Downloaded from rsbl.royalsocietypublishing.org

biology
letters

An analytical model assessing the potential threat to natural habitats from insect resistance transgenes: continuous transgene input

Colleen K Kelly, Michael Bowler and Felix Breden

Biol. Lett. 2006 **2**, 293-297
doi: 10.1098/rsbl.2006.0444

References This article cites 16 articles, 1 of which can be accessed free
http://rsbl.royalsocietypublishing.org/content/2/2/293.full.html#ref-list-1

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Biol. Lett.* go to: **http://rsbl.royalsocietypublishing.org/subscriptions**

This journal is © 2006 The Royal Society

Downloaded from rsbl.royalsocietypublishing.org

biology
letters

Biol. Lett. (2006) **2**, 293–297
doi:10.1098/rsbl.2006.0444
Published online 9 February 2006

An analytical model assessing the potential threat to natural habitats from insect resistance transgenes: continuous transgene input

Colleen K. Kelly[1,*], Michael Bowler[2] and Felix Breden[3]

[1]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*
[2]*Department of Physics, University of Oxford, Keble Road, Oxford OX1 3RH, UK*
[3]*Department of Biological Sciences, Simon Fraser University, Burnaby BC, Canada V5A 1S6*
**Author for correspondence* (colleen.kelly@zoo.ox.ac.uk).

The potential effects of 'escape' of genetically modified material (transgenes) into natural communities is a major concern in their use. These effects may be limited in the first instance by limiting the proportion of transgene-carrying plants in the natural community. We previously presented an analytical model of the ecological processes governing the relative abundance and persistence of insect resistance (IR) transgenes in a natural community. In that paper, we illustrated the case in which the transgene is input into the community in a single season using data from oilseed rape (OSR) and its known herbivore, *Plutella macropennis*. We found that the transgene is unlikely to have a great impact on the natural community. Here, we extend the model for repeated input of crop pollen carrying the transgene. We show the model output, again using OSR, for continuous input of the transgene over 10 years, the projected commercial lifetime of a transgene without associated undesirable agronomic effects. Our results do not change our original conclusion that the IR transgene need not have a large impact on the natural community and our suggestions for assessing and mitigating any threat still stand.

Keywords: genetically modified organism; GMO; genetically engineered organisms; GEO; invasive species

1. INTRODUCTION

The potential effects of 'escape' of genetically modified material (transgenes) into natural communities is a major concern in their use (Arnaud *et al.* 2003; GM Science Review Panel 2003). These effects may be limited in the first instance by limiting the proportion of transgene-carrying plants in the natural community. In a previous paper, we presented an analytical model that investigates the regulatory effects of ecological processes in governing the relative abundance and persistence of insect resistance (IR) transgenes in a natural community (Kelly *et al.* 2005). Although ecological interactions may be the most important driver predicting the spread of transgenes (Rieseberg & Burke 2001), the focus till then had been primarily from a population genetics perspective, and our model was constructed in recognition of that dearth.

Our model incorporates natural year-to-year variation in herbivore numbers through a development of differential sensitivity (DS) storage dynamics (Kelly & Bowler 2002, 2005; Kelly *et al.* 2005). Storage dynamics focuses on the role of recruitment in population persistence and coexistence (Chesson & Warner 1981; Chesson 2003). DS dynamics describe the interaction between competing species pairs, one of which is more sensitive to environmental fluctuations than the other and unable to recruit when the environment is unfavourable. During more favourable periods, the more sensitive species is able to recruit through outcompeting the less-sensitive species. For the spread of an IR transgene, the relevant environmental factor is herbivory, with its pattern of year-to-year fluctuation. After illustrating the application of our model using oilseed rape (OSR), we concluded that IR transgenes might be maintained at low levels unlikely to have a great impact on the natural environment if possession of the transgene carries even a relatively small cost. A potential cost might be a stimulation by the transgene of protein-production in order to enhance insect-resistance properties, accompanied by a lower growth rate in the seedling (cf. Kelly & Hanley 2005).

In our original model, we examined population evolution after a single episode of IR transgene input into the wild-type population had occurred. Such a situation might arise when the associated agronomic traits are undesirable and the transgenic crop is only planted when it is known that the coming year will bring heavy herbivore loads. The previous version of our model is also applicable to instances of naturally occurring mutations that affect plant-defence properties or in the introduction of an herbivore-resistant invader species that may interbreed with its native competitor. Here, we offer a variation of our model that determines the consequences of multiple instances of gene flow. The variation may be applied to either a continuous or an intermittent but repeated period of use of the transgene. We show the results of a potential of 10-year commercial lifetime such as might be possible for an agronomically more benign transgene. We again use OSR as an example because of the accessibility of suitable data, but the model is of much more general use, being applicable to any system involving annual plants with a seed bank and fluctuating pest levels.

2. THE MODEL

For the population under natural conditions, the number of seeds in the seed bank in year $t+1$, x^+, is the sum of the number remaining L and the number recruited R

$$x^+ = L + R, \tag{2.1}$$

where L has the form $(1-K)x$ and where K is the long-term rate at which seeds are lost from the seed bank.

Received 13 January 2006
Accepted 23 January 2006

© 2006 The Royal Society

Downloaded from rsbl.royalsocietypublishing.org

With interbreeding, the recruitment term is broken into a sum of factors of the form

$$R=\sum[d][m], \tag{2.2}$$

where d is the number of seeds endowed with the appropriate alleles by females and m is the frequency with which pollen containing the complementary allele is encountered. In Kelly *et al.* (2005), we considered three varieties drifting through the Hardy–Weinberg landscape under ecological pressure, ww, wg and gg where w is the wild-type allele and g the gene modification; pollen was proportional to the number of adults of a given variety present in the population. If there is continued input of g pollen, the eqns (2.3) of Kelly *et al.* (2005) are modified. The nature of the modification is to add to the terms in $[m]$ an external source of g pollen. The within-population pollination probabilities in eqn (2.3) of Kelly *et al.* (2005), p_i, are changed in $[m]$ as follows

$$p_{ww}\rightarrow p_{ww}(1-\varepsilon),$$
$$p_{wg}\rightarrow p_{wg}(1-\varepsilon),$$
$$p_{gg}\rightarrow p_{gg}(1-\varepsilon)+\varepsilon,$$

where ε is the probability of successful pollination by pollen arriving from outside the community. Eqns (2.3) of Kelly *et al.* (2005), which describe the evolution with time of the density of seeds x_i of variety i, then become

$$\left.\begin{aligned}
x_{ww}^{+}&=(1-K_{ww})x_{ww}+(1-\varepsilon)[Y_{ww}y_{ww}+0.5Y_{wg}y_{wg}]\\
&\quad\times[p_{ww}+0.5p_{wg}]\\
x_{wg}^{+}&=(1-K_{wg})x_{wg}+(1-\varepsilon)\{[Y_{ww}y_{ww}+0.5Y_{wg}y_{wg}]\\
&\quad\times[p_{gg}+0.5p_{wg}]+[Y_{gg}y_{gg}+0.5Y_{wg}y_{wg}]\\
&\quad\times[p_{ww}+0.5p_{wg}]\}+\varepsilon[Y_{ww}y_{ww}+0.5Y_{wg}y_{wg}]\\
x_{gg}^{+}&=(1-K_{gg})x_{gg}+(1-\varepsilon)\{[Y_{gg}y_{gg}+0.5Y_{wg}y_{wg}]\\
&\quad\times[p_{gg}+0.5p_{wg}]\}+\varepsilon[Y_{gg}y_{gg}+0.5Y_{wg}y_{wg}]
\end{aligned}\right\}, \tag{2.3}$$

where x_i^{+} is the value one time step later than x_i, Y_i is the seed yield/adult and y_i is the number of adults of variety i at a site. The sum of the recruitment terms in square brackets in equation (2.3) is the total seed yield

$$Y_{ww}y_{ww}+Y_{wg}y_{wg}+Y_{gg}y_{gg},$$

for any value of the fraction of external pollination ε; for $\varepsilon=0$, eqns (2.3) of Kelly *et al.* (2005) are of course recovered. The external input ε can be a function of time; we have simply switched on a fixed value at a time $t=0$, when $x_{wg}=x_{gg}=0$, and switched it off again T years later, when the field is no longer sown with this particular modification.

Eqns (2.5) of Kelly *et al.* (2005) employ the convenient variables $z_i=(K_ix_i)/Y_i$. These are scaled expressions for the seed densities and have the advantage that their evolution equations have behaviour determined almost entirely by ratios of biologically significant parameters. For slow change, z_i is equal to y_i, the fraction of sites occupied by adult plants. The modifications are trivially carried through from equations (2.3), rewriting the densities of adult plants y_i and the pollination probabilities p_i in terms of the variables z_i and the new equations read

$$\left.\begin{aligned}
z_{ww}^{+}&=(1-K_{ww})z_{ww}+\frac{K_{ww}(1-\varepsilon)}{D_2}\\
&\quad\times\left[\frac{z_{ww}}{a^{*}}+0.5Y^{*}z_{wg}\right]\left[\frac{z_{ww}}{a^{*}\eta^{*}}+0.5z_{wg}\right]\\
z_{wg}^{+}&=(1-K)z_{wg}+\frac{K(1-\varepsilon)}{D_2}\left[\frac{z_{ww}}{a^{*}}\left(\frac{1}{Y^{*}}+\frac{1}{\eta^{*}}\right)+z_{wg}\right]\\
&\quad\times[z_{gg}+0.5z_{wg}]+\frac{K\varepsilon}{D_1}\left[\frac{z_{ww}}{a^{*}Y^{*}}+0.5z_{wg}\right]\\
z_{gg}^{+}&=(1-K)z_{gg}+\frac{K(1-\varepsilon)}{D_2}[z_{gg}+0.5z_{wg}]^2\\
&\quad+\frac{K\varepsilon}{D_1}[z_{gg}+0.5z_{wg}]
\end{aligned}\right\}, \tag{2.4}$$

where

$$D_2=\left(\frac{z_{ww}}{a^{*}}+z_{wg}+z_{gg}\right)\left(\frac{z_{ww}}{a^{*}\eta^{*}}+z_{wg}+z_{gg}\right)$$

$$D_1=\frac{z_{ww}}{a^{*}}+z_{wg}+z_{gg}.$$

Y^{*} is the ratio of seed yields Y/Y_{ww}, a^{*} the relative advantage of the transformed over the untransformed type and η^{*} the ratio of pollen production η/η_{ww}. If $\varepsilon\rightarrow 0$, eqns (2.5) of Kelly *et al.* (2005) are recovered.

Equations (2.3) and (2.4) can be evolved from an initial situation in which only the ww variety is present and it becomes evident that in the early stages ($z_{ww}\approx 1$)

$$x_{wg}^{+}-x_{wg}\approx\varepsilon Y_{ww},$$

since the initial density of adult plants of variety ww is unity, Y_{ww} seeds are produced per site and of these a fraction ε are wg seeds. After n early steps

$$x_{wg}\approx n\varepsilon Y_{ww}.$$

Similarly the scaled variable z_{wg} obeys

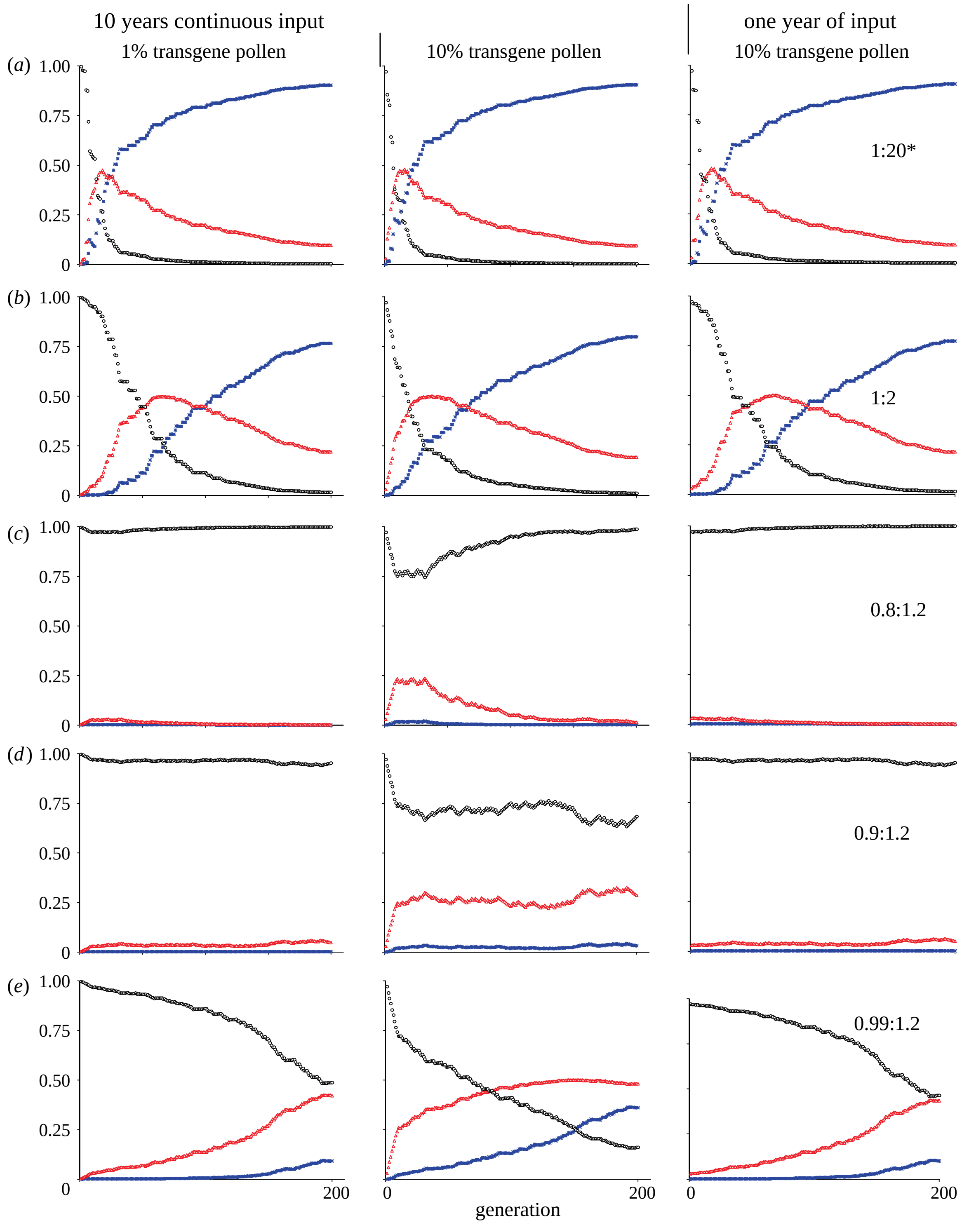
$$z_{wg}^{+}-z_{wg}\approx\frac{K\varepsilon}{Y^{*}}.$$

As expected, x_{wg} and z_{wg} increase linearly with time early on. x_{gg} and z_{gg} will be negligible until the wg variety has built up—we are only allowing g pollen into the environment, not gg crop seed.

3. MODEL OUTPUT

Iterations of the model over 200 generations show that the progress of the transgene in the wild population does not differ hugely if g pollen is an input for 10 years or for only 1 year (figure 1). For example, if the long-term rate at which seeds are lost

Downloaded from rsbl.royalsocietypublishing.org



*cost:benefit (cost of the transgene when herbivory is low vs advantage of the transgene when herbivory is high). blue = gg; black = ww; red = wg. Costs and benefits are reckoned as performance relative to the ww individual.

Figure 1. Change over 200 generations of wild-type (open black circle), homozygous GM (blue asterisk) and hemizygote (open red triangle) genotypes under differing levels of insect resistance (IR) advantage when herbivory levels are high 35% of the time. The column on the left shows proportions of genotype in the population when there is 1% continuous input of transgene pollen from external sources over 10 years; the centre column shows genotype proportions when external pollen flow is 10% for 10 years; the column on the right shows external pollen flow at 10% for 1 year with no external *g* pollen received thereafter. (*a*), (*b*) The effect of levels of advantage of protection from *Plutella* herbivory recorded for crop systems. Advantage values are calculated as the ratio of seed set of oilseed rape with and without protection from herbivory. For both (*a*) and (*b*) we assume no disadvantage to the IR allele when herbivory is low (Stewart *et al.* 1997; Brown *et al.* 1999). (*c–e*) Effects of differing levels of cost to carrying IR alleles when herbivory is low, projected for non-crop species. Here, the IR advantage at high levels of herbivory is assumed to be 1.2, i.e. at high herbivory, the wild-type plant produces 80% the number of seeds per seed sown as individuals carrying the IR allele. In all cases, $K_{ww}=K=0.3$ (K=long-term rate at which seeds are lost from the seed bank; Roberts & Boddrell 1983).

Downloaded from rsbl.royalsocietypublishing.org

from the seed bank K is equal to 0.3 (30% per year), the seed yield per adult Y_i is equal for wild and transgene types and the probability of successful pollination from an external g pollen source is 3%, then $z_{wg} \approx 10^{-2}t$ (only about one-third of seeds in the bank are the latest crop). If the external g pollen source were removed after 10 years, about 10% of plants in the wild would be the *wg* variety. Once the g pollen source is removed, the considerations discussed in Kelly *et al.* (2005) take over and the progress of the transgene would follow the trajectory mapped in fig. 1 and table 2 of the earlier study.

However, the rate of g pollen input—whether low *or* high—can become irrelevant very rapidly. If the modified allele has an overwhelming advantage or suffers no disadvantage, then it will take over the wild-type population (figure 1*a*) rather quickly from a very low level. Where neither of these conditions hold, the results from various levels of continuous g pollen input do not differ greatly from those inferred starting from a single injection (reading across figure 1). In general, it is not the pattern of pollen injection that determines whether untransformed plants can be maintained at a high level (above 75%; reading from right to left in figure 1*c* and *d*), but rather the differences in costs incurred by the transgene in the background of the natural genome (compare figure 1*d* with *e*, with costs equal to 10 and 1%, respectively). If the IR advantage at high levels of herbivory is 1.2, then a disadvantage of 0.8 at low levels means no cause for concern, 0.9 is marginal and 0.99 should be avoided.

4. DISCUSSION

We observe that continuous input of the transgene into the wild population over a realistic period of time does not produce a hugely different result to single-season input of the transgene. Thus, we are left with much the same conclusion as that we reached in our previous study: the effects of IR transgenes need not pose an immediate threat to natural communities. Transgene-carrying plants can be restricted to a low proportion of the natural population provided that there is some suitable level of 'cost' associated with the transgene—which can be assessed with the methods discussed in Kelly *et al.* (2005). Persistently low levels of transformed plants will limit or eliminate potential 'knock-on effects' to other parts of the natural community such as herbivores and their predators and parasites.

The possibility that as much as 10% of the pollination will be derived from sources outside the natural population (figure 1, central column) is likely to be extreme. Studies of pollen movement in OSR indicates such movement levels to be unlikely (Cresswell *et al.* 2002, 2004; Cresswell & Osborne 2004). Moreover, such pollen may be less effective than the wild-type pollen and even when effective, may produce offspring capable of producing fewer seeds than the pure wild-type (Hauser *et al.* 1998; Pertl *et al.* 2002). We have chosen 10 years as the possible commercial lifetime of an OSR transgene although it is not unlikely that it will be less (J. Durkin 2005, personal communication).

Nonetheless, we do not propose that our model can be used as a justification for the release of untested IR transgenes. Rather, our model is intended as a tool for more efficient investigation of the potential risk to natural communities from the effects of individual transgenes. The modification of our model here presented offers a way to examine the effect of differing use of regimes, and it is possible to use our model to specify the length of a continuous input regime as well as a use regime that varies over time in its input into the natural community.

Although we have used a lepidopteran herbivore to illustrate our model, our model may be applied in risk assessment and mitigation for any sort of foliage-damaging system. Furthermore, with minor modifications, it may also be applied to risk assessment/mitigation for seed predators, for pathogens or for other soil-borne agents of plant damage (Kelly *et al.* 2005).

We thank Jonathan Durkin for his information on current agricultural practices. C.K.K. thanks Merton College for its hospitality during the writing of this paper.

Arnaud, J.-F., Viard, F., Delescluse, M. & Cugen, J. 2003 Evidence for geneflow via seed dispersal from crop to wild relatives in *Beta vulgaris* (Chenopodiaceae): consequences for the release of genetically modified crop species with weedy lineages. *Proc. R. Soc. B* **270**, 1565–1571. (doi:10.1098/rspb.2003.2407)

Brown, J., McCaffrey, J. P., Harmon, B. L., Davis, J. B., Brown, A. P. & Ericson, D. A. 1999 Effect of late season insect infestation in yield, yield components and oil quality of *Brassica napus*, *B. rapa*, *B. juncea* and *Sinapis alba* in the Pacific Northwest region of the United States. *J. Agric. Sci. Cambridge* **132**, 281–288. (doi:10.1017/S0021859699006413)

Chesson, P. 2003 Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. *Theor. Popul. Biol.* **64**, 345–357. (doi:10.1016/S0040-5809(03)00095-9)

Chesson, P. L. & Warner, R. R. 1981 Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* **117**, 923–943. (doi:10.1086/283778)

Cresswell, J. E. & Osborne, J. L. 2004 The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow. *J. Appl. Ecol.* **41**, 539–546. (doi:10.1111/j.0021-8901.2004.00912.x)

Cresswell, J. E., Osborne, J. L. & Bell, S. A. 2002 A model of pollinator-mediated geneflow between plant populations with numerical solutions for bumblebees pollinating oilseed rape. *Oikos* **98**, 375–384. (doi:10.1034/j.1600-0706.2002.980302.x)

Cresswell, J. E., Davies, T. W., Patrick, M. A., Russell, F., Pennell, C., Vicot, M. & Lahoubi, M. 2004 Aerodynamics of wind pollination in a zoophilous flower *Brassica napus*. *Funct. Ecol.* **18**, 861–866. (doi:10.1111/j.0269-8463.2004.00917.x)

GM Science Review Panel 2003 GM science review (first report): an open review of the science relevant to GM crops and food based on interests and concerns of the public. London: Department of Trade and Industry pp. 109–194

Hauser, T. P., Jørgensen, R. B. & Østergård, H. 1998 Fitness of backcross and F_2 hybrids between weedy *Brassica napa* and oilseed rape (*B. napus*). *Heredity* **81**, 436–443. (doi:10.1038/sj.hdy.6884250)

Downloaded from rsbl.royalsocietypublishing.org

Kelly, C. K. & Bowler, M. G. 2002 Coexistence and relative abundance in forest tree species. *Nature* **417**, 437–440. (doi:10.1038/417437a)

Kelly, C. K. & Bowler, M. G. 2005 A new application of storage dynamics: differential sensitivity, diffuse competition and temporal niches. *Ecology* **86**, 1012–1022.

Kelly, C. K. & Hanley, M. E. 2005 Juvenile growth and palatability in congeneric British herbs. *Am. J. Bot.* **92**, 1586–1589.

Kelly, C. K., Bowler, M. G., Breden, F. M., Fenner, M. & Poppy, G. M. 2005 An analytical model assessing the potential threat to natural habitats from insect resistance transgenes. *Proc. R. Soc. B* **272**, 1759–1767. (doi:10.1098/rspb.2005.3131)

Pertl, M., Hauser, T. P., Damgaard, C. & Jørgensen, R. B. 2002 Male fitness of oilseed rape (*Brassica napus*), weedy *B. rapa* and their F_1 hybrids when pollinating *B. rapa* seeds. *Heredity* **89**, 212–218. (doi:10.1038/sj.hdy.6800131)

Rieseberg, L. H. & Burke, J. M. 2001 The biological reality of species: gene flow, selection, and collective evolution. *Taxon* **50**, 47–67.

Roberts, H. A. & Boddrell, J. E. 1983 Seed survival and periodicity of seedling emergence in eight species of Cruciferae. *Ann. Appl. Biol.* **103**, 301–304.

Stewart, C. N., All, J. N., Raymer, P. L. & Ramachandran, S. 1997 Increased fitness of transgenic insecticidal rapeseed under insect selection pressure. *Mol. Ecol.* **6**, 773–779. (doi:10.1046/j.1365-294X.1997.00239.x)