



## STRUCTURAL DEFENCES IN PLANTS AGAINST HERBIVORES- A REVIEW

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### ABSTRACT

Plants have developed various defence mechanisms to protect themselves against herbivores, a topic that has fascinated researchers for decades. These mechanisms enable plants to thrive even in environments with intense herbivore pressure. The threats to plants are diverse, including insects, mammals, reptiles and microorganisms. Despite this, plants possess robust defence, both constitutive and inducible. Constitutive defences viz., physical and chemical barriers, exist before herbivore attacks, while inducible defence are activated upon attack. Direct plant defence includes anti-nutritional strategies and toxicity, limiting food supply or reducing nutrient value. Physical defences viz., waxes, trichomes, spines, and sclerophyllous leaves hinder herbivores physically, while chemical defence viz., toxic metabolites, disrupt herbivore physiology. Indirect defence involves attracting natural enemies of herbivores. Understanding these complex interactions is crucial for optimizing crop protection strategies. Future research should adopt a holistic approach, integrating environmental factors and utilizing advanced biological methodologies to further elucidate plant-herbivore dynamics.

**Key words:** Plant defence mechanisms, Herbivore interactions, structural defences, evolutionary arms race, inducible defences, constitutive defences, secondary metabolites, plant-herbivore dynamics, physical barriers, chemical deterrents, trichomes, sclerophylly, spinescence, anti-nutritional strategies, microbiome interactions

The enduring fascination with how plants defend themselves against herbivores has spurred extensive research over decades (Agrawal and Fishbein, 2006). Studies reveal that plants thrive in environments, which are abundant with herbivores due to their capacity to withstand or rebound from intense herbivore pressure (Hartley and Jones, 1997). The spectrum of threats plants may face in nature spans mammals, reptiles, arthropods, bacteria, and particularly, insects, which employ diverse feeding strategies. Despite this array of challenges, plants are equally well defended against those threats. Even the most susceptible host plant of an insect species is not defenceless (Agrawal and Fishbein, 2006). Nonetheless, our comprehension of these defence mechanisms remains incomplete, which underscores the necessity for deeper insights into complex plant-herbivore interactions, which are crucial for crop optimization. The interplay between plants and herbivores mirrors a perpetual evolutionary dance, where the emergence of new offensive tactics prompts corresponding adaptations in successful consumers and the development of novel defensive mechanisms elicits responses from adept defenders. These evolutionary arms race continually shape the dynamic relationship between plants and herbivores over time, underscoring the intricate balance of adaptation and counter-

adaptation driving ecological interactions.

### Estimate of number of organisms

Of the total estimated number of species on the earth today, insects alone contribute around 56% of the species, among which most of the insects directly or indirectly depend on plants for food and shelter (Purvis and Hector, 2000; Tyagi et al., 2024). This shows the diversity of threats to plants, so they should develop defence strategies to fight against these threats (Fig. 1). Throughout their extensive interaction and coevolution with herbivorous insects, plants have developed a diverse array of defence mechanisms to combat insect attacks. These defences can be broadly categorized into pre-formed (constitutive) and inducible defences. Constitutive defences encompass physical and chemical barriers that are present even before an insect attack occurs. On the other hand, inducible defences refer to defensive mechanisms that are triggered and activated specifically in response to an insect attack.

### Plant defence system

1. Direct plant defences can be broadly divided into anti-nutrition and toxicity. Anti-nutrition mechanisms include limiting food

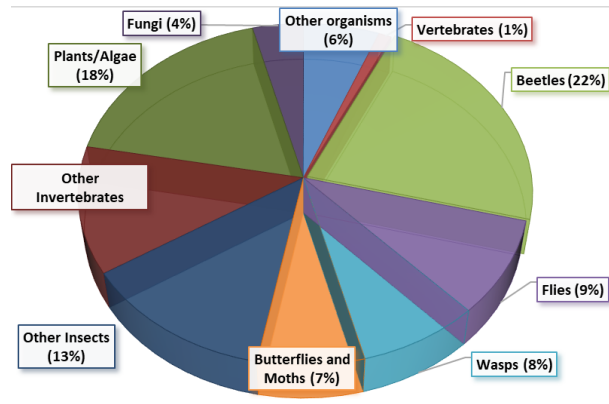
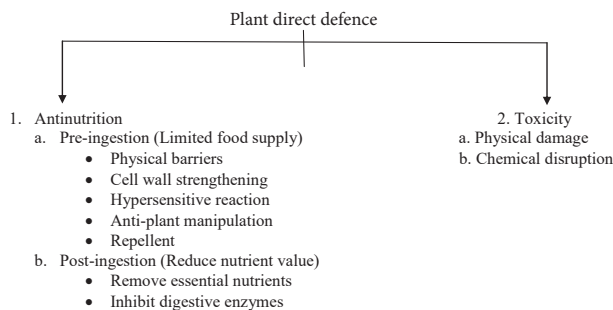


Fig. 1. The number of named species

supply before ingestion and reducing nutrient value after ingestion. Toxicity arises from disrupting insect structures or inhibiting chemical pathways in the insect (Chen, 2008).



Indirect plant defence mechanisms can be categorized into two types: constitutive and inducible. Constitutive defences are always present and include features such as extrafloral nectar, food bodies, and domatia. Domatia are specialized structures on plants that provide shelter for insects, mites, or fungi. On the other hand, inducible defences are activated in response to specific stimuli, involving the production of various elicitors such as enzymes, fatty acid-amino acid conjugates, sulfoxy fatty acids, fragments of cell walls, peptides, and esters. These elicitors stimulate hormone pathways, including jasmonic acid (JA), salicylic acid (SA), and ethylene (ET). The activation of these pathways leads to the production of a wide range of volatile compounds, such as terpenes, volatile indoles, aldehydes, ketones, esters, alcohols, and nitrogenous compounds. These volatiles serve as signals to attract natural

enemies like predators, parasites, and omnivores, thereby helping to control pest populations (Aljory and Chen, 2018).

### Structural defences

Plant defences against herbivores encompass both physical and chemical strategies, with physical defences serving as the frontline protection mechanism in plant-herbivore interactions (Fig. 2). These structural defences are crucial in deterring herbivores, forcing them to overcome significant barriers before accessing the host plant (Kariyat et al., 2018). Present on leaves and stems, these physical structures not only hinder herbivore feeding by making it difficult to grasp and consume the plant but also provide resilience against environmental stressors such as drought, evapotranspiration, and solar radiation (Kariyat et al., 2018). These defences are particularly effective against chewing herbivores like caterpillars, which have strong mandibles that allow them to eat plant tissues (Kariyat and Portman, 2016). The pressure exerted by herbivores has driven host plants to develop specialized defence mechanisms meticulously regulated to reduce the herbivore's harmful impact on their growth, development and fitness (Kariyat and Portman, 2016). Physical defences include various types such as plant waxes, pubescence (trichomes), spinescence (thorns, spines and prickles), sclerophylly (hardened leaves) and raphides (needle-shaped crystals of calcium oxalate or calcium carbonate found in leaves) (Hanley et al., 2007).

### Conceptualization of Plant evolution and Insect Defense

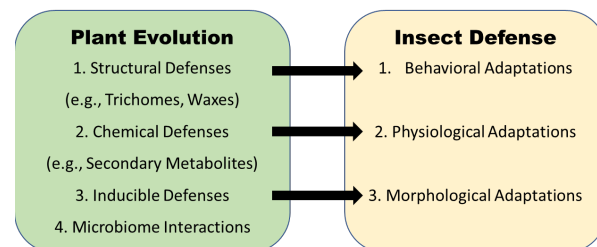


Fig. 2. Plant evolution and insect defence

**Plant waxes:** The plant cuticle, which is the outermost layer of plant cell walls, is composed of lipids and hydrocarbons and plays a crucial role in plant-insect interactions. Made up of cutin and wax, the cuticle forms a thin, hydrophobic barrier around aerial parts of the plant, giving the leaf surface a three-dimensional structure (Jetter et al., 2008). Epicuticular waxes, an essential component of plant cuticles, have multiple ecological and physiological functions, protecting against various stresses (Federle et al., 1997; Whitney

and Federle, 2013). These waxes deter caterpillar movement by making the leaf surface slippery, resulting in prolonged crawling and foraging behaviour rather than feeding. This effect has been observed in diamondback moth caterpillars placed on cuticular extracts of resistant and susceptible genotypes of canola (*Brassica napus* L.) and glossy leaf varieties of collard greens (*Brassica oleracea* var. *viridis* L.) (Justus et al., 2000; Stoner, 1997). Additionally, the hydrophobic materials in these waxes, such as aliphatic chains of alkanes, primary and secondary alcohols, fatty acids, ketones, alkyl esters and acids, not only enhance plant defences as a chemical barrier but also serve as cues for insects to locate their hosts (Jetter et al., 2008; Lewandowska et al., 2020).

Epicuticular waxes are essential in caterpillar feeding, providing host recognition cues (Liu et al., 2023). This thick layer, rich in alkanes, alcohols and chlorophyll, offers visual and chemical signals to herbivores. Besides aiding in host recognition, these compounds have multiple functions. For example, free amino acids and soluble carbohydrates in the plant waxes of wild leek and maize encourage oviposition by the European corn borer, *Ostrinia nubilalis* (Hubner), while the alkane blend in *Brassica napus* L. leaf wax attracts Diamondback moths, *Plutella xylostella* (Linnaeus), for oviposition (Barbero, 2016). Additionally, epicuticular waxes contain semiochemicals that act as sex pheromones and kairomones, attracting parasitoids and predators of herbivores after herbivory, thus facilitating multi-trophic interactions (Dutton et al., 2000). Furthermore, these waxes protect plants in various ways, with some wax chemicals acting as feeding deterrents (Kariyat et al., 2019a).

Caterpillars have developed various physiological and behavioural adaptations to overcome the challenges posed by the hydrophobic and glossy wax layer, which restricts their movement and grip on plant surfaces. These adaptations allow them to establish themselves on plants and begin feeding successfully. For instance, cabbage butterfly (*Pieris brassicae* L.) caterpillars produce water-soluble phenolic compounds that moisten the leaf surface, helping adult butterflies to firmly attach eggs to Brassicaceae leaves (Fatouros et al., 2012). Additionally, *P. brassicae* has evolved mechanisms to ingest and detoxify the glucosinolates found in the dense wax layer of Brassicaceae plants, facilitating their growth and development. In a remarkable example of specialization, the giant geometrid (*Biston robustum*

Butler) can modify the chemistry of its outer integument based on the chemicals present in the cuticular wax layer, mimicking the surface chemistry of plants - a phenomenon known as phytomimesis (Akino, 2005). This chemical camouflage allows larvae to blend with their host plants, evading detection by predators. Despite the significant role of waxes in plant defence against herbivores, caterpillars, particularly those with a long history of co-evolution with their host plants, have evolved behavioural and morphological adaptations to counteract these defences.

**Trichomes:** Plants have developed various ways to defend themselves against herbivorous insects, one of the earliest being the use of tiny hairs called trichomes (Nandi et al., 2022). Caterpillars find it difficult to walk on a leaf surface. Even if waxes do not deter them, their movement is hindered by a dense array of trichomes, which serve as an additional physical barrier (Kariyat et al., 2017, 2018). Trichomes, which can be unicellular or multicellular extensions of epidermal cells, have diverse functions and structures. Despite their small size, they play essential roles in protecting plants from both biotic and abiotic stresses, such as extreme environmental conditions, temperature fluctuations, heavy metal detoxification, and high soil salinity (Karabourniotis et al., 2020; Bosorogan et al., 2023). Furthermore, trichomes are crucial in defending against herbivores and can be broadly categorized into two types: non-glandular and glandular trichomes.

Non-glandular trichomes are sharp, pointed structures that do not secrete substances but act as physical barriers to caterpillar movement. These trichomes are mainly considered mechanical obstacles that impede herbivores, thereby preventing feeding damage. By disrupting the caterpillar's skin upon contact or blocking access to the leaf surface, they prolong foraging periods without corresponding feeding. As a result, neonate larvae are at higher risks of desiccation, starvation, or reduced feeding efficiency (Kariyat et al., 2018; Despland, 2018), making them less active and more prone to injury. These trichomes have significant entrapment capabilities, ensnaring and puncturing soft-bodied insects, and thus serve as effective feeding deterrents. For instance, neonate tobacco hornworm (*Manduca sexta* L.) caterpillars struggle to feed on Solanaceae species with trichomes, leading to their starvation, desiccation, and ultimately death (Kariyat et al., 2013; 2017). These trichomes serve as effective defences against herbivores due to their ability to mechanically trap insects, hindering

their movement and weakening them through physical injury. Additionally, they act as potent deterrents to feeding, causing significant damage by ensnaring and piercing soft-bodied insects. For example, hook-shaped trichomes found in plants such as French bean (*Phaseolus vulgaris* L.) and passion flower (*Passiflora* spp.) can be lethal to herbivores like the sciarid fly (*Bradysia pauper*) and larvae of brush-footed butterflies (Gepp, 1977). Research on species like *Lycopersicon* spp. (Solanaceae) has shown that non-glandular trichomes can dramatically increase herbivore mortality rates, particularly affecting neonate *Helicoverpa armigera* (Hübner) due to entrapment (Simmons et al., 2004). Overall, non-glandular trichomes play a crucial role in deterring herbivory by influencing insect mass, feeding behavior, foraging patterns, adult egg-laying, larval development, mortality rates, and overall fitness (Kariyat et al., 2018; 2019).

Glandular trichomes serve as a defence mechanism by producing toxic secondary metabolites that deter or eliminate herbivores. They activate jasmonic acid (JA)-mediated defences and act as physical barriers, often secreting sticky exudates, toxins and bioactive compounds from their glandular heads. These substances deter herbivores by disrupting their metabolic pathways upon contact (Hare, 2005). For example, trichomes can synthesize proteinase inhibitors that bind to herbivores' digestive enzymes, impairing their ability to digest food. They may also release volatile terpenes that attract predators and parasitoids of feeding caterpillars (Biswas et al., 2009). In specific species like *Lycopersicon* spp., the chemicals released by glandular trichomes cause severe irritation and trap potato tuber moth, *Phthorimaea operculella* (Zeller) neonates due to methyl ketones (2-tridecanone, 2-undecanone) and sesquiterpenes found in the globular cells of their trichomes. Similarly, chemical exudates from glandular trichomes of *L. hirsutum* and *L. pennellii* have been observed to entrap larvae of *H. armigera*, leading to their mortality (Simmons et al., 2004). In plants such as *Solanum lycopersicum* L., herbivore movement can rupture glandular trichomes, triggering the expression of JA-mediated defence genes even before leaf damage occurs (Planelló et al., 2022). Likewise, in the *Nicotiana tabacum* - *M. sexta* system, glandular trichomes release volatiles upon caterpillar damage that attracts predators (Kariyat et al., 2018).

Caterpillars have developed specialized strategies to thrive on plants rich in trichomes, employing morphological, physiological, and behavioural

adaptations. For instance, caterpillars like *M. sexta* have evolved the ability to shave trichomes to access plant tissues, while others construct silk networks to navigate safely through trichome-laden foliage (Wilkens et al., 1996). In contrast, species such as *Heliconius charithonia* (L) have adapted their anatomy to avoid trichomes altogether (Fordyce and Agrawal, 2001). Some caterpillars exhibit social facilitation, aiding collective feeding efforts. They employ behaviours like "mowing" to navigate around trichomes, while others develop physiological adaptations for detoxification. Post-feeding grooming behaviours also play a role in mitigating plant defences. These diverse strategies significantly enhance survival, particularly for early instars vulnerable to the lethality of trichomes. The repertoire of tactics employed by lepidopterans to overcome plant defences underscores their evolutionary creativity and adaptability (Despland, 2019).

**Spinescence:** Spinescence is a term that refers collectively to plant structures such as spines, thorns, and prickles. Spines are pointed projections that typically arise from petioles, midribs, veins, or stipules. Thorns, on the other hand, are sharp-pointed branches made of wood, while prickles are sharp outgrowths from the epidermis or cortex of an organ (Grubb, 1992). While some spines may serve additional functions like reducing radiation flux or aiding in climbing, the primary evolutionary purpose of most spinescence is likely defence against herbivores (Grubb, 1992). These structures can cause mechanical injuries to the mouth, digestive tract, and external body parts of large herbivores, and they may also introduce pathogenic bacteria and fungi into herbivore bodies. Many plants use conspicuous warning colors to signal the danger posed by these sharp structures (Ronel and Lev-Yadun, 2012).

The effectiveness of spinescence in deterring herbivores is supported by several studies. For example, research on European holly (*Ilex aquifolium*) showed that shrubs with highly spiny leaves were significantly less likely to be eaten by large ungulates compared to plants with fewer spines (Obeso, 1997). In East Africa, the substantial thorns of *Acacia tortilis* not only protect leaves from herbivores like goats but also safeguard the axillary meristems, crucial for leaf regeneration (Gowda, 1996). Experiments where spines and thorns were removed further underscored their protective role. Removing thorns from *A. drepanolobium* led to a threefold increase in mammal browsing of new foliage (Milewski et al., 1991). Similarly, removing

thorns from various spinescent shrub species in South Africa's Eastern Cape region increased herbivory rates by bushbucks (*Tragelaphus scriptus*) and Boer goats (*Capra hircus* L.), primarily by allowing these herbivores to take larger bites (Wilson and Kerley, 2003).

*Parasa lepida* Cramer, originating from southern China, has expanded its presence in central Japan, where it infests various broad-leaved trees. Rose prickles, which arise from epidermal tissues, exhibit diverse forms and densities across different rose varieties (Kellogg et al., 2011). Slug caterpillar *P. lepida* often becomes ensnared in the prickles of roses, resulting in immobilization and eventual death. Observations conducted in the rooftop garden of Osaka City Hall revealed instances of *P. lepida* larvae trapped amidst dense prickles on rose twigs, suggesting a potential deterrent effect on mid-sized herbivores. The distinct locomotion pattern and reduced thoracic legs of Limacodid caterpillars heighten their susceptibility to entrapment. Understanding the relationship between inter-prickle spacing and herbivore size is crucial for elucidating plant-insect interactions. While rose prickles have traditionally been viewed as a defence mechanism against larger herbivores, they may also serve to deter mid-sized herbivorous insects, highlighting their multifaceted role in plant defence mechanisms (Yamazaki et al., 2014). Further research in this area is warranted to deepen our understanding of these dynamics.

**Sclerophylly:** Sclerophylly, denoting hard-leaved characteristics typically manifests as small, relatively thick leaves with a thickening of all lamina tissues. This adaptation may serve multiple purposes, including leaf support, resistance to wilting, and conservation of water or nutrients (Lamont et al., 2002). Leaves exhibiting scleromorphic features represent an extreme in food quality, being tougher, lower in nitrogen and water, and richer in secondary compounds. Such attributes decrease the palatability and digestibility of plant material, ultimately constraining herbivore fitness (Grubb, 1986). The thickening process involves all lamina tissues, encompassing the cuticle, outer epidermal walls, and often a hypodermis layer. However, it's important to note that not all thick leaves are classified as sclerophylls. Sclerophyllous leaves typically have diminished concentrations of essential nutrient elements like nitrogen, phosphorus, and calcium. Plant defences against herbivores can be either chemical, mechanical or a combination of both (Moore et al., 2004). Numerous studies have

shown that nonvertebrate herbivores are deterred by scleromorphic structures. For example, Bjorkman and Anderson (1990) observed in South America that butterfly larvae tended to avoid feeding on toughened leaves of blackberry (*Rubus bogotensis*). In Hong Kong, Choong (1996) described how larvae of three lepidopteran species avoided feeding on structurally toughened leaf veins produced by *Castanopsis fiss* when given a choice between pairs of saltmarsh plant species. Similarly, in experiments with saltmarsh plants, *Armases cinereum* consistently preferred plants with softer leaves (Pennings et al., 1998).

Despite their ecological significance in influencing leaf lifespan, insect herbivore abundance and patterns of herbivory across leaf age, leaf mechanical properties remain relatively understudied. Leaf toughness exerts significant evolutionary pressure on herbivores, imposing constraints on herbivore body size, mammal dentition and digestion, insect herbivory patterns, and adaptations (Hanley et al., 2007). Leaf structures are intricate and multifaceted, yet their role in plant defence remains largely unexplored. Recent research emphasizes the need for a comprehensive examination of mutual defences, including both chemical and mechanical aspects, with a renewed focus on leaf toughness as a pivotal mechanical trait. This resurgence of interest underscores the importance of understanding how mechanical properties such as toughness, strength, thickness, vein patterns and density, as well as cuticle structures and barriers like hairs and trichomes, deter herbivores (Read and Stokes, 2006). Leaf veins, characterized by their toughness, nutrient scarcity and thick cell walls, serve as protective barriers for the nutrient-rich leaf lamina. For small herbivores such as insects, feeding on tough leaf material presents a challenge, suggesting that they encounter foraging trade-offs. Breaking down tough leaf tissue requires significant energy, necessitating specialized mandibles. As insects undergo moulting and grow, they develop larger mandibles with wider gaps, presumably providing more force for breaking down tougher material (Ibanez et al., 2013). Malishev and Sanson (2015) found that leaf mechanical properties effectively deter feeding by smaller insect herbivores and may pose greater constraints on feeding than chemical defences along the leaf surface. The selective evolution of larger head sizes and increased force appears to be advantageous for larvae feeding on tougher tissues. Additionally, actively avoiding tougher, more costly-to-fracture tissues like veins along the leaf body likely represents an adaptive behaviour.

**Raphides:** Inorganic calcium oxalate crystals are prevalent in the plant kingdom, appearing in various forms and shapes across a wide range of plant taxa (Franceschi and Nakata, 2005). These crystals are widespread, occurring in more than 215 plant families and about 74% of angiosperm families, and can be found in nearly all plant organs and tissue types (Horner et al., 2012). They can constitute anywhere from 1% to over 90% of a plant's dry mass, with morphological classifications including crystal sand, raphides, druse, styloid and prismatic forms (Franceschi and Nakata, 2005), each exhibiting unique variations in shape and size. Raphides, needle-shaped crystals, are particularly common, forming densely packed bundles in specialized cells known as crystal idioblasts found in various plant tissues from green algae to flowering plants (Horner and Wagner, 1995). These crystals and other shapes have served as valuable taxonomic, pharmacognostic and toxicological markers. Studies have investigated their development and formation, revealing the presence of a cortical microtubule network in raphide crystal idioblasts that influences their ellipsoidal shape (Kostman and Franceschi, 2000). Given the diversity of crystal shapes and their widespread occurrence, multiple hypotheses have emerged regarding their plant functions. These proposed functions encompass defence against herbivory, calcium regulation, plant protection, detoxification (e.g., heavy metals or oxalic acid), ion balance, tissue support, plant rigidity, and even light manipulation (Franceschi and Horner, 1980). While some hypotheses lack robust evidence, accumulating research supports roles in calcium regulation, plant protection, and metal detoxification (Franceschi and Nakata, 2005).

While our comprehension of plant defence mechanisms has made significant strides, several challenges persist. Firstly, there remains a gap in our knowledge concerning the intricate dynamics of plant-herbivore interactions, particularly for less researched plant species and the adaptations of herbivores. Secondly, research often examines individual defence mechanisms separately, missing opportunities to grasp how these mechanisms work together synergistically. A more holistic approach could unveil deeper insights into their combined effectiveness. Thirdly, environmental factors like climate change and habitat modification are frequently underestimated in their influence on both plant defence strategies and herbivore behavior. Integrating these variables into studies is crucial for a more comprehensive understanding of plant defences in their natural contexts.

### Role of secondary metabolites

Plant secondary metabolites play a pivotal role in plant defence against herbivores, serving as chemical deterrents, toxins, or signaling molecules that disrupt herbivore feeding, growth, or reproduction. These compounds are not essential for basic plant functions but are synthesized in response to environmental stresses such as herbivory, pathogen attack, or abiotic stressors. They can be broadly categorized into several classes, including alkaloids, terpenoids, phenolics, and glucosinolates, each with distinct mechanisms of action and ecological roles (Divekar et al., 2022). Alkaloids, for example, often act as potent toxins that interfere with herbivore nervous systems or metabolic processes upon ingestion. Terpenoids, including volatile terpenes, can repel herbivores through their strong odors or disrupt herbivore feeding behavior by affecting digestion or nutrient uptake. Phenolics, such as tannins and flavonoids, can inhibit digestive enzymes or form complexes with proteins, reducing nutrient availability to herbivores (Roaa, 2020). Glucosinolates, found predominantly in the Brassicaceae family, are activated upon tissue damage and can deter herbivores through their bitter taste or by releasing toxic breakdown products. The specific mechanisms of action of these secondary metabolites often involve intricate biochemical interactions between plants and herbivores. Herbivores, in turn, may evolve mechanisms to detoxify or sequester these compounds, leading to co-evolutionary arms races where plants continually adjust their chemical defences and herbivores develop counter-adaptations. Understanding the role of plant secondary metabolites in defence not only informs strategies for sustainable agriculture, pest management, and crop improvement but also enriches our understanding of ecological interactions and the evolutionary processes that shape biodiversity in natural ecosystems. Thus, elucidating these defence strategies at molecular, biochemical, and ecological levels remains a crucial endeavor in contemporary plant biology research (War et al., 2020; Divekar et al., 2022).

### Trade-offs in plant defence

Plant defence mechanisms indeed involve significant trade-offs, primarily in the allocation of limited resources. Plants must balance investment between growth and defence due to resource constraints. When plants allocate resources toward defence, such as producing secondary metabolites or structural defences like thorns or tough leaves, they often divert resources away from processes like growth, flowering

and reproduction (Matyssek et al., 2012). Studies on the trade-offs underscore that plants under herbivore attack or pathogen infection may prioritize defence at the expense of growth and reproduction. For instance, when induced to produce defensive compounds in response to herbivory, plants may experience reduced photosynthetic efficiency or slower growth rates (Kerchev et al., 2012). Similarly, the allocation of resources to defensive structures like lignin or increased cell wall thickness can impede nutrient uptake and allocation for growth and reproduction (Lambers et al., 2019). Understanding these trade-offs is crucial for agriculture and ecological conservation efforts. Balancing plant defence with growth is a delicate ecological dance, impacting not only individual plant fitness but also ecosystem dynamics and biodiversity. Thus, elucidating the mechanisms underlying these trade-offs is essential for sustainable agriculture and ecosystem management in a changing environment (Salgado and Luarte et al., 2023).

### Future thrusts

Employing systems biology methodologies, such as genomics, transcriptomics, and metabolomics, can provide a comprehensive view of plant defence mechanisms and their regulation. Conducting field studies in diverse ecological settings can reveal the complex interactions between plants, herbivores, and their environment, offering valuable insights into real-world dynamics. Investigating the role of plant-associated microbiomes in mediating plant defences and herbivore interactions could uncover novel mechanisms and strategies for pest management. Bridging fundamental research with applied agricultural practices can lead to the development of eco-friendly pest management strategies that harness natural plant defences. Integrating computational modelling and data analytics can help simulate and predict plant-herbivore interactions under various scenarios, aiding in the design of targeted interventions. By addressing these drawbacks and embracing future research thrusts, we can deepen our understanding of plant defence mechanisms and pave the way for more effective pest management strategies and sustainable agriculture practices.

### CONCLUSIONS

The intricate dance between plants and herbivores, particularly insects, underscores the dynamic nature of evolutionary pressures shaping both sides. Plants have evolved an impressive array of defence mechanisms,

ranging from physical barriers like waxes, trichomes, spines, and sclerophylly to chemical deterrents such as toxic secondary metabolites and calcium oxalate crystals. These defences act not only as direct deterrents but also as cues for attracting natural enemies of herbivores, contributing to a complex web of plant-insect interactions. Furthermore, the classification of plant defences into direct and indirect categories highlights the multifaceted nature of their strategies. Constitutive defences provide a constant level of protection, while inducible defences are activated in response to herbivore attacks, demonstrating the flexibility and adaptability of plants in the face of evolving threats. However, despite our growing understanding of plant defence mechanisms, there remains much to uncover. The nuanced adaptations of herbivores to circumvent these defences, as evidenced by caterpillars' morphological, physiological, and behavioural adaptations, highlight the ongoing arms race between plants and herbivores. Ultimately, delving deeper into the intricacies of plant-herbivore interactions is crucial not only for understanding ecological dynamics but also for optimizing agricultural practices. By deciphering the mechanisms underlying plant defences, we can better harness nature's strategies to enhance crop resilience and sustainability in the face of evolving pest load.

### AUTHOR CONTRIBUTION STATEMENT

BNB designed, conceived and wrote the original draft; SRJ revised and edited the manuscript. Both authors have read and approved the manuscript.

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### CONFLICT OF INTEREST

No conflict of interest.

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