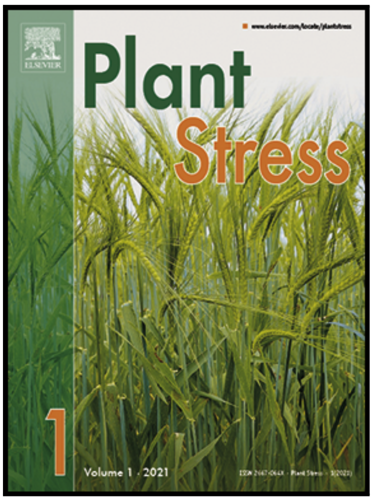


Harnessing molecular insights into plant biophysical traits: Prospects for priming defense against insect pests

Sangeetha Srinivasan Vadivel Murugan , Murugan Marimuthu ,
Jaba Jagdish , Yogendra Kalenahalli , Trevor M. Volp ,
Balasubramani Venkatasamy , Srinivasan Thulasy ,
Kumar K. Krish

PII: S2667-064X(26)00082-5
DOI: https://doi.org/10.1016/j.stress.2026.101299
Reference: STRESS 101299

To appear in: *Plant Stress*

Received date: 15 September 2025
Revised date: 30 January 2026
Accepted date: 14 February 2026

Please cite this article as: Sangeetha Srinivasan Vadivel Murugan , Murugan Marimuthu , Jaba Jagdish , Yogendra Kalenahalli , Trevor M. Volp , Balasubramani Venkatasamy , Srinivasan Thulasy , Kumar K. Krish , Harnessing molecular insights into plant biophysical traits: Prospects for priming defense against insect pests, *Plant Stress* (2026), doi: https://doi.org/10.1016/j.stress.2026.101299

Highlights

- Plant biophysical traits contributing to pest resistance across diverse crops and pests were reviewed.
- The underlying molecular interactions governing these biophysical traits and their role in resistance were examined.
- Reported genes and QTLs associated with key biophysical traits conferring resistance were summarized.
- Potential strategies and future directions for crop improvement towards durable insect pests' resistance were highlighted

Harnessing molecular insights into plant biophysical traits: Prospects for priming defense against insect pests

Sangeetha Srinivasan Vadivel Murugan, Murugan Marimuthu*, Jaba Jagdish, Yogendra Kalenahalli,

Trevor M. Volp, Balasubramani Venkatasamy, Srinivasan Thulasy, Kumar K. Krish

Authors' affiliation

Sangeetha Srinivasan Vadivel Murugan
Department of Agricultural Entomology,
Tamil Nadu Agricultural University,
Coimbatore, Tamil Nadu, India.
ORCID ID: 0009-0009-0557-3645

***Corresponding Author**
Murugan Marimuthu
Department of Agricultural Entomology,
Tamil Nadu Agricultural University,
Coimbatore, Tamil Nadu, India.
Phone Number: 82200 06226
E-mail: entomurugan@rediffmail.com; muruganmarimuthu@tnau.ac.in
ORCID ID: 0000-0002-7485-1153

Jaba Jagdish
Entomology Unit,
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT),
Hyderabad, Telangana, India.
E-mail: jaba.jagdish@gmail.com; jagdish.jaba@icrisat.org
ORCID ID: 0000-0002-4834-8845

Yogendra Kalenahalli
Cell Molecular Biology and Trait Engineering Unit,
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT),
Hyderabad, Telangana, India.
ORCID ID: 0000-0001-7200-6215

Trevor M. Volp
Queensland Department of Primary Industries, Toowoomba, Queensland, Australia
E-mail: trevor.volp@daf.qld.gov.au
ORCID ID: 0000-0003-1646-1154

Balasubramani Venkatasamy
Controller of Examinations,
Tamil Nadu Agricultural University,
Coimbatore, Tamil Nadu, India.
ORCID ID: 0000-0001-6797-3016

Srinivasan Thulasy
Department of Agricultural Entomology,
Tamil Nadu Agricultural University,
Coimbatore, Tamil Nadu, India.
ORCID ID: 0000-0003-0135-5869

Kumar K. Krish
Department of Plant Biotechnology,
Tamil Nadu Agricultural University,
Coimbatore, Tamil Nadu, India
ORCID ID: 0000-0002-9827-2295

Abstract

Among plant biotic stresses, insect pests are of major concern as they directly damage plant tissues and also act as vectors for plant pathogens. The co-evolution of crops and insect pests poses persistent challenges to agricultural productivity worldwide. Chemical insecticides have long served as the primary means of pest control. However, their indiscriminate use has resulted in increased production costs, environmental and ecosystem disruption, and increased risks to human health. These limitations underscore the need for sustainable, non-chemical pest management strategies that can effectively integrate and enhance existing Integrated Pest Management (IPM) programs. One of the most sustainable components of IPM is host plant resistance (HPR), in which plants employ antixenosis and antibiosis as defense strategies mediated through various biophysical, biochemical and behavioral responses. Cultivated genotypes and their wild relatives exhibit diverse resistance mechanisms against insect pests. Key biophysical traits contributing to resistance include leaf glossiness, trichome density, pod and leaf sheath pigmentation, plant vigor, pod wall thickness, cuticle thickness, lignification and other structural defenses. These biophysical traits are regulated by complex molecular and metabolic pathways that determine pest resistance. Understanding the genetic basis of these biophysical traits provides valuable opportunities for identifying and manipulating specific resistance-related genes. Deciphering the complex plant biophysical traits and their genetic basis of resistance, offers promising avenues for immune priming by developing improved crop varieties through new breeding techniques (NBTs). By integrating ecological, genetics and breeding perspectives, this review provides a coherent framework for harnessing plant biophysical traits through modern breeding and genome editing to achieve durable and sustainable insect resistance.

Keywords

Biotic stress, Host plant resistance, Biophysical traits, Genetic basis of resistance, Molecular and metabolic pathways, Plant defense, Pest resistance

1. Introduction

Agriculture faces persistent challenges from various biotic and abiotic stressors, particularly insect pests, which pose a significant threat to production and productivity. These insect pests are responsible for reducing nearly one-fifth of global agricultural yield each year, despite the implementation of multiple management strategies (Junaid and Gokce, 2024). Although conventional insecticides remain the primary means of pest control in most agricultural systems, their use increases production costs and elevates risks to the environment and human health (Devine and Furlong, 2007). To address these concerns, alternative strategies such as host plant resistance (HPR) can offer a sustainable and effective solution for crop protection.

The HPR refers to the ability of plants to defend themselves against insect pests through heritable traits that influence the extent of pest damage, and can serve as a fundamental component of sustainable long-term pest management strategies (Schoonhoven et al., 2005; Sharma, 2016). HPR is categorized mainly into three types - antixenosis, antibiosis and tolerance (Fig. 1). Schuman and Baldwin (2016) proposed a dichotomous scheme distinguishing resistance (traits limiting plant injury) from tolerance (traits minimizing yield loss per injury unit), with resistance further classified into constitutive (e.g., leaf morphology) and inducible (e.g., induced chemical responses) and direct (e.g., leaf morphology or antibiosis) and indirect (attracting natural enemies of the herbivores). These categories of plant resistance mechanisms are governed by the plant's biophysical and biochemical characteristics, which influence insect behavior and development. Biophysical traits in particular play a crucial role during the early stages of plant-insect interactions by influencing insect host finding and settling behaviors.

Crop wild relatives (CWRs), the ancestors and close relatives of cultivated crops (Komal et al., 2023), constitute diverse morphological traits that provide natural defense against herbivores. Structural features such as leaf glossiness, trichomes, pod or sheath pigmentation, pod wall thickness, cuticle thickness, lignification, and overall plant vigor act as the first line of defense against insect attack (Jaba et al., 2021). These traits create unfavorable conditions for insect development or physically hinder feeding and oviposition. Among these structural defenses, non-glandular trichomes have been widely recognized for their role in defense (Jaba et al., 2021). For example, hairy cotton varieties show resistance to leafhoppers (*Empoasca* spp.) and thrips (*Frankliniella* spp.) (Padmavathi and Padmaja, 2022), while the other structural traits, like solid-stem in wheat (*Triticum aestivum*), effectively suppress wheat stem sawfly (*Cephus cinctus* Norton) (Szczepaniec et al., 2015). Extending this concept to seed-associated traits, seed texture and color influence bruchid infestation: smaller and shinier seeds received lower oviposition rates than larger and, duller seeds. In black gram (*Vigna mungo* Hepper), small black seeds show less infestation than larger green seeds (Ponnusamy et al., 2014). Thus, harnessing these traits through de novo domestication and the introgression of insect-resistant genes from CWRs offers a powerful strategy to enhance desirable traits in cultivated crops.

Despite the importance of morphological traits in conferring resistance, their effectiveness is highly environment-dependent. Some traits may repel generalist herbivores but inadvertently attract specialist feeders, indicating an evolutionary constraint in pest resistance (Thiel et al., 2020). Likewise, traits are often specific to feeding guilds; for instance, leaf toughness may deter chewing insects, but provide little resistance against gall-forming pests (Caldwell et al., 2016). Resistance within a feeding guild tends to be positively correlated, whereas resistance across guilds may be weak or absent (Maddox and Root, 1990). These complexities highlight the importance of exploring CWRs, which generally possess stronger pest resistance than domesticated crops and represent a valuable genetic resource for breeding (Bohra et al., 2022). Harnessing this natural diversity through crop improvement programs, integrated with advances in genetics, offers a path towards developing insect-resistant cultivars. In this context, the present review highlights the major biophysical traits underlying plant resistance to insects and discusses their integration into new breeding techniques (NBTs) for sustainable pest management. Accordingly, the following section focuses on the constitutive biophysical traits that enable plants to protect themselves against herbivorous insect attack.

2. Biophysical traits conferring insect resistance

Plants protect themselves against herbivorous insects using their constitutive biophysical traits (Fig. 2; Tables 1 and 2). Additionally, volatile-mediated attraction of natural enemies enables plants to indirectly suppress insect populations through increased predation and parasitism. A plant's defense against herbivory may not depend on a single trait but involve a combination of traits (Agrawal and Fishbein, 2006). Some plant species possess distinct defensive components, including morphological traits and phytochemical substances that influence the behavior and physiology of herbivores encountering them. The morphological and structural traits of the host plants influence insect mating, oviposition, and feeding. Combinations of resistance mechanisms include morphological traits that affect insect host selection behavior. The size, shape, and temporal expression of plant traits are closely linked to resistance against insect pests and are often integrated with underlying chemical defense systems. In response, insects have evolved specialized attachment and locomotion mechanisms that enable effective interaction with diverse plant surface structures (Borodich et al., 2024). Consequently, natural selection may have modified the architecture of terrestrial plants to prevent insect attachment, thereby imposing evolutionary constraints and limiting the range of insect groups capable of colonizing them.

2.1 Morphological and color-related plant traits

Plant appearance and color influence insect host selection behavior by altering visual cues during host recognition, leading to increased resistance. For example, rice *Oryza sativa* cultivars, with narrow lumens, tight leaf sheaths, strong tissues, and ridged stems, are resistant to stem borers (*Chilo suppressalis* Walker, *Scirpophaga incertulas* Walker, *S. innotata,* and *Sesamia inferens* Walker) and sugarcane *Saccharum officinarum* cultivars with loose leaf sheaths exhibit reduced susceptibility to mealybugs *Saccharicoccus sacchari* Cockerell (Sadasivam and Thayumanavan, 2003). In rice, a combination of tightly wrapped leaf sheaths with hairy upper surfaces, narrowly ridged stems, and stronger hypodermal layers provide resistance against the rice stem borer *C. suppressalis* (Sadasivam and Thayumanavan, 2003). Colored rice, including black, crimson, and purple varieties, is less susceptible to storage pests such as the rice weevil *Sitophilus oryzae* Linnaeus than white rice varieties (Jena et al., 2018). Leaf morphology also influences oviposition choice, for example, the plant mirid *Creontiades signatus* Distant prefers cotton genotypes with standard leaf types over okra leaf types (Armstrong et al., 2019). Sclerophylly is a plant trait characterized by hard, stiff, and often thickened leaves resulting from increased lignification, thereby contributing to the plant's defense by limiting herbivore damage (Hanley et al., 2007). For example, tightly packed husks on sweet corn hybrids protect the ear tip against pests such as the cob borer *Helicoverpa armigera* Hubner and the aphids *Melanaphis sorghi* Theobald. Sorghum genotypes with specific leaf colors and panicle shapes repel the spotted stem borer, *Chilo partellus* Swinhoe (Okosun et al., 2021). For instance, sorghum with open panicles had lower *H. armigera* infestation rates than those with compact panicles (Okosun et al., 2021). Also, traits in sorghum, such as deep pigmentation of leaf sheaths, early vigor, and glossy leaves, conferred resistance to the shoot fly *Atherigona soccata* Rondani (Arora et al., 2021). Development and survival of fall armyworm (FAW) *Spodoptera frugiperda* Smith, were adversely affected by sorghum flavonoids, associated with plant color (Grover et al., 2022). FAW larvae showed reduced preference for maize *Zea mays* Linnaeus cultivars with harder and darker leaves (Prassana et al., 2022). The volatiles released by the leaves and their color affected the oviposition of FAW moths on maize (Matova et al., 2020). Cotton leaves of different colors showed varying levels of whitefly resistance, and the presence of gossypol glands had a detrimental impact on whitefly *Bemisia tabaci* Gennadius populations (Rizwan et al., 2021). Furthermore, the number of sympodia (reproductive branches) was identified as a useful morphological trait for selection of pest resistance (Aherkar et al., 2023).

The changes in leaf color constitute a visible and reliable phenotypic indicator of physiological stress and host resistance during insect pest infestation (Mahanta et al., 2024). For example, infestation by wood-boring pests disrupts water and nutrient transport in trees, leading to changes in leaf water content, chlorophyll level, transpiration, and photosynthesis (Luo et al., 2023). These physiological changes are reflected in visible traits, especially leaf color (Liu et al., 2021). Such color changes indicate different stages of infestation and may serve as a useful phenotypic indicator of host resistance or susceptibility.

2.2 Non glandular trichomes

Trichomes are hair-like projections on the plant epidermis of leaves, stems, and roots and may be glandular or non-glandular, differing widely in size, shape, and structure. Non-glandular trichomes impact an insect's ability to move, settle, feed, and survive because they capture, immobilize, and impale insects and provide mechanical resistance (Chu et al., 2003). For instance, the tiny, hooked epidermal trichomes in the French bean, *Phaseolus vulgaris* Linnaeus, have a detrimental effect on *Aphis craccivora* Koch colonies (Riddick and Simmons, 2014). Likewise, trichome density on the lower leaf surface affected the infestation of the bean fly *Ophiomyia phaseoli* Tryon in soybean *Glycine max* (L.) Merrill during early plant stages (Faiz et al., 2021).

Trichomes can deter insect oviposition, as shown by the documented negative associations between oviposition rates and trichome presence. For example, tomato *Solanum lycopersicum* Linnaeus genotypes with higher glandular trichome densities had lower oviposition rates and were less appealing to whiteflies *B. tabaci* than genotypes with fewer trichomes (Oriani and Vendramim, 2010). Higher trichome density in soybean cultivars reduced oviposition by the cabbage looper *Trichoplusia ni* Hubner (Gobbi et al., 2023).

Wild relatives of pigeonpea, such as *Cajanus scarabaeoides* Thouars and *C. acutifolius* Maesen and their derivative introgression lines having glandular trichomes were not preferred by *H. armigera* females for egg laying (Sharma et al., 2001, Jaba et al., 2021; Sharma et al., 2022). Non-glandular trichome density of type C and D in pigeonpea hybrids ICPH 3461 and ICPH 3762 and cultigens BSMR 853, ICPL 332WR offered resistance against pod borer complex (Ambidi et al., 2022) and trichomes in sorghum showed resistance to shoot fly (Arora et al., 2021). The rice variety, Qingliu, exhibited a higher leaf trichome density, which prevented feeding by third-instar *Cnephalocrocis medinalis* Guenee, thereby causing reduced larval relative growth rates and greater mortality compared to susceptible TN1 (Guo et al., 2019). The density and hardness of sugarcane trichomes influenced oviposition choice and survival of pests, such as the sugarcane stem borer *Sesamia nonagrioides* Lefebvre. Sugarcane cultivars, such as SP70-1143, which exhibit increased trichome density and hardness, demonstrate partial resistance to these pests, thereby limiting their population expansion and the crop loss (Malekshah et al., 2022). However, whitefly *B. tabaci* preferred to oviposit and feed on leaves with thick and lengthy trichomes, due to increased microhabitat and protection from natural predators. Whiteflies preferred eggplant *Solanum melongena* Linnaeus cultivars with trichomes in lower densities and shorter lengths (Hasanuzzaman et al., 2016). Cassava (*Manihot esculenta* Crantz) cultivars with pubescent leaves were more resistant to cassava green mite *Mononychellus tanojoa* Bondar, than glabrous ones (Ezenwaka et al., 2018).

Trichome density can also increase in developing leaves in response to herbivory on older leaves, while remaining unchanged in older leaves; these changes can occur within a matter of days or weeks (Agrawal et al., 2009). For example, when the leaf beetle *Phratora vulgatissima* Linnaeus feeds on the canopy of grey willow *Salix cinerea* Linnaeus, the tree produces new leaves with higher trichome density (Dalin and Björkman, 2003).

Unlike the above reported interactions, wheat plants with higher trichome density attracted more *S. frugiperda* females for oviposition (Liu et al., 2022a). Also, some insects, such as the whitefly *B. tabaci* prefer to oviposit and feed on leaves with thick and lengthy trichomes, due to increased microhabitat and protection from natural predators (Riahi et al., 2023).

Trichomes also interfere with insect feeding by exerting both pre- and post-ingestive effects. Pre-ingestive effects caused insects to spend more time foraging than consuming food as they must avoid trichomes to reach the underlying plant material (Steward et al., 2019). Ingestion of trichomes affected the insect's digestive system, particularly the peritrophic membrane, thereby hampering growth and development (Kariyat et al., 2017). When the feeding behavior of the aphid *Rhopalosiphum padi* Linnaeus was studied across 203 wild emmer wheat accessions with varying morphological traits, trichome density was the most important variable in the plant's defensive mechanism (Singh et al., 2021). African (NERICA) rice varieties (1, 4, and 10) having significantly lower glandular trichome densities than the Japanese cultivar Nipponbare suffered more damage from the rice skipper *Parnara guttata* Bremer & Grey and the grasshopper *Oxya japonica* Thunberg (Andama et al., 2020). A positive correlation between the abundance of natural enemies and trichome density is also evident. For example, *Typhlodromalus aripo* De Leon, a mite predator of *M. tanojoa*, preferred leaves from pubescent cassava cultivars over glabrous leaves infested with the pest mite as the pubescent leaf trichomes emit volatile blooms that draw *T. aripo* and remain within pubescence-rich leaf regions, improving their predatory behavior (Onzo et al., 2012).

2.3 Glandular trichomes

Glandular trichomes form a combination of biophysical and biochemical defenses against insect pests. Glandular trichomes produce, store, and occasionally release diverse metabolites, including polysaccharides, organic acids, proteins, terpenoids, alkaloids, and polyphenols (Glas et al., 2012). The secondary metabolites produced by glandular trichomes naturally resist herbivores through antixenosis and antibiosis effects. Glandular trichomes occur in two forms: peltate and capitate. Peltate trichomes are shorter and include unicellular or bicellular stalks and a large multicellular secretory head comprising numerous secretory cells. Capitate trichomes have multicellular stalks of varying length and number, with smaller unicellular heads (Werker, 2000). Dicots frequently have glandular trichomes, which release substances poisonous to insects (Glas et al., 2012).

Tomato and its CWRs possess glandular (I, IV, VI, and VII) and non-glandular (II, III, V, and VIII) trichomes (Glas et al., 2012). Wild progenitors of cultivated tomatoes synthesize a multitude of acyl sugars and volatiles in their type-I/IV and type-VI trichomes, respectively, which may contribute to insect resistance (Kortbeek et al., 2021). Insect movement disrupted and ruptured glandular trichomes, releasing protease inhibitors (Ghosh et al., 2023) that reduced the insect performance by inhibiting protease activity. Glandular trichomes also play an important role in herbivore-induced plant defense by releasing volatile compounds. Wounding or herbivore damage initiates the synthesis of jasmonic acid (JA) through the octadecanoid pathway, which upregulates the synthesis and discharge of volatiles from glandular trichomes (Glas et al., 2012). The volatile blooms released from plants protected them through bottom-up effects on biology and top-down effects by recruiting natural enemies of herbivorous insects. Application of methyl jasmonate (MeJA) to plants induced the synthesis of terpenoids, defense proteins, acyl sugars, and alkaloids in glandular trichomes, thereby priming them against herbivory damage.

When chewing insects feed on plant surfaces densely covered with glandular trichomes, their mandibles frequently become clogged with the sticky exudates, hindering feeding. The glandular trichome exudates of chickpea *Cicer arietinum* Linnaeus that contain succinic, oxalic, and malic acids prevented pod damage by the larvae of the pod borer, *H. armigera* (Golla et al., 2018). The sesquiterpene (E)-β-farnesene in the glandular trichomes of the wild potato *Solanum berthaultii* Hawks attracted the parasitoid wasp *Diaeretiella rapae* Curtis of aphid *Myzus persicae* Sulzer but repelled *M. persicae* (Gibson and Pickett, 1983). The type VI glandular trichomes of certain *Solanum* species released the sesquiterpenes R-curcumene and 7-epizingiberene, which deterred *B. tabaci* (Kennedy, 2003).

Thus, the glandular trichomes play multifunctional roles in plant–insect interactions. They exert direct negative effects on herbivores by deterring feeding, inhibiting larval development and conferring indirect defensive benefits by mediating tritrophic interactions. This underscores that glandular trichomes do not act solely as physical or chemical barriers but also serve as ecological signaling platforms, balancing herbivore deterrence with the recruitment of parasitoids and predators. Harnessing this dual role through breeding or biotechnological approaches could enhance sustainable pest management by reinforcing both direct and indirect plant defense mechanisms.

2.4 Plant surface silicon (Si)

Plants acquire silicon (Si), which increases plant resistance and reduces damage from diseases, insects, and non-insect pests by boosting the plant's innate abilities through constitutive or induced pathways (Alhousari and Greger, 2018). The deposition and accumulation of bioavailable *Si,* either in the form of amorphous hydrated *Si* or biogenic opals, particularly in the epidermal cells of leaves, stems and roots, increase both direct and indirect resistance to insect pests (Alhousari and Greger, 2018). *Si* increased the hardness and abrasiveness of plant tissues by causing mandibular damage to phytophagous insects during feeding, resulting in less plant damage (Frew et al., 2016) and slowing their development (Johnson et al., 2020). *Schistocerca gregaria* Forskal and *Spodoptera exempta* Fabricius are prominent insects that avoid *Si*-rich grass plants (Massey et al., 2006). FAW larvae feeding on artificial food enriched with *Si* showed higher mandible wear than those fed only artificial diets (Acevedo et al., 2021). The stalk borer *Eldana saccharina* Walker larvae’s mandibles were worn down as they continuously consumed hard plant tissues rich in Si, thereby minimizing the damage they inflicted on the plants (Kvedaras et al., 2009).

Si deposits act as a mechanical barrier for feeding by sucking insects, preventing stylets from piercing the cell wall (Verma et al., 2021). In other cases, increasing callose *Si* deposition stops insects from sucking sap and reduces their food intake (Hao et al., 2008; Yang et al., 2017). In addition to providing mechanical protection, *Si*-mediated defenses increase the synthesis of defensive proteins, enzymes, and secondary metabolites, leading to direct defenses in some plant species (Reynolds et al., 2016). For example, aphids and other phloem-feeding insects avoid abrasive phytoliths; however, their feeding-induced damage can still trigger *Si*-mediated responses (Alhousari and Greger, 2018). Furthermore, the *Si*-triggered changes in volatile profiles that attract natural enemies, along with *Si*-mediated defenses, provide both direct and indirect plant defenses (Kvedaras et al., 2010; Leroy et al., 2019; Liu et al., 2017b).

Si deposits also form a physical barrier in root systems, which has a major effect on root-feeding insects. For example, soil-applied *Si* fertilizers enhanced *Si* uptake in sugarcane and the grass *Brachiaria brizantha* Stapf, which reduced the brown root stinkbug *Scaptocoris carvalhoi* Becker nymphs (Souza et al., 2009). This also increased nymphal mortality and shortened the lifespan of the spittlebug *Mahanarva fimbriolata* Stal (Korndörfer et al., 2011). In the case of rapeseed *Brassica napus* Linnaeus, root applied *Si* at the seedling and early bud stages increased the root diameter, stem lignin and SiO_2 accumulation and breaking strength (Kuai et al., 2017). In addition to regular *Si* fertilizers, SiO_2 nanoparticles also contribute to root mediated plant defense. For example, applying silicate as well as SiO_2 nanoparticles to fenugreek *Trigonella foenum-graecum* Linnaeus, increased *Si* uptake and accumulation, xylem cell wall lignification, cell wall thickness, *phenylalanine ammonia lyase* (*PAL*) activity and protein concentration in seedlings *(*Nazaralian et al., 2017).

2.5 Surface/Epicuticular waxes (EWs)

Epicuticular waxes (EWs) form the plant's outermost barrier, and are the first resistance-related trait encountered by herbivorous insects during host contact. EWs also shield plant surfaces from biological stress and desiccation, thereby serving as a crucial interface in the tri-trophic interaction (Van Poecke, 2007). It creates a slippery layer or crystals on the leaf surface, limiting herbivores' ability to grip and feed on host plants (Mitchell et al., 2016). Surface waxes influence mobility, oviposition, and feeding, imparting insect resistance by interfering with the insect's sense organs at the tarsi and mouthparts by sending negative chemical and tactile stimuli (Dhanyalakshmi et al., 2019). This distorts the physiological processes of stimulus processing and response.

Rice plants have evolved an array of physical defenses, including EWs, to protect themselves against insect herbivores. In this context, rice water weevil *Lissorhoptrus oryzophilus* Kuschel and FAW caused more damage when rice expressed lower EWs due to mutations, suggesting higher pest susceptibility at lower EW levels (Bernaola et al., 2021). The wax content in rice sheaths increased as plants grew and their leaves developed, thereby reducing insect attacks (Balakrishnan et al., 2024).

In sorghum plants, wax components such as α-amyrin and isoarborinone increase following aphid infestation, indicating their role in induced defense responses (Cardona et al., 2023). Surface waxes altered rind hardness, which remained an essential element in reducing the sugarcane borer *Diatraea saccharalis* Guenee (White et al., 2006).

Concomitantly, the correlation between wax blooms and pest resistance varies across plant species and is complex, as their function can differ by pest species (Canassa et al., 2021). Surface wax also acts as a strong stimulus for insects to lay their eggs on host plants, in contrast to its ability to repel many insects. During the host selection process, insects use particular wax components, such as long-chain alkanes, to select their host plants. These alkanes in the glossy-leaved *Brassica oleracea* Lour encouraged the diamondback moth (DBM) *Plutella xylostella* Linnaeus adults to lay eggs. Interestingly, neonate larvae did not prefer these plants (Wang et al., 2020) and hence, they may act as a death trap for the pest. Contrarily, the wax bloom on cabbage *B. oleracea* var. *capitata* Linnaeus leaves offered protection against feeding and oviposition by pests, such as the mustard beetle *Phaedon cochleariae* Fabricius and the DBM (Lewandowska et al., 2020). In the case of sesame *Sesamum indicum* Linnaeus, the presence of C_6 compounds in the cuticular wax provided optimal ovipositional signals to generalist feeders (Roy, 2021).

In onion, thrips *Thrips tabaci* Lindeman caused minor damage when fed glossy or semi-glossy leaves containing lower levels of EWs, such as hentriacontanone-16 (H16) and higher concentrations of other waxes, such as fatty alcohols and alkanes. Hence, breeding onions for optimal wax profiles can result in thrips-resistant cultivars (Munaiz et al., 2020).

As previously stated, certain herbivores prefer to live or lay eggs on plants with prominent EW blooms, while others are more susceptible to reduced wax blooms. Minimum level of wax blooms in peas, for example, have been associated with reduced densities of the aphid *Acyrthosiphon pisum* Harris, but the same plants suffered severe damage from leaf weevil *Sitona lineatus* Linnaeus (Eigenbrode et al., 2000). In some cases, these wax blooms affect the attachment of natural enemies to plant surfaces, thereby minimizing indirect effects of plant defense (Eigenbrode, 2004). Still, crop varieties with reduced waxy blooms compared to normal ones enhanced the foraging efficiency of insect predators and therefore, reduced pest populations. For example, resistant cabbage varieties with reduced wax bloom facilitated the activity of insect predators, such as *Chrysoperla plorabunda* Fitch, *Orius insidious* Say, and *Hippodamia convergens* Guérin-Méneville, reducing DBM and aphid *Brevicoryne brassicae* Linnaeus populations (Eigenbrode et al., 2000). Interestingly, insect oviposition may modify the composition of plant cuticular waxes; however, egg parasitoids are known to detect these modifications and trace their host eggs. Supporting this, the oviposition of the large cabbage white butterfly *Pieris brassicae* Linnaeus on *Arabidopsis* altered the wax composition, specifically the fatty acids tetracosanoic acid and tetratriacontanoic acid, which attracted the egg parasitoid *Trichogramma brassicae* Bezdenko (Blenn et al., 2012). Overall, epicuticular waxes play multifaceted roles in plant–insect interactions, conferring both deterrent and attractive effects; therefore, their functional diversity must be carefully considered in breeding programs and molecular manipulation using genomic approaches aimed at improving insect resistance.

3. Ecological and genetic influences on biophysical trait–mediated resistance

The effectiveness of biophysical traits is strongly influenced by ecological context and genetic background, resulting in variable outcomes across insect species and environments. Structural defenses such as trichomes, silicon deposition, and epicuticular waxes can impede insect feeding, movement, and oviposition; however, their defensive value is often contingent on the herbivore's feeding guild and biological traits. For instance, high trichome density commonly deters chewing insects and it may also exert neutral or contrasting effects on sap-feeding pests. At the same time, *Si*-based defenses tend to confer greater resistance against mandibulate insects than against piercing–sucking species (Reynolds et al., 2016). Biophysical traits also influence multitrophic interactions in which moderate trichome density can facilitate the activity of predators and parasitoids by improving prey retention, whereas excessive trichome cover or thick wax layers may hinder natural enemy movement and reduce biological control efficiency.

Despite the importance of biophysical traits in insect population buildup on host plants, their expression is strongly influenced by environmental conditions. As environmental conditions change dramatically across local and global scales, functional research on the ecological implications of variations in plant traits has become increasingly crucial for ecosystem sustainability (Zhan et al., 2022). Abiotic factors such as soil *Si* availability, drought, and temperature further affect trait expression, leading to variable resistance outcomes under field conditions (Cooke et al., 2016). In addition, substantial genetic variation exists among crop genotypes and CWRs in the expression of these traits, which offers opportunities for resistance breeding but also highlights the need to evaluate potential trade-offs (Mitchell et al., 2016). Recognizing these ecological and genetic influences is essential for the effective deployment of biophysical traits in sustainable pest management through resistance breeding programs.

4. Genetic basis of resistant traits

There are two types of plant defense traits: qualitative (provides strong, specific and less durable resistance against certain insect species or biotypes and involves mechanisms like toxin production (e.g., alkaloids) or structural barriers (e.g., trichomes) and quantitative (provides partial and more durable resistance, reducing insect damage rather than completely preventing it which involves traits such as thickened cell walls, secondary metabolites, or changes in plant morphology). This resistance is further categorized according to the number of genes that control it: one (monogenic), a few (oligogenic), or many (polygenic). Polygenic resistance is more difficult to integrate into plant breeding programs than monogenic and oligogenic resistance (Padmavathi and Padmaja, 2022) (Table 3). Quantitative resistance is regulated by many quantitative trait loci (QTLs) with small contributory effects by each QTL, enabling partial resistance against a broad range of insect biotypes (Pilet-Nayel et al., 2017) besides involvement in different biological activities in plants, including regulation of morphological phenotypes and developmental processes imparting pest resistance (Zhang et al., 2013) (Table 4).

There is a knowledge gap regarding the genes underlying plant morphological traits that influence HPR against various insect pests. However, new molecular tools have been developed to detect genomic regions associated with those specific phenotypes. One such tool is QTL mapping, which is frequently used to discover trait-contributing regions on chromosomes (Sehgal et al., 2016). QTL mapping uses two methods: linkage analysis and association mapping. The former refers to the preliminary identification of QTLs within a biparental population's genome, whereas the latter is the discovery of the precise locations of trait-controlling genomic regions in a collection of germplasm that identify the genes driving quantitative traits (Yu et al., 2011). Based on this general genetic basis of resistance, the following section focuses on the specific gene networks and regulatory pathways that govern key biophysical traits involved in insect defense.

5. Gene networks influencing biophysical traits

5.1 Plant leaf traits

Insect-resistant cotton can be developed by manipulating genes linked to traits such as frego bract (a mutation that causes cotton bracts to be narrow and twisted, exposing the buds), nectariless, okra leaf type, and hairiness (Egan and Stiller, 2022). Cotton with okra-leaf shapes exhibited greater resistance to the boll weevil *Anthonomus grandis* Boheman, pink bollworm *Pectinophora gossypiella* Saunders, and the whitefly *B. tabaci* (Chu et al., 2002), which was ascribed to their lower attraction to insects due to a smaller leaf area. In *Gossypium hirsutum*, a single semi-dominant gene controlled the okra leaf trait with F1 generations displaying sub-okra traits (Zhu et al., 2008). The okra leaf gene *ghokra*, which encodes homeodomain leucine zipper class I proteins Gorai.002G244000 and Gorai.002G244200, regulating leaf shape (Zhu et al., 2016), is amenable to genomic selection.

Cotton plants expressing frego bracts resist boll weevil infestations by interfering with oviposition, a trait inherited in a simple monogenic manner, regulated by a single recessive gene (Sajjid et al., 2008). Wang Kangwen et al. (2023) discovered and mapped 14 potential *frego bract* (*FG*) genes on cotton chromosome A03, which are candidates for molecular breeding approaches to develop resistant genotypes.

5.2 Plant color

Plant pigments, such as anthocyanins and carotenoids, offer color-based resistance. Anthocyanin hyperaccumulation has been linked to increased defense against biotic stresses such as herbivory (Malone et al., 2009; Mitsunami et al., 2014). The color intensity and pattern are determined by genes that regulate pigment production pathways (Sharma et al., 2022). In purple sorghum genotypes, flavonoid biosynthesis genes are overexpressed, providing defense against FAW. Upon herbivory, the resistant genotype SC1345 accumulated higher levels of flavonoids, indicating a metabolic shift of precursors away from lignin biosynthesis toward the flavonoid pathway (Grover et al., 2022). WRKY transcription factors, including *SbWRKY86*, were hypothesized to play a role in sorghum's defense against sugarcane aphid *Melanaphis sacchari* Zehntner. When *M. sorghi* infested the resistant sorghum line SC265, several genes were expressed at higher levels (Puri et al., 2023).

In cabbage *Brassica* sp., the purple color develops primarily due to the accumulation of anthocyanins. Several genes involved in the anthocyanin biosynthetic pathway, such as *PAL*, *cinnamate-4-hydroxylase* (*C4H*), *chalcone synthase* (*CHS*), *chalcone isomerase* (*chi*), *flavanone 3- hydroxylase* (*F3H*), *flavonoid 3'- hydroxylase* (*F3'H*), *dihydroflavonol 4- reductase* (*DFR*), *anthocyanidin synthase* (*ANS*), and *udp-glucose flavonoid 3-o-glucosyltransferase* (*UFGT*), are upregulated in purple cabbage compared to green cabbage (Zhang et al. 2016). Transcription factors like *R2R3-myeloblastosis* (*MYB*), *basic helix-loop-helix* (*bHLH*), and *WD40* (forming the MBW complex) regulated these structural genes. Transformation experiments confirmed that a specific gene, named *DARK-PUR*, similar to *BrMYB2*, was responsible for the primary determinant of purple coloration in Chinese cabbage *Brassica rapa* Linnaeus (Liu et al., 2022b). Cotton with red color leaves defended the cotton aphid, *Aphis gossypii* Glover, and suffered reduced foliar damage compared to green-leaved cotton (Hamilton and Brown, 2001). A single partially dominant gene controlled this red color of cotton leaves (Din et al., 2016).

In the tissues of radish *Raphanus sativus* Linnaeus, the genes involved in the anthocyanin biosynthesis pathway - *DFR, Udp-glycosyl transferase78D2 (UGT78D2), transparent testa* 12 (*TT12*), and *caprice* (*CPC*) exhibited differential expression across various tissues. Furthermore, *RsDFR.9c* and *RsUGT78D2.2c* were identified as possible key regulators of anthocyanin production, contributing to purple coloration in radish (Liu et al., 2024). In the Chinese cabbage cultivar 11S91, the dominant purple-head trait is controlled by the regulatory gene *R2R3-MYB*, *BrMYB2*, located on chromosome A07 (He et al., 2020b). The expression profiles of 86 anthocyanin biosynthesis genes in 11S91 and its breeding parents demonstrated an upregulation of *B. rapa MYB2* and *BrTT8* and downregulation of *BrMYBL2.1*, *BrMYBL2.2*, and *B. rapa lateral organ boundaries domain* (*BrLBD39.1*) during growth. This was accompanied by a significant and continuous upregulation of the gene *BrPAL3.1*, early biosynthesis genes such as *BrCHSs*, *BrCHIs*, *BrF3Hs*, and *BrF3'H*, key late biosynthesis genes including *BrDFR1*, *BrANS1*, *BrUF3GT2*, *BrUF5GT*, *B. rapa malonyl transferase* (*Br5MAT*), and *B. rapa p-coumaroyl transferase* (*Brp-Cout*); as well as transport genes *B. rapa glutathione s-transferase 1* (*BrGST1*) and *BrGST2* (He et al., 2020a).

5.3 Trichome development

Several proteins unite to form complexes in molecular regulatory networks of trichome formation in plants (Fig. 3). In *A. thaliana*, the MBW protein complex containing the R2R3-*MYB* transcription factor *glabra 1* (*GL1*), the *bHLH* transcription factors *GL3* and *enhancers of glabra 3* (*EGL3*), and the *WD40* repeat protein *transparent testa glabra 1* (*TTG1*) (Schellmann et al., 2007) promoted trichome initiation by activating the transcription of the homeodomain protein *GL2* (Wei et al., 2019). The nearest phylogenetic relationships between *Arabidopsis* (Brassicales) and *Gossypium* (Malvales) species suggested that a similar regulatory mechanism for leaf trichome initiation may exist in these species (Lee et al., 2006). The key genes that govern trichome initiation were identified at the T1 locus on chromosome 6 (Lacape and Nguyen, 2005). Multiple QTLs linked to fiber fineness, length, elongation, color, and length uniformity were also found in the T1 locus (Wan et al., 2007). Thus, the T1 locus, which contains genes involved in several epidermal trichome formation pathways, is a prospective region to consider for molecular insect resistance breeding programs.

Genotyping by sequencing (GBS) studies have explored genomic regions in cotton (*Gossypium arboreum* Linnaeus) that regulate hairy/pubescent leaf and stem phenotypes. This study focused on *GaKAN2*, a member of the *kanadi* family, and its role in trichome development. Genome-wide scanning with transcriptomic analysis identified seven *GaKAN* genes that were significantly expressed in the stem and root, and *GaKAN2* was also upregulated in other tissues. Silencing of the *GaKAN2* gene decreased the single-cell trichomes and reduced the internodal distance, highlighting its role in trichome development and plant growth. This research laid the groundwork for further manipulation of *GaKAN2* genes to enhance cotton trichomes and plant development, potentially improving plant defense against insect herbivory (Ren et al., 2024). The susceptibility or resistance of *Gossypium* species against sucking insect pests is related to the extent of hairiness (Dhamayanthi et al., 2020).

In barley *Hordeum vulgare* Linnaeus, trichomes provide resistance against aphids, *Rhopalosiphum maidis* Fitch, *R. padi* and *Sitobian avenae* Fabricius. Two key genes responsible for trichome production in barley have been identified. The first gene, *pubescent leaf blade 1* (*Pub1.a*), is a dominant variant located on chromosome 3H and is prevalent in most of the wild barley genotypes, leading to short hairs spreading along the smaller leaf veins on the upper and lower leaf surfaces. The second gene is *hairy leaf sheath 1* (*Hsh1.a*), a dominant mutation on chromosome 4H that induces hairiness at base of the leaf sheaths in barley. The density of these hairs varies between cultivars and is influenced by growing conditions. These trichomes hinder pest movement and feeding (Hansson et al., 2024).

Other cultivated crops have different genes and transcription factors responsible for trichome formation and distribution. For instance, trichome initiation and elongation in rice are regulated by the transcription factor *hairy leaf 6* (*HL6*) (Sun et al., 2017). A pair of dominant genes in rice, *OsGL6* on chromosome 6, which is allelic to the *HL6* gene, governs variation in the hairy phenotype. Transgenic rice lines overexpressing *OsGL6* showed an increased trichome initiation compared to wild lines (Xie et al., 2020). As regulators of trichome development in rice, *OsSPL10* and *OsWOX3B* were found to be important, and their regulated expression was achieved through *OsSPL10* binding to the *HL6* promoter (Li et al., 2021a). In wheat, six candidate genes (*TraesCS3A02G406000*, *TraesCS3A02G414900*, *TraesCS3A02G440900*, *TraesCS7D02G145200*, *TraesCS3A02G149200*, and *TraesCS3A02G152400*) were identified for trichome-related traits (Fan et al., 2023). Tolerance against flea beetle *Phyllotreta cruciferae* Goeze and DBM was achieved by introducing the *A. thaliana* trichome regulatory gene *AtGL3* into semi-glabrous canola *B. napus*, which increased the trichome density, enabling resistance to pests (Alahakoon et al., 2016).

Despite extensive characterization of genes regulating trichome initiation and density, most functional insights to date have come from model species, particularly *Arabidopsis*. In crops, the direct contribution of trichome-related genes to insect resistance is often inferred rather than experimentally validated. These limitations highlight the need for crop-specific functional studies on trichomes and for the evaluation of ecological trade-offs under field conditions.

5.4 Glandular trichomes

MYB transcription factors regulate the initiation of most glandular trichomes (Fig. 3). Among the glandular trichomes, the capitate types were regulated by the interaction of *cyclins* (*CYC*) and *homeodomain-leucine zipper* (*HD-ZIP*) transcription factors. In contrast, the *bHLH* transcription factors controlled the peltate type (Feng et al., 2021). Studies on mutants in domesticated tomatoes have provided insights into trichome developmental regulation involving genes such as *woolly* (*WO*) (a *homeodomain-leucine zipper IV* (*HD-ZIP IV*) gene), and the *hairless* (*HL*) (a *specifically rac1-associated* (*SRA1*) gene) (Yang et al., 2011; Kang et al., 2016). A phenotype resembling the glabrous organs of some CWRs was produced through the tomato hairs absent (h) mutation. In *Solanum habrochaites* Knapp & Spooner glandular trichomes, biosynthetic genes involved in the production of the sesquiterpene (Sst2 locus located at chromosome 8) and methyl ketone and terpenes, *z-isoprenyl pyrophosphate synthases* (*zFPS*) and *santalene and bergamotene synthase* (*SBS*) were identified that significantly inhibited caterpillars and aphids (Sallaud et al., 2009). It allows the transfer of these biosynthetic pathway genes through wide breeding of CWRs with cultivated tomatoes and subsequent selection (Gasparini et al., 2023). The tomato hairless (*HL)* mutant expressed bending and swelling of type VI trichomes, which impaired terpene synthesis and decreased resistance against the tobacco hornworm *Manduca sexta* Linnaeus (Kang et al., 2016). Development of fewer glandular leaf trichomes and production of lower levels of terpene content occurred by the overexpression of tomato B-type cyclin gene, *SlCYCB2*, and its direct transcriptional activator *SlMYB75*, which significantly increased susceptibility against *Spodoptera litura* (Fabricius) and spider mites *Tetranychus* sp. (Gasparini et al., 2023; Gong et al., 2021).

The gossypol excreted by glandular trichomes is deposited in small and darkly pigmented lysigenous glands on the leaf canopy of *Gossypium* spp. A map-based cloning strategy was used in tetraploid cotton to clone the *Gossypium pigment gland formation* (*GoPGF*) gene, which is regulated by a *bHLH* transcription factor (Ma et al., 2016). Its role in regulating glandular trichomes was functionally validated using virus-induced gene silencing (VIGS), which demonstrated that silencing *GoPGF* resulted in the glandless phenotype. Further, the insufficient production of acyl sugars in tomato, due to the absence of type IV and other glandular trichomes, resulted in inadequate pest protection (Blanco-Sánchez et al., 2021). Furthermore, wild relatives of the tomato have been widely utilized as sources of resistance traits for introgression into cultivated varieties to manage pests and diseases. Notably, trichome-mediated resistance from *Solanum pimpinellifolium* Linnaeus accession TO-937 was introgressed into cultivated tomato. The resulting inbred line BC5S2 effectively resisted *Tomato yellow leaf curl virus (TYLCV)* because of the interruptions to virus transmission by its vector *B. tabaci* (Rodríguez-López et al., 2020). This was linked to the presence of type IV glandular trichomes on the leaves and secretion of acyl sugars in the glandular exudates. However, the density of type IV trichomes and production of acyl sugars were limited at the early growth stages of these tomato inbreds. The feeding by the zoo phytophagous predator *Nesidiocoris tenuis* Reuter on young BC5S2 tomato plants caused over 50% increase in type IV trichome density and increased acyl sugar production due to upregulated expression of the acyl sugar biosynthesis gene *dihydrolipoamide branched chain transacylase E2* (*BCKD-E2*) (Riahi et al., 2023). Therefore, pre-planting release of these predators and their feeding on tomato at the nursery stage may upregulate these genes, leading to trichome-rich plants.

5.5 Si-mediated physical defense

The genetics underlying *Si* accumulation in plants is intricate, which involves several critical genes and transporters (Fig. 4). Monocots, such as rice, sugarcane, maize, and other cereals, absorb *Si* in substantial amounts compared to dicots, facilitated by specific *Si transporters* (Ma et al., 2007). Key transporter genes first identified in rice include *low Si* (*LSi1* and *LSi2*), encoding aquaporin-like proteins, where *LSi1*, the initial *Si influx* transporter facilitates the uptake of ortho silicic acid ($Si(OH)_4$) into root cells, while *LSi2* acts as a *Si efflux transporter* (*SiET4*), moving *Si* from roots to the xylem for transport to shoots (Leroy et al., 2019).

Subsequently, homologs of *Si influx* and *efflux* transporters have been identified in barley (*HvLSi1*, *HvLSi6*, *HvLSi2*) (Chiba et al., 2009), wheat (*TaLSi1*) (Montpetit et al., 2012), maize (*ZmLSi1*, *ZmLSi6*, *ZmLSi2*), and pumpkin *Cucurbita pepo* Linnaeus (*CmLSi1*, *CmLSi2*) (Mitani et al., 2009). In rice, a *SiET4* gene that encodes for *Si* accumulation and deposition in leaves has been reported. Functional validation revealed that *SiET4* knockouts led to abnormal *Si* deposition (Mitani-Ueno et al., 2023). Additionally, the *drooping leaf* (*DR*) gene, which encodes a *gdsl* esterase in rice, regulates *Si* deposition in leaves; mutations in *DR* result in reduced *Si* accumulation and a drooping leaf phenotype (Yu et al., 2020). *SiET* genes, such as *OsLsi3* in rice, are reported to be responsible for loading *Si* into the xylem. In horsetail millet *Equisetum arvense* Linnaeus, the *SiET* genes *EaLSi2-1* and *EaLSi2-2*, the highest *Si* accumulators, were reported (Dabravolski and Isayenkov, 2024). In sorghum, the gene *siliplant 1,* which encodes a protein that precipitates *Si* in leaf silica cells, was identified (Kumar et al., 2020) and may be useful for developing insect resistance.

Varietal comparisons in rice revealed that higher expression levels of *LSi1* and *LSi2* correlated with greater *Si* accumulation in japonica varieties, such as Nipponbare, than in indica varieties, such as Kasalath (Ma et al., 2007). Marker assisted selection (MAS) can be used to select genotypes with enhanced ability to accumulate *Si* in their tissues. This process involves identifying genetic markers linked to QTLs or major genes that control *Si* uptake and deposition in plants. By combining these *Si*-related traits with existing pest resistance genes, we can develop varieties that leverage both the direct effects of *Si* and its defense-enhancing properties, to develop a more durable pest management strategy.

Although *Si*-related genes and transporters have been identified, the genetic regulation of *Si*-mediated insect resistance remains incompletely understood. *Si* accumulation is strongly influenced by soil availability, water status, and root uptake efficiency, which can limit the predictability of resistance under field conditions. Furthermore, most evidence for *Si*-based resistance is physiological rather than genetic, and the downstream molecular mechanisms linking *Si* deposition to insect deterrence require further investigation.

5.6 Surface/Epicuticular wax (EW) production

During stress due to plant-pathogen or insect interactions, several EW genes are upregulated (Fig. 5) (Xue et al., 2017). Concurrent upregulation of genes involved in synthesizing EW and defense products, such as cytochrome P450 (*CYP*), *WRKY, MYB* transcription factors and *CHS,* were identified. In *A. thaliana*, EWs synthesis-related *eceriferum* protein family enzymes (*CER4*, *CER6*, and *CER10*), *fatty acyl-acp thioesterase B* (*FATB*), and *glossy 8* (Bonaventure et al., 2003; Dietrich et al., 2005; Rowland et al., 2006; Zheng et al., 2005), wax transporters, *CER5* and *white-brown complex homolog 11* (*WBC11*) (Bird et al., 2007; Pighin et al., 2004), and transcription factors, *shine 1* (*SHN1*), *MYB30*, *MYB96*, and *wax production 1* (*WXP1*) (Broun et al., 2004;

Raffaele et al., 2008; Seo et al., 2011) were documented. These homologous genes were also reported in other cultivated crops.

The interaction between rice and brown planthopper (BPH) *Nilaparvata lugens* Stal feeding is characterized by pronounced cell wall modifications, which serve as a key defensive strategy positioning the cell wall as a principal "battleground" in plant–insect interactions (Silva-Sanzana et al., 2020). The cell wall-modifying enzymes (CWMEs) present in salivary secretions of *N. lugens* help them to penetrate the extracellular matrix of epidermal cells using their stylet (Van Bel and Will, 2016). To defend against *N. lugens* feeding, rice plants used an alternative array of CWMEs to strengthen their cell walls. Numerous signaling mechanisms regulating this resistance have been identified, including salicylic acid (SA) and jasmonic acid (JA). In *N. lugens* infested rice sheaths, regulation of lipid metabolism, particularly lipid-mediated signaling and wax production, was also observed (Li et al., 2021). In response to environmental stress, phospholipase enzymes hydrolyze membrane phospholipids, producing signaling molecules such as phosphatidic acid, diacylglycerol, phosphoinositides, and inositol polyphosphates (Singh et al., 2012), which trigger the synthesis of resistance building biomolecules via downstream pathways.

The fatty acid elongase complex in the endoplasmic reticulum facilitates the elongation of fatty acids into very long-chain fatty acids (VLCFAs) (Wang et al., 2017), which are transformed into cuticular wax and delivered to the cuticle (Xue et al., 2017). The cuticle acts as the outermost hydrophobic layer of aerial organs, protecting plants from abiotic and biotic stresses. In the rice variety Quingliu, resistance against *C. medinalis* and *N. lugens* was associated with increased expression of genes related to lipid signaling. Phospholipase C (*Os02g0588500*), two phospholipase D enzymes (*Os08g0401800, Os02g0120200*), as well as five genes encoding lipid transfer proteins (*Os03g0718800*, *Os12g0114500*, *Os06g0643500*, *Os07g0175600*, *Os10g0505500*) were expressed in Quingliu (Li et al., 2021b).

In sorghum, several resistant 'R' genes and transcription factors associated with EW biosynthesis have been documented in a genome-wide association (GWA) study. This study also found 37 putative genes related to sorghum EW biosynthesis and transport, including those involved in fatty acid synthesis (*3-oxoacyl-[acyl-carrier-protein (ACP)] synthase III*), wax regulation (*ankyrin repeat protein, bHLH-MYC,* and *R2R3-MYB* transcription factors), and wax transport (*ABC transporter, lipid exporter ABCA1, multidrug resistance protein, inositol 1,3,4-trisphosphate 5/6-kinase,* and *CYP*) (Elango et al., 2020). These identified candidate genes could be used as molecular markers in breeding programs to manipulate EW in sorghum.

Cuticular lipids and wax crystal structures on maize leaves influenced host-plant selection behavior and resistance against insects, such as FAW. The density and structure of wax crystals differed between the upper and lower maize leaves, affecting FAW larval movement. Larvae moved farther on the smooth upper leaves than the lower ones with dense wax crystals (Xavier Chiriboga et al., 2021). The *glossy 6* gene in maize is crucial for the intracellular transport of cuticular waxes from their site of biosynthesis to the plant surface. A mutation in the *glossy 6* gene resulted in reduced EW accumulation, increased cuticle permeability, and decreased drought tolerance, indicating that *glossy 6* is important for wax deposition on the leaf surface (Li et al., 2019).

Recent transcriptomic studies have shown that in Arabidopsis, the accumulation of wax and cutin monomers is positively regulated by wounding through the JA signaling pathway. This regulation involved JA-responsive genes (*CYP96A4*) that interacted with *CER1* and *CER2*, the core enzymes in wax biosynthesis, and also modulated *CER3* activity to influence aldehyde synthesis in wax accumulation (Huang et al., 2024).

Generally, the EW and cutin monomers act as physical barriers against various biotic and abiotic factors, preventing excess water loss during drought and insect feeding. In some cases, the chemical composition of these surface waxes directly affects insects and pathogens. Anticipating this trait of cutin monomers, the genes responsible for their synthesis can be directly activated in the plant system, allowing plants to directly resist biotic attacks and achieve combined resistance involving both physical and chemical traits.

Beyond considering the minor variations in foliage color among plant species, the relative differences in the Degree of Linear Polarization (DoLP) are also a more useful plant cue than plant shape, foliage color, or intensity. It was shown that a decreased DoLP, resulting from significant epidermal wax, led to a matte appearance that encouraged pests to lay eggs. Female *P. rapae* laid their eggs on the cabbage and rutabaga form of *B. napus*, which had an EW layer that gave their leaves a matte finish. In order to make plants less susceptible to specific insect herbivores, breeding for the development of plant genotypes with leaves containing higher/reduced wax content is essential, as this can change foliar surface traits and the polarization of their reflections (Blake et al., 2019).

Genes involved in pigmentation and secondary metabolite biosynthesis have been widely associated with insect resistance; however, their effects are frequently reflected through direct and indirect strategies of plant defense. In many cases, changes in pigmentation correlate with altered insect behavior rather than direct toxicity, making causal relationships difficult to establish. Additionally, pigmentation traits are strongly influenced by plant developmental stage and environmental conditions, and their stability across environments remains insufficiently explored. Further studies are required to clarify the consistency and functional relevance of pigmentation-mediated resistance in crops.

6. Epigenetic regulation of defense structures

Epigenetic mechanisms, such as DNA methylation, histone modification, and small RNA–mediated regulation, play an important role in modulating plant biophysical traits associated with insect resistance (Kooke et al., 2015). Such regulations are largely mediated by conserved gene networks that control various defense-related biophysical structures (Alonso et al., 2019), which are discussed in the following sections.

6.1 Trichome development

Epigenetic regulation, particularly miRNA-mediated control of transcription factors, plays a central role in trichome initiation, density, and patterning. In *A. thaliana*, miR319 regulates trichome branching and development by targeting *teosinte branched cycloidea proliferating cell factor 4* (*TCP4*), which positively regulates *glabrous inflorescence stems* (*GIS*), a key activator of trichome formation (Vadde et al., 2018). Similarly, the microRNA156 (miR156)-*squamosa promoter binding protein-like* (*SPL*) module governs trichome distribution during vegetative and reproductive transitions. miR156 suppresses multiple *SPL* genes, particularly SPL9, which directly activates the trichome repressors *trichomeless1* (*TCL1*) and *triptychon (TRY)*, thereby negatively regulating trichome initiation independent of the canonical GL1 pathway (Yu et al., 2010).

Although *A. thaliana* provides the most detailed mechanistic insights into epigenetic control of trichome development, increasing evidence indicates that miRNA-mediated and epigenetic regulation of trichome traits is conserved across crops. In cotton (*Gossypium* spp.), miR828 and miR858 target MYB transcription factors regulating fiber (specialized trichome) initiation and elongation, with additional chromatin-level regulation influencing trichome-associated defensive traits (Huang et al., 2019). In tomato (*S. lycopersicum*), epigenetic mechanisms regulate the expression of the HD-ZIP IV gene *woolly*. This regulation controls downstream TCP transcription factors such as miR319–TCP, thereby determining trichome type and density, which are linked to insect resistance (Schommer et al., 2008; Yang et al., 2011; Xu et al., 2018).

In cucumber (*C. sativus*), expression of trichome regulators *CsGL1*, *CsGL3*, and *CsTTG1* is influenced by epigenetic mechanisms (Chen et al., 2014), while in rice (*Oryza sativa*), miRNA-associated and epigenetic regulation of epidermal cell-fate genes such as *OsGL1* and *WOX* family members control hair-like structures affecting insect feeding behavior (Li et al., 2016). Together, these studies demonstrate that epigenetic and miRNA-mediated regulation of trichomes and trichome-like structures extends beyond model plants. However, functional validation of specific miRNA–gene modules in crops remains limited compared with *Arabidopsis*. Also, direct evidence linking DNA methylation and histone modifications of trichome regulatory genes to insect resistance in crops remains scarce and represents an important area for future research.

6.2 Epicuticular waxes (EWs) and cuticle-based resistance

EWs and cuticular lipids form the first physical interface between plants and insects, which influences insect adhesion, feeding behavior, and host recognition. The biosynthesis and deposition of waxes are controlled by complex gene networks that are increasingly recognized to be epigenetically regulated. Core wax biosynthetic genes such as *CER1*, *CER3*, *KCS*, *FAR*, and *WSD1*, which regulate very-long-chain fatty acid elongation and alkane formation, are under transcriptional and chromatin-level regulation, including histone modifications mediated by *AP2/ERF* transcription factors such as *DEWAX* (Go et al., 2014). However, more research is needed to better understand the regulatory mechanisms underlying EWs and cuticular lipid production and deposition. This will facilitate the design of our approach to selecting breeding and molecular strategies to incorporate the resistant trait into cultivable genotypes successfully.

7. Improvement of biophysical traits in plants through New Breeding Techniques (NBTs) against insect pests

Recent advances in genetic engineering and plant biotechnology have opened new avenues for strengthening HPR against insect pests (Tyagi et al., 2020). Wild relatives of crops harbor significantly greater insect-resistant traits than domesticated varieties, with the different levels of gene pool serving as the richest source of resistance genes/alleles. Conventional backcrossing approaches often faced limitations, yet they contributed to the breeding of insect resistance. More recently, marker-assisted backcrossing (MAB) has facilitated the targeted introgression of desirable resistance genes from wild species into cultivated crops, improving the efficiency and precision of resistance breeding. Genome-based tools now allow the identification of insect-resistant QTLs, while biotechnological approaches, such as genome editing, can directly manipulate genes underlying biophysical traits that influence insect–plant interactions. These methods collectively accelerate the development of insect-resistant cultivars with enhanced durability and specificity.

Biotechnological innovations such as CRISPR–Cas9 offer opportunities to precisely modify resistance-associated loci with minimal off-target effects (Padmavathi and Padmaja, 2022). While genome editing has been extensively used to enhance tolerance to bacterial, viral, and fungal pathogens (Vats et al., 2019), its applications in insect resistance are still emerging. Insects rely on external morphological cues, including leaf color, to recognize and select suitable host plants. Accordingly, changes in plant pigmentation have been shown to influence host preference and feeding behavior (Komal et al., 2023). For example, pigmentation-based resistance has been demonstrated in red-leaf tobacco (*Nicotiana tabacum* Linnaeus), where modification of the anthocyanin pathway led to the accumulation of red leaf color, deterring herbivores such as *H. armigera* and *S. litura* (Malone et al., 2009). In addition, some studies have demonstrated that color pigmentation can be effectively altered using the CRISPR–Cas9 genome editing system. Phytoene dehydrogenase (PDS) genes encode key enzymes in the carotenoid biosynthesis pathway and are essential for leaf pigmentation, photoprotection, and plant responses to both biotic and abiotic stresses. In *Populus tomentosa* Carriere, the application of CRISPR–Cas9 system enabled the successful generation of targeted endogenous mutations by the simultaneous disruption of two PDS genes, *PtoPDS1* and *PtoPDS2* (Fan et al., 2015), which facilitated the enhancement of endogenous defense mechanisms and contributed to improved insect resistance in *Populus*.

In addition to color-related traits, several other host resistance mechanisms have been successfully enhanced through targeted genome editing of key defense-related genes. For example, in the barley cultivar Golden Promise, CRISPR–Cas9-mediated editing of β-1,3-glucanase genes reduced callose degradation in sieve tubes, leading to an increased callose deposition. As a consequence, the growth of aphids *R. padi*, was significantly impaired due to restricted uptake of phloem sap (Moon et al., 2022). Similarly, trichome-based resistance from pigeonpea CWR *C. scarabaeoides* Thouars has been introgressed into cultivated backgrounds, producing lines with high densities of specific trichome types that confer moderate to strong resistance to *H. armigera* (Ngugi-Dawit et al., 2020; Sharma et al., 2022; Volp et al., 2023; Dhanyakumar et al., 2025). Likewise, some barley lines with resistance genes derived from *Hordeum vulgare* ssp. *spontaneum* Thellung, which enhanced aphid resistance (Ahman et al., 2019), and cabbage genotypes with cuticular wax-related genes (e.g., *BoI013612*, *CGL2*) that influence insect oviposition and feeding behavior (Liu et al., 2017a; Huo et al., 2022) were developed. Together, these highlights demonstrate that modifications in biophysical traits such as trichome density, pigmentation, and cuticular wax deposition offer practical avenues for insect pest management.

Beyond these structural traits, cell wall modifications involving secondary cell wall components, such as lignin, which serve as mechanical barriers against herbivory (Liu et al., 2018; Santiago et al., 2013), need to be improved to increase resistance. Interestingly, the tryptamine-to-serotonin pathway contributes to plant resistance by strengthening cell walls and related biophysical traits that deter insect feeding. In rice, CRISPR–Cas9-mediated deletion of the *CYP71A1* gene, which encodes tryptamine 5-hydroxylase, enhanced tryptamine-to-serotonin conversion and conferred increased resistance to striped stem borer *C. suppressalis* and *N. lugens* (Lu et al., 2018). In sweet potato *Ipomoea batatas* (Linnaeus) Lamarck, wound-induced small RNAs (miR828 and sRNA8105) suppressed negative regulators of the phenylpropanoid pathway, resulting in upregulated lignin biosynthesis and enhanced defense against insect damage (Lin et al., 2013). Similarly, in apple, overexpression or silencing of the *MdDEWAX* gene altered cuticular wax accumulation, affecting stress tolerance and potentially influencing pest resistance (Man et al., 2024). These findings emphasize that a deeper understanding of the molecular basis of biophysical traits, coupled with targeted manipulation of candidate genes and QTLs, can guide breeding programs toward the development of insect-resistant cultivars. Thus, an integration of conventional breeding with wild relative introgression and the use of precise genome editing tools provides a powerful framework for exploiting morphological traits in sustainable pest management.

8. Challenges in adopting NBTs in the improvement of biophysical traits in plants against insect pests

Breeding for insect resistance in crops is crucial for sustainable crop production, but it has several challenges. Developing resistant cultivars with enhanced morphological traits is a complex and time-consuming process that requires identifying and introducing effective resistance genes or traits from diverse genetic resources, including CWRs. In this context, the application of NBTs to biophysical trait–mediated insect resistance presents both opportunities and constraints. NBTs such as CRISPR/Cas systems enable precise modification of genes regulating trichomes, wax biosynthesis, pigmentation, and silicon uptake; however, many of these traits are polygenic and quantitatively inherited, limiting the effectiveness of single-gene interventions (Chen et al., 2019; Kumari et al., 2022). One key difficulty is the limited availability of known genes governing those resistant traits and the need to continuously search for new sources of resistance, as pests can evolve to overcome existing resistance. Methodological challenges include target gene selection, unintended pleiotropic effects, and the need for reliable phenotyping under field conditions (Mitchell et al., 2016). Even with advances in genomics and molecular breeding tools, the identification and pyramiding of multiple resistance genes remains challenging, especially in minor crop species, due to limited whole-genome data. Looking ahead, continued exploration of genetic resources, including wild relatives, will be necessary to identify novel resistance genes and traits. Considering pleiotropic effects, such as editing genes associated with biophysical mechanisms of resistance, which may unintentionally affect growth, yield, or other plant functions, leading to trade-offs between defense and productivity. On the other hand, assessing the success of genome-edited biophysical traits requires extensive phenotyping under field conditions, which is time-consuming and labor-intensive.

In addition, ecological considerations such as trait stability across environments and interactions with non-target organisms are of major concern, where genome-edited modification of structural traits such as trichomes, wax layers, or *Si* accumulation may influence multitrophic interactions by altering herbivore behavior as well as the efficiency of natural enemies. Changes in surface traits can affect predator movement, parasitoid host-searching efficiency, and non-target insect interactions, highlighting the need for ecological risk assessment beyond target pest suppression. Also, the expression of many biophysical traits is environmentally sensitive, and edited phenotypes may exhibit variable performance across agroecological zones, seasons, or stress conditions, potentially affecting the durability of resistance.

On the other hand, regulatory frameworks governing genome-edited crops (Kumar et al., 2020) influence the practical deployment of these approaches. India has adopted a case-by-case framework for genome-edited crops (Buchholzer et al., 2023). Since improvements in biophysical traits can be achieved through Site-Directed Nuclease (SDN-1 and SDN-2) genome-editing approaches without the introduction of foreign DNA (Kumar et al., 2020), these modifications are subject to regulatory relaxation. According to guidelines emulated by the Department of Biotechnology, Government of India, New Delhi, SDN-1 and SDN-2 genome-edited plants lacking foreign DNA are exempt from genetically modified organisms (GMO) regulations. However, they require institutional oversight, biosafety assessment, and environmental evaluation prior to confined field trials and release. These regulatory requirements underscore the importance of integrating ecological validation with molecular precision to ensure the safe and responsible deployment of NBT-derived biophysical traits in agriculture. Most importantly, genome-edited crops face public concerns, impacting their acceptance and commercialization, especially in certain countries. Therefore, NBTs should be viewed as complementary tools that integrate molecular insights with ecological validation and conventional breeding, rather than as standalone solutions.

9. Conclusion and future prospects

The deployment of plant biophysical trait-based resistance is essential for improving cultivated crops to meet the growing demand for food production while minimizing yield losses caused by insect pests. Identification of crop and insect-specific biophysical traits, along with their associated candidate genes, provides valuable opportunities to enhance resistance in elite cultivars and supports sustainable pest management strategies. Marker assisted selection (MAS) can facilitate the identification and introgression of such genes into breeding programs. At the same time, the integration of multiomics approaches, including genomics, transcriptomics, proteomics, and metabolomics, will deepen our understanding of plant-insect interactions and enable more targeted interventions.

Recent advances in genome editing technologies, such as CRISPR/Cas9, base editing, and prime editing, further expand the potential to fine-tune biophysical traits associated with insect resistance with high precision and reduced off-target effects. However, the successful application of these approaches requires addressing key challenges, including the polygenic nature of many biophysical traits, potential pleiotropic effects, adaptive responses of insect pests, and regulatory and public acceptance constraints. Emphasis on field level validation, biosafety assessment, and the integration of precision genome editing with advanced breeding strategies and ecological principles will be critical for the development and deployment of durable insect resistant crop varieties, ultimately contributing to global food security and sustainable agricultural systems under changing pest dynamics. Overall, this review integrates current knowledge while recognizing existing limitations, and provides a realistic framework to guide future research and breeding efforts aimed at exploiting biophysical traits for sustainable insect resistance.

Declarations

Ethics approval and consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and material: Not applicable

Competing Interest: The authors declare that they have no competing interests.

Funding: This work did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Acknowledgment

All the authors acknowledge the Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore, and the International Crop Research Institute for Semi-Arid Tropics, Hyderabad, India, for providing necessary support and facilities. The first author acknowledges the Department of Science and Technology, Ministry of Science and Technology, Government of India, New Delhi, India, for DST INSPIRE FELLOWSHIP/2023/IF230020.

Authorship contribution statement

Sangeetha Srinivasan Vadivel Murugan: Writing – original draft, Visualization, Software, Formal analysis, Conceptualization. **Marimuthu Murugan:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Jagdish Jaba:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Kalenahalli Yogendra:** Writing – review & editing, Formal analysis, Conceptualization. **Trevor M. Volp:** Writing – review & editing**.** **Balasubramani Venkatasamy:** Writing – review & editing. **Srinivasan Thulasy**: Writing – review & editing. **Kumar K. Krish**: Writing – review & editing.

References

Acevedo, F.E., Peiffer, M., Ray, S., Tan, C.W., Felton, G.W. 2021. Silicon-mediated enhancement of herbivore resistance in agricultural crops. Front. Plant Sci 12:631824 http://dx.doi.org/10.3389/fpls.2021.631824.

Agrawal, A.A., & Fishbein, M. 2006. Plant defense syndromes. Ecology 87(sp7), S132–S149. https://doi.org/10.1890/0012-9658(2006)87[132:pds]2.0.co;.

Agrawal, A. A., Fishbein, M., Jetter, R., Salminen, J. P., Goldstein, J. B., Freitag, A. E., & Sparks, J. P. 2009. Phylogenetic ecology of leaf surface traits in the milkweeds (*Asclepias* spp.): Chemistry, ecophysiology, and insect behavior. New Phytol 183(3), 848–867. https://doi.org/10.1111/j.1469-8137.2009.02897.

Aherkar, S. S., Deshmukh, S. B., Konde, N. M., Paslawar, A. N., Joshi, T., Messmer, M. M., & Riar, A. 2023. Studies on morphophysiological and biochemical parameters for sucking pest tolerance in organic cotton. Agriculture 13(7), 1402. https://doi.org/10.3390/agriculture13071402.

Ahman, I., & Bengtsson, T. 2019. Introgression of resistance to *Rhopalosiphum padi* L. from wild barley into cultivated barley facilitated by doubled haploid and molecular marker techniques. Theor. Appl. Genet. 132(5), 1397–1408. https://doi.org/10.1007/s00122-019-03287-3.

Agrawal, A.A., & Fishbein, M. 2006. Plant defense syndromes. Ecology 87(sp7), S132–S149. https://doi.org/10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2.

Alahakoon, U. I., Taheri, A., Nayidu, N. K., Epp, D., Yu, M., Parkin, I., Hegedus, D., Bonham-Smith, P., & Gruber, M. Y. 2016. Hairy canola (*Brassica napus*) re-visited: Down-regulating TTG1 in an AtGL3-enhanced hairy leaf background improves growth, leaf trichome coverage, and metabolite gene expression diversity. BMC Plant Biol 16, 1–25. https://doi.org/10.1186/s12870-015-0680-5.

Alhousari, F., & Greger, M. 2018. Silicon and mechanisms of plant resistance to insect pests. Plants 7(2), 33. https://doi.org/10.3390/plants7020033.

Alonso, C., Ramos-Cruz, D. and Becker, C., 2019. The role of plant epigenetics in biotic interactions. New Phytol 221(2), pp.731-737. https://doi.org/10.1111/nph.15408.

Ambidi, V., Bantewad, S., Prasad Mishra, S., Hingane, A., & Jaba, J. 2021. Morpho-biochemical parameters associated with resistance to pod borer complex of pigeonpea. Pak. J. Zool 1–7. https://doi.org/10.17582/journal.pjz/20200703050747.

Andama, J. B., Mujiono, K., Hojo, Y., Shinya, T., & Galis, I. 2020. Nonglandular silicified trichomes are essential for rice defense against chewing herbivores. Plant Cell Environ 43(9), 2019–2032. https://doi.org/10.1111/pce.13775.

Armstrong, J. S., Coleman, R. J., & Sétamou, M. 2009. Oviposition patterns of *Creontiades signatus* (Hemiptera: Miridae) on okra-leaf and normal-leaf cotton. Ann. Entomol. Soc. Am 102(2), 196–200. https://doi.org/10.1603/008.102.0202.

Arora, N., Mishra, S. P., Nitnavare, R. B., Jaba, J., Kumar, A. A., Bhattacharya, J., Sohu, R. S., & Sharma, H. C. 2021. Morpho-physiological traits and leaf surface chemicals as markers conferring resistance to sorghum shoot fly (*Atherigona soccata* Rondani). Field Crops Res 261, 108029. https://doi.org/10.1016/j.fcr.2020.108029.

Arora, N., Bhattacharya, J., Shankhapal, A. R., Mishra, S. P., Desale, A., & Jaba, J. 2025. Shoot fly resistance in sorghum: An overview. J. Appl. Entomol 1–15. https://doi.org/10.1111/jen.1340.

Arora, N., Mishra, S. P., Nitnavare, R. B., Jaba, J., Kumar, A. A., Bhattacharya, J., Sohu, R. S., & Sharma, H. C. 2021. Morpho-physiological traits and leaf surface chemicals as markers conferring resistance to sorghum shoot fly (*Atherigona soccata* Rondani). Field Crops Research 261, 108029. https://doi.org/10.1016/j.fcr.2020.108029.

Arshad, M., Ghafoor, A., & Qureshi, A. S. 2005. Inheritance of qualitative traits and their linkage in blackgram [*Vigna mungo* (L.) Hepper]. Pak. J. Bot 37(1), 41–46. https://api.core.ac.uk/oai/oai:CiteSeerX.psu:10.1.1.533.7836.

Aruna, C., Bhagwat, V., Madhusudhana, R., Sharma, V., Hussain, T., Ghorade, R., Khandalkar, H., Audilakshmi, S., & Seetharama, N. 2011. Identification and validation of genomic regions that affect shoot fly resistance in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet 122, 1617–1630. https://doi.org/10.1007/s00122-011-1559-y.

Balakrishnan, D., Bateman, N., & Kariyat, R. R. 2024. Rice physical defenses and their role against insect herbivores. Planta 259(5), 110. https://doi.org/10.1007/s00425-024-04381-7.

Beale, M. H., Birkett, M. A., Bruce, T. J., Chamberlain, K., Field, L. M., Huttly, A. K., Martin, J. L., Parker, R., Phillips, A. L., & Pickett, J. A. 2006. Aphid alarm pheromone produced by transgenic plants affects aphid and parasitoid behavior. Proc. Natl. Acad. Sci. U.S.A 103(27), 10509–10513. https://doi.org/10.1073/pnas.0603998103.

Bergvinson, D., & García-Lara, S. 2006. Consensus mapping for field and storage pest resistance in tropical maize. In S. Higman (Ed.), International Plant Breeding Symposium. CIMMYT.

Bernaola, L., Butterfield, T. S., Tai, T. H., & Stout, M. J. 2021. Epicuticular wax rice mutants show reduced resistance to rice water weevil (Coleoptera: Curculionidae) and fall armyworm (Lepidoptera: Noctuidae). Environ. Entomol 50(4), 948–957. https://doi.org/10.1093/ee/nvab038.

Bird, D., Beisson, F., Brigham, A., Shin, J., Greer, S., Jetter, R., Kunst, L., Wu, X., Yephremov, A., & Samuels, L. 2007. Characterization of *Arabidopsis* ABCG11/WBC11, an ATP binding cassette (ABC) transporter that is required for cuticular lipid secretion. Plant J 52(3), 485–498. https://doi.org/10.1111/j.1365-313X.2007.03252.x.

Blake, A. J., Go, M. C., Hahn, G. S., Grey, H., Couture, S., & Gries, G. 2019. Polarization of foliar reflectance: Novel host plant cue for insect herbivores. Proceedings of the Royal Society B: Biological Sciences 286(1915), 20192198. https://doi.org/10.1098/rspb.2019.2198.

Blanco-Sánchez, L., Planelló, R., Llorente, L., Díaz-Pendón, J. A., Ferrero, V., Fernández-Muñoz, R., Herrero, Ó., & de la Peña, E. 2021. Characterization of the detrimental effects of type IV glandular trichomes on the aphid *Macrosiphum euphorbiae* in tomato. Pest Manag. Sci 77(9), 4117–4127. https://doi.org/10.1002/ps.6437.

Blenn, B., Bandoly, M., Küffner, A., Otte, T., Geiselhardt, S., Fatouros, N. E., & Hilker, M. 2012. Insect egg deposition induces indirect defense and epicuticular wax changes in *Arabidopsis thaliana*. J. Chem. Ecol 38, 882–892. https://doi.org/10.1007/s10886-012-0132-8.

Bohra, A., Kilian, B., Sivasankar, S., Caccamo, M., Mba, C., McCouch, S. R., & Varshney, R. K. 2022. Reap the crop wild relatives for breeding future crops. Trends Biotechnol 40(4), 412–431. https://doi.org/10.1016/j.tibtech.2021.08.009.

Bonaventure, G., Salas, J. J., Pollard, M. R., & Ohlrogge, J. B. 2003. Disruption of the FATB gene in *Arabidopsis* demonstrates an essential role of saturated fatty acids in plant growth. Plant Cell 15(4), 1020–1033. https://doi.org/10.1105/tpc.008946.

Borodich, F. M., Gao, Z., Gorb, E. V., Gorb, S. N., & Jin, X. 2024. Wax protrusions on anti-adhesive plant surfaces and their interactions with insect adhesive pads: A mechanical interpretation. Biomimetics 9(7), 442. https://doi.org/10.3390/biomimetics9070442.

Boughton, A. J., Hoover, K., & Felton, G. W. 2005. Methyl jasmonate application induces increased densities of glandular trichomes on tomato, *Lycopersicon esculentum*. J. Chem. Ecol 31, 2211–2216. https://doi.org/10.1007/s10886-005-6228-7.

Broun, P., Poindexter, P., Osborne, E., Jiang, C.-Z., & Riechmann, J. L. 2004. WIN1, a transcriptional activator of epidermal wax accumulation in *Arabidopsis*. Proceedings of the National Academy of Sciences 101(13), 4706–4711. https://doi.org/10.1073/pnas.0305574101.

Buchholzer, M. and Frommer, W.B., 2023. An increasing number of countries regulate genome editing in crops. New Phytol 237(1). https://doi.org/10.1111/nph.18333.

Caldwell, E., Read, J., & Sanson, G. D. 2016. Which leaf mechanical traits correlate with insect herbivory among feeding guilds? Ann. Bot 117(2), 349–361. https://doi.org/10.1093/aob/mcv178.

Canassa, V. F., Baldin, E. L. L., Sacilotto, M. G., Lourenção, A. L., & Fanela, T. L. M. 2021. Assessing the resistance of collard greens genotypes to the cabbage aphid (*Brevicoryne brassicae*) (Hemiptera: Aphididae). Phytoparasitica 49, 633–644. https://doi.org/10.1007/s12600-021-00882-3.

Cardona, J. B., Grover, S., Bowman, M. J., Busta, L., Kundu, P., Koch, K. G., Sarath, G., Sattler, S. E., & Louis, J. 2023. Sugars and cuticular waxes impact sugarcane aphid (*Melanaphis sacchari*) colonization on different developmental stages of sorghum. Plant Sci 330, 111646. https://doi.org/10.1016/j.plantsci.2023.111646.

Chalwe, A. 2012. Manipulating morphological traits of cassava to enhance host plant resistance and biological control of cassava green mite in Zambia (Master's thesis). University of KwaZulu-Natal, Pietermaritzburg. http://hdl.handle.net/10413/10056.

Chen, K., Wang, Y., Zhang, R., Zhang, H. and Gao, C., 2019. CRISPR/Cas genome editing and precision plant breeding in agriculture. Annu. Rev. Plant Biol 70(1), pp.667-697. https://doi.org/10.1146/annurev-arplant-050718-100049.

Chen, S.-P., Kuo, Y.-W., & Lin, J.-S. 2023. Defense responses in sweet potato (*Ipomoea batatas* L.) against biotic stress. Plant Sci 337, 111893. https://doi.org/10.1016/j.plantsci.2023.111893.

Chiba, Y., Mitani, N., Yamaji, N., & Ma, J. F. 2009. *HvLsi1* is a silicon influx transporter in barley. Plant J 57(5), 810–818. https://doi.org/10.1111/j.1365-313X.2008.03728.x.

Chu, C. C., Natwick, E. T., & Henneberry, T. J. 2002. *Bemisia tabaci* (Homoptera: Aleyrodidae) biotype B colonization on okra- and normal-leaf upland cotton strains and cultivars. J. Econ. Entomol 95(4), 733–738. https://doi.org/10.1603/0022-0493-95.4.733.

Chu, C. C., Natwick, E. T., Chen, T. Y., & Henneberry, T. J. 2003. Analyses of cotton leaf characteristics effect on *Bemisia tabaci* (Homoptera: Aleyrodidae) biotype B colonization on cotton in Arizona and California. Southwest. Entomol 28(4), 235–240.

Cook, J., Wichman, D., Martin, J., Bruckner, P., & Talbert, L. 2004. Identification of microsatellite markers associated with a stem solidness locus in wheat. Crop Sci 44(4), 1397–1402. https://doi.org/10.2135/cropsci2004.1397.

Cooke, J., DeGabriel, J.L. and Hartley, S.E., 2016. The functional ecology of plant silicon. Funct. Ecol 30(8), 1270-1276. https://www.jstor.org/stable/48582223.

Cui, J.Y., Miao, H., Ding, L.-H., Wehner, T. C., Liu, P.-N., Wang, Y., Zhang, S.-P., & Gu, X.-F. 2016. A new glabrous gene (*csgl3*) identified in trichome development in cucumber (*Cucumis sativus* L.). PLoS One 11(2), e0148422. https://doi.org/10.1371/journal.pone.0148422.

defenseDabravolski, S. A., & Isayenkov, S. V. 2024. The physiological and molecular mechanisms of silicon action in salt stress amelioration. Plants 13(4), 525. https://doi.org/10.3390/plants13040525.

Dalin, P., & Björkman, C. 2003. Adult beetle grazing induces willow trichome defense against subsequent larval feeding. Oecologia 134, 112–118. https://doi.org/10.1007/s00442-002-1093-3.

Dethier, V. G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8(1), 33–54. https://doi.org/10.2307/2405664.

Devine, G. J., & Furlong, M. J. 2007. Insecticide use: Contexts and ecological consequences. Agric. Hum. Values 24, 281–306. https://doi.org/10.1007/s10460-007-9067-z.

Dhamayanthi, K. P., Rameash, K., Manivannan, A., Sheeba, A., & Abirami, S. 2020. Studies on leaf hairiness and sucking pest resistance in Egyptian cotton (*Gossypium barbadense* L.). J. Entomol. Zool. Stud 8(1), 591–594. https://cicr.org.in/wp-content/uploads/SC-FA-AMani05.pdf.

Dhanyakumar, O., Ranjitha, M., Yogendra, K., Revanayya, G., Sharma, H.C., Taggar, G.K., Murugan, M. and Jaba, J., 2025. Decoding plant resistance mechanism in pigeonpea (*Cajanus cajan*) against major insect pests: Decade of efforts and emerging directions. Plant Stress, p.101089. https://doi.org/10.1016/j.stress.2025.101089.

Dhanyalakshmi, K. H., Soolanayakanahally, R. Y., Rahman, T., Tanino, K. K., & Nataraja, K. N. 2019. Leaf cuticular wax, a trait for multiple stress resistance in crop plants. In Abiotic and Biotic Stress in Plants. Intech Open. https://doi.org/10.5772/intechopen.84565.

Dietrich, C. R., Perera, M. A. D., Yandeau-Nelson, M. D., Meeley, R. B., Nikolau, B. J., & Schnable, P. S. 2005. Characterization of two GL8 paralogs reveals that the 3-ketoacyl reductase component of fatty acid elongase is essential for maize (*Zea mays* L.) development. Plant J 42(6), 844–861. https://doi.org/10.1111/j.1365-313X.2005.02418.x.

Din, Z., Malik, T., Azhar, F., & Ashraf, M. 2016. Natural resistance against insect pests in cotton. J. Anim. Plant Sci 26(5), 1346–1353.

Egan, L. M., & Stiller, W. N. 2022. The past, present, and future of host plant resistance in cotton: An Australian perspective. Front. Plant Sci 13, 895877. https://doi.org/10.3389/fpls.2022.895877.

Eigenbrode, S. 2004. The effects of plant epicuticular waxy blooms on attachment and effectiveness of predatory insects. Arthropod Struct. Dev 33(1), 91–102. https://doi.org/10.1016/j.asd.2003.11.004.

Eigenbrode, S., Kabalo, N., & Rutledge, C. 2020. Potential of reduced-wax bloom oilseed *Brassica* for insect pest resistance. J. Agric. Urban Entomol 17(2), 53–63. https://www.cabidigitallibrary.org/doi/full/10.5555/20003018550.

Eigenbrode, S. D., Trumble, J. T., Millar, J. G., & White, K. K. 1994. Topical toxicity of tomato sesquiterpenes to the beet armyworm and the role of these compounds in resistance derived from an accession of *Lycopersicon hirsutum* f. *typicum*. J. Agric. Food Chem 42(3), 807–810. https://doi.org/10.1021/jf00039a042.

Elango, D., Xue, W., & Chopra, S. 2020. Genome wide association mapping of epi-cuticular wax genes in *Sorghum bicolor*. Physiol. Mol. Biol. Plants 26(8), 1727–1737. https://doi.org/10.1007/s12298-020-00848-5.

Esch, J. J., Chen, M., Sanders, M., Hillestad, M., Ndkium, S., Idelkope, B., Neizer, J., & Marks, M. D. 2003. A contradictory *GLABRA3* allele helps define gene interactions controlling trichome development in *Arabidopsis*. Development 130(24), 5885–5894. https://doi.org/10.1242/dev.00812.

Ezenwaka, L., Del Carpio, D. P., Jannink, J.-L., Rabbi, I., Danquah, E., Asante, I., Danquah, A., Blay, E., & Egesi, C. 2018. Genome-wide association study of resistance to cassava green mite pest and related traits in cassava. Crop Sci 58(5), 1907–1918. https://doi.org/10.2135/cropsci2018.01.0024.

Faiz, M. F., Hidayat, P., Winasa, I. W., & Guntoro, D. 2021. Effect of soybean leaf trichomes on the preference of various soybean pests on field. IOP Conf. Ser.: Earth Environ. Sci 694(1), 012046. https://doi.org/10.1088/1755-1315/694/1/012046.

Fan, D., Liu, T., Li, C., Jiao, B., Li, S., Hou, Y. and Luo, K., 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in *Populus* in the first generation. Sci. Rep 5(1), p.12217. https://doi.org/10.1038/srep12217.

Fan, H., Xu, J., Ao, D., Jia, T., Shi, Y., Li, N., Jing, R., & Sun, D. 2023. QTL mapping of trichome traits and analysis of candidate genes in leaves of wheat (*Triticum aestivum* L.). Genes 15(1), 42. https://doi.org/10.3390/genes15010042.

Feng, Z., Bartholomew, E. S., Liu, Z., Cui, Y., Dong, Y., Li, S., Wu, H., Ren, H., & Liu, X. 2021. Glandular trichomes: New focus on horticultural crops. Hortic. Res 8(1), 158. https://doi.org/10.1038/s41438-021-00592-1.

Franceschi, V. R., Krokene, P., Christiansen, E., & Krekling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytol 167(2), 353–376. https://doi.org/10.1111/j.1469-8137.2005.01436.x.

Frew, A., Powell, J. R., Sallam, N., Allsopp, P. G., & Johnson, S. N. 2016. Trade-offs between silicon and phenolic defenses may explain enhanced performance of root herbivores on phenolic-rich plants. J. Chem. Ecol 42, 768–771. https://doi.org/10.1007/s10886-016-0734-7.

Gandikota, M., De Kochko, A., Chen, L., Ithal, N., Fauquet, C., & Reddy, A. R. 2001. Development of transgenic rice plants expressing maize anthocyanin genes and increased blast resistance. Mol. Breed 7, 73–83. https://doi.org/10.1023/A:1009657923408.

Gasparini, K., Gasparini, J., Therezan, R., Vicente, M. H., Sakamoto, T., Figueira, A., Zsögön, A., & Peres, L. E. 2023. Natural genetic variation in the *HAIRS ABSENT* (H) gene increases type-VI glandular trichomes in both wild and domesticated tomatoes. J. Plant Physiol 280, 153859. https://doi.org/10.1016/j.jplph.2022.153859.

Gaucher, M., Juillard, A., Nguyen, B.-H., Viller, N., Ernenwein, C., Marion, D., Brisset, M.-N., & Bakan, B. 2024. Formulated hydroxy fatty acids from fruit pomaces reduce apple scab development caused by *Venturia inaequalis* through a dual mode of action. Front. Plant Sci 14, 1322638. https://doi.org/10.3389/fpls.2023.1322638.

Ghosh, P., Jagadish, K. S., Purushothama, M. G., Hanson, P., Rakha, M., Sotelo-Cardona, P., Vaddi, S., & Srinivasan, R. 2023. Performance of wild tomato accessions and elucidation of resistance against invasive pest *Phthorimaea absoluta* damage under tropical conditions. Horticulturae 9(2), 143. https://doi.org/10.3390/horticulturae9020143.

Gibson, R., & Pickett, J. 1983. Wild potato repels aphids by release of aphid alarm pheromone. Nature 302(5909), 608–609. https://doi.org/10.1038/302608a0.

Glas, J. J., Schimmel, B. C., Alba, J. M., Escobar-Bravo, R., Schuurink, R. C., & Kant, M. R. 2012. Plant glandular trichomes as targets for breeding or engineering of resistance to herbivores. Int. J. Mol. Sci 13(12), 17077–17103. https://doi.org/10.3390/ijms131217077.

Go, Y.S., Kim, H., Kim, H.J. and Suh, M.C., 2014. *Arabidopsis* cuticular wax biosynthesis is negatively regulated by the *DEWAX* gene encoding an AP2/ERF-type transcription factor. Plant Cell 26(4), 1666-1680. https://doi.org/10.1105/tpc.114.123307.

Gobbi, P. C., Fagundes, J. P. R., Silva, L. R., Motta, F. B., Cunha, U. S., Duarte, A. F., Oliveira, A. C., & Rosa, A. P. 2023. Oviposition behavior and foliar consumption of *Chrysodeixis includens* (Lepidoptera: Noctuidae) in soybean genotypes. Cienc. Rural 54, e20220474. https://doi.org/10.1590/0103-8478cr20220474.

Golla, S. K., Rajasekhar, P., Sharma, S. P., Hari Prasad, K. V., & Sharma, H. C. 2018. Antixenosis and antibiosis mechanisms of resistance to pod borer, *Helicoverpa armigera* in wild relatives of chickpea (*Cicer arietinum*). Euphytica 214(1), 6. https://doi.org/10.1007/s10681-018-2168-5.

Gols, R., Bukovinszky, T., van Dam, N. M., Dicke, M., Bullock, J. M., & Harvey, J. A. 2008. Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild *Brassica* populations. J. Chem. Ecol 34, 132–143. https://doi.org/10.1007/s10886-008-9429-z.

Gong, Z., Luo, Y., Zhang, W., Jian, W., Zhang, L., Gao, X., Hu, X., Yuan, Y., Wu, M., & Xu, X. 2021. A *SlMYB75*-centred transcriptional cascade regulates trichome formation and sesquiterpene accumulation in tomato. J. Exp. Bot 72(10), 3806–3820. https://doi.org/10.1093/jxb/erab086.

Griese, E., Pineda, A., Pashalidou, F. G., Iradi, E. P., Hilker, M., Dicke, M., & Fatouros, N. E. 2020. Plant responses to butterfly oviposition partly explain preference–performance relationships on different brassicaceous species. Oecologia 192(3), 463–475. https://doi.org/10.1007/s00442-019-04590-y.

Grover, S., Shinde, S., Puri, H., Palmer, N., Sarath, G., Sattler, S. E., & Louis, J. 2022. Dynamic regulation of phenylpropanoid pathway metabolites in modulating sorghum defense against fall armyworm. Front. Plant Sci 13, 1019266. https://doi.org/10.3389/fpls.2022.1019266.

Guo, T.-W., Liao, C.-T., & Chuang, W.-P. 2019. Defensive responses of rice cultivars resistant to *Cnaphalocrocis medinalis* (Lepidoptera: Crambidae). Arthropod-Plant Interact 13(4), 611–620. https://doi.org/10.1007/s11829-019-09673-4.

Hamilton, W. D., & Brown, S. 2001. Autumn tree colours as a handicap signal. Proc. R. Soc. Lond. B Biol. Sci 268(1475), 1489–1493. https://doi.org/10.1098/rspb.2001.1672.

Han, G., Li, Y., Yang, Z., Wang, C., Zhang, Y., & Wang, B. 2022. Molecular mechanisms of plant trichome development. Front. Plant Sci 13, 910228. https://doi.org/10.3389/fpls.2022.910228.

Hanley, M. E., Lamont, B. B., Fairbanks, M. M., & Rafferty, C. M. 2007. Plant structural traits and their role in anti-herbivore defense. Perspect. Plant Ecol. Evol. Syst 8(4), 157–178. https://doi.org/10.1016/j.ppees.2007.01.001.

Hansson, M., Youssef, H. M., Zakhrabekova, S., Stuart, D., Svensson, J. T., Dockter, C., Stein, N., Waugh, R., Lundqvist, U., & Franckowiak, J. 2024. A guide to barley mutants. Hereditas 161(1), 11. https://doi.org/10.1186/s41065-023-00304-w.

Hao, P., Liu, C., Wang, Y., Chen, R., Tang, M., Du, B., Zhu, L., & He, G. 2008. Herbivore-induced callose deposition on the sieve plates of rice: An important mechanism for host resistance. Plant Physiol 146(4), 1810–1820. https://doi.org/10.1104/pp.107.111484.

Hasanuzzaman, A. T. M., Islam, M. N., Zhang, Y., Zhang, C.-Y., & Liu, T.-X. 2016. Leaf morphological characters can be a factor for intra-varietal preference of whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) among eggplant varieties. PLOS One 11(4), e0153880. https://doi.org/10.1371/journal.pone.0153880.

He, Q., Lu, Q., He, Y., Wang, Y., Zhang, N., Zhao, W., & Zhang, L. 2020a. Dynamic changes of the anthocyanin biosynthesis mechanism during the development of heading Chinese cabbage (*Brassica rapa* L.) and *Arabidopsis* under the control of *BrMYB2*. Front. Plant Sci 11, 593766. https://doi.org/10.3389/fpls.2020.593766.

He, Q., Wu, J., Xue, Y., Zhao, W., Li, R., & Zhang, L. 2020b. The novel gene *BrMYB2*, located on chromosome A07, with a short intron 1 controls the purple-head trait of Chinese cabbage (*Brassica rapa* L.). Hortic. Res 7, 97. https://doi.org/10.1038/s41438-020-0319-z.

Huang, G., Huang, J.Q., Chen, X.Y. and Zhu, Y.X., 2021. Recent advances and future perspectives in cotton research. Annu. Rev. Plant Biol 72(1), 437-462. https://doi.org/10.1146/annurev-arplant-080720-113241

Huang, B., Wu, W., & Hong, Z. 2021. Genetic loci underlying awn morphology in barley. Genes 12(10), 1613. https://doi.org/10.3390/genes12101613.

Huang, H., Wang, Y., Yang, P., Zhao, H., Jenks, M. A., Lü, S., & Yang, X. 2024. The *Arabidopsis* cytochrome P450 enzyme CYP96A4 is involved in the wound-induced biosynthesis of cuticular wax and cutin monomers. Plant J 118(5), 1619–1634. https://doi.org/10.1111/tpj.16701.

Humphries, J. A., Walker, A. R., Timmis, J. N., & Orford, S. J. 2005. Two WD-repeat genes from cotton are functional homologues of the *Arabidopsis thaliana TRANSPARENT TESTA GLABRA1* (TTG1) gene. Plant Mol. Biol 57(1), 67–81. https://doi.org/10.1007/s11103-004-6768-1.

Huo, Z., Xu, Y., Yuan, S., Chang, J., Li, S., Wang, J., Zhao, H., Xu, R., & Zhong, F. 2022. The AP2 transcription factor *BrSHINE3* regulates wax accumulation in non-heading Chinese cabbage. Int. J. Mol. Sci 23(21), 13454. https://doi.org/10.3390/ijms232113454.

Jaba, J., Devrani, A., Agnihotri, M., & Chakravarty, S. 2017. Screening of chickpea cultivars against pod borer *Helicoverpa armigera* (Hübner) under unprotected conditions. J. Exp. Zool 20(2), 835–843. http://oar.icrisat.org/id/eprint/10333.

Jaba, J., Bhandi, S., Deshmukh, S., Pallipparambil, G. R., Mishra, S. P., & Arora, N. 2021. Identification, evaluation and utilization of resistance to insect pests in grain legumes: Advancement and restrictions. In Genetic enhancement in major food legumes: Advances in major food legumes 197–230. Springer. https://doi.org/10.1007/978-3-030-64500-7_7.

Jena, M., Rath, P. C., Mukherjee, A. K., Raghu, S., Guru, P. P., Basana, G. G., & Prasanthi, G. 2018. Exploring new sources of resistance for insect pests and diseases of rice. In Rice Research for Enhancing Productivity, Profitability and Climate Resilience (p. 542).

Johnson, S. N., Rowe, R. C., & Hall, C. R. 2020. Silicon is an inducible and effective herbivore defense against *Helicoverpa punctigera* (Lepidoptera: Noctuidae) in soybean. Bull. Entomol. Res 110(3), 417–422. https://doi.org/10.1017/S0007485319000798.

Junaid, M. D., & Gokce, A. F. 2024. Global agricultural losses and their causes. Bull. Biol. Allied Sci. Res 9(1), 66. https://doi.org/10.54112/bbasr.v2024i1.66.

Kang, J.-H., Campos, M. L., Zemelis-Durfee, S., Al-Haddad, J. M., Jones, A. D., Telewski, F. W., Brandizzi, F., & Howe, G. A. 2016. Molecular cloning of the tomato *Hairless* gene implicates actin dynamics in trichome-mediated defense and mechanical properties of stem tissue. J. Exp. Bot 67(18), 5313–5324. https://doi.org/10.1093/jxb/erw292.

Kariyat, R. R., Smith, J. D., Stephenson, A. G., De Moraes, C. M., & Mescher, M. C. 2017. Non-glandular trichomes of *Solanum carolinense* deter feeding by *Manduca sexta* caterpillars and cause damage to the gut peritrophic matrix. Proc. R. Soc. B Biol. Sci 284(1849), 20162323. https://doi.org/10.1098/rspb.2016.2323.

Kennedy, G. G. 2003. Tomato, pests, parasitoids, and predators: Tritrophic interactions involving the genus *Lycopersicon*. Annu. Rev. Entomol 48(1), 51–72. https://doi.org/10.1146/annurev.ento.48.091801.112733.

Komal, J., Desai, H.R., Samal, I., Mastinu, A., Patel, R.D., Kumar, P.D., Majhi, P.K., Mahanta, D.K. and Bhoi, T.K., 2023. Unveiling the genetic symphony: Harnessing CRISPR-Cas genome editing for effective insect pest management. Plants 12(23), p.3961. https://doi.org/10.3390/plants12233961.

Kooke, R., Johannes, F., Wardenaar, R., Becker, F., Etcheverry, M., Colot, V., Vreugdenhil, D. and Keurentjes, J.J., 2015. Epigenetic basis of morphological variation and phenotypic plasticity in *Arabidopsis thaliana*. Plant Cell 27(2), 337-348. https://doi.org/10.1105/tpc.114.133025.

Korndörfer, A. P., Grisoto, E., & Vendramim, J. D. 2011. Induction of insect plant resistance to the spittlebug *Mahanarva fimbriolata* Stål (Hemiptera: Cercopidae) in sugarcane by silicon application. Neotrop. Entomol 40, 387–392. https://doi.org/10.1590/S1519-566X2011000300013.

Kortbeek, R. W., Galland, M. D., Muras, A., van der Kloet, F. M., André, B., Heilijgers, M., van Hijum, S. A., Haring, M. A., Schuurink, R. C., & Bleeker, P. M. 2021. Natural variation in wild tomato trichomes: Selecting metabolites that contribute to insect resistance using a random forest approach. BMC Plant Biol 21, 70. https://doi.org/10.1186/s12870-021-03070-x.

Kuai, J., Sun, Y., Guo, C., Zhao, L., Zuo, Q., Wu, J., & Zhou, G. 2017. Root-applied silicon in the early bud stage increases the rapeseed yield and optimizes the mechanical harvesting characteristics. Field Crops Res 200, 88–97. https://doi.org/10.1016/j.fcr.2016.10.007.

Kumar, S., Adiram-Filiba, N., Blum, S., Sanchez-Lopez, J. A., Tzfadia, O., Omid, A., Volpin, H., Heifetz, Y., Goobes, G., & Elbaum, R. 2020. Siliplant1 protein precipitates silica in sorghum silica cells. J. Exp. Bot 71(21), 6830–6843. https://doi.org/10.1093/jxb/eraa258.

Kumar, A., Kumar, R., Singh, N. and Mansoori, A., 2020. Regulatory framework and policy decisions for genome-edited crops. In CRISPR/Cas Genome Editing: Strategies and Potential For Crop Improvement (193-201). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-42022-2_9.

Kumari, P., Jasrotia, P., Kumar, D., Kashyap, P. L., Kumar, S., Mishra, C. N., Kumar, S., & Singh, G. P. 2022. Biotechnological approaches for host plant resistance to insect pests. Front. Genet 13, 914029. https://doi.org/10.3389/fgene.2022.914029.

Kvedaras, O.L., Byrne, M.J., Coombes, N.E. and Keeping, M.G., 2009. Influence of plant silicon and sugarcane cultivar on mandibular wear in the stalk borer *Eldana saccharina*. Agric. For. Entomol 11(3), 301-306. https://doi.org/10.1111/j.1461-9563.2009.00430.x

Kvedaras, O. L., An, M., Choi, Y., & Gurr, G. 2010. Silicon enhances natural enemy attraction and biological control through induced plant defenses. Bull. Entomol. Res 100(3), 367–371. https://doi.org/10.1017/S0007485309990265.

Lacape, J.-M., & Nguyen, T.-B. 2005. Mapping quantitative trait loci associated with leaf and stem pubescence in cotton. J. Hered 96(4), 441–444. https://doi.org/10.1093/jhered/esi052.

Lanning, S., Fox, P., Elser, J., Martin, J., Blake, N., & Talbert, L. 2006. Microsatellite markers associated with a secondary stem solidness locus in wheat. Crop Sci 46(4), 1701–1703. https://doi.org/10.2135/cropsci2005.10-0379.

Larkin, J. C., Oppenheimer, D. G., Lloyd, A. M., Paparozzi, E. T., & Marks, M. D. 1994. Roles of the *GLABROUS1* and *TRANSPARENT TESTA GLABRA* genes in *Arabidopsis* trichome development. Plant Cell 6(8), 1065–1076. https://doi.org/10.1105/tpc.6.8.1065.

Lavanya, C., Vishnuvardhan Reddy, A., Dutta, B., & Bandopadhyay, R. 2018. Classical genetics, cytogenetics, and traditional breeding in castor bean. In The Castor Bean Genome (33–65). Springer. https://doi.org/10.1007/978-3-319-97280-0_3.

Lee, J. A. 1985. Revision of the genetics of the hairiness-smoothness system of *Gossypium*. J. Hered 76(2), 123–126. https://doi.org/10.1093/oxfordjournals.jhered.a110036.

Lee, S.B., Kaittanis, C., Jansen, R. K., Hostetler, J. B., Tallon, L. J., Town, C. D., & Daniell, H. 2006. The complete chloroplast genome sequence of *Gossypium hirsutum*: Organization and phylogenetic relationships to other angiosperms. BMC Genomics 7, 61. https://doi.org/10.1186/1471-2164-7-61.

Leroy, N., De Tombeur, F., Walgraffe, Y., Cornélis, J.-T., & Verheggen, F. J. 2019. Silicon and plant natural defenses against insect pests: Impact on plant volatile organic compounds and cascade effects on multitrophic interactions. Plants 8(11), 444. https://doi.org/10.3390/plants8110444.

Lewandowska, M., Keyl, A., & Feussner, I. 2020. Wax biosynthesis in response to danger: Its regulation upon abiotic and biotic stress. New Phytol 227(3), 698–713. https://doi.org/10.1111/nph.16571.

Liu, Y., Zhan, Z., Ren, L., Ze, S., Yu, L., Jiang, Q., Luo, Y., 2021. Hyperspectral evidence of early-stage pine shoot beetle attack in Yunnan pine. For. Ecol. Manag. 497, 119505 https://doi.org/10.1016/j.foreco.2021.119505.

Luo, Y., Huang, H., Roques, A., 2023. Early monitoring of forest wood-boring pests with remote sensing. Ann. Rev. Entomol. 68, 277–298. https://doi.org/10.1146/annurev-ento-120220-125410.

Lu, H.P., Luo, T., Fu, H.W., Wang, L., Tan, Y.Y., Huang, J.Z., Wang, Q., Ye, G.Y., Gatehouse, A.M., Lou, Y.G. and Shu, Q.Y., 2018. Resistance of rice to insect pests mediated by suppression of serotonin biosynthesis. Nat. plants 4(6), 338-344. https://doi.org/10.1038/s41477-018-0152-7.

Mahanta, D.K., Bhoi, T.K., Komal, J., Samal, I. and Mastinu, A., 2024. Spatial, spectral and temporal insights: Harnessing high-resolution satellite remote sensing and artificial intelligence for early monitoring of wood boring pests in forests. Plant Stress 11, p.100381. https://doi.org/10.1016/j.stress.2024.100381.

Mitchell, C., Brennan, R.M., Graham, J. and Karley, A.J., 2016. Plant defense against herbivorous pests: exploiting resistance and tolerance traits for sustainable crop protection. Front. Plant Sci 7, p.1132. https://doi.org/10.3389/fpls.2016.01132.

Moon, T.T., Maliha, I.J., Khan, A.A.M., Chakraborty, M., Uddin, M.S., Amin, M.R. and Islam, T., 2022. CRISPR-Cas genome editing for insect pest stress management in crop plants. Stresses 2(4), 493-514. https://doi.org/10.3390/stresses2040034.

Nazaralian, S., Majd, A., Irian, S., Najafi, F., Ghahremaninejad, F., Landberg, T., & Greger, M. 2017. Comparison of silicon nanoparticles and silicate treatments in fenugreek. Plant Physiol. Biochem 115, 25–33. https://doi.org/10.1016/j.plaphy.2017.03.009.

Ngugi-Dawit, A., Hoang, T. M. L., Williams, B., Higgins, T. J., & Mundree, S. G. 2020. A wild *Cajanus scarabaeoides* (L.) Thouars, IBS 3471, for improved insect-resistance in cultivated pigeonpea. Agronomy 10(4), 517. https://doi.org/10.3390/agronomy10040517.

Oki, N., Komatsu, K., Sayama, T., Ishimoto, M., & Takahashi, M. 2012. Genetic analysis of antixenosis resistance to the common cutworm (*Spodoptera litura* Fabricius) and its relationship with pubescence characteristics in soybean (*Glycine max* (L.) Merr.). Breed. Sci 61(5), 608–617. https://doi.org/10.1270/jsbbs.61.608.

Okosun, O. O., Allen, K. C., Glover, J. P., & Reddy, G. V. 2021. Biology, ecology, and management of key sorghum insect pests. J. Integr. Pest Manag 12(1), 4. https://doi.org/10.1093/jipm/pmaa027.

Onzo, A., Hanna, R., & Sabelis, M. W. 2012. The predatory mite *Typhlodromalus aripo* prefers green-mite induced plant odours from pubescent cassava varieties. Exp. Appl. Acarol. 58, 359–370. https://doi.org/10.1007/s10493-012-9595-0.

Oriani, M. A., & Vendramim, J. D. 2010. Influence of trichomes on attractiveness and ovipositional preference of *Bemisia tabaci* (Genn.) B biotype (Hemiptera: Aleyrodidae) on tomato genotypes. Neotrop. Entomol 39, 1002–1007. https://doi.org/10.1590/s1519-566x2010000600024.

Padmavathi, C., & Padmaja, P. 2022. Insect resistance in field crops. Indian J. Entomo l84(Special Issue, December), 1–28. https://doi.org/10.55446/IJE.2022.911.

Painter, R. H. (1958). Resistance of plants to insects. Annu. Rev. Entomol 3(1), 267–290. https://doi.org/10.1146/annurev.en.03.010158.001411.

Pattanaik, S., Patra, B., Singh, S. K., & Yuan, L. 2014. An overview of the gene regulatory network controlling trichome development in the model plant, *Arabidopsis*. Front. Plant Sci 5, 97, 103. https://doi.org/10.1242/dev.126.4.671.

Phi, C. N., Fujita, D., Yamagata, Y., Yoshimura, A., & Yasui, H. 2019. High-resolution mapping of GRH6, a gene from *Oryza nivara* (Sharma et Shastry) conferring resistance to green rice leafhopper (*Nephotettix cincticeps* Uhler). Breed. Sci 69(3), 439–446. https://doi.org/10.1270/jsbbs.19029.

Pighin, J. A., Zheng, H., Balakshin, L. J., Goodman, I. P., Western, T. L., Jetter, R., Kunst, L., & Samuels, A. L. 2004. Plant cuticular lipid export requires an ABC transporter. Science 306(5696), 702–704. https://doi.org/10.1126/science.1102331.

Pilet-Nayel, M.L., Moury, B., Caffier, V., Montarry, J., Kerlan, M.C., Fournet, S., Durel, C.E. and Delourme, R., 2017. Quantitative resistance to plant pathogens in pyramiding strategies for durable crop protection. Front. Plant Sci 8, p.1838. https://doi.org/10.3389/fpls.2017.01838.

Ponnusamy Duraimurugan, P. D., Pratap Aditya, P. A., Singh, S. K., & Gupta, S. 2014. Evaluation of screening methods for bruchid beetle (*Callosobruchus chinensis*) resistance in green gram (*Vigna radiata*) and black gram (*Vigna mungo*) genotypes and influence of seed physical characteristics on its infestation. Vegetos 27, 60–67. http://dx.doi.org/10.5958/j.2229-4473.27.1.011.

Prasanna, B.M., Bruce, A., Beyene, Y., Makumbi, D., Gowda, M., Asim, M., Martinelli, S., Head, G.P. and Parimi, S., 2022. Host plant resistance for fall armyworm management in maize: relevance, status and prospects in Africa and Asia. Theor. Appl. Genet 135(11), 3897-3916. https://doi.org/10.1007/s00122-022-04073-4.

Puri, H., Grover, S., Pingault, L., Sattler, S. E., & Louis, J. 2023. Temporal transcriptomic profiling elucidates sorghum defense mechanisms against sugarcane aphids. BMC Genomics 24(1), 441. https://doi.org/10.1186/s12864-023-09529-5.

Raffaele, S., Vailleau, F., Leger, A., Joubès, J., Miersch, O., Huard, C., Blée, E., Mongrand, S., Domergue, F., & Roby, D. 2008. A MYB transcription factor regulates very-long-chain fatty acid biosynthesis for activation of the hypersensitive cell death response in *Arabidopsis*. Plant Cell 20(3), 752–767. https://doi.org/10.1105/tpc.107.054858.

Ren, X., Yang, L., Muhammad, Y., Xie, Y., Lin, X., Yu, L., Cao, Y., Ding, M., Jiang, Y., & Rong, J. 2024. The *GaKAN2*, a KANADI transcription factor, modulates stem trichomes in *Gossypium arboreum*. Mol. Genet. Genomics 299(1), 19. https://doi.org/10.1007/s00438-024-02098-6.

Reynolds, O. L., Padula, M. P., Zeng, R., & Gurr, G. M. 2016. Silicon: Potential to promote direct and indirect effects on plant defense against arthropod pests in agriculture. Front. Plant Sci 7, 744. https://doi.org/10.1007/s00438-024-02098-6.

Riahi, C., Urbaneja, A., Fernández-Munoz, R., Fortes, I. M., Moriones, E., & Pérez-Hedo, M. 2023. Induction of glandular trichomes to control whitefly-transmitted viruses in tomato crops: Modulation by the natural enemy *Nesidiocoris tenuis*. Phytopathology 00–XX. https://doi.org/10.1094/phyto-11-22-0440-y.

Riddick, E. W., & Simmons, A. M. 2014. Do plant trichomes cause more harm than good to predatory insects? Pest Manag. Sci 70(11), 1655–1665. https://doi.org/10.1002/ps.3772.

Rizwan, M., Abro, S., Asif, M. U., Hameed, A., Mahboob, W., Deho, Z. A., & Sial, M. A. 2021. Evaluation of cotton germplasm for morphological and biochemical host plant resistance traits against sucking insect pests complex. J. Cotton Res 4(1), 1–8. https://doi.org/10.1186/s42397-021-00093-5.

Rodríguez-López, M. J., Moriones, E., & Fernández-Muñoz, R. 2020. An acylsucrose-producing tomato line derived from the wild species *Solanum pimpinellifolium* decreases fitness of the whitefly *Trialeurodes vaporariorum*. Insects 11(9), 616. https://doi.org/10.3390/insects11090616.

Rowland, O., Zheng, H., Hepworth, S. R., Lam, P., Jetter, R., & Kunst, L. 2006. CER4 encodes an alcohol-forming fatty acyl-coenzyme A reductase involved in cuticular wax production in *Arabidopsis*. Plant Physiol 142(3), 866–877. https://doi.org/10.1104%2Fpp.106.086785.

Roy, N. 2021. Synergism in host selection behavior of three generalist insects towards leaf cuticular wax of sesame cultivars. Neotrop. Entomol 50(5), 812–827. https://doi.org/10.1007/s13744-021-00892-0.

Sadasivam, S., & Thayumanayan, B. 2003. Molecular host plant resistance to pests. CRC Press.

Sajid-ur-Rahman, T. A., Ashraf, M., & Malik, S. A. 2008. Inheritance of frego bract and its linkage with fibre and seed traits in cotton. Pak. J. Bot 40(4), 1621–1626. https://mail.pakbs.org/pjbot/PDFs/40(4)/PJB40(4)1621.pdf.

Sallaud, C., Rontein, D., Onillon, S., Jabes, F., Duffé, P., Giacalone, C., Thoraval, S., Escoffier, C., Herbette, G., & Leonhardt, N. 2009. A novel pathway for sesquiterpene biosynthesis from Z, Z-farnesyl pyrophosphate in the wild tomato *Solanum habrochaites*. Plant Cell 21(1), 301–317. https://doi.org/10.1105/tpc.107.057885.

Santiago, R., Barros-Rios, J., & Malvar, R. A. 2013. Impact of cell wall composition on maize resistance to pests and diseases. Int. J. Mol. Sci 14(4), 6960–6980. https://doi.org/10.3390/ijms14046960.

Satish, K., Srinivas, G., Madhusudhana, R., Padmaja, P., Reddy, R. N., Mohan, S. M., & Seetharama, N. 2009. Identification of quantitative trait loci for resistance to shoot fly in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet 119(8), 1425–1439. https://doi.org/10.1007/s00122-009-1145-8.

Schellmann, S., Hülskamp, M., & Uhrig, J. 2007. Epidermal pattern formation in the root and shoot of *Arabidopsis*. Biochem. Soc. Trans 35(1), 146–148. https://doi.org/10.1042/bst0350146.

Schoonhoven, L. M., Van Loon, J. J., & Dicke, M. 2005. Insect–plant biology. Oxford University Press.

Schuman, M. C., & Baldwin, I. T. 2016. The layers of plant responses to insect herbivores. Annu. Rev. Entomol 61(1), 373–394. https://doi.org/10.1146/annurev-ento-010715-023851.

Sehgal, D., Singh, R., & Rajpal, V. R. 2016. Quantitative trait loci mapping in plants: Concepts and approaches. In V. R. Rajpal, S. R. Rao, & S. N. Raina (Eds.), Molecular breeding for sustainable crop improvement (Vol. 2, pp. 31–59). Springer. https://doi.org/10.1007/978-3-319-27090-6_2.

Selvaraju, K., Shanmugasundaram, P., Mohankumar, S., Asaithambi, M., & Balasaraswathi, R. 2007. Detection of quantitative trait locus for leaffolder (*Cnaphalocrocis medinalis* (Guenée)) resistance in rice on linkage group 1 based on damage score and flag leaf width. Euphytica 157(1), 35–43. https://doi.org/10.1007/s10681-007-9394-6.

Seo, P. J., Lee, S. B., Suh, M. C., Park, M. J., Go, Y. S., & Park, C. M. 2011. The MYB96 transcription factor regulates cuticular wax biosynthesis under drought conditions in *Arabidopsis*. Plant Cell 23(3), 1138–1152. https://doi.org/10.1105/tpc.111.083485.

Sharma, H. C. 2001. Crop protection compendium: *Helicoverpa armigera*. Commonwealth Agricultural Bureaux International. http://www.cabi.org/c&c/about/contributors-p-s1.

Sharma, S., Jaba, J., Rao, P. J., Prasad, S., Gopal, N. T. V. V., Sharma, H. C., & Kilian, B. 2022. Reaping the potential of wild *Cajanus* species through pre-breeding for improving resistance to pod borer, *Helicoverpa armigera*, in cultivated pigeonpea (*Cajanus cajan* (L.) Millsp.). Biology 11(4), 485. https://doi.org/10.3390/biology11040485.

Silva-Sanzana, C., Estevez, J. M., & Blanco-Herrera, F. 2020. Influence of cell wall polymers and their modifying enzymes during plant–aphid interactions. J. Exp. Bot 71(13), 3854–3864. https://doi.org/10.1093/jxb/erz550.

Simmons, A. T., & Gurr, G. M. 2005. Trichomes of *Lycopersicon* species and their hybrids: Effects on pests and natural enemies. Agric. For. Entomol 7(4), 265–276. https://doi.org/10.1111/j.1461-9555.2005.00271.x.

Singh, A., Pandey, A., Baranwal, V., Kapoor, S., & Pandey, G. K. 2012. Comprehensive expression analysis of rice phospholipase D gene family during abiotic stresses and development. Plant Signal. Behav 7(7), 847–855. https://doi.org/10.4161/psb.20385.

Singh, A., Dilkes, B., Sela, H., & Tzin, V. 2021. The effectiveness of physical and chemical defense responses of wild emmer wheat against aphids depends on leaf position and genotype. Front. Plant Sci 12, 667820. https://doi.org/10.3389/fpls.2021.667820.

Souza, E. A. d., Moraes, J. C. d., Amaral, J. L. d., Liberato, R. D., Bonelli, E. A., & Lima, L. R. 2009. Application effect of calcium silicate in *Brachiaria brizantha* cv. Marandu on the nymph population of the brown root stinkbug, soil chemical characteristics, and plant and dry matter production. Cienc. Agrotecnol 33(6), 1518–1526. https://doi.org/10.1590/S1413-70542009000600009.

Steward, R. A., Fisher, L. M., & Boggs, C. L. 2019. Pre- and post-ingestive defenses affect larval feeding on a lethal invasive host plant. Entomol. Exp. Appl 167(4), 292–305. https://doi.org/10.1111/eea.12769.

Sun, W., Gao, D., Xiong, Y., Tang, X., Xiao, X., Wang, C., & Yu, S. 2017. Hairy leaf 6, an AP2/ERF transcription factor, interacts with OsWOX3B and regulates trichome formation in rice. Mol. Plant 10(11), 1417–1433. https://doi.org/10.1016/j.molp.2017.09.015.

Szczepaniec, A., Glover, K. D., & Berzonsky, W. 2015. Impact of solid and hollow varieties of winter and spring wheat on severity of wheat stem sawfly (Hymenoptera: Cephidae) infestations and yield and quality of grain. J. Econ. Entomol 108(5), 2316–2323. https://doi.org/10.1093/jee/tov207.

Taggar, G. K., & Gill, R. S. 2012. Preference of whitefly, *Bemisia tabaci*, towards black gram genotypes: Role of morphological leaf characteristics. Phytoparasitica 40(5), 461–474. https://doi.org/10.1007/s12600-012-0247-z.

Thiel, T., Gaschler, S., Mody, K., Blüthgen, N., & Drossel, B. 2020. Impact of plant defense level variability on specialist and generalist herbivores. Theor. Ecol 13, 409–424. https://doi.org/10.1007/s12080-020-00461-y.

Tyagi, S., Kesiraju, K., Saakre, M., Rathinam, M., Raman, V., Pattanayak, D., & Sreevathsa, R. 2020. Genome editing for resistance to insect pests: An emerging tool for crop improvement. ACS Omega 5(33), 20674–20683. https://doi.org/10.1021/acsomega.0c01435.

Vadde, B.V.L., Challa, K.R. and Nath, U., 2018. The TCP 4 transcription factor regulates trichome cell differentiation by directly activating *GLABROUS INFLORESCENCE STEMS* in *Arabidopsis thaliana*. Plant J 93(2), pp.259-269. https://doi.org/10.1111/tpj.13772

Van Bel, A. J., & Will, T. 2016. Functional evaluation of proteins in watery and gel saliva of aphids. Front. Plant Sci 7, 1840. https://doi.org/10.3389/fpls.2016.01840.

Van Poecke, R. M. 2007. Arabidopsis-insect interactions. The Arabidopsis Book, 5, e0107. https://doi.org/10.1199/tab.0107.

Varella, A. C., Talbert, L. E., Hofland, M. L., Buteler, M., Sherman, J. D., Blake, N. K., Heo, H. Y., Martin, J. M., & Weaver, D. K. 2016. Alleles at a quantitative trait locus for stem solidness in wheat affect temporal patterns of pith expression and level of resistance to the wheat stem sawfly. Plant Breed 135(5), 546–551. https://doi.org/10.1111/pbr.12398.

Vats, S., Kumawat, S., Kumar, V., Patil, G. B., Joshi, T., Sonah, H., Sharma, T. R., & Deshmukh, R. 2019. Genome editing in plants: Exploration of technological advancements and challenges. Cells 8(11), 1386. https://doi.org/10.3390/cells8111386.

Verma, K. K., Song, X.-P., Tian, D.-D., Guo, D.-J., Chen, Z.-L., Zhong, C.-S., Nikpay, A., Singh, M., Rajput, V. D., & Singh, R. K. 2021. Influence of silicon on biocontrol strategies to manage biotic stress for crop protection, performance, and improvement. Plants 10(10), 2163. https://doi.org/10.3390/plants10102163.

Volp, T. M., Zalucki, M. P., & Furlong, M. J. 2023. *Helicoverpa armigera* preference and performance on three cultivars of short-duration pigeonpea (*Cajanus cajan*): The importance of whole plant assays. Pest Manag. Sci 79(2), 627–637. https://doi.org/10.1002/ps.7230.

Vosman, B., Kashaninia, A., van't Westende, W., Meijer-Dekens, F., van Eekelen, H., Visser, R. G., de Vos, R. C., & Voorrips, R. E. 2019. QTL mapping of insect resistance components of *Solanum galapagense*. Theor. Appl. Genet 132, 531–541. https://doi.org/10.1007/s00122-018-3239-7.

Wainhouse, D., Cross, D., & Howell, R. 1990. The role of lignin as a defense against the spruce bark beetle *Dendroctonus micans*: Effect on larvae and adults. Oecologia 85, 257–265. https://doi.org/10.1007/BF00319411.

Wan, Q., Zhang, Z., Hu, M., Chen, L., Liu, D., Chen, X., Wang, W., & Zheng, J. 2007. T1 locus in cotton is the candidate gene affecting lint percentage, fiber quality and spiny bollworm (*Earias* spp.) resistance. Euphytica 158, 241–247. https://doi.org/10.1007/s10681-007-9446-y.

Wang, K., Wang, X., Wang, J., Liang, Y., Pei, X., Ren, X., Xing, W., Zhang, X., Peng, Y., Zang, X., & Xiongfeng, M. 2023. Fine mapping of the frego bract gene *fg* in cotton. Cotton Sci 35(3), 173–180. https://doi.org/10.11963/cs20230015.

Wang, R., Xue, Y., Fan, J., Yao, J.-L., Qin, M., Lin, T., Lian, Q., Zhang, M., Li, X., & Li, J. 2021. A systems genetics approach reveals *PbrNSC* as a regulator of lignin and cellulose biosynthesis in stone cells of pear fruit. Genome Biol 22(1), 1–23. https://doi.org/10.1186/s13059-021-02531-8.

Wang, S., Wang, J.-W., Yu, N., Li, C.-H., Luo, B., Gou, J.-Y., Wang, L.-J., & Chen, X.-Y. 2004. Control of plant trichome development by a cotton fiber MYB gene. Plant Cell 16(9), 2323–2334. https://doi.org/10.1105/tpc.104.024844.

Wang, X., Guan, Y., Zhang, D., Dong, X., Tian, L., & Qu, L. Q. 2017. A β-ketoacyl-CoA synthase is involved in rice leaf cuticular wax synthesis and requires a CER2-LIKE protein as a cofactor. Plant Physiol 173(2), 944–955. https://doi.org/10.1104/pp.16.01527.

Wang, X., Kong, L., Zhi, P., & Chang, C. 2020. Update on cuticular wax biosynthesis and its roles in plant disease resistance. Int. J. Mol. Sci 21(15), 5514. https://doi.org/10.3390/ijms21155514.

War, A.R., Paulraj, M.G., Ahmad, T., Buhroo, A.A., Hussain, B., Ignacimuthu, S. and Sharma, H.C., 2012. Mechanisms of plant defense against insect herbivores. Plant Signal. Behav 7(10), pp.1306-1320. https://doi.org/10.4161/psb.21663.

Wei, L., Jiang, H., & Chuan, S. 2008. Genetic analysis of related phenotypes of functional leaf in rice heading stage. Mol. Plant Breed 6(5).

Wei, Z., Cheng, Y., Zhou, C., Li, D., Gao, X., Zhang, S., & Chen, M. 2019. Genome-wide identification of direct targets of the TTG1–bHLH–MYB complex in regulating trichome formation and flavonoid accumulation in *Arabidopsis thaliana*. Int. J. Mol. Sci 20(20), 5014. https://doi.org/10.3390/ijms20205014.

Weidenbach, D., Jansen, M., Franke, R. B., Hensel, G., Weissgerber, W., Ulferts, S., Jansen, I., Schreiber, L., Korzun, V., & Pontzen, R. 2014. Evolutionary conserved function of barley and Arabidopsis 3-ketoacyl-CoA synthases in providing wax signals for germination of powdery mildew fungi. Plant Physiol 166(3), 1621–1633. https://doi.org/10.1104/pp.114.246348.

Werker, E. 2000. Trichome diversity and development. Adv. Bot. Res 31, 1–35. https://doi.org/10.1016/S0065-2296(00)31005-9.

White, W.H., Tew, T.L. and Richard, E.J., 2006. Association of sugarcane pith, rind hardness, and fiber with resistance to the sugarcane borer. J. Am. Soc. Sugar Cane Technol 26, 87-100. https://www.cabidigitallibrary.org/doi/full/10.5555/20073160754.

Whitehill, J. G., Henderson, H., Schuetz, M., Skyba, O., Yuen, M. M. S., King, J., Samuels, A. L., Mansfield, S. D., & Bohlmann, J. 2016a. Histology and cell wall biochemistry of stone cells in the physical defense of conifers against insects. Plant Cell Environ 39(8), 1646–1661. https://doi.org/10.1111/pce.12681.

Whitehill, J. G., Henderson, H., Strong, W., Jaquish, B., & Bohlmann, J. 2016b. Function of Sitka spruce stone cells as a physical defense against white pine weevil. Plant Cell Environ 39(11), 2545–2556. https://doi.org/10.1111/pce.12810.

Whitehill, J. G., Yuen, M. M., Chiang, A., Ritland, C. E., & Bohlmann, J. 2023. Transcriptome features of stone cell development in weevil-resistant and susceptible Sitka spruce. New Phytol 239(6), 2138–2152. https://doi.org/10.1111/nph.19103.

Whitehill, J. G., Yuen, M. M., Henderson, H., Madilao, L., Kshatriya, K., Bryan, J., Jaquish, B., & Bohlmann, J. 2019. Functions of stone cells and oleoresin terpenes in the conifer defense syndrome. New Phytol 221(3), 1503–1517. https://doi.org/10.1111/nph.15477.

Xavier Chiriboga, M., Amanuel, T., Islam, S. S., & Zeyaur, K. 2021. Evaluation of African maize cultivars for resistance to fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) larvae. Plants 10(2), 392. https://doi.org/10.3390/plants10020392.

Xie, Y., Yu, X., Jiang, S., Xiao, K., Wang, Y., Li, L., Wang, F., He, W., Cai, Q., & Xie, H. 2020. OsGL6, a conserved AP2 domain protein, promotes leaf trichome initiation in rice. Biochem. Biophys. Res. Commun 522(2), 448–455. https://doi.org/10.1016/j.bbrc.2019.11.125.

Xue, D., Zhang, X., Lu, X., Chen, G., & Chen, Z.-H. 2017. Molecular and evolutionary mechanisms of cuticular wax for plant drought tolerance. Front. Plant Sci 8, 621. https://doi.org/10.3389/fpls.2017.00621.

Yang, C., Li, H., Zhang, J., Wang, T., & Ye, Z. 2011. Fine-mapping of the woolly gene controlling multicellular trichome formation and embryonic development in tomato. Theor. Appl. Genet 123(4), 625–633. https://doi.org/10.1007/s00122-011-1612-x.

Yang, L., Han, Y., Li, P., Li, F., Ali, S., & Hou, M. 2017. Silicon amendment is involved in the induction of plant defense responses to a phloem feeder. Sci. Rep 7(1), 4232. https://doi.org/10.1038/s41598-017-04571-2.

Yeats, T.H. and Rose, J.K., 2013. The formation and function of plant cuticles. Plant Physiol 163(1), pp.5-20. https://doi.org/10.1104/pp.113.222737.

Yu, N., Cai, W.J., Wang, S., Shan, C.M., Wang, L.J. and Chen, X.Y., 2010. Temporal control of trichome distribution by microRNA156-targeted SPL genes in *Arabidopsis thaliana*. Plant Cell 22(7), pp.2322-2335. https://doi.org/10.1105/tpc.109.072579

Yu, H., Xie, W., Wang, J., Xing, Y., Xu, C., Li, X., Xiao, J., & Zhang, Q. 2011. Gains in QTL detection using an ultra-high density SNP map based on population sequencing relative to traditional RFLP/SSR markers. PLoS one 6(3), e17595. https://doi.org/10.1371/journal.pone.0017595.

Yu, Y., Woo, M.-O., Rihua, P., & Koh, H.-J. 2020. The DROOPING LEAF (DR) gene encoding GDSL esterase is involved in silica deposition in rice (*Oryza sativa* L.). PLoS one 15(9), e0238887. https://doi.org/10.1371/journal.pone.0238887.

Zhan, X., Chen, Z., Chen, R. and Shen, C., 2022. Environmental and genetic factors involved in plant protection-associated secondary metabolite biosynthesis pathways. Front. Plant Sci 13, p.877304. https://doi.org/10.3389/fpls.2022.877304.

Zhang, N., Sun, Q., Li, H., Li, X., Cao, Y., Zhang, H., Li, S., Zhang, L., Qi, Y., & Ren, S. 2016. Melatonin improved anthocyanin accumulation by regulating gene expressions and resulted in high reactive oxygen species scavenging capacity in cabbage. Front. Plant Sci 7, 197. https://doi.org/10.3389/fpls.2016.00197.

Zhang, Y., Lübberstedt, T., & Xu, M. 2013. The genetic and molecular basis of plant resistance to pathogens. J. Genet. Genomics 40(1), 23–35. https://doi.org/10.1016/j.jgg.2012.11.003.

Zheng, H., Rowland, O., & Kunst, L. 2005. Disruptions of the *Arabidopsis* enoyl-CoA reductase gene reveal an essential role for very-long-chain fatty acid synthesis in cell expansion during plant morphogenesis. Plant Cell 17(5), 1467–1481. https://doi.org/10.1105/tpc.104.030155.

Zhong, R., Cui, D., & Ye, Z. H. 2019. Secondary cell wall biosynthesis. New Phytol 221(4), 1703–1723. https://doi.org/10.1111/nph.15537.

Zhu, Q.-H., Zhang, J., Liu, D., Stiller, W., Liu, D., Zhang, Z., Llewellyn, D., & Wilson, I. 2016. Integrated mapping and characterization of the gene underlying the okra leaf trait in *Gossypium hirsutum* L. J. Exp. Bot 67(3), 763–774. https://doi.org/10.1093/jxb/erv494.

Zhu, W., Liu, K., & Wang, X.-D. 2008. Heterosis in yield, fiber quality, and photosynthesis of okra leaf-oriented hybrid cotton (*Gossypium hirsutum* L.). Euphytica 164, 283–291. https://doi.org/10.1007/s10681-008-9732-3.

Table 1. Biophysical traits associated with insect resistance in crop cultivars

Crop	Pest	Plant Character	Reference
Sorghum	Shoot fly *Atherigona soccata* Rondani	Leaf glossiness, plant vigor, trichomes, and leaf-sheath pigmentation	(Arora et al., 2021)
	Aphid *Melanaphis sacchari* Zehntner	Greater plant height and greater distance between two leaves and the presence of waxy lamina	
	Midge *Contarinia sorghicola* Coquillett	Long glumes that do not open during anthesis, fast ovary growth in sorghum panicle, short floral parts, short glume, length short ovary girth	
Pearl millet	Head miner *Heliocheilus albipunctella* De Joannis	Presence of involucre bristles, their density, length, and orientation	
Cowpea	Pod sucking bug *Riptortus pedestris* Fabricius	Trichomes on pods	
Pigeonpea	Gram pod borer *Helicoverpa armigera* Hubner	High density of non-glandular trichomes on pods, Pod wall thickness, small pods with deep constriction between seeds	(Sharma et al., 2009)
	Pod fly *Melanagromyza obtusa* Malloch	Pod wall thickness, trichome density	
Soyabean	Pod fly *Melanagromyza sojae* Zehntner Whitefly *Bemisia tabaci* Gennadius	Trichome length	(Ambidi et al., 2022)
	Pod borer *Helicoverpa zea* Boddie Cut worm *Spodoptera exigua* Hubner Soyabean looper *Pseudoplusia includens* Walker	Leaf tip pubescence	
Groundnut	*H. armigera*, *S. litura*	Stem thickness, leaflet shape, leaf length, leaf hairiness, standard petal length, stipule and peg length	(Sharma et al., 2003)
	H. armigera	Dark green and small leaves	(Arora et al., 2021)
Chick pea	*H. armigera*	Pod shape, pod wall thickness, and crop duration	(Jaba et al., 2017)
Black gram	White flies *Bemisia tabaci* Gennadius	Erect trichomes	(Taggar and Gill, 2012)

Table 2. Source of biophysical traits and sources of resistance against insect pests in crops

Crop	Insect	Trait	Source of Resistance	References
Maize	Fall army worm *Spodoptera frugiperda* Smith	Leaf toughness and leaf trichome	*Z. mays* subsp. parviglumis	(Mammadov et al., 2018)
Cotton	*Helicoverpa* sp.	Smooth leaf type	*Gossypium somalense*	
	Jassids *Amrasca biguttula* Ishida	Hairiness	*G. barbadense* *G. hirsutum* *G. raimondii*	
	Flea hopper *Pseudatomoscelis seriatus* Reuter	Pilose trait and square structure impacting stylet penetration	*G. hirsutum* "Pilose"	
Pigeonpea	*H. armigera* Hubner	Non glandular Type C and D Trichomes	*Cajanus scarabaeoides*	(Aruna et al., 2011)
			Cajanus scarabaeoides *Cajanus acontifolius*	(Sharma et al., 2022)
Cow pea	Pod sucking bug *Clavigralla tomentosicollis* Stal	Pod trichomes	*Vigna vexillata*	
Tomato	Fruit borer *H. armigera*	Glandular Type IV Trichomes	*Lycopersicon hirsutum* f. glabratum, *L. hirsutum* *L. pennellii*	(Simmons et al 2005)
	Thrips *Bemisia argentifolii* Bellows & Perring			
	Green peach aphid *Myzus persicae* Sulzer			
	Cut worm *Spodoptera exigua* Hubner		*Lycopersicon hirsutum* f. glabratum *L. hirsutum*	(Eigenbrode and Trumble, 1993)
	Potato tuber moth *Phthorimaea operculella* Zeller	Glandular Types IV and V Trichomes	*Lycopersicon hirsutum*	

Table 3. Genes governing the biophysical traits in crops for resistance against major pests

Crop	Pest	Biophysical traits	Genes	References
Cotton	Boll weevil *Anthonomus grandis* Boheman	Frego bract	Single recessive gene	(Green,1955)
	Aphids *Aphis gossypii* Glover	Red colored leaves	Single partial dominant gene	
	Pink bollworm *Pectinophora gossypiella* Saunders Whitefly *Bemisia tabaci* Gennadius	Okra leaf shaped	Single semi-dominant gene	(Zhu et al., 2016)
Black gram	Pod borer *Helicoverpa armigera* Hubner	Pod pubescence	Single dominant gene	(Arshad et al., 2005)
Castor	Leaf hopper *Empoasca flavescens* Fabricius	Stem color	Single dominant gene	(Lavanya et al., 2018)
		Waxy blooms		
Sorghum	Shoot fly *Atherigona soccata* Rondani	Glossy leaves	Single recessive gene; Additive and non-additive genes	(Arora et al., 2025) (Padmavathi and Padmaja, 2022)
		Trichome density	Additive and non-additive genes	(Padmavathi and Padmaja,2022)
Sorghum	Stemborer *Chilo partellus* Swinhoe	Number of nodes	Additive	
	Green bug *Schizaphis graminum* Rondani	Stalk length	Dominant	(Johnson et al., 1981)

Table 4. QTLs governing the biophysical traits in crops for resistance against major pests

Crop	Pest	Biophysical trait	QTL	Location on chromosome	Reference
Rice	Rice leaf folder *Cnephalocrocis medinalis* Guenee	Width and length of flag leaf	RM 3412	Chr 1	(Selvaraju et al., 2007)
			qRLR-3 qRLR-4	Chr 3 Chr 4	(Wei et al., 2008)
	Green leafhopper *Nephotettix virescens* Distant	Leaf lamina thickness	qGRH 4.2	Chr 4	(Phi et al.,2019)
Wheat	Wheat stem fly *Cephus cinctus* Norton	Stem solidness	Qss.msub-3AL.b	Chr 3A	(Cook et al., 2004)
			Qss.msub-3BL	Chr 3B	(Varella et al., 2016)
			Qss.msub-3DL	Chr 3D	(Lanning et al., 2006)
Maize	Maize weevil *Sitophilus granarius* Linnaeus	Grain hardiness	bnlg 1007 bnlg 2180 bnlg 1556 phi 002 umc 128 bnlg 609	Chr 1 Chr 1 Chr 1 Chr 1 Chr 1 Chr 5	(Bergvinson and García-Lara, 2006)
Sorghum	Shoot fly *Atherigona soccata* Rondani	Leaf glossiness	QGsdsr 3 QGsdsr 5 QGsdsr 6 QGsdsr 10	SBI 3 SBI 5 SBI 6 SBI 10	(Satish et al., 2009)
			QGsdsr 1 QGsdsr 2 QGsdsr 4.1 QGsdsr 4.2	SBI 1 SBI 2 SBI 4 SBI 4	(Aruna et al., 2011)

			QEg28.dsr-10	SBI 10	(Gorthy et al., 2017)
		Trichome density on upper surface	QTdu.dsr 10.1 QTdu.dsr 10.2	SBI 10 SBI 10	(Satish et al., 2009)
			QTdu.dsr 7	SBI 7	(Aruna et al., 2011)
		Trichome density on lower surface	QTdl.dsr 1.1 QTdl.dsr 1.2	SBI 1 SBI 1	(Gorthy et al., 2017)
			QTdl.dsr 4 QTdl.dsr 6 QTdl.dsr 10.1 QTdl.dsr 10.2	SBI 4 SBI 6 SBI 10 SBI 10	(Satish et al., 2009)
			QTdl.dsr 3	SBI 3	(Aruna et al., 2011)
Soyabean	Common cut worm *Spodoptera litura* Fabricius	Pubescence length	qPL-1-1 qPL-1-1 qPL-3-1 qPL-4-1 qPL-12-1 qPL-12-2 qPL-12-3 qPL-12-4 qPL-14-1	Chr 1 Chr 1 Chr 3 Chr 4 Chr 12 Chr 12 Chr 12 Chr 12 Chr 14	(Li et al., (2022)
		Pubescence density	qPD-1-1 qPD-8-1	Chr 1 Chr 8	

			qPD-11-1 qPD-11-2 qPD-12-1 qPD-12-2 qPD-12-3	Chr 11 Chr 11 Chr 12 Chr 12 Chr 12	
Potato	Leafhopper *Empoasca fabae* Harris	Long and erect pubescence	qRslx1 qRslx2	Chr 7 Chr 12	(Oki et al., 2012)
	Colorado potato beetle *Leptinotarsa decemlineata* Say	Glandular trichome Type A	TG 119 TG 63	Chr 6 Chr 10	(Bonierbale et al., 1994)
		Glandular trichome Type B	TG 441 TG 379	Chr 5	
Tomato	White fly *Bemisia tabaci* Gennadius *Trialeurodes vapororium* Westwood	Glandular trichome type IV and V	Wf – 1	Chr 2	(Vosman et al., 2019)

Figure Legends

Fig. 1 Insect resistance mechanisms and causal factors

The figure illustrates the overall mechanisms of host plant resistance (HPR), along with the different categories and the underlying causal factors associated with each category of resistance. Created with BioRender.com.

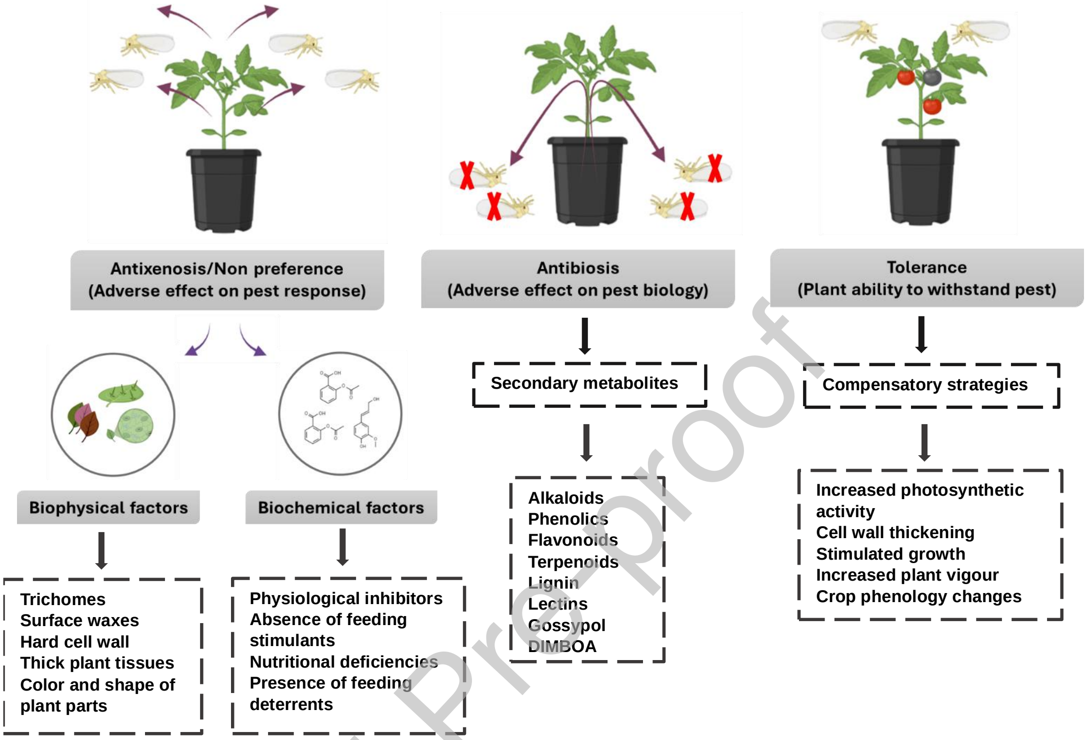


Fig. 2 Biophysical traits imparting resistance to crop insect pests

The figure illustrates various biophysical traits of plants that contribute to resistance against pests. Created with BioRender.com.

Fig. 3 Genes governing trichome development in plants

The figure illustrates the transcription factors and corresponding genes that regulate glandular and non-glandular trichomes, which contribute to biophysical resistance against insect pests. Created with BioRender.com.

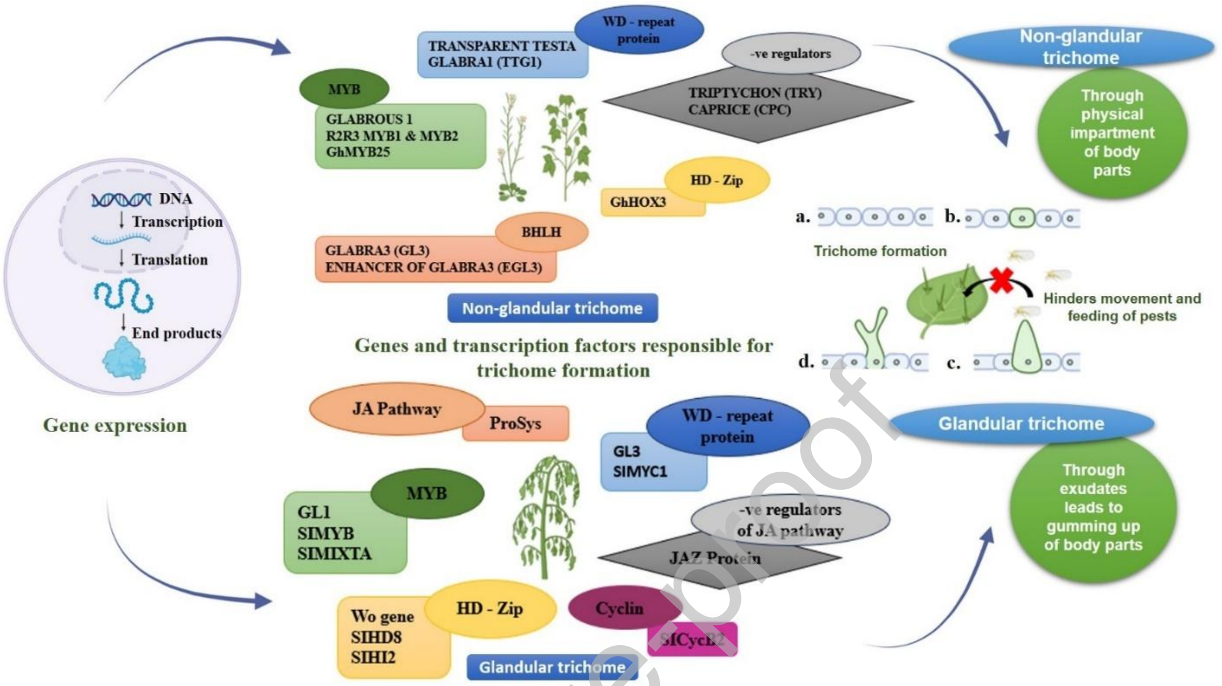


Fig. 4 Genes responsible for silica accumulation in plants

The figure illustrates the genes involved in silica transport and accumulation in plants, which contribute to forming a physical barrier against insect pests. Created with BioRender.com.

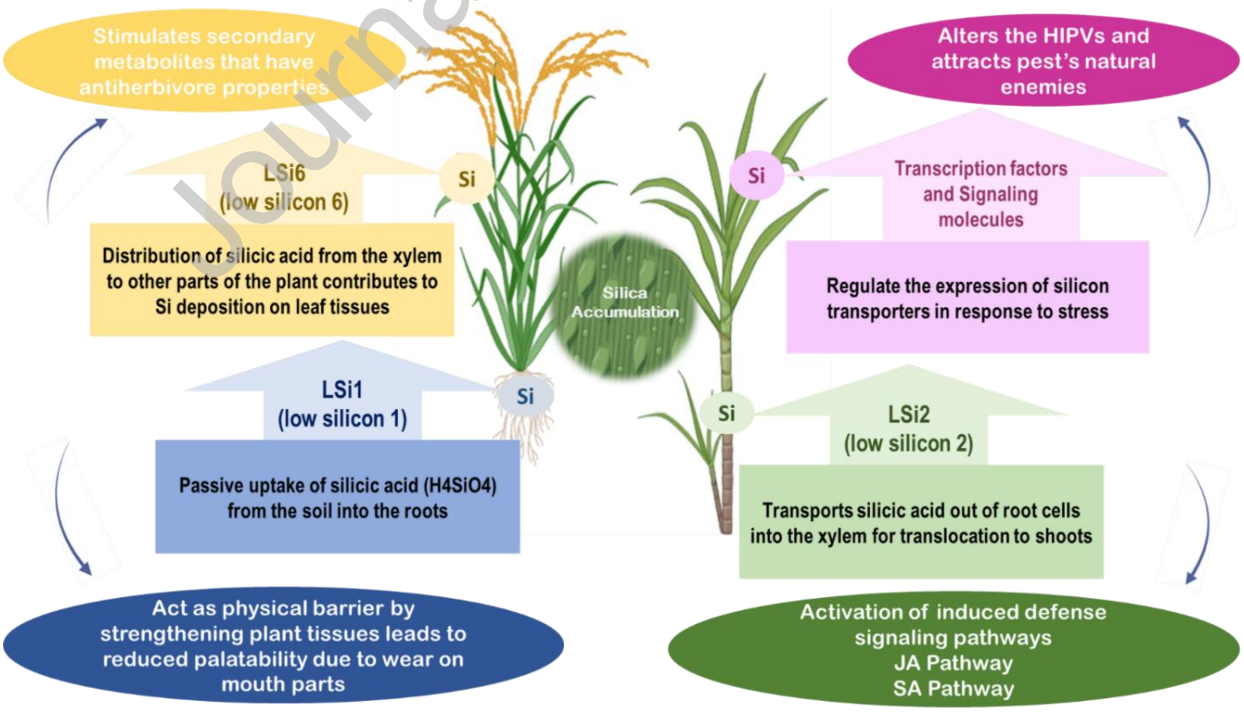
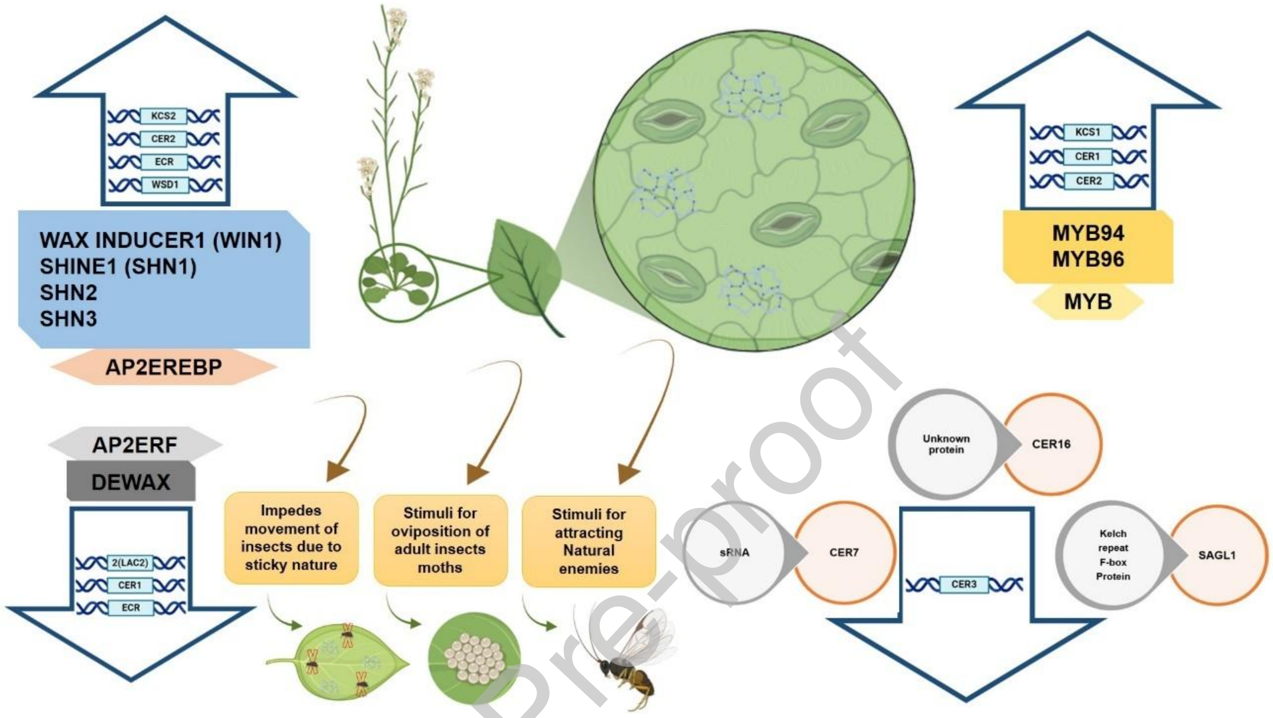


Fig. 5 Molecular biogenetic pathway of epidermal wax production in plants

The figure illustrates the genetic pathways and regulatory mechanisms involved in the production of epidermal wax on the plant surface, where upward arrows represent upregulation and downward arrows represent downregulation of genes contributing to increased/decreased EWs, highlighting their varied roles in influencing insect–plant interactions. Created with BioRender.com.



Declaration of Interest Statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors are not an Editorial Board Member/Editor-in-Chief/Associate Editor/Guest Editor for this journal and was not involved in the editorial review or the decision to publish this article.