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The role of phytophagy by predators in shaping plant interactions with their pests

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ABSTRACT

Zoophytophagy is common among predacious arthropods, but research on their role in plant-herbivore interactions is generally focused on predation effects whereas their phytophagy is largely neglected. Our recent study revealed the ability of zoophytophagous predators to induce defense related traits and to affect herbivore performance apart from predation through the plant. Additionally, we show here that predator-exposed plants suffer less damage compared to unexposed plants. Thus, zoophytophagous organisms likely shape community structure by both their predation on herbivores and their phytophagy. Here, we consider zoophytophagous predators as plant vaccination factors and outline how their dual role in affecting herbivores may impact their use in biological pest control. Because plant responses to phytophagy and phytopathogens are known to interact, zoophytophagous predators may also affect plant-pathogen interactions. When we consider these indirect interactions with different plant pest organisms, we will likely better understand the ecology of the complex relationships among plants, herbivores and predators. Moreover, a comprehensive knowledge on the effects of the phytophagy of predators in these ecological interactions will potentially allow us to enhance sustainability in pest control.

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Natural enemies of herbivorous insects can interact with plants and herbivores at diverse levels. First, plant defense to herbivory involves several indirect defense traits such as volatile signals emitted by damaged plants that guide predators and parasitoids to their prey as well as refugia (e.g. domatia) and food rewards (e.g., extrafloral nectar) that retain them on plants.[1-2] Second, plants employ a series of direct defenses against herbivores[3-4] that can also impact the organisms that feed on the herbivores.[5-6] Natural enemies, on the other hand, suppress herbivore populations either directly through predation or affect herbivore performance indirectly e.g. due to an altered herbivore behavior in the presence of predators, which is referred to as non-consumptive effect.[7-8] Many natural enemies of herbivores are zoophytophagous and feed on both herbivores and plant tissues. Although effects of this phytophagy on plant defense and thereby on herbivores may play a significant role in plant-herbivore-predator interactions, these are barely investigated so far.

Zoophytophagous predators comprise a large group of natural enemies that have a high potential in controlling plant pests. In particular, the family Miridae includes predator species such as *Macrolophus pygmaeus* and *Nesidiocoris tenuis* which are routinely used in biological pest control[9] while many more species are under consideration for application in the field.[10-11] Nevertheless, a growing concern about the use of zoophytophagous predators in biological control is relevant to incidences of plant damage by certain species, especially *N. tenuis* which causes necrotic rings in vegetative and reproductive parts.[9-12] This damage may even result in yield reduction and, therefore, require control measures against the predators.[13-14] However, even predators that do not severely damage the plant may affect herbivore performance through plant responses they induce with their phytophagy.

Our recent study demonstrated for the first time that phytophagy by predators can elicit plant defense responses.[15] Similar to pure herbivores, the

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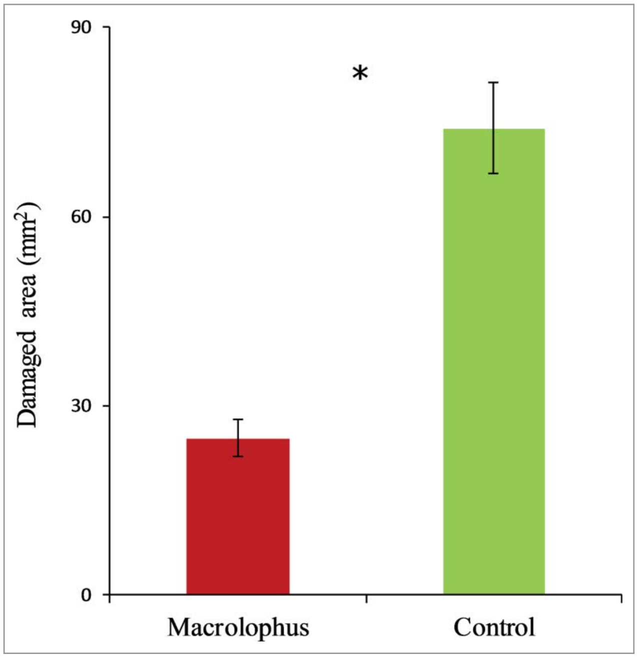

Figure 1. Spider mite damage on predator exposed tomato plants is significantly reduced relative to control (unexposed) plants. Tomato plants were exposed to two *M. pygmaeus* females for a period of 4 d (see ref. 15 for detailed description of methods regarding systemic effects of plant exposure to the predator). Subsequently, plants were infested with 10 spider mite females per leaflet for 7 d (3 terminal leaflets per plant, N = 4 plants per treatment). Leaf area damage was assessed as described in Cazaux et al.[23] Bars represent the means (± SE) for predator exposed (Macrolophus) and unexposed (Control) plants. Statistical significance was determined by Student's *t*-test ($^{*}P < 0.05$).

zoophytophagous *M. pygmaeus* induces proteinase inhibitor (PI) activity and transcript accumulation of the *PI-II* gene in the local and in distally younger tomato leaves. Plant PIs are well-established anti-herbivore defense traits that are mediated by the jasmonic acid (JA) signaling pathway.[16] In line with that, spider mites (*Tetranychus urticae*) performed worse on tomato plants previously exposed to phytophagy by this predator. Here, we provide additional data from these experiments which show that the reduced *T. urticae* performance on predator exposed plants is accompanied by a reduced leaf area damage on these plants (Fig. 1). The feeding damage by spider mites on control plants corresponded to 6.3 % of the total leaflet area (74.1 mm^2) but only 2.8 % of the total leaflet area (24.9 mm^2) when plants were previously exposed to *M. pygmaeus* (Student's *t*-test; $t = -6.296$; $df = 6$; $P < 0.05$). Though it is known that omnivorous herbivores, such as thrips can induce JA-mediated plant defenses,[17] effects of plant defenses induced by omnivorous predators on plant pest insects were only barely addressed. However, de Puysseleyr et al.[18] showed that oviposition by *Orius laevigatus* predators on tomato plants resulted in a decreased thrips infestation level and recently Pérez-Hedo et al.[19] revealed that tomato plants exposed to *N. tenuis* are induced in the wound-responsive phytohormones JA and absicic acid and are altered in their volatile emissions so that the plants are less attractive for whiteflies and more attractive for whitefly parasitoids. Together with our study revealing the elicitation of direct plant defense traits that negatively impact spider mites by the phytophagy of *M. pygmaeus*,[15] these studies show that zoophytophagous predators can increase plant resistance beyond predation. Thus, all three trophic levels can be affected by the plant responses to the phytophagy of many predators, which may therefore be a hidden factor shaping ecological community structures. Moreover, this additional layer of interactions suggests implications for the use of zoophytophagous predators for pest control that require further investigation to potentially enhance their efficiency in biological control by integrating this neglected factor of phytophagy.

In this context, we propose a concept of vaccinating plants with predators (Fig. 2) with the aim to prepare plants for subsequent herbivore attack. This concept is based on our finding that exposing young (2-week old) tomato plants to a low number of predators for a period of only four days is enough to negatively impact *T. urticae* performance even when the plants get older (4-week old plants).[15] The practice of infesting young tomato plants with zoophytophagous predators before transplanting them in the field is not new; this method is suggested as a 'pre-release strategy' for *N. tenuis* on tomato plants aiming an early establishment of this predator.[20] Taking into account that *M. pygmaeus* is not considered as harmful for tomato plants as *N. tenuis*,[9] we add on the pre-release strategy and propose the vaccination of young plants with this predator to obtain 'ready-to-defend' plants against herbivory (Fig. 2). This concept should be further tested under field conditions including also other herbivores than spider mites as for instance, plant exposure to predators did not affect whitefly performance.[15] Moreover, it needs to be verified that the activation of plant defense by predators on young plants does not lead to costs in terms of plant yield.

Considering the interactions between different plant signaling pathways that mediate plant responses to different stresses, the notion that zoophytophagous predators elicit anti-herbivore plant defenses suggests further implications for other interactions between plants and their environment. For example, the antagonistic interaction between salicylic acid (SA)-mediated plant defense responses against pathogens and the JA-mediated anti-herbivore defense is well-established. As a consequence, 'predator-vaccinated plants' could be less resistant against phytopathogens or pathogen-infected plants may be more strongly affected by

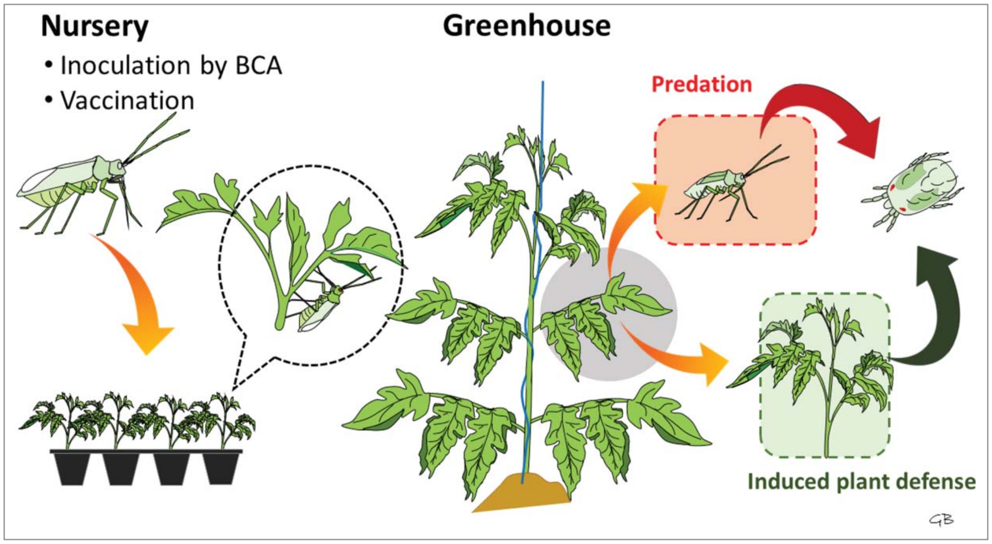

Figure 2. The 'plant vaccination' concept. Tomato plants are exposed to the predator (biological control agent, BCA) ovipositing adults in the nursery. 'Vaccinated' plants are afterwards transplanted in the greenhouse. Besides bearing predator nymphs (direct predator effect -Predation), transplants are indirectly protected against spider mite attack for at least two more weeks through plant defenses elicited by the predators as shown by Pappas et al.[15]

a predator's phytophagy. Indeed, a recent study showed that *M. pygmaeus* can cause more severe damage symptoms on tomato plants infected with Pepino mosaic virus (PepMV) than on non-infected plants.[21] Therefore, we suggest that the effect of zoophytophagous predators in biological control should be investigated in the context of threatening herbivores but also phytopathogens as the plant responses they elicit may affect the plant resistance to both differently.

We conclude that ecological studies on plant-predator interactions require more focus on the role of phytophagy by predators in shaping ecological communities. Considering also that many of these predators are important biological control agents it can be anticipated that pest management methods may be improved via studying zoophytophagy in relation to plant resistance. For example, zoophytophagous predators may be adversely affected by plant defenses as was shown for *Orius insidiosus* on tomato plants bearing anti-herbivore resistance genes[22] and therefore plant defenses may either diminish predator efficiency or shift their feeding behavior to become more zoo- than phytophagous. Such effects should be taken into consideration in the process of developing plant cultivars with resistance against herbivores and/or combining these cultivars with natural enemies in the context of integrated pest management.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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