

Project title: Compendium of Pest Forecasting Models

Project number: CP 127

Project leader: Rosemary Collier, University of Warwick

Report: Final Report

Previous report: N/A

Key staff: Nataliya Tkachenko

Location of project: Warwick Crop Centre, University of Warwick

Industry Representative: David Martin, Plant Systems

Date project commenced: 1 February 2014

**Date project completed
(or expected completion date):** 31 July 2014

DISCLAIMER

AHDB, operating through its HDC division seeks to ensure that the information contained within this document is accurate at the time of printing. No warranty is given in respect thereof and, to the maximum extent permitted by law the Agriculture and Horticulture Development Board accepts no liability for loss, damage or injury howsoever caused (including that caused by negligence) or suffered directly or indirectly in relation to information and opinions contained in or omitted from this document.

Copyright, Agriculture and Horticulture Development Board 2020. All rights reserved.

No part of this publication may be reproduced in any material form (including by photocopy or storage in any medium by electronic means) or any copy or adaptation stored, published or distributed (by physical, electronic or other means) without the prior permission in writing of the Agriculture and Horticulture Development Board, other than by reproduction in an unmodified form for the sole purpose of use as an information resource when the Agriculture and Horticulture Development Board or HDC is clearly acknowledged as the source, or in accordance with the provisions of the Copyright, Designs and Patents Act 1988. All rights reserved.

AHDB (logo) is a registered trademark of the Agriculture and Horticulture Development Board.

HDC is a registered trademark of the Agriculture and Horticulture Development Board, for use by its HDC division.

All other trademarks, logos and brand names contained in this publication are the trademarks of their respective holders. No rights are granted without the prior written permission of the relevant owners.

The results and conclusions in this report are based on an investigation conducted over an extended period. The conditions under which the experiments were carried out and the results have been reported in detail and with accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with interpretation of the results, especially if they are used as the basis for commercial product recommendations.]

AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

[Name]

[Position]

[Organisation]

Signature Date

[Name]

[Position]

[Organisation]

Signature Date

Report authorised by:

[Name]

[Position]

[Organisation]

Signature Date

[Name]

[Position]

[Organisation]

Signature Date

CONTENTS

| | |
|--|----------|
| GROWER SUMMARY | 1 |
| Headline..... | 1 |
| Background..... | 1 |
| Summary | 1 |
| Financial Benefits | 6 |
| Action Points..... | 6 |
| | |
| SCIENCE SECTION | 7 |
| Introduction | 7 |
| Materials and methods | 8 |
| Results | 1439 |
| Day Degree Models for Aphids overwintering in the egg stage: | 42 |
| - Willow carrot aphid | 42 |
| - Lettuce root aphid..... | 42 |
| - currant lettuce aphid | 42 |
| Discussion | 44 |
| Conclusions | 45 |
| Knowledge and Technology Transfer | 45 |
| References | 46 |

GROWER SUMMARY

Headline

The equations for seven of the MORPH pest models have been extracted and summarised so that they are available to others. Simpler versions of the models have been built in EXCEL and validations of these initial versions confirm that the approach is valid.

Background

Over the last 20 years, funding from Defra and HDC in particular has enabled the development of a variety of models for forecasting pest outbreaks, some of which have been used very successfully to target control measures. Such models can also be used to predict the future impact of climate change on pest insects. Unfortunately, changes in funding strategies mean that these bespoke models are no longer supported in terms of software upgrades and some will become inaccessible in the longer term as operating systems change.

The aim of this project is to focus on pest insects and to develop a compendium of pest models in spreadsheet format that can be used directly with inputs of current weather data, or could be transferred by commercial companies to more complex systems. The reason for building 'simple' models is to 1) make them readily accessible, 2) make them more resilient to upgrades in operating systems and 3) ensure that they can be modified over time without the need for specialist programming expertise. Many of these are day-degree models, but others are complex (such as the Monte Carlo models for carrot fly and cabbage root fly). The compendium could be applicable to all sectors of horticulture and indeed could incorporate pests of arable crops and potato – and could be extended to 'diseases'. The compendium could also be extended to link to other resources e.g. HDC Factsheets.

Summary

The objectives of the project were to:

1. Create the pest compendium structure using representative models.
2. Incorporate Monte-Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) and day-degree models (lettuce-root aphid, willow-carrot aphid, currant-lettuce aphid) into the spreadsheet-based tool.
3. Validate models using corresponding MORPH outputs (i.e. using the same set of weather data to run the models in MORPH and the pest compendium).

The pest compendium structure was built in EXCEL. The advantage of EXCEL is that it is a well-supported commercial software package that will continue to be supported into the future and it is relatively simple to program. The disadvantage from the point of view of MORPH is that EXCEL will not accommodate the full size and complexity of the Monte-Carlo models (cabbage root fly, carrot fly etc) and it is not possible to produce such a full graphical output as with the MORPH software.

The equations used in the Monte-Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) and day-degree models (lettuce-root aphid, willow-carrot aphid, currant-lettuce aphid) have been described and presented in tables within the body of the report. An example (for cabbage root fly) is shown in Table 1. For the Monte Carlo models, the tables also include the estimated low temperature threshold for each stage of development and the coefficient of variation, which describes the 'spread' of development, since within any population, some insects develop more rapidly than others, giving the typical shapes of the 'curves' provided by insect sampling data (Figure 1). The lower thresholds in these tables are those estimated by linear extrapolation and may not necessarily be the 'true' functional threshold.

The four Monte Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) were incorporated into the EXCEL structure. As illustrated in Table 1, the models contain a number of equations which describe the rate of insect development in relation to temperature (air or soil) and these models also incorporate variability in the insect population, taking account of the fact that some insects in a population develop more rapidly than others. In MORPH, there is an imaginary insect population, usually of 500 individuals, and each individual in this population is followed through each generation and its development is summarised in the output with that of the 499 others. EXCEL will not deal with this very large computing procedure and so the models have been adapted to follow different 'groups' of insects rather than individuals through each generation, to give the estimated dates of 10% and 50% activity as MORPH does.

Table 1. Equations for the cabbage root fly model. The lower threshold temperatures were estimated by linear extrapolation and may not be the ‘true’ functional thresholds.

| Phase of insect development | Equation | Lower threshold temperature °C | Coefficient of variation (%) |
|---|---|--------------------------------|------------------------------|
| Early spring emergence (ESE) <i>Describes post-diapause development of overwintering pupae of the early-emerging biotype (the most prevalent)</i> | CRF1 = 0.5785*TEMP-1.981 | 6 | 28 |
| Late spring emergence (LSE) <i>Describes post-diapause development of overwintering pupae of the late-emerging biotype</i> | CRF2 = 0.592+2.2525*EXP(-EXP(-0.274*(TEMP-12.49))) | 7 | 23 |
| Pre-oviposition period (first batch) (POP1) <i>Describes maturation period of first batch of eggs</i> | CFR3 = 1.4049*TEMP-10.68 | 8 | 10 |
| Pre-oviposition period (second batch) (POP2) <i>Describes maturation period of second batch of eggs</i> | CRF4 = 1.5*(1.4049*TEMP-10.68) | 8 | 10 |
| Egg and larval development (ELD) <i>Describes development from time egg is laid until pupa is formed</i> | CFR5 = 0.836+5.66*(EXP(-EXP(-0.1473*(TEMP-16.17)))) | 6 | 13 |
| Pupal development (PD) <i>Describes development of pupa until adult emerges</i> | CRF6 = 0.01+11.0*(EXP(-EXP(-0.104*(TEMP-14.28)))) | 4 | 7 |

As an example, Table 2 shows the sequence of the equations in the EXCEL cabbage root fly model through the generations. The model ‘divides’ because each generation lays two batches of eggs and this leads to more than one estimate of the timing of each ‘event’ as the model progresses.

The day-degree models (lettuce-root aphid, willow-carrot aphid, currant-lettuce aphid) are much simpler than the Monte Carlo models. These have also been described within the body of the report (lower threshold temperature and estimated day-degree sum required to reach the predicted event) and have been incorporated into the compendium.

Table 2. Sequence of equations in the EXCEL cabbage root fly model for early-emerging flies through the generations.

| Generation | Early-emerging flies | | | | | | | |
|------------|----------------------|------|------|------|------|------|------|------|
| 1 | ESE | | | | | | | |
| 1 | POP1 | | | | POP2 | | | |
| 1 | ELD | | | | ELD | | | |
| 1 | PD | | | | PD | | | |
| 2 | POP1 | | POP2 | | POP1 | | POP2 | |
| 2 | ELD | | ELD | | ELD | | ELD | |
| 2 | PD | | PD | | PD | | PD | |
| 3 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 |
| 3 | ELD | ELD | ELD | ELD | ELD | ELD | ELD | ELD |

The models were validated by running the MORPH models and the EXCEL models using the same sets of weather data, which were those provided by Plantsystems Ltd to run the pest forecasts.

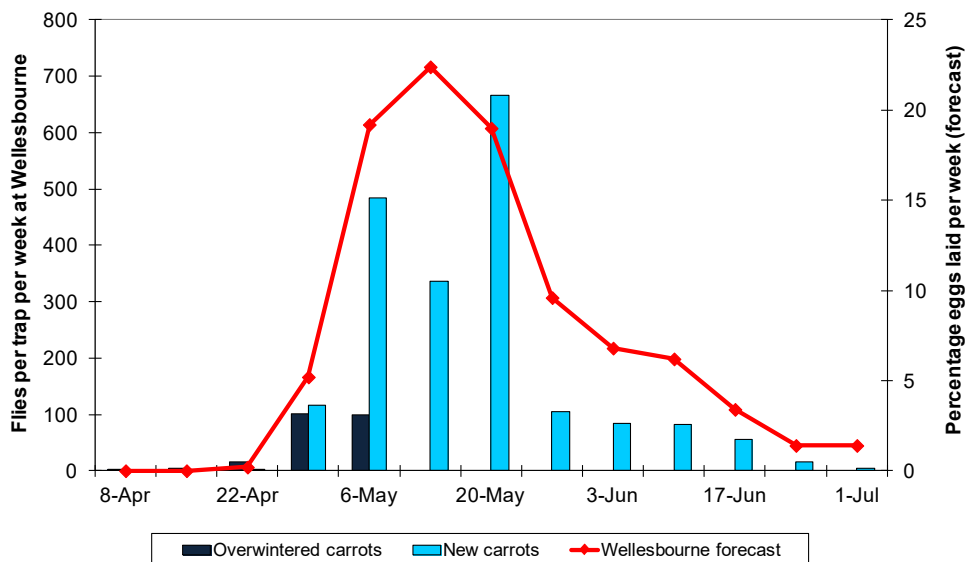


Figure 1. First generation carrot fly at Wellesbourne in 2014 – monitoring data (number of flies per sticky trap per week) compared with output from the MORPH carrot fly model and showing the ‘spread’ of development in the first generation.

Table 3. Validations of the EXCEL model for early spring emergence – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| Validation sites | EXCEL | | | | MORPH | | | | Difference in days (EXCEL-MORPH output) | | | |
|--------------------------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|---|-----|-----------|-----|
| | Emergence | | Eggs laid | | Emergence | | Eggs laid | | Emergence | | Eggs laid | |
| | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% |
| 2012 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 22-Mar | 30-Mar | 02-May | 19-May | 25-Mar | 01-Apr | 03-May | 24-May | -3 | -2 | -1 | -5 |
| Kent | 24-Mar | 01-Apr | 08-May | 11-May | 25-Mar | 01-Apr | 01-May | 14-May | -1 | 0 | 7 | -3 |
| Lancashire | 20-Mar | 27-Mar | 08-May | 22-May | 22-Mar | 28-Mar | 01-May | 24-May | -2 | -1 | 7 | -2 |
| Nottinghamshire | 28-Mar | 09-Apr | 10-May | 22-May | 30-Mar | 11-Apr | 09-May | 24-May | -2 | -2 | 1 | -2 |
| Scotland | 31-Mar | 16-Apr | 25-May | 27-May | 02-Apr | 17-Apr | 24-May | 29-May | -2 | -1 | 1 | -2 |
| Suffolk | 29-Mar | 10-Apr | 18-May | 22-May | 31-Mar | 11-Apr | 11-May | 25-May | -2 | -1 | 7 | -3 |
| Yorkshire | 29-Mar | 09-Apr | 20-May | 23-May | 30-Mar | 10-Apr | 11-May | 25-May | -1 | -1 | 9 | -2 |
| SECOND GENERATION | | | | | | | | | | | | |
| Cornwall | 07-Jul | 26-Jul | 17-Jul | 04-Aug | 16-Jul | 31-Jul | 26-Jul | 12-Aug | -9 | -5 | -9 | -8 |
| Kent | 08-Jul | 18-Jul | 19-Jul | 28-Jul | 09-Jul | 19-Jul | 20-Jul | 02-Aug | -1 | -1 | -1 | -5 |
| Lancashire | 12-Jul | 24-Jul | 24-Jul | 06-Aug | 11-Jul | 25-Jul | 23-Jul | 07-Aug | 1 | -1 | 1 | -1 |
| Nottinghamshire | 10-Jul | 23-Jul | 19-Jul | 30-Jul | 17-Jul | 26-Jul | 25-Jul | 07-Aug | -7 | -3 | -6 | -8 |
| Scotland | 04-Aug | 13-Aug | 12-Aug | 22-Aug | 09-Aug | 18-Aug | 18-Aug | 05-Sep | -5 | -5 | -6 | -14 |
| Suffolk | 02-Jul | 10-Jul | 12-Jul | 22-Jul | 04-Jul | 15-Jul | 18-Jul | 30-Jul | -2 | -5 | -6 | -8 |
| Yorkshire | 21-Jul | 30-Jul | 27-Jul | 08-Aug | 24-Jul | 03-Aug | 03-Aug | 16-Aug | -3 | -4 | -7 | -8 |
| THIRD GENERATION | | | | | | | | | | | | |
| Cornwall | 15-Sep | 08-Oct | 02-Oct | 29-Oct | 18-Sep | 27-Sep | 04-Oct | 13-Oct | -3 | 11 | -2 | 16 |
| Kent | 02-Sep | 12-Sep | 12-Sep | 25-Sep | 08-Sep | 15-Sep | 17-Sep | 30-Sep | -6 | -3 | -5 | -5 |
| Lancashire | 13-Sep | 05-Oct | 09-Oct | 28-Oct | 07-Sep | 25-Sep | 14-Sep | 13-Oct | 6 | 10 | 25 | 15 |
| Nottinghamshire | 08-Sep | 29-Sep | 26-Sep | 28-Oct | 13-Sep | 25-Sep | 25-Sep | 15-Oct | -5 | 4 | 1 | 13 |
| Scotland | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| Suffolk | 24-Aug | 02-Sep | 04-Sep | 11-Sep | 12-Sep | 19-Sep | 01-Oct | 10-Oct | -19 | -17 | -27 | -29 |
| Yorkshire | 04-Oct | 01-Nov | 10-Nov | 14-Nov | 30-Sep | 10-Oct | 11-Oct | 29-Oct | 4 | 22 | 30 | 16 |
| 2013 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 20-Apr | 27-Apr | 31-May | 04-Jun | 23-Mar | 28-Apr | 18-May | 05-Jun | 28 | -1 | 13 | -1 |
| Kent | 26-Apr | 03-May | 25-May | 01-Jun | 27-Apr | 04-May | 13-May | 02-Jun | -1 | -1 | 12 | -1 |
| Lancashire | 06-May | 13-May | 03-Jun | 09-Jun | 08-May | 14-May | 30-May | 08-Jun | -2 | -1 | 4 | 1 |
| Norfolk | 26-Apr | 03-May | 03-Jun | 06-Jun | 28-Apr | 03-May | 12-May | 08-Jun | -2 | 0 | 22 | -2 |
| Scotland | 11-May | 18-May | 03-Jun | 09-Jun | 11-May | 18-May | 28-May | 07-Jun | 0 | 0 | 6 | 2 |
| Suffolk | 22-Apr | 26-Apr | 21-May | 01-Jun | 22-Apr | 26-Apr | 09-May | 28-May | 0 | 0 | 12 | 4 |
| Yorkshire | 11-May | 20-May | 05-Jun | 11-Jun | 13-May | 20-May | 30-May | 10-Jun | -2 | 0 | 6 | 1 |
| SECOND GENERATION | | | | | | | | | | | | |
| Cornwall | 31-Jul | 08-Aug | 09-Aug | 20-Aug | 24-Jul | 01-Aug | 31-Jul | 13-Aug | 7 | 7 | 9 | 7 |
| Kent | 19-Jul | 26-Jul | 26-Jul | 04-Aug | 21-Jul | 29-Jul | 28-Jul | 09-Aug | -2 | -3 | -2 | -5 |
| Lancashire | 30-Jul | 08-Aug | 08-Aug | 20-Aug | 04-Aug | 12-Aug | 13-Aug | 24-Aug | -5 | -4 | -5 | -4 |
| Norfolk | 30-Jul | 07-Aug | 08-Aug | 18-Aug | 27-Jul | 10-Aug | 04-Aug | 21-Aug | 3 | -3 | 4 | -3 |
| Scotland | 01-Aug | 11-Aug | 13-Aug | 25-Aug | 05-Aug | 13-Aug | 15-Aug | 26-Aug | -4 | -2 | -2 | -1 |
| Suffolk | 07-Jul | 17-Jul | 17-Jul | 26-Jul | 07-Jul | 19-Jul | 17-Jul | 30-Jul | 0 | -2 | 0 | -4 |
| Yorkshire | 04-Aug | 15-Aug | 15-Aug | 25-Aug | 09-Aug | 18-Aug | 17-Aug | 28-Aug | -5 | -3 | -2 | -3 |
| THIRD GENERATION | | | | | | | | | | | | |
| Cornwall | 04-Oct | 20-Oct | 20-Oct | n/a | n/a | n/a | n/a | n/a | | | | |
| Kent | 04-Sep | 17-Sep | 17-Sep | 28-Sep | 08-Sep | 15-Sep | 21-Sep | 29-Sep | -4 | 2 | -4 | -1 |
| Lancashire | 01-Oct | 22-Oct | 18-Oct | 27-Oct | n/a | n/a | n/a | n/a | | | | |
| Norfolk | 29-Sep | 14-Oct | 15-Oct | 27-Oct | 19-Sep | 27-Sep | 29-Sep | 13-Oct | 10 | 17 | 16 | 14 |
| Scotland | 20-Oct | 27-Oct | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| Suffolk | 19-Aug | 28-Aug | 27-Aug | 04-Sep | 27-Aug | 04-Sep | 02-Sep | 19-Sep | -8 | -7 | -6 | -15 |
| Yorkshire | 20-Oct | n/a | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| 2014 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 21-Mar | 02-Apr | 04-May | 12-May | 22-Mar | 01-Apr | 22-Apr | 16-May | -1 | 1 | 12 | -4 |
| Kent | 16-Mar | 23-Mar | 15-Apr | 24-Apr | 15-Mar | 21-Mar | 06-Apr | 30-Apr | 1 | 2 | 9 | -6 |
| Lancashire | 08-Apr | 16-Apr | 07-May | 12-May | 10-Apr | 17-Apr | 28-Apr | 17-May | -2 | -1 | 9 | -5 |
| Norfolk | 31-Mar | 06-Apr | 03-May | 12-May | 01-Apr | 07-Apr | 24-Apr | 17-May | -1 | -1 | 9 | -5 |
| Scotland | 26-Apr | 05-May | 25-May | 31-May | 27-Apr | 05-May | | | -1 | 0 | | |
| Suffolk | 18-Mar | 27-Mar | 19-Apr | 27-Apr | 16-Mar | 22-Mar | 07-Apr | 04-May | 2 | 5 | 12 | -7 |
| Yorkshire | 13-Apr | 22-Apr | 11-May | 17-May | 13-Apr | 22-Apr | 04-May | 18-May | 0 | 0 | 7 | -1 |

An example of the comparison of the EXCEL and MORPH outputs for one of the Monte Carlo models is shown in Table 3 (early-emerging cabbage root flies). In general, there is fairly close agreement in predictions for the early-emerging flies; most of the outputs were similar. However, there are a few larger differences that need to be investigated and further consideration must be given to how to interpret the outputs when the population 'divides' (Table 2) to give more than one estimate of the timing of a certain event. The major differences were with the third generation and again, further consideration is needed to determine how to interpret the output so that the proportion of insects completing a third generation can be estimated as well as the timing of activity. Finally, some discrepancies may be because the effect of high temperatures on the incidence of pupal aestivation has not been incorporated into this version of the model.

For the late-emerging flies only the timings of first generation activity were compared. These were all very similar. For the simpler Monte Carlo models (pollen beetle and large narcissus fly) outputs from the two versions of the models were very similar. There were no differences in output between the two versions of the day-degree models.

Overall, the validations of these initial versions of the EXCEL models confirm that the approach is valid. The more complex models require some further modification in places.

Please note: AHDB Horticulture understands that pests and disease decision support tools are a guide to decision making and users should not rely just on these tools to make management decisions.

Financial Benefits

There are no immediate direct financial benefits from this research but the aim is to prevent the loss of information in which the HDC and Defra have invested previously.

Action Points

At this stage, growers do not need to do anything differently. In future the output from the models may be in a different format but currently the output from the MORPH models is available in the HDC Pest Bulletin on the Syngenta web site.

SCIENCE SECTION

Introduction

Over the last 20 years, funding from Defra and HDC in particular has enabled the development of a variety of models for forecasting pest outbreaks, some of which have been used very successfully to target control measures. Such models can also be used to predict the future impact of climate change on pest insects. However, changes in funding strategies mean that these bespoke models are no longer supported in terms of software upgrades and some will become inaccessible in the longer term as operating systems change.

In addition, Defra Projects AC0301 and AC0310 (Warwick University and Rothamsted Research) explored the possible impacts of climate change on a range of agricultural production systems, mainly crops. With help from industry, key crop management/crop growth stages and key pests and diseases were identified for each crop. Where models did not exist and, where feasible, simple mathematical relationships with temperature/rainfall (generally identified from the literature) were used with the UK climate change projections to predict the impact of climate change. Such relationships could also be used to predict pest outbreaks in real time.

The aim of this project is to focus on pest insects and to develop a compendium of pest models in spreadsheet format that could be used directly with inputs of current weather data, or could be transferred by commercial companies to more complex systems. The reason for transferring the models onto the spreadsheet platform is to make them 1) readily accessible and 2) more resilient to upgrades in operating systems and 3) to ensure that they can be modified over time without the need for specialist programming expertise to deal with bespoke software. Many of these would be day-degree models, but others would be more complex (such as the carrot fly and cabbage root fly models). The compendium could be applicable to all sectors of horticulture and indeed could incorporate pests of arable crops and potato – and could be extended to ‘diseases’. The compendium could also be extended to link to other resources e.g. HDC Factsheets.

The models could then be used for real-time predictions, although the newer models would require validation before the industry would have a high level of confidence in them. In some cases field data are already available to undertake validations.

Materials and methods

The objectives of the project were to:

1. Create the pest compendium structure using representative models.
2. Incorporate Monte-Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) and day-degree models (lettuce-root aphid, willow-carrot aphid, currant-lettuce aphid) into the spreadsheet-based tool.
3. Validate models using corresponding MORPH outputs (i.e. using the same set of weather data to run the models in MORPH and the pest compendium).

1. Create the pest compendium structure using representative models.

The pest compendium structure was created in EXCEL.

Uploading weather data

When the model opens and all the relations are established, the programme prompts the user to the directory where the weather data files are stored (Figure 2). This can either be a local directory or a pre-established location on the server. If the user wants the model 'to memorise' the previous location, after the completion of the simulation, they should save the spreadsheet. The forecasting period starts with data from 1st February (usually the coldest part of the year).

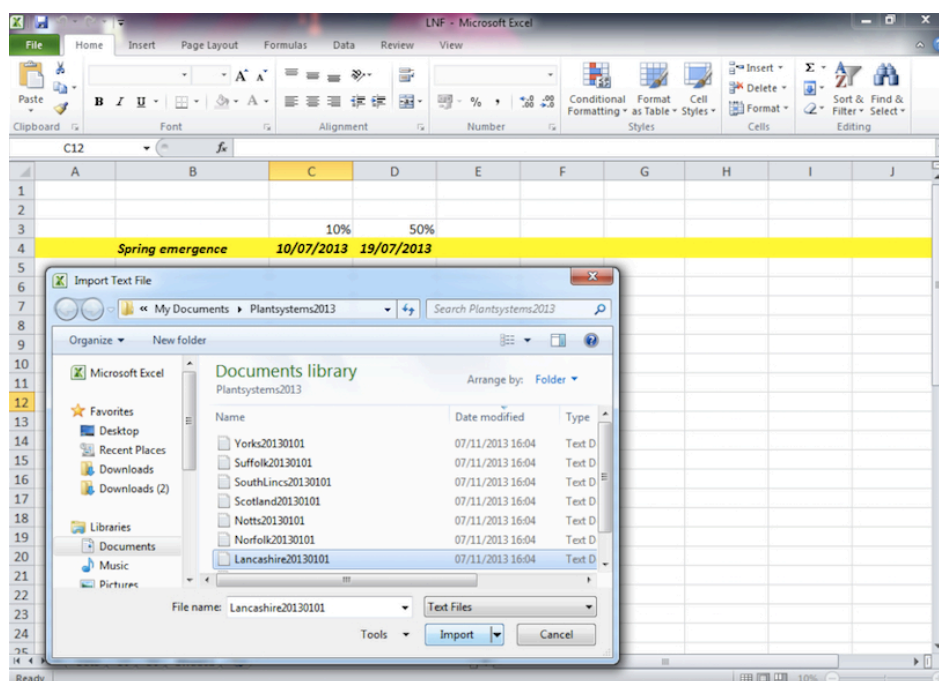


Figure 2. Screenshot showing prompt to upload weather data.

Data and 'controls'

The data imported can be inspected and checked on the first tab, which is named 'Data' (Figure 3). The 'controls' – the CVs and the low temperature thresholds for the equations used by the particular model are stored on this page. These can be altered manually.

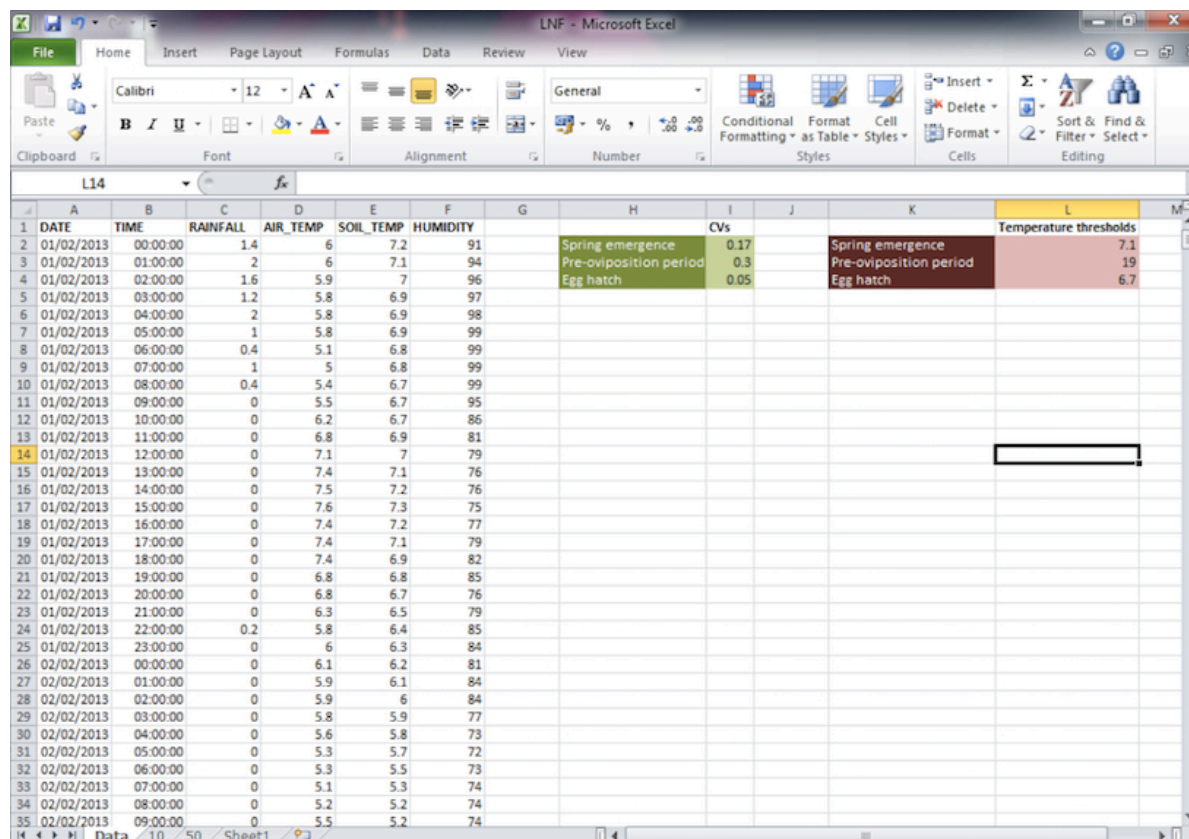


Figure 3. Screenshot showing 'Data' tab.

The progress of the models and the output are presented in separate tabs and will be described below for each type of model.

2. Incorporate Monte-Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) and day-degree models (lettuce-root aphid, willow-carrot aphid, currant-lettuce aphid) into the spreadsheet-based tool.

Monte Carlo models in MORPH

These models simulate the passage of a population of individuals through the egg, larva, pupa and adult stages of one or more generations (Phelps et al., 1993). For each stage, the percentage development is calculated each day by integrating the appropriate development rate curve (developed from laboratory experiments undertaken at a range of constant temperatures). This percentage is accumulated over days until it reaches 100. At this point the individual moves to the next stage. Variation in temperature is incorporated via the integration procedure.

Within any population, some insects develop more rapidly than others, giving the typical shapes of the 'curves' provided by insect sampling data (Figure 4).

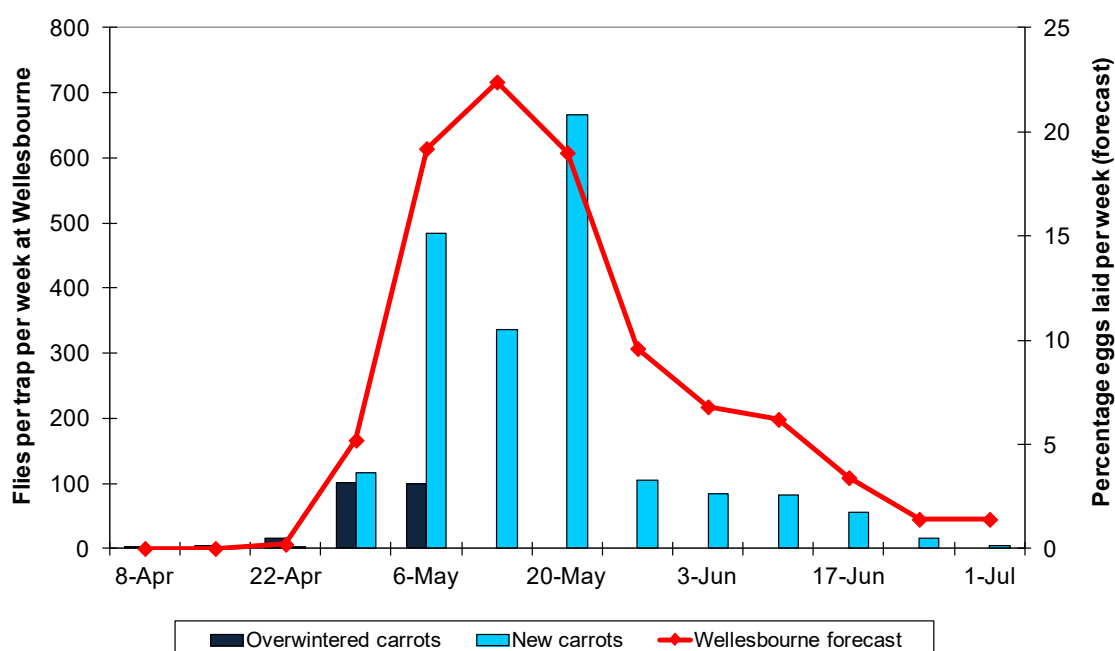


Figure 4. First generation carrot fly at Wellesbourne in 2014 – monitoring data (number of flies per sticky trap per week) compared with output from the MORPH carrot fly model and showing the 'spread' of development in the first generation.

For the Monte Carlo models in MORPH, variability within the insect population is incorporated by assuming that at any instant, the rates of development of a population held at a constant temperature are normally distributed. There is no link between the stages; therefore a 'slow' adult does not necessarily produce a 'slow' egg. In MORPH, at the beginning of each development stage an individual is allocated its 'position' in the normal distribution at random and it retains this position until it enters the next stage, when it is allocated a new position in that distribution, again at random. The mean percentage development per day is calculated by integrating the appropriate rate equation and then adjusting it according to the position in the distribution and the coefficient of variation. This treatment of variability in the insect population uses a considerable amount of computing power.

The aim of the pest models to model the timing of activity rather than changes in population size as the species simulated are mobile pests of ephemeral crops where immigration is important numerically and will depend on factors that cannot be predicted. Thus the MORPH program models the development of a fixed population of 500 individuals. If the population dynamics were being simulated then each adult would produce many eggs and the numbers in the simulation would increase in each generation. The simulation model can also include various types of intervention such as thresholds below or above which development does not occur.

Incorporation of MORPH models into EXCEL

The existing MORPH models and associated information were used to identify the key equations to be moved into EXCEL. Other relevant information on temperature thresholds and coefficients of variation (CV) related to the rates of insect development was also identified and is summarised in the Results section.

EXCEL cannot provide the large amount of space and computing power that the Monte Carlo models require and therefore a pragmatic approach was taken to adapting them for EXCEL. Instead of 'following individual insects through their development, the EXCEL models follow fractions of the population (10%, 20%, 30%, 40%, 50%) to determine when each of these completes a development stage.

In addition, the random element included in the MORPH version of the Monte Carlo models is not part of the EXCEL models and because of this, each run of the MORPH models will provide a slightly different output, the output from the EXCEL models is 'constant'.

Presentation of the Monte Carlo models in EXCEL

The models are presented as a sequence of equations, which represent consecutive development stages and which are linked by the condition of stage completion (cumulative development rate =100). The sequences of stages are repeated across several fractions of the population (e.g., 10%, 20%, 30%, 40%, 50%) to demonstrate the temporal development of different proportions of the insect population, this is 'similar' to the MORPH software (e.g. 10% of the population of eggs were laid by the 6th June 2014).

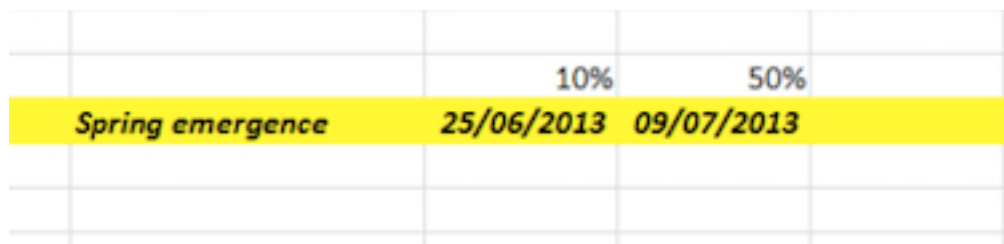
Each tab is divided into a static part and the scrollable part (Figure 5). The static part of the page replicates the weather data from the 'Data' tab and the scrollable part represents the relational sequence of the development stages for a particular fraction of the population; both the 'percentage' of development completed daily and the accumulated development over time. Once the cumulative development for a stage reaches 100% then that part of the population moves into the next stage of development and starts 'accumulating' development in this next stage.

| | A | B | C | D | E | F | G | H | I | J | K | L | M | N |
|----|------------|----------|----------|----------|-----------|----------|------------|------------|------------|----------|-----------|-----------|---------|----------|
| 1 | Date | Time | Rainfall | Air temp | Soil temp | Humidity | SE_mean | SE_rates | SE_cumul | POP_mean | POP_rates | POP_cumul | EH_mean | EH_rates |
| 2 | 01/02/2013 | 00:00:00 | 1.40 | 6.00 | 7.20 | 91.00 | 0.03970833 | 0.04835934 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 3 | 01/02/2013 | 01:00:00 | 2.00 | 6.00 | 7.10 | 94.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 4 | 01/02/2013 | 02:00:00 | 1.60 | 5.90 | 7.00 | 96.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 5 | 01/02/2013 | 03:00:00 | 1.20 | 5.80 | 6.90 | 97.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 6 | 01/02/2013 | 04:00:00 | 2.00 | 5.80 | 6.90 | 98.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 7 | 01/02/2013 | 05:00:00 | 1.00 | 5.80 | 6.90 | 99.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 8 | 01/02/2013 | 06:00:00 | 0.40 | 5.10 | 6.80 | 99.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 9 | 01/02/2013 | 07:00:00 | 1.00 | 5.00 | 6.80 | 99.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 10 | 01/02/2013 | 08:00:00 | 0.40 | 5.40 | 6.70 | 99.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 11 | 01/02/2013 | 09:00:00 | 0.00 | 5.50 | 6.70 | 95.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 12 | 01/02/2013 | 10:00:00 | 0.00 | 6.20 | 6.70 | 86.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 13 | 01/02/2013 | 11:00:00 | 0.00 | 6.80 | 6.90 | 81.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 14 | 01/02/2013 | 12:00:00 | 0.00 | 7.10 | 7.00 | 79.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 15 | 01/02/2013 | 13:00:00 | 0.00 | 7.40 | 7.10 | 76.00 | 0.03970833 | 0 | 0.04835934 | 0 | 0 | 0 | 0 | 0 |
| 16 | 01/02/2013 | 14:00:00 | 0.00 | 7.50 | 7.20 | 76.00 | 0.03970833 | 0.04835934 | 0.09671868 | 0 | 0 | 0 | 0 | 0 |
| 17 | 01/02/2013 | 15:00:00 | 0.00 | 7.60 | 7.30 | 75.00 | 0.03970833 | 0.04835934 | 0.14507802 | 0 | 0 | 0 | 0 | 0 |
| 18 | 01/02/2013 | 16:00:00 | 0.00 | 7.40 | 7.20 | 77.00 | 0.03970833 | 0.04835934 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 19 | 01/02/2013 | 17:00:00 | 0.00 | 7.40 | 7.10 | 79.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 20 | 01/02/2013 | 18:00:00 | 0.00 | 7.40 | 6.90 | 82.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 21 | 01/02/2013 | 19:00:00 | 0.00 | 6.80 | 6.80 | 85.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 22 | 01/02/2013 | 20:00:00 | 0.00 | 6.80 | 6.70 | 76.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 23 | 01/02/2013 | 21:00:00 | 0.00 | 6.30 | 6.50 | 79.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 24 | 01/02/2013 | 22:00:00 | 0.20 | 5.80 | 6.40 | 85.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 25 | 01/02/2013 | 23:00:00 | 0.00 | 6.00 | 6.30 | 84.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 26 | 02/02/2013 | 00:00:00 | 0.00 | 6.10 | 6.20 | 81.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 27 | 02/02/2013 | 01:00:00 | 0.00 | 5.90 | 6.10 | 84.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 28 | 02/02/2013 | 02:00:00 | 0.00 | 5.90 | 6.00 | 84.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 29 | 02/02/2013 | 03:00:00 | 0.00 | 5.80 | 5.90 | 77.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 30 | 02/02/2013 | 04:00:00 | 0.00 | 5.60 | 5.80 | 73.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 31 | 02/02/2013 | 05:00:00 | 0.00 | 5.30 | 5.70 | 72.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 32 | 02/02/2013 | 06:00:00 | 0.00 | 5.30 | 5.50 | 73.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |
| 33 | 02/02/2013 | 07:00:00 | 0.00 | 5.10 | 5.30 | 74.00 | 0.03970833 | 0 | 0.19343736 | 0 | 0 | 0 | 0 | 0 |

Figure 5. Screenshot showing how the models are presented.

Presentation of the outputs

The results are looked up and extracted onto the 'Results' page of the spreadsheet Figure 6). This summarises, for example, the dates of 10% and 50% emergence in the spring, or 10% and 50% egg-laying.



| | 10% | 50% |
|-------------------------|-------------------|-------------------|
| Spring emergence | 25/06/2013 | 09/07/2013 |

Figure 6. Screenshot showing an example of the output.

Limitations of the Monte Carlo models in EXCEL

Because of limitations with 'computing power' the EXCEL models only follow deciles up to 50%. Usually, information provided as part of the MORPH outputs is restricted to 10% and 50% 'activity' and so this is in itself not a limitation. The EXCEL models do not provide information on 'individual' insects and so it is not possible to replicate the types of graph produced by MORPH. Thus it will be necessary to think of another way of representing the information graphically if this is considered useful.

For the two more complex models, cabbage root fly and carrot fly, further consideration is required of how best to interpret the outputs.

Presentation of the day-degree models

The day-degree models are presented in a similar EXCEL format and the weather data are uploaded in the same way.

3. Validate models using corresponding MORPH outputs

The models were validated by running the MORPH models and the EXCEL models using the same sets of weather data, which are those provided by Plantsystems to run the pest forecasts.

Results

CABBAGE ROOT FLY

Description of the original MORPH model

The relationship between the rate of development and temperature was established by rearing each stage (egg, larva, pupa, adult) at a range of constant temperatures between 5 and 30°C and plotting the rate of development (1/time to 50% completion of the stage) against temperature. For stages where the rate of development was related to temperature, either linear or non-linear (Gompertz) rate equations were fitted to the data. The six rate equations used are shown in Table 1. The low temperature thresholds for each stage were estimated by experiment and linear extrapolation (post-diapause development of early flies; Collier & Finch, 1985a; post-diapause development of late flies; Collier *et al*, 1989; non-diapause development; Collier & Finch, unpublished) whilst the upper threshold temperatures were set at 30°C. Above 30°C cabbage root fly mortality starts to increase, the lethal temperatures for egg and pupal survival being 35 and 33.5°C respectively (Coaker & Finch, 1971).

Intra-specific variation in the rate of insect development was estimated for each stage using coefficients of variation (CV) derived from laboratory experiments by calculation the mean rate of development at each constant temperature. In the case of the cabbage root fly, CVs ranged from 7-28% (Table 4).

The series of development rate equations formed the basis of the simulation model and were linked together in a program (Phelps *et al*, 1993). The conditions for induction of diapause (Finch & Collier, 1988) and aestivation (Finch & Collier, 1985) were built into the model at the appropriate stages, as were the initial proportions of the early- and late-emerging biotypes (Finch & Collier, 1983).

The program was used to simulate the development of cohorts of 500 individuals (Phelps *et al*, 1991), and at every stage, each of the 500 individuals was randomly allocated a development equation from a normal distribution based on the mean and CV estimated from the rate equation for the appropriate stage. At the start of each new stage, normally-distributed development equations were randomly re-allocated to the 500 individuals.

The forecast started from 1 February, chosen because this is often the coldest period in the year when development of individual cabbage root flies is most highly synchronised (Collier & Finch, 1983) and because over 50% of the overwintering cabbage root fly population have generally completed diapause development by this date and are competent to begin post-diapause development once soil temperatures rise in the spring (Coaker & Wright, 1963; Collier & Finch, 1983).

Starting with the post-diapause stage, the development of each individual was accumulated on a daily basis, using the appropriate rate equation and soil temperatures. Daily development was accumulated until post-diapause development was completed (100% development). The individual, now a newly-emerged adult, then moved on to the next stage, the pre-oviposition period, to repeat the process using the appropriate development equation and air temperatures. It was assumed that a proportion of cabbage root flies went on to lay a second batch of eggs and this proportion was set at 50% of the initial population. There was little experimental data to substantiate this.

Progress continued through the series of stages taking account of periods when aestivation or diapause were likely to occur. It was assumed that diapause was induced in those cabbage root flies which were eggs after 31 July each year (Finch & Collier, 1988) and that these individuals did not, therefore, contribute to a third generation. Aestivation was induced according to the equation given by Finch & Collier (1985). It was assumed that pupae were only sensitive to aestivation-inducing conditions during the first 30% of the pupal stage and that no pupae aestivated at temperatures below 20°C whilst all pupae aestivated above 27°C. At temperatures between 20 and 27°C the proportion of pupae entering aestivation increased linearly, with 50% entering aestivation at 23.5°C. This was incorporated into the model by assigning an aestivation threshold to each insect, based on a normal distribution. Whilst in aestivation, pupae ceased development.

The model was used to predict the daily distribution of adult emergence and egg-laying activity (out of a total of 500 individuals per generation) throughout the year and could be used to estimate, for example, times of 10% and 50% activity in each generation, the number of weeks when activity was likely to be high and the likely occurrence of a large third generation.

Meteorological data used in the forecast

The cabbage root fly forecast requires soil temperatures at a depth of approximately 6 cm for simulating development of the egg, larva and pupal stages. Air temperatures are required to model the period of egg maturation, from adult emergence to oviposition, which may take as long as a month at the time of the first generation in April-May (Collier & Finch, 1985).

Table 4. Equations for the cabbage root fly model. The lower threshold temperatures were estimated by linear extrapolation and may not be the 'true' thresholds.

| Phase of insect development | Equation | Lower threshold temperature °C | Coefficient of variation (%) |
|---|---|--------------------------------|------------------------------|
| Early spring emergence (ESE) <i>Describes post-diapause development of overwintering pupae of the early-emerging biotype (the most prevalent)</i> | CRF1 = 0.5785*TEMP-1.981 | 6 | 28 |
| Late spring emergence (LSE) <i>Describes post-diapause development of overwintering pupae of the late-emerging biotype</i> | CRF2 = 0.592+2.2525*EXP(-EXP(-0.274*(TEMP-12.49))) | 7 | 23 |
| Pre-oviposition period (first batch) (POP1) <i>Describes maturation period of first batch of eggs</i> | CFR3 = 1.4049*TEMP-10.68 | 8 | 10 |
| Pre-oviposition period (second batch) (POP2) <i>Describes maturation period of second batch of eggs</i> | CRF4 = 1.5*(1.4049*TEMP-10.68) | 8 | 10 |
| Egg and larval development (ELD) <i>Describes development from time egg is laid until pupa is formed</i> | CFR5 = 0.836+5.66*(EXP(-EXP(-0.1473*(TEMP-16.17)))) | 6 | 13 |
| Pupal development (PD) <i>Describes development of pupa until adult emerges</i> | CRF6 = 0.01+11.0*(EXP(-EXP(-0.104*(TEMP-14.28)))) | 4 | 7 |

Description of the EXCEL model

For this model, two independent packages were developed, representing simulations for the early-emerging and late-emerging flies. The results were compared directly with the corresponding MORPH modules ('early' and 'late' emergers). The sequence of the cabbage root fly model is summarised in Table 5. The effect of high temperatures on the incidence of pupal aestivation has not been incorporated into this version of the model, nor has the induction of diapause.

Table 5. Sequence of equations in the EXCEL cabbage root fly model through the generations.

| Generation | Early-emerging flies | | | | | | | |
|------------|----------------------|------|------|------|------|------|------|------|
| 1 | ESE | | | | | | | |
| 1 | POP1 | | | | POP2 | | | |
| 1 | ELD | | | | ELD | | | |
| 1 | PD | | | | PD | | | |
| 2 | POP1 | | POP2 | | POP1 | | POP2 | |
| 2 | ELD | | ELD | | ELD | | ELD | |
| 2 | PD | | PD | | PD | | PD | |
| 3 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 |
| 3 | ELD | ELD | ELD | ELD | ELD | ELD | ELD | ELD |

| Generation | Late-emerging flies | | | |
|------------|---------------------|------|------|------|
| 1 | LSE | | | |
| 1 | POP1 | | POP2 | |
| 1 | ELD | | ELD | |
| 1 | PD | | PD | |
| 2 | POP1 | POP2 | POP1 | POP2 |
| 2 | ELD | ELD | ELD | ELD |

Validation of the EXCEL model

Outputs from the MORPH and EXCEL versions of the cabbage root fly models are compared in Tables 6 and 7. For this validation, where the population 'divides' (from the second generation onwards), the different estimates of the timing of an event were averaged.

For the early-emerging flies, most of the outputs were similar (taken as within 7 days) (Table 6). However, further consideration must be given to how to interpret the outputs

when the population 'divides' to give more than one estimate of the timing of a certain event (Table 5).

The major differences were with the third generation and further consideration is needed to determine how to interpret the output so that the proportion of insects completing a third generation can be estimated. In addition, some discrepancies between the MORPH and EXCEL outputs may be because the effect of high temperatures on the incidence of pupal aestivation has not been incorporated into this version of the model.

For the late-emerging flies only the timings of first generation activity were compared. These were all very similar (Table 7).

Table 6a. Validations of the EXCEL model for early spring emergence – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| Validation sites | EXCEL | | | | MORPH | | | | Difference in days (EXCEL-MORPH output) | | | |
|--------------------------|-----------|--------|-----------|--------|-----------|--------|-----------|--------|---|-----|-----------|-----|
| | Emergence | | Eggs laid | | Emergence | | Eggs laid | | Emergence | | Eggs laid | |
| | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% |
| 2012 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 22-Mar | 30-Mar | 02-May | 19-May | 25-Mar | 01-Apr | 03-May | 24-May | -3 | -2 | -1 | -5 |
| Kent | 24-Mar | 01-Apr | 08-May | 11-May | 25-Mar | 01-Apr | 01-May | 14-May | -1 | 0 | 7 | -3 |
| Lancashire | 20-Mar | 27-Mar | 08-May | 22-May | 22-Mar | 28-Mar | 01-May | 24-May | -2 | -1 | 7 | -2 |
| Nottinghamshire | 28-Mar | 09-Apr | 10-May | 22-May | 30-Mar | 11-Apr | 09-May | 24-May | -2 | -2 | 1 | -2 |
| Scotland | 31-Mar | 16-Apr | 25-May | 27-May | 02-Apr | 17-Apr | 24-May | 29-May | -2 | -1 | 1 | -2 |
| Suffolk | 29-Mar | 10-Apr | 18-May | 22-May | 31-Mar | 11-Apr | 11-May | 25-May | -2 | -1 | 7 | -3 |
| Yorkshire | 29-Mar | 09-Apr | 20-May | 23-May | 30-Mar | 10-Apr | 11-May | 25-May | -1 | -1 | 9 | -2 |
| SECOND GENERATION | | | | | | | | | | | | |
| Cornwall | 07-Jul | 26-Jul | 17-Jul | 04-Aug | 16-Jul | 31-Jul | 26-Jul | 12-Aug | -9 | -5 | -9 | -8 |
| Kent | 08-Jul | 18-Jul | 19-Jul | 28-Jul | 09-Jul | 19-Jul | 20-Jul | 02-Aug | -1 | -1 | -1 | -5 |
| Lancashire | 12-Jul | 24-Jul | 24-Jul | 06-Aug | 11-Jul | 25-Jul | 23-Jul | 07-Aug | 1 | -1 | 1 | -1 |
| Nottinghamshire | 10-Jul | 23-Jul | 19-Jul | 30-Jul | 17-Jul | 26-Jul | 25-Jul | 07-Aug | -7 | -3 | -6 | -8 |
| Scotland | 04-Aug | 13-Aug | 12-Aug | 22-Aug | 09-Aug | 18-Aug | 18-Aug | 05-Sep | -5 | -5 | -6 | -14 |
| Suffolk | 02-Jul | 10-Jul | 12-Jul | 22-Jul | 04-Jul | 15-Jul | 18-Jul | 30-Jul | -2 | -5 | -6 | -8 |
| Yorkshire | 21-Jul | 30-Jul | 27-Jul | 08-Aug | 24-Jul | 03-Aug | 03-Aug | 16-Aug | -3 | -4 | -7 | -8 |
| THIRD GENERATION | | | | | | | | | | | | |
| Cornwall | 15-Sep | 08-Oct | 02-Oct | 29-Oct | 18-Sep | 27-Sep | 04-Oct | 13-Oct | -3 | 11 | -2 | 16 |
| Kent | 02-Sep | 12-Sep | 12-Sep | 25-Sep | 08-Sep | 15-Sep | 17-Sep | 30-Sep | -6 | -3 | -5 | -5 |
| Lancashire | 13-Sep | 05-Oct | 09-Oct | 28-Oct | 07-Sep | 25-Sep | 14-Sep | 13-Oct | 6 | 10 | 25 | 15 |
| Nottinghamshire | 08-Sep | 29-Sep | 26-Sep | 28-Oct | 13-Sep | 25-Sep | 25-Sep | 15-Oct | -5 | 4 | 1 | 13 |
| Scotland | n/a | n/a | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| Suffolk | 24-Aug | 02-Sep | 04-Sep | 11-Sep | 12-Sep | 19-Sep | 01-Oct | 10-Oct | -19 | -17 | -27 | -29 |
| Yorkshire | 04-Oct | 01-Nov | 10-Nov | 14-Nov | 30-Sep | 10-Oct | 11-Oct | 29-Oct | 4 | 22 | 30 | 16 |
| 2013 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 20-Apr | 27-Apr | 31-May | 04-Jun | 23-Mar | 28-Apr | 18-May | 05-Jun | 28 | -1 | 13 | -1 |
| Kent | 26-Apr | 03-May | 25-May | 01-Jun | 27-Apr | 04-May | 13-May | 02-Jun | -1 | -1 | 12 | -1 |
| Lancashire | 06-May | 13-May | 03-Jun | 09-Jun | 08-May | 14-May | 30-May | 08-Jun | -2 | -1 | 4 | 1 |
| Norfolk | 26-Apr | 03-May | 03-Jun | 06-Jun | 28-Apr | 03-May | 12-May | 08-Jun | -2 | 0 | 22 | -2 |
| Scotland | 11-May | 18-May | 03-Jun | 09-Jun | 11-May | 18-May | 28-May | 07-Jun | 0 | 0 | 6 | 2 |
| Suffolk | 22-Apr | 26-Apr | 21-May | 01-Jun | 22-Apr | 26-Apr | 09-May | 28-May | 0 | 0 | 12 | 4 |
| Yorkshire | 11-May | 20-May | 05-Jun | 11-Jun | 13-May | 20-May | 30-May | 10-Jun | -2 | 0 | 6 | 1 |
| SECOND GENERATION | | | | | | | | | | | | |
| Cornwall | 31-Jul | 08-Aug | 09-Aug | 20-Aug | 24-Jul | 01-Aug | 31-Jul | 13-Aug | 7 | 7 | 9 | 7 |
| Kent | 19-Jul | 26-Jul | 26-Jul | 04-Aug | 21-Jul | 29-Jul | 28-Jul | 09-Aug | -2 | -3 | -2 | -5 |
| Lancashire | 30-Jul | 08-Aug | 08-Aug | 20-Aug | 04-Aug | 12-Aug | 13-Aug | 24-Aug | -5 | -4 | -5 | -4 |
| Norfolk | 30-Jul | 07-Aug | 08-Aug | 18-Aug | 27-Jul | 10-Aug | 04-Aug | 21-Aug | 3 | -3 | 4 | -3 |
| Scotland | 01-Aug | 11-Aug | 13-Aug | 25-Aug | 05-Aug | 13-Aug | 15-Aug | 26-Aug | -4 | -2 | -2 | -1 |
| Suffolk | 07-Jul | 17-Jul | 17-Jul | 26-Jul | 07-Jul | 19-Jul | 17-Jul | 30-Jul | 0 | -2 | 0 | -4 |
| Yorkshire | 04-Aug | 15-Aug | 15-Aug | 25-Aug | 09-Aug | 18-Aug | 17-Aug | 28-Aug | -5 | -3 | -2 | -3 |
| THIRD GENERATION | | | | | | | | | | | | |
| Cornwall | 04-Oct | 20-Oct | 20-Oct | n/a | n/a | n/a | n/a | n/a | | | | |
| Kent | 04-Sep | 17-Sep | 17-Sep | 28-Sep | 08-Sep | 15-Sep | 21-Sep | 29-Sep | -4 | 2 | -4 | -1 |
| Lancashire | 01-Oct | 22-Oct | 18-Oct | 27-Oct | n/a | n/a | n/a | n/a | | | | |
| Norfolk | 29-Sep | 14-Oct | 15-Oct | 27-Oct | 19-Sep | 27-Sep | 29-Sep | 13-Oct | 10 | 17 | 16 | 14 |
| Scotland | 20-Oct | 27-Oct | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| Suffolk | 19-Aug | 28-Aug | 27-Aug | 04-Sep | 27-Aug | 04-Sep | 02-Sep | 19-Sep | -8 | -7 | -6 | -15 |
| Yorkshire | 20-Oct | n/a | n/a | n/a | n/a | n/a | n/a | n/a | | | | |
| 2014 | | | | | | | | | | | | |
| FIRST GENERATION | | | | | | | | | | | | |
| Cornwall | 21-Mar | 02-Apr | 04-May | 12-May | 22-Mar | 01-Apr | 22-Apr | 16-May | -1 | 1 | 12 | -4 |
| Kent | 16-Mar | 23-Mar | 15-Apr | 24-Apr | 15-Mar | 21-Mar | 06-Apr | 30-Apr | 1 | 2 | 9 | -6 |
| Lancashire | 08-Apr | 16-Apr | 07-May | 12-May | 10-Apr | 17-Apr | 28-Apr | 17-May | -2 | -1 | 9 | -5 |
| Norfolk | 31-Mar | 06-Apr | 03-May | 12-May | 01-Apr | 07-Apr | 24-Apr | 17-May | -1 | -1 | 9 | -5 |
| Scotland | 26-Apr | 05-May | 25-May | 31-May | 27-Apr | 05-May | | | -1 | 0 | | |
| Suffolk | 18-Mar | 27-Mar | 19-Apr | 27-Apr | 16-Mar | 22-Mar | 07-Apr | 04-May | 2 | 5 | 12 | -7 |
| Yorkshire | 13-Apr | 22-Apr | 11-May | 17-May | 13-Apr | 22-Apr | 04-May | 18-May | 0 | 0 | 7 | -1 |

Table 6b. CVs and thresholds used in validations of the EXCEL model for early spring emergence.

| | CVs | | Temperature thresholds |
|--------------------------|------|----------|------------------------|
| Early spring emergence | 0.28 | ESE | 6 |
| Pre-oviposition periods | 0.1 | POP -1 | 8 |
| Egg & larval development | 0.13 | POP -2 | 8 |
| Pupal development | 0.07 | ELD -1 | 6 |
| | | ELD -2 | 6 |
| | | PD -1 | 6 |
| | | PD -2 | 6 |
| | | POP -11 | 8 |
| | | POP -12 | 8 |
| | | POP -21 | 8 |
| | | POP -22 | 8 |
| | | ELD -11 | 6 |
| | | ELD -12 | 6 |
| | | ELD -21 | 6 |
| | | ELD -22 | 6 |
| | | PD -11 | 6 |
| | | PD -12 | 6 |
| | | PD -21 | 6 |
| | | PD -22 | 6 |
| | | POP -111 | 8 |
| | | POP -112 | 8 |
| | | POP -121 | 8 |
| | | POP -122 | 8 |
| | | POP -211 | 8 |
| | | POP -212 | 8 |
| | | POP -221 | 8 |
| | | POP -222 | 8 |
| | | ELD -111 | 6 |
| | | ELD -112 | 6 |
| | | ELD -121 | 6 |
| | | ELD -122 | 6 |
| | | ELD -211 | 6 |
| | | ELD -212 | 6 |
| | | ELD -221 | 6 |
| | | ELD -222 | 6 |

Table 7a. Validations of the EXCEL model for late spring emergence – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| | EXCEL | | MORPH | | Difference (EXCEL-MORPH) | |
|--------------|----------|----------|----------|----------|--------------------------|----------|
| | 10% eggs | 50% eggs | 10% eggs | 50% eggs | 10% eggs | 50% eggs |
| 2013 | | | | | | |
| Cornwall | 1-Jul | 12-Jul | 30-Jun | 17-Jul | 1.5 | -4.5 |
| Kent | 29-Jun | 11-Jul | 28-Jun | 18-Jul | 1.5 | -6.5 |
| Lancashire | 7-Jul | 16-Jul | 6-Jul | 24-Jul | 1.0 | -7.5 |
| Lincolnshire | 25-Jun | 6-Jul | 22-Jun | 11-Jul | 3.5 | -4.5 |
| Norfolk | 24-Jun | 8-Jul | 24-Jun | 16-Jul | 0.5 | -7.5 |
| Nottingham | 2-Jul | 12-Jul | 30-Jun | 18-Jul | 2.0 | -5.5 |
| Scotland | 9-Jul | 20-Jul | 8-Jul | 25-Jul | 1.0 | -4.5 |
| Suffolk | 19-Jun | 28-Jun | 15-Jun | 4-Jul | 4.5 | -5.5 |
| Yorkshire | 12-Jul | 24-Jul | 11-Jul | 1-Aug | 1.0 | -8.0 |
| | | | | | | |
| 2014 | | | | | | |
| Cornwall | 6-Jun | 17-Jun | 28-May | 22-Jun | 9.5 | -5.0 |
| Kent | 30-May | 13-Jun | 30-May | 17-Jun | 0.5 | -4.0 |
| Lancashire | 12-Jun | 24-Jun | 13-Jun | 4-Jul | -0.5 | -9.5 |
| Lincolnshire | 6-Jun | 16-Jun | 5-Jun | 23-Jun | 1.5 | -7.0 |
| Norfolk | 6-Jun | 17-Jun | 5-Jun | 25-Jun | 1.0 | -8.0 |
| Nottingham | 11-Jun | 24-Jun | 11-Jun | 4-Jul | 0.5 | -9.5 |
| Scotland | 9-Jul | 20-Jul | 7-Jul | 28-Jul | 2.0 | -7.5 |
| Suffolk | 22-May | 3-Jun | 18-May | 7-Jun | 4.0 | -4.0 |
| Yorkshire | 16-Jun | 2-Jul | 17-Jun | 8-Jul | -0.5 | -6.0 |
| | | | | | | |

Table 7b. CVs and thresholds used in validations of the EXCEL model for early spring emergence.

| | CVs | | Temperature thresholds |
|--------------------------|------|----------|------------------------|
| Late spring emergence | 0.23 | LSE | 7 |
| Pre-oviposition periods | 0.1 | POP -1 | 8 |
| Egg & larval development | 0.13 | POP -2 | 8 |
| Pupal development | 0.07 | ELD -1 | 6 |
| | | ELD -2 | 6 |
| | | PD -1 | 6 |
| | | PD -2 | 6 |
| | | POP -11 | 8 |
| | | POP -12 | 8 |
| | | POP -21 | 8 |
| | | POP -22 | 8 |
| | | ELD -11 | 6 |
| | | ELD -12 | 6 |
| | | ELD -21 | 6 |
| | | ELD -22 | 6 |
| | | PD -11 | 6 |
| | | PD -12 | 6 |
| | | PD -21 | 6 |
| | | PD -22 | 6 |
| | | POP -111 | 8 |
| | | POP -112 | 8 |
| | | POP -121 | 8 |
| | | POP -122 | 8 |
| | | POP -211 | 8 |
| | | POP -212 | 8 |
| | | POP -221 | 8 |
| | | POP -222 | 8 |
| | | ELD -111 | 6 |
| | | ELD -112 | 6 |
| | | ELD -121 | 6 |
| | | ELD -122 | 6 |
| | | ELD -211 | 6 |
| | | ELD -212 | 6 |
| | | ELD -221 | 6 |
| | | ELD -222 | 6 |

CARROT FLY

Description of the original MORPH model

Carrot flies overwinter in the soil either as diapausing pupae or as larvae (Wright & Ashby, 1946). Diapause is induced during late summer/autumn in pupae, which form from 6-60% of the overwintering population (Wright & Ashby, 1946; Burn & Coaker, 1981; Collier & Finch, 1994). Declining photoperiods do not influence the occurrence of diapause (Stadler, 1970) which is induced in the pre-pupal stage in response to low temperatures (Stadler, 1970; Burn & Coaker, 1981; McLeod *et al.*, 1985). However, Brunel & Missonier (1968) showed that sensitivity to diapause-inducing conditions increased from late summer to autumn and that the threshold temperature for diapause induction and therefore the percentage of pupae entering diapause, increased from early July to late August.

Later-developing insects remain as larvae throughout the winter and continue to feed on carrot roots, gradually increasing the level of damage. They then form pupae in early spring (Burn & Coaker, 1981). Although soil temperatures at the time of pre-pupal formation in early spring are similar to those inducing diapause in October to December, non-diapause pupae are formed (Burn & Coaker, 1981). This is because sensitivity to diapause-inducing conditions of low temperature declines from November to March and therefore prevents spring-formed pupae from entering diapause. Insects which have overwintered as larvae, forming pupae during the spring, tend to emerge earlier than those which have overwintered as diapausing pupae (Biernaux, 1968; Burn & Coaker, 1981; McLeod *et al.*, 1985). The temperature requirements for overwintering development have been studied in the UK (Burn & Coaker, 1981; Collier *et al.*, 1994b) and in North America (McLeod *et al.*, 1985; Stevenson & Barszyc, 1989)

Details of the life-cycle of the carrot fly were summarised by Dufault & Coaker (1987). Newly-emerged carrot flies require a few days to mature their eggs which then require several days' incubation prior to hatching. Larval development proceeds through three instars and is followed by pupation and pupal development, which culminate in the emergence of the next adult generation. The durations of most stages in the life-cycle of the carrot fly are temperature-dependent and the temperature requirements for development of these stages of development (egg-adult) have been investigated in Europe by van't Sant (1961); Burn (1980); Collier & Finch (1996) and in North America by Stevenson (1981) and McLeod *et al.* (1985). There is evidence that pupal aestivation can

be induced in response to high (>24°C) temperatures (van't Sant, 1961; McClanahan & Niemczyk 1963; Stadler, 1970).

The studies by Collier et al., (1994b) and Collier & Finch (1996) on carrot fly development provided the basis for the carrot fly forecasting model. Additional information on the life-cycle and further data on development times were obtained from other published studies. The modelling procedure is described in detail by Phelps *et al* (1993) but will be summarised in the following description of the model.

The relationships between the rates of development and temperature were established for each stage (e.g. egg, larva, pupa, adult) by plotting the mean rate of development (percentage development completed per day) against temperature. Where one or more studies were comparable, all data were included.

For those stages where rates of development were proportional to temperature, either linear or non-linear (Gompertz) rate equations were fitted to the data. These equations formed the basis of the simulation model and were linked together in the program. Lower development thresholds were estimated by extrapolation from linear equations or from other biological data. Upper development thresholds were set at 30°C, as being at the extreme of temperatures normally experienced in the field. The fitted rate equations and estimated lower thresholds (from linear extrapolation) are shown in Table 8.

The variation in the rate of insect development was estimated for each stage in the life-cycle using coefficients of variation (CV) derived from laboratory experiments by calculating the mean rate of development and its variance at each constant temperature (Table 5). This variation was included in the model by simulating the development of cohorts of 500 individuals. At the start of each new stage of the life-cycle, each of the individuals was randomly allocated a 'personal' development rate in such a way that at each temperature the resulting frequency distribution of rates was compatible with a normal distribution with the required mean and variance.

The forecast was started from 1 February. This date was chosen because this is normally the coldest time of the year. The percentage of insects overwintering as larvae was

specified at the start of the model. The model began with diapause and post-diapause development by overwintering pupae and pupation and pupal development by overwintering larvae. The percentage development of each individual insect was accumulated using the appropriate rate equations and hourly soil temperatures, until each stage was completed (100% development). The individual, now a newly-emerged adult, was then moved to the next stage, the pre-oviposition period. The simulation was run on this stage using the appropriate development equation and hourly air temperatures. Progress continued through each of the stages in the insects' life-cycle, including those periods when aestivation or diapause were likely to occur.

The induction of diapause was modelled according to data obtained from studies by Stadler (1970) and McLeod *et al* (1985). Individual insects were randomly allocated a diapause threshold temperature between 11.5 and 15.5°C. If the soil temperature remained below this temperature for 10 days continuously then diapause was induced (McLeod *et al.*, 1985) and the insect no longer contributed to the population in the current year. Aestivation is induced at temperatures of 21-25°C (van't Sant, 1961; McClanahan & Niemczyk, 1963; Brunel, 1968; Stadler, 1970). At Wellesbourne, an increasing proportion of carrot fly pupae were induced into aestivation as the temperature was increased from 24 - 30°C. However pupae only responded to high temperatures for a relatively short period, soon after their formation. Once they had passed this sensitive stage, they merely developed faster in response to the high temperatures. Aestivation ended and development resumed as soon as temperatures fell. In the model, aestivation was induced when temperatures rose above 24°C and persisted as long as the high temperatures persisted.

The model was used to predict carrot fly emergence and egg-laying activity throughout the year. It was used 1) to estimate the times of 10% and 50% activity in each generation, 2) the number of weeks when fly activity was high and 3) the likely occurrence of a third generation of flies.

The carrot fly forecast used maximum and minimum soil temperatures at a depth of 6 cm to model the development of egg, larval and pupal stages. Maximum and minimum air temperatures were required to model the period from adult emergence to oviposition.

Description of the EXCEL model

Unlike the cabbage root fly model, and due to its complexity, the carrot fly model was divided into separate packages at the start, to accommodate each of the two overwintering stages (diapause pupae and larvae). The sequence of the model is summarised in Table 9. The effect of high temperatures on the incidence of pupal aestivation has not been incorporated into this version of the model, nor has the induction of diapause.

Table 8. Equations for the carrot fly model. The lower threshold temperatures were estimated by linear extrapolation and may not be the 'true' thresholds.

| Phase of insect development | Equation | Lower threshold temperature °C | Coefficient of variation (%) |
|--|---|--------------------------------|------------------------------|
| Larval and pupal development in the spring (LDPDS) | $CF1 = 1.134 + 3.137 * \text{EXP}(-\text{EXP}(-0.3144 * (\text{TEMP} - 13.557)))$ | 4.2 | 27 |
| Diapause and post-diapause development (DPDD) | $CF2 = 0.857 + 1.525 * \text{EXP}(-\text{EXP}(-0.415 * (\text{TEMP} - 11.51)))$ | -1.23 | 10 |
| Pre-oviposition period (first batch) (POP1) | $CF4 = 1.866 * \text{TEMP} - 13.94$ | 7.5 | 49 |
| Pre-oviposition period (second batch) (POP2) | $CF5 = 3.53 * \text{TEMP} - 22.7$ | 6.4 | 76 |
| Egg stage (ES) | $CF6 = 1.1265 * \text{TEMP} - 5.824$ | 5.2 | 7 |
| Larval stage (LS) | $CF7 = 1.236 + 1.93 * \text{EXP}(-\text{EXP}(-0.621 * (\text{TEMP} - 12.27)))$ | -1.2 | 17 |
| Pupal development (PD) | $CF3 = 0.77 + 3.96 * \text{EXP}(-\text{EXP}(-0.339 * (\text{TEMP} - 12.32)))$ | 2.1 | 13 |

Table 9. Sequence of equations in the EXCEL carrot fly model through the generations.

| Generation | Overwinterers as a larva | | | | | | | | Overwinterers as a pupa | | | | | | | |
|------------|--------------------------|------|------|------|------|------|------|------|-------------------------|------|------|------|------|------|------|------|
| 1 | LDPDS | | | | | | | | DPDD | | | | | | | |
| 1 | POP1 | | | | POP2 | | | | POP1 | | | | POP2 | | | |
| 1 | ES | | | | ES | | | | ES | | | | ES | | | |
| 1 | LS | | | | LS | | | | LS | | | | LS | | | |
| 1 | PD | | | | PD | | | | PD | | | | PD | | | |
| 2 | POP1 | | POP2 | | POP1 | | POP2 | | POP1 | | POP2 | | POP1 | | POP2 | |
| 2 | ES | | ES | | ES | | ES | | ES | | ES | | ES | | ES | |
| 2 | LS | | LS | | LS | | LS | | LS | | LS | | LS | | LS | |
| 2 | PD | | PD | | PD | | PD | | PD | | PD | | PD | | PD | |
| 3 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 | POP1 | POP2 |
| 3 | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES | ES |
| 3 | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS | LS |

Validation of the EXCEL model

The outputs from the MORPH and EXCEL versions of the carrot fly model are compared in Table 10. For this validation, where the population 'divides' (from the second generation onwards – Table 9), the different estimates of the timing of an event were averaged. However, further consideration must be given to how to interpret the outputs when the population 'divides' to give more than one estimate of the timing of a certain event (Table 8).

There were some major differences with the third generation (not presented) and further consideration is needed to determine how to interpret the output so that the proportion of insects completing a third generation can be estimated. Some discrepancies may also be because the effect of high temperatures on the incidence of pupal aestivation has not been incorporated into this version of the model.

Table 10a. Validations of the EXCEL model for carrot fly – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| Validation sites | EXCEL - larva overwinterers | | | | EXCEL - pupa overwinterers | | | | MORPH single output | | | | Difference - larva (EXCEL - MORPH) | | | | Difference - pupa (EXCEL - MORPH) | | | |
|-------------------------------|-----------------------------|--------|-----------|--------|----------------------------|--------|-----------|--------|---------------------|--------|-----------|--------|------------------------------------|-----|-----------|-----|-----------------------------------|-----|-----------|-----|
| | Emergence | | Eggs laid | | Emergence | | Eggs laid | | Emergence | | Eggs laid | | Emergence | | Eggs laid | | Emergence | | Eggs laid | |
| | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% |
| First generation 2012 | | | | | | | | | | | | | | | | | | | | |
| Cornwall | 21-Apr | 08-May | 10-May | 26-May | 2-May | 21-May | 18-May | 30-May | 28-Apr | 12-May | 22-May | 30-May | -7 | -4 | -12 | -4 | 4 | 9 | -4 | 0 |
| Kent | 19-Apr | 07-May | 06-May | 22-May | 29-Apr | 17-May | 11-May | 27-May | 26-Apr | 07-May | 12-May | 25-May | -7 | 0 | -6 | -3 | 3 | 10 | -1 | 2 |
| Lancashire | 16-Apr | 06-May | 13-May | 26-May | 28-Apr | 20-May | 17-May | 28-May | 23-Apr | 08-May | 22-May | 28-May | 14 | 14 | -9 | -2 | 5 | 12 | -5 | 1 |
| Nottinghamshire | 24-Apr | 13-May | 12-May | 26-May | 3-May | 24-May | 17-May | 31-May | 27-Apr | 12-May | 21-May | 29-May | -3 | 1 | -9 | -3 | 6 | 12 | -4 | 2 |
| Scotland | 27-Apr | 20-May | 24-May | 31-May | 7-May | 29-May | 24-May | 21-Jun | 01-May | 20-May | 25-May | 09-Jun | -4 | 0 | -1 | -9 | 6 | 9 | -1 | 12 |
| Suffolk | 23-Apr | 10-May | 13-May | 25-May | 4-May | 21-May | 20-May | 30-May | 01-May | 11-May | 23-May | 29-May | -8 | -1 | -10 | -4 | 3 | 10 | -3 | 1 |
| Yorkshire | 23-Apr | 12-May | 15-May | 27-May | 3-May | 24-May | 21-May | 2-Jun | 28-Apr | 15-May | 23-May | 30-May | -5 | -3 | -8 | -3 | 5 | 9 | -2 | 3 |
| Second generation 2012 | | | | | | | | | | | | | | | | | | | | |
| Cornwall | 21-Jul | 11-Aug | 25-Jul | 17-Aug | 25-Jul | 14-Aug | 30-Jul | 22-Aug | 10-Aug | 19-Aug | 16-Aug | 30-Aug | -20 | -8 | -21 | -12 | -16 | -5 | -17 | -8 |
| Kent | 11-Jul | 31-Jul | 16-Jul | 08-Aug | 14-Jul | 5-Aug | 19-Jul | 12-Aug | 28-Jul | 08-Aug | 04-Aug | 17-Aug | -17 | -8 | -18 | -9 | -14 | -3 | -16 | -5 |
| Lancashire | 19-Jul | 06-Aug | 23-Jul | 13-Aug | 20-Jul | 9-Aug | 24-Jul | 16-Aug | 03-Aug | 14-Aug | 11-Aug | 23-Aug | -15 | -8 | -19 | -9 | -14 | -5 | -17 | -7 |
| Nottinghamshire | 20-Jul | 7-Aug | 24-Jul | 14-Aug | 23-Jul | 12-Aug | 26-Jul | 18-Aug | 04-Aug | 15-Aug | 12-Aug | 23-Aug | -15 | -8 | -19 | -8 | -12 | -3 | -17 | -4 |
| Scotland | 11-Aug | 28-Aug | 16-Aug | 8-Sep | 12-Aug | 13-Sep | 17-Aug | 17-Oct | 25-Aug | 10-Sep | 06-Sep | 25-Sep | -14 | -13 | -21 | -17 | -13 | 3 | -20 | 22 |
| Suffolk | 12-Jul | 30-Jul | 18-Jul | 7-Aug | 15-Jul | 5-Aug | 21-Jul | 13-Aug | 28-Jul | 08-Aug | 05-Aug | 18-Aug | -16 | -9 | -17 | -10 | -13 | -3 | -15 | -5 |
| Yorkshire | 26-Jul | 14-Aug | 31-Jul | 21-Aug | 29-Jul | 19-Aug | 3-Aug | 27-Aug | 12-Aug | 23-Aug | 18-Aug | 03-Sep | -17 | -9 | -17 | -13 | -14 | -4 | -15 | -7 |
| First generation 2013 | | | | | | | | | | | | | | | | | | | | |
| Cornwall | 30-Apr | 16-May | 15-May | 6-Jun | 28-Apr | 18-May | 14-May | 6-Jun | 21-Apr | 05-May | 18-May | 06-Jun | 9 | 11 | -3 | 0 | 7 | 13 | -4 | 1 |
| Kent | 8-May | 26-May | 20-May | 10-Jun | 28-Apr | 19-May | 10-May | 6-Jun | 21-Apr | 09-May | 11-May | 02-Jun | 17 | 17 | 10 | 9 | 7 | 10 | -1 | 4 |
| Lancashire | 23-May | 7-Jun | 3-Jun | 17-Jun | 8-May | 31-May | 27-May | 10-Jun | 03-May | 19-May | 27-May | 09-Jun | 20 | 19 | 7 | 9 | 5 | 12 | 0 | 1 |
| Lincolnshire | 17-May | 1-Jun | 29-May | 14-Jun | 5-May | 23-May | 15-May | 9-Jun | 30-Apr | 13-May | 20-May | 07-Jun | 17 | 19 | 10 | 7 | 5 | 10 | -5 | 2 |
| Norfolk | 11-May | 28-May | 1-Jun | 15-Jun | 6-May | 24-May | 19-May | 13-Jun | 02-May | 11-May | 19-May | 11-Jun | 9 | 17 | 14 | 5 | 4 | 13 | 0 | 3 |
| Scotland | 4-Jun | 18-Jun | 13-Jun | 30-Jun | 25-May | 11-Jun | 2-Jun | 23-Jun | 21-May | 02-Jun | 04-Jun | 17-Jun | 14 | 16 | 9 | 13 | 4 | 9 | -2 | 7 |
| Suffolk | 5-May | 17-May | 16-May | 8-Jun | 3-May | 19-May | 13-May | 9-Jun | 29-Apr | 08-May | 14-May | 07-Jun | 6 | 9 | 2 | 1 | 4 | 11 | -1 | 2 |
| Yorkshire | 7-Jun | 21-Jun | 14-Jun | 1-Jul | 22-May | 12-Jun | 2-Jun | 21-Jun | 16-May | 03-Jun | 02-Jun | 18-Jun | 22 | 18 | 12 | 13 | 6 | 9 | 0 | 3 |
| Second generation 2013 | | | | | | | | | | | | | | | | | | | | |
| Cornwall | 31-Jul | 21-Aug | 4-Aug | 29-Aug | 30-Jul | 22-Aug | 3-Aug | 30-Aug | 08-Aug | 19-Aug | 15-Aug | 28-Aug | -8 | 3 | -11 | 2 | -9 | 3 | -11 | 2 |
| Kent | 26-Jul | 16-Aug | 29-Jul | 23-Aug | 21-Jul | 14-Aug | 24-Jul | 20-Aug | 01-Aug | 15-Aug | 07-Aug | 24-Aug | -6 | 2 | -9 | -1 | -11 | -1 | -14 | -4 |
| Lancashire | 6-Aug | 28-Aug | 10-Aug | 6-Sep | 2-Aug | 22-Aug | 6-Aug | 30-Aug | 11-Aug | 20-Aug | 18-Aug | 30-Aug | -5 | 9 | -7 | 7 | -9 | 3 | -12 | 0 |
| Lincolnshire | 26-Jul | 18-Aug | 29-Jul | 24-Aug | 19-Jul | 13-Aug | 23-Jul | 20-Aug | 31-Jul | 14-Aug | 06-Aug | 22-Aug | -5 | 5 | -8 | 3 | -12 | -1 | -14 | -1 |
| Norfolk | 5-Aug | 25-Aug | 9-Aug | 2-Sep | 29-Jul | 24-Aug | 01-Aug | 01-Sep | 07-Aug | 21-Aug | 15-Aug | 30-Aug | -2 | 5 | -5 | 3 | -9 | 4 | -13 | 2 |
| Scotland | 17-Aug | 12-Sep | 22-Aug | 28-Sep | 8-Aug | 6-Sep | 14-Aug | 22-Sep | 17-Aug | 28-Aug | 24-Aug | 09-Sep | 0 | 15 | -2 | 19 | -9 | 9 | -10 | 13 |
| Suffolk | 17-Jul | 9-Aug | 20-Jul | 16-Aug | 15-Jul | 10-Aug | 19-Jul | 17-Aug | 29-Jul | 12-Aug | 04-Aug | 21-Aug | -12 | -3 | -15 | -5 | -14 | -2 | -16 | -4 |
| Yorkshire | 19-Aug | 14-Sep | 23-Aug | 27-Sep | 10-Aug | 4-Sep | 15-Aug | 18-Sep | 16-Aug | 29-Aug | 22-Aug | 10-Sep | 3 | 16 | 1 | 17 | -6 | 7 | -7 | 8 |

Table 10b. CVs and thresholds used in validations of the EXCEL model for carrot fly.

| | CVs | | | Temperature thresholds |
|-------------------------------------|------|--|--------|------------------------|
| Larval & pupal development (spring) | 0.27 | | LPD | 4.2 |
| Pre-oviposition period 1 | 0.49 | | POP1 | 7.5 |
| Pre-oviposition period 2 | 0.76 | | POP2 | 6.4 |
| Egg stage | 0.07 | | ES1 | 5.2 |
| Larvae stage | 0.17 | | ES2 | 5.2 |
| Pupae stage | 0.13 | | LS1 | 2 |
| | | | LS2 | 2 |
| | | | PD1 | 2.1 |
| | | | PD2 | 2.1 |
| | | | POP11 | 7.5 |
| | | | POP12 | 6.4 |
| | | | POP21 | 7.5 |
| | | | POP22 | 6.4 |
| | | | ES11 | 5.2 |
| | | | ES12 | 5.2 |
| | | | ES21 | 5.2 |
| | | | ES22 | 5.2 |
| | | | LS11 | 2 |
| | | | LS12 | 2 |
| | | | LS21 | 2 |
| | | | LS22 | 2 |
| | | | PD11 | 2.1 |
| | | | PD12 | 2.1 |
| | | | PD21 | 2.1 |
| | | | PD22 | 2.1 |
| | | | POP111 | 7.5 |
| | | | POP112 | 6.4 |
| | | | POP121 | 7.5 |
| | | | POP122 | 6.4 |
| | | | POP211 | 7.5 |
| | | | POP212 | 6.4 |
| | | | POP221 | 7.5 |
| | | | POP222 | 6.4 |
| | | | ES111 | 5.2 |
| | | | ES112 | 5.2 |
| | | | ES121 | 5.2 |
| | | | ES122 | 5.2 |
| | | | ES211 | 5.2 |
| | | | ES212 | 5.2 |
| | | | ES221 | 5.2 |
| | | | ES222 | 5.2 |
| | | | LS111 | 2 |
| | | | LS112 | 2 |
| | | | LS121 | 2 |
| | | | LS122 | 2 |
| | | | LS211 | 2 |
| | | | LS212 | 2 |
| | | | LS221 | 2 |
| | | | LS222 | 2 |

| | CVs | | Temperature thresholds |
|--|------|--------|------------------------|
| Diapause and post-diapause development | 0.27 | LPD | 2 |
| Pre-oviposition period 1 | 0.49 | POP1 | 7.5 |
| Pre-oviposition period 2 | 0.76 | POP2 | 6.4 |
| Egg stage | 0.07 | ES1 | 5.2 |
| Larvae stage | 0.17 | ES2 | 5.2 |
| Pupae stage | 0.13 | LS1 | 2 |
| | | LS2 | 2 |
| | | PD1 | 2.1 |
| | | PD2 | 2.1 |
| | | POP11 | 7.5 |
| | | POP12 | 6.4 |
| | | POP21 | 7.5 |
| | | POP22 | 6.4 |
| | | ES11 | 5.2 |
| | | ES12 | 5.2 |
| | | ES21 | 5.2 |
| | | ES22 | 5.2 |
| | | LS11 | 2 |
| | | LS12 | 2 |
| | | LS21 | 2 |
| | | LS22 | 2 |
| | | PD11 | 2.1 |
| | | PD12 | 2.1 |
| | | PD21 | 2.1 |
| | | PD22 | 2.1 |
| | | POP111 | 7.5 |
| | | POP112 | 6.4 |
| | | POP121 | 7.5 |
| | | POP122 | 6.4 |
| | | POP211 | 7.5 |
| | | POP212 | 6.4 |
| | | POP221 | 7.5 |
| | | POP222 | 6.4 |
| | | ES111 | 5.2 |
| | | ES112 | 5.2 |
| | | ES121 | 5.2 |
| | | ES122 | 5.2 |
| | | ES211 | 5.2 |
| | | ES212 | 5.2 |
| | | ES221 | 5.2 |
| | | ES222 | 5.2 |
| | | LS111 | 2 |
| | | LS112 | 2 |
| | | LS121 | 2 |
| | | LS122 | 2 |
| | | LS211 | 2 |
| | | LS212 | 2 |
| | | LS221 | 2 |
| | | LS222 | 2 |

POLLEN BEETLES (*Meligethes* spp.)

Description of the original MORPH model

The relationships between the rate of *Meligethes* development and temperature were used to develop a simulation model for forecasting the summer migration of beetles into susceptible horticultural brassica crops. The modelling procedure is described in Phelps *et al.*, (1993).

The model, which simulates development of *Meligethes* from 1 February (the coldest period of the winter), is based on equations derived from biological data collected at Wellesbourne. Linear and non-linear (Gompertz) equations were fitted to each set of data to describe the relationship between rate of development during a particular phase of the insects' life-cycle and temperature (Phelps *et al.*, 1993). Egg and larval development, both of which occur on the host-plant, were regarded as one phase of beetle development and soil-based stages of pupation and pupal development were regarded as another. The most appropriate equation to describe each phase of development was selected by maximum likelihood analysis and inspection of residuals.

Meligethes development was summarised using equations for the four phases:

1. Development until emergence of beetles in the spring.
2. Egg maturation until egg laying.
3. Egg and larval development until fully-fed larvae drop from plants.
4. Pupation and pupal development until beetles emerge in summer.

The fitted equations are shown in Table 8. The variation in the rate of development was estimated for each phase, using coefficients of variation (CV) derived from the laboratory experiments, by calculating the mean and variance of the rate of development at each constant temperature (Phelps *et al.*, 1993). The CVs for the equations derived for the four phases of beetle development are shown in Table 11.

The facility to include an activity threshold for beetle migration in the summer was also built into the MORPH model. For the initial model runs it was estimated that few beetles were caught when the air temperature was below 18°C. Lower development thresholds for the other phases in the life-cycle were also included.

The MORPH version of the model was run for a population of 500 insects in each phase of development using weather data obtained from Agrometeorological stations. The output included the forecast times of beetle emergence in the spring, of egg laying and of the summer migration.

Table 11. Equations for the pollen beetle model. The lower threshold temperatures were estimated by linear extrapolation and may not be the 'true' thresholds.

| Phase of insect development | Equation | Lower threshold temperature °C | Coefficient of variation (%) |
|--------------------------------|---|--------------------------------|------------------------------|
| Spring development | $PB1 = 3.326 + 7.55 \cdot \exp(-\exp(-0.336 \cdot (T - 15.005)))$ | 4.4 | 45 |
| Egg maturation | $PB2 = 1.568 + 60 \cdot \exp(-\exp(-0.110 \cdot (T - 29)))$ | 7.4 | 21 |
| Egg and larval development | $PB3 = 0.4835 \cdot T - 0.86$ | 1.8 | 16 |
| Pupation and pupal development | $PB4 = 0.3668 \cdot T - 2.382$ | 6.5 | 11 |

Description of the EXCEL model

The model used the same principles as the cabbage root fly and carrot fly models but the sequence is much simpler as there is only one generation per year and the sequence of equations is as shown in Table 11. The facility to include an activity threshold for beetle migration in the summer has not been built into the EXCEL model yet.

Validation of the EXCEL model

The outputs from the MORPH and EXCEL versions of the pollen beetle model are compared in Table 12. For the EXCEL model a threshold of 10°C was used for the last 3 stages of development. In most cases they were in close agreement.

Table 12a. Validations of the EXCEL model for pollen beetle – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| Validation sites | | EXCEL | | | | MORPH | | | | Difference (MORPH - EXCEL) days | | | |
|-------------------|-------------|--------|--------|--------|--------|--------|--------|--------|--------|---------------------------------|-----|--------|-----|
| | | Spring | | Summer | | Spring | | Summer | | Spring | | Summer | |
| | | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% |
| Cornwall | 2014 | 23-Feb | 6-Mar | 13-Jul | 25-Jul | 23-Feb | 07-Mar | 10-Jul | 21-Jul | 0 | -1 | 3 | 4 |
| Kent | 2014 | 23-Feb | 6-Mar | 25-Jun | 9-Jul | 23-Feb | 06-Mar | 25-Jun | 17-Jul | 0 | 0 | 0 | -8 |
| Lancashire | 2014 | 6-Mar | 18-Mar | 11-Jul | 23-Jul | 08-Mar | 20-Mar | 06-Jul | 18-Jul | -2 | -2 | 5 | 5 |
| Norfolk | 2014 | 24-Feb | 7-Mar | 2-Jul | 15-Jul | 25-Feb | 07-Mar | 30-Jun | 12-Jul | -1 | 0 | 2 | 3 |
| Scotland | 2014 | 19-Mar | 10-Apr | | | 25-Mar | 12-Apr | 02-Aug | 09-Aug | -6 | -2 | | |
| Suffolk | 2014 | 25-Feb | 10-Mar | 18-Jun | 2-Jul | 23-Feb | 08-Mar | 21-Jun | 02-Jul | 2 | 2 | -3 | 0 |
| Yorkshire | 2014 | 10-Mar | 21-Mar | 18-Jul | 30-Jul | 10-Mar | 22-Mar | 10-Jul | 22-Jul | 0 | -1 | 8 | 8 |
| | | | | | | | | | | | | | |
| Cornwall | 2013 | 4-Mar | 21-Mar | 30-Jul | 12-Aug | 04-Mar | 21-Mar | 27-Jul | 06-Aug | 0 | 0 | 3 | 6 |
| Kent | 2013 | 16-Mar | 12-Apr | 17-Jul | 27-Jul | 16-Mar | 11-Apr | 18-Jul | 27-Jul | 0 | 1 | -1 | 0 |
| Lancashire | 2013 | 13-Apr | 23-Apr | 29-Jul | 12-Aug | 13-Apr | 24-Apr | 30-Jul | 12-Aug | 0 | -1 | -1 | 0 |
| Norfolk | 2013 | 15-Apr | 23-Apr | 24-Jul | 6-Aug | 15-Apr | 24-Apr | 01-Aug | 11-Aug | 0 | -1 | -8 | -5 |
| Scotland | 2013 | 1-May | 11-May | 1-Aug | 19-Aug | 30-Apr | 11-May | 07-Aug | 20-Aug | 1 | 0 | -6 | -1 |
| Suffolk | 2013 | 2-Apr | 16-Apr | 14-Jul | 24-Jul | 01-Apr | 12-Apr | 26-Jul | 07-Aug | 1 | 4 | -12 | -14 |
| Yorkshire | 2013 | 25-Apr | 5-May | 5-Aug | 18-Aug | 28-Apr | 07-May | 04-Aug | 16-Aug | -3 | -2 | 1 | 2 |

Table 12b. CVs and thresholds used in validations of the EXCEL model for pollen beetle.

| | CVs | | Temperature thresholds |
|--------------------------------|------|--------------------------------|------------------------|
| Spring development | 0.45 | Spring development | 4.4 |
| Egg maturation | 0.21 | Egg maturation | 10 |
| Egg and larval development | 0.16 | Egg and larval development | 10 |
| Pupation and pupal development | 0.11 | Pupation and pupal development | 10 |

LARGE NARCISSUS FLY

Description of the original MORPH model

The equations for the large narcissus fly model are based on the work described in Collier and Finch (1992). Eggs, larvae, pupae and adults of the large narcissus fly (*Merodon equestris*) were reared at a series of constant temperatures between 9–24°C. Egg development required from 37 days at 9°C to 7 days at 21.5°C. The low-temperature threshold for development was 6.7°C. Larvae reared at 14–24°C were fully-grown after 18 weeks, but it took much longer for such insects to pupate, and adult flies emerged only after about 45 weeks of development. Large narcissus flies enter diapause during the larval stage and overwinter as fully-fed larvae, forming pupae in the following spring. Post-winter pupation and pupal development took from 169 days at 10°C to 36 days at 21.5°C. Of this, pupal development required from 91 days at 10°C to 19 days at 21.5°C. The low-temperature threshold for post-winter pupation and pupal development was 7.1°C, and for pupal development alone, 7.2°C.

Females maintained at or below 19°C laid few eggs, whereas some females kept at or above 21.5°C laid more than 100 eggs (mean 69 ± 36). Approximately 50% of females maintained at or above 21.5°C laid less than 10 eggs during their lifetime. The mean egg-laying time was 6 to 9 days. Although temperatures at or below 19°C inhibited mating, once a female had mated, such temperatures did not prevent oviposition.

The equations for the large narcissus fly model are shown in Table 13.

Table 13. Equations for the large narcissus fly model. The lower threshold temperatures were estimated by linear extrapolation and may not be the 'true' thresholds.

| Phase of insect development | Equation | Lower threshold temperature °C | Coefficient of variation (%) |
|-----------------------------|---|--------------------------------|------------------------------|
| Spring emergence | $LNF1 = 0.953 + 1.375 * \text{EXP}(-\text{EXP}(-1.6 * (\text{TEMP} - 13.962)))$ | 7.1 | 17 |
| Pre-oviposition period | $LNF2 = 1.412 * \text{TEMP} - 17.9$ | 19 | 30 |
| Egg hatch | $LNF3 = 0.9651 * \text{TEMP} - 6.531$ | 6.7 | 5 |

Description of the EXCEL model

The model used the same principles as the cabbage root fly and carrot fly models but the sequence is much simpler as there is only one generation per year and the sequence of equations is as shown in Table 13.

Validation of the EXCEL model

The outputs from the MORPH and EXCEL versions of the large narcissus fly model are compared in Table 14. In general, there was a close fit between the two versions of the model.

Table 14a. Validations of the EXCEL model for large narcissus fly – by comparing outputs from the EXCEL model with outputs from the MORPH model.

| Validation sites | Emergence 2012 | | Emergence 2012 (MORPH) | | Difference in days (MORPH - | | Emergence 2013 | | Emergence 2013 (MORPH) | | Difference in days (MORPH - | |
|------------------|----------------|--------|------------------------|--------|-----------------------------|-----|----------------|--------|------------------------|--------|-----------------------------|-----|
| | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% | 10% | 50% |
| Cornwall | 25-May | 04-Jun | 24-May | 02-Jun | 1 | 2 | 25-Jun | 09-Jul | 21-Jun | 07-Jul | 4 | 2 |
| Kent | 26-May | 03-Jun | 26-May | 03-Jun | 0 | 0 | 27-Jun | 05-Jul | 25-Jun | 02-Jul | 2 | 3 |
| Lancashire | 26-May | 05-Jun | 25-May | 04-Jun | 1 | 1 | 02-Jul | 11-Jul | 30-Jun | 10-Jul | 2 | 1 |
| Suffolk | 29-May | 08-Jun | 28-May | 07-Jun | 1 | 1 | 08-Jun | 16-Jun | 05-Jun | 13-Jun | 3 | 3 |
| Scotland | 22-Jun | 06-Jul | 18-Jun | 27-Jun | 4 | 9 | 08-Jul | 16-Jul | 01-Jul | 15-Jul | 7 | 1 |
| Yorkshire | 06-Jun | 23-Jun | 05-Jun | 21-Jun | 1 | 2 | 10-Jul | 19-Jul | 09-Jul | 19-Jul | 1 | 0 |

Table 14b. CVs and thresholds used in validations of the EXCEL model for large narcissus fly.

| | CVs | | Temperature thresholds |
|------------------------|------|------------------------|------------------------|
| Spring emergence | 0.17 | Spring emergence | 7.1 |
| Pre-oviposition period | 0.3 | Pre-oviposition period | 19 |
| Egg hatch | 0.05 | Egg hatch | 6.7 |

DAYDEGREE MODELS FOR APHIDS OVERWINTERING IN THE EGG STAGE

The day-degree models described below were incorporated into a single spreadsheet, which, when opened, provides a prompt for the data file. The accumulated day-degrees are presented graphically together with a horizontal line indicating the target day-degree sums for each species (Figure 7).

Willow-carrot aphid (*Cavariella aegopodii*)

The forecast is based on accumulated day-degrees (D°) from 1 February (base 4.4°C). The base temperature of 4.4°C is an estimate as no detailed laboratory studies have been undertaken to determine the threshold temperature. Information from the Rothamsted Suction trap captures at Wellesbourne and Kirton was used to estimate the mean number of D° from 1 February until the first aphid of the year is caught in a suction trap (the start of the migration to carrot). This is after 360D°.

Lettuce root aphid (*Pemphigus bursarius*)

The forecast is based on accumulated day-degrees (D°) from 1 February (base 4.4°C). The base temperature of 4.4°C is an estimate as no detailed laboratory studies have been undertaken to determine the threshold temperature. The information was collected in projects funded by the HDC, Defra and LINK (Collier *et al.*, 1994a; Collier & Harrington, 2001; Tatchell *et al.*, 1998). The start of the migration of winged aphids from poplar to lettuce occurred after 672D° had been accumulated since 1 February. Monitoring data collected during the projects (e.g. Collier *et al.*, 1994a) were compared with this forecast, which was shown to give adequate early warning of the start of aphid migration.

Currant-lettuce aphid (*Nasonovia ribisnigri*)

The forecast is based on accumulated day-degrees (D°) from 1 February (base 4.4°C). The base temperature of 4.4°C is an estimate as no detailed laboratory studies have been

undertaken to determine the threshold temperature. The information was collected in projects funded by the HDC and LINK (Collier & Harrington, 2001; Tatchell et al., 1998). The mean numbers of day-degrees accumulated until the first aphid was found and until peak numbers of aphids were found were 507D° and 935D° respectively. Comparisons between observed and predicted dates showed that this forecast is likely to be accurate to within a 2-3 week period.

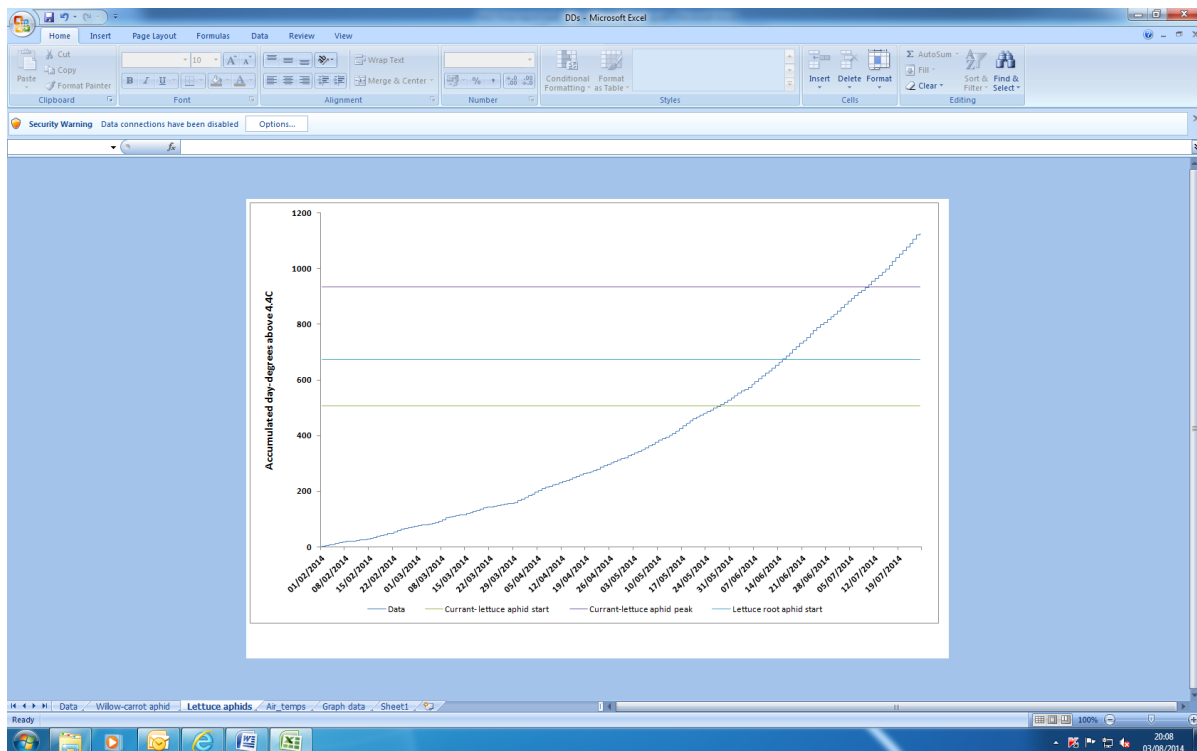


Figure 7. Screenshot of output of day-degree forecast for lettuce aphids.

Discussion

Translation of the Monte Carlo models into EXCEL spreadsheets provides a considerable challenge and this is principally because EXCEL will not deal with the size and complexity of the MORPH models. Thus there had to be some compromises in terms of output in particular. The limitations of the EXCEL versions of the Monte Carlo models described above will be reiterated here. Firstly, because of limitations with ‘computing power’ the EXCEL models currently only ‘follow’ deciles up to 50%. Since information provided to growers as part of the MORPH outputs is usually restricted to 10% and 50% ‘activity’ this is in itself not a limitation. However, the EXCEL models do not provide information on ‘individual’ insects and so it is not possible to replicate the types of graph produced by

MORPH. Thus it will be necessary to think of another way of representing the information graphically if this is considered useful.

In addition, at this stage, some of the other 'interventions' incorporated into MORPH (pupal aestivation in cabbage root fly and carrot fly) have not been incorporated yet into the EXCEL versions and this may account for some of the deviations between the outputs from the versions of the models.

For the two more complex models, cabbage root fly and carrot fly, further consideration is required of how best to interpret the outputs. This is firstly because the population 'divides' as the model progresses and secondly because the output for the third generation is not presented as clearly in EXCEL as in MORPH – in that it is not possible currently to estimate the proportion of the population entering the third generation. Further consideration of how the output is presented is required.

Conclusions

- The information on which seven of the pest models are based has been documented in this report.
- A first attempt has been made to incorporate the Monte Carlo models (cabbage root fly, carrot fly, pollen beetle, large narcissus fly) into an EXCEL format.
- The EXCEL models are 'simpler' because there is a limit to the 'computing power'.
- Overall, the validations of the initial versions of the EXCEL models confirm that the approach is valid. The more complex models require some further modification in places.

Please note: AHDB Horticulture understands that pests and disease decision support tools are a guide to decision making and users should not rely just on these tools to make management decisions.

Knowledge and Technology Transfer

Output from the MORPH versions of the pest models is currently available as part of the AHDB Horticulture Pest Bulletin and the information is available from the Syngenta web site.

References

- Biernaux, J. (1968). Observations sur l'hibernation de *Psila rosae* F. *Bull. Rech. agron. Gembloux* 3, 241-248.
- Brunel, E. & Missonier, J. (1968). Etude du developpement nymphal de *Psila rosae* Fab. (Dipteres Psilides) en conditions naturelles et experimentales: quiescence et diapause. *Comptes Rendus des Seances de la Societe de Biologie et des ses Filiales (Paris)* 162, 2223-2228.
- Burn, A. J. (1980). The natural mortality of the carrot fly. (*Psila rosae* F.) PhD thesis. University of Cambridge. UK.
- Burn, A.J. & Coaker, T.H. (1981). Diapause and overwintering of the carrot fly, *Psila rosae* (F.) (Diptera: Psilidae). *Bulletin of Entomological Research* 71, 583-590.
- Coaker, T. H. & Finch, S. (1971). The cabbage root fly, *Erioischia brassicae* (Bouche). *Report of the National. Vegetable. Research. Station.* 1970: 23-42.
- Coaker, T. H. & Wright, D. W. (1963). The influence of temperature on the emergence of the cabbage root fly (*Erioischia brassicae* (Bouche)) from overwintering pupae. *Annals of Applied Biology* 52, 337-343.
- Collier, R. H. & Finch, S (1983). Completion of diapause in field populations of the cabbage root fly (*Delia radicum*). *Entomologia experimentalis et applicata* 34, 186-192.
- Collier, R. H. & Finch, S. (1985). Accumulated temperatures for predicting the time of emergence in the spring of the cabbage root fly, *Delia radicum* (L.) (Diptera: Anthomyiidae). *Bulletin of Entomological Research* 75, 395-404.
- Collier, R.H. & Finch, S. (1996). Field and laboratory studies on the effects of temperature on the development of the carrot fly (*Psila rosae* F.). *Annals of Applied Biology* 128, 1-11.
- Collier, R.H. & Finch, S. (1992). The effects of temperature on development of the large narcissus fly (*Merodon equestris*). *Annals of Applied Biology*, 120, 383-390.
- Collier, R.H., Davies, J., Roberts, M., Leatherland, M., Runham, S. & Blood-Smyth, J. (1994a). Monitoring and forecasting the times of attack of the lettuce root aphid, *Pemphigus bursarius* L. *Integrated Control in Field Vegetable Crops. IOBC/WPRS Bulletin* 1994, 17 (8), 31-40.

- Collier, R.H., Elliott, M.S. & Finch, S. (1994b). Development of the overwintering stages of the carrot fly, *Psila rosae*, (Diptera:Psilidae). *Bulletin of Entomological Research* 84, 469-476.
- Collier, R.H. & Finch, S. (1996). Field and laboratory studies on the effects of temperature on the development of the carrot fly (*Psila rosae* F.). *Annals of Applied Biology* 128, 1-11.
- Collier, R.H. & Harrington, R. (2001). Outdoor lettuce: Refinement and field validation of forecasts for the aphid pests of lettuce foliage. *Final Report 1999-2001 HDC Project FV162e*.
- Dufault, C. P. and T. H. Coaker. 1987. Biology and control of the carrot fly *Psila rosae* F. *Agricultural Zoology reviews* 2:97-134.
- Finch, S. & Anderson, M. (1989). Laboratory studies on late-emergence in the cabbage root fly (*Delia radicum*). *Entomologia experimentalis et applicata* 50, 233-240.
- Finch, S & Collier R. H. (1983). Emergence of flies from overwintering populations of cabbage root fly pupae. *Ecological Entomology* 8, 29-36.
- Finch, S. & Collier, R. H. (1985). Laboratory studies on aestivation in the cabbage root fly (*Delia radicum*). *Entomologia experimentalis et applicata* 38, 137-143.
- McClanahan, R.J. & Niemczyk, H.D. (1963). Continuous rearing of the carrot rust fly, *Psila rosae* (Fab). *Canadian Entomologist* 95, 827-830.
- McLeod, D.G.R., Whistlecraft, J.W. & Harris, C.R. (1985). An improved rearing procedure for the carrot rust fly (Diptera:Psilidae) with observations on life history and conditions controlling diapause induction and termination. *Canadian Entomologist* 117, 1017-1024.
- Phelps, K., Collier, R.H., Reader, R.J. & Finch, S. (1993). Monte Carlo simulation method for forecasting the timing of pest insect attacks. *Crop Protection* 12, 335-342.
- Stadler, E. (1970). Beitrag zur Kenntnis der Diapause bei der Mohrenfliege (*Psila rosae* Fabr. Diptera: Psilidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 43, 17-37.
- Stevenson, A.B. & Barszcz, E.S. (1989). Diapause status of the overwintering generation of the carrot rust fly, *Psila rosae* (Fab.) (Diptera:Psilidae), in Ontario. *Canadian Entomologist*, 121, 921-928.
- Stevenson, A.B. (1981). Development of the carrot rust fly, *Psila rosae* (Diptera:Psilidae) relative to temperature in the laboratory. *Canadian Entomologist* 113, 569-574.

- Tatchell, G.M., Ellis, P.R., Collier, R.H., Chandler, D., Mead, A., Wadhams, L.J, Parker, W.E., Blood Smyth, J. & Vice, E. W. (1998). Integrated pest management of aphids on outdoor lettuce crops. *Final Report 1994-98 MAFF LINK Project P 131, HDC Project FV 162. 77 pp.*
- Van't Sant, L.E. (1961). Levenswijze en bestrijding van de wortelvlieg (*Psila rosae* F.) in Nederland. *Versl. landbouwk. Onderz. Ned.* 67, 1-131.
- Wright, D.W. & Ashby, D.G. (1946). Bionomics of the carrot fly (*Psila rosae* Fab.). II. Soil populations of carrot fly during autumn, winter and spring. *Annals of Applied Biology* 33, 263-270.