

# A new release of INSIM: A temperature-dependent model for insect development

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For many practical purposes it is useful to predict the development rate of insects, for instance because not all stages of a pest insect are equally damaging crops. As insects are poikilothermous, their developmental rate is strongly influenced by temperature. In the literature the duration of the development of egg, larval and pupal stages of insects is mostly reported at constant temperatures. In an orchard or in crop fields however, fruit growers might like to predict when some stages of pest insect can be expected based on the current temperature. Measures to eradicate such a pest species can then be taken at the right time.

Here, we present a new version of the age-structured insect simulation model INSIM that was originally developed by Diederik and Mols (1996). The model is re-implemented in MATLAB and can now simulate multiple seasons. It calculates the occurrence of insect stages during the year based on daily minimum and maximum temperatures. The model needs detailed information on sex ratio, relative mortality and developmental times at different temperatures. Furthermore, it is necessary to know the threshold value for the development, and the threshold value for the reproduction of adults. If more than one generation is simulated, similar information of reproductive capacity of adults is needed. The model can also take into account that there are individual differences in development time, resulting in a dispersion of stages. We describe the input tables for the program in detail and give the outcome for the western corn root borer *Diabrotica virgifera virgifera*.

*Keywords:* degree-day, phenology, prediction, dynamics

In orchards earwigs *Forficula auricularia* (L.) are polyphagous predators of pest species, like several apple aphid species and pear psyllid (Solomon *et al.* 2000). These species are important for integrated pest management in such environ-

ments, but both the amounts of earwigs and the time at which they appear show a large variation over the years. The timing of the appearance of adults is related to the temperature, and there are rules of thumb that relate this to the temperature sum above a threshold temperature (Helsen *et al.* 1998).

Mols *et al.* (1998) describe one of the first studies that used a more precise estimation of temperature-dependent development for discovering optimum moments for monitoring and control. They studied three *Orthosia* species. Larval emergence and development were predicted, with the Quick Basic computer program INSIM. Results of the simulations with the model (Diederik & Mols 1996) were in close agreement with field observations. The heat sum for embryonic development was determined by the model as 72 degree days above a developmental threshold of 7.0°C. This model was also successfully used to predict the emergence of *Dasineura tetensi* adults (Cross & Crook 1999) and the reproduction of the western corn rootworm, *Diabrotica (virgifera) virgifera* (Hemerik *et al.* 2004).

The INSIM program that was used in these examples, uses the development rate values as measured under laboratory conditions. The model calculates daily development amounts from daily maximum and minimum air temperatures and the temperature sum as an accumulation of these amounts. The model uses boxcar trains (see Goudriaan & van Roermund 1989) to simulate developmental dispersion. When we tried to use the Quick Basic implementation of INSIM, we discovered several shortcomings of the program: (1) the necessary data was not easily imported into INSIM, although the help function told us that space-delimited text files in a certain format should work, (2) the program could not run for a longer time span than a year, which is not enough for simulating the life cycle of, for instance, click beetles (Elateridae) that can live 3-7 years as wireworms in the soil (Kabanov 1975), and (3) if the program was used without reproduction and with constant developmental rate for a few stages, some new eggs were introduced due to numerical errors after a while. These shortcomings of the original INSIM program made it hard to start simulating insects for which temperature data could be found in the literature. Therefore, we decided to develop a new implementation of INSIM. Here we report the results of some simple tests and the results for the development of *D. virgifera* (Hemerik *et al.* 2004).

## **MATERIAL AND METHODS**

### **Structure of the INSIM model**

INSIM applies the boxcar train technique (Goudriaan & van Roermund 1989) to simulate the distribution of individuals over the various life stages. In this approach each particular life stage (called the 'boxcar train') is subdivided in several substages (classes or 'boxcars'). It uses the 'escalator boxcar train' for stages

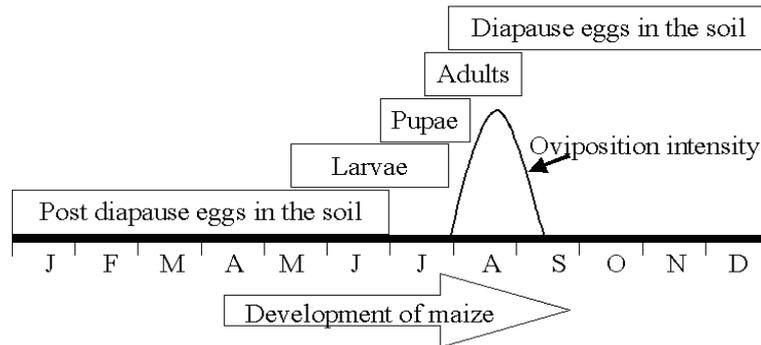


Figure 1. The life cycle of the uni-voltine western corn rootworm in the course of one year.

that have a negligible variance in development rates and the ‘fractional boxcar train’ to apply an individual variance in development. In this latter case, the number of boxcars cannot take any number. The new implementation of INSIM calculates the optimal number of boxcars and the optimal step size of the Euler integration (see Goudriaan & van Roermund 1989). The average development time, the dispersion in development time and the mortality rate at each time step in the simulation are determined by linear interpolation of tables in which these values are given for different temperatures.

## Simulation example

### Life cycle and feeding habits of the western corn rootworm

The species *D. virgifera* is uni-voltine and thus completes one generation per year (Fig. 1). In the soil, during summer, female deposit their eggs. These hibernate and hatch in late May or in early June. *D. virgifera*’s first larval stage feeds on fine root hairs and burrows into the root tips of corn whereas later stages. The white ‘worms’, i.e. larval stages two and three, feed on primary roots. Larvae of the third instar pupate in the soil and emerge as adults in July and August. Males emerge before the females. Mating takes place soon after emergence. Females start ovipositing after two weeks. The adult beetles are approximately 5-6 mm long and feed on corn silk or leaf tissue. The duration of each stage (egg, larval instars L<sub>1</sub>-L<sub>3</sub> and pupae) depends mainly on temperature.

### Necessary inputs

The implementation of the model for *D. virgifera* in INSIM requires information concerning (a) the sex ratio, (b) the life cycle, (c) the temperature-dependent development in each life stage, (d) the threshold values for development in these life stages, (e) the temperature-dependent mortality, (f) a threshold value for oviposition and (g) the age-dependent number of eggs laid per female per day at certain temperatures. All this information is entered in INSIM as a tab-delimited text file, with labeled (square brackets) tables. We explain all tables that are needed as input for INSIM in detail.

Table 1. In table [overview] the coupling of the life stages is defined.

| [overview]     |          |              |         |
|----------------|----------|--------------|---------|
| Name           | Symbol   | Input        | Classes |
| egg            | egg      | NaN          | 10      |
| Diapause eggs  | Diapeggs | egg          | 5       |
| L1 Female      | FL1      | 0.5*Diapeggs | 5       |
| L2 Female      | FL2      | FL1          | 10      |
| L3 Female      | FL3      | FL2          | 10      |
| Pupal Female   | FPup     | FL3          | 10      |
| Preoviposition | Preovi   | FPup         | 5       |
| Adult female   | FAdult   | Preovi       | 5       |

Table 2. An example of a table that contains the temperature-dependent development and mortality data (for the female second larval instar [FL2]).

| [fl2] |                  |                    |                         |
|-------|------------------|--------------------|-------------------------|
| temp  | Development time | Standard deviation | Relative mortality rate |
| 0     | NaN              | NaN                | NaN                     |
| 5.5   | 43.1             | 1.8                | 0.0073                  |
| 7.8   | 30.4             | 1.7                | 0.01036                 |
| 8.3   | 28.6             | 1.7                | 0.01102                 |
| 9.6   | 24.7             | 1.7                | 0.01275                 |
| 9.7   | 24.4             | 1.7                | 0.01288                 |
| 9.8   | 24.2             | 1.7                | 0.01301                 |
| 10.5  | 22.6             | 1.6                | 0.01394                 |
| 11.2  | 21.2             | 1.6                | 0.01487                 |
| 15    | 15.8             | 1.5                | 0.01992                 |
| 18    | 7.1              | 0.5                | 0.01961                 |
| 21    | 5.4              | 0.6                | 0.01544                 |
| 24    | 4.9              | 0.9                | 0.02378                 |
| 27    | 4.1              | 0.6                | 0.0177                  |
| 30    | 3.4              | 0.6                | 0.04096                 |
| 31.5  | 3.5              | 0.5                | 0.16566                 |

In the table [overview] the name (not obligatory) and symbol (obligatory, preferably short) for each stage in the life cycle of the insect are denoted (see Table 1). The sequence of developmental stages is defined in another column where it is stated from which of the other stages the input stems for the current stage. It should be noted that ‘NaN’ (or ‘not a number’) stands for no developmental input for the egg stage. This stage gets its input from the reproduction by adults (see below, where we describe the table [reproduction]). Note that the input for the L1 female states that it is 0.5\*Diapeggs. Here we assumed a 1:1 sex ratio to assure that we are only modeling female stages. The last column gives the number of classes into which the stage should be subdivided in the computer program.

After having defined the life cycle as described above tables for each stage should be defined separately, e.g. [table] **FLz** (Table 2). For each temperature for which data on development time and mortality are known from the literature a row is added to the table for the stage. The first row below the headers ‘temperature’, ‘development time’, ‘standard deviation’ and ‘relative mortality rate’ should hold the threshold temperature for development followed by NaN repeated three times. The example given in Table 2 includes ‘development time’ and the ‘standard deviation’ both in days. It should be noted that in INSIM for MatLab it is also possible to define a table with row headers ‘temperature’, ‘development rate’, ‘standard deviation’ and ‘relative mortality rate’. In that case ‘development rate’ and its ‘standard deviation’ are both presumed to be given as rate per day. The ‘relative mortality rate’ has also the dimension per day. At a temperature of for instance 31.5°C the relative mortality rate is 0.16566 per day (Table 2). This implies that during the mean development time of 3.5 days a fraction  $1 - \exp(-0.16566 * 3.5) = 0.44$  of the individuals have died. So for calculating the input for INSIM if we know that a fraction  $f$  has died during the total development time  $D$ , then we can compute the relative mortality rate  $m$  as  $(-\ln(1-f))/D$ .

This far we have defined the life cycle and the temperature-dependent development and mortality in a total of nine tables (one for the overview and one for each stage). We however, have not dealt with reproduction yet. The table for the reproducing stage, here the adult females of *D. virgifera*, **FAdult**, is defined as table [reproduction] **FAdult** → **egg** (see Table 3). The number of classes that has to be defined for oviposition in table [reproduction] is the same number as the number of classes for the reproducing stage, which was defined in the [overview] table, here 5. The number of eggs per day per class of adults is read from Table 3 (with linear interpolation). For instance in the last row of Table 3 it states that at a temperature of 30°C the adult females have an egg production of 12.3809 per day during the first 1/5th part of their average development time of their adult life. During the second 1/5th of their adult life the egg production

Table 3. Age-dependent and temperature-dependent reproduction (from Elliott *et al.* 1990). At each temperature, the maximum longevity is divided into five classes of equal length. Reproduction is given as the number of eggs laid per day in these classes.

| [REPRODUCTION] FAdult → egg |         |         |         |         |         |
|-----------------------------|---------|---------|---------|---------|---------|
| Temp.                       | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 |
| 15                          | 0.0000  | 0.0000  | 0.0000  | 0.0000  | 0.0000  |
| 16                          | 1.1429  | 4.5714  | 4.2857  | 4.2857  | 0.5714  |
| 19.5                        | 2.8571  | 10.3571 | 3.9286  | 1.4285  | 1.0714  |
| 23                          | 9.6428  | 7.8571  | 2.8571  | 0.9523  | 0.0000  |
| 26.5                        | 15.2380 | 11.4285 | 1.9047  | 0.9523  | 0.0000  |
| 30                          | 12.3809 | 10.0000 | 7.1400  | 3.5714  | 0.0000  |

Table 4. An example of the start of a climate file that includes the daily minimum ( $T_{\min}$ ) and maximum temperature ( $T_{\max}$ ).

debiltdiab.txt

| t   | $T_{\min}$ | $T_{\max}$ |
|-----|------------|------------|
| 1   | -1.4       | 1.2        |
| 2   | -4.1       | 0          |
| 3   | -5.3       | -0.1       |
| 4   | -6         | -0.1       |
| 5   | -5.5       | 1.9        |
| ... | ...        | ...        |

is 10 eggs per day and so on. In the INSIM program the total egg production is calculated using a simple matrix multiplication.

The last required input table is the file with daily minimum and maximum temperature for a period of one year or longer e.g. **debiltdiab.txt** (see Table 4 for the first rows). In the temperature file three different columns have to be defined: ‘day number’, ‘the minimum temperature on that day  $T_{\min}$ ’ and ‘the maximum temperature on that day  $T_{\max}$ ’. In the simulation INSIM uses equation 1 for determining the current temperature from the minimum and maximum temperatures on that day. The day starts at midnight with the minimum temperature from the file and at noon the maximum temperature is reached. Thereafter, the temperature starts falling again up to the next midnight, where the next day starts with the new minimum temperature.

$$T(t) = \left( \frac{T_{\max} + T_{\min}}{2} \right) - \left( \frac{T_{\max} - T_{\min}}{2} \right) \cos(2\pi t) \tag{1}$$

### How to use INSIM for MatLab

After having made a Tab-delimited text file, say **filename.txt**, with all necessary information on the life cycle, the temperature-dependent development in each life stage including threshold values for development, the temperature-dependent mortality, and the age-dependent number of eggs laid per female per day at certain temperatures together with a threshold value for oviposition first INSIM for MatLab has to be installed. For the installation procedure, we refer to <http://www.aew.wur.nl/uk/insim/> where INSIM for MatLab will be freely available as part of the package GRIND for MatLab. After the installation INSIM for MatLab can be started in Matlab by typing: ‘insim **filename.txt** [return]’, and ‘time [return]’. If the text file is correct, the simulation results for the time span of one year will appear in two figures: one figure with the minimum and maximum temperatures in the course of the year and the second figure with the appearance and disappearance of life cycle stages throughout the

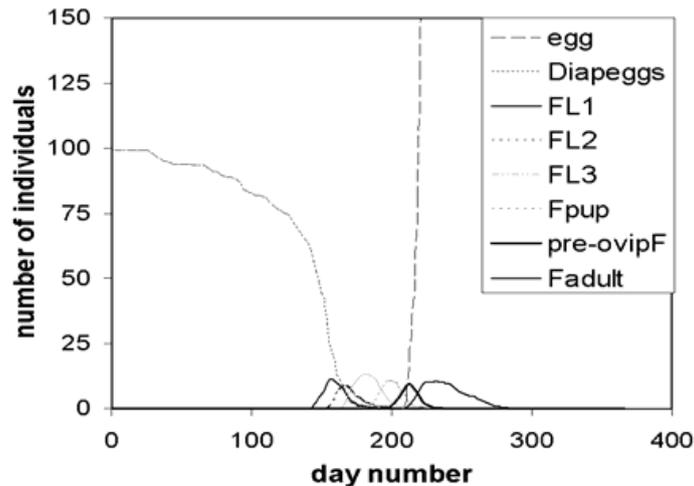


Figure 2. The occurrence of the different female stages of *D. virgifera* in the course of one year. From the left to the right the diapause eggs are starting to develop from January 1 onwards, and only around day 150 the first larval stage appears, the pupae appear around day 150 and both the ovipositing females (Fadult) and the eggs start to appear at day 210.

simulated year. For insects with a life cycle that lasts more than one year the simulation time can be set at the preferred length, say 1000, by typing 'simtime 0 1000' in MatLab after the 'insim filename.txt [return]' command line. It should be noted that we also plan to have at least one fully worked out example on the website and a more detailed manual.

## RESULTS

The first test of INSIM for MatLab was comparing the results of a single stage with a constant death rate at different temperature with an exponential decay function. This first test was easily passed and the deviation between the exponential model and the simulation was smaller than in the original Quick Basic implementation of INSIM.

In a second test we tested a single stage with a fixed development time of 100 days and a standard deviation of 20 days. The average development time and dispersion of last substage closely resembled a gaussian curve with a standard deviation of 20 days.

Finally we modelled the development of *D. virgifera* using the files **day\_diab.txt** (with the [overview] table, the tables for the different stages, the initial values in the stages and the reference to the name of the temperature file) and the temperature file **debiltdiab.txt** to get the resulting time plots. From these the one with the occurrence of the life cycle stages throughout one year is reproduced in Figure 2. We compared the resulting occurrences with the data provided by EPPO (1995) (Table 5). A rather good similarity exists.

Table 5. Simulated and observed occurrences of the stages of the western corn root-worm, *D. v. virgifera*.

|                          | Occurrence interval in INSIM | Occurrence near Zhagreb <sup>1</sup> |
|--------------------------|------------------------------|--------------------------------------|
| First larval instar      | 24 May – 29 June             | Late May to end June                 |
| Second larval instar     | 5 June – 7 July              |                                      |
| Third larval instar      | 14 June – 25 July            |                                      |
| Pupae                    | 4 July – 4 August            |                                      |
| Pre-oviposition female   | 18 July – 15 August          | Start end June                       |
| Ovipositing adult female | 31 July – 1 Oct              | Stop 9 Oct                           |

<sup>1</sup> according to EPPO report (1995)

## CONCLUSION

The advantages of the current implementation of the INSIM model are that

- (1) temperature-dependent development and survival can be easily provided to the MatLab programme in a Tab-delimited text file,
- (2) the program is suitable for insects with egg to egg development times that exceed one calendar year,
- (3) the program is suitable for insect with life stages that have different developmental thresholds
- (4) the program is faster and more flexible than the original Quick Basic programme,
- (5) the new program is user friendly, and last but not least:
- (6) it will be freely available from the internet (<http://www.aew.wur.nl/uk/insim/>).

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