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Ecological effects of cultivation on the machair sand dune systems of the Outer Hebrides, Scotland

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Abstract. The machair sand dune systems of the Outer Hebrides of Scotland are a unique habitat, which is rare within both a global and European context. Unusually, the machair habitat also represents an agricultural resource that is very important to the Hebridean people, having been subject to both grazing and cultivation throughout the historical period. Following designation as an Environmentally Sensitive Area (ESA) in 1988, the machairs of South Uist have been studied with the aim of understanding the links between agricultural practice and their plant community and ecosystem dynamics. This research focused primarily on the effects of cultivation practices and their role in maintaining plant species richness and community and ecosystem stability.

Within two carefully selected areas, the successional plant communities of machair at different stages of recovery following ploughing and cultivation of cereals and potato patches or 'lazy beds' were identified at both a macro- and micro-level. Investigations of the vegetation recovery processes on turves taken from newly ploughed land indicated that the initial stages of recolonization are characterized primarily by rapid vegetative reproduction and growth, although re-vegetation by seeds is also an important factor. The implications of these findings for the long-term management of machair plant communities are discussed and in particular the need to maintain old cultivation practices such as shallow ploughing. The need for more detailed research into both seed banks and seed rain and into processes of vegetative reproduction is stressed.

Keywords: Conservation management; Plant community; Sand dune ecology; Succession; Vegetation dynamics; Vegetative reproduction.

Abbreviations: DCA/DECORANA = Detrended CORrespondence ANAlysis; ESA = Environmentally Sensitive Area; SSSI = Site of Special Scientific Interest; TWINSPAN = Two-Way INdicator SPecies ANalysis.

Nomenclature: Clapham et al. (1981) and Stace (1991, 1997) for vascular plants; Hubbard (1984) for grasses; Pankhurst & Mullin (1991) for the regional flora; Dobson (1992) for lichens; Watson (1981) for mosses and liverworts.

Introduction

The sand dune machairs of the Outer Hebrides of Scotland (Fig. 1) are renowned for their ecological interest and value. The UK Biodiversity Action Plan (Anon. 1999) gives a total of 40 000 ha for the global extent of machair with 30 000 ha of this occurring on the Outer (20 000 ha) and Inner (6500 ha) Hebrides, with small areas on the western Scottish mainland (1000 ha) and on Orkney and Shetland (2500 ha). Their rarity on a global scale, in addition to their geomorphological, archaeological and landscape importance, means that conservation and careful management of machair systems is vital (McKirdy & Foxwell 1985; Angus 1994, 1996; Owen et al. 1996; Anon. 1999). This was recognized by the designation of most of the machair as an Environmentally Sensitive Area in 1988, in addition to various existing Sites of Special Scientific Interest (SSSIs) and two National Nature Reserves (NNRs) (Angus 1996). However, with increasing environmental and anthropogenic interference, there is a need for the further development of suitable conservation strategies for these communities.

Machair is best envisaged as an interrelated system of habitats and communities (Angus 1994, 1996), centred on the machair dune grassland plains that predominate in many areas. However, these are only part of a much wider range of habitats, extending from the beach through foredunes, dune grassland, dune slacks, lochs, loch margins and fens to the 'blackland', which is the name given to those areas where the calcareous sands have been blown up over the inland peats (Anon. 1999).

Human populations and environment have played a significant role in shaping the origin and development of machair systems (Boyd & Boyd 1990; Gilbertson et al. 1995, 1996a; Owen et al. 1996; Angus 1996, 1997). Examination of natural and anthropogenic disturbance is therefore essential to a full understanding of machair ecological processes. However, there has been very little previous research to quantify the responses and adaptations of machair plant communities and ecosystems to the effects of either natural or anthropogenic disturbance.

In recent years, an increased interest in the environmental, ecological and historical machair has been evident (Ranwell 1974, 1977, 1980 a,b; Anon. 1979; Pankhurst & Mullin 1991; Gilbertson et al. 1996a; Angus 1997). However, although the phytosociology of the Hebridean machairs is now well documented (Dickinson et al. 1971; Pankhurst 1991; Dargie 1993; Gilbertson et al. 1994, 1995; Kent et al. 1994, 1996; Owen et al. 1996, 1998; Rodwell 2000), and particularly in Dargie (1998), very little is understood of the underlying processes, plant ecophysiology and plant community dynamics that maintain machair systems. Until recently, with the exception of the work of Crawford (1989, 1990), these phytosociological studies had also largely ignored the cultivated areas of machair that are the subject of this paper. However, Dargie (1998) mapped all arable land and fallows, including separation into oats and rye, potatoes and turnips and associated dry and wet fallows.

Erosion of coastal dunes, as a result of the extreme climatic environment of the Outer Hebrides, is the most common natural disturbance on the machair (Angus & Elliot 1992). Anthropogenic disturbances are chiefly due to the agricultural practices of grazing and cultivation, including ploughing for the growing of cereal crops and digging of 'lazy-beds' where sand/soil is heaped into ridges and furrows for potato production. Although the traditional crofting practices which operate in the Outer Hebrides are fundamental to the creation of species-rich sub-community types (Anon. 1989; Angus 1996, 1997), changes in agricultural practices may accelerate natural erosional processes on the machair (Gilbertson et al. 1996b; Crawford 1997). The deflation of dunes during severe storms and winter gales, in conjunction with inappropriate agricultural methods, leads to widespread sand-blow, re-deposition of sand and subsequent burial of the machair vegetation.

Crofting practices in the Outer Hebrides

Agriculture on South Uist and in the Outer Hebrides in general, follows the long-established methods of crofting management. Crofters hold a traditional right to cultivate the machair and agriculture is the most widespread form of land use (Mather & Ritchie 1977). The croftlands of the Uists are concentrated on the exposed and low-lying coastal machairs (Mather & Ritchie 1977; Grant 1979), which are cultivated to support a limited amount of both arable and winter grazing. *Avena strigosa*, *Secale cereale* and an indigenous form of bere (*Hordeum* spec.) are the main cereal crops, and are used as winter feed for livestock. In addition, small patches, known as 'lazy-beds', where sand is ploughed and heaped into ridges, with intervening furrows, are devoted to the production of potatoes for domestic consumption.

The machair soils are impoverished in terms of nutrients, which means that successive crops cannot be taken for any significant length of time. Machair soils are highly deficient in organic matter, potassium and phosphorus, as well as certain trace elements. To overcome nutrient deficiencies, stock are often grazed on machair in winter and moved onto the 'blackland' in summer, allowing growth of a fodder crop on the machair. This represents a local form of transhumance. Traditional fertilizers, notably seaweed, are important for their property of raising soil humus content (Kerr 1954). In contrast, artificial fertilizers reduce the humus in the soils, resulting in changes in soil stability, tilth and water-holding capacity (Boyd & Boyd 1990). Use of artificial fertilizers also leads to a reduction in species richness.

In response to the nutrient deficiency of the soil, traditional machair cropping operates on a rotational system, so that, in any one machair, large areas are left fallow. Strips of arable and fallow land of different ages are a characteristic feature of the machairs of South Uist and are an important element in the mosaic of machair habitats. Preparation of the machair land for cropping follows established historic methods and the type of seedbed favoured for the growth of cereals has not changed for centuries, since horse ploughing was employed to prepare the land for seeding (Grant 1979). Compared with these traditional methods, modern systems and machinery are highly unsuitable and most ploughing is accomplished through the use of 'old trailed, narrow set, tractor ploughs' (Grant 1979, p. 531). The shallow ploughing characteristic of the Uists results in a series of narrow furrows that are held together by turf. To minimize the risk of erosion, ploughing does not typically begin until late March at the earliest (Knox 1974). Cereal seeds are then sown into the furrow tracks and covered by harrowing.

In combination, the effects of modern ploughing and reseeding techniques, herbicides, pesticides and fertilizers can be dramatic. Various authors have considered (e.g. Mather & Ritchie 1977; Randall 1983; Anon. 1989; Angus 1996; Crawford 1990, 1997) that the botanical and aesthetic value of the Hebridean machairs is attributable to the operation of the traditional crofting practices. Colourful successional plant communities occur during the fallow periods and these may also be characterized by a diverse invertebrate fauna (Randall 1983). Traditional crofting management is closely adapted to the machair environment and has been a major factor in the development of the ecosystem (Anon. 1989). Ranwell (1980b) indicated the need for further detailed study of the influences of traditional cultivation on the development of machair soil and vegetation systems. Although the effects of differing grazing regimes and practices on machair vegetation are relatively well documented (e.g. Randall 1980) the effects of arable cultivation are less well known.

In 1988, a total of 7500 ha of machair situated on the islands of North and South Uist, Benbecula, Barra and Vatersay was designated as an Environmentally Sensitive Area (ESA) (Anon. 1989; Angus 1996). Under section 18 of the Agriculture Act 1986, the Machair ESA Scheme offers crofters financial incentives, on a voluntary basis, to manage their land using traditional low-impact techniques. The ESA prescriptions encourage the crofters to limit the use of damaging fertilizers, herbicides and pesticides and to use traditional crofting methods such as shallow ploughing and the application of natural organic fertilizers such as seaweed and dung. Entrants to the scheme are also expected to cultivate land on a rotational basis and to protect the machair from overstocking and re-seeding practices.

In an attempt to establish the pattern of arable weed succession in fallow fields, Crawford (1989, 1990) chronicled the relationship between arable weed communities and the various methods of crop management in operation on the Outer Hebrides. However, there remains a dearth of information with regard to the dynamics of the plant communities of cultivated machair.

Aims

This paper aims to describe the plant associations of cultivated machair through floristic survey of spatial chronosequences of both ploughed and lazy-bedded land at two sites on South Uist, namely, Drimsdale and Kildonan (Fig. 1). The processes of regrowth following ploughing were also studied in detail by monitoring species regrowth and recolonization on recently ploughed turves. A particular aim was to evaluate the importance of vegetative reproduction and regrowth in recolonization.

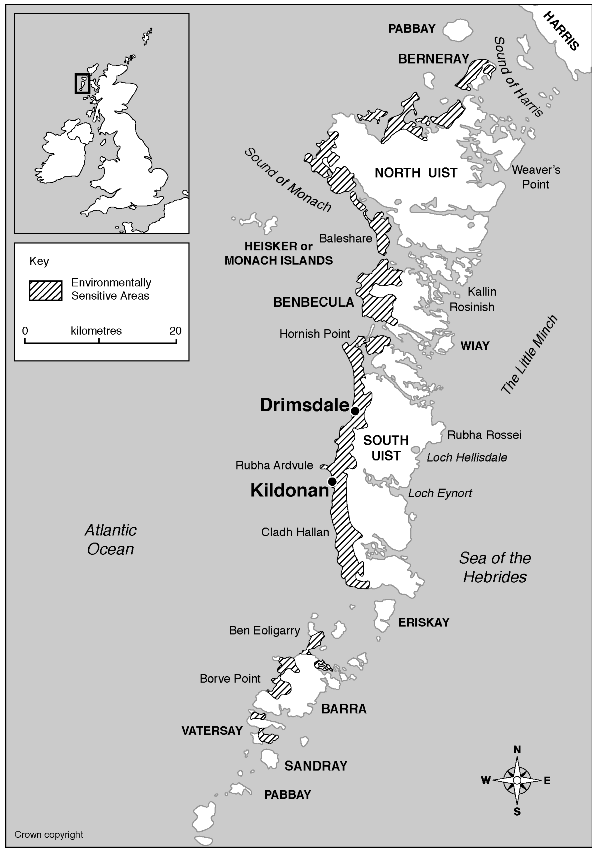


Fig. 1. The location of the research sites at Kildonan and Drimsdale within the Machair Environmentally Sensitive Area (ESA) of the Outer Hebrides.

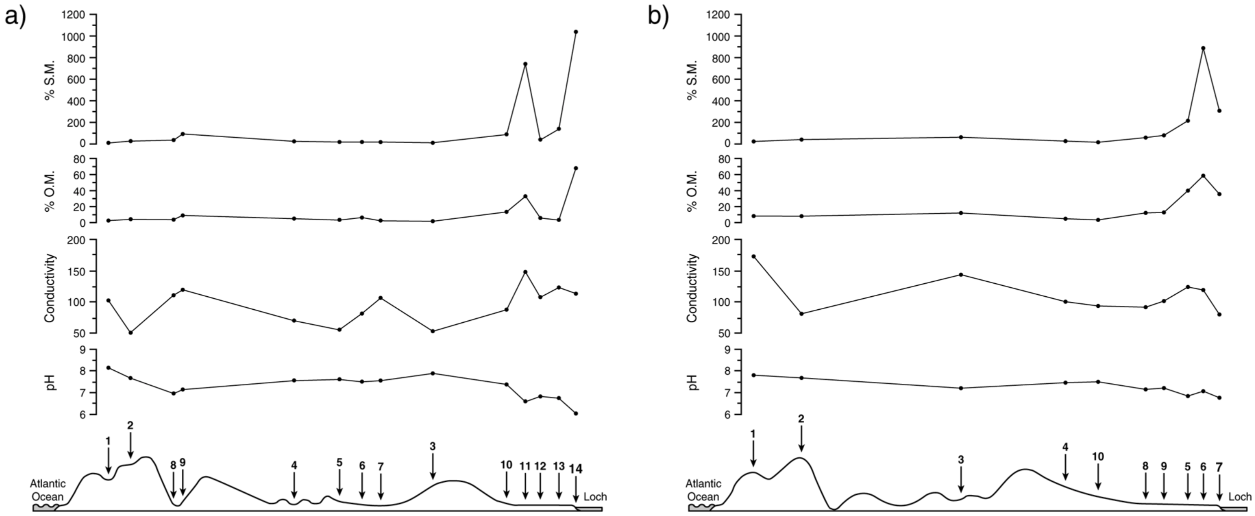
Methods

Site selection

Angus (1996) and English Nature (Anon. 1999) have stated that in terms of botanical, landscape, ornithological and geomorphological interest, the South Uist machairs constitute the best examples of Hebridean machair systems. Two field sites, at Kildonan and Drimsdale (Fig. 1), were carefully selected to provide two typical but differing examples of machair vegetation that were subject to cultivation.

At Kildonan, the machair is subject to grazing by domestic sheep and some cattle and the area has a large population of feral rabbits. During winter, the township gates are opened and the whole area of machair land becomes common grazing for both sheep and cattle. The machair plain is subject to both plough and spade cultivation with the production of both cereals and potatoes. The vegetation of the whole machair system at Kildonan is described in detail in Owen et al. (1998). 14 plant communities and sub-communities were defined using Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979a) and their similarities to those detailed more widely for the machair systems of South Uist, Barra and Vatersay, by Kent et al. (1996) were noted. These community types and their relative positions across the dune complex are shown in Fig. 2a.

The Drimsdale research area lies within the Loch Druidibeg National Nature Reserve. Owen (1998) has described the plant communities and sub-communities in detail and these are summarized in Fig. 2b. Formed as a crofting township in 1924 (Ritchie 1971), cereal crops are cultivated on a rotational basis, while production of potatoes for domestic consumption is concentrated in an area of lazy beds towards the north end of the site. Hay fields are situated in the wetter areas. As at Kildonan, the township gates are opened during the winter months to allow common grazing.



TWINSPAN• group	Community type
Group 1	SD6 *Ammophila arenaria* mobile dune community
Group 2	Mature *Ammophila arenaria* mobile dune community
Group 3	SD7 semi-fixed dune grassland•
Group 4	SD8 *Festuca rubra-Galium verum* fixed dune community•
Group 5	SD8 *Festuca rubra-Galium verum* fixed dune community. Cultivated
Group 6	SD8 *Festuca rubra-Galium verum* fixed dune community. Under potato patch cultivation•
Group 7	SD8 *Festuca rubra-Galium verum* fixed dune community. Under arable cultivation•
Group 8	MG11 *Festuca rubra-Agrostis stolonifera-Potentilla anserina* lowland inundation grassland. Dune slacks
Group 9	Low damp machair. Dune slacks
Group 10•	Wet matrix machair. Previously cultivated
Group 11•	Wet matrix machair grading to loch margin•
Group 12•	Wet matrix machair•
Group 13•	*Eleocharis palustris* swamp community•
Group 14	*Menyanthes trifoliata* bed community

TWINSPAN• group	Community type
Group 1	SD6 *Ammophila arenaria* mobile dune community
Group 2	SD8d *Festuca rubra-Galium verum* fixed dune grassland, *Ranunculus acris-Bellis* • *perennis* sub-community•
Group 3	SD8F *Festuca rubra-Galium verum* fixed dune grassland, fallow after arable tillage•
Group 4	SD8d *Festuca rubra-Galium verum* fixed dune grassland, *Ranunculus acris-Bellis*• *perennis* sub-community. Previously cultivated
Group 5	MG11 *Festuca rubra-Agrostis stolonifera-Potentilla anserina* lowland inundation grassland.•
Group 6	MG11 *Festuca rubra-Agrostis stolonifera-Potentilla anserina* lowland inundation grassland • grading to S4 *Phragmites australis* swamp•
Group 7	S4 *Phragmites australis* swamp, *Galium palustre* sub-community•
Group 8	MG5 *Cynosurus cristatus-Centaurea nigra meadow.* Roadside verge•
Group 9	MG5 *Cynosurus cristatus-Centaurea nigra meadow.* Managed for hay•
Group 10	Newly ploughed and seeded arable field

Fig. 2. Generalized sections through the machair dune systems at **(a)** Kildonan and **(b)** Drimsdale to illustrate major plant community types (NVC) and associated variation in key environmental variables derived from detailed description of the dunes presented in Owen et al. (1998) for Kildonan and Owen (1998) for Drimsdale.

Description of agricultural plant communities at Drimsdale and Kildonan

The first part of the research aimed to describe the plant communities of the two major types of cultivated land on the machair: land under cereal cultivation and land used for production of potatoes known as lazy-bedding.

Cereal land at Drimsdale

A survey of the plant communities of agriculturally disturbed machair was undertaken at Drimsdale during July 1996. Use of aerial photographs and consultation with crofters enabled an approximate chronology of the cereal field systems at Drimsdale to be drawn up. Quadrats were positioned within four distinct vegetation types:

1. Newly-ploughed and seeded dry machair;
2. Previously-ploughed and cropped dry machair, fallow for one year;
3. Previously-ploughed and cropped dry machair, fallow for two years;
4. Wet machair previously managed for cereal-cropping, but judged fallow for ca. two years.

Newly-ploughed and seeded dry machair represented the most abundant vegetation types and 48 1m × 1m quadrats were described from these. A total of 24 quadrats were recorded for each of the remaining three areas. Plant species abundance was recorded using subjective assessment of percentage cover (Kent & Coker 1992).

Kildonan potato patches

During July 1996, plant communities of lazy-bedded machair were examined within a five-stage potato patch spatial chronosequence on the dry machair plain at Kildonan, where five adjacent plots, each 5 m × 20 m in size had been put down to potatoes in successive years. Quadrats were recorded from all five stages of this spatial chronosequence, representing newly ploughed and planted, one-year fallow, two-year fallow, three-year fallow and greater than four-year fallow potato patches. Each quadrat consisted of a 50 cm × 50 cm section of wire garden mesh, subdivided into a grid of four hundred 2.5 cm × 2.5 cm squares. Given the small size of each of the potato patches, only 10 quadrats were randomly located within each patch. In order to assess

the micro-associations of species at each quadrat location, five of the 400 squares comprising each quadrat were randomly selected for sub-sampling, using a table of random numbers as co-ordinates. Each 2·5 cm× 2·5 cm square, therefore, represented a 'micro-quadrat'. For consistency, the southernmost side of the mesh section was always designated as the x-axis. The species present within each of the five micro-quadrats were noted and their abundances recorded on a scale of 1-4, where:
1 = 1 or 2 individuals of a species;
2 = 1 or 2 individuals to a quarter of a square;
3 = one quarter to one half of a square;
4 = one half to one full square.

Bare sand was recorded in each 'micro-quadrat' as percentage cover.

Analysis of vegetation data

Definition and classification of agricultural plant community types at Drimsdale and Kildonan was achieved using TWINSPAN (Hill 1979a). Default cut levels for defining pseudospecies were applied to the Drimsdale cereal land quadrat data. Cut levels for defining pseudospecies during TWINSPAN analysis of the Kildonan potato patch micro-community data were designated as 0, 1, 2, 3 and 4. Since no environmental data were collected during the survey, Detrended Correspondence Analysis (DCA) (Hill 1979b; Hill & Gauch 1980) was considered to be the most suitable ordination method (Kent & Coker 1992). However, Podani (1997) and Oksanen & Minchin (1997) have indicated that the original DECORANA program of Hill (1979b) is sensitive to the input-order of the data. Subsequent testing has shown that this was due to insufficiently strict criteria for defining stability within iterations and an error in the axis rescaling algorithm. Ordination of the floristic data was, therefore, accomplished using the updated DECORANA program (Oksanen & Minchin 1997).

Vegetation processes in newly ploughed machair

Collection and maintenance of plant material

Turves of newly ploughed machair, each ca. 35 cm × 15 cm × 10 cm in size, were collected from a single area of cereal land at Drimsdale in late April 1997. The land had been fallow for at least five years prior to ploughing and corresponded to the Group 3 – SD8F *Festuca rubra-Galium verum* fixed dune grassland, fallow after arable tillage, shown in Fig. 2. Collection of the turves occurred approximately 10 days after ploughing. The turves were transferred to a bed of fresh machair sand in individual shallow plastic trays. Three turves, designated T1, T2 and T3, were transplanted to the trays in the inverted position in which they had been found in the field; with a layer of dead and senescing vegetation on their undersides, and bare sand on their uppermost surfaces. The remaining three turves, T4, T5 and T6, were transferred to the trays in an 'original' position, so that the original layer of vegetation was exposed on the uppermost surface of the turf and the bare sand of the ploughed surface lay on the bed of dune sand. The trays were positioned in a polythene tunnel for the duration of the investigation. Each turf was watered daily from above with a fine rose to prevent excess disturbance.

Measurement of species composition

The species composition of each turf was recorded by means of a 20 cm × 10 cm section of wire garden mesh, centrally-situated and secured in place by wooden stakes. Using a grid of these dimensions ensured that the majority of the turf surface was sampled, whilst excluding the uneven edges of vegetation at the extremities. Each mesh section consisted of a grid of 50 2 cm × 2 cm squares. The local rooted frequency of each species on each turf was determined by recording its presence or absence in each of the 50 squares. Presence/absence data were then converted to give a percentage score for each species (Kent & Coker 1992). Species composition was recorded at fortnightly intervals from mid-May 1997 for a total of 20 weeks. The investigation was terminated in the first week of October 1997.

Results

Description of agricultural plant communities at Drimsdale and Kildonan

Cereal land at Drimsdale

In total, 81 species were found in the 120 quadrats recorded during the survey of agricultural land at Drimsdale. TWINSPAN identified five plant communities (Table 1).

DCA output and an outlier quadrat

Analysis of all 120 quadrats taken from agricultural land at Drimsdale resulted in a distorted ordination due to the presence of one outlier quadrat. Examination of the data indicated that this sample was the only quadrat in the survey characterized by the presence of *Matricaria discoidea*. The removal of the sample, followed by reanalysis of the data set resulted in the quadrat ordination plot presented in Fig. 3. The TWINSPAN group membership of samples (Table 1: Groups 1 – 5) is superimposed in Fig. 3a and field membership is overlaid in Fig. 3b.

Table 1. Summary of plant community groups produced by TWINSPAN analysis of all 120 quadrats of the Drimsdale agricultural vegetation survey, July 1996.

Group	No. of quadrats	Characterizing species	% constancy by group (≥ 50 %)	Associated species (26 - 50 % constant by group)
1	49	Bare sand	98	*Agrostis stolonifera*
		Hordeum spec.	98	*Bellis perennis*
		Festuca rubra	98	*Plantago lanceolata*
		Anagallis arvensis	82	*Erodium cicutarium*
		Senecio jacobaea	80	*Stellaria media*
		Papaver rhoeas	80	
		Achillea millefolium	71	
		Ranunculus acris	71	
		Potentilla anserina	71	
		Sonchus asper	71	
		Sinapis arvensis	71	
		Myosotis arvensis	69	
		Trifolium repens	61	
		Poa humilis	61	
		Viola arvensis	53	
2	23	Bare sand	100	*Saxifraga tridactylites*
		Bellis perennis	100	*Ranunculus repens*
		Festuca rubra	100	*Cerastium diffusum*
		Prunella vulgaris	96	*Cirsium arvense*
		Myosotis arvensis	96	*Papaver rhoeas*
		Viola tricolor	87	*Euphrasia officinalis**
		Veronica arvensis	87	*Brachythecium* spec.
		Hordeum spec.	87	*Rumex acetosella*
		Achillea millefolium	83	*Anagallis arvensis*
		Arenaria serpyllifolia	78	*Daucus carota*
		Cerastium fontanum	78	*Stellaria media*
		Sherardia arvensis	74	*Geranium molle*
		Plantago lanceolata	74	
		Agrostis stolonifera	74	
		Poa humilis	70	
		Senecio jacobaea	61	
		Ranunculus acris	61	
		Erodium cicutarium	52	
		Potentilla anserina	52	
		Bryum capillare	52	
3	19	Bare sand	100	*Potentilla anserina*
		Festuca rubra	100	*Veronica arvensis*
		Senecio jacobaea	100	*Rhytidiadelphus squarrosus*
		Bellis perennis	100	*Arenaria serpyllifolia*
		Prunella vulgaris	95	*Cerastium diffusum*
		Trifolium repens	95	*Myosotis arvensis*
		Achillea millefolium	95	*Viola tricolor*
		Ranunculus repens	89	*Homalothecium lutescens*
		Brachythecium spec.	84	*Ranunculus acris*
		Poa humilis	84	
		Euphrasia officinalis	79	
		Tortula ruraliformis	74	
		Bryum caespiticium	74	
		Linum catharticum	68	
		Plantago lanceolata	68	
		Agrostis stolonifera	68	
		Cerastium fontanum	68	
		Erodium cicutarium	68	
		Lotus corniculatus	63	
		Hordeum spec.	63	
		Geranium molle	53	
4	16	*Festuca rubra*	100	*Ranunculus repens*
		Bellis perennis	100	*Dactylorhiza fuchsii*
		Trifolium repens	100	*Juncus bufonius*
		Rhinanthus minor	100	*Taraxacum brachyglossum*
		Vicia cracca	100	*Cirsium arvense*
		Cerastium fontanum	94	*Trifolium pratense*
		Holcus lanatus	94	*Equisetum fluviatile*
		Ranunculus acris	94	*Leontodon autumnalis*
		Bare sand	94	*Myosotis arvensis*
		Hordeum spec.	94	
		Plantago lanceolata	88	
		Rumex acetosella	88	
		Potentilla anserina	88	
		Prunella vulgaris	81	
		Brachythecium spec.	81	
		Euphrasia officinalis	69	
		Agrostis stolonifera	69	
		Carex flacca	63	
		Senecio jacobaea	63	
		Poa humilis	63	
5	13	Bare sand	100	*Ranunculus repens*
		Trifolium repens	100	*Plantago lanceolata*
		Bellis perennis	100	*Veronica arvensis*
		Achillea millefolium	92	*Lotus corniculatus*
		Festuca rubra	85	*Rumex acetosella*
		Poa humilis	85	
		Ranunculus acris	85	
		Hordeum spec.	85	
		Thalictrum minus	77	
		Euphrasia officinalis	77	
		Brachythecium spec.	77	
		Vicia cracca	77	
		Senecio jacobaea	77	
		Potentilla anserina	77	
		Cerastium fontanum	69	
		Prunella vulgaris	62	
		Myosotis arvensis	62	
		Viola tricolor	54	
		Agrostis stolonifera	54	

**Euphrasia officinalis* is taken as an species aggregate.

Potato patches at Kildonan

37 species were recorded from a total of 250 micro-quadrats taken from the five-year potato patch spatial chronosequence at Kildonan, during July 1996. TWINSPAN identified seven plant micro-communities (Table 2).

DCA output

The quadrat ordination diagram produced as a result of DCA is presented in Fig. 4. The TWINSPAN group membership (Table 2: Groups 1 - 7) of each quadrat is superimposed in Fig. 4a, while the patch age of quadrats is superimposed in Fig. 4b.

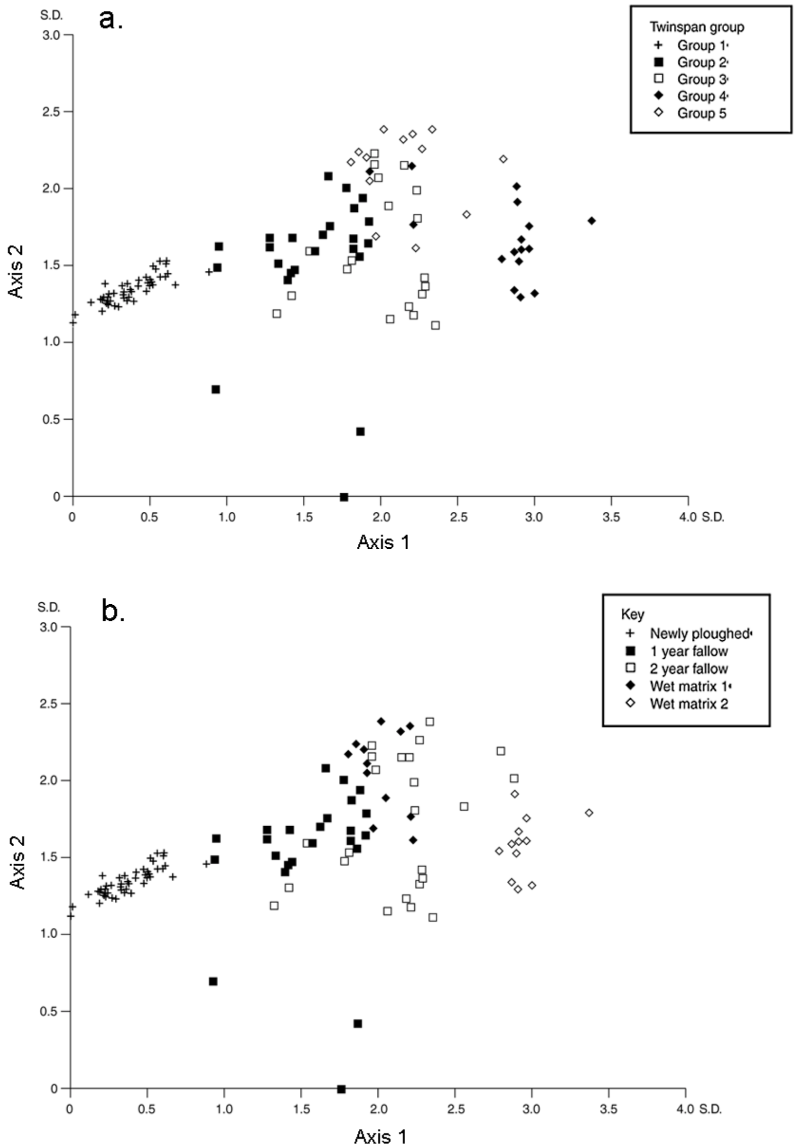


Fig. 3. Quadrat ordination derived from Detrended Correspondence Analysis of the 120 quadrats recorded during the agricultural vegetation survey at Drimsdale, July 1996, with one outlier quadrat removed with **(a)** TWINSPAN groups (1 - 5) from Table 1 superimposed. **(b)** field membership of quadrats superimposed. SD = units of average standard deviations of species turnover; eigenvalues: axis 1 = 0.562; axis 2 = 0.207.

Vegetation processes in newly ploughed machair

The turves transplanted to the trays in the ‘original’ position showed the greatest species diversity over the duration of the investigation with 27, 24 and 20 species recorded on turves T4, T5 and T6, respectively (Table 3). 17 plant species were common to turves T4, T5 and T6 (Table 3).

Of the three turves transplanted to the trays in an ‘inverted’ position, T1 was the most species-rich: 15 plant species were recorded over the 20-week experimental period. Turves T2 and T3 were re-colonized by 11 and 10 species, respectively (Table 3). However, only seven species were common to turves T1, T2 and T3. Five species occurred on all six turves: *Bellis perennis*, *Festuca rubra*, *Agrostis stolonifera*, *Lotus corniculatus* and *Ranunculus repens*. *Arenaria serpyllifolia*, *Ranunculus acris*, *Plantago lanceolata*, *Lophocolea bidentata* and *Cardamine pratensis* were the least common species and did not occur on more than one turf (Table 3).

For clarity, only the most commonly occurring spe-

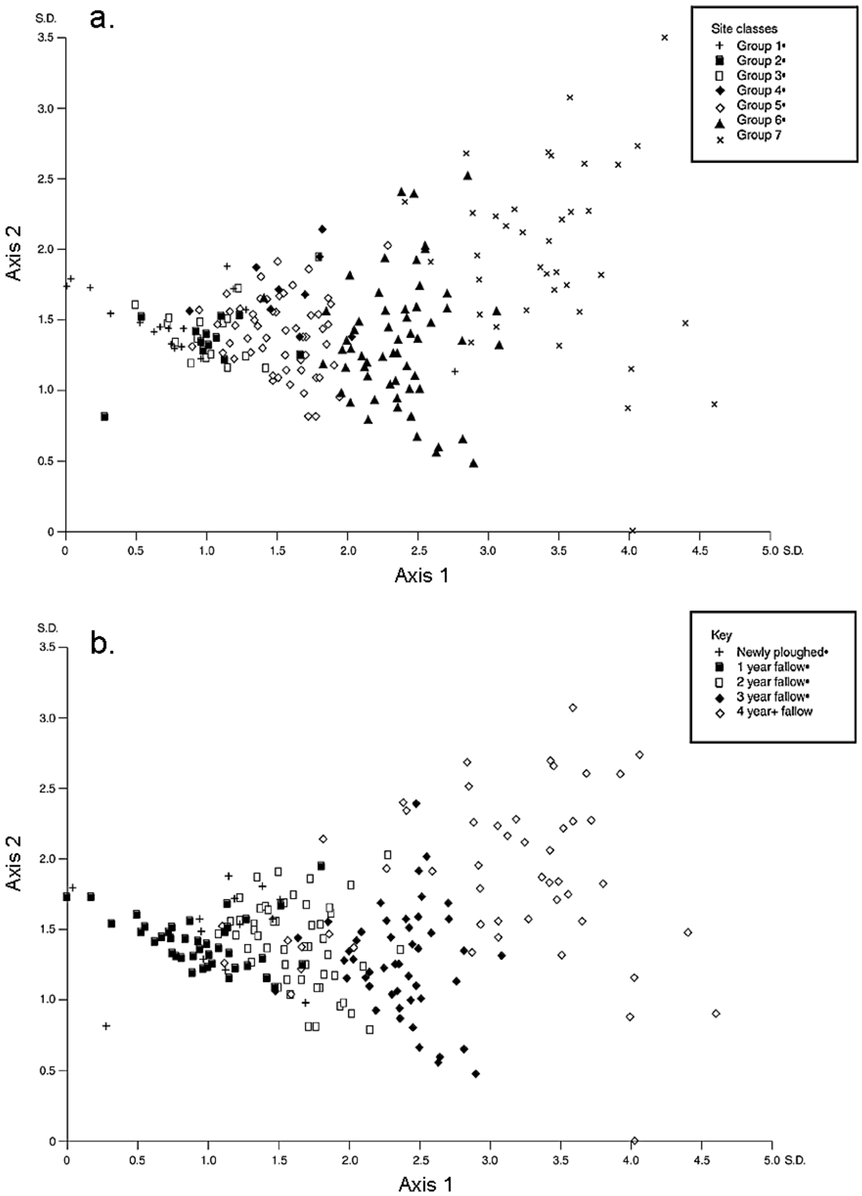


Fig. 4. Quadrat ordination derived from Detrended Correspondence Analysis of 250 micro-quadrats recorded across the five-year potato patch spatial chronosequence at Kildonan, July 1996 with (**a**) TWINSPAN groups superimposed; (**b**) quadrat membership of the 5-yr patch spatial chronosequence superimposed. SD = units of standard deviations of species turnover; eigenvalues: axis 1 = 0.593; axis 2 = 0.330.

cies or those with recovery patterns of particular note are discussed below. There was only a small decrease in the amount of bare sand present on each turf over the 20-week period of the investigation on the 'inverted' turves (Fig. 5), while the 'original position' turves (Fig. 6) show a very much more marked decrease. On both sets of turves, following its initial increase, *Poa humilis* showed a decrease in total frequency. Each turf was also characterized by a steady increase in cover of *Festuca rubra* as the investigation progressed. Similar trends in each of the six turves were witnessed for *Bellis perennis*, *Lotus corniculatus*, *Agrostis stolonifera* and *Ranunculus repens* (Figs. 5 and 6).

Increases in cover over the 20-week period were recorded for *Trifolium repens* and *Potentilla anserina* on turves T4, T5 and T6 (Fig. 6), and for *Stellaria media* on turves T1, T2 and T3 (Fig. 5). Frequencies of moss and liverwort species on turves T4, T5 and T6, notably *Rhytidiadelphus squarrosus, Homalothecium lutescens, Plagiomnium rostratum* and *Tortula ruralis* ssp. *ruraliformis*, were not dramatically increased or decreased but remained relatively constant throughout the course of

Table 2. Summary of plant micro-community groups produced by TWINSPAN analysis of all 250 micro-quadrats taken from the five-year potato patch spatial chronosequence at Kildonan, July 1996.

Group	No. of quadrats	Characterizing species	% constancy by group (≥ 50%)	Associated species (26 - 50% constant by group)
1	51	Bare sand	100	
2	16	Bare sand	100	
		Ranunculus repens	88	
		Viola tricolor	56	
		Stellaria media	50	
		Erodium cicutarium	50	
3	17	Bare sand	100	*Stellaria media*
				Erodium cicutarium
				Agrostis stolonifera
4	13	Bare sand	100	*Festuca rubra*
		Viola tricolor	54	*Plantago lanceolata*
5	56	Bare sand	100	*Senecio jacobaea*
		Agrostis stolonifera	59	
		Festuca rubra	54	
		Ranunculus repens	50	
6	59	Bare sand	95	*Agrostis stolonifera*
		Festuca rubra	86	*Trifolium repens*
		Bellis perennis	80	
7	38	*Festuca rubra*	100	*Rhytidiadelphus squarrosus*
		Homalothecium lutescens	63	*Plantago lanceolata*
				Litter
				Poa humilis
				Bare sand

the investigation (Fig. 6). In contrast, on the 'inverted' turves, recovery of mosses was much poorer and they did not colonize until late in the investigation: *Tortula ruralis* ssp. *ruraliformis* appeared on T1 at time 5, whereas *Rhytidiadelphus squarrosus* appeared on T3 at time 8 (Fig. 5). A number of species characteristically colonized the turves in the later stages of the investigation. These included *Myosotis arvensis* on T1, T2, T3 (Fig. 5) and T5 (Fig. 6); *Geranium molle* L. on T1 and T2; *T. repens* on T1 and T2; *Cerastium fontanum* on T1 and T3 (Fig. 5); *Viola tricolor* on T1, T5 and T6 (Figs. 5 and 6); *Arenaria serpyllifolia* on T2 (Fig. 5); *Erodium cicutarium* on T4 and T5 and *Cardamine pratensis* on T6 (Fig. 6).

Discussion

Description of agricultural plant communities at Drimsdale and Kildonan

Cereal land at Drimsdale

TWINSPAN analysis of the vegetation data from the cereal land identified five plant communities. Subsequent ordination of the data by DCA identified the first axis as the most ecologically significant. The ordering of quadrats along this first axis was strongly related to sample site age (Fig. 3b) and represented a successional gradient from newly ploughed machair to machair at a relatively advanced stage of recovery following

Table 4. Species present in TWINSPAN Group 1 of the Drimsdale agricultural vegetation survey and their presence or absence on experimental ploughed turves T1, T2, T3, T4, T5 and T6. + = species present on turf; - = species absent from turf.

Species	Turf: 'Inverted' T1	T2	T3	'Original' T4	T5	T6
Festuca rubra	+	+	+	+	+	+
Agrostis stolonifera	+	+	+	+	+	+
Bellis perennis	+	+	+	+	+	+
Stellaria media	+	+	+	+	-	+
Trifolium repens	+	+	-	+	+	+
Myosotis arvensis	+	+	+	-	+	-
Potentilla anserina	-	-	-	+	+	+
Senecio jacobaea	-	-	-	+	+	+
Achillea millefolium	-	-	-	+	+	-
Erodium cicutarium	-	-	-	+	+	-
Ranunculus acris	-	-	+	-	-	-
Plantago lanceolata	-	-	-	+	-	-
Papaver rhoeas	-	-	-	-	-	-
Poa humilis	-	-	-	-	-	-
Viola arvensis	-	-	-	-	-	-
Anagallis arvensis	-	-	-	-	-	-
Sinapis arvensis	-	-	-	-	-	-
Sonchus asper	-	-	-	-	-	-
Hordeum spec.	-	-	-	-	-	-

Table 3. Plant species recorded from experimental ploughed turves T1, T2, T3, T4, T5 and T6 over the course of the 20-week investigation. Where: + = species present on turf; - = species absent from turf.

Species	Turf: 'Inverted' T1	T2	T3	'Original' T4	T5	T6
Bellis perennis	+	+	+	+	+	+
Festuca rubra	+	+	+	+	+	+
Agrostis stolonifera	+	+	+	+	+	+
Lotus corniculatus	+	+	+	+	+	+
Ranunculus repens	+	+	+	+	+	+
Stellaria media	+	+	+	+	-	+
Geranium molle	+	+	-	+	+	+
Trifolium repens	+	+	-	+	+	+
Poa humilis	+	+	-	+	+	+
Cerastium fontanum	+	-	+	+	+	+
Myosotis arvensis	+	+	+	-	+	-
Tortula ruralis spp. *r-formis*	+	-	-	+	+	+
Holcus lanatus	+	-	-	+	+	+
Prunella vulgaris	+	-	-	+	+	+
Rhytidiadelphus squarrosus	-	-	+	+	+	+
Viola tricolor	+	-	-	+	+	-
Potentilla anserina	-	-	-	+	+	+
Plagiomnium rostratum	-	-	-	+	+	+
Homalothecium lutescens	-	-	-	+	+	+
Senecio jacobaea	-	-	-	+	+	+
Linum catharticum	-	-	-	+	+	-
Erodium cicutarium	-	-	-	+	+	-
Veronica arvensis	-	-	-	+	+	-
Cirsium arvense	-	-	-	+	+	-
Bryum spec.	-	-	-	+	+	-
Achillea millefolium	-	-	-	+	+	-
Galium verum	-	-	-	+	-	+
Arenaria serpyllifolia	-	+	-	-	-	-
Ranunculus acris	-	-	+	-	-	-
Plantago lanceolata	-	-	-	+	-	-
Lophocolea bidentata	-	-	-	+	-	-
Cardamine pratensis	-	-	-	-	-	+
Total number of species	15	11	10	27	24	20

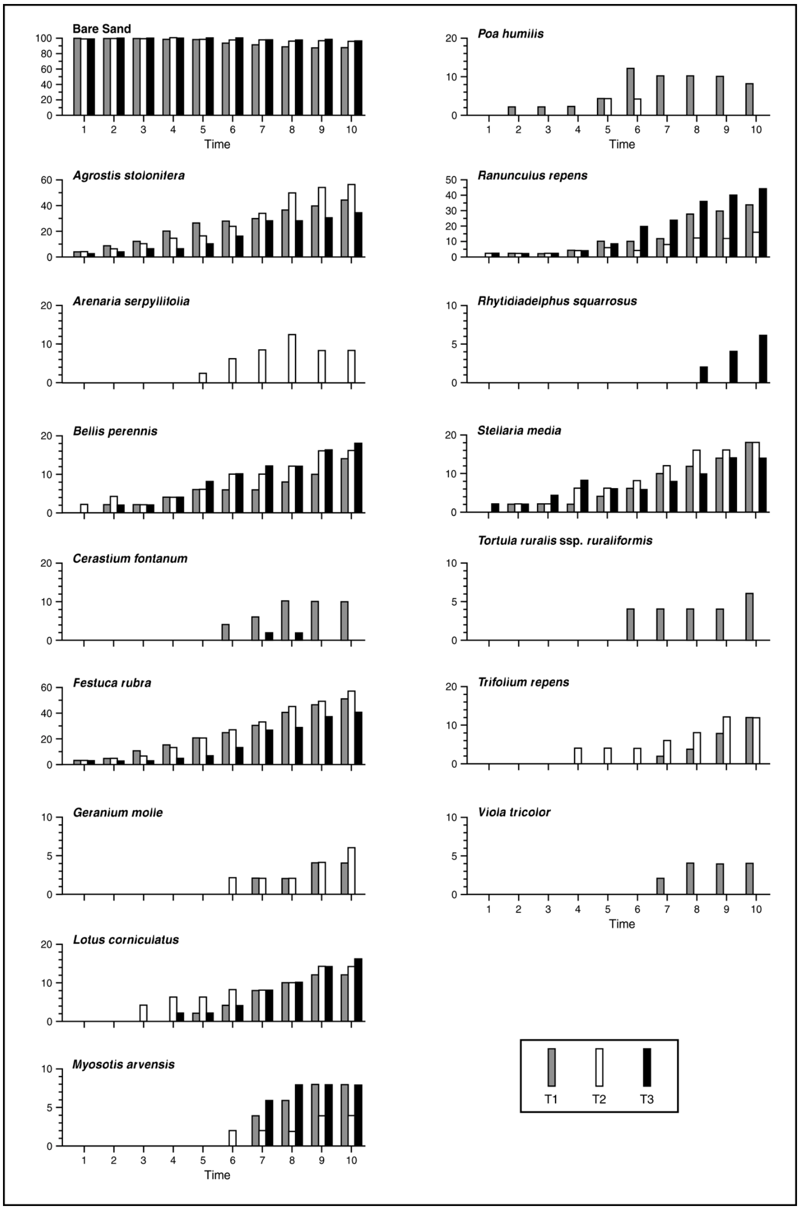


Fig. 5. Recovery of various machair species following ploughing on experimental turves T1, T2 and T3 ('inverted' position) as illustrated by changes in percentage frequency over a period of 20 weeks.

cultivation. However, it is also apparent that Axis 1 represented a gradient from dry to wet machair, as ploughing typically has a desiccating effect on machair soils (Crawford 1990). Quadrats from newly ploughed areas were, therefore, positioned to the extreme left of the ordination, whereas quadrats taken from the wetter mesotrophic grassland were situated to the extreme right of the diagram (Fig. 3b).

The early successional stages of cultivated dry machair derived from analysis of the Drimsdale data relate well to previous accounts by Crawford (1988, 1990) and Dargie (1993, 1998). The moderate to high frequencies of *Trifolium repens*, *Senecio jacobaea* and *Festuca rubra* in Group 1 (Table 1) must be due to their ability to colonize bare sand surfaces by means of vegetative rhizomes, runners and other similar organs (Gimingham 1964; Grime et al. 1988) and indicate that the initial processes of surface fixation are in progress at an early stage (3 - 4 months) following disturbance. TWINSPAN analysis of data collected during the course of this survey indicated that *Anagallis arvensis*, *Papaver rhoeas*, *Sinapis arvensis*, *Myosotis arvensis* and *Viola arvensis* were the ruderal species most significantly and frequently associated with the cereal crops of dry machair at Drimsdale. Crawford (1990) also identified *Viola arvensis* and *Sinapis arvensis*, along with *Chrysanthemum segetum*, *Anchusa arvensis*, *Valerianella locusta*, *Lamium purpureum* and *Euphorbia helioscopia*,

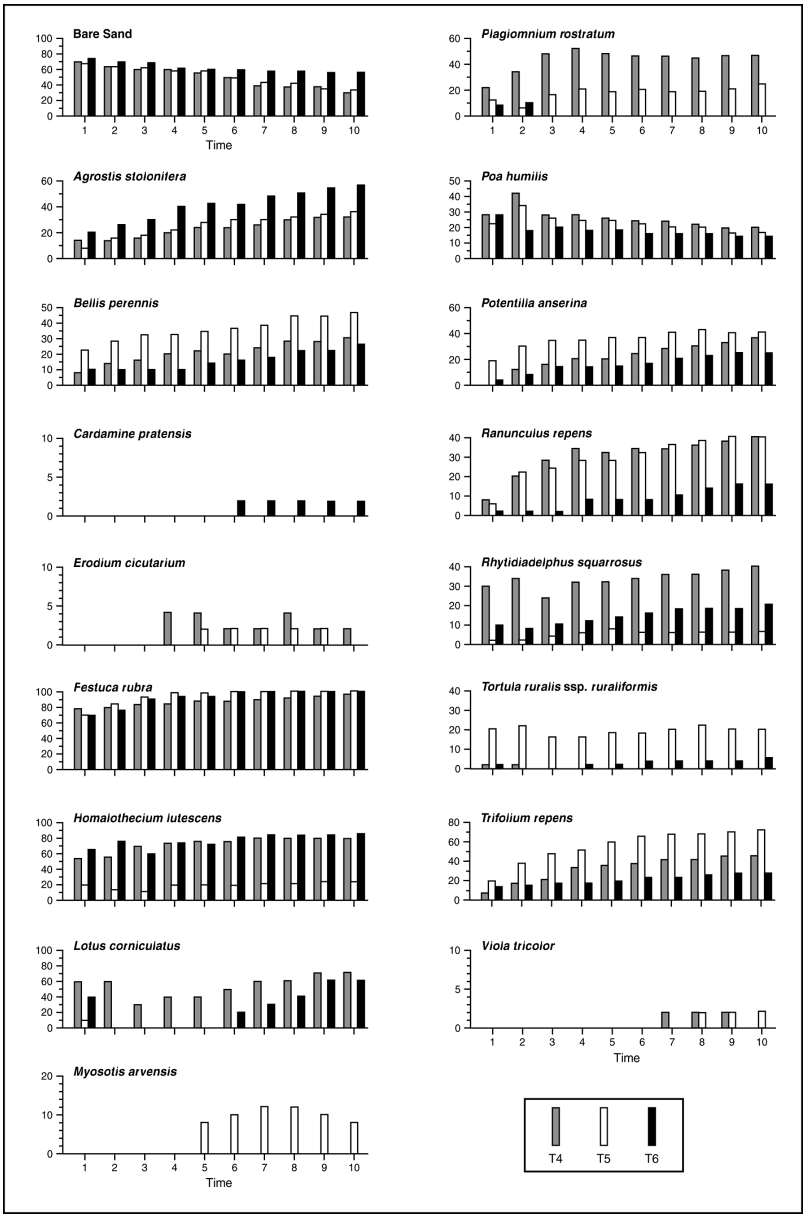


Fig. 6. Recovery of various machair species following ploughing on experimental turves T4, T5 and T6 ('original position') as illustrated by changes in percentage frequency over a period of 20 weeks.

as characteristic weeds of cultivated machair in North and South Uist. Crawford (1990) indicated that although these ruderal species may remain important elements of the community into the first fallow year, they are typically overshadowed by the presence of other species including *Viola tricolor*, *Ranunculus repens*, *Myosotis arvensis*, *Cerastium diffusum* and *Erodium cicutarium*. A similar pattern was recorded for the one-year fallow arable land surveyed at Drimsdale: increases in frequency of *Viola tricolor*, *Ranunculus repens*, *Myosotis arvensis*, *Cerastium diffusum* and *Erodium cicutarium* were mirrored by a sharp decrease in numbers, or total disappearance, of several previously-abundant ruderal species. The increased surface stability of one-year fallow relative to newly ploughed land was reflected by the occurrence of *Bryum capillare* and *Brachythecium* spec. in Group 2 (Table 1) at 52% and 35% constancy, respectively.

At the two-year fallow stage (Group 3 Table 1), most of the ruderal species which characterized the communities of newly-ploughed and one-year fallow land were absent, and the vegetation was dominated by *Festuca rubra*, *Senecio jacobaea*, *Bellis perennis*, *Prunella vulgaris*, *Trifolium repens* and *Achillea millefolium*. In this respect, the species composition of vegetation taken from land fallow for two years is highly comparable to the early successional stages described by Crawford (1988, 1990) and Dargie (1993, 1998). In addition to the increasing occurrence of species characteristic of a machair grassland, including *Euphrasia officinalis* agg., *Lotus corniculatus* and *Poa humilis* (Gimingham 1964), the increased stability and maturity of the two-year fallow vegetation relative to previous successional stages is reflected by the increasing frequencies of bryophyte species, notably *Bryum caespiticium*, *Brachythecium* spec., *Tortula ruralis* ssp. *ruraliformis*, *Rhytidiadelphus squarrosus* and *Homalothecium lutescens*.

It was not possible, prior to the survey, to produce a specific chronology of the wet matrix field systems, although they were judged to have been fallow for ca. two years. However, the position of Group 4 (Table 1) relative to Group 5 (Table 1) on the first DCA ordination axis (Fig. 3a), in conjunction with increased species diversity, suggests that the former was at a later stage of recovery following agricultural management. In contrast, the proximity of quadrats from Group 5 (Table 1) to quadrats from Group 3 (Table 1) on the first ordination axis, suggests that vegetation characteristic of Group 5 is closely related to the two-year fallow vegetation of dry machair. It is, therefore, likely that the community represented by Group 5 is characteristic of a relatively early successional stage but separation from Group 4 may also be related to disturbance caused by trampling effects of grazing animals, with these wetter Group 4 communities having both *Juncus bufonius* and *Equisetum fluviatile* as associated species (Table 1). Separation of quadrats on the second axis of the ordination (Fig. 3) is thus probably related to disturbance and wetness effects within the later stages of the successional sequence.

Thus this survey re-affirmed the role of anthropogenic factors in modifying machair vegetation and the importance of agricultural vegetation types as components of the machair systems of South Uist.

Potato patches at Kildonan

Analysis of micro-quadrat data collected from the five-year potato patch spatial chronosequence at Kildonan during July 1996 indicated the presence of a clear successional sequence, from newly ploughed and planted land to that at a late stage of recovery (Fig. 4b).

In terms of numbers of micro-communities characterizing each stage of recovery, the one-year fallow patch was the most diverse. TWINSPAN identified three different micro-communities from this successional stage (Table 2: TWINSPAN Groups 2, 3 and 4; Fig. 4a), all of which related well to the community previously identified as TWINSPAN Group C during the Kildonan survey reported by Owen et al. (1998). The presence of *Festuca rubra* and *Plantago lanceolata* as associated species in Group 4 (Table 2) is suggestive of the early stages of surface fixation, as Gimingham (1964) considered these species to be important during the initial fixation of bare sand.

Increased surface stability at the two-year fallow stage is indicated by increased quantities of *Festuca rubra* and the presence of other surface fixers, notably *Agrostis stolonifera*, *Ranunculus repens* and *Senecio jacobaea* (Gimingham 1964). Gimingham (1964) considered *Bellis perennis* to be characteristic of the later stages of surface fixation and this species does not appear in the TWINSPAN-defined communities until the three-year fallow stage. Although the previously-ploughed cereal land at Drimsdale was characterized by the presence of *Homalothecium lutescens*, *Bryum caespiticium* and *Brachythecium* spec. at an intermediate stage of recovery, the micro-communities of both the two and three-year fallow potato patches at Kildonan showed no comparable colonization by bryophytes. Surface-fixing bryophytes do not appear in the communities of the Kildonan potato patches until the four-year fallow stage, suggesting that the potato patches are slower to re-vegetate than equivalent areas of cereal land. One possibility is that desiccation effects are greater on potato patches, where ploughed ridges tend to be more exaggerated in terms of relief. However, this idea requires further investigation.

Comparison of the numbers of species within the cereal land quadrats (Table 1) with the potato patches (Table 2) shows the very much greater species richness of the cereal succession. This is partly due to the small size of the potato patches compared with the arable fields and resulting species-area effects but also demonstrates the importance of the additional ‘arable’ component of the cereal land.

Vegetation processes in newly ploughed machair

All experimental turves showed an ability to re-establish vegetation cover following disturbance by ploughing and a steady reduction in the total cover of bare sand was a consistent feature across all six turves (Figs. 5 and 6). Recovery of vegetation cover was most rapid on turves T4, T5 and T6 (Fig. 6). This rapid re-vegetation can be primarily attributed to the non-destructive ploughing methods employed on South Uist, which leave the vegetation cover relatively intact. Additionally, the turves were collected ca. 10 days after ploughing: turves T4, T5 and T6 had not, therefore, been in an ‘inverted’ period for any length of time and it is assumed that the turves were removed from the field before the decomposition processes were fully initiated.

Although re-vegetation of turves T1, T2 and T3 was somewhat slower, with bare sand remaining the dominant feature throughout the course of the investigation, colonization followed a similar pattern to that witnessed for T4, T5 and T6. *Agrostis stolonifera* made a rapid increase in cover during the course of the experiment on all six turves. This species is capable of extensive vegetative reproduction (Grime et al. 1988), and it is likely that the cutting action of the plough produced a number of detached shoots that were able to root to form new individuals. The high relative growth rate of *Agrostis stolonifera* (Grime et al. 1988) may also have been an important factor in the rapid increase in cover recorded for this species during the investigation.

Festuca rubra was the dominant plant species on all six turves at the close of the investigation (Figs. 5 and 6). It is likely that rhizomes, severed by the action of the plough, played an important part in the regeneration of this species (Grime et al. 1988). Increases in frequency by *Festuca rubra* were generally accompanied in each case by an associated decrease in the cover of *Poa humilis* (Figs. 5 and 6). A similar pattern, whereby an increase in the amount of *Festuca rubra* corresponded with a decrease in the amount of *Poa humilis*, was recorded by Hewett (1970) in his paper on the recolonization of sand dunes following extensive marram planting.

Bellis perennis, *Lotus corniculatus* and *Ranunculus repens* are three further species observed to have successfully re-colonized all of the ploughed turves (Figs. 5 and 6). Differences in their speed of recolonization are probably related to their varying modes of growth and reproduction. *Bellis perennis* exhibits a rosette growth form, while *Ranunculus repens* can proliferate via stolons and has been shown to have a rapid turnover of ramets (Grime et al. 1988). Overall, recovery of *Lotus corniculatus* on the six turves was more gradual than that of *Bellis perennis* or *Ranunculus repens*, and must be due to the fact that this species has a limited capacity for vegetative regeneration only (Grime et al. 1988).

The successful recovery of *Stellaria media* on turves T1, T2 and T3 may also be due to recolonization by vegetative means (Fig. 5). *Stellaria media* is a characteristic species of disturbed soils; regeneration on the three 'inverted' turves may have occurred, to some degree, by cuttings taking root (Grime et al. 1988). The good recovery shown by *Trifolium repens* and *Potentilla anserina* on T4, T5 and T6 (Fig. 6) is likely to be due to their capacity for vegetative spread (Grime et al. 1988). Keever (1950) and Egler (1954) have also indicated the role of vegetative propagules of perennial plants in the re-vegetation of agricultural field systems.

Species recorded on the ploughed turves that are not capable of regeneration by vegetative means must have re-colonized by seed present in the form of a soil seed bank. It is likely that the action of the plough was integral in bringing seeds to the surface (Roberts & Feast 1973), resulting in appropriate environmental conditions for breaking dormancy, followed by germination and establishment. *Myosotis arvensis*, *Geranium molle*, *Cerastium fontanum*, *Viola tricolor*, *Arenaria serpyllifolia*, *Erodium cicutarium* and *Cardamine pratensis* are all assumed to have regenerated by seed. Keever (1950, 1979) indicated that agricultural land cultivated during spring or summer is generally characterized by the post-cultivation germination of a population of winter annuals that were dispersed during the previous autumn. Of the seven species that are assumed to have germinated on the ploughed turves, four are classified as winter annuals (Grime et al. 1988). In addition, the colonization of T1, T2 and T3 by germinating seeds may be attributed to the fact that winter annuals are largely dependent on areas of bare ground for their successful establishment (Grime 1979).

Although recolonization via a soil seed bank clearly played a role in the re-vegetation of all six turves, success was somewhat limited. This poor establishment via seed may be due to the nature of the seed bank itself. Burrows (1990) and Cavers & Benoit (1989) maintain that the qualitative and quantitative representation of seeds in the soil seed bank is dependent on the previous cultivation history of the site: seeds in the bank may have been dormant or non-viable, or the number of seeds present in the ploughed turves may not have been particularly high. The majority of dune species are winter annuals (Packham & Willis 1997), that typically do not have innately dormant seeds and are, therefore, poorly represented in seed banks (Keever 1950). The rapid, efficient recovery of vegetative species compared with that of species reproducing by seed, may be partly accounted for by the fact that each experimental turf was removed from the field during April 1997, before flowering and seed-set. Regeneration by seed was, therefore, limited to germination of those propagules laid down in the seed bank during the autumn of 1996.

Field observations of the land from which all six turves were removed indicated that newly-ploughed machair is typified by the presence of 19 plant species (Drimsdale agricultural vegetation survey, TWINSPAN Group 1, Table 1). Experimental turves T1 - T6 are directly comparable to this ploughed land, in that all are assumed to have the same seed bank present. However, due to their 'inverted' position during the course of the investigation, turves T1 - T3 are more directly comparable to this ploughed land than turves T4 - T6. Of the 19 species recorded on ploughed land at Drimsdale, only seven occurred on T1, T2 and T3 (Table 4).

The results of this investigation suggest, therefore, that there are three main sources of colonizing machair species following disturbance by ploughing. These are: (1) roots, shoots and stolons capable of vegetative recolonization, i.e. vegetative propagules;

(2) seeds in the sand prior to ploughing i.e. seeds present in a soil seed bank;
(3) seeds arriving on the sand surface after ploughing i.e. seeds arriving in the seed rain.

The rhizomes, bulbs, corms, specialized roots and other vegetative fragments of the perennial machair species are clearly the most successful and rapid colonizers of ploughed land. However, although clearly a factor in the re-vegetation of ploughed land, successful colonization by seed will ultimately depend on the nature and extent of the seed bank and seed rain. Further research is required into the relative roles of both seed rain and seed banks within these agricultural communities.

Conclusion

The research presented in this paper confirms that agriculture and more particularly, cultivation, has been and still is an important factor in maintaining the botanical interest of Hebridean machair systems. Historically, agriculture has played an integral part in the development of Scottish machairs and it is certain that the Hebridean machairs would not exist in their present form without the influences of past agricultural management, including grazing by domestic animals, but also particularly the cultivation practices of ploughing and lazy-bedding (e.g. Randall 1983; Anon. 1989). Ingrouille (1995) describes the machairs of Scotland as an example of how human activity can modify vegetation and suggests that floristic differences between Scottish and Irish machairs (e.g. Akeroyd & Curtis 1980; Bassett & Curtis 1985) are largely related to the continuing importance of human influence in the former. Although agricultural usage of Scottish and Irish machairs was comparable until the end of the 19th century (Angus 1994), it is interesting that the potato famine was probably instrumental in the decline of the cultivation of the machairs of Ireland.

Clear sets of spatial chronosequences for both ploughed fields and potato patches have been identified and described in terms of floristic changes, showing that centuries of agricultural practice have resulted in the formation of the now typical machair vegetation types, incorporating colourful fallows and diverse old-field successions.

Recolonization by machair species following ploughing has been shown to occur primarily through vegetative processes; a response that permits rapid re-vegetation of traditionally cultivated shallow ploughed sites. Observations during the course of the investigation indicated that the processes of vegetative recolonization were in operation at 10 days after ploughing, and some species, e.g. *Festuca rubra* and *Agrostis stolonifera*, had reached a relatively advanced stage of recovery ca. 3 weeks after cultivation. The buried viable population of plants present in the soil as dormant bulbs, corms, tubers and buds on rhizomes, is frequently termed, 'the bud bank' (Harper 1977). However, there is no literature relating to the size and composition of machair bud banks. An assessment of the extent of vegetative reserves in machair soils could be undertaken in much the same way as described for the evaluation of seed banks (Warr et al. 1993). This would re-affirm the relative importance of vegetative versus sexual reproduction in the machair habitat.

An investigation into the effects of different ploughing techniques, in particular a comparison of traditional shallow ploughs with contemporary deep ploughs, would give an insight into the significance of established and modern farming methods for recolonization by vegetative means. Modern machinery ploughs deeper than the traditional shallow ploughs of crofters (Grant 1979). Deep ploughing completely destroys the surface vegetation, resulting in desiccation and disintegration of the turf, and ultimately limits the capacity for recolonization of the bare sand by vegetative means. It can be hypothesized, for example, that contemporary machinery would plough too deep to permit effective recolonization of the bare surface by vegetative means. This theory could be tested through simulating the effects of shallow and deep ploughing, burying vegetative fragments to different depths to determine at what depth re-growth fails.

Contemporary ploughs are more destructive than the traditionally employed shallow ploughs that merely turn the surface vegetation. It can, therefore, be assumed that the traditional shallow ploughing creates vegetative fragments which are of a suitable size to effect recolonization. However, it is likely that the more destructive contemporary methods would create relatively smaller fragments. The effects of established and contemporary ploughing methods on vegetative recolonization could, therefore, be further appraised through cutting vegetative fragments into different-sized pieces and determining which are most successful in re-vegetating bare sand.

Intensive farming also encourages the use of agrochemicals to supplement nutrient levels in the soil and eradicate unwanted plant species. Widespread and indiscriminate application of herbicides would decimate populations of the rarer arable weed species characteristic of machair cultivation systems. Modern farming practices have already caused the eradication of many weed species from the majority of agricultural habitats on mainland Britain (Angus 1994). Traditionally, seaweed is used to improve nutrient loading of the machair sands. However, increased use of commercial fertilizers will affect soil stability, structure and hydrology, which will, in turn, directly lead to associated changes in the vegetation of the machair systems. Agricultural activity has been instrumental in creating the structure and composition of the machair, and, while it is clear that agriculture is essential to maintain the diversity of the vegetation, it is equally important to restrict this activity to traditional crofting methods.

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References

Anon. 1979. The natural environment of the Outer Hebrides (ed. J.M. Boyd). *Proc. Roy. Soc. Edinb.* 77B: 1-651.

Anon. 1989. *Environmentally Sensitive Areas in Scotland – A first report*. Department of Agriculture and Fisheries for Scotland, Edinburgh.

Anon. 1999. *UK Biodiversity group – Tranche 2 action plans. Volume V – Maritime species and habitats. Machair habitat action plan*. English Nature, Peterborough.

Akeroyd, J.R. & Curtis, T.G.F. 1980. Some observations on the occurrence of machair in Western Ireland. *Bull. Irish Biogeogr. Soc.* 4: 1-12.

Angus, S. 1994. The conservation importance of machair systems of the Scottish islands, with particular reference to the Outer Hebrides. In: Baxter, J.M. & Usher, M.B. (eds.) *The islands of Scotland: a living marine heritage*, pp. 95-120. HMSO, Edinburgh.

Angus, S. 1996. Natural heritage conservation in the Southern Outer Hebrides. In: Gilbertson, D., Kent, M. & Grattan, J. (eds.) *The Outer Hebrides: the last 14,000 years*, pp. 227-250. Sheffield Academic Press, Sheffield.

Angus, S. 1997. *The Outer Hebrides: the shaping of the islands*: The White Horse Press, Cambridge/Isle of Harris.

Angus, S. & Elliott, M.M. 1992. Erosion in Scottish machair with particular reference to the Outer Hebrides. In: Carter, R.W.G., Curtis, T.G.F. & Sheehy-Skeffington M.J. (eds.) *Dunes: geomorphology, ecology and management for conservation*, pp. 93-112. Balkema, Rotterdam.

Bassett, J.A. & Curtis, T.G.F. 1985. The nature and occurrence of sand-dune machair in Ireland. *Proc. R. Irish Acad.* 85B: 1-20.

Boyd, J.M. & Boyd, I.L. 1990. *The Hebrides – a natural history*. Collins New Naturalist, London.

Burrows, C.J. 1990. *Processes of vegetation change*. Unwin Hyman, London.

Cavers, P.B. & Benoit, D.L. 1989. Seed banks in arable land. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds.) *Ecology of soil seed banks*, pp. 309-328. Academic Press, London.

Clapham, A.R., Tutin, T.G. & Warburg, E.F. 1981. *Excursion Flora of the British Isles.* 3rd. ed. Cambridge University Press, Cambridge.

Crawford, I.C. 1988. *National sand dune vegetation survey. Site Report No. 64. Drimsdale, South Uist. Contract Surveys Report No. 114.* Nature Conservancy Council, Peterborough.

Crawford, I.C. 1989. *The machairs of the Uists: land use and vegetation*. Contract Survey 64. Nature Conservancy Council, Peterborough.

Crawford, I.C. 1990. Agriculture, weeds and the Western Isles machair. *Trans. Bot. Soc. Edinb.* 45: 483-492.

Crawford, I.C. 1997. The conservation and management of machair. *Bot. J. Scot.* 49: 433-439.

Dargie, T.C.D. 1993. *Sand dune vegetation survey of Great Britain. Part 2 - Scotland.* Joint Nature Conservation Committee, Peterborough.

Dargie, T.C.D. 1998. *Sand dune vegetation survey of Scotland: Western Isles.* 3 vols. Scottish Natural Heritage Research, Survey and Monitoring Report No. 96. Scottish Natural Heritage, Battleby, Perth.

Dickinson, G., Mitchell, J. & Tivy, J. 1971. The application of phytosociological techniques to the geographical study of vegetation. *Scot. Geogr. Mag.* 87: 84-102.

Dobson, F.S. 1992. *Lichens – an illustrated guide to the British and Irish species*. 3rd. ed. Richmond Publishing Company, Slough.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition – a factor in old-field vegetation development. *Vegetatio* 4: 412-417.

Gilbertson, D., Kent, M., Weaver, R.E., Wathern, P., Mulder, Y.-L., Brayshay, B.A. & Gill, W.J. 1994. The vegetation of the Tangaval Peninsula: present and past. In: Branigan, K. & Foster, P. (eds.) *Archaeological research on Ben Tangaval*, pp. 15-30. Sheffield Academic Press, Sheffield.

Gilbertson, D., Kent, M., Schwenninger, J.-L., Wathern, P., Weaver, R. & Brayshay, B.A. 1995. The machair vegetation of South Uist and Barra in the Outer Hebrides of Scotland: its ecological, geomorphic and historical dimensions. In Butlin, R.A. & Roberts, N. (eds.) *Ecological relations in historical times – human impact and adaptation*, pp. 17-44. Blackwell Scientific, Oxford.

Gilbertson, D., Kent, M. & Grattan, J. 1996a. The Sheffield Environment and Archaeology Research Campaign in the Outer Hebrides. In Gilbertson, D., Kent, M. & Grattan, J. (eds.) *The Outer Hebrides: the last 14,000 years*, pp. 1-4. Sheffield Academic Press, Sheffield.

Gilbertson, D., Grattan, J. & Schwenninger, J.-L. 1996b. A stratigraphic survey of the Holocene coastal dune and machair sequences. In: Gilbertson, D., Kent, M. & Grattan, J. (eds.) *The Outer Hebrides: the last 14,000 years*, pp. 72-101. Sheffield Academic Press, Sheffield.

Gimingham, C.H. 1964. Maritime and sub-maritime communities. In: Burnett, J.H. (ed.) *The vegetation of Scotland*, pp. 67-142. Oliver and Boyd, Edinburgh.

Grant, J.W. 1979. Cereals and grass production in Lewis and the Uists. *Proc.Roy. Soc. Edinb.* 77B: 527-533.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* John Wiley & Sons, Chichester.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative plant ecology*. Unwin Hyman, London.

Harper, J.L. 1977. *Population biology of plants*. Academic Press, London.

Hewett, D.G. 1970. The colonisation of sand dunes after stabilisation with marram grass (*Ammophila arenaria*). *J. Ecol.* 58: 653-668.

Hill, M.O. 1979a. *TWINSPAN – a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes.* Department of Ecology and Systematics, Cornell University, Ithaca, NY.

Hill, M.O. 1979b. *DECORANA – a FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging.* Department of Ecology and Systematics, Cornell University, Ithaca, NY.

Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47-58.

Hubbard, C.E. 1984. *Grasses – a guide to their structure, identification, uses and distribution in the British Isles.* 3rd. ed. Penguin Books, London.

Ingrouille, M. 1995. *Historical ecology of the British flora.* Chapman & Hall, London.

Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. *Ecol. Monog.* 20: 229-250.

Keever, C. 1979. Mechanisms of plant succession in old fields of Lancaster County, Pennsylvania. *Bull. Torr. Bot. Club* 106: 299-308.

Kent, M. & Coker, P. 1992. *Vegetation description and analysis – a practical approach.* Belhaven Press/John Wiley & Sons, London.

Kent, M., Brayshay, B., Gilbertson, D., Wathern, P. & Weaver, R. 1994. A biogeographical study of the plant communities and environmental gradients on South Uist, Outer Hebrides, Scotland. *Scot. Geogr. Mag.* 110: 85-99.

Kent, M., Weaver, R.E., Gilbertson, D.D., Wathern, P. & Brayshay, B.A. 1996. The present-day machair vegetation of the southern Outer Hebrides. In: Gilbertson, D., Kent, M. & Grattan, J. (eds.) *The Outer Hebrides: the last 14,000 years*, pp. 133-145. Sheffield Academic Press, Sheffield.

Kerr, D.H. 1954. Machair land in the Outer Isles. *Scot. Agric.* 34: 157-161.

Knox, A.J. 1974. The agricultural use of machair. In: Ranwell, D.S. (ed.) *Sand dune machair 1*, p. 19. Institute of Terrestrial Ecology, Norwich.

Mather, A.S. & Ritchie, W. 1977. *The beaches of the Highlands and Islands of Scotland.* Countryside Commission for Scotland, Perth.

McKirdy, A.P. & Foxwell, E.A. 1985. Sand dunes: their coast protection function and the Geological Conservation Review. In: Doody, P. (ed.) *Sand dunes and their management – Focus on nature conservation 13*, pp. 11-19. Nature Conservancy Council, Peterborough.

Oksanen, J. & Minchin, P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J. Veg. Sci.* 8: 447-454.

Owen, N.W. 1998. *Plant ecology and community dynamics of machair systems in the Outer Hebrides*. Ph.D. Thesis, University of Plymouth.

Owen, N.W., Kent, M. & Dale, P. 1996. The machair vegetation of the Outer Hebrides: a review. In: Gilbertson, D., Kent, M. & Grattan, J. (eds.) *The Outer Hebrides: the last 14,000 years*, pp. 123-131. Sheffield Academic Press, Sheffield.

Owen, N.W., Kent, M., Dale, P. & Ramsay, P. 1998. The vegetation of Kildonan machair, Isle of South Uist, Outer Hebrides, Scotland. *Scot. Geogr. Mag.* 114: 34-41.

Packham, J.R. & Willis, A.J. 1997. *Ecology of dunes, salt marsh and shingle*. Chapman and Hall, London.

Pankhurst, R.J. 1991. The vegetation of the Outer Hebrides. In: Pankhurst, R.J. & Mullin, R.J. (eds.) *Flora of the Outer Hebrides*, pp. 38-48. Natural History Museum Publications, London.

Pankhurst, R.J. & Mullin, J.M. 1991. *Flora of the Outer Hebrides*. Natural History Museum Publications, London.

Podani, J. 1997. On the sensitivity of ordination and classification methods to variation in the input order of data. *J. Veg. Sci.* 8: 153-156.

Randall, R.E. 1980. Effects of grazing on the machair of the Monach Isles. In: Ranwell, D.S. (ed.) *Sand dune machair 3*, pp. 7-11. Institute of Terrestrial Ecology, Norwich.

Randall, R.E. 1983. Management for survival: a review of the plant ecology and protection of the machair beaches of north-west Scotland. In: McLachlan, A. & Erasmus, T. (eds.) *Sandy beaches as ecosystems – Proceedings of the 1st International Symposium on sandy beaches*, pp. 733-740. Dr. W. Junk, The Hague.

Ranwell, D.S. (ed.) 1974. *Sand dune machair 1.* Institute of Terrestrial Ecology, Norwich.

Ranwell, D.S. (ed.) 1977. *Sand dune machair 2.* Institute of Terrestrial Ecology, Norwich.

Ranwell, D.S. (ed.) 1980a. *Sand dune machair 3*. Institute of Terrestrial Ecology, Norwich.

Ranwell, D.S. 1980b. Biological influences in some units of sand dune landscapes. In: Ranwell, D.S. (ed.) *Sand dune machair 3*, pp. 29-34. Institute of Terrestrial Ecology, Norwich.

Ritchie, W. 1971. *The beaches of Barra and the Uists: a survey of the beach, dune and machair areas of Barra, South Uist, Benbecula, North Uist and Berneray*. Countryside Commission for Scotland, Perth.

Roberts, H.A. & Feast, P.M. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *J. Appl. Ecol.* 10: 133-143.

Rodwell, J.S. (ed.) 2000. *British plant communities – Volume 5: Maritime communities and vegetation of open habitats.* Cambridge University Press, Cambridge.

Stace, C. 1991. *New flora of the British Isles.* Cambridge University Press, Cambridge.

Stace, C. 1997. *New flora of the British Isles.* 2nd. ed. Cambridge University Press, Cambridge.

Warr, S.J., Thompson, K. & Kent, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progr. Phys. Geogr.* 17: 329-347.

Watson, E.V. 1981. *British mosses and liverworts*. 3rd. ed. Cambridge University Press, Cambridge.

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