Available online at www.sciencedirect.com
SCIENCE DIRECT®
ELSEVIER
Biological Conservation 119 (2004) 1–18
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

Review

The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK

Kevin J. Walker [a,*], Paul A. Stevens [b], David P. Stevens [c], J. Owen Mountford [a], Sarah J. Manchester [a], Richard F. Pywell [a]

[a] NERC Centre for Ecology and Hydrology Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK
[b] NERC Centre for Ecology and Hydrology Bangor, University College of Wales Bangor, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK
[c] Countryside Council for Wales, Plas Penrhos, Penrhos Road, Bangor, Gwynedd LL57 2LQ, UK

Received 13 May 2003; received in revised form 28 October 2003; accepted 28 October 2003

Abstract

Intensive agriculture has resulted in the loss of biodiversity and the specialist flora and fauna associated with the semi-natural grasslands of low-intensity pastoral systems throughout northwest Europe. Techniques employed to restore and re-create these grasslands on agricultural land in the UK are reviewed. Extensive cutting and grazing management have been shown to diversify improved swards and facilitate re-colonisation on ex-arable soils, although rates of re-assembly of plant communities with affinity to existing semi-natural grasslands have generally been slow. On former agriculturally improved swards, nutrient depletion has accelerated this process, especially where ‘‘gaps’’ for establishment have been created. Similarly, on ex-arable soils ‘‘nutrient stripping’’ and sowing with diverse seed mixtures has led to the rapid development of species-rich swards. On free draining brown earths such an approach may be required to restore grassland communities where soil phosphorous concentrations exceed semi-natural levels by more than 10 mg/l (using Olsen’s bicarbonate extractant). However, the appropriateness of this threshold for other soil types requires further sampling. Although restored grasslands are likely to contribute to national biodiversity targets success will ultimately depend on the reinstatement of the communities and ecological functions of semi-natural references. Although this is technically feasible for a few plant assemblages, less is known about the re-assembly of microbial and faunal communities, or the importance of trophic interactions during grassland succession. As a consequence, more research is required on the functional attributes of semi-natural grasslands, as well as the methods required to restore localised types, novel nutrient depletion techniques, the ‘‘phased’’ introduction of desirable but poor-performing species and the performance of different genotypes during grassland restoration.

Keywords: Grassland diversification; Nutrient depletion; Phosphorous; Seed-limitation; Soil fertility

Contents

* Corresponding author. Tel.: +44-1487-772446; fax: +44-1487-773467.
E-mail address: kwal@ceh.ac.uk (K.J. Walker).

0006-3207/$ - see front matter
doi:10.1016/j.biocon.2003.10.020

1. Introduction

Habitat conversion from natural and semi-natural vegetation to intensive agriculture is the single biggest factor in the present biological diversity crisis (Lawton and May, 1995). In northwest Europe this has resulted in significant declines in the extent of low-intensity pastoral systems that developed following the advent of animal husbandry during the Neolithic (Poschlod and Wallis-DeVries, 2002). Over the last 50 years, many of these grasslands have been ploughed-up for cultivation with arable crops or re-seeded (Blackstock et al., 1999) and productivity increased by drainage and the application of fertilisers and herbicides, allowing earlier, repeated cutting for silage and stocking rates to be increased (Hopkins and Hopkins, 1994). As a result grassland specialists have been replaced by a few generalists that thrive in productive, human-altered environments (McKinney and Lockwood, 1999). Models of habitat loss suggest that this process has produced an "extinction debt", a pool of species that will eventually go extinct unless natural and semi-natural habitats are repaired or restored (Tilman et al., 1994). Human efforts to restore degraded habitats are, therefore, likely to become an increasingly important aspect of biodiversity conservation (Dobson et al., 1997).

In the UK, a number of government funded initiatives have been introduced to reverse declines in the extent of semi-natural communities. Schemes such as Environmentally Sensitive Areas (ESAs) and Countryside Stewardship (CS) in England, Tir Gofal in Wales, Rural Stewardship in Scotland and Countryside Management (and ESAs) in Northern Ireland offer substantial opportunities for the restoration and re-creation of semi-natural habitats on agricultural land (Coates, 1997). In addition, quantitative targets for re-establishing different types of semi-natural lowland grassland have been provided in a series of Habitat Action Plans (HAPs) (UK Biodiversity Steering Group, 1995; UK Biodiversity Group, 1998), as part of the Government's response to the 1992 Rio Convention (Table 1). The attainment of these expansion targets will clearly require effective and pragmatic management methodologies for the restoration of grasslands of conservation value. This has led to a number of long-term experimental trials on a range of grassland types (e.g., Hopkins et al., 1999; Mountford et al., 1996; Pywell et al., 2002; Smith et al., 2000; Tallowin and Smith, 2001).

We review the recent literature on the restoration of semi-natural lowland grasslands included in the UK Biodiversity Action Plan (BAP) (Table 1). In particular, we focus on the effectiveness of techniques to overcome high soil fertility and seed-limitation on both formerly improved grassland (i.e., restoration) and arable precursors (i.e., re-creation). We, therefore, exclude grassland creation on non-agricultural land (e.g., industrial wastes), translocation of grassland from one site to another and the rehabilitation of grasslands already conforming to one or more of the HAP types (Critchley et al., 2004). The nomenclature of plant species follows Stace (1997), but for National Vegetation Classification (NVC) communities (Rodwell, 1991, 1992), plant names follow Flora Europaea (Tutin et al., 1964 and seq.).

2. Key constraints to grassland restoration

The conversion of semi-natural grassland to intensive agriculture imposes a number of abiotic and biotic constraints on restoration. In particular, the impoverishment of lowland species-pools (and seed sources) through habitat loss and fragmentation has meant that

Table 1
Biodiversity Action Plan (BAP) priority lowland semi-natural grassland types in relation to British National Vegetation Classification Communities (NVC), European alliances and number of studies included in this review

BAP grassland type (2010 re-establishment target)	National Vegetation Classification (NVC) community	Code[a]	Phytosociological alliance	No. studies[c]
Upland hay meadow (50 ha)	*Anthoxanthum odoratum–Geranium sylvaticum* grassland	**MG3**[b]	Polygono-Trisetion	2
Lowland meadow (500 ha)	*Alopecurus pratensis–Sanguisorba officinalis* grassland	**MG4**[b]	Cynosurion cristati	3
	Cynosurus cristatus–Centaurea nigra grassland	**MG5**	Cynosurion cristati	20
	Cynosurus cristatus–Caltha palustris grassland	**MG8**	Calthion palustris	3
Lowland dry acid grassland (500 ha)	*Festuca ovina–Agrostis capillaris–Rumex acetosella* grassland	**U1**	Plantagini-Festucion ovinae	5
	Deschampsia flexuosa grassland	**U2**[b]	Violion caninae	0
	Agrostis curtisii grassland	**U3**[b]	Violion caninae	0
	Festuca ovina–Agrostis capillaris–Galium saxatile grassland	U4	Violion caninae	3
Lowland calcareous grassland (1000 ha)	*Festuca ovina–Carlina vulgaris* grassland	CG1	Xerobromion	0
	Festuca ovina–Avenula pratensis grassland	**CG2**[b]	Bromion erecti	4
	Bromus erectus grassland	**CG3**	Bromion erecti	5
	Brachypodium pinnatum grassland	**CG4**	Bromion erecti	0
	Bromus erectus–Brachypodium pinnatum grassland	**CG5**[b]	Bromion erecti	0
	Avenula pubescens grassland	**CG6**[b]	Bromion erecti	0
	Festuca ovina–Hieracium pilosella–Thymus praecox/pulegioides grassland	CG7	Koelerio-Phleion phleoidis	0
	Sesleria albicans–Scabiosa columbaria grassland	CG8	Bromion erecti	0
	Sesleria albicans–Galium sterneri grassland	**CG9**[b]	Bromion erecti	0
Purple moor-grass and rush pasture (500 ha)	*Juncus subnodulosus–Cirsium palustre* fen-meadow	M22	Calthion palustris	0
	Juncus effusus/acutiflorus–Galium palustre rush pasture	M23	Juncion acutiflori	0
	Molinia caerulea–Cirsium dissectum fen-meadow	**M24**[b]	Junco conglomerati-Molinion	1
	Molinia caerulea–Potentilla erecta mire	M25	Junco conglomerati-Molinion	1
	Molinia caerulea–Crepis paludosa mire	M26	Molinion caeruleae	0

[a] Communities in bold are those for which Critchley et al. (2002) provide summary statistics for soil properties (pH, P, K, Mg, total N, organic matter, carbon:nitrogen, available water capacity).
[b] Where these figures are based on less than 10 samples.
[c] Some studies include more than one NVC type.

grassland re-establishment has usually been seed-limited (Poschlod et al., 1998; Bullock et al., 2002). Furthermore, the widespread loss of farming practices that formerly transported grassland species between sites (e.g., shepherding, folding, hay-strewing) has meant that many grassland species are now isolated within a "sea" of intensively farmed land (Strykstra et al., 1997; Poschlod and Bonn, 1998). Similarly, agricultural intensification has also impoverished the transient or short-lived seed banks of grassland species which are poorly adapted to the frequent disturbance associated with intensive cropping and reseeding (Bakker et al., 1996, 1997). These decline rapidly after the removal of the surface vegetation (McDonald, 1993; Milberg and Hansson, 1994; Smith et al., 2002) and tend to be replaced by annual and weedy species (Graham and Hutchings, 1988; Hutchings and Booth, 1996a; McDonald et al., 1996; Bekker et al., 1997). Given these constraints, few target species are likely to reach isolated sites unaided.

Low levels of soil fertility are associated with high species co-existence on a wide range of semi-natural lowland grasslands (Janssens et al., 1998). As a consequence, one of the most important abiotic constraints to grassland restoration is high residual soil fertility associated with repeated fertiliser applications, possibly accentuated by aerial deposition of nitrogen (N) pollutants (Bobbink et al., 1998). For example, repeated applications of N have been shown to produce species-poor swards across a range of soil types (e.g., Mountford et al., 1993; Silvertown et al., 1994; Smith, 1994) as well as maintain high yields of competitive species even after the cessation of fertiliser inputs (van Duuren et al., 1981; Marrs et al., 1991; Berendse et al., 1992; Mountford et al., 1996). Furthermore, high nutrient levels are likely to promote the growth of competitive grasses and weedy perennials which have been shown to dominate the early stages of grassland restoration and re-creation, greatly restricting opportunities for the establishment of species more typical of semi-natural swards (Bakker, 1989; Bakker and Berendse, 1999; Smith et al., 2002).

On acid soils the application of liming agents, such as ground limestone or marl, to acid soils, elevates soil pH levels to six or above, thereby inhibiting the restoration of calcifugous assemblages (Gough and Marrs, 1990; Marrs, 1993). As a consequence, the reduction to less than pH 5 is usually a prerequisite to the re-establishment of acid grassland and heathland communities. Conversely, the addition of nitrogenous fertilisers can have an acidifying effect (to ca. pH 5) on neutral and calcareous soils (Hayes and Sackville Hamilton, 2001).

The application of nitrogenous fertilisers can also cause significant changes to the soil microbial and fungal communities of semi-natural grasslands (Bardgett and McAlister, 1999; Donnison et al., 1999). Although the functional implications for restoration are as yet unclear, the soil communities of diverse grasslands tend to be dominated by fungal pathways of decomposition and mycorrhizae networks (Bardgett, 1996; Ozinga et al., 1997; Smith et al., 2003). These are likely to play a key role in driving ecosystem functions, such as nutrient capture and productivity, as well as controlling the breakdown of key nutrients such as P (van der Heijden et al., 1998) and community composition and structure during early phases of succession (Grime et al., 1987; Gange et al., 1993).

3. The restoration of lowland grasslands using extensive management

3.1. Diversifying improved grasslands using cutting and grazing management

The reinstatement of extensive cutting and grazing regimes, following the cessation of fertiliser inputs, can cause measurable changes in the composition, productivity and diversity of formerly improved swards (Bakker, 1989). Although largely dependent on soil type and previous management, these changes have usually been associated with a reduction in the cover of competitive grasses (Table 2). For example, in west Wales, the cover of *Lolium perenne* declined much more rapidly, and to lower levels, on shallow freely draining soils of an upland fringe site with high precipitation than on the deeper soils of a lowland site (Fig. 1(a)) (Hayes et al., 2000; Hayes and Sackville Hamilton, 2001). The difference in the *L. perenne* decline between these two sites presumably reflected the more rapid leaching of soil nutrients under higher precipitation at the upland site, where the lower fertility is likely to have reduced the cover of competitive grasses more rapidly and to a greater extent than at the lowland site. Likewise, in an N addition experiment on a lowland peat in Somerset, *L. perenne* declined to lower levels on plots that had formerly received lower amounts of N fertiliser (Mountford et al., 1994, 1996). On agriculturally improved hay-meadows in the Netherlands, declines in dominant grasses following the cessation of fertiliser inputs have been more modest (Table 2). For example it took 13 years for *Holcus lanatus* to decline from between 30% and 60% to less than 5% cover at two sites under a cutting regime (Olff and Bakker, 1991) whereas at another site on a clay soil both *L. perenne* and *Elytrigia repens* persisted at high frequency for over 10 years (Oomes, 1990).

In response to re-instatement of extensive management and/or cessation of fertiliser inputs, changes in species-richness have generally been positive, but relatively modest (Table 2). For example, in experimental trials at Trawsgoed in west Wales extensively managed plots had between 5–15 species (per 4 m^2) more than fertilised controls after 8 years of extensive management (Fig. 1(b)) (Hayes and Sackville Hamilton, 2001). Likewise, in an N addition experiment in Somerset, the apparent rate of increase on unfertilised plots was about 1 species per m^2 per year (Mountford et al., 1996) whereas in the Netherlands, the rate of increase was more modest (1 species per 4 m^2 per 4 years) (Bakker, 1987), presumably because of the more impoverished species pools within and around the restoration sites. In northern England, results from a single study suggest that the restoration of upland hay-meadows (NVC type MG3) may take over 20 years using extensive management alone (assuming a linear increase in species-richness) (Smith et al., 2002).

In most studies the cessation of fertiliser applications has led to a rapid reduction in herbage yields to around 4 tonne/ha. In west Wales, for example, productivity on experimental plots roughly halved after 4 years relative to controls (Hayes et al., 2000; Hayes and Sackville Hamilton, 2001), whereas at other sites productivity either declined more gradually (e.g., Smith et al., 2000), remained stable at low levels (e.g., Olff and Bakker, 1991), or initially declined then increased again due to increased atmospheric N deposition during the study period (e.g., Berendse et al., 1992).

Inter-relationships between species richness and productivity have been discussed by Oomes (1992) who suggested that sward productivities of 4–6 tonne/ha or less are required for high species coexistence. However,

Table 2
Details of changes following the cessation of fertiliser applications and reinstatement of extensive cutting or grazing regimes in UK and Dutch studies

Site name	Grassland type	Soil type	Treatment	Changes following cessation of fertiliser inputs[a]				Years	Source[c]
				Dominant grasses[b]	Species diversity	Dry matter yield (control)	Key nutrients		
1. UK									
Colt Park	MG3	Brown earth	Cut and grazed twice	↓ *As*, *Pp*	↑	4 t/ha (5 t/ha)	nd	8	1
Trawsgoed	MG5	Brown earth	Cut twice and grazed	↓ *Lp*	↑↑	4–5 t/ha (9 t/ha)	↓ P	8	2
Pwllpeiran	MG5/U4	Acid brown earth	Cut and grazed	↓↓ *Lp*	↑	4–5 t/ha (8 t/ha)	↓ P	4	3
Tadham	MG5/8	Peat	Cut and grazed	↓ *Lp*	↓	6 t/ha (9 t/ha)	↓ yield NP	4	4
Little Wittenham	CG2	Clay loam	Grazed	= *Lp*, *As*	↑	nd	nd	5	5
2. Netherlands									
Loefvledder	Hay-field	Peat	Cut once	↓ *Hl*, *As*	↑	8–3 t/ha	↓ NPK	14	6
Westerholt	Hay-field	Sandy podzol	Cut once	↓ *Hl*	=	= (3 t/ha)	↓ P	14	6
Oomes 1	Improved meadow	Humic sand	Cut twice	↓↓ *Lp*, *Fp*	↑	10–4 t/ha	= NPK	13	7
Oomes 2	Improved meadow	Heavy clay	Cut twice	↓ *Lp*, *Er*	=	10–5 t/ha	↓ yield NPK	10	7
Wageningen	Improved meadow	Sand	Cut twice	↓ *Lp*, *Pt*		11–6 t/ha (3 years)	nd	17	8

[a] Changes as follows: ↓↓, marked decrease; ↓, slight or gradual decrease; ↑↑, marked increase; ↑, slight or gradual increase; =, stable; nd, no data.
[b] Codes for the dominant grass species are as follows: *As*, *Agrostis stolonifera*; *Er*, *Elytrigia repens*; *Fp*, *Festuca pratensis*; *Hl*, *Holcus lanatus*; *Lp*, *Lolium perenne*; *Pp*, *Poa pratensis*; *Pt*, *Poa trivialis*.
[c] *Source*: 1, Smith et al. (2000); 2, Hayes and Sackville Hamilton (2001); 3, Hayes et al. (2000); 4, Mountford et al. (1994, 1996) and Tallowin et al. (1998); 5, Bullock et al. (1994); 6, Olff and Bakker (1991); 7, Oomes (1990); 8, Berendse et al. (1992).

in most studies only modest diversification has followed a decline in productivity due to seed-limitation (e.g., Olff and Bakker, 1991; Berendse et al., 1992) and the persistent effects of fertiliser applications on competitive interactions (e.g., Mountford et al., 1996). As a consequence, changes in vegetation composition have generally been insufficient to result in major shifts between community types (e.g., from NVC type MG7 to MG5). For example, it has been estimated that it would take 70–90 years for fertilised plots in the Park Grass Experiment at Rothamsted, England, to revert to *Cynosurus cristatus–Centaurea nigra* grassland (NVC type MG5) (Dodd et al., 1994). Similarly, on a number of Somerset meadows which had been cultivated and reseeded, the development of a "typical" MG5 sward took over a century to develop despite high initial rates of colonisation from adjacent species-rich pastures (Gibson, 1998).

On formerly improved swards, the reduction of soil nutrients through the removal of hay is also likely to take many years. Bakker (1987) estimated that only 1% of total P and exchangeable potassium (K) and 2.5% of total N in the nutrient pool were removed annually by this method, although even these low levels were considerably greater than off-take by grazing animals alone. Berendse et al. (1992) found that N outputs in a single hay-crop were balanced by atmospheric inputs and only amounted to roughly one-third of inputs via mineralisation from organic matter. However, removal of two hay-crops per year removes more nutrients and has generally hastened reversion of vegetation composition when compared with a single crop regime (e.g., Olff and Bakker, 1991; Hayes and Sackville Hamilton, 2001).

Where comparisons have been made, cutting and removal of a hay-crop with aftermath (and sometimes spring) grazing has generally been more successful than either cutting or grazing alone (Hayes et al., 2000; Smith et al., 2000; Hayes and Sackville Hamilton, 2001). Such management has been shown to accelerate reductions in residual soil fertility as well as optimise conditions for the colonisation and establishment of target species. The disturbance caused by aftermath grazing, in particular, opens up the sward and creates germination gaps which are colonised by forb seed from the hay crop (or seed sown deliberately to introduce new species) and from normal colonisation by seed brought by the wind or other dispersal agents such as sheep (Smith et al., 2000). In contrast, hay cutting without aftermath grazing has been shown to favour coarse grasses whereas grazing alone encourages the establishment of undesirable weed species (Hayes and Sackville Hamilton, 2001).

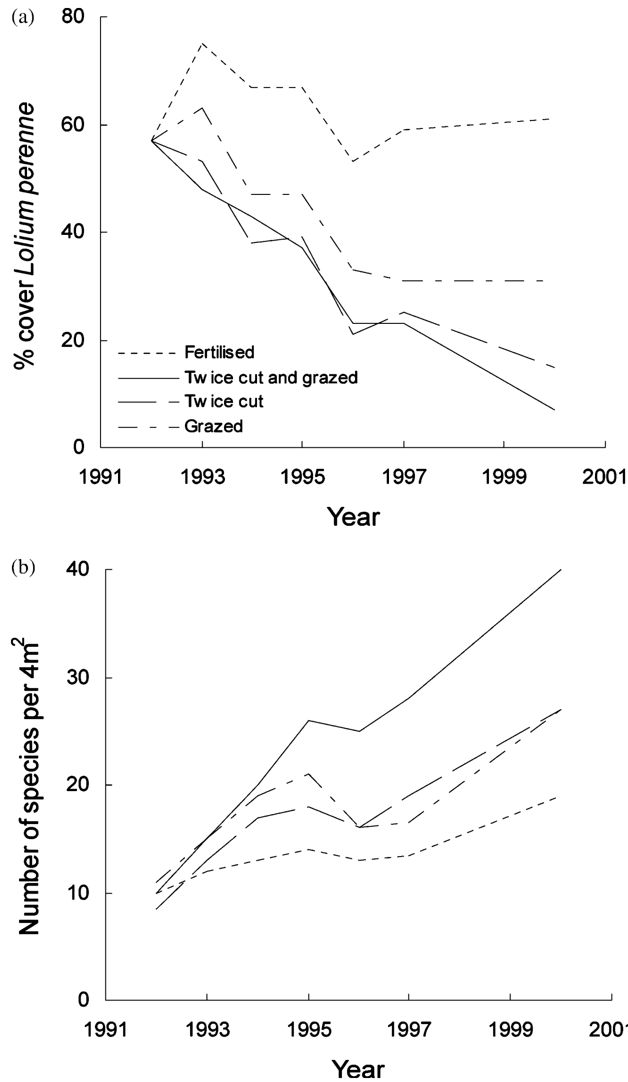

Fig. 1. Changes in (a) the mean cover of *Lolium perenne* and (b) the number of species under a range of cutting and grazing regimes following the cessation of fertiliser application on an improved grassland at Trawsgoed Research Farm, west Wales (Hayes and Sackville Hamilton, 2001).

3.2. Facilitating natural colonisation on ex-arable soils

In the UK, many semi-natural grasslands originated during the 18th and 19th centuries from the grazing of abandoned arable land converted to pasture at times of low grain prices (Gibson, 1998). However, the relative "immaturity" of many of these grasslands suggests that historical rates of re-assembly have generally been very slow (Gibson and Brown, 1991a). For example, seed limitation has been shown to constrain the development of chalk grassland on two former arable fields in the UK (Graham and Hutchings, 1988; Gibson and Brown, 1991b; Hutchings and Booth, 1996a). At both sites, chalk grassland species, which were present in adjacent grasslands, made little contribution to the seed bank or reverting vegetation community and were generally confined to the margins of both sites. The greatest diversity of chalk grassland species were found on plots that had either been grazed (e.g., Gibson et al., 1987) or cut (e.g., Hutchings and Booth, 1996b).

4. Techniques to overcome abiotic constraints

4.1. Reduction of soil fertility

Although key soil nutrients, such as P, will decline by natural leaching, the annual rate of loss is usually very low (Johnston and Poulton, 1977; Gough and Marrs, 1990; Marrs et al., 1991). As a result a number of restoration techniques, intended to remove or fix these pools, have been investigated (Table 3) (Marrs, 1993).

The rationale behind arable cropping is that more nutrients, in particularly soil P, are removed from the soil by the crop than are added as inputs (Marrs et al., 1998). However, increased off-take of nutrients within the crop has not always been followed by significant reductions in soil concentrations (e.g., Marrs et al., 1998; McCrea et al., 2001). On formerly improved grassland soils this has been caused by increased mineralisation of organic P in the soil humus following cultivation (McCrea et al., 2001), whereas on ex-arable soils plant-available P removed via cropping has been rapidly replaced by mineralisation from larger non-available pools (Marrs et al., 1998). As a consequence, cropping has been ineffective where large reductions in soil nutrients have been required for restoration (e.g., Marrs, 1993; Marrs et al., 1998). In contrast, the applications of N and K, followed by cutting, have been shown to significantly increase the off-take of P over three years in a formerly improved grassland in Devon (Tallowin et al., 2002). Using a linear depletion function, Tallowin et al. (2002) estimated that it would take about 12 years to reduce P to semi-natural levels using this technique compared to at least 25 years on the unfertilised plots.

Deturfing has been shown to remove large nutrient pools from the uppermost centimetres of a range of soil types (Table 3) (Hopkins et al., 1999) as well as significantly reducing the yield of P in some target species (Tallowin and Smith, 2001). However, in Holland, deturfing (sod-cutting) has been shown to increase mineralisation rates and mineral N concentrations on some acid soils (de Graaf et al., 1998). In addition, deturfing is unlikely to be an acceptable operation on land entered into agri-environment schemes as it may damage underlying archaeological features and impair the future agricultural potential of the soil (Swash and Belding, 1999).

The addition of chemical materials that adsorb available nutrients, such as P, provide an alternative,

Table 3
Details of changes in pH and phosphorous (P) in UK studies

Site name	NVC	Soil type	Land-use	Treatment	Change in pH[a]	Change in P	Years	Source[d]
Trawsgoed	MG5	Brown earth	Pasture	Cut and grazed	–5.5–5.3	↓ 20–12 ppm (phosphate)	8	1
Pwllpeiran	MG5/U4	Acid brown earth	Pasture	Cut and grazed	–6.0–5.4	–7-ca. 4 mg/kg	4	2
Culm grasslands	M24	Clay/stagnogley	Pasture	Deturfing	nd	↓ 24–10 mg/kg	4	3
ESA (six sites)[b]	CG/MG	Various	Pasture	Deturfing	nd	↓ Herbage yield at four sites	2	4
Euston	U1	Sand	Arable	Deturfing	nd	↓ 22–15 mg/l	5	5
Honington	U1	Sandy loam	Arable	Deturfing	nd	↓ 40–24 mg/l	5	5
ESA (five sites)[c]	CG3/MG5	Various	Arable	Deep cultivation	–6.9–6.5	–28–23 mg/l	4	6
Minsmere	U1	Sandy loam	Arable	Cropping	= Variable (6–7)	= Variable (5–20 mg/kg)	6	7
Compton Park	MG5	Sandy silt loam	Pasture	Cropping	–6.4–6.1/6.3	↑ Increased mineralisation	2	8
Euston	U1	Sand	Arable	Sulphur (3–6 tonne/ha)	↓ 5.7–4.3	↑ 27–>50 mg/l	5	5
Minsmere, Field 66	U1	Sandy loam	Arable	Sulphur (1–2 tonne/ha)	↓ 6.5-ca. 4	↓ 19–5 mg/l	3	9, 10
Minsmere, Field 66	U1	Sandy loam	Arable	Bracken	↓ 6.5–4/4.5	↓ 35/30–<5 mg/kg	3	9, 10
Minsmere, Field 66	U1	Sandy loam	Arable	Pine chippings	↓ 6.5–5.5	↓ 25/30–<5 mg/kg	3	9, 10
Mount Pleasant	U1	Podzol	Arable	Pyritic peat	↓ 6/7–3/4	↓ nd	5	11
Minsmere	U1	Sandy loam	Arable	Iron sulphate	↓ 6.6–5.7	↓ 8.5–5.4 mg/kg	1	12
Minsmere	U1	Sandy loam	Arable	Aluminium sulphate	↓ 6.6–5.8	↓ 8.0–4.7 mg/kg	1	12
Rhôs Llawr-cwrt	M25	Stagnogley	Pasture	Aluminium sulphate	nd	↑ Adsorption capacity	2	13

[a] Changes as follows: ↑, overall increase; ↓, overall decline; -, slight decline; =, stable; nd, no data.
[b] See Fig. 2 for names of sites.
[c] See Fig. 4 for names of sites.
[d] *Source*: 1, Hayes and Sackville Hamilton (2001); 2, Hayes et al. (2000); 3, Tallowin and Smith (2001); 4, Hopkins et al. (1999); 5, Bhogal et al. (2000); 6, Pywell et al. (2002); 7, Marrs et al. (1998); 8, McCrea et al. (2001); 9, Owen and Marrs (2000a,b); 10, Owen et al. (1999); 11, Dunsford et al. (1998); 12, C. Stuckey (unpublished data); 13, Adams et al. (1999).

albeit potentially toxic, method for reducing soil fertility. The adsorption of phosphate by oxides and hydroxides of iron (Fe) and aluminium (Al) has long been recognised as a key mechanism for reducing P availability to plants (Wild, 1988). As a result, a range Fe- and Al-rich materials (e.g., calcium oxide, aluminium sulphate, iron sulphate and iron chloride) have been tested for their potential usefulness in restoration (Codling et al., 2000). Of these, aluminium sulphate has been shown to increase P adsorption capacity on an improved pasture in Wales (Adams et al., 1999) and reduce P availability on a sandy soil in East Anglia (C. Stuckey, unpublished data). In the latter study, iron (ferric) sulphate and a combination of Al and Fe (Ferral 20/60) were also shown to be effective. In addition, iron oxide has been shown to increase P uptake by *Holcus lanatus* on a heavy clay soil, suggesting that it may be used to boost off-take of P when combined with cutting (Tallowin, 1997). However, due to a number of potentially toxic side effects, these treatments are unlikely to be acceptable on or near sensitive sites.

As a consequence, a number of more benign alternatives have been tested but with limited success. These include the dilution of nutrient pools by deep cultivation (Pywell et al., 2002), the addition of inert materials such as rubble, quarry waste or lignitic clay (Marrs, 1993; Tallowin, 1997; Tallowin and Smith, 2001) and the addition of bark or straw to increase the microbial biomass and enzyme activity (Török et al., 2000). In addition, Gibson (1995) describes how burning ("pare and burn") was formerly used in the UK to exhaust available nutrients on calcareous soils.

4.2. Soil acidification

In the UK, a range of acidifying materials have been applied to former arable soils in an attempt to reduce soil pH as a precursor to the restoration of heathland and acid grassland communities (Table 3). Elemental sulphur (S) has often been preferred because of its relative cheapness and immediate effect (Owen et al., 1999). Where initial soil pH levels were between pH 6 and 7, an application rate of 1–3 tonne S/ha has been sufficient to establish semi-natural pH levels (ca. pH 3–5) and acid grassland swards at a range of sites in eastern England (Bhogal et al., 2000; Owen and Marrs, 2000a,b). In contrast, higher rates have been required to establish *Calluna vulgaris* and to suppress ruderal species, although rates above 8 tonne S/ha have produced extremely acid conditions (<pH 3) that were detrimental to the growth of target species (Owen and Marrs, 2000a; Pywell et al., 2000). The application of pyritic peat has been shown to produce a similar acidifying effect on a sandy soil (Dunsford et al., 1998), as have the application of chemical amendments intended to immobilise soil P (C. Stuckey, unpublished data).

In contrast, cheaper and potentially less toxic alternatives have proved less effective (Owen et al., 1999). At Minsmere in East Anglia, the addition of pine chippings to a sandy soil did not produce a significant reduction in pH, whereas bracken was less effective than S in inhibiting the establishment of ruderal species which subsequently suppressed the growth of acid grassland and heathland species (Owen et al., 1999).

5. Techniques to overcome biotic constraints

5.1. Diversifying improved grasslands using species introduction

Direct over-sowing of improved swards with seed mixtures offers a simple and cost-effective method for diversifying grassland provided that "gaps" for establishment are created by grazing or mechanical disturbance (Table 4). For example, at Trawsgoed in Wales, two hay-cuts a year, combined with aftermath grazing, gave the highest rate of establishment of five sown herbs (Fig. 1(b)) (Jones and Hayes, 1999). Similar results were obtained on an improved meadow in northern England where the development of *Anthoxanthum odoratum–Geranium sylvaticum* grassland (NVC type MG3) occurred most rapidly on sown plots which were hay-cut and grazed twice (Smith et al., 2000).

Mechanical disturbance of the sward has been shown to have similar effects on species diversity (Hopkins et al., 1999). In a multi-site experiment, deturfing gave the greatest increase in diversity at five (of six) sites in England and Wales (Fig. 2). This approach was particularly effective because it not only reduced soil fertility but also removed the seed bank of weedy species. In contrast, differences between other seed introduction methods (slot-seeding, harrowing, rotavation and plug-planting) were small, but on sites where these methods were effective, harrowing and rotavation treatments generally resulted in the establishment of more species than slot-seeding and plug-planting.

The addition of the hemi-parasite *Rhinanthus minor* into improved swards may have a similar effect to deturfing by reducing the vigour of competitive grasses and therefore providing suitable micro-sites for the establishment of grassland herbs (Davies et al., 1997). Given the promising results of studies on host-parasite interactions (e.g., Davies and Graves, 2000) and effects on grassland diversity (e.g., Davies et al., 1997; Smith et al., 2000), this technique deserves further consideration as a means of diversifying improved swards in the UK.

An alternative to over-sowing is direct drilling of seed mixtures into a "weed free" slot. This technique (often known as slot- or strip-seeding) is particularly suited for restoration purposes because it requires only a fraction of the seed needed to re-seed large areas. The success of

Table 4
Details of changes following attempts to diversify improved grasslands in UK studies

Site name	NVC	Soil type	Treatment (no. sown species)	Establishment of introduced species[a]	Years	Source[c]
Trawsgoed	MG5	Brown earth	Over-sowing (5)	Greatest on plots cut and grazed once	8	1
Colt Park	MG3	Brown earth	Over-sowing (44)	Greatest on plots cut and grazed twice	8	2
ESA (six sites)[b]	CG/MG	Various	Oversowing/rotovation/deturf (23)	Deturf > disturbance > slot-seeding	5	3
Monks Wood	MG5	Calcareous clay	Slot-seeding (12)	Establishment low (7 spp. 20–50%)	2	4
Upwood Meadow	MG4/5	Calcareous clay	Slot-seeding (14)	Establishment low (<20%); autumn sown > spring sown	2	4
Cople	MG5	Clay	Slot-seeding (15)	Establishment low (<20%); autumn sown = spring sown	2	4
Little Wittenham	MG5	Clay	Slot-seeding (2)	*Rm* spread furthest in cut plots; very little spread of *Lv*	5	5
ESA (six sites)[b]	CG/MG	Various	Slot-seeding (23)	Less effective than over-sowing and rotovation/deturf	5	3
ESA (six sites)[b]	CG/MG	Various	Plug-planting (12)	Initially high, two species persisted; limited spread	5	3
Monks Wood	MG5	Calcareous clay	Plug-planting (14)	Initially high (>90%) declining to 46%; limited spread	2	4
ADAS Drayton	MG5	Calcareous clay	Plug-planting (19)	14 species >70% ; 10 species spread	5	6
Somerset	MG5	Silty clay loam	Plug-planting (25)	>60% on least fertile, grazed plots	2	7
Wicken Fen	MG5	Peat loam	Plug-planting (6)	Initially >80% for 4 species declining to <20%	4	8
Culm grasslands	M24	Stagnogley	Seedling–planting and deturfing (14)	Greatest on deturf plots	4	9

[a] *Rm*, *Rhinanthus minor*; *Lv*, *Leucanthemum vulgare*.
[b] Includes the following sites (as in Fig. 2); South Downs (CG2/3), South Wessex Downs (CG2/3), Pennine Dales (MG3/5), Radnor (MG5/U4), Blackdown Hills (MG5/U4) and Somerset (MG5/8).
[c] *Sources*: 1, Jones and Hayes (1999); 2, Smith et al. (2000); 3, Hopkins et al. (1999); 4, Wells et al. (1989); 5, Coulson et al. (2001); 6, Boyce (1995); 7, Davies et al. (1996); 8, Barratt et al. (2000); 9, Tallowin and Smith (2001).

this technique in the UK, however, has been limited (Table 4). On a range of sites in England and Wales, slot-seeding was less successful than deturfing and mechanical disturbance in increasing species richness (Fig. 2) (Hopkins et al., 1999). Similarly, survival rates and spread of introduced species have been limited on other sites by competitive interactions, herbivory and climatic factors (Wells et al., 1989). Furthermore, the establishment of some species has been shown to be highly individualistic and dependent on management regime (Coulson et al., 2001). For example, differences in the spread of *Rhinanthus minor* and *Leucanthemum vulgare* on an improved hay-meadow in Oxfordshire were attributable to dispersule structures and earlier seed-set in *R. minor* (significant spread) and unspecialised seeds and later flowering in *L. vulgare* (little spread).

One of the simplest ways to diversify species-poor grasslands is to insert container-grown plants (plug-plants) into an established sward (Barratt, 1999). This method has a number of advantages over seeding methods, particularly when seed is scarce (e.g., when collected from plants of a particular genetic provenance), or when restoration involves the introduction of mid- to late-successional species that are vulnerable to competition or have seed dormancy mechanisms (Boyce, 1995; Hopkins et al., 1999). However, despite high initial survival rates in most studies (e.g., Wells et al., 1989; Boyce, 1995; Davies et al., 1996; Hopkins et al., 1999), subsequent losses, and limited dispersal, has led some authors to question its utility for large-scale restoration (Hopkins et al., 1999).

5.2. Re-creation on ex-arable land

In the UK, the favoured method for re-creating species-rich grasslands on ex-arable soils has been direct seeding with mixtures of suitable species (Table 5). This technique, which was pioneered by Terry Wells in the 1970s (Wells et al., 1989, 1994), has now been tested on a range of soil types (e.g., Pywell et al., 2002).

Early work on calcareous soils showed the relative speed by which grasslands could be re-created. For example, at Royston Heath in Hertfordshire, the sowing of 37 chalk grassland species led to the rapid development of a species-rich community (NVC type CG3) virtually indistinguishable from the adjacent calcareous grassland (Fig. 3(a)) (Wells, 1990; Wells et al., 1994; Pakeman et al., 2002). Similar results were obtained at

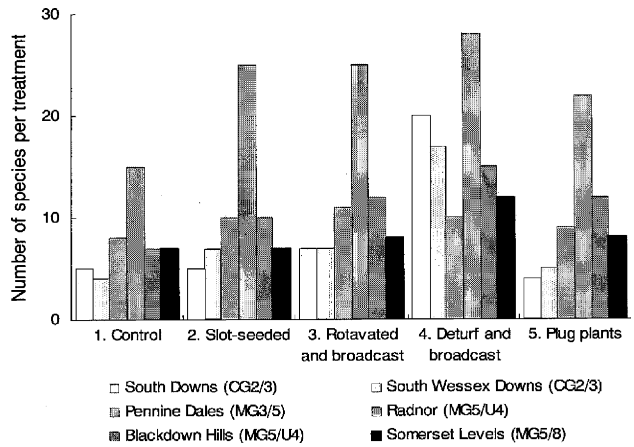

Fig. 2. Mean number of herbs in improved swards in relation to site and restoration treatment 2 years after the cessation of fertiliser inputs (Hopkins et al., 1999). At each site a randomised block design was used with four replicates of each of the five treatments and a plot size of 6 m × 4 m. Species introduction treatments were based on different methods of sward disturbance without complete cultivation: (1) control (undisturbed existing sward); (2) slot-seeding of a grassland seed mixture; (3 and 4) over-sowing of the same mixture with two levels of soil disturbance (deep rotovation to provide 50% bare ground and deturfing) and (5) transplanting plug-plants into an undisturbed sward. Seed mixtures contained between ca. 35 and 40 species, with the composition varying between sites and with forbs making up about 80% by weight of the seeds mixture. Twelve species were introduced as plug-plants at each site. All sites were lightly grazed by sheep in late October–November and again the following spring (see Hopkins et al. (1999) for further details).

St. Catherine's Hill in Hampshire, where the sowing of 47 species led to a community indistinguishable from the reference (CG2c) within 2 years, with the highest seeding rate (4 g/m^2) giving the best results (Stevenson et al., 1995).

Other studies have highlighted the superior performance of species-rich (NVC) mixtures in facilitating grassland re-assembly (van der Putten et al., 2000; Mortimer et al., 2002a), especially when combined with disturbance regimes, such as deep cultivation (Fig. 4) (Pywell et al., 2002). Furthermore, the inoculation of sown swards with soil and turf transplants from a semi-natural grassland has also been shown to increase species diversity by between 3 and 6 species per plot at one site in Buckinghamshire (Mortimer et al., 2002a).

The results from studies on neutral soils have been broadly similar. For example, the sowing of species-rich herb mixtures on a semi-improved heavy clay soil at Monks Wood in Cambridgeshire led to the development of a *Cynosurus cristatus–Centaurea nigra* grassland (NVC type MG5) within 3 years (Pywell et al., 1996), whereas at two sites in Scotland, sowing followed by cutting and aftermath grazing by cattle was sufficient to restore and maintain the same grassland type over 9 years (Christal et al., 2001). As with calcareous grasslands, deep cultivation and seeding appears to be the most effective technique. For example, in a recent multisite study, Pywell et al. (2002) showed that uncultivated plots were more fertile and weedy, whereas those sown with fewer species were much less similar to the target grasslands, regardless of cultivation regime (Fig. 4).

Although less information is available on the restoration of ancient flood-meadows, studies in Oxfordshire have shown the regeneration of *Alopecurus pratensis–Sanguisorba officinalis* grassland (NVC type MG4) on former arable land using commercial seed mixtures (Manchester et al., 1998) and seed harvested from ancient meadows (McDonald, 1993, 2001). In one study, 39 out of 58 (81%) meadow species established after 3 years despite high soil fertility and a predominance of weeds in the seed bank at the receptor site (McDonald, 1993). However, the lack of subsequent recruitment of meadow species has led to a stable grassland community which bears only partial similarity to its semi-natural donor site (McDonald, 2001).

On acid soils, the restoration of heathland has been constrained by high soil pH (>pH 4) and competition from ruderal species (e.g., *Agrostis gigantea*, *Senecio jacobaea* and *Urtica dioica*) (Dunsford et al., 1998; Owen and Marrs, 2000a). In contrast, the establishment of acid grassland on the same soils has proved much more straightforward, particularly when combined with an acid amendment such as S. On a former arable field at Minsmere in Suffolk, a rate of 2 tonne S/ha not only reduced soil pH but also helped to reduce the vigour of ruderal species (Owen and Marrs, 2000b), allowing establishment of 12 of 16 sown species in less than 2 years. In contrast, the addition of bracken litter or pine chippings was less effective in controlling vigorous ruderals but did give some establishment of sown species. Similar results have been reported from two sites in Suffolk, where a mixture of heathland and acid grassland species was sown onto untreated, S-amended, deturfed or cultivated ex-arable soils (Pywell et al., 2000). Although there was some regeneration of Ericaceous species after 5 years, particularly on sulphur amended plots at one site (Euston), the re-created communities were more similar to the regional *Festuca ovina–Agrostis capillaris–Rumex acetosella* acid grassland reference (NVC type U1).

On arable soils nurse crops (e.g., *Lolium multiflorum*, cereal crops or cornfield annuals) have been sown with species mixtures in order to improve the establishment of target species as they provide effective shelter for seedlings during the early stages of succession, as well as suppressing excessive weed growth (Mitchley et al., 1996). However, most studies have recorded few beneficial effects (e.g., Pywell et al., 2002) and in one study the abundance of *L. multiflorum* was detrimental to the early establishment (first 3–4 years) of a lowland wet grassland sward (Manchester et al., 1997).

Another influence on the success of species introduction is the composition of the seed mixture itself.

Table 5
Details of changes following attempts to re-create lowland grassland on ex-arable land in UK studies

Site name	NVC	Soil type	Treatment[a]	Similarity to NVC target community[b]	Years	Source[c]
Royston Heath	CG3	Calcareous loam	Cut	>70% similarity to CG3	20	1
Bradenham	MG/CG	Grey rendzina	Cut	Diverse mixture = greatest similarity to target	4	2
Monks Wood	MG5	Calcareous clay	Cut	Similar to MG5	15	3
ESA (three sites)	MG5a	Alluvial gley/brown sand	Cut and grazed	>65% similarity to MG5	5	4
ESA (two sites)	CG3b	Calcareous brown earth	Cut and grazed	>50% similarity to CG3	5	4
Somerford Mead	MG4	Alluvium	Cut and grazed	81% of sown species established	3	5
SAC (two sites)	MG5	Brown earth/gley	Cut and grazed	Similar to MG5; highest diversity on cut and grazed plots	2	6
St. Catherine's Hill	CG2c	Calcareous brown earth	Deturf/rotavate	>60% similarity to CG2 at highest seeding rate (4 g/m^2)	2	7
Bradenham	MG/CG	Grey redzina	Soil/turf transplants	Diversity increased by 3–6 species per plot	4	2
River Ray	MG4/5/8	Clay	Hay-bales, seed mixtures	Greatest diversity on sown plots > hay-bales > nat. regen.	1	8
Euston/Honnington	U1	Sandy loam	Sulphur and grazed	>80% similarity to U1 at both sites	5	9
Minsmere	U1	Sandy loam	Sulphur and grazed	Greatest similarity to U1 at 2 t S/ha plots	3	10

[a] NVC seed mixtures were sown at all sites.
[b] % similarity calculated using Tablefit (Hill, 1996).
[c] *Sources*: 1, Wells et al. (1994); 2, Mortimer et al. (2002a); 3, Pywell et al. (1996); 4, Pywell et al. (2002); 5, McDonald (1992); 6, Christal et al. (2001); 7, Stevenson et al. (1995); 8, Manchester et al. (1998); 9, Pywell et al. (2000); 10, Owen and Marrs (2000a,b).

Although relatively species-poor grass mixtures can facilitate the development of reference communities over short timescales, more diverse mixtures tailored to the reference community have been shown to give more rapid results (e.g., Manchester et al., 1998; Pywell et al., 2002; Mortimer et al., 2002b). In most cases these mixtures have included species supplied by a commercial producer, or alternatively, as seeds harvested directly from "donor sites", within hay-bales or sweepings. This latter technique has a number of advantages (e.g., assurance of local provenance, introduction of species which are not commercially available, low cost). However, it should be borne in mind that the timing of the initial hay-cut will determine the composition of the species that are introduced. Furthermore, certain species (usually herbs) are likely to be lost as a result of differences in after-ripening (e.g., Manchester et al., 1998), although the use of fresh hay may to overcome this problem, particularly when combined with very late cuts from species-rich meadows (Jones et al., 1995; Mortimer et al., 2002b).

6. Species considerations during grassland restoration

6.1. Poor versus good performers

A recent study of performance of species sown in 25 grassland restoration experiments has shown that many desirable grassland species tend to perform poorly within re-created communities (Pywell et al., 2003). These included a range of stress-tolerators, habitat specialists and species of infertile habitats (e.g., *Centaurea nigra*, *Festuca ovina*, *Galium saxatile*, *Rumex acetosella*, *Sanguisorba officinalis*, *Scabiosa columbaria* and *Thymus polytrichus*). In contrast, "successful" species tended to be good competitors with persistent seed banks, habitat generalists and species characteristic of fertile grasslands. In addition, these species performed increasingly well through time, suggesting that restored grasslands are developing into closed, productive communities, where opportunities for seedling recruitment are rare.

These findings suggest that restored or re-created grasslands tend to lack characteristic species which are often constant components of diverse NVC communities (e.g., MG4-5, U1, CG2 and CG7). Pywell et al. (2003) suggest a number of ways to increase the establishment of these desirable species, including the selection of low fertility sites, the manipulation of abiotic factors (e.g., soil fertility) in order to encourage germination or recruitment, or the "phased" introduction of species over several years after restoration when environmental conditions are more favourable and less dynamic.

6.2. Provenance

The inclusion of non-native genotypes within seed mixtures used in habitat restoration has led to concerns

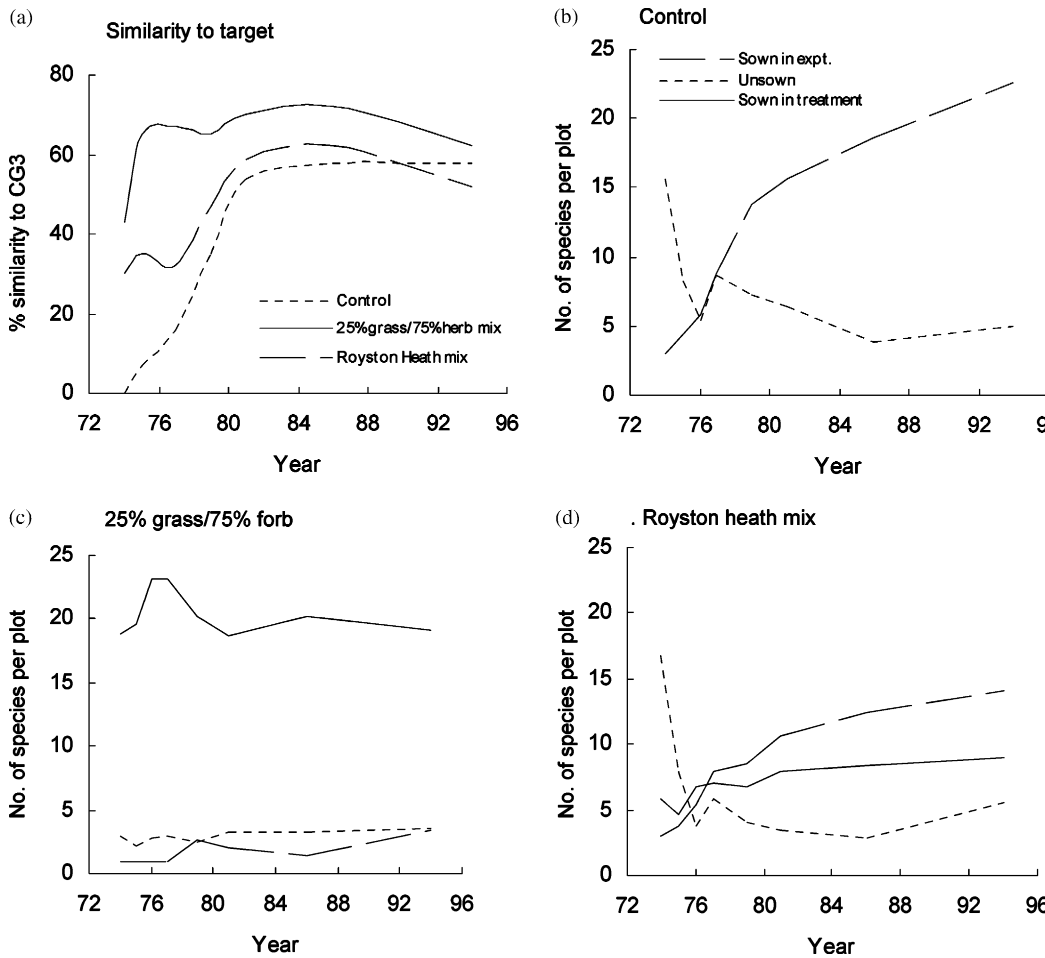

Fig. 3. The overall similarity to *Bromus erectus* grassland (NVC type CG3; Rodwell, 1992) and mean number of sown and unsown species present in plots (2 m × 5 m) in the Royston grassland re-creation experiment (Pakeman et al., 2002; Wells, 1990; Wells et al., 1994). Graph (a) shows the similarity (%) of a selection of treatments (calculated using Tablefit (Hill, 1996)) to CG3. Graphs (b)–(d) show the number of sown (divided into species sown in the plot and species sown elsewhere in the experiment) and unsown species within the following treatments; (b) control, no seed sown, (c) "25% grass/75% forb" grassland seed mixture (6 grasses, 1 sedge and 30 forbs) and (c) "Royston Heath" grassland seed mixture (2 grass, 1 sedge and 14 forbs all collected from the adjacent chalk grassland).

over the potential effects through competition and crossing with native species (Akeroyd, 1984; Stevens and Blackstock, 1997). This has led to the view that local genotypes should be used in habitat restoration to conserve the genetic integrity of local populations and patterns of native genetic diversity (e.g., Sackville Hamilton, 2001). Hybridisation between non-native and local genotypes in particular, may disrupt these patterns, cause the dilution of native gene-pools, and significantly reduce the fitness of subsequent hybrid generations (e.g., Keller et al., 2000). There is also an awareness that the use of local, pre-adapted genotypes, may increase rates of establishment (e.g., Jones et al., 2001) and guard against the introduction of potentially invasive genotypes, which, once freed from their natural enemies and pathogens, become increasingly competitive (Gray, 2002).

However, it has been shown that local genotypes do not necessarily have superior fitness, and hybrids between local and introduced genotypes do not necessarily have low fitness (Wilkinson, 2001). Similarly, the extent to which novel genetic information benefits native populations remains to be tested. Despite these caveats, there is growing recognition that use of material of local provenance should be more fully integrated into agri-environment schemes in the UK (Bullock et al., 2003). There is also an awareness that the superior performance of certain ecotypes in some studies (e.g., Barratt et al., 1999; Jones and Hayes, 1999) suggests that matching the habitat of a species during restoration may be more important than obtaining local seed that may come from a dissimilar habitat (Wilkinson, 2001; Gray, 2002).

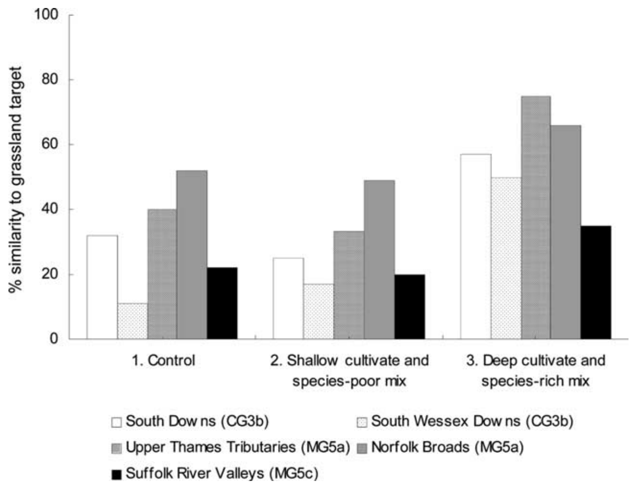

Fig. 4. The similarity of restored grassland on five ex-arable sites in relation to site and treatment 5 years after they were last cultivated (Pywell et al., 2002). Treatments were based on two levels of soil disturbance and species richness: (1) control; (2) shallow cultivation with a species-poor (ESA) grass mixture and (3) deep cultivation and sown with a species-rich (NVC) mixture. The species-rich mixture was designed to create the composition of target NVC communities and typically comprised 25–41 species, of which 80% by weight were grasses and 20% herbs. In contrast, the species-poor mixture typically included 6–8 common grasses. All the sites were cut for hay in July and the aftermath grazed by sheep.

7. Discussion

7.1. Rates of re-assembly

On agricultural land, seed-limitation and high soil fertility are the most important constraints to restoration. On sites that have received minimal inputs of fertiliser, extensive management has been sufficient to overcome these constraints and restore calcareous and mesotrophic grasslands of conservation value in less than 20 years (e.g., Gibson et al., 1987; Mountford et al., 1996). In these studies hay-cutting and aftermath grazing have been shown to reduce the cover of competitive grass species, overall biomass yield and in some cases soil fertility, with cutting and grazing being more successful than either cutting or grazing alone. In contrast, where soils have received repeated fertiliser inputs natural reversion to species-rich grassland has been shown to take several decades, even on sites adjacent to natural seed sources. In contrast, nutrient-stripping (e.g., deep cultivation, deturfing) and seed addition on ex-arable soils has led to the re-creation of species-rich grasslands in less than 10 years (Table 5). Similarly, on improved swards nutrient-stripping, combined with the introduction of species either as transplants or seed mixtures, have been shown to accelerate declines in key nutrients such as P and facilitate the establishment of characteristic species. However, overall rates of reversion have generally been slower presumably because microsite limitation and competitive exclusion have reduced the establishment and spread of introduced species. In both cases, the stability of these “replica” communities over the longer term needs to be evaluated, as does their function relative to semi-natural reference systems.

7.2. Reference levels for soil fertility

Habitat restoration clearly needs to consider the soil nutrient and pH levels at the site to be restored, and the extent to which these differ from semi-natural references. Ideally these should be compared to a local semi-natural grassland, or alternatively published values for BAP priority grasslands (Table 1) (Critchley et al., 2002). These data show that semi-natural levels of extractable P and exchangeable K are typically in the range 4–11 mg/l (with the exception of NVC type U1) and 76–210 mg/l respectively, whereas pH levels range from pH 4.9 to 6.1 on acid grasslands, pH 6–6.4 on mesotrophic grasslands, and pH 6.8–7.9 on calcareous grasslands. However, these figures should be treated with caution for a number of reasons. First, soil nutrients are notoriously variable and display marked regional variations in response to differences in land-use, soils and climate. For example, levels of soil P and pH appear to be slightly lower on mesotrophic grasslands in the more oceanic parts of the UK (Chambers et al., 2000). Second, the values for some communities included in Critchley et al. (2002) were based on a small number of samples (Table 1) (e.g., MG3-4, U2-3, CG2, CG5, CG6, CG9 and M24). Finally, values for P differ markedly from other studies because of the different extractants used. For example, Janssens et al. (1998) suggest that, on soils rich in organic matter, sites for grassland restoration should have extractable P concentrations between below 50 mg/kg (5 mg/100 g), i.e., above 4–11 mg/l. However, comparisons between the two datasets are difficult because the extractant used by Janssens et al. (acetate EDTA) is known to be more powerful than Olsen’s bicarbonate (Läkanen and Erviö, 1971). As a result we suggest that the Critchley et al. (2002) figures are used to guide grassland restoration schemes in the UK. Other datasets which provide useful regional soil data include Gilbert et al. (1996), Blackstock et al. (1998) and Stevens et al. (1998).

The rates at which P declined in experiments in central west Wales (Hayes et al., 2000; Hayes and Sackville Hamilton, 2001) suggest that where soil extractable P levels are less than 10 mg/l, above values for NVC types given by Critchley et al. (2002), then hay cutting and extensive grazing techniques may be sufficient to restore semi-natural levels in less than a decade. In general, such sites would normally be given highest priority where resources for restoration are limited. In contrast, where soil extractable P levels are greater than 10 mg/l, above a desired NVC type more interventionist techniques (e.g., deturfing, deep cultivation and chemical amelioration) are likely to be required to achieve the same results in less than a decade.

However, great caution should be taken when applying this threshold as these studies were undertaken on brown earth soils in an oceanic part of the UK with moderate to a high rainfall, and there is likely to be considerable site-to-site variation in the rate of P decline, particularly in relation to soil type (e.g., Oomes, 1990; Marrs et al., 1991; Olff and Bakker, 1991). Furthermore, it is evident from survey data that soil P is very variable, even under the diverse vegetation of traditional hay meadows. For example, Smith et al. (2000) found that vegetation change at Colt Park occurred despite the uniformly moderate-high levels of soil phosphate across all treatments. This suggests that in some cases at least, soil P may be an indication of past fertiliser rather than a present day problem. The low diversity of fertilised swards, and low fungal/bacterial ratios, is more likely to be a result of repeated N addition which are rapidly lost from the soil once fertiliser applications are curtailed, therefore leaving the P that is often applied with it. As a result P may be more useful as an indicator of past practice which can be ignored when the availability of seed of missing species or soil pH are key factors constraining restoration success. Further work is therefore urgently required to evaluate the importance of soil P (as well as other key nutrients) for grassland restoration as well as the applicability of the threshold presented above over a broader range of environmental conditions and NVC grassland types.

7.3. Restoration end-points

Although restored grasslands are likely to contribute to national biodiversity targets, success will ultimately depend on the reinstatement of the communities and ecological functions of semi-natural references (Ormerod, 2003). This has long been acknowledged as "the acid test" of ecological theory. However, in recent years ecologists have begun to question whether restoration is actually contributing to national conservation objectives or merely replacing one degraded ecosystem with another (Dobson et al., 1997).

From a botanical perspective the findings of this review suggest that the re-creation of species-rich grasslands of conservation value is technically feasible within a relatively short period of time. Indeed, many restored grasslands are often indistinguishable from NVC communities from a botanical point of view (e.g., Fig. 3(a)). However, the re-assembly of invertebrate assemblages appears to be a much slower process. In part, this may be due to the absence of poor-performing plant species on restoration sites, but also because many stenotopic invertebrates are unable to disperse between isolated sites (Mortimer et al., 2002a). This has important implications, not only in terms of the invertebrate value of restored grasslands, but also for the establishment of certain grassland species (e.g., *T. polytrichus* and *Helianthemum nummularium*) which are dependent on the presence of certain invertebrate species (Pywell et al., 2003). Other processes about which we know even less include the development of food and pollinator webs, trophic interactions as well as the functional roles of soil microbial and fungal communities during secondary succession.

8. Conclusions

The findings presented in this review suggest that extensive management can be used to the restore or recreate species-rich grasslands on formerly improved agricultural soils although, due to high residual soil fertility and seed limitation, the rates of re-assembly have been very slow. As a consequence nutrient depletion is likely to accelerate this process where "gaps" for establishment are created on formerly improved swards or diverse seed mixtures are sown on ex-arable soils. However, the review has also highlighted a number of key areas which require further research:

1. Soil P has been shown to be a key limiting nutrient for the restoration and re-creation of some grassland types. However, further sampling is required in order to test its importance (as well as the role of other key nutrients) as well as the appropriateness of the 10 mg/l threshold presented in this paper across a range of soil types and starting conditions.
2. More sampling is required in order to refine the soil nutrient and pH "target levels" for grassland recreation as well as the functional attributes of semi-natural assemblages, in particular the role of soil microbial and faunal soil communities and trophic interactions during community re-assembly.
3. Further research is required on the restoration/re-creation of localised BAP priority grassland types which lack detailed experimental work (U2-3, CG1, CG4-9, M22-23 and M26) or where community re-assembly has only been studied at a few sites (e.g., MG3 and M24-25).
4. Further research is also required to test the efficacy and practicality of novel nutrient depletion techniques such as the application of iron and aluminium residues across a range of starting conditions (e.g., soil type, fertility and pH).
5. More information is required on the performance of species during grassland recreation and restoration as well as experimental research on the establishment of desirable but poor-performing species.
6. Further research is required to assess the impact of non-native genotypes, introduced through restoration, on native infraspecific diversity. In particular,

more information is required on the scale of introduction as well as the potential effects through crossing and competition with native species.

Acknowledgements

This work was funded by the Countryside Council for Wales, Scottish Natural Heritage and the Joint Nature Conservation Committee (contract FC 73-01-273A). The authors would like to thank Micheal Burke, Brian Chambers, Nigel Critchley (all ADAS), Michael Hayes, Alan Hopkins, Jerry Tallowin (all IGER), Jane MacKintosh (Scottish Natural Heritage), Jo Gilbert (RSPB), Roger Smith (Newcastle University) and Clifford Stuckey (Centre for Ecology and Hydrology) for access to unpublished information. We are also grateful to Tim Blackstock, Carrie Rimes and Clare Burrows (all Countryside Council for Wales), Richard Jefferson, Clare Pinches and Heather Robertson (all English Nature) and Steve Ormerod for valuable discussion and advice. Two anonymous referees also made constructive comments on the original manuscript.

References

Akeroyd, J., 1984. Seeds of Destruction? Non-native Wildflower Seed and British Floral Biodiversity. Plantlife, London.

Adams, W.A., Roughley, G., Young, R.J., 1999. An experimental study to re-establish *Molinia–Juncus* pasture from improved grassland at Rhôs Llawr-cwrt National Nature Reserve. Countryside Council for Wales Contract Science Report No. 355, Bangor.

Bakker, J.P., 1987. Restoration of species-rich grassland after a period of fertilizer application. In: VanAndel, J. (Ed.), Disturbance in Grasslands. Dr. W. Junk, Dordrecht, pp. 185–200.

Bakker, J.P., 1989. Nature Management by Grazing and Cutting. Kluwer, Dordrecht.

Bakker, J.P., Poschlod, P., Strijkstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics for restoration ecology. Acta Botanica Neerlandica 45, 461–490.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology and Evolution 14, 63–68.

Bardgett, R.D., 1996. Potential effects on the soil mycoflora of changes in the UK agricultural policy for upland grasslands. In: Frankland, J.C., Magan, N., Gadd, G.M. (Eds.), Fungi and Environmental Change. Cambridge University Press, Cambridge, pp. 163–183.

Bardgett, R.D., McAlister, E., 1999. The measurement of soil fungal:bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate grasslands. Biology and Fertility of Soils 29, 282–290.

Barratt, D.R., 1999. Habitat diversification using plug-plants: realising a growing potential? A review of the current situation in the UK. Journal of Practical Ecology and Conservation 3, 11–22.

Barratt, D.R., Walker, K.J., Pywell, R.F., Sparks, T.H., 1999. Variation in the responses of infraspecific variants of wet grassland species to manipulated water levels. Watsonia 22, 317–328.

Barratt, D.R., Mountford, J.O., Sparks, T.H., Walker, K.J., Warman, E.A., Garbutt, A., 2000. The effects of field elevation and water levels on the establishment of plug-plants in an ex-arable grassland. Aspects of Applied Biology 58, 425–430.

Bekker, R.M., Verweij, G.L., Smith, R.E.N., Reine, R., Bakker, J.P., Schneider, S., 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? Journal of Applied Ecology 34, 1293–1310.

Berendse, F., Oomes, M.J.M., Altena, H.J., Elberse, W.Th., 1992. Experiments on the restoration of species-rich meadows in the Netherlands. Biological Conservation 62, 59–65.

Bhogal, A., Chambers, B.J., Cross, R.B., 2000. Reversion of intensive arable land to grass heath and *Calluna* heath: soil fertility aspects. Report to the Ministry of Agriculture, Fisheries and Food (BD1501), Agriculture, Development and Advisory Service (ADAS), Gleadthorpe.

Blackstock, T.H., Rimes, C.A., Stevens, D.P., Jefferson, R.G., Robertson, H., Mackintosh, J., Hopkins, J.J., 1999. The extent of semi-natural grassland communities in lowland England and Wales: a review. Grass and Forage Science 54, 1–18.

Blackstock, T.H., Stevens, D.P., Stevens, P.A., Mockridge, C.P., Yeo, M.J.M., 1998. Edaphic relationships among *Cirsio–Molinietum* and related wet grassland communities in lowland Wales. Journal of Vegetation Science 9, 431–444.

Bobbink, R., Hornung, M., Roelefs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86, 717–738.

Boyce, D.V.M., 1995. Survival and spread of wildflowers planted into ex-agricultural grassland. Journal of Practical Ecology and Conservation 1, 38–44.

Bullock, J.M., Hill, B.C., Dale, M.P., Silvertown, J., 1994. An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. Journal of Applied Ecology 31, 493–507.

Bullock, J.M., Moy, I., Pywell, R.F., Coulson, S.J., Nolan, A.M., Caswell, H., 2002. Plant dispersal and colonization processes at local and landscape scales. In: Bullock, J.M., Kenward, R.E., Hails, R. (Eds.), Dispersal Ecology. Blackwell Scientific Publications, Oxford, pp. 279–302.

Bullock, J.M., Brown, V.K., Peel, S., Brown, R., Everett, S., Gray, A., Pywell, R.F., Smallshire, D., McIntyre, D., Diack, I., Mortimer, S., 2003. Genetic provenance of seed mixtures for habitat restoration. Bulletin of the British Ecological Society 34 (2), 14–17.

Chambers, B.J., Critchley, C.N.R., Fowbert, J.A., Bhogal, A., Rose, S.C., 2000. Soil nutritional status and botanical composition of grassland in welsh environmentally sensitive areas. Report to the Ministry of Agriculture, Fisheries and Food (BD1429), ADAS, Gleadthorpe.

Christal, A., Davies, D.H.K., Warren, J., MacKintosh, J., 2001. The management of long-term set-aside for nature conservation. Botanical Journal of Scotland 49, 415–424.

Coates, D., 1997. UK policy for ESAs. In: Sheldrick, R.D. (Ed.), Grassland Management in Environmentally Sensitive Areas. In: British Grassland Society Occasional Symposium, vol. 32. British Grassland Society, Reading, pp. 5–11.

Codling, E.E., Chaney, R.L., Mulchi, C.L., 2000. Use of aluminium- and iron-rich residues to immobilise phosphorus in poultry litter and litter-amended soils. Journal of Environmental Quality 29, 1924–1931.

Coulson, S.J., Bullock, J.M., Stevenson, M.J., Pywell, R.F., 2001. Colonisation of grassland by sown species: dispersal versus microsite limitation in responses to management. Journal of Applied Ecology 38, 204–216.

Critchley, C.N.R., Chambers, B.J., Fowbert, J.A., Sanderson, R.A., Bhogal, A., Rose, S.C., 2002. Association between lowland grassland plant communities and soil properties. Biological Conservation 105, 199–215.

Critchley, C.N.R., Burke, M.J.W., Stevens, D.P., 2004. Conservation of lowland semi-natural grasslands in the UK: a review of monitoring results from agri-environment schemes. Biological Conservation 115, 263–278.

Davies, A., Kendle, A.D., Bisgrove, R.J., Marder, J., 1996. Effects of interactions between site, management and species on the planned establishment of wildflowers in grasslands. Aspects of Applied Biology 44, 377–384.

Davies, D.M., Graves, J.D., Elias, C.O., Williams, P.J., 1997. The impact of *Rhinanthus* spp. on sward productivity and composition: implications for the restoration of species-rich grasslands. Biological Conservation 82, 87–93.

Davies, D.M., Graves, J.D., 2000. The impact of phosphorus on interactions of the hemiparasitic angiosperm *Rhinanthus minor* and it host *Lolium perenne*. Oecologia 124, 100–106.

Dobson, A.P., Bradshaw, A.D., Baker, A.J.M., 1997. Hopes for the future: restoration ecology and conservation biology. Science 277, 515–522.

Dodd, M.E., Silvertown, J., McConway, K., Potts, J., Crawley, M., 1994. Application of the British National Vegetation Classification to the communities of the Park Grass Experiment through time. Folia Geobotanica Phytotaxanomica 29, 321–334.

Donnison, L.M., Griffith, G.S., Hedger, J., Hobbs, P.J., Bardgett, R.D., 1999. Management influences on soil microbial and fungal communities of botanically diverse hay-meadows in northern England and Wales. Soil Biology and Biochemistry 32, 253–263.

Dunsford, S.J., Free, A.J., Davy, A.J., 1998. Acidifying peat as an aid to the reconstruction of lowland heath on arable soil: a field experiment. Journal of Applied Ecology 35, 660–672.

van Duuren, L., Bakker, J.P., Fresco, L.F.M., 1981. From intensively agricultural practices to haymaking without fertilisation – effects on moist grassland communities. Vegetatio 46/7, 241–258.

Gange, A.C., Brown, V.K., Sinclair, G.S., 1993. Vesicular–arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. Functional Ecology 7, 616–622.

Gibson, C.W.D., 1995. Chalk Grasslands on Former Arable Land: a Review. Bioscan, Oxford.

Gibson, C.W.D., 1998. South Somerset SSSIs: a study of neutral grassland succession. English Nature Research Report No. 266. English Nature, Peterborough.

Gibson, C.W.D., Watt, T.A., Brown, V.K., 1987. The use of sheep grazing to re-create species-rich grassland from abandoned arable land. Biological Conservation 42, 165–183.

Gibson, C.W.D., Brown, V.K., 1991a. The nature and rate of development of calcareous grassland in southern Britain. Biological Conservation 58, 297–316.

Gibson, C.W.D., Brown, V.K., 1991b. The effects of grazing on local colonisation and extinction during early succession. Journal of Vegetation Science 2, 291–300.

Gilbert, J.C., Higginbottom, P.R.G., Gowing, D.J.G., Bradley, R.I., Kerr, D.M., Leeds-Harrison, P.B., Spoor, G., Godwin, R.J., 1996. The Habitat Creation Model. A model to assess the viability of converting arable land into semi-natural habitat. Report to the Ministry of Agriculture, Fisheries and Food. Cranfield University, Silsoe.

Gough, M.W., Marrs, R.H., 1990. A comparison of soil fertility between semi-natural and agricultural plant communities: implications for the creation of species-rich grassland on abandoned agricultural land. Biological Conservation 51, 83–96.

de Graaf, M.C.C., Verbeek, P.J.M., Bobbink, R., Roelofs, J.G.M., 1998. Restoration of species-rich dry heaths: the importance of appropriate soil conditions. Acta Botanica Neerlandica 47, 89–111.

Graham, D.J., Hutchings, M.J., 1988. A field investigation of germination from the seed bank of a chalk grassland ley on former arable land. Journal of Applied Ecology 25, 253–263.

Gray, A., 2002. The evolutionary context: a species perspective. In: Perrow, M.R., Davy, A.J. (Eds.), Handbook of Ecological Restoration. In: Principles of Restoration, vol. 1. Cambridge University Press, Cambridge, pp. 66–80.

Grime, P.J., Mackey, J.M.L., Hilier, S.H., Read, D.J., 1987. Floristic diversity in a model system using experimental microcosms. Nature 328, 420–422.

Hayes, M.J., Sackville Hamilton, N.R., 2001. The effect of sward management on the restoration of species-rich grassland: a reassessment of IGER's grassland restoration experiment, Trawsgoed. Countryside Council for Wales Contract Science Report No. 438, Bangor.

Hayes, M.J., Sackville Hamilton, N.R., Tallowin, J.R.B., Buse, A., Davies, O., 2000. Methods of enhancing diversity in upland environmentally sensitive area swards. Report to the Ministry of Agriculture, Fisheries and Food (BD1424), Institute of Grassland and Environmental Research, Aberystwyth.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396, 69–72.

Hill, M.O., 1996. TABLEFIT, Version 1.0, for Identification of Vegetation Types. Institute of Terrestrial Ecology, Monks Wood.

Hopkins, A., Hopkins, J.J., 1994. UK grasslands now: agricultural production and nature conservation. In: Haggar, R.J., Peel, S. (Eds.), Grassland Management and Nature Conservation. In: British Grassland Society Occasional Symposium, vol. 28. Blackwell, London, pp. 10–19.

Hopkins, A., Pywell, R.F., Peel, S., Johnson, R.H., Bowling, P.J., 1999. Enhancement of botanical diversity of permanent grassland and impact on hay production in Environmentally Sensitive Areas in the UK. Grass and Forage Science 54, 163–173.

Hutchings, M.J., Booth, K.D., 1996a. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and seed rain. Journal of Applied Ecology 33, 1171–1181.

Hutchings, M.J., Booth, K.D., 1996b. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. Journal of Applied Ecology 33, 1182–1190.

Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F., Oomes, M.J.M., 1998. Relationships between soil chemical factors and grassland diversity. Plant and Soil 202, 69–78.

Johnston, A.E., Poulton, P.R., 1977. Yields on the exhaustion land experiment and changes in the NPK content of the soils due to cropping and manuring 1852–1975 (Report of Rothamsted Experimental Station 1976, Part 2). Rothamsted Experimental Station, Rothamsted.

Jones, A.T., Hayes, M.J., 1999. Increasing floristic diversity in grassland: the effects of management regime and provenance on species introduction. Biological Conservation 87, 381–390.

Jones, A.T., Hayes, M.J., Sackville Hamilton, N.R., 2001. The effect of provenance on the performance of *Crataegus monogyna* in hedges. Journal of Applied Ecology 38, 952–962.

Jones, G.H., Trueman, I.C., Millet, P., 1995. The use of hay strewing to create species-rich grasslands (i) general principles and hay strewing versus seed mixes. Land Contamination and Reclamation 3, 104–107.

Keller, M., Kollman, J., Edwards, P.J., 2000. Genetic introgression from distant provenances reduces fitness in local weed populations. Journal of Applied Ecology 37, 647–659.

Läkanen, E., Erviö, R., 1971. A comparison of eight extractants for the determination of plant available micronutrients in soils. Acta Agralia Fennica 123, 223–232.

Lawton, J.H., May, R.M. (Eds.), 1995. Extinction Rates. Oxford University Press, Oxford.

Manchester, S.J., Treweek, J.R., Mountford, J.O., Pywell, R.F., 1997. The success of nurse crops in the establishment of species-rich lowland wet grassland. In: Sheldrick, R.D. (Ed.), Grassland Management in Environmentally Sensitive Areas. In: British Grassland Society Occasional Symposium, vol. 32. British Grassland Society, Reading, pp. 260–261.

Manchester, S.J., Treweek, J.R., Mountford, J.O., Pywell, R.F., Sparks, T.H., 1998. Restoration of a target wet grassland commu-

nity on ex-arable land. In: Joyce, C.B., Wade, P.M. (Eds.), European Wet Grasslands: Biodiversity, Management and Restoration. John Wiley & Sons, London, pp. 277–294.
Marrs, R.H., 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. Advances in Ecological Research 24, 241–301.
Marrs, R.H., Gough, M.W., Griffiths, M., 1991. Soil chemistry and leaching losses of nutrients from semi-natural grassland and arable soils on three contrasting parent materials. Biological Conservation 57, 257–271.
Marrs, R.H., Snow, C.S.R., Owen, K.M., Evans, C.E., 1998. Heathland and acid grassland creation on arable soils at Minsmere: identification of potential problems and a test of cropping to impoverish soils. Biological Conservation 85, 69–82.
McCrea, A.R., Trueman, I.C., Fullen, M.A., 2001. A comparison of the effects of four arable crops on the fertility depletion of a sandy silt loam destined for grassland habitat creation. Biological Conservation 97, 181–187.
McDonald, A.W., 1992. Succession in a 3-year-old flood-meadow near Oxford. Aspects of Applied Biology 29, 345–352.
McDonald, A.W., 1993. The role of seedbank and sown seeds in the restoration of an English flood-meadow. Journal of Vegetation Science 4, 395–400.
McDonald, A.W., Bakker, J.P., Vegelin, K., 1996. Seed bank classification and its importance for the restoration of species-rich flood-meadows. Journal of Vegetation Science 7, 157–164.
McDonald, A.W., 2001. Succession during the re-creation of a flood-meadow 1985–1999. Applied Vegetation Science 4, 167–176.
McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenisation: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14, 450–453.
Milberg, P., Hansson, M.L., 1994. Soil seed bank and species turnover in a limestone grassland. Journal of Vegetation Science 5, 35–42.
Mitchley, J., Buckley, G.P., Helliwell, D.R., 1996. Vegetation establishment on chalk marl spoil: the role of nurse grass species and fertiliser application. Journal of Vegetation Science 7, 543–548.
Mortimer, S.R., Booth, R.G., Harris, S.J., Brown, V.K., 2002a. Effects of initial site management on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land. Biological Conservation 104, 301–313.
Mortimer, S.R., Toller, A., Masters, G.J., Brown, V.K., 2002b. Efficacy of hay-spreading to increase the botanical diversity of agriculturally-improved chalk grassland. In: Frame, J. (Ed.), Conservation Pays? Reconciling Environmental Benefits with Profitable Grassland Systems. In: British Grassland Society Occasional Symposium, vol. 36. British Grassland Society, pp. 141–144.
Mountford, J.O., Lakhani, K.H., Kirkham, F.W., 1993. Experimental assessment of the effects of nitrogen addition under haycutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. Journal of Applied Ecology 30, 321–332.
Mountford, J.O., Tallowin, J.R.B., Kirkham, F.W., Lakhani, K.H., 1994. Effects of inorganic fertilisers in flower-rich hay-meadows in the Somerset Levels. In: Haggar, R.J., Peel, S. (Eds.), Grassland Management and Nature Conservation. In: British Grassland Society Occasional Symposium, vol. 28. British Grassland Society, Reading, pp. 74–85.
Mountford, J.O., Lakhani, K.H., Holland, R.J., 1996. Reversion of vegetation following the cessation of fertiliser application. Journal of Vegetation Science 7, 219–228.
Olff, H., Bakker, J.P., 1991. Long-term dynamics of standing crop and species composition after the cessation of fertiliser application to mown grassland. Journal of Applied Ecology 28, 1040–1052.
Oomes, M.J.M., 1990. Changes in dry matter and nutrient yields during the restoration of species-rich grasslands. Journal of Vegetation Science 1, 333–338.
Oomes, M.J.M., 1992. Yield and species density of grasslands during restoration management. Journal of Vegetation Science 3, 271–274.
Ormerod, S.J., 2003. Restoration in applied ecology: editor's introduction. Journal of Applied Ecology 40, 44–50.
Owen, K.M., Marrs, R.H., Snow, C.S.R., Evans, C., 1999. Soil acidification – the use of sulphur and acidic plant materials to acidify arable soils for the re-creation of heathland and acidic grassland at Minsmere, UK. Biological Conservation 87, 105–121.
Owen, K.M., Marrs, R.H., 2000a. Creation of heathland on former arable land at Minsmere, Suffolk, UK: the effects of soil acidification on the establishment of *Calluna* and ruderal species. Biological Conservation 93, 9–18.
Owen, K.M., Marrs, R.H., 2000b. Acidifying arable soils for the restoration of acid grasslands. Applied Vegetation Science 3, 105–116.
Ozinga, W.A., Van Andel, J., McDonnell-Alexander, M.P., 1997. Nutritional soil heterogeneity and mycorrhiza as determinants of plant species diversity. Acta Botanica Neerlandica 46, 237–254.
Pakeman, R.J., Pywell, R.F., Wells, T.C.E., 2002. Species spread and persistence: implications for experimental design and habitat re-creation. Applied Vegetation Science 5, 75–86.
Poschlod, P., Bonn, S., 1998. Changing dispersal processes in the central European landscape since the last ice age – an explanation for the decrease of plant species richness in different habitats? Acta Botanica Neerlandica 47, 27–44.
Poschlod, P., Kiefer, S., Traenkle, U., Fischer, S., Bonn, S., 1998. Species richness in calcareous grasslands is affected by dispersability in space and time. Applied Vegetation Science 1, 75–90.
Poschlod, P., WallisDeVries, M.F., 2002. The historical and socio-economic perspective of calcareous grasslands – lessons from the distant and recent past. Biological Conservation 104, 361–376.
van der Putten, W.H., Mortimer, S.R., Hedlund, K., van Dijk, C., Brown, V.K., Leps, J., Rodriguez-Barrueco, C., Roy, J., Diaz Len, T.A., Gormsen, D., Korthals, G.W., Lavorel, S., Santa Regina, I., Smilauer, P., 2000. Plant species diversity as a driver of early succession in abandoned fields: a multisite approach. Oecologia 124, 91–99.
Pywell, R.F., Wells, T.C.E., Sparks, T.H., 1996. Long-term dynamics of reconstructed species-rich grassland communities. Aspects of Applied Biology 44, 369–376.
Pywell, R.F., Warman, L., Walker, K.J., Sparks, T.H., 2000. Reversion of intensive arable land to grass heath and *Calluna* heath: vegetation aspects. Report to the Ministry of Agriculture, Fisheries and Food (BD1502), Institute of Terrestrial Ecology, Monks Wood.
Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland: assessing the limiting processes using a multi-site approach. Journal of Applied Ecology 39, 294–309.
Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L., Walker, K.J., Rothery, P., 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology 40, 65–77.
Rodwell, J.S. (Ed.), 1991. British Plant Communities. In: Mires and Heaths, vol. 2. Cambridge University Press, Cambridge.
Rodwell, J.S. (Ed.), 1992. British Plant Communities. In: Grasslands and Montane Communities, vol. 3. Cambridge University Press, Cambridge.
Sackville Hamilton, N.R., 2001. Is local provenance important in habitat creation? A reply. Journal of Applied Ecology 38, 1374–1376.
Silvertown, J., Dodd, M.E., McConway, K., Potts, J., Crawley, M., 1994. Rainfall, biomass variation and community composition of the Park Grass Experiment. Ecology 75, 2430–2437.
Smith, R.S., 1994. The effects of fertiliser on plant species composition and conservation interest in UK grassland. In: Haggar, R.J., Peel, S. (Eds.), Grassland Management and Nature Conservation. British Grassland Society Occasional Symposium 28, Reading, pp. 64–73.

Smith, R.S., Shiel, R.S., Millward, D., Corkhill, P., 2000. The interactive effects of management on the productivity and plant community structure of an upland meadow: an 8-year field trial. Journal of Applied Ecology 37, 1029–1043.

Smith, R.S., Shiel, R.S., Millward, D., Corkhill, P., Sanderson, D.A., 2002. Soil seed banks and the effects of meadow management on vegetation change in 10-year meadow field trial. Journal of Applied Ecology 39, 279–293.

Smith, R.S., Shiel, R.S., Bardgett, R.D., Millward, D., Corkhill, P., Rolph, G., Hobbs, P.J., Peacock, S., 2003. Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of meadow grassland. Journal of Applied Ecology, 40.

Stace, C.A., 1997. New Flora of the British Isles, second ed. Cambridge University Press, Cambridge.

Stevens, D.P., Blackstock, T.H., 1997. Genetics and nature conservation in Britain: the role of the statutory country agencies. In: Tew, T.E., Crawford, T.J., Spencer, J.W., Stevens, D.P., Usher, M.B., Warren J. (Eds.), The Role of Genetics in Conserving Small Populations. British Ecological Society Symposium, Joint Nature Conservation Committee, Peterborough, pp. 193–203.

Stevens, P.A., Bell, S.A., Brittain, S.A., Hughes, S., Lowe, J.A.H., 1998. Soil/vegetation interactions in lowland grasslands. summary. Countryside Council for Wales Contract Science Report No. 305, Bangor.

Stevenson, M.J., Bullock, J.M., Ward, L.K., 1995. Re-creating semi-natural communities: effect of sowing rate on establishment of calcareous grassland. Restoration Ecology 3, 279–289.

Strykstra, R.J., Verweij, G.L., Bakker, J.P., 1997. Seed dispersal by mowing machinery in a Dutch brook valley system. Acta Botanica Neerlandica 46, 387–401.

Swash, G., Belding, R., 1999. Arable Reversion in Environmentally Sensitive Areas and Countryside Stewardship Schemes. Guidelines for Project Officers. Farming and Rural Conservation Agency.

Tallowin, J.R.B., 1997. Methods for rapid depletion of soil nutrient availability in extensively managed grasslands within ESAs. Report to the Ministry of Agriculture, Fisheries and Food (BD0310), Institute of Grassland and Environmental Research, Okehampton.

Tallowin, J.R.B., Kirkham, F.W., Smith, R.E.N., Mountford, J.O., 1998. Residual effects of phosphorous fertilisation on the restoration of floristic diversity to wet hay meadows. In: Joyce, C.B., Wade, P.M. (Eds.), European Lowland Wet Grasslands: Biodiversity, Management and Restoration. John Wiley & Sons, London, pp. 249–263.

Tallowin, J.R.B., Smith, R.E.N., 2001. Restoration of a *Cirsio–Molinietum* fen-meadow on an agriculturally improved pasture. Restoration Ecology 9, 167–178.

Tallowin, J.R.B., Smith, R.E.N., Pywell, R.F., Goodyear, J., Martyn, T., 2002. Use of fertiliser nitrogen and potassium to reduce soil phosphorous availability. In: Frame, J. (Ed.), Conservation Pays? Reconciling Environmental Benefits with Profitable Grassland Systems. In: British Grassland Society Occasional Symposium, vol. 36. British Grassland Society, Reading, pp. 163–166.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Török, K., Szili-Kovacs, T., Halassy, M., Toth, T., Hayek, Zs., Paschke, M.W., Wardell, L.J., 2000. Immobilization of soil nitrogen as a possible method for the restoration of sandy grassland. Applied Vegetation Science 3, 7–14.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M., Webb, D.A., 1964–1980. Flora Europaea, vols. 1–5. Cambridge University Press, Cambridge.

UK Biodiversity Group, 1998. Tranche 2 Action Plans. Volume II. Terrestrial and Freshwater Habitats. HMSO, London.

UK Biodiversity Steering Group, 1995. Biodiversity: the UK Steering Group Report. Volume 2: Action plans. HMSO, London.

Wells, T.C.E., 1990. Establishing chalk grassland on previously arable land using seed mixtures. In: Hillier, S.H., Walton, D.W.H., Wells, D.A. (Eds.), Calcareous Grasslands – Ecology and Management. Bluntisham Books, Huntingdon, pp. 169–170.

Wells, T.C.E., Cox, R., Frost, A., 1989. Diversifying grasslands by introducing seed and transplants into existing vegetation. In: Buckley, G.P. (Ed.), Biological Habitat Reconstruction. Belhaven, London, pp. 283–298.

Wells, T.C.E., Pywell, R.F., Welch, R.C., 1994. Management and restoration of species-rich grassland. Report to the Ministry of Agriculture, Fisheries and Food (BD0306), Institute of Terrestrial Ecology, Monks Wood.

Wild, A. (Ed.), 1988. Russell's Soil Conditions and Plant Growth. Longman, London.

Wilkinson, D.M., 2001. Is local provenance important in habitat creation? Journal of Applied Ecology 38, 1371–1373.