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Defense strategies and associated phytohormonal regulation in *Brassica* plants in response to chewing and sap-sucking insects

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Plants have evolved distinct defense strategies in response to a diverse range of chewing and sucking insect herbivory. While chewing insect herbivores, exemplified by caterpillars and beetles, cause visible tissue damage and induce jasmonic acid (JA)-mediated defense responses, sucking insects, such as aphids and whiteflies, delicately tap into the phloem sap and elicit salicylic acid (SA)-mediated defense responses. This review aims to highlight the specificity of defense strategies in *Brassica* plants and associated underlying molecular mechanisms when challenged by herbivorous insects from different feeding guilds (i.e., chewing and sucking insects). To establish such an understanding in *Brassica* plants, the typical defense responses were categorized into physical, chemical, and metabolic adjustments. Further, the impact of contrasting feeding patterns on *Brassica* is discussed in context to unique biochemical and molecular *modus operandi* that governs the resistance against chewing and sucking insect pests. Grasping these interactions is crucial to developing innovative and targeted pest management approaches to ensure ecosystem sustainability and *Brassica* productivity.

KEYWORDS

herbivore feeding pattern, defense responses, *Brassica*, chewing herbivores, sap-sucking

1 Introduction

The co-evolutionary arms race between plants and herbivorous insects has shaped the fascinating diversity of defense strategies observed in nature (Kareiva, 1999; Fürstenberg-Hägg et al., 2013). Plants have developed sophisticated defense responses to counter insect attacks, adapting to different herbivore feeding guilds. These defense responses are intricately connected to signaling pathways such as Jasmonic acid (JA), Salicylic Acid (SA), and Ethylene (ET) (War et al., 2012). These signaling pathways can regulate direct and indirect plant defense strategies that effectively deter, repel, and combat herbivorous insects (Kunkel and Brooks, 2002; Bari and Jones, 2009; Checker et al., 2018). The coordination of these defense pathways enables plants to deploy tailored and multifaceted responses, enhancing their ability to withstand and adapt to herbivores attack (Rejeb et al., 2014; Checker et al., 2018; Aftab and Roychoudhury, 2021).

Brassica, globally recognized as the second largest oilseed crop after soybean, holds a prominent position in the agricultural landscape (Attia et al., 2021). With an annual global production of around 72 million metric tons, this versatile crop plays a pivotal role in addressing food security, owing to its diverse uses, including oil extraction and as a crucial component in human diets (Mabry et al., 2021; Chen et al., 2023). However, *Brassica* crops face significant annual losses due to biotic stressors, particularly insect pests (Warwick, 2011; Baldwin et al., 2021). Approximately, 50-60% of *Brassica* crop production is believed to be susceptible to losses caused by insects and mites (Poveda et al., 2020). The worldwide pest management of crop plants including *Brassica* plants highly relies on insecticides which poses great environmental risks (Warwick, 2011). The susceptibility of *Brassica* crops to a multitude of insect pests and concerns regarding insecticide treatments underscore the pressing need for comprehensive understanding and the development of effective and sustainable control strategies to mitigate yield losses and safeguard its economic significance.

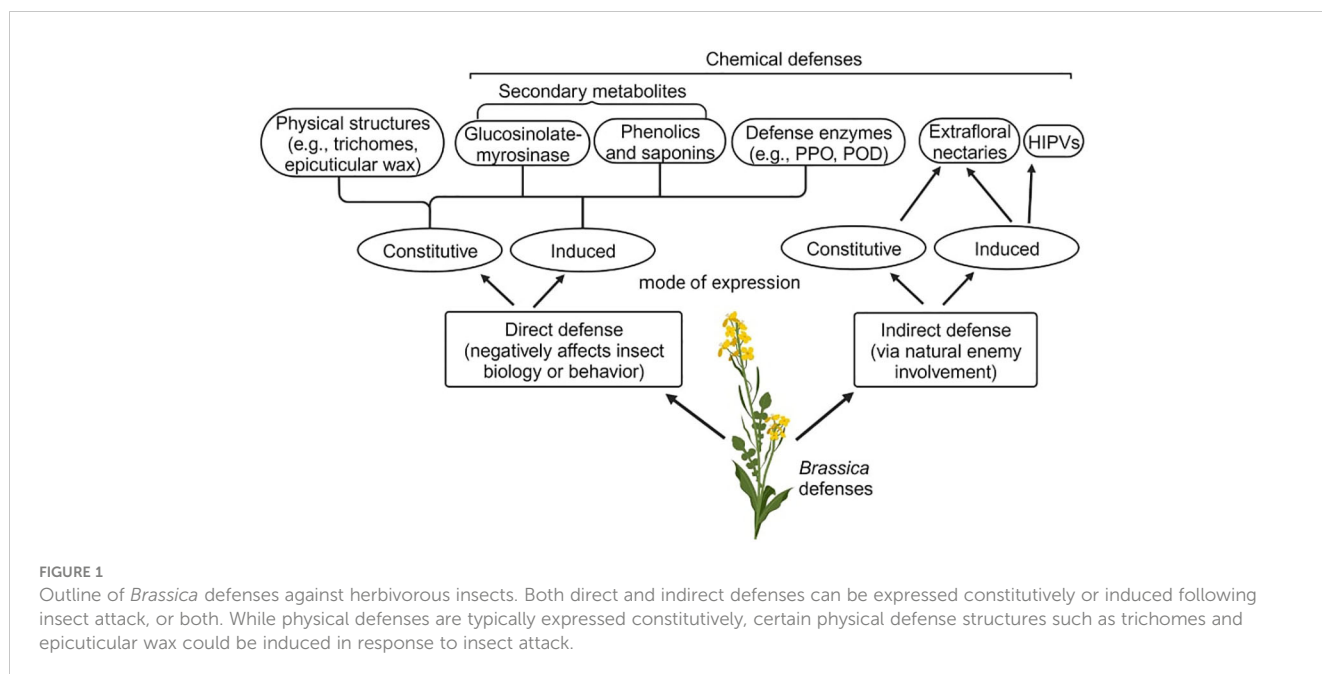
The plant immune system plays a pivotal role in shaping the dynamic interplay between plants and insect herbivores (Zhou and Zhang, 2020). As plants have evolved diverse defense strategies in response to varied feeding patterns of chewing and sucking insects, the importance of understanding these intricate molecular mechanisms requires specific attention (War et al., 2018). The ability of plants to discern and mount tailored defense responses, such as JA-mediated defenses against chewing insects and SA-mediated defenses against sucking insects, showcases the sophistication of their immune system (Nguyen et al., 2016; Stroud et al., 2022). Recognizing the specificity of these defense strategies is not only essential for comprehending plant-insect interactions but also holds immense significance for devising targeted pest management strategies (Vega-Álvarez et al., 2023). In the context of *Brassica* plants, where distinct physical, chemical, and metabolic adjustments contribute to defense (Ahuja et al., 2011), unravelling the intricacies of the plant immune system is key to developing innovative approaches that enhance ecosystem sustainability and ensure the productivity of *Brassica* crops.

This review primarily focuses on the interactions between herbivorous insects and plants belonging to the *Brassica* genus. Focusing on *Brassica*, we aim to provide a comprehensive synthesis of how chewing and sucking behaviors influence the activation of defense strategies mainly relying on involvement of JA and SA, the underlying molecular mechanisms (a specific focus on SA-JA crosstalk), and the impact on physical defense traits. Investigating *Brassica*'s responses, we highlight valuable insights into the broader mechanisms governing plant-insect interactions and defense strategies. In summary, this review will delve into the intricate interplay between herbivore feeding guilds and plant defense responses, with a specific emphasis on the unique attributes observed in *Brassica* species. By shedding light on the evolutionary trajectories of defense strategies, this study seeks to contribute to our understanding of the dynamic interactions between insects and plants in shaping the ecological landscape.

2 Defense responses and their mode of expression in *Brassica* against herbivorous insects

Plants have been coexisting with and facing endless challenges from herbivorous insects for hundreds of millions of years. Plants, including *Brassica* species, have evolved an arsenal of defense strategies to combat herbivore attack (Gatehouse, 2002; Ahuja et al., 2010). Plant defenses are broadly classified as direct and indirect defenses. Direct defenses are plant traits (e.g., trichomes, secondary metabolites) that reduce their susceptibility to insect herbivores or negatively affect insect biology or behavior (Chen, 2008; War et al., 2012). Indirect defenses are traits (e.g., herbivore-induced plant volatiles (HIPVs), extrafloral nectaries) that promote the attraction or efficacy of natural enemies of herbivorous insects such as predators and parasitoids (Heil, 2008; Aljibory and Chen, 2018). Both direct and indirect defenses can be expressed constitutively (i.e., always present in plants) or induced following insect attack. The metabolic costs of induced defenses are considered to be lower than constitutive defenses, particularly when insect pressure is sporadic (Karban, 2011), and there could be a trade-off between constitutive and induced defense responses (Zhang et al., 2008). Plant phytohormone signaling networks, particularly JA and SA signaling pathways play crucial roles in optimizing plant defenses against insect herbivores (Verma et al., 2016). In particular, the JA signaling cascade is considered a master regulator of induced plant responses to insect attack (Erb et al., 2012).

Brassica plants show a diverse array of direct physical and chemical defenses against herbivorous insects (Figure 1). Among physical defenses, epicuticular wax and trichomes account for one of the first lines of defenses against herbivores. For example, the presence of epicuticular wax was found to enhance *Brassica oleracea* resistance to the diamondback moth (*Plutella xylostella*), flea beetles (*Phyllotreta* spp.), and cabbage stink bugs (*Eurydema* spp.) (Bohinc et al., 2014; Silva et al., 2017). Although such morphological structures are constitutive defenses in *Brassica* plants, trichome density and epicuticular wax composition can be



induced when challenged by insect herbivores (Traw and Dawson, 2002; Blenn et al., 2012).

The primary direct chemical defense in *Brassica* is the production of nitrogen- and sulfur-containing secondary metabolites known as glucosinolates (GS) that negatively affect insect herbivores (Hopkins et al., 2009; Jeschke et al., 2021), specifically generalist insects such as *Spodoptera littoralis* and *Mamestra brassicae* (Jeschke et al., 2017). GS are diverse in their structures (i.e., more than 130 known compounds) and are expressed constitutively in *Brassica* (Hopkins et al., 2009; Agerbirk and Olsen, 2012). The composition of GS in the family Brassicaceae varies depending on plant species, plant organs, ontogenetic stages, agricultural practices, and environmental conditions (Textor and Gershenson, 2009; Ahuja et al., 2010). Although GSs per se could be toxic to insects (Kim et al., 2008), they become highly toxic when hydrolyzed by a specific enzyme called myrosinase and converted to toxic compounds such as isothiocyanates and nitriles (Agrawal and Kurashige, 2003; Wittstock et al., 2016). Both GSs and myrosinase are stored in adjacent but separate cells and GSs only encounter the enzyme when plant tissues are mechanically damaged by insect feeding (Hopkins et al., 2009).

Even though Brassicaceous plants possess GSs constitutively, their levels, particularly that of indole GSs, in tissues can be induced rapidly and substantially following shoot or root herbivory by insects (van Dam and Raaijmakers, 2006; Travers-Martin and Müller, 2007; Textor and Gershenson, 2009). Insect attack can cause a redistribution of GSs in different organs or *de novo* synthesis of GSs in both attacked (i.e., local induction) and non-attacked (i.e., systemic induction) tissues (Hopkins et al., 2009; Touw et al., 2020). Likewise, the levels of myrosinase enzyme in plant tissues might increase upon insect feeding in some cases (Pontoppidan et al.,

2003; Travers-Martin and Müller, 2007; Cachapa et al., 2021), although the impacts of such induction on plant defenses remain uncertain (Textor and Gershenson, 2009).

Considering that some specialist herbivores such as *Pieris rapae* and *P. xylostella* can neutralize GS (Ratzka et al., 2002; Wittstock et al., 2004), other secondary metabolites such as phenolic compounds (e.g., flavonoids) and terpenoids (e.g., saponins) can confer direct resistance to specialist insects (Badenes-Perez et al., 2014; Ibrahim et al., 2018; Kovalikova et al., 2019). Moreover, cultivated *Brassica* plants can produce antioxidant defense enzymes such as polyphenol oxidase (PPO) and peroxidase (POD) and defensive proteins such as trypsin proteinase inhibitors (TPI) to defend specialist insects (Khattab, 2007; Ahmed et al., 2022). All these secondary metabolites and antioxidant enzymes can be present in *Brassica* constitutively or induced following insect attack, or both (Ibrahim et al., 2018; Kovalikova et al., 2019).

Brassicaceous plants produce herbivore-induced plant volatiles (HIPVs) when attacked by pest herbivores (Figure 1), including glucosinolate breakdown products such as nitriles and isothiocyanates (Uefune et al., 2012; Mathur et al., 2013c; Zhou and Jander, 2022). The emission of HIPVs can deter insect herbivores (Verheggen et al., 2013) and attract their natural enemies, thus facilitating the top-down control of herbivorous insects (Puente et al., 2008; Mathur et al., 2013c). Furthermore, *Brassica juncea* can produce extrafloral nectaries as an indirect defense, which can be present in plants constitutively, but the amount of nectar production could be induced following insect feeding (Figure 1) (Mathur et al., 2013a). The possession and induction of such nectaries could support natural enemies of herbivores by providing alternative foods (Jamont et al., 2013; Mathur et al., 2013a).

3 Impacts of herbivore feeding patterns on *Brassica* defense mechanisms

3.1 Jasmonic acid-mediated defenses in response to chewing insects

The majority of all known herbivorous insects belong to the orders, Coleoptera and Lepidoptera, that physically consume the plant tissues with their mouth parts evolved for chewing (Schoonhoven et al., 2005). For example, caterpillars follow a special pattern when feeding, removing uniform pieces of leaf tissue in a highly choreographed and predictable manner (Howe and Jander, 2008). Plants have developed various intricate mechanisms to perceive and respond to damage caused by chewing insects. The direct attack by chewing insects orchestrates a prompt and targeted host plant response, commencing a cascade of molecular events that yields in activation of JA-mediated plant defenses (Walling, 2000; Bari and Jones, 2009). Upon detection of chewing damage, plants release specific signals, such as damage-associated molecular patterns (DAMPs) and herbivore-associated molecular patterns (HAMPs) (Mithofer and Boland, 2008; Stahl et al., 2018; Uemura and Arimura, 2019). These signals are perceived by the plant receptors, triggering a signaling cascade that ultimately leads to the synthesis and accumulation of JA signaling.

As the core signaling pathway, JA is activated in response to herbivore chewing and wounding damage. The biosynthesis and signaling of JA have been reviewed elsewhere in detail (Hou and Tsuda, 2022; Kundu et al., 2023). Briefly, JA biosynthesis exist in various cellular compartments, primarily in the chloroplasts, peroxisomes, and cytosol (Staswick and Tiryaki, 2004; Erb et al., 2012; Wasternack and Hause, 2013). The precursor of JA biosynthesis is the unsaturated fatty acid linolenic acid (LA) which is derived from membrane phospholipids. Lipoxygenase (LOX) oxidize LA to 13-hydroperoxylinolenic acid (13-HPOT) which is afterward converted to 12-oxophytodienoic acid (OPDA) following two oxidation phases, allene oxide synthase (AOS) and allene oxide cyclase (AOC) (Ruan et al., 2019). Following the transportation of OPDA from chloroplast to the peroxisome, enzymatic reactions finally yield JA and its derivatives in cytosol (Erb et al., 2012; Ruan et al., 2019).

JA is perceived by F-box protein coronatine insensitive1 (COI1) which forms the SCF (Skp1-Cullin-F-box) E3 ubiquitin ligase complex, SCF^{COI1} (Yan et al., 2013). When JA is absent, jasmonate zim-domain (JAZ) proteins interact with transcription factors (TFs), repressing their activity (Katsir et al., 2008). For example, JAZ deficient mutants lead to increased expression of diverse transcript factors that yielded elevated resistance against the chewing insect *Trichoplusia ni* (Guo et al., 2018). JA-Ile binding to COI1 triggers the degradation of JAZ through the 26S proteasome (Ruan et al., 2019). This molecular cascade facilitates the activation of the transcription factor MYC2 and its homologs, culminating in the induction of JA-responsive genes harboring the G-box motif (CACATG) (Schweizer et al., 2013). Noteworthy participants in this regulatory network

include auxiliary factors, exemplified by the mediator subunit MED25. Another significant transcription factor that is regulated by JAZ, Ethylene Insensitive 3 (EIN3) induces expression of ethylene-responsive TFs (ERFs) such as Octadecanoid-responsive AP2/ERF domain protein 59 (ORA59) (Vos et al., 2013). The MYCs constitute a significant group of TFs in response to chewing insects since they construct a mechanism that prioritize the responses to chewing damage and associated cues (Erb et al., 2012). The evidence clearly suggested that chewing insect feeding causes overexpression of MYC2 branch of JA pathway that activates JA-responsive genes, such as Vegetative Storage Protein 2 (VSP2) (Sheard et al., 2010). Furthermore, other TFs such as MYC3 and 4 interact with MYC2 and activate JA-mediated plant defense mechanisms against the damage by *S. littoralis* that induces JA accumulation in *Arabidopsis* (Schweizer et al., 2013; Schmiesing et al., 2016).

The genetic manipulation studies have revealed that several genes in JA signaling are overexpressed and play significant roles in response to chewing insects. For example, several LOX genes, *lox2*, *3*, *4*, and *6*, despite their distinct spatial expression, are induced upon wound damage (Wasternack and Hause, 2013). The *lox Arabidopsis* plants become severely susceptible to attack by *S. littoralis* feeding and artificial wounding with varying results for combinations of *lox* mutants (Glauser et al., 2008; Chauvin et al., 2013). Similarly, AOS-deficient *Arabidopsis* plants are susceptible to *S. littoralis* while AOS-overexpressed plants have enhanced resistance to this pest (Laudert et al., 2000). JA-mediated plant defenses against *S. littoralis* are completely impaired in *coi1 Arabidopsis* plants as well (Bodenhausen and Reymond, 2007). Similarly, *H. armigera* feeding was increased on *myc Arabidopsis* plants and decreased on MYC2-overexpressed *Arabidopsis* plants (Dombrecht et al., 2007). Other examples include the knockout of *JAR* and *JOX* genes, which results in an impaired JA signaling pathway that could not enhance resistance against wounding and *Mamestra brassicae*, respectively (Suza and Staswick, 2008; Caarls et al., 2017).

JA-mediated chemical defenses of *Brassica* plants include several classes of secondary metabolites such as GSs, flavonoids, terpenoids, alkaloids, proteinase inhibitors (Howe and Jander, 2008). GSs are the predominant secondary metabolites present in *Brassica* plants, and most of the genes involved in GS biosynthesis are JA-inducible. The expression of these genes is governed by a functional regulatory module constituted by MYC and MYB TFs (Erb and Reymond, 2019). For instance, *Arabidopsis* feeding by *S. exigua* activates the JA pathway, resulting in an enhanced accumulation of GSs (Mewis et al., 2005). Notably, the genes participating in the biosynthetic pathway of GS are induced by JA, facilitated by the involvement of the bHLH TFs MYC2, MYC3, MYC4, and MYC5 (Yang et al., 2011; Schweizer et al., 2013). A coordinated functioning of MYB TFs is responsible for distinct branches of GSs biosynthesis, namely, methionine-derived aliphatic GS (MYB28, MYB29, and MYB76) and tryptophan-derived indole GS (MYB34, MYB51, and MYB122), which directly interact with MYC TFs, conferring resistance against *S. littoralis* (Gigolashvili, Berger, et al., 2007; Gigolashvili, Yatusевич, et al., 2007; Gigolashvili et al., 2008, 2009; Schweizer et al., 2013). The overexpression profile of MYB TFs such as MYB28 and MYB51 caused increased production of aliphatic and indole GS, respectively

both of which adversely affected *S. exigua* (Gigolashvili, Berger, et al., 2007; Gigolashvili, Yatusевич, et al., 2007). In contrast, a double mutant *myb28 myb29* lacking aliphatic GS was more susceptible to the feeding activity by *Mamestra brassicae* (Beekwilder et al., 2008).

JA-mediated expression of different transcript factors can cause release of other secondary metabolites in addition to GSs. For example, *Arabidopsis* JAZ proteins interacting with bHLH TF MYB, regulate anthocyanin biosynthesis (Qi et al., 2011). In the presence of JA-Ile, the JAZ proteins are degraded, leading to the accumulation and overexpression of the WD-repeat-bHLH-MYB complex (Goossens et al., 2017). JA and its methyl esters MeJA are key elicitors of terpenoid indole alkaloid (TIA) biosynthesis. The key components of JA, including the JA co-receptor Coronatine Insensitive 1 (COI1) and the five JASMONATE ZIM-domain proteins CrJAZ1/2/3/8/10 have been characterized for their roles in regulating TIA biosynthesis (Patra et al., 2018). Terpenoids and GLVs often comprise a large and diverse portion of the volatile blends emitted by intact as well as damaged *Brassica* plants (van Poecke et al., 2001; Mumm et al., 2008).

Altogether, JA mediates various plant defenses against multiple attackers, especially herbivorous insects (Zhang et al., 2017). The biosynthetic pathways that lead to specialized metabolites especially secondary compounds such as terpenoids, alkaloids and GSs have been proven to be induced by the JA signaling pathway (De Geyter et al., 2012; Goossens et al., 2017). For example, *Arabidopsis* plants lacking GS biosynthesis responsive genes are highly susceptible to a wide range of chewing herbivores (Erb et al., 2012). *Arabidopsis fah1-7* deficient in the sinapoyl malate enzyme exhibits increased susceptibility to *P. brassicae* (Onkokesung et al., 2016), whereas reduced levels of kaempferol 3,7-dihamnoside in MYB75 overexpression lines correlate with increased *P. brassicae* performance.

JA defends plants indirectly by attracting natural enemies of insect pests through volatile emissions (Ozawa et al., 2008; Kappers et al., 2010). Parasitoids exhibit a keen ability to recognize HIPVs that are associated with their specific hosts and host plants. In specialized parasitoids, this ability may be innate (De Moraes et al., 1998), whereas generalist parasitoids learn to distinguish between different HIPV blends (Cardé and Bell, 1995). Natural enemies are responsive to common terpenoids, such as monoterpene (E)-ocimene and the monoterpene alcohol linalool (Dicke et al., 1990; Du et al., 1998), the methylene monoterpene (3E)-4,8-dimethyl-1,3,7-nonatriene, the methylene sesquiterpene (3E,7E)-4,8,12-dimethyl-1,3,7,11-tridecetraene (Dicke et al., 1990; Khan et al., 1997) and the sesquiterpene (E)- β -caryophyllene (Flint et al., 1979; Rasmann et al., 2005; Xiao et al., 2012). The emission levels of HIPVs are changed by *P. rapae* that attract parasitic wasps *Cotesia rubecula* (van Poecke et al., 2001; van Poecke and Dicke, 2002). The parasitism of *P. rapae* caterpillars by *C. rubecula* enhances plant fitness, increasing plant reproduction (van Loon et al., 2000). The perception ability of natural enemies of HIPVs emitting host plants may highly depend on survival strategy. For example, the specialist *Cotesia rubecula* can discriminate between induced host plants exposed to the damage by host larvae parasitized by conspecifics, while the generalist *C. glomerata* was unable to perform such a discrimination (Fatouros et al., 2005).

3.2 Salicylic acid-mediated defenses in response to sap-sucking insects

Sap-sucking insects encompassing a diverse array of pests, including aphids, whiteflies, thrips and so on, have a pivotal position in the functioning network of tropic levels. Sap-sucking insects exhibit distinct mouthpart morphology that are evolved based on their survival strategies. Several groups including aphids, mealybugs, psyllids and whiteflies search for a feeding site in the phloem veins, extending their stylets through cuticle, epidermis, and mesophyll (Walling, 2008). Thrips and mites suck the epidermal and mesophyll cell contents, puncturing using tube-like mouthparts while leafhoppers feed both on phloem and xylem contents (Mewis et al., 2005; Walling, 2008). The sap-sucking mouth parts do not cause a great damage on plant tissues by individual sap-suckers when compared with chewing insects while the sap-sucking damage may still have importance for plant immune system, especially when attacked by a settled population (Schoonhoven et al., 2005; Zhao et al., 2009). The significance of sap-sucking insects to plant immunity is not limited to tissue damage since an array of elicitors may accompany these pests while invading the host plants. Salivary, gut and honeydew endosymbiotic bacteria, salivary and ovipositional components, and associated plant pathogens such viruses may be involved in their attack on host plants (Wari et al., 2019). Once sap-sucking insects launch an attack on plant vascular tissues, plants induce SA-mediated defense responses.

SA is produced via two different signaling pathways; the isochorismate (IC) pathway, located in the chloroplast of plant cells and mediated by IC-synthase (ICS), and the phenylalanine ammonium (PA)-mediated by PA-lyase (PAL) pathways both of which are derived from chorismate (Dempsey et al., 2011). The core metabolite required for both signaling pathways is chorismate which is the main source of SA production in *Arabidopsis* (Wildermuth et al., 2001). *Arabidopsis* plants possess two ICS promoters, ICS1 and ICS2 which govern the chorismate-isochorismate conversion (Macaulay et al., 2017). The ICS1 promoter have WRKY and MYB TF binding sites which play roles in plant response against herbivores. These ICS enzymes individually or in combination can yield isochorismate (Strawn et al., 2007). IC amino acid conjugation producing isochorismate-9-glutamate, results in SA accumulation via *avrPphB* Susceptible3 (PBS3), a process exclusively characterized in *Arabidopsis*, followed either by spontaneous decomposition or enzymatic conversion via Enhanced Pseudomonas Susceptibility 1 (EPS1) (Jagadeeswaran et al., 2007; Nobuta et al., 2007; Rekhter et al., 2019; Torrens-Spence et al., 2019). The transportation of IC from chloroplast to cytosol requires Enhanced Disease Susceptibility 5 (EDS5) protein, a MATE transporter (Nawrath and Métraux, 1999; Nawrath et al., 2002). The studies with ICS mutants clearly revealed that SA can still be synthesized and accumulated. Further assessments including PAL-deficient plants have demonstrated that this SA biosynthesis in *Arabidopsis* continues via PAL pathway (Mauch-Mani and Slusarenko, 1996; Hu et al., 2010). However, there is a possible interplay between ICS- and PAL-mediated SA accumulation since a significant reduction was observed in ICS-mediated SA accumulation, when *Arabidopsis* plants lacked PAL activity. In PAL

-mediated SA pathway, chorismate is converted to Phenylalanine that derivates *Trans*-cinnamic acid (t-CA) and then produces SA via benzoic acid (BA) via Abnormal Inflorescence Meristem 1 (AIM1) functioning (Dempsey et al., 2011).

The involvement of SA signaling in plant defense systems could be either independent of or dependent on NPR1, a master regulator of plant defense mechanisms. In an NPR1-dependent manner, redox signals influence the activity of NPR1. For example, activated THIOREDOXIN h5 can reduce disulfide bonds in NPR1, causing monomerization and nuclear translocation of NPR1 (Figure 2) (Spoel et al., 2009). The NPR1 was first identified in a screening of *Arabidopsis* mutants that were unable to activate the expression of PR genes or disease resistance (Cao et al., 1994; Delaney et al., 1994; Shah et al., 1997). The promoter region of the NPR1 gene involves W-box sequences, which function as binding sites for WRKY family proteins. The mutations in the W-box sequences impair the expression levels of NPR1 which underscores the significance of WRKY TFs in regulation of SA-NPR1 signaling (Yu et al., 2001). NPR1 functions in two places namely the cytoplasm and the nucleus. The cytosolic NPR1 functioning is more related to its interplay with JA-responsive TFs, that finally yields their SA-JA crosstalk (Figure 2A), while nuclear NPR1 is responsible for resistance development in response to stress factors. NPR1 directly interacts with TGA TFs and NIMIN proteins. The TGA TFs directly interact with PR-1 gene through binding to the activation sequence-1 (*as-1*) in its promoter region (Lebel et al., 1998). The requirement of SA for interactions between NPR1 and TGA TFs is highly TGA factor-specific. Interestingly, the presence of SA may also induce the expression of NIMIN1, NIMIN2, and NIMIN3 genes while NIMIN1 adversely affects SA-NPR1 signaling (Weigel et al., 2001, 2005). NIMIN1 overexpression has a significant role which causes induction of ETI and SAR, while its reduced regulation enhances the induction of PR-1 gene by SA. NPR1 is not always required for plant defenses. Transcription of several genes such as PR may require NPR1-independent SA signaling. The TFs responsible for SA-dependent and NPR1-independent resistance cover WHIRLY (WIH) and MYB genes. For example, SA can induce the single-stranded DNA binding activity of WHY, in an NPR1-independent manner (Desveaux et al., 2004). Furthermore, MYB30 positively regulates the pathogen-induced HR in an SA-dependent, NPR1-independent manner (Raffaële et al., 2006).

SA-mediated defense networks are interconnected, and the expression of certain genes, such as ACD6, ALD1, PAD4, EDS1, EDS5, EPS1, ICS1/2, AIM1 PAL and PBS3/WIN3, is inducible by SA, suggesting a mechanism of signal amplification involving both upstream and downstream components in the SA pathway. For example, feeding by *M. persicae* on *Arabidopsis* rosette leaves significantly induced the overexpression profiles of two genes: NPR1-dependent SA-associated genes PR-1 and BGL2 (Moran and Thompson, 2001). *Bemisia tabaci* feeding on *Arabidopsis* plants induced both local (PR1, BGL2, PR5, SID2, EDS5, PAD4) and systemic (PR1, BGL2, PR5) gene induction (Zarate et al., 2007).

The main secondary metabolite group in *Brassica* plants consists of GSs even when attacked by sap-sucking insects. For example, *M. persicae*-infested *Arabidopsis* plants release elevated levels of

phenylpropanoid and isochorismate (van Poecke, 2007; Louis et al., 2012), which are highly dependent on and sensitive to the genes involved in SA biosynthesis. Furthermore, aphid infestation on *Arabidopsis* causes volatile derivatives of indolyl-GS and isothiocyanates (Mewis et al., 2005, 2006). Furthermore, feeding activity by *M. persicae* can cause *Arabidopsis* plants to release several terpenoids and the green leaf volatile, methyl salicylate (MESA) (Aharoni et al., 2003; van Poecke, 2007; Tholl and Lee, 2011).

The SA-mediated plant defenses are known to negatively affect the sap-sucking attackers while providing significant cues for foraging natural enemies. Methyl salicylate (MeSA), a volatile analogue of SA, attracts *Coccinella septempunctata* L. after infestation by the soybean aphid, *Aphis glycines* Matsumura (Zhu and Park, 2005). Salicylic acid analog, BTH (benzo-(1,2,3)-thiadiazole-7-carbothioic-acid S-methyl ester) enhances the suppression of *A. gossypii* without negative effects on the predatory larva *C. carnea* (Moreno-Delafuente et al., 2020).

3.3 The evolution of SA-JA crosstalk in response to herbivore feeding guilds

The induction of plant defense mechanisms commences upon perceiving the herbivore feeding and oviposition associated specific cues including DAMPs and MAMPs (Acevedo et al., 2015). Plants, upon recognition of these patterns, activate several intriguing signaling networks, including mitogen-activated protein kinase (MAPK) such as wound-induced protein kinase (WIPK), SA-induced protein kinase (SIPK) signaling cascades (Seo et al., 1995; Nürnberger and Scheel, 2001; Bonaventure, 2012; Acevedo et al., 2015). These signals are known to both positively or negatively regulate the defense-responsive phytohormones, JA and SA signaling pathways and corresponding downstream transcriptional responses (Jagodzik et al., 2018). These two signaling pathways are among the most significant pathways that are induced following herbivore attack and may frequently crosstalk.

The JA-SA crosstalk is reciprocally antagonistic in which the activation of one signaling pathway inhibits the counterpart (Thaler et al., 2012). This crosstalk is governed by the specific genes inherent to respective pathway that strategically disables the antagonist (Hickman et al., 2019). The crosstalk, as a clear advantage for plants, enhances the strategy of optimal energy and resource allocation for the most effective defense response, therefore, potentially plays a central role in the evolutionary regulation of plant defense mechanisms (Thaler et al., 2012). Therefore, plants have to first perceive the herbivores and associated cues and, afterward, develop the most suitable defense mechanism which are generally subject to crosstalks.

The establishment of defensive plant responses against insects highly depends on the phytohormonal signaling pathway and the regulative involvement of TFs that are central to crosstalks. The most commonly studied TFs involved in plant-insect interactions are MYCs, ERFs, MYBs, and WRKYs (Figure 2A). A growing body of evidence has demonstrated a clear suppression of both MYC and ERF branches of JA in SA-JA crosstalk. The well-known direct targets of JAZ repressors are closely related to bHLH factors, MYC2,

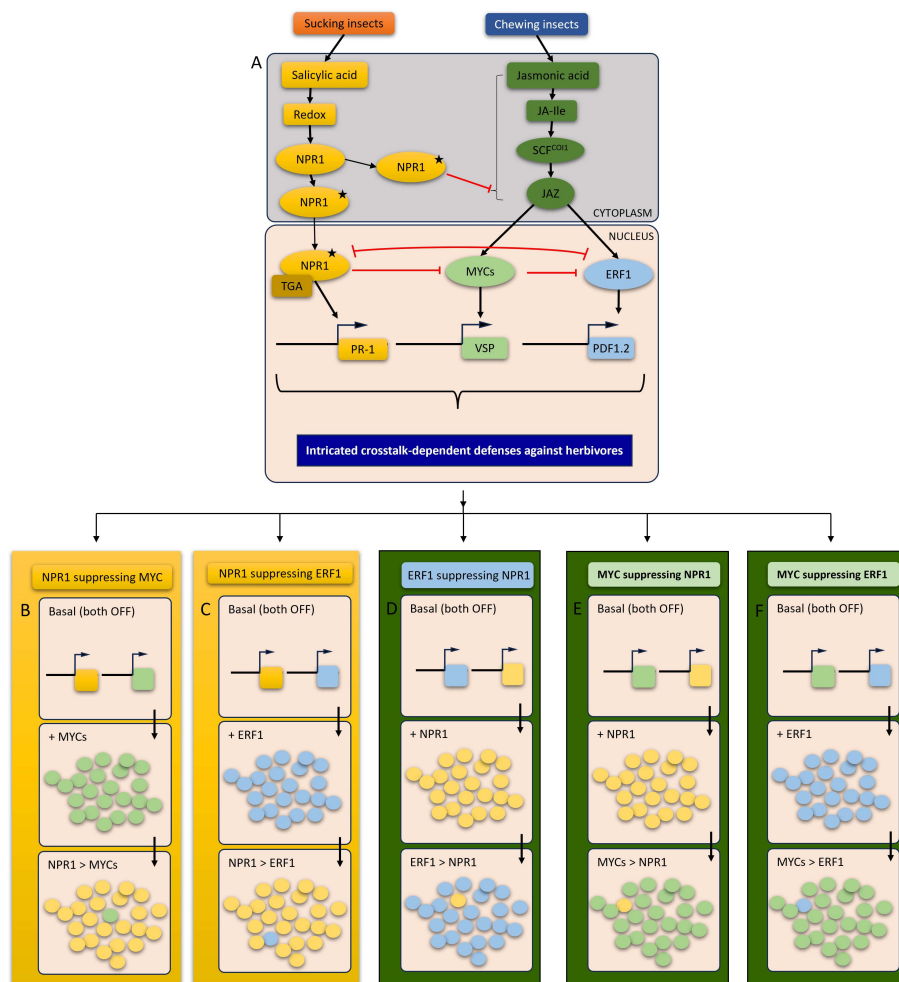


FIGURE 2

A schematic representation of SA-JA crosstalks in response to herbivory: (A) An overview of SA and JA induction in response to different feeding guilds depicting that chewing insects are more prone to induce JA-responsive plant defenses and sucking insects exhibits the tendency to trigger SA-responsive plant defenses. The overview of SA-JA cross-talk that is represented by red lines demonstrating the orientation of reciprocal suppression by respective transcription factors (TFs). The proposed models suggest two (cytosolic and nuclear) crosstalks steps between SA and JA via activated NPR1 (carrying a star). NPR1 activation occurs through the induction of a transition from an oligomeric state (NPR without star) to a monomeric state (with star), a prerequisite for its effective functioning. The activated NPR1 may participate directly in crosstalk, either within the cytoplasm or following translocation into the nucleus. The molecular consequences of possible crosstalk models as a function of reciprocal suppression effects of respective TFs. The side by side panels, (B–F) are consisted of three steps, first box showing the basal level of two TFs (boxes with two squares) which means plants are not under attack and the defense mechanisms are not induced, the second box showing the induced TF upon herbivory and the third box showing the suppressive effect of the antagonistic TFs. (B) indicates the suppression of MYC TFs by NPR1 that refers to SA-dependent plant responses are in control. (C) shows the suppression of ERF TFs by NPR1 that refers to SA-dependent plant responses are in control. (D) depicts the suppression of NPR1 by ERF1 and MYC, respectively, that refers to JA-dependent plant responses are in control. (E) shows the suppression of NPR1 by ERF1 and MYC, respectively, that refers to JA-dependent plant responses are in control. (F) depicts the crosstalk within JA signaling pathway which results in suppression of ERF1 by MYC. The arrows in (B–F) panels indicate the direction of working scheme of crosstalks between TFs. The circles in each box (under (B–F) panels) depicts the induction of respective TF while a single circle of suppressed TF is intentionally left in each crosstalk final to show the suppressive effect of the suppressor TF. The colors of squares and circles in (B–F) are based on the colors of TFs (NPR1, MYCs and ERF1 and respective genes) in panels (A) and (B) The background of panels (B–F) are based on SA and JA signaling pathways.

MYC3, and MYC4 (Fernández-Calvo et al., 2011). AtMYC2, for example, was reported to act downstream of JA and to regulate JA-dependent herbivore resistance (Dombrecht et al., 2007). These three MYCs, interacting with MYB proteins, regulate defense against insect herbivory by binding to a G-box motif found in the promoter of GS biosynthesis genes (Schweizer et al., 2013). The feeding damage of *P. rapae* on *Arabidopsis* plants induced JA pathway through the activation of the transcript factor, MYC2 and JA-responsive marker gene, VSP2 expression (Figure 2B) (De

Vos et al., 2005; Verhage et al., 2011; Vos et al., 2015). Furthermore, the feeding of *P. rapae* on *Arabidopsis* strongly inhibited the other TFs of JA pathway, ERF-branch which includes the marker gene PDF1.2 (Verhage et al., 2011). The MYC2-branch including VSP2 marker gene is known to regulate the defenses in response to wounding and chewing damage by insects while ERF-branch that covers high expression levels of PDF1.2 contributes plant defense in response to sucking insects (Figure 2B) (De Vos et al., 2005). In *Arabidopsis*, both of the JA-responsive genes PDF1.2 and VSP2 are

highly sensitive to suppression by SA. Therefore, SA-dependent plant defense mechanisms suppresses both MYC and ERF branches of JA pathway (Figures 2A, B). WRKY TFs are considered to be responsible for the regulation of expression of *NPR1* and, accordingly, SA-dependent defenses (Bakshi and Oelmüller, 2014). For example, the overexpression of *WRKY70* enhances the expression of SA-responsive PR genes which plays suppressive roles against JA-responsive *PDF1.2*, the complete mechanism of which is *NPR1*-dependent (Li et al., 2004). Furthermore, the antagonistic effect of SA on JA signaling was shown to be controlled by *NPR1* functioning in the cytosol (Spoel et al., 2003; Pieterse and Van Loon, 2004), with very recent findings indicating that *NPR1* physically interacts with MYCs for suppression of JA-responsive genes (Figure 2A) (Nomoto et al., 2021). The cytosolic *NPR1* suppresses JA signaling in cooperation with other cytosolic factors such as *MPK4* and *PAD4* while nuclear *NPR1* suppresses *MYC2* (Figure 2B) (Pieterse et al., 2009; Nomoto et al., 2021).

The chewing insects have to overcome and manipulate the host plant for their own benefit so that they employ some other cues by activating the antagonistic signaling pathway of SA against JA. The compounds in salivary excretion of *S. exigua* namely, glucose oxidase (GOX), causes suppression of JA-regulated plant defense in *Arabidopsis* by activation of systemic acquired resistance (Weech et al., 2008). Furthermore, SA inhibited induced resistance of *Arabidopsis* in response to *S. exigua* through alteration of JA-dependent defense mechanisms such as defense protein activity and GS induction (Cipollini et al., 2004). Foliar treatment of *Arabidopsis* plants with egg extracts of two chewing herbivores, *P. brassicae* and *S. littoralis* significantly reduced the activation of several JA-responsive marker genes, the majority of which consists of MYC branch, and the employment of SA-deficient *sid2-1* plants confirmed this suppression was controlled by SA (Figure 2B) (Bruessow et al., 2010). In comparison with chewing or wounding damage by *P. brassicae* and *S. littoralis* that induce accumulation of JA (Bruessow et al., 2010; Onkokesung et al., 2016), the involvement of egg-derived elicitors can cause a reversed induction of plant defenses through SA-JA crosstalk (Bruessow et al., 2010).

Interesting host manipulative engagements by insect pests with different feeding guilds covers a reversed version of crosstalk when compared to the case with chewing insects. These manipulative engagements suggest that JA-SA crosstalk may stem from the suppression of SA-responsive WRKY TFs by MYC branch of JA. For example, a previous study revealed the increased *B. brassicae* density with simultaneous *P. xylostella* infestation lowered the expression profile of WRKY and increased the expression profile of *MYC2* (Figures 2A, B) (Kroes et al., 2015). Furthermore, the infestation of *Brassica napus* plants with *B. brassicae*, exhibiting similar effects with JA treatments, had negative effects on the growth and development of the chewing pest, *P. xylostella* (Nouri-Ganbalani et al., 2018). The removal of the *COI1* receptor and MYC branch of JA resulted in a high-level accumulation of SA (Spoel and Dong, 2008). This manipulation is apparently not only for the benefit of the first attacker but also for the plant itself since they experience more intriguing defense responses. This seems quite phenomenal since a general understanding has suggested that JA mediates plant defenses upon feeding damage by chewing

herbivores or artificial wounding and induces direct and indirect responses against the attacker and its natural enemies (Titarenko et al., 1997; Bruinsma et al., 2009).

In contrast to chewing insects, sap-sucking insect-induced plant defenses that are highly dependent on the attacker and feeding damage. For example, sap-sucking insect species associated with higher cell damage are more prone to induce JA-dependent plant responses while those with lower cell damage can induce SA dependent responses. For example, the higher level of JA-responsive marker gene, *PDF1.2* and respective plant defense mechanisms of *Arabidopsis* in response to *B. brassicae* and *F. occidentalis* when compared with *M. persicae* is likely corresponded to relatively greater cell damage during the process of reaching the phloem as a function of distinct probing behavior (Cole, 1997; Moran et al., 2002; De Vos et al., 2005). For aphid species, *M. persicae*, the crosstalk seems more complex as such SA dependent plant responses with PR-1 and BGL-2 and JA-dependent responses with *PDF1.2* and *LOX2* constitute a simultaneous expression for both pathways while SA-responsive expression was dominative over JA-responsive marker genes (Moran and Thompson, 2001). However, further factors rather than cell damage can interfere with plant defense responses to sap-sucking insects. In *Arabidopsis* plants that suffered *Eurydema oleracea* feeding activity, *PDF1.2* gene expression was suppressed by the activation of *PR1a* and *ICS1* (Ederli et al., 2020). Therefore, an attack by *E. oleracea* clearly activates SA pathway and suppresses JA defenses (Costarelli et al., 2020). Similarly, in response to *B. tabaci*, the gene transcripts responsive to SA (*PR1*, *BGL2*, *PR5*, *SID2*, *EDS5*, *PAD4*) were activated while those responsive to both MYC2 and ERF branches of JA (*PDF1.2*, *VSP1*, *FAD2*, *FAD3*, *FAD7*, *THI2.1*, *COI1*) were either suppressed or non-respondent (Kempema et al., 2007; Zarate et al., 2007; Zhang et al., 2013).

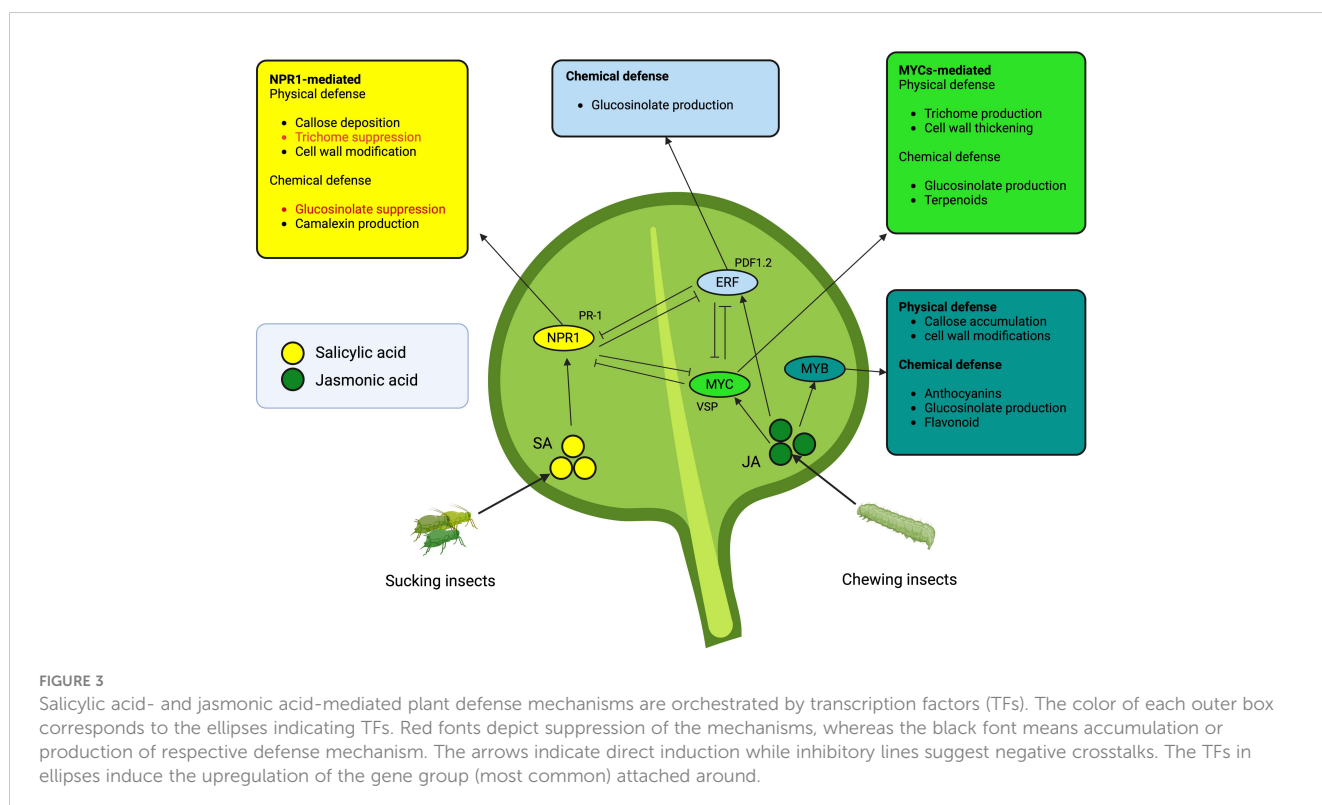
In general, one signaling pathway is expected to suppress the other since a crosstalk between JA and SA prioritizes one signaling defense pathway over the other in response to herbivore attack. The expression of marker genes of both signaling pathway may be due to a concentration-dependent degree of crosstalk (Moran and Thompson, 2001; Mur et al., 2006; Spoel et al., 2007).

Insect attack could induce plant defense mechanisms other than JA and SA. For instance, *P. brassicae* egg deposition in *Arabidopsis* plants has been shown to cause localized cell death, callose accumulation, and the production of reactive oxygen species (Little et al., 2007). The induction of these defense mechanisms in response to oviposition-associated cues can manipulate host plants defenses for the benefit of the ovipositing pest, preventing other attackers (Orlovskis and Reymond, 2020). Plants facing antagonistic attackers may develop intricate defense systems that hinder their ability to respond effectively to secondary attackers. This complexity arises from the activation of signaling pathways by the primary attackers, rendering it challenging for plants to reversely crosstalk, while protecting the balance of resource allocation, and thereby rendering them more susceptible to subsequent assaults from secondary attackers (Vos et al., 2015). Whether this is the case depends highly on the concentrations and combinations of activated defensive proteins and VOCs upon triggered signaling pathway (Smith and Boyko, 2007; Howe and Jander, 2008).

3.4 Glucosinolate biosynthesis and regulation in *Brassica*

Glucosinolates are pivotal plant defense compounds in *Brassica*, exhibiting structural and ecological diversity (Hopkins et al., 2009). The intricate regulatory network governing GS biosynthesis dynamically responds to stress, immune triggers, and herbivory, thereby influencing plant fitness (Zukalová and Vasak, 2002; Bruce, 2014; Mitreiter and Gigolashvili, 2021) (Figure 3). The evolutionary significance of GSs is underscored by the interplay of genes, TFs, and hormonal cues (Schweizer et al., 2013; Mitreiter and Gigolashvili, 2021). Subgroup 12 R2R3 MYB TFs (e.g., MYB28, MYB29) positively regulate GSs, forming complexes with bHLH proteins, while Subgroup IIIe bHLHs (e.g., MYC2, MYC3) modulate GS types in response to phytohormones like jasmonate (Gigolashvili et al., 2008; Seo and Kim, 2017; Millard et al., 2019). Hormonal interactions, especially the JA-SA crosstalk, highlight nuanced control mechanisms governing plant immunity and GS production (Tsuda et al., 2009; Guo et al., 2013). Upon plant damage, GSs initially biologically inert, become potent through myrosinase-driven hydrolysis, yielding compounds responsible for toxicity and herbivore deterrence (Bones and Rossiter, 1996). Over 130 GS structures exist, predominantly within *Brassica* (Newton et al., 2009; Textor and Gershenson, 2009). Herbivory induces GS production, with indolic GSs showing a consistent 1.2- to 20-fold increase, irrespective of the herbivore type (Sontowski et al., 2019). The jasmonate signaling cascade activates TFs controlling GS biosynthesis, while the functions of myrosinase-associated proteins remain inadequately studied.

Insect herbivores from different feeding guilds can influence glucosinolate biosynthesis and regulation in plants (Hopkins et al., 2009; Textor and Gershenson, 2009). Sucking herbivores, exemplified by aphids, generally induce fewer changes in GSs and associated gene expression compared to chewing insects like beetles and caterpillars (Barth and Jander, 2006; Sato et al., 2019). This distinction is rooted in aphids' feeding behavior, targeting single phloem cells and spatially separating them from myrosinase, potentially avoiding the trigger for glucosinolate breakdown (Barth and Jander, 2006). Despite the typically low induction of GSs in response to sucking herbivores, recent investigations into *M. persicae* feeding on *Arabidopsis* revealed the induction of specific indolic GSs, such as 4-methoxyindol-3-ylmethyl glucosinolate, suggesting a crucial role in insect-host interactions even in the absence of myrosinase (Agerbirk et al., 2009). Another study in *Arabidopsis* showed that infestation by *M. persicae* and *B. brassicae* induces genes associated with indole GSs synthesis (Mewis et al., 2006; Kuśnierczyk et al., 2007), and *B. brassicae* infestation leads to GSs accumulation (Nouri-Ganbalani et al., 2018). However, contradictory results were observed in *B. juncea-fruticulosa* introgression lines infested by *L. erysimi*, with impacts on varying GS content (Palial et al., 2018). In *B. juncea*, transcripts related to biosynthetic pathways, including GSs, were induced in response to *A. craccivora*, whereas attenuated by *L. erysimi* infestation (Duhlian et al., 2020). In *B. rapa* infested by *L. erysimi*, the total GS content was enhanced, while those infested by *M. persicae* released lower levels (Blande et al., 2007). Slight stress by *B. brassicae* also enhanced leaf growth and increased GS emission in the bulb, the main storage organ of *B. rapa* (Sotelo et al., 2014). Considering the



impact of herbivory on the GS-myrosinase defense system, sucking herbivores are known to trigger an increase in myrosinase enzyme activity or transcript levels (Siemens and Mitchell-Olds, 1998; Pontoppidan et al., 2005) or may have no effect (Travers-Martin and Müller, 2007). A separate study investigating the influence of *B. brassicae* infestation on the myrosinase-glucosinolate system in *B. napus* has reported induction of genes associated with this defense system (Pontoppidan et al., 2003). However, contradictory results have also been documented; for instance, in *Arabidopsis* infested by *B. brassicae*, a consistent decrease in myrosinase transcript levels was observed (Kuśnierczyk et al., 2007).

Similar to sucking herbivores, chewing herbivores significantly influence the regulation of GSs in plants. For example, generalist *S. exigua* and specialist *P. rapae* larvae, two recognized chewing herbivores, play a crucial role in shaping GS concentrations in different ecotypes of *Arabidopsis*. The impact is observed in both aliphatic and indole GSs, with a more pronounced effect on indole GS, consistent with patterns seen in herbivore-attacked plants (Mewis et al., 2006; Textor and Gershenson, 2009; Gols et al., 2018). The feeding activity of *S. exigua* and *P. rapae* induces similar GS profiles after induction, demonstrating a consistent response to different chewing herbivores (Kos et al., 2012). In *B. oleracea*, *P. rapae* induces significant changes, leading to increased foliar concentrations of GSs compared to undamaged plants (Broekgaarden et al., 2007; Poelman et al., 2008). Caterpillar-induced slight stress on young *B. rapa* plants enhances bulb mass and results in a contrasting regulation of aliphatic and indolic GSs (Sotelo et al., 2014). Chewing herbivores' impact on GS composition is evident in *Arabidopsis*, where *S. exigua* increases aliphatic GS content, and *P. rapae* slightly induces indole GSs. Additionally, *D. radicum* larval infestation upregulates indole GS synthesis genes in both low and high GS varieties of *B. rapa* (Sontowski et al., 2019). Recent studies on primary roots of *B. oleracea* reveal that leaf herbivores cause an increase in the expression of the indole GS biosynthesis gene *CYP81F4*, highlighting intricate regulatory mechanisms in plant defense against chewing herbivores (Karssemeijer et al., 2022). In summary, the intricate and varied responses in glucosinolate regulation underscore the specificity of plant-herbivore interactions and the adaptive strategies of *Brassica* plants to different feeding behaviors of insect herbivores (Supplementary Table 1).

3.5 Physical defenses in *Brassica* against insect herbivores

Brassica plants employ an array of physical defenses to shield themselves from herbivores and environmental challenges. These defenses encompass various components, including trichomes (Mathur et al., 2011; Hao et al., 2019), the cuticle (Khattab, 2007), the leaf surface (Eigenbrode and Espelie, 1995; Ahuja et al., 2010), and thorns or hairs (Traw, 2002) (Figure 3). It is worth noting that predictions suggest that both physical and chemical defense traits can be induced independently, without necessitating trade-offs. However, it is observed that the induction of physical traits may be comparatively weaker due to higher construction costs and time

delays (Barton, 2016). These physical defense mechanisms, when combined with chemical defenses enhance the capacity to deter herbivores, form a comprehensive defense strategy for *Brassica* plants against herbivory and environmental stressors (Mostafa et al., 2022). Insect feeding patterns exert substantial influence on the physical defense mechanisms of *Brassica* plants, specifically impacting callose deposition, leaf thickness, and trichome density (Kos et al., 2012; Mathur et al., 2013b; Will et al., 2013; Rubil et al., 2022) (Figure 3). These responses typically manifest as alterations in trichome density, becoming noticeable within a timeframe of days to weeks (Dalin et al., 2008).

The impact of herbivore feeding on the physical defenses of *Brassica* plants has not been extensively studied. Only a limited number of investigations have been conducted, primarily focusing on chewing herbivores such as the larvae of *P. rapae* (Agren and Schemske, 1993; Traw, 2002; Traw and Dawson, 2002), *Trichoplusia ni* (Traw and Dawson, 2002), and *Spodoptera* species (Mathur et al., 2011). These studies have revealed that herbivore infestation significantly enhances the production of trichomes as a physical defense mechanism in *Brassica* plants against invading herbivores. In contrast, transcriptomic analysis of sucking herbivores feeding on *Brassica* plants revealed an induction in the gene expressions responsible for callose deposition [Callose synthase 1 (*CALS1*), vitamin C defective 2 (*VTC2*)], cell wall modifications [O-methyltransferase family 2 protein, vitamin C defective 2 (*VTC2*), and Xyloglucan endotransglycosylase 6 (*XTH6*)], and trichome production [Glabrous 1 (*GL1*)] (Kempema et al., 2007; Kuśnierczyk et al., 2008; Broekgaarden et al., 2011) Supplementary Table 1.

The alteration of the cell wall, as observed in response to sucking herbivores, could discourage aphids by strengthening the barriers to probing (Thompson and Goggin, 2006). The host preference of *M. persicae* is impacted by *XTH* genes in *Arabidopsis* (Divol et al., 2007). Similarly, O-methyltransferase, found within the phenylpropanoid pathway, plays a role in the synthesis of lignin, a chemical compound known for imparting structural integrity to the cell wall (Whetten and Sederoff, 1995; Zhao et al., 2021). This function potentially serves as a defense mechanism against insects.

3.6 Other secondary metabolites in *Brassica*

In addition to extensively discussed compounds such as JA, SA, GSs, and physical defense mechanisms against sucking and chewing insect herbivores, it is crucial to acknowledge the significant contributions of other secondary metabolites. The secondary metabolites such as tannins, flavonoids, phenols, glycosides, terpenes, green leaf volatiles, phytoalexins, and camalexins are integral elements in the intricate defense strategies employed by *Brassica* plants against insect pests and pathogens (Simmonds, 2003; Ahuja et al., 2010; Cartea et al., 2010; Ibrahim et al., 2018). However, insect herbivory can alter their production and content in the plant. Chewing insect infestations, exemplified by flea beetles *Phyllotreta nemorum* and *P. brassicae* in *B. oleracea*, have been

linked to an increase in polyphenols (Kovalikova et al., 2019). Additionally, *P. brassicae* caterpillar infestation in *B. oleracea* exhibited elevated levels of phenols, condensed tannins, and flavonoids, particularly in JA-treated plants (Ibrahim et al., 2018). The influence of *P. brassicae* caterpillar infestation on *B. nigra* resulted in significant alterations to sugars and phenolic compounds, with a specific impact on flavonol glucosides and hydroxycinnamic acid derivatives (Ponzio et al., 2017). Moreover, *P. brassicae* caterpillar feeding in *B. nigra* led to the accumulation of TCAs and phenylpropanoids while depleting amino acids (Papazian et al., 2019). Similarly, caterpillar infestation induces the emission of green-leaf volatiles and isothiocyanate in *B. rapa* (Verheggen et al., 2013).

Sap-sucking insect infestation also alters the secondary metabolite profile of *Brassica* plants. For example, aphid infestation in *Brassica* genotypes (*B. fruticulosa*, *B. juncea*, *B. rapa*) consistently led to a reduction in flavonols, total sugars, and free amino acids. Conversely, total phenols exhibited a reversed pattern, with a significant increase in phenol content in *Brassica* genotypes with minor exception for *B. fruticulosa* (Palial et al., 2018). Similarly, an induction in camalexin accumulation in *A. thaliana* has been recorded in response to *B. brassicae* infestation (Kuśnierczyk et al., 2008). In contrast, aphid *B. brassicae* feeding on *B. oleracea* resulted in a significant decrease in sugars, amino acids, and total soluble protein levels, accompanied by increased lipid peroxidation (malondialdehyde content) in infested leaves compared to healthy plants (Khattab, 2007). Notably, another study on *B. oleracea* found that aphid herbivory, induced by *B. brassicae* and the generalist *M. persicae*, did not affect the levels of flavonoids upon infestation (Khan et al., 2011). Additionally, numerous studies have reported an increase in the emission of volatile organic compounds (VOCs) from *Brassica* sp. plants upon insect herbivore infestation. These emissions differ in quality and quantity depending on the insect feeding guilds (Verheggen et al., 2013). For instance, *Brassica* sp. plants infested with aphids showed an elevated level of VOCs in blends, including terpenes (monoterpenes and sesquiterpenes), (E)- β -farnesene, β -pinene, and (E)-2-hexanol (Verheggen et al., 2013; Najjar-Rodriguez et al., 2015). In summary, sap-sucking insect infestation induces complex changes in *Brassica* plants, affecting secondary metabolites and volatile organic compounds. This nuanced interaction highlights the diverse adaptive strategies employed by plants in response to insect herbivores.

Orchestrating signaling pathways, TFs interplay with the production of defensive compounds and structures in *Brassica* plants, playing a pivotal role in the intricate network of defense mechanisms against diverse insect feeding guilds. In *Brassica*, the transcription factors NPR1 and ETR1 are vital for enhancing total GS content in response to insect feeding (Mewis et al., 2005). Moreover, MYB transcription factors, specifically MYB28, MYB29, MYB34, and MYB122, play a pivotal role in elevating the expression of genes within the glucosinolate biosynthetic pathway, contributing to enhanced glucosinolate accumulation (Guo et al., 2013). The MYB/MYC model, involving MYB28, MYB29, MYC2, MYC3, and MYC4, influences aliphatic GS accumulation (Li et al., 2014). MYC2, a transcriptional activator in the MYC2-branch of

the JA pathway, contributes to the wound-response and defense against insect herbivores (Verhage et al., 2011). Transcription factors, including MYB, NAC, WRKY, ERF (AtERF38), and MYC (bHLH), are pivotal in regulating secondary metabolites such as flavonoids and terpenoids, and contribute to the synthesis of lignin and cell wall thickening in plants (Owji et al., 2017; Wasternack and Strnad, 2019; Huang et al., 2023). R2R3 MYB, basic helix-loop-helix (bHLH), and WD40 proteins constitute major families regulating flavonoid and anthocyanin biosynthesis in *Brassica* (Chiu et al., 2010). Key transcription factors from the MYB and bHLH families, such as GLABRA1 (GL1), MYB5, MYB23, GLABRA3 (GL3), ENHANCER OF GLABRA3 (EGL3), and TRANSPARENT TESTA 8 (TT8), play a central role in regulating trichome development in *Brassica* (Chiu et al., 2010). Overexpressing NAC transcription factors NST1 and NST2 induces secondary wall thickening in *Brassica*, enhancing physical defense mechanisms (Yang et al., 2020). In conclusion, the interplay of transcription factors in *Brassica* plants, including NPR1, ETR1, MYBs, MYCs, and others, orchestrates a sophisticated defense network against diverse insect feeding guilds. Their regulatory roles span from glucosinolates and other secondary metabolite biosynthesis to different physical defense mechanisms, establishing a comprehensive and efficient response to biotic challenges.

4 Conclusion and future prospects

In summary, this review highlights the pivotal role of distinct defense mechanisms in *Brassica* plants when confronting chewing and sucking herbivores, involving JA-mediated pathways for the former and SA-mediated pathways for the latter. Additionally, we discuss how these pathways cross talk under herbivores attack. This specificity may enable the development of targeted pest management strategies, reducing reliance on environmentally harmful insecticides and promoting ecosystem sustainability. Categorizing defense responses into physical, chemical, and metabolic adjustments establishes a comprehensive framework for enhancing resilience to herbivores. The paper underscores the intricate interplay between herbivore feeding patterns and plant defense responses, providing valuable insights into the co-evolutionary dynamics between *Brassica* plants and insects.

Understanding the impact of insect herbivores' diverse feeding patterns on plants involves a complex interplay of rapid and slow events at local and systemic levels. Recent findings by Ali et al., (2024), suggest that identifying these pathways enables the artificial induction of plant defense systems through mimicking the damage patterns caused by mechanical damage, thereby providing a controlled and sustainable approach. Investigating cross-talk between JA and SA pathways offers promise for developing a unified approach, allowing for specific adjustments based on insect feeding patterns, contributing to innovative and sustainable pest control methods. Tailoring plant defense strategies based on insights into insect feeding patterns can facilitate the development of resistant cultivars, optimizing plant resistance to prevalent herbivores in specific regions and improving crop success compared to non-resistant varieties. Analysing the relationship

between insect herbivore feeding guilds and glucosinolate dynamics offers valuable genetic insights. This understanding can be leveraged to engineer resistant plant varieties through precise genetic modifications, such as gene knockouts or additions. These findings not only contribute to unravelling the plasticity of plant defenses against herbivores but also hold significance for the strategic management of *Brassica* in agroecosystems.

Author contributions

JA: Conceptualization, Investigation, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. AT: Conceptualization, Investigation, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. TI: Writing – original draft, Writing – review & editing. SM: Writing – original draft, Writing – review & editing. MM: Funding acquisition, Writing – original draft, Writing – review & editing. AK: Funding acquisition, Writing – original draft, Writing – review & editing. RC: Writing – original draft, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2024.1376917/full#supplementary-material>

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