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Author contributions and project funding

2 – Phytophagy of omnivorous predator *Macrolophus pygmaeus* affects performance of herbivores through induced plant defences

Nina Xiaoning Zhang, Gerben J. Messelink, Juan M. Alba, Robert. C. Schuurink, Merijn R. Kant & Arne Janssen

NXZ, GJM, JMA and AJ conceived and designed the experiments. NXZ performed the experiments, JA and NXZ collected the plant hormones. NXZ and AJ analysed the data. NXZ wrote the manuscript, all authors commented and corrected it.

3 – Herbivores avoid host plants previously exposed to their omnivorous predator *Macrolophus pygmaeus*

Nina Xiaoning Zhang, Daan van Wieringen, Gerben J. Messelink & Arne Janssen

NXZ, GJM and AJ conceived and designed the experiments. NXZ and DW performed the experiments. NXZ and AJ analysed the data and wrote the manuscript, all authors commented and corrected it.

4 – Omnivore induces production of plant volatiles that attract a specialist spider mite predator

Nina Xiaoning Zhang, Joke Andringa, Jitske Brouwer, Juan M. Alba, Ruy W. J. Kortbeek, Gerben J. Messelink & Arne Janssen

NXZ, GJM and AJ conceived and designed the experiments. NXZ, JA and JB performed the predator olfactometer experiments, NXZ, JMA and RWJK collected and analysed the volatiles. NXZ and AJ analysed the data and wrote the manuscript, all authors commented and corrected it.

5 – Plant feeding by an omnivorous predator affects plant phenology and omnivore performance

Nina Xiaoning Zhang, Gerben J. Messelink, Sunny Verdonkschot & Arne Janssen

NXZ, GJM and AJ conceived and designed the experiments, NXZ and SV performed the experiments, NXZ and AJ analysed the data and wrote the manuscript, all authors commented and corrected it.

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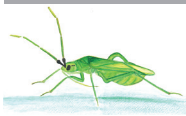
Summary



Omnivory is a common phenomenon in many food webs. It is defined as feeding on more than one tropic level, for example a predator feeding on plants and herbivores. Omnivory occupies a central position in food web ecology as it can influence persistence and stability of populations in fundamental ways. Whereas the predation behavior of omnivorous predators has been extensively studied, the consequences of plant feeding by omnivores have received relatively little attention. Recently, it has been shown that omnivorous predators induce plant defences that affect the performance of herbivores. But on a community level, the interplay between effects of plant feeding by omnivorous predators and the plant-mediated interactions among omnivorous predators, herbivores and natural enemies is still poorly understood. In this thesis, I studied the ecological consequences of plant responses induced by the omnivorous predator *Macrolophus pygmaeus*, for a community of plants, herbivores and their natural enemies.

Like many other omnivores, this predator is used for biological pest control. The advantage of using omnivores is that by feeding on plant tissue, pollen and nectar, their populations can establish and persist in crops without the presence of pests. So, when pests enter the crop, these armies of predators can efficiently suppress them or keep their density at low levels. The study of omnivores in plant-herbivore-predator communities is therefore important for fundamental as well as applied reasons.

In Chapter 2, I show that *M. pygmaeus* induces plant defences in sweet pepper plants, which negatively affects the performance of spider mites and thrips, but not of aphids. I further found that the jasmonic acid pathway, which is involved in induced plant defences, was activated, but the salicylic acid pathway, also involved in induced plant defences, was not. Moreover, the abscisic acid pathway was activated. Hence, phytophagy by the omnivorous predator induced direct plant defences resulting in decreasing performance of herbivores on the same plant. These results suggest that the omnivorous predator can decrease the density of herbivores by directly killing them but also indirectly through plant defences induced by the omnivore.

Omnivores present on plants may affect the host plant choice of herbivores by preying on them as well as by decreasing the quality of host plants. Therefore, in Chapter 3, I further investigated the effect of previous exposure of plants to the omnivorous predator *M. pygmaeus* on the host plant choice of the three herbivore species used in Chapter 2. In agreement with their performance (Chapter 2), I found

that spider mites and thrips preferred clean plants over plants previously exposed to the omnivore. Aphids did not show such preference, but a higher proportion of aphids left exposed plants than unexposed plants. These results show that omnivorous predators can not only decrease herbivore densities on plants by killing them and by decreasing their performance through induction of direct plant defences, but also by affecting herbivore host plant selection.

Important cues used by herbivores during host plant choice are plant volatiles. Some volatiles are constitutively produced by plants, but others are induced by herbivore feeding. Because omnivores also feed on plants, they may also induce the production of plant volatiles. Inspired by the results of CHAPTER 3, in CHAPTER 4 I asked whether plant feeding by *M. pygmaeus* induced the production of plant volatiles and how this affected the performance of the phytoseiid *Phytoseiulus persimilis*, a predatory mite of spider mites. I found that the predatory mites preferred volatiles from plants previously exposed to the omnivore over volatiles from clean plants, even when the prey was absent. To understand the interactions between the two predators, I further investigated whether the omnivore would interfere with the attraction of predatory mites to plants with their common prey, spider mites. Predatory mites were equally attracted by plants previously exposed to the omnivore and subsequently infested by spider mites and plants infested with spider mites. In contrast, the predators were more attracted by volatiles from plants infested with prey and subsequently exposed to the omnivore than plants infested with prey but not exposed to the omnivore, suggesting that the omnivores indeed can interfere with the searching behaviour of the predatory mites. These responses were surprising because *M. pygmaeus* can feed on all stages of *P. persimilis*. I therefore further investigated responses of predator mites to exposed plants after having gained experience with both cues from volatiles and from omnivores from these plants. I found that such experience resulted in a loss of the preference for volatiles emitted by exposed plants. I also analyzed the volatiles from the headspace of clean and exposed plants using gas chromatography-mass spectrometry. Exposed plants indeed produced different volatile blends than clean plants, and some of the volatile compounds were similar to those induced by spider mites and attractive to *P. persimilis*. Hence, the omnivore induced the production of plant volatiles, which attracted other predators and likely also influenced the host plant choice by the herbivores (CHAPTER 3). Obviously, interactions between the omnivore and the predatory mite, especially those mediated by plants, require further study.

The effects of herbivory on plant performance and the subsequent effects on the herbivores have been extensively studied. In contrast, the consequences of plant feeding by omnivore for plant performance are less studied, nor are the subsequent effects of plant performance on omnivore performance. Therefore, in CHAPTER 5, I

investigated the effects of the presence of the omnivorous predator on plant performance by evaluating plant growth and reproduction. I showed that plants with the omnivore produced fewer leaves and open flowers, suggesting a negative effect of the omnivore on plant performance. However, exposed plants and clean plants produced similar numbers and biomass of fruits. Moreover, flowers developed faster into fruits on plants with the omnivore, suggesting a positive effect of the omnivore on fruit development. Most interestingly, the numbers of seeds in fruits on plants with the omnivore was five times higher than on clean plants, suggesting that the presence of the omnivore was beneficial to the plant. Possibly, flower visiting by the omnivore increased pollination, resulting in higher seed production. This increased pollination may then result in an increased allocation of resources to fruit production at the expense of flower production. This may explain the lower numbers of flowers on plants exposed to the omnivore. In addition, I found that the survival and reproduction of the omnivore was higher after plants started flowering than before flowering. Moreover, the survival and reproduction of the omnivore was positively correlated with the numbers of flowers on the plants. So higher numbers of flowers would be beneficial to the omnivore, however, plants produced fewer flowers when the omnivore was around, which suggests a negative effect of the changes in plant phenology on omnivore performance.

In this thesis, I only studied plant-mediated interactions between the omnivorous predator, three herbivores and one predator species. However, the plant-associated food webs usually are more complex, resulting in many more potential interactions among plants, herbivores, omnivores and predators. A next step in further research might be the positioning of plant-herbivore-predator-omnivore interactions in the context of complex food webs as this may alter the consequences of these interactions for population and community persistence and stability in fundamental ways. Such focus on overall food web interactions very likely asks for a combination of empirical and modelling approaches.

Samenvatting

Omnivoren zijn organismen die zich voeden op meer dan één trofisch niveau – denk bijvoorbeeld aan een predator die zich voedt met zowel planteneters (herbivoren) als met planten. Omnivorie komt veel voor in voedselwebben en neemt een centrale plaats in binnen de ecologie omdat het bepalend is voor de persistentie en stabiliteit van populaties en levensgemeenschappen. Het predatiegedrag van omnivore predators is uitgebreid bestudeerd, maar de gevolgen van het zich voeden met planten is veel minder onderzocht. Onlangs is aangetoond dat omnivoren, wanneer ze zich met een plant voeden, de verdediging tegen vraat in die plant induceren en dat deze verdediging het functioneren van herbivoren op dezelfde planten beïnvloed. Het is echter nog niet duidelijk hoe de geïnduceerde verdediging van de plant door vraat door omnivoren de levensgemeenschappen van herbivoren en predators beïnvloedt. Voor dit proefschrift bestudeerde ik de ecologische gevolgen van de reactie van planten op fytofagie door de omnivore predator *Macrolophus pygmaeus* in een gemeenschap van planten, herbivoren en predators.

Macrolophus pygmaeus wordt gebruikt voor biologische plaagbestrijding, zoals vele andere omnivoren. Het voordeel van omnivoren voor biologische bestrijding is dat populaties zich kunnen vestigen zonder dat er plagen aanwezing zijn, omdat ze zich kunnen voeden met plantenmateriaal, zoals blad, stuifmeel en/of nectar. Als een plaaginsect dan later het gewas invadeert, kan dit legertje van omnivoren de plaagpopulaties efficiënt onderdrukken. De studie van de rol van omnivoren in gemeenschappen van planten, herbivoren en predators is daarom niet alleen van fundamenteel belang, maar heeft ook praktische relevantie.

In Hoofdstuk 2 laat ik zien dat vraat door *M. pygmaeus* de verdediging van paprikaplanten induceert, met negatieve gevolgen voor de voortplanting van trips en spintmijten, maar niet voor die van bladluizen. Ik vond ook dat de door jasmonzuur gereguleerde verdedigingsrespons werd geactiveerd, maar niet de door salicylzuur gereguleerde respons. Verder werd de abscisinezuur-route geactiveerd. Deze resultaten suggereren dat de omnivoor de dichtheden van herbivoren op een plant direct kan verlagen door predatie, maar ook indirect, door de inductie van plantenverdediging.

Dit suggereert ook dat herbivoren die nadeel ondervinden van de door de omnivoor geïnduceerde defensie mogelijk een voorkeur hebben voor planten die niet geïnduceerd zijn. Ik onderzocht daarom de waardplantkeuze van dezelfde drie herbivoren in Hoofdstuk 3. Spintmijten en trips bleken een voorkeur te hebben voor schone planten boven planten die eerder blootgesteld waren aan de omnivoor, in overeenkomst met de negatieve effecten van de geïnduceerde defensie op deze twee herbivoren. Bladluizen hadden geen voorkeur, maar een groter percentage bladluizen verliet de blootgestelde planten dan de schone planten. Dit laat zien dan omnivoren de dichtheden van herbivoren op planten niet alleen kunnen verlagen door predatie en door negatieve effecten op de reproductie van de herbivoren door de inductie van plantenverdediging (HOOFDSTUK 2), maar ook door het beïnvloeden van het waardplant-selectiegedrag van de herbivoren.

Vluchtige stoffen behoren tot de belangrijkste stimuli die herbivoren gebruiken wanneer ze op zoek zijn naar waardplanten. Sommige vluchtige stoffen worden altijd door de plant afgescheiden, maar andere komen pas vrij als de planten worden aangevallen door herbivoren, of wanneer omnivoren zich met de plant voeden. Geïnspireerd door de resultaten van HOOFDSTUK 3 besloot ik daarom te onderzoeken of *M. pygmaeus* inderdaad aanzet tot de productie van vluchtige stoffen als deze wants zich met de plant voedt. Ook bestudeerde ik of het zoekgedrag van de roofmijt *Phytoseiulus persimilis* wordt beïnvloed door deze vluchtige stoffen. Het is bekend dat deze roofmijt aangetrokken wordt door de vluchtige stoffen die planten maken als ze worden aangevallen door spintmijten, de prooi van de roofmijt. Ik vond dat de roofmijten ook werden aangetrokken door de vluchtige stoffen van planten die tevoren waren blootgesteld aan de omnivoor (HOOFDSTUK 4). Vervolgens bestudeerde ik of de omnivoor interfereert met de aantrekking van de roofmijten door planten met spintmijten. De roofmijten vertoonden geen voorkeur bij de keuze tussen planten met spintmijten die wel of niet tevoren waren blootgesteld aan de omnivoor, maar ze prefereerden planten die eerst waren geïnfecteerd met spintmijten en vervolgens werden blootgesteld aan omnivoren boven planten met spintmijten die niet werden blootgesteld. Dit laat zien dat de omnivoren inderdaad interfereren met het zoekgedrag van de roofmijten. Deze resultaten waren verrassend omdat de omnivoor alle ontwikkelingsstadia van de roofmijt kan aanvallen. Ik onderzocht daarom de respons van predators die ervaring hadden opgedaan met de vluchtige stoffen van de plant en de omnivoor. Roofmijten met deze ervaring hadden geen voorkeur meer voor deze vluchtige stoffen. Ook analyseerde ik de vluchtige stoffen van schone planten en planten die waren blootgesteld aan omnivoren met gas-chromatografie en massaspectrometrie en vond dat blootgestelde planten inderdaad ander vluchtige componenten afgeven dan schone planten, en dat sommige van deze componenten overeenkomen met de vluchtige stoffen die worden geïnduceerd door spintmijten en aantrekkelijk zijn voor de roofmijt. Concluderend heb ik laten zien dat de omnivoor de productie van vluchtige stoffen door de plant induceert en dat deze aantrekkelijk zijn voor andere predatoren. Ze hebben waarschijnlijk ook een rol gespeeld in de waardplantkeuze van de herbivoren (HOOFDSTUK 3). Het is duidelijk dat de interacties tussen de omnivoor en de roofmijt verder moeten worden bestudeerd, vooral de interacties die via de plant verlopen.

De effecten van herbivorie op planten en de effecten van de verdediging van planten geïnduceerd door deze herbivorie op herbivoren zijn uitgebreid bestudeerd, maar er is nog heel weinig bekend over de effecten van fytofagie van omnivoren op planten en, via de geïnduceerde plantenverdediging, weer op de omnivoren. Ik heb daarom deze effecten bestudeerd in HOOFDSTUK 5. Ik laat zien dat planten blootgesteld aan omnivoren minder bladeren en bloemen produceren, suggererend dat de omnivoren een negatief effect hebben op de plant. De blootgestelde planten produceerden echter evenveel en even zware vruchten en hun bloemen ontwikkelden zich sneller tot vruchten, die bovendien vijf keer zoveel zaden bevatten als de schone planten, hetgeen een positief effect van de omnivoor op de plant impliceert. Misschien dragen de omnivoren bij aan de bestuiving van de bloemen door ze te bezoeken, wat tot hogere zaadproductie kan hebben geleid. Deze bestuiving zou tot een verschuiving van energie en nutriënten naar de productie van vruchten kunnen leiden, ten koste van de productie van bloemen, hetgeen het lagere aantal bloemen van de blootgestelde planten kan verklaren. Ik vond ook dat de overleving en voortplanting van de omnivoor positief waren gecorreleerd met het aantal bloemen aan de planten. Meer bloemen zou dus goed zijn voor de omnivoren, maar planten die blootgesteld waren aan omnivoren vormden juist minder bloemen, hetgeen een negatief effect suggereert van de door de omnivoor geïnduceerde veranderingen in de planten op de omnivoren.

In dit proefschrift heb ik mij beperkt tot het bestuderen van gemeenschap bestaande uit één plantensoort, één omnivoor, drie herbivoren en één predator. Voedselwebben van geleedpotigen op planten zijn echter veelal complexer, wat leidt tot een veelvoud van potentiële interacties. Een logische volgende stap is dan ook het onderzoeken van de consequenties van deze interacties in meer complexe voedselwebben en hun effecten op de persistentie en stabiliteit van levensgemeenschappen. Dit vereist een combinatie van experimenten en theoretische studies met behulp van populatiedynamische modellen.

Curriculum vitae

Xiaoning Zhang (Nina) was born in Anyang (Henan province, China) in 1985. In 2005 she was admitted as a bachelor student (Plant Protection major) at the Forest College of the Henan University of Science and Technology. Since the second year of her bachelor, she showed great interest in entomology and ecology. She started working as a volunteer, performing experiments, sampling insects and preparing insects for reference collections for courses and the college museum, guided by prof. Dingxu Li. Under the supervision of prof. Li, she finished her first bachelor internship in 2008 (bachelor thesis: Effects of high temperature shocks and delayed mating on the hawthorn spider mite, *Tetranychus viennensis* Zacher). In 2009, she did her second bachelor internship under the supervision of prof. Julian Chen at the Institute of Plant Protection of the Chinese Academy of Agricultural Sciences (IPP-CAAS) in Beijing. After obtaining a bachelor degree in Agriculture (July 2009), she started her master study at CAAS, majoring in Agricultural Entomology and Pest Control. In 2012, she went to Gembloux Agro-Bio Tech at the University of Liege (Belgium) for a three-month internship in the laboratory of prof. Frederic Francis. In 2013 she completed her master thesis (Insecticidal and deterrent activities of extracts from *Macleya cordata* to wheat aphids) under the supervision of prof. Julian Chen and prof. Dengfa Cheng and she obtained a master degree in Agriculture at CAAS. The same year, she obtained a scholarship from the Chinese Scholarship Council to start a PhD in The Netherlands. She started her PhD working with dr. Gerben Messelink at the Wageningen University & Research (Greenhouse Horticulture Plant Research). Three months later, she moved to the University of Amsterdam to continue her PhD under the supervision of prof. Maurice Sabelis, dr. Arne Janssen, and dr. Gerben Messelink in the Population Biology group of the Institute of Biodiversity and Ecosystem Dynamics (IBED).

Publications

Zhang NX, van Wieringen D, Messelink GJ, et al (2018) Herbivores avoid host plants previously exposed to their omnivorous predator *Macrolophus pygmaeus*--submitted

Zhang NX, Messelink GJ, Verdonkschot S, et al (2018) Plant feeding by an omnivorous predator affects plant phenology and omnivore performance--submitted

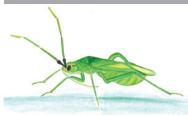
Zhang NX, Messelink GJ, Alba JM, et al (2018) Phytophagy of omnivorous predator *Macrolophus pygmaeus* affects performance of herbivores through induced plant defences. Oecologia 186:101–113

Zhang NX, Chen J, Cheng D, et al (2014) Biological activity of *Macleaya cordata* extracts against three species of wheat aphids. Plant Protection 40(3):187-190 (in Chinese)

Zhang NX, Chen J, Cheng D, et al (2012) Insecticidal activities of *Macleaya cordata* extracts on wheat aphids. Proceedings of the 2012 Annual Meeting of the Chinese Society of Plant Protection, Beijing, China, 25-26 October, p. 532. Chinese Agricultural Sci-Tech Press, Beijing, China (in Chinese)

Li D, Zhang NX, Yang Y, et al (2010) Effects of high temperature shocks on hawthorn spider mite, *Tetranychus viennensis* Zacher. Acta Ecologica Sinica 30(16): 4437–4444 (in Chinese)

Li D, Juan T, Guo Y, Zhang NX, et al (2009) Effects of delayed mating on the reproduction of the hawthorn spider mite, *Tetranychus viennensis* Zacher. Acta Entomologica Sinica 52(12): 1312–1318 (in Chinese)



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