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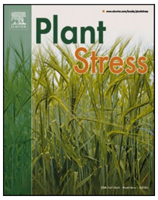

Review

Decoding plant resistance mechanism in pigeonpea (*Cajanus cajan*) against major insect pests: Decade of efforts and emerging directions

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ABSTRACT

Pigeonpea (*Cajanus cajan* (L.) Millsp.) is an important food and nutritional security crop, widely cultivated in the semi-arid regions of Asia and Sub-Saharan Africa. However, its productivity is hindered by various abiotic and biotic stress factors, including numerous insect pests that infest and damage the crop at all stages of development, both in the field and during post-maturity stage/ storage conditions. Host plant resistance (HPR) has emerged as a critical tool in the sustainable management of insect pests in pigeonpea as a vital legume crop. This review synthesizes key breakthroughs in understanding and applying HPR. It focuses on decades of development and recent advances in identifying resistant/tolerant pigeonpea genotypes and the mechanisms underlying their plant defense for major insect pests. Moreover, emphasis is placed on biochemical, morphological, and genetic traits conferring resistance to significant pests of pigeonpea. In addition, innovations in molecular breeding, genomics, and phenotyping are accelerating the development of pest-resistant genotypes, offering alternatives to chemical control and enhancing crop resilience. In this review, we explored emerging research directions, including multi-omics approaches, gene-editing techniques, and novel breeding techniques, thereby expanding our understanding of host-insect interactions and facilitating precision breeding research. This comprehensive review and opinion underscore the potential of HPR in integrated pest management (IPM) for pigeonpea and highlight future pathways for improving insect pest resistance and ensuring food security in pigeonpea-producing regions across the globe.

1. Introduction

Pigeonpea (*Cajanus cajan* (L.) Millsp.) is an essential legume crop cultivated extensively in tropical and subtropical regions, playing a vital role in global food security and agricultural sustainability (Pranati et al., 2024; Saxena et al., 2002). It is valued for its high protein content, drought tolerance, and ability to fix atmospheric nitrogen by nearly 76 %, thereby improving soil health (Bakala et al., 2024; Mhango et al., 2020; Pranati et al., 2024). However, pigeonpea production is significantly constrained by various biotic stresses, particularly major economic damage caused by insect pests (Volp et al., 2025). Major pests of pigeonpea include pod borer *Helicoverpa armigera* (Hüb.) (Lepidoptera: Noctuidae), legume spotted pod borer *Maruca vitrata* F. (Lepidoptera: Crambidae) and pod fly *Melanagromyza obtusa* (Mall.) (Diptera: Agromyzidae). Their damages lead to considerable yield losses, necessitating urgent and effective management strategies (Sharma, 2016). To combat these insect pests, farmers' use of insecticides leads to the development of insecticide resistance in the insect population, resulting in residual toxicity in pigeonpea grains, which affects both human and environmental health (Harischandra et al., 2021).

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Over the past few decades, host plant resistance (HPR) has been considered a valuable, eco-friendly, and sustainable strategy for managing insect pest challenges in pigeonpea (Sharma, 2016). Deciphering resistance mechanisms in pigeonpea is essential for developing pest-resistant or tolerant genotypes. Resistance is primarily due to antixenosis, where plant traits, such as glandular and non-glandular trichomes, deter pests from feeding or laying eggs (Karrem et al., 2025). The antibiosis mechanism affects larval survival, growth, and reproduction, leading to a reduction in the fitness of the insect (Vishal et al., 2023). Moreover, In the cultivated pigeonpea, there is a low level or inconsistency in the resistance to pod borer, *H. armigera* (Sujana et al., 2008). However, the genetic background of crop wild relatives (CWRs) of pigeonpea (*C. cajan*) is a valuable source of resistance through the HPR mechanism, and it helps the breeding programs in enhancing the resistance or tolerance in cultivated pigeonpea (Sharma, 2016). Selecting pigeonpea genotypes that are naturally resistant to insect pests with pre-breeding initiatives has facilitated the transfer of desirable genes from wild species into the cultivated gene pool (Sharma et al., 2022). These improved cultivars, derived from cultivated and wild relatives, can significantly enhance pest resistance. Moreover, genetic engineering efforts have led to the development of *Bt* (*Bacillus thuringiensis*) and plant-derived genes of pigeonpea resistant to *H. armigera* addressing the limitations of traditional breeding. Moreover, due to limited field-level data on the efficacy, biosafety, and adoption of Bt-pigeonpea, its development remains largely confined to controlled environments, and regulatory approval for open field cultivation has not yet been granted in any country across Asia or Africa (Das et al., 2016; Sharma et al., 2002).

Moreover, the advanced molecular approaches have heightened our ability to decipher plant resistance strategies, including physical barriers, biochemical defenses, and molecular signaling networks that deter insect pests in legumes (Razzaq et al., 2023). Additionally, Integrating multi-omics approaches such as genomics, transcriptomics, metabolomics, and proteomics into plant breeding programs provides a comprehensive understanding of host plant resistance, enabling the identification of key genes, regulatory networks, and metabolic pathways involved in plant defense mechanisms while integrating proteomics and metabolomics provide insights into the importance of proteins and metabolites for defense responses (Mahmood et al., 2022; Varadharajan et al., 2025). Indeed, these multi-omics strategies driven by genetic and metabolic diversity form a strong foundation for advanced pigeonpea breeding against insect pests (Gothe et al., 2024; Sai Reddy et al., 2022). Furthermore, genome editing tools have the potential to greatly improve the genetic improvement of pulse crops to make them more resilient to stress (Vamshi et al., 2025). Recently, CRISPR/Cas9 mutagenesis of the UDP-glycosyltransferase (*GmUGT*) gene enhanced soybean resistance to *H. armigera* and *Spodoptera litura* F. by altering flavonoid biosynthesis and strengthening defense mechanisms (Zhang et al., 2022). In pigeonpea cultivation, HPR strategies enhance pest resilience and reduce the reliance on insecticides, thereby lowering production costs and providing significant benefits to small and marginal farmers in semi-arid regions (Sharma and Ortiz, 2002). Moreover, exploring genetic diversity in pigeonpea and its wild relatives is crucial for identifying new resistance traits that can enhance HPR strategies (Sharma, 2016). Developments in HPR have supported sustainable, redefined integrated pest management (IPM) and aligned with One Health goals (Pretty and Pervez Bharucha, 2015; Sharma and Ortiz, 2002).

This review provides an overview of the current developments in host plant resistance mechanisms in pigeonpea against major insect pests, reviewing the progress achieved over the past decades, recent progress, and identifying future directions. Integrating multidisciplinary approaches, including multi-omics, molecular breeding, and gene editing, is essential for enhancing the durability of resistance and promote eco-friendly agricultural practices.

2. Global insights into pigeonpea cultivation and insect pest damage

Globally, pigeonpea is cultivated on approximately 5.38 million hectares, with a production of 4.58 million tons and an average productivity of 1,538.56 kg/ha (FAOSTAT, 2023). The overall country-wise contributions to area, production, and productivity are presented in Fig. 1 (source: FAOSTAT, 2023, generated using R version 4.1.1).

Pigeonpea is susceptible to many insect pest species, though only a few cause significant economic damage (Shanower et al., 1999). Among the most economically damaging pests were further categorized based on pigeonpea crop developmental stages, such as (i) Vegetative stage, (ii) Flowering stage, (iii) Post-flowering and pod filling stage, and (iv) Post-maturity stage (Fig. 2; Table 1).

2.1. *Vegetative stage*

During the vegetative stage, *C. cajan* faces damage from various insect pests. Among Polyphagous defoliators, including hairy caterpillars (*Spilosoma obliqua* Walk., *Amsacta* spp., *Chrysodeixis chalcites* (Esper.), *Acanthoplusia orichalcea* F., and *Euproctis* spp., which feed on leaves and other plant parts, severely threatening pigeonpea in the Asia and Africa regions (Sharma et al., 2010) and leaf webber, *Grapholita critica* Meyr., also cause damage during the vegetative leaf stage.

Sap-sucking Hemipteran pests pose a serious threat to crop productivity by using specialized stylets to extract nutrient-rich phloem sap, thereby weakening plants and reducing vigor (Twayana et al., 2022). In pigeonpea, leafhoppers (jassids), particularly *Empoasca kerri* (Pruthi), have recently emerged as major pests. Their feeding causes leaf distortion, vein thickening, and dark green coloration. Heavy infestations during the vegetative stage often lead to flower drop and pod development failure, significantly affecting yield. Moreover, Aphids (*Aphis craccivora* Koch, *Aphis fabae* Scop., *Myzus persicae* Sulz.), prevalent in Asia and Africa, attack young shoots, flowers, and pods, causing stunted growth (Singh and Oswalt, 1992). Likewise, cow bugs (*Otinotus oneratus* Walk., *Oxyrachis tarandus* F.) feed on sap from tender shoots, reducing plant height and vigor, particularly in early crop stages (Seni, 2021; Sharma et al., 2010). Scale insects (*Ceroplastodes cajani* Mask., *Icerya purchasi* Mask.), leaf miner, *Liriomyza huidobrensis* (Blanchard), while not primary pests of annual pigeonpea, frequently infest perennial varieties, completing their life cycle in 2–3 weeks and dispersing via windborne nymphs (Sharma et al., 2010). Eriophyid mites (*Aceria cajani* Mitra) target the lower surfaces of young leaves, causing curling and stunting, and transmitting sterility mosaic disease across pigeonpea-growing regions in India, Myanmar, and Bangladesh (Keerthi et al., 2022). Two-spotted spider mites (*Tetranychus urticae* Koch) induce necrosis in young leaves and stems, leading to defoliation and potential plant death in India and Eastern Africa (Zhang ZhiQiang, 2003).

Root and stem feeders have a significant impact on plant establishment and overall crop survival. Ash weevils (*Myllocerus undecimpustulatus* Faust) are notorious for causing ragged leaf margins as adults, while their larvae feed on roots underground (Khajuria et al., 2015). In recent years, the stem fly (*Ophiomyia phaseoli* Tryon), which lays eggs on tender plant parts, with larvae tunneling into stems and disrupting nutrient transport, has been recorded in Asia, Africa, and Australia, leading to plant wilting, death, or main shoot damage (Singh and Oswalt, 1992). The combined impact of these pests during the vegetative phase necessitates IPM strategies to mitigate damage and ensure sustainable pigeonpea production.

2.2. *Flowering stage*

During pigeonpea flowering, *M. vitrata* damages buds, flowers, and developing pods by webbing them together, leaving frass and causing significant yield loss 5–25 % on average and can surge to 70–80 %, especially in early-maturing genotypes. Its webbed feeding behavior

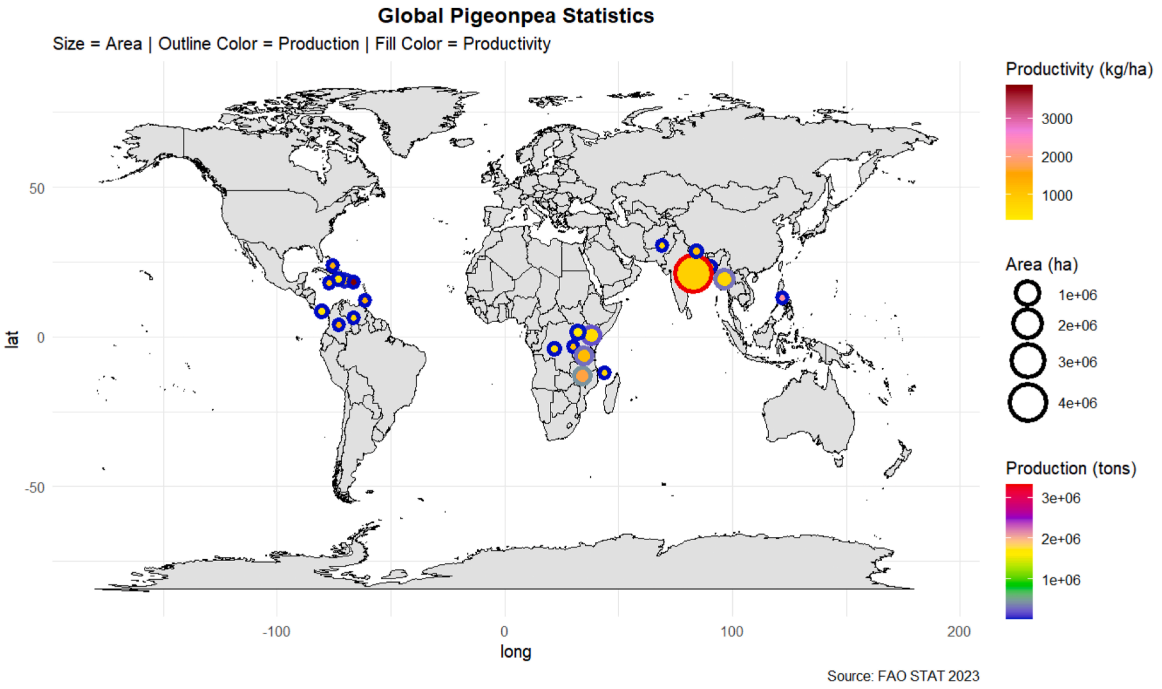

Fig. 1. This map illustrates global pigeonpea statistics during the year 2023, where circle size indicates harvested area (ha), circle outline color reflects total production (tons), and fill color gradient represents productivity (kg/ha). Where, e+06 means 10^6 of pigeonpea by country in 2023, according to FAOSTAT and the current values are represented in USD.

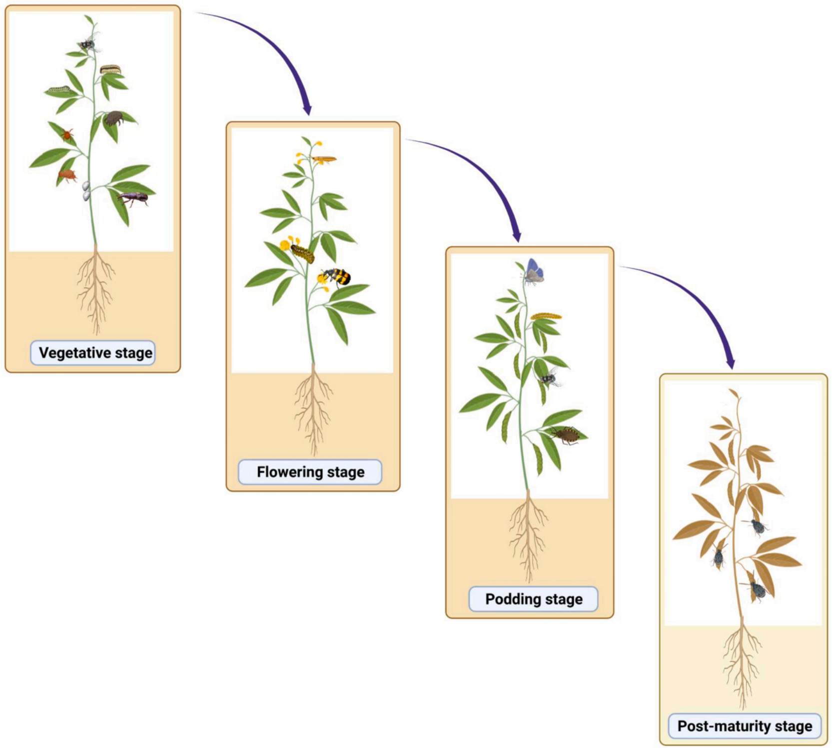

Fig. 2. Temporal occurrence of insect pests across different physiological stages of the crop and their feeding behavior: (A) Insect pest infestation during the vegetative stage, affecting seedling establishment and early plant growth; (B) Pest dynamics at the flowering stage, targeting floral structures and impacting successive flowering; (C) Insect feeding activity during the pod-filling stage, leading to direct damage to developing seeds and yield loss.

makes it difficult to control with most insecticides, and it is emerging as a major pest in legumes (Dhanyakumar et al., 2020; Srinivasan et al., 2021). It also reduced flower retention, leading to lower pod formation and yield loss (Sharma, 2016). Thrips (*Megalurothrips usitatus* Bagn.), common in India and Eastern Africa, infest floral buds and flowers during the flowering stage, causing bud abortion and severe flower

Table 1
Major insect pests of pigeonpea crop during different cropping stage.

Crop developmental stages	Insect pests' common names & scientific names	Distribution	Nature of feeding and damage habit	References
Vegetative Stage	Pod Borer, *H. armigera* (Lepidoptera: Noctuidae)	Asia, Europe, Africa, Australia, and South America	Larvae feed on young leaflets by scraping away green tissue, leaving translucent patches that reduce the plant's photosynthetic capacity. It also feeds on flowers and immature pods.	(Fürstenberg-Hägg et al., 2013; Keerthi et al., 2022)
	Hairy caterpillars, *S. obliqua* (Lepidoptera: Arctiidae); *Amsacta* spp. (Lepidoptera: Erebidae) *C. chalcites* *A. orichalcea* (Lepidoptera: Noctuidae) *Euproctis* spp (Lepidoptera: Lymantridae)	Widely distributed in Asia and Africa	All these polyphagous defoliator larvae feed on young and old leaves and multiple plant parts. This broad feeding range poses a significant threat to agricultural and natural ecosystems.	(Sharma et al., 2010; Singh and Oswalt, 1992)
	Leaf Webbers, *G. critica, Leguminivora ptychora* Meyr (Lepidoptera: Tortricidae)	India	The larva is creamy-yellow and is commonly found binding leaves together while feeding on chlorophyll from within the webbed enclosure. Leaflets are bound with silk, allowing the larva to feed while staying inside the protective web. Infestation begins at the seedling stage and can continue through the reproductive stage, during which the larvae feed within flower buds and young pods.	(Singh and Oswalt, 1992)
	Eriyophid mite, *A. cajani* (Acarina: Eriophyidae)	India, Myanmar, Nepal, Sri Lanka, Thailand and Bangladesh	Major concentration in the younger leaves. on the lower surface of leaves in the diseased plants	(Keerthi et al., 2022)
	Two-Spotted spider mite, *T. urticae* (Acarina: Tetranychidae)	India and Eastern Africa	Necrosis can develop in young leaves and tender stems. Severe infestations by certain species may cause leaves to brown, defoliation, or even plant death	(Singh and Oswalt, 1992; Zhang ZhiQiang, 2003)
	Aphids, *A. craccivora, A. fabae, M. persicae* (Hemiptera: Aphididae)	Asia and Africa	Aphids infest young shoots, flowers, and pods, extracting sap from these plant parts.	(Singh and Oswalt, 1992)
	Cow bugs, *O. oneratus, O. tarandus* (Hemiptera: Membracidae)	India	Nymphs and adults feed on sap from tender shoots. Heavy infestations during the early crop growth may result in stunting and reduced plant growth.	(Seni, 2021; Sharma et al., 2010)
	Scale insects, *C. cajani, I. purchasi* (Hemiptera: Coccidae)	India	Scale insects extract fluids from tender stems, shoots, and leaves. While not major pests of annual pigeonpea, they frequently infest perennial varieties. Their life cycle completes in 2–3 weeks, with mobile nymphs dispersing by wind while adult females remain in colonies.	(Sharma et al., 2010)
	Ash weevils, *M. undecimpustulatus* (Coleoptera: Curculionidae)	Asia and Africa	Adult weevils generally chew the leaflets along the margins, causing a ragged effect. Larvae live in the soil, where they feed mainly on roots.	(Khajuria et al., 2015)
	Stem fly, *O. phaseoli* (Diptera: Agromyzidae)	Asia, Africa and Australia	Adult stem fly lay eggs on the plant's tender parts. Upon hatching, the larvae bore into stems, disrupting nutrient flow and causing wilting or death of young plants.	(Singh and Oswalt, 1992)
Flowering stage	Spotted pod borer, *M. vitrata* (Lepidoptera: Crambidae)	Asia, Africa, Australia and Latin America	larvae cause extensive damage to floral buds and flowers. The characteristic symptom is the webbing together of flowers, pods, and leaves with frass often on pods and shoot tips.	(Dhanyakumar et al., 2020; Srinivasan et al., 2021)
	Thrips, *M. usitatus* (Thysanoptera: Thripidae)	India and Eastern Africa	Heavy infestation of thrips can lead to the shedding of buds and flowers	(Sharma et al., 2010)
	Blister beetles, *M. pustulata* and *M. phalerata* (Coleoptera: Meloidae)	Asia and Africa	Adults feed on the flowers, tender pods and young leaves, resulting in fewer pods	(Dialoke et al., 2014; Singh and Oswalt, 1992)
Post-flowering and pod filling stages	Pigeonpea Pod Fly, *M. obtusa* (Diptera: Agromyzidae)	South and Southeast Asia	Larvae/maggot bores into the pod and feeds on developing seed during vegetative stage of the crop.	(Shanower et al., 1998; Sharma et al., 2010)
	Pod Borer, *H. armigera* (Lepidoptera: Noctuidae)	Asia, Europe, Africa, Australia, and South America	Larvae feed on young leaflets by scraping away green tissue, leaving translucent patches that reduce the plant's photosynthetic capacity. It also feeds on flowers and immature pods.	(Fürstenberg-Hägg et al., 2013; Keerthi et al., 2022)
	Pod sucking bugs, *Clavigralla gibbosa* Spinola, *C. scutellaris* West wood, *C. tomentosicollis* Stal, *R. dentipes* and *A. curvipes* (Hemiptera: Coreidae). *N. viridula* (Hemiptera: Pentatomidae)	Africa and Asia	These bugs suck sap from developing seeds through the pod wall, making seed shrivelled with dark patches often associated with saprophytic fungi. Attacked seeds do not germinate and are also not acceptable as food	(Sharma et al., 2010; Singh and Oswalt, 1992)
	Plume moth, *E. atomosa, S. anisodactylus* (Lepidoptera: Pterophoridae)	Asia, Africa and Australia	Larvae bore into the developing pods and feed on tender seeds. The pupa, which appears like a larva, is often found attached to the pod's surface or on the pedicel.	(Keerthi et al., 2022; Sharma et al., 2010)
	Blue butterfly, L. *boeticus* (Lepidoptera: Lycaenidae)	Europe, Africa, South and Southeast Asia, and Australia.	It causes damage to buds, flowers and tender pods. It is less significant than other pod borers.	(Keerthi et al., 2022)

(*continued on next page*)

Table 1 (*continued*)

Crop developmental stages	Insect pests' common names & scientific names	Distribution	Nature of feeding and damage habit	References
Post-maturity stage	Bruchids, *C. maculatus, C. analis*, and *C. chinensis* (Coleoptera: Bruchidae)	Asia and Africa	These insects begin their infestation when the pods are in the ripening stage in the field and are subsequently carried with grain into the stores resulting in considerable yield losses	(Keerthi et al., 2022)

shedding. Their impact on pod formation and yield is worsened under hot, dry conditions when their populations surge (Sharma et al., 2010). Blister beetles (*Mylabris pustulata* Thun. and *Mylabris phalerata* Pall.), found in Asia and Africa, feed on pigeonpea flowers, tender pods, and young leaves at the flowering stage, reducing pollination and pod formation. Severe infestations can significantly impact seed production (Dialoke et al., 2014).

2.3. Post-Flowering and podding stage

During the post-flowering and pod-filling stages, the pod borer *H. armigera* is widespread across Asia, Africa, Australia, and parts of South America. Its larvae feed on young leaves, flowers and pods completely by creating circular holes on pods that reduce overall plant yield losses 25–35 % and, in severe cases, up to 90–100 % (Keerthi et al., 2022). Additionally, pigeonpea pod fly *M. obtusa*, bores into developing pods and feeds on tender seeds, causing shriveled and damaged seeds, and are common in South and Southeast Asia and Eastern Africa. This reduces seed viability and marketability, significantly impacting the yield of 25 to 30 % (Shanower et al., 1999; Sharma, 2016; Sharma et al., 2010) and due to internal feeding habit, most of the existing insecticides are less effective for managing this pest. Even the pod wasp, *Tanaostigmodes cajaninae* LaSalle, also damages developing pods (Lateef et al., 1985).

Pod-sucking bugs (*Clavigralla* spp., *Riptortus dentipes* F.*, Anoplocnemis curvipes* F.*, Nezara viridula* L.) in Africa and Asia pierce pod walls to suck sap from developing seeds, causing shriveling, dark patches, and fungal contamination. Infested seeds often fail to germinate and are unfit for consumption. Plume moths (*Exelastis atomosa* Wals., *Sphenarches anisodactylus* Walk.) and the blue butterfly (*Lampides boeticus* L.) bore into pods and feed on developing seeds, causing direct seed loss. Plume moths also pupate on pod surfaces, reducing crop quality (Sharma et al., 2010).

2.4. Post-Maturity stage

Bruchids (*Callosobruchus maculatus* F.*, Callosobruchus analis* F.*, Callosobruchus chinensis* L.) infest pigeonpea pods during ripening and continue damaging seeds in storage across Asia and Africa cause loss up to 30–40 % of seeds. Their grubs develop inside seeds, causing weight loss, reduced seed viability, and contamination, making grains unfit for consumption or planting (Keerthi et al., 2022).

Overall, pigeonpea insect pests cause yield losses ranging from 30 % to 80 %, depending on the severity of the pest and management practices. Pod borers (*H. armigera* and *M. vitrata*) are considered the most damaging pests, resulting in significant economic losses in Asia, Africa, and the Australian regions. Moreover, other insect pests affecting pigeonpea include pod fly *M. obtusa,* which infests developing pods and seeds, leading to reduced seed viability, quality, appearance, and germination rates in India and the eastern African region.

3. Current understanding of HPR in pigeonpea and achievements

Resistance is a fundamental aspect of a plant defense system, enabling it to counteract insect pests by influencing their physiology, life cycle, and behavior, thereby minimizing damage to growth and development (Dicke and Baldwin, 2010). In this context, HPR is one of the eco-friendly approaches to pest management. In this approach, the selection of naturally occurring genetic variants that confer resistance to insect pests through favorable morphological, chemical, or biological traits. This concept involves developing or selecting plant varieties that can withstand pest attacks, reducing the damage these pests cause while minimizing the need for chemical pesticides. HPR is particularly valuable in IPM strategies, as it aligns with environmental sustainability, reduces economic input costs, and promotes ecological balance.

3.1. Categories and mechanisms of resistance

HPR functions through three main categories: antixenosis, antibiosis, and tolerance (Vishal et al., 2023). Overall, antixenosis (non-preference) of a host plant happens when a plant's structural and phenotypic conditions make it possess unsuitable morphological traits for insects' ability to oviposit and seek shelter, thereby deterring pests. Antibiosis affects insect life cycles through plant-produced biochemical compounds that reduce growth, fecundity, and survival. Tolerance enables plants to endure pest damage with minimal yield loss, promoting resilience and coexistence (Sharma and Ortiz, 2002).

3.2. Plant-induced defense systems

Generally, plant-induced defense systems are dynamic responses activated upon insect herbivory or pathogen attack, enhancing plants' ability to resist pests (Dicke and Baldwin, 2010). These defenses are broadly categorized into direct and indirect mechanisms. Direct defenses involve structural modifications like increased trichome density and biochemical changes, including the production of toxic secondary metabolites, proteinase inhibitors (PIs) and plant lectins that deter insect feeding (Coley et al., 2006; Guarino et al., 2021; Howe and Schaller, 2008). Indirect defenses recruit natural enemies of pests by releasing volatile organic compounds (VOCs) to attract parasitoids and predators (Karaca et al., 2024; Pérez-Hedo et al., 2021; Wang et al., 2021). Induced resistance is often regulated by phytohormonal pathways, primarily jasmonic acid (JA) and salicylic acid (SA), which orchestrate a cascade of molecular and physiological changes (Anil et al., 2014; Guerreiro and Marhavý, 2023; Mithöfer and Maffei, 2017).

Exogenous application of jasmonic acid (JA) and salicylic acid (SA) in pigeonpea enhances plant defenses against the spotted pod borer, *M. vitrata.* JA treatment notably increases secondary metabolites like tannins, phenols, and protease inhibitors, leading to reduced larval growth and digestive efficiency in *M. vitrata.* While SA also induces defensive responses, its effects are less pronounced compared to JA (Khokhar et al., 2024, S. 2023). Moreover, resistance can influence crop growth patterns by reallocating resources to compensate for damage, ensuring continued development despite pest pressure (Schultz et al., 2013). This multifaceted defense system protects the plant and contributes to sustainable pest management by reducing reliance on chemical insecticides.

3.3. Biophysical factors for plant defense

Biophysical traits contribute significantly to plant resistance against insect pests. However, plant traits such as trichome density and morphology, pod wall thickness, pigmentation, seed hardness, and pod architecture disrupt pest mobility and feeding efficiency. Additionally, delayed flowering and extended maturity enable temporal escape from peak infestation periods (Fürstenberg-Hägg et al., 2013; Sharma, 2016; War et al., 2012).

In pigeonpea, biophysical characteristics play a significant role in plant resistance against insect pests, mainly through antixenosis mechanisms that deter feeding and oviposition (Sharma, 2016). The higher densities of both glandular and non-glandular trichomes in CWRs of pigeonpea, such as *Rhynchosia aurea* (Willd.) DC., *Cajanus scarabaeoides* (L.) Thou., and *Cajanus acutifolius* (Benth.) Maesen, are associated with reduced oviposition preference by adult *H. armigera* (Sharma et al., 2009; Sujana et al., 2008). Variations in trichome density and length impact larval weight gain in *M. vitrata*, further contributing to plant resistance (Sunitha et al., 2008) (Table 2). Recently, a total of 96 pigeonpea CWR's were screened for resistance to *H. armigera* with *C. scarabaeoides* accessions (ICP 15716, 15718, 15726) showing the lowest damage and larval performance. *R. suaveolens* (ICP 15867) also showed strong resistance. Pod trichome density, length, and width were key resistance traits (Karrem et al., 2025). In general, extra-early and determinate genotypes of pigeonpea are more vulnerable to pod borer infestation due to their synchronized flowering and pod-setting (cluster pod setting), which creates a concentrated period of food availability for the pod borers (Sharma, 2016). Moreover, plant architecture strongly influences *H. armigera* preference in cultivated pigeonpea, especially during reproductive stages (Volp et al., 2023). Plants with flowers and pods are preferred for oviposition due to their structural suitability and higher nutritional value for larvae. Moreover, traits such as specific pod features—like thickness and deep purple or green coloration without stripes—deter larval feeding and movement, thereby affecting pest performance (Sharma, 2016; Vishal et al., 2023; Volp et al., 2024).

However, the constitutive morphological traits such as pod length, pod angle, growth habit, and longer trichomes in *C. cajan* genotypes (AL 1747 and ICPL 332WR) act as inherent physical barriers that hinder *M. vitrata* larval movement and feeding, thereby reducing pod damage (Vishal et al., 2023; Wubneh and Taggar, 2016a). Moreover, delayed flowering and maturity in genotypes such as ICPL-98008, ICPL 332WR, and SM-30 act as escape mechanisms by avoiding overlap with peak pest infestations (Wubneh and Taggar, 2016a). Seed hardness and a higher seed coat proportion provide mechanical resistance against bruchids (*C. chinensis* and *C. maculatus*), restricting larval penetration and reducing storage losses (Naik et al., 2021) (Table 2). These biophysical traits in pigeonpea and its wild relatives represent valuable resistance resources that can be exploited in pre-breeding programs.

3.4. *Biochemical factors for plant defense*

Direct chemical defences are mediated by diverse secondary metabolites that disrupt the metabolic functions of insects, particularly during the larval stage (Al-Khayri et al., 2023; Upadhyay et al., 2024). Another crucial aspect of resistance is the induced biochemical responses, where plants swiftly activate and produce secondary metabolites such as alkaloids, flavonoids, and phenolics that act as toxins, feeding deterrents, or insect growth regulators (Wari et al., 2022). These compounds interfere with pests' biological functions, such as digestion, reproduction, and survival, thereby reducing their ability to thrive on the plant. Furthermore, some plants exhibit induced resistance, where exposure to insect attack triggers systemic responses that enhance their ability to withstand future infestations (Flors et al., 2024; War et al., 2012).

In pigeonpea, few attempts have been made to identify the biochemical traits that play a crucial role in plant defense against insect pests by affecting insect physiology, development, and feeding behavior. Antibiosis, a key biochemical defense mechanism, has been observed in pigeonpea CWR genotypes such as *C. acutifolius, Cajanus cajanifolius* (Haines) Maesen*, Cajanus sericeus* (Baker) Maesen*, Paracalyx scariosa* (Roxb.) Ali*, C. scarabaeoides*, and *Cajanus albicans* (Wight & Arn.) Maesen. These wild genotypes exhibit traits that negatively affect the biology of *H. armigera*, such as prolonging its post-embryonic development and reducing larval survival and reproductive success (Sharma et al., 2022; Sujana et al., 2008). The delayed development in insects is often attributed to plant-derived secondary metabolites and antinutritional compounds that impair their growth. Furthermore, defense-related enzymes such as peroxidase and superoxide dismutase (enzymatic antioxidants), along with polyphenol oxidase, contribute significantly to plant resistance. These enzymes, together with secondary metabolites like total phenols, flavonoids, tannins, and lectins, play vital roles in defense against *H. armigera*. In particular, polyphenol oxidase is involved in phenol oxidation, a well-documented mechanism that deters herbivory (Mareyam et al., 2020; Sharma et al., 2022). High phenol concentrations, particularly in flowers, have been linked to reduced nutritional value and increased toxicity, thereby limiting insect feeding and development in resistant pigeonpea genotypes, such as ICPL 98003 and ICPL 332WR, against *M. vitrata* (Sunitha et al., 2008; Vishal et al., 2023). Similarly, phenolic compounds, including isoquercitrin, quercetin, quercetin-3-methyl ether, and a stilbene, were identified. While quercetin and its derivatives had little effect, the stilbene deterred *H. armigera* larvae. Resistant cultivars showed higher isoquercitrin levels, lower quercetin levels, and a greater stilbene-to-quercetin-3-methyl ether ratio (Green et al., 2003). Moreover, high phenol concentrations act as antifeedants, reducing larval survival and pest infestation on pod borers (Sahoo and Patnaik, 2003; Sujana et al., 2008; Vishal et al., 2023). Specific phenolic compounds such as benzoic acid, p-nitrophenol, and orcinol have also been identified as potent deterrents against *H. armigera*. Genotypes with higher concentrations of these compounds exhibit strong resistance by reducing larval damage and feeding activity (Banu et al., 2007; Devi et al., 2013). Additionally, post-ingestive adaptations at the gut level, involving the regulated release of digestive enzymes, play a crucial role in driving physiological plasticity (Sarate et al., 2012).

3.4.1. *Antinutritional factors for plant defense*

Plants employ various antinutritional factors to defend against insect pests by interfering with their digestion, metabolism, and overall development. Key compounds, including lectin-related proteins, tannins, protease inhibitors, and alpha-amylase inhibitors (α-AIs), play a significant role in resistance mechanisms (Sathish et al., 2024, K. 2023). Lectin-related proteins, found in *C. scarabaeoides, C. cajanifolius*, and *Cajanus platycarpus* (Benth) Maesen, exhibit antibiosis effects by disrupting insect digestion and metabolism, reducing the survival and reproductive success of bruchids, *C. chinensis* and *C. maculatus* (Jadhav et al., 2012; Mishra and Panigrahi, 2017). Additionally, Tannins and flavonoids, present in resistant pigeonpea genotypes such as ICP 89049, ICP 7035, ICPL 332WR, ENT 11, Dholi dwarf DB, and *C. platycarpus* (ICPW 66), serve as antifeedants, deterring insect feeding and reducing larval growth (Table 2). These compounds disrupt digestive enzymes and create antinutritional effects on insect development, increasing larval mortality (Naik et al., 2021; Sharma, 2016; Sharma et al., 2022; Vishal et al., 2023). Biochemical analysis of *H. armigera* gut proteinases showed diet and developmental stage-dependent variation. Larvae fed on chickpea exhibited 2.5- to 3-fold higher proteinase activity than those on pigeonpea, cotton, and okra. Serine proteinases dominated, with metalloproteases, aspartic, and cysteine proteases also detected, especially in early instars. Activity peaked in the fifth instar and declined in the sixth. Higher proteinase activity on artificial diets with non-host PIs suggests a potential for selecting effective PIs for pest resistance (Patankar et al., 2001). Non-host crop trypsin-like proteinase activity, along with the production of inhibitor-insensitive proteinase shows potential for developing *H. armigera*-resistant genotypes (Harsulkar et al., 1999). Additionally, PIs ppLPI-1, showing homology from pigeonpea (cv. BSMR 736) and acetone-precipitated ppLPI-1 demonstrated significant inhibitory activity against bovine trypsin and *H. armigera* gut proteinases in solution assays (Shaikh et al., 2018).

Table 2
Effects of some of the bio-physical, bio-chemical and antinutritional factors on pigeonpea insect pests.

Different plant characters governing resistance	Genotype/Accession	Possible mode of action	Targeted insects	References
Bio-physical				
Non-glandular trichomes (trichome type C and D) were associated with resistance	*R. aurea, C. scarabaeoides, C. sericeus, C. acutifolius,* and *Flemingia bracteata*	Oviposition non-preference due to more trichome density	*H. armigera*	(Sharma et al., 2009)
Antixenosis	*C. acutifolius* (ICPW 1); *C. albicans* (ICPW 13 and 14); *C. sericeus* (ICPW 159 and 160); *C. platycarpus* (ICPW 68); *C. scarabaeoides* (ICPW 83, 90, 94, 125, 137, 141 and 280); *Paracalyx scariosa* (ICPW 207) and *R. aurea* (ICPW 210)	Oviposition non-preference due to more trichome density	*H. armigera*	(Sujana et al., 2008)
Trichome density on leaves and Trichome length on pods	*C. cajan* (ICPL 98003)	Trichome density on leaves and Trichome length on pods affect the percentage of larval weight gain in the resistance genotypes	*M. vitrata*	(Sunitha et al., 2008)
High trichome density on leaves and pods (177.33 and 43.33 trichomes/4.6 cm^2, respectively). Long trichome length on leaves and pods (66.26 and 180.83 µm, respectively). Wide pod angle (65°). Indeterminate growth habit and early maturity	*C. cajan* (AL 1747)	Physical deterrence, reduced larval feeding and weight gain, and decreased pod damage. Impairs larval movement and feeding; decreases larval survival and pod damage. Creates an unfavorable micro-environment for larval survival and feeding. Avoidance of the peak infestation period, faster recovery from pest damage.	*M. vitrata*	(Wubneh and Taggar, 2016b)
Trichome Length (0.59 mm). Trichome Density (123.5 per 4.5 mm^2). Pod Length (8.27 cm). Delayed Flowering (143.5 days to 50 %). Delayed Maturity (212 days to maturity).	*C. cajan* (ICPL-98008) SM-30 ENT-11 SM-146 ICP-13198	Acts as a physical barrier, limiting larval movement and feeding. Higher density reduces pod damage by limiting larval feeding. Longer pods recorded less pod damage. Higher phenol concentrations deter insect feeding. Late flowering reduces synchronization with peak pest incidence. An extended crop cycle, avoiding peak pest attack periods.	*M. vitrata*	(Devi et al., 2013)
Seed hardness and High seed coat proportion	*C. cajan* (ICP 89049, IPA 37, Dholi dwarf DB)	Mechanical resistance, preventing larval penetration.	Bruchids *(C. chinensis, C. maculatus).*	(Naik et al., 2021)
Bio-chemical				
Antibiosis	*C. acutifolius* (ICPW 1), *C. cajanifolius* (ICPW 29), *C. sericeus* (ICPW 160), *P. scariosa* (ICPW 207), *C. scarabaeoides* and *C. albicans.*	Post-embryonic development period is prolonged in insects	*H. armigera*	(Sujana et al., 2008)
Peroxidase, Superoxide dismutase, Polyphenoloxidase and total phenols	*C. cajan* (ICP12142 and LRG-41)	Phenol oxidation is one of the defense strategies against herbivorous insects.	*H. armigera*	(Mareyam et al., 2020)
High phenol in flower	*C. cajan* (ICPL 98003)	Antinutritional activity	*M. vitrata*	(Sunitha et al., 2008)
Low amino acid content in pod coats (1.40–1.52 mg/g) and seeds (1.39–1.55 mg/g). Low protein content in pod coats (6.5–8.9 %) and seeds (16.1–18.2 %). Low sugar content in pod coats (2.91–3.44 %) and seeds (2.86–3.51 %). High phenol content in pod coats (6.33–8.97 mg/g) and seeds (7.64–9.49 mg/g).	*C. cajan* (H 892, ICPL 83024, AS 46, T21, AS 36)	Limits larval growth and development. Reduces nutritional value and suppresses pest infestation. Decreases palatability, reducing pest feeding. Acts as an anti-feedant, decreasing larval survival.	*H. armigera*	(Sahoo and Patnaik, 2003)
Benzoic Acid. p-Nitrophenol. Orcinol.	*C. cajan* (ICP 13201)	It is in higher concentration among tolerant genotypes and deters insect feeding. Acts as an anti-feedant, reducing larval damage. It is in the highest concentration among the three phenols, strongly associated with insect resistance.	*H. armigera*	(Banu et al., 2007)
Phenolic Acids (Benzoic Acid, p-Nitrophenol, Orcinol)	*C. cajan* (ICP 13201)	Higher phenol concentrations deter insect feeding.	*H. armigera*	(Devi et al., 2013)
Antinutritional				
Lectin-related proteins	*C. scarabaeoides* (ICPW-094, 095), *C. cajanifolius* (ICPW-030, 031) and *C. Platycarpus* (ICPW-067, 068)	Antibiosis mechanism (Interfering with their digestion and metabolism)	*C. maculatus, C. chinensis*	(Jadhav et al., 2012; Mishra and Panigrahi, 2017)

(*continued on next page*)

Table 2 (*continued*)

Different plant characters governing resistance	Genotype/Accession	Possible mode of action	Targeted insects	References
Tannin content. Lectin-related proteins. Protease inhibitors (PIs). Flavonoids and Phenolics. Alpha-amylase inhibitors (α-AIs).	ICP 89049, Dholi dwarf DB. *C. scarabaeoides* (ICPW 130), *C. platycarpus* (ICPW 66, ICPW 68), *C. cajanifolius* (ICPW 31). *C. cajanifolius* (ICPW 31), ICPW 30. *C. cajanifolius* (ICPW 31), *C. platycarpus* (ICPW 66), Inter-specific derivative A 4–10–7–19. *C. scarabaeoides* (ICPW 130), *C. platycarpus* (ICPW 68). *C. scarabaeoides* (ICPW 130), ICP 89049, IPA 37.	Limits egg adhesion and larval entry. Antifeedant effect with reduction of larval growth. Severe growth retardation and formation of larval-pupal, as well as pupal-adult intermediates *H. armigera* larvae fed with *C. platycarpus* Kunitz inhibitor Disrupts digestive enzymes and causes larval mortality. Interferes with insect digestion and reduces growth rate. Toxic to larvae; affects metabolism. Reduces starch digestion; weakens larvae.	Bruchids (*C. chinensis, C. maculatus*) and Pod borer, *H. armigera.*	(Naik et al., 2021; Gujjarlapudi et al., 2023;Sathish et al., 2024, K. 2023)

Moreover, α-AIs are key defenses against *H. armigera*, with nitrite acting as a potent mixed non-competitive inhibitor of its gut α-amylase. In some pigeonpea genotypes, significant upregulation of nitrate reductase and increased nitrite accumulation in moderately resistant genotypes indicated their role in resistance. Nitrite reductase activity was also higher in these genotypes. A negative correlation between NR, NiR, nitrite levels, and pod damage further confirmed their involvement in resistance against *H. armigera* (Kaur et al., 2014). Together, these mechanisms provide a multi-layered defense strategy that strengthens plant resistance and offers valuable genetic resources for breeding insect-resistant crop varieties, ultimately contributing to a pest management strategy.

4. Progress made in understanding the genetic basis of pigeonpea breeding for resistance/tolerance lines to insect pests

Genetic variation is essential for developing new recombinant genotypes, leading to improved crop varieties. Plant breeders primarily rely on the primary gene pool, as it allows for easy hybridization and selection (Swarup et al., 2021). Pigeonpea is unique because self- and cross-pollination systems operate simultaneously under natural conditions. Historically, the approaches of pigeonpea breeders may have limited the effective utilization of genetic variation, especially in the context of outcrossing on selection efficiency and used breeding procedures outlined for self-pollinated crops (Saxena, 2008). Moreover, several cultivars have been developed using the primary gene pool by focusing on desired traits. Unfortunately, many disease and insect resistance sources are unavailable in the primary gene pool. Still, some promising lines were identified in CWRs in the secondary and tertiary gene pools of pigeonpea. The secondary gene pool, consisting of compatible species, has been successfully used for breeding high-protein pigeonpea, cytoplasmic male sterility (CMS), and biotic stress resistance/tolerance. In contrast, the tertiary gene pool, which includes species not crossable through conventional breeding, has been less commonly utilized in pigeonpea crop improvement (Choudhary et al., 2013; Saxena, 2008).

The development of pigeonpea varieties resistant to insect pests depends on the availability of resistance genes and an understanding of their inheritance (Rubiales et al., 2015). HPR is governed by several minor genes (polygenic resistance) or single significant genes (monogenic/oligogenic resistance). However, advances in system biology and genomics have significantly facilitated the precise introgression of both polygenic and monogenic resistance traits (Sandhu and Kang, 2017; Sharma et al., 2002).

4.1. Genomics and pre-breeding: status and perspective

Developments in pigeonpea breeding and pre-breeding approaches for insect resistance have focused on understanding the genetic basis of HPR. Traditional breeding approaches, such as selection for resistant genotypes, have been complemented by genomic tools, including quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), and marker-assisted selection (MAS) (Satheesh Naik et al., 2024). Moreover, incorporating resistance genes from CWRs has emerged as a promising strategy and provides genetic diversity (Green et al., 2006; Sharma et al., 2013). Several wild *Cajanus* species, especially those from the secondary gene pool, which are cross-compatible with cultivated pigeonpea, have been used for the genetic improvement of pigeonpea (Mallikarjuna et al., 2011). Notably, *C. scarabaeoides, C. acutifolius, C. platycarpus, Cajanus reticulatus* (F.Muell.) Maesen, *C. sericeus,* and *C. albicans* have been reported to have resistance to major insect pests of pigeonpea (Kameswara Rao et al., 2003; Sharma et al., 2009, 2020; Sujana et al., 2008).

Only a few attempts have been made to identify molecular markers and quantitative trait loci for insect pest resistance in pigeonpea, providing valuable genetic resources for breeding programs. In past decades, QTL studies on *H. armigera* resistance identified the pod borer resistant gene (PPB1) as a key locus that was linked to non-glandular short trichomes in an F_2/F_3 population using Random Amplified Polymorphic DNA (RAPD) and Inter Simple Sequence Repeat (ISSR) markers (Mishra et al., 2013). Similarly, pod borer resistance, measured as the percentage of pod damage (antibiosis), was evaluated in an F_2 population using Start Codon Targeted marker (SCoT), RAPD, and ISSR markers (Sahu et al., 2015). Moreover, antibiosis resistance mechanisms against *E. atomosa* were investigated in F_2, F_3, and BC_1F_1 populations using RAPD and Sequence Characterized Amplified Region (SCAR) markers. A total of 143 RAPD markers were screened to detect marker-trait associations linked to plume moth resistance (PPM1 gene) (Mishra et al., 2015). By using 18 SCoT, 5 ISSR, and 143 RAPD markers, resistance in an F_2 population was evaluated against the pod borer blue butterfly (L. *boeticus*), which resulted in the identification of the blue butterfly resistant gene PBB1. Their work focused on field screening and antixenosis (trichome-based resistance) (Sahu et al., 2015). However, this research was extended in F_2, F_3, and BC_1 populations, using 85 Simple Sequence Repeat (SSR) markers, 143 RAPD markers, and nine ISSR markers to identify qPBB2.1 (Mishra et al., 2016) (Table 3).

Few studies have been conducted on the inheritance of resistance, and the first study focused on *H. armigera* resistance in F_1, F_2, and BC populations, specifically examining antibiosis, which affects larval survival and development. Resistance to pod fly (*M. obtusa*) was examined in F_1, F_2, and BC populations using field pod damage ratings to assess resistance levels in different genetic backgrounds (Verulkar et al., 1997). However, resistance is associated with specific trichome types and densities on the pod surface. Inheritance studies across generations (F_1, F_2, BC_1, and F_3) showed that single dominant genes control both pod borer resistance and key trichome traits. These traits can be effectively

Table 3
QTL mapping and Inheritance studies for major insect pests in pigeonpea.

Insect pest	Population type	Marker system	No. Markers used	Name of the QTLs	Trait studied	References
QTL Mapping Studies						
Pod borer, (*H. armigera*)	F2/ F3	RAPD, ISSR	150 RAPD and 12 ISSR	PPB1	Non-glandular short trichomes	(Mishra et al., 2013)
	F2	SCoT, RAPD, ISSR	18 SCoT, five ISSR and 143 RAPD	PPB1	Antibiosis (% pod damage)	(Sahu et al., 2015)
Plume moth, (*E. atomosa*)	F2/F3/ BC1F1	RAPD, SCAR	143 RAPD markers	PPM$_1$	Antibiosis	(Mishra et al., 2015)
	F2	ScoT, RAPD, ISSR	18 SCoT, five ISSR and 143 RAPD	PPM1	Field screening and antixenosis studies (Trichome)	(Sahu et al., 2015)
	F2/F3/ BC1	SSR, RAPD, ISSR	85 SSRs, 143 RAPD and 9 ISSR	qPPM2.1	Field screening and antixenosis studies under lab conditions	(Mishra et al., 2016)
Blue butterfly, (L. *boeticus*)	F2	SCoT, RAPD, ISSR	18 SCoT, five ISSR and 143 RAPD	PBB1	Field screening and antixenosis (Trichome) studies	(Sahu et al., 2015)
	F2/F3/ BC1	SSR, RAPD, ISSR	85 SSRs, 143 RAPD and 9 ISSR	qPBB2.1	Field screening and antixenosis studies under lab conditions	(Mishra et al., 2016)
Inheritance studies						
Pod borer, (*H. armigera*)	F2/F3/BC1	–	–	–	Trichomes (A, B, C and D)	(Aruna et al., 2005)
Pod borer, (*H. armigera*)	F1/F2/BC	–	–	–	Antibiosis	(Verulkar et al., 1997)
Pod fly, (*M. obtusa*)	F1/F2/BC	–	–	–	Field pod damage rating	(Verulkar et al., 1997)

introduced into cultivated pigeonpea through hybridization and selection (Aruna et al., 2005) (Table 3).

At the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India, pre-breeding attempts are made by utilizing CWRs, and different resistance components from various wild *Cajanus* species are being integrated into a single pigeonpea cultivar. To achieve this, two four-way complex crosses were developed in the genetic backgrounds of ICPL 87119 [(ICPL 87119 × *C. acutifolius*) × (ICPL 87119 × *C. scarabaeoides*)] and ICP 8863 [(ICP 8863 × *C. acutifolius*) × (ICP 8863 × *C. scarabaeoides*)], which resulted in the development of over 2300 introgression lines (ILs) (Sharma and Upadhyaya, 2016). Subsequent field evaluations have identified 156 ILs with reduced pod borer damage, and further screening refined this to 21 ILs with improved resistance. These ILs, carrying novel resistance alleles, can enhance pod borer resistance in cultivated pigeonpea (Sharma et al., 2022).

Furthermore, breeding with *C. platycarpus* broadened genetic diversity in pigeonpea, by introducing resistant related genes by using hormone-aided pollination, embryo rescue, tissue culture, and backcrossed progeny, which showed variations in plant traits and a new CMS source that is potentially resistant to pod borer, bruchids, and pod fly (Mallikarjuna et al., 2011).

Overall, these recent findings provided essential insights into genetic resistance mechanisms in pigeonpea, aiding in the development of insect-resistant cultivars through marker-assisted selection. The use of diverse molecular markers across multiple studies highlights the complexity of host-plant resistance and underscores the importance of integrating genomic tools in breeding programs (Fig. 3).

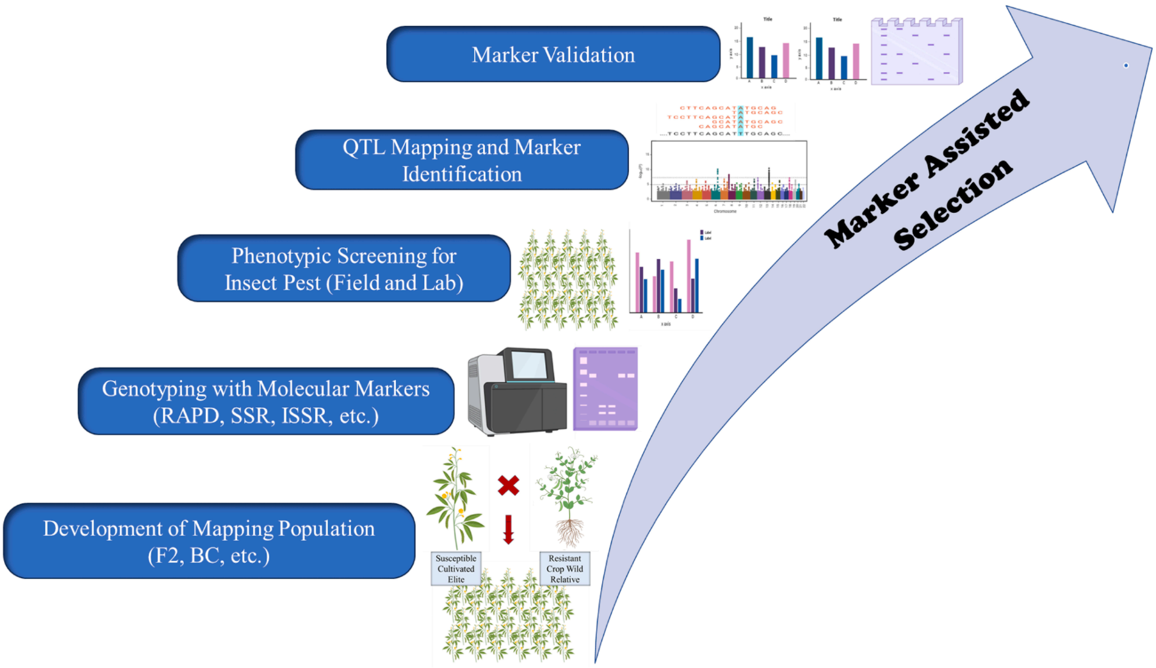

Fig. 3. Advanced pigeonpea breeding strategies using crop wild relatives (CWRs) to develop introgression lines with improved resistance and/or tolerance to insect pests, by harnessing genetic diversity to strengthen host plant defense and improve pest management in cultivated crops.

4.2. Transcriptomics

The integration of pan-genomics and transcriptomics has greatly advanced the identification of resistance genes in pigeonpea. Transcriptomic studies, particularly RNA sequencing (RNA-seq), have uncovered differentially expressed genes (DEGs) involved in insect resistance, such as those encoding protease inhibitors, secondary metabolites, and signaling molecules (Njaci et al., 2021; Swathi et al., 2016). By analyzing gene expression in response to pest infestation, these approaches reveal key regulatory pathways and defense mechanisms (Tyagi et al., 2022). Comparative transcriptomics between wild *Cajanus* species and cultivated pigeonpea further enables the discovery of resistance-associated genes related to antixenosis, antibiosis, and induced systemic responses (Purohit et al., 2021; Varshney et al., 2017), facilitating the deployment of novel resistance genes for genetic improvement (Satheesh Naik et al., 2024).

Although earlier studies on resistance potential have declined in focus, CWRs of *Cajanus* species remain underutilized, primarily due to challenges such as linkage drag and cross-incompatibility. However, recent transcriptomic comparisons between *C. platycarpus* and cultivated *C. cajan* under pod borer infestation have revealed that *C. platycarpus* mounts a more rapid and robust defense through dynamic transcriptomic reprogramming. Functional analyses have highlighted key defense-related pathways, including systemic acquired resistance (SAR), redox homeostasis, and reconfiguration of primary metabolic processes (Rathinam et al., 2025, 2019). Furthermore, RNA-seq findings were validated by transient expression of resistance genes [(Chitinase 4 (*CHI4*), Indole-3-Acetic Acid–Amido Synthetase (*IAAS*), and *C75A1*) in *Nicotiana benthamiana* Domin, demonstrating their efficacy against *H. armigera*. qPCR results confirmed these insights, offering valuable leads for developing durable pod borer resistance in pigeonpea (Rathinam et al., 2019). Additionally, in *C. platycarpus,* surges in herbivory-induced reactive oxygen species (ROS) cause redox post-translational modifications (PTMs) of methionine-rich proteins, leading to oxidative damage. Methionine sulfoxide reductases (MSRs) maintained redox balance, with *C. platycarpus* MSR A2 (*CpMSRA2*) and *CpMSRB1* showing herbivore-induced expressions. Differential lipid peroxidation and antioxidant enzyme activity indicated effective redox management (Rathinam et al., 2022).

Similarly, *C. scarabaeoides* showed the key genes involved in cytokinin, ethylene, JA, and calcium signaling and identified the transcriptional factors WRKY, MYB, bHLH, ERF, NAC, and bZIP, which showed differential gene expression (Njaci et al., 2021). In *C. scarabaeoides*, resistance to *H. armigera* is linked to systemic immune responses regulated by microRNAs (miRNAs). Totally 211 conserved miRNAs were identified in uninfested leaves, while 98 were differentially expressed that targeted defense-related genes and their overlap with infested tissues suggests miRNA-driven systemic signaling in pod borer resistance (Malhotra et al., 2022).

The biochemical basis of *H. armigera* resistance in *C. platycarpus* focused on the flavonoid biosynthesis pathway. Transcript quantification in *H. armigera*-fed plants showed up to 11-fold upregulation of key flavonoid pathway genes, accompanied by increased naringenin, quercetin, and delphinidin, which correlated with stunted larval growth on flavonoid-enriched diets (100 ppm) (Tyagi et al., 2022). *C. platycarpus* Flavonoid 3′,5′-Hydroxylase isoform 2 (*CpF3′5′H_2*) gene from *C. platycarpus* was tracked as a key gene for *H. armigera* resistance. It showed more substantial upregulation (4.6-fold) than its cultivated counterpart. Transgenic tobacco overexpressing *CpF3′5′H_2* had reduced leaf damage, increased larval mortality, and increased accumulations of flavonoids and polyphenols, confirming its role in herbivore deterrence (Tyagi et al., 2023). Additionally, the overproduction of catechins (epigallocatechin (EGC) and epigallocatechin-3-gallate (EGCG)) in the pod borer-resistant *C. platycarpus* during herbivory prompted an investigation into their effects on *H. armigera*. Larvae fed a 100 ppm EGCG diet showed significant reductions in growth. RNA-seq analysis revealed 62 differentially expressed genes in *H. armigera* larvae, which are linked to detoxification and lipid metabolism. Upregulation of lipase and fatty acid-binding protein 2-like, along with downregulation of delta9-FADS-like, indicated disrupted fat metabolism. qPCR and enzyme assays also confirmed increased lipolysis and reduced lipogenesis, with altered levels of stearic and oleic acids (Rathinam et al., 2023).

4.3. Metabolomics

Metabolomics helps identify defense-related metabolites and pathways in wild *Cajanus* species that contribute to insect resistance in pigeonpea. Key compounds like flavonoids, phenolics, and terpenoids involved in antixenosis and antibiosis may be uncovered by comparing biochemical changes under pest infestations (Upadhyay et al., 2024). The targeted and un-targeted metabolomics information generated may provide insights to support the development of insect-resistant pigeonpea varieties through metabolic trait selection.

Mechanistic insights into biochemical and metabolic responses of *C. platycarpus* compared to cultivated *C. cajan* under *H. armigera* infestation over 96 hours revealed that *C. platycarpus* exhibited significant metabolic shifts, including reduced primary carbohydrates, selective amino acid regulation, and JA pathway activation, indicating a more vigorous defense response. It also increased specific sugar alcohols and maintained ROS balance, effectively limiting nutrient availability to the insect pest (Dokka et al., 2024).

4.4. Proteomics

Proteomics aids in identifying defensive proteins and pathways in pigeonpea CWRs that enhance insect resistance. Key defense mechanisms like PIs, lectins, and ROS scavenging were identified by analyzing differentially abundant proteins (DAPs) during pest attacks. Comparative studies between wild and cultivated *Cajanus* species enumerated the array of proteins involved in secondary metabolism and signaling during pest infestation.

Advanced quantitative proteomic analysis of *C. scarabaeoides* (IBS 3471) identified variations in key defense-related proteins. *H. armigera* larvae fed on its leaves showed significant growth inhibition. Differentially abundant proteins (dDAPs), particularly those involved in ROS scavenging and signaling, along with insect-resistant proteins such as a cysteine proteinase inhibitor and a lectin domain-containing receptor kinase, contributed to its enhanced defense (Ngugi-Dawit et al., 2021). Furthermore, proteomic analysis confirmed the introgression of *H. armigera* resistance traits from IBS 3471 into cultivated pigeonpea (ICPL 20338), with elevated levels of insecticidal proteins—such as lectins and cysteine proteinase inhibitors—observed in the hybrids and their derivatives (Ngugi-Dawit et al., 2020).

Comparative proteomics of *C. platycarpus* revealed a multi-layered resistance mechanism against *H. armigera*, characterized by the upregulation of defense-related proteins involved in structural reinforcement such as microtubule assembly, lignin synthesis and stress responses. The differential abundance of these proteins underscores the species' potential as a valuable source of insect resistance (Rathinam et al., 2020).

In the present omics era, integrating multi-omics strategies is essential to decipher complex plant responses to biotic stress, offering insights into resistance genes, regulatory networks, and bioactive compounds. These tools, combined with conventional breeding, can significantly enhance insect resistance in pigeonpea (Fig. 4) (Muthamilarasan et al., 2019; Kang et al., 2019; Wang et al., 2017).

5. Current development of genetic engineering/genome editing in pigeonpea

Genetic engineering and transgenic approaches offer effective alternatives to enhance pigeonpea resistance against significant insect pests by introducing specific resistance genes, such as *Bt* toxins and

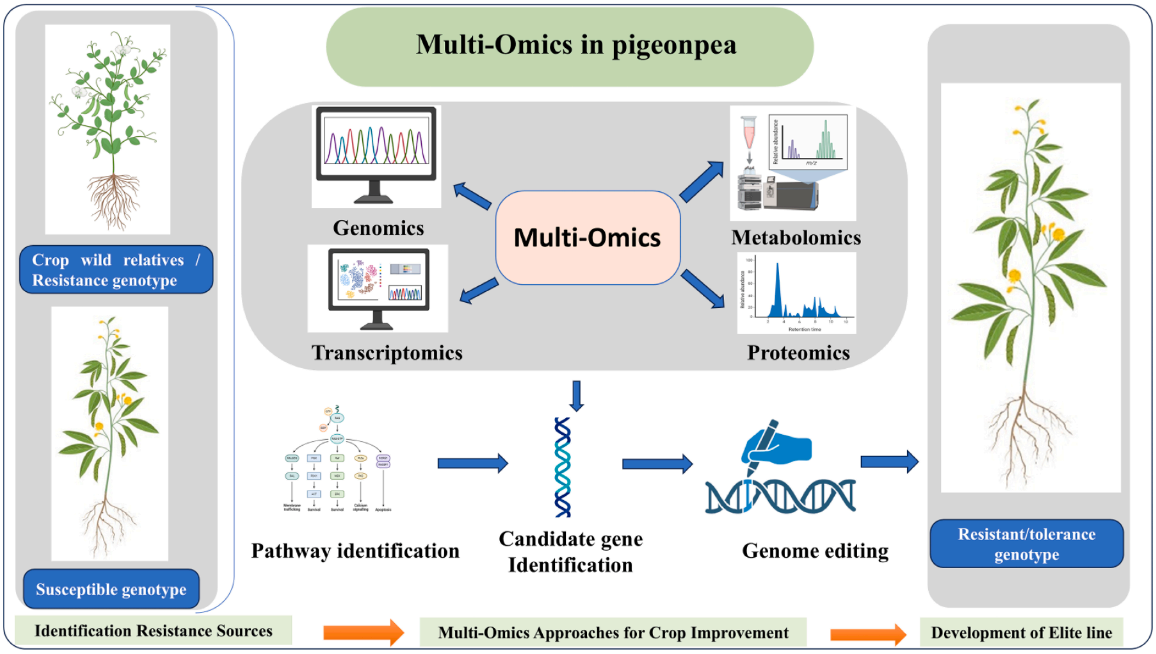

Fig. 4. Comprehensive overview of multi-omics strategies for enhancing insect resistance in pigeonpea: Integrating genomics, transcriptomics, proteomics, and metabolomics to identify resistance traits and accelerate breeding for sustainable pest management.

plant-derived insecticidal genes (Talakayala et al., 2020). Despite numerous efforts over the last decades, few reports of transgenic *Bt* pigeonpea have been developed to express different *Bt* insecticidal proteins (Ghosh et al., 2014; Krishna et al., 2010). The expression of *cry2Aa* in transgenic pigeonpea resulted in resistance to *H. armigera*, reducing larval weight and length ranging from 13.32 % to 47.13 % and 42.33 % to 64.95 %, respectively (Baburao and Sumangala, 2018; Singh et al., 2018). Additionally, transgenic pigeonpea plants expressing the *cry1Ab* gene exhibited significant resistance to *M. vitrata*, with larvae showing up to 53.8 % weight loss and no adult emergence after feeding on these plants. The *cry1Ab* gene demonstrated stable inheritance and expression across T_1 to T_3 generations (Singh et al., 2023).

Moreover, stacking of multiple *Bt* genes improves the durability of resistance in pigeonpea. *Agrobacterium tumefaciens*-mediated transformation was used to introduce *cry1Ac* and *cry2Aa* genes into pigeonpea. T_0 transformants were confirmed through PCR and protein expression, while T_1 events were validated via Western and Southern blot analyses. Twelve *cry1Ac* and 11 *cry2Aa* single-copy transgenic events were developed, which recorded 80–100 % mortality of *H. armigera* larvae in bioassays. Further, the insect-resistant phenotype was found to be stably inherited in the T_2 generation (Ghosh et al., 2017). The cry genes, synthetic *cry1E-C* (replacement of 58 amino acids from *cry1Ea* with 70 homologous amino acids of *Cry1Ca*), *cry1Ab, cry1Ac*, and chimeric *cry1AcF* (fusion of N-terminal and domain II from *cry1Ac* and the C-terminal domain from *cry1F*) were also used to develop *Bt* transgenic pigeonpea (Ghosh et al., 2014; Krishna et al., 2011; Ramu et al., 2012).

A key development in transgenic crop is the creation of marker-free plants that retain desired traits while eliminating selectable marker genes post-transformation. In pigeonpea, the synthetic crystal protein Syn *cry1Ab* was expressed using tissue-specific promoters like *RuBisCo* (*rbcS*), resulting in 90 % mortality of second-instar *H. armigera* larvae. The bar marker gene was removed using a *Cre* recombinase system, with a recombination frequency of up to 35.71 %. Marker-free, insect-resistant lines were established in the next generation through genetic segregation, supporting the development of clean, trait-specific transgenics (Sarkar et al., 2021).

Genome editing tools can potentially revolutionize pulses' genetic enhancement for stress resilience. These tools enable precise DNA modifications, facilitating a deeper understanding of molecular responses to environmental cues and enhancing stress tolerance in pulse crops (Vamshi et al., 2025). The comparative analysis of *CHI4 chitinases* from *C. platycarpus* revealed variations in key amino acids that influenced substrate binding affinity to chitin, the primary structural component of the insect peritrophic matrix, as confirmed by docking analysis with a minimum binding energy of −8.7 kcal/mol. Furthermore, heterologous expression in tobacco validated its insecticidal activity against *H. armigera* (Rathinam et al., 2021). Moreover, Recent developments in genome editing such as Clustered Regularly Interspaced Short Palindromic Repeats associated protein 9 (CRISPR-Cas9) and RNA interference (RNAi) based genome editing offer new avenues for improving pigeonpea's defense against insect herbivores and emerging promising strategy for enhancing resistance in pigeonpea against insect pests by silencing essential genes for pest survival. In *M. vitrata*, a major pigeonpea pest, RNAi targeted three key genes-Alpha-amylase, Chymotrypsin-like serine protease, and Tropomyosin-using two approaches: direct dsRNA injection and host-delivered RNAi through transgenic pigeonpea plants (cv. Pusa 992). Both methods effectively reduced gene expression, increased larval mortality, and decreased feeding (Chatterjee et al., 2022). Moreover, a pigeonpea-specific CRISPR/Cas9 genome editing system has been developed to address productivity challenges arising from biotic stresses. Targeting the phytoene desaturase (PDS) gene, crucial for carotenoid biosynthesis, the system used the CcU6_7.1 promoter and a Cas9 gene driven by the potato ubiquitin promoter. *Agrobacterium*-mediated transformations achieved editing efficiencies of 8.80 % in planta and 9.16 % *in vitro*, confirmed by albino phenotypes and sequence mutations. By optimizing transformation methods, a 15.2 % efficiency was achieved, supporting functional genomics and trait improvement in pigeonpea (Prasad et al., 2024; Senthil et al., 2025).

6. Summary of the bibliometric analysis of pigeonpea host plant resistance mechanism

From PubMed (https://pubmed.ncbi.nlm.nih.gov/), we compiled a total of 71 papers and the over-visualization of the bibliometric analysis was done using VOS viewer. This bibliographic network visualization mapped key research trends in pigeonpea (*C. cajan*) resistance to *H. armigera*, emphasizing the integration of genomics, metabolomics, and proteomics. The central themes revolved around host plant resistance (HPR), gene editing (CRISPR/Cas), high-throughput sequencing, and insect resistance mechanisms. Keywords such as flavonoids, biochemical compounds, and digestive enzymes (amylases, chymotrypsin, and insect proteins) suggest a strong focus on plant-insect interactions at both the molecular and biochemical levels. The presence of RNA interference (RNAi), transcriptomics, and genetic variability underscores the importance of modern biotechnological approaches in breeding pest-resistant pigeonpea varieties.

Additionally, the network highlighted emerging research areas, including pre-breeding, biodiversity conservation, and food supply, indicating a broader interest in sustainable pest management and crop improvement strategies. The clustering of keywords suggests that researchers are linking multi-omics approaches (genomics, metabolomics, and proteomics) with host-plant resistance mechanisms, aiming to identify bioactive compounds and genetic traits responsible for insect resistance. The visualization also highlights the importance of integrating molecular breeding with ecological and biochemical strategies to develop resilient pigeonpea varieties, thereby ensuring food security and promoting sustainable agricultural practices (Fig. 5).

7. Challenges and limitations

The cultivated pigeonpea (*C. cajan*) faces several significant challenges because of its narrow genetic base, which restricts the diversity of the resistance gene pool. This limited genetic diversity hampers efforts to broaden resistance against insect pests, making it increasingly difficult for breeders to develop robust varieties that can withstand various threats. Additionally, when desirable traits from wild relatives are incorporated into cultivated varieties, introgression breeding encounters multiple difficulties, including cross-compatibility issues that can prevent successful hybridization and linkage drag, where unwanted traits are inherited along with the desired ones. Complex inheritance patterns associated with resistance traits make selection a challenging process. Moreover, new pest biotypes pose a serious risk, as evolving pest populations can break existing resistance mechanisms, undermining the efforts. Compounding these challenges is the limited research on certain CWRs of pigeonpea, which are underutilized due to the lack of comprehensive genomic data that could facilitate their incorporation into breeding programs. Moreover, implementing *Bt* pigeonpea in field cultivation presents drawbacks, including regulatory constraints and ethical and environmental issues in the majority of countries. This highlights the need for a balanced approach to pest management that considers genetic resistance and sustainable agricultural practices.

8. Future prospects

Exploring untapped CWRs offers promising opportunities for identifying novel resistance traits that can enhance the resilience of cultivated pigeonpea through pre-breeding and speed breeding, thereby accelerating the transfer of these resistance-related genes. By leveraging molecular breeding approaches such as genomic selection (GS) and GWAS, we can rapidly identify and deploy resistance genes to improve pest management. Additionally, RNAi and genetic transformation facilitate the development of transgenic pigeonpea varieties resistant to insect pests. At the same time, CRISPR-Cas-based gene editing technology allows for the precise integration of beneficial resistance traits from wild relatives or editing of the susceptibility, causing genes to be edited precisely to make the plant resistant/tolerant. Furthermore, breeding efforts must also consider climate resilience, multi-trait/pest resistance,

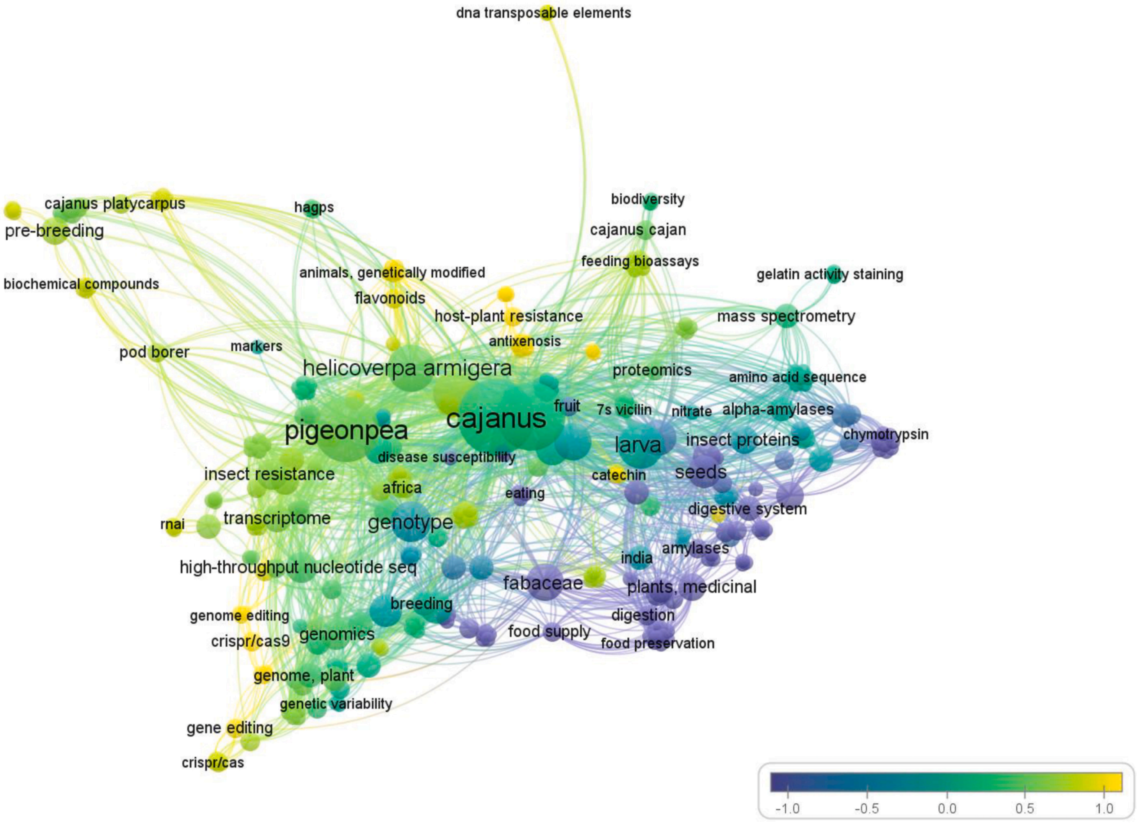

Fig. 5. Bibliometric network visualization of research trends in pigeonpea host-plant resistance against major insect pests between 2000 and 2025 based on all keywords.

and testing of existing tolerance genotypes under different climate variables (temp/elevated CO_2), as climate change is likely to alter pest dynamics and plant-insect interactions, necessitating the development of varieties that can withstand both pest pressures and the challenges posed by changing environmental conditions. By focusing on innovative, sustainable, and precision-based approaches, pigeonpea breeding programs can develop robust cultivars capable of thriving in dynamic and resource-limited agricultural systems.

9. Conclusion

Over the past decade, significant efforts have been made in identifying and utilizing resistance traits in pigeonpea and its CWRs, showcasing successful strategies that enhance the crop's resilience against various insect pests. The implications of these developments are far-reaching, particularly for food security, as HPR plays a vital role in ensuring the sustainability and resilience of pigeonpea production systems worldwide. However, due to the challenges in incorporating high levels of insect resistance, pigeonpea breeding has received comparatively less attention from breeders. To accelerate breeding progress, a deeper understanding of plant defense mechanisms is needed. While single-omics approaches provide valuable insights, they often fall short of capturing the full complexity of stress responses. By combining conventional and molecular breeding, durable insect resistant pigeonpea varieties can be developed. Although the existing few genotypes expressing moderate resistance can avoid one or two insecticide sprays, they still make a significant difference by reducing cultivation costs, which favors the large majority of small and marginal farmers in Asia and Africa. Ultimately, integrating HPR with IPM strategies will be key to improving crop productivity while reducing dependence on chemical pesticides.

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CRediT authorship contribution statement

Onkarappa Dhanyakumar: Writing – original draft, Visualization, Software, Formal analysis, Conceptualization. **Marigoudar Ranjitha:** Writing – original draft, Visualization, Software, Formal analysis, Conceptualization. **Kalenahalli Yogendra:** Writing – review & editing, Visualization, Supervision, Resources, Formal analysis, Conceptualization. **Gothe Revanayya:** Writing – original draft, Visualization, Software, Formal analysis, Conceptualization. **Hari C. Sharma:** Writing – review & editing. **Gaurav Kumar Taggar:** Writing – review & editing. **Marimuthu Murugan:** Writing – review & editing, Visualization, Supervision, Software, Resources, Conceptualization. **Jagdish Jaba:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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.

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Supplementary materials

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Data availability

Data will be made available on request.

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