



# The effect of plant development on thrips resistance in *Capsicum*

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## Abstract

Western flower thrips [*Frankliniella occidentalis* (Pergande)] is a worldwide pest insect that causes damage in pepper cultivation, so growers would benefit from host plant resistance. The objectives of this study were (1) to evaluate the effect of plant age on thrips resistance using nine *Capsicum* accessions with different levels of thrips resistance at three different plant ages, and (2) to study the effect of leaf age on thrips resistance in a resistant and a susceptible pepper accession. The fraction of first instar larvae that did not develop into second instar was used as a measure for thrips resistance. Our results show that plants start to develop thrips resistance when they are between 4 and 8 weeks old. This transition was most marked on the resistant accession CGN16975, on which about 50% of the L1 larvae developed into the next stage on 4-week-old plants, whereas none of them developed beyond the L1 stage on 8- or 12-week-old plants. Furthermore, it is shown that youngest fully opened leaves of the resistant accession CGN16975 are significantly more resistant to thrips than older leaves; 89% of the L1 larvae did not develop into the next stage on the youngest leaves, whereas 57% did not develop beyond the L1 stage on the oldest leaves. Young leaves of the susceptible accession CGN17219 are more susceptible than older leaves; 9 versus 52% of the L1 larvae did not develop into the next stage on young and old leaves, respectively. These findings can be used to improve integrated pest management strategies.

**Keywords** Host plant resistance · Plant age · Leaf age · *Frankliniella occidentalis*

## Introduction

Thrips is a worldwide pest insect in agricultural and horticultural crops (Kirk and Terry 2003). The most important thrips species in *Capsicum* in Europe is western flower thrips [*Frankliniella occidentalis* (Pergande)], causing constraints to pepper production both in the field and in the greenhouse (Siemonsma and Kasem 1994; Tommasini and Maini 1995). Thrips can damage plants both directly and indirectly. Direct

damage is caused by feeding on the leaves, flowers and fruits, resulting in their deformation, reduced plant growth, altered carbon allocation and thus reduced yield (Welter et al. 1990; Shipp et al. 1998). Very characteristic is the “silvery damage” which is caused by thrips piercing the plant cells with their stylet-shaped mouth and sucking out the cell content, leaving silver leaf scars (Chisholm and Lewis 1984). Indirect damage is caused by the viruses they transmit, of which tomato spotted wilt virus (TSWV) is the most important one in pepper (German et al. 1992).

It is difficult to control thrips because of their high reproductive rate, short life cycle and cryptic behaviour (Cloyd 2009). Monitoring the thrips population and limiting its growth to prevent an outbreak is therefore important. This can at least partly be accomplished by using cultural, mechanical, physical and biological control (Mouden et al. 2017). In addition to these protective measures, it is highly desirable to identify plants that have a natural source of resistance against thrips, either constitutive or induced. Host plant resistance can be found in several plant species and in several forms (Smith 2005; Broekgaarden et al. 2011), for example, by the presence of a modified epicuticular wax

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layer on leaves of cabbage (Voorrips et al. 2008; Znidarcic et al. 2008), or by the production of specific compounds such as acylsugars that have a negative effect on insects (Mirn-ezhad et al. 2010; Glas et al. 2012).

Host plant resistance to insects has been found in a large number of crops. In some cases, the resistance is only expressed at specific plant developmental stages. For instance, the epicuticular lipids that play a role in resistance against herbivorous insects can vary with plant part, plant age and environmental condition (Eigenbrode and Espelie 1995). Another example is the increasing resistance in a *Brassica oleracea* cultivar against cabbage whitefly when these plants grow older (Broekgaarden et al. 2012). Similar findings have been reported in resistance of *Solanum lycopersicum* against tomato leaf miner (Leite et al. 2001). In addition, it has been shown that resistance levels may vary in different parts of the plant (De Kogel et al. 1997; Leiss et al. 2009).

Host plant resistance in pepper against thrips may also be affected by plant development. Maharijaya et al. (2011) screened several pepper accessions when the plants were 12 weeks old. Larval development and mortality was determined on the youngest fully opened leaves only (Maharijaya et al. 2012). Therefore, it is not known whether the host resistance against thrips that was identified by Maharijaya et al. (2011) changes during plant development, and whether the resistance varies between plants of different ages and leaves of different ages.

The aims of this study are to determine whether or not the resistance in pepper against thrips changes during plant development, and whether or not the level of resistance varies between leaves of the pepper plant. Based on previous studies on the effect of plant development on insect resistance (De Kogel et al. 1997; Leite et al. 2001; Leiss et al. 2009; Broekgaarden et al. 2012), we hypothesised that the level of resistance to thrips in young leaves increases with plant age, and that thrips resistance decreases with leaf age.

## Materials and methods

### Plant material and growing conditions

To study whether plant age affects thrips resistance, we used the same nine *Capsicum* accessions as Maharijaya et al. (2012), which were classified as susceptible, intermediate resistant and fully resistant to thrips, based on the damage to the youngest fully opened leaves by female adults of *F. occidentalis* and development of first instar larvae (L1). Seeds were obtained from the Centre of Genetic Resources, the Netherlands. Three groups of four plants of each accession were sown with a 4-week interval in potting compost in a greenhouse of Unifarm, Wageningen University and

Research, Wageningen, the Netherlands. Plants were grown at 25 °C, with a photoperiod of L16:D8, and 70% RH. No insecticides were applied. Thrips were controlled biologically using the predatory hemipteran *Orius laevigatus* (Fieber) (Entocare C.V., Wageningen, the Netherlands). Plants were watered three times per week, two times per week nutrients were added. The three youngest fully opened leaves of each plant were evaluated for thrips resistance 12 weeks after the first group of plants was sown, so at plant ages of 12, 8 and 4 weeks, respectively. Plants were not yet flowering when the youngest fully opened leaves were collected.

To study whether different levels of thrips resistance are found in leaves of different ages, we selected one resistant (CGN16975) and one susceptible (CGN17219) accession. Five plants of each accession were sown and grown in the same conditions as the plants of the plant age experiment. At a plant age of 12 weeks we collected leaves of five age classes (1–5, corresponding to a leaf age of about 0, 2, 4, 6 and 8 weeks, respectively) for use in a detached leaf assay for thrips resistance (Additional material 1, Electronic Supplementary Material 1). Three leaves of each leaf age class were collected per plant. These leaves were the three youngest fully opened leaves of each plant at a plant age of 12, 10, 8, 6 and 4 weeks. Plants of CGN16975 and CGN17219 had 4 and 6 real leaves, respectively, at a plant age of 4 weeks. Plants of both accessions showed the same number of leaves at a plant age of 6 weeks or older. The plants did not flower until after the leaves were evaluated for thrips resistance at the plant age of 12 weeks.

Plants from accessions CGN16975 and CGN17219 were used to determine the thrips damage in a no-choice whole plant damage assay. Five plants of each accession were sown and grown in the same conditions as the plants of the plant age experiment. Four weeks after sowing, the plants were enclosed in thrips-proof sleeves to prevent thrips from escaping from the plant.

Three plants from accession CGN16975 were used to study oviposition by female thrips. From each plant the main stem was removed at a plant age of 20 weeks, and the largest side branch that emerged from the base of the main stem was enclosed in a thrips-proof sleeve to prevent thrips from escaping. Each side branch contained at least 40 old and 40 young leaves. The plants were flowering at the start of the oviposition experiment.

### Thrips rearing

A population of *Frankliniella occidentalis* (acquired from Greenhouse Horticulture of Wageningen University and Research, Bleiswijk, the Netherlands) was reared on *Phaseolus vulgaris* beans in glass rearing pots covered with thrips-proof gauze in a growth cabinet at 25 °C, L16:D8, 70% relative humidity. Female adults were allowed to lay

eggs on snack cucumbers for 24 h, after which the thrips were brushed off and the cucumbers were kept in the growth cabinet at 25 °C. After 4 days, new synchronised first instar larvae (L1) emerged (Mollema et al. 1993).

### Detached leaf assay

Each detached leaf, selected as discussed in the Plant material section, was placed with the petiole in a droplet of 1.5% water agar in a Petri dish (BD Falcon, tight-fit lid 50 × 9 mm). Five synchronised L1 larvae were placed on each detached leaf. The Petri dish was firmly closed to prevent the larvae from escaping. The Petri dishes were incubated at 25 °C in a growth cabinet. The developmental stage of each thrips was determined at day 3, 5 and 7 post infestation. The fraction of larvae that did not develop from the first into the second larval stage (from L1 to L2) was used as a measure for thrips resistance. Larval development was more consistent as a measure for thrips resistance than larval survival. In some replicates, survival was affected by the condensation of water causing droplets on the lids of the firmly closed Petri dishes after 5–7 days that caused some larvae to drown. Since under optimal conditions, first instar larvae develop into second instar larvae in 1–2 days (Lublinkhof and Foster 1977), larval development was not affected by the formation of water droplets, and was therefore selected as resistance criterion.

### Whole plant damage assay

For the whole plant damage assay, female adults were carefully collected by using an aspirator and anaesthetised with carbon dioxide (CO<sub>2</sub>). When 7 weeks old, plants were infested each with 20 female adult thrips. To ensure high thrips pressure, the infestation was repeated 1 week later. The five most damaged leaves of each plant were scored for

silvering damage, caused by thrips feeding, when the plants were 10 weeks old. The plants did not yet flower when they were scored. The damage scale is shown in Table 1.

### Oviposition

For the oviposition assay, female adults were carefully collected by using an aspirator and anaesthetised with CO<sub>2</sub>. Each selected side branch was infested with 75 adult females. After 3 days, the 40 oldest and 40 youngest leaves of each side branch were removed and each leaf was placed in a separate Petri dish as described above. All adult thrips were removed. The leaf area was determined by analysing pictures of the leaves in ImageJ 1.51f (Schneider et al. 2012). The Petri dishes were incubated at 25 °C in a growth cabinet. Emerged larvae were counted and removed on 6, 8 and 10 days after the initial infestation. As the average development time from egg to the first instar is 3–4 days at 25 °C, we assumed that all viable eggs were hatched within 10 days after infestation (McDonald et al. 1998; Zhang et al. 2007). The average leaf area of young leaves and the average leaf area of old leaves, respectively, were used to determine the number of larvae per cm<sup>2</sup> of leaf area per leaf age category.

### Statistical analysis

The fractions of larvae arrested at the L1 stage were transformed as  $y = \arcsin(\sqrt{x})$ . Analysis of variance (ANOVA) was carried out to test for significant differences in larval development between plants and leaves of different ages. For the plant and leaf age experiment, a two-way ANOVA was carried out to determine the effects of age, accession and the interaction between age and accession, respectively. When significant *F* values ( $P < 0.05$ ) were obtained, all mean values in the plant and leaf age experiment, respectively, were compared using Fisher's Protected

**Table 1** Evaluation scale for a whole plant thrips damage assay

Leaf damage scale	Description	% of silvering damage
1	No damage	0
2	Tiny silvering spots	<0.1
3	Some small spots near the mid vein or edge of the leaf	0.1–1
4	Moderate number of spots near the mid vein or edge of the leaf, or some small spots more regularly distributed over the entire leaf	1–2
5	Moderate number of spots, more regularly distributed over the entire leaf	3–5
6	Intermediate between 5 and 7	6–10
7	Many silvering spots over the entire leaf	11–20
8	Intermediate between 7 and 9	21–40
9	Very heavy silvering, large leaf surface area damaged	>40

The five most affected leaves of each plant were evaluated. The damage scale is adapted from Linders et al. (2010)

least-significant-difference (LSD) test. For the whole plant damage assay, a Mann–Whitney  $U$  test was used to determine whether the differences between damage score of the most affected leaves of the two tested accessions were significant. For the oviposition assay, a Wilcoxon matched-pairs signed-ranks test was used to determine whether the differences between emerged larvae on old and young leaves per  $\text{cm}^2$  of leaf area were significant. These statistical analyses were conducted using GenStat 18th edition (VSN International 2015).

## Results

### Plant age experiment

The two-way ANOVA showed a significant interaction between accession and plant age in their effect on the fraction of larvae arrested at the first instar stage ( $P < 0.001$ , Table 2). A significant effect of plant age on larval development was

**Table 2** Two-way ANOVA results for the effects of plant age and *Capsicum* accession on larval development of *Frankliniella occidentalis*

Source of variation	d.f.	Sum of squares	Mean square	$F$ ratio	$P$
Plant age	2	3.90	1.95	27.87	<0.001
Accession	8	28.86	3.61	51.62	<0.001
Plant age–accession	16	5.40	0.34	4.83	<0.001
Residual	183	12.79	0.07		
Total	209	50.95			

found in six of the nine tested accessions (Table 3). In five of these accessions (PRI1996112, PRI1996236, CGN17042, CGN20503 and CGN16975), a significantly lower average fraction of L1 was found after 7 days when the plants were 4 weeks old, compared to the plants from the same accession that were 8 or 12 weeks old. In one of the accessions, the most susceptible accession CGN17219, a significantly higher average fraction of L1 was found after 7 days in 4-week-old plants compared to 8- and 12-week-old plants. We did not find a significant difference between 8- and 12-week-old plants among all tested accessions.

### Leaf age experiment

To study the possible effect of leaf age on resistance, we selected the most susceptible and the most resistant accession from the plant age experiment, CGN17219 and CGN16975, respectively. The two-way ANOVA showed a significant interaction between accession and leaf age on larval development ( $P < 0.001$ , Table 4). Leaf age affected larval development in the resistant and susceptible accession in opposite ways (Table 5). In the resistant accession, we found that on the youngest fully opened leaf the fraction of L1 larvae was significantly higher than on leaves of the other ages. In the susceptible accession, we found that larval development significantly increases as leaf age decreases.

Furthermore, it was shown that the differences in larval development when comparing leaves of the same age between the susceptible and resistant accession were significant when the leaf was 6 weeks or younger (Table 5). The largest contrast between the accessions was found in the youngest leaves. When leaves were 8 weeks old, no

**Table 3** Larval development of *Frankliniella occidentalis* in nine *Capsicum* accessions at different plant ages

Accession code	Accession	Level of resistance <sup>a</sup>	Average Fraction of L1 (7dpi) per plant age <sup>b</sup>		
			4 weeks	8 weeks	12 weeks
CGN17219	<i>C. chinense</i> no 4661	S (2.6)	0.06 (bc)	0.00 (a)	0.00 (a)
PRI1996108	<i>C. chinense</i> PI281428	S (2.9)	0.11 (cd)	0.17 (cde)	0.13 (cd)
PRI1996112	<i>C. chinense</i> PI315023	S (2.8)	0.02 (ab)	0.37 (defg)	0.29 (def)
PRI2004001	<i>C. annuum</i> Bruinsma Wonder	M (1.8)	0.43 (cdefgh)	0.18 (cde)	0.15 (cde)
CGN22817	<i>C. frutescens</i> Lombok	M (1.4)	0.24 (def)	0.40 (fgh)	0.30 (efgh)
PRI1996236	<i>C. annuum</i> Laris	M (1.1)	0.17 (cde)	0.45 (h)	0.43 (gh)
CGN17042	<i>C. baccatum</i> no1553	R (0.8)	0.30 (efgh)	0.77 (i)	0.88 (ij)
CGN20503	<i>C. annuum</i> Bisbas	R (0.6)	0.32 (efgh)	0.88 (ij)	0.93 (j)
CGN16975	<i>C. annuum</i> AC1979	R (0.3)	0.47 (h)	1.00 (k)	1.00 (k)

At the indicated plant age, the three youngest fully opened leaves of four plants of the same accession were infested with five L1 larvae in a detached leaf assay and 7 days later, the fraction that remained in L1 stage was determined (average fraction of L1)

<sup>a</sup>Based on the results of previous screening by Maharijaya et al. (2011), in which damage scores were given (0=no injury, 3=severe injury, S susceptible, M intermediate resistant, R resistant)

<sup>b</sup>All means followed by the same letter are not significantly different (Fisher's protected LSD test,  $P > 0.05$ )

**Table 4** Two-way ANOVA results for the effects of leaf age and *Capsicum* accession on larval development of *Frankliniella occidentalis*

Source of variation	d.f.	Sum of squares	Mean square	F ratio	P
Leaf age	4	0.84	0.21	4.54	0.002
Accession	1	8.49	8.49	183.12	<0.001
Leaf age–accession	4	5.56	1.39	29.99	<0.001
Residual	134	6.21	0.05		
Total	143	21.11			

**Table 5** Larval development of *Frankliniella occidentalis* in a resistant (CGN16975) and a susceptible (CGN17219) pepper accession on leaves of different ages

Leaf age	Average fraction of L1 <sup>a</sup>	
	CGN16975	CGN17219
1	0.89 (a)	0.09 (e)
2	0.69 (b)	0.15 (e)
3	0.58 (bc)	0.31 (d)
4	0.61 (b)	0.46 (c)
5	0.57 (bc)	0.52 (bc)

The leaves were tested for larval development when the plant was 12 weeks old in a detached leaf assay, by infesting each leaf with five L1 larvae and determining the fraction of larvae that remained in the L1 stage at 7 days after infestation (average fraction of L1). Leaves of ages 1–5 were about 0, 2, 4, 6 and 8 weeks old at time of testing, respectively

<sup>a</sup>All means followed by the same letter are not significantly different (Fisher's protected LSD test,  $P > 0.05$ )

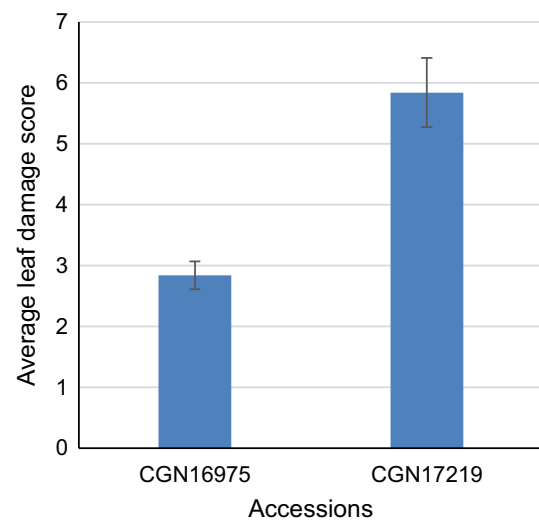
significant differences between the resistant and susceptible accession were found.

### Whole plant damage assay

In addition to the leaf age experiment, the most resistant accession CGN16975 and most susceptible accession CGN17219 were also used in a no-choice whole plant damage assay when plants were 10 weeks old. The damage was determined by evaluating the five most damaged leaves in five plants of these two accessions. Most thrips damage was found on the oldest leaves in both accessions. Thrips damage score was significantly higher for the susceptible accession CGN17219 than for the resistant accession CGN16975 (Fig. 1).

### Oviposition assay

Plants of the resistant accession CGN16975 were used in an oviposition assay to study whether there is a difference in oviposition on young and old leaves. The total number of



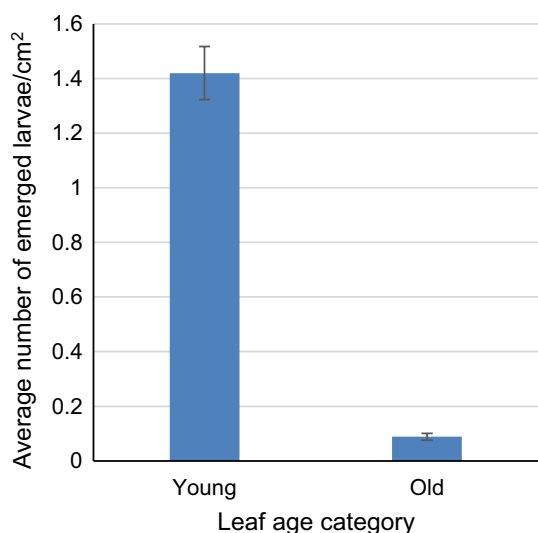
**Fig. 1** Average leaf damage score of the five most affected leaves of five whole plants of the resistant accession CGN16975 and the susceptible accession CGN17219. Each plant was infested twice with twenty female adult *Frankliniella occidentalis* when the plants were 7 and 8 weeks old. The damage of each of the five most affected leaves per plant was scored according to the scale given in Table 1 when the plants were 10 weeks old. The error bars indicate the standard error. The average leaf damage score for CGN16975 was significantly lower than the score for CGN17219 ( $P < 0.001$ )

emerged larvae per cm<sup>2</sup> of leaf area at 10 days after infestation was determined. A significantly higher number of larvae per cm<sup>2</sup> emerged from young leaves compared to old leaves (Fig. 2).

## Discussion

### Plant age affects thrips resistance

We showed that on 4-week-old plants of all accessions L1 larvae can develop to the L2 stage, although there are significant differences between the accessions. Between plant ages of 4 and 8 weeks, we observed an increased resistance in five of the accessions (Table 3). This transition was most marked on CGN16975, the most resistant accession included in this study, on which about half of the L1 larvae were able to develop into the next stage on 4 weeks old plants; whereas on 8- or 12-week-old plants they did not develop at all beyond the L1 stage. This finding suggests that thrips resistance increases with plant age. Differences in insect resistance between plants of different ages is also found in other crops. For instance, *Bemisia tabaci* (Gennadius) resistance in *Solanum pennellii* L. is higher in 20-week-old plants than in 6-week-old plants (Van den Oever-Van den Elsen et al. 2016), and 12-week-old *Brassica oleracea* L. plants have higher resistance to the whitefly *Aleyrodes proletella* L.



**Fig. 2** Average number of emerged larvae per cm<sup>2</sup> of leaf area in young and old leaves of three lower side branches of three plants of CGN16975 at 10 dpi. Each side branch was infested with 75 female adult *Frankliniella occidentalis* for 3 days. Up to 10 days after infestation, the emerged larvae on the 40 youngest and 40 oldest leaves of each side branch were counted. The error bars indicate the standard error of the mean. The average number of emerged larvae per cm<sup>2</sup> was significantly lower in old leaves compared to young leaves ( $P < 0.001$ )

than 6-week-old plants (Broekgaarden et al. 2012). Whether the resistance that is developing with plant age in the resistant *Capsicum* accessions is constitutive (also present in the absence of the thrips) or induced by thrips feeding remains an open question. Further research may shed light on this. We also observed a clear interaction between plant age and accession. In contrast to resistant accessions, susceptible accessions do not show a significant increase in thrips resistance when plant age increases.

### Leaf age affects thrips resistance

We observed significant differences in thrips resistance between young and older leaves of the resistant accession CGN16975 and the susceptible accession CGN17219. When comparing the leaves between the two accessions, no significant difference in thrips resistance was found between the oldest leaves of the resistant and susceptible accession; on these leaves, almost half of the L1 larvae develop into the next stages on both accessions. In the resistant accession CGN16975, the youngest fully opened leaves show the highest thrips resistance. A similar observation was made in *Senecio*, in which Leiss et al. (2009) found a significant positive correlation between leaf age and silvering damage in a choice assay, suggesting a higher thrips resistance in younger leaves. Another example of higher insect resistance in younger leaves is described by Alvarez et al. (2014),

who found that green peach aphid *Myzus persicae* (Sulzer) resistance in younger leaves of potato was higher than in older leaves. In contrast, the susceptible pepper accession CGN17219 shows a higher larval development on younger leaves compared to older leaves. The contrasting effect on larval development on the resistant and susceptible accession can explain the observed interaction between leaf age and accession in their effect on larval development. The higher larval development on younger leaves of the susceptible accession may be explained by higher nutrition and water contents of young compared to old or senescent leaves (Mattson 1980; Boege and Marquis 2005). A similar observation was made by De Kogel et al. (1997), who observed a higher thrips reproduction on apical leaves compared to middle or basal leaves, both in a choice and non-choice study on three partially resistant and one susceptible cucumber accession. These studies used different methods and criteria than we did, so a direct comparison with the outcomes of these studies is not possible. However, these results suggest that in general, young leaves are better suited for thrips performance than older leaves, but that resistance, if present, is expressed most strongly in the younger leaves, resulting in a trade-off. The differences in thrips resistance between young and old leaves in both the resistant and the susceptible accession might be related to the levels of defence compounds. In general, young leaves often contain higher concentrations of defence compounds than older leaves (McCall and Fordyce 2010).

The results from the leaf age experiment agree with our observations in the whole plant damage assay. The average damage score of all leaves evaluated for thrips damage per accession shows that the resistant CGN16975 plants received a significantly lower damage score than the susceptible CGN17219. This difference is found despite the lower level of thrips resistance in the older leaves compared to the youngest leaves within plants of the resistant accession, indicating that the thrips resistance in the youngest leaves does reduce whole plant thrips damage. In this no-choice experimental set-up, the thrips caused silvering damage to the older leaves in the resistant accession as well, which raises the question whether the thrips oviposit on the older leaves, enabling them to reproduce on this accession. In potato, Alvarez et al. (2014) showed that young leaves were resistant to the green peach aphid, but that the insects survive and reproduce on older leaves. The oviposition assay showed that female adult thrips oviposit on both old and young leaves. Despite the resistance against thrips in the young leaves, females laid a significantly higher number of eggs per cm<sup>2</sup> on young leaves compared to old leaves, suggesting that the resistance in the young leaves is useful, as newly emerged larvae on young leaves are directly exposed to host plant resistance. Badenes-Perez et al. (2014) described a similar observation in plants of the genus *Barbarea*: *Plutella*

*xylostella* L. laid more eggs on young leaves compared to older leaves although the abundance of two plant secondary metabolites that were suggested to play a role in plant defence and feeding deterrence was higher in young leaves.

Based on these findings, we formulated the following hypothesis. In general, leaf nutritional quality decreases as leaves grow older (Mattson 1980; Boege and Marquis 2005). Because of the better leaf quality, thrips larvae perform better on young leaves than on old leaves of susceptible accessions. In resistant accessions, the resistance is highly expressed only in young leaves, thus preventing the thrips to develop there. During ageing of the leaves the resistance factor decays, resulting in similar levels of susceptibility in the older leaves of both resistant and susceptible accessions. As female adult thrips strongly prefer to oviposit on young leaves of a resistant plant, this suggests they are unable to detect or react to (a) resistance factor(s) that affect first instar larvae negatively. Therefore, a high resistance level in young leaves is useful for the plant despite the susceptibility of older leaves.

### Implications for plant resistance breeding and integrated pest management

This study provides information to improve the methods to determine host resistance against thrips in *Capsicum*. The plant age experiment shows that the level of thrips resistance can be determined when plants are 8 weeks old instead of 12 weeks old, because no significant difference in thrips resistance in 8 and 12 weeks old plants was found. The leaf age experiment shows that the largest contrast in thrips resistance between a resistant and a susceptible accession was found in the youngest leaves, indicating that a comparison between these leaves could provide most information on the mechanism of the resistance based, e.g. on gene and protein expression and metabolite profile. The whole plant damage assay shows that, although the older leaves of the resistant accession do not provide resistance against thrips, the resistance in the younger leaves does affect thrips damage, probably because oviposition predominantly takes place on these young leaves as shown by the oviposition assay. Therefore, this study shows that CGN16975 is a potential donor for host plant resistance against thrips.

The outcome of this study also provides information for pest management and crop protection. Considering that female adults can lay four to five eggs per day in an optimal environment in the absence of pollen (Van Rijn et al. 1995), the number of thrips can still increase rapidly and can subsequently cause large damage to the plant as almost half of the L1 can develop into L2 in young resistant plants. Therefore, it is important to protect plants until thrips resistance is fully expressed. It is recommended to use protection measures in combination with host plant resistance to limit

the growth and spread of the thrips population. Extra protection can be provided for instance by applying UV-reflective mulch (Reitz et al. 2003) or by using water or sticky traps with attractive volatiles (Teulon et al. 1993; Koschier et al. 2000; Tang et al. 2016), leading to a decrease in number of *F. occidentalis* adults. Moreover, using a natural predator such as *Orius insidiosus* in an early plant stage can lead to a much greater decrease in number of *F. occidentalis*, thus keeping the thrips population below the economic threshold (Ramachandran et al. 2001).

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