Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

# Monocot crop–aphid interactions: plant resilience and aphid adaptation

De-Fen Mou[1,*], Pritha Kundu[1], Lise Pingault[1], Heena Puri[1], Sanket Shinde[1] and Joe Louis[1,2]

Globally, aphids cause immense economic damage to several crop plants. In addition, aphids vector several plant viral diseases that accelerate crop yield losses. While feeding, aphids release saliva that contains effectors, which modulate plant defense responses. Although there are many studies that describe the mechanisms that contribute to dicot plant–aphid interactions, our understanding of monocot crop defense mechanisms against aphids is limited. In this review, we focus on the interactions between monocot crops and aphids and report the recently characterized aphid effectors and their functions in aphid adaptation to plant immunity. Recent studies on plant defense against aphids in monocot-resistant and -tolerant crop lines have exploited various 'omic' approaches to understand the roles of early signaling molecules, phytohormones, and secondary metabolites in plant response to aphid herbivory. Unraveling key regulatory mechanisms underlying monocot crop resistance to aphids will lead to deeper understanding of sap-feeding insect management strategies for increased food security and sustainable agriculture.

**Addresses**
[1] Department of Entomology, University of Nebraska-Lincoln, Lincoln, NE 68583, USA
[2] Department of Biochemistry, University of Nebraska-Lincoln, Lincoln, NE 68583, USA

Corresponding author: Louis, Joe (joelouis@unl.edu)
[*] Current address: Department of Entomology and Nematology, Everglades Research and Education Center, University of Florida, Belle Glade, FL 33430, USA.

**Current Opinion in Insect Science** 2023, **57**:101038

This review comes from a themed issue on **Pests and resistance**

Edited by **Anna Whitfield** and **Dorith Rotenberg**

Available online 25 April 2023

https://doi.org/10.1016/j.cois.2023.101038

## Introduction

Aphids are one of the most damaging pests that feed on the phloem sap of diverse plants. Aphids, such as other sap-feeding insects, utilize their slender stylets present in their mouth parts to feed on the plant sap and inflict severe damage to host plants. Aphid honeydew, which is the digestive waste product, deposited on the leaf surface, facilitates fungal growth and negatively impacts the photosynthetic capability of plants. Additionally, aphids act as vectors of several plant pathogens [1,2]. Aphid-transmitted viruses also manipulate the host physiology [3•], which further enhances the impact of aphid colonization on host plants and intensifies yield losses.

In the last two decades, significant progress has been made in understanding the dicot plant–aphid interactions at the molecular–genetic level. For example, there are several studies that used *Arabidopsis*–aphid pathosystem to understand the plant defense mechanisms against sap-feeding insects. Availability of complete genome sequences and the ease with which the plants can be transformed may have led to rapid knowledge accumulation on dicot plants and the dicot plant–aphid interactions. On the contrary, we know little about monocot crop–aphid interactions, especially at the physiological, molecular, and biochemical levels. Technological advances and availability of novel genome-editing tools in the recent years are significantly contributing to the development of effective methods for transformation of monocot crops [4,5], which could potentially be exploited to characterize monocot crop responses against phloem-feeding insects. In this review paper, we summarize our current understanding of monocot crop–aphid interactions with specific emphasis on the genes, metabolites, and/or molecular mechanisms that modulate monocot crop resistance to aphids and how aphids adapt to plants. With these foci, we will conclude by highlighting the importance of filling the knowledge gaps in monocot crop–aphid interactions and suggestions for future research directions.

## Monocot crops as host of aphids

Monocot crops such as maize, wheat, rice, barley, and sorghum are among the world's economically significant crops, and hence damage by sap-feeding insects to these crops has severe economic consequences. For instance, greenbugs (*Schizaphis graminum*), which comprise of multiple biotypes, are very serious pests of wheat, barley, sorghum, and many other grasses, and cause significant crop losses in the United States [6].

**Figure 1**

Representative images of aphids on host plants. *Left panel*: corn leaf aphid; *Middle panel*: greenbug; *Right panel*: sugarcane aphid.

Greenbugs are also responsible for vectoring barley yellow dwarf virus (BYDV) and maize dwarf mosaic virus. Different aphid species vector BYDV in wheat and can cause grain losses ranging from 5% to 80% [7]. Sugarcane aphid (*Melanaphis sacchari*) is another destructive aphid causing up to 50–100% yield losses in sorghum in 25 sorghum-grown states in the United States since 2013 [6,8]. Similarly, corn leaf aphid (*Rhopalosiphum maidis*) is a significantly important pest on maize and other grasses, causing yield losses through direct feeding on crops and vectoring plant disease viruses [9]. Representative images of these sap-sucking aphids are shown in Figure 1.

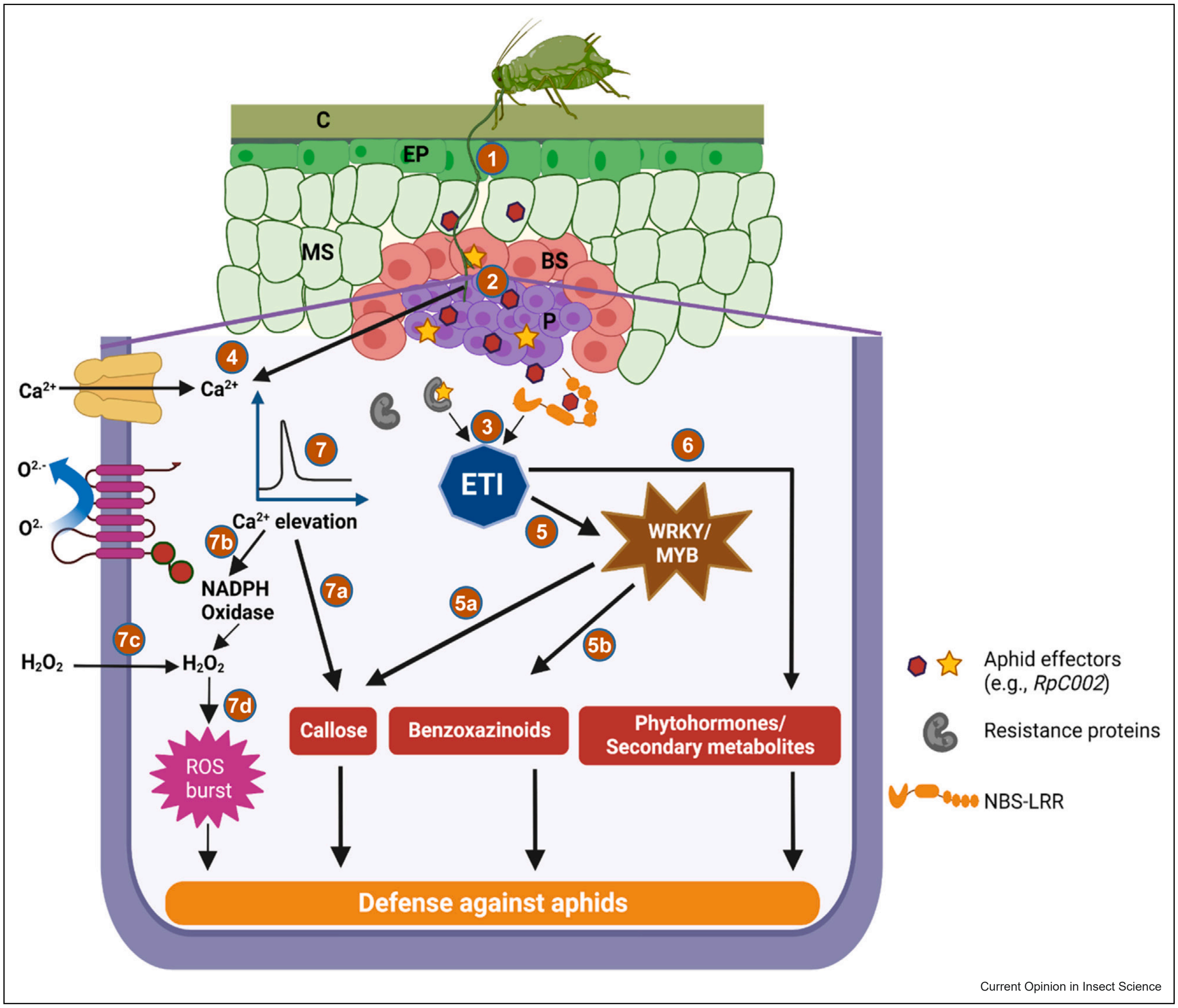
## Aphid effectors

While feeding on the host plant, aphids release salivary factors that can manipulate the plant defenses. These 'factors' or herbivore-associated molecular patterns are recognized by the plant pattern recognition receptors, leading to trigger the pattern-triggered immunity [10]. Aphid feeding also leads to the release of effectors, which can suppress the plant defense responses [11,12]. The recognition of effectors by the resistance (R) proteins further triggers effector-triggered immunity (ETI) in the host plants [13]. Essentially, these effector molecules determine successful entry and aphid colonization on host plants (Figure 2).

In the past decade, characterizing aphid effectors has been facilitated by the advancement of omics techniques and enabled prediction of putative or candidate effectors in a wide range of aphid species [14•]. Although many studies were focused on identifying effectors of aphids that feed on dicot plants, studies related to characterizing salivary effectors of aphids that feed on monocot crops have gained momentum in recent years. Intriguingly, it is suggested that aphid salivary effectors interact with plants in a host species-specific manner, which may have occurred due to plant–aphid coevolution [15]. For example, MpC002 (salivary protein C002 of *Myzus persicae*) expression in its host plants *Arabidopsis* and *Nicotiana* enhanced susceptibility to *M. persicae*, however, the expression of ApC002 (C002 ortholog of *Acyrthosiphon pisum*) did not enhance susceptibility to *M. persicae* [16]. Escudero-Martinez et al. (2020) also observed similar results when bird cherry-oat aphid (*R. padi*) effectors (*RpC002* and *Rp1*), orthologs of *M. persicae* effectors (*MpC002* and *Mp1*), expressed in barley, promoted susceptibility to *R. padi* but reduced susceptibility to *M. persicae* [17••]. However, when expressed in *Arabidopsis* and *N. benthamiana*, *RpC002* and *Rp1* promoted susceptibility to *M. persicae* [17••]. Taken together, these studies demonstrated the host plant specificity of aphid effectors. Additionally, comparison of aphid effector orthologs revealed that the effectors are fast-evolving due to high nonsynonymous versus synonymous nucleotide substitution rates, which could potentially contribute to host specialization and diversification [16,18].

Identifying and characterizing aphid effectors are critical for understanding the complex defense mechanisms involved in monocot crop–aphid interactions. Recent studies have discovered and characterized novel aphid effector proteins and shed light on aphid effectors associated with defense suppression in monocots. For example, the grain aphid (*Sitobion miscanthi*) salivary effector protein *Sm9723*, which was specifically expressed in the aphid salivary glands, was highly expressed after feeding on wheat plants [11]. The silencing of *Sm9723* using nanocarrier-mediated dsRNA delivery system resulted in decreased fecundity and survival of the grain aphid on wheat plants. Further, monitoring of aphid feeding behavior patterns using the electrical penetration graph demonstrated shortened phloem sap consumption and prolonged nonprobing by *Sm9723*-

**Figure 2**



Model depicting plant defense signaling in monocot crop–aphid interactions. Utilizing the slender stylets present in the mouth region, aphids penetrate the host cells on their way to the phloem tissue to uptake the nutrients present in the phloem sap (1). While maneuvering different plant tissues, aphids release effectors to modulate the plant defense responses (2). Upon recognition of the effectors by the plant R proteins or NBS–LRR proteins, monocot plants induce ETI (3). The aphid effectors also induce $Ca^{2+}$ ion fluxes (4), which along with ETI-mediated defenses, results in further downstream activation of defense responses. ETI induces several TFs (5) and results in induction of different phytohormones, secondary metabolites, BXs, and callose deposition that may provide resistance to aphids (5a, 5b, 6). Aphid feeding-induced $Ca^{2+}$ ion fluxes (7) also lead to the accumulation of callose deposition (7a) as well as activation of the nicotinamide adenine dinucleotide phosphate oxidase complex (7b), resulting in oxidative ROS burst-mediated hypersensitive response leading to cell death (7c, 7d). This figure is prepared based on the data compiled from several monocot crop plants' response to aphid feeding. C: cuticle; EP: epidermal cells; MS: mesophyll cells; BS: bundle sheath cells; P: phloem.

silenced aphids compared with control aphids on wheat plants [11]. Transient overexpression of *Sm9723* in *N. benthamiana* demonstrated inhibition of BAX- and INF1-induced programmed cell death, suppression of callose deposition, and decreased expression of jasmonic acid (JA)- and salicylic acid (SA)-related defense genes, suggesting that *Sm9723* may be involved in suppressing direct defenses in host plants [11].

Similar to the grain aphid, the greenbug salivary effector protein *Sg2204* enhanced wheat susceptibility to greenbugs [12]. Silencing *Sg2204* in greenbug resulted in reduced aphid feeding and performance on host plants. On the other hand, overexpression of *Sg2204* in wheat enhanced greenbug feeding and promoted aphid body weight and fecundity compared with the control wheat plants [12]. Additionally, expression of greenbug *Sg2204* in *N. benthamiana* inhibited BAX- and INF1-induced programmed cell death, suppressed callose deposition, and SA- and JA-related gene expressions [12]. Likewise, expression of bird cherry-oat aphid effector proteins, *Rp1* and *RpC002*, in barley, promoted barley susceptibility to *R. padi* by suppressing expression of defense-related genes [17••]. Further characterization of *Rp1*-transgenic barley plants revealed reduced expression of plant hormone signaling genes, suggesting that *Rp1* may enhance susceptibility to *R. padi* by suppressing plant defenses [17••]. In *Arabidopsis*, aphid feeding promotes premature leaf senescence and enhances the upregulation of a subclass of *SENESCENCE ASSOCIATED GENES* (*SAG*) [19,20]. Aphid feeding-induced leaf senescence acts as a defense mechanism to potentially counter the ability of aphids to colonize host plants [21]. *R. padi* feeding on barley plants also induced the expression of a gene encoding a *SAG-12-like* cysteine protease, which is involved in hypersenescence [22]. In contrast, expression of *SAG-12-like* gene was strongly reduced to basal levels in *Rp1*-transgenic barley plants compared with the wild-type control plants. Collectively, these data suggest that similar to the results with *Arabidopsis*–aphid interactions, monocot crops may also modulate senescence-associated physiological and developmental changes to curb the aphid colonization. However, whether the senescence-associated changes in monocot crops have a direct or indirect effect on aphid fecundity and colonization has not been tested. In Table 1, we summarize the recently identified aphid effectors of monocot crops. However, functional evaluation is needed for the studies that proposed putative effector candidates (e.g. [15]).

## Plant defense elicitors

Unlike aphid effectors that suppress plant defenses, elicitors trigger plant defense responses. Several studies have shown that aphid feeding on different monocot crops triggers plant defense responses [23–27]. However, how these elicitors are being perceived and induce defenses in monocot crops, and the molecular/biochemical function of these aphid elicitors, remains to be determined. Interestingly, it was shown that the application of a protein elicitor PeaT1, which is isolated from the fungal pathogen *Alternaria tenuissima*, induces nonspecific systemic resistance in wheat and rice against drought [28] and virus pathogen [29]. Exogenous application of PeaT1 in wheat induced SA and JA accumulation and enhanced the production of more trichomes and quantity of wax, which resulted in decreased reproduction, growth rate, and prolonged nonprobing duration of the English grain aphid (*Sitobion avenae*) [30]. PeaT1 application also enhanced plant resistance to aphids in dicot plants, such as in tomato and cucumber plants against *M. persicae* [31,32] and strawberry plants against buckthorn potato aphid (*Aphis nasturtii*) [33]. Thus, exogenous application of elicitors may contribute to aphid integrated pest management (IPM) by reducing the frequent insecticide use and resulting in a lower probable emergence of pesticide-resistant aphid population.

## Plant perception of aphid effectors

As discussed before, aphids use their stylets to maneuver different tissues in the plants. Once aphid stylet enters the cell wall, several intricate molecular interactions determine resistance or susceptibility to the aphid pests [1,34]. Nucleotide-binding site–leukine-rich repeat (NBS–LRR) genes are the largest class of plant resistance genes that encode proteins that contain NBS–LRR domains, and these genes play a critical role in plant resistance to aphids [35]. For example, the *Dn4* gene in wheat has been reported to provide resistance against the Russian wheat aphid, *Diuraphis noxia* [36]. In sorghum, the *RMES1* (resistance to *Melanaphis sacchari* 1) locus has been identified to contain five genes, namely, *Sb06g001620*, *Sb06g001630*, *Sb06g001640*, *Sb06g001645*, and *Sb06g001650*, which encode for three NBS–LRR proteins beside an RNA-binding protein and an innate immunity-associated WD40 protein [37]. Additionally, 79 NBS–LRR genes were discovered using whole-genome-wide analysis in sorghum [13]. Among those, one *NBS* gene (*Sobic.003G325100*) was highly expressed in response to greenbug feeding on the sorghum plants for 4- and 6 days post infestation (dpi), indicating its significance in plant defense against aphids [13]. Similarly, inheritance of sugarcane aphid resistance in a cross between the susceptible and resistant sorghum lines identified a single dominant locus, which associated with increased expression of several NBS–LRR genes [38], further bolsters the potential role of these genes in monocot crops in providing resistance to aphids.

### Early signaling molecules

When aphid effectors are recognized by the plant receptors, a number of secondary messenger molecules, including calcium ($Ca^{2+}$) channels, reactive oxygen species (ROS), mitogen-activated protein kinases (MAPK), and transcription factors (TFs), have been documented to play a critical role in triggering defenses [39]. For instance, overexpression of IQD1, a nuclear protein with calmodulin (CaM)-binding domain, provides resistance to *Trichoplusia ni* and *M. persicae* in *Arabidopsis* [40]. Green peach aphid feeding on *Arabidopsis* resulted in rapid rise in cytosolic $Ca^{2+}$ influx, which was regulated by the interaction between the plant defense coreceptor BRASSINOSTEROID INSENSITIVE-ASSOCIATED KINASE1 (BAK1), the plasma membrane ion channels GLUTAMATE RECEPTOR-LIKE 3.3 and 3.6 (GLR3.3 and GLR3.6), and the vacuolar ion channel TWO-PORE CHANNEL1 [41]. Pretreatment of wheat seeds with $CaCl_2$ resulted in significant upregulation of *TaCaM* genes as well as callose synthase genes, thereby rendering plants resistant to greenbugs [42]. However, the underlying mechanisms involved in $Ca^{2+}$-regulated defense signaling upon aphid infestation are yet to be explored in monocot crops. Additionally, a recent study with sorghum–sugarcane aphid interactions reported the induced expression of several ROS-scavenging enzymes besides $H_2O_2$ at 3, 6, and 9 dpi in the resistant line compared with the susceptible sorghum line [43]. Thus, $Ca^{2+}$ and ROS have emerged as critical factors inducing the plant defense signaling upon aphid infestation in monocot crops. However, further work is required to understand the underlying mechanisms by which these factors modulate defenses in monocot crops.

Upon activation of membrane-bound channels and receptors, leading to $Ca^{2+}$ and $H_2O_2$ accumulation, subsequent downstream events occur that lead to phosphorylation and transcriptional activation. In wheat, feeding by greenbugs upregulated genes in the MAPK–WRKY pathway and ROS-scavenging activities (2 and 6 hours post infestation [hpi]) [44]. Silencing of wheat *Associated with Dn resistance 1* (*Adnr1*), an NBS–LRR gene that contained integrated WRKY domains (NLR-ID), attenuated resistance response and supported higher numbers of Russian wheat aphids compared with control plants [45]. Additionally, a genome-wide association study identified a WRKY TF, *SbWRKY86*, as a key gene responsible for providing sorghum resistance to sugarcane aphids [46•]. Further, heterologous expression of *SbWRKY86* in *Arabidopsis* and *N. benthamiana* significantly reduced green peach aphid proliferation [46•]. Overexpression of *SbWRKY86* in *Arabidopsis* enhanced callose deposition, which acts as a defense mechanism to curb aphid colonization in host plants [46•]. Similarly, wheat TF *MYB31* functions as a regulator of the genes involved in the biosynthesis of benzoxazinoids (BXs) [47•], which are indole-derived secondary metabolites in monocot crops. RNA-seq analysis identified upregulation of two *TaMYB31* homologous genes in wheat after feeding by bird cherry-oat aphids. Further, *TaMYB31*-silenced wheat plants significantly reduced BX metabolites and supported higher numbers of aphids compared with the control plants [47•]. Collectively, these studies provide interesting examples to further tease apart how these rapid signals induced within the first minute after aphid invasion on monocot crops trigger downstream defense responses.

## Phytohormones and secondary metabolites

Phytohormones and secondary metabolites play a key role in protecting plants from various biotic and abiotic stresses. SA is one of the major phytohormones triggered in monocot and dicot plant systems upon attack by different aphid species [25,48]. SA is derived from either phenylalanine or isochorismate by the action of phenylalanine ammonia lyase (PAL) and isochorismate synthase, respectively [49]. Genome-wide analysis of *PAL*

**Table 1**

**Aphid effectors and elicitors on monocot crops.**

| Effector | Aphid | Host | Plant response | Mechanism | Reference |
|---|---|---|---|---|---|
| *RpC002* | *Rhopalosiphum padi* | Barley | Enhanced plant susceptibility to aphids | Unknown | [17] |
| *Rp1* | *R. padi* | Barley | Enhanced plant susceptibility to aphids | Suppressed genes related to plant defenses and senescence-associated gene (*SAG-12-like*) | [17] |
| *Sm9723* | *Sitobion miscanthi* | Wheat | Enhanced plant susceptibility to aphids | Inhibited BAX- and INF1-induced programmed cell death, suppressed callose deposition, and JA-/SA-related defense genes | [11] |
| *Sg2204* | *Schizaphis graminum* | Wheat | Enhanced plant susceptibility to aphids | Inhibited BAX- and INF1-induced programmed cell death, suppressed callose deposition, and JA-/SA-related defense genes | [12] |
| PeaT1 (elicitor) | *Sitobion avenae* | Wheat | Provided resistance to aphids | Induced SA and JA accumulation and enhanced the production of more trichomes and quantity of wax | [30] |

**Table 2**

**Plant genes/defense compounds in monocot crop–aphid interactions.**

| Gene/compound | Name of gene/metabolite | Host | Aphid | Plant response | Reference |
|---|---|---|---|---|---|
| Gene | Thionin genes (*AK252675* and *AK359149*) | Barley | *Rhopalosiphum padi* | Provided resistance to aphids | [22] |
| Gene | *Adnr1* (*Associated with Dn resistance 1*) | Wheat | *Diuraphis noxia* | NBS–LRR gene containing integrated WRKY domains provided resistance to aphids | [45] |
| Gene | *CaM* | Wheat | *Schizaphis graminum* | Enhanced callose upon aphid feeding, thereby providing resistance to aphids | [42] |
| Transcription factor | *WRKY86* | Sorghum | *Melanaphis sacchari* | Provided resistance to aphids | [46] |
| Transcription factor | *MYB31* | Wheat | *R. padi* | Regulator of the genes involved in the BX pathway and provided resistance to aphids | [47] |
| Phytohormone | SA | Sorghum | *M. sacchari* | Provided resistance to aphids | [50] |
| Phytohormone | JA | Sorghum | *M. sacchari* | Deterred aphids on settling the host plant | [55] |
| Phytohormone | Abscisic acid and cytokinins | Sorghum | *M. sacchari* | Provided tolerance to aphids | [53] |
| Phytohormone | 12-oxo-phytodienoic acid | Maize | *R. maidis* | Enhanced resistance to aphids by enhancing callose accumulation | [23] |
| Phytohormone | Ethylene | Maize | *R. maidis* | Aphid feeding induced several genes involved in ethylene pathway and provided resistance to aphids | [63] |
| Signaling molecule | ROS | Sorghum | *M. sacchari* | Aphid feeding induced several genes involved in ROS pathway | [43] |
| Secondary metabolite | Phenylpropanoids and flavonoids | Sorghum | *S. graminum* | Aphid feeding induced several genes involved in phenylpropanoid and flavonoid pathways | [57] |
| Secondary metabolite | Long-chain alcohols | Sorghum | *M. sacchari* | Enabled aphids to settle on host plant | [26] |
| Secondary metabolite | Terpenoids | Maize | *R. maidis* | Aphid feeding induced several genes involved in terpenoid biosynthesis pathway | [63] |
| Sugars | Trehalose and fructose | Sorghum | *M. sacchari* | Provided resistance to aphids | [55] |

family genes in sorghum demonstrated that eight *PAL* genes were highly induced after sugarcane aphid infestation in the aphid-resistant sorghum line [50•]. Exogenous application of SA also enhanced sorghum resistance to sugarcane aphids [50•]. A recent proteomic study on sorghum–sugarcane aphid interaction also identified enhanced accumulation of several SA-marker proteins such as pathogenesis-related proteins after aphid feeding [51], suggesting the significance of SA-mediated defenses in protecting sorghum plants against sap-feeding insects. In wheat, exogenous application of SA also enhanced resistance to English grain aphid (*Sitobion avenae*) [52]. Interestingly, SA was not a key player in providing sorghum tolerance, in which a plant can withstand or recover from damage caused by insects, to sugarcane aphids [53••]. It was hypothesized that the tolerant plants maintain their growth and development by not activating the SA-mediated defense pathway, because elevated SA levels may inhibit plant growth and development [53••,54]. Instead, it was reported that the sorghum plants utilize abscisic acid and aphid feeding-induced cytokinins to 'tolerate' aphid's attack on sorghum plant aphids [53••].

The dual role of JA has been recently reported in sorghum–sugarcane aphid interactions [55•]. At early time points (6 and 24 hpi), JA deters the aphids on settling, however, at a later time point (7 dpi), JA acts as a susceptibility factor that promoted sugarcane aphid fecundity on sorghum plants. Moreover, JA influences the sugar metabolism, which modulates the aphid reproduction on sorghum plants. Sorghum plants impaired in JA synthesis had elevated levels of aphid feeding-induced trehalose and fructose, which had a direct negative impact on SCA fecundity [55••]. In another genome-wide association study, sorghum plants that were exposed to aphids identified several genes related to JA pathway along with CaM-dependent protein kinases, WRKY TFs, and flavonoid biosynthesis [56]. Sequential herbivory on sorghum plants revealed that the sorghum plants pre-infested with greenbugs negatively impacted sugarcane aphid proliferation, however, aphid numbers were comparable when the sorghum plants were pre-infested with sugarcane aphids [57]. Greenbug pre-infested sorghum plants induced the expression of SA and JA defense-responsive marker genes and flavonoid pathway genes and impacted subsequent sugarcane aphid colonization on sorghum plants [57]. Recently, it has also been shown that the long-chain fatty alcohols present in the cuticular wax contents of young sorghum plants influenced host plant selection by aphids [26]. However, the presence of long-chain fatty alcohols did not alter sugarcane aphid survival and reproduction on sorghum plants [26]. In several economically important monocot crops, for example, maize, barley, and wheat, various secondary metabolites have been reported to act as either toxic or growth inhibitors against a wide range of aphids [58]. In maize, BX or BX-derived metabolites were involved in enhanced callose accumulation, thereby providing increased resistance to aphids [59,60]. Ultimately, monocot crops utilize a combination of strategies to resist aphid invasion and the interplay among phytohormones and secondary metabolites plays a critical role in tailoring plant resistance to biotic stresses (Figure 2). Important plant genes/defense compounds in monocot crop–aphid interactions are listed in Table 2.

## Conclusions and future directions

We have only begun to scratch the surface of the mechanisms underlying monocot crop defense mechanisms to aphids and how aphids adapt to these plant defense responses. Elucidating these mechanisms will unravel the key regulatory mechanisms underlying monocot crop resistance to sap-feeding aphid pests. Most studies conducted on monocot crop–aphid interactions are performed in a controlled environment, requiring a successful lab-to-field transition. Future studies should also consider the impact of plant- and aphid-associated microorganisms, host attack by multiple aphids and diverse pests, which will further shed light on understanding the monocot crop–aphid multitrophic interactions in natural and agricultural conditions. Although there are many recent studies that focus on transcriptomic, proteomic, and metabolomics data, the impact of aphid's feeding on monocot epigenome is yet to be explored. Previously, it was shown that the DNA methylation in pea aphids could impact aphid development through interacting with juvenile hormone, a key endocrine signal in insects [61]. Thus, it is plausible that the modification of the aphid's epigenome may enable aphids to acquire new host plants [62••]. Likewise, the mechanisms involved in the epigenetic variation in the monocot crops after aphid feeding may provide new insights on the adaptation and the regulation of the monocot crop defense mechanisms. Future research in this direction may also play a crucial role in understanding the intricacies behind host specificity and pest compatibility.

## Data Availability

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

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We apologize to colleagues for not being able to include many interesting and relevant papers due to the space constraints. Figure 2 is created using BioRender (Biorender.com). This work is supported by US National Science Foundation CAREER Grant IOS-1845588 and United States Department of Agriculture-National Institute of Food and Agriculture (USDA-NIFA) Grant 2022-67013-36882 awarded to Joe Louis.

## References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Nalam V, Louis J, Shah J: **Plant defense against aphids, the pest extraordinaire**. *Plant Sci* 2019, **279**:96-107.

2. Jayasinghe WH, Akhter MS, Nakahara K, Maruthi MN: **Effect of aphid biology and morphology on plant virus transmission**. *Pest Manag Sci* 2022, **78**:416-427.

3. • Ray S, Casteel CL: **Effector-mediated plant–virus–vector interactions**. *Plant Cell* 2022, **34**:1514-1531.

This paper has provided a comprehensive list of hemipteran effectors associated with plants and viruses.

4. Ahmar S, Mahmood T, Fiaz S, Mora-Poblete F, Shafique MS, Chattha MS, Jung K-H: **Advantage of nanotechnology-based genome editing system and its application in crop improvement**. *Front Plant Sci* 2021, **12**:663849.

5. Bredow M, Natukunda MI, Beernink BM, Chicowski AS, Salas-Fernandez MG, Whitham SA: **Characterization of a foxtail mosaic virus vector for gene silencing and analysis of innate immune responses in *Sorghum bicolor***. *Mol Plant Pathol* 2023, **24**:71-79.

6. Harris-Shultz K, Armstrong S, Jacobson A: **Invasive cereal aphids of North America: biotypes, genetic variation, management, and lessons learned**. *Trends Entomol* 2019, **15**:99-122.

7. Aradottir GI, Crespo-Herrera L: **Host plant resistance in wheat to barley yellow dwarf viruses and their aphid vectors: a review**. *Curr Opin Insect Sci* 2021, **45**:59-68.

8. Bowling RD, Brewer MJ, Kerns DL, Gordy J, Seiter N, Elliott NE, Buntin GD, Way MO, Royer TA, Biles S, *et al*.: **Sugarcane aphid (Hemiptera: Aphididae): a new pest on sorghum in North America**. *J Integr Pest Manag* 2016, **7**:12.

9. Pointeau S, Jaguenet E, Couty A, Dubois F, Rambaud C, Ameline A: **Differential performance and behavior of the corn leaf aphid, *Rhopalosiphum maidis*, on three species of the biomass crop miscanthus**. *Ind Crops Prod* 2014, **54**:135-141.

10. Bos JIB, Prince D, Pitino M, Maffei ME, Win J, Hogenhout SA: **A functional genomics approach identifies candidate effectors from the aphid species *Myzus persicae* (green peach aphid)**. *PLoS Genet* 2010, **6**:e1001216.

11. Zhang Y, Liu X, Fu Y, Crespo-Herrera L, Liu H, Wang Q, Zhang Y, Chen J: **Salivary effector Sm9723 of grain aphid *Sitobion miscanthi* suppresses plant defense and is essential for aphid survival on wheat**. *IJMS* 2022, **23**:6909.

12. Zhang Y, Liu X, Francis F, Xie H, Fan J, Wang Q, Liu H, Sun Y, Chen J: **The salivary effector protein Sg2204 in the greenbug *Schizaphis graminum* suppresses wheat defence and is essential for enabling aphid feeding on host plants**. *Plant Biotechnol J* 2022, **20**:2187-2201.

13. Zhang H, Huang J, Huang Y: **Identification and characterization of plant resistance genes (R genes) in sorghum and their involvement in plant defense against aphids**. *Plant Growth Regul* 2022, **96**:443-461.

14. • Zogli P, Pingault L, Grover S, Louis J: **Ento(o)mics: the intersection of 'omic' approaches to decipher plant defense against sap-sucking insect pests**. *Curr Opin Plant Biol* 2020, **56**:153-161.

This review summarizes plant response to sap-sucking insects using 'omic' approaches and suggests using a holistic approach to better understand plant-sap-feeding insect interactions.

15. Nicolis VF, Burger NFV, Botha A-M: **Whole-body transcriptome mining for candidate effectors from *Diuraphis noxia***. *BMC Genom* 2022, **23**:493.

16. Pitino M, Hogenhout SA: **Aphid protein effectors promote aphid colonization in a plant species-specific manner**. *Mol Plant-Microbe Int* 2013, **26**:130-139.

17. •• Escudero-Martinez C, Rodriguez PA, Liu S, Santos PA, Stephens J, Bos JIB: **An aphid effector promotes barley susceptibility through suppression of defence gene expression**. *J Exp Bot* 2020, **71**:2796-2807.

This study enhanced our understanding of the role of aphid effectors in enhancing susceptibility in monocot crops. This study not only identified a new effector of the bird cherry-oat aphid on barley but also demonstrated the role of effectors in suppressing plant defense gene signaling in barley.

18. Boulain H, Legeai F, Guy E, Morlière S, Douglas NE, Oh J, Murugan M, Smith M, Jaquiéry J, Peccoud J, *et al.*: **Fast evolution and lineage-specific gene family expansions of aphid salivary effectors driven by interactions with host-plants**. *Genome Biol Evol* 2018, **10**:1554-1572.

19. Louis J, Leung Q, Pegadaraju V, Reese J, Shah J: ***PAD4*-dependent antibiosis contributes to the *ssi2*-conferred hyper-resistance to the green peach aphid**. *Mol Plant-Microbe Int* 2010, **23**:618-627.

20. Louis J, Gobbato E, Mondal HA, Feys BJ, Parker JE, Shah J: **Discrimination of Arabidopsis PAD4 activities in defense against green peach aphid and pathogens**. *Plant Physiol* 2012, **158**:1860-1872.

21. Pegadaraju V, Knepper C, Reese J, Shah J: **Premature leaf senescence modulated by the Arabidopsis *PHYTOALEXIN DEFICIENT4* gene is associated with defense against the phloem-feeding green peach aphid**. *Plant Physiol* 2005, **139**:1927-1934.

22. Escudero-Martinez CM, Morris JA, Hedley PE, Bos JIB: **Barley transcriptome analyses upon interaction with different aphid species identify thionins contributing to resistance**. *Plant Cell Environ* 2017, **40**:2628-2643.

23. Varsani S, Grover S, Zhou S, Koch KG, Huang P-C, Kolomiets MV, Williams WP, Heng-Moss T, Sarath G, Luthe DS, *et al.*: **12-oxo-Phytodienoic acid acts as a regulator of maize defense against corn leaf aphid**. *Plant Physiol* 2019, **179**:1402-1415.

24. Zogli P, Alvarez S, Naldrett MJ, Palmer NA, Koch KG, Pingault L, Bradshaw JD, Twigg P, Heng-Moss TM, Louis J, *et al.*: **Greenbug (*Schizaphis graminum*) herbivory significantly impacts protein and phosphorylation abundance in switchgrass (*Panicum virgatum*)**. *Sci Rep* 2020, **10**:14842.

25. Koch KG, Palmer NA, Donze-Reiner T, Scully ED, Seravalli J, Amundsen K, Twigg P, Louis J, Bradshaw JD, Heng-Moss TM, *et al.*: **Aphid-responsive defense networks in hybrid switchgrass**. *Front Plant Sci* 2020, **11**:1145.

26. Cardona JB, Grover S, Busta L, Sattler SE, Louis J: **Sorghum cuticular waxes influence host plant selection by aphids**. *Planta* 2023, **257**:22.

27. Cardona JB, Grover S, Bowman MJ, Busta L, Kundu P, Koch KG, Sarath G, Sattler SE, Louis J: **Sugars and cuticular waxes impact sugarcane aphid (*Melanaphis sacchari*) colonization on different developmental stages of sorghum**. *Plant Sci* 2023, **330**:111646.

28. Shi F, Dong Y, Zhang Y, Yang X, Qiu D: **Overexpression of the PeaT1 Elicitor gene from *Alternaria tenuissima* improves drought tolerance in rice plants via interaction with a myo-inositol oxygenase**. *Front Plant Sci* 2017, **8**:970.

29. Zhang W, Yang X, Qiu D, Guo L, Zeng H, Mao J, Gao Q: **PeaT1-induced systemic acquired resistance in tobacco follows salicylic acid-dependent pathway**. *Mol Biol Rep* 2011, **38**:2549-2556.

30. Li L, Wang S, Yang X, Francis F, Qiu D: **Protein elicitor PeaT1 enhanced resistance against aphid (*Sitobion avenae*) in wheat**. *Pest Manag Sci* 2020, **76**:236-243.

31. Basit A, Farhan M, Abbas M, Wang Y, Zhao D-G, Mridha AU, Al-tawaha ARMS, Bashir MA, Arif M, Ahmed S, *et al.*: **Do microbial protein elicitors PeaT1 obtained from *Alternaria tenuissima* and PeBL1 from *Brevibacillus laterosporus* enhance defense response against tomato aphid (*Myzus persicae*)?** *Saudi J Biol Sci* 2021, **28**:3242-3248.

32. Javed K, Javed H, Qiu D: **Biocontrol potential of purified elicitor protein PeBL1 extracted from *Brevibacillus laterosporus* Strain A60 and its capacity in the induction of defense process against cucumber aphid (*Myzus persicae*) in cucumber (*Cucumis sativus*)**. *Biology* 2020, **9**:179.

33. Mouden S, Bac-Molenaar JA, Kappers IF, Beerling EAM, Leiss KA: **Elicitor application in strawberry results in long-term increase of plant resilience without yield loss**. *Front Plant Sci* 2021, **12**:695908.

34. Jaouannet M, Rodriguez PA, Thorpe P, Lenoir CJG, MacLeod R, Escudero-Martinez C, Bos JIB: **Plant immunity in plant-aphid interactions**. *Front Plant Sci* 2014, **5**:663.

35. Boissot N, Thomas S, Chovelon V, Lecoq H: **NBS-LRR-mediated resistance triggered by aphids: viruses do not adapt; aphids adapt via different mechanisms**. *BMC Plant Biol* 2016, **16**:25.

36. Liu X, Smith C, Gill B: **Identification of microsatellite markers linked to Russian wheat aphid resistance genes *Dn4* and *Dn6***. *Theor Appl Genet* 2002, **104**:1042-1048.

37. Wang F, Zhao S, Han Y, Shao Y, Dong Z, Gao Y, Zhang K, Liu X, Li D, Chang J, *et al.*: **Efficient and fine mapping of *RMES1* conferring resistance to sorghum aphid *Melanaphis sacchari***. *Mol Breed* 2013, **31**:777-784.

38. Tetreault HM, Grover S, Scully ED, Gries T, Palmer NA, Sarath G, Louis J, Sattler SE: **Global responses of resistant and susceptible sorghum (*Sorghum bicolor*) to sugarcane aphid (*Melanaphis sacchari*)**. *Front Plant Sci* 2019, **10**:145.

39. Zebelo SA, Maffei ME: **Role of early signalling events in plant-insect interactions**. *J Exp Bot* 2015, **66**:435-448.

40. Levy M, Wang Q, Kaspi R, Parrella MP, Abel S: **Arabidopsis IQD1, a novel calmodulin-binding nuclear protein, stimulates glucosinolate accumulation and plant defense**. *Plant J* 2005, **43**:79-96.

41. Vincent TR, Avramova M, Canham J, Higgins P, Bilkey N, Mugford ST, Pitino M, Toyota M, Gilroy S, Miller AJ, *et al.*: **Interplay of plasma membrane and vacuolar ion channels, together with BAK1, elicits rapid cytosolic calcium elevations in Arabidopsis during aphid feeding**. *Plant Cell* 2017, **29**:1460-1479.

42. Wang J, Song J, Wu X-B, Deng Q-Q, Zhu Z-Y, Ren M-J, Ye M, Zeng R-S: **Seed priming with calcium chloride enhances wheat resistance against wheat aphid *Schizaphis graminum* Rondani**. *Pest Manag Sci* 2021, **77**:4709-4718.

43. Pant S, Huang Y: **Elevated production of reactive oxygen species is related to host plant resistance to sugarcane aphid in sorghum**. *Plant Signal Behav* 2021, **16**:1849523.

44. Zhang Y, Fu Y, Wang Q, Liu X, Li Q, Chen J: **Transcriptome analysis reveals rapid defence responses in wheat induced by phytotoxic aphid *Schizaphis graminum* feeding**. *BMC Genom* 2020, **21**:339.

45. Nicolis V, Venter E: **Silencing of a unique integrated domain nucleotide-binding leucine-rich repeat gene in wheat abolishes *Diuraphis noxia* resistance**. *Mol Plant-Microbe Int* 2018, **31**:940-950.

46. • Poosapati S, Poretsky E, Dressano K, Ruiz M, Vazquez A, Sandoval E, Estrada-Cardenas A, Duggal S, Lim J-H, Morris G, *et al.*: **A sorghum genome-wide association study (GWAS) identifies a WRKY transcription factor as a candidate gene underlying sugarcane aphid (*Melanaphis sacchari*) resistance**. *Planta* 2022, **255**:37.

This study demonstrated the role of the newly identified WRKY transcription factor in providing sorghum resistance to sugarcane aphids.

47. • Batyrshina ZS, Shavit R, Yaakov B, Bocobza S, Tzin V: **The transcription factor *TaMYB31* regulates the benzoxazinoid biosynthetic pathway in wheat**. *J Exp Bot* 2022, **73**:5634-5649.

This study discovered a previously unknown regulatory function of the transcription factor *TaMYB31* in the BX pathway resistance to aphids in wheat.

48. Hu Z, Zhong X, Zhang H, Luo X, Wang Y, Wang Y, Liu T, Zhang Y, Wang X, An H, *et al*.: ***GhMYB18* confers *Aphis gossypii* Glover resistance through regulating the synthesis of salicylic acid and flavonoids in cotton plants**. *Plant Cell Rep* 2023, **42**:355-369.

49. Dempsey DA, Vlot AC, Wildermuth MC, Klessig DF: **Salicylic acid biosynthesis and metabolism**. *Arab Book* 2011, **9**:e0156.

50. • Pant S, Huang Y: **Genome-wide studies of *PAL* genes in sorghum and their responses to aphid infestation**. *Sci Rep* 2022, **12**:22537.

This study showed *PAL* genes enhance sorghum resistance to sugarcane aphid through regulating SA-mediated defense responses.

51. Grover S, Cardona JB, Zogli P, Alvarez S, Naldrett MJ, Sattler SE, Louis J: **Reprogramming of sorghum proteome in response to sugarcane aphid infestation**. *Plant Sci* 2022, **320**:111289.

52. Feng J-L, Zhang J, Yang J, Zou L-P, Fang T-T, Xu H-L, Cai Q-N: **Exogenous salicylic acid improves resistance of aphid-susceptible wheat to the grain aphid, *Sitobion avenae* (F.) (Hemiptera: Aphididae)**. *Bull Entomol Res* 2021, **111**:544-552.

53. •• Grover S, Agpawa E, Sarath G, Sattler SE, Louis J: **Interplay of phytohormones facilitate sorghum tolerance to aphids**. *Plant Mol Biol* 2022, **109**:639-650.

This study provides information on how phytohormone modulates plant tolerance in an aphid tolerant sorghum plant. The study offers valuable insights on tolerant plants, while most of other studies focused on resistant plants.

54. van Butselaar T, Van den Ackerveken G: **Salicylic acid steers the growth–immunity tradeoff**. *Trends Plant Sci* 2020, **25**:566-576.

55. •• Grover S, Puri H, Xin Z, Sattler S, Louis J: **Dichotomous role of jasmonic acid in modulating sorghum defense against aphids**. *Mol Plant-Microbe Int* 2022, **35**:755-767.

A key study that discovered dichotomous role of JA in sorghum defense to aphids. JA deters early aphid colonization in sorghum, but enhanced sorghum susceptibility at later time points by modulating fructose and trehalose levels.

56. Punnuri SM, Ayele AG, Harris-Shultz KR, Knoll JE, Coffin AW, Tadesse HK, Armstrong JS, Wiggins TK, Li H, Sattler S, *et al*.: **Genome-wide association mapping of resistance to the sorghum aphid in *Sorghum bicolor***. *Genomics* 2022, **114**:110408.

57. Puri H, Ikuze E, Ayala J, Rodriguez I, Kariyat R, Louis J, Grover S: **Greenbug feeding-induced resistance to sugarcane aphids in sorghum**. *Front Ecol Evol* 2023, **11**:1105725.

58. Smith CM, Chuang W-P: **Plant resistance to aphid feeding: behavioral, physiological, genetic and molecular cues regulate aphid host selection and feeding: plant resistance to aphid feeding**. *Pest Manag Sci* 2014, **70**:528-540.

59. Meihls LN, Handrick V, Glauser G, Barbier H, Kaur H, Haribal MM, Lipka AE, Gershenzon J, Buckler ES, Erb M, *et al*.: **Natural variation in maize aphid resistance is associated with 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one glucoside methyltransferase activity**. *Plant Cell* 2013, **25**:2341-2355.

60. Ahmad S, Veyrat N, Gordon-Weeks R, Zhang Y, Martin J, Smart L, Glauser G, Erb M, Flors V, Frey M, *et al*.: **Benzoxazinoid metabolites regulate innate immunity against aphids and fungi in maize**. *Plant Physiol* 2011, **157**:317-327.

61. Walsh TK, Brisson JA, Robertson HM, Gordon K, Jaubert-Possamai S, Tagu D, Edwards OR: **A functional DNA methylation system in the pea aphid, *Acyrthosiphon pisum***. *Insect Mol Biol* 2010, **19**:215-228.

62. •• Shih P-Y, Sugio A, Simon J-C: **Molecular mechanisms underlying host plant specificity in aphids**. *Ann Rev Entomol* 2023, **68**:431-450.

This publication provides a comprehensive review of aphid host specificity and current understanding and knowledge gaps in underlying molecular mechanisms of aphid host plant specificity.

63. Pingault L, Varsani S, Palmer N, Ray S, Williams WP, Luthe DS, Ali JG, Sarath G, Louis J: **Transcriptomic and volatile signatures associated with maize defense against corn leaf aphid**. *BMC Plant Biol* 2021, **21**:138.