A STUDY OF MESOTROPHIC GRASSLAND SUCCESSION IN SOUTH SOMERSET

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Abstract

The mesotrophic (= neutral) grasslands occurring within a narrow compass of countryside in south Somerset, near the Dorset border, have been identified as among the botanically richest examples of MG5 *Cynosurus cristatus-Centaurea nigra* grassland (Rodwell 1992) known in England. This diversity is in part attained through species characteristic of each of the three MG5 sub-communities – the *Lathyrus pratensis* (MG5a), *Galium verum* (MG5b) and *Danthonia decumbens* (MG5c) sub-communities – growing together in intimate association. Fields of known ages and different past treatments such as ploughing, but now all under similar management, were surveyed to reveal differences in plant species composition attributable to age since treatment. Predictable effects of past ploughing and disturbances such as arable cropping and reseeding with rye-grass were found. Sowing with hay-seed in one field surprisingly produced very species-rich grassland within only a few decades. Despite this, differences were detectable between grasslands of different ages. Younger grasslands could be very rich in species, including those regarded as 'constants' of MG5 and as good indicators of agriculturally unimproved grassland. However the full mixture of species characteristic of the three sub-communities, and particularly those typically associated with the MG5c sub-community, may take more than a century to develop. This suggests that the time required for species-rich mesotrophic grassland communities to develop is of a similar order of magnitude to that reported for species-rich calcareous grasslands. The findings should be treated with caution as they are based on a small number of fields, all of them species-rich, occurring in close proximity to one another. However, this preliminary description of succession in MG5 grasslands in south Somerset is presented here in the hope that it will stimulate its testing by observation and experiment elsewhere.

INTRODUCTION

Calcareous grasslands are the best known species-rich, open ground communities to most British ecologists. Ancient chalk grasslands in particular are often cited as examples of communities which have dense species-packing within small areas as well as being rich in species on a larger scale (eg Tansley 1939; Rodwell 1992). This has resulted in a great deal of attention being given to the mechanisms by which species diversity in calcareous grasslands is generated and maintained. A particular focus of this work has been the role of ecological succession, and the typical timescales required, in the development of species-rich grassland communities reverting from arable farmland or other origins (Tansley and Adamson 1925; Wells *et al.* 1976; Gibson and Brown 1991; Gibson 1995; Hirst *et al*. 2005).

The consensus is that species-rich calcareous grasslands, in all but the most exceptional circumstances, take at least a century to develop, ie reach a stage where recognisable plagioclimax vegetation is present. Knowledge of this timescale has been important both in informing attempts to re-create these grasslands (Walker *et al*. 2004) and in safeguarding existing ancient grassland sites (Jefferson *et al*. 1999).

Calcareous grasslands are not the only British plant communities displaying such exceptional species diversity. Among the grassland communities described in the National Vegetation Classification (NVC) by Rodwell (1992), there are several mesotrophic (= neutral) and acidic grassland communities with 45 or more species in 2 x 2m quadrat samples, a number comparable with the richest ancient calcareous grasslands. These include communities such as *Arrhenatherum elatius-Filipendula ulmaria* tall-herb grassland (MG2) and *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (U4), the latter having as many as 62 species per sample. Some flush and small-sedge mire communities can be equally rich (Rodwell 1991).

Despite the recognition of the nature conservation value of these species-rich non-calcareous grasslands (NCC 1989; Jefferson and Robertson 1996) and their rapid decline, virtually nothing is known about the time it takes for them to develop or the processes involved. Experimental work has been limited to quantifying the deleterious effects of agricultural improvement (eg Mountford *et al.* 1993) or documenting the slow process of recovery after the application of modern agricultural fertilisers ceases (Olff and Bakker 1994).

In one of the few studies of non-calcareous grasslands, Hirst *et al*. (2005) used a chronosequence approach, looking at the timescale of succession, in their study of the effects of *c*. 60 years of physical disturbance from tank activity on ungrazed, species-poor *Arrhenatherum elatius* (MG1) grassland growing in mosaics with species-rich calcareous grassland. The present paper is an attempt to describe a chronosequence for *Cynosurus cristatus-Centaurea nigra* grassland (MG5), a community forming the main mesotrophic grassland of conservation importance in lowland England (Jefferson and Robertson 1996).

Work on the impacts of grazing on these mesotrophic grasslands has revealed that they can have species-packing as dense as any other ancient grassland community (Gibson 1997). Particularly species-rich examples were found in several areas of western England between Somerset and Worcestershire, containing up to 45 species in one square metre – more than any MG5 sample had in *four* square metres according to Rodwell (1992, 64–5: floristic table MG5) – and more than 60 in the 2 x 2m area comparable with Rodwell's quadrat samples (Gibson 1997). Since then, equally rich examples have been found in Wales (D. Stephens, pers. comm.).

The richest single site included in Gibson's (1997) study was at Grove Farm, south Somerset, close to the Dorset border near the village of Hardington Mandeville. The site includes a network of MG5 fields, many ploughed and some reseeded during the memory of the then owner and his family. Taken together, these fields provide a unique opportunity to investigate the species composition of grassland in fields of known age on the same soils and under the same current management. A pair of fields also suitable for the study occurs nearby, at Hardington Moor National Nature Reserve (NNR).

The present paper, based on a report written by Charlie Gibson (Gibson 1998), presents the results of an analysis of quadrat data from these fields designed to extract a best estimate of successional changes in MG5 grassland in this area of south Somerset. It is assumed that these fields are representative of others of their age within the same general area, but whether the successional changes described here are applicable to mesotrophic grassland more widely will become clear only after comparable studies have been undertaken elsewhere.

METHODS

The sites

The two sites are within Sites of Special Scientific interest (SSSIs) less than 3km apart: Grove Farm SSSI lies on the north-facing lower slopes of Pen Hill (ST 513 096), and is privately owned with no public access; Hardington Moor NNR faces south on the slope below Coker Hill (ST 515 128). Fields included in the study were selected because they had known, and apparently relatively simple, management histories. Further fields of MG5 grassland were available but rejected because of uncertain management or, in sites remote from the main group, because they lacked nearby 'controls' of undisturbed ancient grassland. The fields studied comprised the following (GF prefix: Grove Farm fields; HN prefix: Hardington Moor fields):

GF76R *South-eastern part of Plain Close pasture*. ST 5130 0956. Arable on 1808 estate map, but pasture on 1844 Tithe map. Ploughed in 1976 and immediately reseeded with rye-grass mixture. Since then grazed as cattle pasture with the other fields on Pen Hill. Assumed age at time of survey: 20 years.

GFCRR *Barley Plot.* ST 5101 0977. Recorded as pasture in both 1808 and 1844. Ploughed post-World War II, with 2–3 years of crops in the 1970s, followed by reseeding as a rye-grass pasture. Since then cattle pasture. Assumed age: 20 years.

GF60R *Higher Dampier's Ground.* ST 5142 0963. Arable in 1808 and 1844, assumed followed by a long period of pasture until *c*. 1960 when it was ploughed and then reseeded, not with rye-grass but with 'hay-seed', using seed from the indigenous hay crop. Used as cattle pasture since. Assumed age: 35 years.

GF52TS *Ope Field.* ST 5136 0937. Pasture in both 1808 and 1844, but ploughed and subsoiled in 1952, subsequently cattle pasture with the rest. Assumed age: 45 years.

GFU1 *South-western field of Plain Close.* ST 5120 0949. Pasture in 1808, 1844 and assumed subsequently. Now grazed with cattle with the remaining Pen Hill fields. High density of large ant-hills. Assumed age: 200+ years.

GFU2 *North-western part of Plain Close.* ST 5121 0969. Arable in 1808 but pasture by 1844 and assumed subsequently. Grazed by cattle with the remaining fields, but with evidence of recent 'poaching' (bare ground resulting from concentrations of animal hooves, often in wet conditions) not seen elsewhere in the sampled fields. High density of large ant-hills. Assumed age: 160 years.

GFU3 *Field east of Higher Dampier's Ground (*and separated from it by a large ancient hedgerow). ST 5153 0965. Estate map of 1808 labels 'arable' over both this field and Higher Dampier's Ground, but likely to refer to only Higher Dampier's Ground because of separation. Pasture by 1844 and assumed subsequently. High density of large ant-hills. Assumed age: 200+ years.

HNU *Southern portion of Hawkins Hill pasture*. ST 5145 1266. Pasture on 1843 Tithe map and no record of ploughing or other disturbance. Reportedly the part of the NNR most similar to HNP before the latter was ploughed. Managed in the same way as HNP, except that it received farmyard manure in 1996. Assumed age: 200+ years.

HNP *Coker Hill.* ST 5152 1293. Arable in 1843, but described as ancient species-rich grassland until ploughed and cropped for two years in 1984–5. Since then it has reverted to grassland (without any deliberate reseeding) and has been managed by hay-cutting and aftermath grazing by cattle. Assumed age: 12 years.

Site environmental factors

Values were given to a series of environmental variables which included: age since last ploughing in years; reseeding with a 'modern' rye-grass (*Lolium perenne*) mixture with fertiliser; 'hay-seed' reseeding; subsoiling; evidence of poaching. Sward height and percentage of bare ground were recorded within the quadrat samples, as described below.

Quadrats

Field survey was carried out in 1997. Six quadrats were located within each field by a 'random walk' method (see Gibson 1997). Each quadrat was 1m square, divided into 25 20cm square cells. Before placing the quadrat, three estimates of sward height were made using a drop-disc (Anon 1986). The quadrat was then placed in position and a full vascular plant species list recorded within each cell. The percentage of bare ground was estimated by eye for the whole quadrat. Within each field, sampling was restricted to areas of MG5 grassland, or to its assumed precursors in the case of recently disturbed/early successional fields. Ant-hills and patches of scrub were excluded from sampling.

Multivariate assessment procedure

Data analyses were carried out largely using CANOCO (ter Braak 1992). Detrended correspondence analysis (DCA) was used to explore the data structure and check for anomalies which might suggest the need for data transformation, exclusion of outlying samples or species, or any other modification. Investigation of the effects of key variables was carried out by detrended canonical correspondence analysis (DCCA), with relations between environmental variables and vegetation built up stepwise. Variables were only included if they had an individual effect at a significance level of $p<0.01$. A partial DCCA analysis was used to factor out the effects of all variables except age as 'covariables', leaving an estimate of the extent to which species composition was being determined by age of grassland. For a fuller explanation of these and other analyses see Gibson (1998).

Attributes of the vegetation chosen to illustrate the effects of age and other variables included: (a) species richness; (b) species diversity as measured by Williams' alpha (Southwood 1974) to show evenness as well as richness; (c) mesotrophic indicator species scores (Rowell and Robertson 1994), in which species scored from 1 to 8 with increasing strength of restriction to agriculturally unimproved mesotrophic grasslands; (d) CANOCO indicators of successional age derived from the partial DCCA analysis described above. Nomenclature follows Stace (2010).

RESULTS

Species richness

The majority of fields contained species-rich vegetation by most standards of comparison (Table 1), with older fields having 30+ species per 1m square. The central row in Table 1 shows species-richness figures for fields having a known age since ploughing and no additional factors affecting them. The top row shows the field subjected to an additional factor (hay-seeding) which would be expected to accelerate development towards a species composition resembling that of an ancient agriculturally unimproved grassland community. The bottom row shows fields with additional factors that might be expected to have had a *negative* effect on floristic composition. The results show that the hay-seeded field and the oldest fields were the richest by a relatively small margin. A field with markedly lower richness (just over half that of the best fields) had been subject to cropping followed by reseeding and relatively 'intensive' grassland management. Poaching in one field appeared to have had no effect on richness.

The greatest difference between fields is shown in the richness of mesotrophic indicator species, being virtually absent from the 1976 cropped and reseeded field and showing a clear successional trend – although the hay-seeded field was again slightly the richest overall. Poaching again apparently had no effect. Patterns in species diversity as measured by Williams alpha were almost identical to those of species richness (Gibson 1998) and so are not shown here.

Multivariate analyses

The pattern shown on the first two axes of the multivariate analysis (DCA) suggests a contrast between successional age or other disturbance and between Hardington Moor and Grove Farm fields (Fig. 1). Quadrats from Hardington Moor scored low on both axes, but those from the recently ploughed field scored higher on axis 2 and lower on axis 1 than did the ancient grassland. Grove

TABLE 1: AVERAGE TOTAL VASCULAR PLANT SPECIES RICHNESS (TOP ROW WITHIN CELL) AND NUMBER OF MESOTROPHIC INDICATOR SPECIES (BOTTOM, ITALICS) PER 1M SQUARE IN FIELDS WITH PARTICULAR PAST HISTORIES, WITH ASSUMED FACTORS AFFECTING RICHNESS

Last ploughed	**1984**	**1976**	**1960s**	**1952**	**200+ yrs**
Assumed positive factor			Hayseed		
			39.8 *18.8*		
No additional factor	28.0 *8.2*	34.7 *13.5*			36.8 *17.9* (3 fields)
		20.7 *2.2*		31.7 *13.2*	37.7 *17.8*
Assumed negative factor		Ryegrass & crop		Subsoiled	Poaching

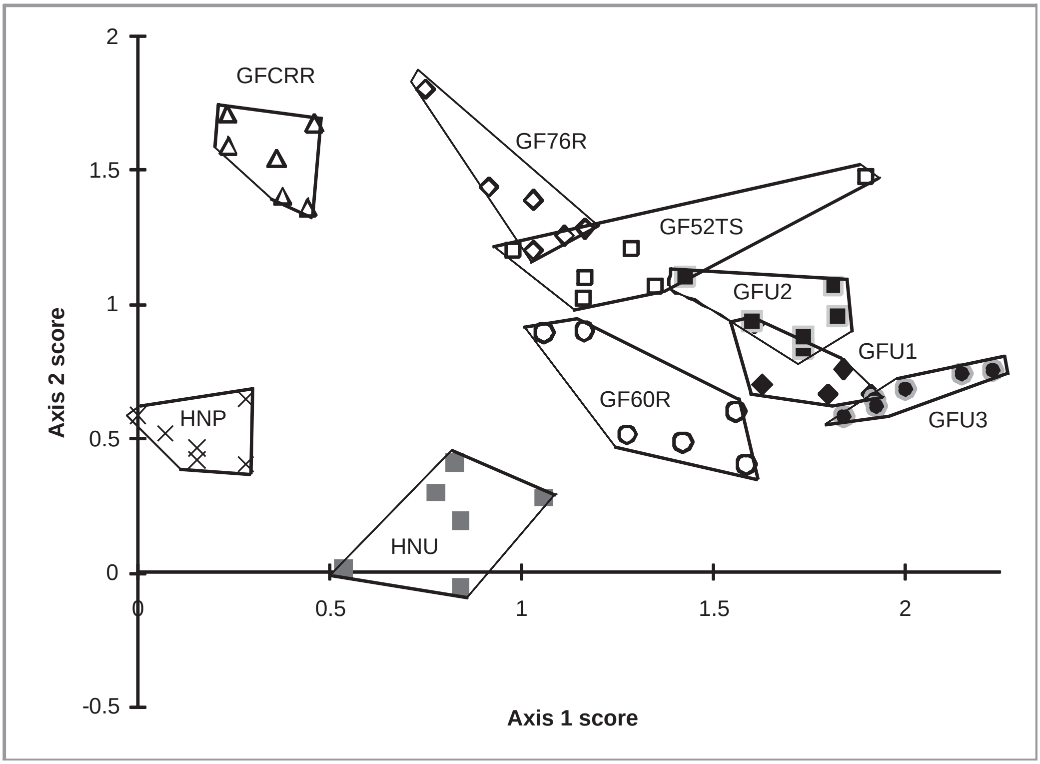

Fig. 1 Quadrat positions on the first two axes of a detrended correspondence analysis (DCA). Polygons enclose six quadrats from each field in the two sampled sites. Solid symbols indicate fields of oldest assumed age

Farm quadrats form a similar and parallel but more extensive series (Fig. 1), with disturbed and/or young fields scoring high on axis 2 and low on axis 1 and ancient grassland scoring lower on axis 2 but with much higher axis 1 scores than the equivalent Hardington Moor field.

Analysis by DCCA identified grassland age, sward height, reseeding, subsoiling and seeding with hay-seed as having significant effects on species composition (Fig. 2). Increasing age was closely associated with low scores on axis 1 and less so with low scores on axis 2 (note direction of arrow). The reseeding effect had a high score on both axes (represented as a point – centroid – because it is a nominal variable). The effect of hay-seeding is associated with low scores on axis 2, while taller swards are indicated with high scores on axis 1 and low scores on axis 2. Note that the youngest field (HNP) was also shut up for hay at the time of survey, so inevitably had a taller sward.

Examination of the species concerned (in Fig. 2) suggests that the formal explanation of the DCCA largely reflects the informal interpretation from the illustrative DCA analysis above (Fig. 1). Species in the upper right quadrant were virtually all ones well known to be associated with disturbance or agricultural improvement, eg *Bromus hordeaceus (= B. mollis), Lolium perenne, Taraxacum* agg. and *Trifolium dubium*. Conversely the taller swards included species such as *Vicia cracca* and *Lathyrus pratensis* which are also associated with hay management (Gibson 1998). Individual effects of the remaining variables were more difficult to disentangle, but an apparent association of *Trifolium medium* with the hay-seeded field is of note.

Successional categories

A partial DCCA analysis (not shown here; see Gibson 1998, fig. 7) factored out the effects of variables other than age. Axis 1 of the resulting ordination revealed a clear relationship between vegetation composition and age, with many species

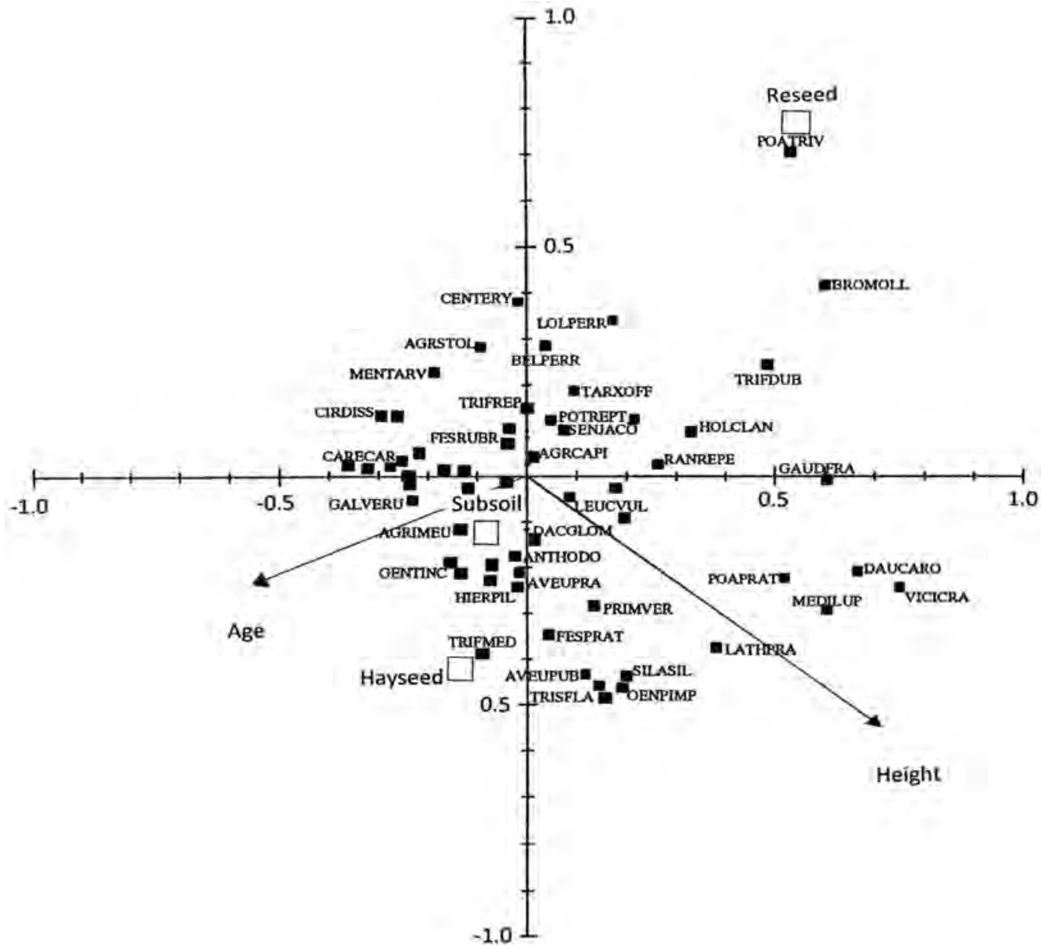

Fig. 2 Species scores and environmental variable influences on the first two axes (axis 1 = horizontal axis) of a detrended canonical correspondence analysis (DCCA) of South Somerset SSSI vegetation data. Only significant (at $p<0.01$) environmental variables are included. Distance from origin indicates magnitude of effect. Nominal variables shown by a data point (□) rather than by an arrow from the origin (ordinal variables)

Labelled species codes are abbreviated and some not shown (for clarity) as: AGRCAPI *Agrostis capillaris* AGRIMEU *Agrimonia eupatoria*, AGRSTOL *Agrostis stolonifera* AJUGREP *Ajuga reptans* ANTHODO *Anthoxanthum odoratum* AVEUPR *Avenula pratensis* AVEUPUB *Avenula pubescens* BELPERR *Bellis perennis* BROMOLL *Bromus hordeaceus subsp. hordeaceus* CARECAR *Carex caryophyllea* CENTERY *Centaurium erythraea* CIRDISS *Cirsium dissectum* DACGLOM *Dactylis glomerata* DAUCARO *Daucus carota* FESPRAT *Schedonora pratensis* FESRUBR *Festuca rubra* GALVERU *Galium verum* GAUDFRA *Gaudinia fragilis* GENTINC *Genista tinctoria* HIERPIL *Pilosella officinarum* HOLCLAN *Holcus lanatus* LATHPRA *Lathyrus pratensis* LEUCVUL *Leucanthemum vulgare* LOLPERR *Lolium perenne* MEDILUP *Medicago lupulina* MENTARV *Mentha arvensis* OENPIMP *Oenanthe pimpinelloides* POAPRAT *Poa pratensis* POATRIV *Poa trivialis aris* POTREPT *Potentilla reptans* PRIMVER *Primula veris* RANREPE *Ranunculus repens* SENJACO *Senecio jacobaea* SILASIL *Silaum silaus* TARXOFF *Taraxacum seedling/sp.* TRIFDUB *Trifolium dubium* TRIFMED *Trifolium medium* TRIFREP *Trifolium repens* TRISFLA *Trisetum flavescens* VICICRA *Vicia cracca* being apparently associated with grassland of a particular age. The spread of species on axis 2 reflected residual variation not explainable by any of the environmental variables or covariables. On axis 1 species associated with younger grasslands had low (negative) scores, those occurring predominantly in older grasslands high (positive) scores, and those found throughout the age range ‘middling’ scores (close to zero). Species were divided on the basis of their axis 1 scores, to produce seven groups, as described below. The ordination diagram is not shown here, but species are listed in Table 2 where they are arranged in order from Group 1, the species most associated with the oldest grasslands, to Group 7, those most associated with the youngest grasslands.

Figure 3 shows the relative contributions made by each of the seven groups to grassland of different ages, irrespective of any additional (either positive or negative) treatments. In Figure 3 grasslands not ploughed since at least 1808 have been given a notional age of 200+ years.

Group 1 species were almost wholly restricted to the oldest grasslands, where they formed an

TABLE 2: SPECIES CATEGORISED INTO DIFFERENT ASSUMED SUCCESSIONAL STAGES FROM DIVISION OF THE FIRST CANONICAL AXIS OF A PARTIAL DCCA (GIBSON 1998: FIG. 7)

Species shown in **bold underline** occurred in ten or more of the 54 quadrats, those in **bold** in five or more quadrats. Sparser species cannot be presumed to be reliably associated with particular stages: they merely happened to be found there in this study. Woody plant seedlings are omitted

Axis 1 score	Species
1: >3.0 Oldest	*Arrhenatherum elatius*, ***Avenula pubescens* (=*Helictotwrichon pubescens*)**, *Blackstonia perfoliata*, *Carex pulicaris*, *Convolvulus arvensis*, ***Schedonorus pratensis* (=*Festuca pratensis*)**, ***Scorzoneroides autumnalis* (=*Leontodon autumnalis*)**, ***Oenanthe pimpinelloides***, *Oenanthe lachenalii* (misidentified as *O. silaifolia*?), ***Anacamptis morio***, *Plantago media*, *Potentilla sterilis*, *Poterium sanguisorba* (=*Sanguisorba minor*), ***Serratula tinctoria***, ***Silaum silaus***, *Betonica officinalis* (=*Stachys officinalis*), ***Tragopogon pratensis***, ***Trisetum flavescens***
2: >2.0	***Avenula pratensis* (= *Helictotrichon pratense*)**, *Brachypodium sylvaticum*, ***Briza media***, ***Cirsium acaule***, ***Danthonia decumbens***, *Pilosella officinarum*, **Polygala vulgaris**, ***Ranunculus acris***, ***Succisa pratensis***
3: >1.0	***Achillea millefolium***, ***Agrimonia eupatoria***, ***Ajuga reptans***, ***Anthoxanthum odoratum***, ***Carex caryophyllea***, ***Carex panicea***, ***Centaurea nigra***, ***Cirsium dissectum***, ***Dactylis glomerata***, *Deschampsia cespitosa*, ***Festuca rubra***, ***Galium verum***, ***Genista tinctoria***, *Heracleum sphondylium*, ***Hypochaeris radicata***, ***Lotus corniculatus***, ***Plantago lanceolata***, ***Potentilla erecta***, ***Primula veris***
4: >0	***Agrostis capillaris***, ***Carex flacca***, ***Cirsium palustre***, ***Cynosurus cristatus***, *Elytrigia repens*, *Euphrasia officinalis* agg., ***Holcus lanatus***, *Hordeum secalinum*, ***Lathyrus pratensis***, ***Leontodon hispidus***, *Leontodon saxatilis*, ***Linum catharticum***, ***Luzula campestris***, *Pedicularis sylvatica*, ***Poa trivialis***, *Potentilla anserina*, ***Ranunculus bulbosus***, ***Taraxacum* agg.**, *Trifolium medium*, ***Trifolium pratense***, ***Trifolium repens***, *Veronica officinalis*, **Viola hirta**, ***Viola riviniana***
5: >-1.0	*Alchemilla vulgaris* agg., ***Bellis perennis***, ***Bromus hordeaceus* subsp. *hordeaceus***, ***Cirsium vulgare***, ***Gaudinia fragilis***, ***Leucanthemum vulgare***, ***Lolium perenne***, *Mentha arvensis*, ***Phleum pratense***, ***Potentilla reptans***, ***Prunella vulgaris***, ***Pulicaria dysenterica***, ***Ranunculus repens***, ***Senecio erucifolius***, ***Senecio jacobaea***, ***Trifolium dubium***
6: >-2.0	***Agrostis stolonifera***, ***Cerastium fontanum***, *Cirsium arvense*, *X Schedolium loliaceum* (= *X Festulolium loliaceum*), *Geranium dissectum*, *Juncus acutiflorus*, **Medicago lupulina**, ***Poa pratensis***, *Rumex acetosa*, ***Sagina procumbens***
7: <-2.01 Youngest	***Centaurium erythraea***, ***Daucus carota***, *Hypericum maculatum*, *Hypericum perforatum*, *Hypericum tetrapterum*, ***Juncus inflexus***, *Veronica serpyllifolia*, **Vicia cracca**

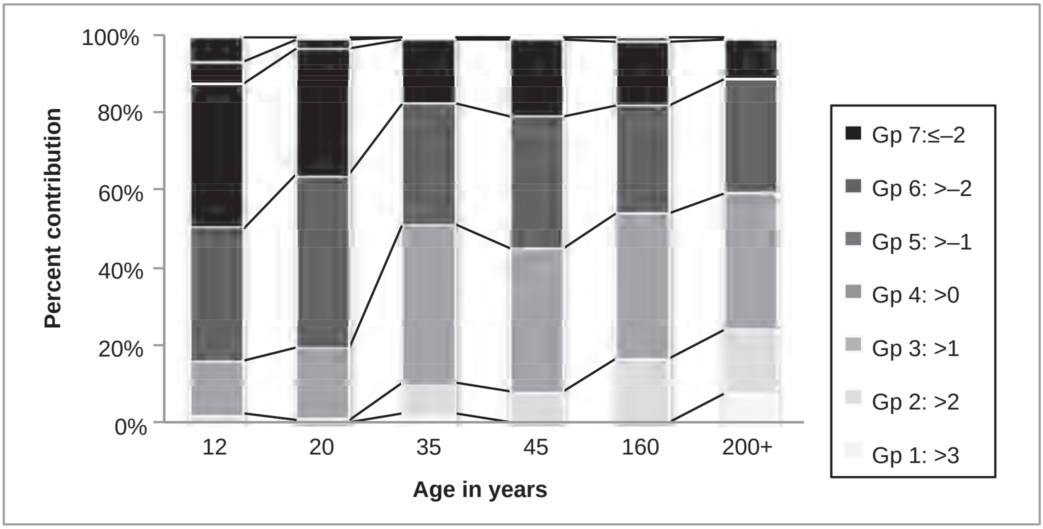

Fig. 3 Relative contribution of successional groups (shown in legend as Gp 1–7, with partial DCA score) to grassland of different assumed age. For details of species groups see Table 2

important yet relatively minor (less than 10% frequency within 20cm x 20cm cells) component of the sward. Two examples of Group 1 species were *Schedonorus pratensis (=Festuca pratensis)*, a surprising member of this group as it is widespread in grasslands elsewhere not noted for their age and, less surprisingly, *Serratula tinctoria* (Fig. 4a).

Group 2 species were virtually absent from the youngest grasslands and only became an important component of the vegetation in grasslands over a century old. This group contained several strong indicators of ancient unimproved grasslands (calcareous and/or mesotrophic), exemplified by *Succisa pratensis* and *Briza media* (Fig. 4b).

Group 3 species, on the other hand, were present as a significant component in early successional grassland, their contribution doubling between grasslands of 20 and 35 years old but showing little change thereafter (Fig. 3). Individual species were sometimes erratic in their relationship, such as *Anthoxanthum odoratum* (Fig. 4c), perhaps as a result of particular conditions in individual fields; but some other species showed a much more even increase, eg *Potentilla erecta* (Fig. 4c).

Group 4 species were a major component of all the grasslands studied, irrespective of age, although overall their contribution tended to decrease slightly from the youngest to the oldest fields (Fig. 3). A large number of Group 4 species showed no particular trend with age, eg *Trifolium pratense* and *Carex flacca* (Fig. 4d).

Groups 5 to 7 clearly defined early succession, with species in Groups 6 and 7, eg *Poa pratensis* (Fig. 4f) only a noticeable component in the youngest grassland sampled, at Hardington Moor. Group 5 species made a significant contribution here, but declined steadily in older grasslands. It is notable that this group contains a number of species which are commonly (and perhaps mistakenly) regarded as signs of 'success' in wildflower grassland creation, such as *Leucanthemum vulgare* (Fig. 4e). One species particularly associated with these younger grasslands was the Nationally Scarce *Gaudinia fragilis* (Fig. 4e), an annual for which there has been much recent debate as to whether it is native or introduced to Britain (Leach and Pearman 2003).

Succession and the MG5 sub-communities

The grasslands at Grove Farm and Hardington Moor are unusual in containing all the species showing a high constancy in MG5 grassland and all those known to be preferential to each of the three MG5 sub-communities (Rodwell 1992), apart from *Koeleria macrantha* (an MG5b preferential) and *Pimpinella saxifraga* (an MG5c preferential). It is noteworthy that these sub-community preferentials are often mixed together in a single quadrat. Twenty

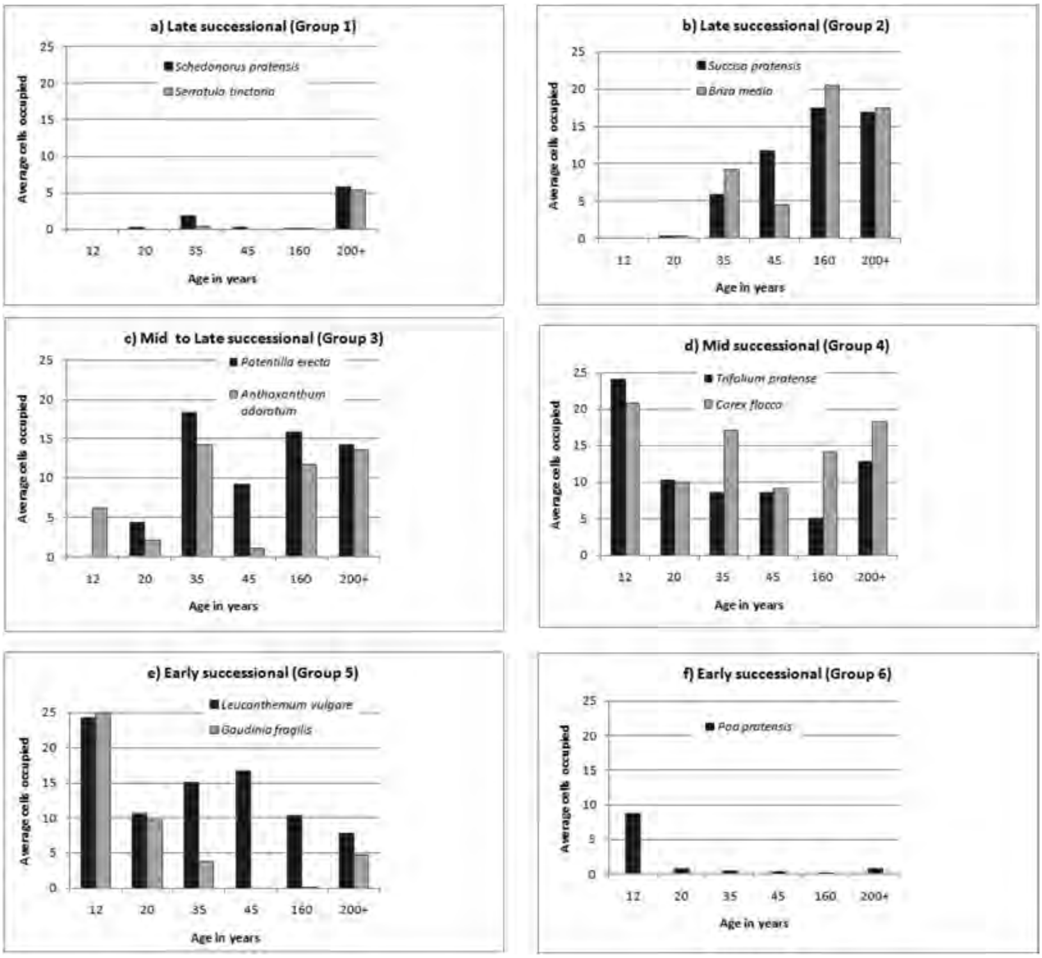

Fig. 4 Examples of individual species frequencies in grassland of different assumed age

of the 25 sub-community preferentials were abundant enough to be encountered in at least one quadrat.

All the MG5 constants fall within Groups 4 and 5 in Table 2, ie they were species which occurred widely across all the fields studied, regardless of age. It is amongst the sub-community preferentials that a successional pattern emerges (Fig. 5). As a group, MG5a (*Lathyrus pratensis* sub-community) preferentials were found to be nearly twice as common in the early successional fields as in the oldest ones. MG5b (*Galium verum* sub-community) preferentials showed no particular pattern, but MG5c (*Danthonia decumbens* sub-community) preferentials showed a marked successional trend. The latter formed only a minor component of the youngest grassland and steadily increased to peak in swards over 100 years old.

DISCUSSION

Age and other variables

In this study, successional age was calculated on the basis of ‘time since last ploughing’. Other disturbance events – eg reseeding, subsoiling, cropping, poaching – varied between fields, and it is likely that different events or *combinations* of events would produce different levels of damage to the grassland and its underlying soils, and would therefore influence the

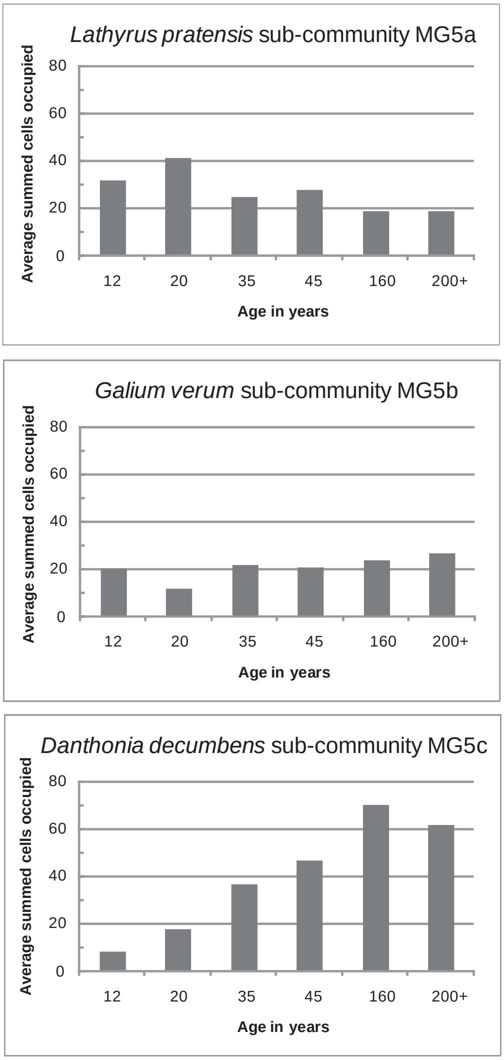

Fig. 5 The contribution made by MG5 sub-community preferentials in grassland of different assumed age

'recovery time' (speed of succession) of individual fields. Nevertheless, it has been possible from the data gathered to derive at least a *preliminary* view of grassland succession in MG5. The results reinforce other studies (Olff and Bakker 1991; Mountford *et al.* 1993) which have shown that reseeding and agricultural improvement cause damage which is long-term and difficult to reverse.

It is noteworthy, however, that 'hay-seeding' at Grove Farm produced a grassland which in only a few decades had become as rich in species – including indicators of high-quality mesotrophic grassland – and as diverse as the oldest fields included in the study. This is reminiscent of Gibson and Brown's (1991) failure to distinguish the wartime ploughed Stony Piece chalk grassland at Aston Rowant NNR from adjacent ancient chalk grassland by analysis of species composition. However, the hay-seeded field differed from the oldest grasslands at Grove Farm in two respects: (1) it emerged as a distinct cluster in the DCA ordination (Fig. 1); (2) it had a much lower cover and frequency of MG5c preferentials which, as already noted, seemed to be particularly associated with grassland more than a century old.

The results presented here should be treated with caution. Firstly, most successional ages and treatments were represented by only one field, and clearly the results may not therefore be representative of similar situations elsewhere. Secondly, and unusually for the late 20th century, the Grove Farm grasslands when disturbed have always had other species-rich grassland patches adjoining them. Thus, quite apart from the buried seed-bank, the potential for relatively rapid recolonisation from neighbouring patches would have been very high – a situation unlike that of many grasslands elsewhere in lowland Britain where individual fields usually occur some distance away from their nearest potential seed sources. Thirdly, despite choosing only those fields with relatively simple management and past history, there may have been unknown or unreported factors complicating the results in individual fields. Lastly, the grasslands at Grove Farm and Hardington Moor are unusually species-rich, and the conclusions presented here may not apply to less species-rich sites.

Why are the older grasslands so species-rich?

The source of this richness lies principally in the fact that a mixture of species preferential to all three of Rodwell's (1992) MG5 sub-communities occur together, often including both calcicoles and calcifuges. Patches of grassland at Grove Farm can readily be found where *Succisa pratensis* (MG5c), *Poterium sanguisorba* (= *Sanguisorba minor*) (MG5b), and *Leucanthemum vulgare* (MG5a) grow intertwined in the same few square centimetres. Without specific information, one must assume that the coexistence of such species reflects temporal and/or spatial edaphic variation at a very small scale.

The cause of this phenomenon at Grove Farm is, however, likely to be less obvious than the clear vertical stratification found in chalk heaths, where sand layers over chalk allow both calcicoles and calcifuges to coexist on a small scale (Watt 1936). The Soil Survey of England and Wales (1984) maps the local soils as Evesham I Association. The deeper soils within this association are calcareous pelosols over clay shales; the essential characteristic of these soils is that they are only slowly permeable and, despite having calcareous layers, develop mottling and a spatial mosaic of different pH at a very small scale. Given the underlying calcareous nature of these soils, it is tempting to speculate that the spatial component which takes time to develop after deep ploughing or other disturbance is patchy acidity. This would be a plausible explanation for the gradual increase in cover/frequency of MG5c preferentials over time, but one which would need specific research to test. The time required to produce these MG5 grasslands is therefore likely to be due to a combination of plant colonisation rates and soil development.

The workings of MG5 succession

The studies reported here did not include any fields in the first few years after ploughing. Even so, the patterns observed broadly agree with those reported in calcareous grassland successions, with one important difference: there appear to be no species which are rare in both early and late succession, but which are common components in the middle decades. There is a strong component of this sort in calcareous grassland succession (Gibson and Brown 1991), comprising mainly robust but relatively short-lived species such as *Pastinaca sativa*, *Knautia arvensis* and *Silene vulgaris*. There were few such species in the fields studied at Grove Farm – although one which did occur, *Daucus carota*, seemed to be restricted to the youngest fields examined.

In contrast, there was a strong component of species which were already present in the youngest grasslands studied and remained a significant proportion of the vegetation throughout. These included the great majority of MG5 constants, as well as some MG5a and MG5b preferentials such as *Leucanthemum vulgare*. This finding may be partly due to the fact that the youngest grasslands studied here had only been under the plough for a short time; in such circumstances species from the original grassland could have survived in the buried seed-bank, or even as vegetative fragments.

Although species strongly associated with the oldest grasslands included many MG5c preferentials (Fig. 5), they also included several species characteristic of more calcareous conditions such as *Avenula pratensis* (= *Helictotrichon pratense*) and *A. pubescens (H. pubescens)*. The oldest grasslands in this study were thus characterised by a mixture of species of varied ecological requirements which have in common only their status as long-lived perennials and their observed slowness in colonisation. Species of nature conservation interest in their own right, such as *Anacamptis morio* and *Oenanthe pimpinelloides*, were usually, but not always, associated with the older grasslands (see Table 2). It seems reasonably clear that while individual species of interest can sometimes appear quite early in the succession, the full species complement characterising these species-rich grassland communities cannot.

Conclusions and consequences

Assuming that the findings of this study can be used as a starting point for developing a more general understanding of mesotrophic grassland succession, there are significant consequences for site safeguard and restoration, and implications too for other studies which depend on manipulating succession.

With respect to site safeguard, it is clear that MG5 grassland may take a similar order of time to acquire its full species complement as that seen in calcareous grasslands, ie well over a century. This is a minimum estimate, as in calcareous grasslands, because it takes no account of the development of specialised fauna and of biological/structural components such as ant-hills. The considerable value and practical irreplaceability of real ancient grasslands is thus emphasised: they have a special interest which cannot be repaired or re-created within normal human timescales. With respect to restoration, the results demonstrate that in certain circumstances (rarely occurring in modern Britain because surviving sites are usually small and/or isolated) attractive, floristically rich grasslands can reappear within a few decades, attaining (as in the hay-seeded field) many *but not all* of the attributes of ancient grasslands. It should be stressed, however, that the presence of a wide range of MG5 constants in a field of ‘new’ MG5 does not mean that a facsimile of an ancient MG5 grassland has been successfully created. Indeed, this aspect of the grassland community – producing a reasonably good 'fit' to MG5 as described in Rodwell (1992) – is probably one of the easier aspects of MG5 grassland to re-create.

As already noted, the fact that this study was limited to a small geographical area and a small number of fields means that the conclusions are only preliminary. It is hoped that they will encourage experimental tests of the findings, and form a foundation for others to extend the observations to grasslands of known age and treatment elsewhere.

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