

Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops

C. Hawes^{1*}, A. J. Haughton², J. L. Osborne², D. B. Roy³, S. J. Clark², J. N. Perry², P. Rothery³, D. A. Bohan², D. R. Brooks², G. T. Champion⁴, A. M. Dewar⁴, M. S. Heard³, I. P. Woiod², R. E. Daniels⁵, M. W. Young¹, A. M. Parish¹, R. J. Scott⁶, L. G. Firbank⁶ and G. R. Squire¹

¹Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK

²Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK

³NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK

⁴Broom's Barn Research Station, Higham, Bury St Edmunds, Suffolk IP28 6NP, UK

⁵NERC Centre for Ecology and Hydrology, Winfrith Technology Centre, Dorchester, Dorset DT2 8ZD, UK

⁶NERC Centre for Ecology and Hydrology, Merlewood, Grange-over-Sands, Cumbria LA11 6JU, UK

Effects of genetically modified herbicide-tolerant (GMHT) and conventional crop management on invertebrate trophic groups (herbivores, detritivores, pollinators, predators and parasitoids) were compared in beet, maize and spring oilseed rape sites throughout the UK. These trophic groups were influenced by season, crop species and GMHT management. Many groups increased twofold to fivefold in abundance between early and late summer, and differed up to 10-fold between crop species. GMHT management superimposed relatively small (less than twofold), but consistent, shifts in plant and insect abundance, the extent and direction of these effects being dependent on the relative efficacies of comparable conventional herbicide regimes. In general, the biomass of weeds was reduced under GMHT management in beet and spring oilseed rape and increased in maize compared with conventional treatments. This change in resource availability had knock-on effects on higher trophic levels except in spring oilseed rape where herbivore resource was greatest. Herbivores, pollinators and natural enemies changed in abundance in the same directions as their resources, and detritivores increased in abundance under GMHT management across all crops. The result of the later herbicide application in GMHT treatments was a shift in resource from the herbivore food web to the detritivore food web. The Farm Scale Evaluations have demonstrated over 3 years and throughout the UK that herbivores, detritivores and many of their predators and parasitoids in arable systems are sensitive to the changes in weed communities that result from the introduction of new herbicide regimes.

Keywords: arable systems; invertebrates; trophic interactions; functional groups; resource limitation

1. INTRODUCTION

The FSEs were designed to compare the impacts of weed management on the diversity and abundance of arable plants and invertebrates in GMHT and conventional crops (Firbank *et al.* 2003). Evidence available at the start of the FSEs indicated that the GMHT and conventional varieties were unlikely to differ substantively in competitive ability with other plants, in the insect defence compounds they produce or in their attractiveness to pollinators (see Squire *et al.* 2003). Nor were the herbicides glyphosate and glufosinate-ammonium, to which

beet, and spring oilseed rape and maize, respectively, are tolerant, any more toxic to insects than the herbicides used widely in conventional arable farming (Breeze *et al.* 1999; Dewar *et al.* 2003; Squire *et al.* 2003). Any effect of GMHT cropping should therefore act primarily through the impact of the herbicides, glyphosate and glufosinate-ammonium, on the arable flora, and then indirectly through transmitted effects to associated invertebrate populations (see Firbank *et al.* 2003).

In typical arable fields in the UK, crop plants produce 10–1000 times more biomass than the weed flora and tend to support a specialist set of arthropods adapted to plentiful but uniform biomass (Andow & Imura 1994). Weeds, by contrast, support a wider range of invertebrate species at lower densities through the provision of a variety of food resources and a more heterogeneous habitat structure (Root 1973; Stinson & Brown 1983; Andow 1991;

*Author for correspondence (chawes@scri.sari.ac.uk).

One contribution of 10 to a Theme Issue 'The Farm Scale Evaluations of spring-sown genetically modified crops'.

Norris & Kogan 2000; Haddad *et al.* 2001). Existing evidence (e.g. Wratten & van Emden 1995; Norris & Kogan 2000) indicates that these invertebrates should show differential sensitivities to change in weed populations or biomass. The more dependent the organisms are on the weed flora, rather than the crop, and the more sedentary and less wide ranging or migratory they are, then the greater their sensitivity to change in the weed flora (Koricheva *et al.* 2000).

The effects of GMHT cropping on the weeds depended on the timing of application and the different efficacies of weed-control regimes compared with conventional crops (Heard *et al.* 2003*a,b*). Within the FSEs, herbicides were applied before, at or near sowing in most conventional half-fields (as is usual), but later, when both crop plants and weeds were larger, in GMHT half-fields (Champion *et al.* 2003). The net effects differed according to the crop species. In beet and spring oilseed rape, the trend to larger initial weed populations in GMHT half-fields was later reversed, resulting in smaller eventual weed biomass than in conventional halves. In maize, the larger initial weed populations in GMHT half-fields were not reversed, probably because of the higher persistence and greater efficacy of the herbicides used in the conventional treatment, resulting in a greater eventual weed biomass under GMHT management. Among crop species and treatments, mean weed biomass ranged from 4 g m^{-2} (geometric mean) in the GMHT treatment in beet to 41 g m^{-2} in the conventional treatment in spring oilseed rape (Heard *et al.* 2003*a*). The invertebrate taxa differed less, and less systematically, between treatments than the weeds (Brooks *et al.* 2003; Haughton *et al.* 2003). Examples of taxa showing consistent effects included Collembola (mainly detritus feeders), which were greater in GMHT treatments, bees and butterflies, which were lower in beet and spring oilseed rape GMHT treatments, and Heteroptera, which also occurred at lower densities in GMHT half-fields towards the end of the growing season (Brooks *et al.* 2003; Haughton *et al.* 2003). Species of carabid beetle showed a mixture of both positive and negative responses to GMHT management (Brooks *et al.* 2003). Strong effects on weeds in GMHT crops were not therefore transmitted to consistent effects in the same direction or of the same magnitude in many of the invertebrate taxa sampled.

Organisms from different taxonomic groups whose geographical distributions do not or only partly overlap might have similar properties and functions in arable systems. The extent to which these properties are affected by changes in management can be assessed through the reclassification of taxa into functional groups and analysis of their responses to GMHT treatment. Functional-group analysis may also provide a more generic basis for modelling system responses to changes in management and allow extrapolation of trends to other ecological situations.

Plants and invertebrates may be assigned to functional groups according to a range of criteria based on biological attributes, resource acquisition strategies, contributions to ecosystem processes or responses to environmental factors (e.g. Haddad *et al.* 2001; Lavorel *et al.* 1997). The method of classification used here and considered most appropriate for the type of data collected in the FSEs was to assign taxa according to their role in the movement of resources from primary production to decomposition (primary

producers, herbivores, pollinators, predators, parasitoids and detritivores) (Lindeman 1942).

The basis of the interaction between these functional groups is the extent to which a change of resource in one of them influences the abundance or biomass of organisms in another (De Feo & Rinaldi 1997; Rosenzweig 1971; Abrams 1993). Accordingly, many studies have attempted to define by experiment or to model the functional form of the relation between resource and consumer (DeAngelis *et al.* 1975; Holst & Ruggie 1997). For at least some part of the relation, the consumer is limited by the resource. However, resource limitation will not occur if the population of the consumer is restricted by other factors, either intrinsic (if consumption, energy conversion and growth rate are already at their physiological maxima) or extrinsic (where populations are kept at low levels through predation, disease, climate, disturbance or human control). Spatial-distribution patterns and foraging strategies also influence the functional form of the relation between scarce prey and highly mobile predators, especially where dispersal behaviour is altered by hunger (Holling 1966). Likewise the functional relation between floral resources and highly mobile pollinating species is complicated by the spatial distribution of resources over the pollinator's foraging range (which may cover many hectares) together with their preferences and navigational ability (Osborne *et al.* 1999; Cresswell *et al.* 2000). The degree of resource limitation also depends on the level of apparency of the resource to the consumer and any direct influence of primary producers on the third trophic level (e.g. through provision of alternative food or shelter).

Despite these complications, the demonstration of an association between consumers and their resources would suggest that the impact of GMHT cropping on invertebrate functional groups acts primarily through changes in the weed flora. This would provide a basis for modelling arable food webs (e.g. Schmitz & Booth 1997) to examine the wider impact of GMHT management on the ecosystem (e.g. Watkinson *et al.* 2000). This paper therefore extends the analyses of individual taxonomic groups in the FSEs, to include a trophic or functional approach aiming to determine whether trends in the populations of herbivores, pollinators, detritivores, predators and parasitoids are driven by differences in weed populations and biomass. Distinction is made in sampling and analysis between invertebrate groups that previous evidence suggests should be sensitive to change in the weed flora and other groups that should be less affected. The former includes sedentary groups inhabiting the weed canopy and litter layer that show numerical responses (through reproduction) to changes in resource availability at a patch scale, herbivores and their natural enemies associated with the weed flora that forage at the field scale, and highly mobile specialist groups that show behavioural responses to resource supply at a regional or landscape scale. Groups likely to be less affected include specialists on the crop plants and wider ranging generalist predators.

2. METHODS

(a) *Sampling*

Sampling methods are described in detail in Brooks *et al.* (2003), Haughton *et al.* (2003) and Heard *et al.* (2003*a*).

Briefly, plants and invertebrates were sampled in 67 spring oilseed rape, 59 fodder maize (including only sites in their first season in the FSEs) and 66 beet sites to compare the ecological effects of conventional and GMHT crop management. Sites were selected to be representative of the geographical distribution and range of conditions under which each of the crops is commercially grown. Crop management was typical of normal commercial practices prevailing at a given site. Field sizes, locations and management, including details of herbicide and pesticide applications, are described fully in Champion *et al.* (2003). Individual fields were split into approximately equal halves such that potential confounding factors (soil type, topography and margin characteristics) were balanced at the field scale. Each treatment was randomly allocated to one half of each field. Sampling was based at fixed locations per half-field along 12 evenly spaced transects projecting 32 m from the crop edge to the field centre.

Ground cover, mean height and development of crop plants at 4 m and 32 m into the field on three transects per treatment were recorded at two-week periods throughout the season (Champion *et al.* 2003). Conventional crop-development schemes were used that identified the growth of plants through vegetative, flowering and fruiting stages (Lancashire *et al.* 1991). Weed abundance was assessed from seedling counts of each species present (Heard *et al.* 2003a). These counts were conducted at 60 fixed locations per treatment in each field, and on three occasions: (i) after sowing but before the first herbicide application to the conventional half (first seedling count); (ii) approximately two weeks after the last herbicide application to the GMHT half of the field (after herbicide count); and (iii) at the end of the growing season before harvest (biomass count). At this third count, samples of weed biomass were also taken as described by Heard *et al.* (2003a).

Predatory and detritivorous invertebrates (mainly Carabidae, Araneae and Collembola) active at the soil surface and the litter layer were sampled by pitfall traps over 14 day trapping periods in May/June, July and August, at 12 sample points per half-field, as described in Brooks *et al.* (2003). Phytophagous, detritivorous, predatory and parasitoid insects living on the weeds and the soil surface were sampled with a vacuum (Vortis) suction sampler in June and August at six sample points per half-field (see Haughton *et al.* (2003) for details of standardized field sampling methods). Pollinators (bees and butterflies) were counted on four 100 m transects into the crop on three occasions in spring oilseed rape and maize fields and on four occasions in beet fields (Haughton *et al.* 2003). As a group, bees and butterflies could be considered generalist flower visitors, playing an important role in the pollination of many weed and crop species in the arable ecosystem. Other flower-visiting insects (e.g. syrphids and some beetles) were not included in the pollinator functional group, as the degree to which they function as pollinators depends to a large extent on the insect species (Proctor *et al.* 1996). Finally, crop herbivores and natural enemies were assessed *in situ* by direct observations for 2 min per plant in which all taxa were counted and recorded. Single crop plants were selected at random 2 m to the right of each of nine transects around each half of the field at 2, 4, 8, 16 and 32 m from the crop edge, giving 45 plants for each half of the field. Surveys were done at periods when significant infestations by the most abundant herbivores were most likely to occur: June and July for spring oilseed rape and beet; July and August for maize. As all sampling methods are biased to particular components of the system, some groups of herbivores may have been

under-sampled (e.g. miners, stem borers). However, this does not invalidate the analysis of or interpretation of trends in the abundance of epigeal guilds. Median sampling dates for each survey across the three sampling seasons (2000, 2001 and 2002) are shown in table 1.

All taxa sampled were classified according to trophic level (crop and non-crop herbivores, pollinators, detritivores, predators and parasitoids) as defined in table 2. Classification was done on the basis of the main trophic function at the species level for Heteroptera and Carabidae, and at the family level for most other groups sampled. Omnivores were not included in the analysis as the relative proportion of plant to animal matter consumed depends on the availability of different resources at the field level and therefore varies greatly from site to site. Predators and parasitoids belonging to the fourth trophic level were amalgamated with the third as the degree of intra-guild predation and the level of parasitism could not be determined from the data gathered. Finally, biomass data would provide a more direct assessment of the transfer of energy across trophic levels than the number of individuals sampled, and would constitute useful further work. Insect number does, however, provide a reasonable indication of trophic-group response to a change in resource availability. The number of individuals in each trophic group per half-field was analysed separately for each sampling method, sampling occasion and over the whole season.

(b) Statistical analysis

A description of the experimental design has been given in detail elsewhere (Perry *et al.* 2003) and is summarized briefly here. Records for each variable analysed were obtained from systematic samples within each of $2n$ half-fields of three spring crops, in a randomized block experimental design, in which the blocks were paired half-fields. 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. To give an approximate indication of abundance, geometric means for each treatment i were calculated from back-transformed values of l_{ij} . The standard analysis of abundance 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 GMHT and conventional treatments on the 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 $t_{0.05}$. Response variables were analysed separately for each occasion. Differences between the treatment effects for samples recorded at different distances into the crop were tested using 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. If half or fewer samples were missing, those missing samples were estimated proportionately. 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 H_0 .

Separate covariate analyses were conducted to detect whether measured treatment effects in one trophic group could be

Table 1. Median sampling dates for vegetation, crop insect, Vortis, bee and butterfly, and pitfall surveys from 2000 to 2002. (Crops were surveyed at two-week intervals from sowing to harvest.)

crop	month	vegetation	crop insect	Vortis	bee and butterfly	pitfall
beet	May	15	—	—	25	—
	June	—	14	19	18	5
	July	26	14	—	16	28
	August	27	—	11	12	22
maize	May	—	—	—	—	—
	June	1	—	12	17	19
	July	26	17	—	14	30
	August	—	12	16	14	22
	September	9	—	—	—	—
spring oilseed rape	May	20	—	—	—	—
	June	16	17	24	14	7
	July	—	12	—	13	23
	August	18	—	7	12	24

Table 2. Level of identification and assigned functional group of invertebrates from Vortis, pitfall and crop-herbivore survey data. (Classification was done at the family level for Collembola, order level for Orthoptera, species level for Heteroptera, and so on; y, present in assigned functional group.)

group	common name	level of identification	functional group classification					mixture or omnivore (excluded)
			herbivore	pollinator	detritivore	predator	parasitoid	
Collembola	springtails	family	y	—	y	—	—	—
Orthoptera	crickets, grasshoppers	order	y	—	—	—	—	—
Thysanoptera	thrips ^a (on crop plants)	order	y	—	—	—	—	—
Hemiptera:								
Heteroptera	true bugs	species	y	—	—	y	—	y
Auchenorrhyncha	leaf hoppers	species	y	—	—	—	—	—
Aphidoidea	aphids ^a	family	y	—	—	—	—	—
Neuroptera	lacewings	order	—	—	—	y	—	—
Lepidoptera:	butterflies and moths	family	—	y	—	—	—	—
Lepidoptera larvae	caterpillars ^a	order	y	—	—	—	—	—
Diptera:								
fly	flies	order	—	—	—	—	—	y
syrrhid larvae	hoverflies	family	—	—	—	y	—	—
Hymenoptera:								
Apocrita	bees	species	—	y	—	—	—	—
Symphyla larvae	sawflies ^a	suborder	y	—	—	—	—	—
Parasitica		superfamily	—	—	—	—	y	—
Coleoptera:								
Coccinellidae	ladybirds	species	y	—	—	y	—	—
Curculionidae	weevils ^a	family	y	—	—	—	—	—
Staphylinidae	rove beetles	family	—	—	—	—	—	y
Carabidae	ground beetles	species	y	—	—	y	—	y
carabid larvae		family	—	—	—	—	—	y
Araneae	spiders	family	—	—	—	y	—	—

^a Groups that include crop herbivores frequently targeted for pest control.

explained by treatment effects in their resource. This was done for natural enemies, herbivores and pollinators, with herbivores and detritivores, plant biomass and dicotyledonous weeds as resource covariates for each consumer group, respectively. Data

were taken from August Vortis samples and July and August bee and butterfly counts to coincide with the plant biomass collection dates. Earlier sample dates were excluded from the covariate analyses as densities of invertebrates tended to be low,

populations may not have had sufficient time to show numerical responses to changes in resource availability, and comparable weed biomass data were lacking. Where a significant effect of treatment in a simple test of the null hypothesis was reduced through inclusion of its resource as a covariate, the implication was that the consumers were showing an indirect response mediated through the change in their resource. If the resource was at the primary level (vegetation), the assumption was that any treatment effect on the resource was a direct effect of herbicide regime.

Simple linear regressions for logarithmically transformed half-field totals were conducted for each of four consumer variables (predators, parasitoids, pollinators and herbivores) on each of three resource variables (herbivores, detritivores and plants). As in the covariate analyses described above, regressions were conducted for data from weed biomass, bee and butterfly counts, and Vortis samples taken in July and August. Interactions between predators active at the ground surface and detritivores inhabiting the litter layer as sampled by pitfall trapping were not included in either the covariate analysis or the regression analysis because of the lack of comparability between these groups in the spatial scale at which they operate, i.e. highly active, generalist and wide-ranging predators at low density cannot be compared meaningfully with highly aggregated sedentary populations of detritivores. For each combination of resource and consumer variable, three regression models were compared: a single line through both treatments; two parallel lines allowing the intercept to vary with treatment; and two separate lines allowing the regression coefficient and intercept to vary with treatment. Discrimination between models was by standard partial *F*-tests on one degree of freedom (Sokal & Rohlf 1981, § 14.9; Perry 1982). In each case the overall regression was tested to establish whether a relation existed between the two variables. The intercept and regression coefficient of the best-fitting model were recorded.

Finally, a generalized linear model with binomial errors and a logit link function was used to analyse treatment differences in the number of spring oilseed rape fields that had reached the flowering stage at two-week periods throughout the growing season.

It might be thought that the multiplicity of hypothesis tests reported in this paper require the use of some Bonferroni adjustment, to adjust the significance level of each. However, we prefer presenting *p*-values of individual tests with estimates of treatment effects and errors of estimation.

3. RESULTS

(a) Crop vegetation and invertebrates

The growth data (cover and height) for conventional and GMHT varieties of each crop from May to September are summarized in table 3. The range of final height, from ca. 0.5 m in beet to 2 m in maize, shows the great difference in canopy structure across crop species. The height and cover of GMHT and conventional varieties were generally similar in all three crops, although GMHT beet was slightly shorter in August, GMHT maize had greater percentage cover in May and was taller in May and June, and GMHT spring oilseed rape had less cover in June and was slightly shorter than conventional varieties in August. Although statistically significant, these small differences between varieties (less than 4.5% cover and less than 7.5 cm in height) were not consistent throughout the

growing season. When in flower, spring oilseed rape is a major nectar and pollen resource for flower-visiting insects, particularly bees and butterflies that are important pollinators. No differences were detected in the number of half-fields in flower between GMHT and conventional spring oilseed rape varieties at any stage during the growing season ($F_{1,5} = 1.84$, $p = 0.233$).

Herbivores, predators and parasitoids living on the crop plants were recorded by direct counts of numbers in the field. The herbivore abundances on the crop plants of beet, maize and spring oilseed rape were largely similar on GMHT and conventional varieties (table 4). This absence of response to treatment remained from the early count to the late count, although herbivore abundance changed greatly between counts. The herbivores in beet, which consisted mostly of aphids, increased about eightfold between these counts, whereas those in spring oilseed rape, mostly aphids and pollen beetles, increased fivefold. The most abundant crop herbivores in maize were thrips (Thysanoptera), which declined in number from the early count to the late count.

The populations of natural enemies recorded on crop plants, mainly aphid specialists, such as coccinellid and syrphid larvae, and parasitic wasps, changed less during the season than populations of herbivores (table 4). Numbers at the later count were 1–16% of the herbivore numbers. No consistent trends between treatments occurred, but statistically significant differences were observed in three instances: the GMHT treatment had fewer parasitoids in beet at the early count in June; there were fewer predators in maize at the later count in August; and fewer parasitoids were found in spring oilseed rape at the later count in July. These effects of treatment observed on small populations did not relate to equivalent responses by crop herbivores to treatment, although covariate analysis indicated that crop herbivore density had a significant positive effect on predator abundance in maize and on parasitoid abundance in spring oilseed rape.

(b) Weed vegetation and invertebrates

Out of approximately 170 weed species recorded, *Chenopodium album* was dominant in beet and maize fields (13% and 14% of the total biomass, respectively), *Polygonum aviculare* was dominant in spring oilseed rape fields (12%) and *Poa annua* was the co-dominant species in all three crops, contributing between 10% and 12% of the total biomass. Total weed populations were higher in the GMHT treatment early in the season as a result of pre-emergence herbicides applied to the conventional treatment at some sites (Champion *et al.* 2003; Heard *et al.* 2003a). The effect was reversed after the GMHT treatment had been sprayed, except in maize where the conventional herbicide was more effective than that used on the GMHT crop. By the end of the season, the weed biomass in the GMHT treatment was lower than in the conventional treatment in beet (4 g m⁻² compared with 22 g m⁻²) and spring oilseed rape (13 g m⁻² compared with 46 g m⁻²) but higher in maize (14 g m⁻² in GMHT compared with 8 g m⁻² in conventional).

The four trophic groups, herbivores, predators, parasitoids and detritivores, living on these weed plants were assessed by Vortis suction sampling. Detritivores (mainly Collembola) were the most numerous group in all three

Table 3. Differences in crop canopy structure (height (cm) and percentage cover) between GMHT and conventional (C) treatments from May to September for three spring-sown crops.

(d is the mean of the differences between GMHT and C treatments.)

crop and month	variable	<i>n</i>	arithmetic mean		<i>d</i> (s.e.m.)	<i>p</i> -value
			C	GMHT		
beet						
May	cover	57	3.84	3.69	-0.15 (0.21)	0.48
June		65	23.91	23.02	-0.90 (0.94)	0.34
July		65	62.29	59.96	-2.32 (1.56)	0.14
August		65	75.87	74.97	-0.90 (1.53)	0.56
September		35	76.54	79.62	3.07 (2.47)	0.22
May	height	57	3.14	3.10	-0.05 (0.18)	0.80
June		65	14.22	14.00	-0.22 (0.62)	0.72
July		65	37.88	36.68	-1.19 (0.88)	0.18
August		65	50.07	47.17	-2.90 (1.05)	0.007**
September		35	53.27	51.25	-2.02 (1.59)	0.21
maize						
May	cover	34	2.87	3.59	0.72 (0.20)	< 0.001***
June		56	11.34	11.82	0.48 (0.50)	0.34
July		58	40.07	41.96	1.90 (1.41)	0.18
August		55	65.87	66.70	0.83 (2.01)	0.68
September		40	63.78	67.23	3.46 (2.33)	0.15
May	height	34	4.43	5.01	0.58 (0.28)	0.04*
June		56	18.45	19.81	1.36 (0.56)	0.02*
July		58	80.70	78.68	-2.03 (3.67)	0.58
August		55	182.00	180.20	-1.81 (4.63)	0.70
September		40	203.50	209.00	5.51 (4.68)	0.25
spring oilseed rape						
May	cover	58	11.27	10.02	-1.25 (0.98)	0.21
June		66	49.71	45.21	-4.49 (1.59)	0.006**
July		66	70.31	70.41	0.10 (1.45)	0.95
August		66	73.07	74.97	1.90 (1.36)	0.17
September		34	69.08	72.14	3.06 (2.77)	0.28
May	height	58	3.31	2.92	-0.39 (0.26)	0.15
June		66	36.54	34.46	-2.08 (1.71)	0.23
July		66	89.10	85.88	-3.22 (2.45)	0.19
August		66	102.47	95.26	-7.21 (2.12)	< 0.001***
September		34	97.68	95.01	-2.66 (2.95)	0.37

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

crops and increased in number from the early sample to the later sample (table 5). The dominant group of herbivores in all three crops was the sap suckers, which consisted mainly of aphids, leafhoppers and mirid bugs. Herbivore populations remained at relatively stable levels through the season in spring oilseed rape and maize, but increased in beet, particularly in the conventional half-fields. The main predator taxa were spiders (Liniphyyidae and Lycosidae), coccinellid larvae and Carabidae. There were three to six times more of these predators at the late count in all crops.

These trophic groups showed a range of treatment effects (table 5). In beet and maize sites, invertebrate functional groups reflected the responses of the weed flora to treatment. In beet, herbivores and parasitoids occurred at lower densities in the GMHT treatment, where weed biomass was also lower by the end of the season. In maize, all four functional groups showed a trend (significant for detritivores) towards higher numbers in the GMHT half-fields where weed biomass was greater by the end of the season. Invertebrates sampled from spring oilseed rape fields showed similar patterns, although the trend for

lower numbers of herbivores in the GMHT treatment was significant only at the earlier sample in June. Over the whole season, predators and parasitoids in spring oilseed rape occurred at lower densities under GMHT management.

The general trend was for greater increases in the ratio of detritivores to herbivores through the season under GMHT than under conventional cropping. In beet, the detritivore-to-herbivore ratio in GMHT treatments was 4.27, approximately double that in the conventional treatment. In spring oilseed rape, the ratios were 11.2 and 8.2 in GMHT and conventional treatments, respectively. In maize, the ratios of detritivores to herbivores were similar across the treatments and through the season as all groups showed a positive response to GMHT management.

(c) *Invertebrates active at the ground surface*

Detritivores (mainly Collembola) active at the ground surface and sampled by pitfall trapping showed significantly higher numbers in the GMHT treatment in beet and maize in August, and in spring oilseed rape in June

Table 4. Mean counts per half-field of crop herbivores and their natural enemies in conventional (C) and GMHT beet, maize and spring oilseed rape on two sampling occasions during the growing season, and respective treatment effects. (Resource as a covariate (in italic type) is shown for each consumer for the latest samples. Mean values are calculated from direct visual counts of all insects from 45 crop plants per half-field. 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 (CI) for R are back-transformed from those for d .)

crop and month	group (with covariate)	<i>n</i>	geometric mean count			treatment <i>p</i> -value	covariate <i>p</i> -value
			C	GMHT	<i>R</i> (95% CI)		
beet							
season total	herbivores	52	149.43	117.43	0.79 (0.61–1.02)	0.09	
	aphids	50	132.00	96.40	0.73 (0.52–1.04)	0.09	
	flea beetles	40	3.14	2.78	0.91 (0.62–1.34)	0.66	
	leaf miners	10	2.37	5.96	2.07 (1.03–4.13)	0.06	
	predators	52	24.05	21.61	0.90 (0.73–1.12)	0.35	
	parasitoids	44	6.87	5.91	0.88 (0.60–1.29)	0.49	
June	herbivores	40	15.82	14.40	0.92 (0.66–1.27)	0.60	
July	herbivores	52	119.40	97.13	0.82 (0.60–1.10)	0.19	
June	predators	33	8.20	7.20	0.89 (0.68–1.17)	0.42	
July	predators	50	18.00	15.90	0.89 (0.69–1.15)	0.40	
	<i>herbivores</i>	50	—	—	0.93 (0.71–1.20)	0.56	< 0.01**
June	parasitoids	22	4.01	2.43	0.69 (0.48–0.97)	0.03*	
July	parasitoids	41	5.34	4.65	0.89 (0.57–1.40)	0.63	
	<i>herbivores</i>	41	—	—	0.92 (0.71–1.47)	0.73	0.46
maize							
season total	herbivores	54	337.18	313.92	0.93 (0.79–1.10)	0.41	
	aphids	54	68.42	57.50	0.84 (0.61–1.17)	0.30	
	thrips	54	151.06	177.60	1.18 (0.98–1.41)	0.08	
	predators	54	33.58	26.52	0.80 (0.63–1.00)	0.06	
	parasitoids	49	14.52	11.39	0.80 (0.57–1.13)	0.21	
July	herbivores	47	164.99	189.77	1.15 (0.93–1.42)	0.18	
August	herbivores	52	100.86	107.11	1.06 (0.74–1.52)	0.74	
July	predators	45	8.79	7.45	0.86 (0.65–1.16)	0.29	
August	predators	52	22.57	17.47	0.78 (0.61–1.00)	0.04*	
	<i>herbivores</i>	52	—	—	0.77 (0.61–0.98)	0.04*	0.04*
July	parasitoids	37	5.55	4.41	0.83 (0.54–1.26)	0.35	
August	parasitoids	44	9.93	7.90	0.81 (0.57–1.17)	0.26	
	<i>herbivores</i>	44	—	—	0.82 (0.57–1.18)	0.27	0.25
spring oilseed rape							
season total	herbivores	64	203.34	220.39	1.08 (0.89–1.31)	0.43	
	aphids	49	26.48	24.30	0.92 (0.61–1.39)	0.71	
	pollen beetles	62	128.11	126.61	0.99 (0.79–1.23)	0.91	
	predators	55	5.61	6.52	1.14 (0.84–1.54)	0.39	
	parasitoids	40	4.56	3.80	0.86 (0.56–1.34)	0.48	
June	herbivores	52	32.99	33.66	1.02 (0.77–1.35)	0.87	
July	herbivores	63	159.18	174.11	1.09 (0.86–1.38)	0.46	
June	predators	27	3.65	4.68	1.22 (0.79–1.89)	0.37	
July	predators	47	4.86	5.14	1.05 (0.76–1.45)	0.75	
	<i>herbivores</i>	47	—	—	1.05 (0.75–1.46)	0.78	0.90
June	parasitoids	20	2.61	3.37	1.21 (0.65–2.26)	0.49	
July	parasitoids	31	4.69	3.23	0.75 (0.47–1.18)	0.18	
	<i>herbivores</i>	31	—	—	0.64 (0.42–0.99)	0.04*	0.03*

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

(table 6). Predators active at the surface (mainly highly mobile generalists including ground beetles and spiders), also sampled by pitfall trapping, showed no significant response to GMHT management.

(d) Pollinators

Approximately 10 times as many pollinators (bees and butterflies) were sampled in spring oilseed rape as in beet or maize owing to the greater resources of pollen and

nectar provided by this crop when in flower. The peak flowering period of spring oilseed rape in July coincided with the maximum number of pollinators sampled (figure 1). Numbers of this trophic group tended to be lower in GMHT treatments in beet and spring oilseed rape, and slightly higher in maize (table 7). These trends were statistically significant for beet in July, August and over the whole season, for spring oilseed rape totalled over the whole season only, and for maize in July.

Table 5. Mean numbers of herbivores, detritivores, predators and parasitoids from Vortis sampling in conventional (C) and GMHT beet, maize and spring oilseed rape on two sampling occasions during the growing season, and respective treatment effects. (Covariate analyses (in italic type) are shown for each consumer for August samples. Mean values are calculated from total numbers of insects in six suction samples per half-field, each sample consisting of five sub-samples. 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 (CI) for R are back-transformed from those for d .)

crop and month	group (with covariate)	<i>n</i>	geometric mean count			treatment <i>p</i> -value	covariate <i>p</i> -value
			C	GMHT	<i>R</i> (95% CI)		
beet							
season total	herbivores	64	17.14	12.27	0.73 (0.58–0.92)	0.01**	
season total	predators	64	15.93	14.73	0.93 (0.79–1.09)	0.38	
season total	parasitoids	64	28.07	16.82	0.61 (0.51–0.74)	< 0.001***	
season total	detritivores	64	59.00	66.75	1.13 (0.91–1.40)	0.29	
June	herbivores	57	24.59	24.43	0.99 (0.74–1.34)	0.97	
August	herbivores	61	49.27	31.16	0.64 (0.53–0.78)	< 0.001***	
	<i>biomass</i>	59	—	—	0.74 (0.53–1.04)	0.08	< 0.001***
June	predators	56	11.37	13.14	1.14 (0.94–1.39)	0.21	
August	predators	61	34.46	30.55	0.89 (0.76–1.04)	0.13	
	<i>herbivores</i>	63	—	—	0.99 (0.82–1.18)	0.89	< 0.001***
	<i>detritivores</i>	63	—	—	0.83 (0.70–0.98)	0.03*	0.28
June	parasitoids	56	13.22	14.82	1.11 (0.88–1.41)	0.37	
August	parasitoids	61	58.01	36.60	0.64 (0.53–0.76)	< 0.001***	
	<i>herbivores</i>	63	—	—	0.69 (0.55–0.86)	0.001**	< 0.001***
June	detritivores	57	56.76	64.70	1.14 (0.83–1.56)	0.44	
August	detritivores	61	115.05	132.96	1.15 (0.88–1.52)	0.32	
maize							
season total	herbivores	56	11.57	15.18	1.29 (0.96–1.73)	0.11	
season total	predators	56	11.09	11.32	1.02 (0.83–1.25)	0.85	
season total	parasitoids	57	13.59	16.84	1.22 (0.96–1.55)	0.09	
season total	detritivores	57	75.80	119.01	1.56 (1.17–2.09)	0.002**	
June	herbivores	44	4.80	7.91	1.54 (1.05–2.24)	0.04*	
August	herbivores	52	6.32	8.60	1.31 (0.96–1.80)	0.09	
	<i>biomass</i>	39	—	—	1.19 (0.82–1.75)	0.35	0.04*
June	predators	41	2.85	2.63	0.94 (0.73–1.22)	0.66	
August	predators	52	9.25	10.21	1.09 (0.86–1.40)	0.46	
	<i>herbivores</i>	52	—	—	0.96 (0.77–1.20)	0.71	< 0.001***
	<i>detritivores</i>	52	—	—	1.02 (0.80–1.31)	0.86	0.04*
June	parasitoids	42	2.24	3.28	1.32 (1.00–1.76)	0.05*	
August	parasitoids	53	12.66	15.77	1.23 (0.93–1.62)	0.15	
	<i>herbivores</i>	53	—	—	1.07 (0.84–1.35)	0.59	< 0.001***
June	detritivores	52	23.33	46.99	1.97 (1.39–2.81)	< 0.001***	
August	detritivores	53	42.07	61.47	1.45 (1.02–2.06)	0.05*	
spring oilseed rape							
season total	herbivores	65	20.75	16.67	0.81 (0.65–1.02)	0.06	
season total	predators	65	14.15	11.88	0.85 (0.73–0.99)	0.04*	
season total	parasitoids	64	55.15	44.09	0.80 (0.68–0.94)	0.009**	
season total	detritivores	64	117.99	125.16	1.06 (0.84–1.34)	0.60	
June	herbivores	53	11.15	7.82	0.73 (0.54–0.98)	0.04*	
August	herbivores	62	9.74	8.47	0.88 (0.70–1.11)	0.26	
	<i>biomass</i>	58	—	—	0.86 (0.64–1.16)	0.31	0.53
June	predators	53	3.03	3.19	1.04 (0.82–1.31)	0.73	
August	predators	62	10.89	9.70	0.90 (0.74–1.10)	0.29	
	<i>herbivores</i>	62	—	—	0.93 (0.77–1.12)	0.45	0.005**
	<i>detritivores</i>	62	—	—	0.86 (0.71–1.04)	0.13	0.05*
June	parasitoids	48	9.79	8.08	0.84 (0.64–1.10)	0.20	
August	parasitoids	61	45.53	39.01	0.86 (0.72–1.02)	0.08	
	<i>herbivores</i>	61	—	—	0.88 (0.74–1.04)	0.14	0.07
June	detritivores	54	33.56	32.23	0.96 (0.68–1.35)	0.81	
August	detritivores	60	79.97	94.49	1.18 (0.97–1.43)	0.11	

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

Table 6. Mean counts of detritivores and predators from pitfall sampling in conventional (C) and GMHT beet, maize and spring oilseed rape on three sampling occasions during the growing season, and respective treatment effects. (Mean values are calculated from total numbers of insects collected over 14 days from 12 pitfall traps per half-field. 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 (CI) for R are back-transformed from those for d .)

crop and month	group	<i>n</i>	geometric mean count			<i>p</i> -value
			C	GMHT	<i>R</i> (95% CI)	
beet						
season total	detritivores	66	352.99	404.21	1.15 (0.97–1.36)	0.15
	predators	66	2295.23	2210.87	0.96 (0.90–1.04)	0.29
May	detritivores	53	197.48	193.30	0.98 (0.79–1.22)	0.85
June		60	67.97	92.40	1.35 (0.98–1.87)	0.06
August		62	55.64	86.18	1.54 (1.17–2.02)	0.004**
May	predators	53	327.29	307.15	0.94 (0.84–1.05)	0.26
June		61	1030.58	1007.86	0.98 (0.89–1.08)	0.62
August		62	956.16	924.36	0.97 (0.87–1.07)	0.52
maize						
season total	detritivores	58	612.64	725.17	1.18 (0.97–1.45)	0.11
	predators	58	1365.39	1345.03	0.99 (0.91–1.07)	0.72
May	detritivores	54	291.97	344.63	1.18 (0.91–1.53)	0.19
June		49	180.81	210.28	1.16 (0.87–1.55)	0.31
August		45	85.62	138.90	1.62 (1.12–2.33)	0.011*
May	predators	54	361.22	354.54	0.98 (0.89–1.09)	0.73
June		49	678.84	690.19	1.02 (0.91–1.14)	0.76
August		45	665.75	693.13	1.04 (0.93–1.17)	0.46
spring oilseed rape						
season total	detritivores	67	528.79	581.81	1.10 (0.95–1.28)	0.21
	predators	67	1628.22	1654.44	1.02 (0.96–1.08)	0.59
May	detritivores	57	172.97	187.16	1.08 (0.89–1.31)	0.44
June		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
May	predators	57	276.83	314.52	1.14 (0.99–1.30)	0.06
June		63	497.36	511.88	1.03 (0.94–1.13)	0.52
August		60	913.88	915.50	1.00 (0.92–1.10)	0.96

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

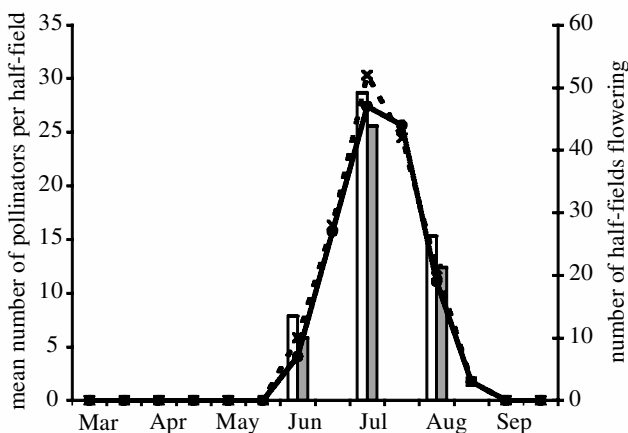


Figure 1. Number of spring oilseed rape half-fields in flower at two-week periods from March to September (dashed line, conventional; solid line, GMHT), and geometric mean number of pollinators sampled in June, July and August from four 50 m transects per half-field (open bars, conventional; grey bars, GMHT).

(e) Association between trophic groups

Interactions between trophic groups were assessed for primary producers, herbivores, pollinators, detritivores,

predators and parasitoids from crop surveys, Vortis samples and bee and butterfly counts taken towards the end of the growing season in August. At this time the sevenfold range of weed biomass across treatments and crops showed a consistent relation with a 2.5-fold difference in herbivore numbers (figure 2a). In turn, where there were lower numbers of herbivores in the GMHT treatments, fewer parasitoids were sampled (figure 2b). Herbivores did not show a consistent relation with predators at this averaging scale (figure 2c). Pollinators tended to occur in higher numbers where numbers of dicotyledonous plants were higher across crops and treatments (figure 2d).

Significant covariate effects of weed biomass on herbivore number and of dicotyledons on pollinator number were detected in both beet and maize fields, but not in spring oilseed rape, where weed mass was higher (tables 5 and 7). Where weed resource was accounted for as a covariate, the effects of GMHT treatment on herbivore number in beet fields and on pollinator number in maize fields disappeared, suggesting that the treatment effect on the consumer was related to the abundance of its resource. Significant effects of herbivores and detritivores on predator numbers were also detected across all crops (table 5).

Regression analysis confirmed that a direct positive correlation existed between consumer (herbivores, predators

Table 7. Mean counts of pollinators (bees and butterflies) in conventional (C) and GMHT beet, maize and spring oilseed rape through the growing season, including counts of dicotyledonous weeds (m^{-2}) as a covariate (in italic type) for July and August counts, and respective treatment effects.

(Mean values are calculated from total pollinators counted along four 100 m transects per half-field. 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 (CI) for R are back-transformed from those for d .)

crop and month (and covariate)	<i>n</i>	geometric mean count			treatment <i>p</i> -value	covariate <i>p</i> -value
		C	GMHT	<i>R</i> (95% CI)		
beet						
season total	60	6.73	4.34	0.69 (0.55–0.86)	0.003**	
May	7	1.92	0.84	0.63 (0.29–1.36)	0.33	
June	13	1.45	2.61	1.47 (0.83–2.60)	0.17	
July	36	3.00	1.86	0.72 (0.54–0.96)	0.03*	
<i>weeds</i>	33	—	—	0.74 (0.55–1.01)	0.06	0.85
August	51	4.68	2.55	0.62 (0.47–0.83)	0.003**	
<i>weeds</i>	49	—	—	0.62 (0.45–0.83)	0.002**	0.04*
maize						
season total	42	3.12	4.02	1.22 (0.87–1.70)	0.24	
June	6	1.67	0.78	0.67 (0.28–1.60)	0.37	
July	20	1.51	3.89	1.95 (1.14–3.34)	0.007**	
<i>weeds</i>	20	—	—	1.33 (0.68–2.57)	0.40	0.005**
August	31	2.78	2.78	1.00 (0.68–1.47)	0.10	
<i>weeds</i>	27	—	—	0.71 (0.48–0.91)	0.90	0.87
spring oilseed rape						
season total	66	63.74	54.60	0.86 (0.74–1.00)	0.05*	
June	41	7.85	5.81	0.77 (0.54–1.10)	0.15	
July	61	28.69	25.61	0.90 (0.68–1.17)	0.43	
<i>weeds</i>	58	—	—	0.95 (0.69–1.30)	0.73	0.17
August	55	15.31	12.40	0.82 (0.66–1.02)	0.08	
<i>weeds</i>	54	—	—	0.80 (0.63–1.02)	0.07	0.76

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

or parasitoids) and resource (weed biomass, herbivores or detritivores) (table 8). Although the amount of resource explained only a low percentage of the variation in the number of consumers (7–23% for insects on crop plants and 13–40% for those associated with the weed flora), significant positive relations were detected between weed biomass and herbivore number, weed herbivore number and natural enemies, detritivores and predators, and crop herbivores and their natural enemies. However, no relation was detected for weed biomass and herbivores in spring oilseed rape, where weed biomass was high, or between spring oilseed rape crop herbivores (mainly pollen beetles) and predators (mainly aphid specialists). Pollinators showed direct significant positive relations with resource availability only in beet fields. In general, the best model was a single fit through all data points, indicating that, although treatment might have affected the mass or population of a trophic group, the form of the association between the groups was not affected by treatment. The exceptions to this were parasitoids against herbivore number in beet, and predators against herbivore number in maize, where the correlation between trophic groups was lower under GMHT management in the former and greater in the latter.

4. DISCUSSION

The measurements of plant and invertebrate functional groups in the FSE arable fields revealed a dynamic system

driven by the cycle of growth and decay of the primary producers, of which the crop provides by far the greatest proportion of the total biomass. Compared with the large seasonal trends in crop growth, very little difference was detected in crop architecture or development between GMHT and conventional varieties, and variations that did occur were unrelated to differences in weed mass. Variations in crop height and cover were therefore likely to be caused by genetic traits of the varieties rather than any differential competitive effect of weeds between treatments (cf. Cipollini & Bergelson 2002). These differences between varieties did not lead to any differences in the abundance of herbivores in any of the three crop species studied, nor in the number of pollinators during the flowering period of spring oilseed rape crops. This confirms previous observations that pollinators show no preference for GMHT or conventional varieties (Picard-Nizou *et al.* 1995; Osborne *et al.* 2001). The few significant effects of treatment on predator and parasitoid groups recorded on crop plants did not relate to comparable differences in their resource or in crop canopy structure, suggesting that these natural enemies may have responded to differences in the availability of alternative food sources or shelter provided by the weed flora (Altieri 1999; Andow 1991; Price *et al.* 1980; Stinson & Brown 1983).

The lack of consistent effects of crop variety on associated invertebrates indicates that the main effect of GMHT cropping was through the impact of glyphosate or glufosinate-ammonium on the weed flora. It would therefore be

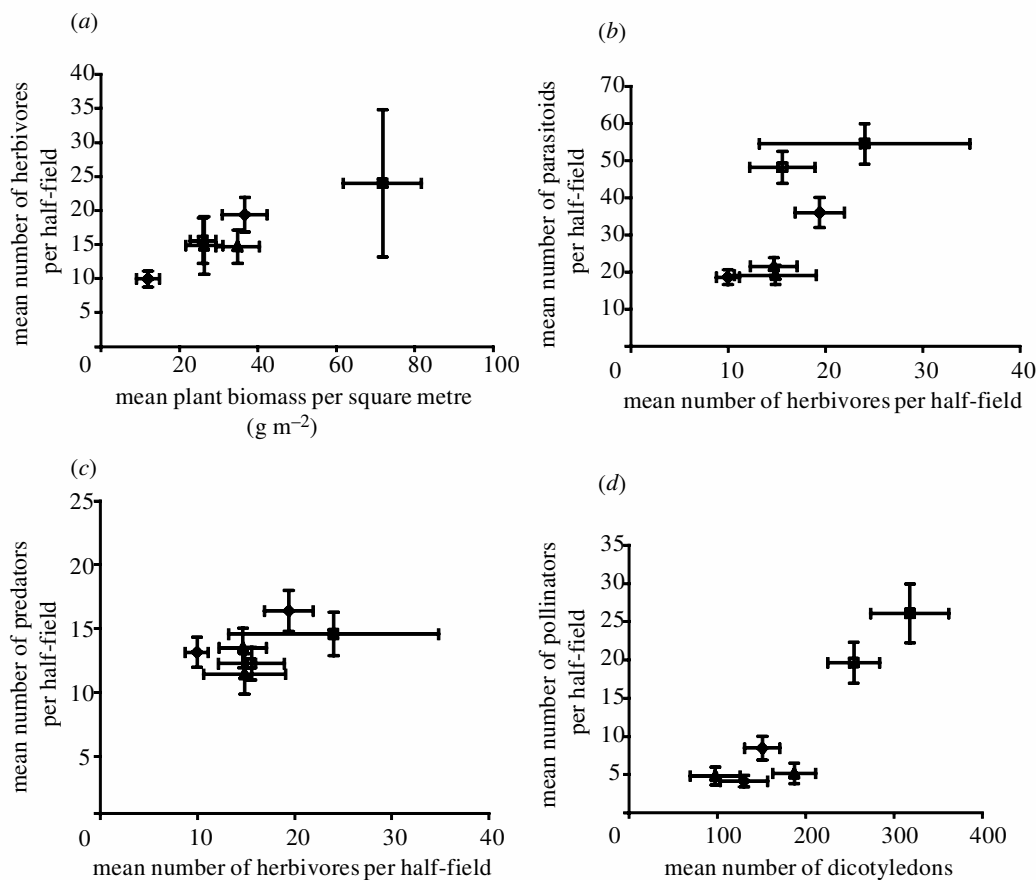


Figure 2. Relation between the untransformed mean (and standard error) number of consumers and resource per half-field, from vegetation surveys, Vortis samples, and bee and butterfly counts taken in August in conventional (filled symbols) and GMHT (open symbols) beet (diamonds), maize (triangles) and spring oilseed rape (squares) sites. (a) Weed biomass and herbivore number; (b) herbivore and parasitoid numbers; (c) herbivore and predator numbers; and (d) weed and pollinator numbers.

predicted that, in the absence of herbicide applications to either treatment, the GMHT crop varieties studied have no inherent impact on arable diversity. By the end of the growing season, weed biomass was lower under GMHT crop management in beet and spring oilseed rape fields, and higher in maize fields compared with conventional management (Heard *et al.* 2003a). Consumer groups associated directly with the weed vegetation (herbivores and their natural enemies) were positively related to the abundance of their resource and showed indirect responses to treatment through these changes in plant mass. This is similar to non-cropped field margins, where plant resources and insects that fed directly on them were higher around GMHT maize fields and lower around GMHT beet and spring oilseed rape fields (Roy *et al.* 2003).

Among the wider-ranging organisms, insects of the pollinator group were the most consistently affected by treatment in the FSEs. Pollinators are active at a much larger spatial scale than the functional groups discussed here, and, being highly mobile, have the potential to respond rapidly to changes in forage availability (Walther-Hellwig & Frankl 2000). Pollinators visiting FSE fields showed positive responses to increased weed biomass, as did weed herbivores. In beet, there is some evidence that the ratio of pollinators to weeds also differed between treatments (the regressions in table 8 have different

intercepts). These differences in pollinator abundance may influence the seed production of insect-pollinated weeds (e.g. Free 1993), thereby amplifying any direct effects of herbicide on the weed flora. To examine this relation further, specificity in feeding preferences would have to be accounted for in future research.

Invertebrates inhabiting the litter layer and those active at the soil surface belonged mainly to generalist predator and detritivore groups. The activity-abundance patterns of polyphagous predators, particularly Carabidae, are influenced by a wide range of factors including prey density, vegetation structure and microclimate (Greenslade 1964; Luff 1975; Honek 1988). Although Brooks *et al.* (2003) found both positive and negative effects of GMHT treatment on different species of Carabidae, this predatory group as a whole did not respond to differences in weed biomass between treatments. In contrast, detritivores (mainly Collembola), which are less mobile and more likely to show rapid numerical responses to food availability, occurred at higher densities in GMHT treatments. This may be caused by differences in the timing of herbicide application (Marshall *et al.* 2003). Compared with conventional management, the later herbicide application to the GMHT treatment resulted in the transfer of a larger quantity of plant material from the above-ground herbivore food web directly to the detritivore food web, thereby increasing the potential for herbivore resource limitation

Table 8. Relations between resource abundance (independent variable) and the abundance of associated herbivorous insects and natural enemies (response variable) in August. (The best-fitting model can be either a single line through both treatments (GMHT and conventional, C), two parallel lines, one through each treatment, or two separate lines fitted to each treatment independently.)

crop/independent variable (x)	response variable (y)	n	best model	regression coefficient (s.e.m.)				percentage variance explained		
				p-value ^a (overall regression)	C	GMHT	p-value (regression coefficient) ^b		C	GMHT
crop herbivores										
beet/herbivores	predators	50	single	< 0.001***	0.27 (0.01)		0.98	0.68	0.73	14.5
beet/herbivores	parasitoids	41	single	0.004**	0.30 (0.10)		0.85	0.11	0.87	8.9
maize/herbivores	predators	52	single	< 0.001***	0.36 (0.06)		0.97	0.59	0.14	23.3
maize/herbivores	parasitoids	44	single	< 0.001***	0.50 (0.11)		0.64	-0.07	0.46	19.7
spring oilseed rape/herbivores	predators	47	no relationship	0.16	0.14 (0.09)		0.96	0.45	0.88	—
spring oilseed rape/herbivores	parasitoids	31	single	0.02*	0.34 (0.14)		0.85	-0.16	0.28	7.7
Vortis										
beet/biomass	herbivores	59	single	< 0.001***	0.24 (0.05)		0.06	0.43	0.25	20.2
beet/herbivores	predators	63	single	< 0.001***	0.28 (0.06)		0.14	0.85	0.99	13.5
beet/herbivores	parasitoids	63	separate	< 0.001***	0.64 (0.09)	0.29 (0.01)	0.009**	0.72	0.92	38.3
beet/detrivores	predators	63	single	< 0.001***	0.25 (0.05)		0.61	0.71	0.07	18.0
maize/biomass	herbivores	39	single	< 0.001***	0.35 (0.06)		0.78	0.08	0.63	27.3
maize/herbivores	predators	52	separate	< 0.001***	0.33 (0.08)	0.63 (0.13)	0.05*	0.73	0.40	26.5
maize/herbivores	parasitoids	53	single	< 0.001***	6.54 (0.06)		0.90	0.69	0.68	40.6
maize/detrivores	predators	52	single	< 0.001***	0.30 (0.06)		0.76	0.51	0.89	22.1
spring oilseed rape/biomass	herbivores	58	no relationship	0.32	0.06 (0.06)		0.19	0.85	0.66	—
spring oilseed rape/herbivores	predators	62	single	< 0.001***	0.39 (0.07)		0.32	0.67	0.66	19.6
spring oilseed rape/herbivores	parasitoids	61	single	< 0.001***	6.31 (0.06)		0.15	1.32	0.32	17.9
spring oilseed rape/detrivores	predators	62	single	< 0.001***	0.26 (0.05)		0.48	0.56	0.29	21.7
bees and butterflies										
beet/total weeds	pollinators	49	parallel	0.02*	0.18 (0.10)		0.14	0.44	0.01*	9.1
maize/total weeds	pollinators	27	no relationship	0.85	0.02 (0.11)		0.35	0.56	0.95	—
spring oilseed rape/total weeds	pollinators	54	no relationship	0.62	0.05 (0.11)		0.84	1.06	0.37	—

p-values are given separately for ^athe best overall regression model, and for tests of treatment differences in ^bregression coefficient and ^cintercept. * p < 0.05; ** p < 0.01; *** p < 0.001.

and enhancing the availability of dead organic matter. Detritivores may also benefit from the lower toxicities of glufosinate-ammonium and glyphosate compared with conventional herbicides to which small soft-bodied invertebrates may be particularly sensitive (Edwards & Stafford 1979).

The positive relations detected between many of the consumer and resource groups sampled indicate that the herbivore and higher trophic levels sampled may be in part controlled by resource availability, i.e. resource was insufficient for the consumer-response curve to reach an asymptote. The only indications of resource surplus, where increases in resource elicit negligible changes in consumer number, were in spring oilseed rape sites between weed biomass and weed herbivores, and between crop herbivores and their predators, where the ratio of herbivores to predators on spring oilseed rape plants was approximately 30 : 1 compared with 5 : 1 and 6 : 1 in beet and maize, respectively.

This pattern in spring oilseed rape is similar to that reported by Koricheva *et al.* (2000) and Siemann *et al.* (1998), who found that herbivore abundance (and species richness) was less dependent on primary production, which was in surplus, and more affected by the abundance of their natural enemies. As in the FSEs, the relation between herbivores and parasitoids was stronger than that between herbivores and predators; one interpretation being a tighter coupling between specialists and their resource than between more generalist consumers and their resource.

Whether or not the positive associations detected between functional groups indicate that these regularly disturbed systems are resource controlled rather than consumer controlled is debatable and requires further investigation. For example, Siemann *et al.* (1998) showed that diversity in the plant layer is positively related to herbivore and predator diversity, indicating an effect of plant diversity on the local arthropod community. However, they suggest that herbivore diversity may equally well be maintained by the predator layer, allowing coexistence of many species regardless of plant diversity. Temporal analysis of trends in the abundances of all three trophic levels under GMHT and conventional crop management is required to distinguish between control by resource and control by natural enemies. Despite these questions, the FSEs have demonstrated over 3 years and throughout the UK that herbivores, detritivores and many of their predators and parasitoids in arable systems are sensitive to the changes in weed communities that result from the introduction of new herbicide regimes.

Given the wide range of conditions over which comparisons in the FSEs were made, the analyses indicate that significant shifts in the abundances of several functional groups would occur if these GMHT crops were grown widely in the UK. The use of GMHT beet and spring oilseed rape as breaks in cereal rotations would depress the populations of herbivores and their natural enemies associated with weed vegetation and enhance the abundance of detritivores. The ratio of detritivores to herbivores in these crops increased through the season to a much greater extent under GMHT compared with conventional crop management, indicating a shift in energy flow from the herbivore food web to the detritivore food web. In

Table 9. Maximum differences in numbers of each functional group between the three crop types, between early and late samples through the season and between GMHT and conventional treatments.

(The magnitude of the difference in each case is indicated as follows: one asterisk, two times; two asterisks, 2–10 times; three asterisks, more than 10 times. Only the weed vegetation itself shows the same magnitude of effect caused by treatment as that caused by season or crop type. All other groups were less affected by herbicide regime than by other factors.)

	difference between crop types	seasonal difference	treatment difference
crop specialists	**	**	no difference
crop natural enemies	**	**	*
weeds (total number)	**	**	**
weed herbivores	*	**	*
weed natural enemies	**	**	*
pollinators	***	**	*
detritivores	**	**	*

contrast to spring oilseed rape and beet crops, management of GMHT maize is likely to be beneficial to most invertebrate functional groups relative to current conventional practice. However, it is essential to place these shifts in context. Differences in the abundances of most groups under GMHT and conventional management were relatively small compared with seasonal trends or with differences between crop species (table 9). Even the enhanced populations resulting from the positive impact of GMHT maize are much lower than the reduced populations that result from the negative impact of GMHT spring oilseed rape (figure 2). These contextual differences should be fully considered when assessing the overall impact of introducing GMHT crops into the UK.

Whether these effects persist beyond the year of the treatment is still uncertain. For example, the trend towards higher densities of weeds in genetically modified crops at the start of the season in which the crops were sown may not persist in subsequent years given that, by the end of the season, seed return for many species was reduced in GMHT crops relative to conventional management (Heard *et al.* 2003b). Further work is required to assess the extent of recovery of plant and invertebrate functional groups after the year in which such treatments are applied. Interpretation of these trends would benefit from a range of further analyses, including (i) estimation of consumer functional and numerical responses; (ii) detailed classification of functional groups for analysis of food-web structure; and (iii) assessment of the relative importance of resource concentration or natural enemies in the regulation of consumer populations (Root 1973). Finally, and following some of the theoretical ideas introduced by Holt *et al.* (1999), the FSE data set provides a unique opportunity to assess the functional diversity of arable systems across trophic levels and to predict the impact of GMHT crop cultivation at regional and landscape scales.

In conclusion, the main effect of treatment was on the weed vegetation, with knock-on effects (i) on the herbivore, predator and parasitoid populations associated directly with this resource at the field scale, (ii) on the detritivores that respond numerically to changes in the quantity of dead plant material at a patch scale, and (iii) on the pollinators that show behavioural responses through foraging activity at a landscape scale. The results are therefore consistent with a more general pattern in plant and invertebrate communities (see, for example, Koricheva *et al.* 2000), in which change in the plant layer has the greatest effect on the relatively sedentary and host-specific herbivores, and the least effect on the more mobile generalists. The abundances of consumer groups were in general positively related to the abundance of their resource, and were therefore negatively affected by GMHT management in beet, positively affected in maize, and showed no effect in spring oilseed rape, where the weed resource was high. These responses to resource availability resulted in a shift in the balance of herbivores to detritivores through the season owing to later application of herbicide resulting in additional input of resource to the detritivore food web. Commercialization of GMHT crops would therefore be likely to have a range of effects on plant and invertebrate functional groups in the long term. The extent and direction of these effects would be dependent on the relative efficacy of conventional and GMHT herbicide regimes and the degree of buffering provided by immigration of more mobile species from surrounding fields.

This work was funded by Defra. Thanks to Nick Sotherton, David Gibbons and Nicholas Aebischer for comments on early drafts. Please refer to the acknowledgements section of the printed issue for a list of all who contributed to the FSEs over the past 3 years. Rothamsted Research receives grant-aided support from the BBSRC.

REFERENCES

- Abrams, P. A. 1993 Effect of increased productivity on the abundance of trophic levels. *Am. Nat.* **141**, 351–371.
- Altieri, M. A. 1999 The ecological role of biodiversity in agroecosystems. *Agric. Ecosyst. Environ.* **74**, 19–31.
- Andow, D. A. 1991 Vegetational diversity and arthropod population response. *A. Rev. Entomol.* **36**, 561–586.
- Andow, D. A. & Imura, O. 1994 Specialisation of phytophagous arthropod communities on introduced plants. *Ecology* **75**, 296–300.
- Breeze, V. G., Marshall, E. J. P., Hart, A., Vickery, J. A., Crocker, J., Walters, K., Packer, J., Kendall, D., Fowbert, J. & Hodgkinson, D. 1999 Assessing pesticide risks to non-target terrestrial plants. Pesticides Safety Directorate, commission no. PN0923. London: Defra.
- Brooks, D. R. (and 32 others) 2003 Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil-surface-active invertebrates. *Phil. Trans. R. Soc. Lond. B* **358**, 1847–1862. (DOI 10.1098/rstb.2003.1407.)
- Champion, G. T. (and 17 others) 2003 Crop management and agronomic context of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. R. Soc. Lond. B* **358**, 1801–1818. (DOI 10.1098/rstb.2003.1405.)
- Cipollini, D. F. & Bergelson, J. 2002 Interspecific competition affects growth and herbivore damage of *Brassica napus* in the field. *Pl. Ecol.* **162**, 227–231.
- Cresswell, J. E., Osborne, J. L. & Goulson, D. 2000 An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol. Entomol.* **25**, 249–255.
- DeAngelis, D. L., Goldstein, R. A. & O'Neill, R. V. 1975 A model for trophic interaction. *Ecology* **56**, 881–892.
- De Fel, O. & Rinaldi, S. 1997 Yield and dynamics of tritrophic food chains. *Am. Nat.* **150**, 328–345.
- Dewar, A. M., May, M. J., Woiwod, I. P., Haylock, L. A., Champion, G. T., Gamer, B. H., Sands, R. J., Qi, A. & Pidgeon, J. D. 2003 A novel approach to the use of genetically modified herbicide-tolerant crops for environmental benefit. *Proc. R. Soc. Lond. B* **270**, 335–340. (DOI 10.1098/rspb.2003.2248.)
- Edwards, C. A. & Stafford, C. J. 1979 Interactions between herbicides and the soil fauna. *Ann. Appl. Biol.* **91**, 125–146.
- Firbank, L. G. (and 18 others) 2003 An introduction to the farm scale evaluations of genetically modified herbicide-tolerant crops. *J. Appl. Ecol.* **40**, 2–16.
- Free, J. B. 1993 *Insect pollination of crops*, 2nd edn. London: Academic Press.
- Greenhouse, S. W. & Geisser, S. 1959 On methods in the analysis of profile data. *Psychometrika* **24**, 95–112.
- Greenslade, P. J. M. 1964 Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* **33**, 301–309.
- Haddad, N. M., Tilman, D., Haarstad, J., Ritchie, M. & Knops, J. M. H. 2001 Contrasting effects of plant richness and composition on insect communities: a field experiment. *Am. Nat.* **158**, 17–35.
- Haughton, A. J. (and 26 others) 2003 Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. *Phil. Trans. R. Soc. Lond. B* **358**, 1863–1877. (DOI 10.1098/rstb.2003.1408.)
- Heard, M. S. (and 12 others) 2003a Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. I. Effects on abundance and diversity. *Phil. Trans. R. Soc. Lond. B* **358**, 1819–1832. (DOI 10.1098/rstb.2003.1402.)
- Heard, M. S. (and 13 others) 2003b Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. II. Effects on individual species. *Phil. Trans. R. Soc. Lond. B* **358**, 1833–1846. (DOI 10.1098/rstb.2003.1401.)
- Holling, C. S. 1966 The functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* **48**, 5–86.
- Holst, N. & Ruggle, P. 1997 A physiologically based model of pest–natural enemy interactions. *Exp. Appl. Acarol.* **21**, 325–341.
- Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. 1999 Trophic rank and the species–area relationship. *Ecology* **80**, 1495–1504.
- Honek, A. 1988 The effect of crop density and microclimate on pitfall trap catches of Carabidae, Staphylinidae (Coleoptera) and Lycosidae (Araneae) in cereal fields. *Pedobiologia* **32**, 233–234.
- Koricheva, J., Mulder, C. P. H., Schmid, B., Joshi, J. & Huss-Danell, K. 2000 Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* **125**, 271–282.
- Lancashire, P. D., Bleiholder, H., Van Den Boom, T., Lange-luddeke, P., Stauss, R., Weber, E. & Witzinger, A. 1991 A uniform decimal code for growth stages of crops and non-crop plants. *Ann. Appl. Biol.* **119**, 561–601.
- Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T. D. A. 1997 Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* **12**, 474–478.

- Lindeman, R. L. 1942 The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–418.
- Luff, M. L. 1975 Some features influencing the efficiency of pitfall traps. *Oecologia* **19**, 345–357.
- Marshall, E. J. P., Brown, V. K., Boatman, N. D., Lutman, P. J. W., Squire, G. R. & Ward, L. K. 2003 The role of weeds in supporting biological diversity within crop fields. *Weed Res.* **43**, 77–89.
- Norris, R. F. & Kogan, M. 2000 Interactions between non-crop plants, arthropod herbivores, and their natural enemies in managed ecosystems. *Weed Sci.* **48**, 94–158.
- Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith, A. D., Reynolds, D. R. & Edwards, A. S. 1999 A landscape scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* **36**, 519–533.
- Osborne, J. L., Carreck, N. & Williams, I. H. 2001 How far do honey bees fly to *Brassica napus* (oilseed rape) crops? In *Apimondia Congr., Durban, South Africa, 28 October–1 November 2001*. CD-ROM paper no. 333, session 14. Irene, South Africa: Document Transformation Technologies.
- Perry, J. N. 1982 Fitting split-lines to ecological data. *Ecol. Entomol.* **7**, 421–435.
- Perry, J. N., Rothery, P., Clark, S. J., Heard, M. S. & Hawes, C. 2003 Design, analysis and statistical power of the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops. *J. Appl. Ecol.* **40**, 17–31.
- Picard-Nizou, A. L., Pham-Delegue, M. H., Kerguelen, V., Doualt, P., Marilleau, R., Olsen, L., Grison, R., Toppan, A. & Masson, C. 1995 Foraging behaviour of honey bees (*Apis mellifera* L.) on transgenic oilseed rape (*Brassica napus* L. var. *oleifera*). *Transgen. Res.* **4**, 270–276.
- Price, P. W., Bouton, C. E., Gross, B. A., McPheron, J. N., Thompson, J. N. & Weis, A. E. 1980 Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *A. Rev. Ecol. Syst.* **11**, 41–65.
- Proctor, M., Yeo, P. & Lack, A. 1996 *The natural history of pollination*. London: Harper Collins.
- Root, R. 1973 Organisation of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**, 95–124.
- Rosenzweig, M. L. 1971 Paradox of enrichment: destabilisation of exploitation ecosystems in ecological time. *Science* **171**, 385–387.
- Roy, D. B. (and 13 others) 2003 Invertebrates and vegetation of field margins adjacent to crops subject to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. R. Soc. Lond. B* **358**, 1879–1898. (DOI 10.1098/rstb.2003.1404.)
- Schmitz, O. J. & Booth, G. 1997 Modelling food web complexity: the consequences of individual-based, spatially explicit behavioural ecology on trophic interactions. *Evol. Ecol.* **11**, 379–398.
- Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. 1998 Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* **152**, 738–750.
- Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*, 2nd edn. New York: W. H. Freeman & Co.
- Squire, G. R. (and 14 others) 2003 On the rationale and interpretation of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. R. Soc. Lond. B* **358**, 1779–1799. (DOI 10.1098/rstb.2003.1403.)
- Stinson, C. S. A. & Brown, V. K. 1983 Seasonal changes in the architecture of natural plant communities and its relevance to insect herbivores. *Oecologia* **56**, 67–69.
- Walther-Hellwig, K. & Frankl, R. 2000 Foraging habits and distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Entomol.* **124**, 299–306.
- Watkinson, A. R., Freckleton, R. P., Robinson, R. A. & Sutherland, W. J. 2000 Predictions of biodiversity response to genetically modified herbicide-tolerant crops. *Science* **289**, 1554–1557.
- Wratten, S. D. & van Emden, H. F. 1995 Habitat management for enhanced activity of natural enemies of insect herbivores. In *Ecology and integrated farming systems* (ed. D. M. Glen, M. P. Greaves & H. M. Anderson), pp. 117–145. Chichester, UK: Wiley.

GLOSSARY

FSE: Farm Scale Evaluation

GMHT: genetically modified herbicide tolerant