Plant Morphological Complexity Impacts Foraging Efficiency of Adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae)

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ABSTRACT   Plant morphological complexity could provide a physical refuge to prey and/or could interfere with foraging activities of a natural enemy. Few studies have rigorously tested the hypothesis that plant structural complexity influences the behavior of natural enemies and thus predator-prey interactions. Thus, we tested the hypotheses that increased plant morphological complexity reduces the predation efficacy and new area search efficiency of *Coccinella septempunctata* L. as a predator of the pea aphid *Acyrthosiphon pisum* Harris. Essential to testing these hypotheses is the use of near-isogenic lines of the pea plant. The *Normal*, *tl*, and *aftl* near-isogenic lines used in experiments manifest distinct levels of morphological complexity ranging from low to high complexity. Further, the use of these genetic isolines allowed us to control, as much as possible, for non-morphological plant characters such as phytochemicals and surface waxes. Increased plant morphological complexity decreased the predator's efficacy with most aphids surviving on the *aftl* plant. Observations on the predator foraging activity suggest that complexity in the form of increased leaf edge to leaf area ratio and increased number of junctions reduced the new area search efficiency of the predator. This study supports the notion that plant complexity can interfere with the foraging success of insect predators.

KEY WORDS   *Acyrthosiphon pisum*, foraging, leaf morphology, *Pisum sativum*, tritrophic interactions

THE OBJECTIVE OF EARLY research on plant structural complexity was to explain patterns of species diversity and abundance (Moran 1980, Lawton 1983, Strong et al. 1984). For instance, Lawton (1983) reviewed data that showed significant correlations between architectural complexity (architecture broadly defined to include a variety of plant attributes such as size and growth form, seasonal development, persistence, and variety of above ground parts) and the species richness of herbivores on the host plant. Species richness declined as the plant architectural complexity decreased. Trees were ranked as the most architecturally complex, followed by bushes and then herbs. Two hypotheses were offered to explain such pattern. One dealt with the absolute size of plants and the other focused on the plant resources made available to herbivores as a consequence of complexity. The resource diversity hypothesis suggested that resources such as a diversity of feeding sites, oviposition and overwintering sites, and escape space are provided with increasing architectural complexity. Lawton (1983) theorized that the architectural complexity of plants afforded a higher degree of 'escape space' to herbivores because the more complex plants provided more refugia to prey. Here we present evidence that plant complexity allows the escape of prey by precluding the predator from an efficient search.

A variety of plant physical characteristics, from trichomes to plant architecture, have been implicated in altering movement, effectiveness, and survival of both insect predators and parasitoids (Pimentel 1961, Evans 1976, Price et al. 1980, Shah 1982, Carter et al. 1984, Treacy et al. 1985, Obrycki 1986, Kareiva and Sahakian 1990, van Lenteren and de Ponti 1990, Stadler and Völk 1991, Grevstad and Klepetka 1992, Hare 1992, Weisser 1995, Walter and O'Dowd 1992, Clark and Messina 1998, Cloyd and Sadof 2000, Roda et al. 2000). For instance, Kareiva and Sahakian (1990) demonstrated the influence of plant morphology on two coccinellid species. *Coccinella septempunctata* L. and *Hippodamia variegata* Goeaze significantly fell more often from normal peas than from leafless peas (leafless peas have tendrils instead of leaflets) with reduced stipules. As a result, coccinellid suppression of aphid cohorts was reduced on the normal leaf/normal stipule plants. As with other plant physical characteristics, the effects of plant morphological complexity are difficult to isolate experimentally from other co-occurring, confounding factors such as plant chemistry. However, Andow and Prokym (1990) managed to study the effects of complexity by manipulating the structure of paper surfaces while holding surface area constant. Their study showed that the parasitoid *Trichogramma nubilale* Ertle & Davis at-
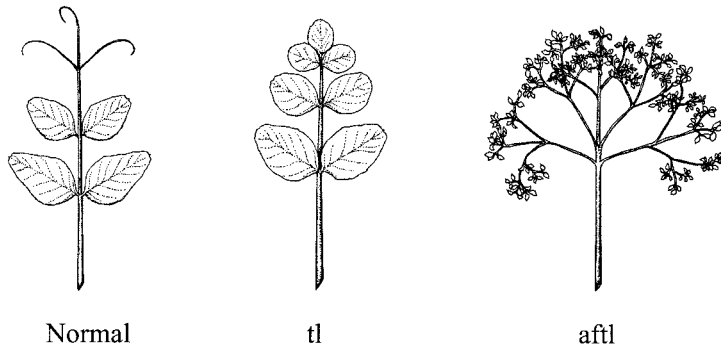
Fig. 1. Leaves of the *Normal*, *tl* and *aftl* near-isogenic pea lines (*Pisum sativum* L.). The *Normal* leaf type is comprised of the rachis, two pairs of leaflets and terminal tendrils. The *tl* leaf mutant is comprised of a rachis and only leaflets. The *aftl* leaf mutant is comprised of a highly branched rachis and tiny leaflets.

tacked 0.94 more egg masses on the simple than on the complex surfaces. Similarly, Lukianchuk and Smith (1997) found a reduction in the number of host eggs parasitized by *Trichogramma minutum* Riley when the parasitoid searched complex surfaces. Tests were done with real leaves and leaf paper models of trembling aspen (*Populus tremuloides* Michx.) and balsam fir (*Abies balsamea* L.). In the test with the real foliage, more egg clusters were found parasitized on the aspen leaves than on the balsam fir needles. There was also a reduction of search success when parasitoids were on real leaves versus the paper models suggesting that *T. minutum* responded to the presence of plant leaf chemicals (Lukianchuk and Smith 1997).

Although the influence of plant structural complexity on parasitoid-host interactions has been studied (Andow and Prokym 1990, Lukianchuk and Smith 1997), no studies have specifically quantified host plant complexity and investigated its effect on insect predator foraging behavior and efficiency. Thus, the objectives of this study were to determine what is the effect of increased plant morphological complexity on predator foraging and to devise a complexity measurement that could be used to predict any such effect. We tested the hypothesis that plant morphological complexity interferes with the foraging activities of *Coccinella septempunctata* as a predator of the pea aphid *Acyrthosiphon pisum* Harris. First, we tested the effect of morphological complexity on the predation efficacy of the beetle. Second, we tested the hypothesis that increased plant morphological complexity reduces the new area search efficiency of the predator. In addition, we asked whether or not the presence of prey interacts with plant complexity to alter the predator's search patterns. Essential to testing these hypotheses was the use of garden pea near-isogenic lines differing only in leaf morphology. The morphological variation in these lines was ranked from low to high complexity. Further, the use of these genetic isolines allowed for the control, as much as possible, of non-morphological plant characters such as phytochemicals and surface waxes which can influence predator movement (Kareiva and Sahakian 1990, Eigenbrode et al. 1998). The near-isogenic lines used

in this study exhibit the leaf mutant genes *af* and *tl*, as well as the reduced stipule *st* gene. These mutant genes alter the normal pea leaf and stipule considerably but are highly specific in their action and do not show a wide range of pleiotropic effects (Wehner and Gritton 1981, Murfet and Reid 1993). Moreover, the near-isogenic lines used did not have any effects on the fecundity, intrinsic rate of increase or within-plant settling location of the pea aphid (Legrand and Barbosa 2000).

Materials and Methods

General Methods. The garden pea (*Pisum sativum* L.) near-isogenic lines selected exhibit *Normal* leaf (AfAfTlTl), *tl* or acacia leaf (AfAftltl), *aftl* or parsley leaf (afaftltl) and *st* or reduced stipule (stst). The genetic background for all of the selected lines is the 'New Line Early Perfection' cultivar. These pea lines display morphological complexity that can be ranked from low to high when comparing leaf structure. *Normal* was the baseline for comparisons and was classified as a simple leaf, *tl* was the intermediate, and *aftl* was the most complex leaf (Fig. 1). In this study, we based the complexity ranking on plant attributes that could influence predator search activity. First, Andow and Prokym (1990) and Lukianchuk and Smith (1997) showed that disruption in the continuity of surfaces was detrimental for parasitoid search success. Thus, in our classification we considered the ratio of leaf edge to leaf area to indicate how much the surface area is partitioned or disrupted. For example, the edge to area ratio of a sample of *Normal* leaves is 0.77, 0.90 for *tl* leaves and 5.32 for *aftl* leaves. Second, surface area is considered because it can impact predator search effort and it naturally varied among the leaf types. Finally, an increase in the number of junctions gives a labyrinthine quality to the leaves and this could lead to an overlap of predator search paths. Whole plant measurements of features used in the complexity are presented in Table 1. Edge for the plants was calculated by measuring the perimeter of leaves and the lengths of stems, rachises and tendrils. The number of junctions were counted as places where an intersec-

Table 1. Classification of plants and characteristics used in the definition of plant morphological complexity

Characteristic[a]	*Normal*	*tl*	*aftl*
Morphological complexity	low	intermediate	high
Leaf area	low: 137.8 cm^2	medium: 194.7 cm^2	high: 807.7 cm^2
Edge	low: 587.9 cm	medium: 714.9 cm	high: 5,019.5 cm
Junctions	same as *tl*: 43	same as *Normal*: 45	higher than *tl* or *Normal*: 72

[a] Numbers under each classification represent measurements of entire plants of similar size as used in experiments.

tion of plant structures occurs and the predator needs to choose a direction. Surface area measurements were made using a CI-202 portable leaf area meter (Cid, Inc., Vancouver, WA). Five readings were taken for each leaf part measured and then averaged. In the *aftl* plant, leaflets are too small to be easily measured and instead the leaflets were classified into four size classes: large, medium, small, and tiny. The area and perimeter of a sample of leaflets in each size category was measured. Ten surface area readings were taken when measuring leaflets in each size category. The area and edge of experimental *aftl* plants were measured by counting the number of leaflets in each size category and calculating the total based on the sample area and edge averages.

Laboratory colonies of the pea aphid were established using apterous adults collected from pea fields planted in Upper Marlboro, MD, and in Storrs, CT. Periodic collections of aphids from the field were incorporated into laboratory colonies. Aphids were kept on the Wando (Southern States, MD) pea cultivar (normal foliage) and maintained in Plexiglas cages at 21 ± 2°C, 16 h light: 8 h dark cycle, and ambient humidity. The predator *C. septempunctata* was introduced from Europe to North America for the biological control of aphids. It is commonly associated with aphid communities of herbaceous plants (Hodek and Honěk 1996). This coccinellid does not show an olfactory response to the prey odor (Nakamuta 1985) and the aphid alarm pheromone (*E*)-β-farnesene does not evoke its intensive search behavior (Nakamuta 1991). Adults and beetle larvae can visually detect prey at a very short distance (on average ≈1 cm for adults) (Stubbs 1980). Recent work has shown that walking *C. septempunctata* adults are attracted to (*E*)-β-farnesene (Al Abassi et al. 2000) and to volatiles from aphid-infested barley plants (Ninkovic et al. 2001). *C. septempunctata* colonies were established using adults collected in Upper Marlboro, MD, Newark, DE, and from Storrs, CT. Larvae were reared individually in 30 ml plastic cups and both larvae and adults were fed pea aphids. Adults were kept in cages at 21 ± 2°C, 16 h light: 8 h dark cycle, and ambient humidity. Aphid and beetle voucher specimens (#UCMS-V2000.1) were placed in the Research Collection of the Connecticut State Museum of Natural History, University of Connecticut, Storrs.

Effect of Plant Morphological Complexity on Predator Efficacy. To test the hypothesis that plant morphological complexity reduces coccinellid efficacy the coccinellid consumption of fourth instar aphids on the *Normal, tl*, and *aftl* pea lines (all of which have re-

duced stipules) was measured. Efficacy describes the capacity to search the plant and is reflected in the maximum number of aphids consumed. Fourth instar nymphs were used as prey to prevent the occurrence of extra aphid nymphs that would be produced by adults. By the end of the experiment the surviving aphids had become adults but most had not yet started to reproduce. The experiment was conducted as four blocks in time and a total of 30 beetles were tested on the *Normal* plants and 31 were tested under each of the *tl* and *aftl* plant treatments. Plants were grown in 15-cm diameter pots using Fafard's 3B potting mix (Agawam, MA) and were used only once for each beetle. When they had nine leaves, plants were placed individually within cylindrical cages made of transparent polycarbonate sheets (60 cm tall, 30 cm in diameter) and white organza mesh covers. On each plant type one aphid was placed on the upper most leaf and four aphids on each of the next lower six leaves for a total of 25 aphids per plant. No aphids were placed on the stem. Cages were randomly placed on a laboratory bench and kept under 21 ± 2°C, ambient humidity and natural light.

All coccinellids were starved before the experiment for 24 h but had been fed ad libitum on pea aphids before the starvation period. One adult coccinellid was introduced into each cage and placed on the stem at the base of the plant. Coccinellids were removed 48 h after the start of the experiment and for each plant type the number and location of surviving aphids recorded; i.e., as being on the bud, stipule, stem, leaf or off the plant. Data were tested to determine if assumptions of normality and homogeneity of variances were met. The numbers of aphids consumed by the beetles on each of the plant types were analyzed with analysis of variance (ANOVA) using PROC MIXED (SAS Institute 1999). Plant treatment and blocks were treated as fixed effects in the model. Least-square means were obtained and they were compared using Tukey's multiple comparison procedure.

An aphid palatability test was conducted to confirm that predation efficacy results from the aforementioned experiment were indeed attributable to plant morphology and not to any differences in aphid palatability because of the plant type serving as food for the aphids. Beetles were individually placed in 30-ml cups and were starved for four hours. Then each was given 20 adult aphids reared on either *Normal* or *aftl* plants both with reduced stipules. The same individual was observed for 3 d at 21 ± 2°C, 16 h light: 8 h dark cycle, and ambient humidity. After each 24-h period the surviving aphids were counted and a new set of 20

aphids was given to the beetles. Ten beetles were tested for each plant type. Data were tested to determine if assumptions of normality and homogeneity of variances were met. A repeated measures model was used in PROC MIXED (SAS Institute 1999) to test the effect of source plant and time on the aphid consumption by the beetles.

Effects of Leaf Morphological Complexity on Predator New Area Search Efficiency. The new area search efficiency of predators on the different plant types was tested both in the presence and absence of prey. In this study, search efficiency is defined as the ability to search plant area with a minimum expenditure of time. Hassell (1978) and Andow and Prokym (1990) defined search efficiency in terms of prey captures per unit time. The definition used here is based on area covered per unit time. This measurement indicates the extent of new area searched by the predator both in the absence or presence of prey. Observations were conducted at the leaf scale for 15 min or until the beetles left the leaf, fell, or flew away. All observations of the coccinellids were made when the predator was on uncaged plants at $20 \pm 2°C$ and ambient humidity. Plants were grown in 15-cm diameter pots using 300-S growing media (Pro-Gro Products Inc., Elizabeth City, NC). Behavioral budgets and observations of the location of the beetles were made using a computer event recorder. The event recorder employed the Observer (V.3) software (Noldus Information Technology 1995).

In experiments involving observations of coccinellids in the presence of prey, five apterous aphid adults were placed on a leaf at a similar location on each of the three isolines. Before introducing the predator, aphids were allowed to settle for 5–15 min until they began feeding. Coccinellids were starved for 24 h before experimentation. Observations were scheduled so that combinations of plant type and aphid presence were all represented during an observation session and at different times of the day. To compare the effects of aphid presence, the same adult coccinellid was tested in the presence and in the absence of prey to minimize the effect of individual differences. After the first test, the coccinellid was fed three adult aphids (or the difference if they had capture any aphids during the test) and was allowed to rest without food until the next test, 24 h later. The order of prey presence or absence was alternated for each new beetle to eliminate order effects. Observations were made of coccinellids on only two leaves per plant (between nodes eight and 10) and each leaf was used once for each beetle under a given pea isoline/aphid presence combination. Twenty-four coccinellids were tested on each pea isoline to give a total of 72 observations.

The behaviors recorded for the coccinellids were: searching (walking on the plant surface while maxillary palps contacted the plant surface), resting (standing still but not as in night time rest), grooming (cleaning legs and mouthparts, extension of wings), eating, and scraping (rubbing of mouthparts on the plant surface at one particular location and sometimes punc-

turing plant). Other events recorded were falling from or flying off the plant. Foraging time constituted the time when coccinellids were observed searching as described above. The number of aphids captured and the number of aphids that dropped from the leaves were recorded. The location of the coccinellid on leaf parts was recorded using a numbering system that identified individual leaf parts or segments. Leaf parts coded for the *Normal* and *tl* plants were rachis, leaflets, and tendrils. Whether or not a coccinellid searched a particular leaf part completely could be determined by noting if it passed through additional numerically coded points on leaf parts. In the *aftl* plants, leaflets are reduced and are grouped at the end of rachioles. Thus, rachioles were coded and the smallest groupings of leaflets were coded as single units. Once a beetle entered these small units it was assumed to search all of the leaflet area.

The coccinellid new area search efficiency was calculated using the location records for each beetle. The individual new area search efficiency was calculated first by multiplying the number of times a beetle entered a leaf part not previously searched by the mean area of those parts and then dividing by the time spent searching that leaf. The leaf parts used in this analysis were only the leaflets because pea aphids are mostly found there (Legrand and Barbosa 2000).

The proportion of time that the coccinellids spent in the different behaviors should have been analyzed simultaneously using multivariate ANOVA. However, the coccinellids spent most or all of their time searching, and the other behaviors (resting, grooming, etc.) were infrequently observed. This created a problem of excess zero observations and a compositional analysis of the data was, therefore, not possible. The frequency of falls from and of flying off the leaves by the beetles was analyzed using Fisher's Exact Test (SAS Institute 1990). Data on the number of aphids captured and that dropped were analyzed with the Kruskal–Wallis one way ANOVA by ranks using PROC NPAR1WAY (SAS Institute 1990). Coccinellid foraging times and data on area search efficiency were analyzed with ANOVA using PROC MIXED (SAS Institute 1999) with plant type and aphid presence as the treatments. To meet assumptions of normality and homogeneity of variances data were log-transformed after adding a constant of one. For the statistical model, individual beetles were treated as a random effect, while plant type, presence of aphids and order of aphid treatment presentation were defined as fixed effects. This model took into account that each beetle had been tested twice on leaves with and without aphids. Least-square means were obtained and they were compared using Tukey's multiple comparison procedure.

Lastly, a small test was carried out to determine which plant feature was mostly responsible for the observed foraging time results because *aftl* leaves increase in complexity in terms of area, edge and junctions. Thus, *aftl* leaf surface area was manipulated so as to make it comparable to that of the *Normal* leaves. Leaflets were removed to reduce area but the number of junctions were kept the same as in original exper-
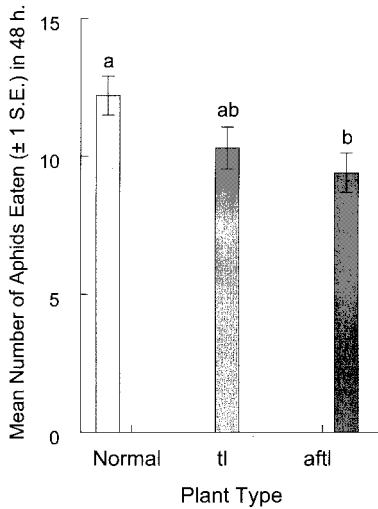
Fig. 2. Number of fourth instar pea aphid nymphs consumed by *C. septempunctata* adults when on plants with increasing morphological complexity. *Normal* plants are defined as simple, *tl* are intermediate, and *aftl* as complex. *P*-values for multiple mean comparisons were adjusted with the Tukey's procedure. Means with a different letter are significantly different at the $\alpha = 0.05$ level.

iments. The foraging time of 15 beetles and 23 beetles was measured on *Normal* leaves and manipulated *aftl* leaves, respectively. Observations were carried out as described above and aphid prey were not present. Data were log-transformed and analyzed using a *t*-test.

Results

Effect of Plant Morphological Complexity on Predator Efficacy. Increases in plant morphological complexity as defined in this study had a significant effect on the predator efficacy. The beetles consumed significantly fewer aphids on the more complex plants as compared with *Normal* plants ($F = 4.12$; df = 2,77; $P = 0.02$) (Fig. 2). Beetles exhibited an intermediate level of aphid consumption while on *tl* plants (intermediate in complexity). However, the efficacy observed on *tl* plants was not significantly different from that observed either on *Normal* or *aftl* plants. The majority of the surviving aphids were found on the leaves (77% for the *Normal*, 83% for *tl* and 84% for *aftl*). Moreover, there were no significant differences in predator consumption of aphids reared on either the *Normal* or *aftl* plants ($F = 0.08$; df = 1,47; $P = 0.78$). Time had a significant effect on the aphid consumption observed for both plant types ($F = 3.64$; df = 2,47; $P = 0.03$). A significant decrease in consumption was observed during the second day likely as a result of beetles becoming satiated from the first meal. Consumption increased again in the third day. The mean number of aphids consumed was 14.6 ± 1.08 and 14.9 ± 1.08 for *aftl* and *Normal* plant sources, respectively.

Effects of Leaf Morphological Complexity on Predator New Area Search Efficiency. Plant morphological complexity had a significant effect on the foraging time of the coccinellid ($F = 11.83$; df = 2,68; $P < 0.0001$) (Fig. 3). Coccinellids on the more complex leaf, *aftl*, had the longest foraging time which was significantly different from the foraging time exhibited on *Normal* leaves ($P = 0.0037$) and from that on *tl* leaves ($P < 0.0001$). The latter two were not significantly different from each other. Aphid presence did not have a significant impact ($F = 2.2$; df = 1,68; $P = 0.1427$) and there was no significant interaction effect between plant morphological complexity and the presence of aphid prey ($F = 0.97$; df = 2,68; $P = 0.3851$). Also, the order of aphid presence treatment to which individual beetles were exposed did not have an effect ($F = 0.95$; df = 1,68; $P = 0.3337$).

Time spent by the coccinellids in other behaviors, other than foraging, made up only a small fraction of the total time spent on the leaves (Table 2). On the leaves with aphids, few of the available prey were
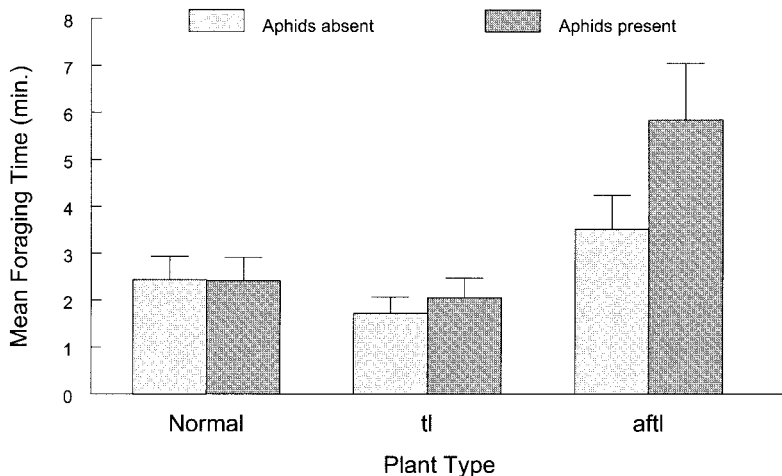

Fig. 3. Influence of plant morphological complexity and aphid prey presence on the foraging time of *C. septempunctata* adults. *Normal* plants are defined as simple, *tl* are intermediate, and *aftl* as complex.

Table 2. Percent of the total residence time spent on various behaviors by *C. septempunctata* when on single leaves of three morphological isolines of the garden pea (Mean ± 1 SE)

Plant & Aphid Treatment	Searching	Eating	Grooming	Resting	Scraping
Normal[a]	92 ± 3	n.a[b]	5 ± 3	0.7 ± 0.7	2.4 ± 2
tl	94 ± 3	n.a.	3 ± 2	2.7 ± 2	0.2 ± 0.2
aftl	89 ± 5	n.a.	9 ± 4	0.9 ± 0.7	0.8 ± 0.8
Normal & aphids	83 ± 6	10 ± 5	4 ± 2	0.8 ± 0.8	1.4 ± 1.4
tl & aphids	83 ± 6	8.4 ± 4	6 ± 3	2.2 ± 2	0
aftl & aphids	90 ± 4	4.5 ± 3	2.5 ± 1	0.6 ± 0.6	1.8 ± 1

Residence time refers to total time spent on plant and does not necessarily equal the 15 min observation period.

[a] *Normal, tl* and *aftl* represent the low, intermediate and most complex leaves, respectively.

[b] n.a. = not applicable.

captured and therefore time spent eating was not extensive. Some coccinellids were observed consuming small amounts of leaf material. This plant material had no aphids and was not contaminated with aphid honeydew, which is known to arrest larval coccinellids (Carter and Dixon 1984). To our knowledge this unusual behavior by *C. septempunctata* of scraping plant surfaces has not been previously reported. Puncturing to imbibe plant sap has been reported as a form of drinking to make up for water loss (Hodek and Honěk 1996).

In addition to effects on foraging time, plant morphological complexity had a significant effect on the new area search efficiency of the coccinellids ($F = 32.22$; df = 2,53; $P < 0.0001$) (Fig. 4). The search efficiency of the coccinellids on the *aftl* leaves was significantly reduced as compared with that obtained from the *Normal* ($P < 0.0001$) or from the *tl* leaves ($P < 0.0001$). The latter two were not significantly different from each other. Neither the presence of aphid prey ($F = 1.21$; df = 1,53; $P = 0.2756$), nor the order of aphid treatment ($F = 1.41$; df = 1,53; $P = 0.2401$) had a significant effect on the new area search efficiency. In addition, there was no significant interaction between plant type and aphid presence ($F = 0.96$; df = 2,53; $P = 0.3878$).

During the 15-min observations, the frequency of adult beetles falling and flying off a leaf was rare. Out of 24 observations for each of the *Normal, tl,* and *aftl* leaves without aphids the number of beetles falling was 4, 6 and 2, respectively, and there was no significant association with leaf morphological complexity ($P = 0.36$). For the leaves with aphids the number of falls was 3, 2, and 4, respectively, and again there was no significant association with leaf morphological complexity ($P = 0.9$). Moreover, plant type did not have a significant effect on the number of aphids that were consumed by predators ($\chi^2 = 2.89$, df = 2, $P = 0.2350$) and on the number of aphids that dropped from the leaves ($\chi^2 = 3.08$, df = 2, $P = 0.2144$). The average number of aphids captured on the *Normal, tl,* and *aftl* plants were 0.2916 ± 0.11, 0.083 ± 0.05, and 0.125 ± 0.06, respectively. Similarly, the average number of aphids that dropped from the *Normal, tl,* and *aftl* plants were 0.916 ± 0.179, 1.16 ± 0.19, 1.375 ± 0.19, respectively.

The test designed to compare *Normal* and *aftl* leaves with similar surface area showed that the time spent foraging is still significantly higher when the beetles are on the manipulated *aftl* leaves than when they are on the *Normal* leaves ($t = 5.06$, df = 36, $P < 0.001$). The mean foraging time of the beetles was 3.2 and 0.92 min (2.28 ± 0.06 and 1.74 ± 0.08 in log units) while they are on the *aftl* and *Normal* leaves, respectively.

Discussion

Coccinellid beetles are important components of the natural enemy complex of aphids in both natural and managed systems (Hodek and Honěk 1996, Hagen et al. 1999). The results presented here support the hypothesis that these predators are negatively influ-
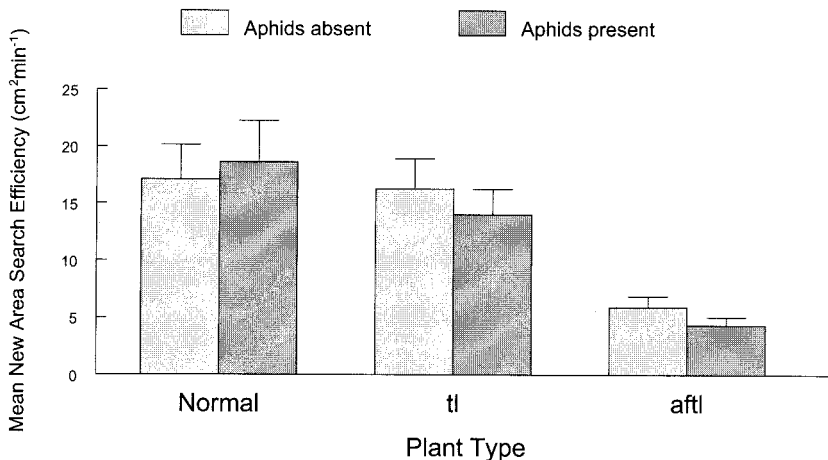

Fig. 4. Influence of plant morphological complexity and aphid prey presence on the area search efficiency of *C. septempunctata* adults. *Normal* plants are defined as simple, *tl* are intermediate, and *aftl* as complex.

enced by increased plant morphological complexity. Although no differences were detected between the intermediate plant and the two extremes, it is clear that changes from the *Normal* to the *aftl* morphology hamper the efficacy of the predator. The aphid palatability test confirmed that the observed efficacy reduction could not be attributed to changes in aphid acceptability by the predator. Beetles exhibited large variability in responses when data on individual consumption are examined and this variability may prevent further detection of differences between the intermediate plant and the two extremes. The observed decrease in predator efficacy in the most complex plants could result in larger aphid populations developing on those plants than on simple ones.

Differences in leaf morphology had an impact on the predator's efficacy (Fig. 2). What can we infer about the role of structural complexity? To help understand why and what aspect of plant morphology altered the predator's efficacy, we need to examine the observations at the leaf scale. One may ask if efficacy results are primarily because of the increased surface area presented by the plants as they are ranked from low to high in complexity. If one compares the two extreme plants, *Normal* and *aftl*, we see that foraging time was greatest when the beetles were on the most complex *aftl* plant (Fig. 3). One could argue that beetles spent so much time searching on *aftl* leaves simply because of the larger surface area available to search. However, leaf observations support an alternate explanation. Coccinellids spent a considerable amount of time searching a small portion of the little leaflets within the most complex *aftl* leaf. The concentration of movements within a portion of the complex leaf kept the beetles from advancing to other parts of the leaf before abandoning it. This overlap of search paths in the same sector resulted in poor new area search efficiency. Indeed, the new area search efficiency results were lowest on the *aftl* leaves (Fig. 4). While *Normal* and *tl* differ in surface area, they have a similar structure as contrasted to the *aftl* leaves. The foraging time and new area search efficiency results from these leaf types are similar and both differ from results obtained with *aftl* leaves. Thus, if surface area was the main factor behind our results, we would expect the three leaf types to produce similar search efficiencies. This suggests that the beetle's search is influenced by the increased complexity mainly in the form of increased partitioning of the surface area and the increase in number of junctions as observed in the *aftl* leaf. The results from tests using manipulated *aftl* leaves support this conclusion. Even though the manipulated *aftl* leaves had similar surface area to that of *Normal* leaves, the beetles still exhibited a significantly greater foraging time than when they were on the simpler *Normal* leaves.

As discussed earlier, new area search efficiency was selected as the parameter to be tested because it allowed the comparison of the three types of plants with and without aphids and allowed for a clear demonstration of the direct effect of plant morphology on *C. septempunctata*. The presence of aphid prey did not interact with the effect of plant morphology on the foraging time and search efficiency of the predator. The presence of prey could have elicited a different mode of search by the beetles. In fact, aphids are more accessible to the predator when found on the more complex *aftl* leaf as compared with the *Normal* leaf. On the *Normal* leaves, some aphids may escape the predator by feeding in the center of the leaf. This type of refuge is not available on the *aftl* plants.

Structural complexity has been shown to influence other insect natural enemies such as the parasitoids *T. nubilale* (Andow and Prokym 1990) and *T. minutum* (Lukianchuk and Smith 1997). In both of these studies, complexity of surfaces was manipulated by cutting the surface and adding more edge and by creating folds. Thus, it appears that *Trichogramma* parasitoids and *C. septempunctata* respond similarly to increased complexity in the form of more edges and junctions. In contrast to the coccinellid, *T. nubilale* females spent more time on simple surfaces than on the complex ones in the absence of hosts (Andow and Prokym 1990). It would appear that the parasitoid's reduction in efficacy may be a result of a low giving up threshold as opposed to the observed coccinellid behaviors. In this work we have shown that plant complexity influences predator efficacy and we have also presented a plausible mechanism behind that reduction. Further testing will be needed to determine the long-term effect of plant complexity on predator-prey dynamics coupled with the fact that coccinellids are only one component of the natural enemy complex of aphids.

Acknowledgments

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