Control of Western flower thrips through jasmonate-triggered plant immunity

Chen, G.

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Author: Chen, G.
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Chapter 1

General introduction

1 Current challenges in agriculture

At present, the agriculture faces different demands. First, it has been predicted that nearly 9.77 billion people will need to be fed by 2050 (UN, 2017). As a consequence, it is estimated that nearly double volume of crop production, compared to 2013, will be required (Ray *et al.*, 2013). And second, there has been an intensification of the global network of ornamental plant species trade that has been accompanied by the increment in their cultivation and the use of pesticides. Increasing the land for the production of horticultural and/or ornamental plants is not the solution, and a great number of researchers have proposed the optimization of plant yield as the most sustainable strategy (Godfray *et al.*, 2010; Foley *et al.*, 2011; Phalan *et al.*, 2011). We need to invest in sustainable agriculture (Garnett *et al.*, 2013), and this might be achieved by optimizing the use of agriculture resources, e.g. water and nutrients (Foley *et al.*, 2011). Also, the generation of high-yield and pest resistant crop varieties through conventional plant breeding or genetic engineering approaches can increase plant yield (Tester & Langridge, 2010). However, most of the cultivated species have been generated by selecting desirable market-related fruit, flower or yield features, while traits conferring resistance to pathogens and herbivores have been lost during the domestication process (Oerke, 2006). As a result, arthropod pests and the diseases they transmit are among the most important factors affecting crop production. Furthermore, these threats are predicted to increase due to current agricultural practices, e.g. monoculture system and global warming (Oerke & Dehne, 2004). To minimize the damaging effects of arthropod pests on horticultural and ornamental crops production, pesticides are used worldwide (Stokstad & Grullón, 2013). However, more than 440 species of insects and mites have been documented to develop pesticide resistances (Roush & Tabashnik, 2012). Moreover, the use of pesticide leads to residue problems in the crops and environment and, therefore, they constitute a threat for untargeted organisms, including humans. European countries have agreed to establish a framework to reduce the adverse effects of pesticides on human health and the environment by promoting the development of Integrated Pest Management (IPM) strategies (directive, 2009). Among these, enhancing host plant resistance by using defense elicitors or the generation of pest resistant cultivars are desirable environmentally-friendly alternatives for pest control.

2 Mechanisms of host plant defense against herbivores

2.1 Constitutive and inducible defenses

To defend themselves against arthropod herbivores, plants have evolved sophisticated defense mechanisms that can be classified into constitutive and inducible. Constitutive defenses are defined as pre-existed morphological or chemical components present in the plant in the absence of herbivory or pathogen infection. Nonetheless, plants may increase their defenses to better protect themselves in response to herbivore or pathogen attacks, i.e. induced defenses (Howe & Jander, 2008). Both constitutive and induced plant defenses can be modulated by the environment as well as by the plant genetics and ontogeny (Karban & Myers, 1989; Franceschi *et al.*, 2005; Köhler *et al.*, 2015). In addition, plants have evolved their immune systems to distinguish their enemies to a certain degree and, thereby, to specifically respond to different types of attacks (Koornneef & Pieterse, 2008). These inducible plant defenses are uniquely initiated after the recognition of molecular patterns associated to herbivory or pathogen attack. These can result from endogenous elicitors derived from injured tissues, the so-called damage-associated molecular patterns (DAMP). Other defense elicitors are components of microbial pathogens (e.g. flagellin, lipopolysaccharides, peptidoglycan, β-glucans and chitin) and they are called pathogen- or microbe-associated molecular patterns (PAMPs or MAMPs). Upon herbivory, plants can recognize this type of attack by detecting herbivore-associated molecular patterns (HAMPs). HAMPs are released from the herbivore's oral secretions, saliva, oviposition fluids, digestive wastes, and/or endosymbionts activity (Mithöfer & Boland, 2008; Basu *et al.*, 2017). Some examples are the oral secretion-related protein glucose oxidase, the fatty acid-amino acid conjugates such as volicitin, sulfated fatty acids such as caeliferins, and peptide fragments such as inceptins (Basu *et al.*, 2017). Also, salivary secretions containing ATP hydrolyzing enzymes and ATP synthase (Wu *et al.*, 2012), digestive wastes like the frass of the caterpillar *Spodoptera frugiperda* (Ray *et al.*, 2015), or endosymbionts in *Diabrotica virgifera* (Barr *et al.*, 2010) all have been documented to serve as HAMPs. Once recognized by plants, HAMPs can elicit the expression of defense-related genes, thereby modifying the physical and/or chemical defensive components of the plant.

Induced plant defenses against arthropod herbivores can be divided into direct and indirect defenses. Direct defenses include morphological features such as cuticles waxes, leaf toughness, spines and trichomes (Barton, 2016) and/or production of specialized metabolites and defensive-related proteins that negatively affect herbivore preference (i.e. host plant selection, oviposition, feeding behavior) and/or performance (i.e. growth rate, development, reproductive success) (Howe & Schaller, 2008). Among the above-mentioned mechanisms, the important defensive role of trichomes has been extensively studied for decades. Trichomes are epidermal hairy structures originated from the epidermal cells of plants, which can be divided into non-glandular or glandular types (Werker, 2000). Non-glandular trichomes are unicellular or multicellular hairs, while glandular trichomes are usually multicellular structures provided with specialized glands that can produce and/or secrete diverse chemical substances (Glas *et al.*, 2012). Non-glandular trichomes can provide physical protection against herbivores, while glandular trichome can provide both a physical and chemical barrier in the leaf surface. Glandular trichomes can produce and secrete different allelochemicals that restrain the survival, growth and fecundity of arthropod herbivores. Although trichomes can be present in the plant before herbivory or pathogen infection, their density and chemistry are modulated by abiotic and biotic factors (Peiffer *et al.*, 2009; Escobar-Bravo *et al.*, 2017). Besides trichome induction, many specialized plant chemicals with toxic or repellent properties against herbivores have been described to be induced by herbivory. Some examples include the production of phenolics, terpenoids, alkaloids, cyanogenic glucosides, and glucosinolates (Karban & Myers, 1989; Bennett & Wallsgrove, 1994; Grubb & Abel, 2006). In addition, plants can increase the production of defensive proteins that limit the nutritional value of plant tissues, such as polyphenol oxidases (PPOs) and proteinase inhibitors (PIs) (Chen, 2008; Howe & Schaller, 2008). Finally, herbivory can also induce indirect plant defenses, which consists on the attraction of the herbivore's enemies, often via the release of volatile organic compounds that serve as predatory cues, or by supplying additional food to the predators such as extrafloral nectar (Wu & Baldwin, 2010).

2.2 Hormone-mediated regulation of induced plant defenses

Induced plant defense responses are mainly controlled by the plant hormones jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) (Smith *et al.*, 2009; Eyles *et al.*, 2010). In general, chewing-biting (like caterpillars) and cell-content feeding insects (like thrips and spider mites) and necrotrophic pathogens activate the JA signaling pathway (Walling, 2000; Glazebrook, 2005), while the SA pathway is induced by biotrophic pathogens and phloem feeding insects (like aphids and whiteflies) (Glazebrook, 2005). Nonetheless, other hormones like gibberellins, cytokinins, abscisic acid, brassinosteroids and strigolactones participate in the regulation of these induced plant defenses (Verma *et al.*, 2016). Hence, JA and SA signaling are fine-tuned by other hormones and they also interact through hormonal crosstalk. For instance, antagonistic effects of SA on JA signaling, and vice versa, have been amply described in the literature (Pieterse *et al.*, 2012).

Jasmonic acid signaling

Upon perception of attack by necrotrophic pathogens, herbivory or wounding, early signaling events like ion fluxes and cell membrane depolarization precede biosynthesis and rapid accumulation of JA in plants (Kessler & Baldwin, 2002; Wasternack & Hause, 2013). JA biosynthesis is initiated in the chloroplast, where α-linolenic acid is released from the galactolipids of chloroplast membranes via the action of phospholipases. These enzymatic reactions generate several oxylipins, including the JA precursor 12-oxo-phytodienoic acid (OPDA). OPDA is transported to the peroxisomes and subjected to a series of β-oxidation steps to generate JA (Wu & Baldwin, 2010). JA can be converted into the volatile component methyl jasmonate (MeJA), or conjugated to amino acids, such as isoleucine (Ile), producing the highly bioactive JA-derivative JA-Ile (Fonseca *et al*, 2009). JA-Ile is perceived by the plant in a dose-dependent manner, and it is crucial for the JA-induced molecular responses (Staswick & Tiryaki, 2004; Howe & Jander, 2008). JA-Ile can be perceived by the F-box protein coronatine insensitive1 (COI1) of the E3 ubiquitin-ligase SKP1-Cullin-F-box complex $\mathrm{SCF}^{\mathrm{COI1}}$ (Sheard *et al.*, 2010). Upon recognition of JA-Ile, COI1 targets the jasmonate ZIM domain (JAZ) transcriptional repressor proteins for degradation via the 26S proteasome. This results in the activation of JA-responsive genes that control, for instance, the synthesis of secondary metabolites (Van Dam *et al.*, 2004), defense-related proteins (Thaler *et al.*, 2001), trichomes (Tian *et al.*, 2014), and volatile organic compounds (Strapasson *et al.*, 2014).

Salicylic acid signaling

SA is rapidly synthesized in plants in response to pathogen infection or attack by phloem feeding insects. It is a phenolic compound that can be synthesized by two different biosynthetic pathways, both requiring chorismate (see also reviewed by Boatwright & Pajerowska-Mukhtar, 2013). The first pathway occurs via the isochorismate synthase, resulting in the production of the SA-precursor isochorismic acid. In the second pathway, chorismic acid is converted into cinnamic acid via phenylalanine. Cinnamic acid is then converted into SA via either benzoic acid or coumaric acid. Activation of the SA-associated defenses is mainly regulated by NONEXPRESSOR OF PR GENES1 protein (NPR1). NPR1 translocates to the nucleus in response to SA accumulation (Ding *et al.*, 2018). Then, NPR1 interacts with TGA transcription factors, resulting in the activation of defense-related genes, including for instance the pathogen-related (PR) genes.

2.3 Local and systemic induced plant defenses

Induction of plant defenses can occur locally at the site of attack and systemically in undamaged parts of the plant located at a substantial distance from the challenged area, which is called as a systemic response (Pieterse *et al.*, 2014). The first publication related to induced systemic defense responses against herbivorous arthropods was reported in the 1970s. Local feeding by Colorado potato beetles resulted in a rapid accumulation of PIs in systemic tissues of tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) plants (Green & Ryan, 1972). Since then, lots of experiments have been conducted to uncover the long-distance signal(s) responsible for induced systemic defenses. It has been proposed that the signal propagation through the plant occur through the transport of mobile signals in the phloem (extracellular pathways) but also trough symplastic (cytoplasmic) pathways. For instance, grafting experiments in tomato have demonstrated that the herbivory-induced JA itself serves as a long distance mobile signal (Sun *et al.*, 2011). In addition, in *Arabidopsis*, it has been shown that local and systemic defense responses are also mediated by reactive oxygen species, electrical signals, and changes in cytosolic Ca^{2+} concentration (see review by Choi *et al.*, 2017).

Although defense-related responses have been reported to occur within minutes in local and systemic tissues, they often vary in their time, organ and magnitude within and among plant species. This variation can be explained by the genetic background, the development plasticity, transmission of long-distance signals, and the vascular architecture of the plant (Van Dam *et al.*, 2001; Arnold & Schultz, 2002; Arimura *et al.*, 2004; Orians, 2005; Howe & Jander, 2008). Importantly, this variation can influence herbivore distribution along the plant canopy, and it can modulate plant-herbivore interactions in specific plant tissues (Lee *et al.*, 2017).

2.4 Within-plant variation of constitutive and inducible defenses

Within an individual plant, leaves of different development stage might differ in their degree of constitutive defenses, and they might respond differently to biotic stresses as well (Takabayashi *et al.*, 1994; Constabel *et al.*, 2000; Bezemer *et al.*, 2004; Steimetz *et al.*, 2012). For instance, young maize leaves have been reported to induce higher levels of 1,4-benzoxazin-3-one derivatives than older leaves (Köhler *et al.*, 2015). In another example, wounding or exogenous MeJA treatments triggered a much stronger expression of PPO in young poplar (*Populus trichocarpa* × *Populus deltoids*) leaves than in older leaves (Constabel *et al.*, 2000). According to the optimal defense theory, this phenomenon can be explained by the higher contribution of young leaves to plant fitness (Harper, 1989; Iwasa *et al.*, 1996; Van Dam *et al.*, 1996). Importantly, this asymmetric distribution of plant defenses along the plant canopy can shape the foraging behavior of arthropod herbivores (Köhler *et al.*, 2015). For instance, many generalist herbivores display preferential feeding for basal and less protected parts of their host plant (Meyer & Montgomery, 1987; Bodnaryk, 1991; Leiss *et al.*, 2009b). Exploring the differences in constitutive and inducible chemical defenses within the plant canopy would help to identify resistant factors and develop plant protection strategies.

2.5 Activation of JA signaling by the *Pseudomonas syringae*-derived phytotoxin coronatine

JA-associated plant defense responses can be artificially activated by natural and synthetic elicitors. For instance, exogenous application of systemin, JA, MeJA, oligogalacturonides, and chitosan all have been documented to induce JA signaling pathway, and to enhance plant resistance to herbivorous arthropods in different plant species (Doares *et al.*, 1995; Bergey *et al.*, 1996; Wu *et al.*, 2008). Another extensively studied example of natural defense elicitors of JA signaling is the phytotoxin coronatine (COR). COR is a polyketide produced by various *Pseudomonas syringae* pathovars, including pv. *atropurpurea, glycinea, maculicola, morsprunorum* and *tomato* (Zhao *et al.*, 2001). COR is composed of two moieties, the polyketide coronafacic acid and coronamic acid (Ichihara *et al.*, 1977; Slawiak & Lojkowska, 2009). Both the structure and function of COR mimic the bioactive molecule JA-Ile. COR binds with high affinity to COI1 and activates the JA signaling pathway (Geng *et al.*, 2014). Yet, this phytotoxin is ca. 1000-fold more active than JA-Ile in activating downstream JA signaling pathway *in vitro* (Katsir *et al.*, 2008). Among the biological activities, COR induces chlorosis, hypertrophy and ET release (Kenyon & Turner, 1990b; Kenyon & Turner, 1990a).

In *Arabidopsis*, *P. syringae* pv. *tomato* infection results in a significant increase in COR levels during the first 24 h, followed by large increases after 48 h (Schmelz *et al.*, 2003). Due to the antagonistic interactions between JA and SA signaling pathways (Takahashi *et al.*, 2004), COR-mediated activation of JA signaling suppresses the SA-dependent defenses responses in the plant (Zhao *et al.*, 2003; Block *et al.*, 2005; Brooks *et al.*, 2005; Uppalapati *et al.*, 2007). Suppression of SA defenses increase the plant susceptibility to *P. syringae*. Hence, in coronatine-insensitive *Arabidopsis* mutants, *P. syringae* elicits both elevated levels of SA and expression of defensive PR proteins, which suppress bacterial growth (Kloek *et al.*, 2001). Notably, activation of JA signaling by COR-producing *P. syringae* strains can alter plant resistance to arthropod herbivores that are susceptible to these defenses (Stout *et al.*, 1999; Cui *et al.*, 2005). This hormonal crosstalk employed by *P. syringae* might set the basis to investigate whether COR and/or other *P. syringae*-derived defense elicitors could be exploited in agricultural systems to increase plant resistance to insect pests.

3 The experimental system

In this thesis I have explored how variations in constitutive and JA-associated inducible defenses correlate with the plant susceptibility to Western flower thrips *Frankliniella occidentalis* in cultivated tomato (*S. lycopersicum*) and chrysanthemum (*Chrysanthemum* × *morifolium* Ramat), two economically important plant species for which Western flower thrips represent one of the most damaging insect pests affecting their production worldwide. In addition, I have investigated whether the exogenous application of *P. syringae*-derived defense elicitors, i.e. COR, might elicit the positive effects of JA on plant defenses against this insect pest.

3.1 The Western flower thrips

Economic impact and biology

Western flower thrips (WFT), *F. occidentalis* (Pergande) (Thysanoptera: Thripidae), was first described in 1895 from specimens collected in California, USA. It has become a global agriculture and horticulture pest since 1970s, when insecticide resistant strain(s) emerged due to intensive pesticide use in Western North American greenhouses (Immaraju *et al.*, 1992; Kirk & Terry, 2003). Since then, WFT has spread to the East North America, and then to Europe and the rest of the world, this being mainly boosted by the global horticulture and floricultural trade (Kirk & Terry, 2003; Wu *et al.*, 2017). In the Netherlands, WFT was first recorded in 1983, on a glasshouse of African violets, and it has become the most common thrips species in Dutch greenhouses (Vierbergen, 2001; Messelink, 2014). It has been estimated to cause annual loses of 55 million euros only in vegetable and ornamental crops cultured in Dutch greenhouses (see also MacDonald *et al.*, 2002).

Several features make WFT a serious agricultural pest. First, it is a highly polyphagous insect that feeds on more than 250 plant species from nearly 60 different families, including fruiting and leafy vegetables, horticultural plants and fruit trees (Lewis, 1997). Second, because of its small size (less than 2.0 mm length) and cryptic habit, it is often unnoticed in the crops until serious levels of infestation take place. Furthermore, typical hiding and feeding behavior in tiny crevices of flowers or leaves makes this pest difficult to control by pesticides (Jensen, 2000). Third, it has a short developmental time and a high reproductive potential. The life cycle of WFT from egg to adult takes from 14 to 21 days to be completed at a moderate temperature (20-25°C) (**Fig. 1**); although it can be shortened to less than 10 days at 30°C (Reitz, 2008). Depending on the host plant species, WFT may produce up to 300 eggs per female, leading to more than 200 offspring per female and up to five generations per year under field conditions (Robb, 1989; Lewis, 1997; McDonald *et al.*, 1998). And fourth, WFT easily develops insecticide resistance due to the short generation time, high fecundity and its haplodiploid sex-determination system (Jensen, 2000).

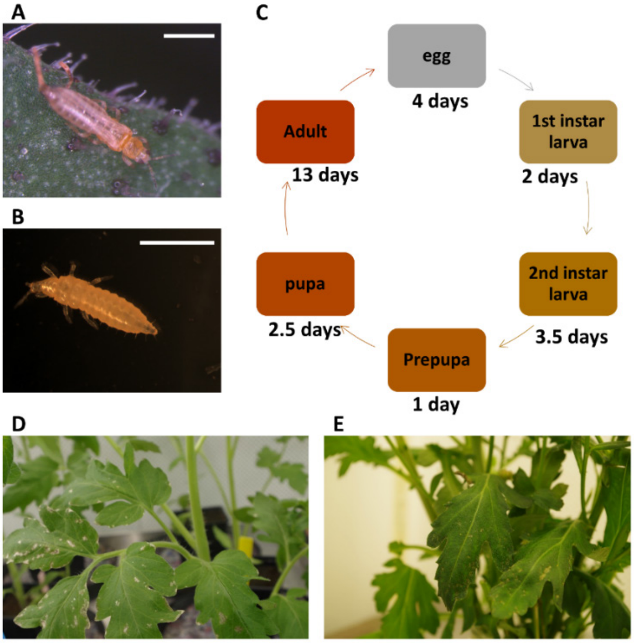

Fig. 1 Development and feeding damage by Western flower thrips. Photographs of (**A**) adult and (**B**) first instar larva of Western flower thrips (*F. occidentalis*). (**C**) life cycle of *F. occidentalis* at 25ºC. Photographs of the typical feeding damage, also termed as "silver damage" on leaves of (**D**) tomato and (**E**) chrysanthemum plants. Scale bars = 0.5 mm. The pictures in A and B were kindly provided by María José Rodríguez.

WFT can cause direct damage by feeding on different parts of the plant (Tommasini & Maini, 1995). WFT penetrates the epidermal and sub-epidermal plant cells with stylet-like mouthparts, sucking out the entire cell sap (Jensen, 2000; Maris *et al.*, 2004). Empty cells are then filled with air resulting in silvery or necrotic patches on leaves, flowers and fruits, which is so-called 'silver damage' (Jensen, 2000). In addition, WFT feeding on developing tissues leads to distortion of flowers and leaves, affecting the photosynthetic ability and fertility of crops and, ultimately, decreasing the crop yield (de Jager *et al.*, 1995; Shipp *et al.*, 2000). Indirect damage by WFT results from the transmission of tospoviruses, of which the *tomato spotted wilt virus* (TSWV) is especially important. It has been estimated that TSWV alone causes an annual economic loss of $19 million in The Netherlands (Rugman-Jones *et al.*, 2010). Until now, more than 1000 plant species belonging to 84 families have been documented to be TSWV hosts, which makes TSWV as one of the most widespread and host-ranged viruses (Parrella *et al.*, 2003). TSWV is transmitted by several species of thrips, of which WFT is one of the most important vectors (Ullman *et al.*, 1989). TSWV is only acquired by first- and second-instar WFT larvae and transmitted by second larval instars or adults (Ullman *et al.*, 1993; Wijkamp & Peters, 1993). As WFT can feed on an ample array of plant species, viruliferous individuals can efficiently transmit the virus across neighboring species.

WFT control in agriculture systems

Current control of WFT mainly relies on the use of insecticides and biological control. Most chemicals, however, have a short-term effectiveness in part due to the cryptic life style of WFT, and a frequent spraying of 3-5 days interval is generally required (Brødsgaard, 1994; Daughtrey *et al.*, 1997; Berndt *et al.*, 2004). General biological control agents of WFT include predatory mites (Gerson & Weintraub, 2007), bugs (Blaeser *et al.*, 2004) and entomopathogenic fungi (Wang & Zheng, 2012). However, biological control is often inefficient because of the limited feeding habit of the predator. For instance, both *Neoseiulus barkeri* Hughes and *Amblyseius cucumeris* Oudenmans primarily prey on WFT first instar larva only (Van der Hoeven & Van Rijn, 1990). Combining two biocontrol control agents, however, seems to not solve this situation and negative interactions might happen between or among biological control agents when simultaneously preying on WFT (Wu *et al.*, 2016). Furthermore, some predators can feed on the plant as well when WFT populations are not very high, thus causing damage in the plant (Briese, 2005).

WFT-plant interactions

WFT feeding induces JA signaling pathway and this response is required to increase plant resistance against this insect (De Vos *et al.*, 2005; Abe *et al.*, 2008; Abe *et al.*, 2009; Kawazu *et al.*, 2012). Accordingly, exogenous application of JAs has been found to increase plant resistance to WFT in cotton (*Aphis gossypii*) (Omer *et al.*, 2001), Arabidopsis (Abe *et al.*, 2008), Chinese cabbage (*Brassica rapa*) (Abe *et al.*, 2009) and tomato (*S. lycopersicum*) (Thaler *et al.*, 2001; Escobar-Bravo *et al.*, 2017). Morphological, chemical and enzymatic-related defenses induced through the activation of JA-dependent defenses (Traw & Bergelson, 2003; Boughton *et al.*, 2005; Tian *et al.*, 2012; Chu *et al.*, 2017; Escobar-Bravo *et al.*, 2017) probably accounts for the enhanced resistance to this insect pest.

Host plant resistance to WFT

Host plant resistance to WFT can be mediated by the constitutive expression of morphological and chemical plant defensive traits, but also by the induction of these or other defenses. For instance, foliar wax content has been found to be negatively correlated with WFT feeding in Gladiolus spp. (Zeier & Wright, 1995). In addition, constitutive levels of certain primary and secondary metabolites, as well as defense enzymes, have been associated with plant resistance to WFT (Mouden *et al.*, 2017). Low concentration of certain aromatic amino acids has been observed to correlate with a reduced WFT feeding damage in lettuce (*Lactuca sativa*), tomato (*S. lycopersicum*), sweet pepper (*Capsicum annuum*) and cucumber (*Cucumis sativus*) (Mollema & Cole, 1996). Variations in constitutive levels of secondary metabolites such as isobutylamide, chlorogenic and feruloyl quinic acid in chrysanthemum (Tsao *et al.*, 2005; Leiss *et al.*, 2009b), jacobine and jaconine in *Senecio (Leiss et al., 2009a)*, trichome-derived acyl sugars in tomato (Mirnezhad *et al.*, 2010), pyrethrins in *Tanacetum cinerariifolium* (Yang *et al.*, 2012), and luteolin and β-alanine in *Daucus carota* L. (Leiss *et al.*, 2013) all have been found to correlate with WFT resistance. Furthermore, genetic engineering for the expression of cysteine proteases inhibitors has been demonstrated to reduce WFT offspring and survival in transgenic potato (*S. tuberosum*) plants (Outchkourov *et al.*, 2004). Notably, induction of certain chemical and morphological defenses has been demonstrated to correlate with WFT resistance or susceptibility as well. For instance, light intensity-mediated reinforcement of type-VI trichome associated chemical defenses has been shown to increase WFT resistance in tomato (*S. lycopersicum*) (Escobar-Bravo *et al.*, 2018). In pepper, Maharijaya *et al.* (2012) showed that while susceptible pepper (Capsicum spp.) accessions induced the production of alkanes and fatty acids in response to WFT infestation, resistant accessions did not.

3.2 Tomato and chrysanthemum

Tomato

Cultivated tomato (*S. lycopersicum* L.) is one of the main consumed vegetable in the world, with an estimated global production of around 177 million tons per year (FAOSTAT, 2016). China, India, EU, USA, Turkey, Egypt, Iran, Brazil, Mexico and Russia produced more than 81% of the total global tomato fruit yield in 2016. In the Netherlands, tomato production was 900 thousand tons in 2016, making tomato production come fifth after potatoes, sugar beet, onions, and wheat (FAOSTAT, 2016). Tomato fruit is a rich source of vitamins A and C, potassium, folic acid and carotenoids, which are positively associated with human health (Giovannucci, 1999; Perveen *et al.*, 2015). Furthermore, carotenoids cannot be synthesized in human tissues, being exclusively obtained from our diet. Tomato fruit also contains other antioxidant compounds, which include flavonoids and phenolic acids (Wardale, 1973). Flavonoids and polyphenols have shown many beneficial properties for human health including anti-cancer, anti-inflammatory, immunomodulatory, and anti-thrombotic activities (Lee & Zhu, 2005; García-Lafuente *et al.*, 2009). Altogether, these features make tomatoes an important nutrient source for the human diet.

Cultivated tomato (*S. lycopersicum* L.) belongs to the Solanaceae family. This family originated in South America and contains many of the most important cultivated plants such as potato, tomato, pepper, eggplant, petunia and tobacco. Tomato breeding for fruit yield, taste and nutritional quality have generated more than 7500 cultivated varieties (Bai & Lindhout, 2007; Korir *et al.*, 2014). Yet, important agricultural traits such as resistance to biotic and abiotic stresses were gradually lost during tomato domestication. As a consequence, most cultivated tomatoes are highly susceptible to a wide array of diseases and arthropod pests, including WFT (Kennedy & Barbour, 1992; Bai & Lindhout, 2007).

One of the main and most important components of tomato defenses against herbivorous arthropods is the leaf trichomes (Kang *et al.*, 2010a; Kang *et al.*, 2010b). Cultivated tomatoes possess non-glandular (type III, V and VIII) and glandular (type I, VI and VII) trichomes types (Glas *et al.*, 2012). Non-glandular trichomes can physically hinder the movement, feeding and oviposition of arthropod herbivores. Type VI glandular trichome, which is the most abundant glandular-type in the leaf surface, can also affect host plant selection and herbivore growth, survival and fecundity (Duffey, 1986). Type-VI glandular trichomes produce and secrete a wide variety of specialized metabolites including terpenoids, phenolics and acyl sugars (Kang *et al.*, 2014). Despite their constitutive expression in the plant, glandular trichome density and chemistry can be induced by the application of JA (Degenhardt *et al.*, 2010; Cevallos-Cevallos *et al.*, 2012; Dobritzsch *et al.*, 2015) or its volatile methyl jasmonate (MeJA) (Boughton *et al.*, 2005; Tian *et al.*, 2012), which can increase tomato resistance to herbivorous arthopods (Escobar-Bravo *et al.*, 2018).

Chrysanthemum

Chrysanthemum [*Chrysanthemum* × *morifolium* Ramat. (Asteraceae)], bred as early as ca. 1000 BC in China and Japan, is one of the economically most important greenhouse ornamentals worldwide (Fletcher, 1992). It is the second most important cutting flowers just after roses in the Netherlands. The Netherlands is also the largest exporting country of cut-chrysanthemum to intra-EU, amount annually to €232 million (Hanks, 2015). The number of chrysanthemum varieties is extremely large, with about 15000 and 6000 listed in Japan and in the National Chrysanthemum Society in Britain, respectively (Teixeira da Silva *et al.*, 2013). Chrysanthemum is primarily propagated asexually by cultivating asexual vegetative stem cuttings (Teynor *et al.*, 1989).

Modern garden chrysanthemums are most likely derived from interspecific hybrids between *Chrysanthemum indicum* and *C. vestitum* native in Eastern Asia being the center of genetic resources of this genus (Zhao *et al.*, 2009). Due to the dense screening and selection of chrysanthemum varieties varying in flower color, size and shape, commercial varieties lacks resistance traits to biotic or abiotic stresses (Teixeira da Silva *et al.*, 2013). Hence, most commercial chrysanthemum cultivars are susceptible to many arthropod pests including the leaf miner *Liriomyza trifolii* (van Dijk *et al.*, 1992), the cotton aphid *Aphis gossypii* (Guldemond *et al.*, 1994) and WFT (*F. occidentalis*) (Leiss *et al.*, 2009b). Yet, there are still variations in the levels of pest resistance. Such variations have been associated to differences in trichome density and antioxidant leaf properties in some cultivars (Leiss *et al.*, 2009b; Deng *et al.*, 2010; He *et al.*, 2011). Thus, determining constitutive and inducible defense traits against arthropod pests in chrysanthemum might be used for the generation of resistant varieties by plant breeding strategies.

4 Outline of this thesis

In **chapter 2** I investigated how JA-mediated induction of tomato defenses against and resistance to WFT is affected by the leaf developmental stage. For this, I measured how JA induced the defensive protein polyphenol oxidase (PPO), type-VI foliar glandular trichome density and accumulation of their associated volatiles in developing and fully-developed leaves. In addition, I assessed the feeding damage by WFT on those leaves. Our results demonstrated that the capacity of tomato leaves to induce JA-associated defenses against WFT is constrained by the leaf development stage, and positively correlated with the levels of WFT resistance along the tomato canopy. Importantly, I also demonstrated that the production of type-VI trichome associated volatiles was differently regulated in developing and fully-developed leaves. These findings have important implications for agriculture, as type-VI trichomes constitute important physical and chemical defenses in tomato against WFT (Escobar-Bravo *et al.*, 2018).

In **chapter 3** I explored the potential use of novel bacteria-derived defense elicitors to activate JA-associated defenses against WFT in tomato. I determined how infiltration with the bacterial pathogen *P. syringae* pv. tomato *(Pst)* strain DC3000, the *Pst*-derived phytotoxin coronatine (COR) or *Pst*-derived medium affected tomato defenses and resistance against WFT. For this, I determined how COR and *Pst* influenced feeding damage by WFT, activation of the JA and SA defenses, type-VI foliar glandular trichome density and leaf chemistry. In addition, I investigated the action of *Pst*-derived culture medium with and without COR, and their interactive effect with pure COR, on tomato resistance to WFT. Our results showed that infiltration of plants with *Pst*, COR or *Pst*-derived culture medium without COR all increased tomato resistance against WFT through the induction of JA-associated defenses, suggesting the presence of non-identified defense elicitors in *Pst*-derived medium. Furthermore, I showed that the *Pst*- or COR-mediated enhancement of tomato resistance against WFT was not explained by the reinforcement of type VI leaf trichome densities, but rather the induction of other JA-associated chemical defenses.

In **chapter 4** I explored the phenotypic diversity in constitutive and inducible defenses against WFT in chrysanthemum. I determined whether variations in constitutive levels of leaf trichome density and oxidative defenses among different chrysanthemum cultivars correlated with the degree of WFT resistance. In addition, I explored whether differences in WFT resistance among a subset of chrysanthemum varieties could be explained by the JA-mediated induction of trichome densities and a defense-related enzyme, PPO. First, our data showed that exogenous application of the phytohormone JA enhanced resistance against WFT in chrysanthemum. However, the phenotypic variation in WFT resistance among chrysanthemum cultivars were not explained by the presence/induction of non-glandular and glandular trichome densities, nor the activity of the defensive protein PPO.

In additional experiments, we observed that local application of JA on chrysanthemum plants did not have a significant effect on WFT resistance. Thus, in **chapter 5** I investigated whether activation of local and systemic chemical responses upon exogenous application of JA varies along the plant canopy in chrysanthemum, and whether it correlates with resistance to WFT. For this, I performed a comprehensive untargeted metabolomic analysis to determine JA-mediated induced chemical responses in local and systemic leaves. Our results showed that local and systemic induction of JA-mediated chemical defenses in chrysanthemum is spatially variable and dependent on the site of the induction. Furthermore, our analyses on the distribution of WFT-associated feeding in the chrysanthemum plant canopy and the metabolomic profiles of basal and apical leaves suggest that higher levels of constitutive and inducible defenses in basal leaves might explain their higher degree of WFT resistance.

In **chapter 6** I summarized and discussed the findings described in this thesis. In addition, I discussed the implications of these findings for the management of WFT in agricultural systems.

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