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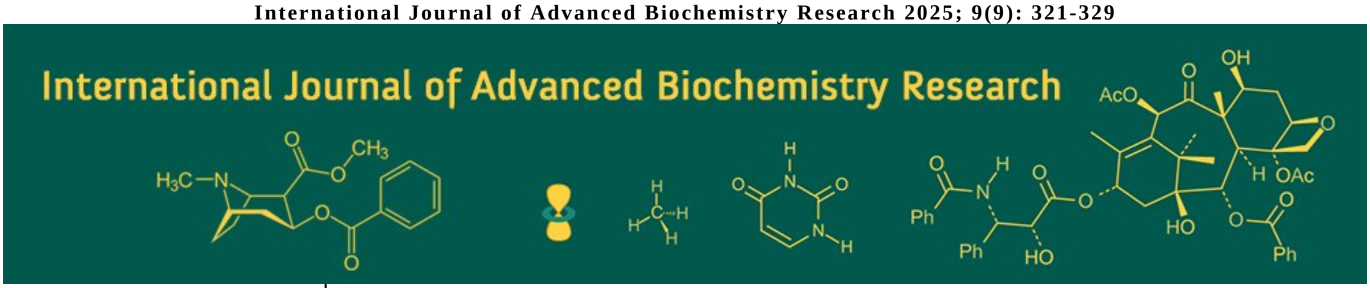

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# Biochemical basis of insect-plant interaction under climate stress: Mechanisms, adaptations and implications for agriculture

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## Abstract

Insect-plant interactions form the backbone of terrestrial ecosystems, influencing biodiversity, ecosystem stability, and agricultural productivity. These interactions are governed by complex biochemical processes that regulate defence, communication, and adaptation. Climate change stressors, including elevated $CO_2$, heat waves, drought, and air pollution, profoundly reshape these biochemical dynamics by altering primary metabolism, secondary metabolites, and hormonal signalling. Such shifts influence insect feeding, detoxification strategies, and the stability of multitrophic networks, ultimately affecting crop protection and pollination services. Insects exhibit remarkable biochemical plasticity, including enzyme adaptation, detoxification, sequestration, and antioxidant defences, allowing them to persist in stressed environments. This review synthesises current understanding of biochemical responses in plants under climate stress, the adaptive mechanisms of insects, and disruptions in tri-trophic signalling. Case studies highlight how stress-modulated metabolites reshape pest dynamics in crops like cotton and ecological relationships in specialist systems such as monarch-milkweed. Understanding these biochemical shifts is vital for designing climate-resilient integrated pest management (IPM) strategies, breeding stress-tolerant cultivars, and applying defence-priming technologies. A systems-level, biochemically informed approach is essential to sustain agriculture under accelerating climate change.

**Keywords:** Insect-plant interactions, primary metabolism, secondary metabolites, volatile organic compounds, insect biochemical adaptations, climate stress, tri-trophic interaction, integrated pest management

## 1. Introduction

Insect-plant interactions are essential ecological relationships that can be antagonistic, commensal, or mutualistic. Antagonism occurs when insects harm plants by feeding on them, reducing growth and health. In contrast, commensalism involves insects benefiting from plants with little or no effect on them, such as aphids extracting sap in small numbers. Mutualistic interactions benefit both partners, as seen in pollination, where insects like bees gain nectar while enabling plant reproduction (Schoonhoven *et al.*, 2005; Belete, 2018) [5]. These diverse interactions not only shape ecosystems but also influence agricultural productivity and reflect the co-evolutionary dynamics between plants and insects, often mediated by complex biochemical signals and adaptive traits.

Plants protect themselves from insect attacks using two main strategies: direct defences and indirect defences. Direct defences include physical barriers such as trichomes, spines, thorns and lignified tissues, and chemical compounds that slow down insect feeding, growth, development, and reproduction. Indirect defences do not harm insects directly, but work by emission of specific volatile compounds that attract predators and parasitoids, functioning as "extended bodyguards" (Howe and Jander, 2008; Dicke and Baldwin, 2010) [33, 20]

Global climate change introduces significant complexity into plant defence systems. The effects of rising temperatures and increased $CO_2$ on basic plant metabolism are primarily known, but their impact on secondary metabolism and defence signalling is unclear. Evidence suggests that higher $CO_2$ levels can suppress jasmonic acid (JA)-mediated defences, which play a key role in protecting plants against chewing insects, while simultaneously enhancing salicylic acid (SA)-mediated pathways that strengthen resistance against pathogens (Belete, 2018; Zavala *et al*., 2017) [5, 104]

This hormonal rebalancing may leave plants more vulnerable to insect herbivores but more tolerant to microbial infections. Such trade-offs highlight the importance of understanding how climate-driven shifts in plant biochemistry will influence future plant-insect interactions and the resilience of agricultural systems.

## 2. Climate Stress and Plant Biochemistry

### 2.1 Primary Metabolism Under Climate Stress

Primary metabolism forms the biochemical foundation of plant growth and defence, encompassing carbon assimilation, nitrogen metabolism, carbohydrate production, and amino acid biosynthesis. These processes are highly sensitive to stressors such as elevated $CO_2$, heat, drought, and ozone, which influence plant-insect interactions.

### 2.1.1 Carbon and Nitrogen Metabolism

Elevated $CO_2$ enhances photosynthetic carbon fixation in $C_3$ plants, increasing biomass and carbohydrate supply, but long-term exposure often leads to photosynthetic acclimation due to carbohydrate feedback inhibition (Ainsworth & Long, 2005; Leakey *et al*., 2009) [2, 50]. Heat and drought stress damage photosystems and limit stomatal conductance, while ozone accelerates oxidative injury, degrades chlorophyll and decreases Rubisco activity (Fiscus *et al*., 2005) [25]. Elevated $CO_2$ also drives nitrogen dilution, lowering tissue protein content and altering C: N ratios (Taub & Wang, 2008) [83]. Heat may temporarily stimulate nitrate reductase activity, but prolonged drought or ozone typically suppresses nitrogen assimilation by impairing root function and reducing enzyme activity (Pell *et al*., 1997; Bloom, 2015) [65, 15]. These shifts reduce plant nutritional quality for herbivores, often reducing their growth and reproduction.

### 2.1.2 Carbohydrates and Amino Acids

Carbohydrates serve as energy reserves and also as signalling molecules in stress adaptation. Elevated $CO_2$ enhances soluble sugars and starch reserves, whereas drought restricts transport and metabolism, and high temperatures deplete reserves through increased respiration (Couée *et al*., 2006; Leakey *et al*., 2009) [17, 50]. Ozone inhibits sugar metabolism via oxidative degradation. Amino acids respond variably: $CO_2$-induced nitrogen limitation lowers total amino acid content due to nitrogen limitation (Taub & Wang, 2008) [83], while drought and salinity promote accumulation of Osmo protectants such as proline, glycine betaine, and GABA (Krasensky & Jonak, 2012) [43]. Heat stress induces synthesis of amino acids required for heat-shock proteins, and ozone alters amino acid balance as part of stress signalling. Since amino acids and sugars are central determinants of herbivore food quality, climate-induced alterations in their availability directly affect insect feeding, growth, and survival.

### 2.2 Secondary Metabolites Under Climate Stress

Secondary metabolites are a chemically varied category of substances crucial for signalling, defence, and environmental adaptability. Among them, terpenes, phenolics, flavonoids, tannins and alkaloids are pivotal in mediating plant-insect interactions. Temperature, increased $CO_2$, ozone, and drought significantly affect their biosynthesis, accumulation, and emission, changing plants' ecological interactions and defence ability.

### 2.2.1 Phenolics, Flavonoids and Tannins

Phenolic compounds derived from the phenylpropanoid and shikimate pathways serve as antioxidants, structural components, and defence molecules. Flavonoids are a large and multifunctional class of phenolics that are highly responsive to abiotic stress. Elevated $CO_2$ often enhances phenolic and tannin production via carbon-nutrient balance (Peñuelas & Estiarte, 1998; Barbehenn & Constabel, 2011) [4, 66]. Drought, UV-B, and ozone further promote their accumulation as scavengers of reactive oxygen species (ROS) (Agati *et al*., 2012) [1]. Tannins interfere with protein digestion, while flavonoids act as UV protectants and signalling molecules. However, due to resource trade-offs, phenolic and tannin levels may plateau or decline under severe or prolonged stress. These compounds generally strengthen defence but vary across species and stress combinations.

### 2.2.2 Terpenes

The most prominent family of secondary metabolites, terpenoids, have two functions: direct defence (toxicity, deterrence) and indirect defence (herbivore-induced volatiles attracting natural enemies). Their biosynthesis and release are highly sensitive to abiotic stress. Elevated temperature and moderate drought stimulate terpene release, whereas severe drought suppresses synthesis (2012 & Llusià, 2003; Loreto & Schnitzler, 2010) [55]. Elevated $CO_2$ produces species-specific outcomes, with some plants accumulating more stored monoterpenes. Ozone often induces terpene release as part of oxidative stress signalling. These shifts strongly influence insect behaviour and multitrophic interactions.

### 2.2.3 Alkaloids

Alkaloids are nitrogen-rich substances acting as neurotoxins and deterrents. Their production depends on nitrogen availability. According to the nitrogen restriction theory, elevated $CO_2$ often results in nitrogen dilution in plant tissues, which lowers alkaloid concentrations (Zavala *et al*., 2013) [102]. Conversely, by upregulating stress-related pathways, drought and other stressors can promote the production of alkaloids (Hartmann, 2007) [30]. These context-dependent responses suggest that climate stress may reduce or enhance plant chemical defences depending on the balance between carbon and nitrogen metabolism.

### 2.3 Signalling Molecules Under Climate Stress

Plant signalling molecules such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) play central roles in coordinating defence responses against herbivores and pathogens. Their biosynthesis and signalling networks are susceptible to climate stress, which can shift defence allocation and alter insect-plant interactions.

### 2.3.1 Jasmonic Acid (JA)

JA is an essential protective regulator against chewing insects by promoting the synthesis of volatile chemical compounds, alkaloids, terpenoids, and proteinase inhibitors. Elevated $CO_2$ frequently suppresses JA signalling due to nitrogen dilution and restricted substrate supply (Zavala *et* *al*., 2008) [103], which weakens inducible defences. In contrast, drought and heat generally enhance JA accumulation, linking it with stomatal regulation and osmotic adjustment (Sharma *et al*., 2013) [77]. Ozone also stimulates JA pathways, since oxidative stress mimics herbivory and activates similar defence cascades (Vuorinen *et al*., 2004) [88].

### 2.3.2 Salicylic Acid (SA)

Salicylic acid (SA) is the primary mediator of resistance against piercing-sucking insects and biotrophic pathogens. It frequently has a negative connection with JA, and stress can upset this equilibrium. Increased $CO_2$ has had a variety of effects. SA signalling may increase in some situations, enhancing pathogen resistance but potentially suppressing JA-based herbivore defence (Zhou *et al*., 2019) [108]. Drought typically induces SA, aiding ROS detoxification and stomatal closure, whereas heat stress can suppress SA and lower disease resistance (Khan *et al*., 2015) [42]. Ozone consistently increases SA accumulation, as part of systemic acquired resistance (Yalpani *et al*., 1994) [97].

### 2.3.3 Ethylene (ET)

Ethylene is a multipurpose hormone that influences defences mediated by JA and SA. Elevated $CO_2$ usually reduces ET synthesis, weakening synergistic defence signalling (Zavala *et al*., 2008) [103]. Heat stress strongly enhances ET, accelerating stress tolerance pathways, senescence, and abscission (Suzuki *et al*., 2014) [82]. Depending on its intensity, drought stress can change defensive activation and growth regulation by raising or lowering ET. According to Booker *et al*. (2009) [10], exposure to ozone causes a sharp rise in ET emissions, which speeds up stress signalling and leaf withering.

### 2.4 Volatile Organic Compounds (VOCs) and Tritrophic Interactions

Plants emit diverse volatile organic compounds (VOCs) that mediate both plant-plant signalling and plant-insect-enemy interactions. Two key groups are green leaf volatiles (GLVs), released immediately after tissue damage, and herbivore-induced plant volatiles (HIPVs), which are produced more slowly in response to insect feeding. These compounds play a central role in indirect defence by attracting predators and parasitoids of herbivores, thereby shaping tri-trophic interactions.

### 2.4.1 Green Leaf Volatiles (GLVs)

GLVs are $C_6$ compounds such as (Z)-3-hexenal, (Z)-3-hexen-1-ol, and (Z)-3-hexenyl acetate, released instantly after mechanical or herbivore damage. They function as “alarm signals”, priming defences in neighbouring plants (Engelberth *et al*., 2004) [21] and providing chemical cues for natural enemies of herbivores (Arimura *et al*., 2009) [3]. GLV release is influenced by climate stress: heat and drought frequently cause an increase in GLV emissions because of increased lipid peroxidation, whereas high $CO_2$ can decrease them (Loreto & Schnitzler, 2010) [55].

### 2.4.2 Herbivore-Induced Plant Volatiles (HIPVs)

HIPVs include terpenoids, phenylpropanoids, and GLVs, produced after herbivore feeding. They attract parasitoids and predators (Turlings & Erb, 2018) [84], while also mediating plant-plant communication. HIPV responses to climate stress are complex: Elevated $CO_2$ often reduces HIPVs, weakening parasitoid attraction (Gouinguené & Turlings, 2002) [28]. High temperature generally increases HIPV release but may alter timing and blend composition (Peñuelas & Staudt, 2010) [68]. Drought can suppress HIPVs due to reduced metabolic activity yet enhance specific compounds as stress signals (Copolovici *et al*., 2014) [16]. Ozone stimulates VOC synthesis but rapidly oxidises HIPVs in the atmosphere, reducing their signalling range (Holopainen & Gershenzon, 2010) [32]. Climate-driven changes in GLVs and HIPVs can disrupt these tritrophic interactions, reducing herbivore suppression or shifting community dynamics (Zavala *et al*., 2017) [104]. For example, reduced HIPV signalling under elevated $CO_2$ may limit parasitoid efficiency, while moderate warming may transiently enhance enemy attraction.

## 3. Insect Biochemical Adaptations

Insects and plants are engaged in a continuous evolutionary arms race, where plants defend themselves with toxic secondary metabolites and insects respond with specialised behavioural, physiological and biochemical mechanisms, which allow them to feed on chemically defended plants (Berenbaum, 2001; Karban and Agrawal, 2002) [7, 40].

### 3.1 Digestive enzymes

Insects play a crucial role in shaping their digestive enzyme activity within the midgut according to the plants they consume, enabling them to efficiently process and extract nutrients from diverse and often chemically defended plant tissues (Kutty and Mishra, 2023; Beran and Petschenka, 2022) [6,48]. Digestive enzymes are thus central to insect adaptation, allowing insects to thrive in varied and sometimes hostile plant environments. Environmental factors such as temperature and elevated $CO_2$ can alter enzyme activity and gut efficiency, but insects compensate by adjusting enzyme secretion to maintain effective nutrient absorption under stress (Zhang *et al*., 2024) [106]. In addition, some plant-feeding insects acquire novel digestive enzyme genes from gut microbes through horizontal gene transfer, providing them with new metabolic tools to digest complex plant materials more effectively (Wang *et al*., 2021) [91].

### 3.2 Detoxification enzymes

Detoxification enzymes in insects (like P450s, GSTs, UGTs) act as biochemical shields that work against toxic plant metabolites, ensuring survival in chemically hostile environments. Insects employ a three-phase detoxification system to counter harmful plant secondary metabolites. In the first phase, ingested compounds are broken down by enzymes such as cytochrome P450s, carboxylesterases, and flavin-containing monooxygenases, either within the insect itself or through symbiotic gut microbes. In the second phase, toxic intermediates undergo conjugation reactions, mediated by enzymes like glutathione S-transferases and glycosyltransferases, which enhance solubility and facilitate excretion. Finally, in the third phase, the modified metabolites are expelled from cells via ATP-binding cassette transporters (Hu *et al*., 2019; Heidel-Fischer and Vogel, 2015; Chen *et al*., 2020) [35,31,15]. Within this framework, *Spodoptera litura* detoxifies the plant defence compound xanthotoxin through UDP-glycosyltransferases (UGTs), whose expression and activity are essential for larval tolerance. Notably, the CncC/MafK transcriptional pathway has been shown to directly regulate UGT expression, thereby mediating xanthotoxin detoxification and illustrating how insects integrate core detoxification phases with transcriptional control mechanisms to adapt to plant chemical defences (yang *et al*., 2025) [98].

### 3.3 Sequestration strategies

The ability of insect herbivores to selectively absorb and store toxic compounds from their host plants is a key trait influencing their survival and success on highly defended plants, especially in environments with numerous natural enemies (Opitz and Muller, 2009) [62]. Insects achieve this through a combination of physiological mechanisms: passive diffusion or active transport proteins such as ABC and SLC transporters, depending on the chemical properties of the compound, move plant-derived toxins—like glucosinolates—into protected storage sites, including the haemolymph, cuticle, or fat body (Dermauw and Van, 2014) [18]. For example, in the milkweed bug (*Oncopeltus fasciatus*), the cardiac glycoside digitoxin is thought to cross the midgut lining passively. In contrast, in the desert locust (*Schistocerca gregaria*) and the American cockroach (*Periplaneta americana*), the midgut prevents this compound from entering (Scudder and Meredith, 1982) [76]. This demonstrates that the ability of plant defence chemicals to cross the gut barrier is a significant factor shaping the evolution of sequestration strategies.

In the poplar leaf beetle (Chrysomela populi), scientists discovered an ABC transporter, CpMRP, strongly expressed in the defensive glands. This protein uses energy from ATP to move salicin, a plant compound ingested by the beetle, into storage vesicles within the glands. Salicin is transformed into salicyl aldehyde, the beetle's primary defensive secretion. When CpMRP is knocked down, the beetles cannot produce their chemical defence, showing that CpMRP plays a crucial role in capturing plant compounds and enabling the beetle's protective chemistry (Strauss, 2013) [80].

Once stored, these compounds are often further processed by detoxification pathways. Enzymes modify the toxins through conjugation (Phase II) and then transport them (Phase III), enabling insects to retain the defensive benefits of the chemicals while avoiding self-harm (Jeckel *et al*., 2022) [39]. Early research in the 1960s and 1970s provided striking evidence of this phenomenon: monarch butterflies feed on toxic milkweed, store the toxins, and become poisonous to predators such as birds (Brower *et al*., 1967; Malcolm, 1994) [11, 57]. Initially thought to be a unique example, subsequent studies have shown that many insect species specialising in toxic plants similarly sequester plant chemicals to enhance their survival (Nishida, 2002; Opitz and Muller, 2009) [61, 62]. These findings illustrate how absorption, storage, and detoxification allow herbivorous insects to exploit plant defences as a powerful protective strategy.

### 3.4 Antioxidant defences

Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidases (GPX) help neutralise reactive oxygen species (ROS) produced in insects during metabolic or environmental stress, thereby protecting cellular components from oxidative damage (Felton and Summers, 1995) [24]; in particular, these enzymes provide defence against oxidative stress induced by plant defence compounds.

## 4. Tri-Trophic Interactions under Climate Stress

In natural ecosystems, plant-insect interactions rarely occur as simple two-way relationships; instead, they often appear in complex tri-trophic systems where plants, herbivores, pollinators, and natural enemies such as parasitoids and predators are linked through intricate biochemical and ecological signals (Turlings and Erb, 2018; Strauss and Irwin, 2004) [84, 81]. These interactions are governed mainly by herbivore-induced plant volatiles (HIPVs), floral traits, and nectar resources, which influence herbivore behaviour and guide natural enemies and pollinators. However, climate stressors—including heat waves, drought, and air pollution alter the quantity, composition, and persistence of these chemical signals, thereby disrupting natural pest control and pollination services.

### 4.1 Plant-Herbivore-Parasitoid Interactions

Plants under herbivore attack emit a diverse blend of herbivore-induced plant volatiles (HIPVs), which play a significant role in indirect plant defences by guiding natural enemies to herbivores. However, these chemical signals are vulnerable to environmental stress. For instance, maize plants showed inconsistent emission patterns of (Z)-3-hexenyl acetate and linalool under herbivory, influencing insect attraction (Block *et al*., 2018) [8]. Similarly, in potato plants, heat stress has been found to modify jasmonate-regulated defence pathways, which in turn shifts both the timing and composition of herbivore-induced volatile emissions such as sesquiterpenes and green leaf volatiles (Zhong *et al*., 2024) [107]. The instability of HIPVs under climate stress has profound consequences for higher trophic levels, particularly parasitoids and predators. Ye *et al*. (2018) [100] demonstrated that in *Spodoptera littoralis*, herbivore-induced volatiles can modify caterpillar odours in ways that reduce their attractiveness to parasitoid *Cotesia marginiventris*, thereby creating unreliable cues that may confuse natural enemies. Drought stress further complicates this defence system. Research on *Arabidopsis thaliana* and other model plants subjected to water limitation revealed an increase in direct defences like phenolic compounds, while indirect defences reduced due to the disruption of volatile-mediated parasitoid attraction (Lin *et al*., 2022) [54].

Beyond plant-herbivore dynamics, adverse weather conditions impair natural enemy foraging. Under combined humidity and temperature stress, Li *et al*. (2024) [106] found that interactions between *Plutella xylostella* (Diamondback moth) and its parasitoid *Diadegma semiclausum* were modified in both species- and age-dependent ways, showing how environmental variability directly affects parasitoid performance. Similarly, Vosteen *et al*. (2020) [87] reported that stormy weather reduced the odour-guided host-finding efficiency of parasitoids by disrupting their ability to detect key HIPVs like (E)-β-caryophyllene and indole. Together, these findings suggest that although plants may enhance biochemical resistance under stress, climate change destabilises HIPV-mediated communication, weakening indirect defences and threatening the stability of tri-trophic networks.

### 4.2 Plant-Pollinator Interactions

Pollinator attraction, another key link in the tri-trophic network, is highly affected by climate stress. Drought consistently reduces floral rewards, including nectar and pollen, lowering pollination success in both wild and crop systems (Waser and Price, 2016; Buchmann and Papaj, 2024) [12, 94]. For instance, a decline in nectar sugars and amino acids directly impairs pollinator health. *Apis mellifera* and *Bombus terrestris* colonies show reduced survival and productivity when foraging in water-limited environments (Wilson Rankin *et al.*, 2020) [96]. Quinanzoni *et al.* (2024) [70] further illustrated that urban and ornamental plants exposed to drought lose their visual appeal and olfactory cues, rendering them less attractive to pollinators.

Air pollutants, particularly ozone ($O_3$), contribute further to disruption by breaking down essential floral volatiles like linalool, benzaldehyde, and (E)-β-ocimene. These substances are crucial chemical cues that lead pollinators such as Bombus terrestris and Apis mellifera to flower resources. Farré-Armengol *et al.* (2016) [23] and Fuentes *et al.* (2016) [26] showed that ozone reduces the stability of floral volatiles, breaking up odour plumes and making pollinators spend more time foraging while visiting fewer flowers. Extending this, Langford *et al.* (2023) [49] showed that polluted air masses distort floral odour trails, making them unreliable over long distances. Along with drought, climate stress weakens plant-pollinator communication, contributing to decline in pollinators, biodiversity loss, and reduced crop yields.

### 4.3 Interactive Stresses and Ecological Trade-offs

Environmental stressors rarely act in isolation but interact in complex and sometimes antagonistic ways. For example, drought can enhance direct volatile-mediated defences in plants while reducing their capacity to attract parasitoids, resulting in a trade-off between self-defence and guiding natural enemies (Lin *et al.*, 2022) [54]. Likewise, Pinto-Zevallos and Blande (2024) [69] highlighted that climate change and air pollution are dual stressors that constrain plants' ability to coordinate defence and reproduction through volatile cues. From a broader ecological perspective, such disruptions exemplify how multi-species interactions are highly vulnerable to environmental stressors, with cascading consequences for biodiversity, ecosystem services, and agricultural stability (Strauss & Irwin, 2004) [81].

In addition to modifying plant signalling, climate stress directly affects insect physiology and behaviour, reshaping host-parasitoid dynamics. Waterman *et al.* (2024) [95] further demonstrated that HIPVs can propagate in rhythmic patterns among neighbouring plants, facilitating defence priming within plant communities, which may be interrupted during environmental extremes. These findings indicate that stress factors may restrict both within-plant and between-plant signalling at the same time, thereby diminishing the ecological reliability of tri-trophic interactions.

## 5. Case studies

### Case study 1: Breaking Chemical Barriers: How Insects Detoxify Plant Defence Metabolites.

According to Kshatriya *et al.* (2024) [44], insect herbivores use detoxification enzymes from large gene families to overcome toxic plant metabolites. These enzymes function to functionalize toxins or conjugate them with polar substituents, reducing toxicity, increasing water solubility, and improving excretion. These enzymes are more abundant in generalists but also present in specialists. Insect microbiomes also play a role in detoxification, processing plant toxins. Detoxification gene families encode enzymes with broad substrate specificity, making insects adept at metabolising diverse plant toxins and synthetic insecticides.

### Case study 2: Effects of Salt Stress on Aphid Development-Related Gene Expression and Secondary Metabolites in Cotton

A study conducted by Wang *et al.* (2015) [89] shows salt stress significantly impacts cotton's secondary metabolites, increasing the accumulation of substances like gossypol, flavonoids, and tannin. These substances are essential for plant defence against aphids and other insect pests. Aphid populations decrease with increased secondary metabolism, leading to gene expression modulation. Secondary metabolites like polyphenols, flavonoids, and alkaloids improve plant tolerance to salt stress and deter insect invasion. Salt stress also affects osmo-protectants like proline and soluble sugars, contributing to cotton stress tolerance and pest resistance.

### Case study 3: Chemical Constraints and Coadaptation in Insect-Plant Evolution

Scriber (2002) [74] stated that coadaptations, chemical limitations, and phenotypic congruence influence the evolution of insect-plant relationships. Plant secondary chemicals constrain insect herbivores, shaping their feeding preferences and evolutionary pathways. Insect adaptation involves complex physiological and behavioural changes, while coevolution aligns insect sensory and metabolic traits with plant chemical profiles, resulting in ecological specialisation.

### Case study 4: Dynamic Modulation of Arabidopsis Jasmonate Pathway during Insect Attack

Verhage *et al.* (2014) [86] recorded that the jasmonate signalling system in Arabidopsis is rewired during insect herbivory to optimise defence responses and minimise growth penalties. This complex network, involving pathways like salicylate and ethylene, fine-tunes plants' response to insect attack. Jasmonate signaling also orchestrates the production of defensive proteins and secondary metabolites, demonstrating the intricacy of plant defense mechanisms in biotic stress.

## 6. Implications for Agriculture and Pest Management

Climate-driven stresses such as heat, drought, and increased $CO_2$ will alter the biochemical composition of plants, which increases insect feeding and disrupts natural enemy regulation (Deutsch *et al.*, 2018) [19]. These stress-induced changes can weaken the stability of traditional pest control approaches because herbivore resistance traits may be reduced while biocontrol efficiency declines (n *et al.*, 2021; Nalam *et al.*, 2021) [60]. Such shifts underline the necessity of integrating plant biochemical responses into future Integrated Pest Management (IPM) strategies.

Abiotic stress leads to a decline in nitrogen levels and secondary defence compounds in plants, which will alter the growth and reproduction (Gupta *et al.*, 2020; Smilanich *et al.*, 2016) [29, 79]. Stress conditions may also increase the tolerance of insecticides and interfere with induced plant defences, further complicating field management (Shrestha *et al.*, 2023; Kumar *et al.*, 2022) [78, 47]. Therefore, it is critical to develop stress-resilient cultivars that are capable of maintaining metabolic defence pathways, such as phenolics, alkaloids, and terpenoids, even under climate extremes, which is becoming increasingly critical (Pandey & Pandey, 2020) [63].

Another promising direction is to use defence priming technologies—chemical elicitors, microbial inoculants, and RNA-based sprays—that activate latent biochemical pathways before pest attack, resulting in faster and stronger defence responses (Mauch-Mani *et al*., 2017; Martinez-Medina *et al*., 2022; Kaur *et al*., 2023) [59, 58, 41]. Combined with biocontrol and cultural practices, priming offers a sustainable solution to reinforce crop resilience. These insights suggest that future agricultural systems must adopt biochemically informed IPM, in which breeding, biotechnology, and agroecological practices are aligned with the realities of climate stress and insect adaptation.

## 7. Future Directions

Future research should move beyond single-stress experiments and adopt multifactorial designs that reflect real field conditions, where heat, drought, elevated CO2 and nutrient limitations act simultaneously. Such approaches will provide more accurate predictions of how plant-insect-natural enemy interactions evolve under climate change (Jamieson *et al*., 2012; Lehmann *et al*., 2020) [38, 52].

A second priority is the application of omics-based tools—including metabolomics, transcriptomics, proteomics, and genome editing—to unravel how plants dynamically regulate biochemical defence pathways under stress. These tools will help identify molecular markers that breeders can exploit to breed for stress-resilient and pest-tolerant cultivars (Pandey & Pandey, 2020) [64]. In particular, CRISPR/Cas-mediated editing of key genes involved in secondary metabolism offers novel opportunities for tailoring crop resistance traits in a climate-smart context (Zhu *et al*., 2020) [109].

Research should also expand its scope beyond herbivory, as parasitoids, pollinators, and soil-dwelling insects are also equally vulnerable to climate stress, and disruptions to their functions may alter ecosystem services and indirectly intensify pest outbreaks (Gillespie *et al*., 2016; Rasmann *et al*., 2014) [27, 71]. Thus, a more holistic approach incorporating mutualists and natural enemies into experimental designs will be crucial for developing ecologically realistic pest management strategies.

Another pressing direction is the integration of plant biochemical responses into pest forecasting and early-warning systems. Current models primarily use temperature-driven population dynamics, but coupling these with stress-induced changes in host quality, pest fitness, and natural enemy efficiency will improve their predictive accuracy (Deutsch *et al*., 2018) [19]. Such climate-adaptive pest models, remote sensing, and AI-driven decision support could guide real-time IPM decisions in farmers' fields.

Finally, a systems-level approach that connects breeding, biotechnology, and agroecology is needed. Developing stress-resilient cultivars, deploying defence priming technologies, and reinforcing biological control must occur in tandem, guided by interdisciplinary research linking molecular biology, ecology, and climate science. This integrated strategy represents the most promising pathway to ensure sustainable pest management in the face of accelerating climate change.

## 8. Conclusion

Climate change is not only altering weather patterns but fundamentally reshaping the biochemical foundations of insect-plant interactions. Under climate stress, plants experience disruptions in primary metabolism, secondary defences, and signalling pathways, which diminish their resistance to herbivory. In response, insects evolve adaptive strategies such as enhanced enzymatic activity, detoxification, and sequestration, enabling them to exploit weakened hosts. These reciprocal shifts destabilise tri-trophic interactions, undermining both natural pest suppression and pollination that are key pillars of agricultural productivity and ecosystem stability. For agriculture, this implies that conventional pest management approaches may prove increasingly inadequate under climate extremes. Addressing this challenge requires a multi-pronged strategy: breeding climate-resilient cultivars, employing biochemical defence priming, and integrating molecular, ecological, and agronomic knowledge within holistic IPM frameworks. By aligning molecular biology with environmental and agricultural practices, we can safeguard food security, sustain biodiversity, and ensure resilient agro-ecosystems in the face of accelerating climate change.

## 9. Disclaimer (artificial intelligence)

The author(s) hereby declare they have not used generative AI technologies such as Large Language Models (Chat GPT, COPILOT, etc.) and text-to-image generators while writing or editing manuscripts.

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## 11. Competing Interests

The author (s) declared that no conflict of interest exists.

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