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Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. I. Effects on abundance and diversity

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We compared the seedbanks, seed rains, plant densities and biomasses of weeds under two contrasting systems of management in beet, maize and spring oilseed rape. Weed seedbank and plant density were measured at the same locations in two subsequent seasons. About 60 fields were sown with each crop. Each field was split, one half being sown with a conventional variety managed according to the farmer's normal practice, the other half being sown with a genetically modified herbicide-tolerant (GMHT) variety, with weeds controlled by a broad-spectrum herbicide. In beet and rape, plant densities shortly after sowing were higher in the GMHT treatment. Following weed control in conventional beet, plant densities were approximately one-fifth of those in GMHT beet. In both beet and rape, this effect was reversed after the first application of broad-spectrum herbicide, so that late-season plant densities were lower in the GMHT treatments. Biomass and seed rain in GMHT crops were between one-third and one-sixth of those in conventional treatments. The effects of differing weed-seed returns in these two crops persisted in the seedbank: densities following the GMHT treatment were about 20% lower than those following the conventional treatment. The effect of growing maize was quite different. Weed density was higher throughout the season in the GMHT treatment. Late-season biomass was 82% higher and seed rain was 87% higher than in the conventional treatment. The difference was not subsequently detectable in the seedbank because the total seed return was low after both treatments. In all three crops, weed diversity was little affected by the treatment, except for transient effects immediately following herbicide application.

Keywords: arable weeds; Britain; genetically modified herbicide-tolerant crops; Farm Scale Evaluations

1. INTRODUCTION

The management of GMHT crops in the FSEs in Britain allows the use of broad-spectrum herbicides, which can provide weed control later in the development of tolerant crops than in conventional non-tolerant varieties (Dewar *et al.* 2000; Strandberg & Pedersen 2002). In principle, GMHT crops can benefit growers by making weed management cheaper (May 2003) and simpler, and allowing more complete control of problem infestations. There may be environmental benefits. For example, cultivation of GMHT crops could reduce the use of persistent herbicides such as atrazine, the most commonly used pre- and post-emergence herbicide in maize (Champion *et al.* 2003). This could increase food resources for birds during the season, reduce surface water leaching, allow the use of conservation or no-till techniques to the benefit of the soil structure and reduce insecticide spraying as a result of insect-pest diversion (Dewar *et al.* 2000, 2003; May 2003). On the other hand, weed control in GMHT crops might be so efficient that some plant species would effectively disappear from the arable landscape. More efficient weed control would diminish the food supply of animals that depend on weeds, and could further reduce populations of threatened animals, including birds (Andreasen *et al.* 1996; Johnson 1999; Buckelew *et al.* 2000; Hails 2000; Watkinson *et al.* 2000; Robinson & Sutherland 2002).

Agricultural intensification since the 1960s has already resulted in many changes to the plants on arable farms (Krebs *et al.* 1999; Wilson & King 2000; Marshall *et al.* 2001). In a survey of the British countryside, the mean numbers of plant species per 200 m^2 quadrat on arable land were 7.62, 7.26 and 6.44 in 1978, 1990 and 1998 (L. Maskell, personal communication, using unpublished data from Countryside Survey; cf. Haines-Young *et al.* 2000). Over a longer time period, many species of arable weed have experienced widespread decline at the 10 km

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square scale (Preston *et al.* 2002). In general, broad-leaved plants (dicotyledons) have decreased and grasses (monocotyledons) have increased (Chancellor 1985; Firbank 1999), but the varieties and abundances of both groups have declined overall (Wilson *et al.* 1995; Donald 1998; Critchley 2000). Out of 62 vascular-plant species listed on the priority list of the UK Biodiversity Action Plan (UK Biodiversity Group 1998), 14 are found exclusively in farmland habitats (Wilson 1999). The existence of a persistent seedbank can buffer the flora against loss, but intensive cropping over many years can reduce seedbanks by one or two orders of magnitude (Roberts 1958; Roberts & Stokes 1965). The impact of these changes on farmland weeds has progressively come to be viewed as a loss of cultural heritage, a matter of concern for conservationists (Wilson & King 2000). There is also evidence that changes in the arable flora can have large effects on vertebrates, especially birds (Potts 1986; Brickle *et al.* 2000; Firbank & Smart 2002).

Several factors are thought to be responsible. They include land drainage, increased use of agrochemicals and fertilisers, loss of ley and fallow from arable rotations and the widespread switch from spring to autumn sowing (Hald 1999; Robinson & Sutherland 2002). The separate impacts of these factors have not been fully elucidated, but experimental evidence on the effects of modern herbicides (as opposed to intensification generally) has consistently suggested that they lead to a reduction rather than an elimination of weed populations at the field scale (Cousens & Mortimer 1995).

Smaller changes have an effect. Changes in the timing of application and the efficacy of herbicides have tended to alter the relative abundance and the dominance relationships of species (Chancellor 1985; Whitehead & Wright 1989; Derksen *et al.* 1995; Marshall *et al.* 2001). Fields can also become weedier again. Experiments with reduced herbicide applications show that the seedbank and flora can recover over several years (Squire *et al.* 2000).

The potential ecological effects of GMHT cropping on the arable-weed flora have to be considered in this context. Experimental evidence suggests that GMHT technology can achieve significantly more efficient control than conventional treatments (Buckmann *et al.* 2000; Dewar *et al.* 2000). Whether such an effect is ecologically important should be considered with reference to the seedbank. The visible weed flora emerging from seed in any season represents a small fraction of the total seedbank. Reduction or removal of the visible flora may temporarily reduce the food available to farmland animals but may have few longer-term implications for floristic diversity if conventional non-GMHT crops are included in the rotation and seed production in these compensates for previous losses.

The weed flora can be altered massively by herbicide treatment, but the seedbank could also change systematically over a year if treatments cause a large difference in seed rain, for example, through reducing the number and size of reproductive individuals or through the harvesting of crops before the weeds reach sexual maturity. In studies where seed rain was largely prevented, the total seedbank density typically decreased over 1 year to 50% of the initial value (Brenchley & Warington 1933; Roberts 1958), a rate of decline later confirmed by controlled sowing of seed populations in soil covered by an arable crop (Lawson *et al.* 1993; Lutman *et al.* 2002). Systematic changes could also occur through the accumulation of smaller effects over time, even though in any one year such changes would not be statistically significant.

The FSEs were designed to determine the effects of cultivating GMHT crops on farmland biodiversity by contrasting a contemporary conventional style of crop management with that recommended for the GMHT crops. The crops studied were beet, *Beta vulgaris* L. ssp. *vulgaris*, maize, *Zea mays* L., and spring oilseed rape, *Brassica napus* L. ssp. *oleifera* (DC.) Metzger. Weeds in the GMHT crops were controlled by the broad-spectrum herbicides glufosinate-ammonium (Bayer CropScience UK Ltd, Cambridge, UK) in maize and spring oilseed rape, and glyphosate (Monsanto UK Ltd, London, UK) in beet. We anticipated that the major ecological effects of GMHT crop management would result from direct and indirect effects of the new herbicide regimes on the vegetation.

The main aim of this and the following paper (Heard *et al.* 2003) is to test whether progressive differences in the weed flora are likely to be caused by a systematic switch to the cultivation of GMHT crops. Specifically we aim first, to test whether differences in the weed flora within the growing season are likely to be caused by a systematic switch to the cultivation of GMHT crops; second, to estimate the magnitude and consider the implications of any differences that are found; and, third, to estimate how any differences found manifest themselves in the first 2 years after GMHT cultivation.

2. METHODS

(a) *Site selection, crop management and sampling layout*

For each crop, about 60 fields were selected from a pool on the basis that they satisfied a number of criteria relating to environmental and farm-management regimes and agricultural intensity. This provided a sample of sites throughout the lowlands of eastern and southern Britain, which was broadly representative of current agriculture (Champion *et al.* 2003). The experiment used a randomised block design in which fields were blocks and the two treatments (GMHT or conventional cropping) were allocated at random to half-fields (Perry *et al.* 2003). After a pilot year in 1999, the experiment ran from 2000 to 2002 (collection of data from the following crops continued into 2003).

Details of crop management, including the timing and type of pesticide applications, are given by Champion *et al.* (2003). All management decisions for the conventional crops were made by the farmers, who were asked to apply 'cost-effective' weed control using their normal practices. Advice on herbicide applications to the GMHT crops was provided by simulated manufacturers' labels and Supply Chain Initiative for Modified Agricultural Crops advisers where necessary. In general the GMHT crops received less herbicide active ingredient per crop with later and fewer applications than the conventional varieties (Champion *et al.* 2003). Inputs for each site were audited by agronomists qualified under the British Agrochemical Supply Industry Scheme. They confirmed that overall the management was appropriate and in line with current conventional practice.

The vegetation was sampled systematically from 12 transects around the edge of each half-field (figure 1). Transects ran from

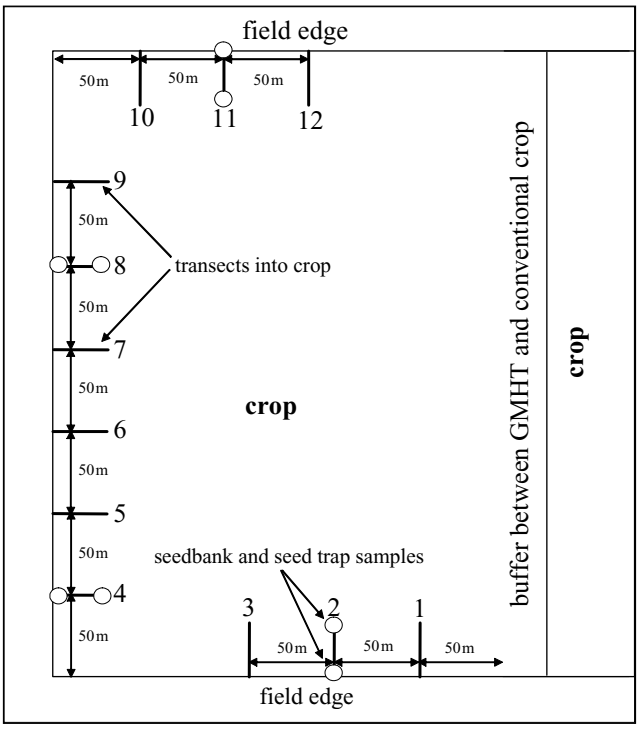


Figure 1. Layout of one half of a split field with transects and sampling plots. Transects into the crop run from the edge of the ploughed area to 32 m into the crop. Note that this shows the maximum distance between transects.

the field margin out into the crop, with sampling points located 2, 4, 8, 16 and 32 m from the field margin. Previous work has shown that species richness and abundance decline rapidly with distance from field boundaries (Marshall 1989; Wilson & Aebischer 1995) and that there is typically little difference between values at 32 m and those in the middle of a field (Critchley & Fowbert 2000).

(b) *Sampling the seedbank*

The seedbank was sampled to compare the effects of treatments on seed densities across a wide range of arable sites. It was not intended to detect all species nor to estimate the seedbank density with a high degree of precision at any one site.

We confirmed the adequacy of sample volumes for the conditions of the experiment by carrying out initial sampling at four sites before they were sown with winter oilseed rape in 1999. Statistical tests showed that eight samples (of 1 l) per treatment (half-field) replicated over the 60 sites envisaged for each crop were sufficient to detect treatment effects in the range of 30–50%. Species-accumulation curves for these sites and for data in the literature also indicated that this sampling strategy would return about half of the species that could be detected at a site (5–20 species per site, the higher figure only from very weedy sites; Squire *et al.* 2000).

Soil was collected for a seedbank count before crops were sown at the start of the experiment (table 1). In the two subsequent years soil was collected at the same sample locations, and at as near as possible to the same time of year as the initial count. Samples were taken at a standard subset of the loci sampled for vegetation: in each half of the split field, on four out of the 12 transects (2, 4, 8 and 11) and at 2 m and 32 m along each transect (to capture potential differences between the edge and the field centre; figure 1). About 1.5 kg of soil was taken to a depth of 0.15 m at each sampling locus using a soil auger or spade, weighed and passed through a sieve with a mesh size of 10 mm. Stones exceeding 10 mm in diameter were removed and weighed. About 1.2 l of the sieved sample was weighed and placed in a plastic tray to a depth of 40 mm. Further small samples were retained and frozen as reference material. The trays were arranged in an unheated glasshouse on benches fitted with capillary matting, which was kept moist. Emergent seedlings were removed and identified. The volume (*ca.* 10 l per treatment) and depth of soil, and the general conditions for emergence, were similar to those in previous studies (Brenchley & Warington 1930, 1933, 1936; Milton 1936; Champness & Morris 1948; Roberts 1958; Roberts & Chancellor 1986).

Typically, 80% of the seedbank emerges in the first flush of seedlings using this technique, but additional seedlings can still appear up to 2–3 years later. In this study, the number of seedlings of each species emerging during the first flush, up to 18 weeks after sample preparation, was taken as the standard measure of seedbank composition. The number of seedlings emerging from a tray was expressed per unit field area to the sampling depth of 0.15 m.

(c) *Counts of individual plants*

Counts of individual plants, identified to species, were made throughout the season and beyond (table 1). During the first growing season (year t) a 'first-seedling' count was made after crop sowing and where possible before the first conventional post-emergence herbicide was applied. An extra 'pre-GM-herbicide' count was made in beet after herbicide had been applied to the conventional crop but before herbicide was applied to the GMHT crop. This extra count was included to provide information about the vegetation at a time when the effect of the two treatments would be very unequal. A 'post-herbicide' count was made in all crops after the last application of GM herbicide (after a suitable delay to allow for mortality) and a 'final' count was made at the time of biomass sampling prior to harvest. In subsequent years ($t + 1$, $t + 2$) growers followed their normal crop rotations and grew crops of their choice in the fields. 'Follow-up' counts ($t + 1$, $t + 2$) were made during May–June at the same locations as all previous counts.

Weeds were counted in quadrats of 0.25 m × 0.5 m (a standard shape for species-richness work; Crawley 1997) with the longest side centred on sampling points 2, 4, 8, 16 and 32 m along each of the 12 transects (figure 1). Exceptionally, when densities of some species were very high (e.g. more than 100 per quadrat, equivalent to 800 plants m^{-2}), counts were made for these species in a half or quarter of the quadrat selected at random. For the final counts in 2001 and 2002, plants were allocated to one of three development classes: plants with fewer than four leaves (excluding cotyledons); plants with four or more leaves but not flowering; and reproductive individuals either flowering or seeding. At all stages, moribund plants were ignored unless they were reproductive individuals dying back after having shed seed.

(d) *Seed rain*

We measured seed rain using a unit-area method, with seed traps placed at ground level. The traps were constructed from three plastic plant pots (0.1 m in diameter and *ca.* 0.1 m high) nested within each other. The bases and lower few centimetres were removed from the inner two pots and a square piece of mesh fabric 250 mm wide with a mesh size of 0.2 mm × 0.4 mm

Table 1. Mean dates of agricultural activities (in italic) for conventional (C) and GMHT treatments, soil sampling for the seedbank and vegetation sampling.
(Years are distinguished as *t*, when the crop was in the ground, and $t + 1$ and $t + 2$ for the two subsequent years. See Champion *et al.* (2003) for more details of crop management.)

sampling occasion	year	beet	maize	spring oilseed rape
soil collection for first seedbank	*t*	April–May	April–May	April–May
sowing of crop	*t*	*21 April*	*8 May*	*20 April*
first seedling count	*t*	18 May	1 June	21 May
pre-GM-herbicide count	*t*	6 June	—	—
first herbicide application—C	*t*	*21 May*	*12 July*	*18 May*
first herbicide application—GMHT	*t*	*8 June*	*14 July*	*7 June*
post-herbicide count	*t*	22 July	22 July	14 July
seed-rain trapping (start–finish)	*t*	May–harvest	May–post-harvest	May–post-harvest
final count and biomass sampling	*t*	30 August	9 September	18 August
soil collection in subsequent years	$t + 1$, $t + 2$	April–May	April–May	April–May
weed counts in following crops	$t + 1$, $t + 2$	May–June	May–June	May–June

was sandwiched between the two. A strip of mesh fabric measuring 50 mm × 200 mm was wrapped around the innermost pot providing a 'ladder' to allow surface-dwelling insects entering the trap to escape. The inner pots were stapled together and all excess mesh was trimmed away. Finally, the two pots, now with a mesh base, were inserted into the third intact pot. Completed traps were sunk into four holes near to the edges of each biomass quadrat at 2 m and 32 m on transects 2, 4, 8 and 11 in each half of the field. Traps were set so that the lip of the uppermost pot was *ca.* 15–20 mm above the soil surface (to reduce insect incursion) and were secured in place using two metal pegs.

In each field, trapping started as soon as anthesis was observed in any of the weed species present. Trapping continued until at least crop harvest and, where possible, after harvest (except for beet, which is harvested by tilling the soil). In general, seeds were trapped from mid-May to late September. Seeds were collected from the traps at approximately two-week intervals. Seeds from all four traps at each transect were pooled during collection and stored in cool dark dry conditions. All seeds were identified to species and classified as 'viable' or 'non-viable'. 'Viable' seeds were those that resisted crushing when squeezed with a pair of fine forceps and had obviously filled seed coats (Forcella *et al.* 1996).

(e) *Biomass of weeds*

Biomass was sampled in the month before harvest, normally before senescence of the weeds. Samples were taken at 2 m and 32 m from the field edge along each transect using a 1 m × 1 m quadrat (which encompassed the quadrat used for individual counts). All weeds rooted within the boundary of the quadrat were cut at ground level, sorted into species, dried for 24 h at 80 °C and weighed.

(f) *Statistical analysis*

The statistical models and analyses developed for the FSEs have been set out in detail elsewhere (Perry *et al.* 2003). Our first objective was to determine whether the total density of weeds (of all species) differed between the GMHT and conventional treatments for each of the three crops. Separately for each crop, the number of individuals in each half-field was analysed by a standard randomized-block ANOVA. The field was the blocking factor, with the treatment (conventional or GMHT) replicated once in each field. Data were log-transformed prior to analysis, with the total count, c_{ij}, per half-field, for treatment i at site j, transformed to $l_{ij} = \log(c_{ij} + 1)$. Sites for which the total whole-field count was zero or one were excluded. Let n be the number of sites remaining to be analysed. The null hypothesis was tested with a paired randomization test using the test statistic $d = \Sigma_j[l_{2j} - l_{1j}]/n$. Further analyses separated the plants into two groups (monocotyledons and dicotyledons) and three development classes. These categories were analysed similarly.

Our second objective was to determine the effects of the treatments on weed biomass. In this analysis the total mass, in grams, w_{ij}, of weeds collected in each half-field was log-transformed to $m_{ij} = \log(w_{ij} + 0.005)$ (the added constant being half of 0.01 g, the minimum measurable mass per sample). Sites for which the total whole-field biomass was zero were removed from the analysis.

Treatment effects were estimated by R, the multiplicative treatment ratio (GMHT/conventional), 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 $t_{0.05}$. For each treatment, the average count across sites was calculated as the geometric mean, defined as the antilog of the mean log-transformed count minus 1.

Differences between treatments for samples recorded at differing distances from the crop margin were tested using a repeated-measures ANOVA (Greenhouse & Geisser 1959), with a term for the treatment × distance interaction. For each particular distance into the field, the half-field total for that distance was deemed to be missing if more than half of the samples were missing. If not more than half of the samples were missing, the half-field total was estimated from the remaining values. If the half-field total for a particular distance was missing, then the overall half-field total was also deemed to be missing, and that site contributed no information towards either the estimated treatment effect or the test of the null hypothesis. With these rules, the percentage of missing values rarely exceeded 5% for any variable.

Separate covariate analyses were used to detect whether treatment effects differed according to the size of the initial seedbank, the environmental zone or, for beet, whether the crop was sugar beet or fodder beet. The whole-field total initial seedbank count was taken as a measure of the overall weed status of each site. Six environmental zones, based on those of Haines-Young *et al.* (2000), were used to define regions of England and Scotland within which climate and topography are similar.

Our third objective was to measure the impact of treatment on species diversity. First, we compared the number of species, S, between treatments. We were not interested in differences that merely reflected N, the number of sampled individuals. The relationship between S and $\log N$ was approximately linear. Therefore we corrected for the number of individuals using ANOVA of S, with $\log N$ as a covariate.

Second, the log-series α index (Taylor *et al.* 1976) was calculated from the total number of species and individuals for all of the sites sampled for a particular crop and treatment. The null hypothesis was tested using 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 of α from totals taken over all sites yields larger values of N than for the covariance analysis, minimizing small-sample bias and reducing the possibility of incorrect ordering (Taylor *et al.* 1976; Kempton & Taylor 1979).

In addition dominance, D, was calculated for each half-field as $D = N_{max}/N$, where N_{max} is the number of individuals of the most abundant species and N is the total number of individuals of all species. This is a version of the Berger–Parker index (Berger & Parker 1970; May 1975), which is easily calculated and depends little on N. After transformation to a logit, $\ln(D/[1 - D])$, the null hypothesis for the dominance response variable was tested as described above. Sites, j, for which either of the two half-field total numbers of individuals over all species, N_{1j} or N_{2j}, was zero or where only one species was present on either side were excluded from all analyses. In addition, sites with totals of fewer than 50 individuals were removed from the dominance analyses calculated for counts.

In reporting the results we refer to treatment differences as significant when $p < 0.05$.

3. RESULTS

(a) *Initial seedbank*

A total of 62 922 individuals and 154 taxa were identified. The ranking of crops by seedbank density was, in descending order, maize, spring oilseed rape, beet (table 2). Generally, the weed species with the highest mean densities were also the most frequently found among sites.

The initial seedbank sample showed that there was no difference between untreated field halves in mean density or number of species within each crop (tables 2–5). Across all crops the geometric mean seedbank density was 2100 m^{-2}. The arithmetic mean number of species per half-field was 14.1, and there was little difference between the crops. Initial species diversity was significantly greater in conventional maize than in GMHT maize (table 3; log-series $\alpha = 14.2$ and 11.9 in conventional and GMHT maize, respectively; $p = 0.014$).

(b) *First seedling count*

A total of 206 taxa were recorded across all sites during the vegetation surveys, with a maximum of 34 species and a minimum of four species emerging per half-field. Total weed counts in all three crops were higher in the GMHT halves ($R = 1.41$, 2.26 and 1.70 for beet, maize and spring oilseed rape, respectively; table 2) with higher dicotyledon emergence and survival in the three crops ($R = 1.60$, 2.80 and 1.61 for beet, maize and spring oilseed rape, respectively; table 4) and significantly more monocotyledons in maize and spring oilseed rape but not in beet ($R = 1.26$ not significant for beet; $R = 1.79$ and 2.13 for maize and spring oilseed rape, respectively; table 5).

There were significantly more species per half-field in GMHT beet than in conventional beet ($S = 16.3$ and 13.5, respectively; table 3). Dominance was lower in GMHT maize ($D = 0.41$) than in conventional maize ($D = 0.46$).

(c) *Pre-GM-herbicide seedling count*

The pre-GM-herbicide seedling count was made only in beet. Overall, the GMHT halves had much higher densities of both dicotyledons ($R = 5.20$; table 4) and monocotyledons ($R = 4.66$; table 5). The difference in densities resulted in widely differing species numbers: 12.8 species per conventional half-field and 20.7 per GMHT half-field. This difference was not significant when the effect of density was allowed for (table 3). There was, however, a highly significant difference in dominance ($D = 0.56$ for the conventional treatment and $D = 0.41$ for the GMHT treatment).

(d) *Plant populations after the application of herbicide to the GMHT crop*

Counts after both GMHT and conventional herbicide treatments had been applied showed differing effects according to crop. In beet, there was no significant difference in plant density (tables 2, 4 and 5). In maize, there were higher densities of both dicotyledons ($R = 3.85$; table 4) and monocotyledons ($R = 2.48$; table 5) in the GMHT treatment. In spring oilseed rape, the opposite effect was apparent, with significantly fewer dicotyledons in the GMHT treatment ($R = 0.58$; table 4) but no difference between treatments in the monocotyledons ($R = 1.30$; table 5).

For maize, there were many more species in the GMHT ($S = 15.5$; table 3) than in the conventional ($S = 9.7$) treatment. Although *ca.* 40% of this difference can be explained by differing plant densities, the remaining 60% cannot, and is highly significant (table 3). The mean dominance of the most abundant species (mostly *Poa annua*; Heard *et al.* 2003) in the conventional maize treatment attained the maximum value recorded in our experiment ($D = 0.60$), and was significantly larger than in the GMHT treatment ($D = 0.41$). In spring oilseed rape, there were more species ($S = 19.1$) in the conventional treatment than in the GMHT treatment ($S = 14.7$). About 43% of this difference can be explained by differing plant densities and the difference is highly significant (table 3). Differences in log-series α (17.0 and 12.6 for conventional and GMHT treatments, respectively) and D (0.38 and 0.45, respectively) also indicate greater diversity in the conventional treatment for this crop.

(e) *Final plant density and biomass*

Plant densities were, with the exception of GMHT beet, higher at the final count than at the previous count. This can be attributed to the continued germination of seedlings throughout the season. Averaging over all crops, about two-thirds of individuals were pre-reproductive and one-third were reproductive.

There were marked differences between crops and treatments. For beet, there were significantly more seedlings in the conventional treatment ($R = 0.77$; table 2). Biomass, however, showed a much larger effect, with roughly a sixfold difference ($R = 0.17$; table 2), which corresponds well with similar differences for dicotyledons

Table 2. Weed seedbank densities (numbers m^{-2} in top 15 cm), plant densities (numbers m^{-2}) and biomasses ($g\ m^{-2}$) per half-field in relation to crop, sampling occasion and treatment.
(Values are geometric means for GMHT and conventional (C) treatments. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. (NB: figures for dicotyledons and monocotyledons in tables 4 and 5 do not sum to the figures in this table because of the use of geometric means). CI, confidence interval.)

sampling occasion, year	*n*	C	GMHT	*R* (95% CI)	*p*-value
beet					
seedbank, *t*	64	1996.1	1779.3	0.89 (0.76–1.05)	0.15
seedling, *t*	64	41.6	58.6	1.41 (1.13–1.76)	0.007**
pre-GM herbicide, *t*	54	25.2	119.5	4.72 (3.27–6.8)	< 0.001***
post-herbicide, *t*	62	32.0	34.8	1.09 (0.85–1.39)	0.51
final, *t*	63	33.0	25.3	0.77 (0.62–0.95)	0.021*
biomass, *t*	62	23.2	3.8	0.17 (0.11–0.26)	< 0.001***
seed rain, *t*	65	620.8	187.6	0.31 (0.19–0.51)	< 0.001***
seedbank, *t* + 1	48	2061.0	1651.9	0.80 (0.67–0.96)	0.015*
follow-up, *t* + 1	48	35.2	30.1	0.86 (0.67–1.1)	0.23
seedbank, *t* + 2	24	1937.0	1601.5	0.83 (0.62–1.1)	0.18
follow-up, *t* + 2	22	32.7	31.6	0.97 (0.68–1.37)	0.85
maize					
seedbank, *t*	57	2266.3	2518.7	1.11 (0.97–1.28)	0.14
seedling, *t*	58	39.0	88.3	2.26 (1.54–3.31)	< 0.001***
post-herbicide, *t*	52	14.4	42.4	2.93 (1.86–4.62)	< 0.001***
final, *t*	45	15.7	48.9	3.08 (2.21–4.29)	< 0.001***
biomass, *t*	40	10.1	18.3	1.82 (0.99–3.33)	0.044*
seed rain, *t*	54	403.9	758.4	1.87 (0.93–3.75)	0.088
seedbank, *t* + 1	25	2805.6	3010.2	1.07 (0.82–1.4)	0.61
follow-up, *t* + 1	15	49.2	39.5	0.80 (0.47–1.38)	0.47
seedbank, *t* + 2	9	1910.6	2038.5	1.07 (0.63–1.79)	0.80
follow-up, *t* + 2	7	6.5	17.3	2.63 (0.13–52.76)	0.81
spring oilseed rape					
seedbank, *t*	65	2065.2	2050.0	0.99 (0.77–1.28)	0.97
seedling, *t*	66	29.4	50.1	1.70 (1.22–2.37)	0.003**
post-herbicide, *t*	62	46.8	32.6	0.70 (0.53–0.91)	0.006**
final, *t*	63	74.9	61.3	0.82 (0.65–1.03)	0.092
biomass, *t*	62	40.8	14.1	0.35 (0.24–0.5)	< 0.001***
seed rain, *t*	65	3023.1	625.9	0.21 (0.13–0.33)	< 0.001***
seedbank, *t* + 1	40	3242.1	2412.3	0.75 (0.59–0.95)	0.018
follow-up, *t* + 1	38	31.3	23.3	0.75 (0.55–1.01)	0.049*
seedbank, *t* + 2	12	2622.7	2113.0	0.81 (0.47–1.39)	0.44
follow-up, *t* + 2	9	40.4	34.7	0.86 (0.41–1.79)	0.57

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

($R = 0.16$; table 4) and monocotyledons ($R = 0.11$; table 5). In maize, the effect was in the opposite direction. For this crop there were significantly more plants in the GMHT treatment ($R = 3.08$; table 2) and this difference was especially marked for reproductive dicotyledons ($R = 4.25$; table 6). The difference for reproductive monocotyledons, although in the same direction ($R = 2.08$), was not significant; neither was that for monocotyledon biomass ($R = 1.58$; table 5). The effect for dicotyledon biomass was relatively large and significant ($R = 3.02$; $p = 0.007$; table 4). In spring oilseed rape, there were widely differing effects on dicotyledons ($R = 0.29$ and 0.52 for biomass and reproductive individuals, respectively; tables 4 and 6) and cmonocotyledons ($R = 0.91$ and 0.94 for biomass and reproductive individuals, respectively; tables 5 and 6). The effects for the densities of pre-reproductive plants were either not significant or, for monocotyledons, significantly in the other direction (table 6). The result is that there was no difference in *overall* plant density in spring oilseed rape (table 2), whereas there was a large and highly significant difference in biomass ($R = 0.35$, $p < 0.001$).

Differences in plant biomass and density in beet were not reflected in effects on diversity: treatment differences for all indices were non-significant (table 3). The markedly greater number of species in GMHT maize than in conventional maize ($S = 13.7$ and 9.2, respectively) can be explained by the difference in plant density and was not significant (table 3). However, for biomass, dominance in the conventional treatment was significantly greater than in the GMHT treatment ($D = 0.59$ and 0.42, respectively; $p = 0.019$). There were no large differences in diversity between the treatments in spring oilseed rape. However, dominance for the final count was significantly larger in the GMHT treatment than in the conventional treatment ($D = 0.52$ and 0.43, respectively; $p < 0.01$).

(f) *Seed rain*

In conventional crops seed-rain counts were highest in spring oilseed rape, followed by beet and then maize (table 2). The directions of treatment effects were the same in all cases as those for biomass, seed rain being lower in the GMHT treatments for beet and spring oilseed rape, and higher in the GMHT treatment for maize. Effects for both monocotyledons and dicotyledons were highly significant for beet and spring oilseed rape (tables 4 and 5). In maize, the dicotyledon seed rain was significantly greater than in

Table 3. Diversity of weed vegetation per half-field in relation to crop, sampling occasion and treatment.
(Indices are as follows: *S*, number of species; α, log-series alpha; and *D*, dominance. Treatment effects for *S* are corrected for plant density by using log (number of individuals) as a covariate; treatment effects for *D* are logits; *p*-values for α and *D* are based on randomization tests.)

sampling occasion, year	index	*n*	C	GMHT	treatment effect	s.e. of effect	*p*-value
beet							
seedbank, *t*	*S*	64	13.59	13.19	–0.17	0.41	0.67
	α	64	14.30	14.54	0.24	—	0.83
	D	43	0.52	0.54	0.07	0.11	0.53
seedling, *t*	*S*	64	13.53	16.33	1.45	0.53	0.008**
	α	64	11.50	12.49	1.00	—	0.17
	D	56	0.46	0.41	–0.19	0.12	0.11
pre-GM herbicide, *t*	*S*	54	12.83	20.65	1.95	1.16	0.097
	α	54	11.92	13.06	1.14	—	0.258
	D	41	0.56	0.41	–0.64	0.15	< 0.001***
post-herbicide, *t*	*S*	62	16.50	15.52	0.27	0.53	0.62
	α	62	14.92	15.30	0.38	—	0.71
	D	49	0.43	0.40	–0.16	0.13	0.24
final, *t*	*S*	63	12.75	11.16	–0.75	0.50	0.14
	α	63	16.00	15.84	–0.15	—	0.91
	D	37	0.39	0.40	0.06	0.14	0.68
biomass, *t*	*D*	61	0.46	0.52	0.36	0.24	0.14
seedbank, *t* + 1	*S*	48	12.94	12.63	0.13	0.55	0.82
	α	48	12.59	12.99	0.40	—	0.69
	D	32	0.44	0.45	0.08	0.12	0.51
maize							
seedbank, *t*	*S*	57	14.19	14.47	–0.00	0.57	0.99
	α	57	14.18	11.86	–2.32	—	0.014*
	D	45	0.48	0.48	–0.07	0.13	0.60
seedling, *t*	*S*	58	14.26	18.76	0.98	0.77	0.21
	α	58	11.81	11.79	–0.02	—	0.98
	D	48	0.46	0.41	–0.23	0.098	0.026*
post-herbicide, *t*	*S*	52	9.71	15.54	3.51	0.73	< 0.001***
	α	52	12.88	14.24	1.36	—	0.32
	D	31	0.60	0.41	–0.78	0.20	0.002**
final, *t*	*S*	45	9.18	13.73	0.94	0.80	0.24
	α	45	14.48	15.33	0.84	—	0.59
	D	20	0.45	0.48	0.11	0.22	0.66
biomass, *t*	*D*	40	0.59	0.42	–0.62	0.25	0.019*
seedbank, *t* + 1	*S*	25	14.28	15.24	0.88	0.93	0.36
	α	25	10.26	11.48	1.21	—	0.087
	D	19	0.50	0.50	–0.13	0.25	0.62
spring oilseed rape							
seedbank, *t*	*S*	64	14.33	14.70	0.20	0.38	0.59
	α	65	14.72	15.53	0.81	—	0.40
	D	44	0.49	0.44	–0.22	0.11	0.046*
seedling, *t*	*S*	65	13.40	14.91	0.35	0.49	0.48
	α	66	11.61	10.71	–0.90	—	0.21
	D	50	0.42	0.44	0.08	0.13	0.51
post-herbicide, *t*	*S*	62	19.13	14.65	–2.54	0.74	0.001***
	α	62	16.96	12.55	–4.42	—	< 0.001***
	D	51	0.38	0.45	0.28	0.12	0.016*
final, *t*	*S*	63	16.32	15.10	–0.62	0.79	0.44
	α	63	15.69	14.35	–1.35	—	0.32
	D	57	0.43	0.52	0.33	0.12	0.009**
biomass, *t*	*D*	62	0.45	0.44	0.19	0.17	0.26
seedbank, *t* + 1	*S*	40	15.57	13.92	–0.63	0.73	0.39
	α	40	12.25	12.63	0.38	—	0.68
	D	37	0.45	0.41	–0.08	0.13	0.56

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

Table 4. Dicotyledon seedbank densities (numbers m^{-2} in top 15 cm), plant densities (numbers m^{-2}) and biomasses ($g\,m^{-2}$) per half-field in relation to crop, sampling occasion and treatment.
(Values are geometric means for GMHT and conventional (C) treatments. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

sampling occasion, year	n	C	GMHT	R (95% CI)	p-value
beet					
seedbank, t	64	926.3	900.1	0.97 (0.82–1.15)	0.76
seedling, t	64	27.5	44.2	1.60 (1.28–2.02)	$< 0.001^{***}$
pre-GM herbicide, t	54	14.8	77.7	5.20 (3.77–7.18)	$< 0.001^{***}$
post-herbicide, t	62	20.6	23.6	1.15 (0.91–1.45)	0.26
final, t	63	20.7	15.1	0.73 (0.6–0.9)	0.006^{**}
biomass, t	62	17.6	2.8	0.16 (0.1–0.26)	$< 0.001^{***}$
seed rain, t	65	507.9	157.8	0.32 (0.19–0.53)	$< 0.001^{***}$
seedbank, $t + 1$	48	1374.9	1045.6	0.76 (0.63–0.93)	0.006^{**}
follow-up, $t + 1$	48	16.7	14.0	0.84 (0.57–1.24)	0.38
seedbank, $t + 2$	24	1084.0	829.6	0.77 (0.56–1.06)	0.10
follow-up, $t + 2$	22	9.6	6.9	0.73 (0.37–1.44)	0.39
maize					
seedbank, $t + 1$	57	1210.8	1337.8	1.10 (0.93–1.31)	0.28
seedling, t	58	24.0	67.5	2.80 (1.75–4.49)	$< 0.001^{***}$
post-herbicide, t	52	6.8	26.7	3.85 (2.32–6.39)	$< 0.001^{***}$
final, t	45	7.6	27.6	3.52 (2.4–5.15)	$< 0.001^{***}$
biomass, t	40	4.2	12.8	3.02 (1.35–6.78)	0.007^{**}
seed rain, t	54	255.9	598.7	2.32 (1.11–4.86)	0.031^{*}
seedbank, 1	25	1529.3	1684.6	1.10 (0.8–1.51)	0.53
follow-up, $t + 1$	15	24.8	19.8	0.80 (0.46–1.4)	0.42
seedbank, $t + 2$	9	1237.6	1082.0	0.88 (0.46–1.66)	0.66
follow-up, $t + 2$	6	6.5	22.0	3.33 (0.09–126.09)	0.73
spring oilseed rape					
seedbank, t	65	1096.1	1084.8	0.99 (0.79–1.24)	0.93
seedling, t	65	20.9	33.8	1.61 (1.15–2.25)	0.01^{**}
post-herbicide, t	62	33.9	19.7	0.58 (0.44–0.78)	$< 0.001^{***}$
final, t	63	48.4	30.8	0.64 (0.5–0.82)	0.002^{**}
biomass, t	62	30.0	8.5	0.29 (0.19–0.42)	$< 0.001^{***}$
seed rain, t	65	2241.0	459.1	0.21 (0.13–0.34)	$< 0.001^{***}$
seedbank, $t + 1$	40	2339.8	1374.2	0.59 (0.44–0.8)	$< 0.001^{***}$
follow-up, $t + 1$	38	12.3	10.0	0.81 (0.51–1.31)	0.41
seedbank, $t + 2$	12	1887.6	1482.5	0.79 (0.48–1.3)	0.35
follow-up, $t + 2$	9	28.0	22.1	0.79 (0.32–1.95)	0.49

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

the GMHT treatment ($R = 2.3$; table 4) but there was no significant difference for monocotyledons ($R = 1.2$; table 5).

(g) *Follow-up seedbank and plant density in following crops*

Seedbank re-sampling showed differences between treatments in the densities of dicotyledon seeds 1 year after ($t + 1$) the initial sowing of beet ($R = 0.76$; table 4) and spring oilseed rape ($R = 0.59$; table 4). It should be noted that, to eliminate any chance of contamination of the food chain, GMHT sugar beet (and some fodder beet) was harvested earlier than the conventional beet. While this did not affect the comparisons of treatments for seed rain (samples were collected simultaneously up until the GMHT harvest date), it could have reduced seed input to the seedbank sampled in the following year. However, we found no significant relationship between $\log R$ and time (days) between harvest dates ($n = 45$; $p = 0.95$). Second-year ($t + 2$) sampling of the seedbank showed comparable magnitudes of effect but these were not significant ($R = 0.77$ and 0.79 for beet and spring oilseed rape, respectively; $p > 0.05$). Similarly, treatment differences for the seedbank of monocotyledons were not significant (table 5). There were no significant effects of treatment on seedbank densities following maize ($t + 1$ or $t + 2$; tables 2, 4 and 5).

Plant density in the following crops averaged 34.8 m^{-2} in the first-year follow-up ($t + 1$). About 88–90% of crops following beet and spring oilseed rape were cereals or other monocotyledonous crops, 5–6% were broadleaved crops and 5–6% of the fields were fallow. By contrast, *ca*. 71% of crops following maize were cereals or other monocotyledonous crops (including 19% repeat maize), 19% were broadleaved crops and 10% were fallow. Treatment differences for plant density in the following crops were mostly not significant. However, the difference for total plant density following spring oilseed rape was narrowly significant ($R = 0.75$; $p = 0.049$; table 2), as was the difference for monocotyledons following beet ($R = 0.69$; $p = 0.03$; table 5).

(h) *Consistency of treatment effects: treatment by covariate interactions*

Out of the 43 significant treatment effects found in tables 2, 4 and 5, none showed a significant

Table 5. Monocotyledon seedbank densities (numbers m^{-2} in top 15 cm), plant densities (numbers m^{-2}) and biomasses ($g\ m^{-2}$) per half-field in relation to crop, sampling occasion and treatment.
(Values are geometric means for GMHT and conventional (C) treatments. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

sampling occasion, year	n	C	GMHT	R (95% CI)	p-value
beet					
seedbank, t	63	672.6	565.7	0.85 (0.68–1.06)	0.13
seedling, t	64	5.4	6.8	1.26 (0.9–1.76)	0.19
pre-GM herbicide, t	54	3.8	18.1	4.66 (2.69–8.08)	$< 0.001^{***}$
post-herbicide, t	62	5.0	4.8	0.96 (0.62–1.48)	0.84
final, t	62	7.0	5.6	0.81 (0.58–1.13)	0.23
biomass, t	62	1.8	0.2	0.11 (0.06–0.22)	$< 0.001^{***}$
seed rain, t	53	77.4	15.6	0.24 (0.14–0.41)	$< 0.001^{***}$
seedbank, $t + 1$	47	463.0	382.1	0.83 (0.62–1.12)	0.20
follow-up, $t + 1$	47	9.1	6.3	0.69 (0.5–0.96)	0.03^{*}
seedbank, $t + 2$	24	593.6	476.9	0.81 (0.46–1.41)	0.46
follow-up, $t + 2$	22	12.6	12.1	0.95 (0.67–1.36)	0.80
maize					
seedbank, t	57	752.3	871.5	1.16 (0.91–1.47)	0.25
seedling, t	58	6.5	11.8	1.79 (1.26–2.55)	0.002^{**}
post-herbicide, t	51	4.2	10.7	2.48 (1.52–4.05)	$< 0.001^{***}$
final, t	45	4.8	14.6	2.88 (1.97–4.21)	$< 0.001^{***}$
biomass, t	40	1.6	2.5	1.58 (0.74–3.35)	0.22
seed rain, t	42	65.0	77.4	1.18 (0.58–2.39)	0.63
seedbank, $t + 1$	25	748.4	983.1	1.31 (0.82–2.08)	0.25
follow-up, $t + 1$	15	10.0	11.2	1.12 (0.6–2.09)	0.71
seedbank, $t + 2$	9	428.6	746.0	1.71 (0.88–3.34)	0.14
follow-up, $t + 2$	7	1.6	3.7	2.16 (0.26–18.21)	0.66
spring oilseed rape					
seedbank, t	64	621.0	696.5	1.12 (0.81–1.54)	0.50
seedling, t	66	4.5	9.7	2.13 (1.5–3.03)	$< 0.001^{***}$
post-herbicide, t	62	6.1	8.0	1.30 (0.9–1.89)	0.15
final, t	63	12.8	20.1	1.56 (1.13–2.14)	0.01^{**}
biomass, t	62	3.4	3.1	0.91 (0.55–1.53)	0.76
seed rain, t	60	197.5	70.4	0.37 (0.22–0.61)	0.002^{**}
seedbank, $t + 1$	40	455.4	524.3	1.15 (0.9–1.45)	0.23
follow-up, $t + 1$	37	9.3	9.1	0.98 (0.68–1.42)	0.92
seedbank, $t + 2$	11	449.2	505.4	1.12 (0.37–3.38)	0.83
follow-up, $t + 2$	9	3.3	4.6	1.40 (0.36–5.42)	0.73

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

treatment × year interaction. There were 10 significant distance × treatment interactions, and, in most of these cases, the treatment effect was significant at all distances from the margin but increased in magnitude with increasing distance into the field. No interaction between treatment and beet crop type (sugar or fodder) was found. Treatment effects were found to differ between environmental zones in two out of 48 analyses. There was only one significant interaction between treatment and initial seedbank density.

4. DISCUSSION

(a) *Detection of treatment differences*

The experiment proved capable of detecting significant effects of treatment for many variables. For comparisons where more than 50 fields had been sampled, treatment differences greater than a factor of 1.5 were, in the main, significant, whereas smaller differences were not significant. Total seed rain in maize, with a multiplicative treatment ratio of 1.87, was an exception in being non-significant.

The lack of significant differences in treatment effects between fodder and sugar beet suggests that the management of these crops was sufficiently similar for them to be treated as one crop for analysis. Similarly, the lack of significant interactions between initial weed density and treatment suggests that farmers did not manage weedy fields differently from clean ones, with the exception of the use of post-emergence herbicide in beet (cf. Champion *et al.* 2003). At a larger scale, the consistency of treatment effects across years, sites and environmental regions implies that the results are representative of what would be found in the wider population of sites across the UK.

(b) *Initial conditions*

The randomization of treatments should mean that the initial conditions were not significantly different. The one significant difference ($p = 0.014$), for log-series α in maize, could easily have arisen by chance given that 18 comparisons were made for the seedbank. Initial seedbank densities varied by two orders of magnitude from *ca.* 300 seeds m^{-2} to *ca.* 25 000 seeds m^{-2}. The highest

Table 6. Plant densities (individuals m^{-2}) per half-field at the final count in each of three development classes, in relation to crop and treatment.
(Values are geometric means for GMHT and conventional (C) treatments. Multiplicative treatment ratio, $R = 10^d$, where d is the mean of the differences between GMHT and C treatments on the logarithmic scale; confidence limits for R are back-transformed from those for d. CI, confidence interval.)

plant type, development class	n	C	GMHT	R (95% CI)	p-value
beet					
dicotyledon, less than four leaves	38	3.8	3.9	1.01 (0.72–1.42)	0.94
dicotyledon, greater than four leaves	39	8.5	9.3	1.09 (0.84–1.42)	0.51
dicotyledon, reproductive	39	7.6	3.4	0.47 (0.33–0.68)	$< 0.001^{***}$
monocotyledon, less than four leaves	31	2.0	3.3	1.58 (1.02–2.44)	0.042^{*}
monocotyledon, greater than four leaves	36	4.7	4.7	1.01 (0.65–1.59)	0.96
monocotyledon, reproductive	30	3.1	1.0	0.38 (0.22–0.67)	0.003^{**}
maize					
dicotyledon, less than four leaves	36	2.1	4.5	1.96 (1.25–3.07)	0.01^{**}
dicotyledon, greater than four leaves	36	3.2	10.9	3.18 (2.19–4.62)	$< 0.001^{***}$
dicotyledon, reproductive	35	1.2	6.2	4.25 (2.6–6.95)	$< 0.001^{***}$
monocotyledon, less than four leaves	29	1.2	1.9	1.44 (0.85–2.42)	0.19
monocotyledon, greater than four leaves	36	2.0	7.0	3.21 (1.99–5.17)	$< 0.001^{***}$
monocotyledon, reproductive	26	1.5	3.5	2.08 (0.93–4.69)	0.072
spring oilseed rape					
dicotyledon, less than four leaves	49	5.2	4.2	0.83 (0.52–1.32)	0.40
dicotyledon, greater than four leaves	53	12.7	14.8	1.16 (0.94–1.44)	0.161
dicotyledon, reproductive	52	18.8	9.7	0.52 (0.36–0.77)	$< 0.001^{***}$
monocotyledon, less than four leaves	41	1.5	4.0	2.44 (1.47–4.05)	0.004^{**}
monocotyledon, greater than four leaves	53	7.2	12.9	1.75 (1.2–2.54)	0.009^{**}
monocotyledon, reproductive	47	3.4	3.2	0.94 (0.56–1.58)	0.79

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

densities are quite large by historical standards (Robinson & Sutherland 2002) and show that very weedy soils are still to be found in the farmed countryside.

(c) *Plant density and biomass*

As treatment effects differed so markedly between crops, most of the results are discussed separately for each crop. Early in the season, plant density in beet was higher under GMHT management, and the treatment ratio increased until glyphosate was applied. This was partly the result of continued germination of seedlings, which under the GMHT treatment doubled in density from 59 plants m^{-2} at the first count to 120 plants m^{-2} at the second count, which followed herbicide application to the conventional crop. At the next count, following glyphosate application to the GMHT crop, plant density was roughly equal in the two halves, but by the end of the season it was significantly lower in the GMHT treatment.

The effects on total biomass were more extreme than for plant density. Herbicide applications resulted in a six-fold greater biomass under conventional management. If we assume that the mass of pre-reproductive plants was negligible, the mean mass of individual reproductive plants was 2.2 g in conventional beet, compared with 0.9 g in GMHT beet. Thus, surviving plants were smaller and less numerous in the GMHT treatment. It appears that the later herbicide application in the GMHT treatment killed the largest weeds. Since glyphosate acts mainly through contact with foliage, larger plants with greater leaf areas are more likely to come into contact with the spray, while smaller weeds can be sheltered by the crop or by larger weeds. The subsequent death of smaller plants overshadowed by beet would explain why weed density was even lower at the final count than after spraying. It seems likely that, if weeds in the GMHT treatment had been treated with glyphosate earlier in the season, plant density, overall biomass and mean size would have been further reduced. This pattern of reduced plant size agrees well with that found by Strandberg & Pedersen (2002) for glyphosate-tolerant fodder beet in Denmark.

The ratio of dicotyledons to monocotyledons was similar for the two treatments over the season. If we calculate the cross-ratio $R_c = R_{\text{dicotyledon}}/R_{\text{monocotyledon}}$, which measures the relative size of the treatment effects for dicotyledons and monocotyledons, we can see that values of R_c were generally in the range 0.9–1.3 (figure 2). However, R_c was 1.4 for the biomass sample, suggesting that monocotyledons were more susceptible to glyphosate than were dicotyledons. Strandberg & Pedersen (2002) also noted that grasses were particularly susceptible to this herbicide.

Plant densities in maize were two to three times higher under GMHT than under conventional management throughout the season. There was a moderate differential effect between dicotyledons and monocotyledons, with dicotyledons showing a threefold difference in biomass, whereas the difference for monocotyledons was half this (figure 2) and not significant. There was no reversal of the effect, and, at the final count, reproductive plants were about 3.6 times as dense under GMHT as under conventional management.

The effect on biomass was smaller, the ratio being 1.8. Under the same assumptions as for beet, the mean mass of individual reproductive plants was 3.7 g in conventional maize, compared with 1.9 g in GMHT maize. Weed biomass in conventional maize was notably low, 10.1 g m^{-2}, being about half of that in conventional beet and a quarter

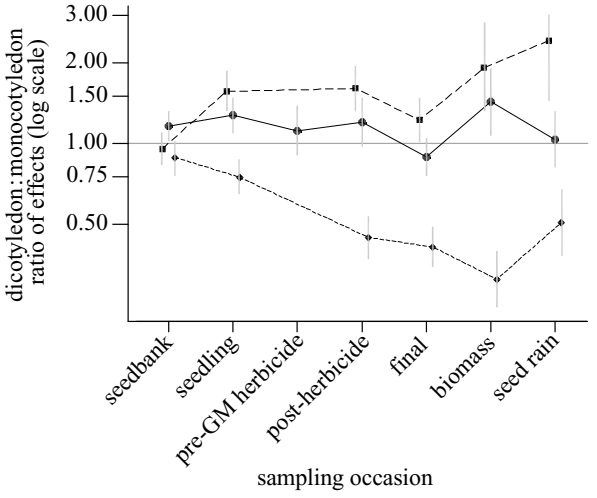


Figure 2. Ratio ($R_{\text{dicotyledon}}/R_{\text{monocotyledon}}$) of multiplicative treatment effects for three crops on weeds in the initial seedbank and during the growing season. Solid line, beet; dashed line, maize; dotted line, spring oilseed rape. Error bars are ± 1 s.e.

of that in conventional spring oilseed rape. The widespread use of herbicides such as atrazine (used in *ca.* 75% of our fields), which persists much longer in the soil than either glyphosate and glufosinate-ammonium (Champion *et al.* 2003), and competition from the maize crop, which invariably overtops all weeds from July onwards, must be major factors contributing to this effect. Kleijn & Verbeek (2000) noted that marginal vegetation beside maize is often poor, and the same applies to vegetation in the crop.

For spring oilseed rape, total plant densities and biomass showed a broadly similar pattern to that found in beet, with a switch from higher densities of plants under GMHT management at the seedling count to lower densities of plants after glufosinate-ammonium had been applied. The biomasses of weeds in conventional half-fields were about three times as large as those on GMHT halves. There was, however, a clear differential effect between monocotyledons and dicotyledons (figure 2), with the biomass of dicotyledons being lower on the GMHT half by a factor of 3.5, whereas monocotyledons were not significantly affected. Under the same assumptions as for beet, the mean mass of reproductive plants was 1.8 g in conventional spring oilseed rape, compared with 1.1 g in GMHT spring oilseed rape.

The reduction in the biomass of weeds under GMHT treatments in beet and spring oilseed rape and its increase in GMHT maize must to some extent alter the resources available to higher trophic levels when compared to conventional treatments. The mortality of larger plants after herbicide application in GMHT beet and spring oilseed rape obviously increased the resources for detritivores mid-season while at the same time reducing food for herbivores. The impacts of these differences are explored in more detail for invertebrates by Hawes *et al.* (2003).

(d) *Seed rain and its effect on the seedbank in following years*

The largest effect for seed rain was the fivefold difference for weeds in spring oilseed rape. A substantial proportion of seed rain was incorporated in the seedbank (Heard *et al.* 2003), and this was sufficient to result in significant treatment differences in the following year, both for the seedbank and for emerged plants. At the time of writing, information on densities in follow-up year 2 is insufficient to draw many conclusions. (Observations to be made during 2003 should correct this.) As would be expected, the follow-on effect for dicotyledons in the seedbank was particularly large ($R = 0.59$), and it is therefore surprising that the effect for emerged dicotyledons was not significant ($R = 0.81$). However, the confidence intervals for these measures do include small values of R.

There was a threefold difference for seed rain in beet, but the overall magnitude of the rain was much smaller, *ca.* 600 seeds m^{-2} in conventional beet, as opposed to *ca.* 3000 seeds m^{-2} in conventional spring oilseed rape. In maize, the total seed rain in the GMHT treatment was *ca.* 800 seeds m^{-2}. The dicotyledon seed rain was more than twice as high in the GMHT treatment as in the conventional treatment. There was, however, no significant difference in any observation made in the next year.

The large drops in seed rain in beet and spring oilseed rape were a direct result of the elimination of larger individuals by the later herbicide sprays. Although many weed species have relatively high growth rates, these were not sufficient to compensate for this loss. These effects are explored at the species level in the companion paper (Heard *et al.* 2003).

The persistence of treatment effects from the seed rain in the soil seedbank in the following year ($t + 1$) shows that the effect of 1 year's seed rain is not negligible. Clearly there was no very sharp decline in the seedbank. Even following crops, such as GMHT beet, in which there was a low seed return, the decline in the seedbank was not large (7%). These declines were certainly smaller than the annual 50% that can be found when land is fallowed. The observed germination rates of 1.4–3.5% were too small to produce a measurable decline. If actual rates are comparable to the 20% hypothesized by Watkinson *et al.* (2000) for *Chenopodium album*, then other causes of loss must be important. Whatever they are, in the longer term a continued reduction in seed return would lead to a change in the age structure of seeds in the soil and possibly to a weakening of the buffer effect (this is discussed further by Heard *et al.* 2003).

(e) *Effects on diversity and dominance*

The indices of diversity used here (table 3) measure different aspects of diversity. Species number, S, and dominance, D, were calculated as mean values for half-fields (D being back-transformed from a logit). Log-series α was calculated by first summing the data over all half-fields and then comparing the numbers of individuals and the numbers of species.

Treatment effects on diversity were transient and mostly rather small. In beet there were notably fewer species in the conventional than in the GMHT half-fields, both at the first count (13.5 and 16.3 species) and in the pre-GM herbicide count (12.8 and 20.7 species). However, after correction for differing numbers of individuals, the second difference was non-significant, because of the very large difference in plant density ($R = 4.7$). After weed control by glyphosate in the GMHT crop, no further differences in diversity were apparent. The most likely explanation of

the temporary effect is a selective early-season response to pre-emergence herbicides, which were used almost exclusively on conventional crops and that may have ceased to be effective after the first few weeks.

In maize, the most significant effects were also transient, with both S and D indicating higher diversity in the GMHT treatment at the post-herbicide count. The value of D in the conventional treatment at this time was 0.60, an exceptionally high value resulting from the dominance of the grass *P. annua*. At the final count, monocotyledons were no longer dominant in the conventional treatment because many dicotyledons germinated towards the end of the season (table 6). Nevertheless, monocotyledons remained more numerous than dicotyledons among reproductive individuals in the conventional treatment (table 6), resulting in a significant treatment effect for dominance, D, in biomass (table 3).

Apart from the significant difference in α for the seedbank in maize (which must surely be the result of chance, given the randomization of treatments), the only other significant effect on α was in the post-herbicide count in spring oilseed rape. The direction of the effect (higher diversity in the conventional treatment) is the same as that indicated by total species number, which reached its second highest value, 19.1 species per half-field, for this treatment and occasion. The difference did not persist to the final count, by which time the population consisted mainly of new recruits (table 6). A high proportion of these recruits in the GMHT treatment were monocotyledons, mainly the grass *P. annua*, which achieved sufficient numerical dominance to produce a significant difference in D, even though the differences in S and α had by then disappeared. The new recruits were small individuals, so that the difference in D for counts did not translate into a difference in D for biomass. Thus the relatively high diversity of weeds in the conventional treatment was a temporary phenomenon, which was later swamped by new recruitment.

For all crops, the major difference between the treatments was the use of selective herbicides on conventional crops and broad-spectrum herbicides on GMHT crops. In principle, selective herbicides should be particularly effective against dicotyledons in a monocotyledonous crop and against monocotyledons in a dicotyledonous crop, whereas broad-spectrum herbicides should be more equal in their effect. The disproportionate losses of dicotyledons when a broad-spectrum herbicide was applied to spring oilseed rape and of monocotyledons when it was applied to maize (figure 2) are exactly what would be expected. The interesting exception is beet. After treatment with glyphosate, there were large differences in density and biomass, but there were no large differences in diversity or in the relative survival of dicotyledons and monocotyledons. It appears therefore that, in this system, diversity was stable in the short term.

There could, however, be cumulative effects over a longer time-scale. There is an obvious cumulative effect expected from the poor reproductive success of all weeds in GMHT beet. If beet is the single dicotyledonous crop in a mainly cereal rotation, then dicotyledonous weeds will selectively be lost from the seedbank. Grasses will be able to reproduce effectively in cereals but many dicotyledons will not. Thus the long-term tendency for the numbers of dicotyledonous weeds to decrease in relation to grass weeds will be reinforced. If this decrease continues to the point where grass weeds predominate even in beet crops, then diversity—though not necessarily whole-field species richness—will certainly be lower.

In the USA, where GMHT crops were introduced in 1996, it has been shown that plant diversity can be systematically affected by GMHT cropping. Across a large latitudinal gradient Petersen *et al.* (2002) showed that, in glyphosate-resistant crops where pre-emergence herbicides were used in addition to glyphosate, weed diversity measured by Shannon's H was lower than in conventional systems. However, in glyphosate-resistant crops receiving only a single post-emergence application of herbicide, weed diversity actually increased because of suppression of the dominant species.

Finally, herbicide-resistant strains of weeds will without doubt become more numerous. No broad-spectrum herbicide is both unselective and completely effective. Invariably, some species are more susceptible than others, so that full killing of all weeds is rarely achieved by a single application (Cousens & Mortimer 1995; Buckmann *et al.* 2000). Furthermore, no broad-spectrum herbicide is so effective that weeds cannot evolve resistance. There are admittedly still rather few weeds resistant to glyphosate, most confirmed reports being of grasses in the genera *Lolium* and *Eleusine*. However, a resistant strain of *Conyza canadensis* (Asteraceae) is spreading rapidly in the USA (VanGessel 2001), and there are anecdotal reports of resistance in *Amaranthus* and *Chenopodium*. It is only a matter of time before resistant plants become widespread. Then diversity is likely to drop, as evolved herbicide tolerance increases the dominance of a few species.

(f) *Longer-term effects*

The key to what will happen in the longer term is the seed rain and its contribution to the seedbank. For example, GMHT maize may not have a very different effect from conventional maize. In both, the dicotyledonous seed rain is low compared with that under conventional spring oilseed rape. Therefore dicotyledons may decrease in the seedbank after a maize crop, whichever maize variety is grown. This would make the longer-term effect of growing maize analogous to that of growing a cereal crop, which for the dicotyledonous *C. album* results in a slow decrease in the seedbank of about 20% per year (Watkinson *et al.* 2000). We do not at present know how frequently a seedbank needs to be replenished in order to sustain a viable population. (Data to be collected during 2003 should help to answer this question.) Replenishment may not need to be very frequent. For the long-term survival of some, perhaps many, species a conventional dicotyledonous crop grown once every 10 years may be sufficient.

In beet and spring oilseed rape, the reduced seed rains in the GMHT treatments had demonstrable effects on the seedbanks in the following year. In the short term, any resulting decline was buffered by the relatively large size of the existing seedbank compared with the new contribution. Thus the loss of 1 year's seed return was not sufficient in itself to produce a large difference in future weed populations. However, relatively small differences could eventually sum to produce a large effect if they were sustained over several crop rotations, say for 10 or more

years. For these crops, just as for maize, calculations taking account of at least one whole rotation are required.

Over this relatively long time-scale there will be further changes. For the FSEs we have used current or (for GMHT crops) currently predicted systems of crop management. An important factor for the future is farmers' attitudes to weeds. Growers may learn to tolerate higher weed densities early in the season, provided that the weeds do not cause economic loss. But there are obvious limits to what is acceptable. High weed densities seriously depress crop yields.

Changes in the timing of herbicide applications are to be expected in the future. This has already happened in the USA, where uptake of GMHT crops was driven by the perceived profitability of cropping. Farmers adjusted the timing to maximize profit. In recent years, glyphosate has been applied earlier in the season and glufosinate later in the season than when GMHT crops were first introduced (J. Orson, personal communication). Such shifts in timing will inevitably affect the impacts of GMHT management on the arable weeds of Britain.

Changes may also occur as a consequence of government regulations. If the environmental disbenefits of very clean fields are in future judged to be unacceptable in Britain, then additional management practices, such as band spraying (Dewar *et al.* 2003) or leaving unsprayed strips along field margins, could be used to reduce the negative impacts of cleanliness. The possibilities for mitigation are numerous, but are beyond the scope of this paper.

(g) *Conclusions*

In conclusion, we have shown significant and variable impacts of GMHT cropping in beet, maize and spring oilseed rape on the arable flora when compared with current commercial practices. Adoption of GMHT beet and spring oilseed rape crops will lead to more effective weed control and accelerate the decline of the weed seedbank that has been going on since the onset of mechanized agriculture. GMHT maize may have the opposite effect. Further studies that incorporate the impacts of crop rotations will help elucidate the impacts of GMHT technology on future long-term trends.

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GLOSSARY

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