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Host plant resistance of tomato plants to western flower thrips

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General introduction

The rapid evolution of resistance to insecticides causes serious problems for the sustainability of crop protection. We are in need for management strategies that reduce over-dependence on synthetic pesticides. The use of natural enemies, biopesticides, natural plant products, and the development of pest-resistant varieties may lead to potentially environmental friendly methods of managing insect pests (Sharma, 2008). It is important to adopt pest control strategies that are: (1) ecologically sound, (2) economically realistic, and (3) publicly acceptable. Host plant resistance and cultural practices can play a major role in pest management (Sharma & Ortiz, 2002; Sharma, 2008). Increasing plant resistance as a tool for pest control is in some cases the only realistic and effective way of pest management.

In nature, plants can defend themselves against insect herbivores in different ways. Wild species of crops are important sources of genes for resistance to biotic and abiotic constraints (Stalker, 1980; Xiao et al., 1996). For example: in cultivated tomato, insect resistance is rare, but it is prevalent in wild accessions of *Lycopersicon* spp. (Sharma, 2008). The potential economic and environmental benefits of improved crop production and quality through breeding with crop wild relatives are highly significant (Sharma, 2008).

In many cases plant resistance is chemically based. Plants produce secondary metabolites: organic compounds that are not directly involved in the normal growth, development or reproduction of plants. It is generally considered that they play a major role in defense against herbivores (Fraenkel, 1959). These secondary metabolites can act as repellents, toxins or plant digestibility reducers.

Tomato is a crop for which breeders have used a wide variety of wild species and a large range of characters (Sharma, 2008). It is a major vegetable in the world. Cultivated tomato is attacked by different pests among which the western flower thrips (WFT), *Frankliniella occidentalis* (Pergande). WFT is a key agricultural pest worldwide causing considerable economic damage. Control of thrips mainly depends on pesticides. However, chemical control of thrips is difficult and costly. Chemical control results in development of insect resistance, residue problems on crops and causes risks to human health and the environment.

Clearly, multiple tactics in the framework of an integrated pest management (IPM) approach are needed. An important part of such a strategy is host plant resistance based on the composition of secondary metabolites in the plant.

Manipulating the metabolomic profile of the plant may have a strong additional advantage. Most secondary metabolites are assumed to have evolved because of their protection against herbivores and pathogens. At the same time many of these secondary metabolites can have a beneficial effect on human health. In fact this is precisely the reason why we select for instance food sources with high levels of anti-oxidants. Therefore, with a proper selection of secondary metabolites it should be theoretically possible to produce crops that are better protected and are healthier at the same time. In this thesis we will study the effects of chlorogenic acid, a well-known and wide spread antioxidant, on tomato resistance against western flower thrips.

Why Tomato?

Tomato, *Solanum lycopersicum* L. (syn. *Lycopersicon esculentum* Mill.) is one of the most consumed vegetables in the world and global production is estimated at around 136 Billion ton per year (FAOSTAT, 2008). Tomato is the 3rd most economically important vegetable crop after potato and onion. Major production countries in descending order include China, USA, India, Turkey and Egypt respectively. Europe contributes 22% of the world's tomato production. In the Netherlands all tomatoes are produced in glasshouses, which cover an area of about 1,257 ha (LEI, 2009). Tomato is worldwide the most important greenhouse vegetable crop with a production of 720 MT and a total value of \$170 Million per year (FAOSTAT, 2008). Tomato is a dietary source of vitamins especially A and C, minerals and fiber, which are important for human nutrition and health. Also, tomatoes are the richest source of lycopene, a phytochemical that protects cells from oxidants that have been linked to human cancer (Giovannucci, 1999; Mutanen et al., 2011). Other antioxidant compounds in tomato fruit include flavonoids and phenolic acids. Flavonoids and phenols are regarded as potentially health benefitting compounds since they are implicated in the prevention of human inflammatory and, cardiovascular diseases as well as cancer (Martin et al., 2004; Tan et al., 2010; Mutanen et al., 2011). Chlorogenic acid (CGA) is the major soluble phenolic in Solanaceous species. In some tomato cultivars CGA represents 75% of the total phenolic contents in green and 35% in ripe fruit (Wardale, 1973). The beneficial health properties, based on its antioxidant properties, include the prevention of cancer (Martin et al. 2004) and atherosclerosis (Laranjinha et al., 1994; Tamagnone et al., 1998). In addition

CGA also shows hepatoprotective, hypoglycemic and antiviral activities (Farah & Donangelo, 2006; Park et al., 2010).

Fresh fruits of tomatoes are used in salads, various culinary preparations, juices, or processed in the form of purees, concentrates, condiments and sauces (Razdan & Mattoo, 2007). Varieties for fresh consumption are cultivated in greenhouses and in the open air, while varieties for processing are only cultivated in the open air (Díez & Nuez, 2008). Today, nearly all the tomato cultivars for the fresh market, as well as an increasing number of cultivars for processing, are hybrids (Díez & Nuez, 2008).

In 1753, Linnaeus placed the tomato in the genus *Solanum*, while Miller classified tomatoes in a new genus, *Lycopersicon* (Díez & Nuez, 2008). The argument over the taxonomic status of the cultivated tomato (*Lycopersicon esculentum* Mill.) has been resolved. Application of molecular techniques (RAPDs, RFLPs) and genomics research has now convinced the research community to place tomato under the genus *Solanum*, namely, *Solanum lycopersicum* L. (Díez & Nuez, 2008).

The tomato is a favorite model system for both classical and molecular genetic studies (Rick & Yoder, 1988). It is a simple diploid with twelve chromosomes as shown with both conventional and molecular markers. Additionally, susceptibility to contamination by *Agrobacterium tumefaciens* allows the application of gene transfer technologies. The important economic crop status of tomato has also contributed to its development as a model genetic system (Rick & Yoder, 1988). Tomato was among the first crops for which molecular markers were suggested for marker-assisted selection (MAS) in breeding (Tanksley & Rick, 1980).

The cultivated tomato *S. lycopersicum* is susceptible to a wide array of arthropod pests (Kennedy, 2003). These include species that feed almost exclusively on foliage, and species that feed on both foliage and fruit (Lange & Bronson, 1981). There are no sufficiently high levels of host plant resistance to allow for significant reductions in the quantity of pesticides used in tomato (Labate et al., 2007). Therefore, the development of cultivars with increased levels of host plant resistance is a major issue in tomato breeding programs (Labate et al., 2007).

Thrips, the thunder-flies

Thrips are a diverse insect order with a worldwide distribution. There are approximately 5800 species described from 9 families (Tipping, 2008). Thrips are small, economically important pest insects, often known as thunder-flies (Tipping, 2008). They feed on more than 600 different wild and cultivated plants (Tipping, 2008). Many thrips are pests of commercial crops due to their damage to leaves, flowers and fruits. The genus *Frankliniella* contains some of the most important thrips pests

such as WFT. This thrips has become one of the most important agricultural pests worldwide over the past 30 years (Kirk, 2002; Reitz, 2009). WFT alone accounts for one third of the publications of all 5000 Thysanoptera species in the past 30 years (Reitz, 2009). It originates from western North America, but in the 1970s and 1980s it spread rapidly across the USA and Canada, and then to Europe and the rest of the world (Kirk & Terry, 2003). It is a significant pest of most crops, including vegetables, ornamentals, fruits, and cotton (Lewis, 1997; Kirk & Terry, 2003). WFT is especially a key pest of greenhouse crops (van Lenteren & Woets, 1988). In Europe, WFT was first detected in the Netherlands in 1983 and by the end of the 1980's, it has been observed in most European countries (Tommasini & Maini, 1995). It is the most common thrips in Dutch glasshouses as observed in a sampling from 1994 until 2000 (Vierbergen, 2001). Forty one thrips species were identified in 359 samples. WFT was observed in 34% of all samples.

The reasons for the major pest status of WFT are four-fold: First, it is highly polyphagous, damaging more than 240 species from 62 different plant families (Lim et al., 2001). Growers frequently need to control it both within the crop and on host weeds within and neighboring to the crop. Second, this pest is an efficient vector of plant viruses, including tomato spotted wilt virus (TSWV), which affects different vegetable crops causing wilting lesions and fruit deformation resulting in considerable crop losses (Cho et al., 1989). Third, thrips often goes unnoticed because of its behavior. Adults and larvae hide and feed in the protected narrow crevices in flowers and foliage (Jensen, 2000). This also makes chemical control difficult. Fourth, WFT develops insecticide resistance, with populations resistant to several different classes of insecticides (Herron & James, 2005).

A typical WFT generation time comprises 22 days, depending on the temperature (Capinera, 2008). At 25- 30 °C, this time can be as brief as 9-13 days (Reitz, 2008). The eggs are about 0.2 mm long and kidney shaped. They take on average 3 days to hatch (Capinera, 2008; Reitz, 2009). Females have a saw-like ovipositor, which they use to deposit eggs into leaves, petioles, and developing fruit (Reitz, 2009). Thrips have two larval stages, followed by a prepupal and a pupal stage. Adults take between 1 and 4 days to reach sexual maturity. Most thrips species overwinter as either adults or as pupae (Capinera, 2008). Under laboratory conditions, females can live up to 5 weeks (Reitz, 2008). Reproduction is parthenogenetic. Unfertilized females produce males, while fertilized females produce one third males and two thirds females (Capinera, 2008). At the beginning of the season, in spring, there are many male thrips to be observed in a glasshouse, while the number of females exceeds in summer.

The direct damage of WFT on plants is caused by oviposition and feeding (Tommasini & Maini, 1995). This pest feeds by penetrating the plant cells with stylet-like mouthparts and sucking out the cell sap (Capinera, 2008). This causes the plant cells to become filled with air, which imparts a silvery appearance, the so called silver damage to foliage, flowers or fruit leading to unmarketable produce (Reitz, 2009). Furthermore, feeding can cause stunted and deformed plants leading to yield losses (Capinera, 2008). WFT causes millions of Euros of damage worldwide. The damage in tomato in the Netherlands alone already accounts for € 13.4 million a year (Lewis, 1997).

By far the greatest damage caused by WFT is its ability to transmit Tospoviruses. WFT is the main vector of TSWV, which causes over \$1 billion in losses annually worldwide (Goldbach & Peters, 1994). Over 1,000 species of plants in 84 families are susceptible to TSWV (Parrella et al., 2003), giving it one of the broadest host ranges of any plant pathogen. This broad host range is clearly related to the distribution of its main vector, WFT. This thrips can reproduce on many different plants. Therefore, viruliferous adults arise from many different sources. Given the fecundity of WFT, large numbers of viruliferous individuals can be present in the environment at any time (Reitz, 2009). Spread and transmission of TSWV can occur in as little as 5 min of WFT feeding (Wijkamp et al., 1996). Adults retain and transmit the virus throughout their lives (Ullman et al., 1993).

Biotypes of WFT

Resistance genes in insect-resistant cultivars may be overcome by the development of insects biotypes that have a natural genetic capability to overcome the properties of plant resistance genes (Smith, 2005). Biotypes have been defined as an individual or population identical in morphology, but showing genetically fixed physiological and/or behavioral differences (Schoonhoven et al., 2005). It is well documented that insects develop resistance against particular insecticides and this problem may be due to the development of resistant insect biotypes (Schoonhoven et al., 2005). This is especially so in greenhouses, an environment in which WFT populations are under intense selection due to constant exposure to insecticides and limited immigration of susceptible individuals (Immaraju et al., 1992b). Since WFT is a pest of many crops, thrips populations are often under constant insecticide pressure, which increases selection for resistance (Reitz, 2009). As such resistance of WFT to pyrethroids, organophosphates and carbamates has been reported (Jensen, 2000). In this view it is also possible that WFT develops biotypes resistant to natural plant defense compounds. Indeed de Kogel et al. (1997) detected evidence of Dutch and Italian WFT biotypes on accessions of cucumber,

Cucurbita sativus L., normally resistant to *F. occidentalis*. Next to biotypes Rugman-Jones et al. (2010) recently reported the existence of two cryptic species of WFT in California.

Control of WFT

Control of WFT is imminent and depends on the use of pesticides. However, the efficacy of chemical control is limited in part due to thrips feeding inside plant organs and in part due to deposition of eggs into sub-epidermal tissues (Robb, 1989; Immaraju et al., 1992; Brødsgaard, 1994). Furthermore, most chemicals have short term effectiveness and frequent spraying is required. Among the insect pests thrips are responsible for most of the pesticide use with sprayings twice a week (Lewis, 1997). As a result vegetables and ornamentals under glass had the highest pesticide application rates in the Dutch agri- and horticulture in 2000 with 14.6 kg/ha active ingredients in tomato (LEI, 2006). However, intensive use of insecticides has been unsafe, leading to problems such as pest recovery, development of resistance, pesticide residues, non-target effects, contamination of the environment, and direct damage to human beings (Sharma, 2009).

Predatory mites and bugs are used for biological control of WFT (Kennedy, 2003; Loomans, 2003). However, this biological control is difficult due to the zero tolerance of ornamentals for export. Furthermore, thrips lacks an obligate diapause. Thrips populations can thus build up very rapidly at the beginning of the season while the natural enemies are still in diapause. Therefore, researchers suggested the use of non toxic compounds such as sugars for reducing pest damage. Sugars have acted as plant hormones that control gene expression and development processes in plants (Sheen et al., 1999). They are used in pest management of apple trees (Lombarkia & Derridj, 2008; Derridj et al., 2009) and against nematodes (Birch et al., 1993a,b; Birch et al., 2009). However, this method seems to be rather unstable, since it is strongly depended on other factors such as environment, cultivar, and agronomic practices (Decoteau, 2005; Dorais et al., 2008).

Seen the problems in thrips control based on the current methods used, host plant resistance forms an important alternative approach to control WFT as part of an integrated pest management approach.

Host plant resistance to WFT

Host plant resistance to WFT has been observed in different plants including vegetables, ornamentals and wild plants. In tomato species, Kumar et al. (1995a) reported high levels of resistance to feeding by nymphs and adults of WFT in the wild tomatoes *Lycopersicum hirsutum* f. *glabratum*, *L. hirsutum* f. *typicum* and *L. pennellii*. He observed a moderate level of resistance in *L. chilense*. They

also reported significant differences in WFT flower infestations among different *Lycopersicon* accessions. However, the underlying mechanisms were not studied. Morphological plant characters such as hairiness, toughness, plant height, number of leaves and leaf surface area were not involved in WFT resistance, neither in chrysanthemum (de Jager et al., 1995) nor in the wild plant *Senecio* (Leiss et al., 2009a). Instead, resistance was influenced by the chemical composition of host plants.

Low concentrations of total aromatic amino acids in cucumber, pepper, lettuce, and tomato, compared to total leaf protein, were correlated with a decrease in damage by WFT (Mollema & Cole, 1996). Overexpression of cystein-protease inhibitors in transgenic chrysanthemums was not related to thrips resistance (Annadana et al., 2002), while multi domain cystein protease inhibitors in transgenic potato were affiliated with thrips resistance (Outchkourov et al., 2004a,b). Potential interference of these multi domain proteins with basic cell functions has hindered a practical function for pest management so far. Recently, two pyrrolizidine alkaloids, jaconine and jacobine, as well as the flavonoid kaempferol glycoside have been identified by NMR to be related to thrips resistance in the wild plant *Senecio* (Leiss et al., 2009a). A metabolomic approach to study WFT resistance in chrysanthemum identified chlorogenic and feruloyl quinic acid as resistance factors (Leiss et al., 2009b).

Mechanisms of host plant resistance in tomato

In the past, selection of crop species for improved agricultural value has been associated with reduced levels of herbivore resistance (Kennedy, 2007). This loss of herbivore resistance is linked to diminished amounts of particular secondary plant metabolites. The secondary plant chemicals, present in the ancestors of the domesticated cultivar, provided natural resistance to pests (Berlinger, 2005). For example 2-tridecanone content in cultivated tomatoes has decreased to 1.5% of the wild tomato species (Williams et al., 1980). Therefore, wild relatives provide valuable source material for insect and disease resistance (Alonso-Blanco & Koornneef, 2000; Kennedy, 2007).

The wild tomato species *S. hirsutum*, *S. peruvianum*, and *S. pennellii* have been reported to be resistant to many tomato insect pests (Gentile et al., 1969; Kumar et al., 1995a; Muigai et al., 2002; Kennedy, 2007). Specifically, accessions of *S. pennellii* showed high levels of resistance to the whitefly, *Bemisia tabaci*/*Bemisia argentifolii* complex (Kennedy, 2003; Berlinger, 2005), the aphids, *Macrosiphum euphorbiae* and *Myzus persicae* (Liedl et al., 1995), two-spotted spider mites, *Tetranychus cinnabarinus* and *T. urticae* (Goffreda et al., 1989), as well as to the larvae of corn earworm, *Helicoverpa zea*, and beet armyworm, *Spodoptera exigua*, (Gentile et al., 1969).

It has been suggested that waxy and shiny leaves as well as variation in leaf area and toughness may act as physical defenses against insect herbivores (Juvik et al., 1994). In tomato trichomes serve as physical barriers and furthermore they produce different allelochemicals which are associated with pest resistance (Williams et al., 1980; Kennedy, 2003). Methyl-ketones, such as 2-tridecanone, present in *S. hirsutum f. glabratum* confers resistance to colorado potato beetle, *Leptinotarsa decemlineata* (Jayanthi et al., 1994; Eigenbrode et al., 1995), spider mite, *Tetranychus evansi* (Kennedy & Sorenson, 1985), the Lepidopterous larvae, *Manduca sexta* and *Heliothis zea*, and the aphid, *Aphis gossypii* (Maluf et al., 2001). Sesquiterpenes in *S. hirsutum f. typicum* are related to resistance against beet armyworm, *S. exigua* (Williams et al., 1980), while acylsugars in *S. pennellii* confer resistance against potato aphid, *M. euphorbiae* (Eigenbrode et al., 1994), silverleaf whitefly, *B. argentifolii* (Goffreda et al., 1989), South American tomato pinworm, *Tuta absoluta* (Liedl et al., 1995) and green peach aphid, *M. persicae* (de Resende et al., 2006). The multiple pest resistance of *S. pennellii* is based on the presence of type IV glandular trichomes and the glucose and sucrose esters of fatty acids (acylsugars) that they secrete (Rodriguez et al., 1993). In contrast cultivated tomato, *S. lycopersicum* does not have any type IV trichomes and does not accumulate acylsugars (Goffreda et al., 1989; Shapiro et al., 1994). Next to the secondary metabolites produced by trichomes, glycoalkaloids and phenols are involved in host plant resistance of tomato to insects. The glycoalkaloid α -tomatine has been suggested as a possible resistance factor in tomatoes to beet armyworm, *S. exigua* (Goffreda et al., 1990), Colorado potato beetle, *L. decemlineata* (Kennedy, 2003), and tomato fruitworm, *H. zea* (Barbour & Kennedy, 1991). Phenolics and flavonoids, are distributed widely among terrestrial plants and are likely among the oldest plant secondary compounds known as plant defense compounds against herbivores and pathogens (Elliger et al., 1981). Phenolics such as CGA and rutin are reported as growth- inhibitors of *H. zea* and *S. exigua* larvae in tomato foliage (Elliger et al., 1981; Kennedy, 2003).

Use of genetic engineering for pest resistance in tomato

Genetic engineering of a secondary metabolic pathway aims to increase the quantity of an individual or a group of specific compounds in a plant species or to transfer a pathway, or part of a pathway, to other plant species (Schowalter, 2006). Insect resistance depends on one locus (monogenic) or many loci (polygenic) that are involved in conferring resistance in different ways. In wild plants, several modes of defense are combined and controlled by a complex system with several loci and multiple alleles at one locus (Verpoorte & Memelink, 2002). Traditional selective breeding can now in some cases be short-circuited by ingenious biotechnological methods. The introduction of

transgenic crops is taking place at a spectacular rate. Helentjaris et al. (1985) demonstrated that DNA-based molecular markers in the form of restriction fragment length polymorphisms (RFLPs) could effectively identify differences between cultivated tomato and wild tomato species. With quantitative trait loci (QTL) mapping, the roles of specific resistance loci can be described, race-specificity of partial resistance genes can be assessed, and interactions between resistance genes, plant development, and the environment can be analyzed. Nienhuis et al. (1987) demonstrated that marker-assisted selection (MAS) could identify QTL associated with insect resistance in tomato. They identified QTL of 2-tridecanone in a cross of *S. lycopersicum* and *S. hirsutum*. Also QTL to whitefly resistance (*B. tabaci*) were identified in a cross of *S. lycopersicum* and *S. habrochaites* (Young, 1996).

Introgression lines (ILs) that contain chromosome segments of wild species in the background of the related cultivated species increase genetic diversity of crop plants without losing the desirable elite phenotype and thus are great resources for crop improvement (Momotaz et al., 2010). ILs are identical for the entire genome except for a single introduced region, and thus variation in the ILs is due to the introgressed segment. The nearly isogenic nature of ILs offers great advantages in genetic studies such as QTL mapping and gene identification (Zamir, 2001). In tomato, several sets of ILs have been developed for wild relatives of tomato, such as introgressions with *S. lycopersicon* and *S. pennellii* (Zamir, 2001; Gur & Zamir, 2004). The *S. pennellii* introgression set comprises 76 lines. In these ILs a marker-defined genomic region of the domesticated variety *S. lycopersicum* M82 was replaced with its homologous interval in the wild species. Over a series of field studies on these lines a number of phenotypic traits were quantified and QTL identified (Eshed & Zamir, 1995). Loci associated with fruit metabolism and yield in the *S. pennellii* introgression set were identified by Schauer et al. (2006). Regarding resistance traits the *S. pennellii* introgression lines were used to map QTL for the accumulation of acylsugars which have been reported to be involved in resistance to various herbivorous insects (Schillmiller et al., 2010).

Transgenic plants

Plant breeding, especially the development of transgenic plants, may offer IPM programs a much needed tool to manage WFT and the diseases it transmits (Eshed & Zamir, 1995; Gur et al., 2004). Significant progress has been made over the past two decades in introducing foreign genes into plants, and this has provided opportunities to modify crops to increase yields, impart resistance to insect pests and diseases, and improve nutritional quality and yield (Morse & Hoddle, 2006). Genetically transformed crops have been deployed for cultivation in different countries (Sharma et al.,

2002). By using biotech applications for “speeding the breeding” in crop improvement programs we can stabilize and increase crop productivity, reduce production costs as well as environmental damage and significantly diminish the production of greenhouse gases (James, 2008). Genetic engineering of tomato has resulted in tomatoes with a doubled amount of CGA by overexpression of hydroxycinnamoyl-CoA quinate hydroxycinnamoyl transferase (HQT), without influencing other phenylpropanoids (Niggeweg et al., 2004). Also Sienkiewicz-Porzucek et al. (2008) produced transgenic tomatoes with increased amounts of CGA using antisense citrate synthase. Increased amounts of CGA in tomato have a dietary benefit for human health due to their antioxidant properties (Elliger et al., 1981). At the same time CGA has been reported to affect herbivores, such as WFT negatively (Leiss et al., 2009b). Due to the unique combination of positive effects on human health and negative effects on thrips, CGA is the substance of choice to develop host plant resistance to thrips.

Aims and scope of the thesis

This thesis explores the resistance of tomato plants to WFT. At first an overview about tomato, WFT and their interactions is presented (this chapter). This is followed by 5 experimental chapters. The first experiment comprises a comparison of thrips resistance between major tomato cultivars and wild tomatoes. Wild species of crops are important sources of genes for resistance to biotic and abiotic stresses. In this study, we explored the natural variation in WFT resistance of the genus *Lycopersicon* by performing bioassays and comparing thrips damage on some wild species and cultivated lines to determine the chemical and mechanical resistance factors in these plants. All plants were subjected to NMR metabolomic analysis to correlate thrips resistance to plant secondary metabolites (Chapter 2). Invasion of pests may lead to rapid local adaptation and the development of biotypes specialized to different hosts. Therefore, host plant adaptation of thrips was studied by observing variation in genetics and performance of Dutch WFT populations (Chapter 3). In this chapter genetic differences between Dutch WFT populations collected on different hosts were analysed with AFLP and the existence of possible cryptic species was tested using mitochondrial barcoding. Feeding damage and reproduction of thrips were examined in different thrips bioassays. A negative effect of CGA in chrysanthemum on WFT has been reported earlier. To study the effects of CGA level in tomato on thrips resistance, transgenic tomatoes with increased amounts of CGA were subjected to thrips infestation and feeding damage was monitored (Chapter 4). Introgression lines (ILs), represent an excellent platform to explore the genetics of multiple biological and chemical traits of agronomical importance. The wild tomato, *S. pennellii* was highly resistance to WFT (Chapter 2). A set of 76

introgression lines between the *S. pennellii* and the cultivated tomato *S. lycopersicum* was used to detect QTLs associated with WFT resistance, secondary metabolites and their co-localization (Chapter 5). Sugars have acted as plant hormones that control gene expression and development processes in plants and sugar spraying of leaves has been used in pest management of different plants. Potentially, it can, therefore be used as a new and more environmentally friendly method of crop protection. We used sugar-sensing, applying sprays of sucrose, fructose and glucose to increase resistance to WFT in a susceptible tomato cultivar (Chapter 6). The summary and conclusions of this thesis are given in Chapter 7.

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