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**Plant architecture and prey distribution influence foraging behavior of the
predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae)**

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Running head: Plant architecture and prey distribution affect predator foraging behavior

24 **Abstract** The arrangement, number, and size of plant parts may influence predator
25 foraging behavior, either directly, by altering the rate or pattern of predator movement,
26 or, indirectly, by affecting the distribution and abundance of prey. We report on the
27 effects of both plant architecture and prey distribution on foraging by the predatory mite,
28 *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), on cucumber (*Cucumis*
29 *sativus* L.). Plants differed in leaf number (2- or 6-leafed), and there were associated
30 differences in leaf size, plant height, and relative proportions of plant parts; but all had
31 the same total surface area. The prey, the twospotted spider mite *Tetranychus urticae*
32 Koch (Acari: Tetranychidae), were distributed either on the basal leaf or on all leaves.
33 The effect of plant architecture on predator foraging behavior varied depending on prey
34 distribution. The dimensions of individual plant parts affected time allocated to moving
35 and feeding, but they did not appear to influence the frequency with which predators
36 moved among different plant parts. Overall, *P. persimilis* moved less, and fed upon prey
37 longer, on 6-leafed plants with prey on all leaves than on plants representing other
38 treatment combinations. Our findings suggest that both plant architecture and pattern of
39 prey distribution should be considered, along with other factors such as herbivore-
40 induced plant volatiles, in augmentative biological control programs.

41

42 **Keywords** Plant architecture; prey distribution; predator foraging behavior; *Tetranychus*
43 *urticae*; *Phytoseiulus persimilis*; biological control

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50 **Introduction**

51 Foraging efficiency in predators and parasitoids is determined by multiple behaviors

52 associated with finding and handling prey or hosts (Vinson 1984; O'Brien et al. 1990).

53 Environmental factors, including the host plant, have an important effect on how natural

54 enemies forage. Host plant effects are mediated by both phytochemical cues and physical

55 structures (Price et al. 1980; Boethel and Eikenbary 1986; Cortesero et al. 2000).

56 Phytochemicals may be released in response to infestation, thus serving as cues for

57 natural enemies while searching for hosts/prey. For example, in phytoseiid mites foraging

58 behavior is modified by herbivore-induced plant volatiles, both in and out of prey patches

59 (Dicke and Sabelis 1988; Dicke 1994; Maeda and Takabayashi 2001). Whether or not

60 plant chemical cues are present, physical structures associated with the plant, broadly

61 described as plant architecture, are known to play a significant role in local foraging

62 behavior (e.g., Thorpe 1985; Kareiva and Sahakian 1990; Grevstad and Klepetka 1992;

63 Clark and Messina 1998a,b; Legrand and Barbosa 2003). Many definitions of plant

64 architecture have been offered (e.g., Andow and Prokrym 1990), but the one we prefer is

65 the spatial arrangement and dimensions of leaves, stems, and branches at a point in time

66 (Cloyd and Sadof 2000). Plant architectural characteristics may influence the direction

67 and rate of natural enemy search, thus affecting searching time and encounter rate with

68 prey or hosts (Legrand and Barbosa 2003; Cloyd and Sadof 2000).

69 We have been studying the foraging behavior of the predatory mite *Phytoseiulus*
70 *persimilis* Athias-Henriot (Acari: Phytoseiidae) on cucumber plants (*Cucumis sativus* L.)
71 to understand variation in biological control efficiency (Gontijo et al. 2010). *P.*
72 *persimilis* is a small (< 0.5 mm long) non-flying predator often used for biological control
73 of the twospotted spider mite (*Tetranychus urticae* Koch, Acari: Tetranychidae) in
74 greenhouses (Gould and Light 1971; Hamlen 1978). Because this predator is so small
75 and must move along a surface to reach its prey, we expected that differences in plant
76 architecture would have a measurable impact on its foraging behavior. Besides plant
77 architecture, prey distribution may affect the foraging success of *P. persimilis* (Zhang et
78 al. 1992; Zhang and Sanderson 1993; Ryoo 1996; Stavriniades and Skirvin 2003). In
79 previous work (Gontijo et al. 2010), we measured prey finding time, consumption, and
80 oviposition rates of *P. persimilis* foraging on either six-leafed or two-leafed cucumber
81 plants on which spider mites were distributed in two patterns: on the basal leaf only or on
82 all leaves. We observed that, while prey distribution affected predator foraging success,
83 under similar prey distributions more predators found prey patches, they found them
84 faster, and they consumed more and laid more eggs on six-leafed plants than on two-
85 leafed plants. In this study we examined specific movement patterns of *P. persimilis* to
86 better understand differences observed in its foraging efficiency.

87 Our focus was to investigate the effects of plant architecture in conjunction with
88 prey distribution on movement patterns of *P. persimilis* on cucumber plants (*Cucumis*
89 *sativus* L.). We were particularly interested in the potential effects these factors would
90 have on initial prey-finding because, once prey are found on a plant, a predator generally
91 will intensify local searching and therefore be more likely to find prey on other plant

92 parts. Our specific objectives were to: 1) quantify the effects of plant architecture on
93 duration and pattern of movement, resting, and feeding by *P. persimilis* on and among
94 plant parts; 2) measure these same variables under different prey distributions; and 3)
95 investigate the possible interaction between plant architecture and prey distribution. We
96 specifically designed our experiment to maintain an equal total plant surface area in order
97 to focus on the impact of plant architectural features, including the sizes and proportions
98 of stems and leaves.
99

100 **Materials and Methods**

101

102 Constructing Plant Architectures

103

104 Seeds of the cucumber cultivar ‘Cumlaude’ were obtained from Hydrogarden Company,

105 Inc. (Colorado Springs, CO) and sown individually into 6.25-cm² pots containing

106 FAFARD[®] Super-Fine Germinating Mix (Conrad Fafard, Inc., Agawam, Massachusetts,

107 USA). Prior to transplanting, seedlings were watered daily and a 20-10-20 fertilizer

108 (Scotts Peters Professional General Purpose 20-10-20, Scotts Company, Marysville,

109 Ohio, USA) was applied three times a week through the irrigation system by dissolving

110 1,048 g of 20-10-20 solid fertilizer into a 75.7 l container of water, which was delivered

111 through a Hozon siphon mixer at a ratio of 1:16 (fertilizer solution:tap water).

112 Thereafter, plants were fertilized whenever watering was required. To avoid competition

113 for light, seedlings were spaced (stem center to stem center) 30 cm apart on a greenhouse

114 bench when the first true leaf was completely expanded. Depending on treatment (see

115 below), seedlings were transplanted at different times and into different sized pots.

116 To create experimental plants with different architectures, we manipulated pot

117 size and transplant date. Specifically, plants assigned to the 2-leafed treatments were

118 transplanted as seedlings into 15.2-cm diam pots when they had four true leaves fully

119 expanded. Plants assigned to the 6-leafed treatments were transplanted as seedlings into

120 10.1-cm diam pots when they had six true leaves fully expanded. The plants transplanted

121 into larger pots at an early stage became taller with larger leaves than those transplanted

122 into smaller pots later in their growth. We removed leaves (petiole and leaf blade) from

123 the taller, larger-leafed plants so that only 2 leaves remained. New growth was removed
124 from the apex of 6-leafed plants to ensure that all plants were subject to pruning; all
125 pruning was done approximately 4 days after final transplant of the 6-leafed plants.

126 We equalized total plant surface area for the two plant treatments. To attain
127 approximately the same total plant surface area but two different architectures, we
128 estimated areas for different plant parts. For the leaves (leaf blades excluding petioles),
129 we established a mathematical relationship between leaf surface area and mid-rib length
130 by scanning leaves for a range of leaf sizes and then generating a regression equation, $y =$
131 $1.091x^2 - 5.817x + 19.477$ ($R^2 = 0.99$, $P < 0.0001$). The leaves were scanned using an HP
132 Scanjet 4850[®] scanner (Hewlett-Packard Company, Palo Alto, California, USA), and the
133 images were converted to surface areas with Scion Image[®] software (Scion Corporation,
134 Frederick, Maryland, USA). Based on this relationship, we created a one-way table in
135 which entering any leaf mid-rib length value would provide an estimate of leaf surface
136 area. Leaf surface areas were multiplied by a factor of two because estimated values
137 were for one side of the leaf only. To measure the surface area of stems and petioles, we
138 constructed a two-way table based on the formula of a cylinder $2*\pi*r*h$ ($\pi = 3.14$, $r =$
139 radius of the cylinder, $h =$ height of the cylinder). By substituting length and diameter
140 measurements for petioles and stems into the formula, we could estimate surface areas for
141 those plant parts. To measure total plant surface area, we summed the surface areas of all
142 plant parts. Differences in surface areas for total plant and plant parts between 2-leaf and
143 6-leaf plants, after alteration, were determined using t-tests (SAS Institute, Cary, North
144 Carolina, USA).

145

146 Experimental Protocols

147

148 *Tetranychus urticae* were obtained from colonies maintained at Kansas State University,
149 Manhattan, Kansas, USA. They were reared on young lima bean plants (*Phaseolus*
150 *lunatus* L.) in 0.3 x 0.6 m plastic flats under a 16:8 L:D photoperiod, and at $25 \pm 2^\circ\text{C}$ and
151 $60 \pm 10\%$ R.H. New lima bean plants were provided every other day. For the
152 experiments, spider mites were distributed on either a single basal leaf or on all leaves for
153 each of the two cucumber plant architectures described above. Leaves designated for
154 spider mites were infested by attaching a bean leaf square containing 10 adult female *T.*
155 *urticae* for 24 h to the lower leaf surface. This resulted in a mixture of adult spider mites,
156 webbing and eggs on infested leaves at the time of predator release. However, in the
157 experiment, only *T. urticae* eggs – which are preferred by *P. persimilis* -- were
158 consumed.

159 *Phytoseiulus persimilis* were purchased from Koppert, Inc. (Romulus, Michigan,
160 USA), and maintained on lima bean plants infested with *T. urticae*. Predators were fed
161 new spider mites by adding infested lima bean plants every other day. The predator
162 population was maintained under the same environmental conditions as described for *T.*
163 *urticae*. Voucher specimens of *P. persimilis* and *T. urticae* have been deposited in the
164 Kansas State University Museum of Entomological and Prairie Arthropod Research
165 under Lot Number 200.

166 The experiment was conducted in a laboratory at Kansas State University. All
167 treatments pertaining to plant architecture and prey distribution were repeated (see
168 below). To begin each test, we placed an adult female predator 24 to 72 h from

169 emergence, which had been deprived of prey for 2 h, at the base of the stem using a fine-
170 haired paint brush. The test age chosen represents a period of peak vigor and
171 reproductive activity for *P. persimilis*. After release, predators were observed
172 continuously for 20 min. This period was selected because preliminary observations
173 indicated that predators moved onto all plant parts at least once during this period.
174 Predators that were released but failed to move during the first five min were removed
175 and replaced. An individual plant was used to test only one predator. During the
176 observation period, the frequency and duration of resting, moving, and feeding, as well as
177 changes in direction and the specific plant location (stem, petiole and leaf) where
178 behaviors occurred, were recorded. Resting was defined as the time that the predator
179 remained stationary; moving represented the time spent walking, regardless of direction;
180 and feeding was defined as the time spent eating (partially or totally) prey eggs.

181

182 Statistical Analyses

183

184 Treatments were blocked through time and 2-3 replicates of each treatment were run per
185 day for a total of 11 replicates at the end of the four-day experiment. The experimental
186 design was a 2 x 2 factorial with two plant architectures (2-leafed and 6-leafed) and two
187 prey distributions (basal leaf only or all leaves). Predator behavioral data were organized
188 for analysis into the following categories: 1) time spent moving and resting on the stem
189 before moving onto a petiole, and moving and resting on the petiole before moving onto a
190 leaf; 2) total time spent moving, resting and feeding on either plant stems, petioles or
191 leaves; 3) total time spent moving and resting on the entire plant; 4) percentage of time

192 spent resting, moving and feeding on either stems, petioles or leaves; 5) percentage of
193 predators that were able to find the first petiole, infested leaf and prey patch; and 6)
194 sequence and probability of predators moving from one plant part to another. To test
195 whether the presence of prey influenced predator behavior, either before or after reaching
196 an infested leaf, we combined behavioral data for leaves within and among plants based
197 on whether or not the leaves were infested with spider mites. The effects of plant
198 architecture, prey distribution, and their interaction were tested using Friedman's
199 ANOVA (SAS Institute 2002) when comparing predator time allocation among different
200 behavioral variables and different plant parts; and ANOVA PROC GLM (SAS Institute
201 2002) when comparing the same behavioral variable across treatments. ANCOVA (SAS
202 Institute 2002) was carried out to test whether or not plant architecture (petiole length)
203 and prey presence could affect the transit time of *P. persimilis* from petiole to leaf. The
204 frequency distribution of *P. persimilis* movement from one part of the plant to another,
205 and the success of the predators in finding prey, were analyzed by Fisher's Chi-square
206 test (SAS Institute 2002). When comparing only two levels of a treatment factor for one
207 dependent response, a t-test was used (SAS Institute 2002).

208

209 **Results**

210

211 Plant Characteristics

212

213 The total plant surface areas were approximately the same for 2- and 6-leafed plants, as
214 designed. However, the surface areas of individual plant parts were significantly

215 different between the two plant architectures (Table 1). For example, 2-leafed plants had
216 longer stems and petioles, and a mean leaf blade surface area that was nearly 3-fold
217 greater than those of 6-leaf plants. Two-leaf plants also had longer internodes, thicker
218 stems and petioles, and were taller than 6-leafed plants. Although 2-leafed plants had
219 fewer internodes, they were taller than 6-leafed plants because the distance from the base
220 to the first internode was longer on 2-leafed plants.

221

222 Effects of Plant Architecture and Prey Distribution

223

224 Regardless of plant architecture or prey distribution, *P. persimilis* spent significantly
225 more time moving (13.78 ± 0.48 min [mean \pm SE]) than resting (3.78 ± 0.41 min) or
226 feeding (2.38 ± 0.46 min) (Friedman's ANOVA, $\chi^2 = 80.38$, $df=2$, $P<0.0001$). In
227 addition, after release onto the stem, all predators walked upward and moved onto a
228 petiole. Fifty percent (22/44; range: 36 – 64%) of the predators turned onto the first
229 (most basal) petiole encountered. Regardless of which petiole was first visited, most
230 (84% [37/44]; range: 73 -100%) moved from the petiole onto the corresponding leaf
231 blade. A much lower percentage (13% [6/44]; range: 0 - 27%) of the predators moved
232 back to a stem, and only one predator stayed on the petiole for the duration of the
233 observation period. Petiole length significantly affected transit time from petiole to leaf
234 blade, with longer petioles on 2-leafed plants associated with longer times predators spent
235 on them (ANCOVA, $F=9.63$, $df=1$, $P=0.035$); whereas presence of prey on the attached
236 leaf blades did not affect transit time (ANCOVA, $F=1.05$, $df=1$, $P=0.311$). Of those
237 predators that moved onto leaf blades, the percentages that remained there were

238 significantly affected by prey distribution (Fisher's, $\chi^2 = 4.65$, $df=1$, $P= 0.048$); on plants
239 with all leaves infested with prey eggs, 70% (12 of 17) stayed on the leaf compared with
240 35% (7 of 20) on plants that had prey on the basal leaf only. Once on an infested leaf, *P.*
241 *persimilis* were more successful in finding a prey patch on the smaller leaves of 6-leafed
242 plants (14 of 16) than on the larger leaves of 2-leafed plants (8 of 17) (Fisher's, $\chi^2 = 6.02$,
243 $df=1$, $P= 0.025$). There was a trend for predators to find prey patches sooner on 6-leafed
244 (4.67 ± 0.65 min) compared to 2-leafed plants (7.23 ± 1.64 min), but the difference in
245 time was not significant (t test, $F=-1.62$, $df=22$, $P= 0.119$).

246 Predators spent more time (ca. 37% more for each plant part) on stems and
247 petioles of 2-leafed plants than on 6-leafed plants (ANOVA GLM, stems: $F = 7.57$, $df=1$,
248 $P = 0.010$; petioles: $F = 7.93$, $df= 1$, $P = 0.02$) (Figure 1). Most of the difference was
249 attributable to time spent moving (ANOVA GLM, stems: $F=10.85$, $df=1$, $P=0.002$;
250 petioles: $F=4.86$, $df=1$, $P=0.033$) as there were no differences in time spent resting among
251 treatments for any plant part (Table 2). Prey distribution had no effect on time spent
252 moving on stems (ANOVA GLM, $F=0.00$, $df=1$, $P=0.975$) or petioles ($F=1.49$, $df=1$,
253 $P=0.229$), nor were there any significant interactions between plant architecture and prey
254 distribution (ANOVA GLM, stems: $F=0.28$, $df=1$, $P=0.597$; petioles: $F=0.21$, $df=1$,
255 $P=0.653$) (Table 2).

256 Compared to stems and petioles, *P. persimilis* females spent considerably more
257 time moving on leaf blades, regardless of plant architecture and prey distribution
258 (Friedman's ANOVA, $\chi^2 = 44.88$, $df=2$, $P<0.0001$) (Figure 1). Predators appeared to
259 walk more slowly on leaf blades than on stems or petioles, and although stops were less
260 frequent, they were slightly longer (average 30 seconds) than on stem and petioles. For

261 each prey distribution, predators spent significantly more time moving on leaf blades of
262 6-leafed plants (9.75 ± 0.88 min) than on those of 2-leafed plants (6.33 ± 0.86) (t test,
263 $F=2.763$, $df=42$, $P=0.008$) (Figure 1). Predators that found prey spent about four minutes
264 feeding, which represents about 25% (range: 21–37%) of the total time on leaf blades.
265 With respect to time spent by *P. persimilis* on different parts of the leaf blade, there was a
266 marginally significant interaction between plant architecture and prey distribution
267 (ANOVA GLM, $F=3.45$, $df=1$, $P=0.07$) (Table 2). That is, when foraging on uninfested
268 leaves (no prey present), predators walked predominantly along the leaf margins;
269 whereas, on infested leaves most of the time was spent in the leaf interior.

270

271 **Discussion**

272

273 The foraging efficiency of natural enemies often decreases in the face of increased plant
274 architectural complexity (e.g., Andow and Prokrym 1990; Geitzenauer and Bernays
275 1996; Cloyd and Sadof 2000; Hoddle 2003; Legrand and Barbosa 2003). However, our
276 results indicate that the effect of plant complexity depends on the specific components of
277 that complexity (e.g., leaf size, internode length) as well as on prey distribution. Thus,
278 the effects of branching pattern, leaf size, and relative differences in surface areas among
279 plant parts need to be carefully evaluated (Gardner and Dixon 1985; Stadler and Völkl
280 1991). Furthermore, different components associated with structural complexity may
281 have different, perhaps opposite, effects on predator foraging. On 6-leafed plants, which
282 have shorter internodes and petioles and smaller leaves than 2-leafed plants, time spent

283 moving was relatively shorter on stems and petioles, but longer on leaves than on 2-
284 leafed plants.

285 Two-leafed plants had thicker stems and petioles, as well as longer internodes and
286 petioles, than 6-leafed plants. Therefore, randomly-searching *P. persimilis* females
287 released at the base of a 2-leafed plant had a larger potential surface area to traverse
288 before reaching a leaf blade than they would on 6-leafed plants. The shorter time
289 predators spent on stems of 6-leafed plants may also be related to the greater frequency of
290 petioles along the stem, which would increase the rate at which petioles are encountered
291 compared to 2-leafed plants. Thus, the effects of plant architecture on predator foraging
292 were cumulative, and in general may result from multiple plant structures, ranging from
293 surface area and microstructural influences to those pertaining to large structural
294 differences such as numbers, kinds and proportions of plant parts.

295 Other studies indicate there may be an inverse relationship between total plant
296 surface area and foraging efficiency for very small natural enemies (Burbutis and Koepke
297 1981; Treacy et al. 1986; Maini et al. 1991; Geitzenauer and Bernays 1996; Wang et al.
298 1997; Cloyd and Sadof 2000). Our study demonstrates that variation in foraging
299 efficiency is not necessarily related to variation in total surface area. That is, although
300 the total surface area of our plants was the same, we still found differences in foraging
301 behavior and efficiency because of the way the area was partitioned. For example, the
302 surface area of individual leaf blades on 2-leafed plants was about 3 times greater than
303 those of 6-leafed plants; and yet predators spent more time moving on leaf blades of 6-
304 leafed plants. This apparent contradiction may be explained by our observation that *P.*
305 *persimilis* spends relatively more time searching leaf edges compared to areas away from

306 the perimeter of the leaf; the tendency for this predator to search leaf edges also was
307 documented previously (Sabelis and Dicke 1985). Because 6-leafed plants had smaller
308 leaf blades, predators may have encountered leaf edges more frequently and, hence, spent
309 more time moving on leaves of 6-leafed plants than on the larger leaves of 2-leafed
310 cucumbers. Increased foraging activity on 6-leafed plants, combined with their smaller
311 leaf areas (which resulted in smaller distances between leaf edges and prey patches), may
312 explain why predators were more successful in finding prey patches on 6-leafed plants
313 compared to 2-leafed plants.

314 *Phytoseiulus persimilis* spent significantly more time moving on the leaf blades of
315 6-leafed plants where prey were located on just the basal leaf compared to plants in
316 which all six leaves contained prey. This difference may be due related to the likelihood
317 that predators would turn onto an infested leaf; on plants with only one infested leaf the
318 chance would be one in six, while on plants on which all leaves were infested any turn
319 would lead to prey. Because predators stop moving and spend more time feeding when
320 they encounter prey patches, when *P. persimilis* find prey patches more quickly (e.g., on
321 plants on which all leaves were infested with prey), they will allocate more time to
322 feeding. Similarly, Yasuda and Ishikawa (1999) found that the ladybird beetle,
323 *Harmonia axyridis* Pallis, spent more time feeding when aphids were distributed evenly
324 than when they were in patches; that is, more time feeding when prey were more easily
325 found. Thus, both plant architecture and prey distribution (number and leaf size) can
326 indirectly affect feeding time and, thus, prey consumption efficiency of *P. persimilis*.

327 The foraging behaviors of predaceous arthropods are important in the acquisition
328 of food and impact on prey populations. As such, understanding the factors that affect

329 foraging behavior may improve the effectiveness and efficiency of biological control
330 programs. For very small natural enemies like predatory mites and many parasitoids,
331 differences in plant architecture and prey distribution may have a profound effect on
332 foraging efficiency and, hence, their effectiveness as biological control agents (Andow
333 and Prokrym 1990; Ryoo 1996; Krips et al. 1999; Skirvin and Fenlon 2001; Stavrinides
334 and Skirvin 2003). Knowing the effects of plant architecture and prey/host distribution
335 on natural enemy behavior will allow better estimates of how many predators or
336 parasitoids to release, and where on the plant to release them, to achieve more efficient
337 and consistent biological control. However, because natural enemies perceive and use
338 plant chemicals during searches for prey/hosts (Turlings et al. 1990; Cortesero et al.
339 2000), examining how plant structure and prey distribution interact with phytochemical
340 cues will provide an opportunity for understanding natural enemy foraging in a broader
341 context. For example, with respect to *P. persimilis*, herbivore-induced plant volatiles are
342 known to modify search behavior both in and out of prey patches (Dicke and Sabelis
343 1994; Maeda and Takabayashi 2001) and in response to prey density (Nachappa et al.
344 2006). This information, when combined with our work on structural effects of cucumber
345 and *T. urticae* distribution on *P. persimilis* behavior (here and see also Gontijo et al.
346 2010), will allow better predictions of prey-finding and local and regional population
347 dynamics in this predator-prey system.

348

349

350

351

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353

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357

358

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Table 1 Means (\pm SEM) of plant part dimensions on manipulated cucumber plants, *Cucumis sativus*. Mean differences between 6- and 2-leafed plants were significant at $P < 0.01$ (t-test) except for total plant surface area ($P > 0.05$).

Plant Type	N	Petiole diam (cm)	Petiole length (cm)	Stem diam (cm)	Base to first internode (cm)	Internode length (cm)	Plant height (cm)	Leaf surface area (cm ²)	Total plant surface area (cm ²)
6-leafed	18	0.32 ± 0.005	3.61 ± 0.06	0.86 ± 0.02	6.89 ± 0.14	0.93 ± 0.02	12.61 ± 0.26	82.98 ± 1.87	554.80 ± 10.05
2-leafed	20	0.45 ± 0.008	7.40 ± 0.09	1.04 ± 0.02	10.50 ± 0.24	2.66 ± 0.05	15.34 ± 0.37	240.60 ± 4.11	551.91 ± 9.90

Table 2 Treatment effects and interactions on *Phytoseiulus persimilis* moving, resting and feeding on stems, petioles and leaves.

architecture		prey distribution		architecture*prey distribution		behavior
<i>F- value</i>	<i>P- value</i>	<i>F- value</i>	<i>P- value</i>	<i>F- value</i>	<i>P- value</i>	
10.85	0.002*	0.00	0.97	0.28	0.59	Moving on stem
1.78	0.18	0.00	0.99	2.68	0.10	Resting on stem
4.86	0.03*	1.49	0.22	0.21	0.65	Moving on petiole
0.22	0.64	0.27	0.60	0.23	0.63	Resting on petiole
8.14	0.006*	1.23	0.27	3.58	0.06	Moving on leaf
0.00	0.97	1.87	0.17	0.72	0.40	Resting on leaf
3.91	0.05*	11.52	0.001*	3.45	0.07	Feeding on leaf

*Significant treatment effect or interaction at $p < 0.05$ (ANOVA, PROC GLM)

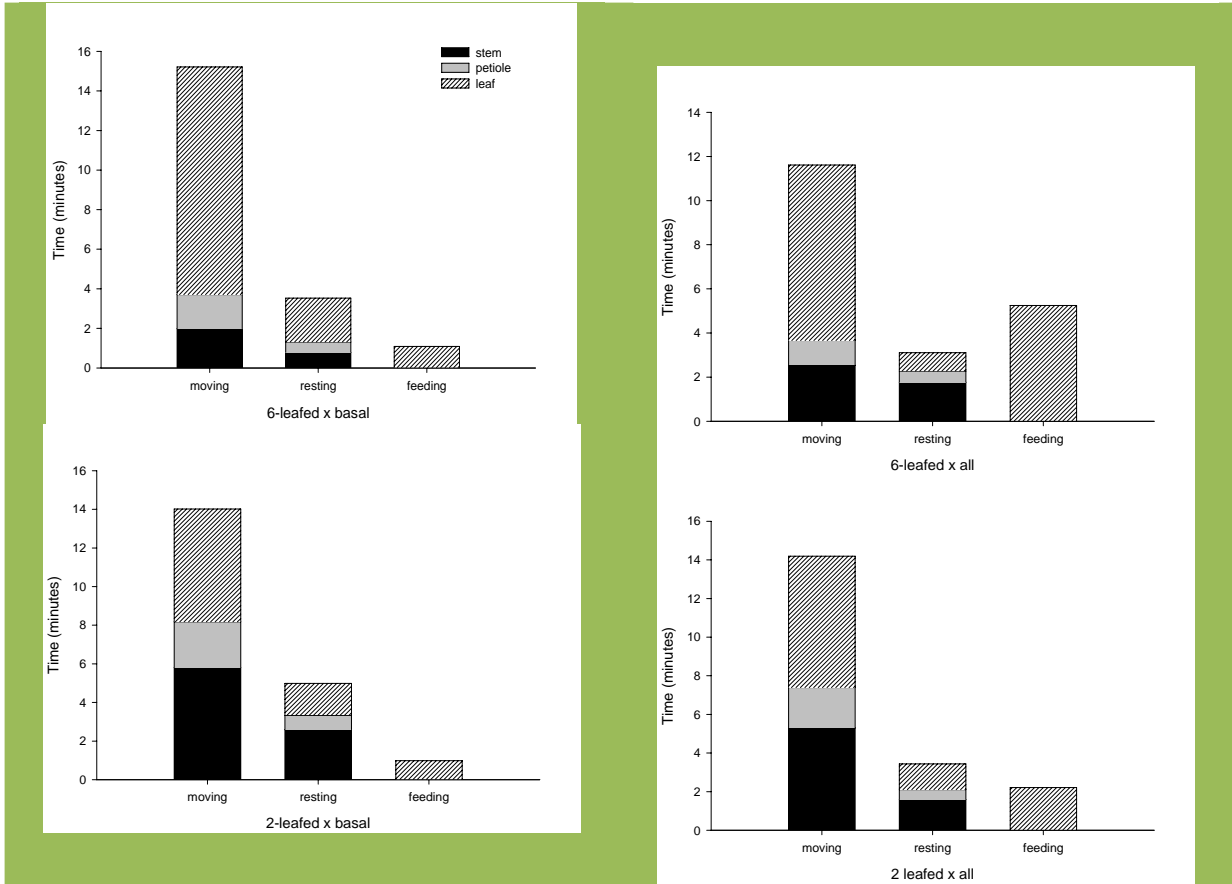


Figure 1. Time spent moving, resting and feeding by *Phytoseiulus persimilis* on stems, petioles and leaves of 6-leafed and 2-leafed plants with either prey on single basal leaf or on all leaves.