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Plant defence: Feeding your bodyguards can be counter-productive

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Abstract

Insect predators often utilize plant cues to locate herbivores and plant food for sustenance when prey is scarce. The capacity of many plants to attract and support predators has sometimes been interpreted as an indirect plant defence system, which has evolved because it reduces the plants' exposure to detrimental herbivores. In accordance with this hypothesis, plant breeders have begun to select for crop varieties that attract and support biocontrol agents. We have tested whether predator proneness to consume herbivores is affected by variation in the plant food quality provided by different *Salix* (willow) varieties. Plant suitability as food for the important biocontrol agent *Anthocoris nemorum* (Common Flower Bug) varied widely between the tested *Salix* varieties. The proneness of *Anthocoris* to consume eggs of the detrimental herbivore *Phratora vulgatissima* also varied between the varieties, consuming eggs at much lower rates on those that provided high quality plant food. The results suggest that plants that provide too good plant food may satiate their "bodyguards", thereby reducing their motivation to hunt for herbivorous prey. Thus, the capacity of plants to support predators may sometimes result in a partially enemy-free space for herbivores – an outcome conflicting with the notion of "indirect defence".

Zusammenfassung

Räuberische Insekten nutzen häufig pflanzliche Signale, um Herbivoren zu lokalisieren sowie pflanzliche Nahrung, wenn die Beute selten ist. Die Fähigkeit vieler Pflanzen, Prädatoren anzulocken und zu unterstützen wurde manches Mal als ein indirektes Verteidigungssystem interpretiert, das sich evolutiv entwickelt hat, weil die Pflanzen dann den schädigenden Herbivoren weniger ausgesetzt sind. In Übereinstimmung mit dieser Hypothese haben Pflanzenzüchter begonnen, Nutzpflanzenvarietäten danach auszuwählen, ob sie Organismen anlocken und unterstützen, die eine Biokontrolle ausüben. Wir haben bei verschiedenen Sorten von Weide (*Salix*) untersucht, ob die Neigung von Prädatoren, Herbivore zu konsumieren, von Änderungen in der Qualität der zur Verfügung gestellten pflanzlichen Nahrung beeinflusst wird. Die Eignung der Pflanzen als Nahrung für die für die biologische Kontrolle wichtigen Blumenwanze *Anthocoris nemorum* variierte stark zwischen den untersuchten *Salix*-Sorten. Die Neigung von *Anthocoris*, die Eier des schädlichen Blattkäfers *Phratora vulgatissima* zu konsumieren, variierte ebenso zwischen den Sorten, wobei auf den Sorten, die eine hohe Qualität der pflanzlichen Nahrung boten, die Eier mit viel geringeren Raten konsumiert wurden. Die Ergebnisse zeigen, dass die Pflanzen, die eine zu hohe Qualität der pflanzlichen Nahrung bieten, ihre "Bodyguards" sättigen und so deren Motivation für die Jagd nach herbivorer Beute vermindern. So kann die Fähigkeit von Pflanzen, Prädatoren zu unterstützen, in manchen Fällen zu einem teilweise feindfreien Raum für Herbivore führen. Dies ist ein Ergebnis, das mit dem Begriff "indirekte Verteidigung" im Konflikt steht.

Keywords: Biocontrol; Trophic cascade; Plant defence; Indirect defence; Omnivory; Top-down control; Predator switching

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Introduction

Predaceous insects may effectively reduce herbivore damage on host plants by consuming herbivores (Schmitz 2008). This realization has spurred a flurry of studies investigating whether plants may actively recruit predators to escape herbivory, and if traits involved in intrinsic "bodyguard" recruitment may be utilized in breeding programs to improve crops (Kessler & Baldwin 2001; Rasmann et al. 2005). As many predators are omnivorous (thus also utilizing plant food, at least during some life stage), it has been suggested that plants may expose nutritious baits (e.g. extra-floral nectaries) to predators, as part of a strategy that makes them attractive as "bodyguard" employers. In this manner, host plants may make it more profitable for omnivorous predators to remain on them for longer times, and in return receive bodyguard services. This hypothesis has received much interest, especially with regard to ant-plant systems where the interactions between these two players are often described in terms of mutualism (Rehr, Feeny, & Janzen 1973; Palmer et al. 2008). In a classic paper, Rehr et al. (1973) showed that ant-acacias could lower their investment in direct defences in parallel with introducing giveaways of extrafloral nectar to herbivore-combating ants. A more recent study even suggested that plants could manipulate the prey preferences of ants by altering the chemical composition of their extrafloral nectar (Wilder & Eubanks 2010).

Most omnivorous predators, however, have not evolved such intimate relationships with individual plant genera. Whether non-specialist predators with a broader diet become more efficient hunters by consuming available plant food is less clear. The crucial issue here is how the availability of non-specific plant-derived food, such as leaves, will affect the predators' features as plant "bodyguards". Though the availability of suitable plant food may encourage omnivorous predators to remain on a certain plant, its effect on the propensity of those predators to hunt for herbivorous prey has been little studied. Most relevant published work has dealt with pollen-feeding predators. In two classic studies, McMurtry and Scriven (1966a, 1966b) found that predators became less prone to hunt for prey as provision of pollen increased – a finding that was subsequently confirmed by Wei and Walde (1997), and Cottrell and Yeargan (1998). However, in another study dealing with the importance of plant reproductive structures Eubanks and Denno (1999, 2000), found that the presence of lima bean pods favoured the development and population growth of predatory bugs, ultimately strengthening top-down regulation of herbivorous aphids.

Fewer studies have investigated the effects of variations in abundance and (especially) quality of plant food on omnivorous predators that utilize non-reproductive plant tissue. An important difference between predators feeding on nectar/pollen and those feeding on plant tissue is that the latter may impose other types of costs on the plant, such as oxidative stress, loss of photosynthetic tissue, and transmission of pathogens. Nevertheless, predators feeding on plant tissue are often considered important biocontrol agents in both agroecosystems (Sigsgaard, Esbjerg, & Philipsen 2006) and natural systems (Kessler & Baldwin 2001).

Agrawal, Kobayashi, and Thaler (1999) showed that plant foliage containing herbivore-induced defence chemicals was unsuitable as food for omnivorous thrips, which switched to feeding on herbivores when they co-occurred and induced the plant's defences. However, interactions between predators that consume non-reproductive plant food, their prey species and host plants warrant further attention due to the current paucity of published information. Unlike previous studies, such as Agrawal et al. (1999), this study focuses on how constitutive (rather than induced) variation in non-reproduction plant tissue mediates the feeding behaviour of omnivorous predators. We use *Salix* clones that differ in leaf chemistry, and hence differs in suitability as food for many herbivores and plant-feeding predators (Stenberg, Lehrman, & Björkman 2010; Stenberg, Lehrman, & Björkman 2011), and hypothesize that predators should consume less animal food (herbivores) on plants with high-quality plant tissue.

Materials and methods

The system

The most important herbivore in coppicing willow (*Salix*) energy forests in Scandinavia is the Blue Willow Beetle (*Phratora vulgatissima*) (Björkman, Dalin, & Eklund 2003; Björkman, Bommarco, Eklund, & Höglund 2004), which may reduce biomass yields by up to 40% (Björkman, Höglund, Eklund, & Larsson 2000). The Common Flower Bug (*Anthocoris nemorum*) is considered an important bodyguard against the Blue Willow Beetle, often consuming a substantial proportion of beetle eggs on host plants (Björkman et al. 2003). However, like most other predatory heteropteran bugs the Common Flower Bug also suck shallowly located fluids from the green parts of the host plant (Lauenstein 1979).

Plant and insect material

Plants: Winter cuttings of four *Salix* clones (Gudrun, Loden, 78021, and 78183) were used. All four clones are commercial varieties used in short rotation energy forestry in Europe, and they differ with respect to leaf chemistry and volatile profiles. For both experiments reported here we used 20 cm cuttings, which were stored in a walk-in freezer (−5 °C) until planting.

The herbivore: P. vulgatissima L. (Coleoptera: Chrysomelidae; Blue Willow Beetle, hereafter BWB) is the most important defoliator of *Salix* in Scandinavia. It is restricted to *Salix* and both adults and larvae skeletonize the leaves. For