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REVIEW PAPER

Thrips advisor: exploiting thrips-induced defences to combat pests on crops

Merel Steenbergen[1], Ahmed Abd-el-Haliem[2], Petra Bleeker[2,3], Marcel Dicke[4], Rocio Escobar-Bravo[5], Gang Cheng[5], Michel A. Haring[2], Merijn R. Kant[6], Iris Kappers[7], Peter G. L. Klinkhamer[5], Kirsten A. Leiss[8], Saioa Legarrea[6], Mirka Macel[9], Sanae Mouden[5], Corné M. J. Pieterse[1], Sandeep J. Sarde[4], Robert C. Schuurink[2], Martin De Vos[10], Saskia C. M. Van Wees[1,*], and Colette Broekgaarden[1]

[1] Plant-Microbe Interactions, Department of Biology, Faculty of Science, Utrecht University, PO Box 800.56, 3508 TB Utrecht, The Netherlands
[2] Department of Plant Physiology, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands
[3] Enza Zaden BV, PO Box 7, 1600 AA Enkhuizen, The Netherlands
[4] Laboratory of Entomology, Wageningen University and Research, PO Box 16, 6700 AA Wageningen, The Netherlands
[5] Plant Sciences and Natural Products, Institute of Biology, Leiden University, PO Box 9500, 2300 RA Leiden, The Netherlands
[6] Molecular & Chemical Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, The Netherlands
[7] Laboratory of Plant Physiology, Wageningen University and Research, PO Box 16, 6700 AA Wageningen, The Netherlands
[8] Wageningen UR Greenhouse Horticulture, PO Box 20, 2665 ZG Bleiswijk, The Netherlands
[9] Molecular Interactions Ecology, Radboud University, PO Box 9010, 6500 NL Nijmegen, The Netherlands
[10] Keygene NV, PO Box 216, 6700 AE Wageningen, The Netherlands

* Correspondence: s.vanwees@uu.nl

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Abstract

Plants have developed diverse defence mechanisms to ward off herbivorous pests. However, agriculture still faces estimated crop yield losses ranging from 25% to 40% annually. These losses arise not only because of direct feeding damage, but also because many pests serve as vectors of plant viruses. Herbivorous thrips (Thysanoptera) are important pests of vegetable and ornamental crops worldwide, and encompass virtually all general problems of pests: they are highly polyphagous, hard to control because of their complex lifestyle, and they are vectors of destructive viruses. Currently, control management of thrips mainly relies on the use of chemical pesticides. However, thrips rapidly develop resistance to these pesticides. With the rising demand for more sustainable, safer, and healthier food production systems, we urgently need to pinpoint the gaps in knowledge of plant defences against thrips to enable the future development of novel control methods. In this review, we summarize the current, rather scarce, knowledge of thrips-induced plant responses and the role of phytohormonal signalling and chemical defences in these responses. We describe concrete opportunities for breeding resistance against pests such as thrips as a prototype approach for next-generation resistance breeding.

Keywords: Cell-content feeder, effectors, herbivorous insect, phytohormone signalling, plant defence, specialized metabolites, thrips, virus, volatiles.

Abbreviations: ABA, abscisic acid; COI1, CORONATINE INSENSITIVE1; DAMP, damage-associated molecular pattern; def-1, *defenseless-1*; BABA, DL-β-aminobutyric acid; ERF, ETHYLENE-RESPONSIVE FACTOR; ET, ethylene; HAMP, herbivore-associated molecular pattern; JA, jasmonic acid; L1, first instar larvae; L2, second instar larvae; PDF1.2, PLANT DEFENSIN1.2; RNA-Seq, RNA sequencing; SA, salicylic acid; TSWV, tomato spotted wilt virus; VOC, volatile organic compound; VSP2, VEGETATIVE STORAGE PROTEIN2.

Introduction

Plants and insect herbivores have been interacting with each other for over 400 million years (Labandeira, 2007). To maximize reproductive success, plants have evolved a plethora of defence mechanisms that can affect herbivores either directly or indirectly. Direct defences rely on plant traits that interfere with host plant selection or herbivore performance (War *et al.*, 2012), while indirect defences rely on the herbivore's natural enemies (Dicke, 2015). Both direct and indirect defences can be displayed constitutively, that is, regardless of the presence of herbivores, but they are more often initiated upon herbivore attack due to the trade-off between plant growth and defence (Züst and Agrawal, 2017).

Herbivore-inducible plant defences are initiated after perception of the herbivore via the recognition of damage-associated molecular patterns (DAMPs; Duran-Flores & Heil, 2016), herbivore-associated molecular patterns (HAMPs; Mithöfer and Boland, 2008), or egg-associated cues (Hilker and Fatouros, 2016) (Fig. 1). Subsequent to herbivore recognition, a signalling cascade is triggered in plant cells that initiates the biosynthesis of specialized metabolites and proteins. The phytohormone jasmonic acid (JA) is considered a key player in the defence regulatory network that is effective against herbivores. The interaction of JA with other hormones, such as ethylene (ET), abscisic acid (ABA), and salicylic acid (SA), permits fine-tuning of the spatiotemporal dynamics of the defence response (Schuman & Baldwin, 2016). Recent evidence suggests that herbivores secrete effectors in their saliva to modulate plant defence responses and establish a compatible interaction with the host plant (Hogenhout and Bos, 2011; Kant *et al.*, 2015; Giron *et al.*, 2016).

There is ample knowledge on the induced plant responses that are activated upon infestation with leaf-chewing or phloem-feeding herbivores (Bonaventure, 2012; Hilker and Fatouros, 2016; Züst and Agrawal, 2016) (Fig. 1). For example, several putative HAMPs (Douglas, 2018), egg-associated elicitors (Reymond, 2013), effector proteins, and resistance genes have been identified (Hogenhout and Bos, 2011; Douglas, 2018). However, such cues have not yet been identified for cell-content-feeding insects such as thrips. These tiny (1.5 mm or less) insects belong to the order Thysanoptera, which comprises over 5500 described species. Their fringed wings, that is, the presence of long hairs (cilia) that form a fringe around the wings (Fig. 2A), allow them to remain airborne despite not being strong flyers (Mound, 2005). Several thrips species are pests of commercial crops (Cannon *et al.*, 2007; Diaz-Montano *et al.*, 2011; Mouden *et al.*, 2017), either because they cause direct damage to plants through feeding or because they act as vectors of economically important plant viruses (Riley *et al.*, 2011). Thrips brings together all the problems of pests in general: they are highly polyphagous, hard to control because of their complex lifestyle and rapid adaptation to pesticides, and are vectors of destructive viruses.

In this review we summarize the current knowledge of thrips-induced plant responses and pinpoint the gaps in knowledge that have to be filled for the development of novel thrips control strategies in agroecosystems. First, we will describe the

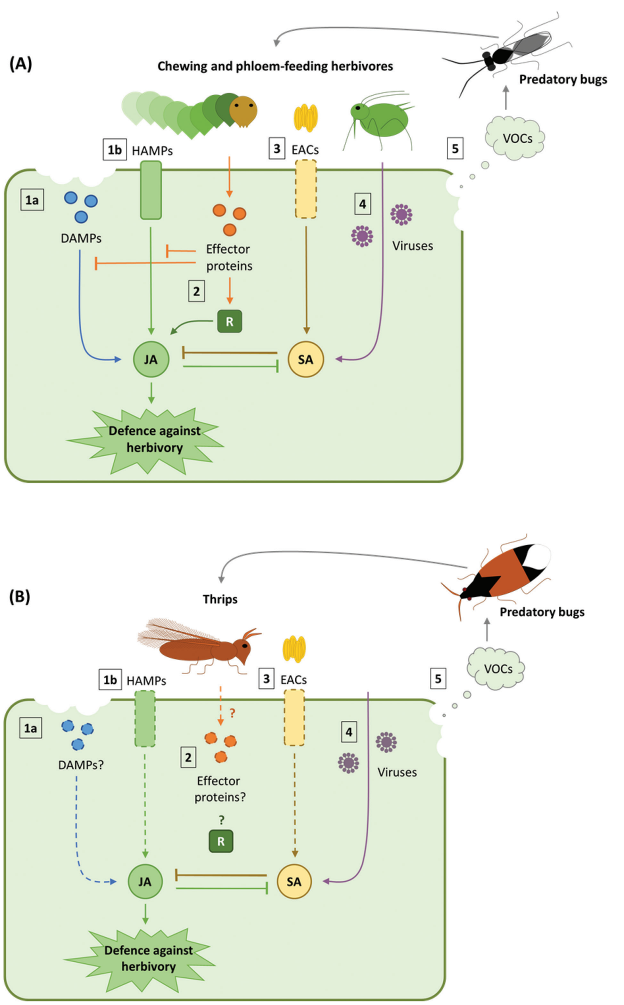

Fig. 1. Molecular components in induced plant responses during feeding by chewing and phloem-feeding herbivores (A) and thrips (B). (A) During feeding by chewing and phloem-feeding herbivores, plant defence responses are initiated upon the recognition of damage-associated molecular patterns (DAMPs) (1a) and herbivore-associated molecular patterns (HAMPs) (1b), which activate the biosynthesis of specialized metabolites, such as the phytohormone jasmonic acid (JA), which in turn regulate effective defences against herbivore attack. Herbivore-derived effector proteins can alter the host's defence response in favour of the insect by suppressing HAMP- or DAMP-induced signalling (2). Plant resistance proteins (R) that recognize pest-derived effector proteins may in turn mount an effective defence response (2). Recognition of insect egg-associated compounds (EACs) triggers salicylic acid (SA) signalling, which through negative crosstalk with the JA response reduces effective plant defences against the herbivore's offspring (3). Viruses transmitted by insects can interfere with induced anti-herbivory defence responses, possibly also mediated by crosstalk effects of virus-induced SA (4). In response to herbivore feeding, plants emit a specific blend of volatile organic compounds (VOCs) to attract natural enemies of the attacker at hand (5). (B) Thrips feeding activates the biosynthesis of JA, resulting in induced plant defences against thrips. In thrips–plant interactions neither DAMPs (1a) nor HAMPs (1b) have been identified yet. Similarly, thrips effector proteins, their plant targets, or plant R proteins have not been isolated yet (2). In addition, it is unknown whether thrips eggs contain EACs that can be recognized by the host plant or trigger SA signalling (3). Tospoviruses are exclusively transmitted by thrips and can interfere with anti-herbivory plant defences, possibly through crosstalk of virus-induced SA with thrips-induced JA signalling (4). In response to thrips feeding, plants emit specific VOCs that can attract predatory bugs, such as *Orius laevigatus*, that feed on thrips (5). Uncharacterized and hypothesized receptors and induced response pathways are indicated with dashed lines.

general aspects of the interaction between thrips and plants. Then, we provide an overview of the current fundamental knowledge of thrips-induced plant responses involving phytohormone signalling and specialized metabolites that play a role in direct and indirect defences. We conclude this review by listing practical opportunities for future research in plant–thrips interactions to improve sustainable crop production methods to fight this pest.

The interaction between herbivorous thrips and plants

Herbivorous thrips feed on leaves, petals, fruits, and/or pollen of green plants, thereby affecting photosynthetic capacity, plant growth, and reproduction (Morse and Hoddle, 2006; Mound, 2005). Female thrips (Fig. 2A) lay their cylindrical or bean-shaped eggs on or into plant tissues that are suitable for their larvae to feed from. Thrips have a haplodiploid sex-determination system, meaning that females and males emerge from fertilized (diploid) and non-fertilized (haploid) eggs, respectively. Larvae (Fig. 2B) that hatch from the eggs develop through two stages (L1 and L2) in which they actively feed, and two non-feeding, soil-dwelling stages (prepupa and pupa) in which they prepare for the adult stage. Both adults and larvae insert their stylets into plant tissue and ingest cell content while feeding (Kindt *et al.*, 2003). Probing plant tissue comprises three distinct behavioural phases: (i) piercing, (ii) salivation, and (iii) ingestion of the cell contents (Kindt *et al.*, 2006). The pierced cells collapse or fill up with air, giving the damaged area a silvery appearance (Fig. 2C). The developmental and reproductive rate of thrips is highly dependent on environmental conditions, including temperature and the nutritional quality of the host plant. For example, the life cycle from egg to adult of the western flower thrips (*Frankliniella occidentalis*) can be completed within 45 days at 15 °C or within 15 days at 30 °C (Cloyd, 2009).

Host plant selection and feeding

Before colonizing a plant, an adult thrips determines the suitability of the potential host via a sequence of pre-alighting and post-alighting behaviours. Pre-alighting host-recognition behaviour, which involves approaching a potential host and landing on it, is mediated by plant volatile organic compounds (VOCs) (Teulon *et al.*, 1999; Koschier *et al.*, 2007; El-Sayed *et al.*, 2009) and/or visual cues such as colour (Childers and Brecht, 1996; Teulon *et al.*, 1999), shape (Mainali and Lim, 2011), or size (Papadaki *et al.*, 2008). For example, *F. occidentalis* is attracted to VOCs emitted by cabbage (*Brassica oleracea*), while VOCs from garlic (*Allium sativum*) are repellent to this thrips species (Cao *et al.*, 2014). Additionally, *F. occidentalis* is more attracted to circular shapes than to other geometrical forms, such as rectangular and triangular shapes (Mainali and Lim, 2010). In deciduous forests, colour has been demonstrated to be a more dominant factor than odours for the orientation of the introduced basswood thrips (*Thrips calcaratus*), the pear thrips (*Taeniothrips inconsequens*), and the native basswood

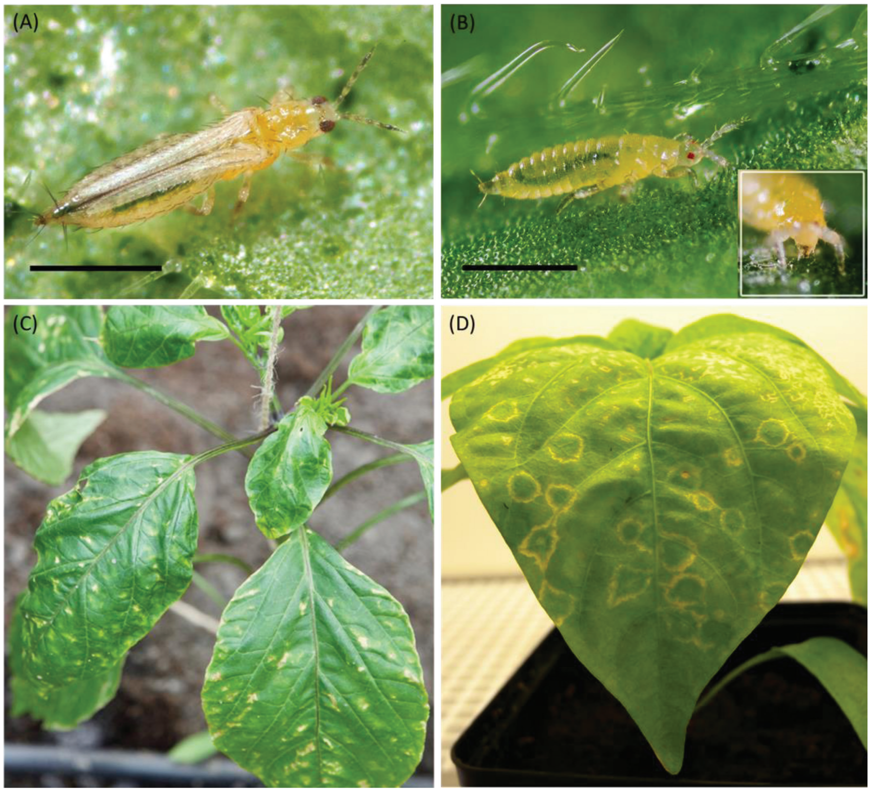

Fig. 2. Thrips development and damage symptoms on pepper (*Capsicum*) plants. (A) Western flower thrips (*F. occidentalis*) adult; (B) stage L2 larva of the same species. Scale bars=0.5 mm. (C) Thrips feeding scars, termed 'silver damage'. (D) Symptoms of tomato spotted wilt virus infection transmitted by thrips. A, B, and D kindly provided by Jan van Arkel (University of Amsterdam).

thrips (*Neohydatothrips tiliae*) (Rieske and Raffa, 1995). Flowers can play an important role in pre-alighting host-recognition behaviour of some thrips species because flowers emit a mixture of VOCs and display distinct visual cues (Boachon *et al.*, 2015; Lim and Mainali, 2009; Mainali and Lim, 2008).

Final acceptance of a plant is guided by post-alighting behaviour to test the plant's suitability for feeding and/or oviposition. The importance of post-alighting testing in host selection by thrips has been shown for *F. occidentalis* interacting with chrysanthemum (*Chrysanthemum morifolium*), in which thrips were more attracted to linalool-emitting flowers but gradually reversed their preference after landing, probably due to test feeding by thrips (Yang *et al.*, 2013). Post-alighting host acceptance, and also subsequent feeding and reproduction, are strongly influenced by the plant's nutritional quality and defences (Baez *et al.*, 2011; Chow *et al.*, 2012; Leiss *et al.*, 2009*b*, 2013; Pobożniak and Koschier, 2014; Wang *et al.*, 2014). For example, transgenic potato (*Solanum tuberosum*) plants overexpressing cysteine proteinase inhibitors, which are known as defensive proteins, deter *F. occidentalis* (Outchkourov *et al.*, 2004). Additionally, leaf age may correlate with nutritional quality and defences, which may cause thrips to prefer older leaves and avoid the better-protected young parts of the plant (Joost and Riley, 2008; Scott-Brown *et al.*, 2016). Hybrids of the ragwort species *Senecio jacobaea* and *Senecio aquaticus* showed a negative correlation between *F. occidentalis* damage and pyrrolizidine alkaloid concentration in the younger leaves (Leiss *et al.*, 2009*a*). Moreover, UV-B radiation can influence the quality of plant tissue for herbivores, through either changes in leaf chemistry and/or reinforcement of the plant cell wall (Lindroth *et al.*, 2000; Stratmann *et al.*, 2000; Rousseaux et al., 2004; Demkura *et al.*, 2010; Kuhlmann and Müller, 2010). For example, solar UV-B radiation strongly reduces damage by the thrips *Caliothrips phaseoli* on soybean (*Glycine max*) leaves (Mazza *et al.*, 1999).

Besides nutritional quality and defence of leaf tissue, pollen can have a significant effect on post-alighting host acceptance as well as on the overall performance of thrips, even allowing the pest to overcome plant resistance (Trichilo and Leigh, 1988). Adding slash pine (*Pinus elliottii*) pollen to leaves of tomato (*Solanum lycopersicum*) or peanut (*Arachis hypogaea*), for example, significantly increased the settling behaviour (landing and residence time) of *F. occidentalis* (Chitturi *et al.*, 2006).

Virus transmission

In addition to the direct damage caused by feeding, thrips also serve as vectors for plant diseases such as tospoviruses (Riley *et al.*, 2011). Members of the *Tospovirus* genus, one of which is the tomato spotted wilt virus (TSWV) (Fig. 2D), can infect thousands of plant species (Whitfield *et al.*, 2005). At present, there are approximately 15 reported thrips species that can serve as vectors for the transmission of 26 different tospovirus species worldwide (Rotenberg *et al.*, 2015). Tospoviruses are generally acquired by immature (L1 and early L2) thrips, when the midgut and salivary glands are still connected, during feeding on a virus-infected plant (Moritz *et al.*, 2004). The efficiency of virus acquisition is highest for L1 larvae and decreases as they develop towards the mature stage (Rotenberg *et al.*, 2015). Once acquired by L1 or early L2 larvae, the virus replicates inside the host vector after a period of latency and can then be transmitted to healthy plants by late L2 larvae and adult thrips (Inoue *et al.*, 2002; De Assis *et al.*, 2004). The transmission of tospoviruses can occur as fast as in a single non-ingesting probe in which the virus enters the plant cell along with the secreted thrips saliva (Kindt *et al.*, 2003). During these probes, the plant cell remains largely undamaged, which promotes virus transmission (Stafford *et al.*, 2011). However, transmission efficiency is dependent on several factors, such as the virus isolate, plant variety, thrips species, and geographical origin (Maris *et al.*, 2003; Nagata *et al.*, 2004; van de Wetering *et al.*, 1999). Viruses can also enhance the transmission efficiency by influencing the probing and host-plant-selection behaviour of thrips (Maris *et al.*, 2004; Ogada *et al.*, 2013; Shalileh *et al.*, 2016). For example, TSWV-infected *F. occidentalis* males showed a significantly higher number of pre-ingestion/salivation probes on jimsonweed (*Datura stramonium*) compared with non-viruliferous thrips. Viruliferous females did not significantly change the number of probes they made, but dispersed more between feeding sites compared with non-viruliferous females; this behaviour probably enhances the spread of the virus (Stafford *et al.*, 2011). These behavioural changes may be related to the fact that TSWV-infected plants are a higher-quality food source for thrips than healthy plants (Belliure *et al.*, 2005; Blanc and Michalakis, 2016), due to increased availability of free nutrients (Shalileh *et al.*, 2016; Shrestha *et al.*, 2012) and/or virus-disrupted plant defences (Abe *et al.*, 2012).

Economic impact

Many thrips species are pests of commercial food crops and ornamentals worldwide due to the damage they cause by feeding and the transmission of viral diseases, which reduce yield and market value (Cannon *et al.*, 2007; Diaz-Montano *et al.*, 2011; Reitz *et al.*, 2011). Thrips are such successful pests because of their life-history characteristics (high reproductive capacity, parthenogenetic reproduction, multi-voltinism), hidden lifestyle (pupation in the soil, thigmotactic behavior), and polyphagous nature (broad host plant range) (Morse and Hoddle, 2006; Reitz *et al.*, 2011). *Frankliniella occidentalis* is considered economically one of the most important pests worldwide as it feeds on plants belonging to at least 60 families and is the primary vector of plant diseases caused by tospoviruses (Morse and Hoddle, 2006; Mouden *et al.*, 2017). Females can produce 40–100 eggs during their life and *F. occidentalis* generally goes through two to seven generation cycles per year on field-grown crops, which can increase to 15 generations under greenhouse conditions (Cloyd, 2009). Other economically important thrips species include the onion thrips (*Thrips tabaci*), the melon thrips (*Thrips palmi*), the common blossom thrips (*Frankliniella schultzei*), and the avocado thrips (*Scirtothrips perseae*) (Hoddle *et al.*, 2003; Cannon *et al.*, 2007; Diaz-Montano *et al.*, 2011; Seal *et al.*, 2014). Although it is hard to precisely determine the total economic loss caused by thrips, annual crop losses due to fruit scarring and the transmission of viral disease are enormous (Hoddle *et al.*, 2003; MacLeod et al., 2004; Riley et al., 2011). Currently, control management of thrips relies mainly on the use of chemical pesticides. However, due to resistance of thrips to these insecticides, there is an urgent need to intensify the search for plant resistance mechanisms (Gao et al., 2012).

Thrips-induced plant defences

Herbivore-induced plant responses are generally organized via a complex network of interacting signalling pathways, orchestrated by several phytohormones, to activate attacker-specific defences (Erb et al., 2012). Many studies have shown that JA is the most important hormone in the regulation of plant defence against herbivores (Wasternack, 2015), and thrips seems to be no exception to this rule (De Vos et al., 2005; Abe et al., 2008; Escobar-Bravo et al., 2017). The activation of the JA-signalling network leads to the production of various compounds that can serve as direct and/or indirect defences (Howe and Jander, 2008; Okada et al., 2015).

Jasmonic acid signalling

Thrips feeding activities have been shown to activate the biosynthesis of JA (Fig. 1) (Abe et al., 2008, 2009) and the expression of JA-responsive genes (Abe et al., 2008, 2009; De Vos et al., 2005; Selig et al., 2016; Escobar-Bravo et al., 2017). From the total set of genes that are differentially expressed in *Arabidopsis thaliana* during *F. occidentalis* feeding, 69% of the genes were JA-responsive (De Vos et al., 2005). In Chinese cabbage (*Brassica rapa* ssp. *pekinensis*) and tomato (*S. lycopersicum*), JA concentrations increased upon *F. occidentalis* infestation, corresponding with increased expression of JA-responsive marker genes (Li et al., 2002; Abe et al., 2009). The activation of the JA pathway most likely reinforces the plant's resistance to thrips, as exogenous application of JA reduces plant susceptibility towards this herbivore (Thaler, 1999; Abe et al., 2009; El-Wakeil et al., 2010), while plants insensitive to JA or deficient in JA accumulation are more susceptible to thrips (Abe et al., 2009). For example, the *S. lycopersicum* mutant *defenseless-1* (*def-1*), which is impaired in JA biosynthesis, was more susceptible to *F. occidentalis* compared with the wild type. However, such differences may not be solely due to differences in induced defences, since the *def-1* mutant also has a lower trichome density than the wild type (Escobar-Bravo et al., 2017). The availability of mineral nutrients in the soil can also affect the plant's degree of JA-dependent resistance. *Arabidopsis thaliana* plants grown under potassium-deficient conditions are less susceptible to thrips attack. This effect is most likely mediated by enhanced JA-associated responses, as some responses to potassium deficiency were dependent on CORONATINE INSENSITIVE1 (COI1), an essential regulator of JA signalling (Armengaud et al., 2010).

The interaction of JA with other phytohormones plays an important role in fine-tuning the magnitude and nature of the final downstream defence response (Pieterse et al., 2012; Schuman and Baldwin, 2016). Research on *A. thaliana* has revealed that the JA pathway consists of two separate branches, which are referred to as the ETHYLENE-RESPONSIVE FACTOR (ERF) branch and the MYC branch (Broekgaarden et al., 2015). ET synergizes the ERF branch to activate, among others, the defence-related gene *PLANT DEFENSIN1.2* (*PDF1.2*), while ABA synergizes the MYC branch to activate, among others, the defence-related gene *VEGETATIVE STORAGE PROTEIN2* (*VSP2*) (Verhage et al., 2011; Vos et al., 2013). Expression levels of both *PDF1.2* and *VSP2* have been shown to increase in *A. thaliana* upon infestation with *F. occidentalis* (De Vos et al., 2005; Abe et al., 2008; Leon-Reyes et al., 2009), suggesting that both branches are thrips-inducible. However, exogenous application of ET, which also activates the expression of *PDF1.2*, enhances the susceptibility of *A. thaliana* to *F. occidentalis* (Abe et al., 2008), suggesting that thrips could potentially interfere with induced plant defences. Manipulation of JA-inducible plant defence has been demonstrated for plant interactions with several herbivorous arthropods (Walling, 2008; Alba et al., 2015; Kant et al., 2015) and is most likely due to the presence of effector proteins in the arthropod saliva (Stafford-Banks et al., 2014; Giron et al., 2016; Jonckheere et al., 2016; Villarroel et al., 2016). However, whether thrips secrete effectors in their saliva to modulate JA-mediated defences and establish a compatible interaction with the host plant is not yet known (Fig. 1).

The finding that *F. occidentalis* is more attracted to, and performs better on, pepper (*Capsicum annuum*) plants infected with TSWV compared with non-infected plants (Maris et al., 2004; Ogada et al., 2013; Shalileh et al., 2016) suggests that viruses can also interfere with plant defences, possibly through the interaction of SA with JA signalling (Fig. 1). In *A. thaliana*, TSWV infection led to increased SA concentrations, resulting in reduced *F. occidentalis*-induced JA-mediated defences (Abe et al., 2012).

Specialized metabolites

Many of the specialized metabolites known to be involved in defence against thrips are constitutively present in the plant (Leiss et al., 2009*b*; Mellway and Constabel, 2009; Mirnezhad et al., 2010; Barbehenn and Constabel, 2011; Yang et al., 2012; Nuringtyas et al., 2012; Wang et al., 2014; Liu et al., 2017), but some have been shown to accumulate in response to thrips infestation. Phenolic compounds, a very common and widespread group of specialized defensive metabolites in plants that confer defence against herbivores, have been found to accumulate in response to thrips infestation (Papadaki et al., 2008; Leiss et al., 2009*b*, 2013; War et al., 2012). For example, *F. occidentalis* feeding resulted in enhanced production of phenols (tocopherols) in resistant pepper (*C. annuum*) accessions, but not in susceptible accessions (Maharijaya et al., 2012). A particular class of polyphenolic compounds that act as feeding deterrent to thrips, but also to many other herbivores, is the tannins (Whittaker and Kirk, 2004; War et al., 2012). A study on alfalfa (*Medicago sativa*) lines with different levels of resistance revealed that the increase in tannin content as a response to infestation with the thrips *Odontothrips loti* was faster in resistant lines than in susceptible lines (Wang et al., 2014).

Some thrips-inducible plant chemicals correlate positively with susceptibility. For example, susceptible pepper (*Capsicum* spp.) accessions mainly induce the production of alkanes and fatty acids in response to *F. occidentalis*, whereas resistant accessions do not (Maharijaya *et al.*, 2012). Additionally, California poppy (*Eschscholzia californica*) and greater celandine (*Chelidonium majus*) respond to *F. occidentalis* feeding by enhancing the production of cytotoxic benzophenanthridine alkaloids, but thrips appear to be able to detoxify these compounds (Schütz *et al.*, 2014). These data suggest that thrips may withstand plant defences not only by manipulating the signalling networks involved (as described above), but also by resisting them directly through metabolic detoxification and/or excretion.

Volatile organic compounds

In response to thrips infestation, plants can change their blend of VOCs to attract natural enemies that predate or parasitize herbivores (Fig. 1), thereby reinforcing the plant's indirect defences (Janssen *et al.*, 1998; Delphia *et al.*, 2007; Maharijaya *et al.*, 2012). For example, VOCs emitted from eggplant (*Solanum melongena*) infested by *T. palmi* attracted the predatory bug *Orius sauteri* (Mochizuki and Yano, 2007). Chrysanthemum (*C. morifolium*) changes its VOC blend upon infestation by *F. occidentalis*, resulting in enhanced attraction of the predatory mite *Neoseiulus* (formerly *Amblyseius*) *cucumeris* (Manjunatha *et al.*, 1998). In tomato (*S. lycopersicum*), the thrips-induced changes in VOC production and composition are most likely dependent on JA, as wild-type plants significantly increased the overall production of terpenes in response to *F. occidentalis* feeding while the JA-deficient mutant *def-1* did not (Escobar-Bravo *et al.*, 2017). Although not shown for thrips specifically, increased production of terpenes has been associated with the enhanced attraction of predators of herbivorous pests (Dicke *et al.*, 1990; Francis *et al.*, 2004; Köllner *et al.*, 2008). Exogenous application of methyl jasmonate restored the repellence in *def-1* tomato (Escobar-Bravo *et al.*, 2017). VOCs emitted from cucumber (*Cucumis sativa*) infested by *F. occidentalis* attracted the predatory mite *N. cucumeris* and the generalist predatory bug *Orius laevigatus* (Venzon *et al.*, 1999), the latter being one of the most effective natural enemies of thrips in agricultural production systems (Weintraub *et al.*, 2011; Ardanuy *et al.*, 2016).

Exploiting thrips-induced plant defences for pest management

Pest thrips generally have broad host ranges and are responsible for the transmission of viruses in many food crops and ornamental plants. Owing to the high genomic variation in virus populations, together with high mutation and recombination rates, monogenic virus resistance can be overcome relatively easily (Drake and Holland, 1999; Harrison, 2002). For example, the widespread introduction of *Capsicum* cultivars carrying the dominant *Tsw* resistance gene generated a selection pressure that resulted in the rapid emergence of resistance-breaking TSWV isolates (Ferrand *et al.*, 2015; Jiang *et al.*, 2016). Therefore, alongside the introduction of virus-resistance genes, simultaneous breeding for vector resistance is an attractive strategy towards durable virus control in agriculture. Enhancing resistance to pests can decrease the transmission of pest-vectored viruses (Maris *et al.*, 2003; Chen *et al.*, 2012; Escobar-Bravo *et al.*, 2016), thereby lowering the selection pressure on the virus and increasing the durability of virus-resistance genes, which could have a large impact on virus outbreaks in monoculture agroecosystems. However, there are cases that illustrate that layered resistance is not necessarily straightforward. For example, JA-induced resistance in wild tomato (*S. lycopersicum* var. *cerasiforme*) reduced *F. occidentalis* feeding by 75%, but this did not lead to a reduction in the transmission of TSWV (Thaler *et al.*, 2002). Additionally, the effectiveness of (induced) resistance against thrips itself can be highly dependent on environmental conditions (Mazza *et al.*, 1999; Armengaud *et al.*, 2010; Demkura *et al.*, 2010; Kuhlmann and Müller, 2010; Escobar-Bravo *et al.*, 2017). These examples underline the importance of understanding the resistance mechanisms and the virus–thrips–plant interactions in order to aid the development of breeding strategies to control both the pest and the viruses they vector. In the following sections we describe several opportunities, including future research directions, for meeting the challenge of exploiting knowledge of thrips-induced plant defences towards more sustainable resistance breeding.

Large-scale screening to identify new resistance traits

Since current breeding initiatives are primarily based on identifying sources of resistance through large-scale screenings of plant populations, developing accurate high-throughput screening methods for thrips resistance is of great interest (Kloth *et al.*, 2012). At present, host plant resistance to thrips is mainly determined by monitoring the damage inflicted and/or thrips behaviour. Thrips damage is usually scored by eye, and parameters monitored during behavioural assays, such as survival and reproduction, are usually recorded manually (Abe *et al.*, 2008, 2009; Maharijaya *et al.*, 2011; Leiss *et al.*, 2013), making these assays labour-intensive and time-consuming. Recently, a high-throughput phenotyping platform has been developed that quantifies thrips behaviour as a proxy of resistance (Fig. 3A). This method allows screening for host plant resistance in a multiple, simultaneous two-choice setup with computerized continuous video tracking, by establishing detailed thrips behavioural parameters over a period of several hours. With a markedly reduced time required and increased resource efficiency, this tool provided comparable resistance scores to manual monitoring of damage inflicted on whole plants (Thoen *et al.*, 2016).

Breeding/engineering for induced defence

Rather than implementing constitutive resistance, breeding (or engineering) crop plants that activate defence only when under attack has a fitness benefit, as resources are reallocated to defence only in times of stress (Pappas *et al.*, 2017). Similarly, inducible VOC emission to attract natural enemies upon

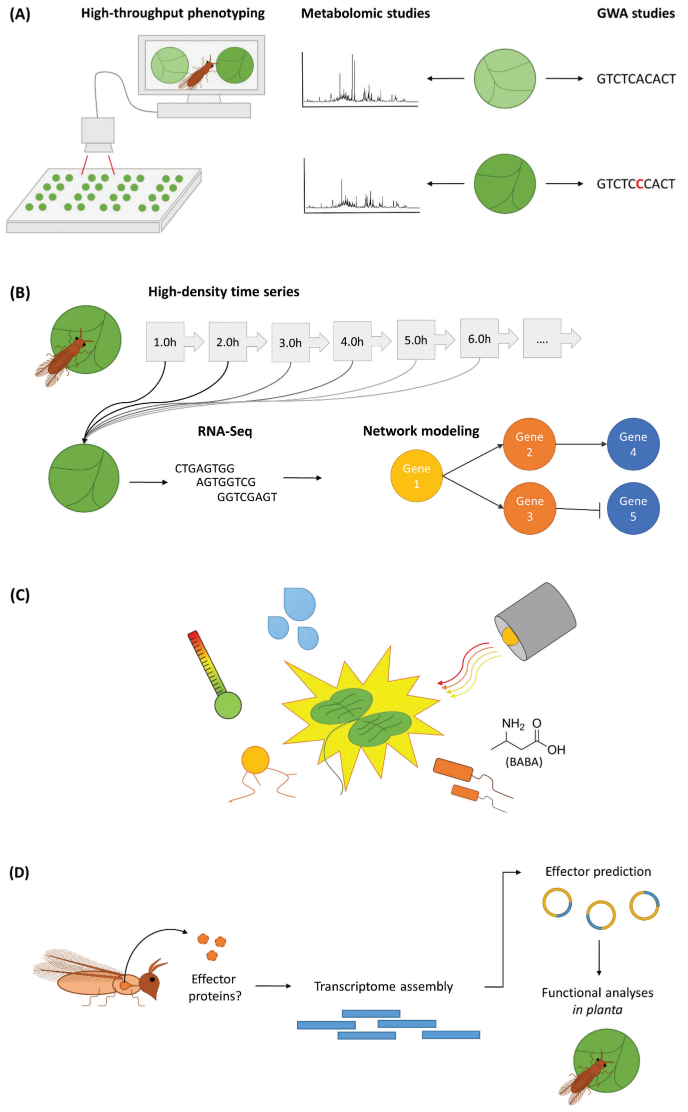

Fig. 3. Strategies to obtain knowledge to enhance plant defence for pest management. (A) Large-scale screenings of plant populations can aid the efficiency of resistance-trait identification. Once different phenotypes have been identified, metabolomic studies along with genome-wide association (GWA) studies can aid the discovery of plant metabolites and genes involved in resistance to thrips. (B) High-throughput transcriptome sequencing (by RNA-Seq) from high-density time series will provide insight into the dynamic gene regulatory network that is induced upon thrips infestation. Such an approach allows the prediction and validation of novel key regulators and their targets for induced defence against thrips. (C) Culture parameters such as water availability, light intensity/quality, and temperature can have a great impact on plant defence induction, and need to be optimized for plant growth and defence. Biostimulants, such as chemical substances or microorganisms, are able to enhance crop quality, for example, by improving nutritional status and priming the plant's defence machinery. (D) Characterization of proteinaceous effectors in thrips saliva will pinpoint important components of plant resistance to thrips. A bioinformatics pipeline can predict putative effectors from the thrips transcriptome, followed by functional analyses *in planta*.

herbivore damage is preferable to avoid 'false' signals—that is, natural enemies may become less responsive to constitutively emitted VOCs in the absence of herbivores (Shiojiri *et al.*, 2010). Identification of the plant's key regulators of induced defences as well as downstream players involved in the gene regulatory network offer ample opportunities for customizing induced defences against thrips. A robust strategy to reveal thrips-induced plant defences is to conduct extensive comparative transcriptomics analyses. RNA sequencing (RNA-Seq) is a powerful tool for capturing the spatiotemporal fluctuations of induced plant defences (Gusberti *et al.*, 2013; Van Verk *et al.*, 2013; Windram *et al.*, 2014; Tzin *et al.*, 2015; Hickman *et al.*, 2017). Conducting computational analysis of RNA-Seq data generated from high-density time series during thrips infestation will elucidate the different phases in time of induced plant defences in compatible and incompatible interactions (Fig. 3B). Such an approach has been successful in predicting and validating novel key regulators and their direct and indirect targets in plant stress signalling networks underlying resistance or susceptibility to other pests and plant pathogens (Windram *et al.*, 2012; Lewis *et al.*, 2015; Coolen *et al.*, 2016).

Besides providing insight in the timing of defence signalling, such an approach allows quantitative mapping of transcripts directly to metabolic pathways in order to elucidate the expected metabolic changes during plant–thrips interactions. Next, metabolomics can aid the discovery of plant metabolites related to induced resistance to thrips (Fig. 3A). In contrast to targeted chemical analyses, untargeted metabolomics has revealed some novel compounds involved in constitutive resistance against thrips (Leiss *et al.*, 2009*a*). Linking metabolomics with transcriptomics or genome-wide association studies can lead to the identification of candidate genes involved in the production of potentially important defence metabolites (Fig. 3A) (Chen *et al.*, 2014). Functional analysis by overexpression or knockdown of individual candidate genes or complete pathways allows validation of important signalling networks, genes, and defensive compounds. The identification of key players in plant defence and increased knowledge of their function in (crop) plants will contribute to breeding of thrips-resistant crop varieties, as they allow a targeted search for genetic variation, allelic variants, and metabolic diversity in (wild) crop germplasm.

Optimizing culturing conditions

Plants are commonly exposed to changing environmental conditions, especially when grown in open-field conditions. In turn, this has a great (temporal) impact on the plant's physiology and chemistry. Plant defence responses to herbivores can be influenced either negatively or positively by environmental (stress) parameters, such as temperature, light intensity/quality, and water availability (Fig. 3C) (Gouinguené and Turlings, 2002; Grinnan *et al.*, 2013; Ballaré, 2014; Suzuki *et al.*, 2014; Coolen *et al.*, 2016; Nguyen *et al.*, 2016; Escobar-Bravo *et al.*, 2017). Depending on the external factor, growth–defence trade-offs occur by prioritizing resources to either growth or defence (Vos *et al.*, 2013). Determining which abiotic conditions influence plant–thrips interactions might help to optimize culture conditions for the reduction of crop damage due to herbivory, while maintaining substantial growth.

The use of UV-B light has been reported to increase constitutive and inducible plant defences against a wide range of pests (Izaguirre *et al.*, 2007; Mewis *et al.*, 2012; Dinh *et al.*, 2013; Zavala *et al.*, 2015), including thrips (Mazza *et al.*, 1999; Demkura *et al.*, 2010; Kuhlmann and Müller, 2010). Reinforcement of UV-B-mediated JA-inducible defences might be used as a tool to increase crop protection against thrips. However, the (modest) effects of UV-B on plant morphology, growth, and yield should be taken into account (Ballaré *et al.*, 2011). Constitutive or primed defences could stop herbivory at an earlier stage, which would minimize the activation of costly defences and eventually reduce the energy investment of replacing consumed plant tissue (Frost *et al.*, 2008; Karban, 2010).

Implementing biostimulants

The industry for biostimulants to improve plant productivity is rapidly growing (Yakhin *et al.* 2016). Treating plants with a biostimulant, which can be a (chemical) substance or a micro-organism, enhances crop quality traits such as improved nutritional status, but can also prime a plant to deploy its defence machinery in a faster, stronger, and/or more sustained manner while under herbivore attack (Fig. 3C) (Pangesti *et al.*, 2013; Du Jardin, 2015; Martinez-Medina *et al.*, 2016). For example, applying the non-protein amino acid DL-β-aminobutyric acid (BABA) to the soil increases pea aphid (*Acyrthosiphon pisum*) mortality on tic bean (*Vicia faba* var. *minor*), pea (*P. sativum*), broad bean (*V. faba* var. *major*), runner bean (*Phaseolus coccineus*), red clover (*Trifolium pratense*), and alfalfa (*M. sativa*) (Hodge *et al.*, 2005). Colonization of *A. thaliana* roots by the plant-growth-promoting rhizobacterium *Pseudomonas simiae* WCS417r (previously known as *Pseudomonas fluorescens* WCS417r) induces systemic resistance to the generalist caterpillar *Spodoptera exigua* by activating the JA pathway (Van Oosten *et al.*, 2008). With regard to resistance to thrips, onion plants (*Allium cepa*) colonized with the endophytic fungi *Clonostachys rosea* ICIPE 707, *Trichoderma asperellum* M2RT4, *Trichoderma atroviride* ICIPE 710, or *Hypocrea lixii* F3ST1 developed significantly fewer feeding scars inflicted by *T. tabaci* (Muvea *et al.*, 2014). Another example of the stimulation of JA-mediated defence responses is through endophytic oviposition by *O. laevigatus*, which is known as a thrips predator but can also significantly reduce *F. occidentalis* feeding damage in tomato (*S. lycopersicum* cv. Moneymaker) by inducing JA-dependent defences. All in all, the incorporation of biostimulants in agricultural practice may constitute a promising approach for thrips control. Their efficacy could be enhanced if we learned more about their molecular mode of action on the plant and, additionally, how the plant regulates establishment of the beneficial microbes in the rhizosphere.

Capture salivary effectors

The success of thrips on many host plants suggests the existence of a common or general mechanism to perturb plant defences that facilitates successful feeding and/or protection of the progeny. One such mechanism could be the transfer of salivary effectors. Pathogen and pest effector proteins and small molecules can alter the host's defence responses and/or promote infection (Hogenhout and Bos, 2011) (Fig. 1). Only very recently, several proteinaceous effectors that suppress plant defence responses have been identified from aphids (Naessens *et al.*, 2015; Kettles and Kaloshian, 2016; Thorpe *et al.*, 2016; Van Bel and Will, 2016; Mondal, 2017) and spider mites (Villarroel *et al.*, 2016; Schimmel *et al.*, 2017). Based on what we know about the feeding habits of thrips, transferred effectors could either exhibit their action locally at the site of feeding/oviposition or at a distance, potentially through 'hitchhiking' on host transport systems such as the symplast (Khang *et al.*, 2010; Giraldo and Valent, 2013; Zebelo and Maffei, 2015). For larvae that start to feed directly after hatching, manipulating local host defences could be of crucial importance. So far, no thrips effectors have been identified, but a similar approach to that used for aphids, hessian flies, and spider mites, using bioinformatic pipelines (Fig. 3D) (Bos *et al.*, 2010; Zhao *et al.*, 2015; Thorpe *et al.*, 2016; Villarroel *et al.*, 2016) to predict potential effectors from transcriptomes of the insect and the tissue they infest, could be taken to fill this knowledge gap on thrips effectors. The identification of a putative orthologue (>65% identity) of the aphid MP46 effector in the salivary-gland and whole-body transcriptomes of *F. occidentalis* (Stafford-Banks *et al.*, 2014) indicates the potential success of such an approach. Functional analyses of candidate effectors can subsequently be performed using RNAi techniques that silence the expression of salivary effectors. Using this technique, the salivary effector gene *C002* was silenced in pea aphids (*A. pisum*), resulting in increased aphid mortality (Mutti *et al.*, 2006). Techniques for transferring RNAi into thrips have already been developed (Badillo-Vargas *et al.*, 2015) and can, for example, be introduced through thrips symbionts (Whitten *et al.*, 2016). Once thrips effectors have been validated, the targets through which these effectors manipulate their host can be identified, which will enable the characterization of the molecular mechanisms involved in the establishment of the thrips–host interaction. For non-genetic engineering breeding approaches, natural mutants or alternative alleles of the target plant protein can then be screened for.

Concluding remarks

Herbivorous thrips are important pests in food and ornamental plant-production worldwide, and possess all the problems of pests in general: they are highly polyphagous, rapidly become resistant to pesticides, and are notorious vectors of plant viruses. With the rising demand for more sustainable, safer, and healthier food-production systems, the development of less invasive and polluting solutions to manage pests is of great importance. Exploiting the natural defence mechanisms of plants against herbivores provides opportunities towards more sustainable resistance breeding. The literature on herbivore-induced plant defences is currently predominantly focused on leaf-chewing and phloem-feeding herbivores, while far less is known about how plants activate their defences in response to the cell-content-feeding thrips (Fig. 1). Even though there is literature demonstrating constitutive defence mechanisms against thrips, functional analyses of defensive compounds that are induced upon thrips attack are lacking. Exploring inducible defences and identifying plant specialized metabolites, VOCs, thrips effectors, and their host's targets can aid the development of cost-efficient thrips-resistant crops. It should also be taken into account that resistance breeding should not be approached from a single-problem point of view (Fig. 3). Abiotic stress factors and thrips-transmitted viruses have a profound impact on the outcome of the plant–thrips interaction. Extending our understanding of the effect of abiotic factors and biostimulants on plant resistance to thrips, and using state-of-the art methods that provide integrated transcriptome and metabolome data of thrips-infested tissue together with high-throughput phenotyping, can aid the battle against these pests. Crop varieties can be developed that are less attractive and suitable for thrips, and possibly other herbivores, to feed from, while being more attractive to natural enemies of these pests and/or allowing lower transmission of viruses.

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