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Short-term successional change does not predict long-term conservation value of managed arable field margins

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ABSTRACT

Field margins have been widely advocated as a means of integrating agronomic and biodiversity objectives and are included in agri-environment schemes across Europe. However, information on the long-term development of field margin plant communities remains limited. We describe a long-term experiment on the effects of field margin management on biodiversity and weed species. Swards were established by natural regeneration or sowing a grass and wildflower seed mixture, and treatments manipulated the frequency and timing of mowing, application of herbicide and leaving of hay. Vegetation was monitored to evaluate the extent to which early conclusions remained valid after 13 years. Although early successional trends suggested that naturally regenerated swards would rapidly become dominated by pernicious perennial weeds, and that sown swards would exclude such species, neither was true in the longer term. Sown swards were eventually invaded by unsown perennials, but they remained distinct from naturally regenerated swards. Plant species richness declined throughout the experiment. Annuals were lost most rapidly from sown swards but, under natural regeneration, loss could be modified by mowing. Perennial species initially increased during natural regeneration before stabilising. In sown swards they declined under all treatments. Species richness in naturally regenerating swards was promoted initially by mowing twice annually. After 13 years, timing and frequency of mowing had no significant effect on species richness although it still influenced sward composition. Leaving cut hay lying produced species-poor swards. We conclude that the choice of establishment and management methods for arable field margins significantly affects the long-term conservation value of the swards.

Key words: agriculture, biodiversity, agri-environment schemes, weed control, mowing regimes, species richness

1. Introduction

The boundaries between fields are one of the principal resources for wildlife in intensively farmed lowland areas in Europe (Marshall and Moonen, 2002), providing a range of habitats, including hedges, ditches and uncropped grassy margins, and connecting larger blocks of semi-natural habitat. In the UK, the potential value of arable field margins has been recognised by the UK Biodiversity Steering Group (Anon, 1995a,b). Widespread degradation and loss of field margins during the agricultural intensification of the second half of the 20^{th} century (e.g. Chapman and Sheail, 1994; Haines-Young et al., 2000; Sotherton and Self, 2000; Chamberlain et al., 2000) has generated many policy initiatives over the last twenty years.

Recent reforms of the Common Agricultural Policy are encouraging European Union member states to switch their farm support mechanism from production-based subsidies to payments conditional on cross-compliance with EU environmental directives (e.g. Ovenden, Swash and Smallshire, 1998; Primdahl et al., 2003). Agri-environment schemes provide incentives for further improvements (Radley, O'Reilly and Jowitt, 2005) and their implementation is currently considered the most important policy instrument through which to reverse widespread biodiversity declines across European agricultural landscapes (Donald and Evans, 2006). In the UK, over five million hectares of land are now covered by Environmental Stewardship agreements (Defra, 2008). This two-tier scheme has a range of environmental objectives, including wildlife conservation, with both tiers incorporating options for restoration and management of uncropped field margins.

Recognition of the importance of field margins for biodiversity conservation triggered many research initiatives designed to inform prescriptions for their restoration and management (Vickery, Feber and Fuller, 2009). Many of these have been short- term and have focussed on early successional stages of habitat re-creation (e.g. Marshall and Nowakowski, 1995; Huusela-Veistola and Vasarainen, 2000; De Cauwer et al., 2005). The new generation of agri-environment schemes has a longer-term focus (with agreements of either five years (Entry Level Stewardship) or ten years (Higher Level Stewardship agreements)) and corresponding requirement for long-term research.

While there have been many studies of successional processes on set aside (e.g. Critchley and Fowbert, 2000; Firbank et al., 2003) and grassland restoration on former arable land (e.g. van der Putten et al., 2000; Pywell et al., 2002; Walker et al., 2004; Donath et al., 2007), few studies have specifically concerned sward development on arable field margins over the longer term (e.g. Bokenstrand et al., 2004). This is surprising given the evidence that relatively small differences in field margin establishment and initial management can result in significant differences to the developing plant (Smith, McCallum and Macdonald, 1997; Critchley et al., 2004; de Cauwer et al., 2005, Westbury et al., 2008) and invertebrate (Feber et al., 1996; Baines et al., 1998; Asteraki et al., 2004; Smith et al. 2008; Woodcock et al., 2008) communities. Studies in other grassland communities have shown that short-term changes do not necessarily predict long-term composition (e.g. Gibson and Brown, 1992). The method of field margin establishment and subsequent management will have significant consequences for the performance of individual species and the conservation value of the resulting sward, and financial and practical implications for the farmer. Elucidating the broad principles of long-term change that are likely to occur in arable field margin composition will help enable ecologically appropriate and cost-effective decisions to be made at the outset.

A large-scale, long-term field experiment at the University of Oxford's Farm at Wytham, Oxford, provided a unique opportunity to answer key questions about succession on field margins adjacent to intensively farmed arable land, and timely guidance for new incentive schemes. The experiment was established in 1987 to evaluate the impact on wildlife, and the implications for crop husbandry, of simple and practical regimes for managing permanent grassy margins around conventionally-farmed fields. The field margins were established on former cultivated field edges either by sowing a wild grass and forb mixture or by allowing natural regeneration. The development of plant species richness, and the fate of key individual species of agricultural concern and conservation interest, was monitored intensively during the establishment phase of the experiment, until 1990. The experiment was maintained for a further ten years and the vegetation recorded again in 2000.

In this paper we use these data to examine the role of the management regimes in determining the species richness and composition of the swards 13 years after their establishment and test the extent to which our conclusions about effective sward management from the early years remained relevant. In particular we addressed the following questions:

Are early trends in succession a guide to longer term species composition?

Does sowing a grass and wildflower seed mixture promote higher species richness than natural regeneration and are these species more or less valuable for wider aspects of biodiversity?

To what extent can species richness and composition of sown and naturally regenerated swards be manipulated by simple mowing regimes in the medium term?

How long do weed populations persist and does this differ with management regime?

We discuss the implications of our results for the restoration of diverse and attractive permanent grass margins around arable fields and, more generically, of other grassland establishment on former arable land.

2. Methods

Two metre wide uncropped margins were created around six arable fields at the Oxford University Farm, Wytham, UK (1˚19' W 51˚47' N) in autumn 1987. They comprised the original (pre-existing) uncropped field margin (approximately 0.5m wide), and a *ca* 1.5m wide fallowed extension onto cultivated land. The fallowed margin extension is the subject of this paper.

Ten treatments were imposed on 50m-long plots in a randomised complete block design with six blocks. Each block was located around a single field, with three blocks located on sandy clay soils and three on clay loam or heavy clay soils. All blocks except one were bounded by hedgerows (the exception was bordered by a track), and the boundary type within each block was the same for all treatment plots. All the experimental fields had a long history of intensive arable use and, in the years prior to establishing the experiment, had been under continuous cereal production. From 1988 onwards they were returned to a rotation, usually with two years of winter wheat, one of winter barley, and the fourth with a break crop of rape, maize or winter beans.

Eight of the treatments formed a 2x4 factorial structure: four were sown with a mixture of wild grasses and forbs and four were allowed to regenerate naturally. They then received one of four cutting regimes: uncut, or cut (with cuttings removed) in (a) summer only (b) spring and summer or (c) spring and autumn. Cutting height was *c*.4-5cm. The plots were first cut in June 1988 and in subsequent years in the last weeks of April, June and September ('spring', 'summer' and 'autumn' respectively). The new margins were rotavated in March 1988 just before the seed mixture was sown. This contained six 'non-aggressive' species of grass and 17 forbs, in a 4:1 ratio, and was sown at 30 kg/ha (Smith *et al*. 1993; Supplementary Material Table S1). All sown species were perennial except for *Torilis japonica*, *Silene latifolia* ssp. *alba* (which can be annual, biennial or perennial), and *Tragopogon pratensis* which is biennial. The remaining two treatments, imposed on naturally regenerating plots, comprised (a) cutting in spring and summer but leaving cut hay *in situ,* and (b) spraying with glyphosate (Roundup, Monsanto Co.; 1.08 kg (a.e.) ha^{-1} (3 l ha^{-1} product) at a volume rate of 175 l ha^{-1}) in late June each year.

The plant species on the margins were monitored at least three times a year until 1990, and again in late July 2000, in three 50x100cm permanent quadrats, situated with their long-axes parallel with the field margin at 15, 25 and 35m along each 50m plot. Relative frequencies were estimated by recording presence/absence of all species rooted within each of eight 25x25cm cells within each quadrat. The frequencies of some key weed species were also monitored in 1991, 1992 or 1993. Species richness is expressed as the mean number of species recorded per quadrat on each plot.

Data for different sampling occasions were initially analysed by 2-way analysis of variance (ANOVA) (blocks x treatments) following appropriate transformation to achieve homogeneity of variance (SAS, 2004). Planned comparisons were used to test for the effects of hay removal (both cut in spring and summer) and herbicide application. A further three-way ANOVA was performed on the eight treatments that formed a 2x4 factorial structure, allowing the treatment effect to be split into main affects of sowing and cutting. We used three sets of planned comparisons to test between: (1) plots that were cut and those left uncut, (2) those cut once and those cut twice and (3) those cut in spring and summer and those cut in spring and autumn.

3. Results

3.1 Species Richness

3.1.1 Temporal trends

Species richness declined over a thirteen-year period. The most rapid decline was after one year, between 1988 and 1989, and under all treatments numbers of species had approximately halved by 2000 (Table 1). Most of the rapid initial decline in species richness was attributable to loss of annuals from the closing swards (Fig. 1). Eighty-seven annual species were recorded on the 50m field margin plots, almost all of which were arable weeds originating either from the seedbank or crop (Smith et al. 1993).

3.1.2 The effects of sowing

Annuals were excluded most rapidly from sown plots, where the numbers of species were significantly lower than in naturally regenerated plots within a year of sowing (Fig.1, Supplementary Material Table S2). By 2000 there were so few annual species in all treatments that the effect of sowing on their numbers could no longer be detected.

Numbers of perennial species initially increased in naturally regenerated plots and then apparently remained stable for the following ten years (Fig. 1). By contrast, in sown plots, they declined throughout the experiment; this decline was most rapid amongst naturally colonising, rather than the sown, species in the early stages of the experiment. Sown species increased to around 70% of the total species complement of sown swards during this period before declining over the next ten years (Fig. 2). After the initial decline, numbers of naturally colonising species in sown swards remained relatively constant, so that, by 2000, they slightly exceeded those of sown species, averaged over all cutting treatments.

Despite the decline, sown plots remained richer in perennial species than naturally regenerated plots throughout the 13-year experiment (Fig. 1). Sown plots accommodated significantly fewer unsown species than were found in naturally regenerated plots (Supplementary Material Table S2).

Very few sown species colonised unsown plots, increasing to an average of just under one per quadrat after 13 years.

3.1.3 The effects of mowing

Mowing (i.e. mown versus unmown) had less impact than sowing (i.e. sown versus natural regeneration) on overall species richness. After 13 years there was no significant main effect of mowing on overall species richness and there were no significant interactions between mowing and sowing. In the establishment years, however, mowing had a significant influence on the development of species richness, with the uncut, naturally regenerated plots being consistently more species-poor than mown plots (Table 1). Plots cut in spring and autumn were consistently the most species rich at that stage, and had significantly more species (both annuals and perennials) than those cut in spring and summer on two sampling dates (November 1988 and June 1989).

Although the mowing regime had no significant effect on overall species richness by 2000, it had a significant influence on the establishment and persistence of sown species in the sown plots. Plots cut twice retained a higher proportion of sown species than those cut once or not at all (Fig. 2). Numbers of sown species were significantly higher in the former after two years and remained so eleven years later (see Supplementary Material Table S3). At this stage, sown plots that were left uncut also had significantly fewer sown species than cut plots. This contrast was also significant when applied to all species, both sown and unsown, in the sown plots ($F_{(1,35)}$=10.29, *P*=0.0021).

Plots in which cut hay was left lying were species-poor throughout the experiment although numbers of species were not significantly lower than in other naturally-regenerated plots, including those cut at the same time, but from which the hay was removed (Table 1).

3.1.4 The effects of spraying

On sprayed plots species richness was lower than under all other treatments on most sampling occasions (Table 1), although this effect was never significant. Annuals continued to form a conspicuous element in the sward and were more numerous than in all other treatments throughout the experiment (Fig. 1, Supplementary Material Table S4). Conversely, numbers of perennial species on sprayed plots were significantly lower than under all other treatments on all sampling occasions from September 1989 onwards (Fig. 1, Supplementary Material Table S4).

3.2 Sward composition

3.2.1 Temporal trends

The changes in species richness of different components of the sward (above) reflected major changes in the relative abundance of many species. Most annual species had declined to very low frequencies by 2000, although they differed in the year in which their numbers peaked (Supplementary Material Figure S1). The most abundant annual (occasionally biennial: Tutin 1980) in 2000, *Bromus hordeaceus* (nomenclature follows Stace 1991), exceptionally, increased over this period but only to a frequency of *ca* 10%. The rank order of abundance of the dominant annuals changed substantially over the course of the experiment with many of the species that were most prominent in the establishment phase disappearing almost completely from the swards within a few years. *Alopecurus myosuroides* and the *Avena* species (predominantly *Avena sterilis*), for example, peaked and declined much more rapidly than *Anisantha sterilis*. Conversely, *Geranium dissectum*, the third commonest annual remaining in the swards in 2000, was only the twenty-second most frequent in 1988.

There were also major changes in the abundance of many perennial species, most of which were likely to have colonised from the hedge bottom or seedbank (Smith et al. 1993). Of the commonest species, *Convolvulus arvensis, Arrhenatherum elatius*, *Dactylis glomerata* and *Holcus lanatus* all increased while *Cirsium arvense, Urtica dioica* and *Elymus repens* declined in the experiment as a whole between 1990 and 2000 (Fig. 3).

3.2.2 The effects of management

These changes in the abundance of individual species over the experiment as a whole (Supplementary Material Figure 1, and Fig. 3) masked often highly significant differences between treatments. Although the contrasting mowing regimes had relatively little effect on species richness (above), they had profound effects on the species composition of the swards (Table 2).

3.2.3 Annual species

Sowing initially substantially reduced the relative frequency of common annual species. When annuals were most abundant sowing had highly significant effects on individual species but, by 2000, most were too infrequent for this effect to be detectable. Annuals both peaked at a lower frequency, and declined more rapidly, in sown than in naturally regenerated plots (e.g. Fig. 4).

The mowing regimes also influenced the abundance of annuals (data not shown) although their effects were generally smaller than that of sowing. For example, by 2000, *B. hordeaceus* was significantly less frequent in plots cut twice than in those cut once ($F_{(1,45)}=8.16$, $P<0.01$) or left uncut. *A. sterilis* was virtually eliminated from these plots (cut twice *v* once: $F_{(1,45)}=21.45$, $P<0.001$) although, in the establishment years, it was significantly more abundant in plots cut in spring and autumn than in those cut in spring and summer (in 1989, 1990 and 1992, $P<0.05$, 0.01 and 0.001 respectively). By contrast, *Avena* species remained significantly more abundant in plots cut in spring and autumn from 1989 onwards ($P<0.001$ in 1989 and 1990) and were restricted to these plots by 2000.

Where cut hay was left *in situ*, *A. myosuroides,* alone amongst the annuals, remained more abundant than under other treatments. In 1989 and 1990, when it was still sufficiently abundant for analysis, it was more frequent in these plots than equivalent plots with hay removed (F=4.13

and 4.49, *P*<0.05). On sprayed plots many annual species remained at relatively high frequencies. For example, in 2000 the mean frequencies of *A. sterilis* and *B. hordeaceus* were *ca* 32% and 55% in these plots, compared with ranges between zero and 10% respectively, under other treatments (cf Fig. 4).

3.2.4 Unsown perennial species

Sowing very effectively reduced the rate of colonisation by perennials during the establishment years of the experiment (Table 3) but, after 13 years, many common perennial species had become as abundant in sown as in naturally regenerated swards (Table 4). Notable exceptions were *Convolvulus arvensis,* which occurred at similar frequencies even in the establishment years, and *P. trivialis* and *D. glomerata*, which still occurred at significantly lower frequencies in sown than in naturally regenerating swards by 2000 (Table 3).

Mowing had relatively little impact on the frequency of common perennials during the early years but, after 13 years, it significantly influenced the abundance of most of these species. The frequency of mowing was more important than its timing: we found no significant differences between plots cut in spring and summer and those cut in spring and autumn for any of the common perennials in 2000.

Among the common species *D. glomerata, C. arvensis and H. lanatus* were all significantly more frequent in mown plots (Fig. 5), with the latter two species also significantly more abundant in plots cut twice than in those cut once (see Supplementary Material Table S5).

Similarly, amongst species that responded negatively to mowing, some were reduced by any mowing and others responded by degree to the numbers of cuts. *A. elatius* was 40% less frequent in plots mown twice than in those cut once or not at all (Fig. 5) while *C. arvense, U. dioica* and *E. repens* were not only more abundant in uncut than in cut plots but were their abundance was also further reduced by cutting twice (Fig. 5, Supplementary Material Table S5). Amongst the commonest perennials, only *P. trivialis* showed no significant response to mowing.

Not removing cut hay substantially increased the abundance of *U. dioica* but did not appear to affect any other common perennial species. By 1990, despite a very significant negative response to an increasing frequency of mowing (above), *U. dioica*, was more abundant in plots that were cut twice a year and in which the hay was left *in situ* than under any other treatment ($F_{(1,45)}$=4.14, P<0.05). By 2000 its frequency in these plots was 27.4%, compared with 1.05% in equivalent plots from which the hay was removed ($F_{(1,45)}$=5.69, P<0.05).

Spraying annually with glyphosate reduced the frequencies of some common perennials to very low levels in 2000, although the frequencies of *A. elatius*, *P. trivialis*, *C. arvense* and *U. dioica* were not significantly affected (Table 5).

3.2.5 Sown species

All sown species declined in frequency in the sown plots, many of them very substantially, between 1990 and 2000 (most abundant species shown in Fig. 6).

In contrast to some of the unsown perennials, none of the commoner sown perennial grasses was significantly more abundant in the absence of mowing, at any stage. *Trisetum flavescens*, *P. pratensis* and *C. cristatus,* were significantly more frequent in cut than in uncut plots from 1989 onwards. By 2000 this difference remained significant for *T. flavescens* (Supplementary Material Table S5) while *C. cristatus* had been lost from uncut plots. By contrast, *Phleum bertolonii* was, most frequent in plots that were left uncut in summer (either cut in spring and autumn or uncut: see Supplementary Material Table S5). Small changes in abundance of common and uniformly distributed grasses such as *Festuca rubra* and *Hordeum secalinum,* were unlikely to be detected by our monitoring method.

Low frequencies of many of the sown species made it difficult to detect significant effects, but most sown forbs that were sufficiently numerous for analysis in 2000 also responded positively to mowing. *Leucanthemum vulgare* was significantly more abundant in cut than in uncut plots ($F_{(1,15)}$=5.53, P=0.025). *Knautia arvensis* was completely lost from uncut plots. *Centuarea nigra* responded by degree to the frequency of cutting: it was least abundant in uncut plots but also significantly less abundant in plots cut once than in those cut twice ($F_{(1,15)}$= 7.82, P=0.014). *Torilis japonica*, the only consistently annual species included in the seed mixture, was, like *P. bertolonii*, most frequent in plots that were left uncut in summer from 1989 until 2000 (1989 $F_{(1,15)}$=8.34, P=0.011; 1990 $F_{(1,15)}$=16.77, P=0.001; 1992 $F_{(1,15)}$=10.01, P=0.006), although this effect was no longer significant in 2000.

4. **Discussion**

4.1 Long term vegetation change

Vegetation is subject to year-to-year fluctuations in composition, resulting from, for example, interspecific differences in responses to changing weather conditions and successional processes. Although we were only able to monitor the longer-term consequences of succession and management on the Wytham field margins once, other monitoring work on the site under the Environmental Change Network programme (Morecroft et al., 2009) explicitly investigated interannual changes in vegetation during this period. This investigation included plots in formerly arable grasslands close to the experimental margins. This and other work (Morecroft et al., 2002

Morecroft et al., 2004) indicated that the main year-to-year differences are in the proportion of annual species within swards, with an increase in annuals following drought, as a result of decreasing grass cover. This was not, however, of such an extent as to change the overall character of the communities. The period 1999-2000 was relatively wet (Morecroft et al., 2004) and it is possible that more annual weed species would have been found following a drier period. However the main differences between treatments are not likely to be substantially affected by this and longer lived species are relatively consistent from year to year.

4.2 Weed control

Our results show that when new field margins are established, annual weeds are a short-lived problem, even in the absence of management. In unmanaged, naturally regenerating swards, both the numbers of annual species, and the frequencies of pernicious annuals, declined to low levels within three years of establishment. This is consistent with other studies of colonisation of former arable land (e.g. Gibson and Brown, 1992; Steffan-Dewenter and Tscharntke, 1997) although many factors, including soil type, nutrient levels, and the supply of propagules, influence the composition of the colonising flora and length of time taken to produce perennial-dominated swards (Donath et al., 2007; Leng et al., 2009). Within the Wytham experiment, the experimental blocks, based around different fields, contributed significantly to the variance in most analyses.

Exclusion of annuals was achieved more rapidly by sowing a wildflower seed mixture than by any of our mowing regimes: the mat-forming habit, particularly of sown grasses such as *F. rubra*, resulted in rapid sward closure. Numbers of annual species and the frequencies of individual species were reduced faster, and peak frequencies were lower, in sown swards irrespective of the mowing regime. Schippers and Joenje (2002) similarly found that all annuals in an annual/perennial mixture sown on an old arable field were lost after two years where management ensured the development of closed perennial swards.

The timing and frequency of mowing could also be used to manipulate the rate of loss of annual species in the establishment phase by influencing seed return and establishment opportunities. Thus, *A. sterilis* and *B. hordeaceus* decreased more rapidly as the frequency of mowing increased: both of these species lack seed dormancy and are dependent on seed dispersal for population maintenance or increase. *Avena* species, despite exhibiting seed dormancy, decreased least rapidly when cut in spring and autumn: summer cutting removed its seeds before they matured, suggesting that seed set and dispersal was also important. *A. myosuroides* was most persistent where hay cut in late June, containing ripe seed, was left lying. Thus, where it is felt necessary to increase the rate of annual weed loss, the management regime can clearly be targeted at the dominant species (Watt et al., 1990).

Our results show that any application of broad spectrum herbicide that opens up gaps on field margins can allow annuals to persist while yielding an overall reduction in species richness and particularly in numbers of perennials. Some perennial weeds were effectively controlled, but other species, including *A. elatius*, *P. trivialis* and *U. dioica* showed little response. Herbicides recommended specifically for controlling broad-leaved weeds in grass field margins (Boatman, 1989) would be expected to be effective in excluding annual grasses by allowing a dense grass sward to develop. However, they also exclude the broadleaved species that have a disproportionate influence on invertebrate and avian diversity by providing nectar sources (Meek et al., 2002; Pywell et al., 2005), structural heterogeneity (Baines et al., 1998; Asteraki et al., 2004) and seeds (Wilson et al., 1999; Vickery et al., 2002). Equally, there is little evidence to show that the use of graminicides to encourage broadleaved species on field margins results in field margin swards dominated by desirable perennial species (Marshall and Novakowski, 1994; Westbury et al. 2008). This experiment shows that swards that are species rich, attractive, and relatively weed-free, can be achieved by sowing and by simple mowing regimes that take account of the phenologies and life histories of the target species.

Whilst annual weeds are a short-lived problem in closing perennial swards, pernicious perennial weeds, with high potential growth rates, might be expected to be more intractable on the enriched soils of arable field margins. In the establishment years, species such as *C. arvense*, *U. dioica* and *E. repens* increased progressively in naturally regenerated plots. By 2000, however, these species had declined over the experiment as a whole, responding negatively, often by degree, to the frequency of mowing. Consistent cutting, only twice a year, over this period can clearly give good control of species such as *C. arvense*, often assumed to require control by herbicide in high-fertility situations.

Sowing initially appeared to be more effective than mowing in controlling perennial weeds. Sown swards largely excluded rhizomatous perennials for at least three years. Marshall (1990) also showed that *E. repens* was excluded from perennial grass swards over a three year period. Similarly, De Cauwer et al. (2008) found that three years after field margins were established, *E. repens* and *U. dioica* were significantly more frequent in unsown compared to sown swards. However, we showed here that the beneficial effect of sowing was relatively short-term and that rhizomatous, weedy perennial species could increase progressively at the expense of less competitive sown grasses.

4. Species richness

Establishing sown swards on field margins has been heavily promoted in agri-environment schemes, originally because of their attractive and tidy appearance and benefits for weed control and, increasingly, to benefit farmland biodiversity, one of the primary objectives of Environmental Stewardship in the UK (Critchley et al., 2006; Marshall et al., 2006). However, several studies have found that species richness starts to decrease after the first year (e.g. Marshall and Nowakowski, 1995; West and Marshall, 1996; De Cauwer et al., 2005), while that of comparable naturally regenerating swards increases and stabilises. De Cauwer et al. (2005) found significant convergence in species richness and vegetation composition between sown and unsown plots after only three years and Warren et al. (2002) after six years. In contrast, Carvell et al. (2007) found that, after three years, field margin swards sown with a diverse wildflower mixture remained substantially different from naturally regenerated ones and provided better quality habitat for bumblebees, although a more species poor mixture proved less stable. There is therefore a degree of uncertainty about the effectiveness of sowing as a tool for enhancing biodiversity in the medium to long term, particularly if a species-poor mixture is used.

Our results suggest that loss of species richness in sown swards is a more long-term process. Species richness declined in sown plots during establishment but this resulted from loss of unsown colonists rather than sown species. Numbers of natural colonists then stabilised over the next ten years but the increasing abundance of rhizomatous perennial species with high potential growth rates, probably accounts for a slow but progressive decline in numbers of sown species. Nevertheless, even after 13 years, sown species still comprised up to 53% of the total in sown swards, and many unsown perennials remained significantly less common in sown than in naturally regenerated swards, consistent with recent demonstrations that resistance to invasion increases with sward diversity (e.g. Fargione et al., 2003; Mwangi et al., 2007). They suggest that invasion resistance increases with niche pre-emption and is stronger within than between functional groups of species. This could explain the much more rapid invasion of the grass-dominated, sown swards by *Convolvulus arvensis* than by *Elytrigia repens,* for example.

The sown swards were more similar in appearance, structure and species composition to local semi-natural grasslands. *Festuca* species included in the sown mixture formed a very dense sward base and persisted at high frequency even after thirteen years. Similarly, Schippers and Joenje (2002) showed that *Festuca* was maintained on field margins when nitrate levels were low, or where there was a gradient in fertility levels. The retention of sown forbs in the sown swards probably improved their quality for many invertebrates compared to naturally regenerated swards. Three years after sowing, they had significantly greater abundance and species richness of Araneae (Baines et al., 1998) and higher abundance of butterflies (Feber et al., 1996), and Auchenorrhyncha (Smith et al., 1993). Haenke et al. (2009) similarly report higher densities of Syrphids in sown than in naturally regenerated field margin strips.

Several studies have found that the rate of loss of sown species in the establishment phase of new field margins can be manipulated by the mowing regime (Schippers and Joenje, 2002; De Cauwer et al., 2005*)*. At Wytham, any mowing in the establishment phase increased the number of perennial species, while mowing in spring and autumn produced the richest swards. This regime also delayed the decline in annuals and appears to have been effective by increasing opportunities for seed return and germination over the winter.

After thirteen years, the timing of mowing was no longer important, but its frequency continued to influence species retention in sown swards. The better retention of sown species in mown plots may result from the selection of more stress tolerant species compared to competitors (sensu Grime et al., 1988). Westbury et al. (2008) found that disturbance of sown swards by annual scarification could result in higher retention of unsown colonists than in mown swards (with hay left *in situ*) in the first four years after sowing. Unsown species retention on the sown Wytham field margins may have been limited by lack of disturbance, although the beneficiaries of scarification were ruderals and competitive perennial colonists, including pernicious weeds. Although 2m-wide margins are still included as an option in current agri-environment schemes, wider margins of 4m or 6m are commonly established. These may provide opportunities for more flexible management, including greater disturbance. However, there is little evidence from other studies that, over the short term at least, an increase in margin width results in greater species richness (e.g. Sheridan et al., 2008). One might predict the establishment phase to be more protracted as distance from the boundary and sources of many perennials increases, and a buffering effect of wider margins may become more apparent over the longer term, but further work is required to elucidate this.

Field margins left to colonise naturally remained significantly less species rich than sown margins even after 13 years, despite perennial species increasing in the establishment phase, and stabilising thereafter. Most species of all types colonised in the first two years of the experiment. Once closed swards had developed, very few new species appeared (Smith et al., 1994). The substantial failure of most sown species to colonise adjacent unsown plots after 13 years illustrates the effectiveness of this competitive exclusion. Although, as on sown plots, species richness in the naturally regenerating swards could be manipulated by mowing in the establishment years, mowing was ineffective for manipulating diversity in the longer term. Mowing sown plots altered the rate of species loss: on naturally regenerated plots few species were lost and the effects of mowing could only be detected in changes in relative abundance.

Even the removal of cut hay – a mantra of conservation management because of its expected effect in reducing soil nutrient levels and increasing sward diversity (Marrs, 1993; Jacquemyn et al., 2003) - did not significantly affect the species richness of naturally regenerated plots on the timescale of our experiment, although plots in which hay was left lying were always relatively species poor. This is consistent with the suggestion that lack of a diversity response to nutrient change on fertile soils is because mid-successional species tend to be competitively equivalent: the initial response to changing nutrient level is likely to be through gradual changes in relative abundance that translates only slowly into changes in species richness (Huston, 1994; Huberty et al., 1998). On sown field margins De Cauwer et al. (2005) recorded a much more rapid impact of leaving hay lying. After only three years, significantly more sown species were retained where hay, cut twice a year, was removed, rather than left lying. The increase that we recorded in *U. dioica* where hay was left lying suggests that nutrient demanding species (Marrs, 1993; Hogg et al., 1995) are likely to thrive at the expense of the slower growing species commonly used in seed mixtures, and result in more rapid loss of species richness than on naturally regenerated swards. Leaving cut vegetation lying may also have a smothering affect sufficient to affect germination and/or survival of seedlings, especially those that require light to germinate.

Few common perennials were significantly affected by mowing during the establishment phase, but after 13 years the most competitive species (*sensu* Grime et al., 1988) were more abundant in the absence of mowing, while most of the sown species, typical of semi-natural grassland, fared better, often by degree, when mown. In established swards, the frequency of mowing had more influence than its timing on the abundance of perennial species that remained common. The timing of mowing might be expected to have less influence on species that propagate by seed, once sward closure restricted germination opportunities. It would, however, be expected to continue to have a substantial influence on other taxa, including granivorous birds (Vickery et al., 2009), small mammals (Shore et al., 2005) and nectar-feeding invertebrates (Marshall et al., 2006; Pywell et al., 2006).

5. Conclusions

The results of this experiment show that short-term experiments on arable field margin establishment are unlikely to provide an accurate insight into the longer term outcomes either for perennial weed control or the development of biodiversity, although they do give an important insight into early successional processes. In particular, we found that different mowing regimes enhanced plant species richness in the establishment years and in the longer-term, with the frequency of mowing becoming more important than its timing. The increase in perennial species with high potential growth rates during the establishment phase was not maintained and was reduced by mowing. Swards established by sowing a wild flower seed mixture effectively excluded perennial as well as annual weeds in the establishment years but not in the longer term. But despite losses of sown species from these swards they remained more species rich than naturally regenerated swards for at least thirteen years**.** They also contained a higher proportion of species typical of semi-natural grassland rather than of disturbed ground.

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Table legends

Table 1. Species richness based on mean numbers of species per quadrat (back transformed from unadjusted log(n+1)-transformed means). 2000 means with the same letter do not differ significantly (Tukey's Test)(analysis was conducted for all dates). NR: natural regeneration. Except where indicated, vegetation was removed from all cutting treatments.

Table 2. Summary of changes in the frequency of the commonest plant species in permanent quadrats on the Wytham field margins between 1990 and 2000. Data are derived from percentage change in mean frequency in the permanent quadrats under each treatment. Treatments:1-uncut, 2-cut in summer, 3-cut in spring and summer (hay removed), 4-cut in spring and autumn, 5-cut in spring and summer (hay left *in situ*, 6-sprayed. Categories: '--' is <-50%; '-' is -50% to -11%; '0' is -10% to +11%; '+' is 12 to =100%, '++' >100%. 'A'absent in 2000 (A) absent in both 1990 and 2000.

Table 3. The significance of the effect of sowing on the frequency of common perennial species. F values for comparison of sown and natural regeneration plots have 1,35 df. nn: non-normally distributed data.

Table 4. Relative abundance of the 12 most common species in sown and natural regeneration plots in 2000, expressed as the percentage of the 576 25x25cm quadrat cells in which they occurred in the paired treatments: sprayed plots and natural regeneration plots in which hay was left lying are excluded. * sown species.

Table 5. The mean frequency of the commonest perennial species in sprayed plots in 2000. Significance levels refer to a planned comparison with frequencies under all other treatments and are based on (angular) transformed, adjusted means.

Figure legends

Fig. 1. Comparison of mean numbers of annual and perennial species per quadrat in sown, natural regeneration and sprayed plots. Data were log(n+1)-transformed prior to analysis. Means are back-transformed and adjusted for block effects.

Fig. 2. Mean numbers of sown species as a proportion of the total number of species in sown plots. Data were angular transformed prior to analysis of the eight factorial treatments. Means are back-transformed and adjusted for block effects.

Fig. 3. Changes in the frequency of the most abundant unsown perennials. Data are the percentage of all quadrat cells in which the species was recorded in early August in 1988 and 2000 and late June 1990.

Fig. 4. Changes in the mean frequency of *Anisantha sterilis* and *Avena* species in sown and natural regeneration plots averaged over cutting and vegetation removal treatments. Data were angular transformed prior to analysis of the eight factorial treatments. Means are back-transformed and adjusted for block effects.

Fig. 5. The effect of different mowing treatments on adjusted mean frequencies of common unsown perennial species in 2000. Spr: spring, aut: autumn. Bars represent 95% confidence intervals.

Fig. 6. Changes in the frequency of the commonest sown species in sown plots. Data are the percentage of all quadrat cells in which the species was recorded in early August in 1988 and 2000 and late June 1990.

Table 1.

Treatment	Date						
	08/88	06/89	09/89	06/90	09/90		07/00
Sow/cut spr+summer	23.1	16.7	14.3	15.0	14.4	a	11.5
Sow/cut summer	23.0	15.0	13.2	14.1	12.3	a	10.9
Sow/cut spr+autumn	24.1	20.3	15.2	18.0	14.9	ab	10.5
Sow/uncut	23.2	15.9	13.0	14.7	12.5	abc	8.8
Nat regen/cut spr+autumn	15.0	11.2	9.5	13.0	11.4	abc	8.5
Nat regen/cut spr+summer	13.7	10.1	9.7	12.4	10.2	abc	8.5
Nat regen/uncut	14.1	8.5	8.4	11.2	10.0	bc	8.0
Nat regen/cut summer	16.8	10.2	9.5	12.2	11.4	bc	8.2
Nat regen/cut spr+summer (hay left lying)	13.3	10.2	8.2	11.6	9.2	c	7.2
Nat regen/sprayed	12.9	9.3	8.6	10.4	9.7	c	7.0

Table 2.

	Treatment									
	Sown plots				Natural regeneration plots					
	1	2	3	4	1	2	5	3	4	6
Sown species:										
Centaurea nigra	--	-	+	+						
Galium verum	--	+	+	--						
Knautia arvensis	A	--	--	-						
Leucanthemum vulgare	--	--	--	--						
Torilis japonica	--	++	--	--						
Cynosurus cristatus	A	--	--	--						
Festuca rubra	-	-	-	-						
Hordeum secalinum	-	-	-	0						
Phleum bertolonii	-	--	--	-						
Poa pratensis	--	--	--	--						
Trisetum flavescens	--	--	--	--						
Natural regen. species										
Anisantha sterilis	--	A	A	A	--	--	--	--	A	-
Arrenatherum elatius	++	++	++	++	++	+	++	++	+	++
Bromus hordeaceus	--	0	--	--	--	--	A	--	--	++
Elymus repens	0	-	--	--	-	--	--	--	-	--
Dactylis glomerata	++	++	++	-	++	++	++	++	-	-
Holcus lanatus	-	0	++	++	0	+	++	++	++	+
Poa trivialis	+	-	--	--	A	A	--	--	A	A
Convolvulus arvensis	+	+	++	+	0	0	+	++	++	-
Geranium dissectum	--	--	--	A	--	--	--	--	-	--
Urtica dioica	-	--	--	(A)	-	-	-	--	--	--

Table 3.

Year	1988		1989		1990		1992		1993		2000	
Arrenatherum elatius	0.00	ns	8.87	**	8.90	**	-		-		0.10	ns
Cirsium arvense	nn		nn		12.68	***	18.89	***	11.33	**	0.57	ns
Convolvulus arvensis	3.19	ns	0.68	ns	0.22	ns	-		-		0.52	ns
Holcus lanatus	nn		26.13	***	5.39	*					1.33	ns
Dactylis glomerata	0.06	ns	2.20	ns	4.11	*	-		-		13.89	***
Elymus repens	0.23	ns	8.11	**	20.22	***	-		-		2.18	ns
Poa trivialis	14.93	***	28.71	***	190.8	***					14.43	***

Table 4.

Sown plots	% of.cells	Unsown plots	% of.cells
*Festuca rubra**	63.2	*Arrenatherum elatius*	53.8
Arrenatherum elatius	50.2	*Poa trivialis*	53.0
*Phleum bertolonii**	47.9	*Elymus repens*	36.5
Convolvulus arvensis	42.4	*Convolvulus arvensis*	33.0
Elymus repens	25.5	*Dactylis glomerata*	28.3
Poa trivialis	24.8	*Lolium perenne*	24.3
Holcus lanatus	24.5	*Holcus lanatus*	21.2
*Hordeum secalinum**	21.0	*Phleum bertolonii*	18.6
*Centurea nigra**	14.6	*Ranunculus repens*	13.4
*Trisetum flavescens**	8.2	*Urtica dioica*	13.0
*Leucanthemum vulgare**	11 .1	*Festuca rubra*	12.5
Lolium perenne	11.1	*Agrostis stolonifera*	10.4

Table 5.

Species	% frequency	$F_{(1,45)}$	*P*	
Arrenatherum elatius	56.81	0.04	0.848	ns
Cirsium arvense	0.12	3.99	0.052	ns
Convolvulus arvense	1.69	8.61	0.005	**
Holcus lanatus	0.49	4.89	0.032	*
Dactylis glomerata	1.70	10.08	0.003	**
Elymus repens	0.47	10.70	0.002	**
Poa trivialis	44.86	0.34	0.562	ns
Urtica dioica	11.50	0.07	0.789	ns