What omnivores don't eat

Nonconsumptive ecological effects of phytophagy by Macrolophus pygmaeus

Zhang, X.

Link to publication

Creative Commons License (see https://creativecommons.org/use-remix/cc-licenses):
Other

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: https://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
General introduction

Omnivores feed on resources from more than one trophic level (Pimm and Lawton 1978). Omnivory is a common phenomenon many food webs, including terrestrial plant-inhabiting communities of arthropods (Polis et al. 1989; Polis and Strong 1996; Coll and Guershon 2002). Earlier theoretical models predicted that omnivory would be rare and would destabilize food webs (Pimm and Lawton 1978), but later research has shown that omnivory is common in nature and may even increase the stability and resilience of food webs (Polis 1991; McCann and Hastings 1997; Fagan 1997). The idea behind this is that by being linked to various species at several trophic levels, omnivores can respond to changes in densities of either of the species, thus decreasing the effects of perturbations (Kondoh 2003).

It has become clear in the last few decades that many terrestrial arthropods are omnivores. Omnivorous predators are increasingly used for biological control of various pests in different crops (Messelink et al. 2012). By feeding on plant tissues or pollen and nectar, populations of omnivores can persist in a crop even when prey density is low. Thus omnivores can make a cropping system more resilient to pest invasions. However, little information is available on the interactions between omnivorous predators and plants, herbivores and other predators. Yet, such information is required for a better understanding of these interactions, which may result in better biological pest control. Whereas the predatory role of omnivores has been studied in detail, there is much less known about the effects of phytophagy on the host plant and the associated food web. In contrast, the interactions between plants and herbivores have been studied extensively. I therefore first review the interactions between herbivores and plants to subsequently focus on omnivore-plant interactions.

Plant-herbivore interactions
Herbivory is one of the most severe threats for plants, causing negative effects on plant growth (Agrawal 2000). Plants employ different types of defences to resist herbivores. Such defences can be displayed constitutively or can be induced. In general, constitutive defences are present all the time, and induced plant defences are reinforced or activated by herbivory. Induced defences involve the production of signalling molecules, which results in the upregulation of biosynthesis of specific compounds such as toxins and digestion inhibitors (Karban and Baldwin 1997; Kant et al. 2015). These compounds act directly against herbivores, reducing their growth,
survival or reproduction (Howe and Jander 2008; Kant et al. 2015), which is referred to as direct plant defence.

Induced direct plant defences can be local, i.e., they are expressed at the damaged site, or systemic, i.e., expressed in plant parts that were not damaged by the herbivores. Phytohormones play important roles in regulating induced defences (Pieterse et al. 2009). The most important hormones involved in induced defences are jasmonic acid (JA), salicylic acid (SA) and the hormone ethylene (Erb et al. 2012; Pieterse et al. 2012). Plant defences can differ qualitatively and quantitatively with the herbivore species attacking the plants (de Vos et al. 2005; Rodriguez-Saona et al. 2010), and time since attack (Kant et al. 2004). Moreover, different defence pathways can affect each other either positively or negatively (Koornneef and Pieterse 2008).

Plants can also reduce damage by herbivores indirectly by involving natural enemies of the herbivores, which is referred to as indirect plant defences (Dicke and Sabelis 1989; Karban and Baldwin 1997; Sabelis et al. 2001). Plants can arrest natural enemies of the herbivores by providing them with food, e.g. nectar and pollen (Pemberton and Lee 1996; Heil et al. 2001; Wäckers 2001), and shelter such as domatia (Walter 1996). Herbivory also results in the production of mixtures of volatiles that are attractive to natural enemies (Turlings et al. 1995; Sabelis et al. 1999; Dicke and van Loon 2000). These plant volatiles do not only emanate from the damaged plant tissue but also systemically from non-damaged tissue (Turlings and Tumlinson 1992; Dicke 1994; Rose et al. 1996; Guerrieri et al. 1999). The volatiles differ qualitatively and quantitatively among plants species (van den Boom et al. 2004), herbivore species feeding on the plants (De Moraes et al. 1998; Birkett et al. 2003), and with the period that herbivores feed on the plants (Takabayashi et al. 1994b; Turlings et al. 1998; Kant et al. 2004), and also vary with other biotic and abiotic factors (Takabayashi et al. 1994a; Dicke and van Loon 2000).

Interactions between omnivores and plants

Until recently, effects of phytophagy by omnivores on plants have not been studied in detail. Perhaps this was caused by most omnivores causing little damage to plants, so there was no reason to expect strong effects on the plants. Since a few years, however, omnivore-plant interactions have received more attention, showing that, like herbivores, several omnivorous predators do induce direct defences when feeding on a plant (De Puysseleyr et al. 2011; Pappas et al. 2015; Pérez-Hedo et al. 2015a,b; Naselli et al. 2016; Bouagga et al. 2018; Zhang et al. 2018). It is known that herbivore-induced direct defences can affect the performance of other herbivores on the same plant (Karban and Baldwin 1997; Howe and Jander 2008; Kant et al. 2015). Likewise, the induction of plant defences by omnivores can affect the performance of herbivores on the same plant. For example, exposure of tomato plants to the
omnivorous predator bug *Orius laevigatus* increases resistance against thrips (De Puysseleyr et al. 2011). In addition, Pérez-Hedo et al. (2015a,b) and Naselli et al. (2016) have shown that three species of omnivorous predators *Nesidiocoris tenuis*, *Macrolophus pygmaeus* and *Dicyphus maroccanus* induced different defence-related pathways. This resulted in different attractiveness of plants to herbivores and natural enemies. The whitefly *Bemisia tabaci* and the lepidopteran *Tuta absoluta* were less attracted by the plants exposed to *N. tenuis* than to clean plants clean plants. Pappas et al. (2015) found that exposing tomato plants to the omnivorous predator *M. pygmaeus* reduced the performance of two-spotted spider mites, but not of greenhouse whiteflies. In conclusion, omnivorous predators can reduce herbivore populations directly by preying on them, but also indirectly through the induction of direct plant defences.

Recently, some evidence has also been presented that phytophagy by omnivores also induces the production of plant volatiles, and these volatiles may affect the searching behaviour of herbivores and natural enemies. Moayeri et al. (2007) showed that the omnivorous predator *Macrolophus pygmaeus* induced production of volatiles in bean plants. A study by Bouagga et al. (2018) showed that feeding by the omnivorous predator *Orius laevigatus* induced the production of volatiles that repelled whiteflies and thrips, but attracted the parasitoid *Encarsia formosa*. Together, these studies show that omnivores can affect other plant-inhabiting arthropods indirectly through the induction of changes in the plant.

In this thesis, I also investigated whether plant feeding by an omnivorous predator induces plant defences, but furthermore investigated the ecological consequences of the induction of these defences. In particular, I address the effects of induced direct plant defences on herbivore performance in Chapter 2, the effects on host plant choice of herbivores in Chapter 3, and the effects on the searching behaviour of a predator in Chapter 4.

Although the literature summarized above clearly shows that phytophagy by omnivores can have important consequences for the interactions among plants, herbivores and predators, it is still unclear how this affects the performance of the host plants and omnivores. Plant defences induced by herbivores are thought to benefit the plant because they decrease the performance of the herbivores and increase the probability that the natural enemies of the herbivores will decimate herbivore populations. In contrast, plant defences induced by omnivores can also reduce herbivore performance, but these defences are even induced in the absence of herbivores. Moreover, the induction of the production of plant volatiles may attract natural enemies without the plant harbouring their herbivorous prey. This suggests that the induction of plant defences by omnivores may not benefit the plants through a decrease in herbivory, but the plants will probably have costs associated with the
induction of defences by the omnivore. I therefore studied the consequences of the induction of plant defences for plant and omnivore performance in Chapter 5.

The study system

*Macrolophus pygmaeus* (Rambur) (formerly identified as *Macrolophus caliginosus* Wagner) (Figure 1.1) is native from and widely distributed in the Mediterranean area (Perdikis and Lykouressis 2000). It is an important omnivorous predator of several generalist crop pests such as whiteflies (Montserrat et al. 2000), thrips (Rudavets and Castañé 1998), aphids (Alvarado et al. 1997), spider mites (Hansen et al. 1999), leaf miners (Arnó et al. 2003) and Lepidoptera species (Urbaneja et al. 2009). It is commercially used for the biological control of spider mites, aphids and whiteflies. Being omnivores, they can also feed on plant tissue (Perdikis and Lykouressis 2000). Plant damage has been observed with high predator densities on tomato, zucchini, and gerbera flowers under experimental conditions, but no such damage has been observed under cropping conditions (Castañé et al. 2011).

Sweet pepper plants, *Capsicum annuum* L., also known as bell pepper (Figure 1.1) are an important crop all over the world. They are cultivated both in open fields and in closed systems such as greenhouses. The most important pests of greenhouse sweet pepper are aphids, spider mites and thrips (Ramakers 2004). Biological pest control is widely used in greenhouse crops. Both generalist and specialist predators are released, for example: the omnivorous predator *M. pygmaeus*, and the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) (Messelink et al. 2012).

The two spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) (Figure 1.2), is one of the most polyphagous herbivores. It feeds on more than 1100

**Figure 1.1** Left: *Macrolophus pygmaeus* female. Right: Sweet pepper plants, *Capsicum annuum*, also known as bell pepper.
plant species (Migeon et al. 2010). Widely distributed all over the world, it is one of the most important pests on many outdoor and protected crops. Due to their short life cycle and abundant progeny, they can reproduce and dramatically increase in numbers when the conditions are favourable, causing severe plant damage (Helle and Sabelis 1985). Spider mites feed on parenchymal cells and avoid damaging the epidermis cells (Bensoussan et al. 2016). Plant feeding by spider mites can induce JA- and SA-related defence pathways (Kant et al. 2004), and their performance often decreases when JA-related defences are induced (Kant et al. 2008). Female spider mites produce silk webs that can protect them from predation by some predators (Helle and Sabelis 1985; Sabelis and Bakker 1992).

The green peach aphid, *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) (Figure 1.3), is the most common species of aphid and attacks various host plant species. Most of the year, females reproduce parthenogenetically, giving birth to nymphs without mating. When the plant quality or climate becomes unfavourable, they start
reproducing sexually (Blackman 1971, 1972). They can reproduce extremely fast, and can cause serious plant damage. They feed from phloem without damaging mesophyll tissue using their long flexible stylets (Walling 2008; Schwarzkopf et al. 2013). Plant feeding by aphids induces SA-related defence pathways, and suppresses JA pathways, to which they are sensitive (Omer et al. 2001; Walling 2008).

The western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (Figure 1.4), native from North America, is an economically important pest in many crops. Thrips are also cell-content feeders like spider mites. Using their mouthparts, they punch holes in both the epidermal cells and mesophyll cells and subsequently, empty the punctured cells with their stylets, resulting in strong plasmolysis and collapse of cells (Hunter and Ullman 1992; van de Wetering et al. 1998). This damage results in silvery discoloration and holes in the plants. Plant feeding by thrips mainly induces JA-related pathways, and thrips are sensitive to JA-pathways.
Female thrips lay their eggs inside plant tissues, which is another source of damage. In addition, thrips are omnivores that can feed not only on plant, but also on vulnerable stages of other herbivores and predators, such as eggs of spider mites and predatory mites (Janssen and Sabelis 1992; Pallini et al. 1998; Faraji et al. 2002).

*Phytoseiulus persimilis* (Figure 1.5) is a predator of spider mites. They can feed on all stages of spider mites, and are not hindered by the webs produced by their prey, making them successful biological control agents of this pest (Helle and Sabelis 1985). These predatory mites can locate their prey from a distance using volatiles emitted by plants infested with spider mites (Sabelis and van de Baan 1983).

**Outline of the thesis**

In Chapter 2, I investigated the effects of phytophagy by *Macrolophus pygmaeus* on the performance of three species of herbivorous prey, the two-spotted spider mite *Tetranychus urticae*, the green peach aphid *Myzus persicae* and the western flower thrips *Frankliniella occidentalis* on sweet pepper plants. It is known that defences induced by herbivores can be local, i.e., they are expressed at the damaged site, and systemic, i.e., expressed in plant parts that were not damaged by the herbivores (Karban and Baldwin 1997). Here, I specifically tested whether induction of defences by the omnivore was local or systemic. To further confirm whether these effects were caused by induced plant defences by the omnivore, I quantified the levels of defence-related plant hormones in leaves from plants exposed to the omnivore and from clean plants.

When herbivores search for host plants, they may encounter plants with or without omnivores, and their performance on plants with omnivores may differ from that on clean plants. Moreover, they may be attacked by the omnivores. Therefore, I investigated the effects of previous exposure of plants to the omnivorous predator *M. pygmaeus* on the host plant choice of the three herbivore species in Chapter 3. This host plant choice can be affected by cues from the omnivorous predators themselves and by the plant defences induced by phytophagy by the omnivore.

The results of Chapter 3 suggest that volatiles were produced by plants exposed to the omnivore. This was further investigated in Chapter 4, where I checked whether plant feeding by *M. pygmaeus* induced the production of plant volatiles and how this affected the performance of *P. persimilis*, a predatory mite of spider mites, one of the herbivores studied here. To confirm that plant volatiles were produced, I also analysed the volatiles from plants exposed to the omnivore and clean plants with gas chromatography-mass spectrometry.

Exposure of plants to the omnivorous predator *M. pygmaeus* can induce plant defences that decrease the performance of herbivores and influence the host plant.
choice of herbivores and behaviour of other predators. Such induction of plant defences by omnivores is intriguing because many omnivores do not cause significant damage to plants, and can effectively protect plants against herbivores, so the induction of plant defences by omnivores is largely redundant. Possibly, this induction of plant defences somehow benefits the omnivores, the plants, or both. Therefore, I investigated the effects of the omnivorous predator *M. pygmaeus* on the plant performance by evaluating plant development and reproduction in Chapter 5. I also investigated the effects of the changes in plant performance on the survival and reproduction of the omnivore.

References
GENERAL INTRODUCTION | CHAPTER 1

Faraji F, Janssen A, Sabelis MW (2002) Oviposition patterns in a predatory mite reduce the risk of egg pre-
Hansen DL, Brodsgaard HF, Enkegaard A (1999) Life table characteristics of Macrolophus caliginosus prey-
ing upon Tetranychus urticae. Entomol Exp Appl 93:267–273
tanarius, is an induced, indirect, defensive response elicited by jasmonic acid. Proc Natl Acad Sci
98:1083–1088
1B. Elsevier, Amsterdam
Hunter WB, Ulman DE (1992) Anatomy and ultrastructure of the piercing-sucking mouthparts and paraglos-
21:17–35
Janssen A, Sabelis MW (1992) Phytoseiid life-histories, local predator-prey dynamics, and strategies for con-
trol of tetranychid mites. Exp Appl Acarol 14:233–250
induction and suppression in herbivore communities. Ann Bot 115:1015–1051
275:443–452
inducible genes in the tomato plant against herbivores with various feeding modes. Arthropod-Plant
Interact 6:221–230
Science 299:1388–1391
Lond B Biol Sci 264:1249–1254
Messelink GJ, Sabelis MW, Janssen A (2012) Generalist predators, food web complexities and biological pest
control in greenhouse crops. In: Integrated pest management and pest control – current and future tac-
tsics. InTech, pp 191–214
caliginosus exploit plant volatiles induced by conspecifics as a sexual synomone. Entomol Exp Appl
123:49–55
greenhouse whitefly (Homoptera: Aleyrodidae) and western flower thrips (Thysanoptera : Thripidae).
Environ Entomol 29:1075–1082
Nesidiocoris tenuis. Int J Mol Sci 17:1210
Omer AD, Granett J, Karban R, Villa EM (2001) Chemically-induced resistance against multiple pests in cot-
ton. Int J Pest Manag 47:49–54
Pallini A, Janssen A, Sabelis MW (1998) Predators induce interspecific herbivore competition for food and
refuge space. Ecol Lett 1:171–176
CHAPTER 1 | GENERAL INTRODUCTION


Schwarzkopf A, Rosenberger D, Niebergall M, et al (2013) To feed or not to feed: plant factors located in the epidermis, mesophyll, and sieve elements influence pea aphid's ability to feed on legume species. PLOS ONE 8:e75298


