Plant Ecology (2005) 181: 255–267
DOI 10.1007/s11258-005-7149-9

The effects of livestock grazing and recreation on Irish machair grassland vegetation

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Received 22 July 2004; accepted in revised form 11 May 2005

Key words: Agriculture, Canonical Correspondence Analysis, Cattle grazing, Coastal dune grassland, Conservation management, Covariable analysis, Detrended Correspondence Analysis, Landscape scale, Rabbit grazing, Sheep grazing, Variance partitioning

Abstract

Machair grassland uniquely occurs over sandy, calcareous soils of coastal sand-plains in dune systems of north-western Scotland and Ireland. This study assesses the plant species composition of Irish machair grassland at a landscape-scale. Machair sites were sampled with quadrats and multivariate analysis was used to assess relationships between species abundance, soil physical variables, livestock grazing and recreation activity. Grazing by cattle and sheep was recorded at most sites, with recreation activities at nearly half the sites. Detrended and Canonical Correspondence Analysis ordinations showed that the main gradients of community composition were related to the key variables of soil calcium carbonate content, soil organic matter content, livestock grazing intensity and recreation pressure. Partial Canonical Correspondence Analysis showed that livestock grazing intensity and recreation pressure explained about twice as much variation as the key soil variables and that rabbit grazing had a much smaller but significant effect. Livestock grazing and recreation activities were shown to be ecologically damaging in terms of having a larger area of bare sand and a lower species diversity. Bare sand can increase the risk of storm damage and reduce habitat heterogeneity by sand-plain deflation. Controls on livestock density, the length of the grazing season and recreation activities are proposed, which we suggest would facilitate vegetation recovery. We highlight the need for local planning authorities, who control coastal development in Ireland, to include agricultural management prescriptions in their machair site management plans.

Introduction

Machair grassland occurs over sandy calcareous soils in the coastal sand-plains of hindshore dune systems in north-western Scotland (Dargie 1993) and Ireland (Curtis 1991). The sand-plains were formed under the influence high wind-speeds by the inland movement of sand and shell fragments, following deglaciation of the region (Ritchie 1979). Typically machair grassland lies behind a dune ridge, on a gently-sloping or undulating deflation surface adjusted down to a water-table or underlying landform such as a raised beach, drift terrace, rock platform or ancient soil (Ritchie 1976, Basset and Curtis 1985, Owen et al. 1996, Angus and Dargie 2002).

Scattered sand-hills and ridges with dune grassland can occur on the machair surface where there has been sand movement in the past. The boundary between dune grassland and machair grassland is marked by an abrupt loss or low frequency of *Ammophila arenaria*. Inland, machair grassland grades into heath or mire communities, often associated with lakes, or oceanic heath and bog, or it has been enclosed for agriculture.

Machair grassland productivity is low, a function of summer soil moisture deficit, winter flooding and small soil concentrations of phosphate, nitrate, potassium, copper and manganese. The low productivity results in a land use, largely for rough grazing. Typical ranges recorded for soil variables are: pH 6.5–8.9, calcium carbonate content 0.2–84%, organic matter content 1–12.5% and the upper humified soil horizon 7–20 cm (Basset and Curtis 1985, Hudson 1991).

The vegetation of machair grassland is related to dune grassland and calcareous grassland. It consists of a closely-grazed species-rich, mesophytic sward dominated by *Festuca rubra*, with other graminoids, dicotyledonous species and bryophytes. Frequent characteristic species of Scottish and Irish machair communities are *Bellis perennis*, *Galium verum*, *Lotus corniculatus*, *Trifolium repens* and *Plantago lanceolata* (Basset and Curtis 1985). Rodwell et al. (2000) and Basset and Curtis (1985) give phytosociological descriptions of machair grassland.

A long history of grazing by cattle, sheep and more recently rabbits, has influenced the development of machair landscapes. Archaeological and historical evidence indicates settlement and agriculture extending at least 5000 years in Scotland (Crawford 1991) and possibly 8000 years in Ireland (Basset and Curtis 1985). Prior to the mid-nineteenth century, there was extensive erosion and sand drift in machair systems, associated with rotational arable agriculture, but currently, machair landscapes are considered to be relatively stable (Angus and Elliot 1992; Basset and Curtis 1985). Angus (1994) outlines the high national and international geomorphological and biological conservation importance of machair dune systems. Machair is listed on Annex I of the Habitats and Species Directive (Commission for the European Community 1992) and has priority status in Ireland.

Machair grassland is typically unenclosed and has multiple owners. Traditional land use is a low-intensity agricultural rotation between patches of unfenced arable crops and winter-grazed cattle (Angus 1994, Owen et al. 1996). Some rotation still occurs in Scottish Island machair (Kent et al. 2003), but there are no data for Ireland. Enclosure by fencing and subsequent agricultural intensification, following agreement by common land users, has led to the loss of much Scottish machair grassland since the Second World War (Boyd and Boyd 1990) but there are no data for Ireland. Currently, the main agricultural use is extensive grazing, with management by small farm enterprises, often with rights of common grazing. Sheep grazing predominates in Scotland, where there is often heavy grazing pressure and a year-round grazing regime (Angus 1994, Kent et al. 2003). There is also recreation pressure, often with unmanaged amenity use (Angus 1994; Basset and Curtis 1985). Angus and Dargie (2002) and Kent et al. (2003) review the conservation management of machair in Scotland.

Plant species composition varies in relation to sand type, sand-plain structure and the duration of winter flooding (Vose et al. 1956; Randall 1976; Dickinson and Randall 1979; Basset and Curtis 1985; Dargie 1993). Community dynamics are also influenced by sand burial (Owen et al. 2004). Whilst moderate to heavy grazing intensity maintains a low grass sward and allows a high species diversity to develop (Vose et al. 1956; Randall 1976), there has been no regional quantitative assessment of community variation in relation to land use intensity. Soil pH, moisture content and organic matter content (a function of soil water status) have been reported to be the main underlying environmental gradients in machair grassland and dune grassland (Kent et al. 1994).

Previous studies of machair grassland have described community gradient structure and species composition based usually on small numbers of sites. Emphasis in early studies was on describing composition in relation to coastal dune to inland machair grassland sequences (Gimingham et al. 1948; Vose et al. 1956; Randall 1976; Dickinson and Randall 1979). Regional phytosociological surveys, with nature conservation objectives, were carried out by Basset and Curtis (1985) in Ireland and by Dargie (1993, 1998, 2000) in Scotland. Quantitative information on regional landscape-scale machair management and relationships between land use and species diversity, however, is lacking. Our study was initiated to assess the plant species composition of Irish machair grassland on sand-plain landforms, in relation to soil structure and current land use and to contribute to the development of machair grassland conservation.

Methods

Vegetation sampling

The study area covers the north-west coast of Ireland, from Malin Head to Galway Bay (Figure 1), an area recognised as containing the Irish machair resource (Curtis 1991). Sampling was restricted to mainland sites (Figure 1) because access to off-shore islands was not practical. Twenty-two machair grassland sites from an inventory of Irish soft coast systems listed by Curtis (1991) were sampled randomly, representing 54% of mainland machair systems. The vegetation sampled, occupied unenclosed, coastal sand-plain with an almost level surface. Machair grassland at each sample site was delimited on 1:10,264 Ordnance Survey maps by stereoscopically interpreting monochrome aerial photographs (Geological Survey of Ireland, 1977, scale 1:30,000) using texture and pattern to eliminate habitats such as dune-ridges and sand-hills with *Ammophila arenaria*, saltmarsh and fen. Site boundaries were modified in the field to take account of recent land use changes such as enclosure. Machair grassland associated with the playing surface of golf courses and Gaelic football pitches was not sampled.

At each sample site, between 1 and 5 sample points were randomly selected in proportion to site area. The vegetation at each point was located in the field by measuring with reference to known landmarks. It was sampled with a 4 m^2 square quadrat, determined from minimal area studies. The cover of all plant species was recorded on a modified Domin scale: 1 – one or two individuals, cover < 1%; 2 – many individuals, cover < 1%; 3 – cover 1–4%; 4 – cover 5–10%; 5 – cover 11–25%; 6 – cover 26–50%; 7 – cover 51–75%; 8 – cover 76–100%. Taxonomic nomenclature follows Stace (1991) for vascular species and Watson (1981) for bryophytes.

Soil variables

Within each quadrat, the percentage cover of bare sand was estimated using the modified Domin scale above. From a soil pit dug at the centre of each quadrat, the surface 5 cm of soil was removed with a 10 cm diameter stainless steel cylinder and transferred to a numbered polythene bag prior to laboratory air-drying in an aluminium-foil dish. The air-dried soil samples were passed through a 2 mm brass sieve to obtain fine earth for analysis. Soil organic matter content was determined, as an indicator of soil moisture status, by a loss-on-ignition method using a muffle furnace set at 430° to avoid loss of calcium carbonate (Allen 1989). Soil calcium carbonate content was determined to assess the content of shell fragments using a calcimetric method (Bascomb 1961). Soil moisture content was not recorded directly because of the effect of rainfall variation and the influence of tides on water table variation during the sampling period. Soil pH was determined with an electronic pH meter after equilibrating in an aqueous 0.01 M solution of calcium chloride (Allen 1989).

Site management variables

Records of site management variables were obtained by interviewing machair users, common-land shareholders and landowners. The density per unit area of cattle and sheep and the number of weeks per year over which the site was grazed were recorded. The presence of rabbits was assessed from field observation of faeces and burrows. Site use for holiday caravans, golf and Gaelic football (a Summer game) was also recorded from field observation. Arable cultivation in the past was determined from common-land shareholders and landowners.

Multivariate analysis

Two-way indicator species analysis (TWINSPAN), a divisive, hierarchical classification (Hill 1994), was carried out to summarise community composition. TWINSPAN default parameters were used, with pseudospecies cut levels set to combine Domin values 5–8 to downweight the influence of abundant species. Domin values 1 and 2 were also combined and given a mid-point cover value of 0.5%. The classification was stopped by inspection to give three groups. To determine the mean percentage cover of species in each group, Domin values were transformed to the mid-point

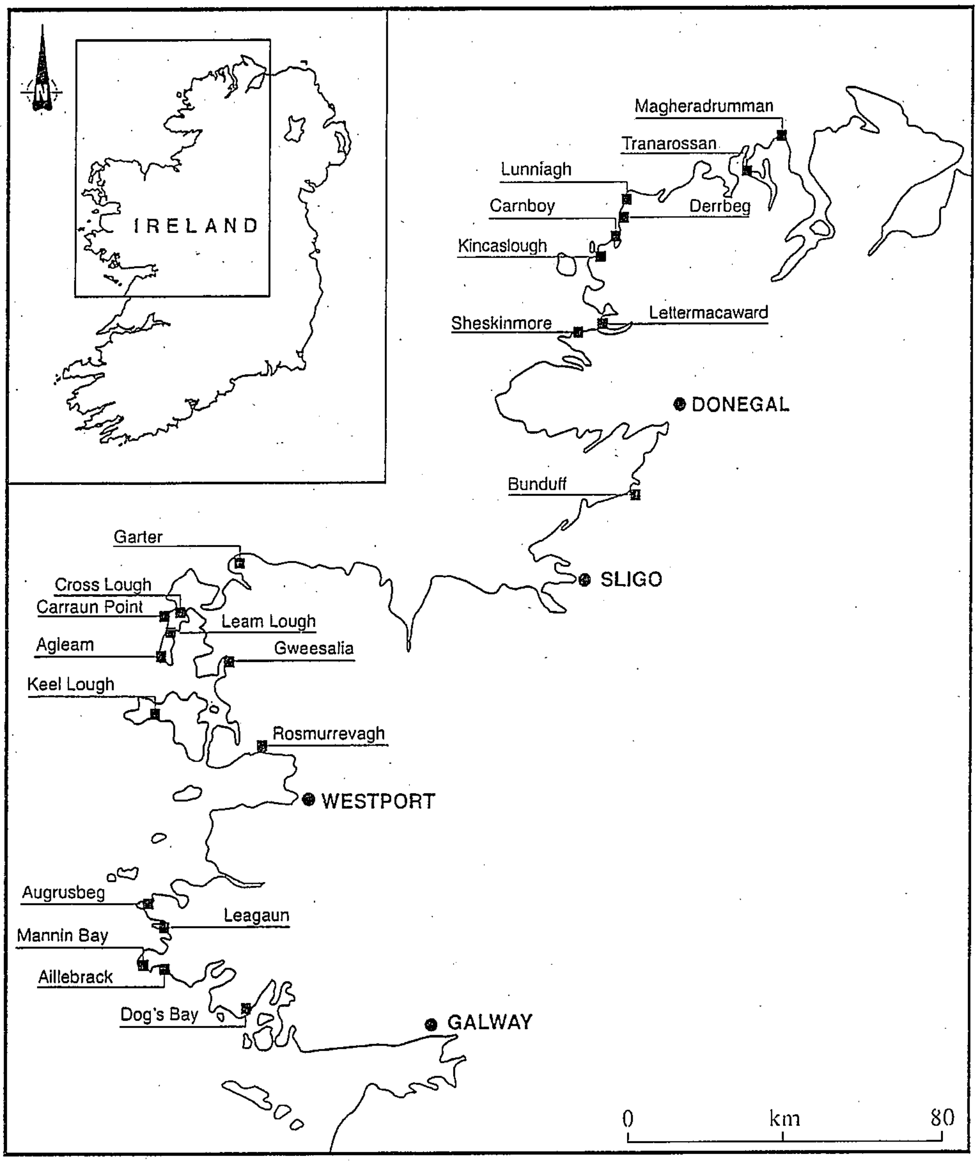

Figure 1. Location map of the study sites.

percentage cover. Comparison with existing vegetation classifications was by table inspection.

Ordinations to analyse relationships between species abundance values, soil physical variables and land use were carried out with the program CANOCO 4.5 (ter Braak and Smilauer 1998). Exploratory ordination indicated that unimodal methods were appropriate, therefore the samples were analysed by Detrended Correspondence Analysis (DCA) to assess community gradient structure. For analysis, Domin values were transformed to mid-point percentage cover values and species with a frequency <5% were deleted. Soil and land use variables were plotted passively (*i.e.*, as supplementary variables) onto the DCA to guide informal interpretation. The percentage area of bare sand, density of cattle and sheep, length of the grazing period, percentage soil organic matter content and percentage calcium carbonate content were log-transformed prior to analysis. The statistical distribution of soil pH was skewed, with most values (69 of the 75 sample quadrats) between 7.0 and 8.1 (standard deviation 0.25) and six quadrats between 5.5 and 6.4. Transformation would not correct this so pH was not included in the ordinations.

Canonical Correspondence analysis (CCA) (ter Braak and Smilauer 1998) was carried out to assess patterns of variation in the species data that could be explained by the measured variables. The amount of variation accounted for by groups of variables representing soil physical attributes, livestock grazing, rabbit grazing and recreation was assessed using a CCA variance partitioning procedure (Bocard et al. 1992). This enabled the amount of unshared variance explained by a group to be assessed by partial analysis, with the other groups used as covariables. The hypothesis of non-significant deviation of variation explained by a variable, from that explained by a random variable, was tested with the Monte Carlo permutation method in CANOCO 4.5 (ter Braak and Smilauer 1998) with 99 unrestricted permutations of the constraining variable. Significance was tested at the $p = 0.05$ level. To clarify the DCA and CCA ordination diagrams, only species with a weighted total abundance >9 were plotted.

Results

TWINSPAN vegetation classification

The first division of the TWINSPAN classification separated Group 3 from Groups 1 and 2 (Table 1), with Group 3 characterised by the TWINSPAN indicator species *Hydrocotyle vulgaris*. The second division separated Groups 1 and 2, with Group 1 characterised by the indicator *Carex arenaria* and Group 2 characterised by the indicators *Senecio jacobaea*, *Holcus lanatus*, *Polygala vulgaris*, and *Euphrasia* spp. In all three groups, *Festuca rubra* was the principle sward-former, with a mean cover >40%. Other abundant species (mean cover >5% or frequency >70% in all groups) were *Bellis perennis*, *Lotus corniculatus*, *Poa pratensis* and *Plantago lanceolata*. There was a high mean number of species per quadrat in each group, with the highest, of 24.7, in Group 2.

There was a high mean soil calcium carbonate and organic matter content in all groups (Table 2) but Group 1 had the highest content. Group 3 had the highest soil organic matter content and Groups 1 and 3 had a high mean area of bare sand. Groups 1 and 2 each had a mean pH of 7.7. Group 3 had a mean pH of 6.5. Grazing by cattle (77%) or sheep (50%) was recorded at most sites (Table 3), with 31% of sites grazed by both sheep and cattle and one site ungrazed. The greatest number of sites (60%) were grazed for 4–6 months during the Summer, with 18% grazed for 10–12 months, *ie.* over the winter. A large proportion of sites (59%) was grazed by rabbits. Past cultivation had occurred at 32% of sites. It was a feature of Group 1, but was no longer carried out. In all three groups public access frequency was >70%. Recreation activity was similar in all groups, with Gaelic football the most frequent.

Detrended correspondence analysis

The first two axes of the DCA accounted for 9.5% and 7.3% of the sample variation respectively (Figure 2a). Ecological data sets frequently have a large proportion of unexplained random and spatial variation (Gauch 1982) but if underlying causes of community structure are identified, this may not be important (Bocard et al. 1992; Okland and Eilertson 1994). The main DCA gradient (Figure 2b) contrasts species indicative of well-drained grassland (*Rumex acetosa* and *Achillea millefolium*), with species indicative of wet soils (*Hydrocotyle vulgaris* and *Succisa pratensis*). A second gradient contrasts species indicative of open sandy habitats (*Plantago coronopus*), with species indicative of more stable grassland conditions (*Holcus lanatus* and *Pseudoscleropodium purum*). The number of species per quadrat was highest in quadrats correlated with the stable grassland part of this gradient (Figure 2c).

Passive overlay of soil variables on the ordination (Figure 2c) shows soil calcium carbonate content correlated with the first axis and soil organic matter content together with the area of bare sand correlated with the second axis. Of the land use variables, sheep density, length of the grazing season and recreation activities were correlated with the area of bare sand (Figure 2c) and the distribution of open habitat species (Figure 2b).

Canonical correspondence analysis

CCA carried out with each variable separately, showed that they all accounted for significant

Table 1. Percentage frequency (*f*) and mean percentage cover (*c*) of species in TWINSPAN Groups 1, 2 and 3.

Species	TWINSPAN group					
	1		2		3	
	f	*c*	*f*	*c*	*f*	*c*
Salix repens	0	0.0	7	0.3	31	5.2
Cochlearia officinalis	0	0.0	7	0.4	31	0.9
Ceratodon purpurea	0	0.0	0	0.0	13	6.3
Succisa pratensis	6	0.1	11	0.2	38	3.5
Carex nigra	0	0.0	4	0.0	44	1.5
Hydrocotyle vulgaris	3	0.2	0	0.0	50	4.9
Plantago maritima	19	1.5	7	0.1	38	2.7
Ranunculus acris	3	0.1	7	0.1	38	1.4
Hieracium pilosella	3	0.6	18	0.7	6	0.1
Calliergon cuspidatum	10	0.4	39	1.7	44	7.5
Mentha aquatica	0	0.0	4	0.3	19	0.1
Pseudoscleropodium purum	6	0.3	18	1.7	13	0.5
Prunella vulgaris	16	0.6	61	3.9	94	4.4
Cynosurus cristatus	16	0.4	46	3.5	50	7.0
Carex flacca	68	3.3	96	10.1	100	26.2
Rhtidadelphus triquetrus	10	0.9	32	2.9	25	3.3
Trifolium pratense	10	0.1	61	1.6	75	2.1
Leontodon taraxacoides	45	0.6	39	0.9	81	2.0
Juncus acutiflorus	19	0.2	4	0.6	31	0.3
Daucus carrota	13	0.1	18	0.1	13	0.1
Homalothecium lutescens	45	2.9	43	4.8	31	3.5
Plantago coronopus	35	2.4	0	0.0	13	1.2
Lolium perenne	6	0.1	36	1.3	6	1.1
Holcus lanatus	10	0.2	71	4.0	38	2.2
Trifolium dubium	10	0.4	11	0.1	6	0.1
Taraxacum officinale	65	1.3	93	2.7	69	1.4
Bellis perennis	97	15.3	100	9.0	100	9.5
Festuca rubra	100	48.0	100	52.8	100	39.6
Euphrasia spp.	19	0.2	79	1.7	38	0.4
Carex arenaria	74	1.8	36	0.6	50	2.5
Rhytidiadelphus squarrosus	45	7.6	82	10.0	56	3.7
Ranunculus bulbosus	87	1.3	100	3.4	50	2.6
Brachythecium albicans	26	5.3	7	0.4	25	2.2
Agrostis stolonifera	87	3.8	57	5.5	69	2.9
Plantago lanceolata	100	9.6	100	8.0	100	4.3
Luzula campestris	84	0.7	71	1.1	56	0.3
Lotus corniculatus	94	8.4	100	10.1	88	2.7
Poa pratensis	84	6.6	71	8.9	56	4.8
Viola riviniana	16	0.1	46	0.4	13	0.1
Sedum acre	16	0.1	11	0.1	13	0.1
Thymus praecox	55	3.9	68	7.4	31	0.3
Trifolium repens	97	17.1	100	7.7	94	2.3
Cerastium fontanum	58	0.9	68	1.2	6	0.2
Cerastium diffusum	61	0.8	61	1.3	25	0.1
Polygala vulgaris	0	0.0	61	0.9	0	0.0
Plagiomnium undulatum	10	0.3	11	0.9	6	0.2
Anthyllis vulneraria	0	0.0	14	0.2	0	0.0
Senecio jacobaea	26	0.2	82	1.3	6	0.0
Galium verum	94	8.1	96	8.3	38	0.6
Plantago major	3	0.0	11	0.1	6	0.0
Veronica chamaedrys	0	0.0	29	2.9	0	0.0
Achillea millefolium	65	3.6	54	0.7	13	0.1
Campanula rotundifolia	13	0.1	14	0.1	0	0.0
Poa annua	13	0.7	11	0.2	0	0.0

Table 1. Continued.

Species	TWINSPAN group					
	1		2		3	
	f	*c*	*f*	*c*	*f*	*c*
Armeria maritima	3	0.0	11	0.3	0	0.0
Rumex acetosa	16	1.2	32	0.6	0	0.0
Brachythecium rutabulum	13	0.1	0	0.0	0	0.0
Mean number of species	18.9		24.7		21.1	
Species range	13–26		18–31		18–26	
Number of quadrats	31		28		16	

Species are listed by location on the first axis of a DCA ordination. Infrequent species not included are: *Ammophila arenaria*, *Barbula* spp., *Briza media*, *Cardamine pratensis*, *Centaurea nigra*, *Epilobium neritoides*, *Fissidens* spp., *Hylocomium splendens*, *Juncus bulbosus*, *Leucanthemum vulgare*, *Lophocolea* spp., *Potentilla anserina*, *Primula vulgaris*, *Rosa pimpinellifolia*, *Sonchus asper*, *Urtica dioica*, *Viola tricolor*.

amounts of variation in the species data. In a CCA with forward selection, however, golf club ownership and sheep density did not contribute significantly. CCA with all variables included accounted for 27% of the total sample variation (Table 4), with the first two axes accounting for 5.5% and 4.6%, respectively. This represents over half the variation accounted for by the first two axes of the DCA ordination.

Each group of variables (the soil physical, livestock and recreation groups) accounted for about one-third of the total variation explained by the CCA (Table 4). In the partial CCA (with covariable analysis), where the effects of each group was assessed independently of the other groups (Table 4), the influence of the groups was reduced. This reduction is a function of the extent to which their ecological explanatory value is shared. The CCA ordination diagrams of species and environment variables (Figure 3) were the same in all major respects as the DCA ordination, with soil calcium carbonate content, soil organic matter content and the area of bare sand/land use variables correlated with the main gradients of species composition. The analysis shows that the soil physical environment, livestock grazing and recreation are important in structuring the species composition of machair grassland and that in comparison, rabbit grazing is much less influential (Table 4).

Table 2. Mean soil and land use variables for each TWINSPAN group (standard deviation is bracketed).

Variable	TWINPSPAN Group					
	1		2		3	
Bare sand cover (%)	8.8	(18.7)	1.5	(7.3)	7.8	(12.8)
pH	7.7	(0.3)	7.7	(0.3)	6.5	(0.8)
Soil calcium carbonate (%)	35.3	(27.5)	24.3	(17.1)	13.6	(16.8)
Soil organic matter (%)	4.2	(5.7)	7.4	(3.5)	11.3	(8.2)
Public access (%)	80.6		71.0		100.0	
Cultivated in the past (%)	54.8		9.7		18.8	
Caravans (%)	12.9		12.9		12.5	
Golf (%)	12.9		6.5		25.0	
Gaelic football (%)	35.5		32.3		37.5	
Rabbits (%)	64.5		51.6		68.8	
Length of grazing season (months)	6.5	(2.7)	5.5	(2.7)	6.6	(2.6)
Cattle density (ha^{-1})	1.1	(1.6)	0.6	(1.0)	0.7	(1.0)
Sheep density (ha^{-1})	1.5	(2.1)	1.1	(2.0)	2.2	(2.9)
Number of quadrats	31		28		16	

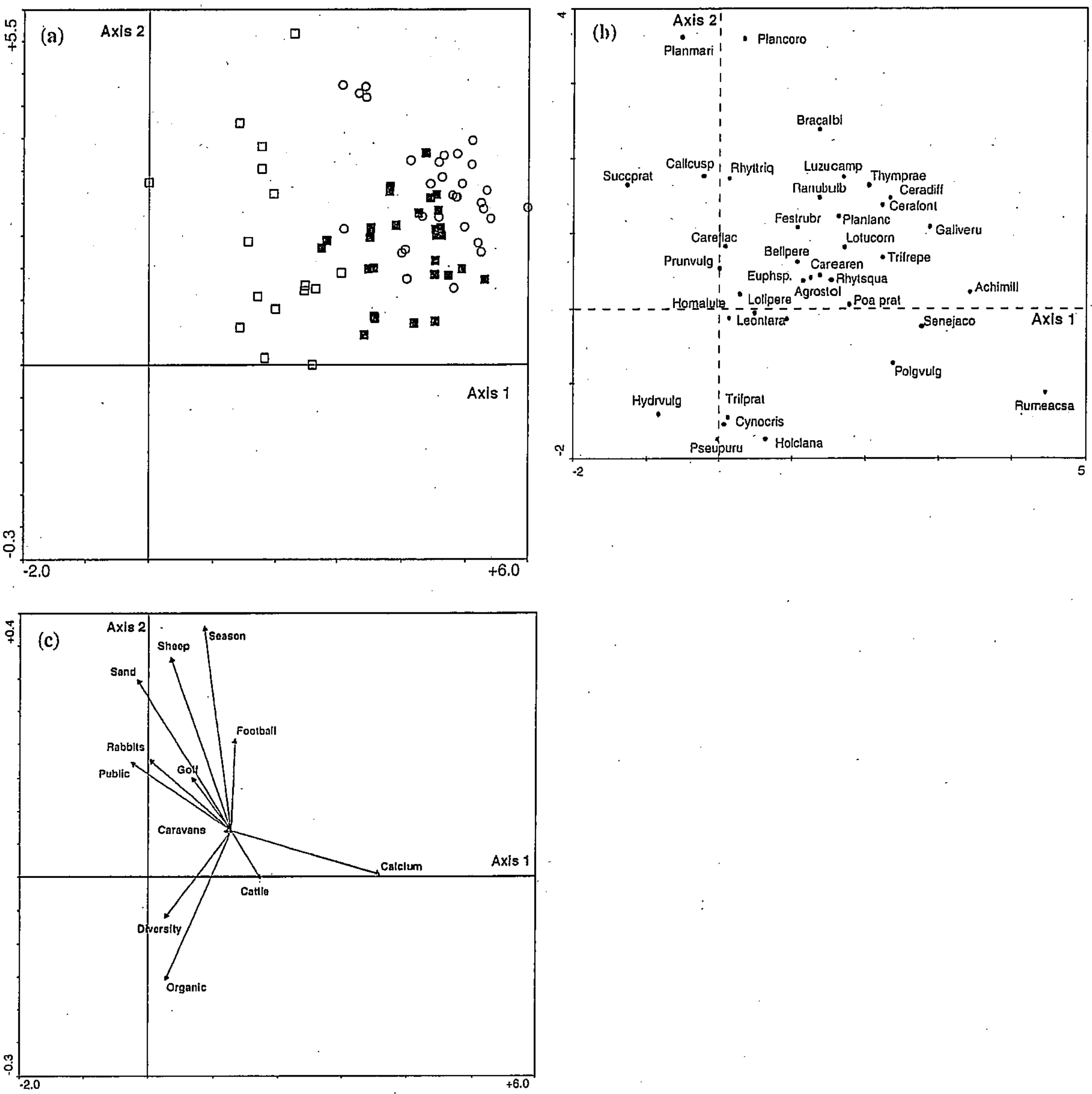

Figure 2. DCA ordination of samples. Eigenvalues: axis 1 = 0.17, axis 2 = 0.13. Gradient lengths: axis 1 = 2.0, axis 2 = 1.8. (a) *Quadrat ordination:* Circles = TWINSPAN group 1; Filled squares = TWINSPAN group 2; Open squares = TWINSPAN group 3. (b) *Species ordination:* Species with a weighted total abundance >9 are presented. Species names: Achimill, *Achillea millefolium*; Agrostol, *Agrostis stolonifera*; Bellpere, *Bellis perennis*; Bracalbi, *Brachythecium albicans*; Callcusp, *Calliergon cuspidatum*; Carearen, *Carex arenaria*; Careflac, *Carex flacca*; Ceradiff, *Cerastium diffusum*; Cerafont, *Cerastium fontanum*; Cynocris, *Cynosurus cristatus*; *Euph* spp., *Euphrasia* spp.; Festrubr, *Festuca rubra*; Galiveru, *Galium verum*; Holclana, *Holcus lanatus*; Hydrvulg, *Hydrocotyle vulgaris*; Leontara, *Leontodon taraxacoides*; Lolipere, *Lolium perenne*; Lotucorn, *Lotus corniculatus*; Luzucamp, *Luzula campestris*; Plancoro, *Plantago coronopus*; Planlanc, *Plantago lanceolata*; Planmari, *Plantago maritima*; Poaprat, *Poa pratensis*; Polyvulg, *Polygala vulgaris*; Prunvulg, *Prunella vulgaris*; Pseu puru, *Pseudoscleropodium purum*; Ranubulb, *Ranunculus bulbosus*; Rhytsqua, *Rhytidiadelphus squarrosus*; Rhyttriq, *Rhytidiadelphus triquetrus*; Rumeacsa, *Rumex acetosa*; Succprat, *Succisa pratensis*; Thymprae, *Thymus praecox*; Trifprat, *Trifolium pratense*; Trifrepe, *Trifolium repens*. (c) *Environment ordination* Environment variable names: Calcium – soil calcium carbonate content; Caravans – site use for caravans and camping; Cattle – cattle density; Football – site used for Gaelic football; Golf – site used for golfing; Organic – soil organic matter content; Rabbits – rabbits present at the site; Sand – area of bare sand in the quadrat; Season – length of grazing season; Sheep – sheep density; Diversity – mean number of species per quadrat.

Table 3. Site land use variables (OSI = Ordnance Survey Ireland).

Site Number	OSI grid ref	Site name	Number of quadrats	Public access	Caravans	Golf	Football	Rabbits	Cultivated in the past	Length of grazing season (months)	Cattle density (ha^{-1})	Sheep density (ha^{-1})
1	F6222	Agleam	1	1	0	0	0	0	0	4.5	1.3	0.7
2	L5944	Aillebrack	1	1	0	1	0	1	0	4.5	0.4	0.1
3	L5558	Augrusbeg	3	1	0	0	0	1	0	4.5	0.9	0.0
4	G7256	Bunduff	4	1	0	0	0	1	0	4.5	2.4	0.0
5	B7823	Carnboy	2	1	0	0	1	0	0	0	0.0	0.0
6	F7508	Corraun point	3	1	0	0	0	1	1	4.5	3.4	0.0
7	F6429	Cross lough	3	1	0	0	0	1	0	4.5	0.1	0.0
8	B8026	Derrybeg	5	1	0	1	1	1	0	10.5	0.0	7.7
9	L6938	Dog's bay	3	1	0	0	1	0	1	4.5	1.0	1.3
10	F8144	Garter hill	5	1	0	0	0	1	1	7.5	0.1	1.3
11	F7412	Gweesalia	2	1	0	0	0	0	0	4.5	1.3	0.0
12	F7227	Keel lough	3	1	1	0	1	1	1	10.5	0.0	6.8
13	B7260	Kincashlough	4	0	0	0	0	0	0	4.5	0.2	0.0
14	L5855	Leagaun	3	0	1	0	0	1	0	3	0.2	0.0
15	F6427	Leam lough	3	1	0	0	0	0	0	4.5	0.5	0.0
16	B7601	Lettermacarward	3	1	0	0	0	1	1	4.5	0.0	0.9
17	B8127	Lunniagh	5	1	0	0	1	0	0	10.5	0.1	2.5
18	C2145	Magh'drumman	5	0	0	0	1	1	0	4.5	0.0	1.6
19	L5847	Mannin bay	4	1	0	0	0	0	1	10.5	4.3	0.0
20	L8596	Rosmurrevagh	2	1	0	1	0	0	1	7.5	3.3	3.1
21	G7069	Sheskinmore	3	1	0	0	0	1	0	4.5	0.2	0.0
22	C1242	Tranarossan	4	1	1	0	1	1	0	7.5	0.1	3.0
		Frequency (%)	–	86.4	13.6	13.6	31.8	59.1	31.8	–	–	–
		Mean (%)	–	–	–	–	–	–	–	5.7	0.9	1.3

Discussion

The species composition of the machair sand-plain grasslands sampled, corresponds to the grassland of unenclosed, mature, Irish coastal sand-plains (Bassett and Curtis 1985). The vegetation of all three TWINSPAN groups has strong affinities with Scottish machair grassland (Gimingham et al.

Table 4. Eigenvalues (eigen) and percent variance accounted for by Canonical Correspondence Analysis with groups of variables and with groups of variables used as covariables.

Group name	Variable name	Group parameters			Group parameters with other groups as covariables		
		Eigen	Percent variance	Percent of total variance	Eigen	Percent variance	Percent of total variance
Physical	Soil calcium carbonate	0.19	38	10	0.14	29	8
	Soil organic matter						
	Bare sand						
Rabbits	Rabbits	0.05	10	3	0.04	8	2
Livestock	Length of grazing season	0.13	27	7	0.11	22	6
	Cattle density						
	Sheep density						
Recreation	Caravans	0.16	33	9	0.15	30	8
	Golf						
	Gaelic football						
	Public access						
	CCA eigenvalue	0.49					
	Total variance (inertia)	1.78	109			90	

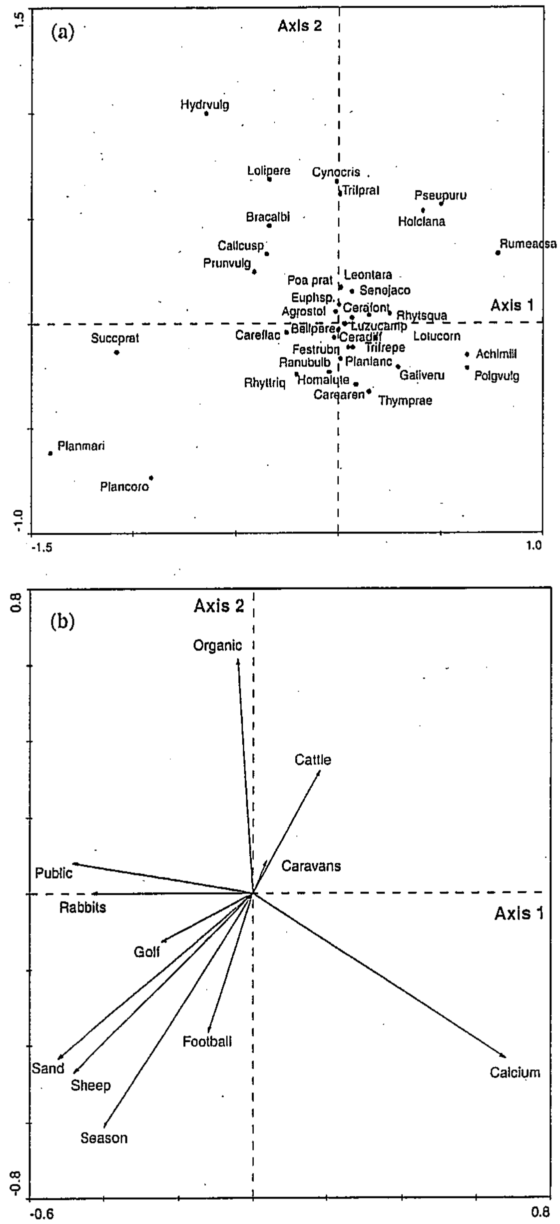

Figure 3. CCA ordination of samples. (a) *Species ordination* Species names: Achimill, *Achillea millefolium*; Agrostol, *Agrostis stolonifera*; Bellpere, *Bellis perennis*; Bracalbi, *Brachythecium albicans*; Callcusp, *Calliergon cuspidatum*; Carearen, *Carex arenaria*; Careflac, *Carex flacca*; Ceradiff, *Cerastium diffusum*; Cerafont, *Cerastium fontanum*; Cynocris, *Cynosuris cristatus*; *Euph* spp., *Euphrasia* spp.; Festrubr, *Festuca rubra*; Galiveru, *Galium verum*; Holclana, *Holcus lanatus*; Hydrvulg, *Hydrocotyle vulgaris*; Leontara, *Leontodon taraxacoides*; Lolipere, *Lolium perenne*; Lotucorn, *Lotus corniculatus*; Luzucamp, *Luzula campestris*; Plancoro, *Plantago coronopus*; Planlanc, *Plantago lanceolata*; Planmari, *Plantago maritima*; Poaprat, *Poa pratensis*; Polyvulg, *Polygala vulgaris*; Prunvulg, *Prunella vulgaris*; Pseupuru, *Pseudoscleropodium purum*; Ranubulb, *Ranunculus bulbosus*; Rhytsqua, *Rhytidiadelphus squarrosus*; Rhyttriq, *Rhytidiadelphus triquetrus*; Rumeacsa, *Rumex acetosa*; Succprat, *Succisa pratensis*; Thymprae, *Thymus praecox*; Trifprat, *Trifolium pratense*; Trifrepe, *Trifolium repens*. (b) *Environment ordination* Environment variable names: Calcium – soil calcium carbonate content; Caravans – site use for caravans and camping; Cattle – cattle density; Football – site used for Gaelic football; Golf – site used for golfing; Organic – soil organic matter content; Rabbits – rabbits present at the site; Sand – area of bare sand in the quadrat; Season – length of grazing season; Sheep – sheep density; Diversity – species density per quadrat.

1948; Dargie 1993) and SD8 *Festuca rubra-Galium verum* fixed dune grassland described by Rodwell (2000). Group 1 corresponds with SD8 *Bellis perennis-Ranunculus acris* sub-community of Rodwell (2000), indicative of relatively dry conditions. Group 2 corresponds with the *Prunella vulgaris* sub-community indicative of wetter conditions. The high frequency of *Hydrocotyle vulgaris* and *Salix repens* in TWINSPAN group 3 indicates its affinity with immature dune-slack (European dune valley) communities (SD13 *Sagina nodosa-Bryum pseudotriquetrum* and SD14 *Salix repens-Campyllium stellatum*) described by Rodwell (2000).

Ecological models of machair sand-plain grassland have largely been developed in studies of machair system zonations inland from coastal dune ridges (Vose et al. 1956; Dickinson et al. 1971; Randall 1976). Kent et al. (1994) and Gilbertson et al. (1995) concluded that variation in species composition of the grassland of active dune fronts, machair grassland, dune slack and peaty soils at the edge of the machair sand-plain, was determined mainly by a gradient of soil moisture and organic matter content and secondarily by soil calcium carbonate content. Gradients related to distance from the coast do not seem to be characteristic of machair sand-plain grassland. Bassett and Curtis (1985), for example, showed that the soil calcium carbonate content of machair sand-plain grassland did not decrease significantly along transects inland, but varied markedly between sites.

Our results support these observations, showing that at the landscape scale, the species composition of the machair sand-plain grassland is structured by soil calcium carbonate content and soil organic matter content. Surface soil pH did not vary greatly, an observation supported by others (Basset and Curtis 1985; Rodwell 2000). We also show that livestock grazing intensity and recreation pressure influence community composition as much as the main soil variables and that the effect of rabbit grazing is significant at the landscape scale. The relatively high proportion of sample variation accounted for by the CCA compared with the DCA and the similarity of their main gradient structure, indicate that the variables in the CCA model are key to explaining community composition (Jongman et al. 1987). Ritchie (1979) proposed that topographic variation within the machair sand-plain (and therefore proximity to the water table) was the principal causal factor influencing species composition. The distribution of soil wetness indicator plant species on the first axis of our DCA ordination and the correlation of high soil organic matter content with the bottom left corner of the environment ordination diagram support this.

Livestock grazing intensity and recreation pressure rank highly in comparison with the key soil variables (organic matter content and soil calcium carbonate content), independently explaining about twice as much variation in species composition. Quadrats with a high livestock grazing intensity and recreation pressure are also shown to have a lower species diversity. These results contrast with studies by Gilbertson et al. (1995), who emphasised the uniformity of machair grassland composition under a range of sheep, cattle and rabbit grazing regimes and took the view that floristic variation in machair dune systems was not directly related to land use. Basset and Curtis (1985) described grazing pressure to be heavy and amenity use to be unmanaged in Irish machair dune systems, but did not quantify the effects on machair grassland. Similarly, Angus (1994) reported recreation pressure on vegetation in Scottish machair systems.

Livestock grazing intensity and recreation activities can influence machair sand-plain grassland at two levels: community composition and substrate stability. At the community level, grazing and recreation disturbance can prevent flowering and seeding and eliminate sensitive species. Also at the community level, small-scale, wind-mediated reworking of sand in the machair sand-plain can promote habitat heterogeneity and species diversity by providing a niche for species of bare sand habitats. Such species are exemplified by winter annuals (*eg*., *Cerastium diffusum*) and maritime species of open habitats (*eg*., *Plantago maritima* and *Plantogo coronopus*). Experimental studies indicate that the main machair grassland perennials are adapted to sand burial and can recover well after disturbance (Owen et al. 2004). This suggests that the ecological condition of machair grassland would respond well to less intensive use.

At the substrate level, high levels of disturbance can initiate sand erosion mediated by wind, particularly under storm conditions. This can lead to a lowering of the sand surface (deflation) and reduced habitat heterogeneity. In this context, Gilbertson et al. (1995) suggested that machair sand-plain deflation and sediment reworking was a result of the impact of major storms rather than land use. We provide evidence that at a landscape-scale, livestock grazing and recreation can lead to an increase in the area of bare sand and thus an increased risk of storm damage.

In the Republic of Ireland, the National Parks and Wildlife Service is responsible for implementing nature conservation management policy. The sectoral policy response to machair biodiversity management has been to designate candidate Special Areas of Conservation (SAC), Special Protection Areas (SPA) and National Heritage Areas (NHA), established under the Annex I of the Habitats and Species Directive (Council Directive 92/43/EEC) and enabling Irish legislation. Farmers owning SAC land, currently receive additional payments under an EEC agri-environment Rural Environment Protection Scheme (REPS), provided they comply with certain management restrictions. The main conclusion of our work in relation to machair agricultural prescriptions, is that the high sheep and cattle grazing intensities recorded are ecologically damaging in terms of the creation of bare sand and reduced species diversity, particularly where there is a long grazing season and recreation activities. The preferred method of grazing management for conservation (Angus and Dargie 2002) is thought to be winter grazing by cattle and stock exclusion during the Summer months to allow seed production. A reduction in summer grazing intensity on Irish machair grassland, particularly by sheep and the initiation of winter grazing (but not a lengthening of the grazing season) is recommended by us for conservation management.

Local planning authorities control coastal development in Ireland. Power et al. (2000) have shown that currently, coastal planning control is piecemeal, responding to events on an *ad hoc* basis. Except for actions requiring planning permission, transparency in decision-making is lacking. Power et al. (2000) advocate a co-ordinated, inter-disciplinary strategy for the conservation and sustainable use of the coastal zone. This approach, addressing management issues through scientifically-based, locally-agreed management plans, has recently been adopted by Donegal County Council, with a view to scaling-up for regional application. The management plans, however, do not consider prescriptions for agricultural land use. Our work suggests that controls on agricultural livestock grazing density and the length and timing of the grazing season would benefit machair grassland conservation.

Acknowledgements

The authors thank Martin Kent for his comments on the manuscript and an unknown referee for helpful suggestions.

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