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Phloem-based whitefly resistance in tomato

Denkers, L.-A.M.

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Summary

The vasculature of a plant consists of two major systems, the phloem and the xylem. The water and minerals taken up by the roots are transported to the shoot through the xylem, while the compounds produced by the plant itself (including sugars, amino acids, lipids, RNAs, specialised metabolites, etc.) are distributed throughout the plant via the phloem. The high concentration of these nutritious, plant-produced compounds makes the phloem a suitable food source for insects, if they have the tools to reach it. The phloem is buried within the plant under multiple cell layers and is thereby protected against most insects, except for the phloem-feeding Hemiptera which include whiteflies and aphids. These insects have developed specialised mouthparts called stylets, with which they penetrate the plant's surface while manoeuvring around the cells before piercing into the phloem vessels. Once they reached the phloem, they inject saliva into the phloem to counteract the wound healing response and maintain a continuous flow of the phloem sap.

This feeding style makes phloem-feeders an ideal vector for many devastating plant viruses. Consequently, whiteflies (*Bemisia tabaci*) and the viruses they vector are a major issue for tomato (*Solanum lycopersicum*) cultivation. In conventional agriculture, the total failure of tomato harvests upon whitefly infestations is prevented by the application of pesticides. Although this can be very efficient, the detrimental non-target effects of most pesticides have led to a demand for more sustainable agricultural practices. A solution for this dilemma can be sought in the wild relatives of crop species, which often harbour a plethora of defence mechanisms. For example, some wild tomato species produce high concentrations of toxic and repellent specialised metabolites in their

glandular trichomes (hairs on the plant's aerial surface), which provide these plants with a strong resistance against whiteflies. However, we also had indications of a resistance mechanism located in the phloem of wild tomato, that might also be based on the presence of specialised metabolites. As the phloem is the main site of interaction between plants and whiteflies, I hypothesized that this is also a location for plants to fight against whiteflies.

The aim of this thesis was therefore to explore the tomato phloem as a site for insect resistance through the identification of phloem-based metabolites that affect the proliferation of *B. tabaci*. To this end, we assessed (1) the developmental success of *B. tabaci* on a set of wild and cultivated tomato plants as a measure of resistance in the host plants and (2) the natural variation in phloem-based specialised metabolites in the wild and cultivated tomato plants, to (3) link the specialised metabolites in the phloem to the resistance phenotype.

First, we reviewed the literature in **chapter 2** to provide an overview of our current knowledge of the role of phloem-based specialised metabolites in plant-insect interactions. Here we found that specialised metabolites in the phloem can have a range of effects on herbivorous insects but can also play a role in mutualistic interactions.

In **chapter 3** we evaluated the resistance to whitefly of four accessions of the wild tomato *S. chmielewskii* by tracking the whitefly nymphal development. On two of the accessions, whitefly nymphs could not fully develop to the final instar stage and these accessions could therefore be considered resistant. These *S. chmielewskii* accessions lack a trichome-based resistance and were used to study phloem-based resistance. With the

use of grafting experiments, we concluded that the *S. chmielewskii* resistance phenotype is likely caused by a factor transported through the vasculature. After metabolomics and inhibitor experiments, we linked the resistance to an increased riboflavin concentration in the resistant accessions.

Because we found this phloem-based resistance in *S. chmielewskii*, we hypothesised that there might be more wild tomato species with phloem-based resistance mechanisms that could be linked to specialised metabolites. We realised that screening many accessions would require a large set of developmental bioassays and untargeted metabolomics analyses. The data analysis following these types of experiments is relatively complex and no Python packages were available to conveniently perform the data analysis. In **chapter 4** we developed a Python package to analyse the data from the bioassays and metabolomics and link the two data types using machine learning.

In **chapter 5** we selected a plant panel consisting of a total of 12 accessions from the wild species *S. chmielewskii*, *S. habrochaites*, *S. pennellii* and a susceptible *S. lycopersicum* cultivar. To omit the strong trichome-based resistance phenotypes of several of the accessions we included, we performed developmental bioassays on susceptible cultivar scions grafted onto wild rootstocks. Next to the two resistant *S. chmielewskii* accessions identified in **chapter 3**, we also identified a *S. habrochaites* accession with a phloem-based resistance phenotype. An untargeted metabolomics analysis of phloem samples of all 13 genotypes showed that the phloem metabolome of (wild) tomato is highly diverse. Using the Phyton package from **chapter 4** and a data analysis method based on Genome Wide

Association Studies we were able to link the resistance phenotype to the phloem metabolite data and pinpoint to metabolic features of interest.

Samenvatting

Het vaatstelsel van een plant bestaat uit grofweg twee systemen, het floëem en het xyleem. Het water en de mineralen die door de wortels worden opgenomen, worden door het xyleem naar de bovengrondse delen vervoerd. Stoffen die door de plant zelf worden geproduceerd (waaronder bouw- en signaalstoffen zoals suikers, aminozuren, lipiden, RNA en gespecialiseerde metabolieten), worden via het floëem vervoerd vanaf de productielocatie naar de locatie waar ze worden opgeslagen of gebruikt in andere processen. Door de hoge concentratie van deze voedzame stoffen is het floëemsap een interessante voedselbron voor insecten, mits ze over de juiste gereedschappen beschikken om het vaatstelsel te bereiken. De floëemvaten liggen ingegraven in meerdere lagen van andere plantencellen die bescherming bieden tegen de meeste insecten. De uitzondering zijn de floëem-voedende insecten van de Hemiptera orde, waar witte vliegen en bladluizen onder vallen. Deze insecten hebben speciale monddelen die samen een lange, bewegelijke buis vormen, genaamd stilet. Met dit stilet kan een insect voorzichtig tussen de plantencellen door bewegen zonder deze ernstig te beschadigen en zo een groot deel van de afweermechanismen van een plant ontwijken totdat de floëemvaten zijn bereikt. Als het insect eenmaal een vat bereikt, wordt het stilet erin geprikt en injecteert het insect eerst speeksel in het floëem voordat er kan worden gedronken. In het speeksel zitten stoffen die wondgenezing tegengaan en ervoor zorgen dat het sap blijft doorstromen.

Dankzij deze manier van eten zijn floëem-voedende insecten een ideale vector (overdrager) voor veel desastreuze plantenvirussen. Witte vliegen (*Bemisia tabaci*) en de virussen die ze bij zich dragen zijn hierdoor dan ook één van de grootste problemen voor de teelt van tomaten (*Solanum*

lycopersicum). In de conventionele landbouw wordt gebruik gemaakt van pesticiden om te voorkomen dat gehele tomaten oogsten verloren gaan. Hoewel het gebruik van pesticiden erg efficiënt kan zijn, is de vraag naar duurzamere landbouwpraktijken toegenomen vanwege de ernstige onbedoelde effecten van pesticiden op mens en natuur. Om dit vraagstuk op te lossen kunnen we te rade gaan bij de wilde soorten die nauw verwant zijn aan gecultiveerde gewassen. In wilde plantensoorten zijn vaak vele afweermechanismes te vinden en zo ook in wilde tomaat. Op sommige wilde tomaatsoorten zijn bijvoorbeeld klierhaartjes te vinden die gespecialiseerde metabolieten (afweerstoffen) maken die afstotend of giftig zijn voor witte vliegen. Daarnaast hadden we ook aanwijzingen voor een afweermechanisme in het floëem van wilde tomaat dat gebaseerd zou kunnen zijn op de aanwezigheid van gespecialiseerde metabolieten in het floëemsap. Aangezien de interactie tussen planten en witte vliegen met name in het floëem plaatsvindt, leek dit mij ook een geschikte locatie voor planten om witte vliegen te bevechten.

Het doel van dit proefschrift was daarom om op ontdekking te gaan in het floëem van wilde tomaat, op zoek naar afweermechanismes die met behulp van gespecialiseerde metabolieten de verspreiding van witte vliegen tegengaan. Deze zoektocht bestond uit het beantwoorden van drie deelvragen. Ten eerste, is er een verschil tussen verschillende wilde tomaatsoorten in hoe goed zij zich tegen witte vliegen kunnen verweren? Ten tweede, kunnen we gespecialiseerde metabolieten vinden in het floëem van wilde tomaat en verschilt de samenstelling hiervan tussen de verschillende soorten? Ten slotte, kunnen we deze gespecialiseerde metabolieten linken aan het verschil in afweer tegen witte vliegen?

We begonnen in **hoofdstuk 2** met het maken van een overzicht van wat er tot nu toe bekend is over gespecialiseerde metabolieten in het floëem en hun rol in de interactie tussen planten en insecten. Hier zagen we dat deze stoffen een grote verscheidenheid aan effecten kunnen hebben op herbivore insecten, maar ook van belang kunnen zijn in mutualistische interacties (een interactie die voor beide partijen voordelig is).

In **hoofdstuk 3** hebben we de afweer van vier accessies (nakomelingen van een in het wild verzamelde plant) van de wilde tomaatsoort *Solanum chmielewskii* geëvalueerd aan de hand van hoe goed witte vliegen zich konden ontwikkelen op deze accessies. Op twee *S. chmielewskii* accessies konden de witte vliegen zich niet volledig ontwikkelen van ei tot volwassenen en deze planten noemden we daarom resistent. Dankzij experimenten op geënte planten konden we vaststellen dat het afweermechanisme in de resistente planten wordt vervoerd door het vaatstelsel. In de resistente planten bleek de riboflavine (vitamine B2) concentratie veel hoger te zijn dan in de vatbare planten. Als we de riboflavine concentratie in de planten manipuleerde, zagen we dat de sterkte van het afweermechanisme ook veranderde. Hierdoor konden we concluderen dat dit afweermechanisme gelinkt is aan riboflavine.

Omdat we in het floëem van *S. chmielewskii* een afweermechanisme hadden gevonden, bedachten we dat er in het floëem van andere wilde tomaatsoorten soortgelijke afweermechanismes aanwezig zouden kunnen zijn. We realiseerden ons ook dat het uitbreiden van het onderzoek naar meer soorten zou resulteren in grote hoeveelheden te analyseren data. Om de complexe analyses van deze grote datasets te vergemakkelijken, hebben we in **hoofdstuk 4** een Python softwarepakket ontwikkeld. Met deze softwaretool kan de gebruiker data analyseren van experimenten waarin de

ontwikkeling van insecten wordt gevolgd. Daarnaast kan met de tool data van ongerichte metabolomics (het analyseren van alle, of zo veel mogelijk, stoffen in een monster) worden opgeschoond. Als laatste kan de gebruiker met behulp van machine learning (een vorm van artificiële intelligentie) de insectontwikkeling linken aan de gemeten stoffen.

In **hoofdstuk 5** hebben we een plantenpanel samengesteld van 12 wilde accessies (waaronder de vier in **hoofdstuk 3** geteste *S. chmielewskii* accessies) en een gecultiveerde lijn, waarin we opnieuw onderzoek zijn gegaan naar afweermechanismen in het floëem. Hier vonden we dat, naast de twee resistente *S. chmielewskii* accessies, ook één *S. habrochaites* accessie een afweermechanisme in het floëem heeft. Na het doormeten van floëem monsters van alle accessies hebben we de data geanalyseerd met behulp van de softwaretool uit **hoofdstuk 4**. Aan de hand daarvan konden we drie, nog naamloze, stoffen aanwijzen die voornamelijk aanwezig zijn in de drie resistent accessies. Hieruit concluderen we dat deze stoffen mogelijk betrokken zijn bij afweermechanismes in het floëem.

Alles bij elkaar kunnen we uit de bevindingen in dit proefschrift concluderen dat er inderdaad afweermechanismes tegen witte vliegen te vinden zijn in het floëem van wilde tomaat. Het floëemsap van wilde en gecultiveerde tomaat bevat een grote verscheidenheid aan stoffen, waarvan sommige mogelijk betrokken zijn bij afweermechanismes tegen floëemvoedende insecten. Er zijn uiteraard nog veel onbeantwoorde vragen, maar het floëem lijkt een veelbelovende locatie voor afweer tegen witte vliegen.

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