

Research and Development

# Final Project Report

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Project title

A generic mathematical model for the Integrated Management of a crop containing antifeedant transgenes

DEFRA project code

RG 0115

Contractor organisation and location

SCRI, Invergowrie, Dundee DD2 5DA, SCOTLAND

Total DEFRA project costs

£

Project start date

01/07/99

Project end date

30/09/02

## Executive summary (maximum 2 sides A4)

In previous research in the laboratory, Birch *et al* (1999) demonstrated the potential transference of undesirable effects of pest-resistant GMO's to species occupying trophic levels higher than those of the target pest organism (e.g. a predator of pest aphids). This case study involved GNA lectin-expressing GM potato (having partial, antibiosis-based resistance to the pest aphid), the peach-potato aphid (*Myzus persicae*), and the 2-spot ladybird (*Adalia bipunctata*). The main observed effects, on both the aphid and the ladybird, were sublethal, through reduced fecundity and reduced adult weight. Reduced female longevity was also observed in the case of the adult ladybird. Similar prey-mediated adverse effects on predators (lethal and non-lethal) have been observed experimentally when fed target pest from *Bt*-expressing crops (e.g. Hilbeck *et al.*, 1998).

The results from such contained, laboratory studies can not be validated at realistic scales in the environment due to restrictions on GM field releases. Modelling crop-pest-predator interactions is, therefore, the only feasible precursor to potential field studies. Such models would have to be constructed from information gained from GM crops in other countries (mainly in North America) and from tri-trophic interactions on non-GM crops in the UK, but would nevertheless lay the foundation for assessing pest-resistant crops should they be trialled in the field or grown commercially in the UK. However, most models developed before the start of this project were unsuitable, since they incorporated neither sublethal effects nor tri-trophic interactions with predator or parasitoid. To develop a predictive capability for pest-resistant GM crops in Europe required a new approach to modelling trophic interactions.

The models were developed in two main stages: first, adapting classical approaches to plant-pest interactions (which did not incorporate spatial interactions explicitly); and second, spatially explicit approaches in which individuals of the crop, pest and predator grow and interact on a spatial lattice, mimicking field patches and whole fields.

Classical, strategic mathematical models were used to explore crop-pest issues in a general way, since this approach can model population scale processes which are applicable across a wide range of systems. The approach was used to understand the dynamics of predator-prey systems in which herbivorous pests compete for a common resource. The models incorporated the potential effects of non-GM and GM crops through parameters defining feeding, energy budget and mortality. The main findings from this phase of the project were related to the incorporation of sublethal effects (here done for the first time), and are presented by Hillier & Birch, (2000; 2002) and Hillier *et al.* (in preparation). They point to the importance of seasonality, through which most of the crop and pest are killed periodically (as in winter in the UK) and plant growth rate as factors having a strong influence on the rate at which toxin-resistant pest genotypes increase within the pest population. Developments of the classical approach had limitations however. The parameters could only be defined at the whole-population scale, and some important features, including individual variation, spatial heterogeneity,

genotype x environment interactions could not be incorporated. Nevertheless, this phase of the work resulted in a detailed exploration of the literature to define ranges of parameters (such as crop growth rate, pest feeding rate and crop-to-pest conversion efficiency).

In the second phase, we developed a individual-based, cellular model incorporating defined parameters for plants, pests and predators. In this tri-trophic model, individual insects (herbivorous pests and their predators) competed on a spatial lattice over time (up to several seasons) for crop resource, in accordance with a set of instructions which related only to that individual and its immediate environment. Instead of trying to solve the model in terms of the mathematical equations describing it, we ran and observed targeted simulations, to see what effects emerged when individuals behaved according to their prescribed rules. Such an approach allowed for the incorporation of the following into the model simulations. (i) Individual insects could be parameterised, leading to natural selection of counter-adapting pest sub-populations inside the model over time through altered ecological fitness. (ii) The simulations were played out on a spatial lattice, which allowed for uneven distributions of GM and non-GM plant populations density across the lattice, simulating pest-susceptible refugia. (iii) As a consequence of this, environment (i.e. anything external to the individual insect) could also be varied from cell to cell in the spatial lattice (e.g. a field or region), providing possible variation to the insect phenotype through its environmental interactions. At this stage, we consider the lattice-based, tri-trophic model to be the most advanced in its area.

Because of the large number of variables and the large datasets generated, statistical analysis techniques were used to quantify model outputs. These carried the risk that complex or subtle mathematical relationships between input and output variables could have been missed, but provided important information additional to that obtained from the strategic models.

The spatially-explicit, individual-based model allows detailed parameterisation for each trophic level (see detailed report) using generic physiological (plant, pest, predator) and behavioural (pest, predator) traits derived from the scientific literature. In principle, it can be adapted to examine any combination of crop, pest and predator. As a test of whether it could be parameterised for a specific case study, typical values for a GM crop type (e.g. oilseed rape) a pest type (e.g. an aphid) and a predator type (e.g. a ladybird) were added to the model to test its functioning and outputs arising from differing GM crop deployment scenarios. Scientific publications on the spatial model are being prepared. This project has broadened appreciation of tri-trophic effects in several ways. The background is that the crop-pest-predator system is intrinsically prone to instability. Change in food quality of the crop to the target pest can lead to large change in the population density of the pest and resulting change, possibly to extinction, of the predator (if no alternative prey of suitable food quality are available). Pests themselves can adapt genetically to change in food quality (through an increase in toxin-resistant biotypes). Stability in the system is therefore preferable, in which toxin-resistant pest biotypes build up very slowly and predators remain in coexistence to control the pest. The following findings should be considered in this context.

- The stability of the system – particularly the coexistence of pest and predator – is strongly affected by the food quality of the crop to the pest (as affected by the GM trait). The degree of reduction in food quality is crucial however. Provided the reduction is not too large, increased stability of the crop-pest subsystem would result, which in turn could lead to an increased likelihood of the predator persisting to regulate the pest. This stabilising effect on the tri-trophic system is likely to be reversed if there was also a reduction in the pest-predator conversion coefficient (as was shown by Birch *et al.* 1999 for the experimental case mentioned above).
- Contextual factors, such as crop growth rate, and seasonality of crop and pest growth – which have mostly been ignored in previous theoretical approaches – should be important in determining the build-up of toxin-resistant pests and the conditions under which crop, pest and predator co-exist. They must therefore be included in future theoretical studies.
- GM crops (or any crops) which retard development or mass gain by the target pest population below set economic thresholds via sublethal effects might be equally as effective in controlling the pest as crops producing lethal toxins; and, indeed, more beneficial for the environment since (i) the selection pressure favouring the fitter (toxin-resistant) pest genotypes is likely to be reduced, and (ii) reducing the pest populations growth rate can potentially stabilise the crop-pest dynamics, thus providing a more steady, constant supply of resource for the pests' natural enemies.

They Project has demonstrated that spatially explicit, tri-trophic models can be constructed based on ecological principles and populated by plants and insects using information mined from the scientific literature. The models developed in the Project are primarily research tools at this stage and require fine-tuning and validation using field data (using GM or non-GM crop data). They have the potential in this capacity to (a) help design cropping arrangements (mixtures, refugia) that will delay counter-adaptation by a pest, (b) help design crop genotypes, both GM and non-GM that are appropriate for advanced pest management strategies, (b) and (c) examine options for sustaining biodiversity while maintaining crop productivity in cropping systems, including or excluding GM. They could also inform and elucidate other tri-trophic case studies that are being carried out in the UK and Europe. Therefore to facilitate dissemination and use of the models, the lattice-based model of crop, pest and predator has been fitted with a *User Interface* which allows tri-trophic interactions to be explored under different scenarios by external scientists with guidance from SCR1 staff. A copy of the User Interface and model are included on a CD submitted with this report. Ultimately, the models have the potential for development as a management tool. Further funding would be required for that development.

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**Scientific report (maximum 20 sides A4)**

Recent data from small-scale, contained release experiments using pest-resistant GM crops (e.g. Hilbeck *et al.* 1998; Birch *et al.* 1999) indicated the potential for adverse effects to be carried through the food chain to beneficial predators of pests. These findings from small scale studies cannot be readily tested at a larger and more realistic field scale in the U.K., due to current restrictions on GM field releases. This limitation on GM field experimentation means that in the U.K. we currently have to rely on modelling potential effects at larger scales, based on published or available information on GM crops from other countries and from studies of the conventional (i.e. produced via plant breeding) pest-resistant crops currently grown in the U.K.

The aim of this project was to build various types of models (classical ordinary differential equation and then individually-based) to examine potential effects of sublethal and lethal anti-insect (referred to as 'anti-feedant' traits in the project title, but actually covering the wider range of possible negative effects on pest survival, growth, dispersal and reproduction) traits in GM crops on the pest and predators of the pest. This was developed firstly using bi-trophic models (pest-resistant GM crop and target pest) and then extended to a tri-trophic model (pest-resistant GM crop, target pest and predators of the pest).

As a basis for comparison and to aid development strategies for sustainable use of future pest-resistant crops, we choose to compare lethal (e.g. *Bt* toxins) and sublethal (e.g. lectins) pest-resistant traits in the crop. This comparison provided a basis to examine effects of resource depletion and altered food quality at the pest and predator levels in the food chain. Our aim was to build in a range of physiological traits and parameters to cover a typical crop, pest and generalist predator into the generic models. Development and testing of the models was carried out largely on a bi- and tri-trophic systems using data for oilseed rape at the crop level, an aphid at the pest level and a ladybird at the predator level. This enabled us to select reasonably realistic parameter values from published literature for the plant, pest and predator life cycle models and feed them into the generic model for testing and analysis.

A bi-trophic model, based on a version of the Lotka-Volterra but modified to examine the effects of fitness differentials in 3 pest sub-populations, was established to explore the interactions and rate of adaptation of a herbivorous pest to a pest-resistant GM crop having logistic growth. This provided a phenotypic model *without* seasonal variability to examine evolution of pest adaptation to the GM pest-resistance trait. Three different pest sub-populations were defined (i.e. susceptible to the GM trait, partially adapted, fully adapted) by differing the parameter values for pest respiration rate and palatability (food value) of the crop. Expressions estimating the rates of increase of the fitter pest types were obtained as a function of food qualities, respiration and mortality rates. Although the model was formulated for single pest resistance gene it could be used and interpreted independently of this, allowing greater flexibility than previously published genetical models which were based on the Hardy-Weinberg equilibrium equation. The effect of using refugia (patches of pest-susceptible crops) on delaying the rate of counter-adaptation in the pest sub-populations was examined. The model demonstrated trade-offs when using pest-susceptible refugia crops; they did slow down pest sub-population adaptation rates (due to decreased fitness differential between pest sub-populations and hence reduced selection pressure for counter-adaptation) but inevitably reduced total crop

yield (primarily due to crop loss in the refugia). It was noted that for this GM deployment strategy to work it requires good mixing of pest sub-populations. Thus, accurate knowledge of pest movement (distances, times) and mating behaviour (synchronicity of pest sub-populations) are critical before designing spatial layouts of pest-susceptible refugia areas within areas of pest-resistant GM crops. For full details see Hillier & Birch 2002a.

We next examined how a sub-population of the pest which was under selection for counter-resistance to the GM trait would spread over space and time. A spatially-explicit reaction-diffusion system model, based on the modified Lotka-Volterra model above, was used. This model incorporated logistic growth of the crop resource and a diffusion term added to account for spatial spread of the pest over time. The model developed is phenotype specific, in which a pest sub-population's fitness (energy reserve for growth and reproduction) is a balance between its resource assimilation rate and its respiration rate. We derived an expression for the rate of spatial spread of the counter-adapting pest sub-population from an initial point source in the field. The model was then used to examine different strategies for delaying pest counter-adaptation to the GM trait. Exploration of the model under different scenarios (principally differing sizes of refuge) revealed that counter-adaptation by the pest could be avoided when sufficiently large refugia areas were deployed, particularly if there was a metabolic cost to counter-adaptation in the pest sub-population. Spread from "hot-spots" of counter-adapting pests could be avoided by deploying refugia of suitable size and spatial positioning. Again, trade-offs were observed between crop yield (plant biomass) and refugia size. Whether or not the use of refugia is desirable will depend on the specifics of the system – the amount of yield loss that occurs, the reduction in the rate of growth of counter-adapting pests caused by the refugia and the cost:benefit balance from using pest-resistant GM crops. Key factors in the model which need to be characterised accurately for particular a crop-pest interaction were identified as the functional form of the pests' movement response to resource suitability and the dispersal mechanisms of the pest. For full details see Hillier & Birch, 2002b. An interesting result from this article was that, when growth of the resistant pest population is restricted by its need to grow in space the form of the growth curve changes from a sigmoidal one as shown in Figure 1, to a linear one – with a significant time lag – as shown in Figure 2. This is in agreement with the results of Peck *et al* 1999, who constructed a rather different spatially explicit model for pest control, and concluded that the difference may well be down to the necessity for the pest to spread in space. Thus, the importance of understanding the role of spatial heterogeneity when making predictions about such systems is highlighted.

Figure 1 Pest adaptation in a spatially *implicit* bi-trophic model

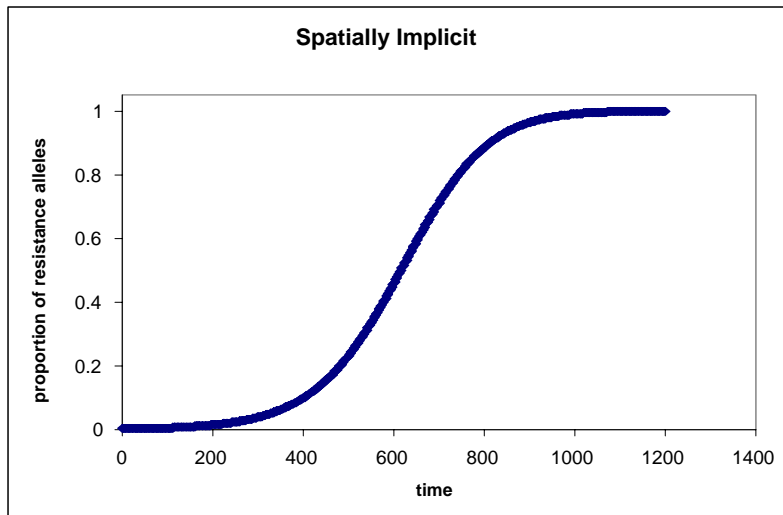
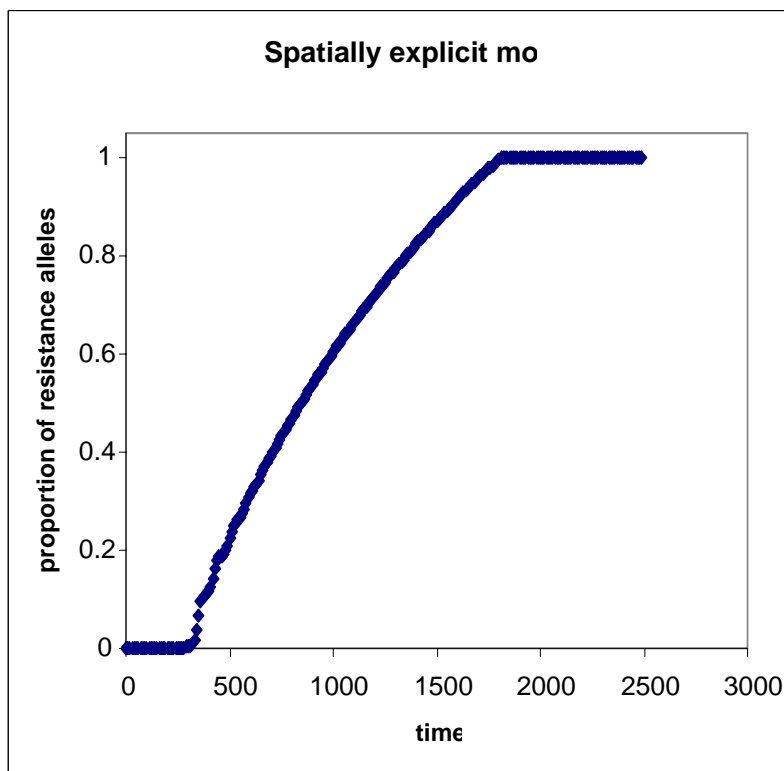


Figure 2 Pest adaptation in a spatially *explicit* bi-trophic model



In the third of the publications (Hillier *et al*, In prep) on this subject we have explored (i), how the influence of environmental fluctuations in resource levels (due to harvesting and resowing), (ii), increased physical realism in the functional response, may affect the prediction of the rate of adaptation derived in Hillier & Birch, 2002a. We also make a comparison of the result to that which might be obtained if toxic pest control measures were used. The results obtained in Hillier & Birch, 2002a seem surprisingly robust, in spite of the rather unrealistic restrictions that were employed to enable analytical solutions of the model.

In order to assess environmental risk in terms of predator extinction our starting point was the following classical tri-trophic model given as follows

$$\begin{aligned}\frac{dC}{dt} &= \theta C \left(1 - \frac{C}{k}\right) - fCA \\ \frac{dA}{dt} &= \phi_A fCA - gAP - \mu_A A \\ \frac{dP}{dt} &= \phi_P gAP - \mu_P P\end{aligned}$$

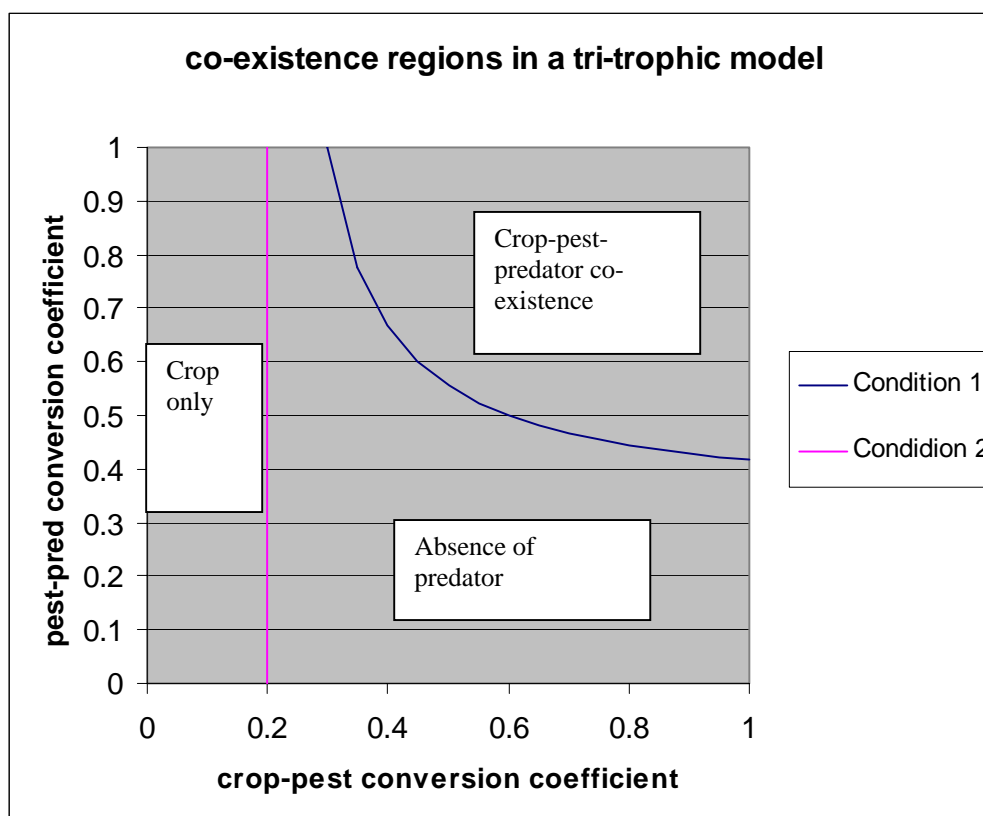
Where C represents crop biomass, A represents pest biomass, and P represent predator biomass. The lower case and Greek letters represent the parameters defining the population traits, and in particular  $\phi_A$  and  $\phi_P$  represent the pest and predator assimilation coefficients respectively for the given crop and pest respectively. The dynamics of such a system can be studied in terms of the values of its parameters, and in particular the food qualities, by which we can arrive at Figure 3.

However the model displayed above also makes assumptions about the uniformity of crop, pest, and predator abundances, and constancy of environment. If the functional responses of the species are changed to represent spatial non-uniformity, or if the crop levels fluctuate to model harvesting and resowing the predictions will change.

The spatially-explicit, individual-based, tri-trophic model was developed to allow all of the constraints encountered above to be relaxed. Results from the above models can then be tested for robustness, when the assumptions employed in their formulation and analyses are relaxed.

The approach is a significant departure from the above, where instead of assuming certain processes and parameters to be important whilst trying to preserve the tractability of the analysis, we instead, intensively parameterise individual objects in the model in terms of their life strategies, and then simulate an ecosystem by advancing the model one time step at a time and observing the outcome.

**Figure 3** Regions of crop, pest and predator persistence in a tri-trophic model.



The model has been built, as a continuation of the work described above, to allow exploration of the issues of pest control and biodiversity management on an annual crop. With this in mind individual plants, herbivores, and predators are programmed to act and make decisions, based largely on their energy budgets, on a 2D spatial grid. The traits of the individuals, determine their ecological strategy, and thus, along with exploitative competition rules, determine the success or failure of individuals or “ecotypes” in the model.

Traits and rules were selected to enable significant variation in strategies between the individuals, although our intent, was to ensure the existence of a clear physiological interpretation, although this was not always the possible, particularly when we are concerned with internal energy budgetting by the pest, were we have used the slightly abstract notions of Free store, and Structural store.

The parameters for herbivores (and predators) are based around 5 different fitness determining components: **(i) Energy budget, (ii) Dispersal, (iii) Reproduction, (iv) Development, and (v) Foraging**. The choice of generic traits and rules can be disputed, since they do not hold for all insects. However, we felt that they were the probably the best rules that can be programmed without especially intensive literature searching and parameterisations, which were beyond the scope of the current project.

The rules for resource demand rates and assimilation efficiencies have come from a literature trawl of much of the insect energy budget work done in the 1960s & 1970s (For example Beddington *et al* 1976, and Hassell *et al* 1976). Gutierrez and colleagues have also extensively employed such models, and the approach can be found summarised in Gutierrez 1996.

Allometric laws governing rates of respiration can be found in Peters 1973. The general rule is that respiration rate increases with the three-quarter power of body mass, and exponentially with temperature. It also increases linearly with distances moved.

The rules for dispersal and reproduction were of our own devising. They allow for several alternative life strategies.

Development rate increases linearly with temperature, and can increase linearly with resource captured. This “thermal time” approach has been much debated, and is unlikely to be validated or invalidated in the near future, although there is plenty of empirical evidence to support it. It is employed for reasons of parsimony, since (being a linear relationship) all it requires is intercepts and slopes.

The model was coded in C++. An NT based visual front end has been coded to facilitate parameterisation of the model and also graphical visualisation of the output. It also allows the user to save plant, pest, and predator parameters, so that a database of well parameterised ecotypes can be acquired over time. A full description of the interface is attached (Matthews & Hillier).

The model allows for a range of different plant distributions to be used (Figure 5). This means that various strategies that propose the spatial mixing of pest resistant with non-pest resistant plants can be tested in order to see whether (i) Mitigation of adverse environmental effects is possible, and (ii), The adaptation of the pest species due to fitness differential can be delayed.

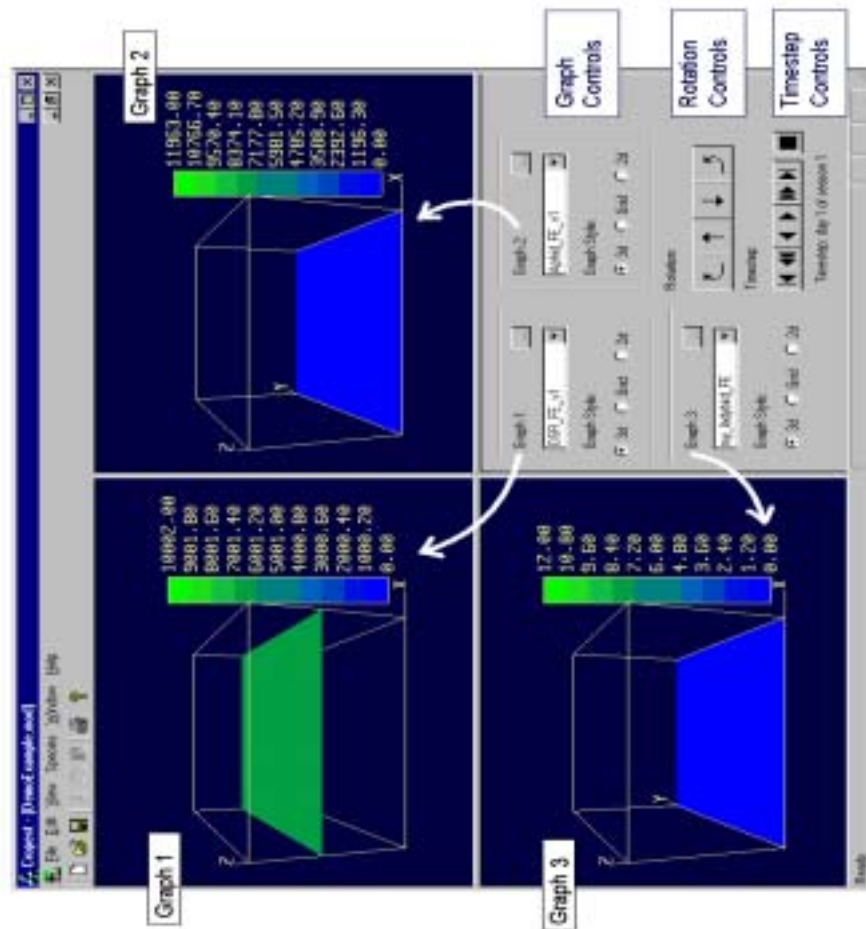
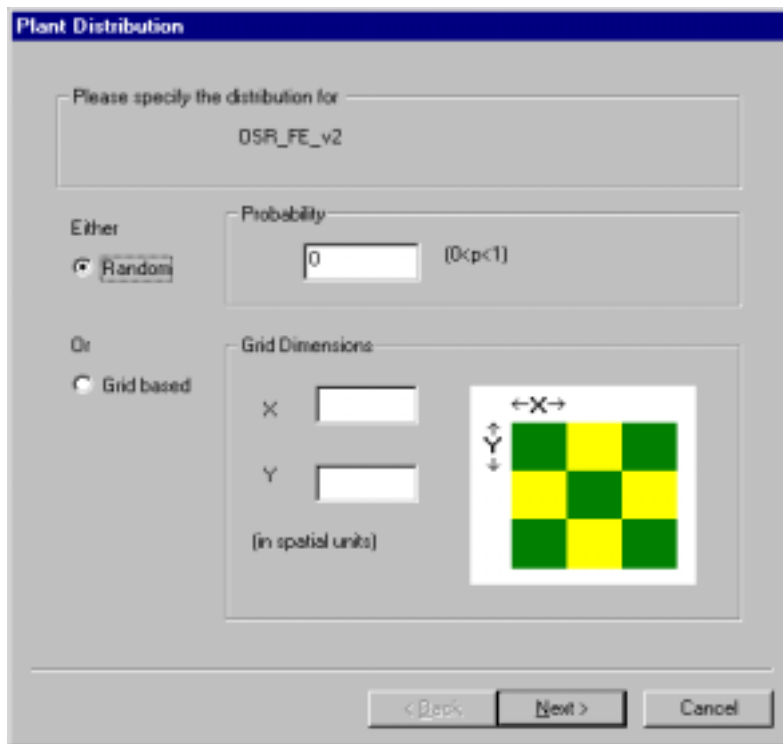


Figure 4 A sample of the output from the model's visual interface



**Figure 5** Example plant distributions allowed by the model interface (See User interface document).

**Detailed description of the parameters used for the final version of the tri-trophic model and instructions for running.**

User-controlled parameters can be categorised into 7 different classes.

1. Environment
2. Plant
3. Herbivore
4. Predator
5. Plant-Herbivore interface
6. Herbivore-Predator interface
7. Initial conditions.

In the herbivore and predator classes (3, 4) the parameters can be put into subclasses for

- a) Energy Budget
- b) Dispersal

- c) Reproduction
- d) Development
- e) Foraging

These are further partitioned as explained below:

### 1.Environment;

E <sub>1</sub>	Lattice length
E <sub>2</sub>	Lattice width
E <sub>3</sub>	Minimum annual temperature
E <sub>4</sub>	Maximum annual temperature
E <sub>5</sub>	Temperature at sowing
E <sub>6</sub>	Season length
E <sub>7</sub>	Number of seasons

### 2. Plant;

PI <sub>1</sub> (1...3)	Maximum Biomass
PI <sub>2</sub> (1...3)	Maximum Phloem
PI <sub>3</sub>	Minimum phloem to biomass ratio for plant growth
PI <sub>4</sub>	Growth rate
PI <sub>5</sub>	Maximum seed mass
PI <sub>6</sub>	Minimum phloem to seed mass ratio for seed production
PI <sub>7</sub>	Development units required for elongation
PI <sub>8</sub>	Minimum temperature to initiate growth
PI <sub>9</sub>	Per day degree development rate

### 3. Herbivore

#### a) Energy Budget

H <sub>1</sub>	Daily food demand rate
H <sub>2</sub>	Food demand rate increase with temperature
H <sub>4</sub>	Respiration rate at base temperature
H <sub>5</sub>	Respiration rate increase with temperature
H <sub>6</sub>	Proportion of assimilated food allocated to energy reserves

#### b) Dispersal

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H <sub>7</sub>	Energy threshold for dispersal
H <sub>8</sub>	Exponent on dispersal probability function
H <sub>9</sub>	Average distance moved during dispersal
H <sub>10</sub>	Energy cost for movement (per spatial unit moved)

## c) Reproduction

H <sub>11</sub>	Egg mass
H <sub>12</sub>	Energy reserves in egg
H <sub>13</sub>	Energy reserves required in adult for egg production
H <sub>14</sub>	Egg laying must not take energy reserves below this
H <sub>15</sub>	Maximum number of reproduction events
H <sub>16</sub>	Egg viability

## d) Development

H <sub>17</sub>	Base temperature of insect
H <sub>18</sub>	Optimal temperature of insect
H <sub>19</sub>	Maximum temperature at which development can occur
H <sub>20</sub>	Daily development at optimal temperature (H <sub>18</sub> ).
H <sub>21</sub>	Additional development occurs if this consumption rate is exceeded
H <sub>22</sub>	Additional development occurring if demand is met

## e) Foraging

H <sub>24</sub>	Plant part that herbivore consumes
H <sub>25</sub>	Overwintering survival rate

**4. Predator**

## a) Energy Budget

Pr <sub>1</sub>	Daily food demand rate
Pr <sub>2</sub>	Food demand rate increase with temperature
Pr <sub>4</sub>	Respiration rate at base temperature
Pr <sub>5</sub>	Respiration rate increase with temperature
Pr <sub>6</sub>	Proportion of assimilated food allocated to energy reserves

## b) Dispersal

Pr <sub>7</sub>	Energy threshold for dispersal
Pr <sub>8</sub>	Exponent on dispersal probability function
Pr <sub>9</sub>	Average distance moved during dispersal
Pr <sub>10</sub>	Energy cost for movement (per spatial unit moved)

## c) Reproduction

Pr <sub>11</sub>	Egg mass
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Pr <sub>17</sub>	Base temperature of insect
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Pr <sub>21</sub>	Additional development occurs if this consumption rate is exceeded
Pr <sub>22</sub>	Additional development occurring if demand is met

## e) Foraging

Pr <sub>24</sub>	Search radius
Pr <sub>25</sub>	Coefficient for preferred prey size
Pr <sub>26</sub>	Exponent for preferred prey size
Pr <sub>27</sub>	Coefficient for tolerance for prey not of preferred size
Pr <sub>28</sub>	Zero tolerance energy threshold for predator
Pr <sub>29</sub>	Min food quality
Pr <sub>30</sub>	Max food quality
Pr <sub>25</sub>	Overwintering survival rate

**5 The Plant-Herbivore Interface**

H <sub>3</sub> (1...#plant types)	Assimilation efficiency
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$H_{23}(1..#\text{plant types})$  Apparancy of plant resource to herbivore

## 6 The Herbivore-Predator Interface

$Pr_3(1...#\text{pest types})$  Assimilation efficiency

$Pr_{23}(1..#\text{plant types})$  Apparancy of herbivores to predator

## 7 Initial Conditions

These may be either random or regular. See the full model description (**Appendix 1**) for details of allowable distributions and controls for setting parameter values.

***A demonstration of the working tri-trophic model, with front-end user interface is included with this report (see CD), along with documentation..***

### Outputs from the project to date:

- a) **Hillier J.G. & Birch A.N.E. (2002)**. A Bi-trophic model for Pest Adaptation to a Resistant Crop, *J. Theor. Biol.*, 215, 305-319.
- b) **Hillier J.G. & Birch A.N.E. (2002)**. Travelling Waves of Resistance in a Bi-trophic Pest Adaptation Model. *J. Theor. Biol*  
( *In press.*)
- c) **Hillier J.G. & Birch A.N.E. (2002)** IOBC Working Group on Breeding for resistance to insects and mites. Rostanga, Sweden, December 2001. "A tri-trophic model to explore insect community response to the introduction of a pest-resistant GM crop". (Invited presentation).
- d) **Birch, A.N.E.**, Jones, A.T., Fenton, B., Malloch, G., Geoghegan, I., Gordon, S.C., **Hillier, J. G.**, and Begg, G. **(2001)**. Resistance-breaking raspberry aphid biotypes: Constraints to sustainable control through plant breeding. *Proceedings of the 8<sup>th</sup> International Rubus and Ribes Symposium, 9<sup>th</sup>-11<sup>th</sup> July 2001* (Invited presentation).
- e) Daniell, T. J., Squires, J. N., **Hillier, J. G.**, Verrall, S. R., Clegg, C. D., Griffiths, B. S., Ritz, K., S. R., Wheatley **(2001)**. Coupling between plants and diversity of nitrite-reducing bacteria in an upland pasture, *9<sup>th</sup> International Symposium on Microbial Ecology, 26-31 August 2001*. (Invited poster presentation).
- f) **Hillier J.G. & Birch A.N.E. (2001)** Royal Entomological Society Special Interest Group on GM Crops. April 2001, Rothamsted, Hertfordshire, U.K. "Modelling environmental impact scenarios for GM pest-resistant crops: Mathematical and theoretical considerations" (Invited presentation).
- g) **Hillier J.G.**, Hawes C, **Squire G.R. & Birch A.N.E. (2000)**. Production and diversity in multi-trophic systems. SCRI Annual Report (1999/2000), pp176-179.
- h) **Hillier J.G.**, **Birch, A.N.E.**, **Squire G.R.** & Hawes C (**refereed paper, in prep**). Pest adaptation in a bi-

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trophic model: Contrasting the effects of lethal and sublethal plant toxins.

i) **Hillier J.G., Birch A.N.E. , Crawford, J., Squire G.R.**, Hawes, C., Maule, M.

j) **(2002)**. Powerpoint presentation: A Spatially-explicit, individual-based, tri-trophic model for pest control  
(*see enclosed CD*).

## Applications of the model in ecology and agronomy

The models developed in the Project are primarily research tools. In constructing them, the project staff have brought together and systematised a great amount of experimental information that was otherwise fragmented in the literature. In particular, some generic aspects of trophic relations – notably the parameters that are used to link resource to consumer in each trophic interaction - can be applied by means of the model to a wide range of circumstances, as follows.

### (a) Design of cropping arrangements (mixtures, refugia)

Insect populations usually become resistant to a practice used to control them only after the majority of susceptible insects have been removed by that control practice. The remaining insects that carry genes for resistance mate with each other and the resulting resistant insect populations subsequently increase in numbers, making control difficult. Examples of control practices that insects have become resistant to include crop rotation, traditional host plant resistance, and pesticides (including sprayable Bt formulations). In order to slow down insect resistance to GM crops expressing insecticidal proteins, scientists have developed various models and Insect Resistance Management (IRM) strategies. The “high dose-structured refuge” model is most widely adopted in countries including USA (Bt maize) and Australia (Bt cotton). This system depends on inter-breeding between potentially resistant pest individuals (i.e. selected on the GM insecticidal crop) and potentially susceptible individuals (from non-insecticidal refugia crop(s) or weed hosts of the pest). The heterozygote pest offspring are then killed by a high dose of the toxin in the GM crop, thus diluting the selection for counter-resistance to the insecticidal toxin in the overall pest population.

Existing mathematical models supporting the use of refugia in GM crops are generally based on the Hardy-Weinberg equation and knowledge of initial gene frequencies (for toxin counter-adaptation) in the target pest population. The models developed in this project go beyond the pest genotype and instead use phenotypic, behavioural and ecological data to predict the fitness of insect sub-populations, based on a balance between resource assimilation and respiration rate in each pest individual. Spatial data for the pest and its host plants are also built into the model. This means that our models can be developed to investigate optimal spatial and temporal distributions of pest-resistant and pest-susceptible plants (e.g. in seed mixes, rows or blocks) to delay counter-adaptation in the pest population. The importance of using spatio-temporal data and models to assist in the design of pest-resistant GM crop deployment strategies is supported by recent field studies (*Proceedings of the Royal Society* 267, 117-122 and 1177-1184). In specific cases where pest sub-populations do not readily inter-breed (e.g. in French studies on European corn borer, where pest sub-populations develop on several wild plant species around maize fields) our model and this recent field data indicate that a strategy based on use of wild host species in adjacent fields as a pest-susceptible refuge is unlikely to delay pest counter-resistance. As a second example, if the target pest readily moves between neighbouring plants to feed during its larval stages, a random seed mixture of resistant and susceptible crop genotypes is unlikely to deliver a sufficiently high toxin dose to kill heterozygote pest genotypes having intermediate toxin tolerance. In this scenario the pest could rapidly counter-adapt to the insecticidal GM toxin. However, in a third scenario, where structured refugia (e.g. large blocks of a pest-susceptible variety) enable toxin-susceptible pest genotypes to readily interbreed with toxin-resistant genotypes, our model predicts, in agreement with Hardy-Weinberg based gene frequency models, that pest counter-resistance to the insect resistance trait can be substantially delayed, particularly if there is a large fitness cost to counter-adaptation in the pest genotype. Confirmation in the field of such fitness costs in pest populations has recently been found in Australian studies on the cotton bollworm *Helicoverpa armigera*; the Bt-resistant strain was found to develop more slowly on conventional cotton than the Bt-susceptible strain and even more slowly on Bt-cotton (CSIRO web report – [www.cotton.pi.csiro.au/publicat/conf/](http://www.cotton.pi.csiro.au/publicat/conf/)). Our models can also be used to explore the rate of spread of GM crop-resistant pests and the potential trade-offs, in terms of crop yield, when pest-susceptible refugia of differing proportions are deployed with a pest-resistant GM crop. These types of exploratory mathematical models, once further developed to include more fully the third trophic level (natural enemies of pests), should assist ecologists and governmental policy makers draw up Insect Resistance Management regulations for maximizing the durability of pest resistance genes in crops (GM or conventional).

### (b) Design of crop genotypes, both GM and non-GM

Genetic improvement programmes that incorporate resistance to invertebrate pests are in place for all major crops in the world. New crop varieties that include GM traits conferring insect resistance are being deployed in many countries outside Europe. The insights gained from this project indicate that, where natural predators have a role in controlling pest populations, greater stability of the crop-pest-predator system will ensue if pest resistance is of a form that impairs growth and reproduction of the pest (i.e. sublethal effects) rather than kills the pest outright. This conclusion applies for both GM and non-GM pest resistance and could be used to define crop ideotypes that fit the local crop-pest-predator system. These ideas on the stability of crop-pest-predator systems could be tested by experiment at the appropriate scale, i.e. in experimental treatments of large enough area to support the life cycle dynamics of pest and predator.

### (c) Exploring options for balancing biodiversity and crop productivity

As originally planned, the model incorporated a simple tri-trophic system, but the capacity to vary the trophic parameters among individual organisms in the model allows the spatially explicit version to explore more complex food webs. Several ecological problems could be examined by the model. For instance, a major issue of interest for arable food webs is whether the mass of resource in the plant or weed layer limits consumers in higher trophic layers. It is generally assumed that such resource-limitation does occur in intensively managed systems, but experimental evidence is lacking. However, the model could be used to explore the parameters of the resource-consumer relation, i.e. the extent to which varying the weed mass affects mass-transfer to herbivores and higher functional groups. A second topic is the way variety in the plant

layer affects the type and abundance of organisms in higher trophic groups. Again, the parameters of individual plants could be varied and the consequent coexistence of invertebrate types (species, traits) examined. The model could be used in such ways to explore major questions in arable ecology, to set hypotheses and to guide experiments. Several generic questions that are likely to arise from the Farm Scale Evaluations of GM crops in GB could be approached using the model.

The models are now being used within SCRI's research programmes on biodiversity in arable fields and integrated pest management. Several possible applications have also been considered with other scientists, for instance in the BBSRC/NERC initiative in Geneflow in Agriculture. Staff at SCRI are most willing to collaborate with external groups in the use of the model for ecological or agronomic purposes. Ultimately, the models constructed in this project have the potential for development as a management tool, for example to optimise biodiversity in relation to production in arable systems. They would however, need further development for this general function.

N. Birch, J. Hillier, GR Squire  
February 2003

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## **Appendix 1:**

### **Cropest: User interface for tri-trophic model**

#### **User Manual (also supplied on CD with demonstration version of model)**

The model was developed at the Scottish Crop Research Institute by Jon Hillier with contributions from Nick Birch (Project Officer), Geoff Squire, Cathy Hawes and John Crawford (now at the University of Abertay Dundee). David Matthews, a graduate student in the Department of Applied Computing at the University of Dundee, constructed this User Interface as a M.Sc. project supervised by Chris Reed from the University of Dundee and Jon Hillier.

The model was funded by DEFRA through Project RGO115.

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## 1. Introduction

The Cropest application provides a visual front end for the Individual-based Tri-trophic model developed at the Scottish Crop Research Institute (SCRI). This manual describes the use of the Cropest interface.

### 1.1. The SCRI model

The model has been built primarily to allow exploration of the issues of pest control and biodiversity management on an annual crop. With this in mind individual plants, herbivores, and predators are programmed to act and make decisions, based largely on their energy budgets, on a 2D spatial grid. The traits of the individuals, along with exploitative competition rules determine the success or failure of individuals or “ecotypes” in the model.

### 1.2. The Cropest interface

The Cropest interface allows a model-run to be set up by defining the participant species, their interactions and initial distributions along with the environmental conditions. The interface then provides a graphical rendition of the output from the model. The output can be reviewed as the model produces it and/or stored for later analysis.

In addition Cropest allows for the separate storage of parameterised species for use in subsequent model runs.

### 1.3. Required Expertise

Cropest is designed to operate under the Windows NT4 operating system. As such, it is assumed that the user is familiar with the use of this operating system.

#### 1.Pull Down Menus

In this manual when a selection from a pull down menu is required the shorthand => will be used. So select ‘File => New...’ means select ‘New...’ from the ‘File’ pull down menu.

## 2. Installation

The Cropest interface and the SCRI model are two independent programs that communicate using files. Once installed correctly the user should only need to access Cropest. The model program will be executed automatically by the interface.

Cropest needs to be installed in the same folder as the model program that it is required to operate. Cropest will only operate an application file named ‘trtr’.

It is suggested that the two programs be installed in a specially created folder.

### 2.1. Installing the software:

Create a ‘New Folder...’ to hold the programs

Copy the two application files: ‘Cropest.exe’ and ‘trtr.exe’ into the New Folder

Create shortcuts to Cropest.exe wherever required (e.g. on the Windows desktop)

### 2.2. Starting the interface

The Cropest interface can be launched in any standard Window’s manner; for instance double clicking on the icon representing the application or a shortcut to it.

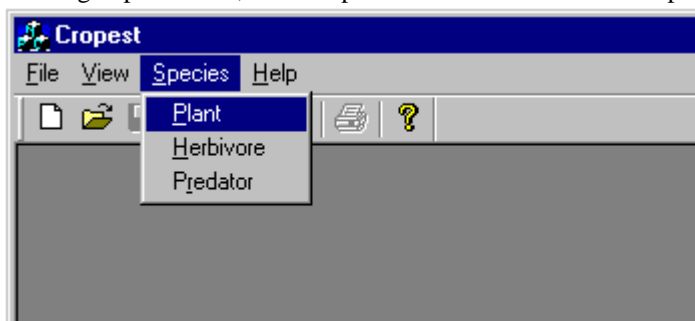
## 3. Defining Species

To gain familiarity with the interface, the defining of species can be looked at first. Species can be defined as part of the process of setting up a model (Chapter 5). They can though also be defined in isolation and then later loaded into models as required. As the definition of a species can involve setting thirty parameters, the ability to save them for re-use will save time

### 3.1. The plant form.

Once the interface is launched a blank screen is presented. To parameterise a species, without running a model, simply select the required trophic level from the ‘Specie’ pull down menu.

Looking at plants first, select ‘Species => Plant’ and the Plant parameterising form (dialog box) will be presented.



**Figure 1: Selecting Plant**

Numbers can now be entered into the boxes to define the plant's characteristics. Please see chapter 4: parameter definitions for an explanation of the parameters.

The screenshot shows a dialog box titled "Plant" with a close button (X) in the top right corner. The dialog is divided into two main sections: "Name" and "Parameters".

The "Name" section contains a single text input field.

The "Parameters" section contains a table of input fields and labels:

	Below Ground	Above Ground-Lower	Above Ground-Upper	
1	<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="0"/>	Maximum Biomass (mgs)
2	<input type="text" value="0"/>	<input type="text" value="0"/>	<input type="text" value="0"/>	Maximum Phloem (mgs)
3	<input type="text" value="0"/>			Minimum phloem to biomass ratio for plant growth
4	<input type="text" value="0"/>			Growth rate (per day)
5	<input type="text" value="0"/>			Maximum seed mass (mgs)
6	<input type="text" value="0"/>			Minimum phloem to seed mass ratio for seed production
7	<input type="text" value="0"/>			Development units required for elongation
8	<input type="text" value="0"/>			Minimum temperature to initiate growth (°c)
9	<input type="text" value="0"/>			Per day degree development rate

On the right side of the "Parameters" section, there are three buttons: "OK", "Cancel", and "Load".

**Figure 2: Plant Form**

If any changes are made to the form then pressing the OK button will offer the user the option to save the plant. This is saved as a file with the extension '.pla'. All of the parameter fields must be given allowable values before the plant can be saved.

Pressing the 'Load' button allows such previously saved plants to be reviewed. If a previously archived plant is loaded and changes are made to its parameters then when the OK button is pressed the option to save these changes is given. The existing .pla file can be overwritten or a new file can be created leaving the original uploaded file untouched.

The Cancel button enables the form to be quit at anytime without saving any changes made.

### 3.2. Herbivores and Predators

Herbivores and predators can be parameterised and stored in a similar way to plants. As they require more parameters to define them, the forms for herbivores and predators are sub-divided into pages.

**Figure 3: Example page from Herbivore form**

Important hint: Once a page has been selected all of the fields on that particular page must be filled before another page can be viewed. If you need to consult another page before filling in a parameter you will need to insert a temporary value before you can change pages.

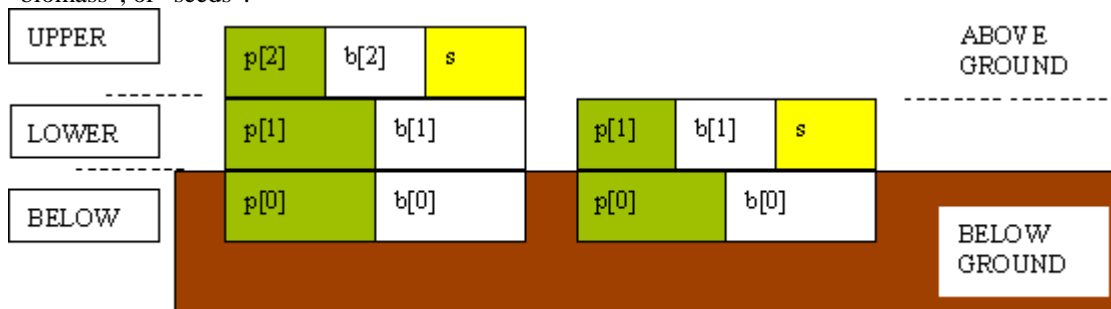
As with plants, herbivores and predators can be archived. The OK, Load and Cancel buttons provide the same functionality as previously described for plants. Herbivores are stored with the file extension .hbv and predators with .prd.

## 4. Parameter Definitions

These are the explanations of the parameters for each type of species:

### 4.1. Plant parameters

Plants have either 5 or 7 compartments depending on their (eventual) height. The compartments are classified as “phloem”, “biomass”, or “seeds”.



**Figure 4: Plant compartments**

So compartments  $p[*]$  and  $b[*]$  correspond to the first 6 boxes in the Plant dialog box.

For *minimum phloem to biomass ratio* we would expect a figure between 0 and 1. Values greater than 1 are allowed but are probably rather high. Plant biomass growth will stop if the overall phloem to biomass ratio is smaller than this figure.

**Growth rate.** The higher this figure is the faster the plants maximum biomass will be achieved. Plant growth is loosely based around the logistic equation. Although *growth rate* can take any value greater than 0, values of greater than, say, 0.2 are likely to be unrealistic.

**Maximum seed mass**, is the optimum that can be obtained if conditions are good and there is no pest damage.

**Minimum phloem to seed mass ratio** is analogous to **minimum phloem to biomass ratio**. Seed production will stop if there is insufficient phloem. Again, any value greater than 0 is allowed.

Development units are day degrees above a threshold of  $T_{base}$ , the **Minimum temperature to initiate growth**. This temperature is in degrees Celsius. For every day that the temperature,  $T$ , is above  $T_{base}$  the plant achieves development units at a rate of **Per day degree development rate** \*  $(T - T_{base})$ . The plant is mature when it has a full development unit, at which point it commences seed production. Thus **Per day degree development rate** should generally be a number between 0 and 1, but much closer to zero. For example, for an oilseed rape a value of 0.0014 gives maturity at a reasonable time based on SCRI weather data.

If the plant is a “tall” one, it will at some point move from possessing 4 (or 5) compartments to 6 (or 7), as it grows taller. This occurs when the number of development units passes a threshold **Development units required for elongation**. Thus, although, this parameter can take any positive real number, it is likely, at its maximum value, to be only slightly larger than 1 (in which case it is still growing significantly taller after seed production has commenced).

## 4.2. Herbivore and predator parameters

The parameters for herbivores (and predators) are based around 5 different fitness determining components: (i) **Energy budget**, (ii) **Dispersal**, (iii) **Reproduction**, (iv) **Development**, and (v) **Foraging**.

The choice of generic traits and rules can be disputed, since they do not hold for all insects. However, we felt that they were the probably the best rules that can be programmed without especially intensive literature searching and parameterisations, which were beyond the scope of the current project.

The rules for resource demand rates and assimilation efficiencies have come from a literature trawl of much of the insect energy budget work done in the 1960s & 1970s (For example Beddington, Hassell, & Lawton). Gutierrez and colleagues have also extensively employed such models, and the approach can be found summarised in Gutierrez 1996.

Allometric laws governing rates of respiration can be found in Peters 1973. The general rule is that respiration rate increases with the three-quarter power of body mass, and exponentially with temperature. It also increases linearly with distances moved.

The rules for dispersal and reproduction were of our own devising. They allow for several alternative life strategies.

Development rate increases linearly with temperature, and can increase linearly with resource captured. This “thermal time” approach has been much debated, and is unlikely to be validated or invalidated in the near future, although there is plenty of empirical evidence to support it. It is employed for reasons of parsimony, since (being a linear relationship) all it requires is intercepts and slopes.

### 4.2.1. Energy budget

In this model the amount of resource that a consumer requires increases in proportion to its own mass. It also increases linearly with temperature.

**Daily food demand rate**,  $D_{base}$ , is the daily resource requirement (as a proportion of own mass) of the insect at its base temperature.

**Food demand rate increase with temperature**,  $D_T$ , is the additional demand (as proportion of own mass) for every degree Celsius above the insect’s base temperature.

Total demand rate appears to vary across species but some species can consume more than their own mass in a day. So if, for example, we suppose demand at the base temperature to be very low, and said that temperature could vary by 10 degrees across a season, reasonable values might be  $D_{base} = 0.1$  and  $D_T = 0.1$ .

**Respiration rate at base temperature**,  $R_{base}$ , is similar to  $D_{base}$ . For many insect species it a value of around 0.02 has been found to be appropriate.

Respiration rate,  $r$ , increases exponentially with temperature according to the law

$$r = R_{base} e^{R_T T}$$

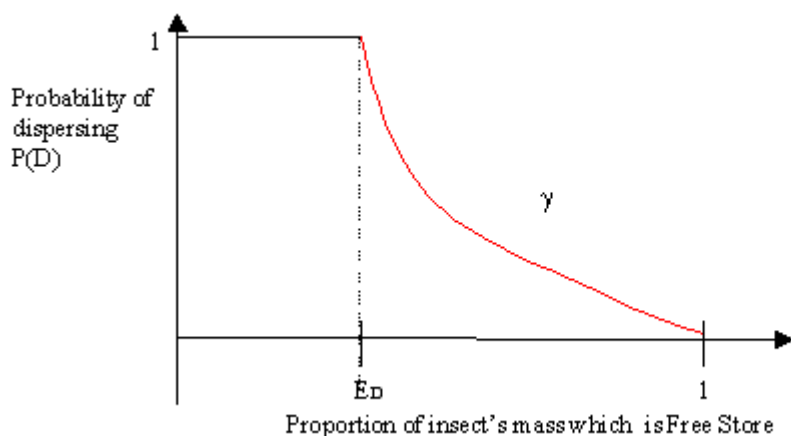
where  $T$  is temperature and  $R_T$  is the **Respiration rate increase with temperature**. Values of around 0.04 are reasonable (Peters 1973).

Our insects consist of 2 energy compartments, Free Store and Structural Store. Free store is energy that is available to meet the costs of reproduction and respiration. **Proportion of assimilated food allocated to energy reserves**, is thus the proportion which is directed to the Free Store. It can take any value between 0 and 1. If it is near 0 then the insect’s strategy becomes very risky since it is unlikely to have a huge energy reserve upon which it can rely if resource is scarce.

## 2. Dispersal

We regard *dispersal* and *foraging* as distinct activities, with *foraging* discussed later.

Insects disperse if they are not getting sufficient energy to satisfy their needs at their current location. This is determined by the level of free store, the probability of dispersal occurring being negatively correlated with the energy reserves of the insect.



**Figure 5: Dispersal probability**

If the proportion of the insect's mass that is free store drops below **Energy threshold for dispersal ( $E_D$  on the graph)** the insect will move. The distance it moves is randomly pulled from a Poisson distribution with mean **Average distance moved during dispersal**. If the proportion of the insect's mass that is Free Store is above the threshold  $E_D$  there is still a chance that the insect will move. The higher the **Exponent on dispersal probability function** ( $\gamma$  on the above graph) is then the less generally mobile the insect will be. We have no good idea for what values  $\gamma$  should take. To simulate a relatively immobile aphid species we have used a value of 100, whereas for some species, say beetles, which can be quite mobile, low values for  $\gamma$  of say 1 to 10 might be more appropriate. There is always a cost to movement. In the model the cost depends on the distance moved and the mass of the insect. Again, we have no clear idea what values **Energy cost for movement** should take, although we have used values between about 0.0001 and 0.001 in practice. It is worth noting that "mobile" insects with low values for  $\gamma$  are unlikely to be able to survive if their cost of dispersal is high.

### 3.Reproduction

**Egg mass** is the total mass of each egg. **Energy reserves in egg** is the amount which is Free Store, thus it is nonsensical for this value to be greater than **Egg Mass**.

When an individual is adult, it will reproduce if the proportion of its mass that is Free Store is above the threshold **Energy reserves required in adult for egg production**. When it reproduces it will use up its free store, as long as the proportion of its mass that is Free Store does not drop below a certain threshold (**Energy reserves must not drop below this**).

An individual can have a certain number of reproduction events before dying (**Maximum number of reproduction events**). For example, some species will only reproduce once, while others will continue to reproduce once they are adult until the end of the growing season.

**Egg viability** is the proportion of eggs laid which are viable. Thus it takes values between 0 and 1.

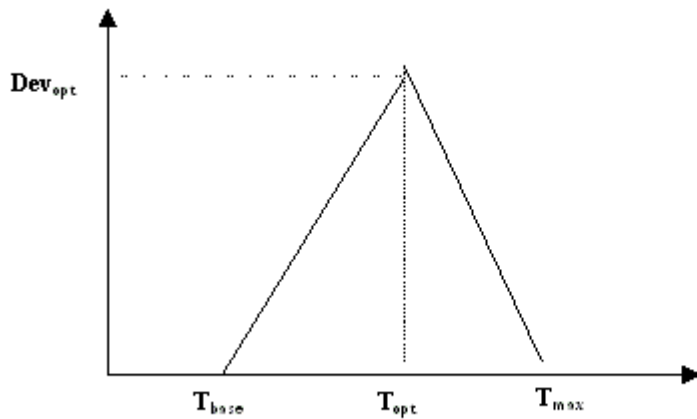
### 4.Development

**Base temperature of insect (degrees Celsius)**.  $T_{base}$ . This is usually above  $0^\circ C$ . Below this temperature the insect is dormant.

**Optimal temperature of insect (degrees Celsius)**.  $T_{opt}$ . At this temperature the development rate of the insect is maximal.

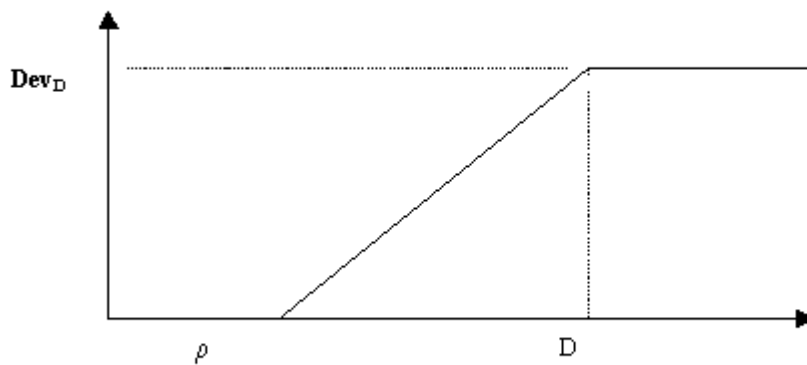
**Maximum temperature at which development can occur (degrees Celsius)**.  $T_{max}$ . If this temperature is exceeded then the insect's development rate drops back down to zero.

**Daily development at optimal temperature. ( $Dev_{opt}$ )**. An insect is adult when its number of development units equals 1. Thus for something like an aphid, which can mature in less than 10 days at optimal temperature a reasonable value might be 0.1. For a ladybird, which might take upwards of 30 days, a value of 0.03 would be more suitable. As the temperature moves away from  $T_{opt}$  the development rate decreases linearly down to zero at either  $T_{base}$  or  $T_{max}$ .



**Figure 6: Daily development at optimal temperature**

In some insect species the resource consumption rate also affects the development rate (e.g. *Adalia decempunctata*, Dixon 1962). We allow for additional development of through the parameters **Additional development ( $Dev_D$ ) occurring if demand ( $D$ ) is met** and **Additional development occurs if this demand is exceeded,  $\rho$** , (as a proportion of mass of self).



**Figure 7: Additional development**

## 5. Foraging

In this case the herbivores and predators have different traits, partly because we allow predators the option of “intelligent” searching. The main differences, however, come about because herbivores generally consume parts of objects that are much larger than themselves, while predators usually consume the whole of objects that are either smaller or equal to themselves in size.

Included among the foraging parameters is the *Overwintering survival rate* of the insect species. This is essentially the probability that any given individual will survive the winter and persist into the next year, so it should take values between 0 and 1.

### 1. Herbivores

**Plant part that herbivore consumes.** This may either be phloem, structure, or seeds.

### 2. Predators

**Search radius.** Predators have the ability to “see” prey in a circle around themselves of this radius. They will move to the cell that they believe has the most suitable prey in it (which cell they believe has the most suitable prey is somewhat dependent on the apparency parameters – discussed later).

Prey choice for predators is rather complicated. We had to consider a number of factors when modeling this:

- (1) As a proportion of mass of self, prey size can vary with predator’s age
- (2) Prey acceptability increases as the predator gets more “hungry”.
- (3) Predators can choose between a number of different prey types.

A day is divided up into a number of sub-units (fixed arbitrarily at 20) over which the predator forages. Although the amount of food required by the predator is set by its demand rate (defined earlier) the items it consumes to meet that demand may vary. In each time sub-unit the preferred size for the prey item is

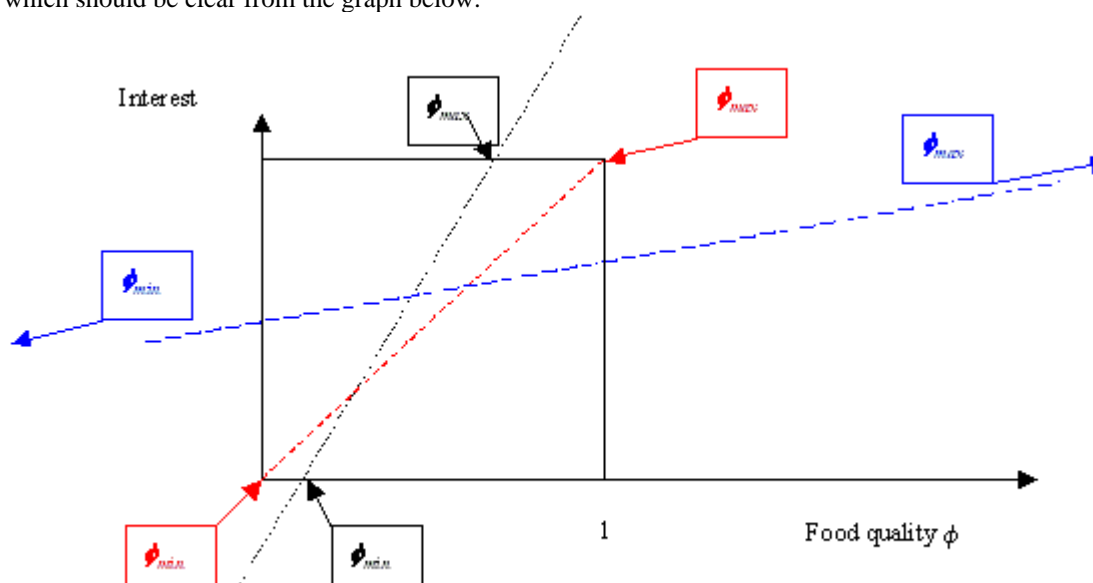
$$cM^\beta$$

where  $c$  is the *Coefficient for preferred prey size*, and  $\beta$  is the *exponent for preferred prey size*. If the proportion of the predator’s mass which is Free Store is at *Zero tolerance energy threshold for predator* ( $FS_{zero}$ ), then the predator will not accept any prey which are not exactly equal in mass to  $cM^\beta$ . If the Free Store is below this threshold then the predator will accept prey of different sizes, the level of tolerance being greater if *Coefficient for tolerance for prey not of preferred size*,  $\sigma$ , is large.

We have no idea of the range of biologically acceptable values, but values that have worked in practice (based loosely around 2-spot ladybirds) are

$$c \approx 0.1, \beta \approx 1, FS_{zero} \approx 0.6, \sigma \approx 0.01.$$

The *Food quality* is also of interest when the predator is choosing its prey items. This parameter, which is essentially a conversion coefficient, and can take values between 0 and 1, will be discussed later. A predator’s level of interest in a prey item will be somewhat dependent on the quality of that prey item. *Minimum quality* ( $\phi_{min}$ ) is the threshold of the conversion coefficient below which the predator is not at all interested, and *Maximum quality* ( $\phi_{max}$ ) is the threshold above which the predator is always interested. Although conversion coefficients themselves should always be between 0 and 1 we allow these parameters to be outside this range for reasons which should be clear from the graph below.



## Figure 8: Food quality

On the black line, the difference between  $\phi_{max}$  and  $\phi_{min}$  is small and the predator has a large difference of interest in prey types even if the difference in their food qualities is low.

On the red line, if the prey conversion coefficient is zero the predator has no interest in it whereas if it is 1 then the predator is completely interested.

On the blue line the difference between  $\phi_{max}$  and  $\phi_{min}$  is very large and the predator does not differentiate much between prey types of different qualities when choosing its prey items.

This provides an explanation of all the basic parameters for individual species. We will now look at these in the context of a complete model.

## 5. Setting Up a Model Run

A full model run consists of defining the parameters for the model and the calculation (by the model software) of the spatial distributions of the participant species for the duration of that model run. Depending on the size of the model defined this may take hours or even days.

To set up a complete model one should be familiar with loading existing species files into a species form (see chapter 3). With this knowledge it is possible to build models using species already parameterised and archived. If one wishes to define one's own species consult chapter 4.

First launch the interface program (see chapter 2).

NB: if the interface is already running it should not be in the process of currently performing a model run. If the Windows taskbar contains the Model icon (see below) it is probable that a model is already in progress. Chapter 6 discusses terminating a running model.

Selecting 'File => New' will initiate the Model wizard which guides the user step by step through the process of defining a model's parameters.

### 5.1. Environmental parameters

The first screen that appears allows the setting of the spatial and temporal size of the model, along with the temperature range. Default values have been provided but these should be altered as required.

New Model

Please enter the following details for the model, then press 'Next'.....

10	Lattice length (spatial units)
10	Lattice width (spatial units)
0	Minimum temperature (°c)
25	Maximum temperature (°c)
15	Temperature at sowing (°c)
150	Season length (days)
3	Number of seasons

< Back   Next >   Cancel

## Figure 9: New model

**Lattice length** and **width** are the length of the lattice in the x and y directions. Run time for the simulation should increase approximately linearly with each Lattice length. Thus, although for the default size of 10 by 10 the model should run quickly, it is worth noting that a lattice of 100 by 100 will take approximately 100 times as long to run.

**Minimum temperature** is the temperature at the start of the simulation and **Maximum temperature** is the peak temperature that can be achieved. **Temperature at sowing** will determine when the plants are sown in the model.

**Season length (days)**: each year will be of this length. Thus for the default values each year will run for 150 days before the plant is harvested and the herbivores and predators go into their over winter phase (see *Overwintering survival rates*, Chapter 4).

**Number of seasons**: the simulation will finish after this many seasons.

When you are satisfied with the numbers entered press 'Next'

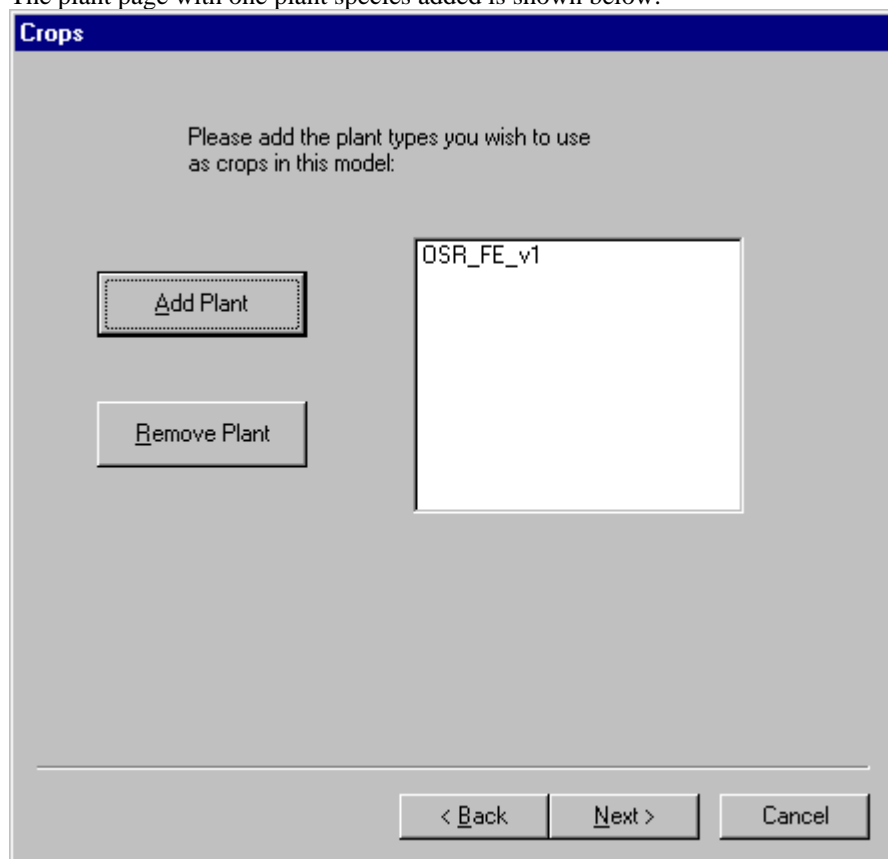
### 5.2. Adding Species

The next three pages allow the addition of any number of species to the model. There is one page each for plants, herbivores and predators. All three pages have an identical format and operate on the same principals. Therefore the plant page is used to demonstrate these pages.

Click on the 'Add Plant' box. A Plant dialog box will now appear. At this point the user can press Load to upload a plant previously defined and saved. Alternatively they may enter parameters manually. Once either method is completed pressing the OK button will add the defined plant to the list of plants.

It is possible to Load a plant from file and then adjust some or all of its parameters. At this point pressing OK, as well as adding the plant to the model (using the altered parameters) will check whether or not to save the altered parameters. The original plant (.pla) file can be overwritten with the altered parameters or a new plant file created.

The plant page with one plant species added is shown below:



## Figure 10: Add plant form

This can be repeated for as many plants as required. If a plant is no longer required it is possible to remove it. Select the plant in the list by left clicking on it. Pressing the 'Remove Plant' button will then remove the highlighted plant from the list.

The forms for adding herbivores and predators to the model operate in the same manner.

It is necessary to add at least one plant and one herbivore to the model.

After the Add Predator page is completed the next page provides a 'Finish' button. It is important to note that once the Finish button is pressed this part of the Model Set-Up Wizard will be complete: it will no longer be possible to add or remove species to the model nor change the environmental parameters. Once Finish is pressed the Wizard moves on to define the species' interactions.

### 5.3. Plant Herbivore interactions.

The interaction between plant and herbivore species is defined by two parameters for each inter-relation. Defining the interaction between crops and pests is done using the Herbivore-Plant interaction page. The user will be presented with one such page for each herbivore present in the model.

**Figure 11: Herbivore Plant interactions**

The name of the herbivore concerned is displayed at the top of the page. A list of plants present in the model is displayed to the left. The parameters defining the relationship between the herbivore and the plant highlighted in the list are displayed in the two boxes to the right.

To enter the required information, select a plant from the list, by left clicking on it, and type the required numbers into the boxes. This must be repeated for every plant in the list.

Two key components of a resource-consumer interaction are the Food Quality and its accessibility of the resource to the consumer. Food quality is defined as the *Assimilation efficiency* of the consumer when eating a given resource. *Apparency* is a parameter expressing how accessible the resource is to the consumer, and thus is a composite parameter which comprises say plant architecture, chemical composition, and foraging behaviour of the consumer. Each individual consumer will look at each individual resource type differently; thus these parameters need to be set for every resource type and every consumer type present.

Although it might be tempting to skip through this tedious part of the process without thought to the parameter values, we would advise against this. Multi-trophic models tend to be *highly* sensitive to these parameters: Species will go through a range of dynamics from extinction, stable persistence, cyclic and chaotic dynamics based on the values defining the resource-consumer interfaces. For guidelines, from our literature searches we have found that *Assimilation efficiency* tend to average at between about 0.25 and 0.4, although there is substantial variation around this mean.

*Apparencies* at the plant-herbivore interface have needed to be quite low to ensure persistence in food chain simulations (up to about 0.1), although this may not be the case in true food webs, in which other species may help to stabilise the system dynamics and facilitate co-existence.

Once the parameters have been added for each herbivore in the model another 'Finish' button is presented. Again at this point, once Finish is pressed it will not be possible to alter the Plant Herbivore interactions.

### 5.4. Predator Herbivore interactions

If any predators are present in the model it will be necessary to define their relationships with the herbivores. Again for each prey type present, each predator needs Assimilation efficiency and apparency parameters set.

The layout and operation of the Predator-Herbivore interaction pages is almost identical to that of the Herbivore-Plant. Except herbivores now appear in the list and each page deals with one predator.

The screenshot shows a software window titled "Predator-Herbivore interaction". At the top, it says "Please select each herbivore from the list and enter its parameters into the boxes". Below this, there are three main sections: 1. "Predator": A text box containing "ladybird\_FE\_v1". 2. "Herbivores": A list box containing "Aphid\_FE\_v1" (highlighted) and "Aphid\_FE\_v2". 3. "Parameters": Two rows of input fields. The first row has a value "3" and a text box, followed by the label "Assimilation efficiency (0<n<1)". The second row has a value "23" and a text box, followed by the label "Apparency of herbivores to predator (0<n<1)". At the bottom of the window are three buttons: "< Back", "Next >", and "Cancel".

**Figure 12: Predator herbivore interaction.**

Again the system *is* sensitive to the parameterisation, and, although values for *Assimilation efficiency* appear to average somewhere between 0.25 and 0.4, we have less idea about what are suitable values for the *Apparencies*.

Once the desired parameters have been entered for all of the predators another 'Finish' page is presented. Again no change to the Predator Herbivore interactions can be made after 'Finish' has been pressed. This will move the wizard on to the initial distribution section.

### 5.5. Initial distributions

It is necessary to supply the initial distributions of the herbivore and predator populations in the model. If there is more than one plant present in the model information concerning their mixture will need to be supplied.

### 6.Plants

In the case that there is only one plant species present in the model, the Set-up Wizard will proceed directly to the distributions for herbivores.

If there are two plants present in the model the following form is presented:

**Plant Distribution**

Please specify the distribution for

Either

Random

Probability  ( $0 < p < 1$ )

Or

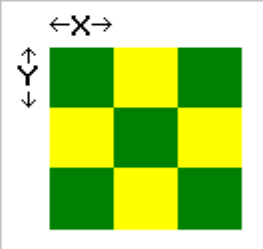
Grid based

Grid Dimensions

X

Y

(in spatial units)



< Back   Next >   Cancel

**Figure 13: Plant distribution-2 Plants.**

The first plant added to the model is assumed to be the main crop. It is only necessary to set the distribution for the second plant. If Random is chosen a probability that the second plant will be sown at any given lattice point is entered. The grid-based choice allows the two plants to be sown in a regular pattern of alternate blocks. The size of these blocks defined by the two parameters, X and Y. X and Y are measured in the same spatial units used to define the lattice size (see Environmental parameters). If X and Y are equal this will give a regular square patterning, like a chessboard. If, say, Y is set to equal the lattice length then this will give a striped pattern of width determined by X. If more than two plants have been added to the model it is only possible to specify a probability for the distributions of the plants. The form to allow this is shown in figure 14:

**Plant Distribution**

Please select each plant in the list and enter its probability into the box:

Plants

- OSR\_FE\_v1
- OSR\_FE\_v2
- OSR\_FE\_v3

Probability

1

$0 < p < 1$

< Back   Next >   Cancel

**Figure 14: Plant Distribution- more than 2 Plants**

Each plant is selected in the left-hand list and a probability for its sowing is entered in the probability box. These probabilities take the range 0 to 1 for each plant. The model averages the probability values to calculate the distribution of the plants.

### **7. Herbivores and predators**

The herbivore and predator distributions are defined as either random or regular using the following form.

**Figure 15: Insect distribution form**

If a *random* distribution is selected then the user has to enter the concentration, that is the average number of insects per plant. If *regular* is selected the user specifies the  $x$  and  $y$  coordinate of a point source. Then enters the number of insects at this point into the 'Population at location'.

If the 'Repeat regularly over grid' box is checked then the sites  $(2x,y)$ ,  $(3x,y)$ ... $(x,2y)$ ,  $(2x,2y)$ ,  $(3x,2y)$ ... etc will also be filled. The 'Population at location' will be ascribed to each of these points.

### 5.6. Running the model

Once all the parameters have been entered the screen informing the user that the model will now be started is displayed. Pressing the 'Finish' button to confirm that you have finished entering all the data starts the model.

The Model program is launched as a minimised window. That is it only appears in the taskbar and should look like so:



**Figure 16: Model program icon**

For details on operation of the interface once the model is running please see chapter 6.

## 6. Viewing a Model Run

Once the model has been started the display will appear as in figure 17. The initial display shows the first plant in graph 1, the first herbivore in graph 2 and the first predator in graph 3. As the model program generates each new timestep's data it will be displayed on the interface.

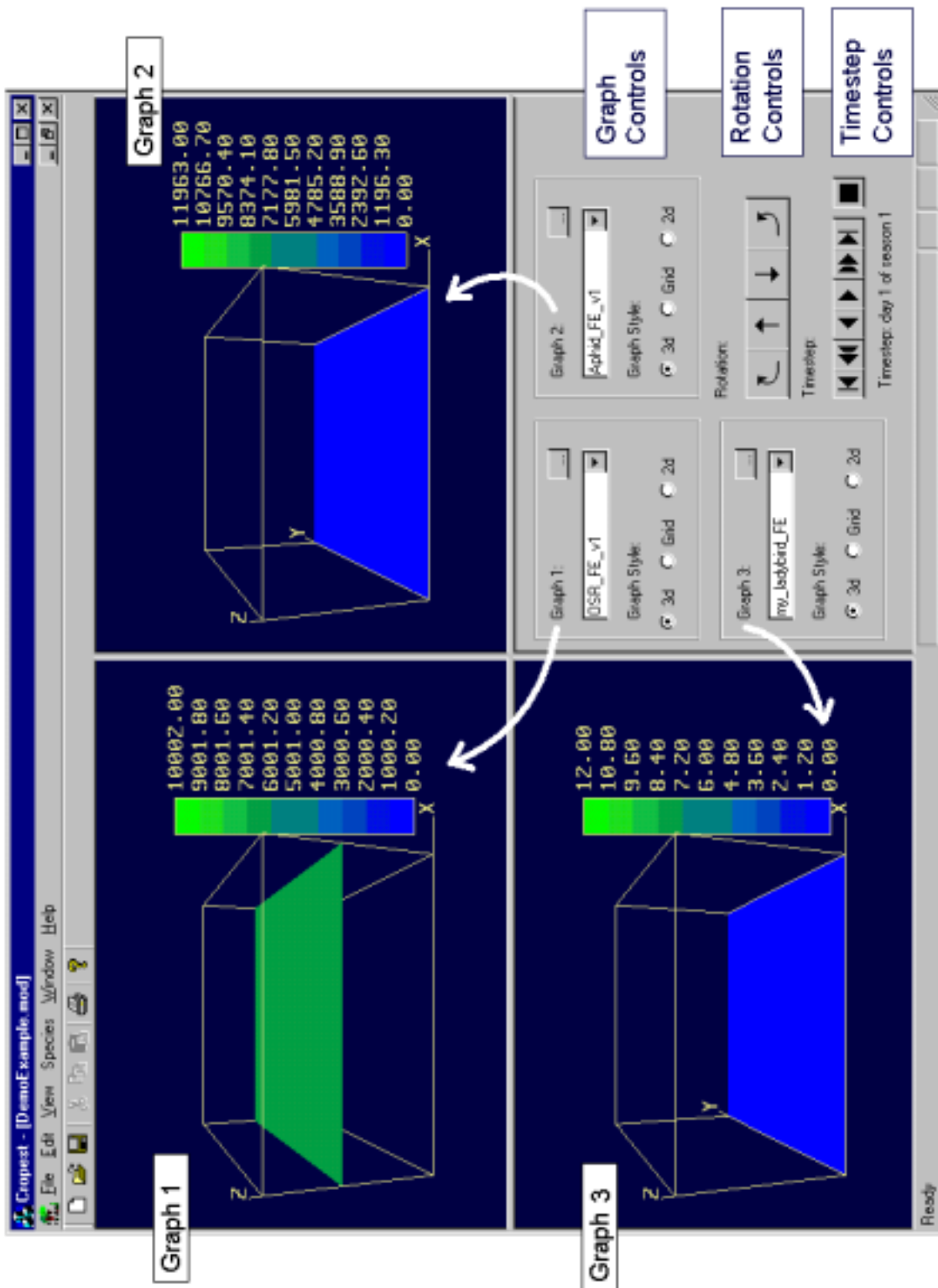
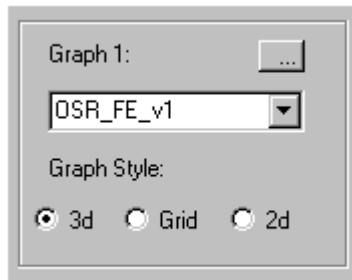


Figure 17: The model viewing interface

## 6.1. Graphs

The name of the species shown in each graph is shown in its respective graph control panel:




**Figure 18: Graph control**

Clicking the down arrow to the right of the species name will present a drop-down list containing the names of all the species present in the model. Clicking on a species name will cause that species data to appear in the relevant graph.

If a plant species is selected the scale on the graph will represent the maximum overall biomass that plant could achieve (The sum of maximum biomass, phloem and seed mass).

For insect species the scale will represent the maximum population achieved by the species. As the eventual maximum population will not be known until a model run has finished this scale will change whilst the model program is still generating output.

The style of the graph can be selected from the three available.

The  button allows the parameters of the species displayed in the graph to be reviewed. The species parameters appear in a form identical to the form used for defining it except that the parameters are read-only.

## 6.2. Rotation

The three graphs can be rotated, in unison, by the use of the four rotation buttons. The button required is simply held down using the mouse until the desired view is achieved. The graphs all move in unison: it is not possible to rotate a graph on its own.

The up and down buttons only allow for a rotation of  $\pm 90^\circ$ .

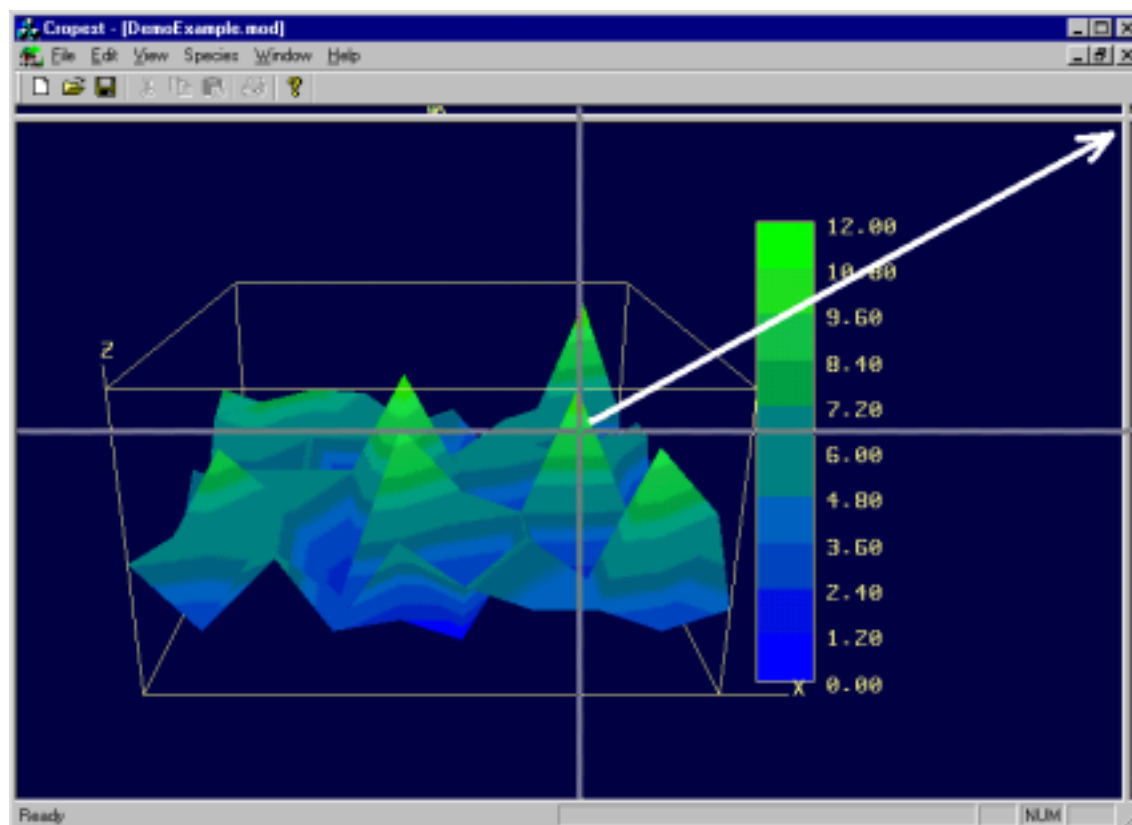
If a graph style is set to 2D it will not appear to rotate. However if the style is later set to 3D or grid the graph's aspect will match that of other graphs that have been rotated.

If the rotation appears slow or jerky this may be because the model program uses a large amount of processing power. Once the model program has generated all the data and closed down the rotation should appear much smoother.

## 6.3. Enlarging

There is no zoom control provided but it is possible to alter portion of the screen allocated to each graph. The bars dividing the graphs can be dragged around the screen. Simply position the mouse over the bar, hold the mouse button down and drag the bar to its new desired location. It is possible to adjust both bars simultaneously by dragging their intersection.

This allows one graph to fill the available screen space as illustrated:










**Figure 19: Enlarging a graph**

#### 6.4. Timestep controls

The timestep control allows the interface to play backwards and forwards through the model output. The current timestep showing on the graphs is displayed below the timestep controls. As with rotation the timestep shown can only be altered for all of the graphs in unison.

The timestep controls are modeled on the controls for a video or audio cassette player and provide the following functions:

-  Jumps back to the first timestep of the model.
-  Plays backwards from the current timestep to the beginning of the model.
-  Moves backward one timestep from the current timestep.
-  Moves forward one timestep from the current timestep.
-  Plays forwards from the current timestep to the end of the model.
-  Jumps forwards to the last timestep of the model.
-  Stops the timestep if it is continuously playing.

It is possible to use the timestep controls to navigate temporally through the model whilst the data is still being generated. In this case the 'last' timestep will be the last timestep for which data has so far been generated.

#### 6.5. Stopping a model run

Important: If it is required to end a model run part way through its generation it should be done by closing the model in the interface. This can be achieved by selecting 'File => Close'.

The program will confirm that you wish to end the model prematurely. The interface will then offer the option to save the model output (See chapter 7). It is possible to archive partially generated models.

It is not recommended to close the model program directly oneself, as this will leave the interface awaiting data. This may cause unexpected and undesired results if a second model run is undertaken.

## 7. Loading and Saving Models

### 7.1. Saving

Once a model has been generated it may be archived for later review, or comparison with other models. This is done by selecting 'File => Save'. If a model is closed without saving it the option to save it will be given before it is closed. Model files are saved with the extension .mod.

Saving a model saves all of the spatial timestep data as well as the parameters for the species involved.

As noted previously, it is possible to save part generated models. It should be noted though that such a model cannot be 're-started'.

Only the data generated prior to the model being stopped will be available for review.

### 7.2. Loading

Loading an archived model is achieved by selecting 'File => Open'. The required model file is then selected and will be displayed.

The model can be reviewed using the controls as outlined in chapter 6.

It is possible open more than one archived model at a time allowing comparisons to be made. The 'Window => Tile' and 'Window => Cascade' options can be used to help organise several models.

It is possible to open archived model whilst another model is in running.

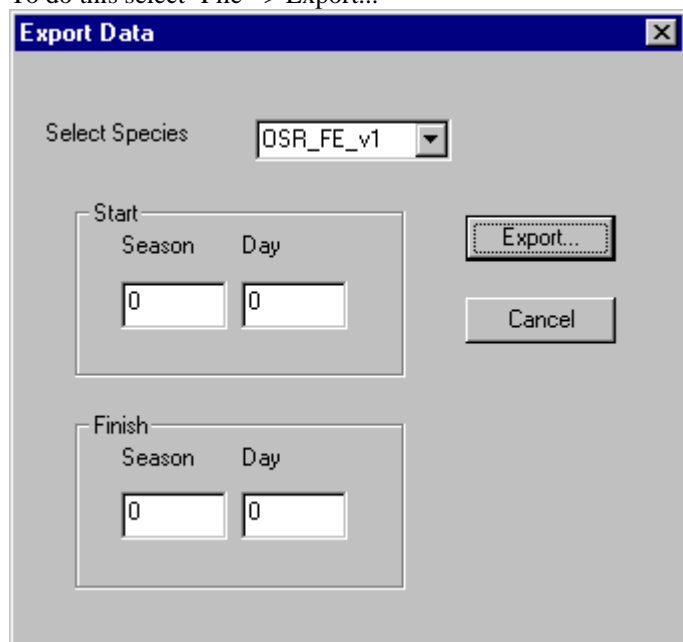
It is not possible to open one archived model twice, simultaneously. This would be useful to compare for instance different timesteps within the same model. The only way this can be achieved is to make a copy of the .mod file, using Windows Explorer. The original and the copy can be opened simultaneously to allow comparisons to be made.

### 7.3. Exporting

The format of the .mod files is such that it can only be read by the interface program. If any analysis of the data is required by other applications it is necessary to create a file of the data legible to other applications.

The interface therefore provides the capability to export the data in a tab delimited text format.

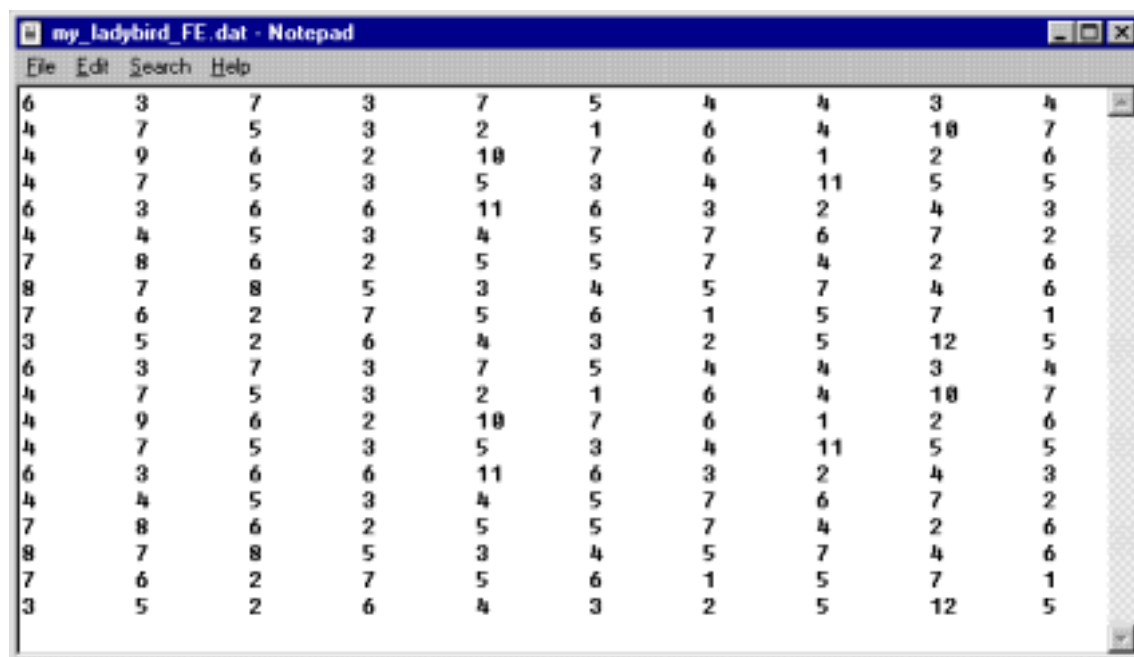
To do this select 'File => Export...'



**Figure 20: Data exporting**

The data for a single species can then be exported for any range of timesteps selected.

The file exported has a .dat file extension. Notepad or Microsoft Excel can read its textual format, for instance.



The image shows a Notepad window titled "my\_ladybird\_FE.dat - Notepad". The window contains a 20x10 grid of numbers. The numbers are arranged in 20 rows and 10 columns. The values in the grid are as follows:

6	3	7	3	7	5	4	4	3	4
4	7	5	3	2	1	6	4	18	7
4	9	6	2	10	7	6	1	2	6
4	7	5	3	5	3	4	11	5	5
6	3	6	6	11	6	3	2	4	3
4	4	5	3	4	5	7	6	7	2
7	8	6	2	5	5	7	4	2	6
8	7	8	5	3	4	5	7	4	6
7	6	2	7	5	6	1	5	7	1
3	5	2	6	4	3	2	5	12	5
6	3	7	3	7	5	4	4	3	4
4	7	5	3	2	1	6	4	10	7
4	9	6	2	10	7	6	1	2	6
4	7	5	3	5	3	4	11	5	5
6	3	6	6	11	6	3	2	4	3
4	4	5	3	4	5	7	6	7	2
7	8	6	2	5	5	7	4	2	6
8	7	8	5	3	4	5	7	4	6
7	6	2	7	5	6	1	5	7	1
3	5	2	6	4	3	2	5	12	5

Figure 21: Exported file opened in Notepad