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Review

Induced plant resistance and its influence on natural enemy use of plant-derived foods

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In response to herbivory, plants employ several inducible defenses to mitigate herbivore damage. These plant-induced responses can trigger subtle changes in plant metabolite composition, altering the profiles of plant-produced exudates such as (extra-) floral nectar and plant guttation. Natural enemies consume these plant-produced exudates, which serve as consistent and nutrient-dense food sources. There is mounting evidence that natural enemies' access to plant-produced exudates impacts their fitness, performance, and life history traits. Nonetheless, the role of induced plant defense on plant-produced exudates and the subsequent effect on natural enemies remains under-researched. This review, thus, highlights the potential role of induced plant defense on the profiles of plant-produced exudates, with a particular emphasis on altered metabolic changes affecting resource nutritional value and consequently the fitness and performance of natural enemies. Future directions and potential implications in biological control practices are also highlighted.

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Introduction

During their coevolution, plants have evolved a complex arsenal of defense mechanisms against insect herbivores [1]. Apart from constitutive defenses, inducible defenses, activated only when herbivore attack occurs, represent a dynamic and adaptive response strategy for plant persistence and survival, frequently against the most potentially harmful intruders [1]. These inducible defenses involve a sophisticated array of traits, including the production of secondary metabolites and the release of volatile organic compounds (VOCs) [1]. The specificity and magnitude of these responses can vary both inter- and intra-specifically dependent on the herbivore species and/or their guilds; in turn, plants can adapt and shape their plasticity in defense to a diverse community of insect herbivores [2]. These inducible changes in plants not only impact insect herbivores but also, at least in terrestrial ecosystems [3], transcend higher trophic levels, potentially impacting the behavior and performance of natural enemies.

The focus of this review is to consider evidence for plant defenses influencing plant-derived foods, such as nectars and pollen, that are all known to be valuable to natural enemies. To sustain their populations and optimize their pest management effectiveness, many natural enemies require supplementary nutrition beyond what is obtained from preying on insect pests [4]. Exudates and other plant-derived materials, such as nectar, extrafloral nectar (EFN), and honeydew, serve as crucial sources of carbohydrates and amino acids for these beneficial organisms, enhancing their fitness, longevity, and reproductive capabilities [5,6]. Understanding and managing the availability and quality of these plant exudates and other plant-derived materials are essential aspects of promoting the efficacy of natural enemies in sustainable pest control practices [4]. Despite significant efforts having been made in recent years studying the effects of plant-derived food sources on the fitness of natural enemies and thereby the overall effectiveness of biological control, the role of induced plant defense on the quality and the nutritional value of these plant-produced exudates and the subsequent effects on natural enemies remains largely under-researched [7].

This article highlights the role of induced plant defense in determining the nutritional value of plant-derived substances as an important fitness and performance-determining food source for natural enemies. In providing an overview of our current understanding, knowledge gaps requiring further exploration are identified, and potential implications for conservation biological control programs are determined and assessed.

Impact of plant-derived foods on natural enemies' traits

Plant-derived foods play a significant role in enhancing biological control by creating an environment that supports and sustains populations of pest-regulating natural enemies [4]. Specifically, these foods provide essential resources that improve the survival, reproduction, and effectiveness of natural enemies, leading to enhanced pest management effectiveness [6,8]. Plant-derived foods can enhance biological control via a range of effects.

Increased lifespan and survival

Accumulating evidence substantiates the positive correlation between the availability of plant-derived nutritional resources and the extended lifespan, as well as increased likelihood of maturation to adulthood, of natural enemies [6,9]. Notably, the ingestion of carbohydrate-rich floral nectar has been associated with increased longevity and heightened survival rates across diverse parasitoid [10–14] and predatory [6,15,16] species. Furthermore, the provision of EFN has demonstrated a profound influence on the biological attributes of natural enemies, significantly supporting adult survival rates and prolonging longevity under both laboratory and field conditions [17–20]. Pollen, likewise, has been identified as a key contributor to the increased survival and longevity of both predatory [6,21] and parasitoid species [22–24]. Honeydew, contingent upon its composition, exerts a substantial impact on parasitoid longevity and survival, with parasitoid individuals exhibiting significantly prolonged lifespans when nourished on the honeydew of their hosts [8,25–27]. Recent investigations by Urbaneja-Bernat et al. [28] have revealed a notable increase in adult longevity among aphid natural enemies (i.e. *Aphidius ervi* and *Chrysoperla rufilabris*) when utilizing plant guttation as a nutritional source that contains several organic compounds (e.g. carbohydrates, proteins, enzymes, and amino acids) and inorganic solutes (e.g. salts, ions), surpassing the effects observed with conventional sugar and protein solutions.

Enhanced growth and reproductive biology

Although reproduction requires food sources that are high in protein, mixtures of prey and non-prey foods usually support greater reproduction of natural enemies rather than each component alone [16], the natural enemies' access to plant-derived foods enhance their growth rate and reproductive traits, resulting in abundant populations [6,8,9,29].

An essential element of parasitoid foraging behavior involves the capability to detect and respond to floral signals that signify the availability of nectaries [9]. In a recent meta-analysis, He et al. [6] found that 45 out of 48 predator species could lay eggs on a diet consisting solely of floral resources. For instance, the adult stages of hoverflies and lacewings rely on nectar and pollen to sustain themselves and to reproduce [6]. In addition, floral nectar is reported to increase egg load, fecundity, egg maturation rate, host searching time, and fitness of parasitoid [10–12,30] and predator [6,16] species. Moreover, the parasitoid access to EFN enhances its foraging and promotes adult populations [17,18]. Nevertheless, little is known on the effect of EFN on the reproductive biology of natural enemies [19]. Many natural enemies are obligatory consumers of pollen during their adult stage [31]. For example, pollen alone significantly shortens the developmental time of the phytoseiid predator *Amblydromalus limonicus* [21] and has been deemed to be the most suitable food for the tachinid parasitoid *Exorista larvarum* [22]. Combined with honey, pollen significantly enhances the fecundity of many natural enemies compared to pollen alone [23,24]. Honeydew, which is a byproduct excreted by many plant-feeding hemipterans, such as aphids, proved to be a good nutrition source, enhancing parasitoid fecundity, increasing their egg loads, and affecting the proportion of male progeny [8,14]. Higher fecundity rate was observed when generalist natural enemies such as *C. rufilabris* fed on plant guttation droplets [28].

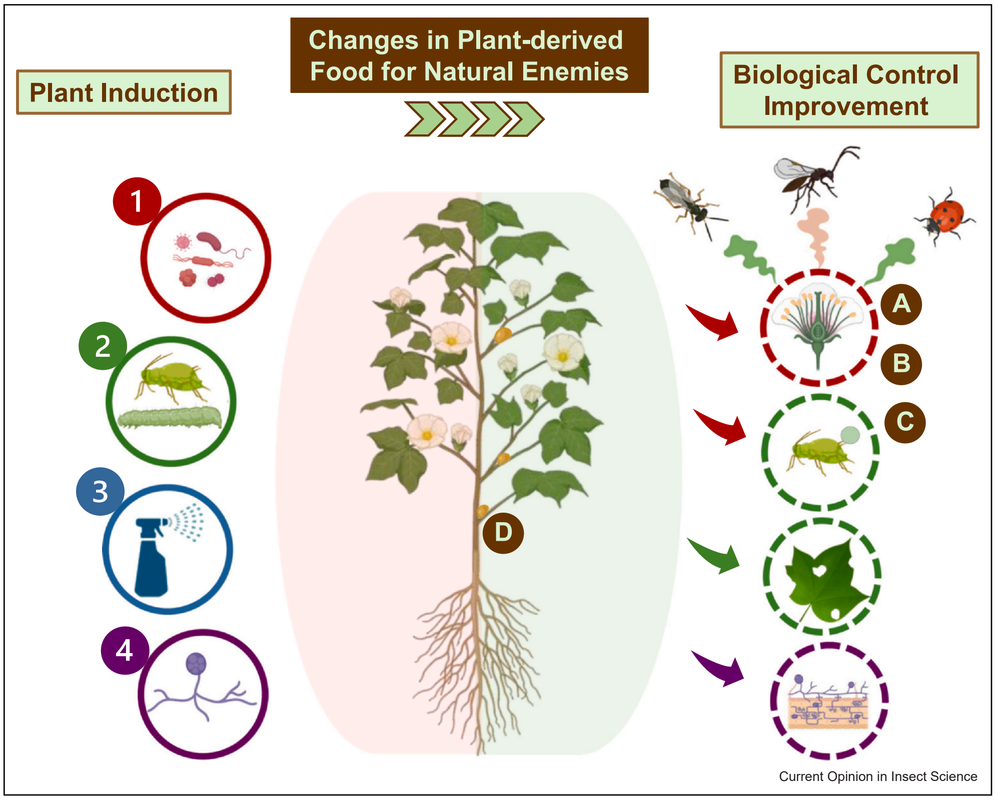
Increased host/prey seeking activity

Well-nourished natural enemies, resourced with floral and plant-driven resources, are more active and effective predators and parasitoids [6,9]. The increased energy gained from nectar consumption and pollen feeding enables predators and parasitoids to search for and consume pest insects more actively, as well as covering larger areas in prey/host seeking, leading to more effective herbivore control and subsequently reducing crop damage [4,6]. As an example, the ingestion of buckwheat nectar substantially prolonged (40-fold) the search duration of the aphid parasitoid *Diaeretiella rapae* compared with individuals provided with water only [30]. In contrast, the host searching time was decreased when parasitoids experienced a lack of energy resources, as starved parasitoids exhibit a broad decline in their foraging endeavors [9]. Honeydew enhanced the host searching behavior of the parasitoid *Aphelinus mali* and also stimulated higher oviposition rates [26].

Induced defense and the natural enemies' plant-derived foods

Induced plant resistance can have both direct and indirect influences on the availability and quality of plant-derived foods as a result of substantial changes in plant physiology, growth patterns, and resource allocation [7]. Among the plant-derived resources for natural enemies discussed in the preceding sections, certain resources (e.g. EFN, floral nectar, and honeydew) have garnered

Figure 1



Schematic representation illustrates how induced plant defense affects the utilization of plant-derived foods by natural enemies. The induction of plant defenses can occur through various mechanisms, including (1) flower association with nectar microbes; (2) real herbivory caused by chewing and sucking insects; (3) simulated herbivory induced by elicitor application; and (4) root interaction with soil microbes. These processes have the potential to influence the nutritional content and palatability of plant-derived foods such as (A) floral nectar; (B) pollen; and (C) honeydew; and (D) EFN for natural enemies' use, which consequently enhance their fitness, performance, and life history traits, ultimately enhancing biological control.

considerable attention in contrast to others. In this section, we will spotlight recently published work exploring the potential impact of induced plant defenses on the nutrient composition of plant-derived foods, consequently influencing the nutritional value and palatability of these foods to natural enemies (Figure 1).

Herbivory

Overall, herbivore attack can elicit both broad-spectrum and targeted responses in plants, reallocating some primary metabolites (e.g. sugars, amino acids, lipids, and steroids) to synthesize defense-related metabolites that protect against herbivory [1]. This, in turn, can qualitatively and quantitatively alter the content of plant-derived foods provided for natural enemies.

Although plants can constitutively produce EFN, several studies have shown that its production can also be induced and increased after above- and/or below-ground herbivore damage [5,19,32,33]; this can also vary between specialist and generalist herbivores [34] and even plant ontogeny (i.e. older vs younger plants) [35]. In addition, foliar herbivory not only induces the production of EFN but also alters its composition modifying the sugar content in nectar [36,37], influencing the foraging behavior of plant-visiting insects. Similarly, herbivory by the specialist *Manduca sexta* induces higher concentration of alkaloids (e.g. anabasine) in tobacco pollen [38]. Cotton exposure to herbivore-induced plant volatiles, mainly sesquiterpene and aromatic VOCs, increased the production of EFN from healthy plants [39]. This induction results in an increase in the sucrose content of EFN, while glucose and fructose are reported to remain unchanged [36]. Nevertheless, other studies have shown that herbivory by the pea aphid, *Acyrthosiphon pisum*, may not induce EFN secretions and even reduces its production [40]. In addition, the production of other traits, such as floral nectar and pollen, was strongly induced in response to herbivory [41].

Microbes association

As sugar-rich resources, plant-derived foods such as floral nectar and honeydew have the capacity to host a diverse array of specialized micro-organisms [42]. These micro-organisms, which are symbiotic (nonpathogenic), play a significant role in altering various traits, including changes in nectary volumes, sugar concentration and types, increased amino acid content, and the synthesis of secondary metabolites [43]. The presence of these beneficial microbes can consequently enhance nutrient availability, thereby impacting both the quantity and quality of plant-derived foods [42]. Mounting evidence suggests that the fermentation process carried out by both yeasts and bacteria can influence the odors of floral nectar [44–46]. Nectar-inhabiting microbes have the capacity to produce *de novo* distinct blends of microbial organic volatile compounds (mVOCs) due to microbial metabolic activities, contributing to flower–insect association [47].

Emerging evidence suggests that the metabolic activity of micro-organisms inhabiting nectars and honeydew plays a pivotal role in modulating nutrient profiles, notably by transforming sugar profiles from disaccharides such as sucrose to monosaccharides such as fructose [43,48]. It is noteworthy that bacteria and yeasts can exert contrasting effects on the characteristics of plant-derived foods. For example, while nectar fermentation by the yeast *Metschnikowia reukaufii* resulted in reduced levels of amino acids without impacting sugar composition, the presence of the bacterium *Gluconobacter* sp. led to elevated concentrations of amino acids and a higher proportion of monosaccharides in the nectar of lopseed plants [49], which may, in turn, impact the performance of nectar consumers such as natural enemies.

Another significant consequence of microbial activity is the modification of nectar [44–46,50,51] and honeydew [52,53] odors, thereby altering the scent profile of plant-derived foods. These mVOCs serve as honest signals of reward quality for insects, such as parasitoids and predators [42,54], at higher trophic levels. Chemical analysis of fermented nectars revealed qualitative and quantitative differences in mVOCs composition between different microbial strains, suggesting that these signals are species-specific and involve intricate sender–receiver dynamics, as odorants derived from fermented nectars may elicit diverse effects in different ecological contexts, including parasitoids [45,51] and bees [44].

Accumulating evidence underscores the significance of microbially produced cues emanating from plant-derived foods in shaping the behavior of natural enemies throughout their life cycles [9,42,54]. For instance, synthetic nectar fermented by *M. reukaufii* exhibited high attractiveness to the aphid parasitoid *A. ervi* [45,50], a trend similarly observed with other microbes, such as the yeast *Metschnikowia gruessii* and the bacterium *Staphylococcus epidermidis*, where their fermented nectars attracted various egg parasitoids of stink bugs [51,55]. The consumption of these microbe-fermented nectars by parasitoids did not, however, affect their survival or longevity [45,46,55]. Additionally, the scent profile of aphid honeydew colonized by bacterial strains has been found to be more attractive to primary aphid parasitoids and their hyperparasitoids [52,56].

In a recent meta-analysis, Hyjazie and Sargent [57] revealed that root association with soil microbes, particularly mycorrhizal fungi, has a positive effect on floral characteristics, including the size of the floral display. In addition, mycorrhizal fungi also promote pollen and nectar quality and quantity [58]. In contrast, nitrogen-fixing rhizobia reduces EFN production by lima beans, leading to fewer ants attracted to rhizobia-associated plants [59]. This suggests that belowground plant interactions mediated by soil microbes also play a crucial role in shaping floral traits and the availability of floral resources, ultimately influencing plant interactions and ecosystem dynamics. However, the impact of root–microbe associations on the plant-derived foods consumed by natural enemies remains largely unexplored.

Elicitor application

The application of elicitors, chemical substances that trigger plant direct and indirect defenses [60,61], could potentially impact the allocation of resources in plants. This may lead to changes in the production of plant-derived foods and the compounds that attract or deter natural enemies.

Under field conditions, lima bean plants under jasmonic acid (JA) exogenous application produced more nectar in both extrafloral nectaries and flowers, attracted more ants, and produced more flowers and seeds than non-induced plants [62]. Likewise, treating legume plants with JA increased the volume of EFN and the mass of sugar per nectary without affecting the sugar concentration [63]. In addition, cotton application with methyl jasmonate (MeJA) increased the production of EFN, without a corresponding increase in yield [64]. Supporting this, both herbivory, using chewing (caterpillar, weevil) and sucking (aphid) herbivores, and MeJA treatment increased EFN secretions of tallow tree, but SA decreased it [65].

A similar pattern of producing high amount of pericarpial and extrafloral nectaries was also observed when plants were subjected to simulated herbivory [66,67]. EFN secretions increased significantly when wild cotton plants were exposed to recurrent simulated herbivory (i.e. two episodes of damage) but not after a single herbivory interaction [68]. These EFN secretions were specifically observed within 24 hours post simulated herbivory, but EFN secretions dropped to initial levels after 7 days [69]. Such induction in EFN production increased the attraction of natural enemies and ants even in the absence or low prey/host density.

Conclusion and future perspectives

The availability and quality of plant-derived foods, including floral nectar, EFN, pollen, honeydew, and plant guttation, play a crucial role in supporting the survival, reproduction, and effectiveness of natural enemies in pest management systems. These plant exudates serve as consistent and nutrient-rich food sources for natural enemies, enhancing their fitness, longevity, and reproductive capabilities. This enables natural enemies to flourish while also further supporting their role in biological control ecoservices and boost integrated pest management strategies while promoting the health of ecosystems [4,70]. The influence of induced plant defense mechanisms on the profiles and nutritional value of these plant-derived foods does, however, remain relatively understudied. The modulation of plant metabolites and the subsequent alteration of plant-produced exudates by induced plant defense responses have significant implications for the ecology of natural enemies. Thus, understanding how induced plant defenses affect the availability, composition, and attractiveness of plant-derived foods is essential for optimizing the efficacy of natural enemies in sustainable pest control practices.

Future research should focus on elucidating the underpinning mechanisms by which induced plant defenses influence the nutritional quality and palatability of plant-derived foods for natural enemies. This includes investigating how induced changes in plant physiology, growth patterns, and resource allocation affect the production and composition of floral and EFN, pollen, honeydew, and plant guttation. Furthermore, studies exploring the interactive effects of induced plant defenses and microbial associations on the nutritional value and attractiveness of plant-derived foods are necessary. This is of necessity a multidisciplinary approach, requiring the integration of expertise from entomology, applied biology, biochemistry, and microbiology, to exploit effectively what has been overlooked. Although there has been increasing interest in using defense elicitors [7,60] and microbial bioactive compounds [42,54] as sustainable and ecologically sound methods for controlling insect pests in agriculture by enhancing the efficacy and fitness of natural enemies, their practical application in agriculture remains in its infancy. Studying these interactions poses significant challenges as controlled environments often fail to capture the complex dynamics of natural ecosystems, while field studies are hindered by high variability and the substantial resources and time required.

Understanding how induced plant defense and microbial activity in plant-derived foods affect the nutritional and odor profiles of these plant exudates, and consequently the foraging behavior of natural enemies, can provide valuable insights into the ecology of plant–microbe–insect interactions. Additionally, research efforts should focus on how changes in the availability and quality of plant-derived foods influence foraging behavior, reproductive biology, and population abundance of natural enemies in agricultural landscapes.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that the content of this manuscript was not affected by any financial, commercial, legal, or professional interest.

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Data access statement

No new data were generated for this review article.

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