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Review

Stomata-mediated interactions between plants, herbivores, and the environment

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Stomata play a central role in plant responses to abiotic and biotic stresses. Existing knowledge regarding the roles of stomata in plant stress is centered on abiotic stresses and plant–pathogen interactions, but how stomata influence plant–herbivore interactions remains largely unclear. Here, we summarize the functions of stomata in plant–insect interactions and highlight recent discoveries of how herbivores manipulate plant stomata. Because stomata are linked to interrelated physiological processes in plants, herbivory-induced changes in stomatal dynamics might have cellular, organismic, and/or even community-level impacts. We summarize our current understanding of how stomata mediate plant responses to herbivory and environmental stimuli, propose how herbivores may influence these responses, and identify key knowledge gaps in plant–herbivore interactions.

Highlights

Plant stomata are emerging as important mediators of interactions between plants and herbivores.

Several components in the oral secretions of herbivores, such as enzymes and phytohormones, that can trigger herbivory-induced stomatal closure have been identified.

Recent evidence suggests that herbivory-induced stomatal changes play important roles in mediating interactions among plants, herbivores, pathogens, and the environment.

State of the art: stomata in abiotic and biotic interactions

Stomata are some of the most important structures in land plants. They are microscopic gates formed between two guard cells that create a passage for the exchange of carbon dioxide (CO_2) and water vapor (H_2O) between plants and the atmosphere [1]. The stomatal aperture is adjusted by shape changes in guard cells and sometimes subsidiary cells (supporting surrounding cells of guard cells) after the plant senses environmental cues, such as humidity, CO_2 concentration, and light. Owing to their ability to control gas exchange, stomata are essential regulators of photosynthesis [2] and transpiration. The detailed signaling pathways – including hormonal regulations involved in stomatal sensing and responses to environmental cues – are well summarized in a previous review [3].

In addition to their roles in plant responses to the abiotic environment, stomata also function in biotic interactions [4]. Many microorganisms exploit stomata to gain access to plant nutrients [5–8]. Pathogens have evolved various strategies to manipulate stomata and allow for easier invasion. The pathogenic bacterium *Pseudomonas syringae* produces a toxin, coronatine, that prevents stomatal closure in a COI-dependent manner (COI, coronatine insensitive 1, a subunit of an E3 ubiquitin ligase) [6]. *Xanthomonas campestris* also produces compounds that manipulate plant stomata [8], and a fungal pathogen of almond and peach, *Fusicoccum amygdali*, is well known for its production of fusicoccin, a toxin that causes stomatal opening by activating proton pumps in guard cells [9]. Another fungal pathogen, *Plasmopara viticola*, exhibits a similar strategy on plants of the family Vitaceae by inducing stomatal opening to facilitate invasion [7]. Oxalic acid produced by many pathogenic fungi is associated with stomatal opening and wilting symptoms in infected plants [5]. Different mechanisms have also evolved in plants to induce stomatal closure as a defense against pathogen invasion. To prevent the entry of pathogenic endophytes, *Arabidopsis thaliana* rapidly closes its stomata after perceiving bacterial molecules via the FLS2 (flagellin sensing 2) receptor [6]. Application of either of two elicitors associated with fungal

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invasion, oligogalacturonic acid or chitosan, induces stomatal closure in tomato (*Solanum lycopersicum*) and Asiatic dayflower (*Commelina communis*) [10], and a bacterial phytotoxin, syringomycin, induces stomatal closure in broad bean (*Vicia faba*) [11]. The phytohormone salicylic acid (SA), which is a central regulator of plant antimicrobial defenses, is essential for stomatal closure upon pathogen attack [12]. These findings highlight the adaptive importance of stomata in interactions between plants and pathogens, leading to the evolution of mechanisms that regulate the stomatal aperture in both plants and pathogens (for a detailed review see [13]). Although the responses of stomata to microorganisms are well studied, our knowledge of the involvement of stomata in interactions between plants and insect herbivores remains extremely limited.

Stomatal closure is known to be a typical response of plants under herbivory. Herbivory can lead to water loss by creating open wounds that increase transpiration (chewing herbivores), removal of liquid from vascular tissues (piercing-sucking herbivores), or damaging root systems [14–16]. Water limitation triggers stomatal closure via the accumulation of the drought-associated phytohormone abscisic acid (ABA) [17]. Physical damage also induces the accumulation of the phytohormone jasmonic acid (JA), that triggers stomatal closure, but it is also observed that methyl jasmonate, other jasmonates, and coronatine (JA mimic) can trigger stomatal opening instead of closure [18]. While the link between stomata and herbivores could be incidental due to responses induced by herbivory, recent discoveries have suggested a key role for stomata in plant–herbivore interactions. Here, we propose that stomata function in specific interactions between plants and insects.

A few studies indicate direct interactions between herbivores and stomata. The authors of [19] found that phytophagous mites of the genus *Raoiella* feed on leaf mesophyll by inserting their stylets into stomata, avoiding penetrating the leaf cuticle and epidermis. Spruce aphids (*Elatobium abietinum*) also feed exclusively through the stomata of their host plants [20], and lace bugs (*Stephanitis pyrioides* and *Stephanitis typica*) feed similarly [21,22]. Besides direct herbivory via stomata, the gall midge (*Cystiphora sonchi*) lays its eggs in the stomata of host plants [23].

Beyond direct interactions between herbivores and stomata, there is evidence suggesting that herbivory indirectly affects stomata in nearby undamaged tissues (Table 1). Mechanical damage to leaves in soybean reduces stomatal conductance, but feeding by Japanese beetles (*Popillia japonica*) does not affect this conductance [24]. Feeding by caterpillars such as *Spodoptera littoralis* and *Manduca sexta* reduces stomatal conductance in cotton (*Gossypium* L) and tobacco (*Nicotiana attenuata*), respectively [25,26]. Damage by phytophagous mites or leaf miners causes systemic stomatal closure in plants [25,27,28], but the mechanisms mediating stomatal closure upon herbivory have not been reported. Due to the lack of comparison between mechanical wounding and herbivore-inflicted damage, it is unclear whether stomatal closure is a generic response to wounding or triggered by specific herbivore-associated molecular patterns (HAMPs).

Stomata-mediated changes in temperature and water availability upon herbivory

Stomatal closure can be potentially beneficial to insect herbivores by increasing the temperature and water content of plant tissues. Leaf damage often leads to a higher rate of transpiration through wounds [24]. Inducing stomatal closure to maintain leaf water content after damage would be beneficial to herbivores [29,30]. Besides herbivores that consume leaf tissues, feeding by piercing-sucking insects, such as aphids, induces stomatal closure, which in turn decreases transpiration and maintains leaf water potential. These changes lead to longer feeding times,

Table 1. Effect of herbivory on plant stomata and photosynthesis

Damage type	Herbivore species	Plant family	Plant species	Photosynthesis	Stomatal response	Refs
Artificial	na[a]	Fabaceae	*Glycine max* cv. Steele	Decrease	na	[106]
Artificial	na	Fabaceae	*Medicago sativa* *Medicago scutellate* *Medicago truncatula* *Melilotus officinalis* *Trifolium hybridum* *Trifolium pratense*	No effect	No effect	[124]
Artificial	na	Fagaceae	*Quercus rubra*	Decrease	Closure	[125]
Artificial	na	Poaceae	*Lolium multiflorum*	Decrease	Closure	[107]
Artificial	na	Poaceae	*Agropyron smithii*	Decrease	na	[108]
Artificial	na	Poaceae	*Bouteloua gracilis*	Decrease/increase	na	[109]
Artificial	na	Rosaceae	*Malus domestica* cv. Holiday	Decrease	na	[105]
Artificial	na	Sapindaceae	*Acer saccharum*	Decrease	Closure	[125]
Chewing	*Helicoverpa zea*	Fabaceae	*Glycine max* cv. Pioneer 93B15	No effect	na	[24]
Chewing	*Helicoverpa zea*	Fabaceae	*Glycine max*	No effect	Closure	[54]
Chewing	*Helicoverpa zea*	Fabaceae	*Solanum lycopersicum* cv. Better Boy	No effect	Closure	[54]
Chewing	*Lymantrria dispar*	Fagaceae	*Quercus robur*	Decrease	Closure	[126]
Chewing	*Manduca sexta*	Solanaceae	*Solanum lycopersicum*	Decrease	Decrease	[127]
Chewing	*Manduca sexta*	Solanaceae	*Nicotiana attenuata*	Decrease	No effect	[128]
Chewing	*Manduca sexta*	Solanaceae	*Nicotiana attenuata*	Decrease	Closure	[26]
Chewing	*Manduca sexta*	Solanaceae	*Nicotiana attenuata*	Decrease	Closure	[74]
Chewing	*Operophtera brumata*	Fabaceae	*Quercus robur*	Decrease	Closure	[73]
Chewing	*Phyllonorycter blancardella*	Rosaceae	*Malus communis*	na	Closure	[28]
Chewing	*Pieris brassicae*	Brassicaceae	*Brassica nigra*	No effect	Closure	[129]
Chewing	*Popillia japonica*	Fabaceae	*Glycine max* cv. Pioneer 93B15	No effect	No effect	[24]
Chewing	*Spodoptera littoralis*	Malvaceae	*Gossypium hirsutum*	No effect	closure	[25]
Chewing	*Trichoplusia ni*	Apiaceae	*Pastinaca satica*	Decrease	na	[110]
Piercing sucking	*Stephanitis pyrioides*	Ericaceae	*Rhododendron mucronatum*	Decrease	closure	[21]
Piercing sucking	*Tetranychus urticae*	Malvaceae	*Gossypium hirsutum*	No effect	closure	[25]
Piercing sucking	*Tetranychus urticae*	Rosaceae	*Fragaria* × *ananassa* cv. Tufts	na	closure	[27]
Piercing sucking	*Tetranychus urticae*	Rosaceae	*Fragaria* × *ananassa* cv. Tufts	Decrease	closure	[130]
Piercing sucking	*Tupiocoris notatus*	Solanaceae	*Nicotiana attenuata*	Increase	No effect	[128]

[a]na, the response was not measured in the selected reference.

and increased aphid abundance [16]. Stomatal closure also regulates the leaf microclimate. Transpiration is one of the main processes that regulates plant temperature; closure of stomata reduces transpiration and elevates leaf temperature [31,32], which could benefit herbivores directly by accelerating their growth [33], shortening vulnerable life stages [34], and reducing the risk of predation from size-limited predators [35] while decreasing spatial overlap between predator and prey [36]. It is important to note that most of these arguments have some support from the literature but remain speculative and are novel hypotheses to be tested.

Stomatal control of plant volatile emissions

Stomata not only control the flow of CO_2 and H_2O but also the release of plant volatile organic compounds (VOCs) [37]. Plant VOCs mediate multiple interactions between plants and their

environment. Enhanced volatile emissions often occur in response to abiotic stress, including drought, heat, and ozone [38]. Biotic stresses such as pathogen infection or herbivory also induce plant VOC emission [39–41]. Herbivore-induced plant volatiles (HIPVs) have received significant research attention due to their prevalence in plants and potential value in agricultural pest management. Many HIPVs attract natural enemies of herbivores [40,42], prime antiherbivore defense [43,44], and function as informational chemicals for plant–plant communication [45].

The rate of VOC release is controlled by several physiological and physicochemical processes, such as the rate of VOC production [46], the activity of associated enzymes in plants [47], the volatility of the compounds [48], their ability to diffuse [49], and stomatal conductance [49,50]. Stomata can limit VOC emission if the decrease in stomatal conductance (g) is larger than the increase in the VOC diffusion gradient (P). The speed of changes in VOC concentration in the intercellular air space controls changes in P. Therefore, whether stomatal conductance can control VOC emissions depends largely on the kinetics of liquid and gaseous concentrations of specific VOCs. The changing speed of P for each VOC depends on its gas–aqueous phase partition coefficient, the Henry's Law Constant (H). VOCs with low H tend to be more soluble in water, and a larger increase in VOC liquid pool size is needed for an increase in VOC gaseous pool size. These VOCs have a slower change in speed for P. Stomata can therefore exert better control over the emission rate of VOCs with low H (for a detailed review see [37]). VOCs that have low H, such as alcohols [e.g., (Z)-3-hexenol [51], 1.6 Pa m^3/mol], carbonyls [e.g., (Z)-3-hexenyl acetate [51], 0.036 Pa m^3/mol; methyl salicylate [51], 0.38 Pa m^3/mol], aldehydes, and oxygenated monoterpenes, are more easily regulated by stomata (for a summary of H see [52]). VOCs with high H tend to partition more into the gaseous phase. A small increase in VOC liquid pool size will lead to large increases in VOC gaseous pool size and therefore a large rise in P. Hence, stomatal conductance has less influence over the release of these VOCs. VOCs with high H, such as monoterpenes (e.g., β-phellandrene [53], 5670 Pa m^3/mol), cannot be controlled effectively by stomata. Interestingly, although many HIPVs with either high or low H are both found to be involved in plant direct/indirect defenses and plant–plant communications, some of the most commonly emitted HIPVs, such as (Z)-3-hexenol, (Z)-3-hexenyl acetate, and methyl salicylate, have a low H [40,42].

The link between the emission rate of the defense-related VOCs and stomatal conductance is an important aspect that has been virtually overlooked. A recent study by our group on a polyphagous caterpillar, *Helicoverpa zea*, revealed a role for salivary glucose oxidase (GOX) in triggering stomatal closure and inhibiting the emissions of (Z)-3-hexenol, (Z)-3-hexenyl acetate, and (Z)-jasmone from plants (VOCs collected from the entire plant) [54]. Although the mechanism underlying inhibition of these volatiles remains hypothetical, the fact that GOX selectively inhibits the emission of HIPVs with low H suggests the likely involvement of stomatal closure. Stomatal closure can directly inhibit the emission of HIPVs with low H for a short period [50], which might benefit herbivores by preventing the attraction of natural enemies during feeding [55]. Close associations between photosynthetic activity and VOC production also suggest that lower stomatal conductance can indirectly inhibit the synthesis of plant VOCs [37].

We hypothesize that the ability to manipulate plant stomata and VOC emission might be an ecologically important trait of insect herbivores. As mentioned earlier, plant VOCs serve myriad functions, including attracting insect natural enemies and triggering plant defense signaling. Feeding is a particularly vulnerable time for herbivores [56]; short-term inhibition of HIPV emission during herbivory reduces the likelihood of detection by natural enemies and subsequently reduces the risk of predation or parasitism [57,58]. Inhibition of HIPV emission also reduces defense elicitation within individual plants [59] and defense priming of neighboring plants [43,59]. Direct

evidence, however, remains limited, and future studies should investigate how common herbivory-induced stomatal closure is and whether it can reduce HIPV emission or even the perception of HIPVs by plants.

Stomata in competitive interactions between herbivores and plant pathogens

Herbivore-induced stomatal closure also potentially influences the competitive relationships between insects and microorganisms. Many pathogens invade plant tissue through stomata [4]. Although it has been shown that some insect herbivores introduce nonpathogenic microbes which elicit SA defense responses and suppress JA defense responses of plants [60], infection by a pathogen can lead to a loss of valuable plant resources for herbivores [61]. It is therefore possible that insect herbivores evolved to reduce plant accessibility for plant pathogens. Salivary GOX is commonly found in many insect herbivores [62–65] and was recently reported to trigger stomatal closure [54]. The GOX in honeybees (*Apis mellifera*) is known to act as a preservative that prevents microbial contamination via its H_2O_2-producing activity [66], similar to many fungi that produce GOX to exclude microbial competitors [67]. Caterpillar salivary GOX may serve similar functions either by directly inhibiting microbial growth by producing H_2O_2 and/or inducing stomatal closure to prevent further infection by plant pathogens [54,68,69]. In contrast to chewing herbivores, attack by piercing-sucking insects, such as aphids, usually induces SA defense responses in plants similar to invasion by some microbes [70,71]. It is therefore likely that the benefit of preventing microbial invasion depends on insect feeding guilds and microbial types. Although there is evidence suggesting a role for stomatal closure in mediating herbivore–microorganism interactions, we speculate that, in some cases, herbivores might also keep the stomata open to facilitate pathogen infection due to the antagonistic nature of SA defense and JA defense [72].

Evidence that insects manipulate plant stomata

There is growing evidence that insect herbivores manipulate stomata (Figure 1). Some studies have shown that either perception of herbivory by plants or manipulation by herbivores leads to altered stomatal responses compared with artificial wounding. Examples of this include interactions between the winter moth larvae (*Operophtera brumata*) and pedunculate oak (*Quercus robur*) and tobacco hornworm (*M. sexta*) and tobacco (*N. attenuata*) [73,74]. The oral secretions of *Pieris brassicae* and *Spodoptera littoralis* larvae both attenuate wound-induced leaf water loss, indicating further stomatal closure compared with mechanical wounding alone [75]. Feeding by leaf miner moth larvae (*Phyllonorycter blancardella*) increases water use efficiency of leaves by 200% compared with intact leaves. The presence of larvae in mined leaves causes more stomatal closure than in mined leaves without larvae, suggesting active manipulation of stomata [76]. These studies suggest that HAMPs induce stomatal closure, but the specific HAMPs involved and the physiological mechanisms that drive closure remain unknown. A study that investigated the function of an insect salivary protein has provided insights into one potential mechanism underlying stomatal closure elicited by HAMPs. Lin *et al*. [54] identified a salivary GOX of *H. zea* larvae that causes stomatal closure in tomato and soybean and determined the key role of H_2O_2-producing GOX in inhibition of HIPV emissions (for the effect of exogenous H_2O_2 on stomatal closure see [77,78]). It is noteworthy, however, that GOX-induced stomatal closure, in this case, was observed only in tomato and soybean. Stomatal conductance in cotton was not affected by GOX.

There is indirect evidence suggesting the broad-scale occurrence of herbivory-induced stomatal closure. For example, GOX activity is commonly found in many caterpillar species (Lepidoptera), and there is a correlation between higher GOX activity and a broader host range [62]. Generalist caterpillars are commonly known to have higher mobility, which exposes them to higher

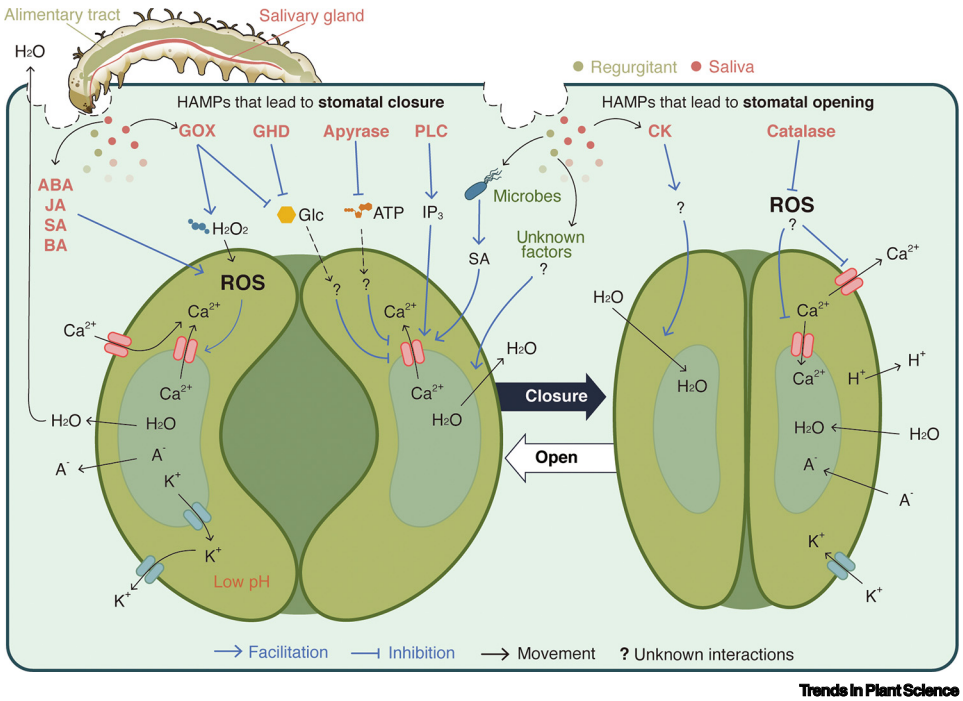

Figure 1. Potential responses of plant stomata to herbivore-associated molecular patterns (HAMPs). Oral secretion (OS) of insect herbivores consists of regurgitant (from the alimentary canal, green texts) and saliva (from salivary gland, red texts). OS components on the left (e.g., ABA, JA, SA, BA, GOX, GHD, apyrase, PLC, microbes) potentially trigger stomatal closure. Phytohormones such as ABA and SA may lead to stomatal closures. Enzymes may produce signaling molecules that trigger stomatal closure, such as H_2O_2 generated by GOX and IP3 generated by PLC. Enzymes may deplete molecules that facilitate stomatal opening. For example, GOX and GHD remove glucose, apyrase removes ATP. Additionally, bacteria from the regurgitant of herbivores may trigger stomatal closure. OS components on the right (e.g., CK and catalase) potentially trigger stomatal opening. Phytohormone CK facilitates stomatal opening. Enzymes (e.g., catalase) may remove molecules (e.g., ROS) that trigger stomatal closure. Abbreviations: A^-, anion; ABA, abscisic acid; BA, benzoic acid; CK, cytokinin; GHD, glucose dehydrogenase; GOX, glucose oxidase; IP3, inositol trisphosphate; JA, jasmonic acid; PLC, phospholipase C; ROS, reactive oxygen species; SA, salicylic acid.

predation risk [55,56]. Therefore, species with a broader host range likely benefit from higher GOX activity that induces stomatal closure and inhibits the emission of HIPVs that attract natural enemies. For example, *Heliothis virescens* larvae that have salivary GOX were reported to reduce HIPV emissions in their host plant *Nicotiana tabacum* [79]. Studies of other generalist caterpillars also revealed their ability to regulate the emission of HIPVs via chemical modulation of plant VOCs [80]. The links between broader host range and the ability to modulate HIPVs indicate that inhibiting HIPV emission might be a common strategy of generalist insect herbivores, but the frequency of occurrence and mechanisms underlying the strategy remain to be investigated.

Damage by specialist herbivores (e.g., *M. sexta*) also triggers stomatal closure and potentially reduces HIPVs that attract natural enemies. However, evidence showing the ability of specialists to trigger stomatal closure remains scarce and its ecological roles remain unclear. In addition to potential inhibition of HIPVs, stomatal closure has been linked to a reduced translocation of secondary metabolites such as nicotine, which is synthesized in roots and transported to leaves in tobacco (*N. tabacum*) [81]. Salivary GOX in *H. zea* larvae and oral secretions in *M. sexta* larvae have been reported to reduce both the stomatal aperture (or conductance) and the concentration of nicotine in plant leaves [54,74,82,83]. One possible explanation for this correlation is reduced water transport that inhibits nicotine translocation from roots to leaves via the xylem.

It is noteworthy that most of the evidence showing the ability of herbivores to manipulate plant stomata focuses on local (e.g., leaf) responses [54,73,75,76]. Only two studies showed evidence for systemic stomatal closure [74] and systemic reduction in specific HIPV emissions [54]. It would be an important future goal to distinguish between local and systemic responses of stomata to herbivory because the ecological impacts of HAMP-induced stomatal changes may depend largely on the response scale. For example, local stomatal closure may inhibit VOC release, but if stomatal closure remains local, plants may still emit enough HIPVs to attract natural enemies at a whole-plant level. We speculate that plants may attenuate the impacts of HAMP-induced stomatal closure by eliciting specific systemic responses. We also hypothesize that specific behaviors of insect herbivores may involve maximizing the effect of HAMP-induced stomatal closure. In the case of *H. zea*, larvae tend to create holes throughout host plants, supposedly maximizing the amount and distribution of oral secretions [54]. Most of these hypotheses, however, remain to be tested.

Many compounds in insect oral secretions are potential modulators of plant stomatal dynamics (Figure 1 and Table 2). Phytohormones such as ABA, SA, and JA function in guard-cell signaling [84], and all three phytohormones have been detected in the saliva of *Spodoptera frugiperda* caterpillars [85]. The presence of phytohormones in insect saliva is not limited to the order of Lepidoptera, they are also present in the orders Hemiptera [86], Hymenoptera [87], and Diptera [88], suggesting that the ability to manipulate plant stomata might be widespread. Phosphatidic acid and/or inositol 1,4,5-trisphosphate produced by phospholipase C (PLC), which is also found in caterpillar saliva [89], is associated with the inhibition of stomatal opening by ABA [90,91]. Additionally, extracellular ATP (eATP), found in the apoplasts of plant cells, modulates stomatal opening in a concentration-dependent manner in which low concentrations (5–15 μM) induce stomatal opening, whereas higher concentrations (150–250 μM) induce closure [92,93]. Apyrases regulate levels of eATP, and application of exogenous apyrase can prevent stomatal opening [92]. ATPases and apyrases are also found in herbivore saliva and thus could help to regulate stomatal opening [94]. Glucose dehydrogenase is commonly found in the saliva of insect herbivores [63,65,95–101] and it oxidizes and reduces the concentration of glucose, an important carbon source that facilitates stomatal opening [102]. Other enzymes that potentially affect stomatal behavior are summarized in Table 2. Although the examples of HAMP-induced stomatal closure remain scarce, we propose that modulation of stomatal behavior by herbivores is much more common than previously recognized. In addition to being a potential adaptive phenotype of herbivores, the possibility that HAMP-induced stomatal closure is an adaptive response of plants should not be disregarded. Closure of stomata could be a response to alleviate the damage by herbivory (e.g., preventing water loss) or even serve as a signal itself that induces antiherbivore defenses by limiting photosynthesis [103]. However, evidence supporting these speculations remains scarce and further investigation is needed to explore the adaptive roles of HAMP-induced stomatal closure.

Stomata as modulators of plant growth and defense

Evidence of direct regulation of stomatal behavior by herbivores remains scarce, but many studies have reported that herbivory influences photosynthesis (Table 1), in part by modulating stomatal responses. Herbivory can inhibit photosynthesis directly through the removal of photosynthetic tissues and indirectly by disturbing vasculature and inducing defense responses [104]. Artificial simulations of chewing damage cause a rapid reduction in photosynthetic activity [105–109]. Feeding by *Trichloplusia ni* caterpillars not only reduces photosynthetic activity by removing leaf tissue but also reduces photosynthesis efficiency in nearby tissues [110]. Feeding by winter moth larvae (*O. brumata*) leads to a significant reduction in photosynthesis in pedunculate oak (*Quercus robur*) compared with undamaged plants and mechanically wounded plants: indirect

Table 2. Components in herbivore oral secretion that potentially modulate plant stomata dynamics

Component in oral secretions	Herbivore type	Herbivore species	Potential impact on stomata	Refs
Amylase	Piercing sucking	*Empoasca fabae*	Starch degradation by amylase is essential for stomatal opening	[131–133]
	Chewing	*Trichoplusia ni*		
Apyrase/atpase	Piercing sucking	*Lygus lineolaris*	Regulate extracellular ATP and prevent stomatal opening	[64,92,94,134,135]
	Chewing	*Helicoverpa zea*		
	Chewing	*Spodoptera exigua*		
	Chewing	*Bombyx mori*		
Ascorbate oxidase	Piercing sucking	*Diuraphis noxia*	Overexpressing ascorbate oxidase reduces stomatal conductance	[136,137]
	Piercing sucking	*Rhopalosiphum padi*		
Beta-glucanase	Piercing sucking	*Empoasca fabae*	Beta-1-3-glucanase degrades callose and inhibits opening or closing of stomata	[101,132,138]
	Chewing	*Spodoptera frugiperda*		
Calreticulin	Chewing	*Bombyx mori*	Calreticulin interacts with ABA signaling and Ca^{2+} which are important regulators of the stomatal response	[134,135,139]
	Chewing	*Spodoptera exigua*		
Catalase	Piercing sucking	*Bemisia tabaci*	Catalase prevents stomatal closure	[96,132,133,136, 140,141]
	Piercing sucking	*Diuraphis noxia*		
	Piercing sucking	*Empoasca fabae*		
	Piercing sucking	*Rhopalosiphum padi*		
	Chewing	*Trichoplusia ni*		
	Chewing	*Vanessa cardui*		
Glucose dehydrogenase	Piercing sucking	*Acyrthosiphon pisum*	Deplete glucose, facilitating stomatal opening and slowing down of dawn stomatal opening	[63,65,95–102,142]
	Piercing sucking	*Bemisia tabaci*		
	Piercing sucking	*Diaphorina citri*		
	Piercing sucking	*Frankliniella occidentalis*		
	Piercing sucking	*Lygus hesperus*		
	Piercing sucking	*Megoura viciae*		
	Piercing sucking	*Metopolophium dirhodum*		
	Piercing sucking	*Myzus persicae*		
	Piercing sucking	*Sitobion avenae*		
	Chewing	*Spodoptera frugiperda*		
Glucose oxidase	Piercing sucking	*Frankliniella occidentalis*	(i). The enzyme produces H_2O_2 that may lead to stomatal closure (ii). Acidification by gluconic acid may lead to stomatal closure (iii). Deplete glucose that facilitates stomatal opening and slows down stomatal opening at dawn	[54,63–65,75,89, 102,142–148]
	Chewing	*Helicoverpa armigera*		
	Chewing	*Helicoverpa zea*		
	Piercing sucking	*Lygus lineolaris*		
	Piercing sucking	*Myzus persicae*		
	Chewing	*Ostrinia nubilalis*		
	Chewing	*Spodo ptera exigua*		
	Chewing	*Spodoptera frugiperda*		
	Chewing	*Spodoptera littoralis*		
Glutathione peroxidase	Piercing sucking	*Acyrthosiphon pisum*	Overexpression of glutathione peroxidase reduces transpiration	[95,133,149]
	Chewing	*Trichoplusia ni*		
Glutathione-*S*-transferase	Chewing	*Bombyx mori*	Antioxidant enzyme that potentially affects stomatal responses	[135,150]
HARP1	Chewing	*Helicoverpa armigera*	HARP1 inhibits JA-regulated responses, potentially interfering with JA-regulated stomatal closure	[151,152]

Table 2. (continued)

Component in oral secretions	Herbivore type	Herbivore species	Potential impact on stomata	Refs
Malate dehydrogenase	Piercing sucking	*Nephotettix cincticeps*	Malate dehydrogenase oxidizes malate which is essential for stomatal opening	[153,154]
NADH dehydrogenase	Piercing sucking	*Myzus persicae*	Cytosolic NADH promotes malate formation and stomatal opening	[65,155]
Peroxidase	Piercing sucking	*Diuraphis noxia*	Inhibition of peroxidase was linked to inhibition of stomatal closure	[101,136,156,157]
	Piercing sucking	*Helopeltis theivora*		
	Piercing sucking	*Rhopalosiphum padi*		
	Chewing	*Spodoptera frugiperda*		
Phospholipase C	Chewing	*Spodoptera frugiperda*	Inositol 1,4,5-trisphosphate produced by phospholipase C is associated with the inhibition of stomatal opening	[89,91]
Polygalacturonase	Piercing sucking	*Lygus Hesperus*	Overexpression of polygalacturonase accelerates stomata opening	[64,98,158]
	Piercing sucking	*Lygus lineolaris*		
Cytokinin	Galling	*Pachypsylla celtidis*	High activity of cytokinin increases stomatal openness	[159–161]
	Leaf mining	*Phyllonorycter blancardella*		
	Piercing sucking	*Tupiocoris notatus*		
Abscisic acid	Chewing	*Spodoptera frugiperda*	ABA is a main regulator of stomatal closure	[85,161,162]
	Galling	*Pachypsylla celtidis*		
Benzoic acid	Chewing	*Spodoptera frugiperda*	Application of benzoic acid leads to lower stomatal conductance	[85,163]
Jasmonic acid	Chewing	*Spodoptera frugiperda*	Jasmonic acid regulates stomatal closure	[85,151]
Salicylic acid	Chewing	*Spodoptera frugiperda*	Salicylic acid regulates stomatal closure	[85,141]
Pseudomonas sp.	Chewing	*Leptinotarsa decemlineata*	Perception of *Pseudomonas syringae* can lead to rapid stomatal closure	[6,60]

inhibition of photosynthesis (40%) was estimated to be higher than the direct effect of leaf area loss (6%) [73]. A similar reduction in photosynthesis upon herbivory was also reported in the *M. sexta–N. attenuata* system [74].

Stomatal closure is likely one of the main causes of herbivore-induced photosynthetic inhibition [26,73,74] and might be part of the antiherbivore defense signaling in plants. Although photosynthesis provides essential molecules for the synthesis of defense-related compounds [111–113], inhibition of growth and photosynthesis usually leads to enhancement in defense [114]. The trade-offs between growth and defense have long been recognized as the result of reallocating resources [115], but recent evidence has suggested that JA-associated signaling networks play a major part in determining this trade-off [116]. Part of the defense signaling network likely involves sensing reductions in carbon assimilation. It was found that higher levels of leaf damage led to enhanced defense responses in tobacco, and it was proposed that plants detect the level of damage by sensing the level of carbon source limitation [103]. Whether herbivory-induced stomatal closure that indirectly reduces carbon assimilation is one of the damage signals/responses that regulates the growth–defense balance requires further investigation.

In contrast to the rapid reduction in stomatal aperture and photosynthesis following herbivory, increases in photosynthetic activity per unit leaf area have also been reported after an attack by chewing insect herbivores [117]. It is noteworthy that the context of each study heavily influences the conclusions of how herbivory affects photosynthesis as many studies have taken measurements of remaining undamaged tissues or regenerated tissue several days after initial attacks

[117] – which is distinct from the studies described in the previous section. Increased photosynthetic activity is likely caused by an increased demand for photosynthate in sink tissues due to direct or indirect inhibition of carbon assimilation (limited source tissue) by herbivory and is associated with plant tolerance and recovery from herbivory [104]. Additionally, increased photosynthesis postherbivory may be a passive response of plants to higher systemic availability of nutrients that limit photosynthesis, such as nitrogen [118], after defoliation, or to improved water status after tissue loss that causes stomata to open and leads to greater photosynthetic activity [119]. Upregulation of photosynthesis could also be an adaptive response to compensate for fitness costs incurred by herbivory and is linked to the plant tolerance of defoliation [120]. The close associations between stomatal dynamics, photosynthesis, defense, and tolerance against herbivory suggest the potential functions for stomata in regulating multiple responses to herbivory. So far, the underlying physiological mechanisms that connect these processes remain unclear.

Concluding remarks and future directions

As sessile organisms, plants constantly face multiple environmental stresses. While many studies have shown the roles of stomata in plant responses to many environmental stresses, there is still a surprisingly limited understanding of the role of stomata in plant–insect interactions. Wound-induced stomatal closure is a commonly observed response in plants and is likely a passive response due to water loss or other associated signaling events, such as the accumulation of JA or SA. It is, however, also emerging that herbivores can directly and/or indirectly modulate plant stomata, and we hypothesize that HAMP-induced stomatal closure serves important ecological functions. Manipulating stomatal closure could have profound and robust benefits for herbivores (Figure 2): (i) reduced water loss of plant tissues, which maintains levels of this

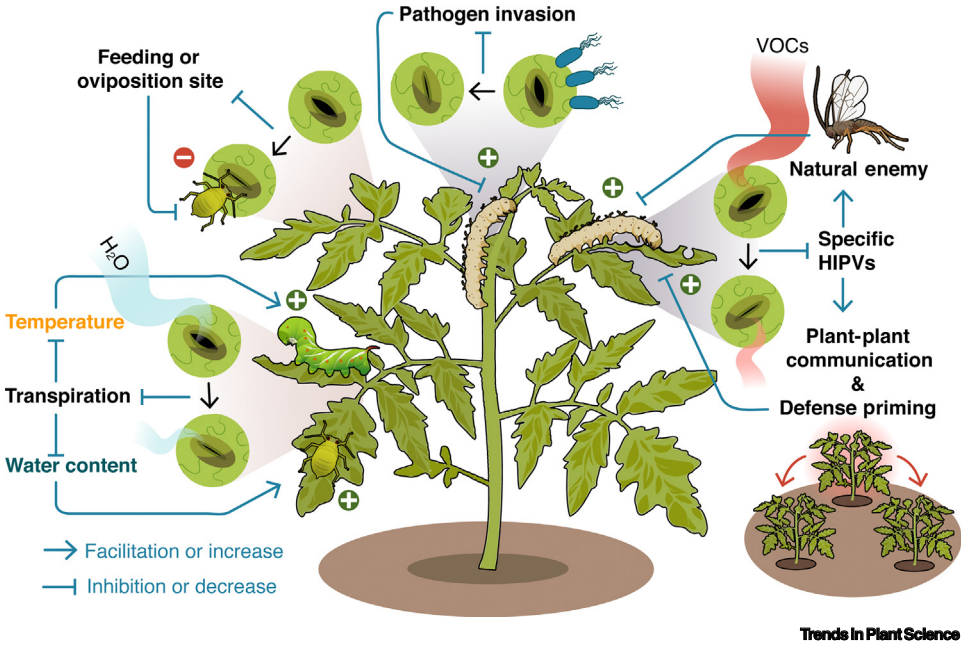

Figure 2. Potential ecological impacts of herbivory-induced stomatal closure. Herbivory-induced stomatal closure may enhance water content of plant tissues and increase its nutritional quality to herbivores. Reduced transpiration by stomatal closure also increases temperature, facilitating insect growth. Stomatal closure reduces feeding and oviposition sites for herbivores that directly interact with stomata. Stomatal closure prevents invasion of plant pathogens and inhibits emission of defense-related volatile organic compounds (VOCs) by plants, subsequently reducing negative species interactions (e.g., competition, parasitism, and predation) to herbivores. Positive signs represent beneficial impacts on herbivores. Negative signs represent detrimental impacts on herbivores. Abbreviation: HIPVs, herbivore-induced plant volatiles.

Outstanding questions

Plant stomatal responses affect photosynthesis and are closely linked to plant growth and defense. Herbivory can alter stomatal apertures and responses to environmental stimuli, but how stomatal responses are incorporated into growth-defense systems in plants is unclear. The adaptive roles of changes in stomatal behavior following herbivory are also unclear.

Although the ability of herbivores to actively modulate plant stomata has been demonstrated in some cases, the frequency of this phenomenon, and its ecological and evolutionary implications, remain unknown.

Herbivory-induced stomatal closure may prevent plant pathogens from invading plant tissues. However, the roles of stomata in competitive interactions between herbivores and plant pathogens have been understudied.

Increasing evidence shows that stomata modulate the release of plant airborne defenses: stomatal closure inhibits the release and uptake of plant volatiles and potentially affects plant–herbivore and plant–plant interactions. However, the signaling/biophysical mechanisms and ecological impacts of stomatal behavior in relation to plant volatile release remain to be investigated.

Herbivory-induced stomatal changes potentially influence the responses of plants to other environmental stresses, such as drought, heat stress, and air pollution. Herbivory may disrupt the plant's ability to protect itself against these stresses. Understanding plant responses to varying combinations of these stresses will be especially important in the face of climate change.

Herbivory-induced stomatal changes have been shown in above-ground herbivory. How below-ground herbivory influences plant stomatal response remains poorly understood. Root damages influence water availability to plants, which affects both below- and above-ground interactions. Understanding how below-ground herbivory influences stomatal response may provide insight into the different ecological impacts between local and

essential nutrient [29,30]; (ii) elevated leaf temperature, which accelerates the growth of poikilothermic herbivores [33]; (iii) reduced competition by inhibiting infection by certain phytopathogenic bacteria; (iv) reduced release of herbivore-induced plant volatiles [121] that would allow natural enemies to locate their herbivore prey/host; and (v) reduced potential for VOC/green leaf volatiles (GLV)-mediated inter/intra-plant signaling/communication [39,122,123]. Although most of these hypotheses remain to be tested they generate a wide range of questions underlying a novel aspect of plant–insect interactions (see Outstanding questions). Stomatal response to herbivory is an underappreciated aspect of plant–insect interactions. Due to the links between stomata and multiple aspects of plant physiology, any manipulations, or changes of stomata due to herbivory, can have molecular, individual, or even community-level impacts. Understanding stomatal responses to herbivory and how herbivores manipulate stomata is an important step towards more comprehensive knowledge of the functions of stomata in plants and their interactions with the environment, which, in turn, could enable the development of pest control and yield optimization strategies. Unveiling these interactions will advance our understanding of stomata-mediated responses that affect plant performance under a changing environment, which is especially important as climate change expands pest ranges and places additional stresses on the plants upon which we rely for food, materials, and renewable energy.

systemic stomatal responses induced by herbivores.

The molecular and physiological mechanisms leading to HAMP-induced stomatal changes remain largely unknown. Plant mutants with impaired phytohormones (e.g., JA, ABA, SA, ethylene), synthesis/sensing, or other signaling components (e.g., H_2O_2, eATP) may serve as excellent tools to understand the proximate reasons for HAMP-induced stomatal changes.

Declaration of interests

There are no interests to declare.

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