

Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil-surface-active invertebrates

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The effects of herbicide management of genetically modified herbicide-tolerant (GMHT) beet, maize and spring oilseed rape on the abundance and diversity of soil-surface-active invertebrates were assessed. Most effects did not differ between years, environmental zones or initial seedbanks or between sugar and fodder beet. This suggests that the results may be treated as generally applicable to agricultural situations throughout the UK for these crops. The direction of the effects was evenly balanced between increases and decreases in counts in the GMHT compared with the conventional treatment. Most effects involving a greater capture in the GMHT treatments occurred in maize, whereas most effects involving a smaller capture were in beet and spring oilseed rape. Differences between GMHT and conventional crop herbicide management had a significant effect on the capture of most surface-active invertebrate species and higher taxa tested in at least one crop, and these differences reflected the phenology and ecology of the invertebrates. Counts of carabids that feed on weed seeds were smaller in GMHT beet and spring oilseed rape but larger in GMHT maize. In contrast, collembolan detritivore counts were significantly larger under GMHT crop management.

Keywords: genetically modified crops; Farm Scale Evaluations; environmental impact; invertebrate biodiversity; Carabidae; Collembola

1. INTRODUCTION

The commercial adoption of GMHT crops would result in marked changes to current herbicide management of conventional arable crops (Firbank *et al.* 2003b). In particular, growing GMHT varieties would enable the use of broad-spectrum herbicides that would normally be toxic to conventional crops. Such herbicides control a wider range of weeds more efficiently than those used in conventional systems during the growing season. Concerns have

been expressed that this could intensify agriculture and exacerbate reported declines in the biodiversity and biomass of the weed vegetation (Krebs *et al.* 1999; Robinson & Sutherland 2002). Conversely, the use of broad-spectrum herbicides could enable greater flexibility of management and result in delayed or fewer applications. If managed correctly, this approach could have benefits for biodiversity at specific times during the year (Dewar *et al.* 2003). Modification of herbicide management could therefore result in changes to the species composition and biomass of weeds, with repercussions for non-target species at higher trophic levels (Firbank & Forcella 2000; Firbank *et al.* 2003b). Invertebrates are an important component of agricultural biodiversity and are often dependent on weed vegetation. It is therefore important to assess the indirect effects of herbicide management of

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GMHT crops on this group within the FSEs (Firbank *et al.* 1999, 2003b).

The in-field weeds of conventionally managed fields support many soil-dwelling and surface-active invertebrates, which have important ecological and conservation functions in providing food for mammals (Pollard & Relton 1970), birds (Brooks *et al.* 1995; Shah *et al.* 2003) and other invertebrates (Bohan *et al.* 2000a). Many of these species, such as the predatory Carabidae (ground beetles), Staphylinidae (rove beetles) and Araneae (spiders) (Speight & Lawton 1976; White & Hassall 1994), also have important ecological and economic roles in the control of pests. The relatively small (< 4 mm) collembolan (springtail) detritivores (Bilde *et al.* 2000) are important for the cycling of nutrients within the soil. The in-field weed vegetation also supports economically important surface-active pest species, notably slugs (Gastropoda: Stylommatophora) (Bohan *et al.* 2000b).

The composition of the in-field weed vegetation has been shown to affect the distributions of soil-dwelling and surface-active invertebrates. The seed-feeding carabid genera *Harpalus* and *Amara* increase in abundance with a greater biomass of weeds (Lorenz 1995) and in the absence of herbicides (Raskin *et al.* 1992). Responses to the density and composition of vegetation, and associated prey, have also been shown widely among the Carabidae (Thomas *et al.* 1997). The money spider *Lepthyphantes tenuis* preferentially colonizes structurally diverse vegetation for web building (Topping & Sunderland 1998), whereas the spider genera *Erigone* and *Oedothorax* colonize more sparsely vegetated areas within arable fields (Alderweireldt 1994). Weed abundance and diversity have also had significant effects on the functional response of Staphylinidae, at the family and species levels (Moreby & Southway 1999; Dewar *et al.* 2003). Slugs are influenced by, and in turn can influence, the species composition of plant communities (Glen *et al.* 1991) and the frequency of plant polymorphisms (Crawford-Sidebotham 1972). Among these groups there are therefore important species likely to respond to anthropogenic perturbations generally (Luff & Woiwod 1995; Kromp 1999) and to the herbicide management that might result from the widespread use of GMHT crops in particular.

This paper describes the effects of the management of GMHT crops on in-field soil-surface-active invertebrates. Effects were assessed in 66 beet, 59 maize and 67 spring oilseed rape sites. It partners the results given in Houghton *et al.* (2003) for plant epigeal and aerially active invertebrates. Many of the species and taxa documented within the Carabidae, Araneae and Collembola are common to both papers. The papers differ, however, in the sampling methodologies adopted. Houghton *et al.* (2003) used a Vortis suction-sampling methodology, whereas this paper reports sampling with pitfall traps, considered to be the most practical way to conduct large-scale surveys of surface-active invertebrates (Spence & Niemela 1994). Unlike Vortis sampling, which is a direct sampling method (Arnold 1994), pitfall trapping relies on individuals approaching and falling into traps. Pitfall-trap captures are a measure of the 'activity-density' of the species around each trap (Ericson 1977). Activity-density is a function of the activity pattern and the density of individuals (Greenslade 1964; Honek 1988) and caution should be

used when interpreting how captures relate to overall population sizes (Sunderland *et al.* 1995). The catches can, however, indicate preferences of invertebrates, such as Carabidae, for different habitat structures at the field level (Hawthorne 1995). They may also relate well to densities when accumulated over longer periods (Baars 1979).

The aim of this paper is to examine the differences in abundance and diversity of groups of surface-active invertebrates between GMHT and conventionally managed crops, and where possible to relate these differences to changes in the weed vegetation brought about by modified herbicide management. Direct observations of the long-term effects on invertebrates of growing GMHT crops either in rotation with conventional crops or on a large commercial scale are outside the scope of this paper. However, possible future implications for the invertebrate groups within such situations are considered. We specifically aim to (i) test the null hypothesis that there is no difference between the management during the growing season of GMHT beet, maize and spring oilseed rape and that of comparable conventional crops on the abundances of Carabidae, Staphylinidae, Araneae, Collembola and Gastropoda, and the diversity of Carabidae; (ii) estimate the magnitude of any observed differences in abundance or diversity; (iii) evaluate the importance of farmland and crop covariates, including: environmental zone; an initial estimate of the seedbank, as a measure of farming intensity; year; distance into crop; a comparison between sugar and fodder beet; biomass; and seed rain; and (iv) discuss how observed differences may result from herbicide effects on weed vegetation.

2. METHODS

The FSEs were designed to evaluate the effects of adopting GMHT crops on farmland biodiversity. They compared the effects of herbicide management of GM crops tolerant to either glyphosate (beet) or glufosinate-ammonium (maize and spring oilseed rape) with those of currently used conventional regimes, for spring-sown sugar and fodder beet, maize and spring oilseed rape. The management employed for both systems was representative of the range used for the crops when grown in a normal commercially viable context (Firbank *et al.* 2003b; Perry *et al.* 2003). Comprehensive details of the ways in which the crops were managed are given in Champion *et al.* (2003). Crops were grown from 2000 to 2002 on 201 farms in the UK that reflected both the typical field size and the current geographical distributions of each crop (Champion *et al.* 2003). During each of these years invertebrates were monitored in a wide range of single fields that were part of a normal commercial rotation. Each of these fields was split into two comparable halves, to which the GMHT and conventional crop treatments were assigned randomly (Perry *et al.* 2003). Invertebrates were sampled at set positions on transects equally distributed between half-fields. Any observed differences in abundance and diversity of groups of soil-surface-active invertebrates between the treatments were expected to be an indirect result of the effects of changes in herbicide management on weed vegetation (Firbank *et al.* 2003b; Squire *et al.* 2003).

An overview of the programme of field sampling and the rationale behind the soil-surface-active invertebrates chosen as indicator groups are given in Firbank *et al.* (2003b). Compre-

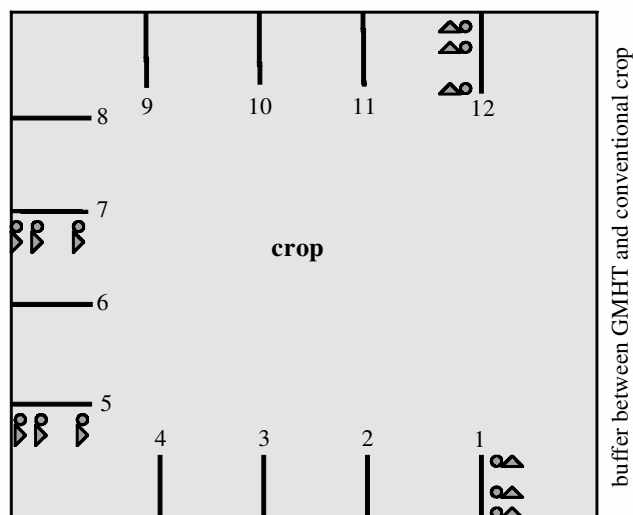


Figure 1. Field layout for arthropod pitfall and gastropod refuge trapping. Schematic diagram of a field showing locations of pitfall traps. This diagram is for an idealized geometry of the split-field design. Traps are placed at positions 2, 8 and 32 m from the edge of the crop along transects 1, 5, 7 and 12. Pitfall and refuge traps are offset 0.5 m and 3.5 m, respectively, from the centre line of these transects. The grey shaded area represents the crop, circles represent pitfall traps, triangles represent refuge traps and the numbered black lines show the transects in the crop.

hensive details of the experimental design, experimental power and statistical analysis are given in Perry *et al.* (2003).

(a) Pitfall trapping for surface-active invertebrates

Pitfall traps were used to survey populations of soil-surface-active invertebrates by modifying the methodology described by Luff (1996). Pitfall traps consisted of 6 cm diameter plastic cups, which were sunk into the ground with the top level with the soil surface. Each was two-thirds filled with a 50 : 50 mixture of tap water and ethylene glycol as a preservative. Twelve traps were distributed evenly across each half-field, with single traps positioned at 2, 8 and 32 m from the crop edge along four of 12 transects (figure 1). All transects were spaced evenly around the edges of half-fields and numbered 1–12 clockwise from the centre of the field. In all cases transect numbers 1, 5, 7 and 12 were used to locate pitfall traps. These transects were chosen to avoid the proximity of other experimental work within the FSE. Trapping was done three times on each field: during May, July and August in spring oilseed rape and beet, and during late May–early June, July and August in maize. On each occasion traps were operated for two weeks. These dates were chosen to reflect the range of species' phenologies across the season and the differing temporal aspects of management. When returned to the laboratory, the samples were preserved by freezing or placement in 70% alcohol, before identification under a binocular microscope. All species of carabid beetles were counted and identified, as were five taxa of Araneae: the families Linyphiidae and Lycosidae, the genus *Pardosa*, *Erigone* agg. (consisting of *E. atra* and *E. dentipalpis*) and the species *Lepthyphantes tenuis*. Collembola and staphylinid beetles were counted at the family level. Nomenclature followed Lindroth (1974), Forsythe (2000), Speight *et al.* (1986) and Aukema (1990) for Carabidae; Fjellberg (1980) for Collembola; Unwin (1988) for Staphylinidae; and Roberts (1993) for Araneae.

(b) Surface trapping for Gastropoda

Gastropoda were sampled by using baited refuge traps. These consisted of upturned 25 cm diameter plastic plant-pot saucers. Sample points were situated at the same positions used for the pitfall trapping, in each half of the field (figure 1). In the first year of the FSEs a single saucer was placed at each sampling point. For both subsequent years, four saucers, arranged in a square configuration with their centres 0.5 m apart, were used at each sample point to increase the capture rate. It should be noted that the lower number of trap saucers used at each sample point in the first year of the FSEs reduced the geometric means reported in the results, but did not affect the expected value of the estimated treatment effect.

The traps were baited with one teaspoon (*ca.* 5 ml) of layers mash, a standard chicken feed available from feed suppliers, placed centrally under each trap when the trap was placed on the soil surface (Young *et al.* 1996). Small gaps were left between the lip of the trap and the soil surface to enable slugs to enter and shelter beneath the trap. A stone or other weight was then placed on top of each trap to prevent it being blown away. Although traps were left in place for between three days and two weeks across all sites, this period before assessment was always equal for each treatment for any given sampling date. Molluscicide baits were not used for trapping (Young *et al.* 1996) because poisoned slugs are difficult to identify and rot rapidly. Pitfall-trap capture could have been affected by the proximity of the refuge traps, owing to the latter providing extra shelter or food resources. To avoid this, gastropods were surveyed at times that were close to, but never concurrent with, pitfall-trap operation. After trapping, the refuge traps and any remaining layers mash were removed from the field.

Trapping was done in late April and in early August for spring oilseed rape, and in May and August for maize and beet. This early and late sampling was designed to assess the population growth through the season which, owing to the multi-generational nature of the gastropods being studied (South 1992), may be sensitive to treatment effects. Multiple trapping, to assess extensively the seasonal population dynamics of this group, was not considered necessary to address the null hypothesis for differences in abundance. The early-season trapping dates were selected to coincide with peak slug damage at the seedling stage of the crop. The timing of sampling was adjusted, where possible, so that the forecast daily air temperature was in the region 10–18 °C, the weather was overcast and the soil surface and vegetation were visibly moist (Young & Port 1991). In August, when the temperature regularly exceeded 18 °C during the day, the traps were assessed before 11.00 whenever possible. If these conditions could not be met, results were removed from the analyses. This occurred for only 6% of trapping dates across all crops; replication remained high overall with the inclusion of at least 40 sites for all reported analyses.

3. STATISTICAL ANALYSIS

(a) Response variables

Where groups were identified to species, selection of appropriate taxa for analysis was informed by their recorded abundance and ecology within the wider context of this study. Analyses were done for total Carabidae and the 15 most commonly captured carabid species. Counts of individuals within the genera *Pterostichus*, *Harpalus*, *Amara* and *Bembidion* were also analysed. Staphylinidae were not identified to species, rather effects on total num-

bers were analysed for each crop. Analyses were completed for total Araneae, Lycosidae, Linyphiidae, *Pardosa* spp., *Erigone* agg., *Oedothorax* spp. and *L. tenuis* in all crops. Total Collembola were analysed, as were the families Entomobryidae, Isotomidae, Poduridae and Sminthuridae. These are four out of the five families recognized by Fjellberg (1980); the Onychuridae were not trapped in sufficient numbers to warrant separate analysis. In the gastropods, only *Deroceras reticulatum* was consistently trapped at all sites. This species is the most common slug pest in the UK (Bohan *et al.* 2000b), and was analysed in addition to total gastropod abundance.

(b) Analysis

A description of the experimental design has been given in detail elsewhere (Perry *et al.* 2003) and is only summarized briefly here. Records for each variate analysed were obtained from systematic sampling within each of $2n$ half-fields of three spring crops, in a randomized block experimental design, in which the blocks were paired half-fields. Most analyses were based on total counts per half-field. The total count, c_{ij} per half-field, for treatment i at site j , was transformed to $l_{ij} = \log(c_{ij} + 1)$. Sites, j , for which the whole-field total count, $c_{1j} + c_{2j}$, was zero or unity were removed from the analyses. The number of sites remaining for each analysis is reported as n , and the number of sites not sampled or removed from the analyses may be calculated as the difference between n and the total number of fields for that crop. To give an approximate indication of trap count, geometric means for each treatment, i , were calculated from back-transformed values of arithmetic means of l_{ij} . The standard analysis of counts was a randomized block ANOVA of the transformed values, l_{ij} , termed the lognormal model by Perry *et al.* (2003). The null hypothesis was tested with a paired randomization test, using as a test statistic $d = \sum_j [l_{2j} - l_{1j}] / n$, the mean of the differences between the GMHT and conventional treatments on a logarithmic scale. The treatment effect was measured as R , the multiplicative ratio of the GMHT treatment divided by the conventional treatment, calculated as $R = 10^d$; confidence limits about R were obtained by back-transformation of the confidence interval of d on the logarithmic scale, derived from the standard error of d and $t_{0.05}$. Where appropriate, differences in the responses to GMHT and conventional treatments between occasions within a year were studied by forming a new response variable, $q_{ij} = l_{ijv} - l_{iju}$ to represent the change in response from occasion u to occasion v ; q_{ij} was then analysed by the standard methods used for l_{ij} as described above.

Differences between the treatment effects for samples recorded from different distances into the crop were tested by using a repeated-measures ANOVA (Greenhouse & Geisser 1959), with a term for the treatment \times distance interaction. For each particular distance into the field, the half-field total for that distance was deemed missing if over half of the samples were missing or invalid. If half or fewer samples were missing, those missing samples were estimated proportionately. This was necessary in fewer than 1.0%, 1.1% and 0.8% of cases for all pitfall samples in beet, maize and spring oilseed rape, respectively. If the half-field total for a particular distance was regarded as missing, then so was the overall half-field total, and that

site contributed no information towards the estimated treatment effect or the test of the null hypothesis.

Covariate analyses were done to detect whether certain of the larger measured effects on invertebrates could be explained by the treatment effects on either the abundance of vegetation, or, in the case of predators, the abundance of their prey. Results are reported where the treatment effect on taxa for the simple test of the null hypothesis was reduced in magnitude and significance by the inclusion of such a half-field covariate and the covariate itself had an important effect. In these cases, the primary effect of the treatment is likely to be on the covariate and the reported response of the taxon is probably an indirect effect, mediated through the covariate. For such analyses the estimate of the multiplicative treatment ratio adjusted for the covariate, R_{adj} , is given together with its associated probability level, p_{adj} , and the probability level, p_{cov} , for the covariate; the first two of these values may be compared with corresponding values for the simple analyses without covariates, reported in the relevant tables. This approach was similar to that taken by Hawes *et al.* (2003) to study interactions at several trophic levels between consumers and resources.

Further, separate covariate analyses were done to detect whether measured treatment effects differed with the whole-field covariates: initial seedbank (Heard *et al.* 2003a), beet grown for either fodder or sugar production and region. The total initial seedbank count was taken as a measure of the intensity of previous management to investigate whether the estimated treatment effect varied with the amount of weed vegetation from previous years, especially for fields with a history of large amounts of weed vegetation. Similarly, consistency of treatment effect was investigated between fodder and sugar beet, which contrast slightly in their management (Champion *et al.* 2003). The six environmental zones (Haines-Young *et al.* 2000; Firbank *et al.* 2003a) of the Institute of Terrestrial Ecology Land Classification of Great Britain (Bunce *et al.* 1996) were used to group sites with similar topography and climate to study the effect of major variation in abiotic factors across the country.

There are many hypothesis tests reported in this paper. Some Bonferroni procedures could be used to adjust the significance level of each, but this is made unnecessary by the provision in the tables of estimates of treatment effects with measures of variability, and the presentation of exact randomization probabilities in addition to significance levels. The misuse of such adjustments was highlighted by Perry (1986).

For Collembola, which showed consistent treatment effects, largely in one direction, for both sampling methodologies, the differences in results between taxonomic groups were examined in plots of the achieved probability level, p , on the logit scale, against the estimated treatment effect, $d = \log R$. This was done for total Collembola, together with the families Entomobryidae, Isotomidae, Sminthuridae and Poduridae, for the combined pitfall-sampled data reported in this paper and Vortis-sampled data reported by Houghton *et al.* (2003).

As well as abundance, three measures of species diversity were calculated for those groups that contained a large species pool, had been identified to species and had adequate sample sizes. The Carabidae was the only taxon

that met these three criteria. Only methods that allowed for the invariably strong relation between number of species, S , and the number of individuals sampled, N , were considered, to avoid apparent changes in species richness that were caused merely by changes in biomass. First, an ANOVA of S was done, using $\log N$ as a covariate. For large sample sizes an approximately linear relation is expected between S and $\log N$. Second, the log-series α index (Taylor *et al.* 1976) was calculated across all the sites sampled for a particular crop; the null hypothesis was tested with a paired randomization test. Log-series α was chosen for its high discriminant ability and its independence of sample size (Taylor *et al.* 1976); calculation across all sites gave larger values of N than for the covariance analysis, minimizing small-sample bias and the possibility of incorrect ordering (Kempton & Taylor 1979). In addition, the diversity measure, D , termed dominance, was calculated for each half-field as $D = N_{\max}/N$, where N_{\max} represents the number of individuals of the most abundant species. This is a version of the simple Berger-Parker index (Berger & Parker 1970; May 1975), which is relatively independent of S and the underlying species frequency distribution (Southwood & Henderson 2000). After transformation of D to a logit, $\ln(D/[1 - D])$, the null hypothesis for the dominance response variable was tested in the standard fashion described above. Sites, j , where either of the two half-field total numbers of individuals, when summed over all species, (N_{1j} or N_{2j}) was zero were excluded from all diversity analyses. Where N_{1j} or N_{2j} was less than 50 or if only one species was present the site was also removed from the dominance analyses.

4. RESULTS

GMHT crop management treatment effects are usually presented here as percentages of geometric mean abundance per half-field relative to the corresponding means for the conventional half-field. The tables presented include the effects for higher-order taxa, species groups and species by year total and individual sampling occasion. Where the patterns of response for individual species followed that for a higher-order taxonomic grouping the results for the higher-order taxon only are presented. Response variables are presented separately for each occasion, unless differences in R between occasions were less than 0.3, in which case results are given for the entire year. Where R differed by more than 0.3 or was significant on one sampling date the results are presented in the text. Results where $p > 0.05$ are highlighted if they are accompanied by large or small values of R , or where they are for year totals representative of a trend including dates with greater significance. Only significant whole-field covariate analyses are presented in the text.

(a) *Carabidae*

The total count of Carabidae was greatest in beet. Counts were about half and 60% of those in beet for maize and spring oilseed rape crops, respectively. *Pterostichus melanarius* and *P. madidus* were clearly the two most dominant species across the year in the three crops, representing 58% and 20% of total Carabidae in beet, 57% and 17% in maize, and 53% and 14% in spring oilseed rape, respectively. Other abundant species included

P. niger, *Harpalus rufipes*, *Bembidion lampros*, *B. tetracolum* and *Nebria brevicollis*.

There was no significant treatment effect on the total capture of Carabidae or the predatory *Pterostichus* genus in any crop (table 1). The response to treatment of all carabids was well summarized by *Pterostichus* spp. Some individual *Pterostichus* spp. appeared more sensitive on specific dates: counts of *P. melanarius* in May–June were 79% of the conventional count in GMHT maize ($p = 0.046$); counts of *P. madidus* in July were 63% greater in GMHT maize ($p = 0.038$). Also yearly counts of *P. niger* were 43% greater in GMHT maize, but only 66% of the conventional in GMHT spring oilseed rape (table 1).

The predatory *Bembidion* spp. were most commonly trapped in May–June, when they comprised 25% of the total capture of carabids, compared with 5% of overall counts across the year. Treatment effects for total *Bembidion* spp. were different between crops: in GMHT maize, counts were 76% of the conventional capture; whereas in GMHT spring oilseed rape, counts were 67% greater than in the conventional treatment. However, the covariate of total weed biomass, which was assessed by sampling shortly before harvest in all crops (see Heard *et al.* (2003a) for methodology), was of high importance in explaining these results for maize ($R_{\text{adj}} = 0.899$, $p_{\text{adj}} = 0.628$, $p_{\text{cov}} = 0.161$) and of some importance in the case of spring oilseed rape ($R_{\text{adj}} = 1.87$, $p_{\text{adj}} = 0.013$, $p_{\text{cov}} = 0.088$). There were no significant effects for total *Bembidion* spp. in beet; however, significant treatment effects were detected for *B. tetracolum*, where counts were lower in the GMHT treatment in May and greater in the GMHT treatment in August (table 1). The weed-biomass covariate again explained much of this treatment effect for August for *B. tetracolum* ($R_{\text{adj}} = 1.486$, $p_{\text{adj}} = 0.176$, $p_{\text{cov}} = 0.054$). Also, measures of weed vegetation in May, made by counting all plants (Heard *et al.* 2003a), explained an important proportion of the treatment effect at this time ($R_{\text{adj}} = 0.509$, $p_{\text{adj}} = 0.445$, $p_{\text{cov}} = 0.005$).

Counts of *Loricera pilicornis* were consistently greater in all GMHT treatments (table 1). The covariate of counts of the collembolan family Entomobryidae, which is a food resource for *L. pilicornis*, from pitfall captures in August explained many of these effects in beet ($R_{\text{adj}} = 1.515$, $p_{\text{adj}} = 0.031$, $p_{\text{cov}} = 0.031$), maize ($R_{\text{adj}} = 1.519$, $p_{\text{adj}} = 0.018$, $p_{\text{cov}} = 0.046$) and spring oilseed rape ($R_{\text{adj}} = 1.304$, $p_{\text{adj}} = 0.821$, $p_{\text{cov}} = 0.069$).

The treatment effects estimated for *Trechus quadristriatus* differed between crops: counts were 37% greater in GMHT beet in August, but 67% of the conventional in GMHT maize over the whole year. There was a treatment \times distance interaction for *T. quadristriatus*, where the difference in counts increased with the distance into the field ($F_{2,115} = 4.09$, $p < 0.02$), in GMHT beet in August. No significant treatment effects were detected for *N. brevicollis* (table 1).

Similar treatment effects were detected for *H. rufipes* and *Amara* spp.: yearly counts were lower than conventional in GMHT beet and spring oilseed rape for *H. rufipes*, but greater in GMHT maize. In GMHT beet, counts of *H. rufipes* were 68% and 58% of the conventional treatment captures across the year and in August, respectively; and in GMHT spring oilseed rape, counts

Table 1. Counts of Carabidae sampled by pitfall traps in conventional (C) and GMHT beet, maize and spring oilseed rape. (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.)

crop and taxa	period	<i>n</i>	geometric mean		<i>R</i> (95% CI)	<i>p</i> -value
			C	GMHT		
beet						
total Carabidae	year	66	1707.18	1576.96	0.92 (0.85–1.01)	0.060
<i>Pterostichus</i> spp.	year	66	1264.39	1172.13	0.93 (0.84–1.02)	0.10
<i>Bembidion</i> spp.	year	61	35.91	35.44	0.99 (0.79–1.24)	0.92
	May	51	35.39	32.78	0.93 (0.72–1.20)	0.56
	July	43	8.53	9.24	1.07 (0.77–1.50)	0.65
	August	40	3.63	5.31	1.36 (0.94–1.98)	0.11
<i>B. tetracolum</i>	year	41	14.75	11.38	0.79 (0.55–1.13)	0.18
	May	31	18.22	10.10	0.58 (0.38–0.87)	0.005**
	July	25	6.75	6.12	0.92 (0.56–1.51)	0.72
	August	13	2.65	5.39	1.75 (1.17–2.63)	0.020*
<i>N. brevicollis</i>	year	45	21.27	17.46	0.83 (0.65–1.06)	0.13
<i>H. rufipes</i>	year	64	46.00	31.12	0.68 (0.55–0.85)	< 0.001***
	May	30	3.93	4.06	1.03 (0.75–1.41)	0.89
	July	53	13.31	12.67	0.96 (0.74–1.24)	0.74
	August	58	43.95	25.02	0.58 (0.44–0.76)	< 0.001***
<i>Amara</i> spp.	year	43	3.45	2.40	0.76 (0.57–1.03)	0.060
	May	25	2.08	2.07	1.00 (0.65–1.54)	0.99
	July	16	2.30	1.81	0.85 (0.55–1.33)	0.42
	August	24	2.35	1.01	0.60 (0.41–0.88)	0.013*
<i>L. pilicornis</i>	year	38	2.13	4.00	1.60 (1.20–2.13)	0.002**
<i>T. quadristriatus</i>	year	65	10.80	12.29	1.13 (0.89–1.42)	0.29
	May	32	3.40	3.42	1.00 (0.70–1.44)	0.98
	July	30	4.21	3.34	0.83 (0.58–1.20)	0.31
	August	58	7.63	10.83	1.37 (1.04–1.80)	0.025*
maize						
total Carabidae	year	58	798.87	812.41	1.02 (0.92–1.13)	0.76
<i>Pterostichus</i> spp.	year	58	479.72	475.64	0.99 (0.88–1.11)	0.88
	May	54	52.70	45.79	0.87 (0.72–1.05)	0.15
	July	49	238.50	264.25	1.11 (0.94–1.31)	0.23
	August	45	368.19	366.08	0.99 (0.87–1.14)	0.92
<i>P. niger</i>	year	38	11.58	16.97	1.43 (1.04–1.97)	0.031*
<i>Bembidion</i> spp.	year	58	52.51	39.72	0.76 (0.62–0.93)	0.004**
<i>N. brevicollis</i>	year	43	8.82	10.16	1.14 (0.84–1.54)	0.39
<i>H. rufipes</i>	year	53	15.36	21.33	1.37 (1.00–1.87)	0.060
	May	34	3.89	4.35	1.10 (0.84–1.42)	0.47
	July	40	6.46	12.18	1.77 (1.24–2.51)	0.004**
	August	41	12.27	17.75	1.41 (0.94–2.13)	0.13
<i>Amara</i> spp.	year	42	1.88	3.58	1.59 (1.20–2.11)	0.002**
	May	25	1.87	3.06	1.42 (1.04–1.93)	0.026*
	July	16	0.50	2.52	2.34 (1.34–4.11)	0.011*
	August	20	1.00	1.63	1.32 (0.80–2.17)	0.27
<i>A. dorsale</i>	year	45	5.46	9.32	1.60 (1.14–2.25)	0.007**
	May	34	3.19	4.42	1.29 (0.88–1.92)	0.19
	July	34	2.60	6.72	2.14 (1.32–3.49)	0.003**
	August	17	2.61	3.93	1.37 (0.84–2.23)	0.17
<i>L. pilicornis</i>	year	43	2.95	5.93	1.76 (1.34–2.30)	< 0.001***
<i>T. quadristriatus</i>	year	48	10.53	6.68	0.67 (0.51–0.87)	0.003**
spring oilseed rape						
total Carabidae	year	67	1023.70	1049.01	1.03 (0.94–1.11)	0.57
<i>Pterostichus</i> spp.	year	67	670.27	685.73	1.02 (0.91–1.15)	0.68
<i>P. niger</i>	year	60	69.13	45.25	0.66 (0.55–0.79)	< 0.001***
<i>Bembidion</i> spp.	year	64	14.90	25.62	1.67 (1.37–2.05)	< 0.001***
<i>N. brevicollis</i>	year	58	22.75	28.84	1.26 (0.97–1.63)	0.10
<i>H. rufipes</i>	year	53	33.58	14.66	0.45 (0.33–0.63)	< 0.001***
	May	24	2.40	3.16	1.22 (0.79–1.88)	0.36
	July	42	9.19	5.38	0.63 (0.44–0.89)	0.011*
	August	49	29.97	10.95	0.39 (0.27–0.55)	< 0.001***

(Continued.)

Table 1. (Continued.)

crop and taxa	period	n	geometric mean		R (95% CI)	p-value
			C	GMHT		
<i>Amara</i> spp.	year	49	5.11	5.21	1.02 (0.78–1.32)	0.92
<i>L. pilicornis</i>	year	58	3.49	4.65	1.26 (1.01–1.57)	0.038*
<i>T. quadristriatus</i>	year	56	6.80	8.88	1.27 (1.00–1.61)	0.060
<i>N. biguttatus</i>	year	53	6.77	9.10	1.30 (1.02–1.66)	0.045*

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 2. Counts of Staphylinidae sampled by pitfall traps in conventional (C) and GMHT beet, maize and spring oilseed rape. (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.)

crop and period	n	geometric mean		R (95% CI)	p-value
		C	GMHT		
beet, year	66	132.89	136.17	1.02 (0.90–1.17)	0.71
maize, year	58	119.45	138.78	1.16 (1.00–1.35)	0.060
spring oilseed rape, year	67	222.22	207.70	0.94 (0.84–1.04)	0.25

were 45%, 63% and 39% of the conventional across the year, in July and in August, respectively. Seeds shed from weeds (seed rain) were assessed throughout the year by using an appropriate trapping methodology (see Heard *et al.* 2003a). The covariate of the annual counts of weed seed rain explained much of this August treatment effect for *H. rufipes* in beet ($R_{adj} = 0.693$, $p_{adj} = 0.02$, $p_{cov} < 0.001$) and spring oilseed rape ($R_{adj} = 0.620$, $p_{adj} = 0.026$, $p_{cov} < 0.001$). For the July result for this species, this covariate was important in explaining a large proportion of the treatment effect ($R_{adj} = 0.774$, $p_{adj} = 0.237$, $p_{cov} = 0.005$). By contrast, in GMHT maize counts of *H. rufipes* were 77% greater than conventional in July, again moderately well explained by the covariate of seed rain ($R_{adj} = 1.652$, $p_{adj} = 0.016$, $p_{cov} = 0.019$). Counts of *Amara* spp. were 60% of conventional counts in GMHT beet in August, but were 59%, 42% and 134% greater in GMHT maize across the year, in May and in July, respectively (table 1). However, the seed-rain covariate was ineffective in explaining these effects. There was a significant treatment \times sampling year interaction for *Amara* spp. in maize in May, where differences in counts were greater in the final year (2002) of sampling ($F_{2,22} = 6.01$, $p < 0.001$).

Counts of *Agonum dorsale* were greater in GMHT maize across the year and in July, by 60% and 114%, respectively. For the yearly analysis there was also a significant treatment \times sampling year interaction ($F_{2,43} = 3.98$, $p < 0.03$). Numbers caught each year were generally greater for the GMHT treatment, and particularly so in 2002 owing to higher captures in the GMHT treatment in May of that year ($F_{2,31} = 3.64$, $p < 0.04$).

(b) Staphylinidae

Staphylinidae were least abundant in maize, where counts were just over half of those in spring oilseed rape. There was no consistent effect of treatment on captures of Staphylinidae in any of the three crops (table 2).

(c) Araneae

Counts of Araneae were greatest in beet and lowest in spring oilseed rape. The Araneae were dominated by the Linyphiidae, which represented 57%, 56% and 61% of all Araneae recorded in beet, maize and spring oilseed rape, respectively. The Lycosidae represented 10%, 10% and 16% of Araneae in beet, maize and spring oilseed rape, respectively. *Oedothorax* spp., *Erigone* agg., *L. tenuis* and *Pardosa* spp. represented 25%, 21%, 5% and 5% of Araneae recorded in beet, 26%, 24%, 6% and 4% in maize, and 16%, 21%, 10% and 5% in spring oilseed rape, respectively.

Total captures of Araneae showed no significant treatment response in any crop (table 3).

Total counts of Linyphiidae were 13% and 27% greater in GMHT spring oilseed rape across the year (table 3) and in August ($p < 0.001$), respectively. The treatment effect for *L. tenuis* was similar to that for total Linyphiidae, with counts that were 22% greater in GMHT spring oilseed rape across the year. Counts of *Oedothorax* spp. were 37% greater in GMHT beet in May ($p < 0.05$); however, in GMHT maize the treatment effect was reversed, and counts were 64% of the conventional across the year.

Captures of the *Erigone* agg. in beet were 30% greater in the GMHT treatment in July ($p < 0.05$) and were 54% and 21% greater (table 3) in GMHT maize and spring oilseed rape, respectively, across the year. The covariate of counts of the collembolan family Entomobryidae (a food resource for *Erigone* agg.) from pitfall captures in July explained many of these effects in beet ($R_{adj} = 1.16$, $p_{adj} = 0.246$, $p_{cov} = 0.115$), but not in maize or spring oilseed rape. There were significant treatment \times distance interactions for *Erigone* agg. in maize ($F_{2,112} = 3.79$, $p < 0.03$) and spring oilseed rape ($F_{2,132} = 6.41$, $p < 0.01$). At 8 m and 32 m into the crop, counts of *Erigone* agg. were relatively greater in both GMHT maize and GMHT spring oilseed rape than at 2 m, where treatment differences were small.

Table 3. Counts of spiders sampled by pitfall traps in conventional (C) and GMHT beet, maize and spring oilseed rape. (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.)

crop and taxa	period	n	geometric mean		R (95% CI)	p -value
			C	GMHT		
beet						
total spiders	year	66	270.47	298.22	1.10 (0.99–1.23)	0.070
Linyphiidae	year	66	135.62	144.28	1.06 (0.95–1.20)	0.30
<i>L. tenuis</i>	year	63	14.41	14.30	0.99 (0.84–1.18)	0.92
<i>Erigone</i> agg.	year	62	35.51	43.21	1.21 (0.96–1.53)	0.11
<i>Oedothorax</i> spp.	year	42	59.93	68.40	1.14 (0.93–1.40)	0.21
Lycosidae	year	63	25.64	28.10	1.09 (0.94–1.27)	0.27
<i>Pardosa</i> spp.	year	61	7.61	10.27	1.31 (1.04–1.64)	0.024*
maize						
total spiders	year	58	265.63	238.42	0.90 (0.80–1.01)	0.060
Linyphiidae	year	58	123.08	133.92	1.09 (0.94–1.26)	0.22
<i>L. tenuis</i>	year	56	14.90	16.51	1.10 (0.93–1.31)	0.27
<i>Erigone</i> agg.	year	57	33.69	52.25	1.54 (1.20–1.97)	0.004**
<i>Oedothorax</i> spp.	year	46	63.53	40.42	0.64 (0.48–0.86)	0.010*
Lycosidae	year	58	27.78	27.43	0.99 (0.87–1.13)	0.85
<i>Pardosa</i> spp.	year	55	11.05	8.76	0.81 (0.65–1.00)	0.06
spring oilseed rape						
total spiders	year	67	209.39	217.03	1.04 (0.94–1.15)	0.50
Linyphiidae	year	67	117.77	133.17	1.13 (1.02–1.25)	0.013*
<i>L. tenuis</i>	year	66	19.92	24.55	1.22 (1.06–1.40)	0.004**
<i>Erigone</i> agg.	year	67	27.42	33.49	1.21 (0.99–1.48)	0.044*
<i>Oedothorax</i> spp.	year	54	27.53	25.25	0.92 (0.74–1.15)	0.49
Lycosidae	year	67	32.85	35.81	1.09 (0.96–1.23)	0.18
<i>Pardosa</i> spp.	year	59	11.86	8.71	0.76 (0.61–0.94)	0.013*

* $p < 0.05$; ** $p < 0.01$.

There were no significant treatment effects for total Lycosidae in any crop (table 3), although counts of *Pardosa* spp. were 31% greater in GMHT beet across the year. However, this result contrasted with those for maize in July and spring oilseed rape across the year, where captures in GMHT crops were 67% ($p < 0.05$) and 76% of the conventional counts respectively (table 3).

(d) *Collembola*

Counts of Collembola were greatest in maize and lowest in beet. More than 99% of the Collembola recorded belonged to the Isotomidae, Entomobryidae, Sminthuridae or Poduridae, which accounted for 56%, 19%, 19% and 6% of Collembola in beet, 46%, 25%, 16% and 13% in maize, and 42%, 36%, 19% and 2% in spring oilseed rape, respectively.

For pitfall traps there was no significant treatment effect for counts of total Collembola across the year in any of the three crops; however, there were within-year effects. Counts of total Collembola were consistently greater in the GMHT treatment in August in beet and maize and in July in spring oilseed rape (table 4). The amount of weed vegetation detritus was not measured directly. Possibly the best surrogate measure of detritus calculable for beet is the difference between the counts of total weeds taken most nearly before and after herbicide application (Heard *et al.* 2003a). Here, this detritus covariate explained much of the treatment effect for total Collembola in August ($R_{\text{adj}} = 1.228$, $p_{\text{adj}} = 0.318$, $p_{\text{cov}} = 0.040$). For spring oilseed rape, the best surrogate was a similar measure, but for

dicotyledons only; this explained much of the treatment effect for total Collembola in July ($R_{\text{adj}} = 1.351$, $p_{\text{adj}} = 0.088$, $p_{\text{cov}} = 0.172$). No simple covariate was found to explain the treatment effect in maize in August; these results differed from those obtained by Vortis-suction sampling (Haughton *et al.* 2003), for which biomass was an effective covariate.

In August, counts of Entomobryidae were 51% greater in GMHT beet and 44% greater in GMHT maize. In July, Entomobryidae counts were also 89% greater in GMHT spring oilseed rape, and 49% greater in beet. Counts of Isotomidae were significantly greater by 42% in GMHT beet across the year, by 41% in May and by 74% in July, and by 33% in GMHT maize across the year and by 185% in August.

There were no significant treatment effects for either the Sminthuridae or the Poduridae. It should be noted that the Poduridae were captured in lower numbers and from fewer fields than the other families.

From the combined Vortis-suction (Haughton *et al.* 2003) and pitfall sampled data for the Entomobryidae, Isotomidae, Sminthuridae, Poduridae and total Collembola, it is clear that in very few instances was the count of Entomobryidae, Isotomidae or all Collembola less in the GMHT treatment (figure 2). Total Collembola were consistently more abundant under GMHT treatments across the year (mean $d = 0.076$, s.e.m. = 0.016), and the treatment effect measured by mean d increased from 0.051 (s.e.m. = 0.024) in May–June to 0.081 (s.e.m. = 0.015) in July–August (table 5).

Table 4. Counts of Collembola sampled by pitfall traps in conventional (C) and GMHT beet, maize and spring oilseed rape. (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.)

crop and taxa	period	<i>n</i>	geometric mean		<i>R</i> (95% CI)	<i>p</i> -value
			C	GMHT		
beet						
total Collembola	year	66	352.99	404.28	1.15 (0.97–1.36)	0.15
	May	53	197.48	193.30	0.98 (0.79–1.22)	0.85
	July	60	67.97	92.40	1.35 (0.98–1.87)	0.061
	August	62	55.64	86.18	1.54 (1.17–2.02)	0.004**
Entomobryidae	year	66	92.29	100.16	1.08 (0.84–1.40)	0.56
	May	52	59.45	47.40	0.80 (0.59–1.09)	0.20
	July	53	20.30	30.76	1.49 (1.02–2.17)	0.039*
	August	59	28.77	43.83	1.51 (1.12–2.02)	0.009**
Isotomidae	year	65	72.13	103.11	1.42 (1.13–1.80)	0.006**
	May	53	43.91	62.32	1.41 (1.05–1.89)	0.025*
	July	56	12.31	22.20	1.74 (1.23–2.48)	0.004**
	August	48	13.08	18.05	1.35 (0.92–1.98)	0.12
Sminthuridae	year	58	50.37	38.33	0.77 (0.57–1.03)	0.075
	May	40	28.60	19.17	0.68 (0.46–1.01)	0.077
	July	53	16.36	12.29	0.77 (0.51–1.14)	0.19
	August	40	9.21	11.24	1.20 (0.77–1.88)	0.39
Poduridae	year	29	17.17	19.46	1.13 (0.71–1.79)	0.62
	May	22	14.56	17.31	1.18 (0.70–1.97)	0.56
	July	17	4.52	5.22	1.13 (0.47–2.69)	0.79
	August	17	4.38	8.37	1.74 (0.66–4.60)	0.29
maize						
total Collembola	year	58	612.64	725.17	1.18 (0.97–1.45)	0.11
	May	54	291.97	344.63	1.18 (0.91–1.53)	0.19
	July	49	180.81	210.28	1.16 (0.87–1.55)	0.31
	August	45	85.63	138.90	1.62 (1.12–2.33)	0.011*
Entomobryidae	year	58	165.08	191.78	1.16 (0.93–1.44)	0.16
	May	52	74.07	74.64	1.01 (0.73–1.40)	0.96
	July	45	48.13	62.87	1.30 (0.97–1.74)	0.086
	August	44	37.92	55.12	1.44 (1.01–2.06)	0.047*
Isotomidae	year	58	144.31	192.46	1.33 (1.05–1.68)	0.025*
	May	53	99.08	121.20	1.22 (0.92–1.62)	0.16
	July	47	33.29	45.55	1.36 (0.97–1.90)	0.067
	August	43	8.92	27.27	2.85 (1.85–4.38)	< 0.001***
Sminthuridae	year	58	66.29	69.96	1.06 (0.77–1.44)	0.76
	May	52	36.20	42.59	1.17 (0.82–1.67)	0.38
	July	45	25.48	29.45	1.15 (0.72–1.84)	0.53
	August	39	7.74	10.53	1.32 (0.77–2.26)	0.31
Poduridae	year	42	11.48	11.52	1.00 (0.55–1.85)	0.99
	May	31	4.01	5.94	1.39 (0.75–2.55)	0.29
	July	25	11.34	5.50	0.53 (0.17–1.63)	0.26
	August	16	14.66	12.95	0.89 (0.27–2.90)	0.85
spring oilseed rape						
total Collembola	year	67	528.79	581.82	1.10 (0.95–1.28)	0.21
	May	57	172.97	187.16	1.08 (0.89–1.31)	0.44
	July	57	97.10	139.68	1.43 (1.10–1.87)	0.011*
	August	60	175.22	198.23	1.13 (0.94–1.37)	0.22
Entomobryidae	year	67	96.62	115.89	1.20 (0.93–1.54)	0.16
	May	53	39.50	41.58	1.05 (0.77–1.43)	0.76
	July	53	20.11	38.83	1.89 (1.26–2.83)	0.003**
	August	55	45.81	60.89	1.32 (0.98–1.79)	0.075
Isotomidae	year	67	199.90	227.17	1.14 (0.97–1.33)	0.11
	May	57	77.02	85.66	1.11 (0.89–1.39)	0.38
	July	53	33.28	38.37	1.15 (0.84–1.56)	0.40
	August	57	66.59	73.43	1.10 (0.86–1.42)	0.46
Sminthuridae	year	66	72.99	68.13	0.93 (0.66–1.32)	0.71
	May	49	32.78	29.49	0.90 (0.62–1.30)	0.58
	July	54	23.37	27.00	1.15 (0.71–1.86)	0.57
	August	49	18.44	17.68	0.96 (0.70–1.31)	0.79
Poduridae	year	46	5.78	7.81	1.30 (0.82–2.07)	0.27
	May	27	3.24	5.24	1.47 (0.81–2.67)	0.20
	July	23	2.45	4.12	1.49 (0.74–2.98)	0.25
	August	27	4.25	4.89	1.12 (0.65–1.94)	0.69

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

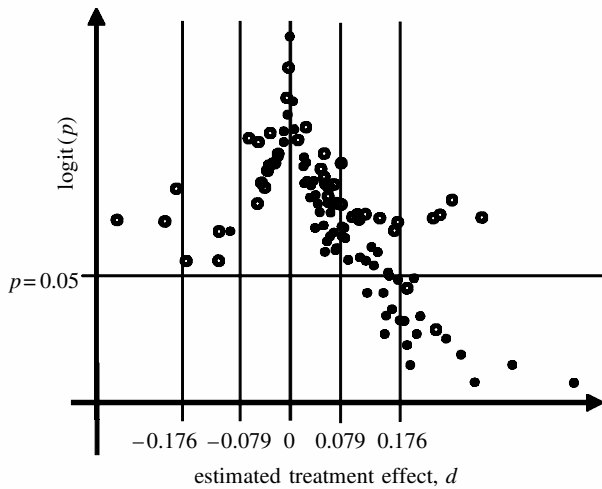


Figure 2. Relationship between randomization probability and estimated treatment effect, d ($d = \log R$), for Collembola at various times during the season. Filled circles, total Collembola, Entomobryidae and Isotomidae; open circles, Sminthuridae and Poduridae. Symbols to the right of $d = 0$ denote occasions when the abundance in GMHT half-fields exceeded that in conventional half-fields; symbols below the line $p = 0.05$ denote occasions when the test of H_0 was significant. Samples were combined from pitfall traps and Vortis suction.

Table 5. Estimated percentages of occasions (generalized linear model, binomial errors, logit link) for which $R > 1$ (i.e. when abundance in GMHT half-fields exceeded that in conventional half-fields), for various categories of Collembola at different times during the season. (Overall, $R > 1$ in 81 out of 105 cases ($t_{105} = 5.2$, $p < 0.001$). Samples combined from pitfall traps and Vortis suction.)

	year total	sampling date	
		May–June	July–August
all Collembola	93	80	96
Entomobryidae	85	62	91
Isotomidae	97	90	98
Poduridae	71	42	81
Sminthuridae	55	27	68

(e) *Gastropoda*

Counts of gastropods were lowest in beet and greatest in spring oilseed rape, where counts were more than twice those in beet. There were no significant treatment effects for total gastropods in any of the three crops (table 6). Counts of *D. reticulatum* were greater in GMHT spring oilseed rape across the year and in August by 44% and 68%, respectively.

(f) *Whole-field covariate analyses investigating consistency*

In the whole-field covariate analyses to study the consistency of treatment effects, in no case was the effect different in direction between sugar beet and fodder beet or regions, and there were no more significant differences than expected by chance between the crop types. Just four out of 45 significant effects revealed a significant dependence of the treatment effect, d , on w , the initial seedbank

assessment (Heard *et al.* 2003a), hardly more than expected by chance. In each case this was summarized well by a simple linear regression of d , the mean of the differences between the GMHT and conventional treatments on a logarithmic scale, on $\log w$. For the carabids, *Amara* spp. in beet, the estimated intercept and regression coefficient were -1.20 and 0.52 , respectively, (s.e. = 0.19 , $p = 0.0090$). Interpretation is aided by noting that, in this example, a twofold increase in the treatment effect is implied for every 3.75-fold increase in weed seed abundance. Hence, for an abundance of around 200 seeds per sample, there was no predicted difference between the treatments; for an abundance of 50 seeds, the predicted value of $R = 10^d$ was 0.48 ; and for an abundance of 800 seeds the predicted value of R was 2.07 . The other intercepts and regression coefficients were as follows. For carabids: *Bembidion* spp. in maize 0.47 and -0.28 , respectively (s.e. = 0.12 , $p = 0.026$); for *T. quadristriatus* in maize 0.57 and -0.35 , respectively (s.e. = 0.17 , $p = 0.043$); and for spiders: *Pardosa* spp. in maize -0.72 and 0.30 , respectively (s.e. = 0.13 , $p = 0.024$).

(g) *Diversity*

Diversity measures were calculated only for Carabidae. Other groups were either not identified to species or, in the case of gastropods, were from relatively species-poor groups where analyses would have little meaning. There was very little evidence of treatment effects in any of the diversity measures, with only dominance in spring oilseed rape showing a significant effect of treatment, where this measure was greater under GMHT cropping. This effect was significant across the year, but was concentrated in July and August (table 7).

5. DISCUSSION

Among the taxa analysed, many exhibited significant responses to treatment in at least one crop on one occasion. For most taxa, where such significant treatment effects occurred, there was an approximately equal likelihood of the direction of the effect; significantly larger abundances in GMHT crops were about as frequent as those in conventional crops. Hence, out of the 91 non-collembolan treatment analyses tabulated in this paper, nine comparisons had estimates of the multiplicative ratio (R), the mean capture in GMHT crops relative to that in conventional crops, of less than 0.67 , compared with 11 with $R > 1.5$. This balance in the direction and magnitude of effects on individual species and species groups probably explains the lack of significance typically observed for the higher taxonomic groupings. A stark departure from this was the Collembola, where counts were consistently greater in GMHT half-fields. For this group seven analyses had $R > 1.5$, compared with only one with $R < 0.67$.

Assessment of the importance of these results for the agricultural ecosystem, however, requires consideration of how responses of surface-active invertebrates are mediated through the indirect effects of GMHT herbicide management of weed vegetation (Heard *et al.* 2003a). Consistent indirect effects were found across functional groups and taxa, and in each crop.

Weed seed feeders, including *Amara* spp. and *H. rufipes*, tended to have smaller counts under GMHT crop man-

Table 6. Counts of Gastropoda sampled by refuge traps in conventional (C) and GMHT beet, maize and spring oilseed rape. (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.)

crop and taxa	period	n	geometric mean			p -value
			C	GMHT	R (95% CI)	
beet						
total gastropods	year	40	4.77	5.15	1.07 (0.78–1.47)	0.66
<i>D. reticulatum</i>	year	34	3.49	4.23	1.16 (0.79–1.72)	0.43
maize						
total gastropods	year	42	7.79	8.96	1.13 (0.83–1.55)	0.40
<i>D. reticulatum</i>	year	36	5.86	5.73	0.98 (0.70–1.38)	0.91
spring oilseed rape						
total gastropods	year	59	10.50	12.10	1.14 (0.89–1.46)	0.30
<i>D. reticulatum</i>	year	47	6.92	10.40	1.44 (1.02–2.03)	0.042*
	May	33	2.69	3.16	1.13 (0.70–1.81)	0.62
	August	36	5.19	9.39	1.68 (1.07–2.63)	0.032*

* $p < 0.05$.

agement in beet and spring oilseed rape but higher counts in maize. This was explained well for *H. rufipes* by total seed rain, but effects on *Amara* spp. could not be similarly explained and may require more detailed investigation of the species composition of seed rain to allow for food preferences. Omnivorous species, such as the highly mobile *T. quadristriatus*, which feeds on seeds and invertebrates, could switch to predation and make use of collembolan prey in the GMHT treatments. This might explain differences in the direction of the treatment effects between crops for this species. Treatment differences for predators with specific preferences for Collembola, such as *L. pilicornis* and *Erigone* agg., tended to reflect the seasonal pattern of counts for specific collembolan families, albeit not significantly. Predators, such as *Bembidion* spp., also showed responses to the vegetation structure of weeds and their density, as either a direct result of increased activity–density (Wallin & Ekbohm 1988) or a preference for structure and microclimate (Baker & Dunning 1975). Most generalist and highly mobile surface-active predators, such as *Pterostichus* spp., and species that use the crop as food, such as the gastropods, were often unaffected by the treatment.

The detritivore Collembola were significantly more abundant in GMHT treatments. For beet and spring oilseed rape crops this was most likely the result of more efficient control of initially greater weed vegetation densities by GMHT herbicide applications (Heard *et al.* 2003a). This would almost certainly produce additional detritus in the GMHT treatments after application. Results for maize are also likely to be partly caused by additional detritus after GMHT herbicide control. However, contrasting effects of herbicide control were observed for maize (Heard *et al.* 2003a), where dicotyledon densities were substantially higher in the GMHT varieties throughout the season, partly as a result of the strong effect of pre-emergence herbicides on some of the conventional crops. Together with differences in the timing of applications, this may have resulted in additional detritus in this crop.

In general, we found that, where there were greater captures in the conventional crops, they often occurred for

particular carabid species, whereas higher GMHT counts were associated with Collembola and linyphiids, such as *Erigone* agg. However, relatively few effects were found for the gastropods. Considering the crops separately, counts across all taxa in the GMHT treatment were often greater in maize, but smaller in beet and spring oilseed rape. These observations for the crops mirrored those found generally in the vegetation analyses (Heard *et al.* 2003a).

(a) Consistency of treatment effects

For comparisons where more than 50 fields were sampled, treatment differences greater than a factor of 1.5 or less than 0.67 were all significant (Perry *et al.* 2003). In addition, few interactions between the treatments and associated covariates were found in the soil-surface-active invertebrate dataset. These findings give confidence that the fields sampled produced consistent results, which may be scaled up to wider populations of invertebrates across a broad spectrum of farming in the UK.

In beet, the lack of significant interactions of the covariate for fodder and sugar crops suggested that the management of these crops was sufficiently similar in the FSEs (Champion *et al.* 2003) for them to be treated as one crop in the analyses. Interactions with environmental zone were also absent. A treatment \times year interaction was noted in only two analyses. This suggests that, as the number of sites is increased, particularly when they are widely distributed over a large geographical area, treatment \times year interactions are minimized. In just four out of 45 significant effects was initial seedbank count a significant covariate. Although the effects were clear, without further experimental studies we have no straightforward explanation for these results. For all other analyses, the consistency of the treatment effects over a range of sites with differing degrees of initial seedbank implied that the indirect effects studied here remained proportionate across zones and treatments. In only three out of the 45 significant results were treatment \times distance interactions apparent, little more than expected by chance. Indeed, these showed little consistency over occasions within a season, and would require experimental manipulation studies to elucidate

Table 7. Diversity of Carabidae in pitfall traps in conventional (C) and GMHT beet, maize and spring oilseed rape crops through the season.

(Indices are number of species (S), log-series α and dominance (D). Values in brackets following values of α are standard errors. The treatment effect for S is calculated after allowance for $\log N$ as a covariate on each half-field, where N represents the number of individuals; that for D is the treatment difference calculated after transformation to logits; p -values for α and D are based on randomization tests.)

crop and date	index	n	value of index		treatment effect	s.e. of effect	p -value
			C	GMHT			
beet							
total	S	66	18.74	18.52	-0.050	0.38	0.90
	α	66	7.55 (0.87)	7.47 (0.87)	-0.071	—	0.86
	D	66	0.64	0.64	0.000	0.056	0.99
May	S	52	13.08	12.98	0.054	0.32	0.87
	α	53	7.78 (1.00)	7.86 (1.09)	0.085	—	0.84
	D	42	0.46	0.48	0.068	0.10	0.51
July	S	61	10.75	10.72	0.057	0.35	0.87
	α	61	6.37 (0.83)	6.57 (0.85)	0.19	—	0.66
	D	60	0.78	0.77	-0.083	0.086	0.34
August	S	62	11.21	11.19	0.16	0.39	0.69
	α	62	5.84 (0.79)	5.75 (0.78)	-0.092	—	0.88
	D	59	0.65	0.65	0.016	0.056	0.78
maize							
total	S	58	18.40	19.02	0.63	0.42	0.14
	α	58	8.35 (0.96)	9.02 (1.00)	0.67	—	0.36
	D	58	0.64	0.63	-0.015	0.066	0.82
May	S	54	12.76	13.22	0.52	0.33	0.13
	α	54	8.22 (1.05)	8.29 (1.06)	0.063	—	0.91
	D	46	0.52	0.56	0.18	0.10	0.10
July	S	49	12.04	12.45	0.15	0.51	0.77
	α	49	6.87 (0.90)	7.72 (0.96)	0.85	—	0.33
	D	46	0.75	0.73	-0.080	0.11	0.49
August	S	45	11.62	11.71	0.057	0.45	0.90
	α	45	6.55 (0.88)	5.79 (0.83)	-0.77	—	0.35
	D	44	0.70	0.69	-0.048	0.074	0.53
spring oilseed rape							
total	S	67	18.06	18.52	0.44	0.43	0.31
	α	67	8.13 (0.93)	8.08 (0.93)	-0.054	—	0.92
	D	66	0.57	0.60	0.12	0.054	0.026*
May	S	57	12.53	12.86	-0.44	0.38	0.25
	α	57	7.52 (1.01)	7.31 (0.98)	-0.21	—	0.72
	D	47	0.43	0.45	0.079	0.080	0.31
July	S	61	9.62	10.00	0.24	0.39	0.53
	α	63	6.57 (0.89)	6.29 (0.86)	-0.28	—	0.59
	D	57	0.69	0.75	0.28	0.079	0.002**
August	S	60	10.95	11.15	0.19	0.35	0.60
	α	60	6.17 (0.82)	6.29 (0.83)	0.11	—	0.84
	D	57	0.63	0.68	0.22	0.076	0.007**

* $p < 0.05$; ** $p < 0.01$.

whether they are real effects or artefacts of the number of analyses examined.

(b) Diversity

The results of the diversity analyses suggest that changes in management resulting from the introduction of GMHT crops might have very little effect on carabid diversity directly, with the possible exception of dominance in spring oilseed rape. This is perhaps not surprising as there is very little treatment effect on total carabid count and it is unlikely that the underlying species frequency distribution would be greatly changed under these circumstances. An apparently contrary result, reported by

Strandberg & Pedersen (2002), was caused by their use of the mean number of taxa per sample, which corrects for sample size in terms of area rather than number of individuals. Here, in only one out of the nine monthly species-richness analyses was $\log N$ clearly not a significant covariate, underlining the importance of correcting for number of individuals (rather than area) in diversity studies. Despite the lack of effects on overall diversity, relative abundances of particular species might be affected, resulting in increased abundance in some trophic groups and decreases in others. The importance of this for biodiversity is explored further in the paper addressing trophic interactions (Hawes *et al.* 2003).

(c) *R* and the geometric mean

It is not straightforward to infer, from a within-season estimate of *R*, what the long-term effect on counts would be within crop rotations if there was future wide-scale GMHT crop management (Heard *et al.* 2003b). First, the invertebrate sampling protocols lacked direct year-to-year comparisons. Second, effects might be transient, and change in subtle ways as a result of interactions between trophic levels. Third, population-dynamic theory (Varley *et al.* 1973) would suggest that mortality effects from one cause may be buffered by a reduction in mortality from some other cause. Fourth, density-dependent effects may hamper attempts to interpret values of *R* as direct increases or decreases. For example, for species that showed a decrease under GMHT crop management relative to the conventional status quo, the equilibrium density might be less than the estimated count for GMHT treatment if the effect were compounded over several years, or somewhere between it and the conventional if there was amelioration resulting from population-dynamic processes. Other generic difficulties also exist in extrapolating the results described here, such as variations in the proportion and number of fields that adopt GMHT crop management and possible changes in rotation and cultivation practices. It should be emphasized that, whereas we have focused attention on relatively large estimated treatment effects ($R < 0.67$ and $R > 1.5$), smaller estimates (*R* closer to unity) could still imply detectable effects on population densities, particularly when compounded over the longer term.

Expectations for changes in the large-scale population geometric mean and growth rate under GMHT cropping will also depend upon the type of response shown by the taxa or species. Taxa may show two classes of response: a behavioural one where a mobile species may choose to disperse into or out of a particular field; and an abundance response where a species of low vagility is directly subject to the management, with direct consequences on local mortality and reproduction. These differences in response modify further the interpretation and use of the geometric mean and *R* for predicting long-term effects. For species that show a direct abundance response, the results might be interpreted as representing a direct modification of the population equilibrium. However, for species that respond behaviourally, the differences observed may reflect the costs of making a foraging or dispersal choice. Such costs could change with the proportion of GMHT fields grown.

The results presented here suggest that the future effects of GMHT cropping may be predictable from the recorded data for GMHT and conventional geometric mean counts and *R*, provided appropriate assumptions are made within a mathematical modelling framework. To test these model expectations, or to develop future approaches to test the environmental impact of other GM traits, it will be imperative to use species or functional groups that are sensitive to management in both possible directions and readily measured by using simple protocols. Data summarized across taxa, such as all Carabidae or all Staphylinidae, do not show the full responses to GMHT crop management of the individual species, and tend to average out large but opposing behavioural or abundance effects. This emphasizes the importance of species-level identification in future studies. However, the detritivore Collem-

bola were clearly sensitive to management and provided adequate power for the detection of effects by using simple pitfall trapping, and so might be appropriate indicators for changing farm systems, including GM crop monitoring (see also Frampton 2001). Seed-feeding carabids, such as *H. rufipes* and *Amara* spp., might provide suitable conraindicators of management effects.

(d) Implications of GMHT crop management: Collembola

The timings of herbicide usage (Champion *et al.* 2003), the dynamics of the weed vegetation (Heard *et al.* 2003a), the relationships between the weed vegetation and the detritivore functional groups (Hawes *et al.* 2003) and covariate analyses all suggest that the high counts of detritivore Collembola under GMHT cropping, here and in Haughton *et al.* (2003), were associated with the production of weed detritus. Increased penetration of light to the soil surface, caused by lower densities of weeds in GMHT beet and spring oilseed rape, could have also contributed to this effect. The light could have stimulated fungal growth on which Collembola can feed (Hopkin 1997). Most taxa discussed here have one generation per year (uni-generational) and may demonstrate, as well as mortality, a dispersal response to treatment through their behaviour. In contrast, the Collembola are multi-generational (Hopkin 1997) and may additionally show an abundance response that is enhanced by reproduction. The Collembola are possibly the only soil-surface-active invertebrate taxa that showed such population-dynamic responses to GMHT crop management within this study.

There was strong consistency in the results for Collembola across families, across crops and across the sampling methods of pitfall traps and Vortis suction (Haughton *et al.* 2003). Such findings for the Collembola could have important implications for farmland biodiversity under GMHT crop management (Rusek 1998). First, this production of additional detritus, which sustains the Collembola, is novel as it occurs only under GMHT crop management. Second, this detritus, which enters the GMHT system after the application of herbicides to GMHT crops, maintains detritivore Collembola numbers until at least July–August. Third, the Collembola counts could explain the responses to GMHT cropping of several uni-generational invertebrate omnivores and predators that may have beneficial agronomic effects, including *L. pilicornis*, *T. quadristriatus*, *Notiophilus biguttatus* and *Erigone* agg. (see Marcussen *et al.* 1999; Bilde *et al.* 2000). Although their importance relative to other taxa is as yet unknown, Collembola are known to be components of the diet of resident farmland birds that have undergone steep declines, including the yellowhammer (*Emberiza citrinella*) and reed bunting (*E. schoeniclus*) (J. D. Wilson, B. E. Arroyo and S. E. Clark, unpublished data).

It is difficult to predict the expected long-term effects of this detritus if GMHT crops were adopted on a large scale; further experimentation is necessary. During the year that the GMHT crop is grown, an increase in the abundance of detritivore Collembola could lead to a significant early-season elevation of predator abundances and subsequent enhanced pest control. However, the importance of this result within long-term rotations remains equivocal. We cannot infer reliably from the results dis-

cussed here whether such effects may persist in future years or under the influence of different cropping rotations. Furthermore, if the successive use of GMHT crops within rotations were to lead to a long-term decline in the abundance of weed vegetation, there would be less plant biomass to produce detritus and a subsequent reduction of the effect on Collembola. Moreover, it is unclear whether any possible advantages for the fitness of predators, such as greater reproductive capability, resulting from increases in collembolan prey in the first year would be sustained subsequently. Hence, the long-term effects of such an influx of detritus on soil functioning and biodiversity are unknown. However, possible effects should be monitored and studied further if GMHT crop management becomes widely adopted.

6. CONCLUSION

GMHT crop management affected the counts of many surface-active invertebrates, with either increasing or decreasing captures, according to the crop and to the phenology and ecology of the species concerned. Usually effects were indirect, and were mediated by herbicide management of weed vegetation, as measured by variables such as biomass at harvest and seed rain. Most effects involving a greater capture in the GMHT treatments occurred in maize, whereas most of the effects involving a smaller capture were in beet and spring oilseed rape. It would be speculative to predict the precise impact, under widespread GMHT cropping, of consequent changes of soil-surface invertebrates on agro-ecosystem function. Recorded effects are likely to be of similar magnitude to possible effects of switches between conventional crop species. Major sources of variation in potential impacts arise from probable changes in herbicide regimes, tillage systems and crop rotations and from possible long-term interactions between weed and invertebrate populations. All of these potential effects depend greatly upon the management of the crops, the rotations and the entire farmed landscape. Within most families or orders, averaging over taxa tended to mask opposing behavioural and abundance effects, thus emphasizing the importance of species-level taxonomy in future studies. However, consistently large increases in captures of detritivore Collembola and some of their predators were seen for all GMHT crops. At the species level, differences in counts of seed-feeding carabids were noticeable for all crops. Collembola and weed seed-feeding carabids may therefore be useful indicator species for future studies of GMHT crop management. These results apply generally to agriculture across Britain, and could be used within mathematical models to predict the likely long-term effects of the widespread adoption of GMHT crops.

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GLOSSARY

- FSE: Farm Scale Evaluation
GM: genetically modified
GMHT: genetically modified herbicide tolerant