

# Adapting the GENESYS gene flow model for GM canola in Australia

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## **Summary**

A spatio-temporal canola gene flow model was constructed based on the equations used for GENESYS (Colbach et al. 2001a; 2001b). The model was simpler in form than GENESYS, because several of the features used in GENESYS are not applicable to the Australian cropping environment.

The model failed to adequately replicate the data from Rieger et al. (2002), largely because of a failure to accurately predict gene flow from fields past 50 m.

Sensitivity analysis determined that canola seed bank decay parameters and the pollen dispersal curve were the main factors influencing the output of the model. The main factors of importance that need understanding are the shape of the pollen distribution curve, the persistence of canola seed in the soil, the ability of old canola seed to germinate and the amount of self-pollination among canola volunteer populations.

In general, the model predicted low rates of gene flow from GM canola crops in the environment. The greatest risk of gene flow was for small non-GM canola fields adjacent to GM canola fields. Any distance of greater than 10 m between canola fields greatly reduced gene flow. Canola volunteer management was predicted to be important in maintaining low GM canola seed banks in fields.

In principle, it would be possible to use GENESYS for other crops; however, the model would need to be re-parameterised for each crop and environment. At a minimum, detailed data on crop seed persistence in the soil, volunteer emergence rates, flower and seed production of crop and volunteers, outcrossing rates and the pollen dispersal function would be needed. Some of this data may already be available, but the rest would need to be gathered for the specific environment(s) of interest.

## **Introduction**

GENESYS is a model developed in France to predict gene flow and persistence of GM canola in a complex cropping system (Colbach et al. 2001a; 2001b). GENESYS attempts to model the effects of cropping system, crop rotation, tillage operations and pollen and seed dispersal on gene flow between GM oilseed rape crops and volunteers in both time and space. GENESYS is based around European cropping environments and it is not clear how well GENESYS will predict pollen flow in the Australian environment.

The aim of this work was to investigate GENESYS for Australian cropping systems, to determine how well it predicts the results obtained by Rieger et al. (2002), to understand the main factors driving the model and to determine the ability of GENESYS to predict dispersal of GM traits in Australian cropping environments.

## **Models**

A licence agreement for use of the software was signed with the developers of GENESYS at INRA; however, the software was not provided for use in time. Therefore, the model was re-built using the equations published in Colbach et al. (2001a; 2001b). The developers have made a number of additions to the software since that time including

segregation of genes and the addition of numerous GM traits. However, the current task does not require these elaborations and the model was developed from the original papers.

A number of changes were made to the model to fit Australian agricultural systems (Table 1). The main changes were as follows:

1). Changes to the seed bank matrix. The original model had a seed bank to 20 cm and allowed considerable deep cultivation. In Australia, cropping systems have moved away from intensive cultivation and towards no-till (D'Emden and Llewellyn 2006). Also recent research indicates no significant difference in canola seed bank behaviour between minimum tillage and no-till cultivation systems (Baker and Preston 2008). Tillage in Australian cropping systems is rarely aggressive and rarely deep. Therefore, a single-layer seed bank model was included.

2) Crop and land use patterns were limited to cereals (represented by wheat), canola and a pulse (represented by faba beans). A number of the land uses in GENESYS (spring crops, set aside) are not used in the canola growing regions of Australia and were not included.

3) The meteorological sub model was not included. In GENESYS, this sub model is mainly used to drive flowering time of canola plants; particularly those in set aside that have been mown, but also volunteers in crop fields. Set aside is not a normal land use in Australia. For the model built it was assumed that all canola plants flowered at the same time, regardless of germination time. This assumption could result in a slight over-estimation of gene flow between plants; however, given that southern Australian cropping environments are often terminated by summer drought limiting flowering time, this assumption is reasonable.

4) Crop sowing rates were reduced to reflect Australian cropping systems in line with recommendations from McRae et al. (2008). Wheat stand establishment was set at 140 plants m<sup>-2</sup>, faba beans at 40 plants m<sup>-2</sup> and canola seeding rate at 100 seeds m<sup>-2</sup>.

5) A crop option for a pulse crop was included in the rotation. This was based on faba bean biology. Faba bean competition against canola was set at 1 in comparison to canola (Felton et al. 2004) and herbicide control of canola volunteers in faba bean crops was set at 90%.

6) Canola crop yield was allowed to vary. In the original GENESYS, canola yield is effectively set at a maximum of 2.5 T ha<sup>-1</sup> by the maximum seed production m<sup>-2</sup>. For the model built, canola yield was allowed to vary by linking the number of flowers m<sup>-2</sup> and the number of seeds pod<sup>-1</sup> to canola yield. The data of Wright et al. (1995) was used to develop the equations. The number of flowers m<sup>-2</sup> was linked to canola yield by the equation:

$$\text{Number of flowers (pods) m}^{-2} = 2084.1 \times (\text{canola yield in T/ha})^{0.7369}$$

The number of seeds per pod was linked to canola yield by the equation:

$$\text{Number of seeds pod}^{-1} = 14.523 + 4.767 \times \ln(\text{canola yield in T/ha})$$

A check was made to ensure that multiplying these two values together and dividing by seed weight (3 g per 1000 seed) correctly estimated the specified yield.

This means that unlike GENESYS, the current model uses yield to determine flower production and seeds per pod.

7) The spatial model used by Colbach et al. (2001b) estimated gene flow from every  $\text{m}^2$  of the source field to every  $\text{m}^2$  of the sink field, both by pollen and seed. In a large landscape of  $40 \text{ km}^2$  this process was exceedingly time consuming. An examination of the decay curve for seed movement used by Colbach et al. (2001b) showed that the proportion of seed travelling more than 5 m was  $4.7 \times 10^{-17}$ . The maximum seed produced in a 50 ha field with 5 T/ha yield is only  $8.3 \times 10^{10}$ . Therefore, it is unlikely the seed movement function would contribute to any significant gene flow with Australian field sizes. Therefore, the seed dispersal function was not included.

An examination of the decay curve for pollen movement demonstrated that pollination events decline rapidly with distance. An examination of pollen movement out of the source field found that >99.5% of all pollen leaving the source field came from the first 50 m of the field. Therefore, the amount of pollen exiting the source field would vary little for large source fields. To simplify the spread model, the amount of pollen leaving the source field was estimated using the pollen dispersal function and summing for the 50 m of the source field closest to the edge. This was then distributed across the landscape according to the pollen decay function. The amount of pollen that reached a sink field of any size and at any distance situated under the pollen curve was summed as the incoming pollen. This was then used to calculate the percentage of pollination events due to pollen arriving from the source field. The incoming pollen divided by the total amount of pollen present in the field (incoming pollen plus resident pollen).

Table 1. Parameters used in the model. Parameters in bold were different to the original GENESYS model and based on Australian data.

Parameter	Value	Equation used
survival of young seeds in the soil - a	1.96	$\exp(-a*\text{time}(\text{months})^b)$
survival of young seeds in the soil - b	0.52	
Survival of old seeds - c	0.08	$1-c*\text{time}(\text{months})$
Seedling emergence - canola	0.925	
Seedling emergence - volunteers	0.81	
Effect of seed age on emergence rate	1	
Maximum rates of adults per seedling	1	
Maximum stand - canola	125	
Herbicide control - wheat	0.95	
<b>Herbicide control - pulse</b>	0.9	
Herbicide control - canola	0	
Crop volunteer competition - cereals	0.3125	
<b>Crop volunteer competition - pulses</b>	1	
Flower production - crop	1500	
Flower production - volunteers	232	
<b>Maximum flower density - canola</b>	2810	$2084.1*\text{Yield}^{0.7369}$
<b>Seed production per flower - crop</b>	16.5	$14.523+4.767*\ln\text{Yield}$
Seed production per flower - volunteers	2.13	
<b>Maximum seed production - canola</b>	50000	
Seed loss - crop	0.05	
Seed loss - volunteer	1	
<b>Canola seed sown</b>	100	
<b>Cereal plant density</b>	140	
<b>Pulse plant density</b>	40	
<b>Canola yield T/ha</b>	1.5	
Gene flow - a	1.213	$(a/2\text{PI})*(\text{distance}^b)$
Gene flow - b	-3.213	
Distance between crops (m)	5	

## Results

### Temporal model

The temporal model was run with a canola-wheat-faba bean-wheat-canola rotation starting with canola in Year 0. Under the conditions used in the simulation, the model predicted canola seed banks would decline rapidly over time (Figure 1). By the time canola was re-planted in Year 4, the seed bank was less than 0.1 seed m<sup>-2</sup>. The model conditions predicted the GM canola seed bank would not build up over time in a 4 year rotation. The model predicted canola volunteers would be highest in the crop immediately after canola and drop to very low densities in subsequent crops (Figure 2).

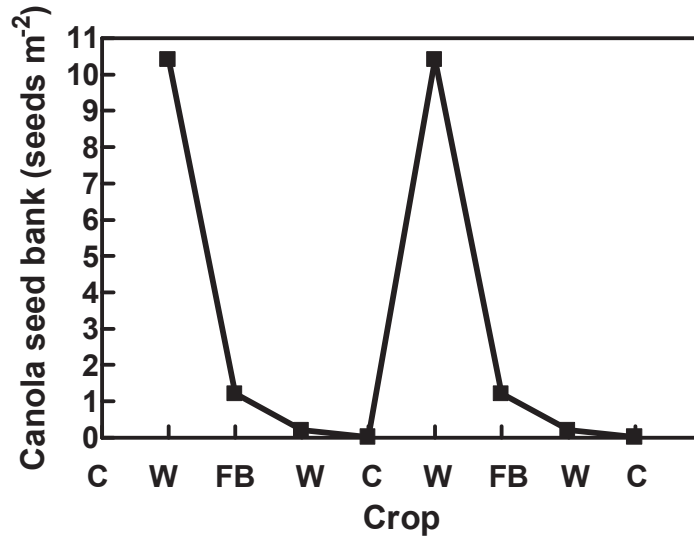


Figure 1. Predicted canola seed bank at seeding during a canola-wheat-faba bean-wheat-canola crop rotation

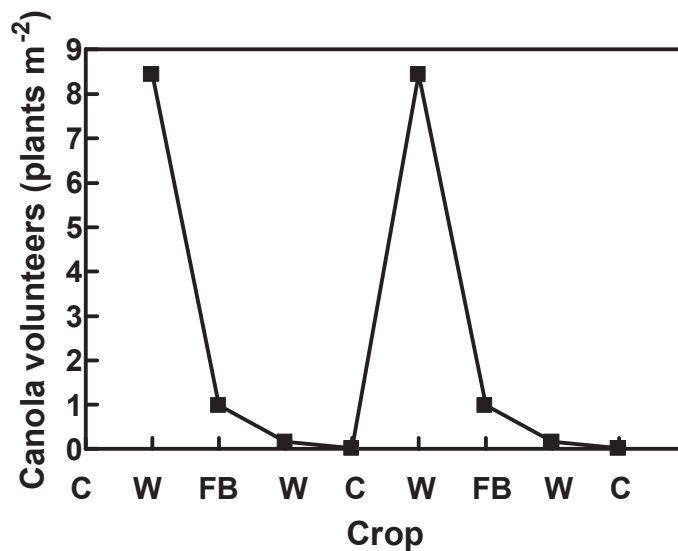


Figure 2. Predicted canola volunteer emergence after crop seeding during a canola-wheat-faba bean-wheat-canola crop rotation

Sensitivity analysis of the temporal model showed the main drivers were the canola seed bank decay characteristics, the ability of old seed to germinate, the level of control of volunteers and the amount of seed shatter. Baker and Preston (2008) reported canola seed banks declined rapidly with time in southern Australia. Baker and Preston (2008) also showed that the ability of old seed to germinate declined at a faster rate than did the seed bank. After 2.5 years considerable canola seed remained in the soil, but that seed was mostly not viable. The GENESYS model operates in the opposite manner with the seed bank declining quickly and germination ability remaining high. While the results from the model were similar to the observed data from the field, the mechanisms are likely to be different. Therefore, under different conditions, the GENESYS model may not reliably predict seed bank decline.

Several factors likely to vary within the Australian cropping system were explored for their effect on persistence of the canola seed bank. The model predicted the canola seed bank would increase with crop yield as a result of a greater number of seeds being shed at harvest (Figure 3). However, the predicted rapid decline in the canola seed bank with time predicted by the model meant the canola seed bank would be very small by the time the next canola crop was planted.

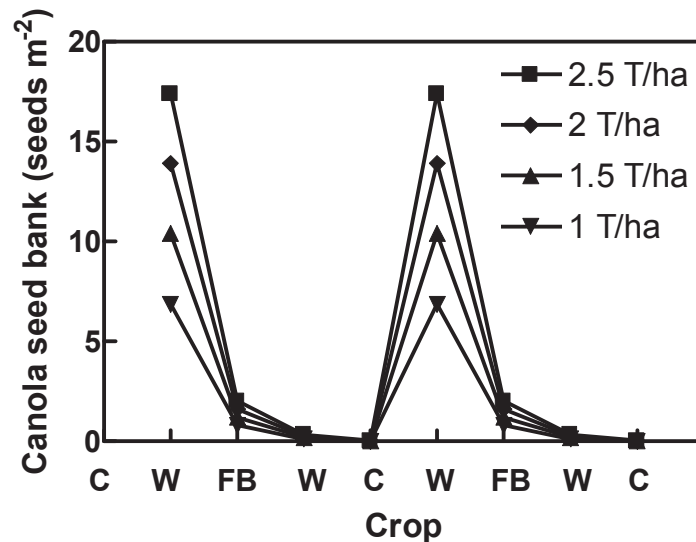


Figure 3. Predicted effect of canola crop yield on canola seed bank at seeding during a canola-wheat-faba bean-wheat-canola crop rotation. Simulations conducted with standard values and canola crop yield varying from 1 to 2.5 T ha<sup>-1</sup>.

The amount of seed shattering at harvest can vary depending on environmental conditions, timing of operations and equipment set up. Gulden et al. (2003) showed seed shatter under Canadian harvest conditions can be as much as 10% of the harvested crop. Simulations varying the amount of seed shatter showed this parameter greatly influenced the predicted canola seed bank in the year after canola was grown (Figure 4). However, the predicted rapid decay in the canola seed bank in the model meant that these differences would almost disappear by the time canola was planted a second time.

Simulations with varying levels of volunteer control were conducted. High levels of volunteer canola control throughout the rotation were predicted to result in low levels of canola seed in the seed bank (Figure 5). Reducing canola volunteer control was predicted to result in replenishment of the canola seed bank from volunteers through the rotation. Consistently poor levels of volunteer canola control were predicted to result in the canola seed bank building up over time. This highlights the importance of volunteer canola control in managing GM canola in the crop rotation.

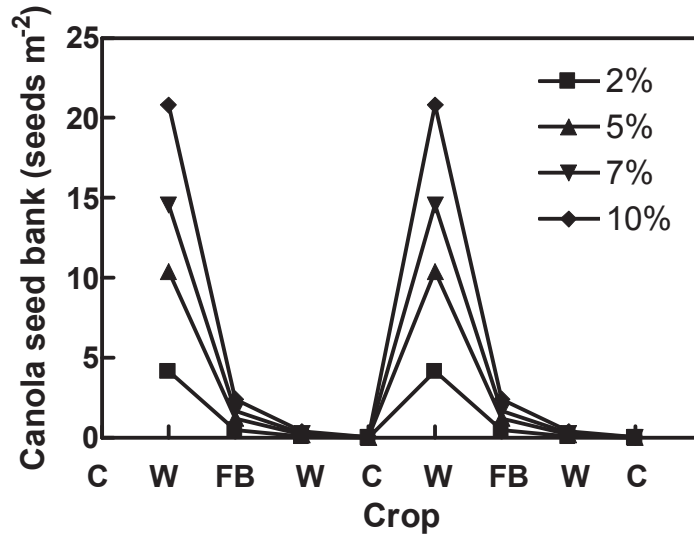


Figure 4. Predicted effect of seed shatter at harvest on persistence of canola seed banks in a canola-wheat-faba bean-wheat-canola crop rotation. Simulations were conducted with standard values and seed shatter varying from 2% to 10%.

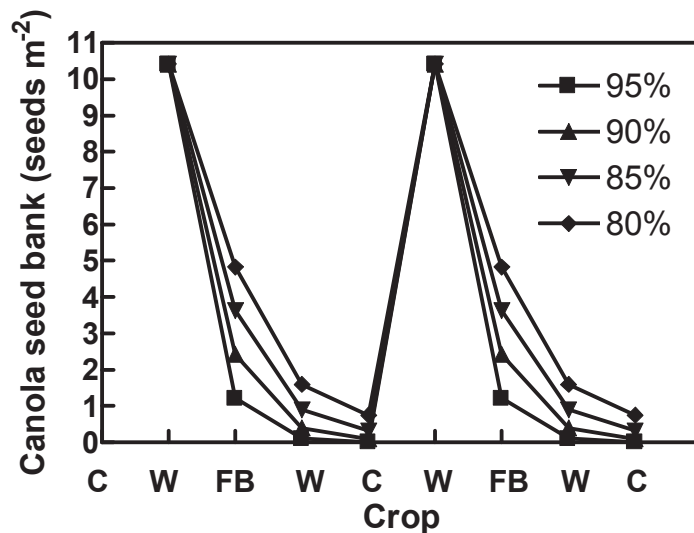


Figure 5. Predicted effect of varying levels of canola volunteer control in subsequent crops during a canola-wheat-faba bean-wheat-canola crop rotation. Simulations were conducted with standard values and volunteer management varying from 80% to 95%.

Changing the rotation in order to grow canola more often was predicted to result in greater potential for canola volunteers to occur in subsequent canola crops. Simulations with canola every 3 years instead of every 4 years predicted an increase in the canola seed bank for the next canola crop by 6-fold. Simulations with canola grown every second year predicted an increase in the canola seed bank for the next canola crop by 50-fold compared to the 4 year rotation.

## Spatial model.

The spatial model was run in an environment with square fields for simplicity, although other field shapes were tested (see below). A distance of 5 m between adjacent crops was used. The model predicted the frequency of pollination events in the recipient field would decline rapidly with distance from the source field (Figure 6). Fields immediately adjacent to the source field were predicted to have more than 100 times the amount of gene flow compared with fields 100 m away. At 2 km from the source field the predicted seed produced as a result of gene flow was less than  $10^{-8}\%$  of the total seed produced. Increasing the gap between adjacent canola fields from 5 m to 10 m reduced the predicted amount of gene flow between fields by approximately 5-fold (not shown).

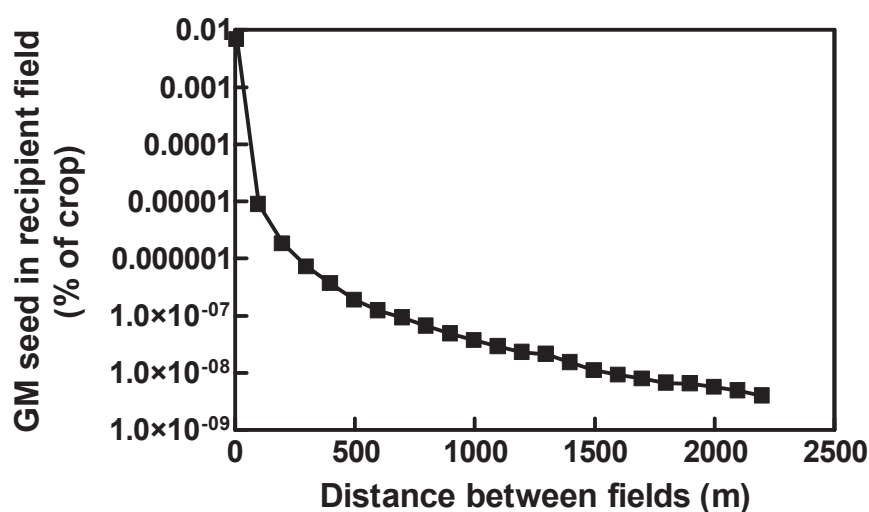


Figure 6. Predicted gene flow from a 50 ha GM canola field to a 50 ha recipient field situated at various distances from the GM canola field.

Sensitivity analysis determined that the shape of the pollen dispersal curve, the recipient field size and the recipient field shape had the largest effects on gene flow. Field shape was only important in the model for fields close to the source field. Extremes of shape parallel or perpendicular to the source field influenced the amount of gene flow to the greatest extent. Rectangular fields parallel to the source field were predicted to have higher levels of gene flow than rectangular fields situated perpendicular to the source field. The model predicted that rectangular fields of 5 ha (71 m x 700 m) situated parallel to a 50 ha source field would have 45% more gene flow than square fields and double the gene flow of rectangular fields situated perpendicular to the source field (not shown). Spatial arrangement of fields in the environment with respect to the source field also mattered. Fields on the diagonal were predicted to have less gene flow than fields adjacent to the source field. Crop yield had no impact on gene flow in the model, because yield in every canola field changed together in the model.

Recipient field size had an impact on predicted gene flow with more gene flow to smaller fields. Adjacent fields of 5 ha in size were predicted to have 3 times more gene flow than 50 ha fields (Figure 7). The difference in gene flow between smaller and larger fields was predicted to decrease with distance from the source field. By 1 km from the source field, the predicted difference in gene flow was less than 2-fold between the smallest and

largest fields. This suggests the highest risks for gene flow are for small fields immediately adjacent to the source field.

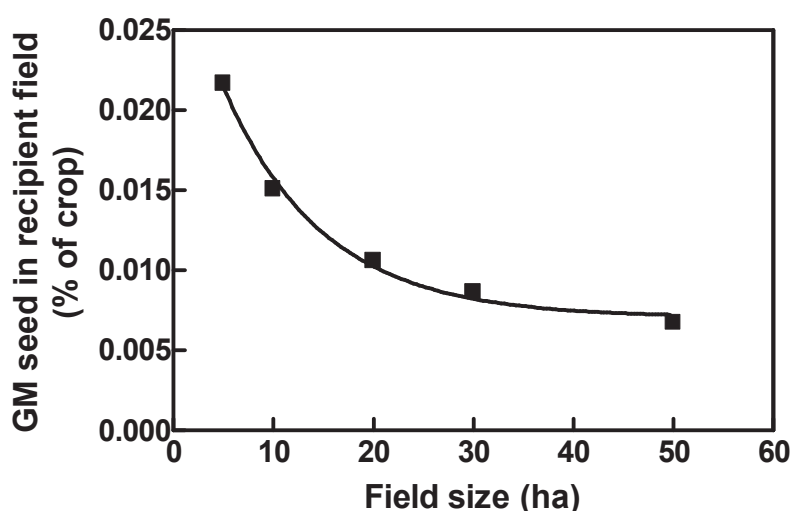


Figure 7. Predicted effect of field size on gene flow from a 50 ha GM canola field to immediately adjacent fields of various sizes.

The level of gene flow predicted by the model was much lower than that observed by Rieger et al. (2002). Two specific features stand out. Firstly, the predicted level of gene flow was more than 10-fold lower than the average observed by Rieger et al. (2002), except for immediately adjacent fields. Colbach et al. (2005) also reported that GENESYS underestimated, by about 10-fold, the amount of gene flow observed in experimental plots in France at distances greater than 50 m. Devaux et al. (2008) examined gene flow from herbicide resistant canola crops in France and reported a similar under-estimation of the true gene flow by the method used in GENESYS. Clearly a different pollen dispersal curve is necessary in order to more accurately predict gene flow. The current dispersal curve used underestimates gene flow with increasing distance. The second factor evident in the Rieger et al. (2002) data is the sporadic, rather than ordered, distribution of gene flow. This suggests that factors other than the leptokurtic pollen distribution are influencing gene flow under Australian conditions.

### Temporal and spatial model

As constructed for the present exercise, the temporal and spatial model resulted in very low levels of GM dispersal across the cropping environment over time. An environment with 81 fields of 50 ha each was simulated with a 9 year rotation. The simulation assumed that GM canola was planted in the central field and conventional canola was planted in 25% of the other fields (Figure 8). The simulation was run for each field over the 9 years of the rotation. The resulting GM canola seed bank populations at seeding of the crop in the 9<sup>th</sup> year are shown in Figure 9.

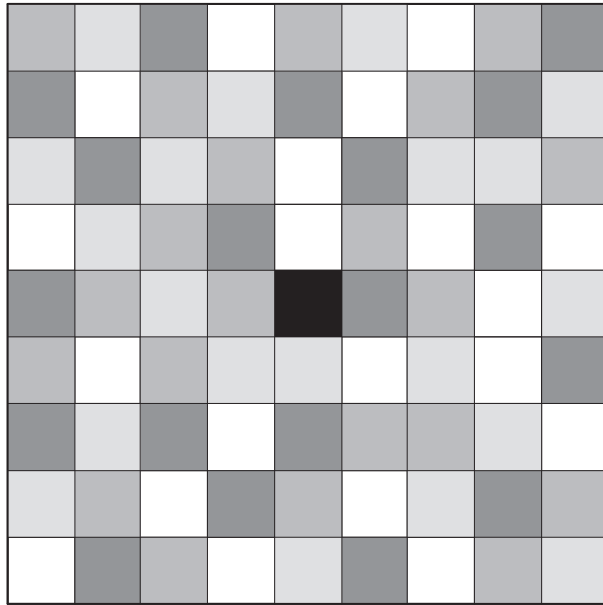


Figure 8. Distribution of crops in year 8 of the landscape used for the spatial-temporal model. Fields were 50 ha in size. The central field (■) was sown to GM canola in Years 0, 4 and 8. The crop rotation was canola-wheat-faba bean-wheat-canola in all fields, but with different starting crops: canola (■), wheat (■), faba beans (□) and wheat (■).

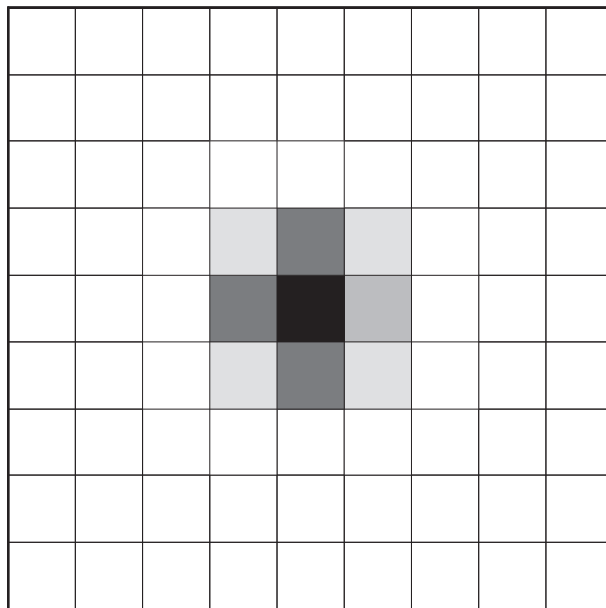


Figure 9. Distribution of GM canola in the landscape from gene flow. GM canola seed numbers per hectare prior to sowing the 9<sup>th</sup> crop: >10,000 (■), <30 (■), <3 (■), <0.01 (■) and <0.001 (□).

Combining the two models predicted GM canola seed banks would be largest in the field where GM canola was grown. Small GM canola seed banks (< 30 seed ha<sup>-1</sup>) were predicted to occur in immediately adjacent fields, regardless of whether canola was grown in those fields at the same time as in the central field. The remainder of the

landscape was predicted to have very small ( $\ll 1$  seed  $\text{ha}^{-1}$ ) GM canola seed banks. The model predicted most fields would have less than 1 GM canola seed field<sup>-1</sup>.

The model predicted GM canola volunteers would be so few at flowering that they would not significantly contribute to gene flow into non-GM fields (frequencies of  $<10^{-7}$  for adjacent fields). However, small non-GM canola volunteer populations could be overwhelmingly pollinated by a GM canola crop present in an adjacent field. This appears to be a flaw in the model in that incoming pollen is simply added to the amount of resident pollen and distributed across all plants. This is an unlikely outcome given that canola is known to have high levels of self-pollination (Hayter and Cresswell 2006).

Gene flow from GM canola to non-GM volunteers was predicted to have a significant impact on the amount of GM seed present in a field. However, under all circumstances, the model predicted low levels of GM canola gene flow to other fields in the environment. This was largely the result of volunteer canola populations, both GM and non-GM, being predicted to decline rapidly in a continuously cropped system.

The results obtained in these simulations were much lower than those reported by Colbach et al. (2001b). Colbach et al. (2001b) reported the model predicting the largest amounts of gene flow to fields sown to oilseed rape or to set aside at the same time as the central field was sown to canola. The model used here does not include set aside. Secondly, the model used here had large fields more typical of Australian cropping systems, whereas Colbach et al. (2001b) used many small fields. Colbach et al. (2001b) also used a combination of spring and winter crops in the rotation, whereas the model used here just included winter crops. Sensitivity analyses conducted by Colbach et al. (2004; 2005) identified sowing date relative to volunteer emergence, survival of seeds in the soil, emergence of volunteers, tillage, crop succession, date of set aside cutting, seed movement and pollen movement as being important factors in determining the amount of GM seed at harvest. Several of these parameters are not important in Australian cropping systems.

## **Conclusions**

### **Parameterise the GENESYS model using Australian canola data.**

As the GENESYS model was not available in time, a simplified version of the model was reconstructed from the equations published in Colbach et al. (2001a; 2001b). The GENESYS model operates on a per plant or per  $\text{m}^2$  basis and data was not available from Australia for many of the variables. In particular, detailed seed bank decline, volunteer emergence and pollen distribution models are required to fully parameterise GENESYS. Where these values were not available from Australia, the French values in Colbach et al. (2001a; 2001b) were used. In correspondence with Dr. Nathalie Colbach of INRA it transpired that the code for GENESYS would not be made available. This limits the number of parameters that could be changed in the model were it available for use.

### **Determine how well the model replicates the canola gene flow pattern determined by Rieger et al. (2002).**

The GENESYS model poorly replicated the gene flow pattern of Rieger et al. (2002). In general, GENESYS underestimated gene flow by more than 10-fold, except for

immediately adjacent fields. Colbach et al. (2005) reported that GENESYS estimated the amount of gene flow observed in experimental plots in France to a distance of about 50 m accurately. After that, GENESYS tended to underestimate gene flow by about 10-fold. Devaux et al. (2008) also reported the pollen distribution equations in GENESYS predicted lower amounts of gene flow than observed in fields. Devaux et al. (2008) suggested the tail of the leptokurtic distribution used for the pollen dispersal model was the problem. The other factor the GENESYS model was unable to replicate was the sporadic distribution of pollination events observed in the data of Rieger et al. (2002). It is clear that pollen dispersal curves estimated from data up to 50 m from the source greatly underestimate gene flow when used to predict gene flow at greater distances.

### **Sensitivity analyses of the model to determine major drivers.**

As constructed here, the major drivers of the model were seed bank survival and pollen distribution for the temporal and spatial models respectively. As no sufficiently detailed data were available for either parameter in Australia, simulations varying these were not explored further. Other factors that influenced the temporal model were the ability of old seed to germinate, the level of control of volunteers and the amount of seed shatter. Other factors that influenced the spatial model were the recipient field size, the recipient field shape and the amount of gene flow from GM canola crops to non-GM volunteers.

The main factors of importance are the shape of the pollen distribution curve, the persistence of canola seed in the soil, the ability of old canola seed to germinate and the amount of self-pollination among canola volunteer populations.

### **Uncertainty associated with the model output with respect to Australia.**

The temporal and spatial models were run separately to examine the influence of a number of variables in the Australian cropping system. The Australian cropping system is much simpler than the system being modelled in GENESYS and this allowed several factors to be discarded. Through all simulations, the model predicted low rates of GM canola persistence and low rates of GM canola gene flow in the environment.

The temporal model provided predictions similar to data on canola volunteers obtained by Baker and Preston (2008), but for different reasons. Baker and Preston (2008) observed that canola seed banks in South Australia declined more slowly than predicted in the model, but that volunteer seedling emergence was much lower. Crop yield and shattering both influenced predicted canola seed banks in the model, but canola volunteer control was much more important. The model predicts that poor canola volunteer control would result in more persistent GM canola seed banks.

The spatial model poorly predicted the data of Rieger et al. (2002), largely as a result of underestimation of gene flow at distance. This is a function of the leptokurtic distribution used in the model. Field size, field shape and field position all influenced the amount of gene flow predicted. The model predicted that small fields immediately adjacent to the GM source field would have the highest percentage of GM seed in the crop. Fields not adjacent to the GM source field were always predicted to receive very low levels of gene flow, regardless of size or shape.

The spatial/temporal model was only run under one set of conditions, simulating 81 fields over 9 years. Pollen movement from GM crops to non-GM volunteers had a large influence on the predictions. The model predicted that pollen movement from GM crops to non-GM volunteers in fields had a greater influence on gene flow between fields than was pollen movement between canola crops. There are two reasons why this occurred. Firstly, the model predicts that all seed set on canola volunteers enters the seed bank whereas most of the seed in canola fields is harvested. Secondly, the model does not take account of self-pollination in canola.

### **Ability of GENESYS to predict gene flow in other crops under Australian conditions.**

GENESYS has been expanded to include multiple GM traits including 3 herbicide resistance traits (Colbach et al. 2005), male sterility, plant height and quality traits (Fargue et al. 2005), as well as other improvements (Colbach et al. 2008). A sugar beet version of the model has also been created (Sester et al. 2008). This demonstrates GENESYS could be used to model gene flow in other crops and in other environments. However, the model would need to be parameterised for each crop and each environment.

Lessons from the sensitivity analysis suggest that the following minimum data are required in order for GENESYS to be used to predict gene flow in the Australian environment:

1. Crop seed soil persistence functions applicable to the environment;
2. Volunteer emergence rates;
3. Flower and seed production of the crop in relation to yield;
4. Flower and seed production of volunteers;
5. Percentage of out-crossing of the crop species; and
6. Pollen dispersal curves to greater than 50 m from the source.

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