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

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27 ABSTRACT

28

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

49

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

52

53 1. **Introduction**

54

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

63

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

75

76 Recognition of the importance of field margins for biodiversity conservation triggered many
77 research initiatives designed to inform prescriptions for their restoration and management
78 (Vickery, Feber and Fuller, 2009). Many of these have been short- term and have focussed on

79 early successional stages of habitat re-creation (e.g. Marshall and Nowakowski, 1995; Huusela-
80 Veistola and Vasarainen, 2000; De Cauwer et al., 2005). The new generation of agri-environment
81 schemes has a longer-term focus (with agreements of either five years (Entry Level Stewardship)
82 or ten years (Higher Level Stewardship agreements)) and corresponding requirement for long-
83 term research.

84

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

101

102 A large-scale, long-term field experiment at the University of Oxford's Farm at Wytham, Oxford,
103 provided a unique opportunity to answer key questions about succession on field margins adjacent
104 to intensively farmed arable land, and timely guidance for new incentive schemes. The
105 experiment was established in 1987 to evaluate the impact on wildlife, and the implications for

106 crop husbandry, of simple and practical regimes for managing permanent grassy margins around
107 conventionally-farmed fields. The field margins were established on former cultivated field edges
108 either by sowing a wild grass and forb mixture or by allowing natural regeneration. The
109 development of plant species richness, and the fate of key individual species of agricultural
110 concern and conservation interest, was monitored intensively during the establishment phase of the
111 experiment, until 1990. The experiment was maintained for a further ten years and the vegetation
112 recorded again in 2000.

113

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

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

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

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

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

124

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

128

129 2. **Methods**

130 Two metre wide uncropped margins were created around six arable fields at the Oxford University
131 Farm, Wytham, UK (1°19' W 51°47' N) in autumn 1987. They comprised the original (pre-existing)

132 uncropped field margin (approximately 0.5m wide), and a *ca* 1.5m wide fallowed extension onto
133 cultivated land. The fallowed margin extension is the subject of this paper.

134

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

143

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

157

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

164

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

173

174 3. Results

175 3.1 Species Richness

176 3.1.1 Temporal trends

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

183

184

185 **3.1.2 The effects of sowing**

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

190

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

199

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

204

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

207

208 **3.1.3 The effects of mowing**

209 Mowing (i.e. mown versus unmown) had less impact than sowing (i.e. sown versus natural
210 regeneration) on overall species richness. After 13 years there was no significant main effect of

211 mowing on overall species richness and there were no significant interactions between mowing
212 and sowing. In the establishment years, however, mowing had a significant influence on the
213 development of species richness, with the uncut, naturally regenerated plots being consistently
214 more species-poor than mown plots (Table 1). Plots cut in spring and autumn were consistently
215 the most species rich at that stage, and had significantly more species (both annuals and
216 perennials) than those cut in spring and summer on two sampling dates (November 1988 and June
217 1989).

218

219 Although the mowing regime had no significant effect on overall species richness by 2000, it had
220 a significant influence on the establishment and persistence of sown species in the sown plots.
221 Plots cut twice retained a higher proportion of sown species than those cut once or not at all (Fig.
222 2). Numbers of sown species were significantly higher in the former after two years and remained
223 so eleven years later (see Supplementary Material Table S3). At this stage, sown plots that were
224 left uncut also had significantly fewer sown species than cut plots. This contrast was also
225 significant when applied to all species, both sown and unsown, in the sown plots ($F_{(1,35)}=10.29$,
226 $P=0.0021$).

227

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

231

232 ***3.1.4 The effects of spraying***

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

237 perennial species on sprayed plots were significantly lower than under all other treatments on all
238 sampling occasions from September 1989 onwards (Fig. 1, Supplementary Material Table S4).

239

240 **3.2 Sward composition**

241 **3.2.1 Temporal trends**

242 The changes in species richness of different components of the sward (above) reflected major
243 changes in the relative abundance of many species. Most annual species had declined to very low
244 frequencies by 2000, although they differed in the year in which their numbers peaked
245 (Supplementary Material Figure S1). The most abundant annual (occasionally biennial: Tulin
246 1980) in 2000, *Bromus hordeaceus* (nomenclature follows Stace 1991), exceptionally, increased
247 over this period but only to a frequency of *ca* 10%. The rank order of abundance of the dominant
248 annuals changed substantially over the course of the experiment with many of the species that
249 were most prominent in the establishment phase disappearing almost completely from the swards
250 within a few years. *Alopecurus myosuroides* and the *Avena* species (predominantly *Avena*
251 *sterilis*), for example, peaked and declined much more rapidly than *Anisantha sterilis*. Conversely,
252 *Geranium dissectum*, the third commonest annual remaining in the swards in 2000, was only the
253 twenty-second most frequent in 1988.

254

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

260

261 **3.2.2 The effects of management**

262

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

268

269

270 **3.2.3 Annual species**

271

272 Sowing initially substantially reduced the relative frequency of common annual species. When
273 annuals were most abundant sowing had highly significant effects on individual species but, by
274 2000, most were too infrequent for this effect to be detectable. Annuals both peaked at a lower
275 frequency, and declined more rapidly, in sown than in naturally regenerated plots (e.g. Fig. 4).

276

277 The mowing regimes also influenced the abundance of annuals (data not shown) although their
278 effects were generally smaller than that of sowing. For example, by 2000, *B. hordeaceus* was
279 significantly less frequent in plots cut twice than in those cut once ($F_{(1,45)}=8.16$, $P<0.01$) or left
280 uncut. *A. sterilis* was virtually eliminated from these plots (cut twice v once: $F_{(1,45)}=21.45$,
281 $P<0.001$) although, in the establishment years, it was significantly more abundant in plots cut in
282 spring and autumn than in those cut in spring and summer (in 1989, 1990 and 1992, $P<0.05$, 0.01
283 and 0.001 respectively). By contrast, *Avena* species remained significantly more abundant in plots
284 cut in spring and autumn from 1989 onwards ($P<0.001$ in 1989 and 1990) and were restricted to
285 these plots by 2000.

286

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

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

294

295 **3.2.4 Unsown perennial species**

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

302

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

308

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

312

313 Similarly, amongst species that responded negatively to mowing, some were reduced by any
314 mowing and others responded by degree to the numbers of cuts. *A. elatius* was 40% less frequent
315 in plots mown twice than in those cut once or not at all (Fig. 5) while *C. arvensis*, *U. dioica* and *E.*
316 *repens* were not only more abundant in uncut than in cut plots but were their abundance was also

317 further reduced by cutting twice (Fig. 5, Supplementary Material Table S5). Amongst the
318 commonest perennials, only *P. trivialis* showed no significant response to mowing.
319
320 Not removing cut hay substantially increased the abundance of *U. dioica* but did not appear to
321 affect any other common perennial species. By 1990, despite a very significant negative response
322 to an increasing frequency of mowing (above), *U. dioica*, was more abundant in plots that were
323 cut twice a year and in which the hay was left *in situ* than under any other treatment ($F_{(1,45)}=4.14$,
324 $P<0.05$). By 2000 its frequency in these plots was 27.4%, compared with 1.05% in equivalent
325 plots from which the hay was removed ($F_{(1,45)}=5.69$, $P<0.05$).
326
327 Spraying annually with glyphosate reduced the frequencies of some common perennials to very
328 low levels in 2000, although the frequencies of *A. elatius*, *P. trivialis*, *C. arvense* and *U. dioica*
329 were not significantly affected (Table 5).

330

331 **3.2.5 Sown species**

332

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

335

336 In contrast to some of the unsown perennials, none of the commoner sown perennial grasses was
337 significantly more abundant in the absence of mowing, at any stage. *Trisetum flavescens*, *P.*
338 *pratensis* and *C. cristatus*, were significantly more frequent in cut than in uncut plots from 1989
339 onwards. By 2000 this difference remained significant for *T. flavescens* (Supplementary Material
340 Table S5) while *C. cristatus* had been lost from uncut plots. By contrast, *Phleum bertolonii* was,
341 most frequent in plots that were left uncut in summer (either cut in spring and autumn or uncut:
342 see Supplementary Material Table S5). Small changes in abundance of common and uniformly

343 distributed grasses such as *Festuca rubra* and *Hordeum secalinum*, were unlikely to be detected
344 by our monitoring method.

345

346 Low frequencies of many of the sown species made it difficult to detect significant effects, but
347 most sown forbs that were sufficiently numerous for analysis in 2000 also responded positively to
348 mowing. *Leucanthemum vulgare* was significantly more abundant in cut than in uncut plots
349 ($F_{(1,15)}=5.53$, $P=0.025$). *Knautia arvensis* was completely lost from uncut plots. *Centuarea nigra*
350 responded by degree to the frequency of cutting: it was least abundant in uncut plots but also
351 significantly less abundant in plots cut once than in those cut twice ($F_{(1,15)}=7.82$, $P=0.014$).
352 *Torilis japonica*, the only consistently annual species included in the seed mixture, was, like *P.*
353 *bertolonii*, most frequent in plots that were left uncut in summer from 1989 until 2000 (1989
354 $F_{(1,15)}=8.34$, $P=0.011$; 1990 $F_{(1,15)}=16.77$, $P=0.001$; 1992 $F_{(1,15)}=10.01$, $P=0.006$), although this
355 effect was no longer significant in 2000.

356

357

358 4. Discussion

359

360 4.1 Long term vegetation change

361

362 Vegetation is subject to year-to-year fluctuations in composition, resulting from, for example,
363 interspecific differences in responses to changing weather conditions and successional processes.

364 Although we were only able to monitor the longer-term consequences of succession and
365 management on the Wytham field margins once, other monitoring work on the site under the
366 Environmental Change Network programme (Morecroft et al., 2009) explicitly investigated
367 interannual changes in vegetation during this period. This investigation included plots in formerly
368 arable grasslands close to the experimental margins. This and other work (Morecroft et al., 2002

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

376

377 4.2 Weed control

378

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

388

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

396

397 The timing and frequency of mowing could also be used to manipulate the rate of loss of annual
398 species in the establishment phase by influencing seed return and establishment opportunities.

399 Thus, *A. sterilis* and *B. hordeaceus* decreased more rapidly as the frequency of mowing increased:

400 both of these species lack seed dormancy and are dependent on seed dispersal for population
401 maintenance or increase. *Avena* species, despite exhibiting seed dormancy, decreased least rapidly
402 when cut in spring and autumn: summer cutting removed its seeds before they matured,
403 suggesting that seed set and dispersal was also important. *A. myosuroides* was most persistent
404 where hay cut in late June, containing ripe seed, was left lying. Thus, where it is felt necessary to
405 increase the rate of annual weed loss, the management regime can clearly be targeted at the
406 dominant species (Watt et al., 1990).

407

408 Our results show that any application of broad spectrum herbicide that opens up gaps on field
409 margins can allow annuals to persist while yielding an overall reduction in species richness and
410 particularly in numbers of perennials. Some perennial weeds were effectively controlled, but other
411 species, including *A. elatius*, *P. trivialis* and *U. dioica* showed little response. Herbicides
412 recommended specifically for controlling broad-leaved weeds in grass field margins (Boatman,
413 1989) would be expected to be effective in excluding annual grasses by allowing a dense grass
414 sward to develop. However, they also exclude the broadleaved species that have a
415 disproportionate influence on invertebrate and avian diversity by providing nectar sources (Meek
416 et al., 2002; Pywell et al., 2005), structural heterogeneity (Baines et al., 1998; Asteraki et al.,
417 2004) and seeds (Wilson et al., 1999; Vickery et al., 2002). Equally, there is little evidence to show
418 that the use of graminicides to encourage broadleaved species on field margins results in field
419 margin swards dominated by desirable perennial species (Marshall and Novakowski, 1994;
420 Westbury et al. 2008). This experiment shows that swards that are species rich, attractive, and
421 relatively weed-free, can be achieved by sowing and by simple mowing regimes that take account
422 of the phenologies and life histories of the target species.

423

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

432

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

441

442 4. Species richness

443

444 Establishing sown swards on field margins has been heavily promoted in agri-environment
445 schemes, originally because of their attractive and tidy appearance and benefits for weed control
446 and, increasingly, to benefit farmland biodiversity, one of the primary objectives of
447 Environmental Stewardship in the UK (Critchley et al., 2006; Marshall et al., 2006). However,
448 several studies have found that species richness starts to decrease after the first year (e.g.
449 Marshall and Nowakowski, 1995; West and Marshall, 1996; De Cauwer et al., 2005), while that

450 of comparable naturally regenerating swards increases and stabilises. De Cauwer et al. (2005)
451 found significant convergence in species richness and vegetation composition between sown and
452 unsown plots after only three years and Warren et al. (2002) after six years. In contrast, Carvell et
453 al. (2007) found that, after three years, field margin swards sown with a diverse wildflower mixture
454 remained substantially different from naturally regenerated ones and provided better quality habitat
455 for bumblebees, although a more species poor mixture proved less stable. There is therefore a
456 degree of uncertainty about the effectiveness of sowing as a tool for enhancing biodiversity in the
457 medium to long term, particularly if a species-poor mixture is used.

458

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

471

472 The sown swards were more similar in appearance, structure and species composition to local
473 semi-natural grasslands. *Festuca* species included in the sown mixture formed a very dense sward
474 base and persisted at high frequency even after thirteen years. Similarly, Schippers and Joenje
475 (2002) showed that *Festuca* was maintained on field margins when nitrate levels were low, or
476 where there was a gradient in fertility levels. The retention of sown forbs in the sown swards

477 probably improved their quality for many invertebrates compared to naturally regenerated swards.
478 Three years after sowing, they had significantly greater abundance and species richness of
479 Araneae (Baines et al., 1998) and higher abundance of butterflies (Feber et al., 1996), and
480 Auchenorrhyncha (Smith et al., 1993). Haenke et al. (2009) similarly report higher densities of
481 Syrphids in sown than in naturally regenerated field margin strips.

482

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

489

490 After thirteen years, the timing of mowing was no longer important, but its frequency continued to
491 influence species retention in sown swards. The better retention of sown species in mown plots may
492 result from the selection of more stress tolerant species compared to competitors (*sensu*
493 Grime et al., 1988). Westbury et al. (2008) found that disturbance of sown swards by annual
494 scarification could result in higher retention of unsown colonists than in mown swards (with hay
495 left *in situ*) in the first four years after sowing. Unsown species retention on the sown Wytham
496 field margins may have been limited by lack of disturbance, although the beneficiaries of
497 scarification were ruderals and competitive perennial colonists, including pernicious weeds.

498 Although 2m-wide margins are still included as an option in current agri-environment schemes,
499 wider margins of 4m or 6m are commonly established. These may provide opportunities for more
500 flexible management, including greater disturbance. However, there is little evidence from other
501 studies that, over the short term at least, an increase in margin width results in greater species
502 richness (e.g. Sheridan et al., 2008). One might predict the establishment phase to be more
503 protracted as distance from the boundary and sources of many perennials increases, and a

504 buffering effect of wider margins may become more apparent over the longer term, but further
505 work is required to elucidate this.

506

507 Field margins left to colonise naturally remained significantly less species rich than sown margins
508 even after 13 years, despite perennial species increasing in the establishment phase, and
509 stabilising thereafter. Most species of all types colonised in the first two years of the experiment.

510 Once closed swards had developed, very few new species appeared (Smith et al., 1994). The
511 substantial failure of most sown species to colonise adjacent unsown plots after 13 years
512 illustrates the effectiveness of this competitive exclusion. Although, as on sown plots, species
513 richness in the naturally regenerating swards could be manipulated by mowing in the
514 establishment years, mowing was ineffective for manipulating diversity in the longer term.

515 Mowing sown plots altered the rate of species loss: on naturally regenerated plots few species
516 were lost and the effects of mowing could only be detected in changes in relative abundance.

517

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

531 mixtures, and result in more rapid loss of species richness than on naturally regenerated swards.
532 Leaving cut vegetation lying may also have a smothering affect sufficient to affect germination
533 and/or survival of seedlings, especially those that require light to germinate.

534

535 Few common perennials were significantly affected by mowing during the establishment phase,
536 but after 13 years the most competitive species (*sensu* Grime et al., 1988) were more abundant in
537 the absence of mowing, while most of the sown species, typical of semi-natural grassland, fared
538 better, often by degree, when mown. In established swards, the frequency of mowing had more
539 influence than its timing on the abundance of perennial species that remained common. The timing
540 of mowing might be expected to have less influence on species that propagate by seed, once sward
541 closure restricted germination opportunities. It would, however, be expected to continue to have a
542 substantial influence on other taxa, including granivorous birds (Vickery et al.,
543 2009), small mammals (Shore et al., 2005) and nectar-feeding invertebrates (Marshall et al., 2006;
544 Pywell et al., 2006).

545

546 5. Conclusions

547

548 The results of this experiment show that short-term experiments on arable field margin
549 establishment are unlikely to provide an accurate insight into the longer term outcomes either for
550 perennial weed control or the development of biodiversity, although they do give an important
551 insight into early successional processes. In particular, we found that different mowing regimes
552 enhanced plant species richness in the establishment years and in the longer-term, with the
553 frequency of mowing becoming more important than its timing. The increase in perennial species
554 with high potential growth rates during the establishment phase was not maintained and was
555 reduced by mowing. Swards established by sowing a wild flower seed mixture effectively
556 excluded perennial as well as annual weeds in the establishment years but not in the longer term.
557 But despite losses of sown species from these swards they remained more species rich than

558 naturally regenerated swards for at least thirteen years. They also contained a higher proportion
559 of species typical of semi-natural grassland rather than of disturbed ground.

560

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562

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567

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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:										
<i>Centaurea nigra</i>	--	-	+	+						
<i>Galium verum Knautia</i>	--	+	+	--						
<i>arvensis Leucanthemum</i>	A	--	--	-						
<i>vulgare Torilis</i>	--	--	--	--						
<i>japonica Cynosurus</i>	--	++	--	--						
<i>cristatus Festuca rubra</i>	A	--	--	--						
<i>Hordeum secalinum</i>	-	-	-	-						
<i>Phleum bertolonii</i>	-	-	-	0						
<i>Poa pratensis</i>	-	--	--	-						
<i>Trisetum flavescens</i>	--	--	--	--						
	--	--	--	--						
Natural regen. species										
<i>Anisantha sterilis</i>	--	A	A	A	--	--	--	--	A	-
<i>Arrhenatherum elatius</i>	++	++	++	++	++	+	++	++	+	++
<i>Bromus hordeaceus</i>	--	0	--	--	--	--	A	--	--	++
<i>Elymus repens</i>	0	-	--	--	-	--	--	--	-	--
<i>Dactylis glomerata</i>	++	++	++	-	++	++	++	++	-	-
<i>Holcus lanatus</i>	-	0	++	++	0	+	++	++	++	+
<i>Poa trivialis</i>	+	-	--	--	A	A	--	--	A	A
<i>Convolvulus arvensis</i>	+	+	++	+	0	0	+	++	++	-
<i>Geranium dissectum</i>	--	--	--	A	--	--	--	--	-	--
<i>Urtica dioica</i>	-	--	--	(A)	-	-	-	--	--	--

Table 3.

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

Table 4.

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

Table 5.

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