ACS
AGRICULTURAL
SCIENCE & TECHNOLOGY

pubs.acs.org/acsagscitech

Review

Chemical Camouflage in Plants: Defensive Science of Stealth against Insect Herbivory

Manisha Parashar, Maniraj Rathinam, Narasimham Dokka, and Rohini Sreevathsa*

Cite This: *ACS Agric. Sci. Technol.* 2025, 5, 1251−1262

Read Online

ABSTRACT: Chemical camouflage is a fascinating and intricate survival strategy that plants have evolved to defend themselves against herbivores and pests. While plant defense mechanisms have long captivated scientific interest, their full potential remains largely untapped in practical applications. This review takes a distinctive interdisciplinary approach, weaving together insights from molecular biology, ecology, and agricultural science to offer a comprehensive perspective on chemical camouflage. It was driven by a shared understanding that integrating plant defense strategies more deeply into agricultural systems could help address urgent challenges such as pest control, crop productivity, and environmental sustainability. With continued research and advances in biotechnology, chemical camouflage could become a key component of future farming—where crops not only protect themselves but also contribute actively to a more productive and sustainable agricultural landscape.

KEYWORDS: *biosemiosis, chemical camouflage, herbivory, volatile organic compounds (VOCs), plant defense*

1. INTRODUCTION

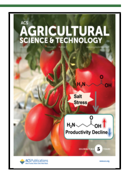
Burgeoning population and climate change have been linked to significant problems for ecosystems, agriculture, and human existence worldwide. As temperatures increase and weather turns erratic, insects, rodents, and microorganisms discover new environments and thrive in areas that were once inhospitable. Among the various stress factors that pose grave challenges to plant growth and productivity, insect pests are of phenomenal priority. Herbivorous insects damage crops by feeding on leaves, stems, and roots, leading to reduced yields and economic losses. Additionally, some insects serve as vectors for diseases, transmitting pathogens to plants, animals, and humans.[1] In forestry, they can cause deforestation by weakening trees, making them vulnerable to secondary infections.[2] These pests' complicate pest control efforts as they not only diminish agricultural production but also alter natural environments. As a consequence, crop loss has risen, particularly in risk areas where pests such as beetles, caterpillars, and aphids have proliferated.[3] Along with inflicting direct damage, the invasion of crops by these pests raises the application of chemical pesticides,[4] potentially harming biodiversity, human health, and environment. Consequently, an urgent need for innovative and environmentally friendly pest management solutions rise with this.

Plants, have long developed intricate and effective defense strategies to counteract these threats. One of the key mechanisms in their defense arsenal is the production of chemical compounds that act as repellents, toxins, or attractants for natural predators of herbivores.[5,6] These compounds, which include alkaloids, terpenoids, and phenolics, are synthesized in response to pest attacks, initiating a chain of biochemical activities that ultimately result in the production of protective substances.[7,8]

This chemical defense response is largely facilitated through the production of volatile organic compounds (VOCs)—a diverse group of low-molecular-weight compounds emitted by plants during their metabolic processes.[9] VOCs play a critical role in plant-environment interactions, attracting pollinators, repelling herbivores, and signaling to neighboring plants or organisms.[10] In response to herbivory, plants release specific VOCs such as green leaf volatiles (GLVs), terpenoids, and phenylpropanoids, which function as both direct defenses, repelling herbivores, and indirect defenses, attracting natural enemies of the pests.[11,12] In a more sophisticated maneuver, plants can alter or hide their chemical signals to mislead or deter pests, masking their presence or even creating the illusion of an uninviting environment.[13,14]

In the natural world, survival often hinges on the ability to hide in plain sight. While animals have long been known to use physical camouflage to blend into their surroundings,[15] plants have perfected a different form of concealment: chemical camouflage.[16] This extraordinary defense mechanism enables plants to outwit herbivores and pests by using biochemical ingenuity to disguise their true identity. It is a process rooted in the release and manipulation of volatile compounds—chemical signals that confuse, repel, or even deceive would-be attackers. Through this chemical stealth, plants effectively create a "stealth barrier" that helps them avoid being eaten or damaged, offering a fascinating example of nature's functional

Received: March 19, 2025
Revised: June 14, 2025
Accepted: June 17, 2025
Published: June 27, 2025



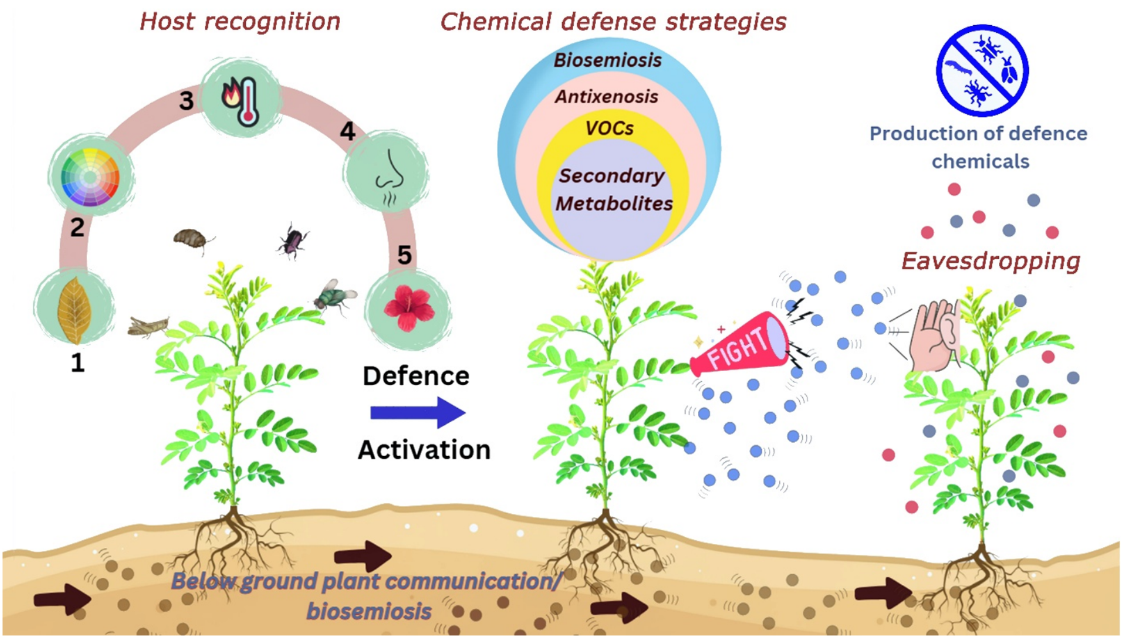


Figure 1. Chemical Camouflage- an invisible defense cloak in plants. (Plant—left to right) Primarily host recognition by insects depends on various cues like preferable plant surface, attractive leaf/ flower color, amenable temperature, preferable odor from plants, congenial plant flowering time. Various strategies like biosemiosis, antixenosis, VOCs and secondary metabolites of chemical camouflage is operated by plants upon cognizance of insects. Exploitation of insect specific defense by neighboring plants happens through eavesdropping, resulting in the release of different defense chemicals including a range of secondary metabolites and VOCs. Plants emanate a blend of VOCs to communicate with one another and with their surroundings, both above- and belowground. Defense- induced VOCs released from plants have been displayed in small colored circles.

Table 1. Parameters for Host Identification by Pests

mechanism	description	examples	references
visual cues	Herbivores use color, size, or shape of plants to identify hosts	Cabbage white butterfly (*Pieris rapae*) targets green brassicas. Grasshoppers favor broad-leaved plants	31,35
chemical cues	Volatile organic compounds (VOCs), secondary metabolites, or surface chemicals guide host selection	Tomato hornworm (*Manduca sexta*) responds to tomato VOCs. Aphids detect specific secondary metabolites in crops	24
nutritional quality	Preference for plants with higher protein, carbohydrate, or nitrogen content	Locusts favor nitrogen-rich grasses. Cattle graze on protein-rich legumes	92
mechanical traits	Herbivores avoid or prefer plants based on physical traits like toughness, trichomes, or spines	Beetles avoid leaves with high trichome density. Deer avoid spiny cacti	93
plant palatability	Taste or texture influences choice; herbivores often avoid bitter or toxic plants	Koalas prefer nontoxic eucalyptus species. Slugs avoid bitter-tasting plants like mustard	94
phenological synchrony	Timing of plant growth (e.g., young leaves or flowers) affects herbivore preference	Gypsy moths target newly emerged oak leaves. Monarch butterflies favor young milkweed.	34
microbial associations	Herbivores are attracted to or repelled by microbial communities (e.g., fungi or bacteria) on plants.	Grasshoppers are deterred by plants with endophytic fungi. Bark beetles are drawn to infected pine trees	35
learned behavior	Some herbivores learn host preferences based on experience or social interaction	Cattle develop a taste for previously unpalatable plants after exposure. Caterpillars learn host plants from maternal oviposition sites	39

adaptations shaped by evolution. The concept of chemical camouflage is not only an impressive evolutionary adaptation, but it also holds significant promise for the future of agriculture. This adaptive strategy can be viewed as a form of chemical deception that not only helps plants avoid predators but also creates a more complex relationship between plants, their environments, and the organisms with which they interact.

Despite the progress in understanding these plant-pest interactions, there has been a relative lack of comprehensive reviews that synthesize the specific mechanisms and biotechnological applications of chemical camouflage.[17] Most research in this area has concentrated on individual components of plant resistance, such as secondary metabolite synthesis or mechanical defenses.[18] While these studies have provided valuable insights, they often overlook the interdisciplinary approach needed to fully grasp the complexities of chemical camouflage. Moreover, while some research has focused on natural occurrences of chemical camouflage, there has been little exploration of how these natural processes can be translated into technological applications, such as genetic engineering of VOC pathways or the creation of synthetic analogues.

This review aims to fill this gap by offering a comprehensive, up-to-date perspective on the science of chemical camouflage and its applications in agriculture. By bringing together insights from various scientific disciplines, this review not only synthesizes previous research but also offers innovative ideas for how chemical camouflage could be used to address critical challenges in agriculture. Through this synthesis, we hope to shed light on how sophisticated chemical defenses of plants can be harnessed to create smarter, more resilient crops that

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

reduce reliance on harmful pesticides and contribute to more sustainable farming practices.

2. THE ART OF THE ATTACK: HOST SELECTION BY PESTS

Pests are not random feeders; they are selective, guided by a host based on factors including plant morphology, nutrient content, and most importantly, chemical cues.[19,20] How do herbivores choose their plant hosts in the first place? This act is a complex and multifaceted process that involves the integration of various sensory cues, allowing pests to identify and evaluate suitable plants for feeding, reproduction, and shelter.[21] They rely on an array of signals from plants they target, that include chemical, visual, tactile, and environmental cues.[22] These signals are not only essential for the herbivore's survival but also play a crucial role in shaping plant-pest interactions.

Having delineated the complexity of herbivore behavior and the importance of host selection, we now delve and outline in Figure 1, the specific aspects that guide this process, each playing a pivotal role in how pests identify and assess potential plant hosts.

2.1. Chemical Cues (VOCs and Surface Chemicals). Chemical signals are central to the host selection process. Plants emit VOCs that serve as long-range chemical signals, guiding pests to their hosts[23] (Figure 1). These VOCs can be attractants or repellents, depending on the pest's preferences and evolutionary adaptations. For example, tomato hornworms (*Manduca sexta*) are attracted to tomato plants because of specific VOCs that tomatoes release during growth.[24] These VOCs signal to the hornworms that the plant is suitable for feeding.[25] On the other hand, glucosinolates in brassicas like cabbage or kale attract cabbage white butterflies (*Pieris rapae*), as these compounds act both as attractants and feeding stimulants[26] (Table 1).

Surface chemicals, such as epicuticular waxes, terpenoids, alkaloids, and phenolics, also play a critical role.[27] For instance, terpenoids produced by certain plants can repel pests or signal the presence of a toxic plant.[28] Alkaloids, on the other hand, are often toxic to herbivores. The presence of these chemicals on the plant's surface helps herbivores assess whether the plant is suitable for feeding or not.[29] For example, nicotine in tobacco acts as a potent deterrent for many herbivores, including some insects[30] (Table 1).

2.2. Visual Cues (Color, Shape, and Movement). Visual cues are another significant factor in host selection, particularly when pests are approaching plants from a distance. Many herbivores are attracted to specific colors that indicate healthy, photosynthetically active plants.[31] For example, green leaves are often an indicator of a healthy, nutritious plant (Figure 1). Many insects, like aphids and caterpillars, are particularly drawn to these green hues.[32] Similarly, yellow can also attract herbivores because it often signals new, tender growth, which is easier to consume.[33]

The shape and size of the plant are also key indicators. For instance, larger plants with abundant leaves, such as the bean plant, may attract herbivores like bean beetles because they offer more surface area for feeding and reproduction.[34] Furthermore, the movement of plant parts can influence pests' decisions. Insects such as grasshoppers may be attracted to the swaying leaves of plants because the movement signals that the plant is alive and likely to be a suitable food source[35] (Table 1).

2.3. Tactile Cues (Texture and Surface Properties). Once a pest lands on a plant, it further evaluates its suitability using tactile cues. Insects use mechano-receptors located on their antennae and mouthparts to assess the plant's surface texture. For example, trichomes (hair-like structures) on the surface of plants like tomato or cucumbers can deter feeding by making it difficult for insects to settle on the plant[36] (Figure 1). Insects like whiteflies may be repelled by the hairy surface of these plants.[37] Similarly, smooth leaves might be more appealing to pests such as aphids because they can easily settle and feed without being obstructed.

The hardness or toughness of plant tissues also plays a role in pest selection. For example, tobacco plants have tough leaves that can deter some pests, while others, such as caterpillars, have evolved to feed on these tougher surfaces by secreting digestive enzymes that break down plant defenses[38] (Table 1).

2.4. Environmental Cues (Light, Humidity, Temperature). Environmental factors such as light, temperature, and humidity can enhance or suppress the effectiveness of chemical, tactile, and visual cues. Temperature and humidity can influence the release of VOCs and the overall health of the plant (Figure 1). For instance, in warmer climates, plants like corn may release more VOCs that attract pests like corn earworms (*Helicoverpa zea*).[39] Similarly, the humidity of the environment can affect the physical characteristics of the plant surface, such as stickiness, which may influence a pest's feeding behavior. For example, certain pests like whiteflies thrive in warm, humid conditions, where their preferred host plants, such as tomato or squash, grow vigorously.[40] In contrast, other herbivores, such as cabbageworms, may be more active under cooler conditions where brassicas are abundant[41] (Table 1).

2.5. Interaction with Other Organisms (Pheromones and Mutualists). Pheromones, that are chemical signals emitted by insects, can also guide herbivores in their host selection. These signals allow herbivores to communicate with others of their species about the location of suitable hosts. For example, female moths like the corn earworm (*H. zea*) release sex pheromones to attract males, who then help to locate host plants.[42] Additionally, mutualistic relationships can influence herbivore behavior. Ants that protect plants like acacia trees from herbivores will often receive food rewards, such as nectar, in return.[43,44] These mutualistic relationships can sometimes affect herbivore feeding choices, as ants may chase away herbivores that attempt to feed on the plants they protect[45] (Table 1). Moreover, the phyllosphere and rhizosphere microbiota play key roles in modulating plant defense responses through the production of volatile organic compounds (VOCs) and signaling. In the phyllosphere, microbial interactions, particularly with bacteria like *Pseudomonas* and *Bacillus*, can trigger induced systemic resistance (ISR), activating plant immune responses and VOC emissions that deter herbivores and attract natural predators. Similarly, the rhizosphere microbiota, through microbial VOCs and root exudates, enhances plant defenses against soilborne pathogens and regulates plant hormones such as jasmonic acid and salicylic acid. Both microbiomes communicate through VOC signaling, initiating systemic defense mechanisms across plant tissues.[46]

2.6. Learned Behavior and Experience. Some pests also exhibit learned behavior, modifying their host preferences based on previous feeding experiences. For example, the cabbage white butterfly (*Pierisrapae*) tends to prefer plants in

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

the Brassicaceae family, like cabbage and kale, because these plants produce glucosinolates, which not only attract but also stimulate feeding[47] (Table 1). Over time, pests like these may learn to associate specific plant odors or chemical signatures with higher nutritional value, shaping their future feeding decisions.[48]

Plants, in turn, have evolved various mechanisms to either attract or repel herbivores, influencing the selection process and, in many cases, leading to coevolutionary arms races between plants and their insect pests.

3. BATTLE OF THE WITS: HOW PLANTS OUTSMART PESTS?

Plants often emit chemical signals that can inadvertently attract herbivores. However, some have evolved strategies to avoid detection by altering or suppressing these signals, a phenomenon known as chemical camouflage. Unlike mechanical defenses like thorns or toughened leaves, chemical camouflage operates on an almost imperceptible level, allowing plants to mask their presence or mimic unpalatable species. One fascinating example comes from wild tobacco plants (*Nicotiana attenuata*), when attacked by herbivores like the tobacco hornworm (*M. sexta*). During the attack, these plants can suppress the emission of certain VOCs that typically distress signal.[49] Rather than emitting distress signals that attract predatory insects, which could inadvertently draw additional herbivores, the plant suppresses its chemical emissions, effectively blending into the surrounding chemical environment. Another example is the case of *Ficus* species, which use chemical mimicry to deter leaf-cutter ants. By producing compounds similar to those found in less palatable or toxic plants, these plants deceive the ants into bypassing their leaves for other, seemingly more suitable, targets.[50] This reduces the chances of sustained herbivory and conserves the plant's resources. Chemical camouflage involves more than just masking or imitation; it may also involve direct deceit. Some orchids, for example, generate substances that imitate ants' alarm pheromones, preventing herbivores from approaching. These plants successfully navigate a complicated ecological web by altering the behavior of both herbivores and predators.[14] This evolutionary arms race between plants and herbivores demonstrates the incredible flexibility of life on earth. Chemical camouflage is more than simply a defensive strategy for plants; it also demonstrates their capacity to sense and adapt to their surroundings. It focuses on a complicated interaction in which survival is determined by subtle, creative techniques rather than overwhelming might. These adaptations showcase their ability to modify chemical signals, manipulate visual cues, adjust life cycles, and fortify structural integrity. By employing these ingenious strategies, plants not only deter predators but also enhance their chances of reproduction and survival. The following are some of the remarkable defensive mechanisms portraying chemical camouflage that illustrate the ingenuity of plant evolution.

3.1. Odor Masking. Odor masking is a complex plant defense system in which plants change or suppress VOCs to avoid detection by herbivores or attract beneficial species. This method includes altering chemical cues that insects use to find appropriate hosts. Plants conceal odors through a variety of ways, including the creation of VOCs, which either neutralize attractant odors or imitate ambient aromas, allowing them to blend in. Odor masking is frequently activated in response to herbivory or environmental stress signals. Plants have complex signaling processes including phytohormones such as jasmonic acid, salicylic acid, and ethylene that control the manufacture of defensive VOCs.[51] When plants sense herbivore activity, they may selectively control the emission of certain VOCs, disrupting the olfactory signals utilized by insects. For example, when maize plants are attacked by herbivores, they release (*Z*)-3-hexenol and indole, which can either mask their own odor or attract predatory insects like parasitic wasps that prey on the herbivores.[52] Similarly, a plant volatile (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) is produced constitutively in many plant species and often induced under insect attack in increased quantities. The production of DMNT masks the insect olfactory receptor and affects its host reorganization.[53,54] Likewise, when plants like the black walnut tree are under herbivore attack, they may release VOCs such as methyl jasmonate and green leaf volatiles (GLVs) to disrupt the herbivores' olfactory cues and confuse them.[55] These masking strategies can be activated by herbivory or environmental stress, involving phytohormones like jasmonic acid, which regulates VOC production and plays a role in disrupting the herbivore's ability to locate the plant.

3.2. Color Masking. Color masking is another clever plant defense technique in which plants change their outward appearance to escape identification by herbivores or to imitate environmental characteristics. This technique may include changes in pigmentation, surface texture, or even the development of reflecting chemicals, which affect how light interacts with the plant surface, making it less apparent to predators. This response is frequently activated to tackle environmental stresses or direct herbivore assaults. Specific metabolic processes are activated, resulting in the buildup of pigments such as anthocyanins, flavonoids, and carotenoids. These pigments can serve two functions: camouflage the plant against the backdrop and indicate unpalatability to potential herbivores. For example, the buttercup (Ranunculus) can adjust its pigmentation to blend with surrounding foliage, reducing its visibility to herbivores.[56] Similarly, some species of mint develop reflective, waxy surfaces on their leaves that scatter light, making them harder to see.[57] Likewise, in some of the tree species autumn leaf color changes affect aphid host recognization. Commonly, red color leaf cannot be seen by aphids' visual spectrum range which provides color masking to the tree.[58]

Color masking has a significant environmental and agricultural impact. Ecologically, it shows how plants have evolved to exploit visual sensory biases in herbivores, resulting in a complex interaction of concealment and deception.

3.3. Change in Flowering Time. Flowering time variation is a unique adaptive technique that plants utilize to avoid herbivory or synchronize with favorable environmental circumstances. Plants can reduce overlap with peak pest activity by changing blooming time or synchronize their reproductive stages with ideal environmental conditions. This phenological adjustment is controlled by intricate genetic and hormonal systems. Photoperiod, temperature oscillations, and herbivore-induced stress signals are common environmental cues that trigger flowering time alterations. Plants under herbivore assault may delay or advance blossoming to decrease pest exposure or to attract natural enemies that provide indirect defense. For example, in response to herbivore pressure, some species of wild oats (*Avena fatua*) may delay flowering until after the peak period of herbivory, thereby reducing their exposure to pests.[59] Similarly, plants like the

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

wild radish (*Raphanus raphanistrum*) can alter their flowering time based on temperature and photoperiod cues, helping them to either avoid herbivores or attract natural predators by blooming when beneficial insects are most active.[60] This adjustment is controlled by plant hormones such as gibberellins, abscisic acid and transcription factors like CONSTANS (CO) and FLOWERING LOCUS T (FT), which regulate the plant's internal clocks and responses to external stimuli.[61] Ecologically, this technique emphasizes the complex connection between plants and their environment, as well as the evolutionary constraints that promote phenological flexibility.

3.4. Mimicry/Biosemiosis. Mimicry and biosemiosis are advanced strategies of plant defense that entail the release of chemical, visual, or behavioral signals to mislead herbivores, predators, or pollinators. Biosemiosis is a process by which living things use and interpret signs to communicate, survive, and interact with their environment. These signs can be anything from light, sound, smell, or chemical signals. These tactics are components of a larger system of plant communication, in which plants convey and decode signals that affect their survival, reproduction, and relationship with other organisms. Mimicry, in particular, occurs when a plant generates a signal that imitates another signal—typically that of a predator, a nonprey species, or a helpful organism, to defend itself or seek assistance. In plant protection, mimicry may appear in various forms. A prevalent type is Batesian mimicry, in which a plant resembles the look or scent of a species that is distasteful or poisonous to herbivores, thus discouraging feeding.[62] For example, certain plants might develop characteristics that mimic toxic plants or release comparable VOCs that herbivores link to harmful or hazardous species.[63] This type of mimicry deters herbivores from coming near, decreasing the chances of herbivory. Another type is Müllerian mimicry, where various toxic or unappetizing plant species develop similarities in appearance.[64] This aids herbivores in learning faster to steer clear of these plants, as they begin to link the similar signals (like taste, smell, or color) with an unpleasant experience. Throughout time, both species gain from a mutual deterrent strategy, resulting in a collaborative evolutionary edge. Alongside visual and chemical mimicry, plants employ biosemiosis—the interpretation and application of signs or signals—within a more intricate signaling framework. In biosemiosis, plants can imitate other organisms and may also interact with different species via a recognized semiotic system of signals. For instance, certain plants imitate the existence of pollinators or helpful insects by emitting particular VOCs that lure these creatures, thereby enhancing pollination or the parasitism of herbivores. Additionally, the below-ground transmission of chemicals plays a crucial role in plant communication and defense. Through root exudates, plants can release specific chemical signals into the soil, which influence neighboring plants or interact with soil microbes to indirectly deter herbivores or attract beneficial organisms. This subterranean signaling system contributes to the broader biosemiotic framework by connecting plants to their immediate ecosystem through shared chemical languages. Moreover, plants exhibit a phenomenon akin to "group immunity", where the defensive mechanisms of individual plants collectively benefit a population. When multiple plants within a community employ mimicry or release defensive signals, they create a shared deterrent effect that amplifies protection against herbivores. This communal strategy, often seen in Müllerian mimicry, reinforces herbivore learning and deters widespread damage.[65] For example, when a population of plants release a consistent pattern of toxic signals or mimicry cues, herbivores more rapidly associate these traits with an undesirable experience, reducing their impact on the group as a whole. In contrast to this phenomena, in a weed plant *Centaurea stoebe* (spotted knapweed), constitutive production of root volatiles increase protein and carbohydrate content in neighborhood plants thus deviating the insect load on to them.[66]

Plants can utilize mimicry via misleading pollination strategies, where they imitate the look or scent of a female insect from a species that comes for mating. Male insects, drawn to the mimic, try to copulate with the flowers, inadvertently aiding in pollination while the plant achieves reproductive success.[67] This type of sexual mimicry is observed in orchids that look like female bees or flies, guaranteeing pollination takes place without any direct advantage to the misled insect.[68] From an ecological standpoint, mimicry and biosemiosis illustrate the fluid interaction between plants and their surroundings, emphasizing the coevolution of signaling mechanisms among plants, herbivores, and other organisms. These mechanisms improve the plant's capacity to adjust to environmental stresses, like herbivory, while promoting interactions that are advantageous for both the plant and its partner organisms. Mimicry and biosemiosis exemplify the intricate and clever qualities present in nature's evolutionary competition.

3.5. Sclerophylly. Sclerophylly denotes adaptation of plants to environmental stresses through the formation of hard, sturdy leaves, stems, or various other plant structures. This structural change features a significant presence of lignin, cellulose, and various robust materials within the plant structures, leading to leaves and stems that are tough, leathery, and resilient to physical harm. Sclerophylly serves as a crucial defense strategy in plants, especially in dry or nutrient-deficient settings, where conserving resources and safeguarding against herbivores are essential for survival. The main role of sclerophylly is to minimize water loss and enhance the plant's defense against herbivores. In regions with limited water, sclerophylly aids in reducing transpiration (the loss of water via stomata), essential for preserving moisture.[69] The tough, sturdy characteristics of sclerophyllous leaves hinder herbivores' ability to chew and digest them, acting as a type of passive defense against herbivory. From a physiological standpoint, the progression of sclerophylly generally correlates with a reduction in leaf dimensions and a rise in leaf density. These alterations increase the difficulty for herbivores to reach the plant's soft tissues, while simultaneously reducing the surface area available for water to evaporate. Moreover, the higher lignin levels in sclerophyllous leaves serve as a barrier to herbivore digestion, since lignin poses challenges for many animals to decompose. Besides its function in defending against herbivores, sclerophylly can also give a plant a competitive edge in tough environmental situations. A well-known example of sclerophylly is seen in Mediterranean plants like the holm oak (*Quercus ilex*), which has thick, leathery leaves rich in lignin and cellulose. This tough leaf structure not only helps the plant conserve water in arid conditions but also makes it more resistant to herbivore. Another example is the Australian eucalyptus tree, which possesses sclerophyllous leaves that are hard, resistant to herbivore damage, and able to retain water during dry periods.[70] With tougher, more resilient

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

Table 2. Biochemical Pathways Underlying Chemical Camouflage

pathway	compound	function in herbivory	references
green leaf volatile (GLV) pathway	hexenal	Deters herbivores by producing a "wounded" signal; acts as a precursor for other volatiles	95
	hexenol	Attracts natural enemies of herbivores; contributes to volatile signaling	12
	hexenyl acetate	Primes defense responses in neighboring plants and attractsparasitoids	96
Jasmonic acid biosynthesis pathway	α-linolenic acid	Serves as the precursor for the entire jasmonic acid biosynthesis pathway	97
	13-hydroperoxyoctadecatrienoic acid (13-HPOT)	Intermediate that channel fatty acid metabolism into defense signal production	98
	12-oxo-phytodienoic acid (OPDA)	Functions as a direct defense molecule and precursor to jasmonic acid	99
	jasmonic acid	Activates defense genes, induces secondary metabolites and protease inhibitors, and disrupts herbivore digestion	100
salicylic acid pathway	salicylic acid (SA)	Enhances systemic acquired resistance (SAR) and mediates defense against herbivores and pathogens	100
	methyl salicylate	Volatile derivative of SA that signals to neighboring plants and recruits predators	101
phenylpropanoid pathway	phenolics	Act as toxins or deterrents against herbivores; contribute to oxidative stress resistance	102
	flavonoids	Provide UV protection and act as feeding deterrents	103
	lignin	Strengthens cell walls, making them harder for herbivores to digest	104
	tannins	Bind to proteins, reducing herbivore digestive efficiency	105
isoprenoid pathway	monoterpenes	Repel herbivores and attract predators; some have direct toxic effects	106
	sesquiterpenes	Function in both direct toxicity and signaling to natural enemies of herbivores	107
	sterols	Interfere with herbivore hormonal systems, disrupting development and reproduction	108
nitrogen-containing secondary metabolite pathway	alkaloids	Act as neurotoxins or feeding deterrents by disrupting nervous system functions	109
	cyanogenic glycosides	Release toxic hydrogen cyanide when plant tissue is damaged	110
	glucosinolates	Break down into toxic compounds like isothiocyanates, deterring herbivory	111
polyol pathway	mannitol	Functions as an osmoprotectant to mitigate oxidative stress caused by herbivory	112
	sorbitol	Protects against cellular damage during stress and aids in wound healing	113
hormonal crosstalk pathway	jasmonic acid	Balances defense against herbivores and pathogens; mediates interaction with other hormones	114
	salicylic acid	Works antagonistically or synergistically with jasmonic acid to fine-tune defenses	115
	ethylene	Modulates defense responses by enhancing jasmonic acid or salicylic acid signaling, depending on the context	116

leaves, plants are able to endure extreme temperatures, physical harm, and dryness. This renders sclerophylly especially prevalent in plants thriving in arid, nutrient-deficient soils, like numerous species found in mediterranean regions, deserts, and alpine areas. From an ecological standpoint, sclerophylly enhances the plant's overall durability, allowing it to withstand extended durations of drought, elevated temperatures, and herbivore threats. Numerous sclerophyllous plants generally exhibit slower growth rates but are very effective at conserving resources. Throughout evolutionary history, this approach has enabled these plants to prosper in settings where alternative plant strategies could struggle.

3.6. Eavesdropping. Eavesdropping in plants refers to their remarkable ability to detect and respond to chemical signals released by neighboring plants, herbivores, or even microorganisms. This adaptive strategy allows plants to pre-emptively activate their defense mechanisms or adjust their behavior to counter potential threats in their environment. Unlike direct internal signaling, eavesdropping involves intercepting VOCs or other external chemical cues to anticipate and mitigate risks. For instance, when a nearby plant is attacked by herbivores, it often releases VOCs like methyl jasmonate or GLVs to alert natural predators or neighboring plants.[71] These signals enable nearby plants to prepare their defenses by producing secondary metabolites, toughening their leaves, or releasing their own VOCs to deter herbivores. Poplar and willow trees, for example, respond to such cues by producing tannins that make their foliage less palatable, while tomato plants detect methyl jasmonate from nearby damaged plants and ramp up the production of proteinase inhibitors that disrupt herbivore digestion.[72] Eavesdropping can also involve exploiting signals emitted by herbivores themselves. Some plants can detect saliva-derived compounds from herbivores and tailor specific defenses in response.[73] Corn plants (*Zea mays*), for instance, recognize cues from feeding caterpillars and release chemicals that attract parasitic wasps, effectively turning herbivore predators into allies.[74] Beyond defense, eavesdropping can confer competitive advantages in resource acquisition. Plants may detect stress signals from their neighbors and adjust their growth strategies accordingly. For example, coyote tobacco (*N. attenuata*) responds to cues from herbivore-damaged neighbors by allocating more resources to reproduction, ensuring its survival and seed production under adverse conditions.[75] Ecologically, eavesdropping integrates plants into a larger communication network, highlighting their role as active participants in a community-wide resilience strategy. By intercepting and interpreting these signals, plants not only enhance their own

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

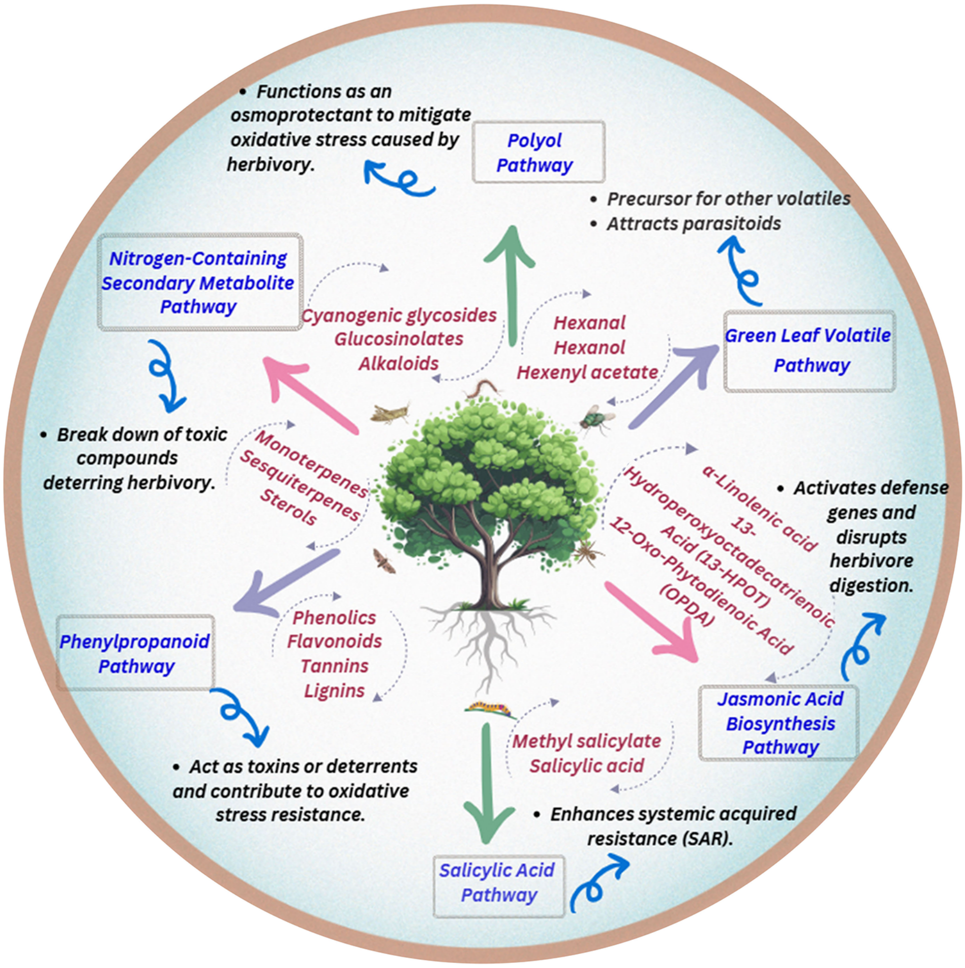


Figure 2. Illustration of plant biochemical defense mechanisms during insect attack underlying Chemical camouflage. Chemical camouflage in plants is supported by various defense pathways that encompass phenylpropanoid pathway, nitrogen containing secondary metabolite pathway, polyol synthesis pathway, green leaf volatile synthesis pathway and JA, SA defense and hormone signaling pathways.The pathways are enclosed in boxes, the compounds involved are mentioned in red and curved arrows points toward the role of these pathways.

survival but also contribute to the collective defense of their ecosystem. This dynamic interaction underscores the complexity and adaptability of plant strategies, demonstrating how they thrive amid constant ecological pressures. Through eavesdropping, plants reveal a sophisticated understanding of their environment, showcasing the evolutionary ingenuity that defines their survival.

4. BIOCHEMICAL PATHWAYS UNDERLYING CHEMICAL CAMOUFLAGE

The biochemical pathways underlying chemical camouflage represent an intricate dance of survival, where plants, locked in an evolutionary arms race with herbivorous pests, deploy an arsenal of defense mechanisms. These strategies are not random but are meticulously orchestrated through specialized biochemical pathways that produce compounds to fend off attackers, attract allies, and warn neighbors. At the heart of this complex interplay lies the green leaf volatile (GLV) pathway, a first line of defense that acts as the plant's early warning system. By producing fatty acid-derived volatiles, this pathway not only repels herbivores but also signals predators and primes nearby plants for impending danger.[76] As the battle intensifies, the jasmonic acid (JA) pathway takes center stage, coordinating an aggressive counterattack (Table 2). Beginning with α-linolenic acid, this pathway activates defense-related genes that manufacture secondary metabolites, protease inhibitors, and antidigestive substances, effectively reducing herbivore damage[77] (Figure 2). In the meantime, the salicylic acid (SA) pathway acts as a chief strategist, orchestrating systemic acquired resistance and calling on predators to fight the invaders, all while bolstering plant defenses against biotic threats.[78] In addition to strengthening the plant's defenses, the phenylpropanoid pathway plays a role in generating a variety of compounds including phenolics, lignin, tannins, and flavonoids.[79] These molecules function to reinforce cell walls, prevent feeding, and defend against oxidative stress and UV harm. Complementing this, the isoprenoid pathway produces terpenoids, acting as both repellents and attractants, while sterols disrupt the hormonal balance of herbivores, stunting their growth and reproduction[80] (Table 2 and Figure 2). Adding to the defensive lineup, the nitrogen-containing secondary metabolite pathway generates a suite of potent compounds like alkaloids, glucosinolates, and cyanogenic glycosides.[81] These substances act as neurotoxins or release reactive compounds upon herbivore attack, ensuring a swift and decisive counterstrike.[82] Meanwhile, the polyol pathway operates as a silent guardian, mitigating stress by producing osmoprotectants like mannitol and sorbitol to protect cells and

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

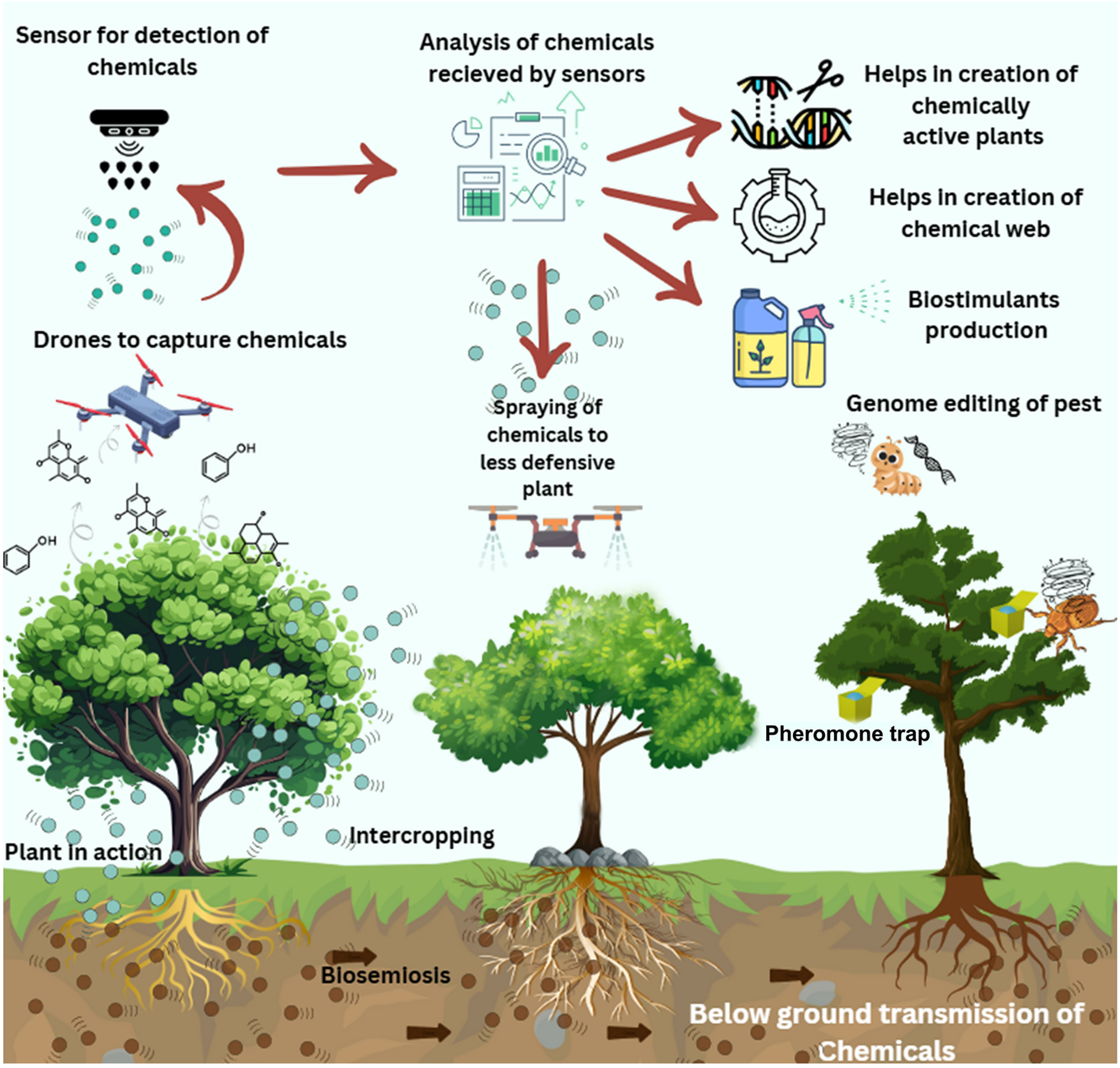


Figure 3. Envisioning and redefining intelligent and futuristic sustainable farming. Ingenious and integrated plant defense strategies utilizing chemical detection, analysis, and deployment. The strength of an agricultural scientist to explore and exploit chemical camouflage in plant lies in the utilization of drones to primarily sense the chemicals and a state of art facility for the detection of chemicals. This identification of chemicals will be utilized further through biostimulant production, intercropping, and pheromone traps to promote sustainable agriculture. Finally biotechnological interventions like genome editing of plants or insects could lead to better management of pests in plants identified as hosts as well as those surrounding them.

promote recovery.[55] Finally, the hormonal crosstalk pathway brings all these defenses into harmony[83] (Table 2). By integrating the signals from jasmonic acid, salicylic acid, and ethylene, this pathway fine-tunes the plant's responses, balancing its energy allocation and ensuring an optimal defense strategy (Figure 2). Together, these pathways weave a story of resilience and adaptation, showcasing the biochemical ingenuity of plants in their fight against herbivores while providing a blueprint for sustainable pest management practices.

5. EFFECTS OF DIFFERENT AGROECOLOGICAL ZONES ON CHEMICAL CAMOUFLAGE

Chemical camouflage strategies, which involve plants producing chemical compounds to mimic or blend in with their environment (e.g., resembling unpalatable plants or using VOCs to deter herbivores), are not equally effective across all agroecological zones, climates, or continents. The effectiveness of these strategies largely depends on local ecological factors, including the specific herbivore and pathogen pressures, the plant's surrounding flora, and climatic conditions.[84] In different agroecological zones or climates, the availability of particular plant species that may serve as models for chemical mimicry can vary, affecting how well the camouflage works. For instance, in arid regions, plants might rely more on drought-resistant compounds and use chemical mimicry to avoid herbivores that are adapted to dry environments.[85] Conversely, in humid or tropical areas, the emphasis might be on deterring herbivores that thrive in wetter, more biodiverse conditions.

Climate also influences the synthesis and stability of the chemicals involved in camouflage. High temperatures or varying humidity levels can affect the production of secondary metabolites, such as alkaloids or terpenoids, altering the plant's ability to effectively camouflage. Additionally, local herbivore species may have different sensitivities to specific chemicals, meaning a strategy that works well in one region might be less effective in another where the herbivores have evolved different resistance mechanisms.

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

6. CHEMICAL CAMOUFLAGE AND BEYOND: DESIGNING FARMS FOR TOMORROW

Hitherto the review has underlined every aspect of chemical camouflage which acts as a shield in protecting plants against pests. However, the broader question lies in effective translation and utilization of this ingenious abilities possessed by the plants. As a result, finding creative and integrative ways that use plant defense mechanisms and modern technology is critical. Biotechnologists are at the vanguard of this effort, developing new techniques and tactics to make agriculture more sustainable and efficient. The core mechanism of this chemical camouflage in plants lies in chemicals and VOCs produced by the plants in the state of stress. We hereby in this section utilize this naturally occurring superpower of plants and propose various ways to effectively translate this in designing the farms of tomorrow.

First and foremost, for effective utilization of the chemicals released by plants during chemical camouflage, need to be trapped and identified. The use of drones and sensors into agricultural techniques is revolutionising precision farming. Drones with hyperspectral and multispectral imaging capability can identify chemical changes caused by stress to monitor crop health.[86] Hence, we proposed the utilization of these devices to sense and capture the chemicals (Figure 3). Next important step would be high throughput identification of these chemicals through sophisticated chromatographic techniques. Furthermore, drones may be later used for precision spraying of pest specific chemicals, targeting fewer defensive plants with specific treatments, therefore increasing crop resistance. This data enables tailored treatments, just where they are required by decreasing waste, lowering environmental impact, and assuring maximum resource utilization.

Post successful identification of defensive chemicals paves a way for other novel strategies. One interesting approach is the use of biostimulants, which are natural or synthetic substances that improve plant growth, stress tolerance, and immunological responses[87] (Figure 3). In this regard, the identified chemicals can be used as biostimulants to protect plants from environmental challenges and improve nutrient absorption, thereby, providing a sustainable alternative to chemical fertilizers and pesticides.[88]

Another novel technique is the study of chemical webs in agricultural environments for successful use of defensive chemicals. Scientists can design plants to emit certain volatile organic chemicals by studying and regulating the intricate chemical interactions that exist between plants, pests, and beneficial species. These manufactured emissions can attract natural pest predators or repel herbivores, restoring ecological balance. Such solutions lessen the need for broad-spectrum insecticides and improve the sustainability of agricultural systems (Figure 3). Through these approaches, the preexisting knowledge can be perfectly utilized for successful pest management.

The practice of intercropping and polyculture is long known to the world but this practice can find its utilization in improving plant group immunity. The preexisting knowledge of plants which has the potential to produce VOCs can be combined with crop species having complementary features to increase biodiversity and environmental resilience.[89] Leguminous crops, for example, may fix atmospheric nitrogen, enriching the soil for nearby plants, while other companion crops repel pests or attract beneficial insects (Figure 3). These technologies not only increase output but also lower the environmental impact of farming.

All the above proposed strategies involve exploration and exploitation of defensive chemicals for using it back on plants. However, various other techniques developed by agricultural scientists can also be extended as a benefit of chemical camouflage seen in certain plant species. Pheromone traps is another innovative technology gaining popularity. These traps use synthetic pheromones that imitate insect communication signals, interrupting pest breeding cycles or repelling pests away from crops[90] (Figure 3). Advances in pheromone manufacturing, storage, and delivery methods are making this technique more affordable and scalable for farmers globally.

Genome editing has emerged as one of the benefactions of scientists to the world. Editing genes of insects, can influence their ability to feed on certain plants. For example, targeting genes responsible for digestive enzymes or taste receptors could make the insects less capable of consuming particular crops. This would limit the insect's ability to cause harm to plants without affecting its overall population dynamics. As with gene drive to spread sterility, targeted gene editing could be used to reduce the fertility of individual insects in a controlled way (Figure 3). This would lower the number of offsprings in the population, but not in a way that would lead to an engineered population collapse. The goal would be to decrease herbivore pressure without driving the population to extinction.

Synthetic biology opens up new opportunities for the development of genetically active molecules and the engineering of plants capable of manufacturing bioactive substances. These designer plants can boost their own defenses or create chemicals that function as biocontrol agents against neighboring crops.[91] This technique necessitates a thorough understanding of metabolic pathways and regulatory networks, making it a promising area of research in agricultural biotechnology.

Therefore, understanding and harnessing the intricacies of plant defense system represents a paradigm change in agriculture. This insight not only increases our knowledge of plant-environment interactions, but also enables the development of more robust and sustainable systems. The combination of these approaches marks a new frontier in agricultural research, with the potential to change future farms. By collating and synthesizing this knowledge, this review serves as a foundational resource for researchers and policymakers. It paves the way for future studies to build on a more comprehensive understanding of chemical camouflage and its transformative potential in agriculture.

AUTHOR INFORMATION

Corresponding Author

Rohini Sreevathsa − *ICAR-National Institute for Plant Biotechnology, New Delhi 110012, India*; orcid.org/0000-0003-4171-6956; Phone: +91-11-25841787; Email: rohinisreevathsa@gmail.com, Rohini.Sreevathsa@icar.gov.in

Authors

Manisha Parashar − *ICAR-National Institute for Plant Biotechnology, New Delhi 110012, India*

Maniraj Rathinam − *ICAR-National Institute for Plant Biotechnology, New Delhi 110012, India*

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251−1262

Narasimham Dokka – *ICAR-National Institute for Plant Biotechnology, New Delhi 110012, India*

Complete contact information is available at:
https://pubs.acs.org/10.1021/acsagscitech.5c00223

Notes

The authors declare no competing financial interest.

■ REFERENCES

(1) Jaisval, G. K.; Dwivedi, H.; Pandey, A.; Jaiswal, S.; Kumar, A.; Kushwaha, D.; Shukla, P. A. Comprehensive Review on Plant Disease Vectors and Their Management. *Int. J. Environ. Clim. Change* **2023**, *13*, 2518–2530.

(2) Balla, A.; Silini, A.; Cherif-Silini, H.; Bouket, A. C.; Moser, W. K.; Nowakowska, J. A.; Oszako, T.; Benia, F.; Belbahri, L. The Threat Of Pests And Pathogens And The Potential For Biological Control In Forest Ecosystems. *Forests* **2021**, *12*, No. 1579.

(3) Regina, T.; Chamola, A.; Ghosh, C. The Impact Of Climate Change On Insects. *Environ. Ecol.* **2024**, *42*, 1774–1782.

(4) Zhou, W.; Li, M.; Achal, V. A comprehensive review on environmental and human health impacts of chemical pesticide usage. *Emerging Contam.* **2025**, *11*, No. 100410.

(5) Khan, F. A.; Anis, S. B.; Badruddin, S. Plant Defenses Against Insect Herbivory. In *Integrated Management Of Arthropod Pests And Insect Borne Diseases*; Cianico, A.; Mukerji, K. G., Eds.; Springer: SG, 2010; pp 189–208.

(6) Sánchez-Sánchez, H.; Morquecho-Contreras, A. Chemical Plant Defense against Herbivores. In *Herbivores*; IntechOpen, 2017.

(7) Bennett, R. N.; Wallsgrove, R. M. Secondary Metabolites In Plant Defence Mechanisms. *New Phytol.* **1994**, *127*, 617–633.

(8) Kefale, H.; You, J.; Zhang, Y.; Getahun, S.; Berhe, M.; Abbas, A. A.; Ojiewo, C. O.; Wang, L. Metabolomic Insights Into The Multiple Stress Responses Of Metabolites In Major Oilseed Crops. *Physiol. Plant.* **2024**, *176*, No. e14596.

(9) Dudareva, N.; Klempien, A.; Muhlemann, J. K.; Kaplan, I. Biosynthesis, Function And Metabolic Engineering Of Plant Volatile Organic Compounds. *New Phytol.* **2013**, *198*, 6–32.

(10) Matsui, K. A Portion Of Plant Airborne Communication Is Endorsed By Uptake And Metabolism Of Volatile Organic Compounds. *Curr. Opin. Plant Biol.* **2016**, *32*, 24–30.

(11) Hammerbacher, A.; Coutinho, T. A.; Gershenzon, J. Roles Of Plant Volatiles In Defence Against Microbial Pathogens And Microbial Exploitation Of Volatiles. *Plant Cell Environ.* **2019**, *42*, 2827–2843.

(12) War, A. R.; Sharma, H. C.; Paulraj, M. G.; War, M. Y.; Ignacimuthu, S. Herbivore induced plant volatiles: their role in plant defense for pest management. *Plant Signalling Behav.* **2011**, *6*, 1973–1978.

(13) Kessler, A.; Mueller, M. B.; Kalske, A.; Chautá, A. Volatile-Mediated Plant–Plant Communication And Higher-Level Ecological Dynamics. *Curr. Biol.* **2023**, *33*, 519–529.

(14) Stevens, M. *Cheats and Deceits: How Animals and Plants Exploit and Mislead*; Oxford University Press, 2016.

(15) Pembury Smith, M. Q. R.; Ruxton, G. D. Camouflage In Predators. *Biol. Rev.* **2020**, *95*, 1325–1340.

(16) Forbes, P. *Dazzled and Deceived: Mimicry And Camouflage*; Yale University Press: U.K., 2011.

(17) Howe, G. A.; Jander, G. Plant Immunity To Insect Herbivores. *Annu. Rev. Plant Biol.* **2008**, *59*, 41–66.

(18) Haouel-Hamdi, S.; Jemâa, J. M. B. Plant Secondary Metabolites for Insect Resistance: Seed–Pest Interaction: An Overview. In *Molecular Dynamics of Plant Stress and its Management*; Shahid, M.; Gaur, R., Eds.; Springer: SG, 2024; pp 351–359.

(19) Borkakati, R. N.; Venkatesh, M.; Saikia, D.; Sasanka, S. A brief review on food recognition by insects: Use of sensory and behavioural mechanisms. *J. Entomol. Zool. Stud.* **2019**, *7*, 574–579.

(20) Powell, G.; Tosh, C. R.; Hardie, J. Host Plant Selection By Aphids: Behavioral, Evolutionary, And Applied Perspectives. *Annu. Rev. Entomol.* **2006**, *51*, 309–330.

(21) Serdo, D. F. Insects' perception and behavioral responses to plant semiochemicals. *PeerJ* **2024**, *12*, No. e17735.

(22) War, A. R.; Paulraj, M. G.; Ahmad, T.; Buhroo, A. A.; Hussain, B.; Ignacimuthu, S.; Sharma, H. C. Mechanisms of plant defense against insect herbivores. *Plant Signaling Behav.* **2012**, *7*, 1306–1320.

(23) Ninkovic, V.; Markovic, D.; Rensing, M. Plant Volatiles As Cues And Signals In Plant Communication. *Plant Cell Environ.* **2021**, *44*, 1030–1043.

(24) Kessler, A.; Baldwin, I. T. Plant responses to insect herbivory: The emerging molecular analysis. *Annu. Rev. Plant Biol.* **2002**, *53*, 299–328.

(25) Kessler, A.; Baldwin, I. T. Plant Responses To Insect Herbivory: The Emerging Molecular Analysis. *Annu. Rev. Plant Biol.* **2002**, *53*, 299–328.

(26) Hopkins, R. J.; van Dam, N. M.; Van Loon, J. J. Role Of Glucosinolates In Insect-Plant Relationships And Multitrophic Interactions. *Annu. Rev. Entomol.* **2009**, *54*, 57–83.

(27) Al-Khayri, J. M.; Rashmi, R.; Toppo, V.; Chole, P. B.; Banadka, A.; Sudheer, W. N.; Nagella, P.; Shehata, W. F.; Al-Mssallem, M. Q.; Alessa, F. M.; et al. Plant Secondary Metabolites: The Weapons For Biotic Stress Management. *Metabolites* **2023**, *13*, No. 716.

(28) Pichersky, E.; Raguso, R. A. Why Do Plants Produce So Many Terpenoid Compounds? *New Phytol.* **2018**, *220*, 692–702.

(29) Agrawal, A. A.; Petschenka, G.; Bingham, R. A.; Weber, M. G.; Rasmann, S. Toxic Cardenolides: Chemical Ecology And Coevolution Of Specialized Plant–Herbivore Interactions. *New Phytol.* **2012**, *194*, 28–45.

(30) Sun, G.; Zhang, X.; Liu, Y.; Chai, L.; Liu, D.; Chen, Z.; Lü, S. Plant Chemical Defenses against Insect Herbivores—Using the Wild Tobacco as a Model. *Phyton* **2024**, *93* (4), 641–659.

(31) Quinn, J. C.; Kessell, A.; Weston, L. A. Secondary Plant Products Causing Photosensitization In Grazing Herbivores: Their Structure, Activity And Regulation. *Int. J. Mol. Sci.* **2014**, *15*, 1441–1465.

(32) Döring, T. F.; Chittka, L. Visual ecology of aphids—a critical review on the role of colours in host finding. *Arthropod-Plant Interact.* **2007**, *1*, 3–16.

(33) Strauss, S. Y.; Zangerl, A. R.Plant-Insect Interactions in Terrestrial Ecosystems. In *Plant-Animal Interactions an Evolutionary Approach*; Wiley, 2002; pp 77–106.

(34) Fürstenberg-Hägg, J.; Zagrobelny, M.; Bak, S. Plant Defense Against Insect Herbivores. *Int. J. Mol. Sci.* **2013**, *14*, 10242–10297.

(35) Yamazaki, K. Gone with the wind: trembling leaves may deter herbivory. *Biol. J. Linn. Soc.* **2011**, *104*, 738–747.

(36) Tabary, L.; Navajas, M.; Tixier, M. S.; Navia, D. Tomato trichomes: trade-off between plant defenses against pests and benefits for biological control agents. *Acarologia* **2024**, *64*, 1232–1253.

(37) Conboy, N. J. Exploring the Use of Plant Volatiles as a Sustainable Control Method for Glasshouse Whiteflies on Glasshouse-Grown Tomato. Ph.D. Thesis, Newcastle University: United Kingdom, 2020.

(38) Tlak Gajger, I.; Dar, S. A. Plant allelochemicals as sources of insecticides. *Insects* **2021**, *12*, No. 189.

(39) Yactayo-Chang, J. P.; Block, A. K. The impact of climate change on maize chemical defenses. *Biochem. J.* **2023**, *480*, 1285–1298.

(40) Nasif, S. O.; Siddiquee, S. Host preference, mode of damage and succession of major insect pests of brinjal. *Ann. Res. Rev. Biol.* **2020**, *35*, 68–78.

(41) Johnsen, S. Modelling Plant-Herbivore Interactions: Cauliflower (Brassica oleracea L. var. botrytis) And Cabbage Maggot (Delia radicum (L.). Ph.D. Thesis, University of California: Berkeley, 1990.

(42) Hillier, N. K.; Baker, T. C. Pheromones of Heliothine Moths. In *Pheromone Communication in Moths: Evolution, Behavior, and Application*; Allison, J. D.; Cardé, R. T., Eds.; University of California Press, 2016; pp 301–333.

https://doi.org/10.1021/acsagscitech.5c00223
ACS Agric. Sci. Technol. 2025, 5, 1251–1262

(43) Gijsman, F.; González, Y.; Guevara, M.; Amador-Vargas, S. Short-Term Plasticity And Variation In Acacia Ant-Rewards Under Different Conditions Of Ant Occupancy And Herbivory. *Sci. Nat.* **2021**, *108*, No. 31.
(44) Koptur, S. Extrafloral Nectary-Mediated Interactions between Insects and Plants. In *Insect-Plant Interactions*; CRC Press, 1992; pp 89−138.
(45) Oliveira, P. S.; Freitas, A. V. Ant−plant−herbivore interactions in the neotropical cerrado savanna. *Naturwissenschaften* **2004**, *91*, 557−570.
(46) Venturi, V.; Keel, C. Signaling in the Rhizosphere. *Trends Plant Sci.* **2016**, *21* (3), 187−198.
(47) Alishah, A. Ecology, Behaviour And Integrated Control Of Cabbage Insect Pests In Tasmania. Ph.D. Thesis, University of Tasmania: Australia, 1987.
(48) Conchou, L.; Lucas, P.; Meslin, C.; Proffit, M.; Staudt, M.; Renou, M. Insect Odorscapes: From Plant Volatiles To Natural Olfactory Scenes. *Front. Physiol.* **2019**, *10*, No. 972.
(49) Kutty, N. N.; Mishra, M. Dynamic Distress Calls: Volatile Info Chemicals Induce And Regulate Defense Responses During Herbivory. *Front. Plant Sci.* **2023**, *14*, No. 1135000.
(50) Bain, A.; Harrison, R. D.; Schatz, B. How To Be An Ant On Figs. *Acta Oecol.* **2014**, *57*, 97−108.
(51) Ponzio, C.; Gols, R.; Pieterse, C. M.; Dicke, M. Ecological And Phytohormonal Aspects Of Plant Volatile Emission In Response To Single And Dual Infestations With Herbivores And Phytopathogens. *Funct. Ecol.* **2013**, *27*, 587−598.
(52) Ameye, M. Uncovering The Priming Potential Of The Green Leaf Volatile Z-3-Hexenyl Acetate: Towards A New Disease Control Tool. Doctoral dissertation, Ghent University: Belgium, 2017.
(53) Hatano, E.; Saveer, A. M.; Borrero-Echeverry, F.; Strauch, M.; Zakir, A.; Bengtsson, M.; Ignell, R.; Anderson, P.; Becher, P. G.; Witzgall, P.; Dekker, T. A Herbivore-Induced Plant Volatile Interferes With Host Plant And Mate Location In Moths Through Suppression Of Olfactory Signalling Pathways. *BMC Biol.* **2015**, *13*, No. 75.
(54) Escobar-Bravo, R.; Lin, P. A.; Waterman, J. M.; Erb, M. Dynamic Environmental Interactions Shaped By Vegetative Plant Volatiles. *Nat. Prod. Rep.* **2023**, *40*, 840−865.
(55) Barbehenn, R. V.; Constabel, C. P. Tannins In Plant−Herbivore Interactions. *Phytochemistry* **2011**, *72*, 1551−1565.
(56) Woodvine, M. A. Cellular Correlates of Heterophyllous Leaf Shape Change in the Freshwater Buttercup Ranunculus Flabellaris Raf. Ph.D. Thesis, University of Toronto: Toronto, Canada, 1999.
(57) Farmer, E. E. *Leaf Defence*; Oxford University Press: UK, 2014.
(58) Döring, T. F.; Archetti, M.; Hardie, J. Autumn Leaves Seen Through Herbivore Eyes. *Proc. R. Soc. B* **2009**, *276*, 121−127.
(59) Back, M.; Pope, T.; Reade, J. Crop Health−Responding To Pests, Weeds And Diseases. In *The Agricultural Notebook*; Soffe, J. S.; Lobley, M., Eds.; Wiley: Blackwell, NJ, 2021; Chapter 4, p 153.
(60) Ritchey, C. M. The Effect Of Anthocyanin On Herbivory In Viola Pedata (Birdfoot Violet). Ph.D. Thesis, Truman State University: Missouri, United States, 1999.
(61) Sharma, M. K. How Plants Adapt to the Photoperiod. *Annu. Res. Rev. Biol.* **2023**, *38*, 17−45.
(62) Lev-Yadun, S. Defensive (Anti-Herbivory) Batesian Mimicry In Plants. *Isr. J. Plant Sci.* **2019**, *66*, 34−51.
(63) Niu, D.; Xu, L.; Lin, K. Multitrophic and Multilevel Interactions Mediated by Volatile Organic Compounds. *Insects* **2024**, *15*, No. 572.
(64) Purser, B. *Jungle Bugs: Masters of Camouflage and Mimicry*; Firefly Books: Buffalo, NY, 2003.
(65) Matthews, R. W.; Matthews, J. R. *Insect Behavior*; Springer Nature: SG, 2010.
(66) Huang, W.; Gfeller, V.; Erb, M. Root Volatiles In Plant−Plant Interactions II: Root Volatiles Alter Root Chemistry And Plant−Herbivore Interactions Of Neighbouring Plants. *Plant Cell Environ.* **2019**, *42*, 1964−1973.
(67) Torezan-Silingardi, H. M.; Silberbauer-Gottsberger, I.; Gottsberger, G. Pollination Ecology: Natural History, Perspectives and Future Directions. In *Plant-Animal Interactions*; Del-Claro, K.; Torezan- Silingardi, H. M., Eds.; Springer International Publishing: Cham, 2021; pp 119−174.
(68) Pellegrino, G.; Bellusci, F.; Palermo, A. M. Who Helps Whom? Pollination Strategy Of Iris Tuberosa And Its Relationship With A Sexually Deceptive Orchid. *J. Plant Res.* **2016**, *129*, 1051−1059.
(69) Guerra, A.; Scremin-Dias, E. Leaf Traits, Sclerophylly And Growth Habits In Plant Species Of A Semiarid Environment. *Braz. J. Bot.* **2018**, *41*, 131−144.
(70) Hanley, M. E.; Lamont, B. B.; Fairbanks, M. M.; Rafferty, C. M. Plant Structural Traits And Their Role In Anti-Herbivore Defence. *Perspect. Plant Ecol. Evol. Syst.* **2007**, *8*, 157−178.
(71) Holopainen, J. K.; Blande, J. D. Where Do Herbivore-Induced Plant Volatiles Go? *Front. Plant Sci.* **2013**, *4*, No. 185.
(72) Iason, G. R.; Villalba, J. J. Behavioral Strategies Of Mammal Herbivores Against Plant Secondary Metabolites: The Avoidance−Tolerance Continuum. *J. Chem. Ecol.* **2006**, *32*, 1115−1132.
(73) Baldwin, I. T.; Kessler, A.; Halitschke, R. Volatile signaling in plant−plant−herbivore interactions: what is real? *Curr. Opin. Plant Biol.* **2002**, *5*, 351−354.
(74) Zhang, W.; Stelinski, L. L.; Mohamed, A.; Wang, G.; Tettamanti, G.; Chen, M.; Hong, M.; Daly, E. Z.; Bruin, J.; Renault, D.; et al. Unlocking agro-ecosystem sustainability: exploring the bottom-up effects of microbes, plants, and insect herbivores. *Integr. Zool.* **2025**, *20*, 465−484.
(75) Ayoub, L.; Yaqoob, M.; Zahoor, S.; Wani, F. F.; Irshad, S. S.; Gull, A.; Sheikh, M. A. Role of Induced Resistance in Insect-Pest Management. In *Plant Resistance to Insects in Major Field Crops*; Kumar, S.; Furlong, M., Eds.; Springer Nature: SG, 2024; Chapter 6, pp 249−277.
(76) Matsui, K.; Engelberth, J. Green Leaf Volatiles—The Forefront Of Plant Responses Against Biotic Attack. *Plant Cell Physiol.* **2022**, *63*, 1378−1390.
(77) Ab Rahman, S. F. S.; Singh, E.; Pieterse, C. M.; Schenk, P. M. Emerging microbial biocontrol strategies for plant pathogens. *Plant Sci.* **2018**, *267*, 102−111.
(78) Saini, N.; Anmol, A.; Kumar, S.; Wani, A. W.; Bakshi, M.; Dhiman, Z. Exploring phenolic compounds as natural stress alleviators in plants-a comprehensive review. *Physiol. Mol. Plant Pathol.* **2024**, *133*, No. 102383.
(79) Kumar, S.; Abedin, M. M.; Singh, A. K.; Das, S. Role of Phenolic Compounds In Plant-Defensive Mechanisms. In *Plant Phenolics In Sustainable Agriculture*; Lone, R.; Shuab, R.; Kamili, N. A., Eds.; Springer: SG, 2020; Vol. *1*, pp 517−532.
(80) Harrewijn, P.; Van Oosten, A. M.; Piron, P. *Natural Terpenoids as Messengers: A Multidisciplinary Study of Their Production, Biological Functions, and Practical Applications*; Kluwer Academic Publishers: Dordrecht, 2001.
(81) Bhatla, S. C.; Lal, M. A. Secondary Metabolites. In *Plant Physiology, Development And Metabolism*; Springer Nature: SG, 2023b.
(82) Wink, M.; Schimmer, O. Molecular modes of action of defensive secondary metabolites. *Ann. Plant Rev.* **2010**, *39*, 21−161.
(83) Robert-Seilaniantz, A.; Grant, M.; Jones, J. D. Hormone Crosstalk In Plant Disease And Defense: More Than Just Jasmonate-Salicylate Antagonism. *Annu. Rev. Phytopathol.* **2011**, *49*, 317−343.
(84) Dettner, K.; Liepert, C. Chemical mimicry and camouflage. *Annu. Rev. Entomol.* **1994**, *39* (1), 129−154.
(85) Zu, P.; Boege, K.; del-Val, E.; et al. Information arms race explains plant-herbivore chemical communication in ecological communities. *Science* **2020**, *368*, 1377−1381.
(86) Caballero, D.; Calvini, R.; Amigo, J. M. Hyperspectral Imaging In Crop Fields: Precision Agriculture. In *Data Handling In Science And Technology*; Elsevier, 2019; pp 453−473.
(87) Yakhin, O. I.; Lubyanov, A. A.; Yakhin, I. A.; Brown, P. H. Biostimulants in plant science: a global perspective. *Front. Plant Sci.* **2017**, *7*, No. 2049.
(88) Rouphael, Y.; Colla, G. Editorial: Biostimulants In Agriculture. *Front. Plant Sci.* **2020**, *11*, No. 40, DOI: 10.3389/fpls.2020.00040.
(89) Barot, S.; Allard, V.; Cantarel, A.; Enjalbert, J.; Gauffreteau, A.; Goldringer, I.; Lata, J.-C.; Le Roux, X.; Niboyet, A.; Porcher, E.

Designing Mixtures Of Varieties For Multifunctional Agriculture With The Help Of Ecology. A review. *Agron. Sustainable Dev.* **2017**, *37*, No. 13.

(90) Laurent, P.; Frérot, B. Monitoring Of European Corn Borer With Pheromone-Baited Traps: Review Of Trapping System Basics And Remaining Problems. *J. Econ. Entomol.* **2007**, *100*, 1797−1807.

(91) Cusumano, A.; Harvey, J. A.; Bourne, M. E.; Poelman, E. H.; de Boer, J. G. Exploiting Chemical Ecology To Manage Hyperparasitoids In Biological Control Of Arthropod Pests. *Pest Manage. Sci.* **2020**, *76*, 432−443.

(92) Van Vuuren, A.; Chilibroste, P. Challenges in the nutrition and management of herbivores in the temperate zone. *Animal* **2013**, *7*, 19−28.

(93) Björkman, C.; Ahrné, K. Influence Of Leaf Trichome Density On The Efficiency Of Two Polyphagous Insect Predators. *Entomol. Exp. Appl.* **2005**, *115*, 179−186.

(94) El-Merhibi, A.; Ngo, S.; Jones, B.; Milic, N.; Stupans, I.; McKinnon, R. Molecular insights into xenobiotic disposition in Australian marsupials. *Australas. J. Ecotoxicol.* **2007**, *13*, 7−18.

(95) Tanaka, T.; Ikeda, A.; Shiojiri, K.; Ozawa, R.; Shiki, K.; Nagai-Kunihiro, N.; Fujita, K.; Sugimoto, K.; Yamato, K. T.; Dohra, H.; et al. Identification of a hexenal reductase that modulates the composition of green leaf volatiles. *Plant Physiol.* **2018**, *178*, 552−564.

(96) Wang, M. H.; Rodriguez-Saona, C.; Lavoir, A. V.; Ninkovic, V.; Shiojiri, K.; Takabayashi, J.; Han, P. Leveraging air-borne VOC-mediated plant defense priming to optimize Integrated Pest Management. *J. Pest Sci.* **2024**, *97*, 1245−1257.

(97) Bhatla, S. C.; Lal, M. A. Jasmonic Acid. In *Plant Physiology, Development and Metabolism*; Springer Nature: SG, 2023a.

(98) Demiwal, P.; Mir, J. I.; Sircar, D. A Non-Invasive Method For Phenotyping Scab-Tolerant Apple Plants Using Volatile Organic Compounds. *Physiol. Plant.* **2024**, *176*, No. e14377.

(99) Böttcher, C.; Pollmann, S. Plant Oxylipins: Plant Responses To 12-Oxo-Phytodienoic Acid Are Governed By Its Specific Structural And Functional Properties. *FEBS J.* **2009**, *276*, 4693−4704.

(100) Kant, M. R.; Jonckheere, W.; Knegt, B.; Lemos, F.; Liu, J.; Schimmel, B.; Villarroel, C.; Ataide, L.; Dermauw, W.; Glas, J.; et al. Mechanisms And Ecological Consequences Of Plant Defence Induction And Suppression In Herbivore Communities. *Ann. Bot.* **2015**, *115*, 1015−1051.

(101) Filgueiras, C. C.; Martins, A. D.; Pereira, R. V.; Willett, D. S. The Ecology Of Salicylic Acid Signaling: Primary, Secondary And Tertiary Effects With Applications In Agriculture. *Int. J. Mol. Sci.* **2019**, *20*, No. 5851.

(102) Pratyusha, S. Phenolic Compounds In The Plant Development And Defense: An Overview. In *Plant Stress Physiology-Perspectives In Agriculture*; Hasanuzzaman, M.; Nahar, K.; Brzozowski, T., Eds.; IntechOpen, 2022; Chapter 7, pp 125−140.

(103) Mathesius, U. Flavonoid Functions In Plants And Their Interactions With Other Organisms. *Plants* **2018**, *7*, No. 30, DOI: 10.3390/plants7020030.

(104) Peracchi, L. M.; Panahabadi, R.; Barros-Rios, J.; Bartley, L. E.; Sanguinet, K. A. Grass Lignin: Biosynthesis, Biological Roles, And Industrial Applications. *Front. Plant Sci.* **2024**, *15*, No. 1343097.

(105) Robbins, C. T.; Hanley, T.; Hagerman, A.; Hjeljord, O.; Baker, D.; Schwartz, C.; Mautz, W. Role Of Tannins In Defending Plants Against Ruminants: Reduction In Protein Availability. *Ecology* **1987**, *68*, 98−107.

(106) Qasim, M.; Islam, W.; Rizwan, M.; Hussain, D.; Noman, A.; Khan, K. A.; Ghramh, H. A.; Han, X. Impact Of Plant Monoterpenes On Insect Pest Management And Insect-Associated Microbes. *Heliyon* **2024**, *10*, No. e39120.

(107) Michelozzi, M. Defensive Roles Of Terpenoid Mixtures In Conifers. *Acta Bot. Gallica* **1999**, *146*, 73−84.

(108) Jing, X.; Vogel, H.; Grebenok, R. J.; Zhu-Salzman, K.; Behmer, S. T. Dietary Sterols/Steroids And The Generalist Caterpillar Helicoverpa Zea: Physiology, Biochemistry And Midgut Gene Expression. *Insect Biochem. Mol. Biol.* **2012**, *42*, 835−845.

(109) Hussain, G.; Rasul, A.; Anwar, H.; Aziz, N.; Razzaq, A.; Wei, W.; Ali, M.; Li, J.; Li, X. Role Of Plant Derived Alkaloids And Their Mechanism In Neurodegenerative Disorders. *Int. J. Biol. Sci.* **2018**, *14*, No. 341.

(110) Vetter, J. Plant cyanogenic glycosides. *Toxicon* **2000**, *38*, 11−36.

(111) Bruce, T. Glucosinolates In Oilseed Rape: Secondary Metabolites That Influence Interactions With Herbivores And Their Natural Enemies. *Ann. Appl. Biol.* **2014**, *164*, 348−353.

(112) Singh, M.; Kumar, J.; Singh, S.; Singh, V. P.; Prasad, S. M. Roles of osmoprotectants in improving salinity and drought tolerance in plants: a review. *Rev. Environ. Sci. Bio/Technol.* **2015**, *14*, 407−426.

(113) Bhattacharya, S.; Kundu, A. Sugars And Sugar Polyols In Overcoming Environmental Stresses. In *Protective Chemical Agents In The Amelioration Of Plant Abiotic Stress: Biochemical And Molecular Perspective*; Roychoudhury, A.; Tripathi, K. D., Eds.; Wiley: Blackwell, NJ, 2020; Chapter 4, pp 71−101.

(114) Lazebnik, J.; Frago, E.; Dicke, M.; Van Loon, J. J. Phytohormone Mediation Of Interactions Between Herbivores And Plant Pathogens. *J. Chem. Ecol.* **2014**, *40*, 730−741.

(115) Hou, S.; Tsuda, K. Salicylic Acid And Jasmonic Acid Crosstalk In Plant Immunity. *Essays Biochem.* **2022**, *66*, 647−656.

(116) Kachroo, A.; Kachroo, P. Salicylic Acid-, Jasmonic Acid-And Ethylenemediated Regulation Of Plant Defense Signaling. In *Genetic Engineering Principles and Methods 28*; Setlow, J. K., Ed.; Springer: SG, 2007; Vol. *28*, pp 55−83.