I and J are located about the middle of the axis, while the most mesic communities (K, L, M and N) have the highest scores.

The second axis represents a gradient from deep soils, with little or no topsoil, short, sparse vegetation and high rabbit numbers, to shallow, potassium-poor soils with more intact topsoils, higher organic content and taller vegetation, which is less preferred by rabbits (Fig. 5a; Table 3). Species of deep soils: exotic species from beside rabbit-burrows (e.g., *Marrubium vulgare* and *Sisymbrium altissimum*) and native species from less-disturbed habitats (e.g., *Helichrysum filicaule*), have low scores on the second axis (Fig. 6a). At the top of the second axis are species of shallow soils, some restricted to the moist channel terrace of Butchers Creek (e.g., *Rumex crispus*), and others to sunny aspects of rock outcrops (e.g., *Brachyglottis southlandicus*, *Coprosma propinqua*), or steep, arid slopes (e.g., *Thymus vulgaris* and lichen species). A trend is less easily discernible among communities on the second axis: samples of Community C occur at the extreme low end of the second axis. Communities D, F and G (of the *Thymus vulgaris*-dominated group) and M and N (the two most mesic communities) are positioned at the top of this axis (Fig. 7a).

The third axis represents a gradient in disturbance. At the left are moist sites which are protected from herbivory, while exposed habitats, where rabbit faeces and bare soil are most abundant, are positioned towards the right (Fig. 5b; Table 3). Total and native species richness decrease along this gradient (Table 3). Species at the extreme left of Axis 3 are native forbs (e.g., *Dichondra repens*, *Pseudognaphalium luteoalbum*), grasses (*Lachnagrostis filiforme*, *Rytidosperma unarede*) and woody species (e.g., *Coprosma propinqua*) of diverse, moist, tor-side communities (Fig. 6b). At the disturbed end of this axis are typically ruderal, predominantly exotic, annual and short-lived perennial species of open, denuded localities (e.g., *Erodium cicutarium*, *Myosotis stricta*, *Veronica verna*) and native ephemeral species (*Ceratocephalus pungens*, *Myosotis pygmaea* var. *minutiflora* and *Myosurus minimus* subsp. *novae-zelandiae*). Communities of the classification show less distinct trends on the third and fourth axes (Fig. 7b). The mesic communities J and K occupy the extreme left of the third axis, while Community A is positioned at the extreme right.

Only 21% of the variation on the fourth axis is explained by environmental factors. Altitude increases, and east aspect and topsoil depth decrease along the fourth axis (Fig. 5b). Slow-growing native woody perennials (e.g., *Coprosma propinqua*), forbs (*Gnaphalium audax*, *Uncinia elegans*) and ferns (e.g., *Asplenium flabellifolium*) occupy the low end of the fourth axis (Fig. 6b). At the opposite extreme are species of 'weedy scrub' (Johnson and Hewitt, 1991), including shrubs of the Butchers Creek channel terrace (e.g., *Cytisus scoparius*, *Ribes uva-crispa*) and their understorey components (e.g., *Senecio jacobaea*). Samples of the *Anthoxanthum odoratum* - *Dactylis glomerata* Community (M) occupy the extreme low end of the fourth axis, while the *Salix fragilis* Community (N) is positioned at the top (Fig. 7b).

Discussion

Comparison with other Central Otago plant communities

The Flat Top Hill reserve contains fewer species than other areas in Central Otago for which counts are published (Partridge *et al.*, 1991; Patrick, 1994). The dry grasslands east of the Main Divide in both the North and South Islands of New Zealand contain few endemic species (Allan, 1937; Wardle, 1963, 1985), and the particularly dry climate of the Alexandra basin may exclude from the reserve a range of exotic species which are found elsewhere in Central Otago. For example, those exotic species which are common in the less arid Luggate area of Central Otago (Wilson *et al.*, 1989), and also important invaders of the dry grasslands of California (e.g., *Aira caryophyllea*, *Bromus mollis*, *Poa annua* and *Rumex crispus*), are restricted to mesic habitats on Flat Top Hill. Low species richness in the reserve may reflect the severity of disturbance by fire, grazing and subsequent erosion of the soils (Cockayne, 1910; Petrie, 1912; Mather, 1982).

Fifty-three percent of vascular plant species present are indigenous, which is similar to the results of other lowland Central Otago surveys, e.g., 56% at Conroys Road (Patrick, 1994) and 48% in the Kawarau Gorge (Partridge *et al*., 1991). Plant communities range in species richness from 1.9 vascular plant species m^{-2} in the Lichen - *Thymus vulgaris* Community (G) to 20.7 species in the *Achillea millefolium* - *Anthoxanthum odoratum* Community (M) (Table 1). A high proportion of the species present on Flat Top Hill are concentrated in steep, shady areas and near rock tors.

Many plant communities presently found on Flat Top Hill have not been described in other parts of Central Otago: in particular the *Sedum acre*-dominated Community C and *Anthoxanthum odoratum* - *Festuca rubra* grassland communities (H to J). Plant communities of the type found on Flat Top Hill are not mentioned in the PNA Report on the adjoining Manorburn Ecological District (Fagan and Pillai, 1992), nor are they clearly represented in the descriptions of Hubbard and Wilson (1988), whose survey included the lower slopes of Flat Top Hill.

Saline areas in lowland Central Otago have been noted for their distinctive flora and fauna (e.g., Patrick, 1989). Although the saline area at Butchers Creek on Flat Top Hill is documented (McIntosh, Beecroft and Patrick, 1992), *Atriplex buchananii* and *Puccinellia stricta* were the only two halophytes found in the present study, each in only one locality.

Raoulia australis-dominated vegetation is widespread throughout lowland Central Otago (Mark, 1965; Hubbard and Wilson, 1988; Wilson *et al*., 1989; Partridge *et al*., 1991), but its species composition varies widely. *Anagallis arvensis*, *Poa maniototo* and *Raoulia beauverdii*, which are abundant in Community B on Flat Top Hill, are not mentioned in the descriptions of other Central Otago "Scabweed" communities. Patches of *Coprosma propinqua* - *Discaria toumatou* shrubland on Flat Top Hill are similar to remnants in the Kawarau Gorge, while *Salix*-dominated vegetation is widespread beside water throughout the Upper Clutha basin. It therefore appears that some of the communities found on Flat Top Hill extend throughout the region, while others are more restricted.

Despite diffuse vegetation boundaries, clear relationships between communities and environmental features are demonstrated in the vegetation pattern of Flat Top Hill. Dasti and Agnew (1994) suggested that low constancy and fidelity of species in the vegetation of low rainfall areas was due to a residual flora, comprising generalists capable of persisting in an environment of variable disturbance and episodic resource availability. Species which survive must retain enough variation to react to these conditions, and directional selection is unlikely.

Factors influencing the vegetation

Water deficit is the most frequent control on biological processes in semi-arid regions. Lowland Central Otago has frequently been referred to as 'desert', or 'semi-desert' (Petrie, 1912; Cockayne, 1928; Zotov, 1938; Mark, 1965) while Williams (1980), Hubbard and Wilson (1988), Wilson *et al*. (1989) and Partridge *et al*. (1991), in studies of different parts of the region, all attributed the vegetation pattern primarily to the effects of differential soil moisture deficiency.

The overriding effect of soil moisture variation (determined by aspect and slope) on the vegetation pattern of Flat Top Hill, is shown in the primary division of the classification as well as on the first axis of the ordination (Figs. 3 and 5). Particular examples may be seen of the effect of soil moisture stress: (a) east of the crest, the vegetation changes abruptly in response to cooler aspect and steeper gradients (Fig 4); (b) small-scale topography has a marked effect upon the water regime and hence vegetation; e.g., remnant *Festuca novae-zelandiae* stands are found on moist soils on steep, shady aspects of spurs, and soils receiving runoff from adjacent rock tors support distinctive, species rich communities.

Soil texture, particularly the coarse component, has been found to be important in other studies of Central Otago vegetation (e.g., Wilson *et al*., 1989; Partridge *et al*., 1991), and soil fertility is clearly a determinant of species distribution in the Luggate area of Central Otago (Wilson *et al*., 1989). In this study, soil texture was correlated with the first division of the classification and with lower ordination axes (Figs. 3 and 5). Soil depth appeared in this study to have a slightly stronger influence on the vegetation than soil texture. However, soil potassium and potassium:sodium ratios have relatively subtle roles in determining vegetation gradients on Flat Top Hill, and are correlated with lower order axes of the vegetation ordination.

While rock tors modify the local environment by shading and increasing moisture runoff to soils at their bases (Fig. 2), they have also been described as 'refugia' for plant species (Johnson and Hewitt, 1991), implying that they provide protection from the disturbances of frequent fire and from grazing. Steep, south-facing slopes not only provide relatively moist habitats, but are also avoided by both sheep and rabbits, which prefer gentle, sunny gradients (Partridge *et al*., 1991). The gradient from less disturbed, species-rich sites in the shelter of rock tors and steep, south-facing slopes, to species-poor sites in sunny, flat localities, where bare soil is most extensive, and rabbit faecal pellets are most numerous, is clearly shown on the third axis of the ordination (Fig. 5b; Table 3).

Changes in vegetation composition due to human disturbance

Isolated mature trees of *Sophora microphylla* (kowhai) and shrubs of *Carmichaelia compacta* (native broom), *Cassinia leptophylla*, *Helichrysum lanceolatum*, *Olearia lineata* and *Olearia odorata* among rock tors and on steep, moist slopes in the reserve might be remnants of the pre- or early-European vegetation of the area. Recruitment of such species may have declined following environmental modification brought about by fires and continual grazing.

The area was once heavily grazed by sheep (Mr P. Dunbier, *pers. comm.*) and the present restricted distribution of palatable native grasses (e.g., *Dichelachne crinita*, *Elymus apricus*, *Elymus solandri*, *Poa colensoi*, *Rytidosperma clavatum* and *Rytidosperma unarede*) may be a response to past sheep grazing. Several species that are presently widespread in the study area (*Anagallis arvensis*, *Cirsium vulgare*, *Epilobium* spp., *Erodium cicutarium*, *Geranium sessiliflorum*, *Raoulia australis*, *R. subsericea*, *Reseda luteola*, *Rumex acetosella*, *Trifolium arvense* and *Verbascum virgatum*) are rarely recorded in sheep faecal samples (Croker, 1959); their persistence may have been favoured under a heavy grazing regime. Although the degradation of vegetation and soils in Central Otago has often been blamed on the rabbit pest, no analysis of rabbit diet has been published. Authors have implied that rabbits compete with sheep for available forage, reducing the stock carrying capacity of the grasslands (e.g., Zotov, 1938).

The invasion of *Sedum acre* and *Thymus vulgaris*

Much of the area of Flat Top Hill today is presently dominated by either *Sedum acre* or *Thymus vulgaris* (Walker, 1994). The former, which predominates on gentle slopes and deeper, silty soils, is rarely grazed by rabbits in the area (Fraser, 1985), and there are few records of its introduction and spread in Central Otago.

T. vulgaris occupies mainly shallow, gravely soils of the lower eastern slopes, parts of the crest, and the steeper west-facing slopes of Flat Top Hill, and appears to be spreading southward in the area. Rabbits will feed on seedlings or new growth of *T. vulgaris* (Wilkinson, Dann and Smith., 1979), but rarely browse adult foliage (Fraser, 1985). Morgan (1989) associated a dramatic increase in the extent of *T. vulgaris* in Central Otago with the reduction of rabbit populations in the 1950s. *T. vulgaris* has a relatively high requirement for soil moisture for germination and the early phases of establishment (Wilkinson *et al*., 1979; Morgan, 1989). It is probable that *T. vulgaris* shrubs initially became established on steeper, rockier slopes of Flat Top Hill in moist years, when forage was abundant in the flatter areas preferred by rabbits. Few vascular plant species survive beneath mature, tall (*c*. 35 cm) stands of *T. vulgaris*, and the mature shrub is highly tolerant of drought (Morgan, 1989). A mature stand of *T. vulgaris* shrubs may therefore have further reduced the abundance of palatable understorey species on steep slopes, which would have discouraged rabbit grazing within such stands. Furthermore, rabbits may have sharpened the boundaries between *Sedum acre*- and *T. vulgaris*- dominated communities, by continually browsing seedlings of *T. vulgaris* on the margins of flatter, preferred areas. Such a self-reinforcing process may be an example of a switch (*sensu* Wilson and Agnew, 1992).

Release from grazing

There are few published studies regarding the effects of a release from grazing in semi-arid short tussock grasslands in New Zealand (Allen, 1993). Although the present knowledge of the attributes of the species is too limited to allow a detailed forecast of the changes that may occur, following the recent control of grazing animals in the reserve, some general predictions can be made.

An increase in the perennial component of semi-arid vegetation following release from grazing has often been recorded (e.g., Orr, 1981) and has recently been demonstrated in Central Otago (Allen *et al*., *in press*). A succession towards perennial grasses and shrubland is most likely to occur on the deeper (<30 cm), finer soils of the wetter, south- and east-facing slopes, east of the main ridge. A resurgence of palatable species may also be expected. However, in the short term, these are likely to be mainly exotic species. In particular, *Thymus vulgaris* seedlings may establish beyond the present range onto more gentle slopes. The competitive advantage of less palatable species (e.g., *Sedum acre*, *Epilobium hectorii*, *Geranium sessiliflorum*, *Poa maniototo*, *Raoulia australis* and *Raoulia beauverdii*) may be weakened. *Dactylis glomerata* may also increase, particularly on cooler aspects; it has been shown to increase when protected from grazing overseas and in New Zealand (Lord, 1990) including Central Otago (Allen *et al*., *in press*). Palatable native herbs and grasses which are presently restricted to protected microsites may also increase in range, but this will depend on their ability to compete with vigorous exotic species. Similarly, although survival of seedlings of *Festuca novae-zelandiae* may be favoured by the cessation of grazing (Lord, 1990), both seedlings and adults may be suppressed by exotic species.

A resurgence of perennial and palatable species may reduce species richness in the reserve. Diversity is generally higher in grazed than in ungrazed grasslands, and this has been demonstrated in the short tussock grasslands of Canterbury (Meurk, Norton and Lord, 1989; Lord, 1990).

Native annuals

Annuals are rare in the New Zealand flora (Allan, 1937), and the presence of the native ephemerals *Ceratocephalus pungens*, *Myosotis pygmaea* var. *minutiflora* and *Myosurus minimus* ssp. *novae-zelandiae* add considerably to the botanical and conservation value of Flat Top Hill. They are found only in spring, in the sparse vegetation of open, saline west-facing toeslopes. A number of exotic ephemerals (*Aphanes arvensis*, *Erophila verna*, *Myosotis discolor* and *M. stricta*) are extremely similar in size, life-cycle and in distribution. The life-cycles of these ephemeral species show many of the characteristics of desert annuals (Fox, 1992). They are well adapted to spring moisture availability and to long summer droughts, showing early and rapid spring growth and reproduction. Jackson and Roy (1986) name three requirements of annual species in grasslands: a ruderal environment (variable, with catastrophic and density-independent mortality - Pianka, 1970), high winter rainfall, and relatively long summer drought. Although winter rainfall is not always high, and summer droughts are not always long, the climate of Central Otago largely fulfills these requirements, and the vegetation has a proportion of annual species.

The ephemerals appear to escape grazing, both by being low-growing, and because their short life cycle coincides with the period of germination of many other species. However, under a reduced grazing regime, palatable and/or perennial species, such as *Agrostis capillaris* and *Poa pratensis*, may invade the presently sparsely vegetated habitats of the ephemerals and compete with them.

Management recommendations

Superficially, Flat Top Hill appears to be a desertified, eroded landscape, infested with weeds and rabbits, and of little value for nature conservation. The pre-human vegetation has been modified by the influence of man, and probably could not be restored by any change in pastoral management. Indeed, the vast majority of the land area is covered by exotic plant species. However, in terms of numbers of species present in the area, the flora of Flat Top Hill is still predominantly native.

The most important management tool is manipulation of grazing intensity. In New Zealand short-tussock grassland, removal of grazing may result in dominance by a few exotic species, and a reduction in total species richness (Meurk *et al.,* 1989). If present management for very low rabbit numbers continues on Flat Top Hill, an increase in the cover of exotic species may be expected. Direct eradication of exotic herbs is not feasible with currently-available techniques, except perhaps locally. Therefore, particularly in the native-ephemeral areas, it may be desirable to allow some level of rabbit grazing. Exotic woody plants (e.g., *Cytisus scoparius* (broom), *Ulex europaeus* (gorse), *Rosa rubiginosa* (sweet brier) and wilding *Pinus* species) are also likely to increase under management for low rabbit numbers, but they are presently sufficiently restricted in their distribution within the reserve that eradication, or at least control, is possible. However, *Thymus vulgaris* is now so widespread in the reserve that control is not presently feasible.

An important feature of the reserve, in terms of natural values, is the presence of remnant shrubs, such as *Aristotelia fruiticosa*, *Carmichaelia compacta* and *Cassinia leptophylla*, especially around rock outcrops east of the main ridge. Occasional shrubs of *Kunzea ericoides* (kanuka) are also present, although no seedlings were observed. It may be possible to encourage the regeneration of native shrubland on the relatively moist slopes above Lake Roxburgh, towards the higher-altitude southern end of the crest, and in moist gullies.

Species dominance in unstable semi-arid regions is often episodic, with species rising to dominance for a period of time, and later being reduced to minor components of the vegetation (Walker and Noy-Meir, 1982). Even relatively long-lived species (e.g., *T. vulgaris*) may not represent permanent features of the landscape in semi-arid Central Otago, and may ultimately be succeeded by other species, e.g., through the action of biological agents such as insects or disease. The inevitability of continuing change in the vegetation must be taken into account in the management of Flat Top Hill.

Acknowledgements

The financial support of the Miss E.L. Hellaby Indigenous Grasslands Research Trust and the J.S.

Tennant Fund is gratefully acknowledged. SW is grateful to Brian Patrick for his enthusiastic support and encouragement, and to Peter Johnson, Allan Hewitt and Ralph Allen for their ideas and advice. Thanks are also due to DoC and Mary Wallace for access, to Ivan Fennessy, Robert Gibson and Graeme Parmenter for data, to Dave Frew and John Reid for accommodation, to Lyall Rishworth and Lewis Sargeant for field assistance, and to Colin Meurk and John Steel for lichen and bryophyte identification. We would like to thank Bill Lee and an anonymous referee for suggested improvements on the manuscript, and Ken Phipps and Richard Gimpel for logistic and technical support in the Botany Department.

References

Allan, H.H. 1937. A consideration of the “biological spectra” of New Zealand. *Journal of Ecology 25:* 116-152.

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

Allen, R.B. 1993. An appraisal of monitoring studies in the South Island tussock grasslands, New Zealand. *New Zealand Journal of Ecology 17:* 61-63.

Allen, R.B.; Wilson, J.B.; Mason, C.R. *(In press).* Vegetation change following exclusion of grazing animals in depleted grassland, Central Otago. *Journal of Vegetation Science*.

Blakemore, L.C.; Searle, P.L.; Daly, B.K. 1987. *Methods for the chemical analysis of soils*. New Zealand Soil Bureau Scientific Report No. 80, Department of Scientific and Industrial Research, Lower Hutt, New Zealand. 103 pp.

Brownsey, P.J.; Smith-Dodsworth, J.C. 1989. *New Zealand ferns and allied plants*. David Bateman, Auckland, New Zealand. 168 pp.

Buchanan, J. 1868. Sketch of the botany of Otago. *Transactions of the New Zealand Institute* 1 (Part III): 22-53.

Cheeseman, T.F. 1925. *Manual of the New Zealand Flora, 2nd Edition*. Government Printer, Wellington, New Zealand. 1163 pp.

Cockayne, A.H. 1910. The natural pastures of New Zealand. I. The effect of burning on tussock country. *Journal of the Department of Agriculture (New Zealand) 1:* 7-15.

Cockayne, L. 1919. An economic investigation of the montane tussock-grasslands of New Zealand. III: Notes on the depletion of the grassland. *New Zealand Journal of Agriculture 19:* 129-138.

Cockayne, L. 1928. *The vegetation of New Zealand*. 2nd Edn. Willhelm Engelmann, Leipzig.

Connor, H.E.; Edgar E. 1987. Name changes in the indigenous New Zealand Flora 1960-1980 and *Nomina Nova* IV, 1963-1986. *New Zealand Journal of Botany 25:* 115 -170.

Croker, B.H. 1959. A method of estimating the botanical composition of the diet of sheep. *New Zealand Journal of Agricultural Research 2:* 72-85.

Dasti, A; Agnew, A.D.Q. 1994. The vegetation of Cholistan and Thal deserts, Pakistan. *Journal of Arid Environments 27:* 193-208.

Fagan, B.; Pillai, D. 1992. *Manorburn Ecological District*. Survey Report for the Protected Natural Areas Programme. Department of Conservation, Wellington, New Zealand. 116 pp.

Fox, G.A., 1992. The evolution of life history traits in desert annuals: adaptation and constraint. *Evolutionary Trends in Plants 6:* 25-31.

Fraser, K.W. 1985 (unpublished). *Biology of the rabbit (*Oryctogalus cuniculus *L.) in Central Otago, New Zealand, with emphasis on its behaviour and its relevance to poison control operations*. PhD thesis, University of Canterbury, Christchurch, New Zealand. 378 pp.

Fraser, K.W. 1988. Reproductive biology of rabbits *Oryctogalus cuniculus* (L.), in Central Otago, New Zealand. *New Zealand Journal of Ecology 11:* 79-88.

Friedel, M.H.; Bastin, G.N.; Griffin, G.F. 1988. Range assessment and monitoring in arid lands: The derivation of functional groups to simplify vegetation data. *Journal of Environmental Management*, 27: 85-97.

Galloway, D.J. 1985. *Flora of New Zealand: Lichens*. Government Printer, Wellington, New Zealand. 662 pp.

Garnier, B.J. 1951. Thornthwaite’s new system of climate classification in its application to New Zealand. *Transactions of the Royal Society of New Zealand 79:* 87-103.

Garnock-Jones, P.J. 1984. *Ceratocephalus pungens* (Ranunculaceae): a new species from New Zealand. *New Zealand Journal of Botany 22:* 135-137.

Garnock-Jones, P.J. 1986. A new status for the New Zealand mousetail (*Myosurus*, Ranunculaceae). *New Zealand Journal of Botany 24:* 351-354.

Gibbs, H.S. 1980. *New Zealand soils - An introduction*. Oxford University Press, Wellington, New Zealand. 115 pp.

Healy, A.J.; Edgar, E. 1980. *Flora of New Zealand: Volume III*. Government Printer, Wellington, New Zealand. 220 pp.

Hill, M.O.; Gauch, H.G. 1980. Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio 42:* 47-58.

Hill, M.O.; Bunce, R.G.H.; Shaw, M.W. 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. *Journal of Ecology 63:* 597-613.

Hubbard, J.C.E.; Wilson, J.B. 1988. A survey of the lowland vegetation of the Upper Clutha District of Otago, New Zealand. *New Zealand Journal of Botany 26:* 21-35.

Jackson, L.E.; Roy, L. 1986. Growth patterns of mediterranean and perennial grasses under simulated rainfall regimes of Southern France and California. *Acta Oecologia, Oecologia Plantarum 7:* 191-212.

Johnson, P.N.; Hewitt, A.E. 1991 (unpublished). *Flat Top Hill*, *Central Otago: Report on soils and vegetation*. Department of Scientific and Industrial Research Land Resources, Dunedin, New Zealand. 24 pp.

Lord, J.M. 1990. The maintenance of *Poa cita* grassland by grazing. *New Zealand Journal of Ecology 13:* 43-49.

Mark, A.F. 1965. Vegetation and mountain climate. *In:* Lister, R.G.; Hargreaves, R.P. (Editors), *Central Otago*, pp. 69-91. New Zealand Geographical Society, Wellington, New Zealand. 195 pp.

Mather, A.S. 1982. The desertification of Central Otago, New Zealand. *Environmental Conservation 9:* 209-216.

Maunder, W.J. 1965. Climatic character. *In:* Lister, R.G.; Hargreaves, R.P. (Editors), *Central Otago*, pp. 46-68. New Zealand Geographical Society, Wellington, New Zealand. 195 pp.

McEwen, W.M. 1987. *Ecological regions and districts of New Zealand*, *Sheet 4, 3rd Revised Edition*. Biological Resources Centre Publication No. 5, Department of Conservation, Wellington, New Zealand. 125 pp.

McGlone, M.S. 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. *New Zealand Journal of Ecology 12 (Supplement):* 115-129.

McGlone, M.S.; Mark, A.F.; Bell, D. 1995. Late Pleistocene and Holocene vegetation history, Central Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand 25*: 1-22.

McIntosh, P.D.; Beecroft, F.G.; Patrick, B. 1992 (unpublished). *Register of saline sites in North and Central Otago*: *Volume II*. Department of Scientific and Industrial Research, Dunedin, New Zealand. 59 pp.

Meurk, C.D.; Norton, D.A.; Lord, J.M. 1989. The effects of grazing and its removal from grassland reserves in Canterbury. *In:* Norton, D.A. (Editor), *Management of New Zealand's natural estate*, pp. 72-75. Occasional Publication No. 1, New Zealand Ecological Society, Christchurch, New Zealand. 119 pp.

Molloy, L.F. 1988. *The living mantle: Soils in the New Zealand landscape*. Mallison Rendel and the New Zealand Society of Soil Science, Wellington, New Zealand. 239 pp.

Moore, L.B.; Edgar, E. 1970. *Flora of New Zealand*: *Volume II*. Government Printer, Wellington, N.Z. 354 pp.

Morgan, R.K. 1989. Thyme in the Central Otago landscape. *In:* Kearsley, G.; Fitzharris, B. (Editors), *Southern Landscapes: Essays in honour of Bill Brockie and Ray Hargreaves,* pp. 213-232. Department of Geography, University of Otago, Dunedin, New Zealand. 360 pp.

New Zealand Meteorological Service, 1983. *Summaries of climatological observations to 1980*. New Zealand Meteorological Service Miscellaneous Publication 177, Wellington, New Zealand. 59 pp.

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

Orr, D.M. 1981. Changes in the quantitative floristics of *Astrebla* spp. (Mitchell Grass) communities in south-western Queensland in relation to trends in seasonal rainfall. *Australian Journal of Botany 29:* 533-545.

Partridge, T.R.; Allen, R.B.; Johnson, P.N.; Lee, W.G. 1991. Vegetation/environment relationships in lowland and montane vegetation of the Kawarau Gorge, Central Otago, New Zealand. *New Zealand Journal of Botany 29:* 295-310.

Patrick, B.H. 1994. Biodiversity in semi-arid Central Otago. *New Zealand Botanical Society Newsletter 35:* 11-12.

Patrick, B.H. 1989 (unpublished). *Lepidoptera of salt-pans of Central Otago*. Department of Conservation, Dunedin, New Zealand. 41 pp.

Petrie, D. 1883. Some effects of the rabbit pest. *New Zealand Journal of Science 1:* 412-414.

Petrie, D. 1895. List of the flowering plants indigenous to Otago, with indications of their distribution and range in altitude. *Transactions of the New Zealand Institute 28:* 540-591.

Petrie, D. 1912. *Report on the grass denuded lands of Central Otago*. New Zealand Department of Agriculture, Industries and Commerce Bulletin, 23, Wellington, New Zealand. 18 pp.

Shannon, C.E.; Weaver, W. 1949. *The mathematical theory of communication.* University of Illinois Press, Urbana, U.S.A. 125 pp.

Stace, C.A. 1991. *New flora of the British Isles.* Cambridge University Press, U.K. 1266 pp.

Thomas, R.F. 1973. *Test methods for soil engineering.* New Zealand Soil Bureau Scientific Report 10E, Department of Scientific and Industrial Research, Lower Hutt, New Zealand. 27pp.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review 38:* 55-94.

Walker, B.H.; Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. *In:* Huntley, B.J.; Walker, B.H. (Editors), *Ecology of tropical savannas*, pp. 577-590. Springer, Berlin, Germany. 669 pp.

Walker, S. 1994 (unpublished). *The vegetation of Flat Top Hill, Central Otago, New Zealand.* MSc thesis, University of Otago, Dunedin, New Zealand. 320 pp.

Wardle, P. 1963. Evolution and distribution of the New Zealand flora, as affected by quaternary climates. *New Zealand Journal of Botany 1:* 3-17.

Wardle, P. 1985. Environmental influences on the vegetation of New Zealand. *New Zealand Journal of Botany 23:* 773-788.

Webb, C.J.; Sykes, W.R.; Garnock-Jones, P.J. 1988. *Flora of New Zealand: Volume IV.* Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand. 1365 pp.

Wilkinson, E.L.; Dann. G.M.; Smith, G.J.S. 1979. *Thyme in Central Otago.* Tussock Grasslands and Mountain Lands Institute Special Publication No. 14, Lincoln College, Lincoln, New Zealand. 30 pp.

Wilson, J.B.; Williams, P.A.; Lee, W.G. 1989. Vegetation composition and segregation in relation to the environment at low altitudes in the Upper Clutha Basin, New Zealand. *New Zealand Journal of Ecology 12:* 103-116.

Wilson, J.B.; Agnew, A.D.Q. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research 23:* 263-336.

Zotov, V.D. 1938. Survey of the tussock grasslands of the South Island of New Zealand. *New Zealand Journal of Science and Technology 20 (A):* 212 -244.