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VEGETATION COMPOSITION AND SEGREGATION IN RELATION TO THE ENVIRONMENT AT LOW ALTITUDES IN THE UPPER CLUTHA BASIN, NEW ZEALAND

Summary: The vegetation of an area of the Upper Clutha basin, New Zealand, with a 'semi-arid' climate, was sampled with 95 quadrats in a nested randomised design. All types of vegetation were sampled, from near-natural to managed pastures. Twenty four environmental factors were measured in each quadrat.

Five 'formations' are described, and 14 'communities' recognised within them, although there are few constant or faithful species. Such weak structure, and relatively weak correlation with the environment, are partly attributed to non-equilibrium. All formations, and many of the communities, are scattered over the area. The most important environmental factors in determining the vegetation are latitude, elevation, soil fertility (especially sulphate) and water.

All sites contain exotic species; some contain only exotics. Correlation between .the sizes of the native and exotic guilds gave no evidence that natives and exotics were competing for niches. The lowest proportion of exotics is at higher elevations and on steeper slopes. Analyses showed a strong gradient from near-natural vegetation to managed pastures, but with no discontinuity. Agricultural communities, especially lucerne fields, include species typical of unmanaged sites in similar conditions.

Keywords: Low-elevation vegetation; Clutha; Central Otago; depleted land; semi-desert; community structure; native and exotic guilds.

Introduction

New Zealand has a generally oceanic climate, but the rain shadow of the Southern Alps creates a dry climate in small areas of the South Island. The driest part is the lowland Upper Clutha basin, where a Thornthwaite moisture index ranging down to -31 rates the climate as "Semi-arid" (Hubbard and Wilson, 1988). Semi-desert vegetation (Cockayne, 1928) has resulted from this climate, combined with disturbances during the last 100 years such as burning, grazing, and gold-mining. The open cover has allowed invasion by many exotic species.

Hubbard and Wilson (1988) described the mixed native/exotic vegetation of the lowland Upper Clutha basin on a broad scale. The present investigation aimed to intensively examine a smaller area, in the northern Upper Clutha basin, across a strong rainfall gradient. A reduced number of samples enabled more rigorous sampling methods to be used, and the environment to be more fully categorised than in previous work.

The study aimed to answer the following questions:

a. What recognisable floristic aggregates (i.e. communities) are present?
b. Is there strong or weak community structure?
c. Do some communities have a greater proportion of native species than others? If so, what factors influence the native:exotic ratio?

Methods

The sampling, in 1979, covered land below 460 m elevation a.s.l. and between NZ Map Series 1 grid line 2020 in the north, 2090 in the south, 1000 in the west and 2020 in the east. A nested sampling scheme was used, making it possible to sample more sites in the time available, and also giving information on both large- and small-scale variation. Within the study area, 16 grid squares (0.91 km x 0.91 km) were selected by restricted randomisation, and within each six quadrats were positioned by further restricted randomisation. A further randomisation of up to 10 m was used in locating the final sampling point.

A quadrat of 1m x 3m was used. All vascular plant and bryophyte species occurring in the quadrat were recorded on a 3-point abundance scale. However, only the presence/absence information is used for the main analyses, because of its greater objectivity.

The following environmental factors were recorded for each site:

Longitude.
Latitude: latitude parallels the gradient in rainfall, from 684 mm in the north of the sample area to 459 mm per annum in the south (New Zealand Meteorological Service, 1984).
Elevation.

Macro-exposure: an 11-point scale; -5 (extremely sheltered), through 0 (neither sheltered by surrounding land on that scale, nor exposed from it), to + 5 (extremely exposed), estimated over a radius of 50 m from the centre of the quadrat.

Micro-exposure: a scale of + = exposed or - = sheltered, comparing the centre with the edges of the quadrat.

Slope: with an Abney level placed on aim rod down the line of maximum slope.

Aspect: Since compass bearings are on a circular scale, this was split into two factors for analysis:

North-aspect: 180 for a due north aspect, through 90 for east or west, to 0 for due south.

East-aspect: 180 for a due east aspect, through 90 for north or south, to 0 for due west.

Rock cover: estimated as a percentage of the ground area.

Pellets: the number of animal faecal pellets in the quadrat.

Three soil samples were taken from each quadrat, at depth 0-15 cm, and bulked. Sieving, followed by mechanical analysis by the hydrometer method of Thomas (1973), separated the soil into diameter classes as a % of total dry soil:

Stone (> 2mm).
Coarse sand (0.2 mm - 2 mm).
Fine sand (0.02 mm - 0.2 mm.
Silt (0.002 mm - 0.02 mm).
Clay (< 0.002 rom).

For statistical analysis, the last four factors were combined into one value, 'sandiness' as:

coarse sand % X 3 + fine sand % - silt % - clay % X 3

The following were estimated in the < 2 mm soil fraction:

Water: expressed on a dry soil basis.

pH: by meter, on a soil:water mixture.

Total nitrogen: by the method of McKenzie and Wallace (1954).

Available phosphate: by the method of Mountier, Grigg and Oomen (1966).

Available potassium:
Available magnesium:
Available calcium:
} extracted with 1 M ammonium acetate and determined by atomic absorption spectrophotometry.

Sulphate: by the method of Sinclair (1973).

Carbon: by wet ashing.

Fertility index: The following factors were combined into one Fertility Index by using the quadrat scores from a Principal Components Analysis (PCA): calcium, potassium, magnesium, carbon and nitrogen. These factors were selected by iteratively eliminating the factor with the smallest communality in a PCA of soil chemical factors. The first axis accounted for 53% of the variation in these factors. This provides an estimate of fertility independent of the bioassay (see below). The index ranged from -1.15 to +0.55. Correlation between the bioassay results and the PCA Fertility Index is +0.62 ($P < 0.001$), though the latter excludes phosphate and sulphate because they were not well correlated with the group above.

Bioassay: The soil (< 10 mm fraction) was bioassayed by determining the shoot dry weight of *Lolium perenne** after 6 weeks growth in a greenhouse in summer, with ample watering. Two replicate pots of each soil were assayed. Analysis of variance showed significant differences in bioassay value between the soils ($p < 0.001$).

The primary analyses of the data were by Cluster Analysis, using the complement of Jaccard's coefficient of similarity and Flexible sorting strategy (beta = -0.25, Lance and Williams, 1967). Ordination was by Detrended Correspondence Analysis (Hill and Gauch, 1980). Species which occured only once were excluded from analyses (i.e. 48 vascular plant species, 2 lichens and 6 mosses). This left 120 species. One agricultural site containing only *Medicago sativa* (lucerne) was excluded, leaving 95 sites.

Correlations between classification fusions and environmental factors were determined by the Mann-Whitney test (Snedecor and Cochran, 1980). Differences are mentioned below only when they are significant ($P < 0.05$).

Results

Classification

The classification is described at the arbitrary levels of five formations (A - E), with 14 communities within these (Table 1). The term 'formation' is used here to indicate a larger grouping than 'community', often with a physiognomic difference; for both terms we accept that the level is arbitrary, and neither term is used to imply any particular level of integration. The communities are named for convenience after

*Nomenclature follows Allan (1961), Moore and Edgar (1970). Cheeseman (1925) and Clapham. Tutin and Warburg (1981) except where indicated.

Table 1: *Frequency of the more common species in the communities: C (constant) = 100%, 9 = 85-94%, 8 = 75-85% etc., 0 = 1-4%, - = absent. Values of species used to name a formation are in italics, those of species used to name a community are in bold. The species are arranged by the inverse classification (gaps separate groups); E (in the left-hand column) = exotic species. The bottom line gives the frequency of each community among the* 95 *quadrats.*

	A_1	A_2	A_3	B_1	B_2	C_1	C_2	D_1	D_2	E_1	E_2	E_3	E_4	E_5
Viola filicaule	4	-	-	-	-	-	-	-	-	-	-	-	-	-
Epilobium tenuipes	3	3	-	-	-	-	-	-	-	-	-	-	-	-
Myosotis discolor	1	3	-	-	1	-	-	1	-	-	-	-	-	-
Cotula serrulata	7	2	-	-	0	-	-	-	-	-	-	-	-	-
Oreomyrrhis rigida	6	-	-	-	-	-	-	-	-	-	-	-	-	-
Stellaria gracilenta	8	2	-	-	1	2	-	-	-	-	-	3	-	-
Poa colensoi	6	5	-	1	2	3	-	-	-	-	-	-	-	-
Raoulia australis	*8*	*5*	-	-	0	-	-	-	-	-	-	-	-	-
Raoulia subsericea	*6*	***C***	-	-	0	2	-	-	-	-	-	-	-	-
Elymus apricus	5	3	-	1	2	-	-	-	-	-	-	-	-	-
Geranium sessiliflorum	*9*	*2*	-	*4*	*3*	*5*	*3*	-	-	-	*1*	-	-	-
Carex breviculmis	9	7	C	1	3	5	-	-	-	-	-	-	-	-
Dichelachne crinita	8	2	3	4	2	-	-	-	-	-	-	-	-	-
Rytidosperma maculatum	8	3	7	4	2	-	-	-	-	-	-	-	-	-
Hypericum gramineum	5	-	**C**	-	1	3	-	-	-	-	-	-	-	-
Leucopogon fraseri	6	3	C	-	1	2	-	-	-	-	-	-	-	-
Raoulia hookeri	*4*	*3*	*7*	3	0	-	-	-	-	-	-	-	-	-
Thelymitra longifolium	4	3	-	-	-	2	-	-	-	-	-	-	-	-
Poa maniototo	2	3	-	-	0	-	-	-	-	-	-	-	-	-
Ophioglossum coriaceum	4	2	-	-	-	-	-	-	-	-	-	-	-	-
E *Acaena agnipila*	7	-	-	7	4	**C**	-	1	-	-	-	-	-	-
E *Anthoxanthum odoratum*	5	-	-	1	3	C	5	-	-	-	-	-	5	-
E *Rosa rubiginosa*	2	-	3	-	0	*C*	*8*	-	-	-	-	-	-	-
E *Crepis capillaris*	C	C	7	6	9	C	5	4	-	**8**	3	3	-	-
E *Rumex acetosella*	7	C	C	9	9	2	8	4	-	3	1	-	3	-
E *Aira caryophyllea*	9	C	C	9	8	5	-	1	-	2	-	-	3	-
E *Vulpia* spp.	8	C	C	9	9	-	3	**C**	-	5	1	-	**C**	-
E *Veronica verna*	8	7	C	9	5	3	-	1	-	2	2	-	-	-
E *Trifolium arvense*	7	8	C	9	5	7	3	5	-	2	1	-	-	-
E *Hypochaeris radicata*	5	8	-	3	3	8	-	1	-	-	-	-	**8**	-
E *Erodium cicutarium*	1	-	-	1	7	-	-	5	7	-	1	3	3	-
E *Bromus tectorum*	5	-	-	*9*	*9*	2	3	8	-	3	-	-	-	-
E *Trifolium glomeratum*	2	-	-	1	5	-	-	4	-	5	3	-	3	-
E *Trifolium dubium*	6	-	-	1	**9**	5	3	5	7	**C**	5	-	8	-
E *Bromus mollis*	5	2	-	*6*	*C*	2	3	3	3	C	C	7	C	-
E *Echium vulgare*	2	-	-	**9**	1	-	-	1	-	-	-	-	-	-
E *Hypericum perforatum*	-	-	-	6	-	3	-	-	-	-	-	-	-	-
E *Verbascum virgatum*	1	-	3	7	1	2	-	-	-	-	-	-	-	-
Dichondra repens	3	-	-	1	2	-	-	-	-	-	-	-	-	-
Oxalis lactea	2	-	-	1	1	2	-	-	-	-	-	-	-	-
Discaria toumatou	4	-	3	-	3	3	3	-	-	-	-	-	-	-
Rytidosperma clavatun	2	-	-	3	2	-	-	-	-	-	-	-	-	-
E *Bromus sterilis*	-	-	-	-	0	2	3	1	3	-	-	-	-	-
E *Hieracium lepidulum*	1	2	-	1	-	8	-	-	-	-	-	-	-	-
Breutelia affinis	1	2	-	-	0	3	-	-	-	-	-	-	-	-
E *Cerastium fontanum*	-	-	-	-	2	3	3	6	-	2	4	-	5	-
E *Festuca rubra*	-	-	-	1	3	7	3	1	-	-	-	-	5	-
E *Holcus lanatus*	-	-	-	-	1	3	-	-	-	2	3	-	5	-

Table 1 Cont...	A,	A,	A,	8,	8,	C,	C,	D,	D,	E,	E,	E,	E.	E,
E *Trifolium subterraneum*	1	-	-	-	2	-	-	3	7	2	2	-	-	-
E *Agrostis capillaris*	1	-	-	-	4	2	-	-	-	-	-	-	-	-
Festuca novae-zelandiae	1	-	-	-	2	7	-	-	-	-	-	-	-	
Aphanes arvensis	1	2	3	-	4	3	-	5	3	2	1	3	3	-
E *Myosotis caespitosa*	-	-	-	-	1	-	5	1	-	-	-	-	3	-
E *Torilis nodosa*	-	-	-	1	0	-	5	-	-	-	1	3	-	-
Kunzea ericoides	1	-	3	1	0	2	5	-	-	-	-	-	-	-
E *Bromus diandrus*	1	-	-	3	3	-	8	3	-	2	1	3	5	-
Muehlenbeckia complexa	1	-	-	-	1	2	5	-	-	-	-	-	-	-
Acaena buchananii	1	-	-	-	1	3	-	-	-	-	-	-	-	-
E *Anagallis arvensis*	1	-	-	-	-	-	5	1	-	-	-	-	3	-
E *Cirsium arvense*	-	-	-	-	-	2	3	1	-	2	1	-	5	-
E *Arenaria serpyllifolia*	1	-	-	-	0	2	-	3	-	-	-	-	-	-
E *A vena sativa*	-	-	-	-	-	-	-	1	-	-	-	-	3	-
E *Capsella bursa-pastoris*	-	-	-	-	-	-	-	9	3	-	-	C	-	-
E *Medicago sativa*	-	-	-	-	1	-	-	5	C	-	-	-	-	-
E *Triticum aestivum*	-	-	-	-	-	-	-	1	-	-	-	3	-	-
E *Cerastium glomeratum*	1	-	-	-	1	-	-	-	-	3	1	7	3	-
E *Cirsium vulgare*	-	-	-	-	0	-	3	-	-	3	-	7	-	-
E *Taraxacum officinale*	-	-	-	-	-	-	-	-	3	-	8	C	5	-
E *Trifolium repens*	-	-	-	-	4	2	-	3	-	8	8	C	8	-
E *Lolium perene*	-	-	-	1	1	2	3	3	7	C	C	C	8	C
E *Poa pratensis*	-	-	-	1	1	2	-	-	3	5	C	-	C	-
E *Hordeum murinum*	-	-	-	-	0	-	3	4	3	3	8	7	-	-
E *Veronica arvense*	-	-	-	-	1	2	3	5	-	5	4	7	5	C
E *Dactylis glomerata*	1	-	-	-	0	-	-	-	3	3	5	-	-	-
E *Cynosurus cristatus*	-	-	-	-	-	-	-	-	-	3	2	3	3	-
E *Agrostis stolonifera*	-	-	-	-	1	-	-	-	-	-	1	-	5	C
E *Juncus articulatus*	-	-	-	-	-	-	-	-	-	-	-	-	3	C
Frequency (%)	14	6	3	7	22	6	4	8	3	6	10	3	4	1

characteristic species, using a combination of overall and within-formation constancy and fidelity.

The main distinction is between Formations A, B, & C versus Formations D & E, corresponding to a distinction between semi-natural vegetation versus agricultural crops and pastures. Many environmental factors (Table 2) correlate significantly with this distinction. The agricultural formations (D & E) occur at lower elevations, on more sheltered and flatter sites, with less rock cover, and loamier, less stony, moister soils that are more fertile and higher in sulphate. The best single predictor of the vegetational split is sulphate (79% correct predictions). This probably reflects the application of sulphate-enriched superphosphate fertiliser. (It should be noted in interpreting such tests that some of the environmental factors are inter-correlated.) The best battery of predictors is geographical position (latitude and longitude), elevation, pH, sulphate, stoniness and PCA Fertility Index. This gives the correct prediction of the A & B & C/D & E distinction in 96% of cases.

A: Scabweed Formation

The mat-forming native scabweeds *Raoulia australis, R. subsericea* and *R. hookeri* are usually present, and often abundant (Table 1). They are rarely found in other formations. Formation A is environmentally separated from the other non-pasture formations B and C by a tendency to occur at higher elevations, with sandy, infertile (by bioassay) soils, but more soil moisture at the time of our survey. These four factors together enable prediction of the Scabweed Formation for 83% of the non-pasture sites. The Scabweed Formation may be split into three communities:

A_1: *Cotula serrulata* Ö*Stellaria gracilenta* Scabweed Community:

C. *serrulata* and S. *gracilenta* are usually present in this community, and very rarely present

Table 2: *Environments of the communities (means).*

	A_1	A_2	A_3	B_1	B_2	C_1	C_2	D_1	D_2	E_1	E_2	E_3	E_4	E_5
Longitude (grid units)	98	62	115	148	91	92	88	87	117	43	147	15	107	172
Latitude (grid units)	1032	1117	1045	977	1049	1005	1044	1073	1075	1181	1014	1196	985	941
Elevation (m)	382	300	254	261	336	348	282	286	274	361	274	335	221	244
Macro-exposure (see text)	1.5	0.7	1.3	0.1	1.0	-0.2	-0.4	-0.3	0.5	-0.5	0.0	0.5	-0.6	0.0
Micro-exposure (cm)	1.3	0.0	-3.2	0.5	0.8	0.3	3.0	0.3	0.0	2.6	0.5	-0.3	0.9	0.0
Slope (^{O})	12	6	21	5	7	16	22	2	3	7	2	0	8	0
North-aspect (^{O}, see text)	120	65	124	127	105	67	123	121	53	80	98	90	81	90
East-aspect(^{O}, see text)	78	68	34	66	79	87	100	76	67	58	89	90	41	90
Rock Cover (%)	7.5	9.8	17.3	4.0	3.5	1.7	24.5	0.1	0.0	0.7	0.0	0.7	0.0	0.0
Pellets (number)	100	103	73	76	117	39	30	83	50	38	51	80	228	0
Stone (%)	23	20	59	19	17	15	55	3	0	4	3	13	2	0
Sandiness (see text)	67	118	172	125	37	45	172	68	58	-43	23	-28	115	12
Water (% of dry soil)	19	17	14	13	19	21	11	17	20	28	23	29	24	35
pH	5.9	5.4	5.6	5.6	5.6	5.7	6.1	5.8	6.0	5.3	6.0	5.5	6.6	5.8
Phosphate (_g cm^{-3})	19	18	15	22	20	20	24	22	15	14	16	35	9	21
Sulphate (_g cm^{-3})	3.1	4.0	3.3	3.9	4.6	2.7	4.0	7.4	6.3	9.0	7.4	9.3	5.0	10.0
PCA fertility index (arbitrary units)	0.05	0.34	0.31	0.20	0.03	-0.03	0.02	0.10 0.01	-0. 13	-0.19	-0.24	-0.61	-0.16	-
Bioassay (arbitary units)	0.93	0.67	0.67	0.69	1.06	1.15	0.87	0.84	1.13	1.31	1.53	1.49	1.14	2.44

elsewhere. The community occurs on slopes above the Clutha river opposite Maori Point and north and south of Luggate, at higher elevations than community A_2 but on sunny north-facing slopes, where the soils are of higher pH and fertility (by bioassay).

Other species often important in community A_1 but absent in communities A_2 and A_3 are *Acaena agnipila, Anthoxanthum odoratum, Trifolium dubium* and the natives *Oreomyrrhis rigida* and *Viola filicaule*.

A_2: *Raoulia subsericea* Scab weed Community: The five species listed above are lacking in Community A_2 but, unlike A_3 *Raoulia subsericea* is present, and usually *Hypochaeris radicata*.

A_3: *Hypericum gramineum* Scabweed Community: Community A_3, is rather poor in species. It contains many of the species normally associated with the scabweeds (e.g. *Leucopogon fraseri, Carex breviculmis),* but is without *Raoulia australis* or *R. subsericea,* and in one case without even *R. hookeri*. Community A_3 is found on the south bank of the Clutha, east of Luggate, on lower elevation sites than the previous two communities and on very stony soils (42-76% stone) with low plant cover. To separate A, from the other two communities, low elevation is the best environmental predictor *(P* < 0.01, Mann-Whitney test) predicting correctly in 91 % of cases.

B: Depleted Pasture Formation

Bromus tectorum and *B. mollis* are often the main species on these low fertility pastures. Casual observation indicates that their contribution to the cover decreases towards the height of summer, and varies greatly from year to year, depending on the intensity and timing of rainfall. Two communities are recognised:

B_1: *Echium vulgare* Depleted Pasture Community: This community comprises rough pasture on the lower terrace towards the east of the area on dry sandy soils with low fertility (by bioassay). *Echium vulgare* is almost constant, and *Hypericum perforatum* and *Verbascum virgatum* are much more frequent than in community B_2.

B_2: *Trifolium dubium* Depleted Pasture Community:
Found on a wider range of sites, such as rough pasture, kanuka *(Kunzea ericoides)* scrub, mixed scrub, scarps, roadsides, etc., this community generally contains *Trifolium dubium,* often with considerable cover. *Erodium cicutarium* is more frequent than in the *Echium* community.

C: Rosa Scrub Formation

Almost all sites of Formation C contain *Rosa rubiginosa,* and some have high cover of *Kunzea ericoides*. Rosa Scrub (C) can occur on steeper slopes (up to 35°) than Depleted pasture (B). Fewer pellets were recorded, but this may be due to the slope. The formation is found through the area, for example on terrace scarps near Albert Town, at the foot of the hill near Luggate, and at Queensberry. Two communities are recognised:

C_1: *Acaena agnipila* Rosa Scrub Community:
Several species are indicators of this community compared to Community C" especially *Acaena agnipila,* but also *Anthoxanthum odoratum, Crepis capillaris, Hieracium lepidulum, Hypochaeris radicata, Festuca novae-zelandiae,* etc.

C_2: *Bromus diandrus* Rosa Scrub Community:
Species more characteristic of this community than of C_1 are the exotics *Bromus diandrus, Torilis nodosa, Verbascum thapsus* and natives *Kunzea ericoides, Muehlenbeckia complexa* and *Myosotis arvensis*. The soil of community C_2 is significantly stonier, more sandy and drier. The latter two factors offer perfect discrimination between sites of communites C_1 and C_2. In their native range *B. diandrus, T. nodosa* and *V. thapsus* are typically found in sandy, dry, open sites (Clapham, Tutin and Warburg, 1962).

D. Paddock Formation

This formation is quite species-poor, with an open canopy. Many sites are lucerne paddocks, and lucerne is rarely found elsewhere. The formation also occurs as wheat fields, in trampled areas such as gateways, and in a water ponding area. *Capsella bursa-pastoris* is frequent, and rarely found elsewhere. Two communities are recognised:

D_1: *Vulpia* Paddock Community:
Overall, this community is more species-rich than D_2. Most of the lucerne fields are included here. *Vulpia* spp. are constant.

D_2: Species-poor Paddock Community:
This communtiy, found only on terrace scarps across the river from Luggate, includes two particularly species-poor lucerne fields and a corner of trampled paddock by a fence. *Vulpia* spp. are absent. No environmental factor is significantly different between D_1 and D_2 but the location of community D_2 means that the sites are exposed, sandy, and infertile.

E: Lolium Pasture Formation

Lolium perenne is almost constant, and usually has high cover. Besides *Lolium-Trifolium* pastures, the community was found in a wheatfield, in a gateway, and in wet and riverside sites. It differs from Formation D in occuring on soil that is more fertile, moister and less sandy.

E_1: *Crepis capillaris - Trifolium dubium* Pasture Community:
This community is found on loamy soils, only in the north of the sampled area. *T. dubium* is constant, and C. *capillaris* more frequent than in communities E_2-E_5.

E_2: *Poa pratensis - Hordeum murinum* Pasture Community:
Occuring towards the southwest of the area, this community is at lower elevations, on sandier soil with higher pH than in community E_1. *Taraxacum officinalis* is more frequent. *Poa pratensis* is constant.

Communities E_1 and E_2 may be differentiated from E_3-E_5 by a combination of factors, but no *single* environmental factor is significantly different. E_1 and E_2 are on loamier soils, with lower water and available phosphate content, and occur towards the east. Consistent indicator species are few, but the weedy *Crepis capillaris* and *Hordeum murinum* are more frequent in E_1 and E_2.

E_3: *Capsella bursa-pastoris* Pasture Community:
This occurs in the north west, around Maungawera, at higher elevations than communities E_4 and E_5 and on east-facing aspects.
The presence of *C. bursa-pastoris* distinguishes E_3 from all other communities of Formation E.

E_4: *Hypochaeris radicata - Vulpia* spp. Pasture Community:
This occurs as high quality pasture, mainly in the very south of the area sampled. In contrast with

communities E_1-E_3 *Hordeum murinum* is notably absent.

E_5: *Juncus articulatus* Pasture Community:
This single site is environmentally distinct from the former community in several factors. It has wetter soil, reflected in the presence of *Juncus articulatus* and *Agrostis stolonifera,* with only two other species present. It is also more fertile (by bioassay) with a higher soil sulphate content. It had no animal pellets, faced less towards the north and more towards the east.

Ordination: Axis 1

This first axis contrasts (on the left) rough pasture, Scabweed Formations, scarps and high-elevation sites, with (right) *Lolium-Trifolium* pastures and low-lying, moist sites (the ordination of sites is not presented).

The latter sites occur at lower elevations, towards the north of the area where rainfall is higher, and on fertile soils (by bioassay and by PCA Fertility Index) high in sulphate (Table 3), factors that partly reflect agricultural activity. Typical species of this end of the axis (Fig. 1) include those deliberately sown in agriculture: *Triticum aestivum* (wheat), *Lolium perenne, Cynosurus cristatus* etc. and agricultural weeds: *Tripleurospermum inodorum, Taraxacum officinale, Hordeum murinum,* etc. These two groups of exotic species combine to dominate the right-hand end of the axis (Fig. 1, Fig. 3). The native species closest to the right-hand end of the axis (and not very close at that) comprise the tree *Kunzea ericoides,* shrubs *Melicytus alpinus, Coprosma propinqua* and *Muehlenbeckia complexa,* and the tussock grass *Poa cita,* all species likely to be less adversely affected by agricultural disturbance than other native species. Thus they probably represent relics. *Poa cita* may be responding directly to increased fertility.

Species frequent at the (left-hand) high-elevation, southern, infertile soil end of the axis are overwhelmingly native. Of the 26 species with negative

Table 3: *Regression of environmental factors on the axes (quadrat scores) from the presence/absence D.C.A. ordination. For each axis is given: 'dir'; the direction of the regression slope* (- *or* +); *'cont'; the percentage contribution to the regression; and 'sig'; the significance of that contribution (.*P = 0.05 - 0.01; **P = 0.01 - 0.001; ...***P< 0.001). The percentage of variation accounted for is given for the alternative ordination, using quantitative information.*

	Axis 1			Axis 2			Axis 3			Axis 4		
	dir	cont	sig	dir	cont	sig	dir	cont	sig	dir	cont	sig
Longitude	+	2		-	9	**	+	0		-	17	***
Latitude	+	11	**	-	17	***	-	0		-	24	***
Elevation	-	37	***	-	0		-	3		-	1	
Macro-exposure	+	1		-	1		+	3		-	1	
Micro-exposure	+	1		+	4		+	12	*	+	2	
Slope	-	1		+	11	**	-	12	*	-	4	*
North-aspect	-	0		+	0		-	1		+	0	
East-aspect	+	0		+	0		-	9		-	5	*
Rock Cover	+	1		-	3		+	0		+	13	***
Pellets	-	1		-	5		-	2		+	0	
Stone	-	2		+	8	*	-	4		+	5	
Sandiness	-	2		+	6	*	+	2		-	2	
Water	-	3		+	11	**	+	3		+	13	***
pH	+	7	*	+	0		-	3		-	0	
Phosphate	+	0		-		*	-	18	**.	+	0	
Sulphate	+	11	**	-	5		-	1		-	6	*
PCA Fertility Index	+	9	*	+	1		-	9		-	8	**
Bioassay	+	14	**	+	15	***	+	17	**	-	0	
Probability of whole regression		0.00000			0.00000			0.00001			0.00000	
Variation in scores accounted for *(%)*		67.7			60.7			51.3			50.4	
Quantitative ordination:												
Variation in scores accounted for (%)		67.7			57.4			54.0			46.5	

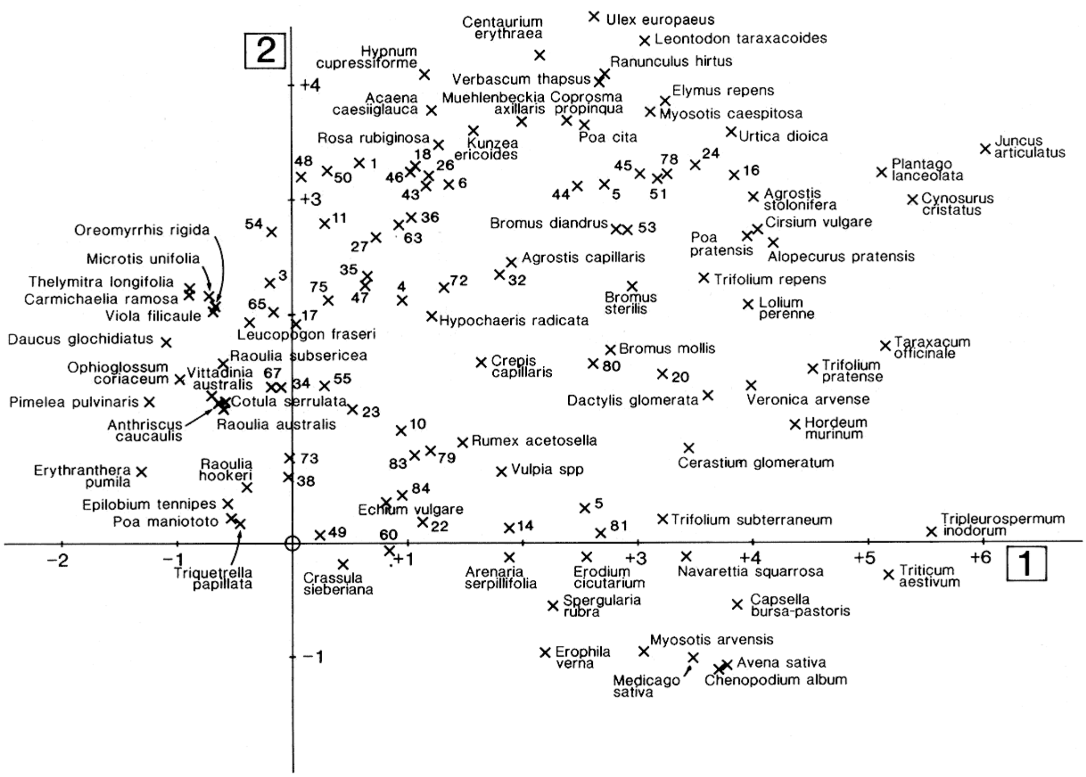

Figure 1: *Ordination of species. axes 1 (left-right) and 2 (up-down). Species numbers (for Fig. 1 and for Fig. 2): 1 Acaena buchananii; 2 Acaena caesiiglauca; 3 Acaena novae-zelandiae; 4 Acaena ovina; 5 Anagallis arvensis; 6 Anthoxanthum odoratum; 7 Anthriscus caucalis; 8 Aphanes arvensis; 9 Arenaria serpyllifolia; 10 Aira caryophyllea; 11 Breutelia affinis; 12 Bromus diandrus; 13 Bromus mollis; 14 Bromus tectorum; 15 Capsella bursa-pastoris; 16 Carduus tenuiflorus; 17 Carex breviculmis; 18 Carex colensoi; 19 Carmichaelia ramosa; 20 Cerastium fontanum; 21 Cerastium glomeratum; 22 Ceratodon purpureus; 23 Cheilanthes sieberi; 24 Cirsium arvense; 25 Cirsium vulgare; 26 Coprosma petriei; 27 Cotula maniototo; 28 Cotula serrulata; 29 Crassula sieberiana; 30 Crepis capillaris; 31 Leucopogon fraseri; 32 Cytisus scoparius; 33 Daucus glochidiatus; 34 Dichelachne crinita; 35 Dichondra repens; 36 Discaria toumatou; 37 Echium vulgare; 38 Elymus apricus; 39 Epilobium tenuipes; 40 Erodium circutarium; 41 Erophila verna; 42 Erythranthera pumila; 43 Festuca novae-zelandiae; 44 Festuca rubra; 45 Galium perpusillum; 46 Geranium microphyllum; 47 Geranium sessiliflorum; 48 Gnaphalium audax; 49 Gypsophila tuberosum; 50 Hieracium lepidulum; 51 Holcus lanatus; 52 Hordeum murinum; 53 Melicytus alpinus; 54 Hypericum gramineum; 55 Hypericum perforatum; 56 Hypochaeris radicata; 57 Lolium perenne; 58 Microtis unifolia; 59 Myosotis arvensis; 60 Myosotis discolor; 61 Ophioglossum coriaceum; 62 Oreomyrrhis rigida; 63 Oxalis lactea; 64 Pimelea pulvinaris; 65 Poa colensoi; 66 Poa maniototo; 67 Polytrichum juniperinum; 68 Raoulia australis; 69 Raoulia hookeri; 70 Raoulia subsericea; 71 Rosa rubiginosa; 72 Rytidosperma clavata; 73 Rytidosperma maculatum; 74 Spergularia rubra; 75 Stellaria gracilenta; 76 Taraxacum officinale; 77 Thelymitra longifolia; 78 Torilis nodosa; 79 Trifolium arvense; 80 Trifolium dubium; 81 Trifolium glomeratum; 82 Trifolium repens; 83 Verbascum virgatum; 84 Veronica verna; 85 Viola filicaule; 86 Vulpia spp.; 87 Vittadinia australis.*

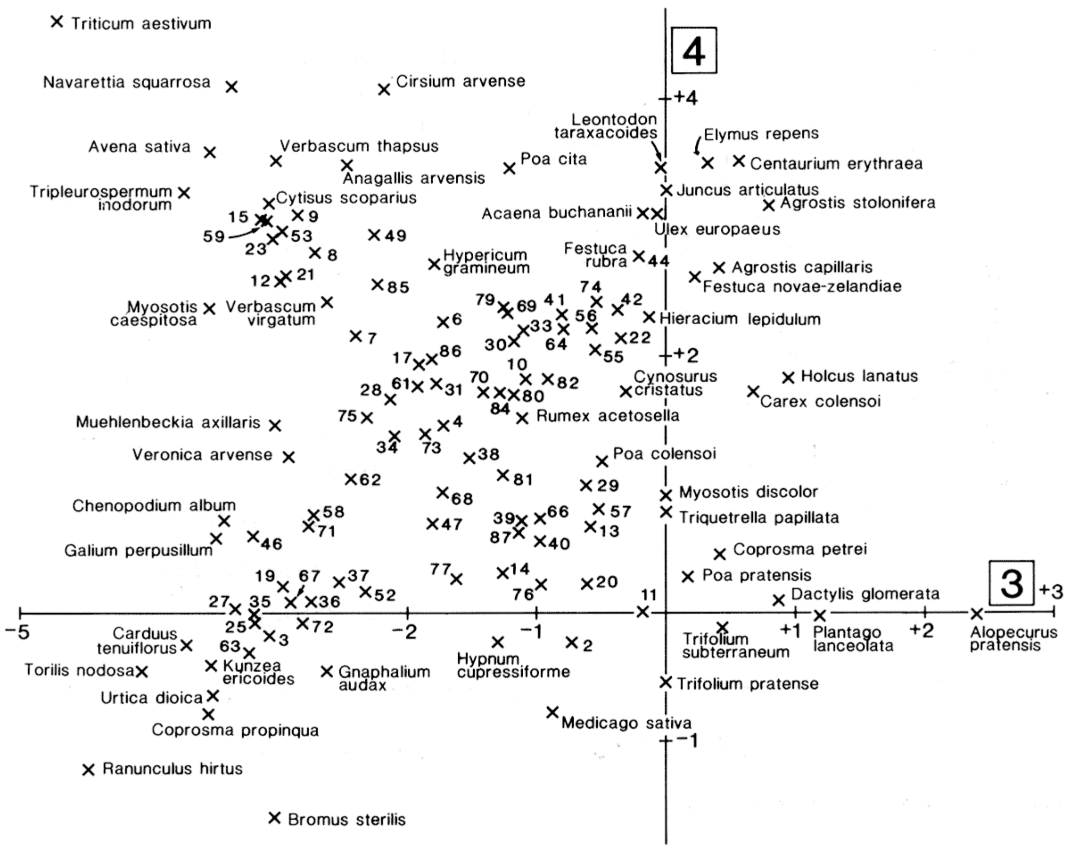

Figure 2: *Ordination of species, axes* 3 *(left-right) and* 4 *(up-down). Species numbers as Fig. 1.*

scores, 25 are native. The one exotic is *Anthriscus caucalis,* a species which in Britain occurs on sandy soils mainly in the more continental south and east regions (Clapham, Tutin and Warburg, 1981), and might therefore be especially suited to the conditions of the Upper Clutha.

Ordination: Axis 2

Sites with high positive scores include scrub (kanuka-dominated and mixed), but also pasture near rivers and other wet sites. The regression indicates they tend to be towards the south and perhaps west of the area, on fertile soils (as indicated by the bioassay, but not by PCA Fertility Index), steeper slopes, but with relatively high water content.

Species characteristic of this end of the Axis 2 vegetational gradient (Fig. 1) include the shrubs *Ulex europaeus, Kunzea ericoides, Coprosma propinqua, Rosa rubiginosa* and *Muehlenbeckia complexa.* Tusssock grasses *Poa cita* and *Festuca novae-zelandiae* are also important here. The environment represented (Table 3) is one where water deficiency is less severe, either because the woody plants can extract water from deep in the profile and give herbs beneath them some protection from desiccation, or else because of a nearby river. They are sites that have been only moderately disturbed.

At the other (negative, lower) end of Axis 2 are flat open sites, including rough pasture, wheat fields

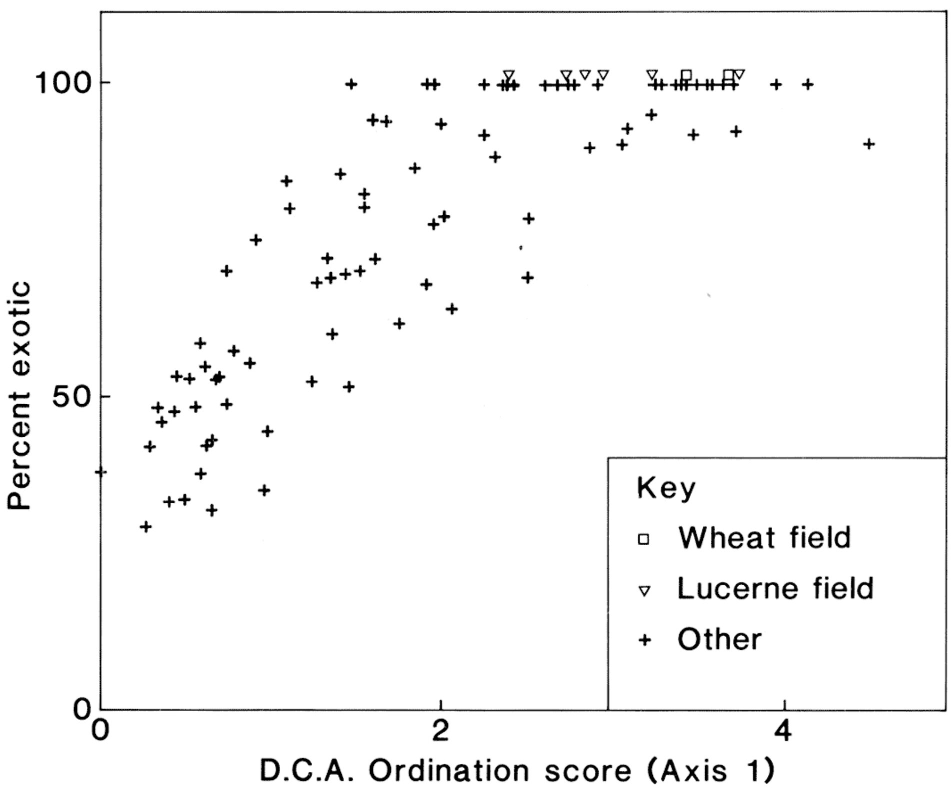

Figure 3: *Native: exotic ratio in relation to Axis I.*

or lucerne fields. The latter fields probably represent rough pasture that has received relatively little agricultural management before becoming arable; lucerne in particular is grown in the Upper Clutha because it is productive in relatively dry infertile soils. The species typical of the rough pasture are therefore still present as weeds, e.g. *Erophila verna* and *Myosotis arvensis*.

Ordination: Axis 3

The high (right-hand) end of Axis 3 comprises typically *Lolium-Trifolium* pastures, generally fertile as seen in the bioassay, but relatively low in phosphate and in other nutrients (as seen in the PCA Fertility Index). They tend to be on flat but locally raised sites. Typical species are *Alopecurus pratense, Holus lanatus* and *Plantago lanceolata*.

At the other (negative, left-hand) end of Axis 3 are wheat fields, kanuka and other scrub, and scree. Species typical of this end of Axis 3 are *Triticum aestivum, Tripleurospermum inodorum, Carduus tenuiflorus* and *Torilis nodosa*.

Ordination: Axis 4

Sites with low scores on Axis 4 occurred in the centre of the area sampled, around Luggate village, across the Clutha from this, and then in the far east of the area sampled. The sites were rather steep, generally with an easterly aspect, dry, but with low rock cover and soil stone content. Nutrient status (by PCA Fertility Index) was low.

Species on sites typical of the low end of Axis 4 are *Bromus sterilis* and *Ranunculus parviflorus*. Some of the sites were lucerne crops, but others were

Lolium-Trifolium pastures (in one case by a fence). kanuka scrub, or *Coprosma propinqua* scrub.

At the other extreme is a mixture of sites: wheat fields, scree slopes, scrub, high-elevation pasture etc., this end of this axis typified by a mixture of species such as *Triticum aestivum,* the pasture weed *Cirsium arvense,* the waste-area Californian weed *Navarettia squarrosa,* and the native tussock *Poa cita*.

Crop species

The ordination includes two species that have clearly been sown quite recently - *Triticum aestivum* (wheat) and *Medicago sativa* (lucerne). Removing them from the analysis makes practically no difference to the first two axes, and little difference to the third and fourth. (Later axes are likely to differ more, since they reflect also differences in the earlier axes.)

Even the sites which contained *T. aestivum* and *M. sativa* are placed in approximately the same positions without them (site ordination. not presented). Thus, in the full ordination, (i.e. including wheat and lucerne fields) lucerne fields are separated most clearly on Axis 2, where the six lucerne fields are in the nine sites at one extreme, and the three most extreme sites are lucerne fields. Omitting wheat and lucerne from the analysis, four 'lucerne' fields are in the extreme nine, and the two most extreme sites are lucerne fields.

Wheat fields are most clearly separated by Axis 3. In the full ordination, two of the three sites at one extreme are wheat fields. Omitting wheat and lucerne, one of the wheat fields remains in the extreme three, though the other is well towards the same end of the axis.

Discussion

Community structure

Community structure in the lowland Upper Clutha basin is weak - there are no clear trends or groupings, so that species presence and absence is not predictable by any simple model. For example, not a single species is constant to any of the five formations (Table 1). Many species are constant to individual communities, although they are almost always found widely in other communities. Communities B. and C, have no constant species. Faithful species are almost as rare. *Viola filicaule* and *Oreomyrrhis rigida* in Community A_1 are the only species faithful to a community; only four more are faithful to a formation. The ordination shows a similar lack of structure, though a little less than that shown by Fig. 4 of Hubbard and Wilson (1988), probably because of the narrower geographical range sampled here and because of the inclusion of agricultural communities. Nevertheless. some species span a wide part of the ordination gradient, for example *Bromus mollis* occurs in quadrats from one end of the ordination to the other. *Trifolium dubium* and *Crepis capillaris* have almost as wide an ecological range.

Hubbard and Wilson (1988) suggested that such weak structure in the lowland Upper Clutha could be because of complicated vegetational relations. stochasticity or non-equilibrium, and gave non-equilibrium as the most likely reason. Non-equilibrium, over the geographical range, is less likely to be because of dispersal, and most likely to be due to slow vegetational response to management changes. Invasion may have been facilitated by the limited native flora adapted to semi-arid conditions, attributed by Wardle (1963) to lack of continuity of presence of dry habitats through the Quaternary. An alternative or additional explantion, is that changes in herbivores, fire, soil disturbance, etc., have created an environment different from that before European man arrived (Moore, 1976; Williams, 1980), and one to which they are not adapted (cf Macdonald and Jarman, 1984). As in other dry parts of New Zealand, the vegetation has shown fluctuations, with no sign of coming to an equilibrium. Moore (1976) attributed this to response to management changes (rabbit control, stocking rate, fire), a response that was. slow because of the longevity of many indigenous species, and because of year-to-year variation in rainfall. Evidence for this instability is seen in reports of waves of dominance by particular species *(Rumex acetosella:* Moore, 1954; *Vittadinia triloba:* Williams, 1980; *Hieracium pilosella:* Makepeace, 1985). Watt (1981) observed similar waves of dominance in dry grassland under constant management but attributed them to subtle changes in the climate, which may be a factor in the Upper Clutha.

All formations are scattered over at least five grid squares (our macro-sampling unit), and all occur in the northern, middle and southern thirds of the sampled area. All but three of the communities occur in at least two of the three latitudinal sampling divisions. One sampling square contained only one community (A_1). Three further squares contained only one formation. However, the norm is for a square to contain a wide variety of communities. A small-scale mosaic is superimposed on regional trends controlled by such factors as rainfall and elevation.

It is often supposed that quantitative data contain more information than presence/absence data. There

Table 4: *Regression of native: exotic ratio (log transformed) on environmental factors. Abbreviations and symbols as in Table* 3.

	dir	cont	sig
Longitude	+	0	
Latitude	+	5	
Elevation	-	50	***
Macro-exposure	-	0	
Micro-exposure	+	5	
Slope	-	10	*
North-aspect	-	1	
East-aspect	-	1	
Rock Cover	+	2	
Pellets	-	0	
Stone	-	4	
Sandiness	-	4	
Water	-	7	
pH	+	0	
Phosphate	+	0	
Sulphate	+	5	
PCA Fertility Index	+	4	
Bioassay	+	2	
Probability of whole regression		0.00000	
Variation in ratio accounted for *(%)*		52.4	

is no evidence for this here. The first axis of the presence/absence ordination has a 67.70% predictability from the environment, the quantitative 67.68%. Over the four axes, the predictability of the quantitative regression is on average slightly lower (Table 3). Weir and Wilson (1987) also found better correlation between the environment and presence/absence data, but on a much smaller scale and in more stable vegetation. Lambert and Dale (1964) reported that mathematically presence/absence data can contain more information.

Native and exotic guilds

A distinction is seen between the native species at the low (left) end of Axis 1 of the ordination (Fig. 1), and exotic species at the other extreme. The weak structure referred to above, however, means that this is only a trend, as the majority of sites have a mixture of native and exotic species (Fig. 3). All sites have at least one exotic species, but 35 sites have no native species.

The proportion of exotic species is lowest at higher elevations and on steeper slopes (Table 4), perhaps because of less disturbance and because native species are better adapted than the exotics to higher elevation environments. Wilson and Sykes (1988) suggest that a negative correlation between numbers in the two guilds would indicate niche limitation; here the correlation is negative (r = - 0.119), but far from significant (P = 0.251). Where the exotic guild is a higher proportion of the community, the total species richness is lower (r = -0.703, P < 0.001).

Arid regions worldwide have been susceptible to invasion by exotics, for example the dry steppes of North America (Forcella and Harvey, 1983; Mack, 1981). In New Zealand, the replacement of native cover by exotic cover began soon after, or even before, organised European settlement (Thomson, 1922), as in California (Burcham, 1956). Even many of the species important in the exotic invasions of California are common to the Upper Clutha - *Aira caryophyllea, Bromus mollis, Erodium cicutarium, Poa annua, Rumex crispus, Vulpia megalura* (Burcham, 1956).

Wilson (1989) discussed the concentration of presences in a site/species two-way table as an indication of the strength of community structure, and used Cramer's (1946) C to measure such concentrations separately for two guilds. Here the native guild (C = 0.093) shows slightly more structure than the exotic guild (0.078), but both are low. Probably the concentration of the native guild is low because of spasmodic relict occurrences, and that of the exotic guild is low because of incomplete invasion, the lack of equilibrium discussed above.

Agricultural and natural communities

Our sampling was unusual in including the whole landscape, from near-natural to intensive agricultural. The vegetational continuity between agricultural and semi-natural sites justifies this approach.

Leaving out the two obviously sown species affected the analysis rather little. Some of the wheat and lucerne fields could have been identified as such from their weed flora. This might be because the weed flora is a remnant from the vegetation present before cultivation. The seed pool may contribute to such persistence. The weed vegetation may also have established following cultivation. In the full ordination the four sites at the end of the axis with wheat fields are scrub sites (two kanuka, two mixed). This suggests that species able to tolerate the shade under scrub are those able to tolerate the shade of the wheat crop (all the wheat weeds were shorter than the wheat). These include the native *Ranunculus parviflorus,* found naturally in shady sites (Allan 1961; Wilson 1982), and apparently pre-adapted to wheat fields. Dale and Thomas (1987) observed that in some Saskatchewan arable fields the weed flora was related to soil and climate rather than to the crop type.

Most prominent among species of lucerne fields are species that are otherwise most abundant in Depleted Pasture (B): *Bromus tectorum, Bromus diandrus, Bromus mollis, Aphanes arvensis, Erodium cicutarium* and *Trifolium dubium*. *Vulpia* spp. are abundant in both A and B formations. Exceptions are *Cerastium fontanum* of Lolium Pasture (E) and *Capsella bursa-pastoris* of other Paddock (D) sites. Probably, lucerne fields were established on sites that had previously borne Depleted Pasture, and some species from those formations remained as weeds, with only C. *fontanum* and C. *bursa-pastoris* invading.

This intensive survey has confirmed the conclusion from an extensive survey (Wilson, 1989) that the natives and exotics now form one set of communities, with overlapping ranges and therefore cannot be separated into distinct communities.

Predictability from the environment

The factors that emerge as particularly important for predicting the vegetation are latitude, elevation, soil fertility (especially sulphate) and water.

Even with the battery of environment factors available, none of the Discriminant Functions Analyses achieve 100% correct predictions between the five formations; the highest is 97%. The highest predictability by a single factor is 84% by slope distinguishing between formations C and D. The environmental factors explain only 68% of ordination position on axis 1 (less for subsequent axes). This probably reflects the effects of past disturbance that is independent of current environmental conditions.

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