

CROP WILD RELATIVES OF LEGUME PULSES: AN UNTAPPED RESOURCES IN INSECT RESISTANCE BREEDING

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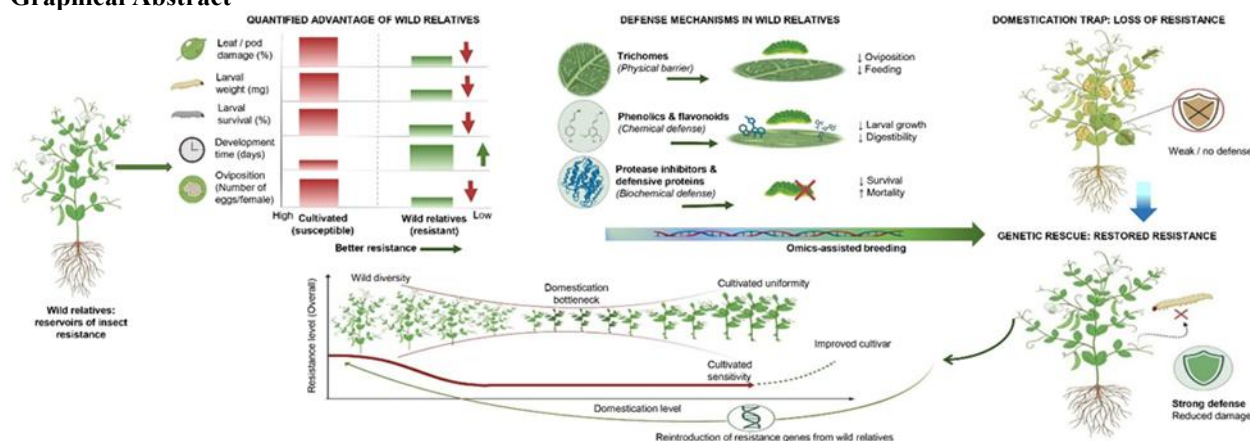
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ABSTRACT

Legume pulses are essential to ensuring food and nutritional security around the world, but remain subject to significant losses due to insects in the field and during storage. Due to domestication bottlenecks, genetic erosion and the loss of defence related traits, resistance remains limited in cultivated legumes and this makes them increasingly susceptible to the challenges posed by a changing climate. Wild legume relatives serve as important reservoirs of resistance to insect pests, and adaptive genetic variation created over time through a dynamic co-evolutionary process with insect enemies. This review brings together ecological, evolutionary, physiological, biochemical, and molecular understanding of resistance mechanisms found in wild legume taxa, which could help improve insect resistance in legumes. Such wild relatives are endowed with a variety of defense mechanisms: structural barriers, secondary metabolites, defense proteins and defense hormones, as well as with various inducible defense mechanisms. Advances in genomic and multi-omics platforms have made it possible to pinpoint resistance loci, candidate genes, and defense-related pathways with direct applications in crop improvement. However, limitations in the use of these are still faced due to reproductive barriers, linkage drag, less genomic resources and small germplasm characterization. A combination of systematic germplasm exploration, standardized phenotyping, and the application of omics-assisted breeding approaches will be essential for developing pest and disease resistant pulse cultivars, ultimately supporting the goal of reduced or eliminated chemical pesticide use in sustainable pulse production systems.

Graphical Abstract



KEYWORDS: wild species; insect resistance; legumes; multi-omics; sustainable breeding.

1. INTRODUCTION

Legume pulses are among the most important crops in global agriculture, ranking just behind grasses, and they play a crucial role in ensuring food and nutritional security for millions of people worldwide (Coyne *et al.* 2020). Legumes rank among the most valuable sources of protein, they're affordable, packed with vitamins and minerals, and boost soil fertility through their role in biological nitrogen fixation (Goodwin 2017; Sonakul and Jirarat 2020; Singh *et al.* 2022), with a total of over 20,000 species and 750 genera in the world. The strategic importance of legumes, valued for their role in sustainable agriculture, is evident in their role in providing food and feed for over 700 million people (Razzaq *et al.* 2023).

Though pulses are important, insect pest damage in both field and storage are a major constraint to quality pulse production. *Helicoverpa armigera*, *Maruca vitrata*, aphids, leafhoppers, pod borers and bruchids are significant pests worldwide that result in significant economic losses (Sharma *et al.* 2017). Climate change is expected to

make these challenges worse, as pest populations grow and long-standing relationships between plants and insects are disrupted (Barah and Bones 2015; Zenda *et al.* 2021). Pest-resistant crop varieties have been created and released for pigeonpea, cowpea, soybean, and field pea to protect against insect damage (Soundararajan *et al.* 2013). The limited resistance found in cultivated germplasm stems from domestication and selective breeding, which have diminished genetic variation and eliminated resistance-associated traits from the available gene pool (Coyne *et al.* 2020; Edwards and Singh 2006).

Wild legume species contain substantial genetic variation and pest-resistance characteristics that have been maintained through extended periods of natural selection driven by exposure to pests (Von Wettberg *et al.* 2018). Numerous wild species of chickpea, pigeonpea, cowpea and other legumes have been identified and deserving for attention on their resistance to major insect pests (Sharma *et al.* 2017). This review critically ascertains insect resistance in wild relatives of legume pulses with a focus on the ecological role, gene pool, distribution, characterization, meta-analysis, resistance mechanisms, evolutionary aspects, omics approach and their potential in breeding for development of insect-resistant cultivars.

2. Wild relatives of legume pulses: Diversity and ecological relevance

As the second-largest family of cultivated crops behind cereals and the third-largest family within the Angiosperms, legumes encompass roughly 800 genera and 20,000 species distributed across every continent except Antarctica (Singh *et al.* 2022). The economic importance of legumes is growing, as they represent 27% of crop production in the world and 33% of human protein needs and further legumes like pasture and forage legumes are a necessary component of animal feed (Smýkal *et al.* 2017).

India possesses a remarkable range of wild legume species from various genera including *Abrus*, *Acacia*, *Alysicarpus*, *Atylosia*, *Bauhinia*, *Canavalia*, *Cassia*, *Dolichos*, *Entada*, *Erythrina*, *Indigofera*, *Lens*, *Mucuna*, *Parkia*, *Parkinsonia*, *Phaseolus*, *Pongamia*, *Prosopis*, *Sesbania*, *Tamarindus*, *Vicia*, *Vigna*, and *Xylia*. These legumes serve as food sources for numerous tribal communities throughout India, who collectively form a substantial portion of the country's population (Janardhanan *et al.* 2003).

Beyond their critical nutritional contribution, legumes provide essential agroecosystem services including atmospheric nitrogen fixation and soil amelioration, which makes them well-suited to farming systems that rely on fewer external inputs like synthetic fertilizers (Guiguitant *et al.* 2020). Crop wild relatives refer to wild plant species that either directly gave rise to domesticated crops or share a closer evolutionary connection to them. These relatives are grouped into primary, secondary, and tertiary gene pools based on how closely related they are to the cultivated species (Kapazoglou *et al.* 2023).

There is a great loss of genetic diversity in cultivated legumes due to domestication processes that have taken place. The genomic diversity of the domesticated pea has been compared to that of its crop wild relative across Europe and the Mediterranean, and is found to be quite large, with cultivated varieties possessing a narrower genetic base (Smýkal *et al.* 2017). Domestication bottlenecks, followed by the shift from subsistence to commercial farming, have made crop varieties highly genetically similar to one another. This has narrowed the genetic diversity of cultivated germplasm, making it more vulnerable to pests and diseases. In addition, modern high-yield varieties tend to prioritize reproductive output over traits related to defense and competitive ability (Coyne *et al.* 2020).

Climate change has emerged as the foremost danger to farm output and global food supply. Projections indicate global temperatures could climb by 2°C to 3°C by the end of this century, a shift expected to take a heavy toll on both living and non-living elements of the environment. Among the most damaging stress factors are erratic rainfall patterns, drought conditions, extreme heat, and soil salinity/sodicity, all of which are driving substantial declines in crop yields (Rajpal *et al.* 2023a). Concurrently, disease causing organisms and insect pests including bruchids, pod borers, aphids, and weevils pose significant challenges to pulse production worldwide (Edwards and Singh 2006). Wild relatives offer a promising answer to these challenges. Through their long evolutionary history, they have encountered and adapted to a wide range of harsh environments, developing the resilience needed to survive difficult conditions. As a result, they carry valuable traits, such as resistance to pests, diseases, and environmental stresses, along with unique nutritional properties that make them useful for improving cultivated crops (Muñoz *et al.* 2017). Chickpea is a legume that plays a major role in food security, particularly in countries like India, Pakistan, and Ethiopia, where roughly 22% of the global population relies on chickpeas and other legumes as their main source of dietary protein (Von Wettberg *et al.* 2018). Many populations of wild relatives face threats from habitat loss and degradation, creating a pressing need to gather and preserve crop wild relatives through approaches that maximize both genetic and environmental diversity. These collections must then be characterized in ways that make them useful for addressing present and future challenges in agriculture.

A global assessment of crop wild relatives shows that the Mediterranean Basin, the Near East, South America, Mesoamerica and parts of Africa and Asia have higher species richness of legume wild relatives, with the majority of the species present on most continents. The regions match the centres of domestication and diversification of crops (Castañeda-Álvarez *et al.*, 2016). The main regions of origin, diversification and distribution of the pulse legumes' wild relatives have been displayed in Figure 1.

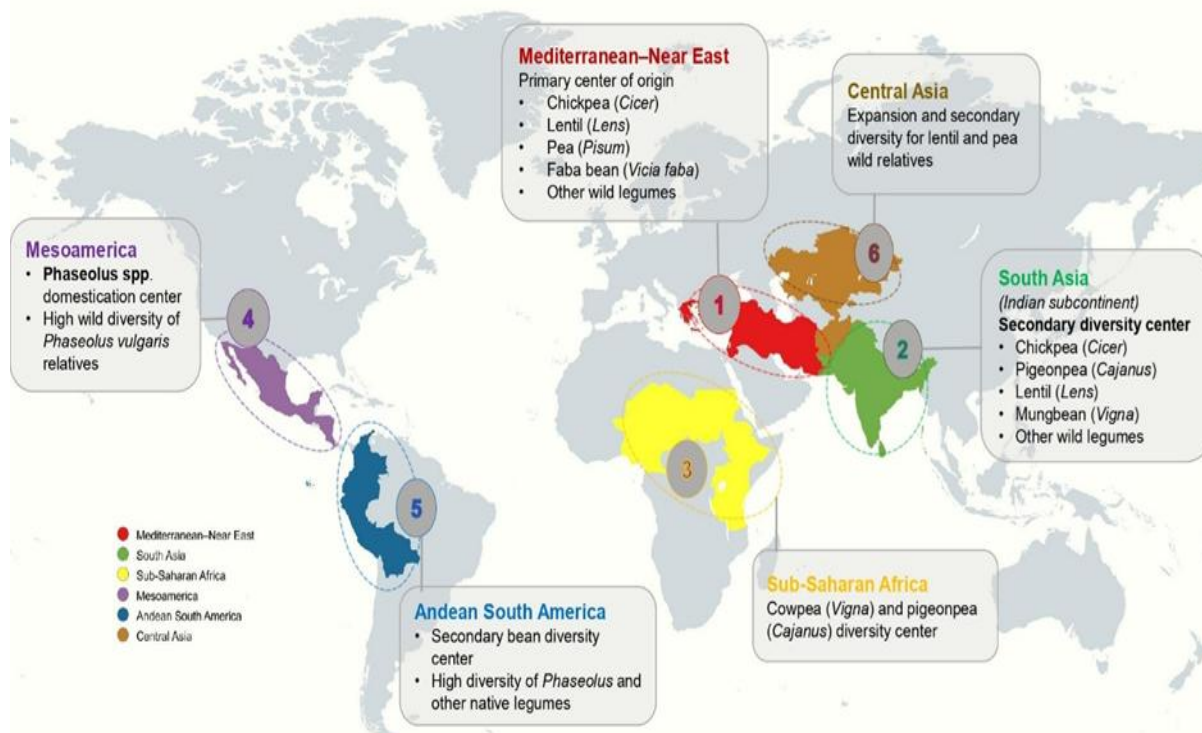


Fig 1. Major geographic centers associated with the origin, domestication, diversification, and distribution of wild relatives of economically important pulse legumes including *Cicer*, *Lens*, *Pisum*, *Phaseolus*, *Vigna*, and *Cajanus* species

Crop wild relatives and adaptive significance

Crop wild relatives (CWRs) form an essential component of plant genetic resources across the globe. They have retained a wide array of adaptive characteristics that have decreased or been lost as a result of crop domestication and modern breeding. Unlike cultivated crops, which are generally chosen for yield, uniformity in managed environments, CWRs are growing in the environments where they belong. They are constantly adapting to various stresses, making them an important stock of genetic variability, especially in the areas of stress tolerance, defence and ecological resistance (Cockel *et al.* 2022).

Crop wild relatives are wild relatives in nature that are taxonomically close to cultivated legumes. These wild relatives serve as reservoirs of untapped genetic diversity that evolved through natural selection without being subjected to the anthropogenic selection pressures imposed during domestication. It has become essential for plant breeders to identify and use the valuable genetic resources found in crop wild relatives to boost genetic gain and meet targeted food demands. Wild relatives serve as potential donors of agronomically valuable traits, encompassing both yield potential and resistance to biotic and abiotic stresses (Singh *et al.* 2022).

Resistance to stress from living organisms, as well as to environmental conditions, is an important attribute conferred by wild legume relatives. A broad spectrum of resistance to insects and diseases, together with tolerance to drought, heat, and salinity and traits linked to high grain yield, has been documented among wild lentil relatives. Evaluations of wild lentil genotypes have uncovered resistance or tolerance to a range of major stresses, including *Ascochyta* blight, *Stemphylium* blight, rust, *Fusarium* wilt, *Sitona* weevil, bruchids, *Orobanche*, powdery mildew, and Anthracnose. Drought tolerance has additionally been documented in *L. nigricans*, *L. orientensis*, and *L. ervoides*, whereas cold tolerance is a feature of *L. culinaris ssp. orientalis*. Among peas, *P. fulvum* stands out as a recognized source of bruchid resistance. Although the use of wild *Cicer* diversity for resistance to environmental stresses has progressed more slowly, chickpea wild relatives likely possess resistance to drought, heat, and cold, with differences in flowering time being especially valuable for improving the crop. (Coyne *et al.* 2020). The scope for countering biotic stress and their fit for adaptation in the newer environment when utilizing the trait in the high yielding cultivar development will be researchable agenda.

Gene pool concept in understanding wild - cultivated relationships

The gene pool classification used in this review follows the concept proposed by Jack Harlan and Jan de Wet (1971) together with subsequent crop-specific revisions adopted for individual legume species. The relationship of wild and cultivated species shown increased genetic distance (Fig. 2).

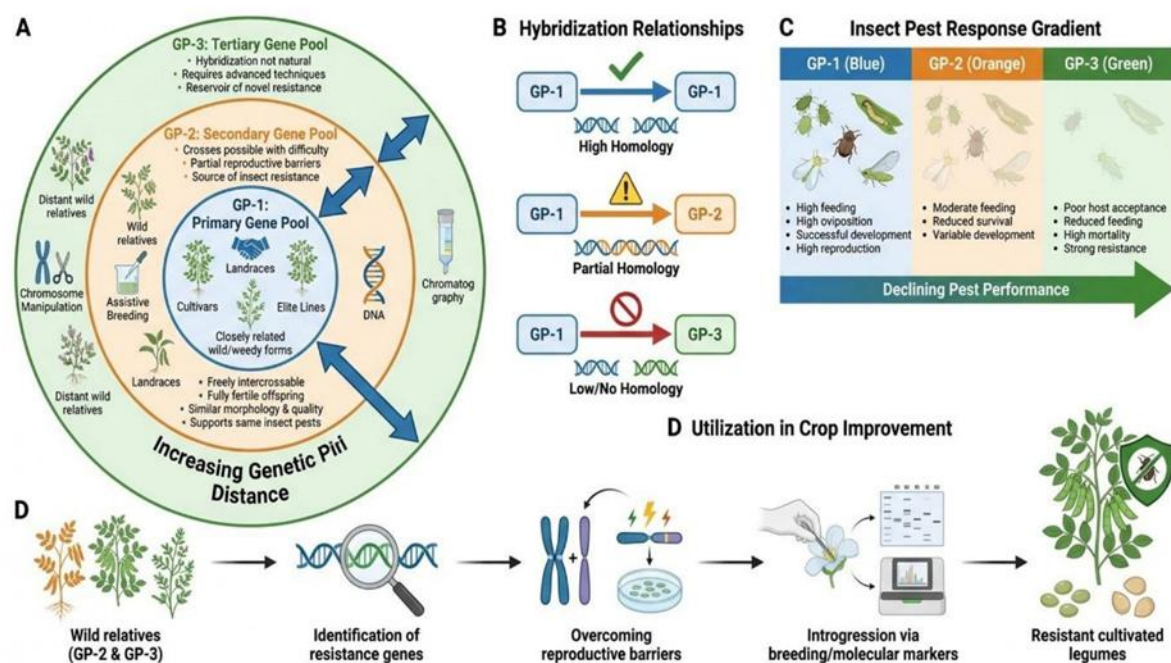


Fig 2. Gene pool relationships among cultivated legumes and their wild relatives showing increasing genetic distance, hybridization barriers, insect pest resistance gradients, and utilization of secondary and tertiary gene pools in crop improvement Wild relatives spanning multiple gene pools have been recognized as valuable sources of resistance to major field and storage insect pests affecting legume pulses (Table 1).

Table 1. Wild germplasm resources associated with insect pest resistance in major pulse crops

Crop Species	Wild Species	Relative	Gene Pool	Target Insect Pest	References
Chickpea (<i>Cicer arietinum</i>)	<i>Cicer bijugum</i> , <i>C. pinnatifidum</i>		GP2	<i>Helicoverpa armigera</i>	Edwards and Singh, 2006; Sharma <i>et al.</i> , 2017; Tripathi <i>et al.</i> , 2020
	<i>C. reticulatum</i>		GP1	<i>H. armigera</i>	Edwards and Singh, 2006
	<i>C. echinospermum</i>		GP1	<i>C. chinensis</i> , Pod borer resistance	Singh <i>et al.</i> , 1998
Pigeonpea (<i>Cajanus cajan</i>)	<i>Cajanus scarabaeoides</i>		GP2	<i>H. armigera</i> , pod fly and bruchids	Sharma <i>et al.</i> , 2009
	<i>C. cajanifolius</i>		GP1	<i>H. armigera</i> and pod fly	Mallikarjuna <i>et al.</i> , 2011
	<i>C. platycarpus</i>		GP3	Pod borer (<i>H. armigera</i>)	Saxena <i>et al.</i> , 2002; Sharma <i>et al.</i> , 2009
	<i>C. acutifolius</i> ,		GP2	pod-feeding insects	Mallikarjuna and Moss, 1995
	<i>C. albicans</i>		GP2	Pod fly and pod wasp resistance	Sharma <i>et al.</i> , 2009
	<i>C. sericeus</i>		GP2	<i>H. armigera</i> , Pod borer complex	Sharma <i>et al.</i> , 2009; Mallikarjuna <i>et al.</i> , 2011

Cowpea (<i>Vigna unguiculata</i>)	<i>Vigna unguiculata</i> <i>subsp. dekindtiana</i>	GP1	Cowpea aphid (<i>Aphis craccivora</i>), Flower thrips (<i>Megalurothrips sjostedti</i>), Bruchid (<i>Callosobruchus maculatus</i>)	Jackai and Doust, 1986; Dongre <i>et al.</i> , 1996; Fatukon <i>et al.</i> , 2012
	<i>V. vexillata</i>	GP3	Pod-sucking bug (<i>Clavigralla tomentosicollis</i>), <i>Maruca vitrata</i>	Jackai and Oghiakhe, 1989
Soybean (<i>Glycine max</i>)	<i>Glycine soja</i>	GP1	Soybean aphid, leaf-chewing insects, defoliators	Hill <i>et al.</i> , 2004; War <i>et al.</i> , 2012
Common Bean (<i>Phaseolus vulgaris</i>)	<i>Phaseolus vulgaris</i> <i>var. aborigineus</i>	GP1	<i>Callosobruchus</i> spp., <i>Zabrotes subfasciatus</i> <i>Acanthoscelides obtectus</i>	Cardona <i>et al.</i> , 1990
	<i>P. coccineus</i>	GP1	Mexican bean weevil (<i>Zabrotes subfasciatus</i>)	Van Schoonhoven <i>et al.</i> , 1983; Singh SP and Schwartz HF 2010
Pea (<i>Pisum sativum</i>)	<i>Pisum fulvum</i>	GP2	Pea weevil (<i>Bruchus pisorum</i>), Pea aphid (<i>Acyrtosiphon pisum</i>)	Hardie <i>et al.</i> , 1995
	<i>Pisum elatius</i> ,	GP1	<i>B. pisorum</i> , <i>A. pisum</i>	Clement <i>et al.</i> , 2002
	<i>P. abyssinicum</i>	GP1	<i>C. chinensis</i>	Hardie <i>et al.</i> , 1995; Smykal <i>et al.</i> , 2012
Lentil (<i>Lens culinaris</i>)	<i>Lens culinaris</i> <i>subsp. orientalis</i>	GP1	Pea aphid (<i>A. pisum</i>)	Gupta <i>et al.</i> , 2006; Tullu <i>et al.</i> , 2010
	<i>Lens odomensis</i>	GP2	Sitona weevil (<i>Sitona</i> spp.)	El-Bouhssini <i>et al.</i> , 2008
	<i>Lens lamottei</i>	GP2	Bruchid pests	Cubero, 1981; Laserna-Ruiz <i>et al.</i> , 2012
	<i>Lens ervoides</i>	GP2	bruchids and Pea aphid (<i>Acyrtosiphon pisum</i>)	Fratini and Ruiz, 2006
	<i>Lens tomentosus</i>	GP3	Pea aphid (<i>A. pisum</i>), <i>Callosobruchus</i> spp.	Tullu <i>et al.</i> , 2010; Singh <i>et al.</i> , 2013
Greengram (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>sublobata</i>	GP1	<i>C. chinensis</i> , Whitefly	Tomooka <i>et al.</i> , 2000; Somta <i>et al.</i> , 2007; Nair <i>et al.</i> , 2019
	<i>Vigna umbellata</i>	GP2	<i>C. chinensis</i> , <i>C. maculatus</i>	Tomooka <i>et al.</i> , 2000; Pandiyan <i>et al.</i> , 2020

Blackgram (<i>V. mungo</i>)	<i>V. mungo</i> var. <i>silvestris</i>	GP1	Bruchids, Whitefly	Dongre <i>et al.</i> , 1996; Tomooka <i>et al.</i> , 2000; War <i>et al.</i> , 2017
	<i>V. stipulacea</i> , <i>V.</i> <i>trilobata</i>	GP2	Bruchids	Somta <i>et al.</i> , 2007; Ventury <i>et al.</i> , 2022

3. Significance of insect pests on legume pulses

The economic impact of insect damage on pulses is high, especially in India, where pulse production and consumption are the largest in the world (Mal *et al.* 2024). Yield losses can be quite high at crop species level. The losses from major pests in Pigeonpea are quite large ranging from 25 to 70% due to pod borers, 10 to 50% due to pod fly, 5 to 25% due to *Maruca* and 10 to 30% due to pod bug (Sharma *et al.* 2017). Loss by insect pest infestation in pigeonpea are estimated at about 33% of the annual production in India. Insect pests are responsible for an estimated 15% annual loss in chickpea production (Saxena *et al.*, 2018). In black gram and green gram, the annual losses are as high as 30% while in cowpea, avoidable losses vary from 66 to 100%, depending on the situation (Anusha *et al.* 2016; Swaminathan *et al.* 2012).

Storage insect pests represent a significant, frequently underestimated source of loss. They can reduce yield after harvest and diminish both the quality and quantity of stored seed. Storage damages are reported up to 50% in key legume crops, such as chickpea, faba bean, lentil and pea, and losses may exceed 70% for smallholder farmers using traditional storage methods (Makhlouf *et al.* 2024). Besides weight loss, annual losses in Indian storage facilities are estimated at 55 to 60 % due to damage caused by storage pests, along with a protein loss of 45.5 to 66.3 % resulting from the same storage pests (Salunkhe and Gaikwad 2025). These qualitative losses make seeds inedible to human, value the market, and cause a reduction in the germination potential (Mal *et al.* 2024). In pigeonpea, screening most of the cultivated entries are susceptible to bruchids and suggested that bruchid control measures are to be initiated in the field itself (Chitra and Soundararajan 2013). Field and storage damage occur in various forms, depending on the developmental stage and part of the plant targeted different feeding zones by the insect pests of legume pulses (Fig.3).

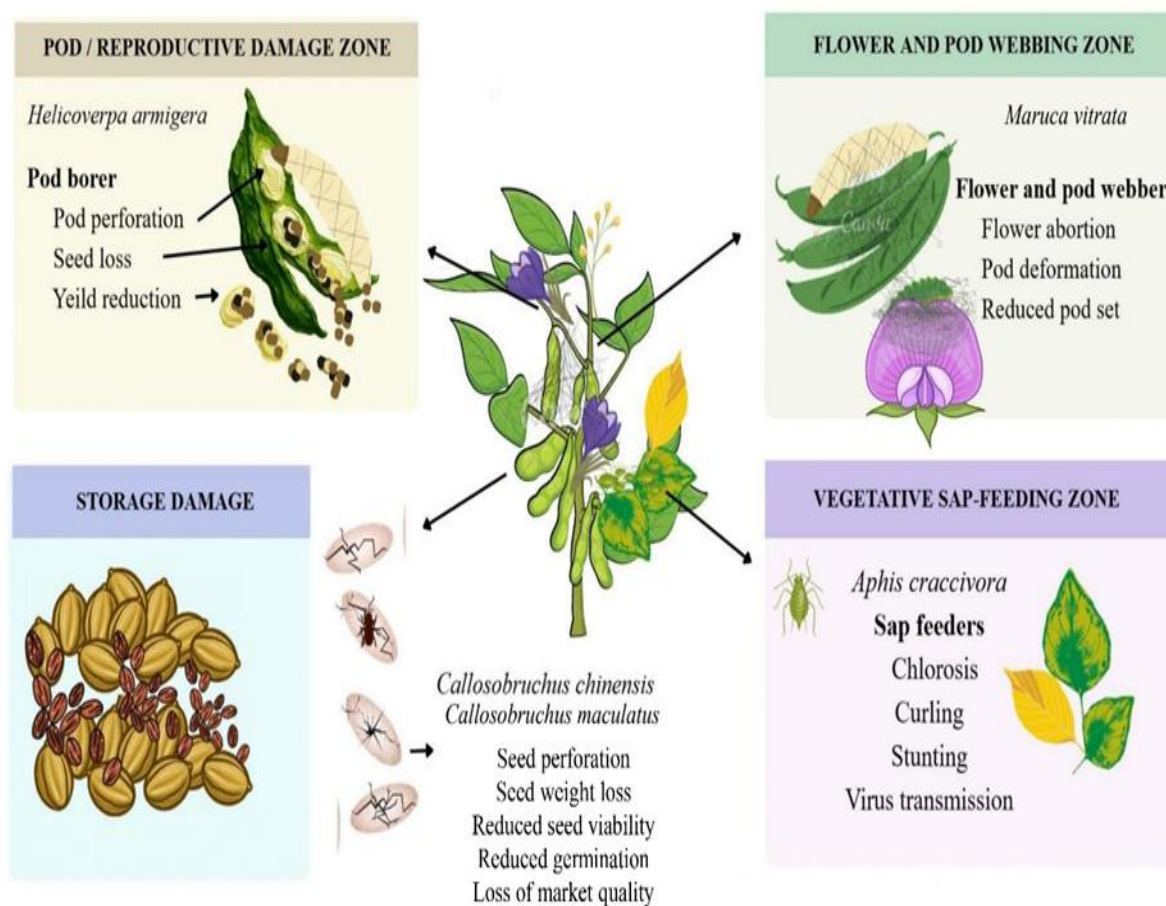


Fig 3. Major insect pest feeding zones and associated damage symptoms in legume pulse crops

4. Characterization and meta-analysis of wild genotypes for resistance to insect pests

Wild genotypes showing resistance to insect pests under both field and storage conditions have been identified in large numbers (Zhang et al. 2017). Wild relatives of pigeonpea and chickpea are regarded as reliable sources of genes for insect pest resistance, and strong resistance to pod borers has been found in wild accessions of chickpea, pigeonpea, and cowpea (Sharma et al. 2017).

Screening studies across multiple legume crops have systematically evaluated for resistance to field level insect pests through various methodologies, revealing that wild relatives consistently demonstrate superior resistance compared to cultivated varieties. In field pea evaluation, specific accessions showed consistently low seed damage against pea weevil, demonstrating significant potential for exploitation in breeding programs (Osuna-Caballero et al. 2024). The wild relatives of chickpea species, including *Cicer bijugum* and *C. reticulatum*, have shown high levels of resistance to *Helicoverpa armigera*, one of the most destructive pod borers affecting leguminous crops (Sharma et al. 2017). Accessions of *C. pinnatifidum*, *C. bijugum*, and *C. echinospermum* demonstrated resistance to bruchid *Callosobruchus chinensis*, indicating broad-spectrum resistance across different pest types (Chaithanya et al. 2024).

An evaluation of ten cowpea accessions for biophysical and biochemical traits linked to *M. vitrata* resistance, benchmarked against resistant and susceptible checks, identified pod trichomes as a key factor negatively correlated with seed damage, while elevated phenol content coupled with low total sugar and protein levels was likewise linked to *M. vitrata* resistance (Sruthi et al. 2024b). In pigeonpea, wild accessions including *Cajanus scarabaeoides* and *C. acutifolius* with specific trichome types are not preferred for egg laying by *H. armigera* females, demonstrating antixenotic resistance mechanism (Karrem et al. 2025). These findings collectively demonstrate the importance of wild relatives as sources of resistance to field insect pests. The accessions identified across pigeonpea (various *Cajanus* species including *C. bracteata*, *C. scarabaeoides*, *C. sericeus*, and *C. acutifolius*) and chickpea showing resistance against pod borers and other field pests (Karrem et al. 2025).

Resistance to storage insect pests, particularly bruchids and storage beetles, has been widely documented across wild legume relatives, with studies reporting consistently lower seed damage and reduced adult emergence in resistant genotypes. Under the single-choice test, screening trials performed with wild and cultivated varieties of pigeonpea revealed that *C. platycarpus* had the least seed damage by *C. chinensis* (4.33%) and under multi-choice test-also it had least seed damage (18.9%) while the cultivated variety ICPL 161 had 59.78% and 74.40% seed damage respectively (Sathish et al. 2022). In wild *Vigna* species screening, accessions of *V. radiata* var. *sublobata*, *V. trilobata*, and *V. umbellata* were identified as resistant to *C. maculatus*, with less adult emergence, lower seed damage, reduced index of susceptibility, and minimal seed weight loss, making them potential donors for resistance breeding programs (Subramaniyan and Narayana 2023). Delayed development period and low adult emergence was recorded in *C. maculatus* cultured on wild type of *Vigna mungo* var. *silvestris* accessions indicated that wild types had strong resistant factors against bruchids (Soundararajan et al. 2013).

The documented resistance wild legume species and accessions display considerable and consistent variability across studies, with some wild taxa showing reliable resistance while others exhibit pest- or location-specific responses. Wild species serve as reservoirs of trait-specific genes, with diversity evident across secondary gene pools and tertiary gene pools being used as donors for specific traits into cultivated varieties (Nacira Muñoz et al. 2017). This species-level variation is further complicated by accession-specific differences, where among identified resistant accessions, resistance levels and mechanisms can vary considerably even within the same species (Quezada-Martinez et al. 2021).

Some wild taxa demonstrated consistent resistance responses across different studies and pest pressures. In case of *Cajanus scarabaeoides*, the accessions ICPW 086, ICPW 097 have been identified as resistant to multiple pests including *Meloidogyne javanica* and various insect pests (Sharma et al. 2017). The strong relationships among the resistance traits observed in the wild *Vigna* accessions indicated significant correlation among the number of seeds lost, seed damage, and the index of susceptibility, and these were the influential principal components to obtain reliable bruchid resistance among cultivars (Subramaniyan and Narayana 2023). Insect resistance associated traits between wild and cultivated genotypic types were used to conduct a meta-analysis with published data to quantitatively evaluate the contribution of wild legume relatives to insect resistance (Fig.4).

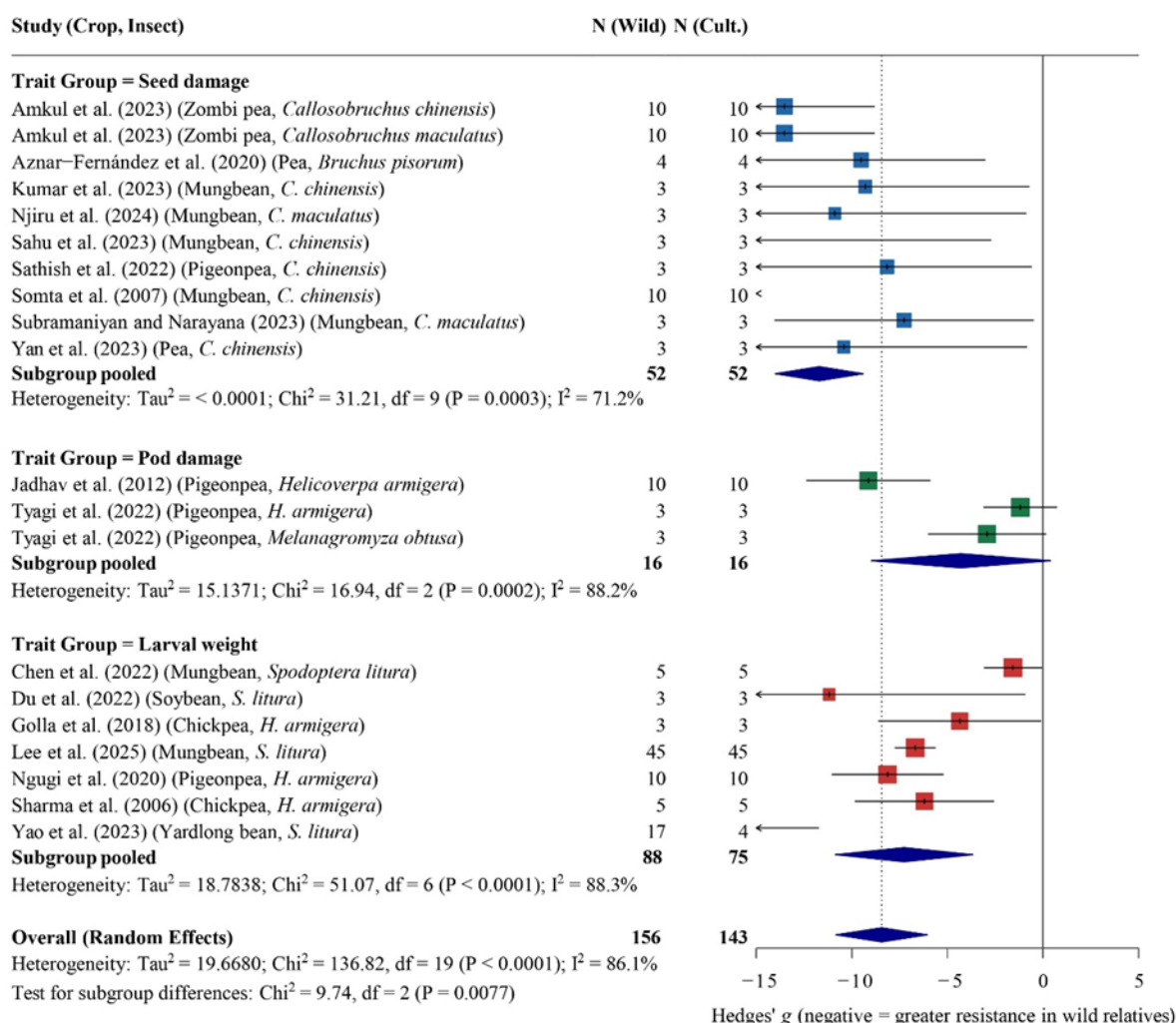


Fig 4. Meta-analysis of major insect resistance traits in wild relatives of pulse legumes compared with cultivated genotypes

Hedges' g (a standardized mean difference) was computed for all major resistance parameters evaluated (seed damage, pod damage, larval weight) in a random-effects model. A random-effects meta-analysis of 20 studies examining insect resistance traits across wild relatives of pulse legumes yielded an overall pooled Hedges' g of -11.71 (95% CI: -14.01 to -9.40), indicating significantly greater resistance in wild accessions compared to cultivated genotypes. Substantial heterogeneity was detected across all included studies ($I^2 = 86.1\%$, $\tau^2 = 19.6680$, $p_{\text{het}} < 0.0001$), suggesting considerable variation in effect sizes across studies, likely reflecting genuine biological differences among crops, insect species, and resistance mechanisms. Subgroup analysis by trait category revealed significant differences among trait groups ($\chi^2 = 9.74$, $df = 2$, $p = 0.0077$). Wild relatives demonstrated the strongest and most consistent resistance advantage for seed damage traits (10 studies; $I^2 = 71.2\%$, $\tau^2 < 0.0001$, $p_{\text{het}} = 0.0003$), where heterogeneity, though statistically significant, was markedly lower than the other subgroups, indicating relatively consistent superiority of wild accessions across *Callosobruchus*-based bioassays. For pod damage traits (3 studies; $I^2 = 88.2\%$, $\tau^2 = 15.1371$, $p_{\text{het}} = 0.0002$), wild relatives also showed superior resistance, though high heterogeneity suggests that pod damage responses vary considerably depending on crop–insect combinations, particularly among *Helicoverpa armigera*-infested pigeonpea systems. Similarly, larval weight studies (7 studies; $I^2 = 88.3\%$, $\tau^2 = 18.7838$, $p_{\text{het}} < 0.0001$) showed that wild relatives consistently suppressed larval performance, reflecting putative antibiotic and antixenotic resistance mechanisms against *Helicoverpa armigera* and *Spodoptera litura* across chickpea, mungbean, soybean, and pigeonpea. Meta-analysis was performed in R-Studio using the ‘meta’ package in R software. Standardized mean differences (Hedges' g) were calculated under a random-effects model, and subgroup analyses were conducted based on resistance trait categories.

A few of the wild relatives were found to be susceptible to specific pests, but resistant to different ones and both antixenosis and antibiotic types of resistance were observed against different insect pests (Rubiales *et al.* 2015). The resistance to a particular pest species may be linked to specific morphological traits, which are not necessarily associated with resistance to another species; and the expression of resistance may be influenced by environmental conditions and pest pressure. Peduncle length and pod angle had effect on expression of resistance to *M. vitrata* in cowpea (Agbim 2023), pod wall thickness and plant growth habit on pod borer (*H. armigera*) damage in

chickpea (Sharma *et al.* 2017). Characterizing resistance in common legume pulses has been done by qualitatively by field screening with damage score based for different insect pests followed by artificial screening methods. The Pest Score Index (PSI) offers a practical means of assessing field resistance and narrowing down entries for subsequent glasshouse and laboratory screening aimed at identifying resistance to particular pod-borer species (Soundararajan and Chitra 2017). PSI score-based method is ideal for most of the pod borer pests in legume crops in categorizing resistant levels.

5. Mechanisms of resistance in wild relatives of legumes for insect pests

The resistance of legume wild relatives is a multifactorial phenomenon, with the result of the co-evolution of plants and insects, which has occurred over many millions of years of insect-plant interactions (Razzaq *et al.* 2023). The co-evolutionary interaction has resulted in the evolution of a large number of defenses, such as structural, biochemical, and physiological changes, which have varying contribution to the overall phenotype of resistance of wild genotypes. The wide range of direct and indirect mechanisms that insects have adapted to defend legumes presents opportunities for both insect protection and legume crops (Edwards and Singh 2006). The mechanism of insect resistance in wild legumes not only includes structural barriers and biochemical compounds but also hormone-regulated pathway systems that are utilized in a coordinated manner (Fig.5). The defense traits associated with wild types triggered by different type of mechanism for each insect (Table 2).

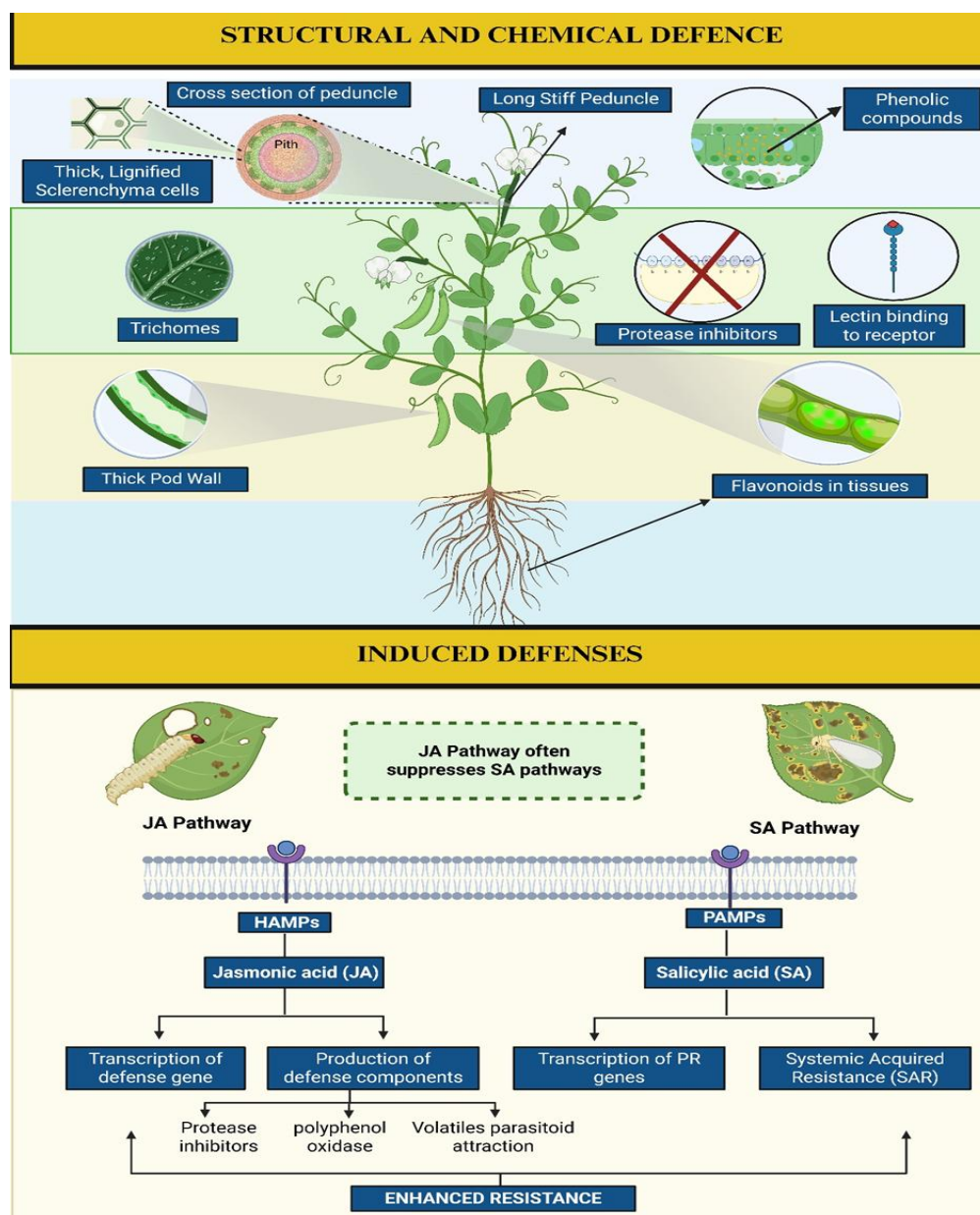


Fig 5. Schematic representation of constitutive structural and biochemical defenses together with inducible hormone-mediated defense pathways associated with insect resistance in wild legume relatives

Table 2. Defense-related insect resistance traits reported in wild pulse germplasm

Defense Category	Specific Trait	Biological Mechanism	Insect Stage	Wild Legume Species	Insect Pest	References
Structural	Tough seed coat	Acting as a physical barrier to entry or feeding	Egg and early larval stage	<i>Vigna radiata</i> var. <i>sublobata</i> , <i>V. trilobata</i>	<i>Callosobruchus</i> spp.	Kaga and Ishimoto, 1998 ; Tomooka <i>et al.</i> , 2000; Somta <i>et al.</i> , 2007
	Dense pod wall trichomes	Restricts larval feeding and penetration and reduces oviposition preference	Adult and larval stages	<i>V. vexillata</i>	<i>M. vitrata</i>	Jackai and Oghiakhe, 1989
	Dense glandular trichomes	Restricts larval movement and feeding and may entrap neonate larvae	Larval stage	<i>Cicer judaicum</i>	<i>H. armigera</i>	Sharma <i>et al.</i> , 2005
	Thick pod wall	Acts as a mechanical barrier reducing larval penetration and feeding within pods	Larval stage	<i>Cajanus scarabaeoides</i>	<i>H. armigera</i>	Sharma <i>et al.</i> , 2009
	High trichome density on pods and leaves	Interferes with oviposition, larval movement and feeding behaviour	Adult and larval stages	<i>Cicer bijugum</i>	<i>H. armigera</i>	Sharma <i>et al.</i> , 2005
	Small pod size and compact pod surface	Reduces oviposition preference and larval establishment within pods	Adult female and early larval stages	<i>Cajanus albicans</i>	<i>Melanagro myza obtusa</i>	Sharma <i>et al.</i> , 2009
	Thick cuticular wax layer	Reduces insect attachment, settling and stylet probing efficiency	Adult stage	<i>Lens culinaris</i> subsp. <i>orientalis</i>	Aphids	Gupta <i>et al.</i> , 2006
	Pod surface pubescence	Discourages oviposition and reduces larval feeding and establishment	Adult and larval stages	<i>Phaseolus acutifolius</i>	Bean pod borers and leaf-feeding insects	Blair <i>et al.</i> , 2006
	Pod and seed coat resistance traits	Reduces oviposition success, larval penetration and seed damage	Egg and larval stages	<i>Pisum fulvum</i>	<i>Bruchus pisorum</i>	Hardie <i>et al.</i> , 1995

Biochemical	Elevated α -amylase inhibitors	Inhibits digestive α -amylase, reducing carbohydrate utilization and larval development	Larval stage	<i>V. mungo</i> var. <i>silvestris</i>	<i>C. maculatus</i>	Soundararajan <i>et al.</i> , 2013; Wisessing <i>et al.</i> , 2010
	High phenolic content	Feeding deterrence and antibiosis reducing larval	Larval stage	<i>Cicer bijugum</i>	<i>H. armigera</i>	Golla <i>et al.</i> , 2020
	Plant lectins	Binding to glycosyl groups in the digestive tract to hinder absorption	Larval stage	Wild <i>Vigna</i> species	<i>Callosobruchus</i> spp.	Gatehouse <i>et al.</i> , 1990; Tomooka <i>et al.</i> , 2000
	Protease inhibitor isoforms	Suppression of serine protease activity in the insect larval midgut	Larval stage	Wild relatives of pigeonpea (<i>Cajanus</i> spp.)	<i>H. armigera</i>	Parde <i>et al.</i> , 2012
	Altered nutrient composition (protein/carbohydrate imbalance)	Creating a nutritional imbalance that reduces insect growth and development	Larval stage	<i>Cicer cuneatum</i>	<i>H. armigera</i>	Golla <i>et al.</i> , 2020
	Elevated flavonoid levels	Antibiosis effects reducing larval survival, pupation and adult emergence	Larval stage	<i>Cicer chros-sanicum</i>	<i>H. armigera</i>	Golla <i>et al.</i> , 2020
	High tannin content	Reduces digestibility, feeding efficiency and larval growth through antibiosis	Larval stage	<i>Cicer judaicum</i>	<i>H. armigera</i>	Stevenson <i>et al.</i> , 2005
	Polyphenol oxidase activity	Oxidative conversion of phenolics reduces palatability, protein availability and larval performance	Larval stage	<i>C. scarabaeoides</i>	<i>H. armigera</i>	Sharma <i>et al.</i> , 2009; Njaci <i>et al.</i> , 2020
	Elevated peroxidase activity	Enhances oxidative defence responses associated with reduced insect feeding and	Larval stage	<i>Lens culinaris</i> subsp. <i>orientalis</i>	Aphids and chewing insects	Gupta <i>et al.</i> , 2006; War <i>et al.</i> , 2012

		larval performance				
	Volatile organic compounds (VOCs)	Alters host selection and deters oviposition by adult females	Adult stage	<i>Cicer reticulatum</i>	<i>H. armigera</i>	Stevenson <i>et al.</i> , 2005; Golla <i>et al.</i> , 2020
	Arcelin seed proteins	Causes larval mortality and delayed development by disrupting digestion and nutrient utilization	Larval stage	<i>Phaseolus vulgaris</i> var. <i>aborigineus</i>	<i>Zabrotes subfasciatus</i>	Cardona <i>et al.</i> , 1990; Osborn <i>et al.</i> , 1988
Physiological	Rapid jasmonic acid signaling	Activates downstream defense genes and anti-herbivore metabolites after infestation	Larval stage	<i>Cajanus scarabaeoides</i>	<i>H. armigera</i>	Njaci <i>et al.</i> , 2020
	Oxidative burst (ROS production)	Generates toxic oxidative environment reducing larval feeding and survival	Larval stage	<i>Cicer bijugum</i>	<i>H. armigera</i>	Golla <i>et al.</i> , 2020
Inducible	Wound-induced phenolic accumulation	Increased phenolics reduce feeding and larval growth	Larval stage	<i>Cicer reticulatum</i>	<i>H. armigera</i>	Stevenson <i>et al.</i> , 2005
	Induced proteinase inhibitor activity	Suppresses larval gut proteases after herbivory	Larval stage	<i>Cicer bijugum</i>	<i>H. armigera</i>	Golla <i>et al.</i> , 2020
	Callose deposition after aphid feeding	Restricts stylet penetration and phloem feeding	Nymph/adult stage	<i>Glycine soja</i>	Soybean aphid	Hill <i>et al.</i> , 2004
	Induced stomatal and water-balance regulation	Maintains tissue integrity and compensatory defense during herbivory	Larval stage	<i>Lens culinaris</i> subsp. <i>orientalis</i>	Aphids and chewing insects	War <i>et al.</i> , 2012

To protect themselves, plants have evolved complex defence strategies including physical features (such as thorns and trichomes) and specialized secondary metabolites which inhibit or directly damage herbivores (Mithöfer and Boland 2012). The structural features like concentration of trichomes and pod morphology have a direct effect on insect behaviour and attack pattern, biochemical defence like secondary metabolites and proteinaceous compounds have an effect on insect growth and survival (Jackai and Oghiakhe 1989). Physiological defense responses triggered by insect attack provide dynamic resistance capabilities that enable wild relatives to respond adaptively to pest pressure, with particular importance in protecting seeds and pods from storage pests (Edwards and Singh 2006).

Morphological and structural defence traits

Morphological and structural traits serve as crucial first-line defenses against insect pests in wild legume relatives, providing physical barriers that reduce insect attack and colonization before more sophisticated defensive mechanisms are engaged (Abebe 2021; Belete 2018; Warschefsky *et al.* 2014). During the domestication process, many of these structural traits were reduced or lost as selection favored attributes associated with yield and palatability rather than defense, whereas wild relatives retain these protective characteristics that contribute significantly to their resistance to insect pests (Smýkal *et al.* 2018). Structural defenses can provide resistance to all categories of insect pests, whether they feed on pods and seeds, foliage, or sap and cell contents (Edwards and Singh 2006).

Trichomes, both glandular and non-glandular, play important roles in defense against various insect pests (Glas *et al.* 2012; Karabourniotis *et al.* 2020). These hair-like outgrowths on the plant epidermis influence insect behavior through physical obstruction and, in the case of glandular trichomes, through organic exudates that provide additional chemical defences (Shvachko *et al.* 2020). Hooked trichomes impede the movement of aphids and potato leafhoppers, while glandular trichomes in various crops affect larval movement and feeding behaviour (Levin 1973). Trichomes on pods of wild cowpea relative *V. vexillata* are partly responsible for resistance to pod-sucking bugs (Jackai and Oghiakhe 1989). Cowpea genotypes investigated for resistance to *Maruca vitrata* implies trichomes on pods emerged as a pivotal component showing a significant negative interaction with seed damage (Sruthi *et al.* 2024a). Beyond trichomes, pod wall thickness and hardness significantly influence resistance, with pod wall thickness affecting *H. armigera* damage in chickpea (War *et al.* 2018). Seed coat texture, thickness, and hardness serve as important defensive structures, with resistance to weevils in cowpea correlating strongly with seed coat thickness, and resistance to hemipteran and lepidopteran pod pests correlating with pod toughness, hull thickness, peduncle length, and seed location within the pod (Edwards and Singh 2006). In common bean, a negative correlation was arrived with tegument hardness and larval penetration, for *Acanthoscelides obtectus* damage (Cabral *et al.* 2024).

Wild relatives of pigeonpea such as *C. scarabaeoides* and *C. acutifolius* with non-glandular trichomes are not preferred by *H. armigera* females for egg laying (Karrem *et al.* 2025) and varieties with pigmented calyx, petioles, pods, and pod tips suffer least damage from legume spotted pod borer *M. vitrata* (Sharma *et al.* 2009). The number of eggs deposited by *Callosobruchus spp.* was affected by seed size, curvature, color, thickness of the seed coat, and smoothness of the seeds (Akhtar *et al.* 2022; Sahu *et al.* 2023; Sathish *et al.* 2022). Feeding deterrence occurs through multiple structural mechanisms, including the physical barriers presented by pod walls and seed coats that impede larval access to nutritious tissues, and trichome-mediated effects that modify feeding surfaces or entrap young larvae in exudates (Nandi *et al.* 2022; Sharma *et al.* 2009). Impaired larval entry or movement represents another critical effect, where neoplasm formation at oviposition sites (Reymond 2013), podwall thickness, and micromorphological traits contribute to reduced larval penetration rates (Hilker and Meiners 2002). Dense hairs on pods of resistant mungbean genotypes make it difficult for adult bruchids to move over pods and decrease both egg laying and adult emergence (Sahu *et al.* 2023; War *et al.* 2018). The stability of morphological traits contributes to their utility in developing durable resistance, as these physical barriers are less subject to environmental fluctuation than chemical defenses and can therefore provide more consistent protection across diverse growing conditions. In African yam bean cultivars, antibiotic factors in the endosperm and the difficulty in obtaining optimal nutrient quantities needed for growth from harder endosperms may be primarily responsible for the relative resistance of seeds (Baiyeri 2024; Ojuederie *et al.* 2021). The identified structural traits in wild relatives offer promising targets for incorporation into breeding programs aimed at developing cultivars with enhanced and sustained resistance to insect pests (Clement *et al.* 1993). But there are several other characters which are not conducive for the cultivated varieties such as hard thorns, spines, thickened fruits need to be eliminated from the outcome of the crossing programmes. Those features can be overcome by repeated backcrossing with cultivated parents or through advanced transgenic or gene specific approaches.

Biochemical basis of resistance in wild legumes

Wild legumes possess diverse arrays of secondary metabolites and defense proteins that constitute the biochemical basis of resistance to insect pests. Plants have developed diverse mechanisms to defend themselves against insect damage, including the production of chemical compounds, and this defense evolution has been shaped by over 350 million years of plant-insect relationships (Razzaq *et al.* 2023). Secondary metabolites do not participate in the normal growth and development of plants but reduce palatability to herbivores, influencing host finding, oviposition, feeding, survival, and growth and development of insects, thereby playing a major role in host plant resistance in grain legumes (Golla *et al.* 2020).

High phenol concentration correlated with resistance, whereas low concentration of total sugar and proteins were also related with reduced damage by *M.vitrata* in cowpea wild types (Sruthi *et al.* 2024a). Other classes of defensive compounds include alkaloids and terpenoids, and those compounds that are antinutritious such as terpenoids give characteristic scent as insect repellents (Njaci *et al.* 2020). The direct defense compounds such as phenolics, glucosinolates, alkaloids, proteinase inhibitors, cyanogenic glucosides, toxins and repellents that provide broad innate protection against insect pests (Razzaq *et al.* 2023).

Studies have shown that the expression of genes encoding secondary metabolites are significantly induced upon infestation in wild genotypes compared to cultivated types, with chalcone synthase, a key enzyme regulating the flavonoid biosynthetic pathway, showing enhanced activity in resistant wild genotypes (Njaci *et al.* 2020). The gut proteinases (GP) have multiple defense strategies in wild relatives, which is not the case in cultivated chickpea. Wild relatives show high variations in protease isoforms, providing multiple mechanisms of defense against gut proteinases (GP) in comparison to cultivated chickpea. In addition, the presence of the trypsin and chymotrypsin inhibitors in wild pulses further hinders digestion and development of insects (Ignacimuthu *et al.* 2000). Protease inhibitors, phenols, flavonoids, terpenoids, α -amylase inhibitors and arcelins (Sakthivelkumar *et al.* 2013) and lectins have roles in reducing larval growth and organic compounds like terpenoids provide insect repellent characteristic smell (Njaci *et al.* 2020; Sagar and Dhall 2018).

The biosynthetic and regulatory pathways of secondary metabolites of flavonoids, terpenes and glucosinolates exhibited higher accumulation in wild genotypes, indicating that there are different tolerance mechanisms that provide broad protection (Njaci *et al.* 2020). Such diversity and concentration of these biochemical defense systems in the wild relatives make them indispensable for the development of insect resistant varieties of legumes (Sagar and Dhall 2018; War *et al.* 2018). However, few of the biochemical defense compounds in the wild types may not be preferred when brought to cultivated varieties due to their poor nutritional quality or their astringent characters. The preference for the developed genotype may be retarded due to their quality though it may have good quality for resistant to pests. By targeting specific tissue compounds or avoiding over production of these secondary chemical constituents may be achieved through genomic approaches.

Physiological defence responses in wild legumes

Wild legume relatives possess physiological defense responses which are dynamic, inducible in response to insect attack and are distinct from structural and chemical defenses, yet offer complementary protection by induction of defense pathways (Edwards and Singh 2006). Plants actively respond to insect herbivory and mechanical wounding by generating distinctive biochemical changes at the wound site or systemically in distant unwounded tissues such as production of the phytohormones, secondary metabolites and proteins with antimicrobial, insecticidal and antioxidant activities (Njaci *et al.* 2020).

Induced defenses can be significant for seed and pod damaging pests as exemplified by the novel form of insect resistance in pea against cowpea or pea weevils, which involves elicitors in the oviposition fluid of these weevils, termed bruchins (Edwards and Singh 2006). These bruchins induce cell division at oviposition sites, leading to neoplastic growth under the eggs that hinders larval entry into the pods and may expose the larvae to abortion, desiccation, and/or predation (Edwards and Singh 2006).

In bean the pod weevil seems to produce a similar response to that of beans and is a good example of how physiological defence responses are induced across legume species (Edwards and Singh 2006). Hormonal regulation is a key component in the co-ordinated physiological defense responses, and jasmonic acid, salicylic acid and ethylene are the major hormones involved in induced resistance. JA, SA, and ET are important plant hormones that can affect the responses of plants to different diseases and pests; they interact with each other in a network of synergism and antagonism (Njaci *et al.* 2020). The octadecanoid pathway involved in JA production is one of the most studied pathways involved in plant defense, and jasmonic acid and its methyl ester trigger a variety of defense responses such as the induction of PI proteins, volatiles, and other defensive compounds (Edwards and Singh 2006). Lipoxygenase, oxophytodienoate reductase, and allene oxide synthase were three important enzymes in JA biosynthesis pathway that exhibited greater accumulation in JA-resistant wild genotypes than their JA-susceptible cultivated controls (Njaci *et al.* 2020). Enhancement of ethylene pathway enzymes such as 2-oxoglutarate, 1-aminocyclopropane-1-carboxylate synthase and 1-aminocyclopropane-1-carboxylate oxidase expression in resistant genotypes after herbivory (Njaci *et al.* 2020). MicroRNAs (miRNAs) have also been found to regulate expression of defense genes in response to herbivory in wild legumes (Malhotra *et al.* 2022). Another important aspect of physiological defense reactions is the calcium signaling pathway which can trigger phosphorylation of transcription factors thereby directly regulating transcription factors activities through calcium dependent protein kinases. Several Ca^{2+} binding proteins were significantly induced in response to attack, indicating an increase in cellular calcium concentration that reaches levels to bind its binding proteins.

6. Omics-based approaches to study insect resistance in wild relatives

Insect resistance in wild relatives is multigenic and quantitative, and cannot be fully understood by the conventional phenotypic screening (Zhang *et al.* 2017). Omics approaches have been increasingly used to study the genetic, transcriptional, protein, and metabolic basis of insect resistance specifically in wild relatives of legumes (Barah and Bones 2015; Das *et al.* 2022; Wani *et al.* 2022). Integration of genomics, transcriptomics, metabolomics, and trait-mapping approaches has accelerated the identification and utilization of insect resistance-associated loci and candidate genes from wild legume germplasm (Fig. 6).

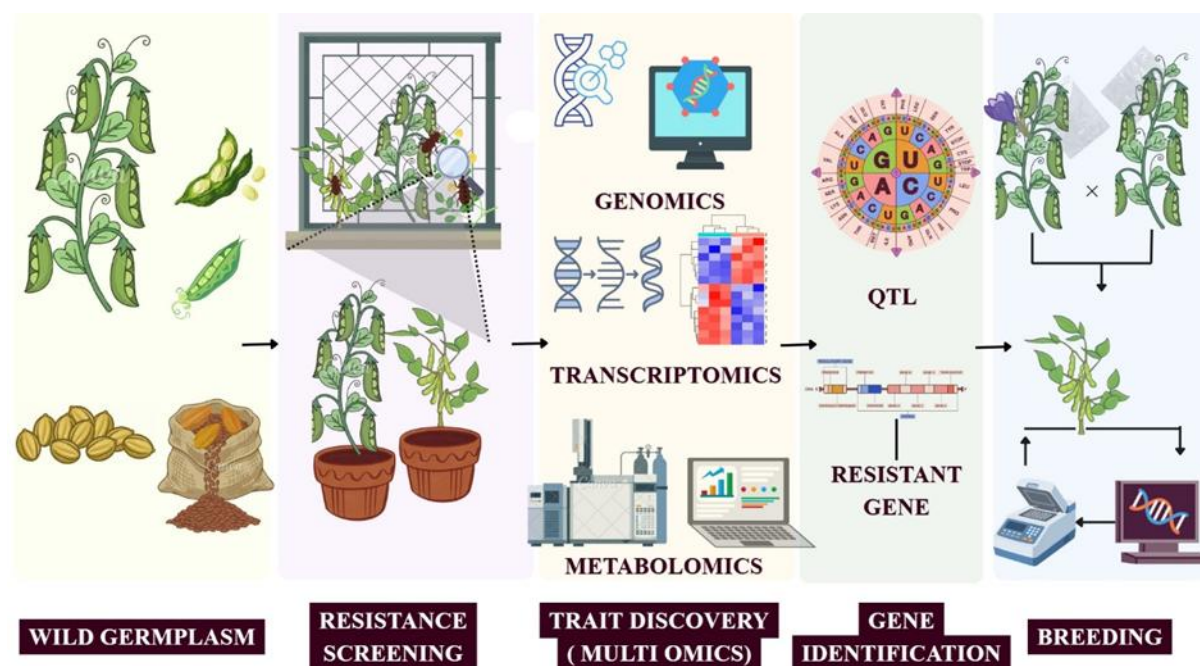


Fig 6. Multi-omics-assisted discovery and utilization of insect resistance traits from wild legume germplasm

Genomics is concerned with the entirety of the DNAs in a given organism, within the framework of abiotic and biotic stress, genomics are also useful in the case of determining quantitative trait loci (QTLs) that allow an organism to withstand particular stress. The analysis of the complex genome set of RNA transcripts under a particular set of conditions using advanced methods as genome-wide sequencing (GWAS) can allow the identification of genetic variations of the desired traits, thereby developing the programs of plants resistant to specific conditions through marker-assisted breeding (Huang 2024).

Genomic studies have revealed numerous resistance-linked loci in wild legumes, with significant genomic divergence observed between resistant wild and susceptible cultivated genotypes (Chang and Hartman 2017; Osuna-Caballero *et al.* 2024). In lentil genetic resources, quantitative trait loci have been identified through genome-wide association studies that help explain plant defense against aphid resistance (Das *et al.* 2022). The availability of whole-genome sequences for legumes including chickpea, pigeonpea, cowpea, and mungbean underpins novel presence or absence of variations that contributes various resistant genes and pathogenesis genes (Dwivedi *et al.* 2023; Jha *et al.* 2023). The genetic diversity maintained in crop wild relatives represents allelic richness that can be harnessed for developing insect-resistant varieties through marker-assisted selection and genomic-assisted breeding approaches (Rajpal *et al.* 2023b; Zhang *et al.* 2017).

Transcriptomics is the study of the complex of RNA transcripts which the genome produces in a given condition. Gene expression patterns at times of stress can help researchers to determine the important regulatory genes in stress conditions. The information is essential in the process of knowing how plants adapt on a molecular scale, and which genetic targets can be used in crop enhancement (Ali *et al.* 2022). High-throughput transcriptome profiling enables the analysis of herbivory-associated gene expression profiles across various plant species, revealing complex signaling networks that coordinate plant defense responses against insect pests (Rubiales *et al.* 2015). A comparative transcriptome analysis of wild blackgram (*Vigna mungo* var. *silvestris*) revealed that several defense-related genes, such as vicilin, trypsin inhibitor, acid phosphatase, thaumatin-like proteins, and receptor kinases, are constitutively expressed and play a role in conferring resistance to *Callosobruchus maculatus*. By identifying 715 differentially expressed genes along with a number of promising candidate resistance genes, this study sheds light on the molecular basis of insect resistance present in wild germplasm. Together, these results highlight the value of wild pulse relatives as an important genetic resource for breeding insect-resistant cultivars through molecular approaches (Raizada and Souframanien 2020).

Comparative transcriptome profiling has been used to identify genes that are upregulated upon infection and differential expression of defense-related genes in mungbean that may play a role in resistance mechanisms (Dayma *et al.* 2025; Singh *et al.* 2022). The resistant wild pigeonpea genotype exhibited clear expression in response to insect attack, with significant increase in accumulation of transcripts related to secondary metabolic pathways viz., flavonoids, terpenes and glucosinolates. Distinct transcriptional signatures identified in wild relatives facilitate the elucidation of specific candidate genes that contribute to insect resistance and the superior defense mechanisms employed by wild pigeonpea relatives against pod borer infestation. Transcription factors associated with insect herbivory including WRKY, MYB, basic helix-loop-helix leucine zipper, Ethylene-Responsive, NAC-domain, and bZIP show differential expressions in response to pod borer infestation. WRKY transcription factors constitute one of the largest families of regulatory proteins involved in insect pest and pathogen defense response, with WRKY3 responsible for wound responses and WRKY6 showing wound

responses significantly amplified when fatty acid-amino acid conjugates from larval oral secretions are introduced into wounds during feeding (Njaci *et al.* 2020).

Proteomics is a study of the overall array of proteins produced in a plant (Aizat and Hassan 2018). The method will provide information on the mechanisms of proteins and their interactions in response to stress. Mass spectrometry is a technique that can be used to identify and determine the quantity of proteins in signal pathways that trigger defense mechanisms to the environmental stresses (Bilbao 2019; Imran *et al.* 2021). Studies have shown differential accumulation of defense-related proteins in resistant genotypes upon pest infestation, with clear separation between resistant and susceptible genotypes evident in proteomic profiles (Rubiales *et al.* 2015). In common bean, protein analysis has identified specific isoforms of storage proteins and defensive molecules that correlate with resistance to storage pests like the bean weevil (Cabral *et al.* 2024).

Proteomics bridges gene expression and observed insect resistance by linking biochemical and molecular defense mechanisms with functional protein expression patterns (Sharma *et al.* 2017). Post-translational modifications such as nitrosylation, nitration, phosphorylation, or ubiquitination may modulate protein activity in response to stress, and proteomics-based approaches for detecting these modifications have been developed and applied in legumes (Rubiales *et al.* 2015).

Metabolomics is crucial for studying the chemical expression of insect resistance because it provides direct insight into the constitutive and induced metabolic compounds that plants use to deter pests (Cuyas and Schwarzenberg 2023; Kumaraswamy *et al.* 2025; Piasecka *et al.* 2019). The coexisting herbivores provoke a metabolome alteration in the plant, which triggers defense metabolites to keep off pests (Jiang *et al.* 2019). Nevertheless, untargeted metabolomics has been effective in deciphering the systematic biochemical reaction of plants to different stresses (Allwood *et al.* 2021). Non-targeted metabolomics LC -Mass spectrometry (LC-MS) can be used to discover endogenous candidate resistance-related (RR) metabolites in plant-herbivore interactions and also give information on phenotypic variations (Anzano *et al.* 2021). Triterpenoid saponins present in lentil include soyasaponin 1 and soyasapogenol A and B, with concentrations in lentil dried plant matter determined to be 0.1-0.5% dry weight, contributing to defense mechanisms against herbivores (Das *et al.* 2022; Sahu *et al.* 2023).

Insect resistance is not governed by a single molecular layer, instead operating through multilayered interactions between genomes, transcriptomes, proteomes, and metabolomes that collectively determine plant defense outcomes (Barah and Bones 2014; Mohamedikbal *et al.* 2025; Chauhan *et al.* 2023)). The adoption of omics methodology including transcriptomics, genomics, proteomics, metabolomics and phenomics is a revolutionary approach to the study of plant resilience to biotic and abiotic stress. This multi-omics framework enables researchers to examine the complex interactions among different biological molecules and their contributions to stress responses to have more efficient crop improvement strategies (Roychowdhury *et al.* 2023). Combining metabolomics with other omics can also provide a whole multi-layered perspective on systems biology connecting genes to function (Rosato *et al.* 2018). Although a coordinated strategy involving the utilization of proteomics, genomics, and other related omics branches of biotechnology has demonstrated potential in enhancing crop improvement initiatives.

7. Challenges and limitations in utilizing wild legumes

Wild relatives represent valuable sources of insect resistance for legume improvement, yet their utilization is constrained by biological, technical, and ecological challenges that fundamentally affect the identification, interpretation, and deployment of resistance traits in breeding programs (Rubiales *et al.* 2015). Chief among the constraints on genetic gain in legume crops are a narrow genetic base stemming from accumulated domestication-syndrome traits, monophyletic evolutionary history, repeated reliance on the same breeding lines, and underuse of wild genetic resources (Singh *et al.* 2022) and faces several challenges, including linkage drag, reproductive barriers, genetic erosion, and habitat loss (Muñoz *et al.* 2017).

The conservation of this genetic diversity faces challenges, as genetic erosion of germplasm in tribal pulses such as *Entada scandense*, *Mucuna monosperma*, *M. gigantea*, *Atylosia goensis*, *Bauhinia vahlii*, *Xylia xylocarpa*, *Parkia roxburghii*, *Vigna radiata* var. *sublobata*, *V. mungo* var. *silvestris*, and *V. grandis* has been noticed (Janardhanan *et al.* 2003). The context of long-term ecological interactions that shape these traits complicates their transfer to agricultural environments, requiring an understanding of the evolutionary history of these plants (Endara *et al.* 2017).

A significant barrier to the utilization of wild relatives is that many species, particularly legumes, remain poorly characterized at the genomic level compared to model crops (Edwards and Singh 2006). The absence of high-quality genomic frameworks restricts the precise identification of resistance-associated genes and alleles (Baucom *et al.* 2021). Limited genomic resources have prevented meaningful comparative analysis to date that might provide clues to the diversification of resistance mechanisms among wild taxa, and consequently insights into key evolutionary history (Watts *et al.* 2023). The lack of genetic baseline information hampers progress in understanding the diversity in insect resistance, limiting the ability to characterize and harness the genetic diversity in this wild gene pool (Shashikala *et al.* 2025).

Draft genome assemblies are typically only 50% to 20% complete for underutilized legumes, and for the taxa which only about sixfold sequencing depth was achieved, the assembly N50 is often shorter than 15 kilobases (Diakostefani *et al.* 2024). Genome-assembly efforts for cultivated lentil and its wild relative *Lens ervoides* have advanced considerably in recent years. The long-read assemblies created for some of the main cultivars and

complete genome assemblies for related species enable understanding of the genomic relationship between the two. Encouraging progress has likewise been made in assembling genomes for cultivated lentil and wild *Lens ervoides*, with long-read assemblies of leading cultivars and complete assemblies of related species clarifying the genomic relationship between them. There are few genomic resources available for the wild legumes, which makes identification of resistance associated loci which are more challenging. Performing comparative analysis with cultivated legumes is more difficult, thereby limiting the rate of understanding of insect resistance diversity in wild taxa (Jha *et al.* 2022; Rubiales *et al.* 2015).

Insect resistance has been evolving over time and has led to the development of various resistance mechanisms, generating a dynamic relationship that has led to the establishment of host utilisation patterns (Després *et al.* 2007). The high biological complexity makes it difficult to interpret reports of resistance across studies because associations between plants and herbivores are sometimes the result of successive evolutionary change and not evolutionary "arms race" (Endara *et al.* 2017). So, general statements about the effectiveness of resistance mechanisms across the range of pests or environments are problematic, and depend on the particular insect biotype (Futuyma and Agrawal 2009; Gougherty and Davies 2021).

Over evolutionary time, biochemical and behavioral adaptations arising from plant–herbivore co-evolution have shaped the specific regulation and expression patterns of plant defenses (Erb and Reymond 2019; Vasantha-Srinivasan *et al.* 2025; Sun *et al.* 2023). Recent research indicates that field-based cross-talk between jasmonic acid (JA) and salicylic acid (SA) pathways produces inconsistent outcomes, with persistent antagonism between the two complicating predictions of defense allocation when biotic and abiotic stresses co-occur (Züst and Agrawal 2017; Gaillard *et al.* 2018; Mangan *et al.* 2025). The expression of resistances in wild relatives is not only a matter of genotype but also strongly driven by abiotic (climate, soil) and biotic (other organisms) environmental factors). Environmental variability can also have significant consequences for resistance evaluation as it can influence the consistency and magnitude of resistance expression across different environments, especially under resource limitations, as that can be expected in agricultural environments.

8. Conclusion and future prospectives

Wild relatives of legume pulses have proven to be irreplaceable reservoirs to counteract biotic stress that have been largely lost or diminished through domestication and intensive breeding. Across the studies reviewed, wild legume taxa consistently outperform cultivated legumes in resistance to field and storage insect pests, a pattern attributable to their ecological adaptation and their morphological, biochemical, and physiological attributes. Their strength is probably due to their remarkably diverse array of defense mechanisms, the morphological architecture viz., trichomes, thickness of pod walls, higher rate of secondary metabolites such as, protease inhibitors, lectins, and hormone-regulated inducible pathways with which they defend themselves against insect enemies. However, the potential use of wild relatives in legume breeding is still not fully realised, due to reproductive barriers, linkage drag, genomic resources and lack of germplasm characterisation. Closing the gap between the recognized value of wild relatives and their actual application in producing resistant cultivars remains among the most pressing priorities for sustainable pulse production.

Advancement in the use of wild legume relatives for insect resistance will require a coordinated effort on the breeding, genomics, and conservation fronts. Although much is known about inheritance of resistance and genetic variation, the process of developing resistant cultivars is still in its early stages, and more concerted activities are desperately needed. Standardized phenotyping platforms combined with multi-environment validation of accessions will be essential for systematically screening secondary- and tertiary-gene-pool material to identify resistance sources that remain stable across diverse agroecological settings. The introduction of new technologies such as GWAS, QTL mapping and multi-omics will speed up the discovery and introgression of resistance loci into high-yielding and nutritionally enhanced cultivars. With the advent of CRISPR-Cas genome editing, new avenues for targeted and precise enhancement of defense characteristics open up. However, long term success will also rely on the development of pre-breeding pipelines, greater in situ and ex situ germplasm conservation, and appropriate breeding targets based on farmers' needs. Bringing together these efforts can help realize the full potential of wild relatives, ultimately yielding more resilient cultivars with reduced pesticide dependence and greater sustainability amid future climate change.

ACKNOWLEDGEMENTS

The authors would like to express their gratitude to the Head of the Department (Agricultural Entomology) and Dean (SPGS), TNAU, Coimbatore, India for providing opportunity and motivation to present, write and work in the area of research through organizing workshops. The authors also thank Director of Research, TNAU, Coimbatore for approval of manuscript (TNAU PUB: 20260013) for submission.

Author contributions

All authors contributed for the concept designing, manuscript preparation. AMRK: Writing – original draft, review and editing, RPS: Mentoring, conceptualization, review and editing, and manuscript correction, PSS, NM: Critical review of the manuscript, MM, SN: Review, analysis of meta-data. All authors read and approved the final manuscript for publication.

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