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Amelioration of biodiversity impacts of genetically modified crops: predicting transient versus long-term effects

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It has been suggested that genetically modified herbicide-tolerant crops may benefit biodiversity because spraying of crops may be delayed until later in the growing season, allowing weeds to grow during the early part of the year. This provides an enhanced resource for arthropods, and potentially benefits birds that feed on these. Thus, this technology could enhance biodiversity. Using a review of weed phenologies and a population model, we show that many weeds are unlikely to benefit because spraying is generally delayed insufficiently late in the season to allow most to set seed. The positive effects on biodiversity observed in trials lasting one or two seasons are thus likely to be transient. For one weed of particular significance (Chenopodium album, fat hen) we show that it is unlikely that the positive effects observed could be maintained by inputs of seed during other parts of the rotation. However, we find preliminary evidence that if spraying can be ceased earlier in the season, then a viable population of late-emerging weeds could be maintained. This strategy could benefit weeds in both genetically modified (GM) and non-GM crops, but would probably lead to reduced inputs in GM systems compared with conventional ones.

Keywords: sugar beet; Chenopodium album; genetically modified crop; weed model; farmland birds

1. INTRODUCTION

A fundamental problem in predicting changes in ecological systems is that the scale at which we can observe systems is less extensive than the scale over which we wish to make predictions. Thus, in the current debates concerning the likely large-scale impacts of the introduction of genetically modified (GM) crops, predictions of impacts on biodiversity over time periods in the order of decades or more are required, and at nationwide spatial scales. However, experiments investigating likely impacts can be conducted only over much shorter periods, typically no more than 2 or 3 years in small-scale field experiments (Firbank 1991; Firbank et al. 1999, 2003; Dewar et al. 2003). In a previous paper we showed that local-scale effects on the abundance of weeds in GM crops might not translate directly into regional-scale effects on the abundance of either weeds or the organisms that rely on them for food (Watkinson et al. 2000).

A recent highly publicized experimental study has explored the short-term positive effects of introducing GM herbicide-tolerant (GMHT) technology on farmland biodiversity (Dewar et al. 2003). This study tested a widely cited hypothesis (Monsanto 2000; Firbank & Forcella 2000; also reported throughout the media) that delayed spraying in GM crops will allow greater biodiversity to develop in these crops. Delayed spraying is possible because weed control is much easier using highly efficient broad-spectrum herbicides, which are effective even on large weeds. In conventional crops weed control is often difficult, and efficiency is generally highest in the early stages of growth. In conventional systems, herbicides are therefore applied early in the growing season. By delaying spraying in GM crops, weeds are given an opportunity to grow, and create a micro-habitat that may be an important habitat and food resource for associated arthropod species. These arthropod species in turn could be a potentially valuable food resource for other species, such as farmland birds, at a time of year when small chicks are maturing. Dewar et al. (2003) have shown that this is indeed potentially the case in GMHT sugar beet (Beta vulgaris L.): delayed spraying, especially when coupled with initial band spraying, leads to increased weed biomass, which in turn results in increased arthropod densities. It should be noted, however, that very late delayed spraying of weeds (a delay as late as August was included) resulted in large crop yield losses and that a delay beyond mid-to-late June would therefore be unlikely in practice with this crop.

The study by Dewar et al. (2003) was concerned entirely with within-season effects, however, and did not address issues of long-term impacts on biodiversity. A long-term perspective is important because the reported benefits of delayed spraying of GM crops will be maintained only if weed species are allowed to set seed. In this paper, we conduct a survey of the phenological characteristics of common arable weeds, and show that many key species are unlikely to produce seed under delayed-spraying regimes. Given this observation two scenarios are possible: first, the benefits reported under delayed spraying may be entirely transient; or, second, the positive effects of delayed spraying may be maintained if there is seed production by weeds during other stages of the rotation. We use population models to test these hypotheses in Chenopodium album (fat hen), an important weed of sugar beet. We use our models to:
(i) predict how the positive effects of delayed spraying will change through time; and
(ii) ask whether the effects of delayed spraying can be maintained through the input of seeds during other parts of the rotation.

Finally, we suggest an alternative mechanism by which GM technology could potentially be used to enhance biodiversity.

2. MATERIAL AND METHODS

(a) Phenology of common weeds in relation to delayed spraying

We compiled data on the phenologies of species that are known to be important in generating food (seed) for birds (Wilson et al. 1999). These plants are also likely to be important resources for insects. For each species we compiled data on:

(i) the minimum time taken to reach flowering; and
(ii) the time between the initiation of flowering and the first production of seeds.

We compiled these data mainly from Grime et al. (1988). For species for which these data are not available in this source, we consulted the Ecoflora (Fitter & Peat 1994).

(b) Model for weed dynamics under delayed spraying

Our model is a modification of that described by Watkinson et al. (2000), which is itself based on an earlier model (Freckleton & Watkinson 1998). The model considers the population dynamics of C. album growing within a five-crop rotation. It is assumed that sugar beet is grown every fifth year, and that C. album is capable of surviving, growing and setting seed only in this crop. In the other 4 years it is assumed that C. album is unable to survive (owing to the efficiency of conventional control), as would be the case if cereals or winter-sown crops were grown. In the years between the sugar beet crops, the population of C. album persists solely as a pool of dormant seed. We relax this assumption below, although we expect that densities of C. album will be low throughout the other parts of the rotation unless appreciable numbers of spring-sown crops are grown or spraying of set-aside occurs late enough in the season to allow C. album to set seed. Generally, other crops (particularly cereals and oilseed rape) are harvested too early in the year (by mid-July) to allow seed production by C. album, even if plants survive control.

The dynamics of emerging seedlings (N) and seeds in the seed bank (S) are given by the following equations (Freckleton & Watkinson 1998; the model parameters and their meanings are summarized in table 1):

\[
N_{t+5} = g(1-m)^4s_m-pN_tf(pN_f) + g(1-m)^5S_t
\]  
\[
S_{t+5} = (1-m)^4(1-g)S_t + (1-m)^5(1-g)s_ms_pN_tf(pN_f).
\]

In equations (2.1) and (2.2), g and m are the emergence and mortality rate of seeds in the seed pool, respectively, s_m is the seed production of an isolated plant experiencing no competition from other weeds or the crop, and the function f describes how seed production changes with competition resulting from increasing weed and crop density. The specific form of f assumed is given in table 1.

Hericidal and mechanical control are modelled through the parameter p, which is the proportion of plants surviving control. We assume that this includes both pre- and post-emergence herbicide applications. We also assume p to include the background mortality of seedlings following germination. The density of mature plants, M, is then given by pN. It is assumed that herbicides are applied early in the growing season. Competition takes place after control has been applied, so that the function f acts on the density of survivors (pN) rather than the density of seedlings (N). Equations (2.1) and (2.2) are readily solved analytically to yield predictions of equilibrium population sizes (Freckleton & Watkinson 1998; see electronic Appendix A, available on The Royal Society’s Publications Web site).

To include the effects of introducing GM technology (or indeed any increase in the efficiency of control), we modified the parameter p (Watkinson et al. 2000). If p_GM is the level of control achieved in a conventional crop, then in a GMHT crop the level of control achieved is

\[
p_{GM} = (1-\gamma)p_c.
\]

The parameter \(\gamma\) is the proportion by which control efficiency is changed under GM crops. A value of \(\gamma = 0\) implies that there is no increase in the efficiency of control under GM crops; a value of \(0 < \gamma < 1\) means that there is an increase in the efficiency of control under GM crops, while for a value of \((1-1/p_c) < \gamma < 0\) control is less efficient in GM crops than in conventional ones. The evidence (see Dewar et al. 2003) is that herbicidal control can be very efficient in GM crops, with the consequence that, in the absence of amelioration practices, \(\gamma\) is closer to one than zero.

Under conventional management the density of surviving weeds is reduced from \(N\) to \(\bar{N}\) very rapidly, as control is applied from the time that the crop is sown. However, under delayed spraying, the density of weeds can be maintained at \(N\), or in the case of band spraying a large fraction of \(N\), for a substantial portion of the initial period of growth. Thus, to assess the possible impacts of delayed spraying in GM crops on the potential abundance of weeds, we consider how introducing GM crops affects \(N\). We started with an equilibrium density, then iterated the model through a number of rotations following the introduction of GM crops in which the control parameter \(\gamma\) was set at values of 0.25, 0.5, 0.75, 0.9 and 1. The control parameter \(p\) was set to yield initial densities of mature plants of \(1 \text{ m}^{-2}\) and \(100 \text{ m}^{-2}\).

(c) Balance of weed density by second source of seed

The effects of delayed spraying on C. album are determined by the emergence of seedlings from the soil seed pool. The survival of weed plants to maturity and seed set is likely to be even lower in GM crops than in conventional ones and, thus, sources of seed from other parts of the rotation are likely to be of importance in determining seed pool densities. Specifically, it could be the case that, even if seed production is very low in the GM crops, small or moderate inputs of seed during other parts of the rotation could maintain a reserve of seeds and hence enhance or maintain the densities of weeds benefiting from delayed spraying. To account for this we make a further modification to the model. We assume that C. album is also capable of growing and setting seed in a second crop in the rotation. We assume that if sugar beet is grown in year 1, then C. album is also capable of...
emerging and setting seed in the crop grown in year 3 (note that the results presented are not dependent on which of the four remaining courses C. album is able to recruit in). In that case, the dynamics of the population become

\begin{equation}
N_{t+2} = g(1-m)S_{t} + \frac{1}{2}(1-g)S_{t-2} \tag{2.4}
\end{equation}

\begin{equation}
S_{t+2} = P_{2} c_{2} N_{t+2} + (1-m)^2 \left(1-g\right)S_{t} \tag{2.5}
\end{equation}

\begin{equation}
N_{t+5} = g(1-m)^{2}S_{t} + \frac{1}{2}(1-g)^{2}S_{t-2} \tag{2.6}
\end{equation}

\begin{equation}
S_{t+5} = (1-m)^{2}\left(1-g\right)S_{t} + (1-m)^{2}(1-g)^{2}S_{t-2} \tag{2.7}
\end{equation}

The new parameter, \( P_{2} \), is the proportion of seedlings surviving control in the second crop. It is assumed that all other model parameters are the same.

In the GMHT crop it was assumed that no plants are capable of surviving to produce seeds, i.e. \( \gamma = 1 \). In the conventional crop it was assumed that the level of control of C. album was \( p_{r} \) in sugar beet and \( p_{r} = p_{c} \) in the second crop. The constant \( c \) varies the level of control in the second crop relative to control in conventional sugar beet. We varied \( c \) to make levels of control in the second crop 25%, 50%, 90% and 100% as efficient as in conventional sugar beet. Equations (2.4)–(2.7) were solved iteratively (using 1000 generations of simulation) to yield the equilibrium density of seedlings emerging in the sugar beet crop in the rotation. We varied \( p_{r} \) between 0.00001 and 0.005 to yield equilibrium densities in the range 0–50 plants m\(^{-2} \).

3. RESULTS

(a) Weed phenology in relation to delayed spraying

Sugar beet, the crop studied by Dewar et al. (2003), is sown from mid-March to mid-April (Solfe 2003), so all weeds that are present in the seed pool and able to germinate at this time of year initiate growth at this time. This sowing time favours spring-germinating weeds such as C. album, Fallopia convolvulus (black bindweed) and Polygonum spp. (knotgrass and other bindweeds), as well as several species with no specialized germination time, such as Capsella bursa-pastoris (shepherd’s purse), Poa annua (annual meadow grass) and Senecio vulgaris (groundsel) (figure 1). The bold line in figure 1 represents the time of sowing of sugar beet. Under conventional herbicide-application regimes, the first herbicide applications occur

Table 1. Summary of mean parameter values used for modelling the population dynamics of Chenopodium album. (Parameters are taken from Freckleton & Watkinson (1998).)

<table>
<thead>
<tr>
<th>parameter</th>
<th>definition</th>
<th>mean value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N )</td>
<td>density of seedlings (m(^{-2} ))</td>
<td>—</td>
</tr>
<tr>
<td>( M )</td>
<td>density of mature plants (m(^{-2} ))</td>
<td>—</td>
</tr>
<tr>
<td>( S )</td>
<td>density of seeds in the soil after germination (m(^{-2} ))</td>
<td>—</td>
</tr>
<tr>
<td>( w_{m} )</td>
<td>weight of an isolated individual (g)</td>
<td>200</td>
</tr>
<tr>
<td>( d )</td>
<td>allometric constant</td>
<td>420</td>
</tr>
<tr>
<td>( k )</td>
<td>allometric coefficient</td>
<td>1.19</td>
</tr>
<tr>
<td>( s_{m} )</td>
<td>seed production of an isolated individual = ( dw_{m}c_{2} )</td>
<td>229 866</td>
</tr>
<tr>
<td>( a )</td>
<td>density response parameter</td>
<td>0.10</td>
</tr>
<tr>
<td>( g )</td>
<td>per annum probability of seed germination</td>
<td>0.10</td>
</tr>
<tr>
<td>( m )</td>
<td>per annum probability of seed mortality and loss of seed to emergence in cereals</td>
<td>0.20</td>
</tr>
<tr>
<td>( e )</td>
<td>competitive equivalence coefficient</td>
<td>1</td>
</tr>
<tr>
<td>( B )</td>
<td>density of sugar beet (m(^{-2} ))</td>
<td>11.11</td>
</tr>
<tr>
<td>( p )</td>
<td>proportion of seedlings surviving control (subscripted ‘c’ for conventional, ‘GM’ for GM crops or ‘c2’ for a second crop in the rotation)</td>
<td>varied</td>
</tr>
<tr>
<td>( \gamma )</td>
<td>control efficiency change in GM crops</td>
<td>varied</td>
</tr>
<tr>
<td>( f(x) )</td>
<td>density-dependent function for seed production in which ( x ) is the density of plants after the application of control</td>
<td>( f(x) = (1 + ax + eB)^{-k} )</td>
</tr>
</tbody>
</table>

We modified the basic model, where C. album is able to recruit only into sugar beet (parameters as in table 1) in the following ways and with the following assumptions.

(i) Weeds emerging late are small (5% or 10% of the maximum size of an isolated individual—this value is suggested by data from Kropff et al. (1992), cited in Freckleton & Watkinson (1998)), with the result that maximum seed production is only 5% or 10% of the baseline value.

(ii) Only a small proportion of weeds are able to establish in this way. (Data from Roberts (1964) indicate that between 1% and 30% of seedlings might emerge in May, for instance, although fields are usually sown between mid-March and mid-April, at which time the bulk of emergence will occur. The figure of 30% may be a considerable overestimate since the bulk of emergence would be expected in the few weeks following the sowing of the crop.) The emergence rate of seeds, \( g \), was therefore varied using values between 1% and 30% of the baseline value.
prior to crop emergence (pre-emergence herbicides), and herbicidal control continues until the crop cover is complete, typically during mid-June. The reason that weeds persist in such a system is primarily because some weeds survive the weed control, with their numbers potentially being comparatively high under conventional herbicides.

Under a delayed-spraying regime in a GM crop, the first application of herbicides could be delayed as late as August (Dewar et al. 2003) included a delay this late). The likely negative impacts on crop yields of allowing weeds to grow this long in competition with the crop (particularly competition arising from weeds growing within rows) would, however, tend to prohibit delays of this length. Some weed species will benefit from a delay in spraying of even a few weeks. These species include Capsella bursa-pastoris, Stellaria media, all of which are capable of producing seed within a few weeks. By contrast, most other species do not initiate flowering until May or June, with the result that, for most weeds, spraying would have to be delayed until July or August for any seed production to occur. A number of other weeds do not begin to flower or produce seed until August or later, and these weeds are unlikely to show any long-term benefits from delayed spraying. These include some species that are extremely important as sources of seeds for farmland birds (Wilson et al. 1999), such as C. album, F. convolvulus and Polygonum aviculare. These species are some of the largest weeds, and hence are also likely to be important as habitat for aerial arthropods. In terms of soil-dwelling arthropods, these weeds are likely to be important when they eventually die because they contribute a large amount of rotting plant material to the soil.

Dewar et al. (2003) indicated that the main species present were bindweeds (F. convolvulus and the knotgrass P. aviculare) and C. album. Surveys suggest that C. album is generally the most important weed occurring in sugar beet (Schroeder et al. 1993). If the positive effects of delaying spraying in the manner reported by Dewar et al. (2003) mainly result from the growth of this species or F. convolvulus and P. aviculare, then we predict that these positive effects on biodiversity are likely to be transient. This is because these weeds would be incapable of producing seeds even if spraying were delayed until August. Only C. bursa-pastoris, P. annua and S. media are likely to promote arthropod populations in the long term. Out of these species P. annua and S. media are regarded as ‘important’ components of the diet of farmland birds, whereas C. bursa-pastoris is not.

(b) Transient effects of delayed spraying

Following the introduction of GM crops, our population model predicts an ultimate reduction in the density of seeds, seedlings and mature plants. This arises because C. album and similar weeds are not capable of setting seed in a GM crop under delayed spraying. Figure 2 shows this effect for populations in which there are high (equilibrium M in the absence of GM crops = 1 m⁻²; figure 2a) and very high (equilibrium M in the absence of GM crops = 100 m⁻²; figure 2b) densities of mature weeds. We concentrate on such high densities as these are representative of areas that are likely to be disproportionately important for farmland biodiversity (Watkinson et al. 2000).

The ratio of the density of emerging weed seedlings (N) to the density emerging under conventional control measures the change in the number of weeds that will survive for a period under delayed spraying, and is 1 in the first year in which GM control is employed. In the case of moderate densities of weeds (figure 2a), there is a rapid decline in the number of seedlings benefiting from delayed spraying, and this is the case even if the net efficiency of control is only marginally higher in the GM system (γ = 0.25). Thus, we predict that, in fields that currently yield high densities of mature weeds that produce seeds, the positive effects recorded by Dewar et al. (2003) will be only transient. If the efficiency of control in the GM...
crop is very high ($\gamma$ is close to 1) then there are potentially large negative impacts in the course of just one or two rotations. Note that the effect of $\gamma$ depends on the density of weeds prior to the introduction of GM crops because the density of weeds prior to GM crops depends in turn on $p_m$ and $\gamma$ is a relative rather than an absolute increase in efficiency of control.

In the case of very high densities of weeds, there is again a rapid reduction in the density of emerging weed seedlings if the efficiency of control in GM crops is very high (figure 2b). There is the possibility of sustained high densities of weed seedlings in this case, but only if the increase in efficiency of control in the GM crops is low.

**Effect of recruitment from a second crop**

Conceivably, the positive effects of delayed spraying could be maintained if there was input of seed at other stages in the rotation. In figure 3 we explore what happens to weed populations if there is a second non-GM crop within the rotation in which $C. album$ is capable of producing seed.

Figure 3 shows the predicted equilibrium density of weed seedlings following the introduction of GM crops, relative to the equilibrium density of weed seedlings in conventional crops. This is the same quantity as plotted in figure 2, and, as shown in figure 2, it takes a value of unity in the year of first application, but only slowly approaches an eventual equilibrium value that, when $\gamma = 1$, is always zero in the absence of a second crop. In figure 3 this is plotted against the density of mature plants ($M$) prior to the introduction of GMHT crops. It is clear from figure 3, that persistent populations occur only when weed densities are originally high. Even in the case where as many weeds persist in the secondary crop as persist in conventional sugar beet, a current mature-plant density of at least 4 plants $m^{-2}$ is required for the weed population even to be able to persist. This would reflect exceptionally poor control of weeds under conventional agricultural methods. In such cases the introduction of GMHT crops may well lead to very dramatic increases in the efficacy of control, with the result that $\gamma$ will be high (close to 1) in currently weedy fields. For most farms, it is likely that the introduction of GMHT sugar beet would have the effects described by the points in the lower left corner of the figure, with the result that the presence of a second crop harbouring $C. album$ would provide no amelioration.
(d) Early cessation of spraying

When the final broad application of herbicide is relatively early in the season, relatively large densities of seeds may be produced at a stable equilibrium density (figure 4). This is because a fraction of germinating seedlings emerge after control has ceased. This means that, even if $\gamma = 1$, i.e. all weeds are controlled in the GM system as assumed in figure 4, some seedlings nevertheless are able to survive because they emerge too late to be subject to herbicide application. Although these results have to be considered as highly tentative, they indicate that it may be possible to develop methods for deploying herbicides that are consistent with maintaining weed populations and their associated biodiversity.

Figure 4. Modelling the potential for positive impacts of the early cessation of spraying on numbers of weed seeds. In this model maximal seed production ($s_m$) is reduced to either 5% (open circles) or 10% (filled circles) of maximal mean seed production (see table 1) since plants emerge later and hence have less time for growth and experience more intense competition from the crop. The proportion of seeds emerging following the cessation of spraying was varied up to 30% of maximal emergence (other parameters are as given in table 1).

4. DISCUSSION

The benefits proposed for GMHT crops basically include increased yields, reduced inputs and more convenient management practices. These benefits seem rather likely. It seems exceedingly likely that introducing GMHT crops will indeed yield a number of positive effects since weed control under broad-spectrum herbicides should be highly effective, with only a few or even single herbicide applications required to achieve very high levels of weed control. However, the likely impacts on biodiversity are of great concern and debate, and indeed this is the single reason why the Farm Scale Evaluation was commissioned (Firbank et al. 1999). In this and a previous paper (Watkinson et al. 2000) we have tried to point out that the short-term results of experiments attempting to evaluate the biodiversity consequences of introducing GMHT crops cannot simply be extrapolated to large spatial and temporal scales. Ignoring a large-scale perspective is dangerous, and large-scale predictions require a modelling approach.

Although it appears that delayed spraying offers only limited prospects for enhancing biodiversity in the long term, our modelling indicates that an early cessation of spraying could yield long-term benefits. This form of management could yield positive effects on biodiversity in conventional systems but is particularly suited to GM systems for two reasons:

(i) management would be less risky from the farmer’s point of view in a GM system, since all early-emerging weeds would be controlled in the GM crops, whereas it is not certain that all early-emerging weeds could be managed in the conventional crop; and

(ii) although the size of the seed pool would be increased, this would not pose a risk to future crops since control in GM crops is highly efficient.

However, if weed levels in non-GM crops were increased then the strategy would be counter-productive and would lead to increased inputs or decreased yields owing to weed competition in other stages of the rotation. As noted in § 3d, however, much work needs to be done to evaluate whether this approach can be implemented in a practical and economic manner.

In evaluating the long-term impacts of possible changes to farming systems, it is important to recognize the likely responses of farmers (Watkinson et al. 2000). One important consequence of recognizing the potential reactions of producers is that in the future it may be necessary to pay farmers to manage in a manner explicitly designed to promote biodiversity, if management conducive to biodiversity is expensive. This conclusion applies to any form of management, not just to the potential introduction of GMHT crops. Moreover, such practices may need to be as explicitly prescribed as to include the form and timing of herbicide application, since these may be critical as the results presented here indicate. Assessments of the biodiversity impacts of changing management are therefore required. Such impact assessments unfortunately have not been performed on the uptake and widespread adoption of many schemes (Kleijn & Sutherland 2003). Thus, irrespective of whether one is considering the introduction of GMHT crops, the introduction of stewardship schemes or some other change, the likely long-term impacts of changes in farm practices should be assessed using a combination of short-term trials and long-term model predictions.

Finally, we note that the modelling in this paper has assumed that weed populations are at an equilibrium value prior to the introduction of GM crops. In fact the evidence is that weed populations have declined precipitously over the past century, and there is nothing to indicate that this decline has been halted (Robinson & Sutherland 2002; Preston et al. 2002). Therefore future declines in weed numbers could be severe even in the absence of the introduction of GM crops. It is owing to the extremely negative impacts of conventional agriculture on farmland biodiversity that there is such concern about the further impacts that GM crops may have. Thus, we are concerned to foster a debate in which the various costs and benefits associated with the various agricultural technologies can be compared to help produce an agricultural system that is supportive of the needs of the farmer, the public and the environment.
This work was funded by Defra. The authors thank A. Dewar for his comments on an earlier draft.

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