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Weeds in fields with contrasting conventional and genetically modified herbicide-tolerant crops. II. Effects on individual species

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We compared the effects of the management of genetically modified herbicide-tolerant (GMHT) and conventional beet, maize and spring oilseed rape on 12 weed species. We sampled the seedbank before and after cropping. During the season we counted plants and measured seed rain and biomass. Ratios of densities were used to calculate emergence, survival, reproduction and seedbank change. Treatments significantly affected the biomass of six species in beet, eight in maize and five in spring oilseed rape. The effects were generally consistent, with biomass lower in GMHT beet and spring oilseed rape and higher in GMHT maize. With few exceptions, emergence was higher in GMHT crops. Subsequent survival was significantly lowered for eight species in beet and six in spring oilseed rape in the GMHT treatments. It was increased for five species in maize and one in spring oilseed rape. Significant effects on seedbank change were found for four species. However, for many species in beet and spring oilseed rape (19 out of 24 cases), seed densities were lower in the seedbank after GMHT cropping. These differences compounded over time would result in large decreases in population densities of arable weeds. In maize, populations may increase.

Keywords: arable weed; demography; genetically modified herbicide-tolerant crops; Farm Scale Evaluations

1. INTRODUCTION

The FSEs in Britain compared the effects of the management of GMHT crops resistant to broad-spectrum herbicides with those of conventional non-tolerant varieties. Two of the GMHT crops, maize and spring oilseed rape, were resistant to glufosinate-ammonium (Bayer CropScience UK Ltd, Cambridge, UK) and the third, beet, was resistant to glyphosate (Monsanto UK Ltd, London, UK). The potential advantages and disadvantages of these to farming have been discussed more fully elsewhere (Heard *et al.* 2003) but their effects on farmland wildlife were uncertain before the trial began.

One major concern, widely expressed, is that weed control in GMHT crops might be so efficient that the loss of some plant species from the arable landscape could be accelerated (Andreasen *et al.* 1996; Johnson 1999; Buckelew *et al.* 2000; Hails 2000; Watkinson *et al.* 2000; Robinson & Sutherland 2002). Agricultural intensification has led to a general reduction in the density of weed seeds in arable soils (Robinson & Sutherland 2002) and widespread declines in their distributions (Preston *et al.* 2002), and has through time altered the communities of weed plants (Marshall *et al.* 2001). However, although it is true to say that herbicides tend to reduce the abundance of weed species, the influence of herbicides on the structure of weed communities is often compounded by other effects of farming (Hald 1999; Krebs *et al.* 1999; Wilson & King 2000).

There is little experimental evidence to suggest that herbicides alone lead to the elimination of a species at the field scale (Cousens & Mortimer 1995). The response of a species to herbicide application depends on its sensitivity to the compounds used. Relatively few weed species are directly targeted by specific herbicides; indeed, products with wider selectivity and with the potential to affect a wide range of non-target species are increasingly being used (Marshall *et al.* 2001). These products include broad-spectrum herbicides such as glufosinate-ammonium and glyphosate. An important question is whether the introduction of GMHT technology simply represents an increase

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in the level of intensification, like the introduction of a new herbicide, or is a major change in agricultural practice.

Many authors have assumed that weed control with broad-spectrum herbicides and a herbicide-tolerant crop will be even more effective than control by existing techniques (e.g. Royal Society 1998; Tester 2001). Very effective within-season control has been demonstrated experimentally with early herbicide applications in glyphosate-tolerant sugar beet (Dewar *et al.* 2000; Strandberg & Pedersen 2002). The use of glyphosate-resistant and glufosinate-ammonium-resistant oilseed rape crops in Canada has allowed growers to 'clean up' weedy fields (Derksen *et al.* 1999). In general, it appears that GMHT weed control can be comparable to and sometimes even more efficient than conventional control in current agricultural practice. There are, however, some exceptions. Scientists advising growers of GMHT soya beans in the southern USA view the technology as providing not better weed control but more flexibility (Firbank & Forcella 2000).

There are few published data on the long-term effects of growing GMHT crops. Anecdotal information from Minnesota, USA, suggests that, when GMHT crops were first introduced, weed plants were generally well controlled, but control became less effective as relatively tolerant species increased and others escaped by germinating late (Firbank & Forcella 2000). Up to the present, empirical studies that have investigated the behaviour of weed populations have been based on data from a few experimental sites collected over a few years' trials. Ideally, predictive models require broadly based parameter estimates (Freckleton & Watkinson 1998; Forcella 1999; Watkinson *et al.* 2000). The many sites used in the FSEs, which cover all the main agricultural areas in Britain, may provide parameter estimates for predicting the impacts of GMHT technology on weed dynamics across a wide geographical range.

In the accompanying paper (Heard *et al.* 2003) we considered the impacts of contrasting GMHT and conventional crop managements on the overall densities of groups of weeds in three spring-sown break crops, *Beta vulgaris* L. ssp. *vulgaris* (beet), *Zea mays* L. (maize) and *Brassica napus* L. ssp. *oleifera* (DC.) Metzger (spring oilseed rape), over 3 years. At the end of the season there was a reduction in the biomasses of weeds in GMHT beet and spring oilseed rape but an increase in maize (Heard *et al.* 2003).

Here, we disaggregate the weeds and consider individual species rather than the two broad groups, dicotyledons and monocotyledons. Specifically, we consider the effects of differential herbicide management on the populations of 12 common weed species. We examine the extent to which changes in herbicide management affected the growth and abundance of these species and the transitions between stages in their life cycles. Our aim is to focus on the sensitivity, magnitude and direction of treatment effects rather than provide a detailed estimation of demographic parameters. We emphasize the potential impacts of the treatments on longer-term dynamics through changes in recruitment, seed production and seedbank composition.

2. METHODS

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

The experimental design and statistical justification for the number of sites used in the trials have been presented in detail elsewhere (Perry *et al.* 2003). Surveys were done in 66 beet, 59 maize and 67 spring oilseed rape fields. Nine sites were planted with maize in two or more consecutive seasons; results from these sites are not considered in this paper. Treatments were arranged in a randomized block experimental design, in which the blocks were individual fields. The fields were split into halves, with differing treatments applied to each half. The treatments (GMHT or conventional cropping) were allocated at random. The experiment ran for 3 years, from 2000 to 2002, with roughly a third of the total fields per crop sown in each year.

Farmers were asked to undertake 'cost effective' weed control in the conventional treatments, as they would for a normal crop. Weed control in the GMHT treatments followed advice provided by simulated manufacturer's labels and Supply Chain Initiative for Modified Agricultural Crops advisers where necessary. The management of all fields and treatments was subsequently audited by qualified agronomists, who deemed 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 (Heard *et al.* 2003). Sampling points were located at 2, 4, 8, 16 and 32 m from the field margin.

(b) *Weed species*

Twelve species were selected for detailed study (table 1). These are among the most frequent and abundant weeds found across the FSEs and elsewhere in British agriculture (Roberts & Chancellor 1986; Marshall *et al.* 2001) and therefore play a major role in arable ecosystems. Many of these species and genera are important in the diet of farmland birds (Wilson *et al.* 1997, 1999). The selected plants vary widely in form, and their traits are representative of the range found in spring-germinating annual arable weeds.

(c) *Sampling the seedbank*

The seedbank was sampled to compare the effects of treatments on changes in the seed densities of the 12 species across the sites after the application of treatments. Soil was collected before crops were sown at the start of the experiment by using a spade or auger (year t). Samples, *ca.* 1.5 kg of soil taken to a depth of 15 cm, were taken from four out of the 12 transects, at 2 m and 32 m along each transect. In two subsequent years ($t + 1$, $t + 2$) soil was collected at the same locations and at roughly the same time of year as the initial samples. About 1.2 l of each sample was passed through a sieve with 10 mm mesh size, weighed and placed in a plastic tray to a depth of 40 mm. The trays were arranged in an unheated glasshouse on benches fitted with capillary matting (kept moist). Emerged seedlings were removed and identified over an 18 week period.

(d) *Counts of individual plants*

On each sampling occasion counts of individuals of the species were taken. A 'first seedling' count was made after sowing (year t) and where possible before the first conventional post-emergence herbicide was applied. A 'final' count was made at the time of biomass sampling before harvest after all treatments

Table 1. Species for which abundance and seasonal dynamics were analysed separately.
(*Sonchus* spp. includes *Sonchus asper* (L.) Hill and *Sonchus oleraceus* L. Seedbank longevity categories are from Thompson *et al.* (1997): 2, persisting more than 1 year but less than 5 years; 3, persisting for at least 5 years. Germination periods are from Williams & Morrison (1987) and Grime *et al.* (1988). Heights are typical maximum heights based on personal observations.)

species	seedbank longevity	germination period	height (m)
Capsella bursa-pastoris (L.) Medik.	2	all year	0.4
Chenopodium album L.	3	spring (some in autumn)	1.0
Fallopia convolvulus (L.) Á. Löve	3	spring	1.0
Lamium purpureum L.	3	all year	0.3
Persicaria maculosa Gray	3	spring	0.8
Poa annua L.	2	all year	0.2
Polygonum aviculare L.	3	spring–late summer	0.3
Senecio vulgaris L.	2	all year	0.4
Sonchus spp.	2	spring (some in autumn)	1.5
Stellaria media (L.) Vill.	2	all year	0.3
Veronica persica Poir.	3	spring	0.3
Viola arvensis Murray	3	all year	0.3

had been applied. In the subsequent year ($t + 1$) a 'follow-up' census was made during May–June at the same locations as previous counts. In 2000, the first year of the trial, only total counts were made on each sampling occasion. In 2001 and 2002, plants were recorded in 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. Counts were made in a $0.25\,\mathrm{m} \times 0.5\,\mathrm{m}$ quadrat, but, exceptionally, when the density of a species was more than 100 plants per quadrat (equivalent to 800 plants m^{-2}), counts were made in a half or quarter of the quadrat selected at random.

(e) *Seed rain*

Seed rain was measured by using a unit-area method, with seed traps placed at the soil surface to estimate the amount of seed actually returned to the soil (Heard *et al.* 2003). The traps, 0.1 m in diameter, were sunk into four holes near to the edge of each biomass quadrat, at 2 m and 32 m from the edge of the field on transects 2, 4, 8 and 11 in each half of the field. Trapping began as soon as anthesis was observed in any of the weed species present in the field. It continued until at least harvest of the crop and where possible after harvest (except for beet, which is harvested by tilling the soil). After setting the traps, seeds were collected at approximately two-week intervals throughout the sampling season. Seeds from all four traps at each transect location were pooled during collection and stored together in cool dark dry conditions. All seeds were identified to species, and classified as 'viable' or 'non-viable' on the basis of their resistance to crushing when squeezed with a pair of fine forceps (Forcella *et al.* 1996).

(f) *Biomass of weeds*

Biomass production was sampled in the month before harvest, normally before senescence of the weed plants. Biomass was measured at 2 m and 32 m from the field edge along each transect by 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 at 80 °C for 24 h and weighed.

3. STATISTICAL ANALYSIS

(a) *Biomasses of individual species*

Our first objective was to compare the impacts of the treatments on the biomasses of individual species at the end of the season. Whereas a simple analysis of treatment ratios was possible for the total biomass of species aggregates (Heard *et al.* 2003), this method had to be adjusted for the analysis of individual species. The reason was that, when the data were disaggregated to species, there were many zero values (figure 1). Zeros were caused not only by absences of a species from whole fields, but also in many cases by a species being absent in one treatment but not the other. With so many unpaired zero values, a simple ratio analysis was not advisable. For a given species, let

N_{00} = number of fields from which species was absent;
N_{01} = number of fields with species only on GMHT half;
N_{10} = number of fields with species only on conventional half;
N_{11} = number of fields with species on both halves;
$N_{++} = N_{00} + N_{01} + N_{10} + N_{11}$.

N_{++} is the total number of fields from which data were available for analysis, including those with absences.

Three methods of analysis, A1, A2 and A3 (table 2), were used to present individual species biomasses. In many cases a species had high biomass in a few fields and small or very small biomasses in the remainder. As an extreme example, *Sonchus* spp. were abundant at only one site in GMHT beet. This meant that geometric mean values calculated by analysis A2 were often very much lower than the arithmetic means. Our approach was to use arithmetic means (A1) as descriptive statistics, not tested for significance, whereas A2 and A3 were both used for significance testing. For A2, the test statistic was, as in Heard *et al.* (2003), d, the mean of the differences between the GMHT and conventional treatments on the logarithmic scale. Specifically, let w_{ij} be the mass in grams of the species collected from field j under treatment i, and let $m_{ij} = \log(w_{ij})$. A standard randomized block analysis of variance was done on these transformed values, using the N_{11} fields in which the species was present in both halves

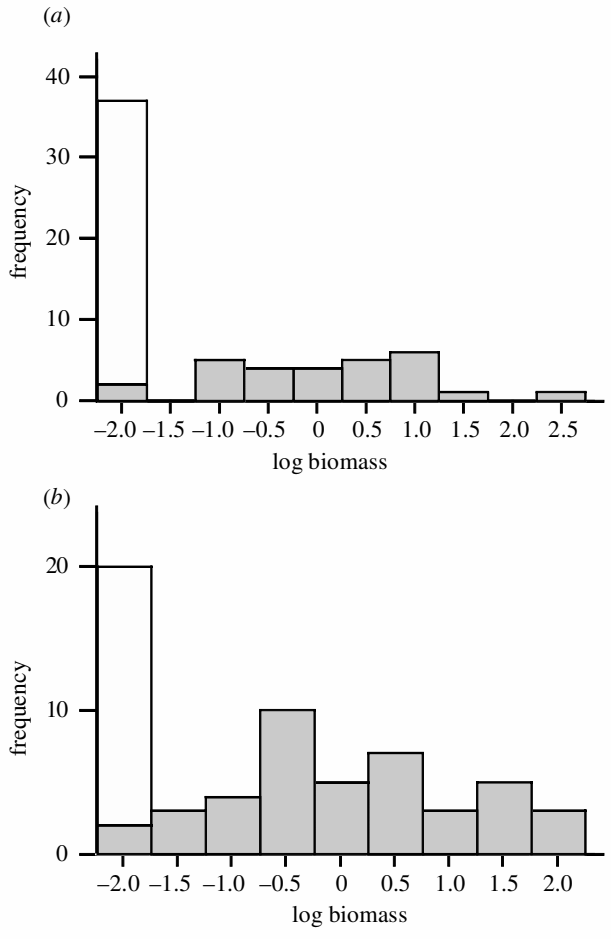

Figure 1. Frequency distributions (number of sites) of *Capsella bursa-pastoris* biomass (grams per 24 m^2) in (*a*) conventional and (*b*) GMHT treatments in beet, showing the frequency of zero values (unshaded boxes) and frequencies in categories of log-transformed biomass (shaded boxes).

as blocks. The null hypothesis was tested with a paired randomization test by using the test statistic $d = \Sigma_j[m_{2j} - m_{1j}]/N_{11}$. Confidence limits about the treatment ratio, $R\ (= 10^d)$, were obtained by back-transformation of the confidence interval of d on the logarithmic scale, derived from the standard error of d and $t_{0.05}$. Analysis A3 used the McNemar test (Sokal & Rohlf 1981) for a difference in matched proportions, with test statistic $(N_{01} - N_{10})^2/(N_{01} + N_{10})$ (table 2) and an exact binomial test. The values from A1 allow potential extrapolation to impacts on abundance in wider populations whereas A2 allows the magnitude of treatment effects to be estimated on an average-field basis.

(b) *Changes in demographic-transition rates*

Our aim was to test for impacts of the treatments on transitions between stages in the life cycle of each species (cf. key-factor analysis; Begon *et al.* 1986). The emergence rate, g, of a species was calculated as the ratio of the number of seedlings emerging to the density of its seeds in the seedbank. The survival rate, s, was calculated as the ratio of the number of reproductive individuals recorded before harvest to the number of seedlings that emerged. The reproductive rate, f, was calculated as the ratio of seeds returned to the soil surface (captured in seed traps) to the number of reproductive individuals counted before harvest. The seedbank-change ratio, b, was calculated by dividing the density of seeds in the seedbank at time $t + 1$, by density at time t. Late-germinating cohorts of seedlings were excluded, under the assumption that only plants established early in the season contributed to final seed production.

Transition rates were calculated by using ratios of total counts across sites. This avoided averaging unreliable ratios resulting from low counts at individual sites in each stage. Note that sites with zero counts in both stages did not contribute to the totals. Log transition rates from one sampling occasion, t, to the next, $t + 1$, were then calculated for each species as the difference $k_i(t) = \log [c_i(t + 1)/c_i(t)]$, where $c_i(t)$ is the total count for the ith treatment at time t, provided that the total exceeded zero. The treatment difference on a logarithmic scale was estimated by using $h(t) = k_2(t) - k_1(t)$. The standard error, s.e.$[h(t)]$, was calculated by using the formula for the approximate variance of the ratio estimate (Cochran 1977). The t-ratio, $t = h/\text{s.e.}[h]$, was then used to test the null hypothesis of no treatment difference. The treatment effect was estimated as the multiplicative ratio (GMHT/conventional) of transition rates $R = 10^h$. Confidence limits about R were obtained by back-transformation of the limits about h, derived from the standard error of h.

It might be thought that the multiplicity of hypothesis tests reported in this paper require the use of some Bonferroni adjustment (Brown & Rothery 1993), to adjust the significance level of each. We prefer instead to give estimates of treatment effects together with measures of variability and p-values. Treatment effects are assessed on a case-by-case basis. In reporting the results we refer to treatment differences as significant when $p < 0.05$.

4. RESULTS

(a) *Biomasses of individual species*

(i) *Testing for treatment differences*

Twenty-seven out of 72 tests were statistically significant at the 5% level, seven being significant using only the analysis method A2 and four using only method A3 (table 3). In eight cases, tests using both A2 and A3 proved significant, and in all of these the effect of the treatment was consistent in direction within crops.

In general, crop biomass was low. Across all crops, maximum arithmetic means were 6.3 g m^{-2} and 7.2 g m^{-2} for *Chenopodium album* in conventional beet and GMHT maize, and 10.3 g m^{-2} for *Poa annua* in conventional spring oilseed rape. Six species were significantly affected by the treatments in beet, eight in maize and five in spring oilseed rape. In these cases biomass, or the proportion of sites with biomass, showed a consistent treatment effect: lower in GMHT beet and rape (with the exception of *Capsella bursa-pastoris* in beet) and higher in GMHT maize.

Two species, *Capsella bursa-pastoris* and *Poa annua*, had significant treatment differences in all three crops. Differences were significant for *Chenopodium album* and *Polygonum aviculare* in beet and spring oilseed rape, *Fallopia convolvulus* in beet and maize and *Sonchus* spp. in maize and spring oilseed rape. Five species differed in only one crop: *Lamium purpureum*, *Stellaria media*, *Veronica*

Table 2. Three methods of analysis used for biomass.

method of analysis	values listed in table	number of observations	test statistic for treatment effect
A1	arithmetic means	N_{++}	not tested
A2	geometric means	N_{11}	d
A3	presences and absences	$N_{01} + N_{10}$	$(N_{01} - N_{10})^2/(N_{01} + N_{10})$

persica and *Viola arvensis* in maize, and *Persicaria maculosa* in beet. The biomass of only one species, *Senecio vulgaris*, was not significantly affected by the treatments in any crop.

In beet and spring oilseed rape, the GMHT treatments generally led to a decrease in biomass in each species. However, the rank abundances of the 12 species were positively correlated between the two different herbicide treatments (for beet, Spearman's rank correlation coefficient, $r_S = 0.71$, $n = 12$, $p = 0.011$; for spring oilseed rape $r_S = 0.78$, $n = 12$, $p = 0.003$). In maize the rank abundance was less consistent across the two treatments ($r_S = 0.54$, $n = 12$, $p = 0.072$).

(ii) *Estimating treatment differences*

In general, the estimated treatment ratios, R, calculated by using methods A1 and A2, were in the same direction (31 out of 36 comparisons), and in particular this was true for all the cases where the difference between treatments was statistically significant at 5% using A2. Rank correlations showed that Rs calculated by each method in beet and spring oilseed rape were highly correlated (for beet, $r_S = 0.87$, $n = 12$, $p < 0.001$; for spring oilseed rape $r_S = 0.83$, $n = 12$, $p = 0.001$) whereas in maize there was little consistency ($r_S = 0.29$, $n = 12$, $p = 0.36$). Thus in beet and spring oilseed rape A1 and A2 generally led to the same qualitative conclusions, especially when the evidence for a difference was strong. Quantitative estimates of R using the two methods often differed, but for the statistically significant species effects, Rs were generally of a similar order.

(b) *Impacts on demographic processes*

(i) *Emergence rate, g*

In beet, g was significantly affected in six out of 12 species, but in all species it was higher in the GMHT treatment (table 4). Emergence rates were variable across these species. In the conventional treatment, 0.6–15.2% of the seedbank emerged, whereas in the GMHT treatment this ranged between 1.1% and 38.3%.

In maize, g was significantly affected in only two out of the 12 species and in these cases the proportion of seeds emerging was roughly twice as high in the GMHT treatment. Though not significant, an increase in g was observed for five other species, and a decrease in three species. Only *Capsella bursa-pastoris* showed little effect of the treatments on mean emergence rate. The ranges of emergence values across all species were 1.2–27.9% in the conventional treatment and 2.1–25.4% in the GMHT treatment.

In spring oilseed rape, six species showed significant treatment effects on g. Five species showed higher rates in the GMHT treatment whereas one had a significantly lower rate. However, across all species, most (nine out of 12) had higher rates in the GMHT treatment. Values across all species in spring oilseed rape ranged from 0.5% to 11.2% in the conventional and from 1.5% to 44.2% in the GMHT treatments.

(ii) *Survival rate, s*

In beet, the survival rates of eight species were significantly affected by the treatments (table 5) and in all these cases survival was lowered in the GMHT treatment when compared with the conventional treatment. Nine out of the 11 species had lower survival rates in the GMHT treatment.

In maize, five species were significantly affected and showed higher survival rates in the GMHT treatment. Two species out of 12 had lower survival rates in the GMHT treatment but these were not significant.

In spring oilseed rape, seven species were significantly affected, with rates in six species lowered in the GMHT treatments. In total, nine out of the 12 species showed lower survival rates in the GMHT treatment. The mean survival rate of one species, *Poa annua*, was higher than that in conventionally managed spring oilseed rape.

(iii) *Reproductive rate, f*

The results for the treatment effects on reproductive rate are presented in table 6. In beet, reproductive rates in three species (*Chenopodium album*, *Poa annua* and *Polygonum aviculare*) were significantly decreased by the GMHT treatment (treatment ratio = 0.10–0.32) and in one species, *Lamium purpureum*, they increased by a factor of 8.3, although this was not statistically significant. In maize, reproductive rates significantly increased in one species (*Veronica persica*) and decreased in another (*Poa annua*). In spring oilseed rape, f was significantly lowered in three species (*Capsella bursa-pastoris*, *Poa annua* and *Polygonum aviculare*) and no species showed a significant increase in reproduction in the GMHT treatment. In general reproductive rates were lower for most species in GMHT beet and spring oilseed rape, whereas in maize just under half of the species showed this response.

(iv) *Seedbank change, b*

In only four cases were the effects of the herbicide treatments on b found to be significant (table 7). In beet, seedbank change was higher in the GMHT treatment for two species: *Fallopia convolvulus* (conventional, $b = 0.62$; GMHT, $b = 1.59$) and *Viola arvensis* (conventional, $b = 1.66$; GMHT, $b = 3.44$). In spring oilseed rape, the opposite effect was true with the ratio lowered in two species, *Capsella bursa-pastoris* (conventional, $b = 2.38$; GMHT, $b = 0.86$) and *Persicaria maculosa* (conventional, $b = 3.57$; GMHT, $b = 1.49$).

In all three crops most species had mean values of $b \geqslant 1$ in both treatments (beet, conventional $n = 7$, GMHT

Table 3. Biomasses of 12 selected species in relation to treatment and crop, analysed according to the methods A1, A2 and A3 listed in table 2.
(Counts N are the numbers of fields without the species (N_{00}) or with the species in one (GMHT N_{01}, conventional (C) N_{10}) or both (N_{11}) half-fields. R_A is the ratio of arithmetic means. 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. p_M is the exact p-value for the McNemar test. CI, confidence interval.)

	A1: arithmetic mean across all sites			A2: geometric mean (sites for which $N_{11} > 0$)					A3: comparison based on N_{01} and N_{10}			
crop and species	C ($g\,m^{-2}$)	GMHT ($g\,m^{-2}$)	R_A	N_{11}	C ($g\,m^{-2}$)	GMHT ($g\,m^{-2}$)	R (95% CI)	p-value	N_{00}	N_{01}	N_{10}	p_M
beet												
Capsella bursa-pastoris	0.25	0.34	1.36	23	0.05	0.08	1.62 (0.57–4.64)	< 0.35	17	19	3	0.001***
Chenopodium album	6.27	1.68	0.27	45	2.69	0.33	0.12 (0.05–0.28)	< 0.001***	7	3	7	0.34
Fallopia convolvulus	0.95	0.28	0.29	26	0.51	0.17	0.33 (0.14–0.81)	0.011*	13	5	18	0.011*
Lamium purpureum	0.08	0.08	0.94	26	0.03	0.03	0.86 (0.29–2.57)	0.78	20	9	7	0.80
Persicaria maculosa	1.42	0.05	0.03	10	1.19	0.08	0.07 (0.02–0.30)	0.006**	36	2	14	0.004**
Poa annua	3.57	1.49	0.42	56	0.47	0.14	0.30 (0.16–0.54)	< 0.001***	1	2	3	1.00
Polygonum aviculare	2.67	0.18	0.07	34	0.58	0.04	0.07 (0.03–0.16)	< 0.001***	6	1	21	< 0.001***
Senecio vulgaris	0.05	0.11	2.10	31	0.02	0.03	1.22 (0.62–2.40)	0.57	14	12	5	0.14
Sonchus spp.	0.19	0.21	1.10	39	0.03	0.03	0.88 (0.36–2.14)	0.78	12	7	4	0.55
Stellaria media	0.55	0.19	0.35	41	0.05	0.02	0.42 (0.16–1.14)	0.086	9	7	5	0.77
Veronica persica	1.68	0.46	0.27	42	0.18	0.08	0.47 (0.15–1.49)	0.20	9	6	5	1.00
Viola arvensis	0.94	0.30	0.33	31	0.38	0.19	0.48 (0.23–1.02)	0.053	14	10	7	0.63
maize												
Capsella bursa-pastoris	0.13	0.87	6.45	14	0.04	0.28	7.32 (1.71–31.32)	0.01**	9	17	0	< 0.001***
Chenopodium album	5.56	7.24	1.30	21	0.92	0.97	1.06 (0.26–4.29)	0.94	8	9	2	0.07
Fallopia convolvulus	0.05	0.22	4.29	8	0.08	0.31	3.86 (0.95–15.61)	0.047*	20	10	2	0.04*
Lamium purpureum	0.17	0.40	2.40	9	0.05	0.08	1.60 (0.35–7.29)	0.54	11	19	1	< 0.001***
Persicaria maculosa	0.33	1.74	5.19	9	0.47	0.30	0.65 (0.02–18.56)	0.79	20	8	3	0.23
Poa annua	5.15	5.58	1.08	37	0.16	1.44	9.16 (3.58–23.46)	< 0.001***	0	2	1	1.00
Polygonum aviculare	1.38	1.10	0.80	17	0.17	0.16	0.94 (0.19–4.73)	0.95	8	10	5	0.30
Senecio vulgaris	0.02	0.13	7.14	17	0.01	0.03	3.33 (0.83–13.35)	0.10	12	6	5	1.00
Sonchus spp.	0.27	0.47	1.76	26	0.04	0.13	3.51 (1.08–11.42)	0.04*	1	11	2	0.02*
Stellaria media	0.64	2.41	3.78	21	0.11	0.39	3.72 (0.71–19.46)	0.12	3	14	2	< 0.001***
Veronica persica	0.47	3.07	6.50	18	0.03	0.52	18.21 (2.39–138.70)	0.008**	9	12	1	< 0.001***
Viola arvensis	0.68	3.11	4.60	13	0.03	0.15	5.20 (0.51–52.91)	0.14	18	9	0	< 0.001***
spring oilseed rape												
Capsella bursa-pastoris	1.51	0.87	0.58	48	0.47	0.23	0.49 (0.24–1.01)	0.05*	4	3	7	0.34
Chenopodium album	9.21	2.10	0.23	37	2.51	0.28	0.11 (0.04–0.30)	< 0.001***	10	3	12	0.035*
Fallopia convolvulus	0.50	0.75	1.49	33	0.26	0.18	0.69 (0.27–1.74)	0.42	12	9	8	1.00
Lamium purpureum	0.13	0.26	1.98	25	0.07	0.13	1.68 (0.54–5.26)	0.36	17	14	6	0.12
Persicaria maculosa	6.80	4.35	0.64	50	1.37	1.50	1.09 (0.59–2.04)	0.76	1	6	5	1.00
Poa annua	10.34	1.27	0.12	51	1.72	0.35	0.20 (0.10–0.40)	< 0.001***	2	3	6	0.51
Polygonum aviculare	9.01	1.13	0.13	30	1.24	0.16	0.13 (0.04–0.48)	0.002**	18	3	11	0.057
Senecio vulgaris	0.09	0.10	1.09	31	0.07	0.04	0.54 (0.26–1.13)	0.12	12	14	5	0.064
Sonchus spp.	0.39	0.19	0.50	41	0.09	0.04	0.48 (0.23–1.01)	0.045*	5	8	8	1.20
Stellaria media	2.90	2.11	0.73	48	0.47	0.29	0.62 (0.26–1.49)	0.25	4	7	3	0.34
Veronica persica	1.06	0.95	0.90	40	0.18	0.16	0.87 (0.31–2.45)	0.77	13	2	7	0.18
Viola arvensis	1.07	2.02	1.89	29	0.62	0.64	1.03 (0.45–2.36)	0.93	22	8	3	0.22

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

Table 4. Emergence rates (ratio of seedlings to seedbank) and their multiplicative treatment ratios (R) for 12 species in relation to crop and treatment, GMHT or conventional (C).
(A dash indicates too few data to estimate the ratio and confidence intervals (CI).)

		emergence			
crop and species	n	C	GMHT	R (95% CI)	p-value
beet					
Capsella bursa-pastoris	37	0.014	0.051	3.64 (1.53–8.58)	0.005**
Chenopodium album	55	0.046	0.114	2.50 (1.53–4.07)	< 0.001***
Fallopia convolvulus	34	0.152	0.383	2.53 (1.72–3.44)	< 0.001***
Lamium purpureum	34	0.064	0.139	2.17 (1.18–3.97)	0.015*
Persicaria maculosa	31	0.020	0.029	1.43 (0.72–2.83)	0.30
Poa annua	60	0.006	0.011	1.84 (0.99–3.40)	0.054
Polygonum aviculare	38	0.049	0.063	1.28 (0.67–2.44)	0.45
Senecio vulgaris	21	0.021	0.066	3.13 (2.40–4.84)	< 0.001***
Sonchus spp.	26	0.000	0.004	—	—
Stellaria media	45	0.046	0.065	1.42 (0.82–2.49)	0.21
Veronica persica	46	0.097	0.128	1.33 (0.60–2.94)	0.48
Viola arvensis	34	0.113	0.253	2.23 (1.31–3.86)	0.005**
maize					
Capsella bursa-pastoris	41	0.105	0.109	1.03 (0.59–1.85)	0.89
Chenopodium album	54	0.054	0.134	2.50 (0.78–7.94)	0.12
Fallopia convolvulus	27	0.279	0.254	0.91 (0.42–2.01)	0.82
Lamium purpureum	31	0.045	0.060	1.33 (0.84–2.18)	0.20
Persicaria maculosa	34	0.089	0.099	1.11 (0.68–1.83)	0.67
Poa annua	57	0.012	0.021	1.75 (1.11–2.75)	0.017*
Polygonum aviculare	39	0.025	0.066	2.65 (1.72–4.01)	< 0.001***
Senecio vulgaris	37	0.062	0.050	0.81 (0.42–1.62)	0.57
Sonchus spp.	4	0.000	0.000	—	—
Stellaria media	50	0.037	0.060	1.61 (0.96–2.73)	0.070
Veronica persica	39	0.036	0.067	1.87 (0.95–3.60)	0.068
Viola arvensis	27	0.075	0.070	0.94 (0.60–1.50)	0.83
spring oilseed rape					
Capsella bursa-pastoris	48	0.040	0.058	1.43 (0.87–2.35)	0.16
Chenopodium album	44	0.037	0.082	2.25 (1.28–4.02)	0.006**
Fallopia convolvulus	29	0.112	0.442	3.94 (2.29–5.32)	< 0.001***
Lamium purpureum	29	0.090	0.078	0.87 (0.67–1.14)	0.30
Persicaria maculosa	33	0.071	0.127	1.78 (1.28–2.48)	< 0.001***
Poa annua	59	0.005	0.015	2.97 (1.42–6.19)	0.004**
Polygonum aviculare	57	0.045	0.069	1.52 (1.01–2.31)	0.045*
Senecio vulgaris	30	0.036	0.046	1.26 (0.72–2.47)	0.34
Sonchus spp.	26	0.000	0.000	—	—
Stellaria media	51	0.027	0.050	1.85 (0.92–3.72)	0.082
Veronica persica	43	0.042	0.048	1.15 (0.67–1.99)	0.60
Viola arvensis	28	0.108	0.071	0.66 (0.54–0.81)	< 0.001***

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

$n = 7$; maize, conventional $n = 8$, GMHT $n = 7$; spring oilseed rape, conventional $n = 11$, GMHT $n = 10$). Despite the general lack of significant treatment effects, several general trends were apparent. The multiplicative treatment ratio (GMHT : conventional) for b in each crop showed that the numbers of species with values less than 1 were 8, 10 and 11 in beet, maize and spring oilseed rape, respectively. Across crops, some species showed consistency in the effects of the treatment. Five species, *Capsella bursa-pastoris*, *Lamium purpureum*, *Poa annua*, *Polygonum aviculare* and *Stellaria media*, were negatively affected in all three crops. In spring oilseed rape and beet, the ratio was less than 1 in two species, *Persicaria maculosa* and *Veronica persica*. Similarly, in maize and spring oilseed rape, *Fallopia convolvulus*, *Senecio vulgaris*, *Sonchus* spp. and *Viola arvensis* all had treatment ratios less than 1. *Chenopodium album* had a ratio less than 1 in beet and maize.

5. DISCUSSION

(a) *Species data and patchy distributions*

We have concentrated on the most abundant and frequent species found in the FSEs. These weeds have been consistent and conspicuous components of the British arable flora for many years (Firbank 1999; Marshall *et al.* 2001), so that they determine not only biotic interactions within fields but also, indirectly, the weed-control strategies used by farmers. Another reason for choosing the most frequent species is that they can be expected to occur in most of the fields. Less frequent species occur by

Table 5. Survival rates (ratio of final densities of reproductive individuals to seedling densities at the first count) and their multiplicative treatment ratios (R) for 12 species in relation to crop and treatment, GMHT or conventional (C).
(A dash indicates too few data to estimate the ratio and confidence intervals (CI).)

		survival			
crop and species	n	C	GMHT	R (95% CI)	p-value
beet					
Capsella bursa-pastoris	19	0.132	0.164	1.24 (0.69–2.51)	0.38
Chenopodium album	33	0.378	0.127	0.34 (0.14–0.78)	0.013*
Fallopia convolvulus	20	0.100	0.048	0.48 (0.28–0.78)	0.005**
Lamium purpureum	17	0.029	0.055	1.89 (0.78–3.05)	0.19
Persicaria maculosa	16	0.399	0.059	0.15 (0.09–0.23)	< 0.001***
Poa annua	33	0.332	0.185	0.56 (0.25–1.24)	0.15
Polygonum aviculare	23	0.221	0.057	0.26 (0.13–0.44)	< 0.001***
Senecio vulgaris	11	0.378	0.100	0.26 (0.07–0.66)	0.012*
Sonchus spp.	16	0.000	0.018	—	—
Stellaria media	28	0.075	0.037	0.50 (0.29–0.83)	0.010*
Veronica persica	24	0.226	0.063	0.28 (0.13–0.62)	0.003**
Viola arvensis	24	0.324	0.096	0.30 (0.17–0.54)	< 0.001***
maize					
Capsella bursa-pastoris	25	0.018	0.216	12.37 (2.38–65.31)	0.004**
Chenopodium album	31	0.033	0.077	2.30 (1.14–4.56)	0.022*
Fallopia convolvulus	16	0.004	0.068	15.38 (5.13–64.97)	< 0.001***
Lamium purpureum	20	0.000	0.044	—	—
Persicaria maculosa	21	0.005	0.017	3.15 (0.93–10.73)	0.065
Poa annua	32	0.180	0.114	0.63 (0.30–1.32)	0.22
Polygonum aviculare	24	0.103	0.038	0.37 (0.09–1.43)	0.14
Senecio vulgaris	22	0.024	0.078	3.29 (0.43–13.68)	0.30
Sonchus spp.	27	0.000	0.013	—	—
Stellaria media	32	0.024	0.092	3.80 (1.16–12.45)	0.029*
Veronica persica	25	0.057	0.286	5.01 (1.77–14.51)	0.004**
Viola arvensis	19	0.091	0.268	2.95 (0.92–9.64)	0.067
spring oilseed rape					
Capsella bursa-pastoris	38	0.348	0.288	0.83 (0.40–1.65)	0.56
Chenopodium album	34	0.841	0.273	0.32 (0.21–0.49)	< 0.001***
Fallopia convolvulus	24	0.451	0.184	0.41 (0.25–0.67)	< 0.001***
Lamium purpureum	26	0.127	0.224	1.76 (0.92–3.21)	0.089
Persicaria maculosa	23	0.316	0.033	0.10 (0.05–0.22)	< 0.001***
Poa annua	43	2.666	0.417	0.16 (0.06–0.43)	< 0.001***
Polygonum aviculare	43	0.806	0.131	0.16 (0.09–0.29)	< 0.001***
Senecio vulgaris	25	0.157	0.252	1.61 (0.54–3.02)	0.56
Sonchus spp.	28	0.112	0.028	0.25 (0.09–0.74)	0.014*
Stellaria media	42	0.566	0.277	0.49 (0.22–1.09)	0.079
Veronica persica	36	0.676	0.487	0.72 (0.42–1.26)	0.24
Viola arvensis	26	0.118	0.217	1.84 (1.08–3.13)	0.028*

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

definition in fewer sites. For them, density and biomass will be averaged over fewer sites, so that few, if any, significant treatment effects would be found.

Even the common species showed wide variations in abundance between fields (figure 1), and the variation within fields was equally striking. One rather extreme example comes from the seedbank of the grass *Poa annua* in conventional maize. In the year $t + 1$, after the experimental crop, 95% of seedbank counts were, before conversion to unit area, in the range 0–200 seeds per half-field, but for one site the value was 2528 seedlings. This result was in turn almost entirely caused by the soil sample from a single location at 2 m from the field edge. An astounding 1856 seedlings emerged from this one sample. Given that the total count from all 32 half-fields in which *Poa annua* was found in year $t + 1$ was 3634, then 51% of the year's total came from that one sample out of 256 (there were eight sample locations per half-field.)

Such extreme values present a serious problem for analysis. If mean densities are estimated as arithmetic means, then they tend to be dominated by results from just a few sites. Nevertheless, results from sites where densities are lower are highly relevant to the question of long-term trends. In particular, an understanding of treatment effects operating at lower densities is essential for any prediction of whether a species is likely to disappear. It was for these reasons that we based analyses of dicotyledons and monocotyledons taken as a whole on geometric means. Unfortunately, when groups are disaggregated to species, geometric means become unreliable because of random variation at low densities. If, for example, a plant is absent in year t but four individuals are counted in year

Table 6. Reproductive rates (ratio of seed rain to density of reproductive individuals at the final count) and their multiplicative treatment ratios (*R*) for 12 species in relation to crop and treatment, GMHT or conventional (C).
(A dash indicates too few data to estimate the ratio and confidence intervals (CI).)

		reproductive rate			
crop and species	*n*	C	GMHT	*R* (95% CI)	*p*-value
beet					
Capsella bursa-pastoris	18	95	363	3.84 (0.68-21.9)	0.12
Chenopodium album	34	105	25.5	0.24 (0.07–0.80)	0.020*
Fallopia convolvulus	16	41.5	10.9	0.26 (0.06–1.23)	0.086
Lamium purpureum	8	6	49.9	—	—
Persicaria maculosa	15	195	49.5	0.25 (0.05–1.29)	0.095
Poa annua	27	84	26.5	0.32 (0.17–0.60)	< 0.001***
Polygonum aviculare	18	32.2	3.1	0.10 (0.02–0.57)	0.012*
Senecio vulgaris	16	212	324	1.53 (0.16–14.3)	0.70
Sonchus spp.	11	—	—	—	—
Stellaria media	18	431	310	0.72 (0.10–5.05)	0.73
Veronica persica	11	33.3	111	3.34 (0.76–14.7)	0.11
Viola arvensis	21	34	26.1	0.77 (0.22–2.66)	0.67
maize					
Capsella bursa-pastoris	16	541	108	0.20 (0.02–2.28)	0.19
Chenopodium album	28	403	276	0.68 (0.18–2.54)	0.56
Fallopia convolvulus	15	501	137	0.27 (0.05–1.45)	0.12
Lamium purpureum	10	—	—	—	—
Persicaria maculosa	14	807	1210	1.50 (0.20–11.45)	0.69
Poa annua	29	121	49.4	0.41 (0.23–0.72)	0.003**
Polygonum aviculare	36	3.8	8.3	2.16 (0.45 – 10.2)	0.33
Senecio vulgaris	11	71.6	82.1	1.15 (0.10–12.55)	0.91
Sonchus spp.	13	—	—	—	—
Stellaria media	21	799	714	0.89 (0.28–2.88)	0.85
Veronica persica	16	15.9	131	8.24 (1.98–34.33)	0.005**
Viola arvensis	14	115	333	2.90 (0.66–12.8)	0.15
spring oilseed rape					
Capsella bursa-pastoris	48	483	148	0.31 (0.13–0.75)	0.01**
Chenopodium album	38	167	339	2.02 (0.46–8.87)	0.35
Fallopia convolvulus	35	134	152	1.14 (0.51–2.52)	0.75
Lamium purpureum	23	24.4	38.6	1.58 (0.57–4.33)	0.37
Persicaria maculosa	29	381	292	0.77 (0.51–1.16)	0.20
Poa annua	46	72.1	30.5	0.42 (0.21–0.87)	0.019*
Polygonum aviculare	40	115.8	36.1	0.31 (0.17–0.57)	< 0.001***
Senecio vulgaris	28	171	172	1.00 (0.36–2.78)	0.99
Sonchus spp.	27	418	332	0.79 (0.17–3.70)	0.76
Stellaria media	39	163	109	0.67 (0.42–1.06)	0.087
Veronica persica	35	41.9	29.4	0.70 (0.24–2.04)	0.51
Viola arvensis	28	102	75.8	0.74 (0.25–2.16)	0.58

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

$t + 1$, then this result has to be excluded from the analysis. There is no tidy solution to this problem. Consequently, the results for individual species are markedly more variable and individually less reliable than those for big groups.

(b) *Effects on species biomass*

Our results indicate that the management of the GMHT crops had significant impacts on the biomasses of all of the weed species. As expected, *Chenopodium album* was the dominant weed in beet, but it also attained high biomasses in spring oilseed rape and maize along with *Poa annua*.

Biomass production in the GMHT treatment was significantly reduced for five species in beet and spring oilseed rape, whereas in maize the opposite effect was true, with seven species showing a general increase in biomass. These significant treatment effects correspond well to those found for total weed biomass (Heard *et al.* 2003). Many species showed similar responses to the GMHT treatments in beet and spring oilseed rape crops, where two different herbicides were used. This contrasted with their response in maize, where the same herbicide as in spring oilseed rape was applied. This suggests that in this experiment it was the interaction between the species and the management associated with a particular GMHT crop rather than sensitivity to the specific herbicides used that determined species responses.

A species that did not follow the general trend was *Viola arvensis*. This weed is known to have low susceptibility to glufosinate-ammonium (Becker *et al.* 2001). Unlike several other dicotyledons, it was equally (geometric mean)

Table 7. Seedbank-change ratios (ratio of seedbank density in spring of the following year to that in the year of the crop) and their multiplicative treatment ratios (R) for 12 species in relation to crop and treatment, GMHT or conventional (C). (CI, confidence interval.)

		seedbank change			
crop and species	n	C	GMHT	R (95% CI)	p-value
beet					
Capsella bursa-pastoris	28	0.78	0.65	0.83 (0.38–1.87)	0.66
Chenopodium album	38	3.24	2.40	0.74 (0.43–1.28)	0.27
Fallopia convolvulus	15	0.62	1.59	2.54 (1.42–5.46)	0.006**
Lamium purpureum	14	1.40	0.91	0.65 (0.38–1.38)	0.31
Persicaria maculosa	16	1.42	0.51	0.36 (0.11–1.10)	0.069
Poa annua	46	0.80	0.58	0.72 (0.47–1.12)	0.14
Polygonum aviculare	28	1.87	1.21	0.65 (0.31–1.34)	0.23
Senecio vulgaris	20	0.63	1.79	2.82 (0.97–6.78)	0.056
Sonchus spp.	27	0.78	1.01	1.29 (0.74–2.06)	0.42
Stellaria media	31	1.13	0.75	0.67 (0.45–1.01)	0.056
Veronica persica	27	1.78	1.04	0.58 (0.26–1.28)	0.17
Viola arvensis	19	1.66	3.44	2.08 (1.39–3.33)	0.002**
maize					
Capsella bursa-pastoris	22	0.74	0.54	0.73 (0.26–2.03)	0.52
Chenopodium album	30	1.79	1.09	0.61 (0.34–1.10)	0.095
Fallopia convolvulus	10	2.10	1.10	0.52 (0.25–1.11)	0.084
Lamium purpureum	10	1.65	1.00	0.61 (0.33–1.39)	0.25
Persicaria maculosa	17	0.84	1.21	1.43 (0.94–2.11)	0.093
Poa annua	32	2.05	1.25	0.61 (0.33–1.11)	0.10
Polygonum aviculare	22	1.72	1.47	0.86 (0.47–1.50)	0.55
Senecio vulgaris	17	1.50	0.53	0.35 (0.13–1.21)	0.096
Sonchus spp.	17	0.98	0.66	0.67 (0.32–1.36)	0.24
Stellaria media	27	0.85	0.73	0.87 (0.40–1.88)	0.71
Veronica persica	18	1.46	1.64	1.12 (0.67–1.92)	0.61
Viola arvensis	13	1.15	0.89	0.78 (0.53–1.15)	0.19
spring oilseed rape					
Capsella bursa-pastoris	36	2.38	0.86	0.36 (0.19–0.70)	0.003**
Chenopodium album	25	3.27	3.76	1.15 (0.26–5.14)	0.84
Fallopia convolvulus	8	2.83	2.00	0.71 (0.33–1.00)	0.052
Lamium purpureum	12	1.19	1.15	0.96 (0.64–1.50)	0.93
Persicaria maculosa	21	3.57	1.49	0.42 (0.24–0.75)	0.005**
Poa annua	38	0.96	0.89	0.92 (0.57–1.51)	0.75
Polygonum aviculare	31	3.10	1.48	0.48 (0.16–1.44)	0.18
Senecio vulgaris	14	1.38	1.10	0.80 (0.24–1.51)	0.25
Sonchus spp.	29	8.59	8.06	0.94 (0.33–2.79)	0.94
Stellaria media	35	2.69	1.86	0.69 (0.36–1.31)	0.25
Veronica persica	18	1.41	1.14	0.81 (0.38–1.65)	0.52
Viola arvensis	15	2.63	1.36	0.52 (0.19–1.50)	0.21

** $p < 0.01$.

or more (arithmetic mean) abundant in GMHT spring oilseed rape than in the conventional variety.

The analyses showed that in some species above-ground biomass might be reduced to very low, even undetectable, values. In beet this agrees with the findings of Dewar *et al.* (2000) and Strandberg & Pedersen (2002) who showed that herbicides used in GMHT crops can give very efficient weed control within a season. The most extreme example here was *Persicaria maculosa*, which was almost completely eliminated in GMHT beet. At least part of the reason is that its seeds do not germinate after the initial flush, returning to a state of secondary dormancy after the annual rise in late-spring temperatures (Grime *et al.* 1988). At the opposite extreme, *Veronica persica* was almost completely eliminated in conventional maize. This species differs from *Persicaria maculosa* in having seeds that show little innate dormancy and are capable of germinating during any month of the year (Grime *et al.* 1988). It is therefore strongly affected by persistent herbicides such as atrazine (applied in about 75% of conventional maize fields), which are used to reduce the effects of early weed competition in a relatively uncompetitive crop.

Senecio vulgaris, which can germinate all through the year, is relatively low growing (table 1) and has a high relative growth rate (Grime *et al.* 1988). It was the only species whose biomass was not significantly affected by the treatments in any of the crops. However, there were large treatment ratios in maize ($R_A = 7.14$; $R = 3.33$; $p = 0.10$; table 3), which suggest that it was strongly reduced by persistent herbicides.

In beet and spring oilseed rape, the effects of the GMHT treatments on biomass did little to affect the rank

Table 8. Transition ratios and their multiplicative treatment ratios (*R*) (GMHT/conventional (C)) for life stages of dicotyledons and monocotyledons in C and GMHT crops.
(Values are based on geometric means in tables 4–6 in Heard *et al.* (2003).)

	dicotyledons			monocotyledons		
	C	GMHT	*R*	C	GMHT	*R*
emergence						
beet	0.030	0.049	1.65	0.008	0.012	1.50
maize	0.020	0.050	2.55	0.009	0.014	1.57
spring oilseed rape	0.019	0.031	1.63	0.007	0.014	1.92
mean for all crops	0.022	0.043	1.90	0.008	0.013	1.65
survival						
beet	0.28	0.08	0.28	0.57	0.15	0.26
maize	0.05	0.09	1.84	0.23	0.30	1.29
spring oilseed rape	0.90	0.29	0.32	0.73	0.47	0.65
mean for all crops	0.26	0.17	0.63	0.46	0.27	0.60
reproductive rate						
beet	67	46	0.69	25	16	0.62
maize	213	97	0.45	43	22	0.51
spring oilseed rape	119	47	0.40	58	22	0.38
mean for all crops	119	60	0.50	40	20	0.49
seedbank change						
beet	1.48	1.16	0.78	0.69	0.68	0.98
maize	1.26	1.26	1.00	0.99	1.13	1.13
spring oilseed rape	2.13	1.27	0.59	0.73	0.75	1.03
mean for all crops	1.59	1.23	0.77	0.79	0.83	1.05

abundance of the 12 weed species. Likewise, there was no significant effect on biomass dominance values in these crops (Heard *et al.* 2003). In maize, however, it is clear that the conventional treatment had a powerful selective effect, which altered the species' rank abundance relationships. Dominance was also affected by the treatments in maize (Heard *et al.* 2003).

(c) *Impacts on species transition ratios*

It is of interest to compare transition rates for individual species with those obtained for the broad categories of species considered by Heard *et al.* (2003). The broad-brush picture (table 8), although based on several individual species with disparate traits, shows some interesting features. Emergence rates were surprisingly consistent between crops but differed markedly according to treatment and between dicotyledons and monocotyledons. The highest emergence, of dicotyledons in GMHT crops, was about 4.3%. Note that this value is subject to two additional uncertainties. The fact that ploughing is ordinarily to *ca*. 20 cm means that seedbank densities in the following crop may be underestimated because of deep burial of seed. Plants also germinated after the first count. Thus the true rate of emergence could be higher or lower than reported here.

Emergence rates for most individual species showed the same general pattern. Six species, *Capsella bursa-pastoris*, *Chenopodium album*, *Persicaria maculosa*, *Poa annua*, *Stellaria media* and *Veronica persica*, all showed increased emergence in the GMHT treatments across all crops. *Fallopia convolvulus* and *Senecio vulgaris* showed higher emergence rates in GMHT beet and spring oilseed rape, but lower emergence in GMHT maize. The lower emergence rates in maize were not significant and were surprisingly at variance with the markedly greater biomasses found for these species in the GMHT treatment at the end of the season.

In the analysis of broad categories (table 8), the rate of survival from seedlings to reproductive adults was generally higher in monocotyledons than dicotyledons. The treatment effects differed by almost an order of magnitude between crops. In maize, the treatment ratio for dicotyledon survival was 1.84, whereas it was 0.28 in beet and 0.32 in spring oilseed rape. Low survival in conventional maize can be attributed to the continuing effects of persistent herbicides. Low survival in GMHT beet resulted from the broad-spectrum herbicide, which was highly effective in this crop. Survival of monocotyledons was higher than that of dicotyledons in beet and maize, but lower than that of dicotyledons in conventional spring oilseed rape.

It is clear that some plants that germinated after the first seedling count were in a reproductive state by the time of the final count. Late germination was particularly large in conventional spring oilseed rape, where the final density of reproductive dicotyledons was only 10% lower than the seedling density at the first count. The term 'survival' for this ratio is therefore not wholly appropriate.

One species with especially high values of 'survival' was *Poa annua*. This can germinate intermittently throughout the season, and clearly did so. Although both glufosinate-ammonium and glyphosate generally resulted in dicotyledons being better controlled in GMHT beet and spring oilseed rape than in the corresponding conventional crops, the survival rate of *Viola arvensis* was remarkably different between the two crops. In beet, the treatment ratio was 0.30; in spring oilseed rape it was 1.84, both values being significantly different from 1. This result accords with the fact, noted in § 5b, that *Viola arvensis* has low susceptibility to glufosinate-ammonium. *Lamium purpureum* also had

higher survival in GMHT treatments, confirming the results of Buckmann *et al.* (2000), who found that *Lamium* spp. were less well controlled by glyphosate than most other weeds, including *Chenopodium album*.

Averaging over broad categories of species, reproductive rates, unlike survival, differed little between crops (table 8). There were clear and consistent differences between treatments and between categories of plants. Plants in GMHT crops had reproductive rates about half of those in conventional crops. Dicotyledons had about three times the reproductive rate of monocotyledons. Both of these differences reflect comparable differences in unit plant mass (Heard *et al.* 2003). Similar broad trends can be seen in the results for individual species (table 6), although there were only eight significant differences out of 36 comparisons. In seven of these cases, the reproductive rate was higher in the conventional crop. However, *Veronica persica* had a higher reproductive rate in GMHT maize than conventional maize.

(d) *Effects on seedbank change*

When species were aggregated in broad categories, there were highly significant treatment effects on the dicotyledon seedbank in beet and spring oilseed rape (Heard *et al.* 2003). The effect in spring oilseed rape, where the seedbank-change ratio was 40% lower in the GMHT treatment than in the conventional treatment (table 8), was particularly marked. In all crops and treatments the seedbank change for dicotyledons was greater than 1. Equally striking is that in beet and spring oilseed rape, the monocotyledons decreased over the same period. The decrease in monocotyledons was about 30% after beet and 25% after spring oilseed rape, with no difference between the treatments. After maize, there was no large decrease in monocotyledons. This is a slightly surprising result given that the monocotyledon seed rain was lower in maize than in spring oilseed rape.

Given the immense variability in the seedbank of *Poa annua*, it is clearly unwise to place too much emphasis on results from a single crop. However, taking all three crops together, it appears that the seedbank of monocotyledons decreased by about 20% in the year of growing GMHT crops, whereas the seedbank of dicotyledons tended to increase. After conventional spring oilseed rape it more than doubled. This shows the potential for large and immediate treatment effects within a season.

When the seedbank-change ratios are disaggregated to species (table 7), some of the same patterns are apparent, but only four out of 36 species treatment effects were significant. Significant effects for *Capsella bursa-pastoris* and *Persicaria maculosa* in spring oilseed rape were in the expected direction, lower in the GMHT treatment. However, treatment ratios greater than 1 for *Fallopia convolvulus* and *Viola arvensis* in beet seem highly improbable, given that the biomass effects were strongly the other way and were either significant or nearly significant. The moderately high significance levels for treatment effects in the seedbank-change ratio for these two species ($p = 0.006$ and 0.002, respectively) may be slightly misleading. When we applied a multiplicative statistical model (based on geometric means; M. S. Heard, unpublished data) the effect for *Fallopia convolvulus* was non-significant, and the significance for *Viola arvensis* was 0.035, which could easily be the result of chance. No simple statistical model fitted the data well.

For the seedbank, we therefore conclude that the data available at the time of writing were not adequate to detect many species effects. During 2003, much further seedbank sampling took place. When the results from this year become available, a clearer picture should emerge.

(e) *Longer-term trends*

The fact that the seedbanks of most dicotyledons increased during the FSEs may appear at odds with the more general patterns of weed population decline across Britain (Preston *et al.* 2002). However, any impacts within a season should be viewed in the context of longer-term cropping patterns, which can have large impacts on weed abundance through time. In Britain, arable rotations are dominated by cereal crops, which are interspersed with 'break' crops such as beet and rape. Many weeds, especially dicotyledons, depend on the break crops for recruitment and reproduction. For example, recruitment of *Chenopodium album* in cereals may be negligible (Watkinson *et al.* 2000).

In the FSEs, emergence rates for dicotyledons were about 4% in the GMHT treatment. This sets a lower bound on the rate of seedbank decline in the absence of replenishment. It is interesting that the seedbank of the monocotyledons decreased by about 20% during the year of growing GMHT crops. Broad-leaved break crops are likely to be less suitable than cereal crops for monocotyledons because of the use of selective conventional herbicides. There was clearly some replenishment of the monocotyledon seedbank, so that the actual rate of monocotyledon decline in the absence of replenishment must be greater than this. When more data are available from results collected in 2003, we should be able to obtain estimates of this important demographic parameter, but from the early results there is only a general indication.

It is already clear that the decline rate for the seedbank in the FSEs was closer to the value of 20% per annum proposed by Watkinson *et al.* (2000) for *Chenopodium album* than to the higher values, up to 50%, reported from several other studies (cf. Heard *et al.* 2003). On the other hand, the increase in the seedbank after conventional spring oilseed rape confirms the potential for rapid changes over relatively short periods (Squire *et al.* 2000; Marshall *et al.* 2001).

None of the 12 species has a very short-lived seedbank. Indeed, dicotyledons that achieve high seed output only in break crops depend necessarily on seeds surviving for *ca.* 5 years. The seedbank is essential for their dynamic stability (Firbank 1993; Freckleton & Watkinson 2002). This pattern of survival, with relatively long intervals between occasional 'good' years (the 'storage effect' *sensu* Chesson 1986; Lutman *et al.* 2002), is most characteristic of species that in natural habitats are found in sand dunes and perennial grasslands (type 4 species; Grubb 1988). For species with transient seedbanks, every year must be at least moderately good. Population survival is therefore likely to be especially sensitive to herbicide effects in a single year (Lintell Smith *et al.* 1999).

The treatment ratio for survival rate (equivalent to the measure of efficiency of weed removal in GMHT crops, *h*; Watkinson *et al.* 2000) was in most cases less than 1.

However, several species had treatment ratios greater than 1 in maize, and at least one such ratio was significantly greater than 1 in spring oilseed rape. Thus, the GMHT treatment was not always more efficient than the conventional control. This was an assumption of the model of GMHT beet developed by Watkinson *et al.* (2000). Another assumption was the total absence of reproduction in cereal crops. Our own data from fields after GMHT crops show that many dicotyledons are present and reproductive in cereals (Heard *et al.* 2003). Their seed return will slow the rate of decline between break crops.

Data from Robinson & Sutherland (2002) indicate that the decline in weed seedbanks in the UK has averaged about 3% per annum since the 1940s. There is no evidence that the trend is not continuing. The only real limit is the cost of weed control. If this long-term rate of decline were compounded with the low seedbank-change ratios, say about 0.7, found for dicotyledons in GMHT beet and spring oilseed rape, then there would be the potential for accelerated species decline under GMHT cropping. In a five course cereal rotation with a break crop grown every 5 years (e.g. Watkinson *et al.* 2000) the additional annual loss would be $(1 - 0.7^{0.2}) = 0.07$, i.e. 7%. The inclusion of more GMHT break crops in a rotation would slightly slow the rate of these declines for some species, but there would be others, such as *Persicaria maculosa* in beet, where decline would be accelerated.

In conventional maize, declines similar in magnitude to those suggested under GMHT beet and spring oilseed rape are presumably already occurring. However, dicotyledon biomass and seed rain were nearly three times greater in GMHT than in conventional maize and were comparable with those in conventional beet. It is quite possible that, under rotations including GMHT maize, weed populations would in the long term be stable or increase. It is also possible that farmers might respond by increasing their levels of weed control across the rotation.

(f) *Conclusions*

With a few exceptions, weed species in beet and spring oilseed rape were negatively affected by the GMHT treatment. On the other hand, several species gained a relative benefit in maize, where persistent herbicides are in conventional use and exert a powerful selective effect. If, in future, GMHT crops are licensed for general release and managed as they were in the FSEs, their introduction will have a large effect on weed populations in the longer term, even if short-term change is somewhat buffered.

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GLOSSARY

FSE: Farm Scale Evaluation
GMHT: genetically modified herbicide tolerant