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Oviposition preference of western flower thrips for cucumber leaves from different positions along the plant stem

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Abstract

While the distribution of herbivorous insects over leaves along the stem often shows a peak at some distance from the apex this does not necessarily reflect an innate preference as alternative explanations can be provided such as impact of predators and inter- or intraspecific competitors. It is of interest to determine which factors shape the distribution of insects over the leaves of a plant. Do leaves from different positions differ in suitability for insects and is that reflected in the insect's preference, or are other factors involved? In this paper we assess how the herbivorous insect western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), chooses among leaves from different positions relative to the apex of cucumber, *Cucumis sativus* (L.) plants. On leaf discs of a susceptible and three partially resistant cucumber accessions, thrips reproduction was highest on apical leaves and lowest on basal leaves. In dual-choice essays thrips females preferred younger leaves over older leaves for oviposition in all cucumber accessions tested, as was predicted from the no-choice assay. This indicates that differences in leaf suitability are an important factor in determining thrips distribution on cucumber plants.

Introduction

Spatial or temporal variation in resistance to insects in plants is well documented (Tingey & Singh, 1980; Kennedy & Barbour, 1992). Leaves at different position relative to the plant apex, or plants of different age can differ in suitability for insects. For example, Reynolds & Smith (1985) showed that top leaves of a resistant soybean cultivar supported higher growth of larvae of the soybean looper, *Pseudoplusia includens* (Walker) (Lepidoptera: Noctuidae), than the lower leaves. In tomato, older plants are more resistant to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) (measured as oviposition rate and pre-adult survival), than younger plants (Bas et al., 1992).

It is expected that insects choose those parts of the plant for oviposition on which they achieve highest reproductive success. As a consequence, the most suit-

able plant parts would support the highest densities of the insect. Such a correlation between suitability of plant parts and density of insects could be disturbed by factors like intra- or interspecific competition and predation.

Western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is a polyphagous insect that forms a major pest in greenhouse crops including cucumber (Mantel & van de Vrie, 1988). Efforts are made to develop thrips-resistant cucumber varieties (Mollema et al., 1995). Soria & Mollema (1995), showed that reproduction of thrips is lower on some resistant cucumber accessions than on a susceptible control. On susceptible cucumber (variety 'Autumn Green'), thrips tend to be most abundant in the youngest parts of the plants (de Kogel, unpubl.) which suggests that young leaves are more suitable for the insect than older leaves. When thrips are able to discriminate between leaves that differ in suitability, indi-

viduals will probably move to the most suitable leaves, explaining higher densities in the youngest parts of the plants.

The aim of the present study is to determine the effect on the reproduction of *F. occidentalis* in a no-choice situation of leaf position relative to the apex and plant age of both a susceptible and three of the partially resistant cucumber accessions, described previously by Soria & Mollema (1995). When differences in suitability for reproduction of *F. occidentalis* are observed, it is expected that the most suitable leaves are preferred by the insect for oviposition. This will be tested in a choice assay. As a measure for oviposition, the number of hatched larvae is used in the experiments as in the study of Soria & Mollema (1995), since numbers of larvae are much easier to determine than numbers of eggs (eggs are laid inside the leaf tissue). However, differences in numbers of hatched larvae can be caused by differences in numbers of eggs produced (oviposition) or by different levels of egg-mortality. Therefore numbers of eggs and numbers of hatched larvae were compared on leaf discs from the set of cucumber accessions studied.

Materials and methods

Plant material and insect manipulation. Four cucumber accessions were used: a susceptible inbred line 'G6' and three accessions, CPRO-DLO numbers 9104, 9140, and 9143, previously selected for low levels of damage after infestation with *F. occidentalis* (Mollema et al., 1993). Plants were grown in an isolated greenhouse at 20–30 °C. *F. occidentalis* was originally collected in 1988 on cucumber at CPRO-DLO (Wageningen, The Netherlands) and since then maintained on flowering cucumber plants, variety 'Autumn Green' in a gauze tent (mesh-size 100 µm) in an isolated greenhouse (Mollema et al. 1990). Thrips were randomly collected from this rearing with an aspirator, shortly anaesthetized with CO₂, and manipulated with a fine brush.

Effect of leaf position and plant age on reproduction. To determine the effect of leaf position and plant age of the four cucumber accessions on reproduction of the thrips, plants of 4.5, 5.5, and 6.5 weeks after sowing were used. Ten adult female thrips were released on leaf discs ($\phi=8$ cm) of basal, middle and apical (youngest unfolded) leaves. Per accession, four plants were used of each plant age. Leaf discs were put

in petri dishes, adaxial side down, on moist tissue paper, covered with plastic film and stored in the climate chamber ($T=24\text{ }^{\circ}\text{C}\pm 1.5\text{ }^{\circ}\text{C}$; r.h.=60%; L16:D8). After 48 h adaptation (Soria & Mollema, 1995), thrips were transferred to fresh leaf discs ($\phi = 8$ cm, 10 females/disc) where they were allowed to oviposit for 24 h. From each accession, four leaf discs per plant age-leaf position combination (from four different plants) were used. After four days the numbers of larvae that had hatched on the leaf discs were counted. Data were analyzed by a three-way ANOVA with as main treatment factors plant age, accession and leaf position. Mean separation test was conducted using LSD ($\alpha=0.05$).

Oviposition preference for leaves from different positions relative to the apex. In the middle of a petri dish, two leaf discs ($\phi=2.5$ cm) were put adaxial side down and side by side on moist tissue paper. Basal (b), middle (m), and apical (a) leaves of 6 weeks old plants were used; five plants per accession. Per accession all possible combinations of the three leaf positions were offered to the thrips (a–a, m–m, b–b, a–m, a–b, m–b), in five replicates per combination. Ten adult females were put on the leaf discs (5 on each disc) and the petri dish was covered with plastic film. Thrips could easily move from one leaf disc to the other. The petri dishes were stored in a climate chamber for 28 h ($T=24\text{ }^{\circ}\text{C}\pm 1.5\text{ }^{\circ}\text{C}$; r.h.=60%; L16:D8 h). Petri dishes were randomized to eliminate the effect of possible gradients of light or temperature in the climate chamber. During the day the position of the adult females was recorded 5 times: they were on either leaf disc or elsewhere in the petri dish. Mean numbers per petri dish were calculated and pooled data from the 4 accessions were analyzed with a two-tailed paired t-test to test for differences in number of females on the two leaf discs from a treatment. After 28 h adult thrips were removed and leaf discs were put separately in wells of tissue culture plates (Greiner, No. 657102; Germany) on 1 ml of tap water. After 4 days numbers of larvae that had hatched from the leaf discs were counted. Data were analyzed by a two-way ANOVA on differences between the number of larvae on the two discs of each combination, with as main treatment factors leaf disc combination and accession.

Reproduction test; numbers of eggs and larvae. To test whether the difference in numbers of larvae produced by *F. occidentalis* on leaf discs from different accessions reflects the number of eggs produced, the

Table 1. Effect of leaf position relative to the apex and plant age of cucumber on reproduction of *F. occidentalis*. Results of ANOVA

Source of variation	df	MS
Plant age	2	1.218ns
Accession	3	33.801***
Leaf position	2	20.264***
Plant age*accession	6	0.679ns
Plant age*leaf position	4	1.328ns
Accession*leaf position	6	2.010**
Plant age*accession*leaf position	12	1.185*
Residual	108	0.594

ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

following experiment was performed. Adult female thrips were put on leaf discs ($\phi=8$ cm) from basal leaves of 4.5 weeks old plants from each accession that were placed adaxial side down in a petri dish with moist tissue paper. The dishes were covered with a transparent plastic film ($14 \mu\text{m}$) and kept in a climate chamber for two days. After this adaptation period 48 females were collected from the petri dishes and put on small leaf discs ($\phi=1.2$ cm, 1 female/disc) from the same accession, that were put adaxial side down on 1 ml of tap water in wells of tissue culture plates (Greiner, No. 662160; Germany). Plates were covered with plastic film and kept in the climate chamber. Adults were removed after 24 h. Twenty four leaf discs were kept in the climate chamber; after 4 days numbers of hatched larvae were counted. The other 24 leaf discs were used to determine the number of eggs. To this end, leaf discs were boiled in water, one day after removal of the adults, in a microwave oven (3 min, 700 Watt). Eggs were clearly visible using a binocular microscope with transmitting light. This experiment was repeated and square root transformed pooled data were analyzed by a two-way ANOVA with accession and developmental stage (egg *versus* larvae) as main treatment factors. The correlation coefficient between numbers of hatched larvae and eggs was also calculated.

Results

Effect of plant age and leaf position on reproduction. Results of ANOVA showed that accession and leaf position had a significant effect on reproduction while plant age did not (Table 1). A significant accession*leaf

Figure 1. Effect of leaf position (apical, middle and basal leaf) of four cucumber accessions on reproduction (number of larvae/female/day) of *F. occidentalis* (mean+s.e.). Bars with the same letter within accessions are not significantly different, $P < 0.05$.

position interaction indicated that the effect of leaf position differed among accessions. This is presented in Figure 1, where data were pooled over the three plant ages. On accession 9104, numbers of larvae on middle and basal leaves were reduced compared to apical leaves, whereas on the other accessions, numbers of larvae were lower on basal leaves compared to apical and middle leaves (difference not significant on 9140). In general, mean reproduction was higher on apical leaves than on basal leaves.

Oviposition preference for leaves from different positions relative to the apex. In all choice situations (a-m, a-b, m-b) significantly more adult females were present on leaf discs from younger leaves (Table 2). Both in the control series (a-a, m-m, b-b) and in the choice series (a-m, a-b, m-b) there is a trend that with increasing leaf age more females are found on neither leaf disc, but elsewhere in the petri dish.

Results of ANOVA on the number of hatched larvae showed that the treatment factor leaf disc combination was significant while accession and interaction were not (leaf disc combination: $df=5$, $MS=88.44$, $P < 0.001$; accession: $df=3$, $MS=7.41$, $P=0.717$, interaction: $df=15$, $MS=12.34$, $P=0.727$; residual: $df=96$, $MS=16.44$). Therefore data were pooled over the four accessions, and 95% confidence limits, based on the experimental error, were calculated to determine if differences within leaf disc combinations were significantly different from zero. There were no differences in numbers of larvae on leaf discs from leaves of the same position (a-a, m-m, b-b), while there were clear differences between pairs of discs from leaves of different

Table 2. Number (mean $\pm$ s.e.) of adult thrips on cucumber leaf discs in a dual-choice assay

Treatment	Disc 1	Disc 2	P	Off
a-a	5.17 $\pm$ 0.34	3.58 $\pm$ 0.30	P<0.05	0.94 $\pm$ 0.18
m-m	4.33 $\pm$ 0.32	4.02 $\pm$ 0.32	P=0.59	1.46 $\pm$ 0.26
b-b	4.27 $\pm$ 0.32	3.47 $\pm$ 0.25	P=0.09	2.06 $\pm$ 0.26
a-m	5.20 $\pm$ 0.35	3.50 $\pm$ 0.38	P<0.05	0.94 $\pm$ 0.16
a-b	6.06 $\pm$ 0.33	2.22 $\pm$ 0.34	P<0.0001	1.54 $\pm$ 0.25
m-b	6.29 $\pm$ 0.44	1.83 $\pm$ 0.27	P<0.0001	1.68 $\pm$ 0.30

a=apical, m=middle and b=basal leaf. Off=number of females not on leaf discs. P-values obtained with two-tailed paired *t*-test.

Figure 2. Oviposition preference of *F. occidentalis* for cucumber leaves from different position relative to the apex. a=apical leaf, m=middle leaf, b=basal leaf. * indicates significant difference, $P<0.05$.

positions (a-m, a-b, m-b) (Figure 2). In all cases more larvae hatched from the younger leaves.

Reproduction test; numbers of eggs and larvae. There were clear differences among accessions in both numbers of eggs and hatched larvae produced by *F. occidentalis* (Table 3). ANOVA indicated a significant effect of accession and not of developmental stage and interaction (accession: $df=3$, $MS=14.92$, $P<0.001$; developmental stage: $df=1$, $MS=1.05$, $P=0.126$; interaction: $df=3$, $MS=0.08$, $P=0.911$; residual: $MS=0.45$). Since there is no significant interaction, there is no differential egg-mortality among accessions. The absence of a significant effect of developmental stage indicates that numbers of eggs and larvae on leaf discs were similar, i.e., egg-mortality was low. A correlation coefficient (r) of 0.99 ($n=4$, $P<0.01$) was calculated between mean numbers of eggs and hatched larvae.

Discussion

The results of the no-choice reproduction test clearly showed that leaf position relative to the apex, and not plant age, had an effect on the number of hatched larvae produced by *F. occidentalis*. This was true for all four cucumber accessions tested. It was also shown that reproduction on the resistant accessions was lower than on the susceptible control which is in agreement with results of Soria & Mollema (1995). In general, the younger leaves of cucumber plants supported higher numbers of hatched larvae than older leaves. In a study on the soybean looper, *Pseudoplusia includens*, on soybean, Reynolds & Smith (1985) also found significant effects of leaf position but not of plant age on insect growth. In their study, the top leaves of the plants were more suitable for the insect than the lower leaves.

In the present study, no effect of plant age was found over a relatively small range of plant ages. In other studies, significant effects of plant age on insects have been found, e.g., a decrease in oviposition rate and pre-adult survival with increasing plant age of the greenhouse whitefly, *Trialeurodes vaporariorum* in tomato (Bas et al., 1992) and a decrease of survival of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) on celery with increasing plant age (Diawara et al. 1994). In these studies, however, differences in plant age were much larger.

It was hypothesized that western flower thrips females would prefer those leaves for oviposition on which they realize the highest reproductive success. In our study we measured the number of larvae produced, assuming that this is correlated with reproductive success. Previous work on the same cucumber accessions, showed that other life history traits that contribute to thrips reproductive success, such as pre-adult survival, correlate well with the observed differences in reproduction on the susceptible and resistant cucumber accessions used in our study (Soria & Mollema, 1995). Furthermore, de Kogel et al. (1997) showed that on cucumber accessions on which thrips have a high reproduction, also r_m is high. On accessions on which reproduction is reduced, also r_m is lower. Therefore the assumption that differences in reproduction correlate with differences in reproductive success seems justified.

It was shown that those leaves on which thrips females produced the highest numbers of larvae in the no-choice assay, were also preferred for oviposition in choice experiments. During the experiment, higher numbers of adult females were found on discs from

Table 3. Numbers of eggs and hatched larvae per female per day on leaf discs of four cucumber accessions (mean $\pm$ s.e., $n=48$). No significant effect of developmental stage according to ANOVA (see text)

Accession	Eggs	Hatched larvae
G6	2.33 $\pm$ 0.26	1.98 $\pm$ 0.23
9104	0.52 $\pm$ 0.11	0.39 $\pm$ 0.08
9140	0.76 $\pm$ 0.13	0.63 $\pm$ 0.13
9143	1.55 $\pm$ 0.20	1.11 $\pm$ 0.18

younger leaves (Table 2). In the control a–a (Table 2) there was a significant difference in number of females between the two discs, in the other controls (m–m and b–b) there was no difference in number of females on the two discs, as expected.

The number of females that were not on either of the leaf discs, but elsewhere in the petri dish increased with increasing leaf age (basal leaves are older than apical leaves) (Table 2). This suggests that thrips behaviour is influenced by leaf age: it seems that thrips spent more time on walking on older leaves than on younger leaves. According to our experiments, older leaves are less suitable for thrips in terms of reproduction and preference. On resistant cucumber plants, reproduction is reduced compared to susceptible plants. Harrewijn et al. (1996) showed, using electrical penetration graph technique, that thrips feeding behaviour is disturbed on these resistant plants; thrips spend less time on feeding and more time on walking. This is consistent with our results.

Thrips preferred younger leaves in all cases. This could explain observations in the greenhouse that thrips are most abundant in the youngest parts of cucumber plants. However, it can not be excluded that other factors such as risk of predation and inter- or intraspecific competition influence the distribution of thrips on the plant. Our experiments were short-term lab-experiments which only provide information about thrips choosing behaviour in the first stage of colonization.

The observed differences in numbers of hatched larvae indeed reflect differences in oviposition (numbers of eggs produced) and not differences in egg-mortality (Table 3). The high correlation between numbers of eggs and larvae indicates that the number of hatched larvae is a good index for oviposition in this case.

The relationship between oviposition preference for different host plants and the performance of off-

spring on those hosts has been studied by several authors (see Thompson, 1988, for examples). The correlation between oviposition preference and performance ranges from good to poor. Several hypotheses that explain a poor relationship between oviposition preference and performance are discussed by Thompson (1988). A positive correlation between oviposition preference and performance is described by Via (1986). She found in populations of *Liriomyza sativae* (Blanchard) (Diptera: Agromyzidae) that females preferred the hosts for oviposition on which they achieved the highest pupal masses.

Oviposition preference for leaves of different age has been described for three whitefly (Homoptera: Aleyrodidae) species in both laboratory and field tests (Walker & Zareh, 1990). The authors found that *Parabemisia myricae* (Kuwana) preferred very young lemon leaves for oviposition. Previously it had been shown that this species only colonizes young leaves because the mature lemon leaf cuticle prevents colonization of mature leaves (for references see Walker & Zareh, 1990). Two other whitefly species, *Aleurothrixus floccosus* (Maskell) and *Dialeurodes citri* (Ashmead), however, do colonize older leaves. The authors showed that these two species preferred older leaves than *P. myricae*. The effect of leaf age on the reproduction of these two species in a no-choice situation was, however, not tested. Based on the data for *P. myricae* it can be predicted that reproduction would be highest on leaves of the preferred age, similar to what we show in the present study on thrips.

It is concluded that thrips females show oviposition preference for leaves from different positions on the plant stem relative to the apex. Thrips preferred leaves from higher positions along the stem; on these leaves they achieved the highest reproduction. It is not yet clear by which mechanisms thrips discriminate between leaves.

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