


REVIEW

Open Access



Phenotypic plasticity plays an essential role in the confrontation between plants and herbivorous insects

Xianzhong Wang¹, Jieyu Kang¹, Huizhong Wang¹, Shigui Wang¹, Bin Tang^{1*} and Jiangjie Lu^{1*} 

Abstract

The interaction between insects and plants is a classic case of coevolution. During the arms race that has continued for 400 million years, the mutualistic (such as pollination and defense assistance) and antagonistic relationships gradually formed and complicated under the selection pressure from phytophagous insects. Thus, plants have developed diverse defense strategies, constantly balancing the relationship between defense and growth. At the same time, insects have evolved the ability to adapt to and resist plant defenses. Throughout this process, phenotypic plasticity has continuously helped both groups adapt to new environments and niches. Epigenetic changes play an important role in the formation of plastic phenotype. These changes allow parental defense traits to be passed on to the offspring, helping the offspring resist insect feeding. Epigenetic changes and genetic variation provide the basis for the formation of new phenotypes, and plants can form stable defense traits under long-term insect feeding pressure. In this review, we summarize the defense strategies of plants and the counter-defense strategies of insects, suggest that phenotypic plasticity plays an important role in this interaction, and discuss the role of epigenetics in the formation of plastic phenotypes.

Keywords Adaptation, Plant defense, Evolution, Insect, Phenotypic plasticity

Introduction

Plant defenses against insect ingestion are varied and highly species-specific (Bustos-Segura et al. 2022; Depalo et al. 2022). Plant defenses can be divided into two categories: static, known as “constitutive defense,” and dynamic, known as “inducible defense.” (Tortorici et al. 2022). These two methods work together to defend against herbivores, especially insects, and protect the normal growth, development, and reproduction

processes (Taggar and Singh 2016). Although the anti-insect compounds or proteins produced during defense formation may be the same, the levels and amounts differ, which is one of the important reasons why different species and even different populations of the same species can adapt to different environments (Mahmood et al. 2022; Jain et al. 2022).

Some studies have shown that insect feeding plays an important role in the formation of plant plasticity phenotypes; in this process, insects, as consumers, also adapt to plant defenses. Some scholars refer to this process of competitive adaptation between insects and plants as an “arms race” (Jones et al. 2022; Guo et al. 2023). Phenotypic plasticity, a widespread phenomenon in nature, refers to the ability of an organism to quickly change its phenotype in response to environmental stimuli or damage (Schneider 2022). Most organismal

*Correspondence:

Bin Tang
tbzm611@hotmail.com
Jiangjie Lu
lujj@hznu.edu.cn

¹ College of Life and Environmental Sciences, Zhejiang Provincial Key Laboratory for Genetic Improvement and Quality Control of Medicinal Plants, Hangzhou Normal University, Hangzhou 310018, China



© The Author(s) 2023. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

traits have some degree of plasticity, which is an indispensable means for organisms to adapt to environmental changes. In addition, phenotypic plasticity is considered a resource for biological evolution (Skinner and Nilsson 2021; Nilsson et al. 2020). Insect ingestion results in mechanical and chemical damage to plants, which induces plant defense responses and transmits signals from the wound site to the whole plant through Ca^{2+} , wound-activated surface potential changes (WASPs), plant hormones, and other pathways (Wu et al. 2022; Kumari et al. 2019). This response is generally short-lived, and importantly, it can lead to the production of a new phenotype without altering genetic information. Interestingly, it has been found that such a 'defensive state' can be passed on to offspring (Adachi-Fukunaga et al. 2022; Velasquez-Vasquez et al. 2022), but the mechanism for this transmission is not yet fully understood.

In this review, three questions about the interaction between plants and insects are addressed.

1. How do plants perceive and respond to insect ingestion?
2. How do insects adapt to plant defenses?
3. What are the reasons for the formation and inheritance of plasticity phenotypes in plant defense?

Plant response to stress is an ongoing focus of research, with a large number of studies focusing on the effects of abiotic stress (such as salt stress, drought stress, low-temperature stress, etc.) on plants. In recent years, there have been great developments in the understanding of plant responses to biological stress (Lin et al. 2023). At the core of this article lies the interaction between plant defense and herbivorous insect adaptation and the role of phenotypic plasticity and epigenetic inheritance in this process (Fig. 1).

Perception and response of plants to insect attack

Insects and land plants have been on Earth together for nearly 400 million years, and the interaction between insects and plants has evolved over this period (Moro et al. 2021; Khramov et al. 2022). A few mutually beneficial relationships exist, including pollination and defense assistance (Salerno et al. 2023). In addition, there are a few plants (such as the genera *Nepenthes*, *Drosera*, and *Dionaea*) that reverse the situation and eat insects as a means of survival. These are often called carnivorous plants (Freund et al. 2022). Plants have developed multiple defense mechanisms over the course of evolution to protect themselves from insects and other herbivores. These defense mechanisms are crucial for the plant's self-protection (Noman et al. 2020). The constitutive defenses and induced defenses

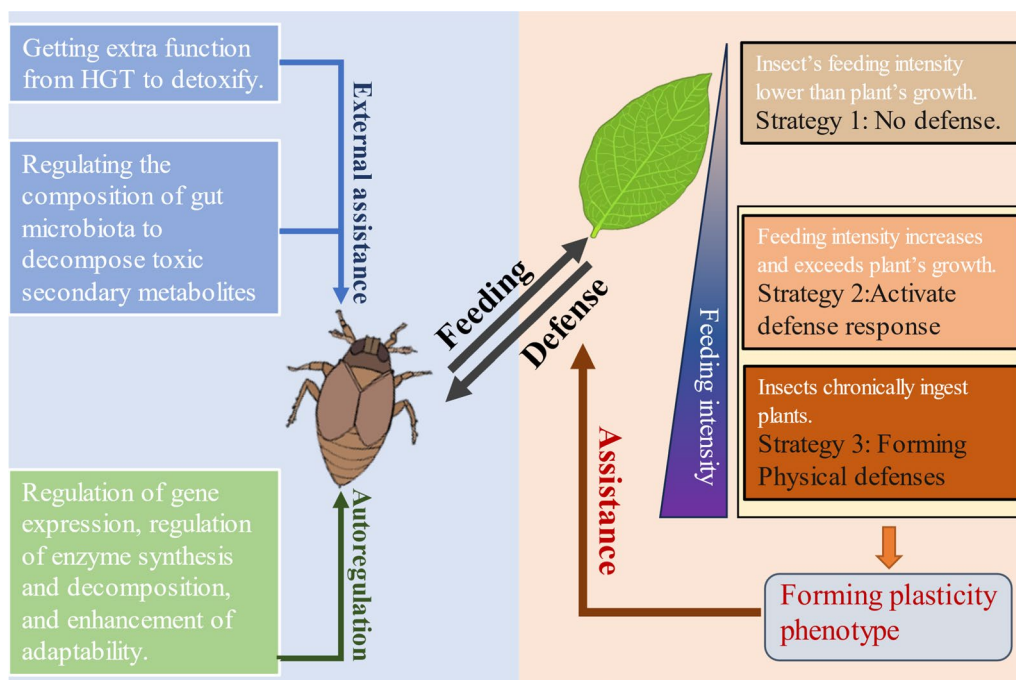


Fig. 1 Simple model of insect and plant interaction. Herbivorous insects use two adaptive strategies to assist them feed safely on plants, self-regulation (green box) and external assistance (blue box). Plants formed different strategies to cope with ingesting from insect depending on the intensity. Among them, strategies 2 and 3, phenotypic plasticity plays a role in defense

are two types of plant defenses that are widely recognized and important for plant survival and reproduction, despite predation (Kesel et al. 2021; Tanaka and Heil 2021). The multiple defense mechanisms of plants effectively reduce the invasive behavior of herbivores. Recognizing herbivore attack is a complex process for plants, as it can activate the plant defense system and prompt appropriate responses to ensure survival in a challenging ecological setting. Understanding the mechanisms underlying this response will aid researchers in enhancing crop resilience against biotic stress.

Over the course of their long-term coexistence, plant perceptual systems have developed to perceive damage, and plants have special receptors to recognize whether the damage was caused by a random factor or by insect feeding (Chavanke et al. 2022; Ge et al. 2022). When damage is determined to be mechanical damage from external factors in nature, the plant does not activate its specific defense system, thus saving energy for growth and reproduction. However, when damage is caused by insect feeding, specific metabolites, mainly fatty acid-amino acid conjugates (FACs) and other so-called herbivore-associated elicitors (HAEs), bind to specific receptors on the cell surface (Jones et al. 2022; Tumlinson 2023). These receptors, known as pattern recognition receptors (PRRs) (Song et al. 2021; Wang et al. 2019), initiate phosphorylation cascades and defense reactions. In recent years, increasing in-depth research on mechanical injury signal transduction has improved the understanding of this signaling system. Cell rupture or even cell wall damage or modification will trigger the defensive response, in which glutamate, peptides, ATP, oligogalacturonides (OGs), high mobility group (HMG) and so on can act as the first messengers to transmit injury information. These are called damage-associated molecular patterns (DAMPs) (Tanaka and Heil 2021; Grissett et al. 2020). Currently, research has identified and analyzed a minimum of 18 species of DAMPs (Hou et al. 2019). DAMPs interact with specific receptors, triggering signal transduction through downstream CaBP responses and phosphorylation cascades. This process regulates damage-related genes (Kanyuka and Rudd 2019). At the same time, these signals are further mediated by short-distance signals such as Ca^{2+} waves and activated wound-activated surface potential change (WASP) signals, or long-distance signals such as glutamate, ROS, and others that transmit damage signals to surrounding tissues, organs, and even the whole organism (Toyota et al. 2018). Some plants also transmit damage signals to other individuals in the population through volatile organic chemicals (VOCs). In this way, the defense response of the whole organism or even the whole population can be activated (Ling et al. 2022).

The initial signaling molecules are now widely believed to come from the damaged cells and damaged cell walls, as well as the attackers' biological components, such as glutamate, ATP, and HMG, which come from the cytoplasm of the damaged cells (Ramachandran et al. 2019), and the destruction of the cell wall under the action of polygalacturonases (PG) produces OGs, insect salivary proteins, etc. (Pontiggia et al. 2020). These signaling molecules bind to cell surface receptors and cause downstream effects in cells (Toyota et al. 2018; Kimura et al. 2020). For example, when glutamate serves as the first messenger, intracellular Ca^{2+} concentration increases and CaBP regulates the expression of damage-related genes. As the same time, the movement of ions in and out of the cell alters the cell's internal and external electrical potential, consequently transmitting the signal to the neighboring cells (Bricchi et al. 2013; Steinhorst and Kudla 2014). When cell wall damage decomposes under the action of PG to produce OGs, which act as the first messenger to transmit damage signals, MAPK is induced to regulate the expression of damage-related genes through receptors (Silva-Sanzana et al. 2022; Oelmüller et al. 2023). In addition, ATP, HMG, and other DAMPs can regulate gene expression in a similar way (Fig. 2). These genes regulate JA synthesis, callose formation, secondary metabolite synthesis, etc., and thus promote callus formation and enhance physical defense formation to repair wounds (Yang et al. 2018; Wang et al. 2021a; Mitra and Baldwin 2014; Fu et al. 2022; Fierke and Stephen 2008). It is worth emphasizing that the contents of damaged plant cells should be followed with interest as a novel kind of DAMPs. There are not many studies on the immune responses caused by small molecules in plants, while most research on DAMP has focused on the metabolites or fragments of fungi and insects. Utilizing small molecules of plants as triggers to enhance plant defense and insect and disease resistance presents a novel approach that can provide a new idea for crops to resist biotic stress.

Current studies have shown that plants can simultaneously defend against attacking insects, but plants cannot properly defend against excessive stress due to energy shortages (Bobadilla et al. 2022). Plants are believed to identify predators by distinguishing variations in insect HAEs, which encompass components like insect saliva, egg effusion, feces, and other substances. This ability allows plants to select the most suitable defense strategy (Zeng et al. 2023). By recognizing PRRs and HAEs on the cell surface, plants can distinguish physical damage from herbivore predation and identify the attacker, thus achieving optimal resource allocation (ul Malook S, Maqbool S, Hafeez M, Karunarathna SC, Suwannarach N 2022). However,

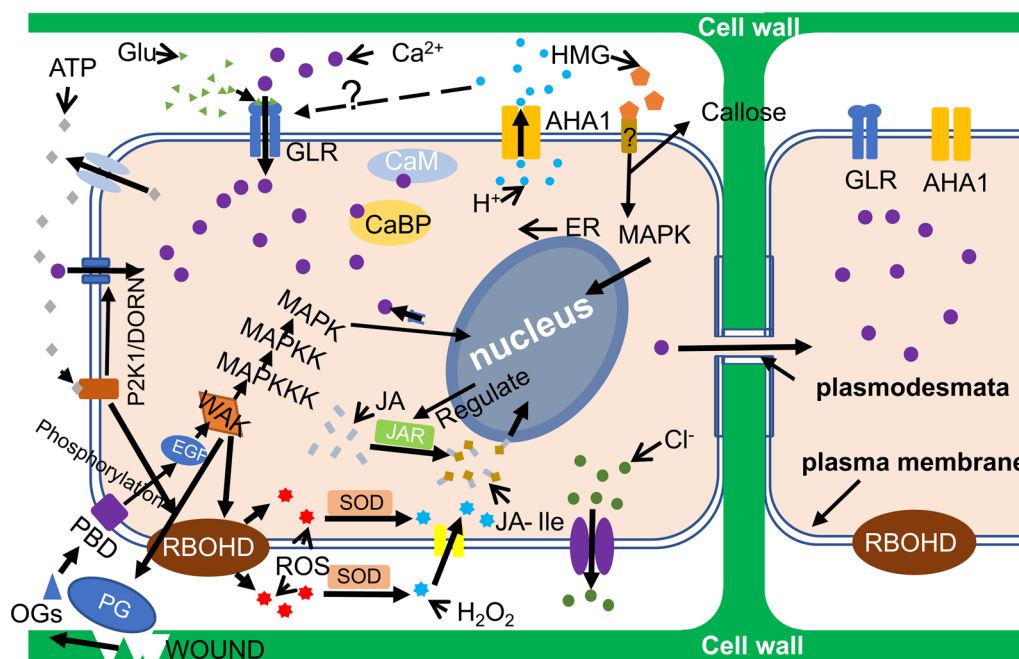


Fig. 2 Schematic diagram of partial DAMPs signal transduction. After cell damage, glutamate and ATP, which are cell contents, dissociate in the periplasmic space. They then bind to nearby cells membrane receptors, such as GLR and P2K1, resulting in the influx of Ca^{2+} and triggering the efflux of Cl^- to polarize cells and create a potential difference. Depolarization is achieved by draining H^+ through the AHA1 receptor channel. It has been proposed that H^+ can also promote depolarization by acting on GLR. Simultaneously, second messengers like Ca^{2+} are transmitted to peripheral cells through plasmodesmata, leading to the generation of similar responses in these peripheral cells. This results in the formation of wound-activated surface potential changes (WASPs). Additionally, Ca^{2+} regulates the expression of relevant genes through CaBP. Cell wall damage induces the production of OGs through the action of PG, which in turn regulates the expression of related genes through the MAPK pathway. This regulation impacts defense mechanisms, specifically the synthesis of JA, the generation of ROS signals, and callose production. The MAPK pathway also regulates HMG as cellular content, although the receptor remains unidentified.

HAE-related research is limited at present, and the mechanism by which plants identify predators is still a focus of research.

Phenotypic plasticity in plant defenses

Phenotypic plasticity, a widespread phenomenon, distinct from the long and slow process of trait formation associated with genetic variation, is the primary means by which organisms rapidly adapt to the environment and cope with stress (Burton et al. 2022). Phenotypic plasticity is the ability of organisms to express different phenotypes based on the biological or abiotic environment, and induced defenses are -related to the formation of plasticity phenotypes in plants (Nagano and Doi 2020; Weiss 2019). Similar to genetic variation, adaptations are not always specific to the environment. Some phenotypically plastic traits allow organisms to alter their traits over a short period to adapt to the environment, which is called an adaptive malleable phenotype. However, neutral or even non-adaptive phenotype also occurs, and these are far from the optimal phenotype (Gibert et al. 2019).

Phenotypic plasticity is essential for plant defense against herbivores

Although phenotypic plasticity is particularly common in insects and contributes to their formation as one of the most diverse animal groups in the world, little is known about how phenotypic plasticity helps them cope with plant defenses. On the contrary, numerous studies tell us that phenotypic plasticity provides powerful adaptive and defensive capabilities in plants (Stotz et al. 2021). Feeding by herbivorous insects is thought to be an important driving force for the generation of plant plasticity phenotypes, and the insect-plant arms race is a major driver of phytochemical diversity (Qu et al. 2022). Feeding by herbivores not only leads to plasticity in the defensive traits of plants, but also has an influence on the floral traits of flowering plants, and indirectly interferes with plant pollination (Rusman et al. 2019a, 2022). Plasticity phenotypes contribute to enhanced survival of plants despite dynamic environments and mobile enemies (Bonser 2021).

In addition to feeding by herbivorous insects, environmental conditions also play a crucial role in the development of the plasticity phenotype in plant defenses.

Different environmental conditions can affect the allocation of plant resources, influencing the balance between defense and growth. For example, nutritional conditions, elevation, and temperature can all affect the phenotypic plasticity of plants (Bakhtiari et al. 2019; Liu et al. 2022a). In particular, nutritional conditions directly affect the balance between plant growth and defense. When nutrient and water supplies are insufficient, plants tend to protect themselves, favoring greater resources and defense. When nutrition is abundant, plants tend to favor growth, development and reproduction, leading to more offspring (Yamawo et al. 2012). This strategy selection may help plants survive under poor environmental conditions and allow populations to recover quickly after conditions improve. The trade-off between defense and growth has long been considered one of the strategies for coping with environmental changes. This trade-off limits the evolution of intraspecific-induced defense but does not have much effect on the evolution of interspecific defense (Agrawal and Hastings 2019). Interestingly, different herbivorous insects and feeding patterns, as well as different environments, can induce completely different plant defense phenotypes, including constitutive and induced defenses.

In conclusion, during the interaction between herbivorous insects and plants, the plant plasticity phenotypes are influenced by herbivorous insects, and the environmental conditions, such as soil nutrient also plays a very important role in this process.

Heredity and epigenetic changes in plant plastic defense phenotype

What is most notable, however, is that plant plastic defense traits and resistance have intergenerational effects, with both chemical defenses that are easy to induce and adjust and broadly effective constitutive defenses being inherited by subsequent generations (Sobral et al. 2021a). Sobral et al. and Quintero et al. suggest that there are differences in phenotypic plasticity across life stages. Both physical and chemical defenses can be induced during infancy, but only chemical defenses can be induced by phenotypic plasticity in adults (Sobral et al. 2021a; Quintero and Bowers 2012). Most of the adaptive phenotypes resulting from phenotypic plasticity usually disappear sometime after the interaction ends, returning to the original phenotype. However, not all phenotypic formation and disappearance occur fixedly, and this resetting phenomenon may persist over several generations with parental influence (Baker et al. 2018). For example, *Solanum carolinense* can transmit defensive traits (i.e., trichome and spine production) to offspring (Nihranz et al. 2022). Some phenotypes, especially morphological changes, may not be recovered

after the end of the interaction (Burggren 2019; Radersma et al. 2020). In contrast, some interactions produce plastic phenotypes and disappearance that start and end within a few seconds. Thus, the time scales of phenotypic responses to interactions are variable and vary considerably, depending perhaps on whether the reaction is chemical, physiological, morphological, or behavioral (Ogran et al. 2020a; Guo et al. 2019).

Predation by herbivorous insects promotes plasticity phenotype formation of plant defenses, and changes in those defenses, especially chemical defenses. Plants are forced to adjust themselves through forming appropriate own phenotypic plasticity to cope with insect feeding stress. But the molecular mechanisms involved in this process remain obscure (Umesh et al. 2021; Qiao and Stepanova 2021).

The nucleotide sequence of DNA determines the sequence of its protein products, but at the level of gene expression regulation, the genetic units of eukaryotes are involved in related chromatin components in addition to the DNA sequence. These can confer occasional genetic changes in cell division and gene expression (Grant-Downton and Dickinson 2005; Francis 2011; Flintoft 2009). Phenotypes formed by defense responses are derived both from phenotypic plasticity and from the evolution of genetic variation in plant populations, and the transgenerational effect of phenotypic plasticity in plants is thought to be due to epigenetics (Tikhodeyev 2020). Epigenetic changes (such as DNA modification, histone modification, and non-coding RNA) are observed in damaged plants (Sobral et al. 2021b; Herrera et al. 2019). There are some findings that link epigenetic changes to plant defense genetics suggest that the damage results in certain epigenetic changes. Furthermore, they observed an increase in the abundance of non-dicer sRNAs, which were found to be associated with nearby genes that had decreased expression in the subsequent generation (Colicchio et al. 2020).

Genetic material with epigenetic characteristics is passed to offspring. This causes the progeny to have a plastic defense phenotypes and increases their chances of survival in infancy by altering dormancy, forming defensive traits or other ways (Vanden Broeck et al. 2018). Although little is currently known about the relationship between epigenetic traits and plant defense formation, several studies have shown a link between the inheritance of phenotypic plasticity and epigenetic changes (Ali et al. 2020; Liu et al. 2022b). Sobral et al. performed experiments with *Raphanus sativus* and showed that herbivore feeding triggers genomic methylation of the target plant and its offspring, and that trichomes, which act as a physical defense, and glucosinolates, which act as a chemical defense, can be induced at the seedling stage. However,

only chemical defenses can be induced in adults (Sobral et al. 2021a). Assmann et al. demonstrated that the induction of *Pst/Hpa* and intergenerational memory of herbivores lasted only one generation in experiments on the interactions of *Arabidopsis*, tomato, and caterpillar, suggesting transcriptional plasticity in response to stress and the existence of strict regulation and powerful reset mechanisms, which prevent stable inheritance of chromatin changes (Rasmann et al. 2012). At present, most relevant studies have focused on epigenetic changes and reprogramming mechanisms of plant defense caused by microbial invasion, and some relevant mechanisms have been studied and reviewed (Buscaill and Rivas 2014). However, there is limited knowledge exists regarding the epigenetic mechanisms underlying plant phenotypic plasticity in herbivorous insects. Some studies have indicated that increased transcriptional plasticity is an important mechanism for widespread feeding in generalist insects, and such transcriptional plasticity and post-transcriptional modifications also appear in the phenotypic plasticity of insects (Richard et al. 2021). Although currently known mechanisms are insufficient to construct a mechanism chain linking interplay to epigenetic changes, there is ample evidence pointing towards the formation of phenotypic plasticity in the process of interaction (Boquete et al. 2021; Duncan et al. 2022).

There are several discoveries about epigenetic changes in plant defense. Epigenetic changes are observed in many plants, such as wild arugula, wild radish, and yellow monkeyflower (Sobral et al. 2021b; Ogran et al. 2020b; Scoville et al. 2011). Epigenetic changes regulate the expression of genes without altering genetic information while also enabling the passage of that information to offspring, creating transgenerational effects of phenotypic plasticity while maintaining the stability of genetic information (Smith and Ritchie 2013; Miryeganeh and Saze 2020; Shea et al. 2011; Gallusci et al. 2023). In conclusion, epigenetic changes in plant chromatin may guide phenotypic plasticity. Transcriptional level regulation and post-transcriptional level modification may play an important role in the formation of phenotypic plasticity (Villagra and Frias-Lasserre 2020).

Moczek believed that phenotypic plasticity provided opportunities for species differentiation, and the tradeoff between plasticity and mutation accumulation determined the diversity at all levels of organisms, enabling the generation of new traits and even new species (Casasa and Moczek 2019). Interaction between plants and insects also has a considerable influence on ecology. Plants constantly cope with insect herbivory, which is thought to be the evolutionary driver for the immense diversity of plant chemical defenses. In this competition, the emergence of new phenotypes disrupts the original

balance, prompting the other side to respond, forcing out the population that cannot adapt, but at the same time, it will lead to the prosperity of the new dominant population until a new equilibrium is reached (Kant et al. 2015; Coley et al. 2018; Maron et al. 2019; Ida et al. 2018). Epigenetics and phenotypic plasticity act as a bridge between species evolution and ecology (Ashe et al. 1826). Herbivorous insects induce phenotypic plasticity of plants while selecting for genetic variation. Both forms of phenotypic variation, and plant phenotypic changes directly and indirectly affect the community diversity of herbivorous insects and the environment as a whole (Hilker et al. 2023; Rusman et al. 2019b).

Adaptation of insects to plants defenses

Insect and plant interactions are the most common animal-to-plant interactions on Earth. Facing plant defenses, especially chemical defenses, insects employ one or more strategies to adapt to host resistance (Wang et al. 2021b). They rely on the regulation of the expression of detoxification-related genes (Vandenhole et al. 2021; Lu et al. 2021). The mutual benefit with intestinal microorganisms and horizontal gene transfer (HGT) are also important means for insects to exclusively feed on a certain type of plant and even become generalists (Coolen et al. 2022; Kirsch et al. 2022). Studying how insects react to plant defenses can help us address pest issues in crop production. Diminishing insects' adaptability to plant defenses can serve as a solution to minimize pesticide use and promote environmentally friendly production.

Research on insect gut microbes has been fruitful, providing new ideas for green pesticide development and ecological environmental governance by using insect gut microbes (Zhang et al. 2022a; Liu et al. 2021). Insect gut microbes, which have been described as a tool kit for the flexible metabolism of insects, are one of the important reasons why insects can decompose pesticides, plant secondary metabolites, and even microplastics (Zhang et al. 2022b; Wei et al. 2022; Fang et al. 2023). In an insect-plant interaction, gut microbes provide the insect with the ability to degrade plant secondary metabolites and enhance the availability of nutrients for the host (Attia et al. 2022; Zhang et al. 2020), while the host provides a stable and nutritionally abundant living environment for the microorganisms; thus, the arrangement is mutually beneficial. Interestingly, some insects not only metabolize plant secondary metabolites into nontoxic substances but also use microorganisms to transform them into substances they need for growth, information transmission, and even immune-related substances (Siddiqui et al. 2022; Yoon et al. 2019). The substances are likely to affect the physicochemical conditions in the gut of the colonized insects, as indicated by Kešnerová et al.

This evidence reinforces the notion that gut microbes help insects decompose plant secondary metabolites. (Kešnerová et al. 2017). The diversity and adjustability of gut microbes provide important tools by which insects can adapt to their hosts (Francoeur et al. 2020; Banerjee et al. 2022), while microbial complexity also provides a variety of functions. For chemical defense substances such as plant flavonoids, phenols, defense proteins, and even cyanides, corresponding microorganisms with the ability to metabolize the substances exist in different insects' guts (Medina et al. 2022; Shukla and Beran 2020). However, the utilization of gut microbes is not limited to insects. Studies have shown that plants can also directly or indirectly regulate the composition of insect gut microbes by influencing them through volatile substances, disrupting the intestinal permeability of insects, affecting their digestive ability, and even altering their immune systems. Mason et al.'s study found that certain plants can inhibit the growth and cause death of fall armyworms (*Spodoptera frugiperda*) through the action of bacteria present in the insect's gut. The combination of physical and chemical defenses from these plants can weaken the armyworms' digestive system, leading to the colonization of harmful bacteria and an increase in the cost of survival for the insects. This ultimately results in slower growth or death (Mason et al. 2019). Chen et al. also found DMNT to be damaging to the PM of *Plutella xylostella* and suppressing PxMucin expression in midgut cells, creating favorable conditions for microbial infections (Chen et al. 2021). In brief, the alteration of gut microbes by plants can make the insects more susceptible to infection and disease (Mason et al. 2022; Gasmí et al. 2019a).

It is an interesting phenomenon that insect gut microbes can be influenced by both sides of the interaction (Alberoni et al. 2021; Li et al. 2022). Here, we propose a hypothesis for this phenomenon: the utilization of insect gut microbiota serves as a battleground for plant–insect interactions, with both parties benefiting from this "neutral resource." The insect gut is a very complex and flexible environment and contains a wide variety of microorganisms, both beneficial and harmful (Schmidt and Engel 2021; Bai et al. 2021). Changes in herbivorous insect hosts exert an influence on the intestinal environment (Yang et al. 2020; Pirttilä et al. 2023). After the intestinal environment changes, microorganisms that can use host plant defense compounds become dominant populations because of better adaptation to environmental changes and then assist insects with resisting plant defense (Mogren and Shikano 2021). However, the dominant population is not always beneficial to insects (Gu et al. 2023). When harmful microorganisms become the dominant population, they may cause damage to

the intestine and reduce insect's digestive and immune capabilities, and even kill them (Gasmí et al. 2019b; Hu et al. 2021). During evolution, some plants got the ability to produce such secondary metabolites, which are beneficial to insects' harmful gut microbes. In their study at Rice, Lou et al. discovered that the attack of the brown planthopper triggers the accumulation of sukranetin in rice. This accumulation significantly inhibits the beneficial endosymbionts of the brown planthopper (Liu et al. 2023). According to the study by Zhu et al., intestinal microorganisms of herbivorous insects mainly come from their diet (Zhu et al. 2021). The intestinal microbiota plays a crucial role in host immunity, digestion, defense, and development (Xu et al. 2022; Wang et al. 2022). Helping insects survive in a new environment, an insect diet shapes the structure of intestinal microbial communities (Wang et al. 2022), and at the same time, the structural adjustment of gut microbes also assists in insect adaptation to host defenses (Zhang et al. 2022c; Lv et al. 2021).

Horizontal gene transfer, which is the movement of genetic information from one genome to another across species (Soucy et al. 2015), was first mentioned in Sukhodolets's article on bacteria (Sukhodolets 1988). HGT exists widely in nature and has been observed in bacteria, fungi, plants, and animals (Arnold et al. 2022; Wang et al. 2020). Recent studies have found that HGT also plays an important role in insect adaptation and response to plant defenses. There are at least 14 insect species belonging to 6 orders that are known to have received plant genetic material through HGT (Gilbert and Maumus 2023). For example, the acyltransferase encoded by the *PMaTI* gene obtained by the whitefly from its host is a key enzyme in the decomposition of phenolic glucosides. The transfer of the acyl group of the phenolic glucosides eliminates the toxicity of these compounds to the whitefly. This ability has enabled the whitefly to become a widespread feeding agricultural pest (Xia et al. 2021). Similar HGT events also occurred in the horizontal transfer of plant cell wall-degrading enzyme (PCWDE) related genes (Bellieny-Rabelo et al. 2020; Shin et al. 2023).

In addition, insect self-resistance to plant defense occurs mainly in two ways: by regulating the expression of self-detoxification related genes and enzyme synthesis and by secreting specific active substances, such as GOX proteins, to reduce the plant injury response (Chen et al. 2022).

Conclusion

The need for environmentally friendly pest control programs has become more and more urgent in the face of the huge losses caused by insect pests and the increasingly serious environmental pollution caused by

inorganic pesticides. Insect pests have been an important problem in crop production since ancient times, affecting both food crops and cash crops. Finding solutions from the plant itself should become an important green control approach, in addition to targeted control from the physiological and biochemical direction of insects. The study of plant defense mechanisms and insect adaptation mechanisms is also an important cornerstone for the development of green pest resistance programs.

Through the interaction between plants and herbivorous insects that has occurred for more than 400 million years, both plants and insects have developed defense and anti-defense mechanisms. Plants have developed large and complex chemical defenses, universal physical defenses, and indirect defense strategies under the pressure of herbivorous insects. Insects adapt to plant defenses by regulating the expression and composition of their enzymes, interacting with microorganisms, and obtaining external genes through HGT. Plants also have a well-developed system to detect herbivores and initiate defense responses. Signals are transmitted to the whole plant through mediators such as Ca^{2+} , WASPs, ROS, and jasmonic acid, triggering the defense response throughout the individual, as plants receive stress information from herbivorous insects through perception and recognition systems. Some plants also transmit signals to other individuals through VOCs, inducing a defense response through this process. These responses regulate the expression levels of related genes through a second messenger and a phosphoric acid cascade. Phenotypic plasticity, an important means of biological adaptation to the environment, plays a crucial role in the interaction between herbivorous insects and plants. Epigenetic changes and posttranscriptional regulation are significant molecular mechanisms for the formation of plastic phenotypes. The future research should delve into epigenetics and examine changes at the transcriptional and posttranscriptional levels to gain a deeper understanding of the internal mechanisms that drive the occurrence and inheritance of plasticity phenotypes, especially focusing on transgenerational effects.

Understanding insect-plant interactions provides a more systematic and clear direction for pest control problems in crop production. Here, we propose three directions for environmentally friendly pest control that should be emphasized. First, we should apply plant defense capabilities to further research on plant damage perception, develop plant vaccines targeting DAMPs and HAEs, stimulate plant defense responses, and enhance crop defense capabilities in an external form to cope with herbivore insects. Secondly, we further studied the internal mechanism of the heritability of plant defense traits, linked the phenotypic plasticity of defense traits with

epigenetics, and used new epigenetic observation methods to explore the genetic puzzle of plasticity of defense traits. Finally, taking insects as the research object, metagenomics and bioinformatics methods should be used to analyze the responses of insect gut microbes to plant defense. It could be used as a control measure by enhance the synthesis of plant-related compounds for sustainable control. In summary, whether promoting the formation of plant defense barriers in the form of plant vaccines or seeking the heritability of defense traits through epigenetics, improving plant defense capabilities as an anti-pest solution should be an important direction for the development of green pest control in the future.

Acknowledgements

The author would like to acknowledge the Hangzhou Normal University Post-graduate Research Innovation Promotion Project (1115B20500401).

Author contributions

Conceptualization, XW and JL; methodology, XW and JK; resources, SW and HW; data curation, BT; writing—original draft preparation, XW; writing—review and editing, JK and JL; supervision, BT and JL. All authors have read and agreed to the published version of the manuscript.

Funding

This work was supported by the National Natural Science Foundation of China (31970346 and 31470407).

Data availability

The data used to support the findings of this study are included in the article.

Declarations

Ethics approval and consent to participate

Not Applicable.

Consent for publication

All authors approve the manuscript for publication.

Competing interests

All authors declare that they have no competing interest.

Received: 17 August 2023 Accepted: 5 December 2023

Published online: 13 December 2023

References

- Adachi-Fukunaga S, Nakabayashi Y, Tokuda M. Transgenerational changes in pod maturation phenology and seed traits of *Glycine soja* infested by the bean bug *Riptortus pedestris*. *Plos One*. 2022;17(3):e0263904.
- Agrawal AA, Hastings AP. Trade-offs constrain the evolution of an inducible defense within but not between plant species. *Ecology*. 2019. <https://doi.org/10.1002/ecy.2857>.
- Alberoni D, Favaro R, Baffoni L, Angeli S, Di Gioia D. Neonicotinoids in the agroecosystem: in-field long-term assessment on honeybee colony strength and microbiome. *Sci Total Environ*. 2021;762: 144116.
- Ali M, Javadi A, Naqvi SH, Batcho A, Kayani WK, Lal A, Sajid IA, Nwogwugwu JO. Biotic stress triggered small RNA and RNAi defense response in plants. *Mol Biol Rep*. 2020;47(7):5511–22.
- Arnold BJ, Huang IT, Hanage WP. Horizontal gene transfer and adaptive evolution in bacteria. *Nat Rev Microbiol*. 2022;20(4):206–18.

- Ashe A, Colot V, Oldroyd BP. How does epigenetics influence the course of evolution? *Philos Trans Royal Soc London Series B Biol Sci*. 1826;2021(376):20200111.
- Attia S, Renoz F, Pons I, Louâpre P, Foray V, Piedra J-M, Sanané I, Le Goff G, Lognay G, Hance T. The aphid facultative symbiont *Serratia symbiotica* influences the foraging behaviors and the life-history traits of the parasitoid *Aphidius ervi*. *Entomol Gen*. 2022;42(1):21–33.
- Bai S, Yao Z, Raza MF, Cai Z, Zhang H. Regulatory mechanisms of microbial homeostasis in insect gut. *Insect Sci*. 2021;28(2):286–301.
- Baker BH, Berg LJ, Sultan SE. Context-dependent developmental effects of parental shade versus sun are mediated by DNA methylation. *Front Plant Sci*. 2018;9:1251.
- Bakhtiari M, Formenti L, Caggia V, Glauser G, Rasmann S. Variable effects on growth and defense traits for plant ecotypic differentiation and phenotypic plasticity along elevation gradients. *Ecol Evol*. 2019;9(7):3740–55.
- Banerjee S, Maiti TK, Roy RN. Enzyme producing insect gut microbes: an unexplored biotechnological aspect. *Crit Rev Biotechnol*. 2022;42(3):384–402.
- Belliény-Rabelo D, Nkomo NP, Shyntum DY, Moleleki LN. Horizontally acquired quorum-sensing regulators recruited by the phop regulatory network expand the host adaptation repertoire in the phytopathogen *Pectobacterium brasiliense*. *mSystems*. 2020. <https://doi.org/10.1128/mSystems.00650-19>.
- Bonser SP. Misinterpreting the adaptive value of phenotypic plasticity in studies on plant adaptation to new and variable environments. *Plant Biol*. 2021;23(5):683–5.
- Boquete MT, Muyle A, Alonso C. Plant epigenetics: phenotypic and functional diversity beyond the DNA sequence. *Am J Bot*. 2021;108(4):553–8.
- Bricchi I, Occhipinti A, Berteà CM, Zebelo SA, Brillada C, Verrillo F, De Castro C, Molinaro A, Faulkner C, Maule AJ, et al. Separation of early and late responses to herbivory in *Arabidopsis* by changing plasmodesmal function. *Plant J*. 2013;73(1):14–25.
- Burggren WW. Phenotypic switching resulting from developmental plasticity: fixed or reversible? *Front Physiol*. 2019;10:1634.
- Burton T, Ratikainen II, Einum S. Environmental change and the rate of phenotypic plasticity. *Glob Change Biol*. 2022;28(18):5337–45.
- Buscaill P, Rivas S. Transcriptional control of plant defence responses. *Curr Opin Plant Biol*. 2014;20:35–46.
- Bustos-Segura C, Gonzalez-Salas R, Benrey B. Early damage enhances compensatory responses to herbivory in wild lima bean. *Front plant sci*. 2022;13:1037047.
- Casasa S, Moczek AP. Evolution of, and via, developmental plasticity: insights through the study of scaling relationships. *Integr Comp Biol*. 2019;59(5):1346–55.
- Chavanke SN, Penna S, Dalvi SG. β -Glucan and its nanocomposites in sustainable agriculture and environment: an overview of mechanisms and applications. *Environ Sci Pollut Res Int*. 2022;29(53):80062–87.
- Chen C, Chen HY, Huang SJ, Jiang TS, Wang CH, Tao Z, He C, Tang QF, Li PJ. Volatile DMNT directly protects plants against *Plutella xylostella* by disrupting the peritrophic matrix barrier in insect midgut. *eLife*. 2021;10:63938.
- Chen W, Saqib HSA, Xu X, Dong Y, Zheng L, Lai Y, Jing X, Lu Z, Sun L, You M, et al. Glucosinolate sulfatases-sulfatase-modifying factors system enables a crucifer-specialized moth to pre-detoxify defensive glucosinolate of the host plant. *J Agric Food Chem*. 2022;70(36):11179–91.
- Coley PD, Endara MJ, Kursar TA. Consequences of interspecific variation in defenses and herbivore host choice for the ecology and evolution of *Inga*, a speciose rainforest tree. *Oecologia*. 2018;187(2):361–76.
- Colicchio J, Kelly J, Hileman L. *Mimulus* sRNAs are wound responsive and associated with transgenerationally plastic genes but rarely both. *Int J Mol Sci*. 2020;21(20):7552.
- Coolen S, R-vd-M M, Welte CU. The secret life of insect-associated microbes and how they shape insect-plant interactions. *FEMS Microbiol Ecol*. 2022. <https://doi.org/10.1093/femsec/fiac083>.
- de Bobadilla MF, Vitiello A, Erb M, Poelman EH. Plant defense strategies against attack by multiple herbivores. *Trends Plant Sci*. 2022;27(6):528–35.
- De Kesel J, Conrath U, Flors V, Luna E, Mageroy MH, Mauch-Mani B, Pastor V, Pozo MJ, Pieterse CMJ, Ton J, et al. The induced resistance lexicon: do's and don'ts. *Trends Plant Sci*. 2021;26(7):685–91.
- Depalo L, Urbaneja A, Gallego C, Fournarakos A, Alonso M, Perez-Hedo M. Eliciting sweet pepper plant resistance to *Aulacorthum solani* and attractiveness on *Aphelinus abdominalis* by exposure to (Z)-3-hexenyl propanoate. *Entomol Gen*. 2022;42(5):743–9.
- Duncan EJ, Cunningham CB, Dearden PK. Phenotypic plasticity: what has DNA methylation got to do with it? *Insects*. 2022;13(2):110.
- Fang J, Wang Y, Hu J, Hoffmann AA, Li L, Yin Z, Yang F, Cao L, Zhu J, Liu Q, et al. Dissecting a mutualistic interaction involving an insect-endosymbiont association. *Entomol Gen*. 2023;43(2):399–407.
- Fierke MK, Stephen FM. Callus formation and bark moisture as potential physical defenses of northern red oak, *Quercus rubra*, against red oak borer, *Enaphalodes rufulus* (Coleoptera : Cerambycidae). *Can Entomol*. 2008;140(2):149–57.
- Flintoft L. EPIGENETICS RNAi protects across the generations. *Nat Rev Genet*. 2009;10(4):220.
- Francis NJ. Gene Regulation: Implications of Histone Dispersal Patterns for Epigenetics. *Curr Biol*. 2011;21(17):R659–61.
- Francoeur CB, Khadempour L, Moreira-Soto RD, Gotting K, Book AJ, Pinto-Tomas AA, Keefover-Ring K, Currie CR. Bacteria contribute to plant secondary compound degradation in a generalist herbivore system. *mBio*. 2020. <https://doi.org/10.1128/mBio.02146-20>.
- Freund M, Graus D, Fleischmann A, Gilbert KJ, Lin Q, Renner T, Stigloher C, Albert VA, Hedrich R, Fukushima K. The digestive systems of carnivorous plants. *Plant Physiol*. 2022;190(1):44–59.
- Fu WJ, Jin GC, Jimenez-Aleman GH, Wang XJ, Song JJ, Li SH, Lou YG, Li R. The jasmonic acid-amino acid conjugates JA-Val and JA-Leu are involved in rice resistance to herbivores. *Plant Cell Environ*. 2022;45(1):262–72.
- Gallucci P, Agius DR, Moschou PN, Dobránszki J, Kaiserli E, Martinelli F. Deep inside the epigenetic memories of stressed plants. *Trends Plant Sci*. 2023;28(2):142–53.
- Gasmi L, Martínez-Solis M, Frattini A, Ye M, Carmen Collado M, Turlings TCJ, Erb M, Herrero S. Can herbivore-induced volatiles protect plants by increasing the herbivores' susceptibility to natural pathogens? *Appl Environ Microbiol*. 2019a;85(1):e01468-e1418.
- Gasmi L, Martínez-Solis M, Frattini A, Ye M, Collado MC, Turlings TCJ, Erb M, Herrero S. Can herbivore-induced volatiles protect plants by increasing the herbivores' susceptibility to natural pathogens? *Appl Environ Microbiol*. 2019b;85(1):e01468-e1418.
- Ge D, Yeo I-C, Shan L. Knowing me, knowing you: Self and non-self recognition in plant immunity. *Essays Biochem*. 2022;66(5):447–58.
- Gibert P, Debate V, Ghalambor CK. Phenotypic plasticity, global change, and the speed of adaptive evolution. *Curr Opin Insect Sci*. 2019;35:34–40.
- Gilbert C, Maumus F. Sidestepping Darwin: horizontal gene transfer from plants to insects. *Curr Opin Insect Sci*. 2023;57: 101035.
- Grant-Downton RT, Dickinson HG. Epigenetics and its implications for plant biology. 1. The epigenetic network in plants. *Ann Bot*. 2005;96(7):1143–64.
- Grissett L, Ali A, Coble AM, Logan K, Washington B, Mateson A, McGee K, Nkrumah Y, Jacobus L, Abraham E, et al. Survey of sensitivity to fatty acid-amino acid conjugates in the solanaceae. *J Chem Ecol*. 2020;46(3):330–43.
- Gu J, Zhang P, Yao Z, Li X, Zhang H. BdNub is essential for maintaining gut immunity and microbiome homeostasis in *Bactrocera dorsalis*. *Insects*. 2023;14(2):178.
- Guo J, Li H, Yang Y. Phenotypic plasticity in sexual reproduction based on nutrients supplied from vegetative ramets in a *leymus chinensis* population. *Front Plant Sci*. 2019;10:1681.
- Guo L, Qiao X, Haji D, Zhou T, Liu Z, Whiteman NK, Huang J. Convergent resistance to GABA receptor neurotoxins through plant-insect coevolution. *Nat Ecol Evol*. 2023. <https://doi.org/10.1038/s41559-023-02127-4>.
- Herrera CM, Medrano M, Pérez R, Bazaga P, Alonso C. Within-plant heterogeneity in fecundity and herbivory induced by localized DNA hypomethylation in the perennial herb *Helleborus foetidus*. *Am J Bot*. 2019;106(6):798–806.
- Hilker M, Salem H, Fatouros NE. Adaptive plasticity of insect eggs in response to environmental challenges. *Annu Rev Entomol*. 2023;68:451–69.
- Hou S, Liu Z, Shen H, Wu D. Damage-associated molecular pattern-triggered immunity in plants. *Front Plant Sci*. 2019;10:646.
- Hu L, Zhang K, Wu Z, Xu J, Erb M. Plant volatiles as regulators of plant defense and herbivore immunity: molecular mechanisms and unanswered questions. *Curr Opin Insect Sci*. 2021;44:82–8.
- Iida TY, Takanashi K, Tamura M, Ozawa R, Nakashima Y, Ohgushi T. Defensive chemicals of neighboring plants limit visits of herbivorous

- insects: associational resistance within a plant population. *Ecol Evol.* 2018;8(24):12981–90.
- Jain M, Amera GM, Muthukumar J, Singh AK. Insights into biological role of plant defense proteins: a review. *Biocatal Agric Biotechnol.* 2022;40:102293.
- Jones AC, Felton GW, Tumlinson JH. The dual function of elicitors and effectors from insects: reviewing the “arms race” against plant defenses. *Plant Mol Biol.* 2022;109(4–5):427–45.
- Kant MR, Jonckheere W, Knecht B, Lemos F, Liu J, Schimmel BC, Villarreal CA, Ataide LM, Dermauw W, Glas JJ, et al. Mechanisms and ecological consequences of plant defence induction and suppression in herbivore communities. *Ann Bot.* 2015;115(7):1015–51.
- Kanyuka K, Rudd JJ. Cell surface immune receptors: the guardians of the plant's extracellular spaces. *Curr Opin Plant Biol.* 2019;50:1–8.
- Kešnerová L, Mars RAT, Ellegaard KM, Troilo M, Sauer U, Engel P. Disentangling metabolic functions of bacteria in the honey bee gut. *PLoS One.* 2017;15(12):e2003467.
- Khranov AV, Naugolnykh SV, Węgierek P. Possible long-proboscid insect pollinators from the early Permian of Russia. *Current Biology : CB.* 2022;32(17):3815–3820.e3812.
- Kimura S, Hunter K, Vaahtera L, Tran HC, Citterico M, Vaattovaara A, Rokka A, Stolze SC, Harzen A, Meißner L, et al. CRK2 and C-terminal phosphorylation of NADPH oxidase RBOHD regulate reactive oxygen species production in arabidopsis. *Plant Cell.* 2020;32(4):1063–80.
- Kirsch R, Okamura Y, Haeger W, Vogel H, Kunert G, Pauchet Y. Metabolic novelty originating from horizontal gene transfer is essential for leaf beetle survival. *Proc Natl Acad Sci USA.* 2022;119(40):e2205857119–e2205857119.
- Kumari A, Chetelat A, Nguyen CT, Farmer EE. Arabidopsis H⁺-ATPase AHA1 controls slow wave potential duration and wound-response jasmonate pathway activation. *Proc Natl Acad Sci USA.* 2019;116(40):20226–31.
- Li Z, Huang S, He X, Ma H, Zhou X, Lin H, Zhang S. Specific enriched acinetobacter in camellia weevil gut facilitate the degradation of tea saponin: inferred from bacterial genomic and transcriptomic analyses. *Microbiol Spectr.* 2022;10(6): e0227222.
- Lin Y-H, Silven JJM, Wybouw N, Fandino RA, Dekker HL, Vogel H, Wu Y-L, de Koster C, GroSse-Wilde E, Haring MA, et al. A salivary GMC oxidoreductase of *Manduca sexta* re-arranges the green leaf volatile profile of its host plant. *Nat Commun.* 2023;14(1):3666.
- Ling S, Rizvi SAH, Xiong T, Liu J, Gu Y, Wang S, Zeng X. Volatile signals from guava plants prime defense signaling and increase jasmonate-dependent herbivore resistance in neighboring citrus plants. *Front Plant Sci.* 2022;13: 833562.
- Liu Q-X, Su Z-P, Liu H-H, Lu S-P, Ma B, Zhao Y, Hou Y-M, Shi Z-H. The effect of gut bacteria on the physiology of red palm weevil, *Rhynchophorus ferrugineus* Olivier and their potential for the control of this pest. *Insects.* 2021;12(7):594.
- Liu H, Su X-Y, Sun Z, Wang C, Shi J-H, Foba CN, Jin H, Wang M-Q. Nitrogen and plant pathogens alter rice plant volatiles mediating host location behavior of *Nilaparvata lugens* and its parasitoid *Anagrus nilaparvatae*. *Entomol Gen.* 2022a;42(4):549–57.
- Liu N, Xu Y, Li Q, Cao Y, Yang D, Liu S, Wang X, Mi Y, Liu Y, Ding C, et al. A lncRNA fine-tunes salicylic acid biosynthesis to balance plant immunity and growth. *Cell Host Microbe.* 2022b;30(8):1124–1138.e1128.
- Liu M, Hong G, Li H, Bing X, Chen Y, Jing X, Gershenzon J, Lou Y, Baldwin IT, Li R. Sakuranetin protects rice from brown planthopper attack by depleting its beneficial endosymbionts. *Proc Natl Acad Sci USA.* 2023;120(23): e2305007120.
- Lu K, Cheng Y, Li Y, Li W, Zeng R, Song Y. Phytochemical flavone confers broad-spectrum tolerance to insecticides in *Spodoptera litura* by activating ROS/CncC-mediated xenobiotic detoxification pathways. *J Agric Food Chem.* 2021;69(26):7429–45.
- Lv D, Liu X, Dong Y, Yan Z, Zhang X, Wang P, Yuan X, Li Y. Comparison of gut bacterial communities of fall armyworm (*Spodoptera frugiperda*) reared on different host plants. *Int J Mol Sci.* 2021;22(20):11266.
- Mahmood S, Kumari P, Kisku AV, Mahapatro GK, Banerjee N, Sarin NB. Ectopic expression of *Xenorhabdus nematophila* chitinase in tobacco confers resistance against *Helicoverpa armigera*. *Plant Cell Tissue Organ Cult.* 2022;151(3):593–604.
- Maron JL, Agrawal AA, Schemske DW. Plant-herbivore coevolution and plant speciation. *Ecology.* 2019;100(7): e02704.
- Mason CJ, Ray S, Shikano I, Peiffer M, Jones AG, Luthe DS, Hoover K, Felton GW. Plant defenses interact with insect enteric bacteria by initiating a leaky gut syndrome. *Proc Natl Acad Sci USA.* 2019;116(32):15991–6.
- Mason CJ, Peiffer M, St Clair A, Hoover K, Felton GW. Concerted impacts of antiherbivore defenses and opportunistic *Serratia* pathogens on the fall armyworm (*Spodoptera frugiperda*). *Oecologia.* 2022;198(1):167–78.
- Medina V, Rosso BE, Soria M, Gutkind GO, Pagano EA, Zavala JA. Feeding on soybean crops changed gut bacteria diversity of the southern green stinkbug (*Nezara viridula*) and reduced negative effects of some associated bacteria. *Pest Manage Sci.* 2022;78(11):4608–17.
- Miryeganeh M, Saze H. Epigenetic inheritance and plant evolution. *Popul Ecol.* 2020;62(1):17–27.
- Mitra S, Baldwin IT. RuBPCase activase (RCA) mediates growth-defense trade-offs: silencing RCA redirects jasmonic acid (JA) flux from JA-isoleucine to methyl jasmonate (MeJA) to attenuate induced defense responses in *Nicotiana attenuata*. *New Phytol.* 2014;201(4):1385–95.
- Mogren CL, Shikano I. Microbiota, pathogens, and parasites as mediators of tritrophic interactions between insect herbivores, plants, and pollinators. *J Invertebr Pathol.* 2021;186:107589.
- Moro A, Blacquière T, Panziera D, Dietemann V, Neumann P. Host-parasite coevolution in real-time: changes in honey bee resistance mechanisms and mite reproductive strategies. *Insects.* 2021;12(2):120.
- Nagano M, Doi H. Ecological and evolutionary factors of intraspecific variation in inducible defenses: insights gained from *Daphnia* experiments. *Ecol Evol.* 2020;10(16):8554–62.
- Nihranz CT, Helms AM, Tooker JF, Mescher MC, De Moraes CM, Stephenson AG. Adverse effects of inbreeding on the transgenerational expression of herbivore-induced defense traits in *Solanum carolinense*. *PLoS One.* 2022;17(10):e0274920.
- Nilsson EE, Ben Maamar M, Skinner MK. Environmentally induced epigenetic transgenerational inheritance and the weismann barrier: the dawn of neo-lamarckian theory. *J Dev Biol.* 2020;8(4):28.
- Noman A, Aqeel M, Qasim M, Haider I, Lou YG. Plant-insect-microbe interaction: a love triangle between enemies in ecosystem. *Sci Total Environ.* 2020;699:134181.
- Oelmlüller R, Tseng YH, Gandhi A. Signals and their perception for remodeling, adjustment and repair of the plant cell wall. *Int J Mol Sci.* 2023;24(8):7417.
- Ogran A, Conner J, Agrawal AA, Barazani O. Evolution of phenotypic plasticity: Genetic differentiation and additive genetic variation for induced plant defence in wild arugula *Eruca sativa*. *J Evol Biol.* 2020;33(2):246.
- Ogran A, Conner J, Agrawal AA, Barazani O. Evolution of phenotypic plasticity: Genetic differentiation and additive genetic variation for induced plant defence in wild arugula *Eruca sativa*. *J Evol Biol.* 2020b;33(2):237–46.
- Pirttilä AM, Brusila V, Koskimäki JJ, Wälilä PR, Ruotsalainen AL, Mutanen M, Markkola AM. Exchange of microbiomes in plant-insect herbivore interactions. *mBio.* 2023;14(2):e0321022.
- Pontiggia D, Benedetti M, Costantini S, De Lorenzo G, Cervone F. Dampening the DAMPs: how plants maintain the homeostasis of cell wall molecular patterns and avoid hyper-immunity. *Front Plant Sci.* 2020;11:613259.
- Qiao H, Stepanova AN. Editorial overview: toward deciphering the molecular basis of plant phenotypic plasticity. *Curr Opin Plant Biol.* 2021;63: 102107.
- Qu J, Bonte D, Vandegehuchte ML. Phenotypic and genotypic divergence of plant-herbivore interactions along an urbanization gradient. *Evol Appl.* 2022;15(5):865–77.
- Quintero C, Bowers MD. Changes in plant chemical defenses and nutritional quality as a function of ontogeny in *Plantago lanceolata* (Plantaginaceae). *Oecologia.* 2012;168(2):471–81.
- Radersma R, Noble DWA, Uller T. Plasticity leaves a phenotypic signature during local adaptation. *Evolut Lett.* 2020;4(4):360–70.
- Ramachandran SR, Kumar S, Tanaka K. Quantification of extracellular ATP in plant suspension cell cultures. *Methods Mol Biol.* 2019;1991:43–54.
- Rasmann S, De Vos M, Casteel CL, Tian DL, Halitschke R, Sun JY, Agrawal AA, Felton GW, Jander G. Herbivory in the previous generation primes plants for enhanced insect resistance. *Plant Physiol.* 2012;158(2):854–63.
- Richard G, Jaquière J, Le Trionnaire G. Contribution of epigenetic mechanisms in the regulation of environmentally-induced polyphenism in insects. *Insects.* 2021;12(7):649.
- Rusman Q, Poelman EH, Nowrin F, Polder G, Lucas-Barbosa D. Floral plasticity: herbivore-species-specific-induced changes in flower traits

- with contrasting effects on pollinator visitation. *Plant, Cell Environ.* 2019a;42(6):1882–96.
- Rusman Q, Lucas-Barbosa D, Poelman EH, Dicke M. Ecology of plastic flowers. *Trends Plant Sci.* 2019b;24(8):725–40.
- Rusman Q, Hooiveld-Knopppers S, Dijksterhuis M, Bloem J, Reichelt M, Dicke M, Poelman EH. Flowers prepare themselves: leaf and root herbivores induce specific changes in floral phytochemistry with consequences for plant interactions with florivores. *New Phytol.* 2022;233(6):2548–60.
- Salerno G, Rebora M, Gorb S. Mechanoecology and chemoeology: physical and chemical interactions between insects and plants. *Insects.* 2023;14(7):657.
- Schmidt K, Engel P. Mechanisms underlying gut microbiota-host interactions in insects. *J Exp Biol.* 2021. <https://doi.org/10.1242/jeb.207696>.
- Schneider HM. Characterization, costs, cues and future perspectives of phenotypic plasticity. *Ann Bot.* 2022;130(2):131–48.
- Scoville AG, Barnett LL, Bodbyl-Roels S, Kelly JK, Hileman LC. Differential regulation of a MYB transcription factor is correlated with transgenerational epigenetic inheritance of trichome density in *Mimulus guttatus*. *New Phytol.* 2011;191(1):251–63.
- Shea N, Pen I, Uller T. Three epigenetic information channels and their different roles in evolution. *J Evol Biol.* 2011;24(6):1178–87.
- Shin NR, Okamura Y, Kirsch R, Pauchet Y. Genome sequencing provides insights into the evolution of gene families encoding plant cell wall-degrading enzymes in longhorned beetles. *Insect Mol Biol.* 2023. <https://doi.org/10.1111/imb.12844>.
- Shukla SP, Beran F. Gut microbiota degrades toxic isothiocyanates in a flea beetle pest. *Mol Ecol.* 2020;29(23):4692–705.
- Siddiqui JA, Khan MM, Bamisile BS, Hafeez M, Qasim M, Rasheed MT, Rasheed MA, Ahmad S, Shahid MI, Xu Y. Role of Insect Gut Microbiota in Pesticide Degradation: A Review. *Front Microbiol.* 2022;13: 870462.
- Silva-Sanzana C, Zavala D, Moraga F, Herrera-Vasquez A, Blanco-Herrera F. Oligogalacturonides enhance resistance against aphids through pattern-triggered immunity and activation of salicylic acid signaling. *Int J Mol Sci.* 2022;23(17):9753.
- Skinner MK, Nilsson EE. Role of environmentally induced epigenetic transgenerational inheritance in evolutionary biology: unified evolution theory. *Environ Epigenet.* 2021. <https://doi.org/10.1093/eep/dvab012>.
- Smith G, Ritchie MG. How might epigenetics contribute to ecological speciation? *Curr Zool.* 2013;59(5):686–96.
- Sobral M, Sampedro L, Neylan I, Siemens D, Dirzo R. Phenotypic plasticity in plant defense across life stages: inducibility, transgenerational induction, and transgenerational priming in wild radish. *Proc Natl Acad Sci USA.* 2021. <https://doi.org/10.1073/pnas.2005865118>.
- Sobral M, Neylan IP, Narbona E, Dirzo R. Transgenerational plasticity in flower color induced by caterpillars. *Front Plant Sci.* 2021b;12: 617815.
- Song W, Forde A, Yu D, Chai J. Structural biology of plant defence. *New Phytol.* 2021;229(2):692–711.
- Soucy SM, Huang JL, Gogarten JP. Horizontal gene transfer: building the web of life. *Nat Rev Genet.* 2015;16(8):472–82.
- Steinhorst L, Kudla J. Signaling in cells and organisms—calcium holds the line. *Curr Opin Plant Biol.* 2014;22:14–21.
- Stotz GC, Salgado-Luarte C, Escobedo VM, Valladares F, Gianoli E. Global trends in phenotypic plasticity of plants. *Ecol Lett.* 2021;24(10):2267–81.
- Sukhodolets VV. Organization and evolution of the bacterial genome. *Microbiol Sci.* 1988;5(7):202–6.
- Taggar GKG, Ranjit Singh: Host plant resistance in *Vigna* sp. towards whitefly, *Bemisia tabaci* (Gennadius): a review. *Entomol Gen.* 2016;36(1):1–24.
- Tanaka K, Heil M. Damage-associated molecular patterns (DAMPs) in plant innate immunity: applying the danger model and evolutionary perspectives. *Annu Rev Phytopathol.* 2021;59:53–75.
- Tikhodeyev ON. Heredity determined by the environment: Lamarckian ideas in modern molecular biology. *Sci Total Environ.* 2020;710: 135521.
- Tortorici S, Biondi A, Perez-Hedo M, Labat R, Zappala L. Plant defences for enhanced integrated pest management in tomato. *Ann Appl Biol.* 2022;180(3):328–37.
- Toyota M, Spencer D, Sawai-Toyota S, Wang JQ, Zhang T, Koo AJ, Howe GA, Gilroy S. Glutamate triggers long-distance, calcium-based plant defense signaling. *Science.* 2018;361(6407):1112–5.
- Tumlinson JH. Complex and beautiful: unraveling the intricate communication systems among plants and insects. *Annu Rev Entomol.* 2023;68:1–12.
- ul Malook S, Maqbool S, Hafeez M, Karunarathna SC, Suwannarach N. Molecular and biochemical mechanisms of elicitors in pest resistance. *Life.* 2022;12(6):844.
- Umesh K, Pandey PC, Kumar M, Pandit S. An untapped plant defense: Eggplant's steroidal glycoalkaloid solanone confers deterrence against the Oriental leafworm *Spodoptera litura*. *Entomol Gen.* 2021;42. <https://doi.org/10.1127/entomologia/2021/1213>.
- Vanden Broeck A, Cox K, Brys R, Castiglione S, Ciatelli A, Guarino F, Heinze B, Steenackers M, Vander Mijnsbrugge K. Variability in DNA methylation and generational plasticity in the lombardy poplar, a single genotype worldwide distributed since the eighteenth century. *Front Plant Sci.* 2018;9:1635.
- Vandenhole M, Dermauw W, Van Leeuwen T. Short term transcriptional responses of P450s to phytochemicals in insects and mites. *Curr Opin Insect Sci.* 2021;43:117–27.
- Velasquez-Vasconez PA, Hunt BJ, Dias RO, Souza TP, Bass C, Silva MC. Adaptation of *Helicoverpa armigera* to soybean peptidase inhibitors is associated with the transgenerational upregulation of serine peptidases. *Int J Mol Sci.* 2022;23(22):14301.
- Villagra C, Frias-Lasserre D. Epigenetic molecular mechanisms in insects. *Neotrop Entomol.* 2020;49(5):615–42.
- Wang X, Zhang Y, Zhang R, Zhang J. The diversity of pattern recognition receptors (PRRs) involved with insect defense against pathogens. *Curr Opin Insect Sci.* 2019;33:105–10.
- Wang H, Sun S, Ge W, Zhao L, Hou B, Wang K, Lyu Z, Chen L, Xu S, Guo J, et al. Horizontal gene transfer of Fhb7 from fungus underlies Fusarium head blight resistance in wheat. *Science.* 2020. <https://doi.org/10.1126/science.aba5435>.
- Wang Y, Li XF, Fan BF, Zhu C, Chen ZX. Regulation and function of defense-related callose deposition in plants. *Int J Mol Sci.* 2021;22(5):2393.
- Wang Y, Yan J, Sun JR, Shi WP, Harwood JD, Monticelli LS, Tan XL, Chen JL. Effects of field simulated warming on feeding behavior of *Sitobion avenae* (Fabricius) and host defense systems. *Entomol Gen.* 2021b;41(6):567–78.
- Wang Q, Liu Y, Yin X. Comparison of gut bacterial communities of *Locusta migratoria manilensis* (Meyen) reared on different food plants. *Biology.* 2022;11(9):1347.
- Wei J, Yang X-K, Zhang S-K, Segreaves KA, Xue H-J. Parallel metatranscriptome analysis reveals degradation of plant secondary metabolites by beetles and their gut symbionts. *Mol Ecol.* 2022;31(15):3999–4016.
- Weiss LC. Sensory ecology of predator-induced phenotypic plasticity. *Front Behav Neurosci.* 2019. <https://doi.org/10.3389/fnbeh.2018.00330>.
- Wu Q, Stolz S, Kumari A, Farmer EE. The carboxy-terminal tail of GLR3.3 is essential for wound-response electrical signaling. *New Phytol.* 2022;236(6):2189–201.
- Xia J, Guo Z, Yang Z, Han H, Wang S, Xu H, Yang X, Yang F, Wu Q, Xie W, et al. Whitefly hijacks a plant detoxification gene that neutralizes plant toxins. *Cell.* 2021;184(13):3588–3588.
- Xu X, De Mandal S, Wu H, Zhu S, Kong J, Lin S, Jin F. Effect of Diet on the Midgut Microbial Composition and Host Immunity of the Fall Armyworm, *Spodoptera frugiperda*. *Biology.* 2022;11(11):1602.
- Yamawo A, Katayama N, Suzuki N, Hada Y. Plasticity in the expression of direct and indirect defence traits of young plants of *Mallotus japonicus* in relation to soil nutritional conditions. *Plant Ecol.* 2012;213(1):127–32.
- Yang L, Li P, Li F, Ali S, Sun XQ, Hou ML. Silicon amendment to rice plants contributes to reduced feeding in a phloem-sucking insect through modulation of callose deposition. *Ecol Evol.* 2018;8(1):631–7.
- Yang FY, Saqib HSA, Chen JH, Ruan QQ, Vasseur L, He WY, You MS. Differential profiles of gut microbiota and metabolites associated with host shift of *plutella xylostella*. *Int J Mol Sci.* 2020;21(17):6283.
- Yoon SA, Harrison JG, Philbin CS, Dodson CD, Jones DM, Wallace IS, Forister ML, Smilanich AM. Host plant-dependent effects of microbes and phytochemistry on the insect immune response. *Oecologia.* 2019;191(1):141–52.
- Zeng J, Ye W, Hu W, Jin X, Kuai P, Xiao W, Jian Y, Turlings TJC, Lou Y. The N-terminal subunit of vitellogenin in planthopper eggs and saliva acts as a reliable elicitor that induces defenses in rice. *New Phytol.* 2023. <https://doi.org/10.1111/nph.18791>.
- Zhang S, Shu J, Xue H, Zhang W, Zhang Y, Liu Y, Fang L, Wang Y, Wang H. The gut microbiota in *Camellia* Weevils are influenced by plant secondary

- metabolites and contribute to saponin degradation. *mSystems*. 2020. <https://doi.org/10.1128/mSystems.00692-19>.
- Zhang X, Wang X, Guo Z, Liu X, Wang P, Yuan X, Li Y. Antibiotic treatment reduced the gut microbiota diversity, prolonged the larval development period and lessened adult fecundity of *Grapholita molesta* (Lepidoptera: Tortricidae). *Insects*. 2022;13(9):838.
- Zhang Z, Peng H, Yang D, Zhang G, Zhang J, Ju F. Polyvinyl chloride degradation by a bacterium isolated from the gut of insect larvae. *Nat Commun*. 2022. <https://doi.org/10.1038/s41467-022-32903-y>.
- Zhang S, Li Z, Shu J, Xue H, Guo K, Zhou X. Soil-derived bacteria endow *Camelia* weevil with more ability to resist plant chemical defense. *Microbiome*. 2022. <https://doi.org/10.1186/s40168-022-01290-3>.
- Zhu L, Zhang Y, Cui X, Zhu Y, Dai Q, Chen H, Liu G, Yao R, Yang Z. Host bias in diet-source microbiome transmission in wild cohabitating herbivores: new knowledge for the evolution of herbivory and plant defense. *Microbiol Spectr*. 2021. <https://doi.org/10.1128/Spectrum.00756-21>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

