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Resistance to western flower thrips in greenhouse cucumber: effect of leaf position and plant age on thrips reproduction

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Summary

Three greenhouse cucumber (*Cucumis sativus* L.) accessions, previously selected for low levels of damage after infestation with *Frankliniella occidentalis* (Pergande), were tested for resistance against *F. occidentalis* in a no-choice greenhouse experiment at the mature plant stage. The three accessions showed a strong reduction in thrips damage compared to the susceptible control. The effects of leaf position and plant age of the four cucumber accessions on the reproduction of *F. occidentalis* were determined in a leaf disc assay. Leaf position had a significant effect on thrips reproduction, whereas plant age, within the test range, had not. In general, reproduction was higher on young leaves. Reproduction as measured on leaf discs from certain leaf positions was strongly correlated with resistance of mature plants in the greenhouse, and can therefore be used as a quick test to screen cucumber accessions for resistance against thrips.

Introduction

Western flower thrips, *Frankliniella occidentalis* (Pergande) is a major pest worldwide. In the Netherlands it is the most serious pest in many vegetable and ornamental crops in greenhouses (Mantel and van de Vrie, 1988). Chemical and biological control are used to control this pest. Chemical control is difficult because *F. occidentalis* has become resistant to many insecticides (Immaraju et al., 1992). Biological control in cucumber crops has specific problems (Mollema et al., 1990; van Rijn and Sabelis, 1990); for instance, pollen is probably needed to sustain predator populations, but in modern female flowering cucumber crops pollen is not available. Host plant resistance could contribute to control this pest, it is often compatible with other control strategies and can therefore play a key role in integrated pest management (de Ponti & Mollema, 1992; Wiseman, 1994).

Cucumber accessions (i.e. a sample of a plant population as conserved in genebank collections) with low levels of damage after infestation with *F. occidentalis* have been selected by Mollema et al. (1993). In their experiments young cucumber plants were used (2–4 weeks old). The most resistant accessions also showed reduced damage levels at the mature plant stage in a greenhouse. The various accessions, however, were all tested at the same time in one greenhouse, i.e. a choice situation. This can lead to an overestimation or underestimation of resistance levels when one accession is preferred by the insect over another. For example, in a test for oviposition preference of the white-backed planthopper, *Sogatella furcifera* (Horvath), for several rice cultivars, differences in oviposition between free-choice and no-choice experiments were observed (Mishra and Misra, 1991). In a free-choice experiment oviposition was lowest on one cultivar compared to the six other cultivars tested. In a no-choice test oviposition on this cultivar was higher than on three others.

Similar differences between choice and no-choice situations have been found by Firempong (1988), who found that the hierarchy of colonization of cowpea cultivars by *Aphis craccivora* (Koch) was different in choice and no-choice situations. Therefore the resistance of three of the cucumber accessions that were previously selected by Mollema et al. (1993) and a susceptible control was assessed in separate compartments of a greenhouse at the mature plant stage, in a no-choice situation.

Spatial or temporal variation for resistance to insects within plants is well documented (Tingey & Singh, 1980; Kennedy & Barbour, 1992). There are, however, no data available on the effect of plant age and leaf position on the resistance of cucumber to *F. occidentalis*. Observations in the greenhouse however, indicated that there is variation in resistance within cucumber plants: thrips tend to be more abundant in the youngest part of the plant suggesting that young leaves are more suitable for thrips than older leaves. In other plant-insect systems variation in degree of resistance within plants has been shown, e.g. in soybean the top leaves are less resistant (measured as larval growth) to the soybean looper, *Pseudoplusia includens* (Walker), than the lower leaves (Reynolds & Smith, 1985). Resistance can also vary with plant age. In tomato, resistance to greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), quantified by measuring several life history components, increases with plant age (Bas et al., 1992). Information on effects of plant age and leaf position upon host plant resistance is a prerequisite for the development of reliable test methods for host plant resistance. Therefore we tested the effect of plant age and leaf position on the reproduction of *F. occidentalis* in susceptible and resistant cucumber accessions using a leaf disc assay. The outcome of the greenhouse experiment and the leaf disc assay are compared, and the correlation between the results of the two tests is discussed.

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, 1995). Plants were grown in an isolated greenhouse at 20–30 °C. *F. occidentalis* was originally collected in 1988 on cucumber at CPRO-DLO

Table 1. Damage (mean $\pm$ SEM) caused by *F. occidentalis* to four cucumber accessions ($n = 3$). Damage in mm² on first leaf measured two weeks after inoculation and damage index to leaves (0 = no damage, 5 = maximum damage) determined 7.5 weeks after inoculation

Accession	Damage $\pm$ SEM 1st leaf (mm ²)	Damage index $\pm$ SEM
G6	623 $\pm$ 78 ^a	3.25 $\pm$ 0.42 ^a
9104	335 $\pm$ 25 ^b	0.27 $\pm$ 0.12 ^b
9140	265 $\pm$ 33 ^b	0.43 $\pm$ 0.10 ^b
9143	224 $\pm$ 14 ^b	0.61 $\pm$ 0.14 ^b

Values followed by the same letter (columns) are not significantly different ($P < 0.05$).

(Wageningen, the Netherlands) and since then maintained on flowering cucumber plants, variety 'Autumn Green' in a gauze tent (mesh-size 100 μ m) in an isolated greenhouse (Mollema et al., 1990). Thrips were collected with an aspirator, briefly anaesthetized with CO₂, and manipulated with a fine brush.

Greenhouse experiment. In this experiment resistance to thrips was determined in a no-choice situation. In 12 separated compartments of a greenhouse, cucumber plants were grown, 12 plants per compartment, 3 compartments per accession. Plants were sown on August 20, 1994. After 3.5 weeks basal leaves were inoculated with 25 first instar larvae (L1) and 25 second instar larvae (L2). Larvae were produced on small cucumber fruits according to Mollema et al. (1993). Two weeks after inoculation damage on the basal leaf was quantified with an Image-Analysis device (Mollema et al., 1992). Seven and a half weeks after inoculation leaves 7 to 16 were given an index value on a scale from 0 (no damage) to 5 (maximum damage). Maximum damage is about 3000 mm² per leaf, which is about 7% of the total area of a full grown cucumber leaf. For each compartment the mean damage was calculated. Data were analyzed by ANOVA (treatment factor accession) and mean separation was conducted using LSD ($\alpha = 0.05$).

Effect of plant age and leaf position on reproduction. To determine the effect of plant age and leaf position 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 put on leaf discs ($\varnothing = 8$ cm) from basal, middle and apical (youngest unfolded) leaves. Of each accession four plants per plant age were used. Leaf discs were put in

Table 2. Effect of plant age and leaf position of four cucumber accessions on reproduction (larvae/female/day, mean $\pm$ SEM) of *F. occidentalis* (n = 4)

Leaf position	Accession	Plant age (weeks)		
		4.5	5.5	6.5
Apical leaf	G6	3.43 $\pm$ 0.57 ^{ab}	4.00 $\pm$ 0.26 ^a	4.26 $\pm$ 0.09 ^a
	9104	1.97 $\pm$ 0.39 ^{cd}	2.58 $\pm$ 0.49 ^{bc}	2.31 $\pm$ 0.50 ^{bcd}
	9140	2.24 $\pm$ 0.29 ^{cd}	1.40 $\pm$ 0.42 ^{efg}	1.81 $\pm$ 0.46 ^{cde}
	9143	2.83 $\pm$ 0.30 ^{bc}	3.47 $\pm$ 0.33 ^{ab}	2.88 $\pm$ 0.16 ^{bc}
Middle leaf	G6	4.09 $\pm$ 0.48 ^a	3.91 $\pm$ 0.44 ^a	4.00 $\pm$ 0.25 ^a
	9104	1.21 $\pm$ 0.49 ^{de}	0.89 $\pm$ 0.32 ^{fg}	1.03 $\pm$ 0.18 ^{ef}
	9140	1.90 $\pm$ 0.36 ^{cd}	2.29 $\pm$ 0.20 ^{cde}	1.63 $\pm$ 0.15 ^{de}
	9143	3.59 $\pm$ 0.51 ^{ab}	2.54 $\pm$ 0.31 ^{bcd}	2.98 $\pm$ 0.42 ^b
Basal leaf	G6	3.80 $\pm$ 0.80 ^{ab}	1.45 $\pm$ 0.19 ^{defg}	2.18 $\pm$ 0.36 ^{bcd}
	9104	0.33 $\pm$ 0.11 ^e	0.94 $\pm$ 0.29 ^{fg}	0.30 $\pm$ 0.06 ^f
	9140	2.14 $\pm$ 0.50 ^{cd}	0.50 $\pm$ 0.07 ^g	1.47 $\pm$ 0.10 ^{de}
	9143	1.80 $\pm$ 0.56 ^{cd}	1.70 $\pm$ 0.43 ^{cdef}	1.78 $\pm$ 0.23 ^{cde}

Means in columns followed by the same letter are not significantly different (P < 0.05).

petri dishes on moist tissue paper, covered with transparent plastic film (14 μ m) and stored in a climate chamber (T = 24 $^{\circ}$ C $\pm$ 1.5 $^{\circ}$ C, r.h. = 60%, 16L:8D h). After 48 hours pre-adaptation, thrips were transferred to fresh leaf discs ($\varnothing$ = 8 cm, 10 females/disc) where they were allowed to oviposit for 24 hours. From each accession, four leaf discs per plant age and leaf position combination 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 main treatment factors of plant age, accession and leaf position. Mean separation test was based on LSD (α = 0.05). Linear (Pearson) correlation between reproduction and log-transformed damage index values from the greenhouse experiment was calculated.

Results

Greenhouse experiment. Damage on the first leaf, measured two weeks after inoculation was significantly lower on 9104, 9140 and 9143 than on susceptible G6 (Table 1), ANOVA indicated a significant effect of accession: df = 3, F = 16.131, P < 0.001. The damage index which was determined 7.5 weeks after inoculation also showed a significant reduction in damage on these three accessions when compared to G6 (ANOVA: df = 3, F = 36.086, P < 0.0001).

Effect of plant age and leaf position on reproduction. Reproduction on accessions 9104, and 9140 was sig-

Table 3. Effect of plant age and leaf position of cucumber on reproduction of *F. occidentalis*. Results of ANOVA

Source of variation	df	F	P
Plant age	2	2.05	0.134
Accession	3	56.91	< 0.001
Leaf position	2	34.12	< 0.001
Plant age*accession	6	1.14	0.343
Plant age*leaf position	4	2.24	0.070
Accession*leaf position	6	3.38	< 0.010
Plant age*accession*leaf position	12	1.99	< 0.05

nificantly reduced in most cases when compared to G6 (Table 2). Reproduction on 9143 was in four of nine comparisons significantly lower than on G6. Results of ANOVA showed that accession and leaf position had a significant effect on reproduction while plant age had not (Table 3). Significant interaction accession leaf position indicates that the effect of leaf position differed among accessions. Accession 9104 showed a very clear leaf position effect i.e. reproduction was highest on apical leaves, intermediate on middle leaves and lowest on basal leaves, whereas in 9140 this effect was not clear. On accession 9143 reproduction was reduced on basal leaves. This also holds for G6, except for plants of 4.5 weeks old. In the latter group of plants there was no reduction in reproduction on basal leaves (Table 2). In general, reproduction is highest on young (apical) leaves. The correlation between reproduction and the log-transformed damage index values from the

Table 4. Correlation (r^2) between log-transformed damage index values from the greenhouse experiment and reproduction of *F. occidentalis* on leaf discs from leaves from different leaf position and plant age (n = 4)

Leaf position	Plant age (weeks)		
	4.5	5.5	6.5
Apical leaf	0.91, P = 0.044	0.51, P = 0.285	0.86, P = 0.075
Middle leaf	0.74, P = 0.138	0.89, P = 0.057	0.87, P = 0.067
Basal leaf	0.87, P = 0.068	0.27, P = 0.482	0.68, P = 0.178

greenhouse experiment is high ($r^2 > 0.85$) in several of the plant age and leaf position combinations (Table 4).

Discussion

It has been shown by Mollema et al. (1993) that the same cucumber accessions as used in our study showed reduced levels of damage ($\text{mm}^2 \times 1000$ measured 6 weeks after inoculation) at the mature plant stage in a choice situation: G6 = 6.6, 9104 = 0.6, 9140 = 0.1, 9143 = 0.1. In the present study it has been demonstrated that in a no-choice test damage levels are comparable to the choice situation. This is important since in practice cucumbers are grown in monoculture (only one cultivar), and resistance to thrips should be effective in such a (no choice) system.

Two weeks after inoculation, all three resistant accessions, 9104, 9140 and 9143, showed less damage than the susceptible G6. Differences in level of damage between 9104, 9140 and 9143 were not significant. The level of damage on 9104 was somewhat higher than on 9140 and 9143. A slightly higher damage level in 9104 is usually found in experiments where damage is quantified two weeks after inoculation with larvae (Balkema et al., unpublished). In contrast, seven and a half weeks after inoculation, i.e. *F. occidentalis* was present for three to four generations, 9104 showed the lowest level of damage, though not significantly different from 9140 and 9143. These contrasting trends between short and long term experiments can be explained by the effect of resistance on the life history of *F. occidentalis*. Reproduction is reduced strongest on 9104 followed by 9140 and 9143 (Table 2). When compared to G6, Soria and Mollema (1995) found that preadult survival is strongly reduced on 9104 and 9140 but to a lesser extent on 9143 (G6 = 57%, 9104 = 5%, 9140 = 3% and 9143 = 18% survival until adult emergence on leaf discs). Developmental time from egg to adult is longer on 9140 than on the other accessions

(Soria & Mollema, 1995). It is evident that in long term experiments all these parameters affect the population growth and consequently the level of damage.

Lewontin (1965) showed that for colonizing species (with high fecundity), changes in developmental time have larger effects on the population growth rate than changes in fecundity. However, when the population growth rate gets low, the relative importance of reproductive output increases (Caswell & Hastings, 1980). Thrips population growth rate is supposedly quite low on the resistant accessions, and therefore differences in reproduction between the accessions will have a great impact on population growth rate and subsequent damage levels on the plant. The relatively strong reduction in reproduction on 9104 may explain why this accession shows the highest resistance level in long term experiments (thrips present for several generations) and not in short term experiments (only larvae present).

The present study shows a significant effect of leaf position and no effect of plant age (in the test range) on reproduction of *F. occidentalis*. In their study on the soybean looper, *Pseudoplusia includens*, on soybean, Reynolds and Smith (1985) also found significant effects on leaf position but not of plant age on insect growth. Similar to our study the top leaves of the soybean plants were more suitable for *P. includens* than the lower leaves. The effect of leaf position on the reproduction of the thrips should be taken into account when performing tests with cucumber accessions: on basal leaves of 4.5 weeks old plants and middle leaves of 5.5 weeks old and middle and top leaves of 6.5 weeks old plants, discrimination between accessions is optimal. The results of reproduction tests on leaf discs taken from leaves from these positions correlate well with resistance levels of mature plants in the greenhouse (Table 4). This indicates that the reduction in damage of the accessions studied is due to resistance rather than tolerance. The reproduction test can therefore be used as a quick test of thrips resistance in these cucumber accessions.

In other studies a significant effect of plant age on resistance to insects has been found, e.g. an increase in resistance with plant age in tomato to the greenhouse whitefly, *Trialeurodes vaporariorum* (Bas et al., 1992) and in resistance of celery to *Spodoptera exigua* (Hübner), measured as survival (Diawara et al., 1994). Differences in plant age in these studies were however much larger than in our experiments. We used relatively young plants, because our aim was to develop a quick test using plants as young as possible.

In conclusion, for the evaluation of resistance in cucumber to *F. occidentalis*, leaf position should be taken into account. In the tested accessions, reduction in reproduction in the leaf disc assay correlates well with reduced damage levels of mature plants in the greenhouse. Therefore the leaf disc assay will be useful in further research on these accessions. It is currently used in the study of responses of different strains of *F. occidentalis* to host plant resistance (de Kogel et al., 1995).

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