

## CHAPTER 22

### MODELLING PLANT CANOPIES FOR BIOCONTROL AND BIODIVERSITY

*Insect movement, networks and lacunarity*

D.J. SKIRVIN

*Warwick HRI, University of Warwick, Warwick, UK*

**Abstract.** Canopy structure has an important role to play in determining the searching patterns of predators of insect pests in crops. The connections between plants within the canopy are crucial in determining the ability of predators to move around the canopy. Virtual plant models provide an ideal method for providing a realistic background for modelling the movement of insects in plant canopies. Experimental simulations of the movement of the predatory mite *Phytoseiulus persimilis* have shown that the time taken for the predator to locate the prey decreases as plants become more connected. However, the time to prey location is increased as the internal structure of the individual plants is increased. These two factors therefore have to trade off against each other to determine the optimal canopy structure for the quickest time to location of prey by predators. There is therefore a need to be able to characterize the structure of real canopies to examine how canopy structure influences the searching success of predators. In this paper we discuss potential methods for the characterization of plant canopies, using virtual plants as a tool to model the canopies, and the potential implications of characterizing plant canopies in relation to biological control and biodiversity.

#### THE IMPORTANCE OF CANOPY STRUCTURE

The plant is a major component of all ecosystems and provides the battleground for the war between insect pests and their natural enemies. It has been shown that plant structure can have a major influence on the success of many natural enemies (Van Haren et al. 1987; Sütterlin and Van Lenteren 1997; Stavrinides and Skirvin 2003). These studies have focussed mainly on the morphological characteristics of the plant leaves, with a particular emphasis on leaf trichomes, showing that increased density of leaf trichomes reduces the searching ability of parasitoids (Sütterlin and Van Lenteren 1997) and predatory mites (Van Haren et al. 1987; Stavrinides and Skirvin 2003).

However, the overall canopy structure, in terms of connections between plants, is also likely to be important, as it will determine the ability of predators to move from

253

*J. Vos, L.F.M. Marcelis, P.H.B. de Visser, P.C. Struik and J.B. Evers (eds.), Functional-Structural Plant Modelling in Crop Production, 253-264.*

© 2007 Springer. Printed in the Netherlands.

plant to plant within the canopy. Zemek and Nachman (1998; 1999) demonstrated, using metal bridges between caged plants, that the number of connections between adjacent plants significantly affected the dispersal of the predatory mite, *Phytoseiulus persimilis* Athais-Henriot (Acari: Phytoseiidae), and its ability to control the pest mite *Tetranychus urticae* Koch (Acari: Tetranychidae). These studies show that canopy structure plays an important role in determining the ability of predators to move around between patches of prey. In the Section "*Ornamental crops as a model system*" describe the current state of research on linking models of pests and predators with virtual plant models to gain an understanding of how canopy structure affects the movement of predators and their ability to locate prey.

In order to understand the role that canopies play in the movement of insects, it is necessary to be able to characterize plant canopies to explain how the connections between plants differ in different canopies, and the impact that changes in connections between plants have on predator and pest movement. However, measuring the connections between and within plants in a canopy is experimentally difficult. This is due to the high probability of knocking or moving individual plants during the counting process, which leads to change in the canopy structure.

Virtual plants (Room et al. 1996; Hanan 1997; Prusinkiewicz et al. 2000) are a powerful method for developing an understanding of the influence of plant canopy on insects. They provide a structured way of developing models of plant canopies, which can then be utilized to determine how different canopies differ in their structure. In the Section "*Characterizing Canopy Structure*", I describe the current research being done to develop a mathematical method for the characterization of plant canopies, with the potential uses of these methods explored in the Section "*Future Directions for canopy structure research*".

## CANOPY STRUCTURE AND BIOCONTROL – THE STORY SO FAR

### *Ornamental crops as a model system*

With the increasing loss of pesticides within the UK horticultural sector, there was a need to develop robust and sustainable biological-control strategies for pests of ornamental crops. As part of research on biocontrol in ornamentals, a simulation model of the biological control of the pest mite, *T. urticae* by the predatory mite, *P. persimilis* was developed (Skirvin et al. 2002). The results of this model showed that the movement of predators was crucial to obtaining successful biological control of the pest. Further research indicated that the number of connections between plants was an important factor governing the movement of the predators (Skirvin and Fenlon 2003). These results combined with existing data (Zemek and Nachman 1998; 1999) indicated the importance of canopy structure in determining the success of biological control in ornamental crops.

Due to the wide diversity of ornamental crops grown in the UK and the large amount of literature data on the movement behaviour of *P. persimilis* (Bernstein 1983; 1984; Sabelis and Van der Baan 1983; Sabelis and Van der Weel 1993; Pels and Sabelis 1999), it was felt that the ornamental crop – *T. urticae* – *P. persimilis*

system provided a good model system on which to develop detailed models to examine the effect of canopy structure on the movement of predators for biological control.

#### *Development of the virtual chrysanthemum model*

As a starting point for the development of detailed models of predator movement, the first stage was to select an appropriate model crop. Chrysanthemum was chosen as *T. urticae* is a major pest of this crop and the plants have a reasonably simple structure, consisting of a main stem and leaves, with a single flower.

Sixteen chrysanthemum plants (cultivar Sunny Regan) were digitized using a sonic digitizer and the Floradig software (Hanan and Room 1997). The data on the plants was then analysed to provide the lengths of the nodes, branching angles of leaves, the length of the petioles and the size of the leaves. From these data, statistical relationships between the architectural variables of the plant and the position of the node were developed. These relationships were then used to develop an L-system model of the plants using the L-studio software (Prusinkiewicz et al. 2000).

The L-system model was used to generate a range of chrysanthemum canopies with different plant spacings, which showed that increasing the plant spacing led to a decrease in the complexity of the canopy structure, but due to a lack of appropriate mathematical analyses, it was not possible to determine the exact differences between the different canopies. Therefore, it was decided to simplify the model, to allow a more systematic examination of the effects of both the within-plant architecture and the connections between plants.

The plant structure was simplified as described in Skirvin (2004). The model simulated plants that have four leaves. Three levels of within-plant spatial complexity were simulated: all four leaves attached to a single node, with the leaves arranged equidistantly around the node (i.e. rotated 0, 90, 180 and 270° around a vertical axis through the node); two leaves attached to a node, with the leaves in each pair on opposite sides of the node, or a single leaf attached to a node (with a 90° around the stem between each node), so that the plants had either 1, 2 or 4 nodes, respectively. This model was then used as the base model for the simulation experiments described below.

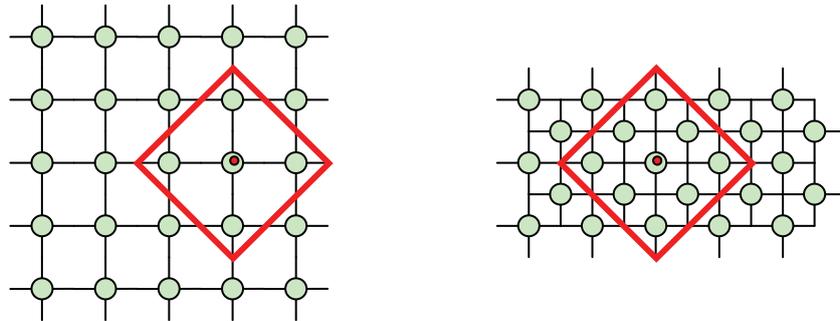
#### *Simulating predator movement – the effect of canopy structure*

Initial simulation experiments looked at the proportion of the leaves and nodes of the plants visited by a single searching predator. The model assumes that the predator uses a random search to locate prey, providing the following set of simplistic rules for predator movement.

- If a predator is on a node it has equal probability of moving to any leaf attached to the current node, other nodes connected to the current node or not moving.
- If a predator is on a leaf that does not touch another leaf, it has equal probability of not moving or moving to the node to which the leaf is attached.

- If a predator is on a leaf that touches another leaf it has equal probability of not moving, moving to the node to which the current leaf is attached or moving to the leaf or leaves that touch the current leaf.
- If a predator is moving between nodes or leaves, or from a leaf to a node and vice versa, it continues moving until it reaches the node or leaf.

Using these rules, the movement of the randomly searching predators was simulated in two types of grids (Figure 1), which differed in their connectedness: a regular grid, where each plant is connected to 4 others, and an offset grid, where each plant is connected to 8 other plants. For both grid types, the within-plant architecture was simulated by the three plant models described above. For each combination of plant size and grid, a total of 999 runs of the experiment were done. These runs were repeated for three different grid sizes (5 by 5, 10 by 10 and 20 by 20 plants), giving a total of 17982 runs of the model.



**Figure 1:** The regular (left) and offset (right) grid patterns for the plants. The diamonds represent the nearest neighbourhood of the plant marked with a dot

The results (analysed using ANOVA) showed that there were significant effects of the connectedness or grid type ( $F = 4442.52$ , d.f. = 1, 17,964,  $p < 0.001$ ) and the within-plant architecture ( $F = 5542.89$ , d.f. = 2, 17,964,  $p < 0.001$ ), and a significant interaction between these two factors ( $F = 158.02$ , d.f. = 2, 17,964,  $p < 0.001$ ). A greater proportion of the leaves and nodes were visited in the offset grid compared to the regular grid, showing that as connectedness increased, the ability of the predator to move through the canopy increased. However, as the within-plant complexity increased from 1 node to 4 nodes, the proportion of leaves and nodes visited decreased. The interaction between these two factors was caused by a non-linear decrease in the proportion of leaves and nodes visited as within-plant complexity increased. These results highlight the complex nature of the interaction between individual plant structure and between plant connections. A plant with a complex (highly branched) architecture is likely to be connected to more plants in a canopy than a simple plant with limited branching. However, the more complex structure means that the randomly searching predator has to spend more time searching within an individual plant.

These results show that canopy structure has a major impact on the movement of the predators, but it does not show the effect that canopy structure has on the ability of predators to locate prey. Therefore, a second set of simulation experiments was carried out to examine the effect of canopy structure on prey location.

The experiment was designed to investigate how the time to location of a static prey by a randomly foraging predator was influenced by two aspects of canopy structure: connectedness and canopy complexity. For each set of simulations, which used the same grid types, plant architectures and grid sizes as the previous experiment, three prey locations were simulated: in one of the four corner plants; on an edge plant; or on any of the plants not on the edge of the grid. For each prey location, the model was run 2,500 times for the 5 x 5 grid, 10,000 for the 10 x 10 grid and 40,000 times for the 20 x 20 grid, with the predator start point being chosen at random for each run of the model.

The time for the predator to locate the prey was output for each run of the model along with the starting location of the predator and the location of the prey. If the prey was not found within 1 million time steps (equivalent to approximately 2–3 days), then it was assumed that the predator did not find the prey (as real predators die of starvation in 2–3days).

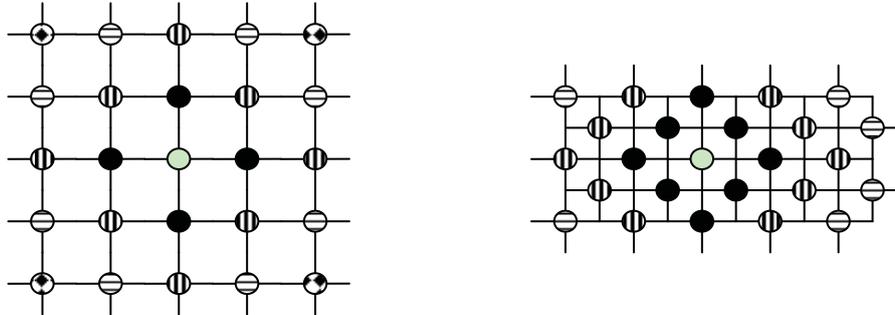
For each run, the starting location of the predator and location of the prey were used to calculate the initial distance of the predator from the prey, in terms of concentric neighbourhoods around the prey location, according to the following equations for regular (1) and offset (2) grids:

$$N = X + Y + Z \tag{1}$$

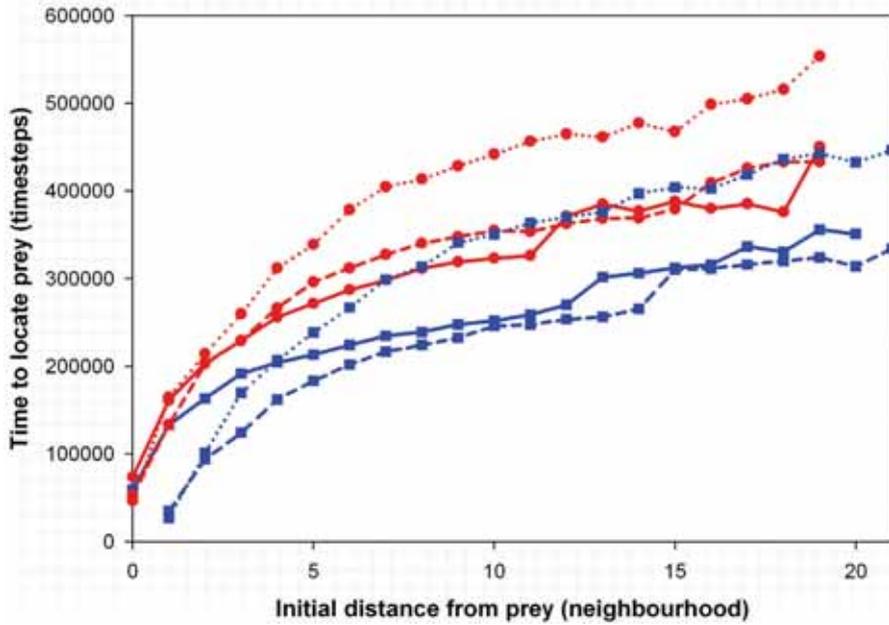
$$N = X/2 + Y/2 + Z \tag{2}$$

where  $X$ ,  $Y$ , and  $Z$  are the distances between the  $x$ ,  $y$  and  $z$  coordinates of the prey and predator locations and  $N$  is the index of distance between plants in terms of the number of concentric neighbourhoods. Neighbourhoods are illustrated in Figure 2 for regular and offset grids, and the value of  $N$  is equivalent to the minimum number of plants a predator must visit to locate the prey. The division by 2 in the offset grid accounts for the larger size of the neighbourhood of a single plant (8 plants touched instead of 4). The mean time to prey location for each distance was then calculated for each of the grid sizes, plant canopy complexities and connectedness, and plotted against the initial distance between predator and prey in terms of neighbourhood distance (Figure 3).

The results show that the time to prey location is related to distance in a non-linear way and that it increases with the distance of the predator from the prey. As the connectedness of the plants is increased, then the time to prey location is shorter (compare regular and offset grids in Figure 1). As the complexity of the plant canopy is increased, then the time to prey location increases.



**Figure 2.** Illustration of the neighbourhoods (1 - solid black, 2 - vertical stripes, 3 - horizontal stripes, 4 - diamonds) for regular (left) and offset (right) grids around a central plant (white)



**Figure 3.** Graph showing the effect of plant canopy complexity [..... - 4 nodes; — — - 2 nodes; — — - 1 node] on the relationship between distance from prey and time taken to locate prey for the 2 levels of plant connectedness [●- touching 4 plants; ■- touching 8 plants]

These results demonstrate the importance of canopy structure in determining the ability of a predator to locate its prey. The fact that a more connected canopy leads to a shorter time to prey location is not surprising, as there are more ways of moving

from one plant to another, but it is the first time it has been demonstrated through simulation. The fact that a more complex canopy leads to a longer prey location time is mainly driven by the separation of the leaves in the vertical plane, as the model assumes that all leaves are of the same area. This means that the predator has to spend more time moving up and down a plant, rather than being able to move horizontally through the canopy. This is more likely to mimic the natural situation in ornamental crops. However, leaf area will be an important factor in determining the connections between plants in a crop canopy, and for ornamental crops, it is likely that there will be a greater connectedness lower in the canopy, where the leaves are larger, than in the upper canopy near the growing tips, where the leaves tend to be smaller. As the majority of pest insects attack the growing tips, the predators will have to move up and down within the canopy in order to locate the pests.

This work has major importance for biological control using walking predators, since it shows that canopy structure needs to be taken into account when deciding on strategies for the introduction of biological-control agents, as the distance of the predator from the prey is not a linear relationship, and the further away the predator is, the longer it takes to locate the prey. This would support the use of dispersed predator introductions rather than point introductions; however, economic factors and the biological features of the predator will affect the most suitable introduction strategy.

#### CHARACTERIZING CANOPY STRUCTURE

##### *Why do we need to characterize canopy structure?*

Although the results of the simulation experiments provide useful information about the effect of canopy structure on the prey location by predators, it is difficult to translate these results to real plant canopies, as currently there is no suitable method of characterizing and quantifying real canopies that will allow comparison between different plant canopies. This is mainly due to the impracticalities of digitizing and measuring real canopies. The bushy growth habit of many ornamental plants means that it would be impossible to measure or digitize a single plant in a canopy without moving it and the other plants around it. This means that measurements could not be made without altering the connections within the canopy, giving a false measure of the canopy connectedness.

However, by digitizing individual plants and creating simulated 'real' canopies, it may be possible to develop quantitative methods that will allow canopies to be characterized, so that comparisons between different digitized 'real' canopies can be made. This section describes two methods that show potential for developing quantitative methods for the comparison of canopy structure.

##### *The L-valued matrix*

The first method is the L-valued matrix (Rodrigue et al. 2006), which is a concept used in transport geography and logistics. For this method, the plant is treated as a

network, with each leaf on the plant forming a node within the network. The L-valued matrix is effectively a matrix that lists the shortest possible distance between every node in the network (i.e. the shortest possible distances between every leaf, assuming movement can only take place along stems and petioles).

To compute the shortest possible distances between leaves, we have developed an algorithm that uses plant signals to traverse the canopy. The signal is released from a single leaf in the canopy in turn, and returns the time taken for the signal to reach every other leaf in the canopy, assuming that the signal moves a single unit of distance in each time step and propagates or reproduces itself at every branching point in the canopy. In this way, we ensure that the signal takes the shortest possible route to each leaf. By allowing the program to release the signal from each leaf in the canopy in turn, we essentially obtain the shortest times (equivalent to distance) for signals to travel between any pair of leaves in the canopy. Because the signal moves at unit distance per time step, this is effectively the shortest distance between pairs of leaves, which is the information required for the L-valued matrix.

Having obtained the L-valued matrix, we can then sum the distances in the matrix, which provides a measure of the accessibility of the canopy, in terms of shortest possible pathways through the canopy. This provides us with an ‘accessibility index’ that we can use to compare plant canopies.

The ‘accessibility indices’ were calculated for the regular and offset grids, with the different levels of internal structure, described in the Section "*Canopy Structure and Biocontrol – the story so far*", and are shown in Table 1. The smaller the value of the accessibility index, the greater the accessibility of the network, i.e. the more connected the canopy is.

**Table 1.** The indices derived from the L-valued matrix for canopies in regular and offset grids, with 1, 2 or 4 nodes of internal structure

<i>Regular</i>			<i>Offset</i>		
<i>1 node</i>	<i>2 nodes</i>	<i>4 nodes</i>	<i>1 node</i>	<i>2 nodes</i>	<i>4 nodes</i>
243	302	352	196	207	280

The indices help to explain the results of the second simulation experiment described in Section "*Canopy Structure and Biocontrol – the story so far*", by showing that the ‘accessibility’ or connectedness of the canopy in an offset grid arrangement with 4 nodes is similar to that of plants arranged in a regular grid with either 1 or 2 nodes. This is consistent with the time to locate prey from these canopies, which were similar (Figure 2).

The L-valued matrix provides a quick and easy method for describing canopy structure in terms of the distances travelled between different parts of the canopy, which is useful when examining the movement of insects within the canopy. However, it does not provide any information about the actual structure of the canopy in space. Therefore, it needs to be used in conjunction with other measures that can provide information about the spatial structure of the canopy itself.

*Lacunarity*

Landscape ecology has many metrics that are used to describe the structure of the landscape, and some of these could have potential for describing the structure of plant canopies. Of particular interest is lacunarity (Plotnick et al. 1993), which provides a method for determining the texture of patterns of spatial dispersion in 1, 2 and 3 dimensions. The method is based on a gliding-box algorithm (Allain and Cloitre 1991), which compares the proportion of empty and non-empty squares within a grid by sliding boxes of different sizes over the grid. By plotting the lacunarity for different box sizes, it is possible to provide information about the structure of the pattern on the grid.

In order to utilize lacunarity measures for characterization of canopy structure, it will be necessary to have volumetric data on the structure of the plants, where a voxel (a 3-D cubic spatial unit in 3-D grid space) is classed as occupied if it contains a part of the plant canopy, and empty if it does not. Using a gliding-cube algorithm (the three dimensional equivalent of the gliding-box algorithm), the lacunarity of the plant canopy can then be calculated.

Current research in this area is focussing on the conversion of simulated 'real' plant canopies from L-system representation to a voxel-based representation, to allow testing of canopies with the gliding-cube algorithm. It is hoped that the lacunarity measures will provide a powerful method for quantifying and comparing plant canopies so that the effect of canopy structure on the movement of predators and pests can be examined in much greater detail.

## FUTURE DIRECTIONS FOR CANOPY STRUCTURE RESEARCH

*Biological control – directed movement*

The simulation experiments on the movement of predator, locating prey in a canopy, have so far focussed on randomly searching predators. There is a wide body of evidence that suggests that predators are able to use chemical cues to locate patches of prey (see review by Vet and Dicke 1992). Therefore, there is a need to simulate the impact of these attractant volatile chemicals on the movement of the predators through the canopy. This can be done by allowing the predators to have directed-movement patterns rather than random-searching patterns.

The inclusion of directed movement is not without its problems, as a predator with no memory could easily end up stuck in a dead end and not be able to move away from it, since as far as it is concerned, it has to move into the dead end to move closer to its prey. Therefore, in simulating directed movement, it will be necessary to examine also the effect of memory. This opens up the possibilities of simulating predators with different memory lengths to determine whether there is an optimal memory length that will benefit the predators.

Another question that is linked with directed movement concerns the distance over which the prey patch can be detected. If the detection distance is larger than the size of the canopy, then the predator will always take the shortest path to the prey;

however, if its detection distance is short, then it may have to move randomly at first until it detects a prey, after which it will move in a directed manner.

At present, the model to allow directed movement is being developed, after which a suite of simulation experiments will be designed to examine the effects of detection distance, memory and the interactions between the two. This should provide much greater information about how predators move through canopies and lead to the development of robust and sustainable strategies for the biological control of crop pests. By understanding how predators move around within a canopy, and the way in which they spread out from release points to locate prey, it should be possible to use the models to develop canopy-specific biological-control strategies that provide rapid control of pests based on the movement patterns of the predators. This will lead to more efficient biological control, and enable biological control to become a more economic method for the control of pests in horticultural crops.

### *Biodiversity*

In the UK, there is increasing interest in the use of habitat manipulations in cropping systems to promote biodiversity in the landscape. However, there is currently little understanding of how different habitats affect biodiversity. Recent research has shown that canopy structure is as important in determining the biodiversity within a habitat as the presence of floral resources (Rebek et al. 2005).

Since there is currently no way of quantifying different plant canopies, it is difficult to determine how changing canopy structure might affect biodiversity within the canopy. The current research on developing a method for characterizing and quantifying canopy structure has potential importance in this area. If the differences between canopies can be quantified then it will be possible to relate the biodiversity of a canopy to the characteristics of that canopy, and to understand which attributes of the canopy (e.g., floral resources, structure, microclimate and light availability) are most important in affecting biodiversity.

Once the key attributes of canopy structure that influence biodiversity have been determined, it will then be possible to develop canopy structure to promote either specific levels of biodiversity or specific functional groups of organisms, such as aphid predators and parasitoids. This will enable the development of habitat manipulations for use in crops that will have the most benefit for pest control.

### SUMMARY AND CONCLUSIONS

Virtual plant models have been extremely useful in beginning to unravel the complex interactions between plant canopy structure and the movement of insects within the plant canopy. Research into the effects of plant canopies on the biological control of insects is still in its infancy, but it is already clear that the success of predators will depend on the connections between the plants and the internal structure of individual plants.

The research in this area is now beginning to mature and will focus on the development of more realistic models of the searching behaviour of insect predators, to determine the effect of factors such as memory and the use of chemical information to detect prey at a distance. This will help in understanding the key factors that determine the efficiency of different predators. It will enable the development of suitable strategies of introducing predators for biological control that take account of the searching behaviour of the predators being introduced.

There is a need to translate the research to real plant canopies, as opposed to the simple canopies simulated so far, if this research area is to have any benefit for crop production. This need will only be realized through the development of a reliable method for characterizing plant canopies and quantifying the differences between them. More research on potential methods is required, to determine the best possible method for comparing different plant canopies. If it proves possible to be able to compare the structure of canopies in a quantifiable way, then this opens up the possibility of understanding the complex interactions between habitat canopy structure and biodiversity, with the potential to develop specific canopy structures that provide the greatest benefit to both crop producers and biodiversity.

#### REFERENCES

- Allain, C. and Cloitre, M., 1991. Characterizing the lacunarity of random and deterministic fractal sets. *Physical Review A*, 44 (6), 3552-3558.
- Bernstein, C., 1983. Some aspects of *Phytoseiulus persimilis* (Acarina: Phytoseiidae) dispersal behaviour. *Entomophaga*, 28 (2), 185-198.
- Bernstein, C., 1984. Prey and predator emigration responses in the acarine system *Tetranychus urticae* - *Phytoseiulus persimilis*. *Oecologia*, 61 (1), 134-142.
- Hanan, J., 1997. Virtual plants: integrating architectural and physiological models. *Environmental Modelling & Software*, 12 (1), 35-42.
- Hanan, J.S. and Room, P.M., 1997. Practical aspects of virtual plant research. In: Michalewicz, M.T. ed. *Plants to ecosystems*. CSIRO, Collingwood, 28-44. Advances in Computational Life Sciences no. 1.
- Pels, B. and Sabelis, M.W., 1999. Local dynamics, overexploitation and predator dispersal in an acarine predator-prey system. *Oikos*, 86 (3), 573-583.
- Plotnick, R.E., Gardner, R.H. and O'Neill, R.V., 1993. Lacunarity indices as measures of landscape texture. *Landscape Ecology*, 8 (3), 201-211.
- Prusinkiewicz, P., Karwowski, R., Měch, R., et al., 2000. L-studio/cpfg: a software system for modeling plants. In: Nagl, M., Schürr, A. and Münch, M. eds. *Applications of graph transformations with industrial relevance: international workshop, AGTIVE'99 Kerkrade, The Netherlands, September 1-3, 1999: proceedings*. Springer, Berlin, 457-464. Lecture Notes in Computer Science no. 1779.
- Rebek, E.J., Sadof, C.S. and Hanks, L.M., 2005. Manipulating the abundance of natural enemies in ornamental landscapes with floral resource plants. *Biological Control*, 33 (2), 203-216.
- Rodrigue, J.P., Comtois, C. and Slack, B., 2006. *The geography of transport systems*. Routledge, Oxford.
- Room, P., Hanan, J.S. and Prusinkiewicz, P., 1996. Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. *Trends in Plant Science*, 1 (1), 33-38.
- Sabelis, M.W. and Van der Baan, H.E., 1983. Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomologia Experimentalis et Applicata*, 33 (3), 303-314.
- Sabelis, M.W. and Van der Weel, J.J., 1993. Anemotactic responses of the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, and their role in prey finding. *Experimental and Applied Acarology*, 17 (7), 521-529.
- Skirvin, D. and Fenlon, J., 2003. Of mites and movement: the effects of plant connectedness and temperature on movement of *Phytoseiulus persimilis*. *Biological Control*, 27 (3), 242-250.

- Skirvin, D.J., 2004. Virtual plant models of predatory mite movement in complex plant canopies. *Ecological Modelling*, 171 (3), 301-313.
- Skirvin, D.J., De Courcy Williams, M.E., Fenlon, J.S., et al., 2002. Modelling the effects of plant species on biocontrol effectiveness in ornamental nursery crops. *Journal of Applied Ecology*, 39 (3), 469-480.
- Stavrínides, M.C. and Skirvin, D.J., 2003. The effect of chrysanthemum leaf trichome density and prey spatial distribution on predation of *Tetranychus urticae* (Acari: Tetranychidae) by *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Bulletin of Entomological Research*, 93 (4), 343-350.
- Sütterlin, S. and Van Lenteren, J.C., 1997. Influence of hairiness of *Gerbera jamesonii* leaves on the searching efficiency of the parasitoid *Encarsia formosa*. *Biological Control*, 9 (3), 157-165.
- Van Haren, R.J.F., Steenhuis, M.M., Sabelis, M.W., et al., 1987. Tomato stem trichomes and dispersal success of *Phytoseiulus persimilis* relative to its prey *Tetranychus urticae*. *Experimental and Applied Acarology*, 3 (2), 115-121.
- Vet, L.E.M. and Dicke, M., 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology*, 37, 141-172.
- Zemek, R. and Nachman, G., 1998. Interactions in a tritrophic acarine predator-prey metapopulation system: effects of *Tetranychus urticae* on the dispersal rates of *Phytoseiulus persimilis* (Acarina: Tetranychidae, Phytoseiidae). *Experimental and Applied Acarology*, 22 (5), 259-278.
- Zemek, R. and Nachman, G., 1999. Interactions in a tritrophic acarine predator-prey metapopulation system: prey location and distance moved by *Phytoseiulus persimilis* (Acari: Phytoseiidae). *Experimental and Applied Acarology*, 23 (1), 21-40.