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Thrips resistance in gladiolus: An eco-metabolomic approach

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GENERAL INTRODUCTION

Sustainable growth and development require minimizing the natural resources and toxic materials used, and the waste and pollutants generated, throughout the entire production and consumption process. This also applies to the production of food and ornamentals the sustainable production of which requires to minimize the use of pesticides. Breeding for resistance becomes more and more important in this respect. Nowadays for many species we can apply molecular tools, such as gene expression studies and mutants to discover mechanisms of host plant resistance. Such methods and techniques become increasingly cheaper and at some point, will become available for all crops. However, the need to reduce pesticides is extremely urgent as was recently again signaled by the reports on the alarming decline of insect species (Hallmann *et al.*, 2017). For some crops, especially polyploids and crops with large genomes the feasible required molecular tools will most likely not become available soon. So the market still calls for fast and cheap alternatives such as morphological or chemical markers. In order to provide these, we first need to study host plant resistance in plants and how it may change depending on environmental conditions or plant development. Based on these ideas we can then develop markers for herbivore resistance. Gladiolus is such a plant species of which the breeding industry is in search for markers that can assist the breeding for resistance against different insect herbivores with thrips being the most urgent one.

HOST PLANT RESISTANCE

To defend against multiple stresses, every plant species has a palette of different traits to combat them. This includes, among others morphological and chemical traits, as a defence against herbivores. Plant morphological traits includes plant size, trichomes, thickened tough cuticula and leaf surface waxes, all which play a role in resistance against the thrips, *Heliethrips haemorrhoidalis* (Scott Brown and Simmonds, 2006). Especially trichomes in tomato have been well studied as a defence mechanism and combine both morphological and chemical traits that contribute to herbivore resistance (Kang *et al.*, 2014; Balcke

et al., 2017; Chen *et al.*, 2018). In addition to the effect of these traits on thrips preference, thrips damage was positively correlated to plant size in chrysanthemum (de Jager *et al.*, 1996; Kos *et al.*, 2014) and tomato (Mirnezhad *et al.*, 2010).

Resistance strategies can be constitutively expressed or induced after damage (Dicke, 1998). Constitutive defenses are always present in plants, while induced defenses are produced when plants are attacked and damaged. Chemical compounds are produced upon attack that may serve against pathogen infections, may affect herbivores or may attract the natural enemies of herbivores. Constitutive defenses are thought to be costly for plants since they use up resources for their biosynthesis, they may be toxic to the plant itself or ecological costs can be present e.g. because the plant becomes more attractive to specialist herbivores (Gershenson, 1994; Purrington, 2000). Most qualitative defence compounds occur in concentrations that are very low (<1%) (Zhao *et al.*, 2005) and therefore costs of biosynthesis are assumed to be low at the level of the whole plant. Aerts and co-workers (1991) showed that the carbon atoms needed for alkaloid formation only amount to 0.4% of the carbon atom flux into respiration. However, in locally induced defenses all energy of the induced area goes into the defense related pathways, resulting in local cell death.

Constitutive chemical defenses produced in plants can act as toxic and repellent compounds as well as digestibility reducers (Fürstenberg-Hägg *et al.*, 2013). Different compounds have been reported to be involved in the constitutive defense of different plant species against thrips: pyrrolizidine alkaloids and flavonoids in *Jacobaea vulgaris* (Leiss *et al.*, 2009a), phenylpropanoids (de Jager *et al.*, 1995; Leiss *et al.*, 2009b) and isobutylamides (Tsao *et al.*, 2003) in the ornamental chrysanthemum, acylsugars in tomato plants (Mirnezhad *et al.*, 2010), the flavonoid luteolin, the phenylpropanoid sinapic acid and the amino acid β -alanine in carrots (Leiss *et al.*, 2013). In transgenic potato plants constitutive defense involved cysteine protease inhibitors that affect the oviposition rates (Annadana *et al.*, 2002) and population development (Outchkourov *et al.*, 2004) of *Frankliniella occidentalis*. Moreover, these proteins suppressed the fecundity and reduced the survival rates of *F. occidentalis* in transgenic potato plants (Outchkourov *et al.*, 2004).

Plants induce defenses after wounding. Defense related genes are upregulated which is in general a fast process. However, an increase in the defence compounds resulting from these changes in gene expression is often only seen after a number of days (e.g Boue, 2000). Various signaling compounds like jasmonate, salicylate and ethylene play a major role in inducing these defense responses (Zhao *et al.*, 2005). Though the signaling pathways seem to be very similar in all plant species, they are coupled to totally different secondary metabolite pathways, which includes, among others, sesquiterpenes, triterpenes, anthraquinones, alkaloids, phenylpropanoids, and polyketides. Jasmonic acid was detected as being involved in induced defense against thrips in wheat cultivars (El-Wakeil, Volkmar and Sallam, 2010; El-Wakeil and Volkmar, 2012), tomato (Escobar-Bravo *et al.*, 2017) and chrysanthemum (Chen *et al.*, 2018). In *Nicotiana tabacum* the volatiles α -humulene and caryophyllene oxide were detected after infestation with thrips (Delphia *et al.*, 2007). Wittstock and Gershenzon (2002) pointed to the risk of relying on induced defences only, because the initial attack may be too rapid or too severe for such damage-induced defenses to be deployed effectively. Induced defense should help to reduce the damage after the attack and help other plant parts to be prepared, which means for plant breeding both systems, induced and constitutive defenses, are important as both are needed for a proper resistance of the plant. Recently, plant resistance to herbivores based on chemical traits has been determined using an eco-metabolomic approach. (Leiss *et al.*, 2009b; Leiss *et al.*, 2013). Such an approach is based on the natural variation present among genotypes or varieties of a particular species.

On top of the enormous variation among and within plant species the detection of metabolites involved in resistance is even more complicated by the fact that many plant metabolites interact in their effects. This may explain why, for instance, in some species (e.g. chrysanthemum, Leiss *et al.*, 2009b) resistance against thrips was correlated with chlorogenic acid while in others such as tomato it was not. As a result of the lack of general patterns it remains necessary to study individual species for which resistance is a problem. One such species is the ornamental gladiolus of which many varieties are severely attacked by insect herbivores.

For such plant species we need to investigate defence under various growing conditions because these may alter the attractiveness of plants to herbivores severely.

Such growing conditions include temperature, nutrient, water, oxygen (Pieterse *et al.*, 2009). For instance, two-spotted spider mites preferred plants of *Sorbus aucuparia* L. and *Acer platanoides* L. grown in the shade environment over plants grown in full sunlight. The first contained less phenolics compounds (Giertych *et al.*, 2008). In *Arabidopsis thaliana*, high light intensity led to a significant change in rosette growth and the composition of B-subunits of protein phosphatase 2A, which significantly decreased aphid fecundity in 3 mutant lines but not in the Columbia wild type (Rasool *et al.*, 2014). Nutrient and water availability influenced pyrrolizidine alkaloids concentration which are well-known chemical defenses in e.g. *Senecio jacobaea* and *S. aquaticus* (*Jacobaea aquatica*) (Kirk *et al.*, 2010). Elevated CO₂ reduced resistance in wild-type tomato plants infested with *Helicoverpa armigera* by decreasing jasmonic acid levels (Guo *et al.*, 2012). In broccoli plants, *Brassica oleracea* var. *italica*, water stress differentially influenced induced defences among cultivars (Khan *et al.*, 2011). Moreover, high photosynthetically active radiation (PAR) induced trichome-associated chemical defense which plays a major role in tomato-thrips interaction (Escobar-Bravo *et al.*, 2018).

In addition to abiotic and biotic stresses, plant resistance changes during ontogeny. Ontogenetic shifts in defense traits can be associated with dramatic changes in the levels of herbivory (Barton and Koricheva, 2010). In *Nicotiana attenuata* (Solanaceae) rosette plants, bolting plants, and flowering plants all contained trypsin protease inhibitors in leaves, stems, and flowers, while seed capsules, seeds, and young seedlings did not contain any protease inhibitors (PIs) (van Dam *et al.*, 2001). In *Plantago lanceolata*, Iridoid glycosides concentrations decreased with plant age and even more strongly with leaf age (Bowers and Stamp, 1993). Likewise, seedling to early juvenile stages of *Penstemon virgatus* (Plantaginaceae) were better defended against the caterpillar *Junonia coenia* (Nymphalidae) than adult stages (Quintero and Bowers, 2013). In tomato, developing leaves were more resistant against thrips than fully developed leaves (Chen *et al.*, 2018). In general young leaves seem better defended against thrips than older leaves (Leiss *et al.*, 2009b; Mirnezhad *et al.*, 2010). However, Visschers *et al.* (2019) could not observe any differences in thrips damage between old and young leaves. Most likely the balance between the nutritional values of leaf and their

concentrations of toxic compounds determine the pattern of resistance over the leaf canopy.

Given the examples above, exploring resistance means that the plant has to be studied during different life-stages and under different environmental conditions and that both constitutive and inducible defense mechanisms should be included. In this thesis, we studied plant defense of the ornamental plant *Gladiolus* for both morphological and chemical traits related to resistance against thrips.

GLADIOLUS

The Netherlands are a leader in the production of flower bulbs worldwide. They generate \$ 756 million in value with 21,000 ha of production area (Benschop *et al.*, 2010). *Gladiolus* is an important flower bulb crop, which comprises 5% of the total bulb production (Benschop *et al.*, 2010). *Gladiolus* is one of the largest genera in Iridaceae family. *Gladiolus* means sword and often *Gladiolus* is called ‘sword lily’ because of the shape of its leaves. The plants are herbaceous, and have lanceolate, unbranched, basal leaves. In addition to bulbs, *Gladiolus* is an important cut flower export product in summer. The *Gladiolus nanus* type, known as mini gladiolus, has been developed for growing in greenhouses in the winter season (Cohen and Barzilay, 1991). In general, *Gladiolus* corms can be planted on beds or ridges of the furrows for flower production. Common *Gladiolus* varieties grow for 110-150 days whilst the nanus type varieties are early flowering *Gladiolus* types that take 70-100 days to bloom.

Besides the use of flowers for decoration purposes, other uses have been explored. Aqueous macerates from *Gladiolus dalenii* corms have been reported to have antidepressant properties in epilepsy-associated depression (Ngoupaye *et al.*, 2013 and Ngoupaye *et al.*, 2014). The extract exhibited both an anticonvulsant and a sedative effect (Ngoupaye *et al.*, 2013). Moreover an antimicrobial and an antifungal activity against *Staphylococcus aureus*, *Bacillus cereus*, *Mycobacterium smegmatis* and *Candida albicans* were reported (Kahrman *et al.*, 2012). These effects were due to the presence of monoterpenes such as limonene and linalool, and sesquiterpene hydrocarbons such as muurolene (Kahrman *et al.*, 2012). *Gladiolus* was reported to contain several triterpenoids and their derivatives such as β -amyryn, lupeol, friedelin, betulin, etc (Zhang *et al.*, 2007). The presence of anthraquinone glycosides in *Gladiolus* was reported by

Abdessemed et al. (2011) and Wang (2003). A new oleanan triterpene was identified in some *Gladiolus* species (El-Shanawany *et al.*, 2009).

Gladiolus has many pest problems such as *Thrips simplex* and *F. occidentalis* which are commonly found in *Gladiolus* (Terry and Lewis, 1997). They cause severe damage on corms, leaves and flowers on *Gladiolus*. Control of thrips mainly depends on fumigating, dipping and spraying insecticides on the corms and plants. However, the continuous application of insecticides results in insect resistance, and has negative impacts on human health and the environment.

THRIPS

Thrips are small pest insects (0.5 to 14 mm in length). *F. occidentalis* is a highly polyphagous pest, damaging more than 240 species from 62 different plant families (Kirk and Terry, 2003). Tipping (2008) estimated that they feed on more than 600 different wild and cultivated plants. Thrips may feed on leaves, flowers and fruits. The genus *Frankliniella* contains some of the most important thrips pests such as Western flower thrips [WFT, *F. occidentalis* (Pergande (Thysanoptera:Thripidae)]. It is a significant pest of most crops, including vegetables, ornamentals, fruits and cotton (Lewis, 1997; Kirk and Terry, 2003). Thrips is especially a key pest of ornamental crops (Tommasini and Maini, 1995). In Europe, WFT was first detected in the Netherlands in 1983 and by the end of the 1980's, it has been observed in most European countries (Tommasini and Maini, 1995). It is the most common thrips in Dutch greenhouses as observed by sampling in the period 1994- 2000 (Vierbergen, 2001).

Thrips often go unnoticed because of their behavior. Adults and larvae hide and feed in the protected narrow crevices in flowers and foliage (Jensen, 2000). This makes chemical control difficult. Moreover, thrips developed insecticide resistance, with populations resistant to several different classes of insecticides (Herron and James, 2005). In addition, this pest is an efficient vector of plant viruses, including tomato spotted wilt virus (TSWV), which affects different vegetables crops (Steenbergen *et al.*, 2018).

Oviposition and feeding behavior of thrips cause direct damage to plants (Mouden *et al.*, 2017). Thrips have piercing-sucking mouthparts which allow them to feed on different types of plant cells (Reitz *et al.*, 2019). Thrips feed by penetrating the plant cells and sucking out the cell sap (Capinera, 2004). Feeding causes the plant cells

to become filled with air which cause a characteristic silver leaf scar, so called silver damage (Denmark and Price, 1998). Feeding leads to yield losses due to stunted and deformed plants (Denmark and Price, 1998).

Thrips is commonly found on *Gladiolus* (Terry and Lewis, 1997). They cause damage on the corms resulting in smaller corms, retardation of growth, and poor flowering. Some corms may even fail to germinate. Damage in the buds and flowers may lead to difficulties in flower formation and opening. Moreover, severely damaged flowers may desiccate and fall off. The variation in *Gladiolus* thrips resistance, primarily to *Thrips simplex* and *F. occidentalis*, has been reported by Terry and Lewis (Terry and Lewis, 1997).

METABOLOMIC STUDIES

Metabolomics is an advanced technology aiming at measuring the full suite of metabolites expressed in a cell or tissue both qualitatively and quantitatively. Obviously, that means it is a tool and not a goal. Metabolomics provides comprehensive information related to all metabolites networks (Weckwerth, 2003) and thus on the functioning of the whole system. Metabolomics based on Nuclear Magnetic Resonance spectroscopy (NMR) provides a very fast and detailed analysis of the biomolecular composition of a crude extract (Verpoorte *et al.*, 2008). It has major advantages of high long term reproducibility and a broad range of detected metabolites and simple absolute quantitation of all compounds as signal intensity is only dependent on molar concentration (Kim *et al.*, 2010). However, a relatively low sensitivity and signal overlap in the NMR spectra are the drawback of NMR as a tool in metabolomics studies (Krishnan *et al.*, 2005).

Metabolomics has been applied as a tool to study plant-insect interactions (J William Allwood, Ellis and Goodacre, 2008; Macel *et al.*, 2010). The comparison of the metabolomes of herbivore resistant and susceptible plants allows identification of metabolites related to host plant resistance (Leiss *et al.*, 2011). Identification of such metabolites using NMR has been done successfully in wild *Jacobaea* species (Leiss *et al.*, 2009a), chrysanthemum (Leiss *et al.*, 2009b) and *Barbarea vulgaris* (Kuzina *et al.*, 2009), as well as in crop plants like tomato (Mirnezhad *et al.*, 2010; Bac-Molenaar *et al.*, 2019) and carrot (Leiss *et al.*, 2013).

AIMS AND SCOPE OF THE THESIS

This thesis explores the resistance of the ornamental plant *Gladiolus* to thrips. The aim is to improve our understanding of its defence against WFT by studying both morphological and chemical traits related to resistance against thrips. We focused on how defence traits were influenced by the abiotic and biotic environment and by plant developmental stages.

This general aim was translated to the following research questions:

1. Is leaf morphology related to the defense against thrips in *Gladiolus*?
2. Does chemical defense play a role in *Gladiolus*? And if so which compounds are involved?
3. Does the spectrum of constitutive defense compounds related to thrips resistance alter qualitatively or quantitatively during plant development? Do thrips damage and concentrations of defense compounds differ between plant organs? Do we find significant changes in defense related metabolites depending on the growth conditions?
4. Do we find an increase in resistance related metabolites after thrips infestation?

In the second chapter of this thesis, we explored the natural variation in thrips resistance dwarf *Gladiolus* by performing bioassays and relating differences in resistance to morphological traits as possible mechanical resistance factors (Chapter 2).

In chapter 3 we first explored the natural variation in resistance against thrips of regular, medium and large size *Gladiolus* varieties. Firstly we added extracts of plants to artificial diets to show that resistance was, at least in part, based on the plant's metabolome. We continued by performing a thrips infestation bioassay in which the damage caused by thrips was measured. To determine the chemical factors involved in resistance, all tested plants were subjected to NMR metabolomics analysis to identify possible markers for constitutive resistance. In addition, we studied the correlation between the density of papillae, a morphological structure identified as being related to WFT resistance in chapter 2, and leaf metabolite concentrations.

In chapter 4 we studied the influence of plant development stages on resistance of *Gladiolus* against WFT and the distribution of WFT damage over plant organs in flowering plants. We used 3 development stages (vegetative stage, generative stage with

buds and generative stages with flowers) of susceptible and resistant *Gladiolus* varieties in a thrips infestation bioassay. Furthermore, we grew plants under different conditions to study their effect on the plant's metabolome. Most experiments to study resistance referred to in the literature were performed in climate chambers under controlled growth conditions. But are these results also valid for the performance of plants under field conditions? Therefore, we compared the metabolomes of plants grown in the field and in the climate chamber (Chapter 4).

In chapter 5 we studied metabolic changes in *Gladiolus* after thrips infestation. We subjected six dwarf *Gladiolus* varieties to thrips infestation and measured the metabolomic changes compared to plants that were not infested (Chapter 5).

In chapter 6 we present the summary and conclusions of this thesis and discuss why the density of papillae is a good marker to be used in breeding programs targeted at thrips resistant *Gladiolus* varieties.

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