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Effects on weed and invertebrate abundance and diversity of herbicide management in genetically modified herbicide-tolerant winter-sown oilseed rape

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We evaluated the effects of the herbicide management associated with genetically modified herbicide-tolerant (GMHT) winter oilseed rape (WOSR) on weed and invertebrate abundance and diversity by testing the null hypothesis that there is no difference between the effects of herbicide management of GMHT WOSR and that of comparable conventional varieties. For total weeds there were few treatment differences between GMHT and conventional cropping, but large and opposite treatment effects were observed for dicots and monocots. In the GMHT treatment, there were fewer dicots and more monocots than in conventional crops. At harvest, dicot biomass and seed rain in the GMHT treatment were one-third of that in the conventional, while monocot biomass was threefold greater and monocot seed rain almost fivefold greater in the GMHT treatment than in the conventional. These differential effects persisted into the following two years of the rotation. Bees and butterflies that forage and select for dicot weeds were less abundant in GMHT WOSR management in July. Year totals for Collembola were greater under GMHT management. There were few other treatment effects on invertebrates, despite the marked effects of herbicide management on the weeds.

Keywords: genetically modified crops; biodiversity; oilseed rape; canola; herbicide management

1. INTRODUCTION

The UK Farm Scale Evaluations (FSEs) were established because of concerns that the introduction of genetically modified herbicide-tolerant (GMHT) crops could have negative impacts upon farmland biodiversity (Firbank *et al.* 2003*a*,*b*). UK farmland biodiversity has declined over the last four decades (Benton *et al.* 2003) with significant reductions recorded in the abundance of some arable weed species (Donald 1998; Robinson & Sutherland 2002) and birds (Gibbons *et al.* 1996; Siriwardena *et al.* 1998; Chamberlain *et al.* 2000; Fuller *et al.* 2002). It was feared that control of weeds in GMHT crops tolerant to broad-spectrum herbicides might be so efficient that it could help to clean up previously weedy fields (Watkinson *et al.* 2000), exacerbating long-term declines in weeds and the wildlife depending on them (Hails 2000). By contrast, others suggested that GMHT crops might ameliorate intensification by delaying and reducing herbicide use (Firbank & Forcella 2000; Carpenter *et al.* 2002) or allowing weeds and associated wildlife to remain in fields for longer (Strandberg & Pedersen 2002; Dewar *et al.* 2003).

Of the crops considered in the FSEs, winter oilseed rape (WOSR) *Brassica napus* L. ssp. *oleifera* is much the most widely grown with 330 000 ha harvested in 2002 (M.R. Thomas, personal communication). Typically, WOSR is a break crop in cereal rotations and is grown one year in every three or four. WOSR is sown from late August to early September and over-wintering may be difficult in dry years if establishment has been poor and the crop is frequently grazed by pigeons (Isaacson *et al.* 2002). WOSR plants form a rosette until March or April, when stem extension begins. Vigorous, dense crops resist broad-leaved weed competition, but slow or sparse crops (late drilled or droughted) may be vulnerable. As WOSR is a broad-leaved crop ('dicot'), selective herbicides can be

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used to control grass ('monocot') weeds and cereal volunteers, while the herbicides most commonly used to control dicots work best when applied pre-emergence. The GMHT SeedLink variety (Bayer CropScience, Cambridge, UK) used in this experiment was modified to be tolerant to the herbicide glufosinate-ammonium, the same herbicide that was used in the spring oilseed rape (SOSR) and maize FSEs. This herbicide has foliar activity against most dicots at a wide range of growth stages, but is less effective on monocot weeds (Petersen 2000), particularly as they become larger.

We have already demonstrated that the herbicide regimes associated with spring-sown GMHT beet, maize and SOSR had direct effects on weeds (Heard *et al.* 2003) and knock-on, indirect effects on invertebrate abundance and diversity (Brooks *et al.* 2003; Haughton *et al.* 2003; Hawes *et al.* 2003; Roy *et al.* 2003). This paper complements these earlier studies by reporting the findings for the final crop in the FSEs, WOSR. As for the spring-sown crops, we test the null hypothesis that there is no difference between the herbicide management of glufosinate-ammonium-tolerant WOSR and that of comparable conventional varieties, in terms of their effect on the abundance and diversity of weeds and invertebrates. We estimate the magnitude of any observed differences in weed and invertebrate abundance or diversity and relate these to herbicide management.

2. METHODS

Site selection procedures followed those published for the spring-sown crops and sought to select fields representative of the spectrum of current UK arable cropping in terms of environmental and agronomic variables (Champion *et al.* 2003). A total of 65 WOSR sites were selected and sown in 2000 (21 fields), 2001 (29 fields) and 2002 (15 fields). The two treatments (GMHT or conventional) were allocated at random to half-fields (Perry *et al.* 2003). Management inputs were applied by the farmers at levels designed to achieve cost-effective weed control. Decisions on weed control applied to the conventionally grown crop and insecticides and fungicides for both crops followed the farmers' normal practice using their normal advisory method. Non-weed control inputs could differ between the treatments based on agronomic or economic need. Weed management of the GMHT crop was based on a draft product label and followed the recommendations made by a Supply Chain Initiative on Modified Agricultural Crops adviser, often in conjunction with the farmer's usual adviser. Only glufosinate-ammonium was applied for weed control. Products used pre-drilling or as desiccants were applied to both conventional and GMHT treatments. Management inputs were recorded and all inputs were audited by agronomists qualified under the British Agrochemical Supply Industry Scheme (Champion *et al.* 2003). In subsequent years, the farmers followed their normal crop rotations and grew the crops of their choice, but under the conditions of the release they were not permitted to grow oilseed rape in the first two years.

The vegetation and invertebrate sampling followed that used in the FSEs of spring-sown crops (Brooks *et al.* 2003; Firbank *et al.* 2003*b*; Haughton *et al.* 2003; Heard *et al.* 2003), although the timing and number of some assessments differed to account for the phenology of WOSR and the timings of management activities. Methods are described only briefly here.

(a) *Weed seedbank*

Baseline estimates of weed seedbank densities were made from soil samples taken at sowing in the first growing season (late August to September, year t) from two locations on each of four transects per treatment to 15 cm depth. All seedlings emerging from the samples during the 18 weeks after collection were identified. Sites where soil was taken after the application of pre-emergence herbicides were not used in the statistical analysis. Seedbank samples were also taken in each of the subsequent two years ($t+1$ and $t+2$) at approximately the same time as the original samples. Seedbank data reported in this paper refer to the first flushes of germination between September/October and December from samples not subject to a winter chill. Owing to the staggered timing of the follow-up assessments, the $t+2$ data were not available for all sites.

(b) *Weed counts*

During the first growing season (year t) individual plants, identified to species, were counted in quadrats (0.25 m$\times$0.5 m) at five locations along 12 transects per treatment. Counts were made after crop emergence in late September/October ('seedling'), after winter from late February to early April ('early spring') and after all herbicides were applied from late April to early June ('post-herbicide'). Just before harvest in June/July, 'final' counts and biomass samples (see §2*c* below) were taken at two locations along 12 transects per treatment. At the early spring and post-herbicide counts in each year, the species were divided into size classes: plants with fewer than four true leaves and plants more than four leaves but not flowering. At the final count an additional category for reproductive individuals was included. 'Follow-up' counts ($t+1$ and $t+2$) were taken during the summer (late May to early July) at the same locations as previously. From 2003, half the number of quadrats (30) were counted compared with previous years.

(c) *Weed biomass and seed rain*

Biomass of weeds was sampled in the month before harvest (June/July) from 24 quadrats (1 m$\times$1 m) per treatment. Samples were identified to species and dried at 80 °C for 24 h before weighing. The return of weed seed to the seedbank ('seed return') was measured using four seed rain traps (0.1 m diameter), emptied every two weeks, at two locations along four transects per treatment between anthesis and crop harvest. All non-crop seeds were identified to species and categorized as viable or non-viable based on seed coat integrity.

(d) *Weed assessments in the field boundary*

Three 10 m transects per treatment were established along the field edges. Estimates of flowering were made in the three features monthly from April to July, weed cover was assessed in June and weed seeding in July (Roy *et al.* 2003). Separate assessments were made for the crop edge (uncropped but 'tilled margin'), any margin strip ('verge') and semi-natural habitat associated with the boundary ('boundary'), as defined by Roy *et al.* (2003).

(e) *Pitfall-trapping soil-surface-active invertebrates*

The pitfall-trapping of soil-surface-active invertebrates

employed the method described by Brooks *et al.* (2003). Pitfall traps, 6 cm diameter, two-thirds filled with a 50 : 50 tap water and ethylene glycol preservative, were positioned at 2, 8 and 32 m from the crop edge along four transects in each treatment. Trapping was conducted in the autumn (September/October), spring (April/May) and summer (June/July). Traps were opened for a two-week period and then removed. The invertebrate taxa were identified and counted as in Brooks *et al.* (2003).

(f) *Vortis suction sampling invertebrates on or around the weeds*

In-field Vortis suction sampling for invertebrates living either on the weeds or on the underlying soil surface was conducted using the method outlined by Haughton *et al.* (2003). Five 10 s suction samples, spaced 1 m apart, were taken at two locations along three transects. Samples for each position were bulked together. Field margin suction samples followed the method set out by Roy *et al.* (2003) and consisted of five 10 s sucks taken 1 m apart in the verge at the end of three transects. Samples were taken on one occasion in the autumn (September/October) and one in the summer (May/June). Identification and counting of the invertebrates were done to the taxonomic levels specified by Haughton *et al.* (2003) and Roy *et al.* (2003).

(g) *Surveying bees and butterflies*

Bees and butterflies were identified and counted using a modified version of the line-transect method developed for the UK Butterfly Monitoring Scheme (Pollard & Yates 1993), as described by Haughton *et al.* (2003). Surveys consisted of four 100 m sections walked into the crop and were conducted in early- (April) and late-spring (May) and early- (June) and mid-summer (July). Bees and butterflies were also surveyed in the tilled margin along three 100 m transects as described by Roy *et al.* (2003). All individuals were identified to the bee and butterfly groups described by Haughton *et al.* (2003) and Roy *et al.* (2003).

(h) *Statistical analysis*

The statistical models and analyses are explained in detail in Perry *et al.* (2003) and are only summarized here. Response variables analysed were counts or weight, totalled over samples from the two treated half-fields at each site, in a randomized block experimental design, with blocks as paired halved-fields. Whole-field total counts of zero or one were removed from analyses, leaving n sites. Variables were analysed by ANOVA (Perry *et al.* 2003), but H_0 was tested with a paired randomization test, using a test statistic, d, the mean of the differences between the GMHT and conventional (C) treatments on a logarithmic scale. Treatment effects were estimated by $R = 10^d$, the multiplicative treatment ratio of the GMHT treatment divided by the conventional; confidence limits about R were obtained from back-transformation of the confidence interval of d on the logarithmic scale, derived from the standard error of d and $t_{0.05}$. Average values were calculated as back-transformed geometric means; biomass and missing values were computed according to methods given in Heard *et al.* (2003).

Covariate analyses followed methods outlined in Brooks *et al.* (2003) to detect whether invertebrate results could be explained by the abundance and biomass of weeds in the field. Estimates of the multiplicative treatment ratio adjusted for the covariate, R_{adj}, are given with associated probability level, p_{adj}, and the probability level, p_{cov}, for the covariate. Further, separate covariate analyses (Firbank *et al.* 2003*a*; Heard *et al.* 2003) were done to detect whether weed or invertebrate treatment effects were consistent across the environmental and management covariates of the baseline seedbank and the six environmental zones of the ITE Land Classification of Great Britain (Firbank *et al.* 2003*c*).

Vegetation counts were inspected to see if treatment effects differed with density (density effect): they were quantified by fitting splines with four degrees of freedom (d.f.) to plots of the difference in count between the two treatments ('GM' and C) on a logarithmic scale $y = \log(N_{GM} + 1) - \log(N_C + 1)$, versus the sum of the counts for the treatments on a logarithmic scale $x = \log(N_{GM} + 1) + \log(N_C + 1)$.

The three measures of species diversity and methods of analysis for all weed species and the Carabidae followed those in Heard *et al.* (2003) and Brooks *et al.* (2003), respectively: (i) the number of species, S, using $\log(N)$, where N represents the total number of individuals, as covariate; (ii) the log-series α index; and (iii) dominance, D, transformed to logits.

3. RESULTS

(a) *Crop management and growth*

The average sowing date was in the first week of September in all three years. Herbicides were applied to conventional crops, on average, 38 days after sowing, including 25 (out of 65) sites treated within the first 7 days and six sites not treated until the following spring. By contrast, GMHT crops were treated on average 91 days after sowing, and this varied greatly between year 2001 (75 days) and years 2000 and 2002 (105 and 103 days, respectively). At 20 sites the GMHT treatment was not treated with herbicides until the following spring (figure 1). Fewer herbicide applications and fewer active ingredients were employed in the FSE conventional treatments than were used nationally in 2002, albeit with slightly higher dosages (data from the Pesticide Usage Survey; M.R. Thomas, personal communication).

Mean crop height was similar for GMHT and conventional crops (figure 1). Mean crop cover varied between treatments slightly, with the greatest difference occurring between around 170 and 200 days from sowing. The greater variation in cover of conventional WOSR may have been owing to the greater number of cultivars grown, as opposed to the single GMHT variety. Mean weed cover was higher on the GMHT crops for the first 200 days or so, but was then greater on the conventional fields, following the later herbicide applications on the GMHT treatment.

(b) *Weed seedbank and weed counts*

As expected, the baseline weed seedbank densities for total weeds, dicots and monocots did not differ significantly between treatments (table 1). The geometric mean total seedbank density of approximately 1660 m^{-2} was composed of roughly equal numbers of monocot and dicot weed seeds. This was slightly lower than the seedbanks found in the spring crops of the FSEs, which ranged from 1800 to 2500 seeds m^{-2} (Heard *et al.* 2003).

At the first seedling count, greater weed densities

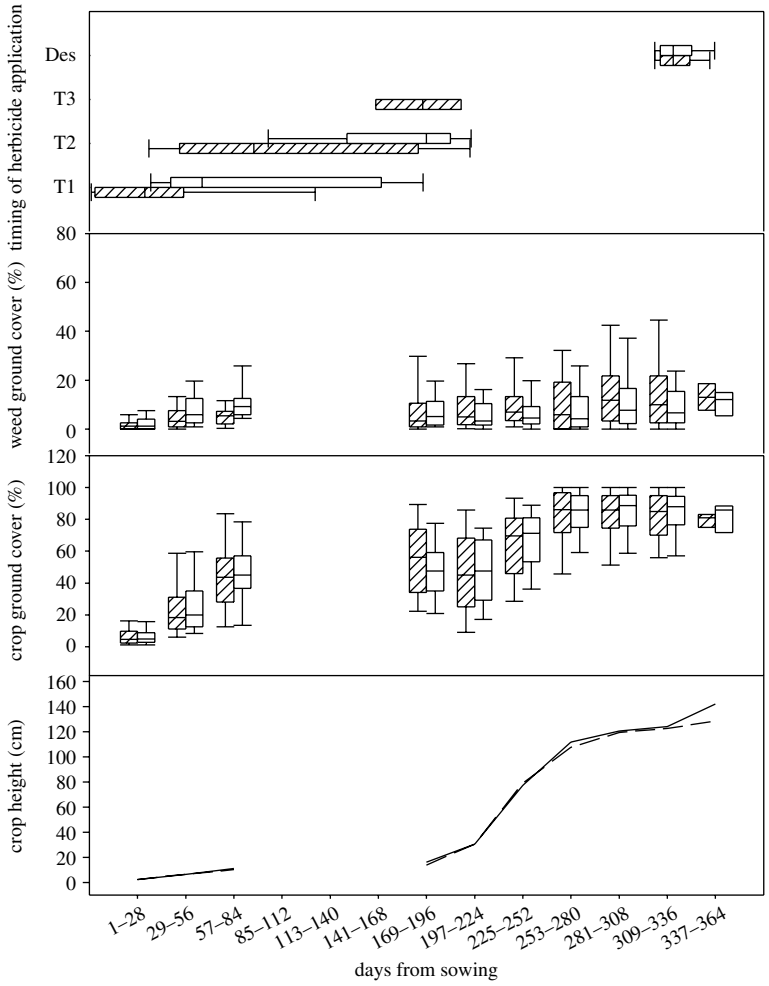

Figure 1. Timing of herbicide applications, percentage weed and crop cover and crop height against the number of days from sowing. Conventional (hatched boxes, dashed lines) and GMHT (open boxes, solid lines) WOSR crops. Boxes span the 25th to 75th percentiles; the line denotes the median; whiskers denote the 10th and 90th percentiles. Four successive treatments (herbicides T1, T2 and T3 and desiccants Des) were applied to conventional ($n=63$, 30, 6 and 41 sites for T1–3 and Des) and GHMT treatments ($n=63$, 18 and 41 sites for T1–2 and Des). Weed and crop cover and crop height assessed on conventional ($n=44$, 62, 12, 20, 59, 61, 59, 64, 43, 6) and GMHT ($n=44$, 63, 11, 20, 57, 62, 59, 62, 42, 6) sites. Assessments of crop height and weed cover were made infrequently over the winter (four sites between 85 and 168 days from sowing) and these data are not included.

($R=2.29$) were found in the GMHT treatment, owing to pre-emergence herbicide use on the conventional treatment, but this effect had disappeared by the early spring count, when both treatments had herbicides applied in 59 of the 65 sites. At the final count, there were more total weeds in the GMHT treatment than the conventional (table 1). However, there were no treatment effects on total weed biomass, seed rain or in weed numbers in the following seasons.

There were larger differences in treatment effect within both dicot and monocot weeds. Initially, both dicots and monocots were more numerous in the GMHT crop, but subsequently, there were significantly fewer dicots but significantly more monocots present in the GMHT than in the conventional crops (table 1, figure 2). Similar, contrasting treatment differences were seen in monocot and dicot plants with more than four true leaves at the early spring count and in plants that were reproductive at the final count (Electronic Appendix, table 1).

Species-level effects on weeds echoed the effects on dicots and moncots. The five most common dicot species occurred on at least 75% of sites and all were at lower abundance in the GMHT crop by the final count (Electronic Appendix, table 2), with lower seed rain and seedbank $t+1$ being observed for the majority of the species. The most abundant weed, the monocot *Poa annua*, was found at 90% of sites and made up 24% of the total seedbank (Electronic Appendix, table 2). *Alopecurus myosuroides* was present on about 50% of sites, reflecting its patchy geographical distribution, and it was controlled well by conventional herbicides (Electronic Appendix, table 2). Three times more of these monocot plants were found at the final count in the GMHT treatment. Wheat and barley crop volunteers occurred in larger numbers in the GMHT treatment at the first seedling count, but later almost disappeared indicating good control by both herbicide regimes.

Weed diversity differed the most between treatments in the early spring, with greater dominance (D) in the GMHT crops ($C=0.45$, GMHT$=0.54$) and greater species richness (S) in the conventional ($C=15.17$, GMHT$=12.89$) crop (table 2).

Table 1. Weed seedbank densities (numbers per metres squared in top 15 centimetres), plant densities (numbers per metres squared), biomass (grams per metres squared) and seed rain (seeds per metres squared) per treatment in relation to sampling occasion.
(Values are geometric means for GMHT and conventional (*C*) treatments. Multiplicative treatment ratio, $R=10^{d}$, where d is the mean of the differences between GMHT and *C* treatments on the logarithmic scale; confidence limits for *R* are back-transformed from those for *d*. N.B.: figures for dicots and monocots in the table do not sum to the figures for total weeds because of use of geometric means. CI, confidence interval; $^{\star}p<0.05$; $^{\star\star}p<0.01$; $^{\star\star\star}p<0.001$.)

sampling occasion, year	geometric mean			*R* (95% CI)	*p*-value
	n	*C*	GMHT		
weeds					
seedbank, *t*	55	1719.8	1598.7	0.93 (0.73–1.12)	0.45
seedling, *t*	65	83.3	190.7	2.29 (1.71–3.07)	<0.001***
early spring, *t*	63	39.5	50.9	1.29 (0.95–1.74)	0.09
post-herbicide, *t*	63	41.0	48.7	1.19 (0.96–1.47)	0.13
final, *t*	65	57.9	69.0	1.19 (1.02–1.40)	0.04*
biomass, *t*	65	40.6	33.5	0.82 (0.57–1.19)	0.28
seed rain, *t*	65	5023.9	3719.9	0.74 (0.47–1.17)	0.18
seedbank, *t*+1	65	2799.4	2625.0	0.94 (0.76–1.16)	0.56
follow-up, *t*+1	50	174.8	214.8	1.23 (0.97–1.56)	0.06
seedbank, *t*+2	49	2941.9	2941.9	1.00 (0.84–1.20)	0.99
follow-up *t*+2	20	37.8	46.7	1.24 (0.77–1.98)	0.38
dicots					
seedbank, *t*	55	712.4	638.3	0.90 (0.73–1.11)	0.31
seedling, *t*	65	28.8	56.2	1.94 (1.43–2.64)	<0.001***
early spring, *t*	63	25.0	16.5	0.66 (0.49–0.89)	0.01**
post-herbicide, *t*	63	29.2	19.8	0.68 (0.54–0.86)	<0.001***
final, *t*	65	37.2	30.3	0.82 (0.68–0.98)	0.04*
biomass, *t*	65	28.0	10.2	0.36 (0.25–0.54)	<0.001***
seed rain, *t*	64	4132.1	1372.9	0.33 (0.20–0.56)	<0.001***
seedbank, *t*+1	65	1543.1	1087.5	0.71 (0.57–0.88)	0.002**
follow-up, *t*+1	50	53.5	37.4	0.72 (0.51–1.00)	0.04*
seedbank, *t*+2	49	1385.6	1074.4	0.78 (0.63–0.97)	0.03*
follow-up *t*+2	20	14.1	8.9	0.64 (0.39–1.06)	0.08
monocots					
seedbank, *t*	55	691.3	723.2	1.05 (0.81–1.34)	0.72
seedling, *t*	65	27.8	83.5	3.00 (1.90–4.74)	<0.001***
early spring, *t*	63	7.5	23.1	3.07 (1.84–5.11)	<0.001***
post-herbicide, *t*	63	7.0	18.5	2.62 (1.69–4.05)	<0.001***
final, *t*	65	10.3	25.9	2.47 (1.74–3.50)	<0.001***
biomass, *t*	65	4.7	13.3	2.86 (1.57–5.19)	0.003**
seed rain, *t*	63	290.1	1407.5	4.80 (2.40–9.61)	<0.001***
seedbank, *t*+1	65	791.3	995.6	1.25 (0.91–1.71)	0.15
follow-up, *t*+1	49	84.3	129.1	1.51 (1.09–2.09)	0.007**
seedbank, *t*+2	49	1038.8	1310.6	1.26 (0.99–1.60)	0.06
follow-up *t*+2	19	18.3	31.4	1.71 (0.99–2.96)	0.04*

(c) *Weed biomass and seed rain*

There were large, but opposite, effects on the biomass and seed rain of dicots and monocots (table 1). Overall, the average of the dicot biomass was over twice as great in the conventional crop, and monocot biomass was nearly three times greater in the GMHT; differences that were similar in direction but not in magnitude to those in post-herbicide and final counts. The weeds in the conventional crops were fewer, but larger. Similarly with seed rain, seed return of dicots was between two (GMHT) and six (*C*) times larger than the original seedbank and between half (*C*) and twice (GMHT) the original seedbank for monocots. Dicot seed rain in the GMHT treatment was one-third that in the conventional, while monocot seed rain in the GMHT treatment was nearly five times that in the conventional. Dominance in the seed rain in the GMHT crop was also greater ($D=0.58$ (*C*), $D=0.70$ (GMHT), table 2).

(d) *Seedbank effects in following years, t+1 and t+2*

In the first following crop $t+1$, dicot seedbanks and seedling counts were significantly greater in the conventional than in the GMHT treatment. Significant differences were observed between numbers of monocot seedlings, consistent with effects on seed rain the previous year, but differences in the seedbank were not detected (table 1). Seedbank densities at $t+1$ had increased from the baseline at rates of 14% (conventional) and 38% (GMHT) for monocots and 70% (GMHT) and 117% (conventional) for dicots. There was relatively little change in dicot seedbanks from $t+1$ to $t+2$, but monocot seedbanks increased 30% on both treatments.

Table 2. Diversity of total weeds and pitfall-trapped Carabidae per treatment in relation to sampling occasion. (Indices are: S, number of species; α, log-series alpha; and D, dominance. Values in brackets after α are standard errors. Treatment effects for S are corrected for plant density by using log(number of individuals) as a covariate; treatment effects for D are after transformation to logits; p-values for α and D are based on randomization tests. Seedbank analyses exclude sites that had been treated with herbicide prior to soil collection; $^{\star}p<0.05$; $^{\star\star}p<0.01$; $^{\star\star\star}p<0.001$.)

sampling occasion, year	index	n	C	GMHT	treatment effect	s.e.m. of effect	p-value
weeds							
seedbank, t	S	55	11.78	11.71	0.003	0.46	0.99
	α	55	12.86	13.98	1.11	–	0.31
	D	32	0.52	0.52	0.002	0.12	0.99
seedling, t	S	65	12.97	16.42	0.55	0.68	0.42
	α	65	8.91	9.43	0.51	–	0.47
	D	61	0.59	0.58	−0.07	0.12	0.55
early spring, t	S	63	15.17	12.89	−2.32	0.53	<0.001***
	α	63	11.48	9.28	−0.22	–	0.01**
	D	53	0.45	0.54	0.37	0.16	0.02*
post-herbicide, t	S	63	16.44	16.19	−0.81	0.48	0.10
	α	63	14.21	12.41	−1.80	–	0.03*
	D	60	0.40	0.50	0.43	0.13	<0.001***
final, t	S	65	16.97	17.23	−0.16	0.57	0.78
	α	65	21.43	18.89	−2.54	–	0.07
	D	61	0.40	0.41	0.04	0.11	0.71
biomass, t	D	65	0.45	0.47	0.05	0.11	0.68
seed rain, t	S	65	13.85	13.00	−0.47	0.52	0.37
	α	65	11.05	10.44	−0.61	–	0.48
	D	54	0.58	0.70	0.54	0.19	0.01**
seedbank, $t+1$	S	65	13.77	13.95	0.31	0.59	0.60
	α	65	14.48	15.56	1.08	–	0.24
	D	51	0.46	0.54	0.31	0.14	0.04*
Carabidae							
year total	S	65	19.6	19.5	−0.24	0.37	0.52
	α	65	9.09	9.55	0.45	–	0.48
	D	63	0.36	0.41	0.22	0.065	0.002**
autumn	S	62	7.87	7.95	−0.043	0.26	0.87
	α	62	5.91	6.94	0.48	–	0.47
	D	47	0.60	0.60	−0.012	0.068	0.87
spring	S	60	12.4	12.6	0.42	0.37	0.26
	α	61	8.64	9.38	0.74	–	0.33
	D	32	0.47	0.42	−0.20	0.14	0.16
summer	S	59	13.8	13.7	−0.32	0.44	0.47
	α	59	7.49	8.13	0.64	–	0.35
	D	54	0.50	0.54	0.15	0.078	0.057

(e) *Consistency of weed treatment effects*

For total dicots at the seedling stage, the fitted splines (figure 3) showed that there was no density effect. However, for the early spring counts, post-herbicide and final counts, total dicots showed a clear density effect, with values of R at low densities being smaller ($R \ll 1$) than those given in table 1 (a more pronounced treatment effect) but values close to one at the largest densities (negligible treatment effect). For all four occasions, total monocots showed a clear density effect, with values of R at low densities being larger ($R \gg 1$) than those given in table 1 (a more pronounced treatment effect) and values close to one at the largest densities (negligible treatment effect).

Some significant year×treatment interactions were found but were largely restricted to the early spring counts for total weeds, dicots and monocots. Interactions between treatment and environmental zone were limited to zone 4 (the lowlands of Scotland; $n=9$) monocots at the seedling, early spring, post-herbicide and final counts that had high R values. The size of the initial seedbank affected one treatment comparison for monocots at the seedling count where high densities at several sites were associated with high R values.

(f) *Weeds in the field boundary*

Analyses of weed cover, flowering and weed seeding in the verge and boundary did not show significant effects of the two treatments (Electronic Appendix, table 3). Effects were limited to the tilled margin where less flowering of the weeds was seen in the GMHT treatment, although weed seeding in July was not affected.

(g) *Tests and estimation of invertebrate treatment effects*

Counts of the majority of invertebrate taxa did not differ significantly between the GMHT and conventional treatments. Of the invertebrates that were affected, bee

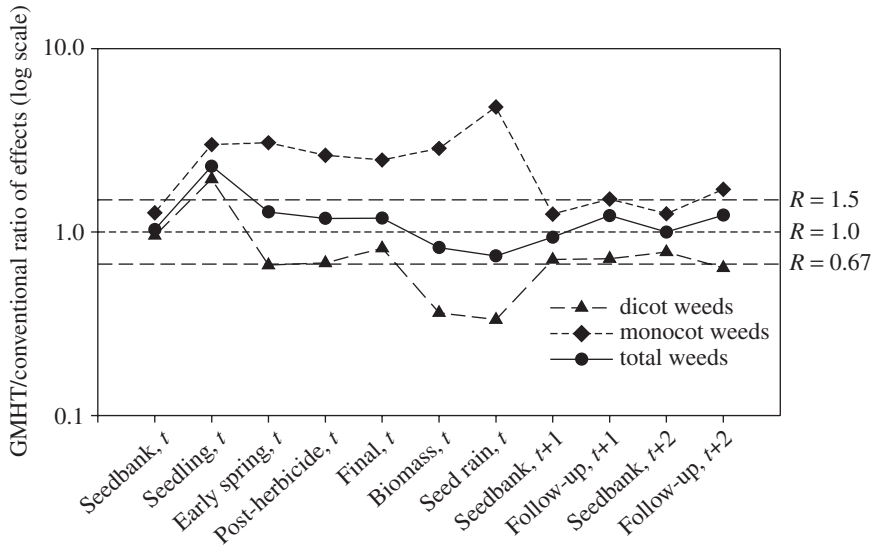

Figure 2. Multiplicative treatment ratio, R (GMHT:conventional), for total weeds, dicots and monocots. Lines represent where the indicator is equivalent in both treatments ($R=1$), or where it is 50% higher ($R=1.5$) or 50% lower ($R=0.67$) in the GMHT than in the conventional.

counts were significantly lower in the GMHT treatment, at 42% of the conventional in July (table 3; Electronic Appendix, table 4), after the WOSR crop had flowered. The lower count of bees in the GMHT treatment was, in the main, due to effects on bumblebees, although these were present in sufficient numbers for analysis at only 12 sites. Counts of the *Pieris* butterflies under GMHT management in July were 59% of those in the conventional treatment at that time. There were no effects of treatment on the total counts of pitfall-trapped carabids, staphylinids or most spider species across the year (table 3). However, significantly fewer Linyphiidae, and particularly *Lepthyphantes tenuis*, were found in the spring pitfall traps in the GMHT treatment. Pitfall counts of total Collembola and the families Entomobryidae, Isotomidae and Sminthuridae were greater in the GMHT treatment, when summed across the year. Counts of species or taxa sampled by suction sampler did not differ between GMHT and conventional treatments in any sampling period or across the year (table 3).

Counts of invertebrates sampled in the tilled margin were similar to those found in the field with the majority of species being found not to differ between the GMHT and conventional treatments (table 3; Electronic Appendix, table 4). Suction-sampled margin Heteroptera were 36% greater adjacent to the GMHT treatments in the summer. Bee counts were significantly lower next to the GMHT treatment, in July, due to *Apis mellifera*, the honeybee, although this species was only recorded in sufficient numbers at nine sites. Counts of *Pyronia tithonus*, the hedge brown, and *Pieris brassicae*, the large white, were significantly lower in the GMHT treatment. Conversely, *P. brassicae* counts in the margin were 94% greater in May under GMHT management.

(h) *Consistency of invertebrate treatment effects*

The covariates for environmental zone and initial seedbank weed–seed counts did not interact significantly with treatment effects.

The flowering Asteraceae were found to explain some of the treatment effect for bumblebees ($R_{adj}=0.52$, $p_{adj}=0.063$, $p_{cov}=0.73$), while total weed biomass explained a proportion of the effect of treatment on the *Pieris* butterfly species ($R_{adj}=0.65$, $p_{adj}=0.049$, $p_{cov}=0.93$). Dicot weed abundance, at the seedling count, explained a significant proportion of the treatment effect for total Collembola ($R_{adj}=1.16$, $p_{adj}=0.071$, $p_{cov}=0.004$), Entomobryidae ($R_{adj}=1.09$, $p_{adj}=0.18$, $p_{cov}=0.036$) and Isotomidae ($R_{adj}=1.14$, $p_{adj}=0.15$, $p_{cov}=0.001$) across the year. Significant relationships were estimated for the pitfall-trapped Staphylinidae ($R_{adj}=1.04$, $p_{adj}=0.53$, $p_{cov}=0.042$) using post-herbicide weed counts and suction sampled spiders ($R_{adj}=0.99$, $p_{adj}=0.21$, $p_{cov}=0.018$) with linear and quadratic terms for weed biomass, while reduced statistical significance was found with the covariates for pitfall-trapped carabids ($R_{adj}=1.03$, $p_{adj}=0.51$, $p_{cov}=0.60$). Only the counts of Heteroptera showed no relationship to post-herbicide weed abundance or total biomass.

(i) *Carabidae diversity*

Carabidae dominance was higher in the GMHT across the year, although log-series α and species richness S did not differ significantly between treatments (table 2).

4. DISCUSSION

These results present a number of interesting similarities with, but some consistent and important differences to, the results for the spring-sown crops in the FSEs. The treatment effects on the dicot weeds, and species within this group, in WOSR were broadly similar to those observed for SOSR, with greater numbers being found in the conventional treatment throughout the year. Marked differences were observed for the monocots, though, which were strongly selected for in the WOSR GMHT treatment. The increase in monocot weeds under GMHT resulted from relatively poor monocot control by late-applied glufosinate-ammonium (Petersen 2000), compared with the pre-emergence herbicides used in the conventional treatments. The consequence of this was a

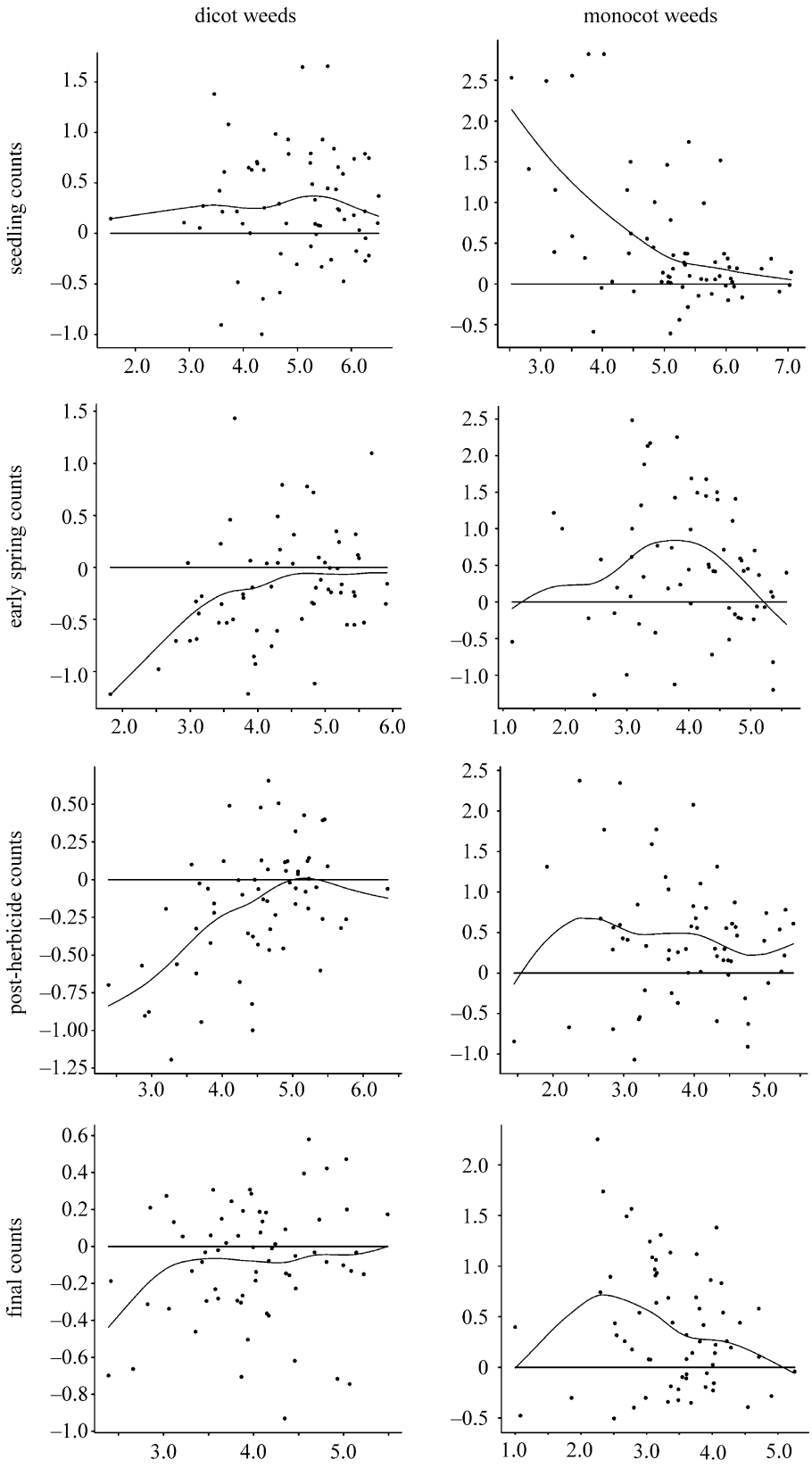

Figure 3. Graphs of counts of total weeds, N, for dicots and monocots, for each of n sites, for samples of seedling, early spring, post-herbicide and final counts. The y-axis for each graph is the difference in count between the two treatments on a logarithmic scale: $\log(N_{GM}+1)-\log(N_C+1)$, for which the mean value is the quantity d (table 2). The x-axis is the sum of the counts for the treatments on a logarithmic scale: $\log(N_{GM}+1)+\log(N_C+1)$, a measure of the overall abundance per field. The equality line, $R=1$ (see fig. 6 of Firbank *et al.* (2003*b*)), is shown for reference as the horizontal line $y=0$. The curve is a smooth spline fitted through the points with four d.f.

Table 3. Counts of high-level taxa, and species with statistically significant effects, sampled in conventional (*C*) and GMHT WOSR.
(Values are geometric means for GMHT and conventional (*C*) treatments. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and *C* treatments on the logarithmic scale; confidence limits for *R* are back-transformed from those for *d*. CI, confidence interval; †, too few sites for analysis; $\star p < 0.05$, $\star\star p < 0.01$.)

protocol and taxa	period	*n*	geometric mean		*R* (95% CI)	*p*-value
			C	GMHT		
pitfall-trapping						
total Carabidae	year	65	497	520	1.05 (0.95–1.15)	0.36
total Staphylinidae	year	65	147	157	1.07 (0.95–1.20)	0.25
total Araneae	year	65	187	177	0.95 (0.87–1.03)	0.21
Linyphiidae	year	65	110	109	0.99 (0.90–1.08)	0.79
	autumn	61	18.0	17.2	0.96 (0.83–1.10)	0.53
	spring	61	23.5	17.1	0.74 (0.62–0.87)	0.002**
	summer	59	65.1	73.2	1.12 (0.97–1.29)	0.10
Lepthyphantes tenuis	year	65	23.4	21.5	0.92 (0.82–1.03)	0.14
	autumn	60	9.50	8.65	0.92 (0.76–1.11)	0.38
	spring	49	3.51	2.14	0.70 (0.53–0.91)	0.011*
	summer	55	11.2	12.6	1.11 (0.91–1.37)	0.29
total Collembola	year	65	620	769	1.24 (1.07–1.43)	0.007**
Entomobryidae	year	64	70.4	83.1	1.18 (1.01–1.37)	0.028*
Isotomidae	year	65	336	423	1.26 (1.07–1.48)	0.009**
Sminthuridae	year	65	39.6	53.5	1.34 (1.05–1.72)	0.021*
	autumn	58	13.8	13.8	1.00 (0.71–1.40)	0.99
	spring	52	13.2	17.8	1.32 (0.94–1.86)	0.12
	summer	56	12.9	19.4	1.46 (1.06–2.03)	0.027*
suction sampling						
total Carabidae	year	53	4.04	4.06	1.00 (0.82–1.23)	0.97
total Heteroptera	year	21	1.77	1.51	0.91 (0.60–1.36)	0.63
total Araneae	year	60	5.43	4.54	0.86 (0.72–1.04)	0.12
total Collembola	year	65	184	186	1.01 (0.85–1.20)	0.89
margin suction sampling						
total Carabidae	year	57	4.05	4.70	1.13 (0.91–1.40)	0.24
Bembidion lampros	year	14	0.72	2.31	1.93 (1.16–3.21)	0.043*
	autumn	12	0.67	2.28	1.96 (1.09–3.54)	0.053
	summer	—	—	—	—	†
total Heteroptera	year	54	3.46	4.47	1.23 (0.95–1.58)	0.11
	autumn	30	1.93	1.88	0.98 (0.67–1.45)	0.92
	summer	47	2.46	3.72	1.36 (1.01–1.83)	0.036*
total Araneae	year	64	18.1	20.8	1.14 (0.92–1.41)	0.21
total Collembola	year	65	121	136	1.12 (0.92–1.37)	0.23
bees and butterflies						
total bees	year	63	14.0	11.3	0.82 (0.64–1.06)	0.10
	April	32	3.51	3.74	1.05 (0.75–1.48)	0.76
	May	44	4.68	4.24	0.92 (0.70–1.22)	0.55
	June	44	6.78	5.12	0.79 (0.54–1.15)	0.20
	July	15	4.79	1.41	0.42 (0.26–0.66)	0.004**
bumble-bees	year	62	9.20	6.93	0.78 (0.60–1.01)	0.053
	July	12	4.26	1.58	0.49 (0.30–0.81)	0.01**
total butterflies	year	56	4.45	3.86	0.89 (0.67–1.19)	0.44
	April	11	1.38	1.61	1.10 (0.44–2.74)	0.82
	May	23	1.80	1.77	0.99 (0.64–1.52)	0.95
	June	26	2.26	1.49	0.76 (0.48–1.21)	0.26
	July	33	5.14	3.43	0.72 (0.51–1.02)	0.062
	year	51	3.73	2.77	0.80 (0.59–1.08)	0.14
Pieris species	July	27	5.62	2.90	0.59 (0.42–0.83)	0.004**
margin bees and butterflies						
total bees	year	64	11.1	10.9	0.98 (0.77–1.25)	0.89
	April	26	2.62	3.95	1.37 (0.85–2.21)	0.20
	May	42	3.31	3.34	1.01 (0.79–1.28)	0.95
	June	51	4.11	4.13	1.00 (0.72–1.39)	0.97
	July	44	3.22	1.88	0.68 (0.48–0.96)	0.043*
Apis mellifera	year	38	3.63	3.98	1.08 (0.72–1.62)	0.72
	July	9	2.75	0.82	0.49 (0.30–0.79)	0.028*

(*Continued.*)

Table 3. (*Continued.*)

protocol and taxa	period	*n*	geometric mean		*R* (95% CI)	*p*-value
			C	GMHT		
total butterflies	year	64	12.7	11.3	0.90 (0.74–1.09)	0.28
	April	28	1.87	2.01	1.05 (0.70–1.56)	0.82
	May	43	3.49	3.09	0.91 (0.69–1.19)	0.48
	June	40	3.30	2.10	0.72 (0.48–1.09)	0.11
	July	55	6.50	6.60	1.01 (0.80–1.28)	0.91
Pieris brassicae	year	34	3.37	1.86	0.66 (0.42–1.01)	0.052
	April	3	0.82	3.31	2.37 (0.16–35.0)	0.83
	May	14	0.67	2.23	1.94 (1.20–3.13)	0.016*
	June	12	1.99	0.74	0.58 (0.24–1.43)	0.23
	July	19	3.72	1.21	0.47 (0.28–0.79)	0.008**
Pyronia tithonus	year	7	3.43	0.71	0.39 (0.18–0.83)	0.049*
	July	7	3.03	0.61	0.40 (0.19–0.84)	0.049*

result for WOSR clearly different from those seen previously in the spring-sown FSEs (Heard *et al.* 2003), with contrasting numbers of dicots and monocots in the GMHT treatment (figure 2). Surprisingly, given the results of the spring-sown crops where changes in weed abundance could be used to explain invertebrate effects (Brooks *et al.* 2003; Haughton *et al.* 2003; Hawes *et al.* 2003; Roy *et al.* 2003), the majority of invertebrate species in the margin and field did not show treatment effects in WOSR. Only the bees and butterflies, which select for the higher dicot numbers in the conventional treatment, and the mainly detritivorous Collembola, which presumably feed upon those larger weeds selectively killed in the GMHT treatment, showed any response.

In conventional WOSR, dicot weeds are not specifically targeted for control because vigorously growing oilseed rape tolerates dicot weed competition and pre-emergence herbicides are effective (Lutman 1989; HGCA 2000). Monocot weed species, however, can be a serious economic problem and are a major factor considered by farmers when designing weed control programmes. Density effects were produced by farmers responding to weed density, for both monocots and dicots, at pre- and post-emergence herbicide applications, respectively. In conventional half-fields, pre-emergence herbicides were applied to control dicots. As monocot densities were weakly negatively correlated with dicots across all sites ($R=-0.132$, $t_{64}=-1.71$, $p=0.093$), sites with low dicot but high moncot densities had no pre-emergence herbicides applied. There was a treatment effect for dicots ($R>1$), but no appreciable density effect at the seedling stage, before the application of post-emergence herbicides to the GMHT half-fields. For sites with increasing dicot densities and low monocot densities, an appreciable and persistent density effect resulted for the monocots, with $R\gg1$. By contrast, on GMHT half-fields, post-emergence application of glufosinate-ammonium was in response to monocot densities; sites with high densities of monocots and low densities of dicots received the largest doses, so there was a strong density effect at these sites, with $R\ll1$. Such density effects may also explain the observed treatment×environmental zone and treatment×initial seedbank interactions. In lowland Scotland (zone 4), for example, eight of the nine sites had received pre-emergence herbicides, in response to high dicot weed counts and the associated dicot seedbank counts, resulting in high monocot *R* values ranging between 0.8 and 4.6. While these findings would suggest that the effects on dicots and monocots may have been in part related to weed density, it should be stressed that this does not change the overall result that dicots were less abundant, and monocots more abundant, in GMHT than conventional crops.

A marked difference between the results for WOSR and those for the spring-sown GMHT crops was that the majority of invertebrate taxa did not respond to treatment. Whereas in the spring-sown crops species from a wide range of groups showed responses that could be related to herbicide-induced changes in monocot or dicot abundance (Brooks *et al.* 2003; Haughton *et al.* 2003; Hawes *et al.* 2003; Roy *et al.* 2003), remarkably few effects were observed in WOSR. This finding may be due, in part, to the WOSR crop itself, which is large, structurally complex and could provide the microclimate preferred by many invertebrates (see Baker & Dunning 1975; Brooks *et al.* 2003) that might otherwise be provided by the weeds. These conditions would be similar in both treatments and might buffer treatment effects on the invertebrates. In turn, interaction effects were found, with total weeds, for some taxa, possibly suggesting that invertebrates might be able to trade-off changes in food and habitat weed resources, between the dicot and monocot weed groupings, and follow trends in total weed abundance or biomass. The pollinator, bee and butterfly, and detritivore Collembola groups did show treatment effects in WOSR, however, and in a manner similar to that found in SOSR. The pollinators, which actively forage for flowering dicot resources, were found in larger numbers in the conventional treatment and could be explained by covariates for the abundance of flowering Asteraceae and total weed biomass. The difference in pollinator numbers between GMHT and conventional treatments also increased through time, as more dicots came into flower. As in the spring-sown crops, Collembola numbers were higher in the GMHT treatment. These effects were, in large part, well explained by the higher abundance of dicot weeds in the GMHT treatments in the autumn. The early presence of these weeds, subsequently controlled in the GMHT treatment, would produce detritus that might sustain the

significantly greater abundance of Collembola in the GMHT treatment over the season.

Within the growing season, the lower abundance of dicots in the GMHT treatment might suggest that bees and butterflies, and other animals that depend upon dicots, would not fare well if GMHT WOSR were widely adopted. Indeed, that groups of bees and butterflies were similarly affected by GMHT herbicide management in spring-sown beet, SOSR and WOSR suggests a consistent effect of GMHT management that might have a negative impact on pollinator abundance, and conceivably on pollination (Allen-Wardell *et al.* 1998). However, the importance of weeds in WOSR crops as forage resources for bees and butterflies is as yet uncertain. The availability of alternative forage, shelter and larval food resources in adjacent habitats during the summer would be critical (Dover & Sparks 2000; Backman & Tiainen 2002) for buffering populations of these mobile groups against the effects of changes in herbicide management, but only if forage reductions do not occur over large contiguous areas (Sherratt & Jepson 1993; Weibull *et al.* 2000; Roy *et al.* 2003). In the longer term, the increase in both the dicot and monocot seedbanks from the baseline to the follow-up sampling indicates the perceived importance of oilseed rape crops in replenishing the weed seedbank within cereal rotations. That the dicot increase was lower and the monocot increase higher in the GMHT crop might suggest that were GMHT WOSR to replace conventional WOSR in typical cereal rotations in the UK, then dicot seedbank abundance might decline from those currently observed, while the monocot seedbank could increase.

In conclusion, this experiment has shown large and important differences in the treatment effects for dicot and monocot weeds, leading us to reject the null hypothesis for weed vegetation. We would expect to see greater numbers of monocots under GMHT WOSR herbicide regimes, as tested, and lower numbers of dicots. Such a decline in dicot abundance might adversely affect pollinator species and those taxa at higher trophic levels, such as some birds, dependent on dicots as a seed food resource. However, for the majority of invertebrate taxa, no systematic effects of glufosinate-ammonium management in GMHT WOSR were observed despite the close linkage between some invertebrate groups and vegetation reported for the spring-sown crops, also tested in FSEs (Brooks *et al.* 2003; Haughton *et al.* 2003; Hawes *et al.* 2003). Only for the bees and butterflies and the Collembola were consistent treatments effects estimated, for which we also reject the null hypothesis.

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