Host plant resistance of tomato plants to western flower thrips

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Effect of sugar spraying on host plant resistance to western flower thrips in tomato

Abstract

Sugar spraying can cause induced plant resistance. In this study we investigated the effects of sugar spraying on the resistance to western flower thrips, WFT, *Frankliniella occidentalis* on tomato. We tested three different sugars: sucrose, fructose and glucose, at four concentrations: 0, 1, 10 and 100 ppm, to induce resistance of the cultivated tomato (var. Moneymaker). Bioassays conducted 2 weeks after sugar treatment showed significantly lower damage compared to bioassays after 24 hours, while such a difference was absent in the control. Only for fructose we detected indications that sugar-spraying may increase plant resistance to thrips. At concentrations of 1 and 10 ppm fructose plants showed less thrips damage compared to control plants. In 10 out of the 12 treatments with fructose, thrips damage was less than in the control. Although this number is significantly higher than can be expected by chance (χ^2 = 5.3, df= 1 and *P* = 0.02), differences were generally small and not significant. Plant leaf stage at the time of sugar spraying, did not affect thrips resistance.

Introduction

Sugars have been shown to control gene expression and development processes in plants acting as signaling molecules similar to classical plant hormones (Sheen et al., 1999). However, the underlying regulatory networks involving multiple signaling pathways are still not properly understood. Environmental stresses, such as pathogen infection and wounding, activate a cascade of defense responses and may also affect carbohydrate metabolism and sugar-responsive genes. It was therefore hypothesized that sugar spraying may also increase plant resistance and indeed several studies showed such positive effects.

Ehness et al. (1997) reported that in red goosefoot, *Chenopodium rubrum,* a treatment with 40 mM D-glucose caused induction of defense responses by an increase in the mRNA of

Phenylalanine Ammonia Lyase (PAL) a key enzyme for plant defense, as well as induction of the carbohydrate metabolism. Similarly, application of 10 ppm sugar sprays of glucose or fructose induced the resistance to western flower thrips (WFT), *Frankliniella occidentalis*, on apple leaves (Derridij, personal communication). Metabolomic analysis of these leaves showed increased amounts of chlorogenic acid (CGA) and the sugar trehalose in the sugar sprayed leaves (Derridj et al., 2009). Induced resistance due to sugar sprays also affects nematodes. Sprays, soil drenches or seed dressings of the naturally occurring sugar analogue DMDP (2,5-Dihydroxymethyle-3, 4-dihydroxypyrrolidinde), isolated from tropical legumes, inhibited different plant parasitic nematodes including the potato cyst nematodes *Globodera pallida, G. rostochiensis* and the virus transmitting nematode *Xiphinema diversicaudatum* (Birch et al., 1993a). Foliar sprays at concentrations of 1 and 10 ppm significantly decreased root galling of *Meloidogyne* spp. nematodes in tomato (Birch et al., 1993a).

Next to the effects on induced resistance, sugar spraying can influence insect behavior by functioning as sensory cues for contact with leaf surfaces (Derridj et al., 1996). Leaf surface sugars are known to influence oviposition in Lepidoptera. They act as egg-lying stimulants as has been shown for myo-inositol and the Spangle butterfly, *Papilio protenor*, (Honda, 1990), dulcito, a stereo- isomer of sorbitol, and the Spindle Ermine,*Yponomeuta cagnagella*, (Roessingh et al., 2000), fructose and the European corn borer, *Ostrinia nubilalis*, (Derridj et al., 1989), fructose, sorbitol and myo-inositol and the codling moth, *Cydia pomonella*, (Lombarkia & Derridj, 2002). A lack of these substances may thus explain resistance to *C. pomonella* in apple trees. Changes in the sugar metabolites on leaf surfaces may, therefore, be used to deter oviposition. Sugar foliar treatments of apple leaves with glucose or fructose at 10 ppm to induce resistance to *C. pomonella,* resulted in significant modifications of the amounts and ratios of sugars and sugar alcohols on the surface of apple leaves (Derridj et al., 2009). Application of synthetic blends of different types and ratios of these sugars and sugar alcohols on the surface of untreated apple leaves led to a significant reduction in oviposition and arrestment of neonate larvae of *C. pomonella.* The mechanism of this oviposition deterrence is still unknown. However, the sugar treated apple leaves contained significantly increased amounts of CGA and the sugar trehalose (Derridj et al., 2009).

Besides the direct effects of sugar spraying on pest resistance also indirect effects by way of increasing populations of predators or parasites have been reported (Azzouz et al., 2004). This increase is thought to be caused by the fact that sugars are a very common supplemental

food source for predators and parasitoids (Jacob & Evans, 1998; Azzouz et al., 2004; Rogers & Potter, 2004). Sprays of sucrose increased the populations of green lacewing, *Chrysoperla rufilabris,* which reduced the number of European corn borer larvae, *O. nubilalis*, before entering the corn stalk (Carlson & Chiang, 1973). Sucrose solution sprayed on a corn field increased the populations of three different Coccinellids, and that of a Chrysopid adult population (Schiefelbein & Chiang, 1966).

In this study, we tested direct effects of sugar spraying on resistance to WFT in tomato. WFT is one of the main pests in tomato production. Thrips has become a key agricultural pest because it is a successful invader, it is highly polyphagous, small of size, and shows an affinity for enclosed spaces. It has a short generation time coupled with asexual reproduction leading to a high reproductive potential (Morse & Hoddle, 2006). Feeding on actively growing tissue leads to distortion, reduction in plant growth and eventually yield loss. Feeding on expanded tissue results in the characteristic silver leaf scars, which affect product appearance and reduce market quality (de Jager et al., 1995). In addition, *F. occidentalis* is the primary vector of tospoviruses of which tomato spotted wilt virus is the economically most important one (Maris et al., 2003).

Consistent productivity and fruit quality of tomatoes are reliant upon sufficient control of insects (Csizky et al., 2005). Currently, mainly pesticides are used for pest control, including WFT. Intensive treatment with insecticides has lead to pesticide resistance, human health risks, death of beneficial insects, and increased contamination of the environment. Biological control is not properly effective and available cultivars do not have sufficiently high levels of pest resistance to allow for significant reductions in the amount of pesticides used in the crop (van Emden & Service, 2004). Due to these problems there is an increasing need for more suitable alternatives. This has stimulated the search for new and more environmentally friendly methods of crop protection, using less toxic or non toxic, ecological plant-derived chemicals.

Because of the serious problem to control WFT in different vegetables and crops, including tomato, our aim was to study the effect of sugar-spraying on host plant resistance to thrips in tomato. The cultivated tomato, *Solanum lycopersicum* L., is a most popular garden vegetable and the 2nd most important vegetable crop in the world based on its per capita consumption (FAOSTAT, 2008). Three different sugars, sucrose, fructose and glucose were used at four different concentrations: 0, 1, 10 and 100 ppm. We tested the application of sugar spray at different leaf stages and different time periods between sugar treatment and start of bioassays. Finally, the effect of sugar treatment on tomato leaf metabolites was studied with Nuclear

Magnetic Resonance Spectroscopy (NMR). We specifically wanted to answer the following questions:

- Does sugar spraying affect host plant resistance to thrips in tomato?
- Do the effects of sugar spraying on resistance depend on the time between sugar treatment and the onset of the bioassay?
- Does the effect of sugar spraying on resistance depend on the type of sugar?
- Is the effect of sugar spraying on resistance concentration depended?
- Does sugar spraying affect the plant's metabolomic profile?
- Does the leaf stage at which plants are treated with sugar spray affect resistance?

Material and methods

The effects of sugar type and concentration on host plant resistance and metabolomic profiles

The cultivated tomato (var. Moneymaker), which is highly susceptible to WFT was used as a host plant. The seeds were directly sown into pots (13 cm Ø) filled with potting soil. Plants were thinned to one plant per pot after one week. Ten replicates for each treatment were grown in a randomized fashion in a climate chamber (L16: D8, 25 °C, 70% RH & 11.36 µmol m^{-2} s^{-1} light intensity) and grown for 5 weeks. Five replicates were used for the thrips bioassay while the other five replicates were used for metabolomics. Plants were sprayed at the 4^{th} leaf stage once at 9:00 h directly after the light was switched on in the climate room. Plants were sprayed with 0.1 ml of three different sugar solutions respectively: fructose, glucose and sucrose at four different concentrations: 0, 1, 10 and 100 ppm. In this experiment, the effects of the sugar treatment on thrips resistance were measured two times: after 24 hours and after 2 weeks. This lead to 120 plants for the bioassays (2 repetitions × 3 sugars × 4 concentrations × 5 replicates) and 120 plants for metabolomics. We intended to do the metabolomic analyses only for those cases where significant effects were detected. In the end this resulted in 15 plants being analysed (see result section). The control plants were sprayed with pure water. A plastic sheet was used to prevent contamination of spraying treatments between plants.

Bioassays. Whole plant bioassays were used to evaluate thrips feeding damage 24 h after spraying and 2 weeks after spraying. The plants were subjected to a non-choice whole plant bioassay as described by Leiss et al. (2009). Whole plants were placed in individual thrips proof

cages consisting of Perspex cylinders (60 cm height, 20 cm diameter) closed on top with nylon gauze of 120 µm mesh size. Twenty adults of WFT, reared on flowering chrysanthemum, were added. One week after the introduction of the thrips silver damage, expressed as the leaf area damaged in mm^2, as well as plant dry mass, were measured.

Statistical analyses. We used general linear models to determine whether sugar spraying affected silver damage. Normal distributions and homogenous variances were confirmed by testing the residuals of the models. A model was set up in which the control treatment was used as a reference. All sugar treatments were compared with the reference. Differences between the sugar treatments and the reference were evaluated using the regression coefficient matrix of the two models. In this matrix, the estimated coefficient of a sugar treatment indicated whether it had suffered more or less damage than the reference and the *P* value showed whether the difference was significant (Crawley, 2005). This is similar to a post-hoc test of an ANOVA model, however such a post-hoc test includes all pair-wise comparisons between groups, and we were mainly interested in testing for differences between a sugar treatment and the control.

Sample collection and extraction procedure for NMR. Plants for NMR analysis were grown under the same as conditions as the plants for the bioassays as described above. From each individual plant the third leaf from below was collected for analysis. Leaves were harvested in the morning of the day the thrips bioassays were started. Each treatment was sampled five times. Immediately after collection, leaves were shock-frozen in liquid nitrogen and stored at -80 °C until extraction. Those samples which showed significant effects of sugar spraying on thrips resistance were ground to a fine powder in a mortar and 50 mg of plant material was transferred to a 2-mL eppendorf tube. The samples were extracted under ultrasonication (15 min) with 1.5 mL of 80% methanol-d_4 in potassium phosphate buffer (90 mM, pH 6.0) containing 0.02% (w/v) trimethyl silyl-3-propionic acid sodium salt- d_9 (TMSP). After centrifugation (13 krpm, 15 min) an aliquot of 800 µL was taken for NMR analysis.

NMR measurements and data analysis. NMR measurements followed the protocol described in Kim et al. (2006). ^{1}H NMR spectra were recorded at 25°C on a 500 MHz Bruker DMX-500 spectrometer (Bruker, Karlsruhe, Germany) operating at a proton NMR frequency of 500.13 MHz. Deuterated methanol was used as the internal lock. Each ^{1}H NMR spectrum consisted of 128 scans requiring 10 min and 26 s acquisition time with the following parameters: 0.16 Hz/point, pulse width (PW) = 30 (11.3 µs), and relaxation delay (RD) = 1.5 s. A pre-saturation

sequence was used to suppress the residual water signal with low power selective irradiation at the water frequency during the recycle delay. Free induction decay (FIDs) were Fourier transformed with a line broadening (LB) = 0.3 Hz. The resulting spectra were manually phased and baseline corrected, and calibrated to the internal standard TSP at 0.0 ppm, using XWIN NMR (version 3.5, Bruker).

The optimized ^{1}H NMR spectra were then automatically binned by AMIX software (v. 3.7, Bruker Biospin). Spectral intensities were scaled to TMSP and reduced to integrated regions of equal width (0.04 ppm) from δ 0.3–10.0. The regions of δ 4.7–5.0 and δ 3.24–3.33 were excluded from the analysis because of the residual signals of water and methanol, respectively. Principle component analysis (PCA) was performed with the SIGMA-p software (version 11.0, Umetrics, Umea, Sweden) with scaling based on the Pareto method.

Further experiments with fructose spraying

Only fructose showed an effect on thrips damage in tomato in the previous experiment (see results section). Therefore, we only used fructose for further experiments. Forty tomato plants were grown as described above. Ten plants each were treated with 0, 1, 10, or 100 ppm fructose at the 4th leaf stage and subjected to a whole plant thrips bioassay 2 weeks after spraying as described above. An additional 10 plants were used to spray 5 plants each at the 2nd and 3rd leaf stage with 10 ppm fructose. This concentration was chosen because it had been the most effective one in the previous experiment. Data were analyzed as described for the previous experiment.

Choice leaf bioassay

A choice leaf bioassay as described by Kumar et al., (1995). The entire leaflets, except lateral ones were cut to form a long petiole. The lateral leaflet from each treatment was placed in a glass jar filled with water. By this way, the samples can absorb enough water during the bioassay which lasts 5 days. From 5 plants each, that were sprayed with 10 ppm fructose at the 2nd, 3rd and 4th leaf stage, and 5 control plants we took a leaflet from the fourth oldest leaf. This led to 20 leaflets in total. These leaflets were divided over 5 cages such that each treatment and the control were represented in each cage. The cages were placed in a complete randomized design in a climate chamber (L16: D8, 25: 20 °C, 70% RH & 11.36 µmol m^{-2} s^{-1} light intensity). Per leaflet, 10 adults of WFT, reared on flowering chrysanthemum, were added and left for five

days. Silver damage, expressed as the leaf area damaged in mm², was visually scored for each leaflet. Data were analyzed as described in the first experiment.

Results

The effects of sugar type and concentration on host plant resistance and metabolomic profiles

No significant differences in thrips damage between sugar treatments and control could be observed after 24 hours (F = 0.043, df= 3, P= 0.988). Sugar treatments reduced silver damage after 2 weeks. This result was marginally significant (F = 1.57, df= 3, P= 0.084). A further indication that sugar spraying affects silver damage comes from the fact that silver damage in the sugar spray treatments was reduced when thrips were put on the plants after 2 weeks compared to after 24 hours (F = 7.354, df =1, P= 0.008), while such an effect was completely absent in the control (F = 0.628, df =1, P= 0.432). For the effects of individual sugars we observed that spraying plants with sucrose and glucose at different concentrations did not have an effect on thrips damage 2 weeks after sugar treatment (F = 0.272, df =3, P= 0.845 and F = 1.35, df=3, P= 0.282, respectively). In contrast, significant differences in silver damage between the different concentrations of fructose were observed (F = 3.429, df= 3, P= 0.0425) (Figure 1 A). Plants sprayed with 1 and 10 ppm fructose showed less thrips damage compared to the control and the treatment with 100 ppm (Figure 1 B).

NMR analysis: PCA analysis of the fructose treatment showed a clear separation of the control group from the treatments with 1 and 10 ppm (Figure 2). Controls contained higher amounts of glucose and aspartic acid. Two components with well known insect resistance properties, the phenylpropanoids, ferulic and caffeic acid, could be clearly identified. Quantification of these metabolites showed no significant differences in ferulic (F = 0.482, df= 2, P= 0.631) nor caffeic acid (F = 0.179, df= 2, P= 0.839) between treatments and control. The concentration of chlorogenic acid was low both in the control and the sugar treatments.

Further experiments with fructose spraying

Although in this experiment fructose spraying showed less thrips damage than the control, at all three concentrations, this was in no case significant (F = 0.099, df= 3, P= 0.96) (Figure 3).

Spraying different leaf stages with 10 ppm fructose in all three cases lead to lower silver damage but again these differences were not significant (F = 1.35, df= 3, P= 0.282) (Figure 4 A).

Choice leaf bioassay

In the leaf bioassay all three fructose treatments showed less damage than the control but differences were not significant (F = 0.13, df= 3, P= 0.94) (Figure 4 B).

Discussion

Although several studies indicated that sugar spraying is a potentially successful strategy to increase herbivore resistance in plants, our study could not demonstrate a clear effect of sugars against thrips on tomato plants. In 10 out of 12 cases in which a fructose spraying was applied we did observe that the treatment showed less thrips damage compared to the control (χ^2 = 5.33, df= 1, P= 0.02). However, in general effects of fructose spraying were only small and non-significant. The levels of reduction in silver damage do not seem large enough to rely on fructose spraying as an effective method of plant protection.

For the remaining sugars tested, sucrose and glucose, we could not observe any effects on induced resistance of western flower thrips in tomato. Nothing is known of the effect of these sugars on feeding of pest species. However, some studies have looked at their effect on oviposition. Similarly to our results, application of sucrose of glucose did not detect any effect on egg laying of the Spangle butterfly, *P. protenor,* on sour orange, *Citrus natsudaidai,* (Honda, 1990). In contrast to fructose, sucrose and glucose as such, did not cause a positive effect on oviposition by *C. pomonella* on apple leaves (Lombarkia & Derridj, 2002). However, blends of these three sugars and sugar alcohols showed a deterrent effect on egg laying in this insect (Derridj et al., 2009). Thus, instead of applying one sugar there may be a blend of several sugars at different concentrations necessary to induce resistance to pests, whereby the different components of the blend work in an additive or synergistic manner.

Potentially effects of sugar spraying on thrips resistance may be present in different cultivars under different conditions (Decoteau, 2005; Dorais et al., 2008; Jaganath & Crozier, 2010). Environmental conditions such as low temperatures, heavy metals, wounding, desiccation, and high irradiance are typical triggers that switch on a biochemical pathway cascade leading to increased secondary product accumulation (Ann Lila, 2006). The effect of

these conditions on sugar-spraying is unknown. Other factors which may interact with the effect of sugar spraying are the time of spraying and solvent preparation (Birch personal communication).

In conclusion: we only observed an indication that sugar spraying may reduce thrips damage for spraying with fructose. However, even for fructose effects were small and not or only marginally significant. This shows that at this stage sugar spraying is not a very promising measure to control thrips damage.

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Figure 1. Effect of sugar spraying on resistance of tomato plants to western flower thrips 2 weeks after treatments with (A) different sugars and B) different concentrations of fructose as tested with a whole plant non-choice bioassay. Means and SE of silver damage, measured as leaf area in mm², are presented. Asterisks and different letters indicate groups that are significantly different from each other at * $P \leq 0.05$.

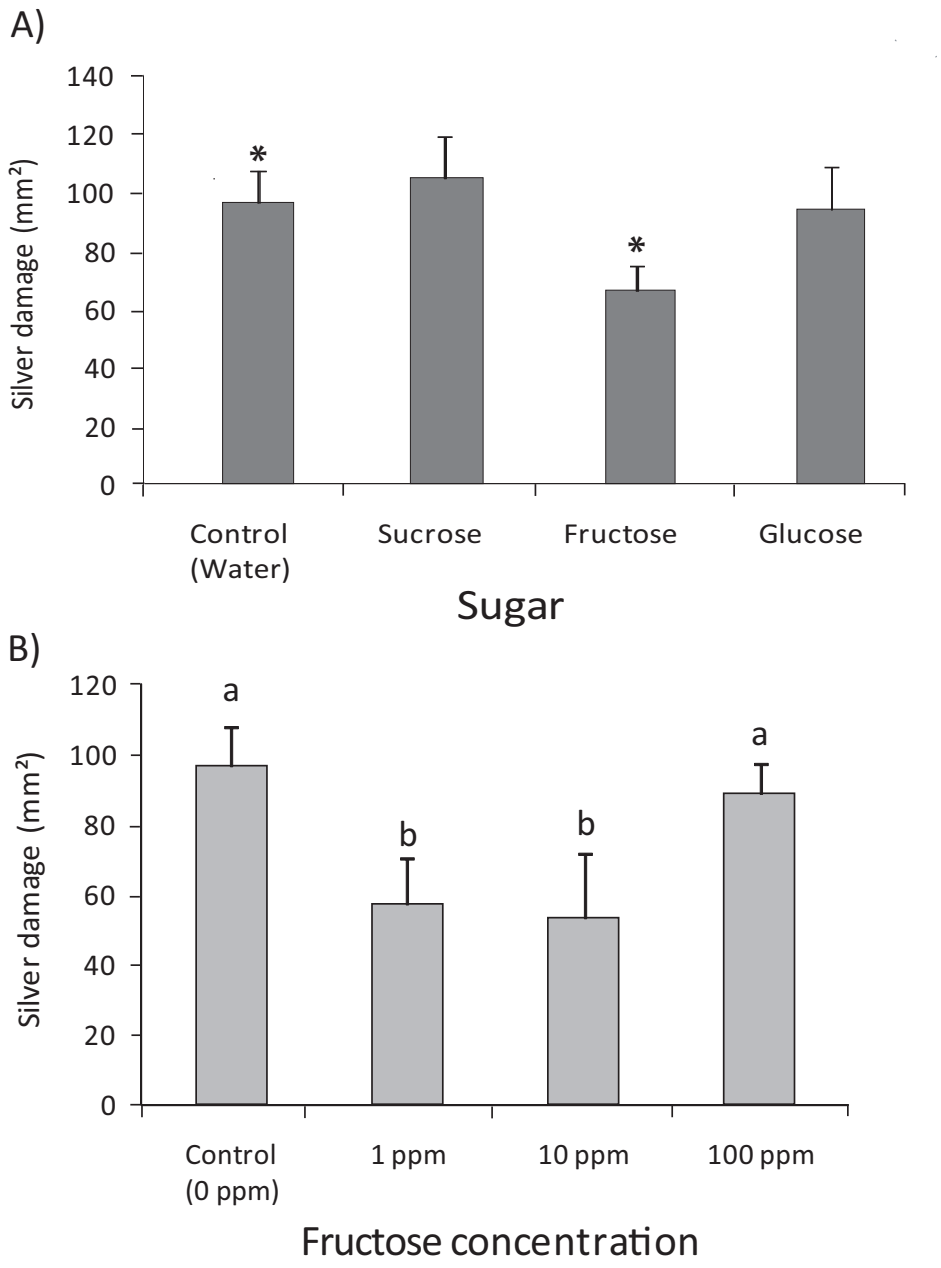
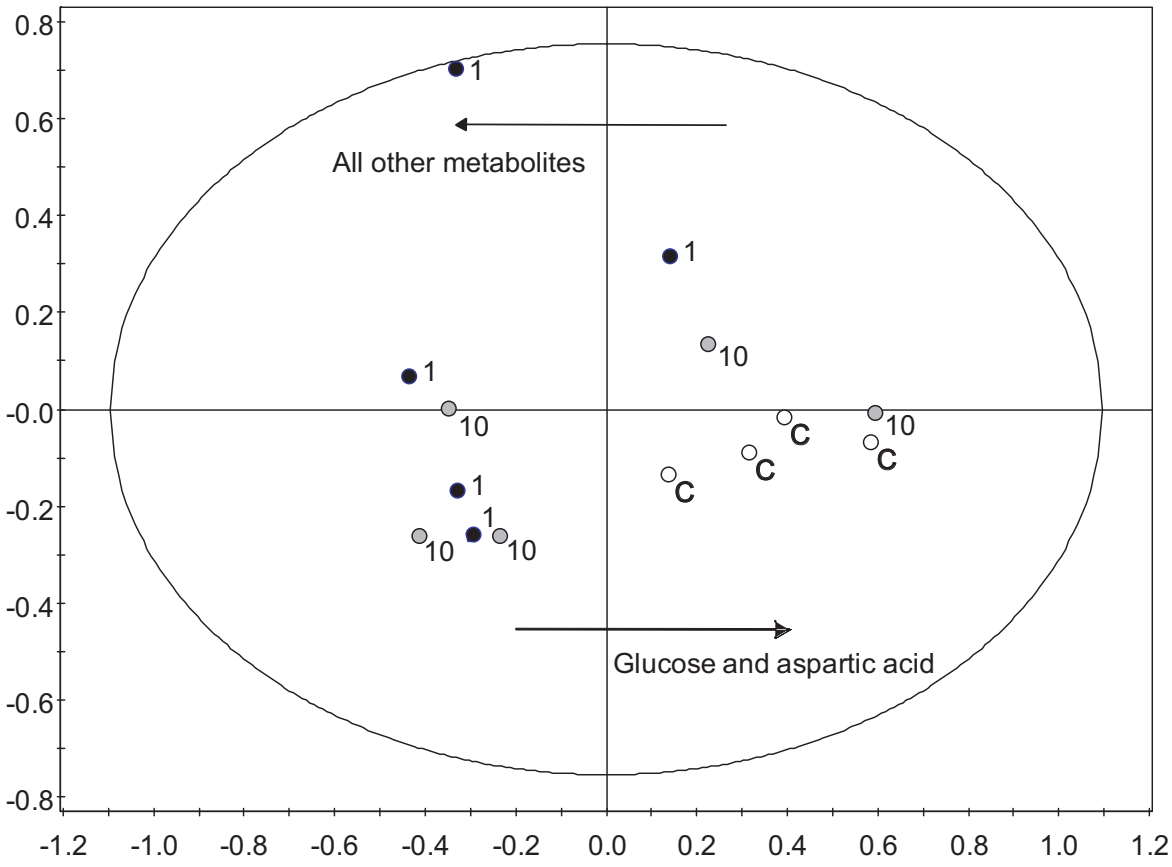


Figure 2. Score plot of principle component analysis (PCA) based on ^{1}H NMR spectra of tomato plants sprayed with 1 and 10 ppm of fructose. C= control, 1= 1ppm, 10= 10ppm.



C= Control, 1= 1ppm, 10= 10ppm

Figure 3. Effect of sugar spraying on resistance of tomato plants to western flower thrips 2 weeks after treatments with different concentrations of fructose as tested with a whole plant non-choice bioassay in the second experiment. Means and SE of silver damage, measured as leaf area in mm^2, are presented. For each concentration 10 replicates were used. Differences between treatments were not significant.

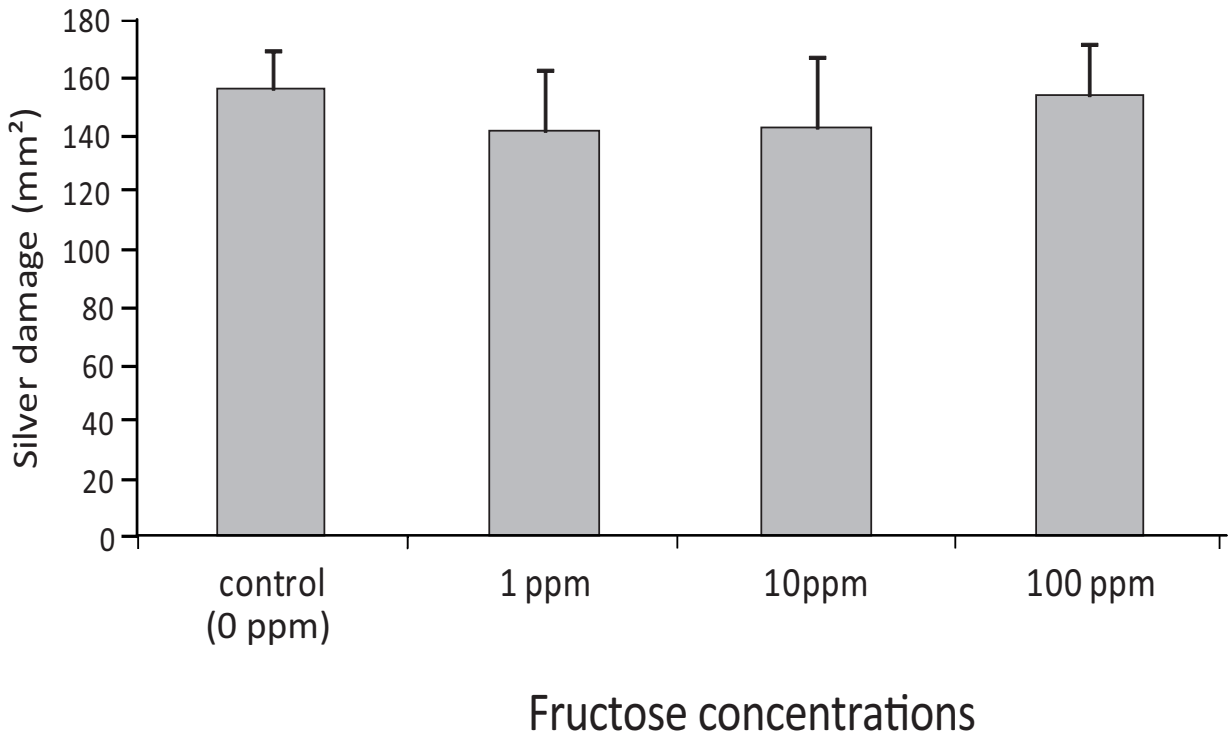


Figure 4: Effect of sugar spraying with 10 ppm fructose at different plant leaf stages on resistance of tomato plants to western flower thrips as tested (A) with a whole plant non-choice bioassay and (B) a choice leaf bioassay. Means and SE of silver damage, measured as leaf area in mm^2, are presented. Five replicates were used for each leaf stage.