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Host plant resistance to thrips (Thysanoptera: Thripidae) – current state of art and future research avenues

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Integrated Pest Management (IPM) is endorsed as the future standard for crop protection worldwide. This holistic concept integrates preventative and curative measures amongst which host plant resistance (HPR) plays an essential role. Up to now HPR has been a somewhat under-utilized tool in pest management due to widespread use of pesticides and technological hindrance. Thrips are key pests in agriculture and horticulture worldwide. Here we provide an overview on the current status of research on constitutive and induced HPR including thrips–host relationships and thrips as virus vectors. We stress modulation of plant defense responses by abiotic and biotic elicitors to increase HPR and provide an outlook on the increasing potential of HPR inspired by the fast advancement of –omics techniques.

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Introduction

Global agriculture is at an important juncture and in a period of great change, whereby Integrated Pest Management (IPM) is endorsed as the future paradigm for crop protection [1]. The holistic concept of IPM emphasizes a systems approach integrating preventative and curative intervention measures amongst which host plant resistance (HPR) plays an essential role. Up to now HPR has been a somewhat under-utilized tool in pest management. Selection for yield, taste or appearance has greatly reduced phenotypic and genetic diversity of cultivated plants often accompanied by a loss of HPR [2]. This was reasonable using pesticides on a large scale. Widely spreading pesticide resistance and, especially for the EU, more stringent pesticide regulations related to apparent risks for human health, beneficial organisms and the environment, reduce pesticide availability which makes established cropping systems highly vulnerable. HPR incorporates varieties which hamper preference, reproduction, feeding and/or transmission of insect-borne pathogens. Thrips species of the family Thripidae are particularly polyphagous and contain key pests of a large variety of ornamentals and vegetables worldwide [3], including western flower thrips (WFT: *Frankliniella occidentalis)*, onion thrips (*Thrips tabaci*) and melon thrips (*Thrips palmi*). In addition to direct feeding damage these species are virus vectors of which tomato spotted wilt virus (TSWV) is the economically most important [4••]. The present review provides an interdisciplinary overview of the current body of knowledge on constitutive and inducible components of HPR to thrips, and discusses the potential of elicitors to modulate plant defenses. Finally, we provide an outlook on the future exploitation of HPR inspired by the fast advancement of -omics techniques.

Host plant resistance to thrips

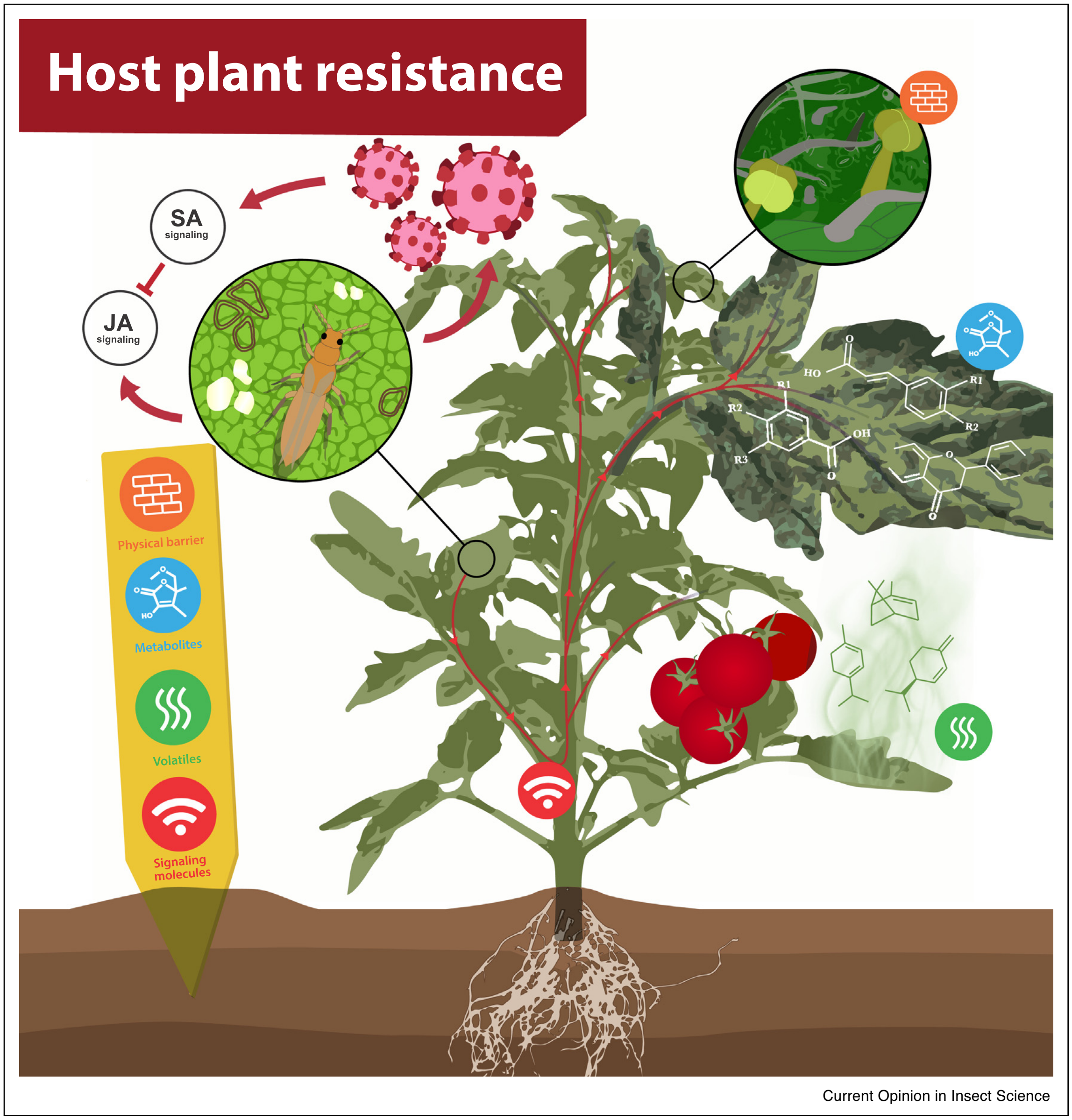
Over the past decades, great effort has been devoted developing plant varieties with resistance to viruses although, resistance to thrips feeding is recently gaining attention [4••,5]. Empirical approaches to HPR often involves phenotypic screening, that is, evaluation of germplasm for resistant genotypes [6–14]. Advances in phenotyping technologies support high-throughput characterization of crop resistance to thrips [8,15]. Moreover, the affordability of current omics technologies fosters a major advancement in connecting genotype-phenotype relationships to enhance our understanding of plant–thrips defense mechanisms [16–21].

HPR results from a complex set of interdependent mechanisms (Figure 1) ranging from morphological barriers to the complex array of signaling molecules of the plant's immune system. These plant-defensive responses are associated with constitutive, thus always present traits, or induced plant traits shaped upon attack or elicitation in the plant's morphology, physiology and/or chemistry producing plant secondary metabolites [13,22]. Both ways are not mutually exclusive and lead to direct or indirect effects through attraction of natural enemies.

Constitutive defense

Constitutive barriers, including morphological leaf traits, form a first line of defense against thrips [7,11,14,23,24]. Many studies are correlative with little consensus concerning the role of leaf traits. For instance, feeding damage by the viruliferous soybean thrips (*Neohydatothrips variabilis*)

Figure 1



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A schematic model for host plant resistance (HPR) to thrips. Thrips face direct constitutive plant defenses such as physical barriers (i.e. leaf pubescence or trichomes), secondary defensive plant metabolites or indirect defenses such as the emission of volatile organic compounds. Upon thrips feeding, damage typically appears as silver scars whereas tospoviruses (depicted by red virus particles), vectored by thrips, lead to chlorotic ringspots (upper left part). Trips attack activates local plant immune responses by jasmonic acid (JA) production which is systemically transported to undamaged plant tissues (red arrow). Tospoviruses induce the salicylic acid (SA) pathway and are capable of manipulating host defenses through SA-JA antagonism to benefit their vector.

was reduced in genotypes with low pubescence [14] whereas, in another study Abdelmaksoud *et al.* [24] reported lower WFT infestations in strawberry cultivars with high densities of non-glandular trichomes. However, in both studies only a small number of genotypes was analyzed, therefore, probably additional not measured traits were interfering. In search for markers associated with thrips resistance, Bac-Molenaar *et al.* [25••] reported that foliar resistance to WFT was independent from glandular trichome density and derived volatile compounds in a mapping population derived from a resistant and non-resistant tomato line. Metabolomic analysis identified leaf α-tomatine and a non-elucidated phenolic compound as putative defense metabolites related to WFT resistance. In addition, glandular trichomes are known for their production of sticky resinous substances, such as acylsugars. Their importance to WFT resistance has been shown by Vosman *et al.* [26]. Ben-Mahmoud *et al.* [27] demonstrated that particular combinations of acylsugars with specific fatty acid profiles, not only reduced WFT oviposition but also lowered incidence of TSVW. Regarding defense compounds Maharija *et al.* [17] reported two capsianosides and a flavonoid to correlate with WFT resistance using metabolite quantitative trait loci (QTL) mapping. Concurrently, capsianosides were negatively correlated with WFT preference and damage in an untargeted metabolomic profiling approach in *Capsicum* whereas, sucrose and malonylated flavone glycosides were related to susceptibility [18]. In addition, plant olfactory cues play a role in direct defenses as composition and magnitude of volatile emission shapes host localization or preferences [28–32]. Moreover, thrips herbivory may also affect plant biochemistry through changes in nutritional host quality [33,34] or by inducing defenses.

Inducible defense – signaling and manipulation

While constitutive defenses have gathered substantial attention in the majority of screening studies, induced resistance is rapidly gaining interest [35]. In contrast to constitutive defenses induced defenses are associated with lower metabolic costs. All plants, whether resistant or susceptible, respond to insect attack by induction of a coordinated defense strategy primarily mediated by endogenous phytohormonal signaling, followed by biochemical cascades activating local and/or systemic defense mechanisms (Figure 1). Among the early plant responses, jasmonic acid (JA) acts as a main regulator of induced thrips defenses [22,36,37]. Pepper plants colonized by WFT enhanced the expression of the JA-related marker genes Ca*LOX2* and CA*PIN* II [37]. Moreover, WFT are susceptible to externally induced JA-mediated defenses. Foliar JA application impaired feeding of WFT [38,39] and increased duration of developmental stages [40]. Unlike adults, feeding activities of WFT larvae were observed to tolerate naturally induced levels of JA-defenses suggesting that artificial induction of JA-regulated defenses overamplifies rather than mimics natural response [41]. Late plant responses include the production of plant secondary metabolites [38,39].

In contrast, thrips-vectored viruses such as TSWV induce the salicylic acid (SA) pathway which indirectly enhances fitness and performance of the vector by exploiting SA-JA antagonism [21]. In addition to immunological plant modulation, viruses modify vector behavioral responses to facilitate virus transmission [42,43]. Such behavioral responses can be mediated by plant-derived cues such as volatile alterations aimed at attracting [44] or repelling vectors [45].

Whether defenses actually enhance plant resistance depends on whether thrips have evolved counter adaptations such as the ability to detoxify and degrade plant toxins [34,46,47]. The underlying molecular components of how thrips feeding modulates induced responses still remains unclear [35]. There are indications that plant responses to thrips are influenced by potential elicitors such as saliva components [48•] and endosymbiotic-borne cues [49].The latter points at the potential of different bacterial groups in manipulating plant defense responses to thrips, highlighting the importance of a multitrophic context when considering thrips–plant interactions.

In complex food webs omnivorous thrips can affect plant-mediated interactions of co-existing herbivorous arthropods such as whiteflies [50] or aphids [51•]. Such dual interactions may even cascade up to the third trophic level by influencing preference and performance of natural enemies [51•]. A study by Ataide *et al.* [41], aimed to disentangle direct and indirect effects of plant defenses, demonstrated that feeding by predatory omnivorous WFT larvae was independent from JA-mediated indirect defense effects on spider mite prey quality.

Modulating defenses by plant resistance inducers

Plant signals inducing resistance are highly conserved among plant species. Accordingly, modulation of plant defenses to increase HPR, through biotic and abiotic elicitors (Figure 2), has a great potential [35].

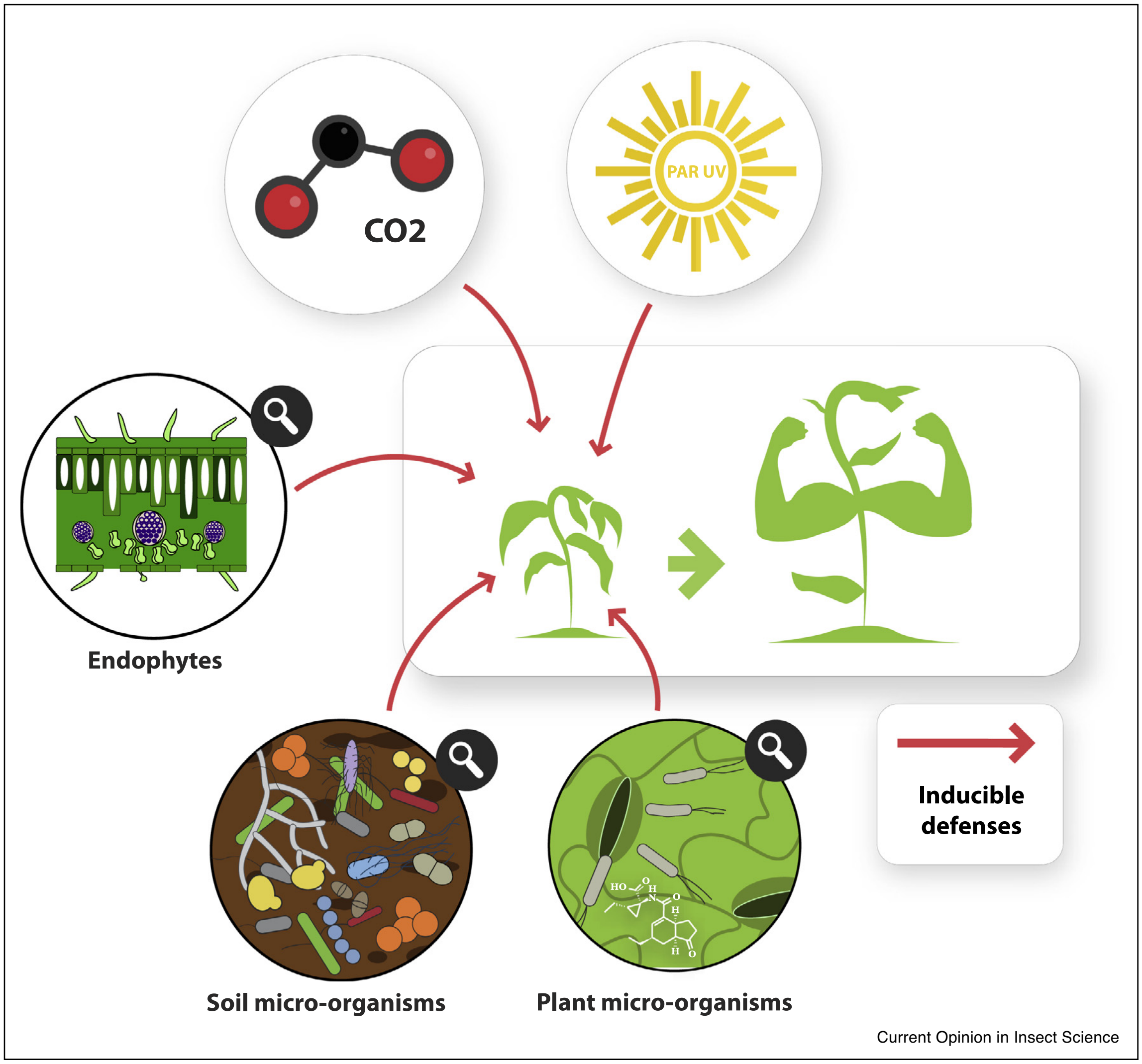
Abiotic elicitors

Environmental factors such as photosynthetically active radiation [52] and ultraviolet light [22,36,53] can mediate HPR to thrips. Exogenously applied calcium chloride improved resistance of kidney bean plants to WFT by extending the larval developmental time [54]. Calcium application only slightly induced the activities of defense-related enzymes whereas more potent defense responses were induced upon subsequent attack, a phenomenon generally referred to as priming. Priming has also been observed in UV-treated chrysanthemum, which experienced a stronger induction of JA signaling after thrips infestation [22]. While JA or its volatile derivative methyl jasmonate are commonly tested synthetic elicitors to mimic thrips induced plant responses [39], not much progress has been made in the development of products based on this mechanism.

Biotic elicitors

Regarding biotic elicitors, a growing body of research is demonstrating how microbial communities mediate plant defense through direct and indirect changes to plant immunity and/or nutrition. Infiltration of tomato leaves with *Pseudomonas syringae* (Pst), producing the JA analogue coronatine, reduced WFT feeding damage by reinforcing plant defense metabolites, such as phenols [55]. *Pst*-derived and filtered culture medium, as well as a coronatine defective *Pst* mutant increased tomato resistance to thrips suggesting that induction of resistance did not require a living *Pst* population but likely depends on other additional defense elicitors. Earthworm-driven modifications of soil properties, particularly

Figure 2



Modulation of plant inducible defenses. Biotic elicitors (soil microbes, plant microbes and endophytes) as well as abiotic elicitors such as ultraviolet light (UV), photosynthetically active radiation (PAR) and CO_2 can be exploited as strategies to induce resistance to thrips.

through increased nitrogen availability and microbial activity, decreased thrips abundance by inducing phenols as defense compounds [56]. Muvea *et al.* [57] reported that colonization of onions by the fungal endophyte *Hypocrea lixii* not only enhanced resistance against *T. tabaci* but also reduced incidence of thrips-transmitted *iris yellow spot virus* (IYSV). There is a growing interest in manipulating soil microbiomes to improve above-ground pest management. Soil microbiomes, conditioned by non-crop plants, induced aboveground resistance in chrysanthemums to WFT [58•], which was positively correlated with the amount of leaf chlorogenic acid as a secondary defense compound.

Host plant resistance – quo vadis?

Development of HPR has been hampered for technological reasons. *A-priori* knowledge on plant metabolites of the crop in question was required for adequate chemical analysis. Concurrently, large-scale screening of thrips HPR on breeding populations was almost impossible since only *in*-vivo bioassays could be performed. The fast advancement of omics-techniques, however, enables a much quicker and comprehensive understanding of HPR to thrips. Genetic engineering has resulted in the first-ever transgenic plant trait targeting thrips [59]. Transgenic cotton expressing a *Bacillus thuringiensis* protein showed substantially less damage to WFT and tobacco thrips (*Frankliniella fusca*) [60•,61]. Gene-editing tools such as CRISPR can further accelerate the introduction of thrips HPR into crops. However, in Europe, varieties based on this technology are subject to the same stringent regulations as conventional genetically modified organisms. Therefore, the combination of metabolomics and QTL mapping identifying markers as selection tools for thrips HPR in conventional breeding programs is a very promising way forward. Especially since quantitative traits depend on the cumulative action of several different genes making it more difficult for thrips to break through this defense. Because of the rapid progress in next generation sequencing more genomic crop sequences are becoming available. However, ornamentals are often polyploid and, although current techniques are fast, data analysis and interpretation are still challenging. The use of metabolomic markers shows potential for thrips HPR screening in these commodities. Next to breeding for conventional HPR, breeding for induced HPR offers a completely new avenue, which needs to be explored. Besides breeding, crop management techniques inducing HPR look promising. The transition to more efficient but energy saving LED light in greenhouses enables the use of ultraviolet light as an abiotic elicitor. Also beneficial microbes, used as biotic elicitors, registered as plant protection products or biostimulants, offer great potential. However, there is still relatively little known about their molecular mode of action and interplay with the plant. While HPR becomes increasingly important in thrips management we should not look at this one-sided. Viruses, vectored by thrips, can impact plant–thrips interactions. Also, HPR may impact biological control organisms. We advocate that HPR to thrips needs to be placed into an IPM context. To fully exploit the potential of HPR, also horizontal integration, thus concurrent protection to a broader spectrum of pests should be taken into consideration.

Conflict of interest statement

Nothing declared.

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- •• of outstanding interest

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