



Universiteit
Leiden
The Netherlands

Control of Western flower thrips through jasmonate-triggered plant immunity

Chen, G.

Citation

Chen, G. (2019, June 25). *Control of Western flower thrips through jasmonate-triggered plant immunity*. Retrieved from <https://hdl.handle.net/1887/74367>

Version: Not Applicable (or Unknown)

License: [Leiden University Non-exclusive license](#)

Downloaded from: <https://hdl.handle.net/1887/74367>

Note: To cite this publication please use the final published version (if applicable).

Cover Page



Universiteit Leiden



The handle <http://hdl.handle.net/1887/74367> holds various files of this Leiden University dissertation.

Author: Chen, G.

Title: Control of Western flower thrips through jasmonate-triggered plant immunity

Issue Date: 2019-06-25

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 & Wallsgrave, 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 SCF^{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 through 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 COII 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 defense 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 losses 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).

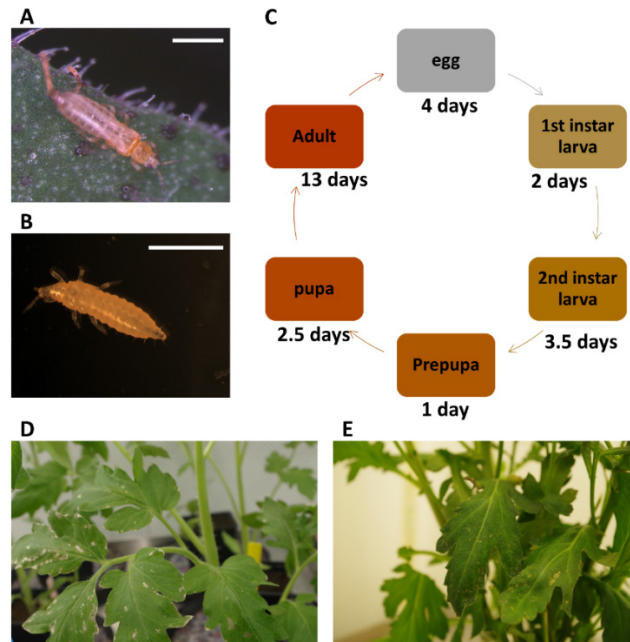


Fig. 1 Development and feeding damage by Western flower thrips. Photographs of (A) adult and (B) first instar larva of Western flower thrips (*F. occidentalis*). (C) life cycle of *F. occidentalis* at 25°C. Photographs of the typical feeding damage, also termed as “silver damage” on leaves of (D) tomato 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 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 arthropods (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* (Guldmond *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.

References

- Abe H, Ohnishi J, Narusaka M, Seo S, Narusaka Y, Tsuda S, Kobayashi M. 2008.** Function of jasmonate in response and tolerance of *Arabidopsis* to thrip feeding. *Plant and cell physiology* **49**: 68-80.
- Abe H, Shimoda T, Ohnishi J, Kugimiya S, Narusaka M, Seo S, Narusaka Y, Tsuda S, Kobayashi M. 2009.** Jasmonate-dependent plant defense restricts thrips performance and preference. *BMC plant biology* **9**: 97.
- Arimura Gi, Huber DP, Bohlmann J. 2004.** Forest tent caterpillars (*Malacosoma disstria*) induce local and systemic diurnal emissions of terpenoid volatiles in hybrid poplar (*Populus trichocarpa* × *deltoides*): cDNA cloning, functional characterization, and patterns of gene expression of (-)-germacrene D synthase, *PtdTPS1*. *The Plant Journal* **37**: 603-616.
- Arnold TM, Schultz JC. 2002.** Induced sink strength as a prerequisite for induced tannin biosynthesis in developing leaves of *Populus*. *Oecologia* **130**: 585-593.
- Bai Y, Lindhout P. 2007.** Domestication and breeding of tomatoes: what have we gained and what can we gain in the future? *Annals of Botany* **100**: 1085-1094.
- Barr KL, Hearne LB, Briesacher S, Clark TL, Davis GE. 2010.** Microbial symbionts in insects influence down-regulation of defense genes in maize. *PLoS one* **5**: e11339.
- Barton KE. 2016.** Tougher and thornier: general patterns in the induction of physical defence traits. *Functional Ecology* **30**: 181-187.
- Basu S, Varsani S, Louis J. 2017.** Altering plant defenses: herbivore-associated molecular patterns and effector arsenal of chewing herbivores. *Molecular Plant-Microbe Interactions* **31**: 13-21.
- Bennett RN, Wallsgrave RM. 1994.** Secondary metabolites in plant defence mechanisms. *New Phytologist* **127**: 617-633.
- Bergey DR, Howe GA, Ryan CA. 1996.** Polypeptide signaling for plant defensive genes exhibits analogies to defense signaling in animals. *Proceedings of the National Academy of Sciences, USA* **93**: 12053-12058.
- Berndt O, Meyhöfer R, Poehling HM. 2004.** The edaphic phase in the ontogenesis of *Frankliniella occidentalis* and comparison of *Hypoaspis miles* and *Hypoaspis aculeifer* as predators of soil-dwelling thrips stages. *Biological Control* **30**: 17-24.

- Bezemer TM, Wagenaar R, Van Dam NM, Van Der Putten WH, Wäckers FL. 2004.** Above-and below-ground terpenoid aldehyde induction in cotton, *Gossypium herbaceum*, following root and leaf injury. *Journal of Chemical Ecology* **30**: 53-67.
- Blaeser P, Sengonca C, Zegula T. 2004.** The potential use of different predatory bug species in the biological control of *Frankliniella occidentalis* (Pergande)(Thysanoptera: Thripidae). *Journal of pest science* **77**: 211-219.
- Block A, Schmelz E, Jones JB, Klee HJ. 2005.** Coronatine and salicylic acid: the battle between *Arabidopsis* and *Pseudomonas* for phytohormone control. *Molecular plant pathology* **6**(1): 79-83.
- Boatwright JL, Pajeroska-Mukhtar K. 2013.** Salicylic acid: an old hormone up to new tricks. *Molecular plant pathology* **14**: 623-634.
- Bodnaryk RP. 1991.** Developmental profile of sinalbin (*p*-hydroxybenzyl glucosinolate) in mustard seedlings, *Sinapis alba* L., and its relationship to insect resistance. *Journal of Chemical Ecology* **17**: 1543-1556.
- Boughton AJ, Hoover K, Felton GW. 2005.** Methyl jasmonate application induces increased densities of glandular trichomes on tomato, *Lycopersicon esculentum*. *Journal of Chemical Ecology* **31**: 2211-2216.
- Briese DT. 2005.** Translating host-specificity test results into the real world: the need to harmonize the yin and yang of current testing procedures. *Biological Control* **35**: 208-214.
- Brødsgaard HF. 1994.** Insecticide resistance in European and African strains of western flower thrips (Thysanoptera: Thripidae) tested in a new residue-on-glass test. *Journal of Economic Entomology* **87**: 1141-1146.
- Brooks DM, Bender CL, Kunkel BN. 2005.** The *Pseudomonas syringae* phytotoxin coronatine promotes virulence by overcoming salicylic acid-dependent defences in *Arabidopsis thaliana*. *Molecular plant pathology* **6**: 629-639.
- Cevallos-Cevallos JM, Gu G, Danyluk MD, van Bruggen AHC. 2012.** Adhesion and splash dispersal of *Salmonella enterica* Typhimurium on tomato leaflets: effects of rdar morphotype and trichome density. *International Journal of Food Microbiology* **160**: 58-64.
- Chen MS. 2008.** Inducible direct plant defense against insect herbivores: a review. *Insect Science* **15**: 101-114.
- Choi WG, Miller G, Wallace I, Harper J, Mittler R, Gilroy S. 2017.** Orchestrating rapid long-distance signaling in plants with Ca²⁺, ROS and electrical signals. *The Plant Journal* **90**: 698-707.
- Chu B, Zhang S, Wang L, Zhu XZ, Luo JY, Wang CY, Lü LM, Cui JJ. 2017.** Genetic regulation of defence responses in cotton to insect herbivores. *AoB Plants* **9**: plx048.
- Constabel CP, Yip L, Patton JJ, Christopher ME. 2000.** Polyphenol oxidase from hybrid poplar. Cloning and expression in response to wounding and herbivory. *Plant Physiology* **124**: 285-296.
- Cui J, Bahrami AK, Pringle EG, Hernandez-Guzman G, Bender CL, Pierce NE, Ausubel FM. 2005.** *Pseudomonas syringae* manipulates systemic plant defenses against pathogens and herbivores. *Proceedings of the National Academy of Sciences, USA* **102**: 1791-1796.
- Daughtrey ML, Jones RK, Moyer JW, Daub ME, Baker JR. 1997.** Tospoviruses strike the greenhouse industry: *INSV* has become a major pathogen on flower crops. *Plant disease* **81**: 1220-1230.
- de Jager CM, Butôt RPT, Klinkhamer PGL, de Jong TJ, Wolff K, van der Meijden E. 1995.** Genetic variation in chrysanthemum for resistance to *Frankliniella occidentalis*. *Entomologia Experimentalis et Applicata* **77**: 277-287.
- De Vos M, Van Oosten VR, Van Poecke RMP, Van Pelt JA, Pozo MJ, Mueller MJ, Buchala AJ, Métraux JP, Van Loon LC, Dicke M *et al.* 2005.** Signal signature and transcriptome changes of *Arabidopsis* during pathogen and insect attack. *Molecular Plant-Microbe Interactions* **18**: 923-937.
- Degenhardt DC, Refi-Hind S, Stratmann JW, Lincoln DE. 2010.** Systemin and jasmonic acid regulate constitutive and herbivore-induced systemic volatile emissions in tomato, *Solanum lycopersicum*. *Phytochemistry* **71**: 2024-2037.
- Deng Y, Chen S, Lu A, Chen F, Tang F, Guan Z, Teng N. 2010.** Production and characterisation of the intergeneric hybrids between *Dendranthema morifolium* and *Artemisia vulgaris* exhibiting enhanced resistance to chrysanthemum aphid (*Macrosiphoniellasanbourni*). *Planta* **231**: 693-703.
- directive. 2009.** Directive 2009/128/EC of the European Parliament and of the Council.

- Ding Y, Sun T, Ao K, Peng Y, Zhang Y, Li X, Zhang Y. 2018.** Opposite roles of salicylic acid receptors NPR1 and NPR3/NPR4 in transcriptional regulation of plant immunity. *Cell* 173: 1-14.
- Doares SH, Syrovets T, Weiler EW, Ryan CA. 1995.** Oligogalacturonides and chitosan activate plant defensive genes through the octadecanoid pathway. *Proceedings of the National Academy of Sciences, USA* 92: 4095-4098.
- Dobritzsch S, Weyhe M, Schubert R, Dindas J, Hause G, Kopka J, Hause B. 2015.** Dissection of jasmonate functions in tomato stamen development by transcriptome and metabolome analyses. *BMC biology* 13: 28.
- Duffey SS. 1986.** Plant glandular trichomes: their partial role in defence against insects. In: Juniper BE, Southwood TE, eds. *Insects and the plant surface*. London, UK: Arnold, 151-172.
- Escobar-Bravo R, Klinkhamer PGL, Leiss KA. 2017.** Induction of jasmonic acid-associated defenses by thrips alters host suitability for conspecifics and correlates with increased trichome densities in tomato. *Plant and cell physiology* 58: 622-634.
- Escobar-Bravo R, Ruijgrok J, Kim HK, Grosser K, Van Dam NM, Klinkhamer PGL, Leiss KA. 2018.** Light intensity-mediated induction of trichome-associated allelochemicals increases resistance against thrips in tomato. *Plant and cell physiology* 59: 2462-2475.
- Eyles A, Bonello P, Ganley R, Mohammed C. 2010.** Induced resistance to pests and pathogens in trees. *New Phytologist* 185: 893-908.
- FAO, IFAD, UNICEF, WFP, WHO. 2017.** *The State of Food Security and Nutrition in the World 2017: Building Resilience for Peace and Food Security*. Rome, FAO.
- FAOSTAT. (2016).** <http://www.fao.org/faostat/en/#data/QC>
- Fletcher JT. 1992.** Disease resistance in protected crops and mushrooms. *Euphytica* 63(1-2): 33-49.
- Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PC *et al.* 2011.** Solutions for a cultivated planet. *Nature* 478: 337.
- Fonseca S, Chini A, Hamberg M, Adie B, Porzel A, Kramell R, Miersch O, Wasternack C, Solano R. 2009.** (+)-7-*iso*-Jasmonoyl-L-isoleucine is the endogenous bioactive jasmonate. *Nature Chemical Biology* 5: 344-350.
- Franceschi VR, Krokene P, Christiansen E, Krekling T. 2005.** Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167: 353-376.
- García-Lafuente A, Guillamón E, Villares A, Rostagno MA, Martínez JA. 2009.** Flavonoids as anti-inflammatory agents: implications in cancer and cardiovascular disease. *Inflammation Research* 58: 537-552.
- Garnett T, Appleby MC, Balmford A, Bateman IJ, Benton TG, Bloomer P, Burlingame B, Dawkins M, Dolan L, Fraser D *et al.* 2013.** Sustainable intensification in agriculture: premises and policies. *Science* 341: 33-34.
- Geng X, Jin L, Shimada M, Kim MG, Mackey D. 2014.** The phytotoxin coronatine is a multifunctional component of the virulence armament of *Pseudomonas syringae*. *Planta* 240: 1149-1165.
- Gerson U, Weintraub PG. 2007.** Mites for the control of pests in protected cultivation. *Pest Management Science: formerly Pesticide Science* 63: 658-676.
- Giovannucci E. 1999.** Tomatoes, tomato-based products, lycopene, and cancer: review of the epidemiologic literature. *Journal of the National Cancer Institute* 91: 317-331.
- Glas JJ, Schimmel BCJ, Alba JM, Escobar-Bravo R, Schuurink RC, Kant MR. 2012.** Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. *International journal of molecular sciences* 13: 17077-17103.
- Glazebrook J. 2005.** Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. *Annual Review of Phytopathology* 43: 205-227.
- Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. 2010.** Food security: the challenge of feeding 9 billion people. *Science* 327: 812-818.
- Green TR, Ryan CA. 1972.** Wound-induced proteinase inhibitor in plant leaves: a possible defense mechanism against insects. *Science* 175: 776-777.
- Grubb CD, Abel S. 2006.** Glucosinolate metabolism and its control. *Trends in Plant Science* 11: 89-100.

- Guldmond JA, Tigges WT, De Vrijer PWF. 1994.** Host races of *Aphis gossypii* (Homoptera: Aphididae) on cucumber and chrysanthemum. *Environmental Entomology* **23**: 1235-1240.
- Hanks G. 2015.** A review of production statistics for the cut flower and foliage sector 2015 (part of AHDB Horticulture funded project PO BOF 002a). *The National Cut Flower Centre, AHDB Horticulture*: 102.
- Harper JL. 1989.** The value of a leaf. *Oecologia* **80**: 53-58.
- He J, Chen F, Chen S, Lv G, Deng Y, Fang W, Liu Z, Guan Z, He C. 2011.** Chrysanthemum leaf epidermal surface morphology and antioxidant and defense enzyme activity in response to aphid infestation. *Journal of Plant physiology* **168**: 687-693.
- Howe GA, Jander G. 2008.** Plant immunity to insect herbivores. *Annual Review of Plant Biology* **59**: 41-66.
- Howe GA, Schaller A. 2008.** Direct defences in plants and their induction by wounding and insect herbivores. In: Schaller A, ed. *Induced plant resistance to herbivory*. New York, NY, USA: Springer Verlag, 7-29.
- Ichihara A, Shiraishi K, Sato H, Sakamura S, Nishiyama K, Sakai R, Furusaki A, Matsumoto T. 1977.** The structure of coronatine. *Journal of the American Chemical Society* **99**: 636-637.
- Immaraju JA, Paine TD, Bethke JA, Robb KL, Newman JP. 1992.** Western flower thrips (Thysanoptera: Thripidae) resistance to insecticides in coastal California greenhouses. *Journal of Economic Entomology* **85**: 9-14.
- Iwasa Y, Kubo T, van Dam NM, de Jong TJ. 1996.** Optimal level of chemical defense decreasing with leaf age. *Theoretical Population Biology* **50**: 124-148.
- Jensen SE. 2000.** Insecticide resistance in the western flower thrips, *Frankliniella occidentalis*. *Integrated Pest Management Reviews* **5**: 131-146.
- Kang JH, Liu G, Shi F, Jones AD, Beaudry RM, Howe GA. 2010a.** The tomato *odorless-2* mutant is defective in trichome-based production of diverse specialized metabolites and broad-spectrum resistance to insect herbivores. *Plant Physiology* **154**: 262-272.
- Kang JH, McRoberts J, Shi F, Moreno JE, Jones AD, Howe GA. 2014.** The flavonoid biosynthetic enzyme chalcone isomerase modulates terpenoid production in glandular trichomes of tomato. *Plant Physiology* **164**: 1161-1174.
- Kang JH, Shi F, Jones AD, Marks MD, Howe GA. 2010b.** Distortion of trichome morphology by the *hairless* mutation of tomato affects leaf surface chemistry. *Journal of Experimental Botany* **61**: 1053-1064.
- Karban R, Myers JH. 1989.** Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* **20**: 331-348.
- Katsir L, Schilmiller AL, Staswick PE, He SY, Howe GA. 2008.** COI1 is a critical component of a receptor for jasmonate and the bacterial virulence factor coronatine. *Proceedings of the National Academy of Sciences, USA* **105**: 7100-7105.
- Kawazu K, Mochizuki A, Sato Y, Sugeno W, Murata M, Seo S, Mitsuhashi I. 2012.** Different expression profiles of jasmonic acid and salicylic acid inducible genes in the tomato plant against herbivores with various feeding modes. *Arthropod-Plant Interactions* **6**: 221-230.
- Kennedy GG, Barbour JD. 1992.** Resistance variation in natural and managed systems. In: Fritz RS, Simms EL, eds. *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics*. Chicago, IL, USA: University of Chicago Press, 13-41.
- Kenyon J, Turner JG. 1990.** Physiological changes in *Nicotiana tabacum* leaves during development of chlorosis caused by coronatine. *Physiological and molecular plant pathology* **37**: 463-477.
- Kessler A, Baldwin IT. 2002.** Plant responses to insect herbivory: the emerging molecular analysis. *Annual review of plant biology* **53**: 299-328.
- Kirk WDJ, Terry LI. 2003.** The spread of the western flower thrips *Frankliniella occidentalis* (Pergande). *Agricultural and Forest Entomology* **5**: 301-310.
- Kloek AP, Verbsky ML, Sharma SB, Schoelz JE, Vogel J, Klessig DF, Kunkel BN. 2001.** Resistance to *Pseudomonas syringae* conferred by an *Arabidopsis thaliana* coronatine-insensitive (*coi1*) mutation occurs through two distinct mechanisms. *The Plant Journal* **26**: 509-522.
- Köhler A, Maag D, Veyrat N, Glauser G, Wolfender JL, Turlings TCJ, Erb M. 2015.** Within-plant distribution of 1, 4-benzoxazin-3-ones contributes to herbivore niche differentiation in maize. *Plant, cell & environment* **38**: 1081-1093.

- Koornneef A, Pieterse CMJ. 2008.** Cross talk in defense signaling. *Plant Physiology* **146**(3): 839-844.
- Korir NK, Diao W, Tao R, Li X, Kayesh E, Li A, Zhen W, Wang S. 2014.** Genetic diversity and relationships among different tomato varieties revealed by EST-SSR markers. *Genetics and Molecular Research* **13**: 43-53.
- Lee G, Joo Y, Kim SG, Baldwin IT. 2017.** What happens in the pith stays in the pith: tissue-localized defense responses facilitate chemical niche differentiation between two spatially separated herbivores. *The Plant Journal* **92**: 414-425.
- Lee WJ, Zhu BT. 2005.** Inhibition of DNA methylation by caffeic acid and chlorogenic acid, two common catechol-containing coffee polyphenols. *Carcinogenesis* **27**: 269-277.
- Leiss KA, Choi YH, Abdel-Farid IB, Verpoorte R, Klinkhamer PGL. 2009a.** NMR metabolomics of thrips (*Frankliniella occidentalis*) resistance in *Senecio* hybrids. *Journal of Chemical Ecology* **35**: 219-229.
- Leiss KA, Cristofori G, van Steenis R, Verpoorte R, Klinkhamer PGL. 2013.** An eco-metabolomic study of host plant resistance to Western flower thrips in cultivated, biofortified and wild carrots. *Phytochemistry* **93**: 63-70.
- Leiss KA, Maltese F, Choi YH, Verpoorte R, Klinkhamer PGL. 2009b.** Identification of chlorogenic acid as a resistance factor for thrips in chrysanthemum. *Plant Physiology* **150**: 1567-1575.
- Lewis T, eds. 1997.** *Thrips as crop pests*. Wallingford, UK: CAB International.
- MacDonald KM, Hamilton JGC, Jacobson R, Kirk WDJ. 2002.** Effects of alarm pheromone on landing and take-off by adult western flower thrips. *Entomologia Experimentalis et Applicata* **103**: 279-282.
- Maharijaya A, Vosman B, Verstappen F, Steenhuis-Broers G, Mumm R, Purwito A, Visser RGF, Voorrips RE. 2012.** Resistance factors in pepper inhibit larval development of thrips (*Frankliniella occidentalis*). *Entomologia Experimentalis et Applicata* **145**: 62-71.
- Maris PC, Joosten NN, Goldbach RW, Peters D. 2004.** Decreased preference and reproduction, and increased mortality of *Frankliniella occidentalis* on thrips-resistant pepper plants. *Entomologia Experimentalis et Applicata* **113**: 149-155.
- McDonald JR, Bale JS, Walters KFA. 1998.** Effect of temperature on development of the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). *European Journal of Entomology* **95**: 301-306.
- Messelink GJ. 2014.** Persistent and emerging pests in greenhouse crops: Is there a need for new natural enemies? *IOBC/wprs Bulletin* **102**: 143-150.
- Meyer GA, Montgomery ME. 1987.** Relationships between leaf age and the food quality of cottonwood foliage for the gypsy moth, *Lymantria dispar*. *Oecologia* **72**: 527-532.
- Mirnezhad M, Romero-González RR, Leiss KA, Choi YH, Verpoorte R, Klinkhamer PGL. 2010.** Metabolomic analysis of host plant resistance to thrips in wild and cultivated tomatoes. *Phytochemical Analysis* **21**: 110-117.
- Mithöfer A, Boland W. 2008.** Recognition of herbivory-associated molecular patterns. *Plant Physiology* **146**: 825-831.
- Mollema C, Cole RA. 1996.** Low aromatic amino acid concentrations in leaf proteins determine resistance to *Frankliniella occidentalis* in four vegetable crops. *Entomologia Experimentalis et Applicata* **78**: 325-333.
- Mouden S, Sarmiento KF, Klinkhamer PGL, Leiss KA. 2017.** Integrated pest management in western flower thrips: past, present and future. *Pest management science* **75**: 813-822.
- Oerke EC. 2006.** Crop losses to pests. *The Journal of Agricultural Science* **144**: 31-43.
- Oerke EC, Dehne HW. 2004.** Safeguarding production—losses in major crops and the role of crop protection. *Crop protection* **23**: 275-285.
- Omer AD, Granett J, Karban R, Villa EM. 2001.** Chemically-induced resistance against multiple pests in cotton. *International Journal of Pest Management* **47**: 49-54.
- Orians C. 2005.** Herbivores, vascular pathways, and systemic induction: facts and artifacts. *Journal of Chemical Ecology* **31**: 2231-2242.
- Outchkourov NS, De Kogel WJ, Wiegers GL, Abrahamson M, Jongma MA. 2004.** Engineered multidomain cysteine protease inhibitors yield resistance against western flower thrips (*Frankliniella occidentalis*) in greenhouse trials. *Plant biotechnology journal* **2**: 449-458.

- Parrella G, Gognalons P, Gebre-Selassie K, Vovlas C, Marchoux G. 2003.** An update of the host range of Tomato spotted wilt virus. *Journal of Plant Pathology* **85**: 227-264.
- Peiffer M, Tooker JF, Luthe DS, Felton GW. 2009.** Plants on early alert: glandular trichomes as sensors for insect herbivores. *New Phytologist* **184**: 644-656.
- Perveen R, Suleria HAR, Anjum FM, Butt MS, Pasha I, Ahmad S. 2015.** Tomato (*Solanum lycopersicum*) carotenoids and lycopenes chemistry; metabolism, absorption, nutrition, and allied health claims—a comprehensive review. *Critical Reviews in Food Science and Nutrition* **55**: 919-929.
- Phalan B, Balmford A, Green RE, Scharlemann JPW. 2011.** Minimising the harm to biodiversity of producing more food globally. *Food Policy* **36**: S62-S71.
- Pieterse CMJ, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees SCM. 2012.** Hormonal modulation of plant immunity. *Annual review of cell and developmental biology* **28**: 489-521.
- Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Van Wees SCM, Bakker PAHM. 2014.** Induced systemic resistance by beneficial microbes. *Annual review of phytopathology* **52**: 347-375.
- Ray DK, Mueller ND, West PC, Foley JA. 2013.** Yield trends are insufficient to double global crop production by 2050. *PLoS one* **8**: e66428.
- Ray S, Gaffor I, Acevedo FE, Helms A, Chuang WP, Tooker J, Felton GW, Luthe DS. 2015.** Maize plants recognize herbivore-associated cues from caterpillar frass. *Journal of Chemical Ecology* **41**: 781-792.
- Reitz SR. 2008.** Comparative bionomics of *Frankliniella occidentalis* and *Frankliniella tritici*. *Florida Entomologist* **91**: 474-476.
- Robb KL. 1989.** Analysis of *Frankliniella occidentalis* (Pergande) as a pest of floricultural crops in California greenhouses. Doctoral thesis. University of California, Riverside.
- Roush R, Tabashnik BE. 2012.** *Pesticide resistance in arthropods*. Springer Science & Business Media.
- Rugman-Jones PF, Hoddle MS, Stouthamer R. 2010.** Nuclear-mitochondrial barcoding exposes the global pest western flower thrips (Thysanoptera: Thripidae) as two sympatric cryptic species in its native California. *Journal of Economic Entomology* **103**: 877-886.
- Schmelz EA, Engelberth J, Alborn HT, O'Donnell P, Sammons M, Toshima H, Tumlinson III JH. 2003.** Simultaneous analysis of phytohormones, phytotoxins, and volatile organic compounds in plants. *Proceedings of the National Academy of Sciences, USA* **100**: 10552-10557.
- Sheard LB, Tan X, Mao H, Withers J, Ben-Nissan G, Hinds TR, Kobayashi Y, Hsu FF, Sharon M, Browse J *et al.* 2010.** Jasmonate perception by inositol-phosphate-potentiated COI1-JAZ co-receptor. *Nature* **468**: 400-405.
- Shipp JL, Wang K, Binns MR. 2000.** Economic injury levels for western flower thrips (Thysanoptera: Thripidae) on greenhouse cucumber. *Journal of Economic Entomology* **93**: 1732-1740.
- Slawiak M, Lojkowska E. 2009.** Genes responsible for coronatine synthesis in *Pseudomonas syringae* present in the genome of soft rot bacteria. *European Journal of Plant Pathology* **124**: 353-361.
- Smith JL, De Moraes CM, Mescher MC. 2009.** Jasmonate- and salicylate-mediated plant defense responses to insect herbivores, pathogens and parasitic plants. *Pest management science* **65**: 497-503.
- Staswick PE, Tiryaki I. 2004.** The oxylipin signal jasmonic acid is activated by an enzyme that conjugates it to isoleucine in Arabidopsis. *The Plant Cell* **16**: 2117-2127.
- Steimetz E, Trouvelot S, Gindro K, Bordier A, Poinssot B, Adrian M, Daire X. 2012.** Influence of leaf age on induced resistance in grapevine against *Plasmopara viticola*. *Physiological and molecular plant pathology* **79**: 89-96.
- Stockstad E, Grullón G. 2013.** Infographic: pesticide planet. A global look at the uses, benefits, and drawbacks of pesticides. *Science*, **341**: 730-731.
- Stout MJ, Fidantsef AL, Duffey SS, Bostock RM. 1999.** Signal interactions in pathogen and insect attack: systemic plant-mediated interactions between pathogens and herbivores of the tomato, *Lycopersicon esculentum*. *Physiological and molecular plant pathology* **54**: 115-130.
- Strapasson P, Pinto-Zevallos DM, Paudel S, Rajotte EG, Felton GW, Zarbin PHG. 2014.** Enhancing plant resistance at the seed stage: low concentrations of methyl jasmonate reduce the performance of the leaf miner *Tuta absoluta* but do not alter the behavior of its predator *Chrysoperla externa*. *Journal of Chemical Ecology* **40**: 1090-1098.

- Sun JQ, Jiang HL, Li CY. 2011.** Systemin/jasmonate-mediated systemic defense signaling in tomato. *Molecular Plant* **4**: 607-615.
- Takabayashi J, Dicke M, Takahashi S, Posthumus MA, Van Beek TA. 1994.** Leaf age affects composition of herbivore-induced synomones and attraction of predatory mites. *Journal of Chemical Ecology* **20**: 373-386.
- Takahashi H, Kanayama Y, Zheng MS, Kusano T, Hase S, Ikegami M, Shah J. 2004.** Antagonistic interactions between the SA and JA signaling pathways in *Arabidopsis* modulate expression of defense genes and gene-for-gene resistance to cucumber mosaic virus. *Plant and cell physiology* **45**: 803-809.
- Teixeira da Silva JA, Shinoyama H, Aida R, Matsushita Y, Raj SK, Chen F. 2013.** Chrysanthemum biotechnology: Quo vadis? *Critical Reviews in Plant Sciences* **32**: 21-52.
- Tester M, Langridge P. 2010.** Breeding technologies to increase crop production in a changing world. *Science* **327**: 818-822.
- Teynor TM, Ascher PD, Widmer RE, Luby JJ. 1989.** Inheritance of flower color in *Dendranthema grandiflora* Tzvelev. (*Chrysanthemum morifolium* Ramat.) using cultivars and inbreds. I. Plastid pigmentation. *Euphytica* **42**: 199-207.
- Thaler JS, Stout MJ, Karban R, Duffey SS. 2001.** Jasmonate-mediated induced plant resistance affects a community of herbivores. *Ecological Entomology* **26**: 312-324.
- Tian D, Peiffer M, De Moraes CM, Felton GW. 2014.** Roles of ethylene and jasmonic acid in systemic induced defense in tomato (*Solanum lycopersicum*) against *Helicoverpa zea*. *Planta* **239**: 577-589.
- Tian D, Tooker J, Peiffer M, Chung SH, Felton GW. 2012.** Role of trichomes in defense against herbivores: comparison of herbivore response to woolly and hairless trichome mutants in tomato (*Solanum lycopersicum*). *Planta* **236**: 1053-1066.
- Tommasini MG, Maini S. 1995.** *Frankliniella occidentalis* and other thrips harmful to vegetable and ornamental crops in Europe. In: Loomans AJM, van Lenteren JC, Tommasini MG, Maini S, Riudavets J, eds. *Biological control of thrips pests*. Wageningen: Wageningen Agricultural University Papers, 1-42.
- Traw MB, Bergelson J. 2003.** Interactive effects of jasmonic acid, salicylic acid, and gibberellin on induction of trichomes in *Arabidopsis*. *Plant Physiology* **133**: 1367-1375.
- Tsao R, Marvin CH, Broadbent AB, Friesen M, Allen WR, Mcgarvey BD. 2005.** Evidence for an isobutylamide associated with host-plant resistance to western flower thrips, *Frankliniella occidentalis*, in chrysanthemum. *Journal of Chemical Ecology* **31**: 103-110.
- Ullman DE, German TL, Sherwood JL, Westcot DM, Cantone FA. 1993.** *Tospovirus* replication in insect vector cells: Immunocytochemical evidence that the nonstructural protein encoded by the S RNA of tomato spotted wilt tospovirus is present in thrips vector cells. *Phytopathology* **83**: 456-463.
- Ullman DE, Westcot DM, Hunter WB, Mau RFL. 1989.** Internal anatomy and morphology of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) with special reference to interactions between thrips and tomato spotted wilt virus. *International Journal of Insect Morphology and Embryology* **18**: 289-310.
- UN. 2017.** World Population Prospects: The 2017 Revision, Key Findings and Advance Tables. *United Nations, Department of Economic and Social Affairs, Population Division. (Working Paper No. ESA/P/WP/248)*.
- Uppalapati SR, Ishiga Y, Wangdi T, Kunkel BN, Anand A, Mysore KS, Bender CL. 2007.** The phytotoxin coronatine contributes to pathogen fitness and is required for suppression of salicylic acid accumulation in tomato inoculated with *Pseudomonas syringae* pv. *tomato* DC3000. *Molecular Plant-Microbe Interactions* **20**: 955-965.
- Van Dam NM, De Jong T, Iwasa Y, Kubo T. 1996.** Optimal distribution of defences: are plants smart investors? *Functional Ecology* **10**: 128-136.
- Van Dam NM, Horn M, Mareš M, Baldwin IT. 2001.** Ontogeny constrains systemic protease inhibitor response in *Nicotiana attenuata*. *Journal of Chemical Ecology* **27**: 547-568.
- Van Dam NM, Witjes L, Svatoš A. 2004.** Interactions between aboveground and belowground induction of glucosinolates in two wild *Brassica* species. *New Phytologist* **161**: 801-810.

- Van der Hoeven WAD, Van Rijn PCJ. 1990.** Factors affecting the attack success of predatory mites on thrips larvae. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* **1**: 25-30.
- van Dijk MJ, Hermans C, de Jong J, van der Meijden E 1992.** The impact of environmental conditions on survival of the leaf miner *Liriomyza trifolii* on *Chrysanthemum* cultivars. *Proceedings of the 8th International Symposium on Insect-Plant Relationships*: Springer: 267-270.
- Verma V, Ravindran P, Kumar PP. 2016.** Plant hormone-mediated regulation of stress responses. *BMC plant biology* **16**: 86.
- Vierbergen G. 2001.** *Thrips palmi*: pathways and possibilities for spread. *EPPO Bulletin* **31**: 169-171.
- Walling LL. 2000.** The myriad plant responses to herbivores. *Journal of Plant Growth Regulation* **19**: 195-216.
- Wang J, Zheng C. 2012.** Characterization of a newly discovered *Beauveria bassiana* isolate to *Frankliniella occidentalis* Perganda, a non-native invasive species in China. *Microbiological Research* **167**: 116-120.
- Wardale DA. 1973.** Effect of phenolic compounds in *Lycopersicon esculentum* on the synthesis of ethylene. *Phytochemistry* **12**: 1523-1530.
- Wasternack C, Hause B. 2013.** Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in *Annals of Botany*. *Annals of Botany* **111**: 1021-1058.
- Werker E. 2000.** Trichome diversity and development. *Advances in botanical research* **31**: 1-35.
- Wijkamp I, Peters D. 1993.** Determination of the median latent period of two tospoviruses in *Frankliniella occidentalis*, using a novel leaf disk assay. *Phytopathology* **83**: 986-986.
- Wu J, Baldwin IT. 2010.** New insights into plant responses to the attack from insect herbivores. *Annual Review of Genetics* **44**: 1-24.
- Wu J, Wang L, Baldwin IT. 2008.** Methyl jasmonate-elicited herbivore resistance: does MeJA function as a signal without being hydrolyzed to JA? *Planta* **227**: 1161-1168.
- Wu S, Gao Y, Smagghe G, Xu X, Lei Z. 2016.** Interactions between the entomopathogenic fungus *Beauveria bassiana* and the predatory mite *Neoseiulus barkeri* and biological control of their shared prey/host *Frankliniella occidentalis*. *Biological Control* **98**: 43-51.
- Wu S, Peiffer M, Luthe DS, Felton GW. 2012.** ATP hydrolyzing salivary enzymes of caterpillars suppress plant defenses. *PloS one* **7**: e41947.
- Wu S, Tang L, Zhang X, Xing Z, Lei Z, Gao Y. 2017.** A decade of a thrips invasion in China: lessons learned. *Ecotoxicology* **27**: 1-7.
- Yang T, Stoopen G, Wieggers G, Mao J, Wang C, Dicke M, Jongsma MA. 2012.** Pyrethrins protect pyrethrum leaves against attack by western flower thrips, *Frankliniella occidentalis*. *Journal of Chemical Ecology* **38**: 370-377.
- Zeier P, Wright MG 1995.** Thrips resistance in *Gladiolus* spp.: potential for IPM and breeding. In: Parker BL, Skinner M, Lewis T, eds. *Thrips Biology and Management. NATO ASI Series (Series A: Life Sciences)*, Boston, MA, Springer, **276**: 411-416.
- Zhao HE, Liu ZH, Hu X, Yin JL, Li W, Rao GY, Zhang XH, Huang CL, Anderson N, Zhang QX et al. 2009.** Chrysanthemum genetic resources and related genera of *Chrysanthemum* collected in China. *Genetic Resources and Crop Evolution* **56**: 937.
- Zhao YF, Jones WT, Sutherland P, Palmer DA, Mitchell RE, Reynolds PHS, Damicone JP, Bender CL. 2001.** Detection of the phytotoxin coronatine by ELISA and localization in infected plant tissue. *Physiological and molecular plant pathology* **58**: 247-258.
- Zhao Y, Thilmony R, Bender CL, Schaller A, He SY, Howe GA. 2003.** Virulence systems of *Pseudomonas syringae* pv. *tomato* promote bacterial speck disease in tomato by targeting the jasmonate signaling pathway. *The Plant Journal* **36**: 485-499.