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Modeling the impact of plant structure on host-finding behavior of parasitoids

Received: 29 September 2000 / Accepted: 5 September 2001 / Published online: 26 October 2001
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Abstract For many parasitoid species, the final step of host location occurs on plants whose structure varies in time and space, altering the capacity of parasitoids to exploit hosts. Plant structure can be defined by its size, heterogeneity and connectivity. We tested the hypothesis that these three components and all possible interactions affect the level of parasitism of *Trichogramma evanescens* and that parasitism can be predicted if the structure of a plant is measured. We quantified and varied the structure of three-dimensional artificial plants to determine which component(s) of plant structure explain variability of parasitism and to develop a model that predicts parasitism by *Trichogramma* females. This model was validated with three natural tritrophic systems. The experiment with artificial plants revealed that plant structure affected host-finding success, which was higher on plants with a simple structure and low on plants with a complex structure. A response surface regression showed that the linear and quadratic terms of connectivity were highly significant, indicating that connectivity best explained the variability in the rate of parasitism obtained. The interaction between connectivity and heterogeneity was also significant. Observed values of parasitism from experiments with three natural tritrophic systems fit predicted values of parasitism generated by the model, indicating that parasitism can be predicted if heterogeneity and connectivity of a plant are known. Consequences of these results in regard to population dynamics, evolution and biological control are discussed.

Keywords Tritrophic interactions · Model · Cabbage · Broccoli · Brussels sprouts

Introduction

Parasitoids evolve in a multitrophic context (Hassell and Waage 1984; Vet and Dicke 1992) and forage at multiple scales (ecosystem, macro-habitat, micro-habitat, patch) but for many parasitoid species the final step of host location takes place on plants whose structure varies in time and space. The definition of plant structure has, until now, often been subjective and many terms have been used to describe this characteristic (Bell et al. 1991). Various models of plant structure have been proposed, some based essentially on structural and phenological characteristics and patterns of growth, but these remain highly descriptive (Ross 1981; Lawton 1983; Tomlinson 1987 and references therein; Cremers and Edelin 1995; Price et al. 1995). Others aimed to quantify structural components such as branch length and branch angles (Honda 1971; Leopold 1971; McMahon 1975; McMahon and Kronauer 1976; Bell et al. 1979; Honda et al. 1981, 1982; Honjo 1995). Fractal geometry has also been used to quantify the structure of habitats and plants (Williamson and Lawton 1991; Foroutan-pour et al. 1999).

Andow and Prokrym (1990) and Bell et al. (1991) recognized three components to plant structure: size (height or volume of a plant), heterogeneity (abundance and diversity of plant parts) and connectivity (abundance of connections between plant parts). These three components define to a large extent the potential searching area and could be the most relevant to foraging parasitoids. Previous studies on the effect of plant structure on foraging behavior of parasitoids and predators have focused on a single component. An increase in plant size was found to decrease significantly the percentage of parasitism of various host species by different species of *Trichogramma* parasitoids (Ables et al. 1980; Thorpe 1985). An increase in connectivity was found to reduce

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host-finding success of *Trichogramma* species (Andow and Prokrym 1990; Lukianchuk and Smith 1997; Romeis et al. 1998), aphidiid wasps (Mackauer and Völkl 1993), predatory wasps (Geitzbauer and Bernays 1996), and coccinellids (Grevstad and Klepetka 1992; Frazer and McGregor 1994).

Polyphagous species of predators and parasitoids often forage on a variety of plant structures used by their prey/hosts. For example, parasitoid species of the genus *Trichogramma* exploit eggs of several lepidopteran species on a large variety of plants, from herbs to large trees (Suverkropp 1997). In nature, size, heterogeneity and connectivity of plants vary and interact and therefore affect host-finding success of parasitoids.

The objectives of this study were (1) to determine the impact of plant structure, defined by different combinations of size, heterogeneity and connectivity, on host finding by *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae); (2) to identify the plant structural component(s) that best explain variability in parasitism; (3) to develop a model of parasitism by using artificial plants, and (4) to validate this model on natural tritrophic systems.

Materials and methods

Three-dimensional artificial plants, on which *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs were placed, were used to study the effect of plant structure on host-finding behavior by *T. evanescens*. The use of artificial plants eliminates the variability of chemical (e.g. volatiles) and physical factors (e.g. color, texture) found in natural plants. The artificial plants consisted of a main stem, two secondary stems, branches, leaves and buds (Fig. 1). The three stems were made of wire covered with green plastic. Branches were in flexible green plastic, whereas leaves were in silk and buds were plastic green push pins. All plant parts were inserted into each other and no glue was used. Size, heterogeneity and connectivity of artificial plants were varied and quantified.

Size (*S*) was defined by the height of the plant, and was quantified by measuring, in centimeters, the main stem. To vary the size, the main stem was cut at four different heights: $S_1=15$; $S_2=30$; $S_3=45$; $S_4=60$ cm. Heterogeneity (*H*) was defined by the relative abundance, per unit area, of structural components. To vary the heterogeneity, we used a constant number of 45 leaves for all plant structures but placed 2, 6, 12 or 45 buds along the main and secondary stems and on branches. Heterogeneity was calculated following the formula of the Shannon-Wiener's index of biodiversity (Barbour et al. 1987), which is, $(-\sum X_i / X_0) (\ln X_i / X_0)$. In that equation, X_i denoted the number of leaves and the number of buds, while X_0 corresponded to the sum of leaves and buds. Four values of heterogeneity were thus obtained: $H_1=0.1$; $H_2=0.3$; $H_3=0.5$; $H_4=0.7$. Connectivity (*C*) was defined by the absolute abundance, per unit area, of connections between plant parts. To vary the connectivity, plants were cut to obtain four values: $C_1=3$; $C_2=24$; $C_3=45$; $C_4=66$.

These variations of size, heterogeneity and connectivity gave 64 different plant structures (4 sizes \times 4 heterogeneities \times 4 connectivities) that were used as treatments. The simplest plant structure consisted of the main stem, 15 cm high, two secondary stems, 45 leaves, 2 buds and 3 connections between plant parts (Fig. 1A). The most complex plant structure consisted of the main stem, 60 cm high, two secondary stems, 45 leaves, 45 buds and 66 connections between plant parts (Fig. 1C). Because most of the surface of the plant consisted of leaves rather than stems or buds, the

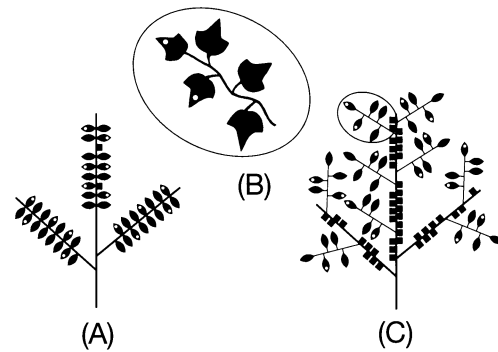


Fig. 1 A Representation of the most simple plant structure; height =15 cm, heterogeneity =0.1, connectivity =3; B a detailed view of one branch and leaves; C representation of the most complex plant structure height =60 cm, heterogeneity =0.9, connectivity =66. The white dots represent the host eggs and the squares represent buds

total surface area of plants varied less between treatments than the other factors. The minimum and maximum values of surface area were 412 and 552 cm². Thus, a simple plant structure had low values of size, heterogeneity and connectivity, and the reverse applied to a complex plant structure.

For all experiments we used female *T. evanescens* reared on cold-killed *E. kuehniella* eggs at 24 \pm 1°C, 50 \pm 5% relative humidity (r.h.) and 16L:8D. Females were less than 6 h old, mated, unfed and naive.

Sixteen cold-killed eggs of *E. kuehniella* were individually glued with mucilage Elmer's glue on the margin of 16 leaves per plant structure (Fig. 1). The same leaves were used for each replicate but they were washed with water between replicates. The main stem of artificial plants was then inserted in a circular wooden base of 18 cm in diameter and three *T. evanescens* females were introduced with a fine brush on one leaf located at the base of the plant. Plants were then covered individually with a closed plastic cylinder, 18 cm in diameter. In order to keep the volumes of the plant and cylinder relatively proportional between treatments, the heights of cylinders were the same as the enclosed plants. A constant humidity level of 40% r.h. was maintained inside the cylinder by using a piece of cotton soaked in saturated salt water. The experimental set-up was then placed in an incubator at 24°C (16L:8D). Parasitized *E. kuehniella* eggs turned black 6 days after parasitization under our experimental conditions and parasitized eggs were therefore counted on the 7th day in order to measure parasitism during the first 24 h of the experiment.

Experimental design and statistical analysis

The three factors (*S*, *H*, *C*) had four levels each, resulting in 64 treatment combinations (4S \times 4H \times 4C) that were replicated 12 times. Due to time and space constraints, only 32 treatment combinations could be tested simultaneously. The experimental set-up consisted in a hierarchical incomplete block design with mini-blocks nested within mega-blocks. The definition of these incomplete blocks satisfied the orthogonality condition (Mead 1988). A first randomization occurred among the three pairs of complete blocks or mega-blocks whereas the second randomization was carried out between the two halves of each complete block or mini-block. Thus, a mega-block was formed by all 64 treatment combinations, whereas a mini-block was formed by only 32 treatment combinations. Preliminary analyses showed that the mean rate of parasitism was statistically different between mini-blocks within a complete block. These differences were related to treatment effects, but there was no statistical difference between mega-blocks. Accordingly, we eliminated the mega-block and mini-block structure and grouped the data into complete blocks. The parasitism ob-

served in one block was much lower than in the other blocks probably because of lower quality hosts. This block was statistically different from the others and it was removed from the analysis in order to be able to use response surface regression. A response surface regression was performed on the mean percentage of parasitism calculated over those five complete blocks, after arcsine square root transformation (Sokal and Rohlf 1995). The stability and robustness of the regression model were assessed using a jackknife procedure (Efron and Tibshirani 1993) in which the percentage of parasitism of each block was predicted by fitting the model to the mean of the four other blocks (see Dutilleul et al. (2000) for a recent application in forest entomology). SAS software, version 6.12 (SAS 1997), was used for all statistical analysis.

To visualize how parasitism varied with heterogeneity and connectivity, we plotted one three-dimensional response surface of the percentage of parasitism against heterogeneity and connectivity. The minimum value of heterogeneity and connectivity was zero, whereas the maximum values were 0.9 and 72, respectively.

Model validation

The validation step compared predicted level of parasitism to values obtained from experiments using *T. evanescens* as parasitoid, eggs of *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae) as host and either cabbage, broccoli or Brussels sprouts as plant. Seeds of cabbage (*Brassica oleracea* L. var. *capitata*, cv. 'Green Bartolo'); broccoli (*Brassica oleracea* var. *italica*, cv. 'Green valiant'); and Brussels sprouts (*Brassica oleracea* var. *gemmifera*, cv. 'Hyb Jade E'), were started in individual cells then, after 6 days were transferred into a growth chamber where the temperature was constant at 25°C. After 12 days, plants were transplanted into 6 l pots and placed in a greenhouse until they reached 80 days old, calculated from the sowing date. The temperature within the greenhouse varied between 22°C and 35°C during the day and between 15°C and 24°C during the night for the duration of experiments. Female *T. evanescens* used in all experiments were reared on cold-killed *E. kuehniella* eggs at 24°C and at 16L:8D. Females were less than 6 h old, mated unfed and naive. *T. ni* was reared in the laboratory on artificial diet (Shelton et al. 1991) at 23±1°C, 65±5% r.h. and 16L:8D. Adults were maintained in cages. To collect eggs, we dipped a strip of polyethylene film into filtered cabbage juice and introduced it into a cage to let the adult females lay their eggs. The polyethylene film was cut into 6 mm² pieces and we made sure that each piece contained one freshly (<12 h) laid *T. ni* egg.

Size, heterogeneity and connectivity of cabbage, broccoli and Brussels sprouts plants of 30, 55 and 80 days old were quantified on 21 plants for each age × crucifer combination and mean values were computed (Table 1). Size was measured from the highest leaf down to ground level. Heterogeneity occurred only on older plants of broccoli and Brussels sprouts while only leaves were present on cabbage. Connectivity was quantified by counting the number of branching, mostly due to leaf stems, on each plant. Values of heterogeneity and connectivity were then incorporated to the equation of the response surface regression model of parasitism to obtain predicted parasitism values for the three plant varieties and the three ages.

Observed values of parasitism for simple (30 day old), intermediate (55 day old) and complex (80 day old) cabbage, broccoli and Brussels sprouts were obtained experimentally. On each plant, a piece of polyethylene film, containing one *T. ni* egg was glued on each side of eight different leaves for a total of 16 eggs per plant. On simple plants, two or three eggs per leaf were glued because they possessed fewer than eight leaves. The eggs were all located within 1 cm of the leaf margin. Plants were then placed in a cage (85×85×100 cm) covered with white muslin located within a greenhouse where the temperature varied between 22°C and 35°C during the day and between 15°C and 24°C during the night. Twenty-five *T. evanescens* females were introduced on a leaf located at the base of the plant. This number was established following preliminary experiments to obtain a measurable level of para-

Table 1 Mean values (±SD) for each component of plant structure and for each plant variety and age. Heterogeneity is expressed as the Shannon-Wiener's index of biodiversity and varied from 0 to 1. Connectivity corresponded to the absolute abundance of connections between plant parts and varied between 1 and 72. *n*=21

Plant age/plant variety	Size (cm)	Heterogeneity	Connectivity
Age=30 days after sowing date			
Cabbage	21.7±1.7	0.0±0.0	6.2±0.7
Broccoli	20.2±2.1	0.0±0.0	4.2±0.6
Brussels sprouts	21.9±2.1	0.0±0.0	8.0±1.0
Age=55 days after sowing date			
Cabbage	35.4±4.8	0.0±0.0	12.5±1.1
Broccoli	41.0±4.3	0.0±0.0	10.5±0.7
Brussels sprouts	40.9±1.8	0.0±0.0	18.6±1.8
Age=80 days after sowing date			
Cabbage	36.3±2.3	0.0±0.0	21.0±1.2
Broccoli	50.5±9.4	0.1±0.1	17.4±1.8
Brussels sprouts	48.5±6.6	0.7±0.05	35.3±7.1

Table 2 Overall analysis of the response surface regression of parasitism of *T. ni* eggs by *T. evanescens* for the experiment with artificial plants

Regression	df	F-ratio	Prob>F
Linear	3	23.99	0.0001
Quadratic	3	5.36	0.0026
Cross-product	3	2.64	0.0589

sitism under the prevailing experimental conditions. The plants were left into the cage for 24 h, after which the 16 eggs of *T. ni* were removed from the plant and incubated. The proportion of parasitized eggs was determined by counting, 7 days later, the number of eggs that turned black. This experiment was replicated 20 times.

A linear regression of predicted versus observed parasitism served to evaluate the performance of the model. Statistical tests using regression procedure were done to determine if there was equality of slopes and if slopes were significantly different from 1. SAS software, version 6.12 (SAS 1997), was used for all statistical analysis.

Results

Parasitism on artificial plants

The response surface regression model had significant linear and quadratic effects and non-significant weaker cross-product effects (Table 2). A more detailed analysis, term by term, revealed that only the linear and quadratic terms of the connectivity component were highly significant, whereas the cross-product of connectivity and heterogeneity was also significant (Table 3). Therefore, the component of plant structure that best explained the variability in the rate of parasitism was connectivity. The equation of the statistical model for the response surface regression is then: Parasitism=1.115 (0.1032)–0.01273 (0.0021) C+0.00454 (0.0022) C×H+8.60×10⁻⁵ (2.22×10⁻⁵) C². Errors of the estimate are in parentheses.

Table 3 Response surface regression analysis of parasitism of *T. ni* eggs by *T. evanescens* for the experiment with artificial plants

Parameter	df	t-value	Prob>t
Size (S)	1	-1.084	0.2832
Heterogeneity (H)	1	-0.058	0.9539
Connectivity (C)	1	-6.132	0.0001
S×S	1	-0.001	0.9992
H×S	1	1.197	0.2364
H×H	1	-1.086	0.2822
C×S	1	1.473	0.1465
C×H	1	2.075	0.0428
C×C	1	3.861	0.0003

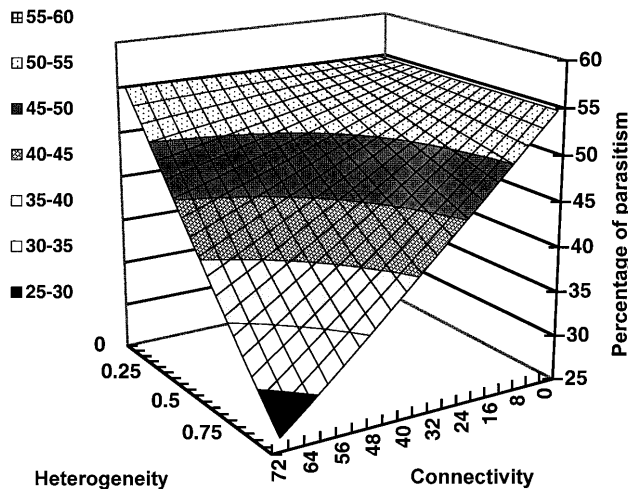


Fig. 2 Response surface of the percentage parasitism of *E. kuhniella* eggs by *T. evanescens* females on artificial plants as a function of heterogeneity and connectivity of these plants. Heterogeneity is expressed as the Shannon-Wiener's index of biodiversity while connectivity corresponded to the absolute abundance of connections between plant parts

An inverse relationship of parasitism as a function of the linear and quadratic terms of connectivity appeared when we plotted parasitism as a function of heterogeneity and connectivity (Fig. 2), and parasitism tended to decrease with increasing values of heterogeneity and connectivity indicating that female parasitoids were more efficient at finding host eggs when foraging on simple plant structure. The values of parasitism were between the interval of 20% and 60%. At low levels of heterogeneity, connectivity had little influence on parasitism but as heterogeneity increased, parasitism declined as connectivity increased (Fig. 2).

The parameters that were significant in the response surface model were stable in the jackknife procedure. These parameters were the coefficients of the linear and quadratic terms of connectivity and, to a lesser degree, the coefficient of the bilinear term of connectivity and heterogeneity. The connectivity linear coefficient ranged from -0.0141 to -0.0118 with a probability of significance of 0.001 for all values, while the quadratic connectivity coefficient ranged from 0.000075 to 0.000100 with

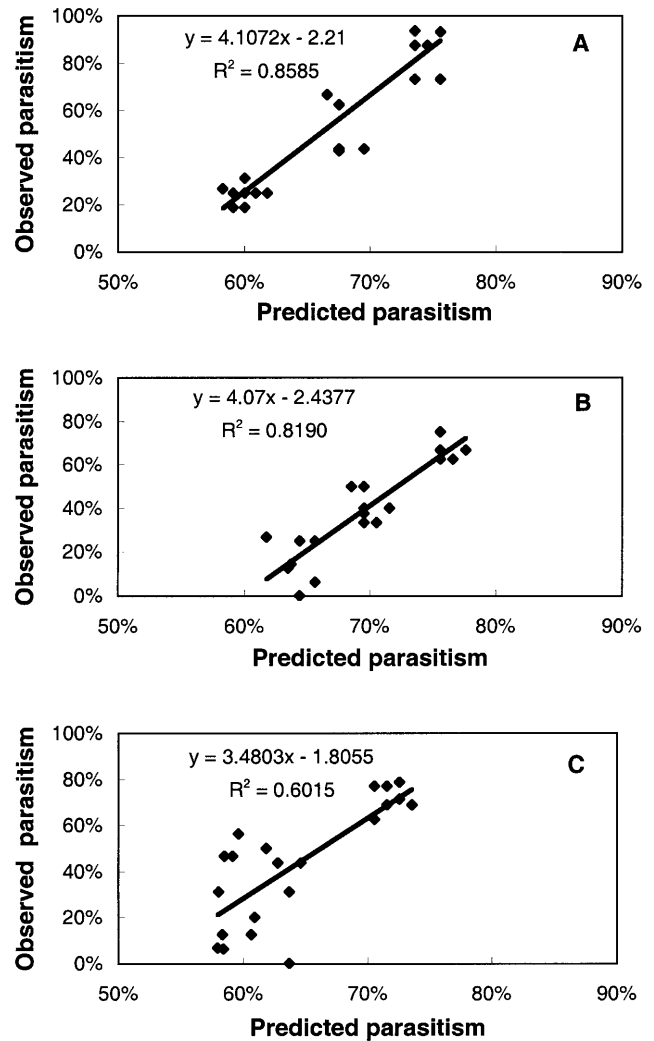


Fig. 3 Observed values of parasitism of *T. ni* eggs by *T. evanescens* against predicted values provided by the response surface model from an experiment with **A** cabbage plants of 30, 55 and 80 days of age, **B** broccoli plants of 30, 55 and 80 days of age, and **C** Brussels sprouts plants of 30, 55 and 80 days of age

a probability of significance below 0.005 in all cases. The bilinear coefficient of connectivity and heterogeneity ranged from 0.0035 to 0.0059, with a probability of significance of 0.011–0.195. Some of the parameters that were not significant in the original response surface model with all five complete blocks changed sign while others sometimes drastically changed in magnitude, but never became significant in the jackknife procedure, with one exception (i.e., linear effect of size when block 5 was removed). On that basis, we considered that our response surface regression model was stable in the frame of our experiment.

Validation of the model

All three regressions of observed versus predicted percentage of parasitism were significant, which gives a

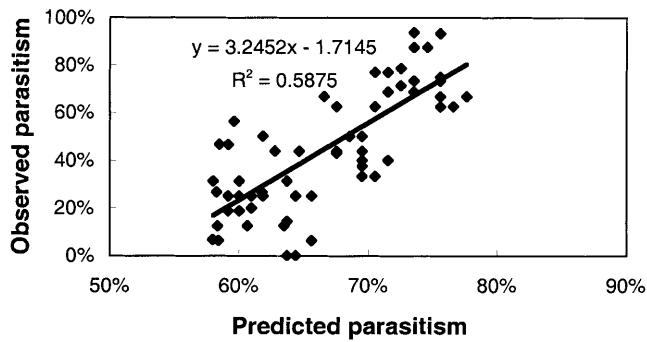


Fig. 4 Observed values of parasitism of *T. ni* eggs by *T. evanescens* against predicted values provided by the response surface model from an experiment with cabbage, broccoli and Brussels sprouts grouped. The solid line represents the simple linear regression of the observed values of parasitism on the expected values

predictive power to the expected values generated by the model ($df=1$, $F=80.75$, $P=0.0001$ for cabbage; $df=1$, $F=121.47$, $P=0.0001$ for broccoli; $df=1$, $F=30.53$, $P=0.0001$ for Brussels sprouts) (Fig. 3 A–C). Slope values varied between 3.4 and 4.1 and all were significantly different from 1 ($df=1$, $t=5.73$, $P=0.0001$ for cabbage; $df=1$, $t=6.12$, $P=0.0001$ for broccoli; $df=1$, $t=2.89$, $P=0.01$ for Brussels sprouts). A test for slopes equality revealed that the three slopes' values were not significantly different from each other ($df=2$, $F=1.24$, $P=0.2976$), which permitted merging of the data from the three plant varieties (Fig. 4) and led to a more general model. The regression presented in Fig. 4 was significant ($df=1$, $F=98.57$, $P=0.0001$). The high R^2 values of all regression models indicate that most of the variability is explained by the model. Observed percentage of parasitism of *T. ni* eggs increased with increasing values of expected parasitism and the observed values of parasitism corresponded well to the expected ones over the 40–80 range (Fig. 3 A–C and Fig. 4).

Discussion

Size, heterogeneity and connectivity define to a large extent the habitats of herbivorous insects and the potential searching area of parasitoids. It was initially thought that all three components may be relevant to foraging *Trichogramma* parasitoids and this is why we varied all three components in our artificial plants. With respect to the scientific objective of determining the plant component that best explained the variability of parasitism, only one of the three main factors and two of the six interactive factors came out significant.

As shown by the results of the response surface regression, connectivity of artificial plants best explained the variability observed in parasitism. The important effect of that component of plant structure may be attributable to the fact that *Trichogramma* searches for hosts on plants mostly by walking (Bigler et al. 1988) and indeed when *T. evanescens* females were observed on similar ar-

tificial plants, flying was noted only when the female left the plant never for within plant movements (Gingras 2001). Chemical stimuli play a major role in the detection of habitat and host plant in *Trichogramma* species (Nordlund 1994) but host location on the host plant is mostly done by walking (Schmidt 1994). Plant connectivity could be less important for parasitoids that search by flying or use chemical cues to directly land near their host.

The absence of significant effect of size and heterogeneity under our experimental conditions does not mean that such effects do not exist or are not important to foraging *Trichogramma* parasitoids. An increase in plant size has been found to decrease host discovery in various *Trichogramma* species (Ables et al. 1980; Thorpe 1985; Wang et al. 1997). Differences in plant configurations may explain the results obtained with these studies that used natural plants and natural hosts and our results where we used artificial plants and cold-killed hosts, which emitted no or few chemical cues. Chemical characteristics of plants and hosts modify searching behavior of parasitoids by increasing searching time or by retaining them in a limited area or patch (Lewis et al. 1975). Because no or few cues were emitted from the artificial system, arrestment effects did not occur and females may have explored most of the plant. Also, the last-cited studies used *T. pretiosum* (Ables et al. 1980), *T. minutum* (Thorpe 1985), and *T. ostrinae* (Wang et al. 1997), while we used *T. evanescens* and, as observed by Thorpe (1985), some *Trichogramma* species are less influenced by plant size than others.

In our experiment with artificial plants, heterogeneity was created by using different numbers of green push pins, simulating buds, over a constant number of 45 leaves. Host-finding success may not be affected by the relative number of plant parts. It could rather be influenced by texture of plant parts (waxy, hairy, smooth leaf surface; plant topography) as revealed by previous studies (Evans 1976; Carter et al. 1984; Juniper and Southwood 1986; Obrycki 1986; Kareiva and Sahakian 1990; Van Lenteren et al. 1995; Sütterlin and van Lenteren 1997).

Plant structure will affect the frequency of host encounters and therefore oviposition success. In a study on the proximate mechanisms of parasitoid foraging decisions, Waage (1979) proposed that responsiveness increases with successive encounters with hosts and decreases in the absence of encounters. Based on our results, responsiveness of parasitoids may reach more frequently the lower level of responsiveness when parasitoids forage on complex plant structure and therefore we could expect lower patch residence time on complex plants.

Because instantaneous host-finding rate of parasitoids is reduced on complex plants, selection pressure for host or prey to occupy these regions preferentially must be strong, and this appears to be true (Askew 1980; Hawkins and Lawton 1987). Availability of hosts to parasitoid is then affected, which in turn has an impact on

population dynamics (Price et al. 1980, 1991). Furthermore, more microhabitats are available within complex plants, which permit greater niche diversification and consequently provide a greater measure of enemy free space (Berdegue et al. 1996). A decrease in host-finding success with an increase in complexity of plant structure may tend to stabilize parasitoid/host interactions (Smith 1972; Crowley 1978) and allow coexistence of both parasitoids and hosts.

Our validation of the model indicated that connectivity, which had significant effect on artificial plants, can predict, at least qualitatively, the effect of plant structure on host finding by *Trichogramma*. By measuring the characteristics of plant structures on three different varieties of crucifer, we were able to obtain a highly significant relationship between predicted and observed values, indicating that our model has a predictive value over a range of plant types. The experimental conditions of the development and the validation of the model differed but the objective of the model was not to predict a precise level of parasitism, which can vary according to the host plant and the host insect, but rather to predict the impact of changes in plant structure on host-finding success of *Trichogramma*.

Results from the experiment with natural plants confirm that we can be confident of our approach in defining and quantifying plant structure. Also, the assumption that size, heterogeneity and connectivity are relevant to foraging female *Trichogramma* appears to be partially right. Modeling the impact of plant structure on host-finding success was achieved, suggesting that we captured the essential biological phenomenon associated with host searching by *Trichogramma* parasitoid on a plant. Because the predictions of the impact of changes in plant structure on host finding hold for three tritrophic systems and under different experimental conditions, the model can thus be trusted. We have then good reasons to believe that such predictions may hold in the field. The model can find application in biological control programs by being a tool helping to plan the number of parasitoids to be released based on quantification of plant structure. Reliable predictions of natural enemy release rates before the onset of a biological control program can provide practitioners with an estimate of the economic feasibility of the releases.

Moreover, the broadly comparable structure of very different plant types and the quantitative approach to plant structure used here for studying parasitoids' responses to plant structure appear to provide a promising avenue for comparative research on plant-herbivore-parasitoid interactions. The challenge remains to collect relevant data on other parasitoid and plant species to test the consistency of the model developed here. Also, future studies should test how the model responds to variation of host density and under semi-field or field conditions where other factors influence host searching.

Acknowledgements We are grateful to Services Bio-Control for their financial support to the project. Our thanks also go to Danielle Thibodeau, Josiane Vaillancourt and Stéphane Dulude for insect rearing and laboratory works, and to François Fournier and

Daniel Cormier for their useful advice on protocols and data analysis. This is contribution 335/2001.10.26 of the Horticultural Research and Development Centre, Agriculture and Agri-Food Canada, Saint-Jean-sur-Richelieu, Québec, Canada.

References

- Ables JRD, McCommas WJ, Jones SL, Morrison RK (1980) Effect of cotton plant size, host egg location, and location of parasite release on parasitism by *Trichogramma pretiosum*. *Southwest Entomol* 5:261–264
- Andow DA, Prokrym DR (1990) Plant structural complexity and host-finding by a parasitoid. *Oecologia* 82:162–165
- Askew RR (1980) The diversity of insect communities in leaf-mines and plant galls. *J Anim Ecol* 49:817–829
- Barbour MG, Burk JH, Pitts WD (1987) *Terrestrial plant ecology*, 2nd edn. Benjamin/Cummings, Don Mills, Ontario
- Bell AD, Roberts D, Smith A (1979) Branching patterns: the simulation of plant architecture. *J Theor Biol* 81:351–375
- Bell SS, McCoy ED, Mushinsky HR (1991) *Habitat structure, the physical arrangement of objects in space*. Chapman & Hall, New York
- Berdegue M, Trumble JT, Hare JD, Redak RA (1996) Is it enemy-free space? The evidence for terrestrial insects and freshwater arthropods. *Ecol Entomol* 21:203–217
- Bigler F, Bieri M, Fritschy A, Seidel K (1988) Variation in locomotion between laboratory strains of *Trichogramma maidis* and its impact on parasitism of *Ostrinia nubilalis* in the field. *Entomol Exp Appl* 49:283–290
- Carter MC, Sutherland D, Dixon AFG (1984) Plant structure and searching efficiency of coccinellid larvae. *Oecologia* 63:394–397
- Cremer G, Edelin C (1995) Etude de l'architecture aérienne de quelques plantes tropicales à ramification basitone: vers une révision du modèle de Tomlinson. *Can J Bot* 73:1490–1503
- Crowley PH (1978) Effective size and the persistence of ecosystems. *Oecologia* 35:185–195
- Dutilleul P, Nef L, Frigon D (2000) Assessment of site characteristics as predictors of the vulnerability of Norway spruce (*Picea abies* Karst.) stands to attack by *Ips typographus* L. (Col. Scolytidae). *J Appl Entomol* 124:1–5
- Efron B, Tibshirani RJ (1993) *An introduction to the bootstrap*. Chapman & Hall, New York
- Evans HF (1976) The searching behaviour of *Anthocoris confusus* (Reuter) in relation to prey density and plant surface topography. *Ecol Entomol* 1:163–169
- Foroutan-pour K, Dutilleul P, Smith DL (1999) Soybean canopy development as affected by population density and intercropping with corn: fractal analysis in comparison with other quantitative approaches. *Crop Sci* 39:1784–1791
- Frazer BD, McGregor RR (1994) Searching behaviour of adult female coccinellidae (Coleoptera) on stem and leaf models. *Can Entomol* 126:389–399
- Geitznauer HL, Bernays EA (1996) Plant effects on prey choice by a vespid wasp, *Polistes arizonensis*. *Ecol Entomol* 21:227–234
- Gingras D (2001) Effect of plant structure on host searching behavior of the egg parasitoid *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) on artificial and natural plants. PhD thesis, Dept. Natural Resource Sciences, McGill University, Canada
- Grevstad FS, Klepetka BW (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* 92:399–404
- Hassell MP, Waage JK (1984) Host-parasitoid population interactions. *Annu Rev Entomol* 29:89–114
- Hawkins BA, Lawton JH (1987) Species richness for parasitoids of British phytophagous insects. *Nature* 326:788–790
- Honda H (1971) Description of the form of trees by the parameters of the tree-like body: effects of the branching angle and the branch length on the shape of the tree-like body. *J Theor Biol* 31:331–338

- Honda H, Tomlinson PB, Fisher JB (1981) Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. *Am J Bot* 68:580–585
- Honda H, Tomlinson PB, Fisher JB (1982) Two geometrical models of branching of botanical trees. *Ann Bot* 49:1–11
- Honjo T (1995) Measurement and modeling of architecture of horticultural plants. *Acta Hort* 399:233–238
- Juniper BE, Southwood TRR (eds) (1986) *Insects and plant surfaces*. Arnold, London
- Kareiva P, Sahakian R (1990) Tritrophic effects of simple architectural mutation in pea plants. *Nature* 345:433–434
- Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. *Annu Rev Entomol* 28:23–39
- Leopold LB (1971) Trees and streams: the efficiency of branching patterns. *J Theor Biol* 31:339–354
- Lewis WJ, Jones RL, Nordlund DA, Gross HRJ (1975) Kairomones and their use for management of entomophagous insects: II Mechanisms causing increase in rate of parasitization by *Trichogramma* spp. *J Chem Ecol* 1:349–360
- Lukianchuk JL, Smith SM (1997) Influence of plant structural complexity on the foraging success of *Trichogramma minutum*: a comparison of search on artificial and foliage models. *Entomol Exp Appl* 84:221–228
- Mackauer M, Völkl W (1993) Regulation of aphid populations by aphidiid wasps: does parasitoid foraging behaviour or hyperparasitism limit impact? *Oecologia* 94:339–350
- McMahon TA (1975) The mechanical design of trees. *Sci Am* 233:92–102
- McMahon TA, Kronauer RE (1976) Tree structure: deducing the principle of mechanical design. *J Theor Biol* 59:443–446
- Mead R (1988) *The design of experiments, statistical principles for practical application*. Cambridge University Press, Cambridge
- Nordlund DA (1994) Habitat location by *Trichogramma*. In: Wajnberg E, Hassan SA (eds) *Biological control with egg parasitoids*. CAB International, Wallingford, UK, pp 155–163
- Obrycki JJ (1986) The influence of foliar pubescence on entomophagous species. In: Boethel DJ, Eikenbary RD (eds) *Interactions of plant resistance and parasitoids and predators of insects*. Ellis Horwood, Chichester, pp 63–83
- Price PW (1991) Evolutionary theory of host and parasitoid interactions. *Biol Control* 1:83–93
- Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Syst* 11:41–65
- Price PW, Andrade I, Pires C, Sujii E, Vieira EM (1995) Gradient analysis using plant modular structure: pattern in plant architecture and insect herbivore utilization. *Environ Entomol* 24:497–505
- Romeis J, Shanower TG, Zebitz CPW (1998) Physical and chemical plant characters inhibiting the searching behaviour of *Trichogramma chilonis*. *Entomol Exp Appl* 87: 275–284
- Ross J (1981) *The radiation regime and the architecture of plant stands*. Junk, The Hague
- SAS (1997) *SAS / STAT user's guide, version 6.12, 4th edn*. SAS Institute, Cary, N.C.
- Schmidt JM (1994) Host recognition and acceptance by *Trichogramma*. In: Wajnberg E, Hassan SA (eds) *Biological control with egg parasitoids*. CAB International, Wallingford, UK, pp 165–200
- Shelton AM, Cooley RJ, Kroening MK, Wilsey WT, Eigenbrode SD (1991) Comparative analysis of two rearing procedures for diamondback moth (Lepidoptera: Plutellidae). *J Entomol Sci* 26:17–26
- Smith FE (1972) Spatial heterogeneity, stability and diversity in ecosystems. *Trans Conn Acad Arts Sci* 44:309–335
- Sokal RR, Rohlf F J (1995) *Biometry, 3rd edn*. Freeman, New York
- Sütterlin S, van Lenteren JC (1997) Influence of hairiness of *Gerbera jamesonii* leaves on the searching efficiency of the parasitoid *Encarsia formosa*. *Biol Control* 9:157–165
- Suverkropp BP (1997) *Host-finding behavior of Trichogramma brassicae in maize*. Ph D Thesis, Dept of Entomology, Wageningen Agricultural University, The Netherlands
- Thorpe KW (1985) Effects of height and habitat type on egg parasitism by *Trichogramma minutum* and *T. pretiosum* (Hymenoptera: Trichogrammatidae). *Agric Ecosyst Environ* 12:117–126
- Tomlinson PB (1987) Architecture of tropical plants. *Annu Rev Ecol Syst* 18:1–21
- Van Lenteren JC, Li ZH, Kamerman JW, Xu R (1995) The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). XXVI. Leaf hairs reduce the capacity of *Encarsia formosa* to control greenhouse whitefly on cucumber. *J Appl Entomol* 119:553–559
- Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annu Rev Entomol* 37:141–172
- Waage JK (1979) Foraging for patchily-distributed hosts by the parasitoid *Nemeritis canescens*. *J Anim Ecol* 48:353–371
- Wang B, Ferro DN, Hosmer DW (1997) Importance of plant size, distribution of egg masses, and weather conditions on egg parasitism of the European corn borer, *Ostrinia nubilalis* by *Trichogramma ostriniae* in sweet corn. *Entomol Exp Appl* 83:337–345
- Williamson MH, Lawton JH (1991) Fractal geometry of ecological habitats. In: Bell SS, McCoy ED, Mushinsky HR (eds) *Habitat structure, the physical arrangement of objects in space*. Chapman & Hall, New York, pp325–348