

Pursuing greener farming by clarifying legume-insect pest interactions and developing marker-assisted molecular breeding

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Abstract

Legumes are important for both food security and sustainable agriculture. Given their relatively high protein content, more than 700 million people worldwide rely on them as food or poultry feeds. They are also important in intercropping systems for improving soil quality, due to their nitrogen-fixing ability. One major challenge to the yield of legumes is infestation by insect pests and pathogens both in the field and during storage. Most farmers have responded by planting resistant strains of legume crops and spraying them with insecticide and fungicide. Nevertheless, the continuous use of biocides, despite their cost-effectiveness, results in resistance development by the pests and pathogens, and raises environmental safety concerns for both humans and off-target beneficial species of insects and microbes. In this review, we discuss the most up-to-date thinking on the interactions between legumes and their insect pests and current farming practices, explain the latest techniques used in identifying molecular markers to aid in the breeding of insect-resistant cultivars, and highlight areas that require further development for effective and ecofriendly integrated pest management.



1. Introduction

Grain legumes (a category which includes soybeans, chickpeas, pigeon peas, cowpeas, field peas, lentils, greengrams, blackgrams, faba beans, and grasspeas) are the main dietary protein sources among vegetarians and form an integral part of the daily diet of human beings all over the world. The cultivation of legumes can contribute to the reduction of malnutrition and improvement of soil fertility (Abate, 2012; Schreinemachers et al., 2014). The total area under soybean, groundnut and pulses cultivation worldwide is estimated at 249 million hectares (FAOSTAT, 2021). Despite the importance of legumes, it has been a struggle to increase their production relative to cereal crops (Foyer et al., 2016).

One major reason is the damage to such crops caused by insect pests. For example, the African bollworm (*Helicoverpa armigera*) alone caused an annual loss in pigeon pea and chickpea production worth US\$645 million (ICRISAT, 1992). Another example is the soybean aphid, *Aphis glycines*, which could cause up to 58% of soybean crop yield loss, worth an estimated US\$2.4 billion annually (Song, Swinton, Difonzo, O'Neal, & Ragsdale, 2006; Tilmon, Hodgson, O'Neal, & Ragsdale, 2011; Wang, Fang, Lin, Zhang, & Wang, 1994). Table 1 summarizes some

Table 1 Summary of the distribution, infestation area and damage caused by different insect pests.

Legume crop	Insect pest	Scientific name	Distribution ^a	Attack area(s)	Infestation rate (IR)/ yield loss (YL)	Reference(s)
Common bean	Bean weevil	<i>Acanthoscelides obtectus</i>	Worldwide	Seed	YL: 13.7%	Allotey, Segwabe, and Randome (2016)
Pea and lentil	Pea aphid	<i>Acyrtosiphon pisum</i>	Worldwide	Leaf, stem and pod	YL: Up to 35.7%	Sandhi and Reddy (2020)
Cowpea	Striped bean weevil	<i>Alcidodes leucogrammus</i>	Africa	Root and stem	IR: 13.8–45.8%	Amoako-Atta (1983)
Cowpea	Coreid pod-bug	<i>Anoplocnemis curvipes</i>	Africa and Iran	Seed	IR: 15.0–17.2%	Koona, Osisanya, Jackai, and Tonye (2004)
Soybean	Velvetbean caterpillar	<i>Anticarsia gemmatalis</i>	North and South America	Leaf	—	Anazonwu and Johnson (1986)
Leguminosae family ^b	Cowpea aphid	<i>Aphis craccivora</i>	Worldwide	Leaf, stem and pod	IR: 32.6% (Cowpea)	Mehrparvar, Madjdzadeh, Mahdavi Arab, Esmailbeygi, and Ebrahimpour (2012); Ofuya (1991)
Broad bean	Black bean aphid	<i>Aphis fabae</i>	Worldwide except Oceania	Leaf, stem and pod	—	Völkl and Stechmann (1998)
Soybean	Soybean aphid	<i>Aphis glycines</i>	Asia, Russia, USA, Canada and Australia	Whole plant	IR: Up to 80%	Venette and Ragsdale (2004)
Chickpea	Semi loopers	<i>Autographa nigrisigna</i>	Asia and Russia	Leaf and pod	—	Sharma et al. (2007)
Soybean	Bean leaf beetle	<i>Ceratoma trifurcata</i>	North America	Leaf, stem and pod	YL: 3.06 kg/ha	Smelser and Pedigo (1992)
Pigeon pea	Pod bug	<i>Clavigralla scutellaris</i>	Africa and Asia	Pod and seed	YL: 35–65%	Shanower, Romeis, and Minja (1999)
Cowpea	African pod bug	<i>Clavigralla tomentosicollis</i>	Africa	Pod and seed	IR: 57.0–60.0%	Koona et al. (2004)

Continued

Table 1 Summary of the distribution, infestation area and damage caused by different insect pests.—cont'd

Legume crop	Insect pest	Scientific name	Distribution ^a	Attack area(s)	Infestation rate (IR)/ yield loss (YL)	Reference(s)
Soybean	Leafhopper	<i>Empoasca terminalis</i>	India and Indonesia	Pod and seed	YL: 26%	Nasruddin, Fattah, Baco, and Said (2015)
Pigeon pea	Leafhopper	<i>Empoasca kerri</i>	India, Bangladesh and USA	Leaf	YL: 10%	Rachappa, Shivayogiyappa, Harischandra, and Yelshetty (2018)
Common bean	Bean ladybeetle	<i>Epilachna varivestis</i>	North America, Japan and Colombia	Leaf	YL: 2–54.9%	Kabissa and Fronk (1986)
Soybean	Limabean pod borer	<i>Etiella zinckenella</i>	Worldwide	Pod and seed	YL: Up to 80%	Kuswanto, Bayu, Baliadi, and Tengkan (2017)
Pigeon pea	Leaf webber	<i>Grapholita critica</i>	Asia	Leaf	YL: 1.3–50.56 kg/ha	Kumar et al. (2014)
Leguminosae family ^b	American bollworm	<i>Helicoverpa armigera</i>	Worldwide	Pod, seed and flower	IR: 20.7–37.0% (Pigeon pea) YL: 12.5–17.8% (Common bean) IR: 16.4–26.3% (Cowpea)	Ali et al. (2009); Karel (1985); Ofuya (1991)
Chickpea	Leaf miner	<i>Liriomyza cicerina</i>	Africa, India, Middle East Asia and Europe	Leaf	IR: Up to 40%	Toker, Erler, Ceylan, and Canci (2010)
Leguminosae family ^b	Legume pod borer	<i>Maruca vitrata</i>	Worldwide	Flower bud and pod	YL: 23.3% (Pigeon pea)	Sharma, Saxena, and Bhagwat (1999)
Cowpea	Flower bud thrips	<i>Megalurothrips sjostedti</i>	Africa and Saudi Arabia	Pod	YL: 20–100%	Singh (1987)
Leguminosae family ^b	Bean flower thrips	<i>Megalurothrips usitatus</i>	Asia and Oceania	Flower	—	Tang et al. (2015)
Pigeon pea	Pod fly	<i>Melanagromyza obtusa</i>	Kenya, Asia, North America, Australia, Papua New Guinea and Colombia	Pod and seed	IR: 29.7–52.0%	Sharma, Bhosle, Kamble, Bhele, and Seeras (2011)

Leguminosae family ^b	Soybean stem fly	<i>Melanagromyza sojae</i>	Egypt, South Africa, Asia, Spain, Australia, Solomon Islands and South America	Stem	YL: 2–51% (Soybean)	Vitorio et al. (2019)
Leguminosae family ^b	Green stink bug	<i>Nezara viridula</i>	Worldwide	Pod	—	Ntonifor and Jackai (1994)
Cowpea	Foliage beetle	<i>Ootheca mutabilis</i>	Africa	Flower and pods	—	Egho (2010a)
Soybean	Stemfly	<i>Ophiomyia centrosematis</i>	Africa, Asia and Australia	Stem and seed	—	Talekar and Lee (1988)
Common bean	Bean stem maggot	<i>Ophiomyia phaseoli</i>	Africa, Asia, USA and Oceania	Stem, leaf and seed	YL: 8–100%	Ochilo and Nyamasyo (2010)
Soybean	Stink bug	<i>Piezodorus guildinii</i>	USA, Cuba and South America	Seed	—	Panizzi and Slansky (1985)
Leguminosae family ^b	Soybean looper	<i>Pseudoplusia includens</i>	Australia, North and South America	Leaf	IR: Up to 91%	Kogan and Cope (1974)
Soybean	Bean bug	<i>Riptortus clavatus</i>	Japan, South Korea and Taiwan	Seed	IR: 43.6–52%	Lee et al. (2004)
Soybean and cowpea	Pod-sucking bug	<i>Riptortus dentipes</i>	Africa	Pod	—	Ntonifor and Jackai (1994)
Soybean	Stink bug	<i>Riptortus pedestris</i>	Asia	Pod and seed	IR: 46.7–56.4%	Li et al. (2021)
Leguminosae family ^b	Fall armyworm	<i>Spodoptera frugiperda</i>	Worldwide	Pod	—	Andrews (1980)
Leguminosae family ^b	Two-spotted spider mite	<i>Tetranychus urticae</i>	Worldwide	Seed	—	Razmjou, Tavakkoli, and Nemati (2009)

^aCAB International (<https://www.cabi.org/>) or EPPO Global Database (<https://gd.eppo.int/>).

^bPolyphagous pest.

of the major global insect pests specific to legumes (Abate, 2012; Abate & Ampofo, 1996; Clement et al., 2000).



2. Mechanisms of host plant resistance against insects

The interaction between the host plant and its insect pests is a continuously evolving form of one-upmanship. Plants have evolved numerous defense mechanisms against insect attacks, including chemical and physical barriers such as volatile compounds that attract the predators of herbivorous insects, secondary metabolites that impart an unpleasant taste or are toxic to herbivores, and increased trichome density as both a physical barrier and a reservoir of antiherbivory compounds. The main mechanisms of host plant resistance are: antixenosis (adverse effects on the behavior of pests), antibiosis (adverse effects on the life history of pests), and tolerance (ease of recovery from insect damage).

2.1 Antixenosis

Antixenosis is also referred to as a nonpreference, in which a plant characteristic poses a chemical or biophysical barrier that deters or repels the arthropod without causing it harm. It may be affected by morphological factors (such as trichomes, waxiness, or pigmentation) or chemical factors (such as phenolic compounds, volatile compounds, enzymes, or other secondary metabolites) that adversely affect the actions of insects, prompting them to choose an alternative host plant. Although this mode of repelling insect pests does not harm them directly, it can increase the pests' exposure to parasitoids or predators by increasing their search time for a more palatable host (Belmain, Haggard, Holt, & Stevenson, 2013). This approach could therefore be part of an integrated pest management (IPM) strategy that incorporates the use of predators or parasitoids of the target insect pest species.

Trichomes have been found in alfalfa/lucerne to offer effective resistance to sapsucking insects such as the potato leafhopper (Shade, Doskocil, & Maxon, 1979). These glandular hairs are likely to provide some level of resistance against other sapsucking pests as well, including aphids (Shade & Kitch, 1983). Trichomes seem also to be able to prevent heavy aphid infestations on chickpeas, as aphids feed more effectively on the areas of these vegetables where trichomes are absent (Edwards, 2001). Trichome secretions often contain the immobilized bodies of young nymphs and larvae of a number

of insect herbivores (Boethel, 1999). Resistance seems to be related to the orientation and size of trichomes in leafhopper-resistant soybeans, rather than their density (Turnipseed, 1977).

Soybean trichome length and density have also been implicated in a plant's resistance to beanflies, whiteflies, pod borers, and bean leaf beetles (Chiang & Norris, 1983; Lam & Pedigo, 2001; Lambert, McPherson, & Espelie, 1995; Talekar & Lin, 1994). Pod trichomes have been found to be involved in Coreid bug resistance (Koono et al., 2002). The morphology of pods and seeds may also lead to resistance against insect herbivory. For cowpeas, resistance to weevils is strongly correlated with seed coat thickness (Kitch, Shade, & Murdock, 1991), while their resistance to hemipteran and lepidopteran pod pests is correlated with a variety of morphological characteristics, including pod toughness, hull thickness, peduncle length, and seed position in the pod (Koono et al., 2002; Tayo, 1989).

2.2 Antibiosis

Antibiosis is defined as a mechanism of pest resistance in which the plant produces an adverse biological effect on the arthropod herbivore, either by killing it or making it too sick to do further damage and cause yield loss. Usually, this resistance mechanism relies on the deployment of plant biochemicals, such as free amino acids, fatty acids, terpenoids, flavonoids and phenolic compounds (Tables 2 and 3), which may weaken an insect attempting to colonize or feed on the plant and harm its biological output (Smith, 2005). Antibiosis is employed in the resistance of pigeon peas and chickpeas to *H. armigera*, resulting in decreased larval survival, decreased fertility, lower weight gain and prolonged larval growth of the herbivore (Kumari, Sharma, & Reddy, 2010). Accessions of wild *Cajanus* spp. (relatives of the pigeon pea) have elevated manifestations of pod borer antibiosis (Sharma, 2005). Antibiosis in the forms of decreased larval and pupal weights, increased larval mortality, extended larval and pupal periods, failure to pupate, reduced fecundity and egg viability contributes to the resistance to *H. armigera* in chickpeas (Narayanamma, Sharma, Gowda, & Sriramulu, 2007). The cowpea cultivar MNC 99-541 F21 demonstrated antibiosis against whitefly (*Bemisia tabaci* biotype B), prolonging the insect's life cycle, and the cowpea genotypes BRS-Urubuquara, Canapu, and TE97-304 G-4 also showed antibiosis toward whitefly, causing elevated nymphal mortality (Cruz, Baldin, de Jesus, & de Castro, 2014).

Table 2 Biochemical substances and mechanisms involved in host plant resistance against insects.

Biochemical substances	Functions and mechanisms	References
Terpenoids (monoterpenoids, sesquiterpenoids, diterpenoids, triterpenoids)	Antibiotic, feeding deterrents, toxicants, oviposition deterrents	Nishida (2002)
Flavonoids (flavonols, flavones, isoflavonoids, anthocyanins)	Phytoalexins, antifeedant, inhibition of mitochondrial oxidation	Ananthakrishnan (1999)
Tannins and lignins	Unpalatability, mechanical barrier postabsorptive inhibition	De Bruxelles and Roberts (2001)
Aldehydes, ketones, alkanes, waxes	Protective layer	Panda and Khush (1995)
Phenolics	Ovicidal, toxicants, photosensitizing insects	Nishida (2002)
Glucosinolates	Antibiotic, toxicant, repellent, irritant	Kliebenstein et al. (2001)
Alkaloids	Digestive enzyme inhibitor, toxicants, interfere in the nerve system, antifeedant, glucosidase inhibitor	Panda and Khush (1995)

Table 3 Protein-derived molecules involved in host plant resistance against insects.

Protein-derived molecules	Function	References
Chitinases	Damage the insect midgut	Falco, Marbach, Pompermayer, Lopes, and Silva-Filho (2001)
Proteinase inhibitors	Digestive enzyme inhibitors	Pompermayer et al. (2001)
Lectins	Increase the absorption of toxic substances, interfere in the absorption of nutrients	Falco et al. (2001)
Polyphenol oxidase	Reduce the nutritive value of the proteins	Falco et al. (2001)
Peroxidase	Hypersensitive response, lignin biosynthesis	Arimura et al. (2000)

Plant secondary metabolites involved in environmental adaptations and stress tolerance can be broadly classified into phenolics, flavonoids, alkaloids, and terpenoids. Terpenoids are the most diverse among these classes of compounds, and play a significant role in the area of chemical ecology (Gershenson & Dudareva, 2007).

Terpenoids are known to mediate interactions between plants and insects (e.g., pollinators, predators, parasitoids, and herbivores). These interactions generally work to the advantage of the plants and to the detriment of the herbivores. The emission of volatile organic compounds (VOCs), including terpenoids, is believed to mediate these interactions. It is believed that the characteristics and effects of the VOC mixture depend on the identity and proportion of the individual components, and that each species of attacking herbivore is susceptible to a specific blend of VOCs (Boncan et al., 2020). The emitted VOCs may include one or a few compounds with toxic, deterrent/repellent, or attractive properties.

Terpenoids are classified (based on the number of carbon atoms they possess) into hemiterpenoids (C₅), monoterpeneoids (C₁₀), homoterpenoids (C₁₁, C₁₆), sesquiterpenoids (C₁₅), diterpenoids (C₂₀), sesterpenoids (C₂₅), triterpenoids (C₃₀), tetraterpenoids (C₄₀), and polyterpenoids (C > 40, higher-order terpenoids) (Boncan et al., 2020). Volatile terpenes (VTs) are terpenoids that are released to interact with the environment, and include hemi-, homo-, mono-, sesqui-, and some diterpenoids. Certain chemical properties, viz. vapor pressure and hydrophobicity, influence the storage and volatility of these terpenoids, while their emission rates and patterns depend on abiotic and biotic factors, including temperature, humidity, seasonality, irradiance, and interactions with other plants and organisms (Yazaki, Arimura, & Ohnishi, 2017).

Terpenoids play essential roles in various biological processes, not only for plant defenses but also for the growth of insects. The well-known methyl farnesoate (MF), farnesoic acid (FA), and juvenile hormone (JH) contain insect sesquiterpenoids (Beran, Kollner, Gershenson, & Tholl, 2019; Cheong, Huang, Bendena, Tobe, & Hui, 2015; Qu, Bendena, Tobe, & Hui, 2018).

Plant tissues with specialized structures, such as secretory cavities, resin canals, latex canals, and glandular trichomes (Holopainen, Himanen, Yuan, Chen, & Stewart, 2013), are involved in the preservation and storage of terpenoids. In the presence of a high concentration of terpinolene, less

damage than usual was caused by *Paropsisterna tigrina* adults in *Melaleuca alternifolia* (Bustos-Segura, Külheim, & Foley, 2015). Besides directly attacking insect pests, terpenoids may also serve as elicitors to activate defense mechanisms in plants against pests. On the other hand, terpenoids that attract herbivores can also serve as bioherbicides that facilitate weed control in rice paddies and other cultivated areas (Mitra, Karmakar, Mukherjee, & Barik, 2017). In addition to promoting crop yield by weed control, pest management, and pollination, terpenoids are also used to improve or change the scents and flavors of food products to suit consumer preferences, through engineering the terpenoid biosynthesis pathways.

2.3 Tolerance

Tolerance is a polygenic trait that helps a plant to tolerate or recover from an insect infestation. It also denotes the degree to which an insect population can be sustained by a plant without significant loss of vigor or yield. However, due to environmental factors, tolerance is more variable than antixenosis and antibiosis. The degree of tolerance is also markedly affected by the age or size and the general vigor of the plant, as well as by the size of the insect-resistant plant population vs the magnitude of the infestation (Belmain et al., 2013).

The degree of reduction in grain yield is also a good indicator of the agronomic efficiency and genotypic ability to withstand damage to insect pests. In chickpeas, better recovery and a lower reduction in grain yield were obtained with the *H. armigera*-tolerant cultivars ICC 12476, ICC 12479 ICC 506 EB, and ICCV 2, than with the vulnerable control ICC 37 (Narayanamma et al., 2007). Pigeon pea cultivars ICPL 98008, ICPL 187-1, ICP 7203-1, T 21, ICPL 332, and ICP 7035 exhibited moderate levels of resistance to *H. armigera* over the growing season. Under unprotected conditions, ICP 7203-1, ICPL 87119, ICPL 187-1, ICPL 84060, and ICPL 332 exhibited lower grain yield losses than the controls, ICPL 87091 and ICPL 87 (Kumari et al., 2010).

To fully utilize resistant cultivars as effective tools in modern pest control schemes, a keen understanding of the types and mechanisms of resistance is required. Some of the pest-resistance mechanisms in legumes are shown in Table 4.

Table 4 Legume-insect interactions and host resistance mechanisms.

Legume crop	Insect pests	Resistance mechanisms	Genetics	References
Soybean (<i>Glycine max</i>)	Stink bugs, <i>Nezara viridula</i>	Antibiosis and antixenosis	Quantitative	Lopes, Destro, Montalvan, Ventura, and Guerra (1997)
	Soybean aphid, <i>Aphis glycines</i>	Antibiosis	<i>Rag1</i>	Li, Zhao, et al. (2004), Li, Hill, and Hartman (2004)
	Potato leafhopper, <i>E. fabae</i>	Antixenosis (trichomes)	Quantitative	Elden and Elgin (1992)
	Various caterpillars: <i>Spodoptera exigua</i> , <i>Pseudoplusia includens</i> , <i>H. zea</i> , <i>H. virescens</i>	Antibiosis, some antixenosis	Recessive or partial dominance, quantitative	Lambert and Kilen (1984); Kilen and Lambert (1986); Kilen and Lambert (1998)
Chickpea (<i>Cicer arietinum</i>)	Pod borers, <i>Helicoverpa armigera</i> and <i>H. punctigera</i>	Chemical antibiosis (trichome exudates)	Quantitative	Yoshida, Cowgill, and Wightman (1997)
Alfalfa (<i>Medicago sativa</i>)	Pea aphid, <i>Acyrtosiphon pisum</i>	Antibiosis	Polygenic	Julier, Bournoville, Landre, Ecalle, and Carre (2004)
	Potato leafhopper, <i>E. fabae</i>	Tolerance	Quantitative	Sorensen and Horber (1974)
Pea (<i>Pisum sativum</i>)	Pea aphid, <i>Acyrtosiphon kondoi</i>	Indirect via leaf	<i>st</i>	Kareiva and Sahakian (1990)
		Morphology	<i>Af</i>	Soroka and MacKay (1990)
	Pea weevil, <i>Bruchus pisorum</i>	Hypersensitivity	<i>Np</i>	Doss et al. (2000)

Continued

Table 4 Legume-insect interactions and host resistance mechanisms.—cont'd

Legume crop	Insect pests	Resistance mechanisms	Genetics	References
Common bean (<i>Phaseolus vulgaris</i>)	Leafhoppers, <i>Empoasca</i> spp.	Tolerance, antixenosis	Quantitative	Galwey and Evans (1982); Kornegay and Temple (1986)
	Mexican bean beetle, <i>Epilachna varivestis</i>	Antibiosis	Recessive, quantitative	Rufener, St. Martin, Cooper, and Hammond (1989)
	Mexican bean weevil, <i>Zabrotes subfasciatus</i>	Antibiosis	<i>Arc</i>	Osborn, Blake, Gepts, and Bliss (1986); Romero-Andreas, Yandell, and Bliss (1986)
	Bean weevil, <i>Acanthoscelides obtectus</i>	Antibiosis	Recessive, quantitative	Kornegay and Cardona (1991)
	Bean pod weevil, <i>Apion godmani</i>	Antibiosis	<i>Agr</i> , <i>Agm</i>	Garza, Cardona, and Singh (1996)

Rag1, Resistance to *Aphis glycines* gene 1; *st*, Reduced stipule gene; *Af*, *Afila* gene; *Np*, Neoplastic pod gene; *Arc*, Arcelin; *Agr*, *A. godmani* resistance; *Agm*: *A. godmani* resistance modifier.



3. Insect-borne plant pathogens

The interactions among insect pests, microorganisms and plants are complex (Franco, Moura, Vivanco, & Silva-Filho, 2017). In these interactions, insect pests are not merely herbivores, but can also act as vectors for the transmission of plant viruses (Whitfield, Falk, & Rotenberg, 2015). Viral diseases are the main biotic stress factors on legume yields in the tropics and subtropics (Sastry & Zitter, 2014). Around 80% of the 1480 known plant viruses rely on insect vectors for transmission (Eigenbrode, Bosque-Pérez, & Davis, 2018). In this section we discuss four major insect pests responsible for transmitting legume viruses, viz. aphids, whiteflies, beetles and thrips (Table 5).

Table 5 Major pest vectors for the transmission of legume crop viruses.

Pest	Crop	Disease	Virus
Aphids	Soybean	Mosaic	Soybean mosaic virus (SMV)
		Dwarf	Soybean dwarf virus (SDV)
	Groundnut	Rosette	Groundnut rosette assistor virus (GRAV)
			Satellite RNA
			Groundnut rosette umbravirus (GRV)
		Mottle	Peanut mottle virus (PeMoV)
		Stripe	Peanut stripe virus (PStV)
Yellow mosaic	Cucumber mosaic virus (CMV)		
Common bean	Common mosaic and black root	Bean common mosaic virus (BCMV), Bean common mosaic necrosis virus (BCMNV)	
		Mosaic due to CMV	CMV
Cowpea	Mosaic due to potyviruses	Cowpea aphid-borne mosaic virus (CABMV), Bean common mosaic virus-blackeye cowpea mosaic strain (BCMv-BICM)	
		Stunt	CMV BCMv-BICM

Continued

Table 5 Major pest vectors for the transmission of legume crop viruses.—cont'd

Pest	Crop	Disease	Virus
	Chickpea	Stunt	Bean leaf roll virus (BLRV), SDV, Beet western yellows virus (BWYV), Legume yellows virus (LYV) and Chickpea luteovirus (CpLV)
		Chlorotic stunt	Chickpea chlorotic stunt virus (CpCSV)
	Pea	Mosaic due to potyviruses	Pea seed-borne mosaic virus (PSbMV) Bean yellow mosaic virus (BYMV)
		Enation mosaic	Pea enation mosaic virus-1 (PEMV-1) Pea enation mosaic virus-2 (PEMV-2)
		Top yellows	BLRV
		Necrotic yellows	Faba bean necrotic yellows virus (FBNYV), Faba bean necrotic stunt virus (FBNSV)
	Faba bean	Leaf roll	BLRV
		Mosaic and necrosis	BYMV
		Yellows and stunt	BLRV FBNYV
	Lentil	Mosaic and mottle	PSbMV CMV
		Bud light	Cowpea serve mosaic virus (CPSMV)
	Soybean	Leaf yellow and roll	Bean pod mottle virus (BPMV)
		Mosaic due to comoviruses	Cowpea mosaic virus (CPMV) and CPSMV
	Cowpea	Mosaic due to sobemovirus	Southern bean mosaic virus (SBMV)
		Chlorotic mottle	Cowpea chlorotic mottle virus (CCMV)
		Mottle	Cowpea mottle virus (CPMov)
		Mottle	Broad bean mottle virus (BBMV)
	Lentil	Mosaic and mottle	Broad bean stain virus (BBSV)

Table 5 Major pest vectors for the transmission of legume crop viruses.—cont'd

Pest	Crop	Disease	Virus	
Thrips	Soybean	Bud blight	Peanut bud necrosis virus (PBNV) and Soybean vein necrosis virus (SVNV)	
		Brazilian bud blight	Tobacco streak virus (TSV)	
	Groundnut	Stem necrosis	TSV	
		Spotted wilt	Tomato spotted wilt virus (TSWV)	
		Bud necrosis	PBNV	
Mungbean and Urdbean	Leaf curl	PBNV		
Whiteflies	Soybean	Yellow mosaic	Begomoviruses (e.g., Bean golden mosaic virus (BGMV))	
	Common Bean	Golden mosaic	BGMV	
		Golden yellow mosaic	Bean golden yellow mosaic virus (BGYMV)	
		Dwarf mosaic	Bean dwarf mosaic virus (BDMV)	
	Cowpea	Golden mosaic and yellow mosaic		Cowpea golden mosaic virus (CGMV)
				Mungbean yellow mosaic India virus (MYMIV)
				Dolichos yellow mosaic virus (DoYMV)
		Mild mottle	Cowpea mild mottle virus (CMMV)	
	Pigeon pea	Yellow mosaic	MYMV, Rhynchosia mosaic virus	
	Mungbean and Urdbean	Yellow mosaic	MYMV, MYMIV and Horsegram yellow mosaic virus (HgYMV)	

3.1 Aphids

Aphids transmit viruses that infect legume crops, which could either kill the plant or significantly reduce the crop yield (Ng & Perry, 2004). For instance, the aphids *A. glycines* can transmit the soybean mosaic virus (SMV) (Rupe & Luttrell, 2008), and the occurrence rate of SMV in a field is highly correlated with the flights of aphids, resulting in huge yield losses (Widyasari, Alazem, & Kim, 2020; Yang et al., 2008).

In Japan, Indonesia, Australia, New Zealand and some parts of Africa, soybean dwarf virus (SDV) is an important soybean disease. This can also be transmitted by aphids such as *A. glycines* (Damsteegt et al., 2011).

Groundnut rosette disease (GRD) is a severe disease of groundnuts in Uganda, and can sometimes result in a complete loss of yield (Okello et al., 2014). GRD is caused by three causal agents: groundnut rosette assistor virus (GRAV), groundnut rosette umbravirus (GRV) and satellite RNA. The transmission of these three agents requires aphids as vectors (Okello et al., 2014). As viral infections in groundnuts cannot be directly controlled once they have gained hold, the control of aphids is the only way of preventing them from spreading further (Alegbejo & Abo, 2002).

Peanut mottle disease, caused by peanut mottle virus (PeMoV), is also spread by aphids, notably *Aphis craccivora* Koch and *Myzus persicae* (Bock, 1973). Another aphid-transmitted virus, peanut stripe virus (PStV), was first reported in China and causes a mild mottle in the seed.

3.2 Whiteflies

Begomoviruses can infect legumes and cause the legume yellow mosaic disease (YMD) (Alabi, Kumar, Mgbechi-Ezeri, & Naidu, 2010). Begomovirus transmission is highly dependent on the whitefly, *B. tabaci* (Hema, Sreenivasulu, Patil, Kumar, & Reddy, 2014; Mar et al., 2017). In India, the yield loss caused by begomoviruses has exceeded \$300 million in mungbean, soybean and black gram (Varma & Malathi, 2005). Whiteflies feed on plant phloem sap through injecting their stylets into the vascular tissue (Morgan et al., 2013). During the ingestion process, the whitefly ingests begomoviruses from the phloem sap, which can then infect other legume crops such as soybeans, common beans, cowpeas, pigeon peas, mungbeans and urdbeans, as the insect moves on to feed on the next plant (Czosnek, Ghanim, & Ghanim, 2005; Hema et al., 2014; Morales & Anderson, 2001).

3.3 Beetles

Beetles can cause mosaic and mottle diseases in several legume crops through the transmission of mosaic and mottle viruses (Bradshaw, Rice, & Hill, 2008). The bean leaf beetle is the main cause of the spread of bean pod mottle virus (BPMV), which causes the young leaves of soybeans to yellow and pucker (Yadav et al., 2015). The transmission of cowpea mosaic virus

(CPMV) is highly dependent on beetles. This virus reduces the plant's fresh weight and reduces the number and weight of pods (Lomonossoff & Shanks, 1999).

3.4 Thrips

Thrips palmi Karny has been reported to be the vector for peanut bud necrosis virus (PBNV), and can spread the virus among several legume crops including soybeans, groundnuts, mungbeans and urdbbeans (Hema et al., 2014; Pensuk, Jogloy, Wongkaew, & Patanothai, 2008; Thekke-Veetil et al., 2020). Recently, the nucleic acid sequences of 12 arthropod viruses and 12 plant viruses were found in the soybean thrips, *Neohydatothrips variabilis*, suggesting that thrips could acquire viruses from various host plants and transmit them to soybeans (Thekke-Veetil et al., 2020).



4. Pest adaptations to plant defenses

The interactions between insects and plants are bidirectional. Plants have evolved different mechanisms to defend themselves against herbivores through physical or chemical barriers. At the same time, insects have also developed counteradaptations by secreting effectors to suppress plant defenses triggered by the initial insect-produced elicitors (Chen & Mao, 2020). For instance, the salivary protein C002 produced by pea aphids (*Acyrtosiphon pisum*) shortens the feeding span of some insects on faba beans (Mutti et al., 2008). Another effector, Armet, has been detected in the phloem sap of infested faba beans, and its knockdown through RNAi shortens aphid feeding and life spans (Wang et al., 2015). Furthermore, the aphid symbiont *Serratia symbiotica* promotes the expression of a histidine-rich Ca^{2+} -binding protein-like gene in the aphid salivary gland to prolong the feeding by its host on *Medicago truncatula*. It does this by suppressing the accumulation of Ca^{2+} and reactive oxygen species (ROS), the initial plant defense response to insect herbivory (Wang et al., 2020). In the soybean aphid *A. glycines*, downregulation of effectors and upregulation of transposable elements have been proposed as putative mechanisms adopted by the insect to counteract soybean aphid resistance (Yates-Stewart et al., 2020). Similarly, nontransient microbiota isolated in the stink bug, *Nezara viridula*, help the herbivore to adapt to soybean defenses (Medina et al., 2018).



5. Worldwide insecticide use in agriculture

Pest management technology has undergone a range of advances in recent decades. The widespread indiscriminate killing of insects, including agricultural pests, through the use of synthetic insecticides in the latter half of the 20th century has given way to more agroecologically sensitive strategies aimed at controlling pest populations by interfering with their reproduction, attracting predators, and using insect pheromone traps. Although the application of synthetic biocides to protect crops against pests and diseases has protected crop yields, the use of these chemicals has had harmful effects both on the environment and on human health. In recent years, attempts have been made to use molecular approaches to develop cultivars or varieties that are resistant to insect pests in grain legumes, in order to reduce reliance on pesticide use and make agriculture more ecofriendly (Sharma, 2016). These molecular approaches include genetic or quantitative trait loci (QTL)-related introgression/pyramiding, marker-assisted selections and wide hybridization for the generation of insect pest-resistant cultivars (Khera et al., 2013).

Total insecticide usage worldwide in agriculture rose from a low in 1994, at 569,465 t, to a peak in 2010, at 720,538 t (Fig. 1A). Average total insecticide application by continent between 1990 and 2019 was highest in Asia, which accounted for 60.3% of the world's total, followed by the Americas (26.2%), Europe (8.3%), Africa (3.8%), and Oceania (1.4%) (Fig. 1B). The top 10 countries with the highest average insecticide usage from 1990 to 2019 were China (272,792.9 t), the USA (79,817.13 t), Brazil (44,011.97 t), India (29,641.23 t), Russia (23,018 t), Japan (12,561.03 t), Turkey (12,600.1 t), Italy (11,305.63 t), Vietnam (11,268.43 t), and Spain at 9799.97 t (Fig. 1C) (FAOSTAT, 2021).



6. Integrated pest management (IPM) and current farming practices

The oldest strategies for controlling insect species were related to modifications in agricultural practices. However, these strategies were soon abandoned or deemphasized with the development of synthetic pesticides, and research on them was largely discontinued. They are reliant on long-term planning because agricultural controls are often proactive rather

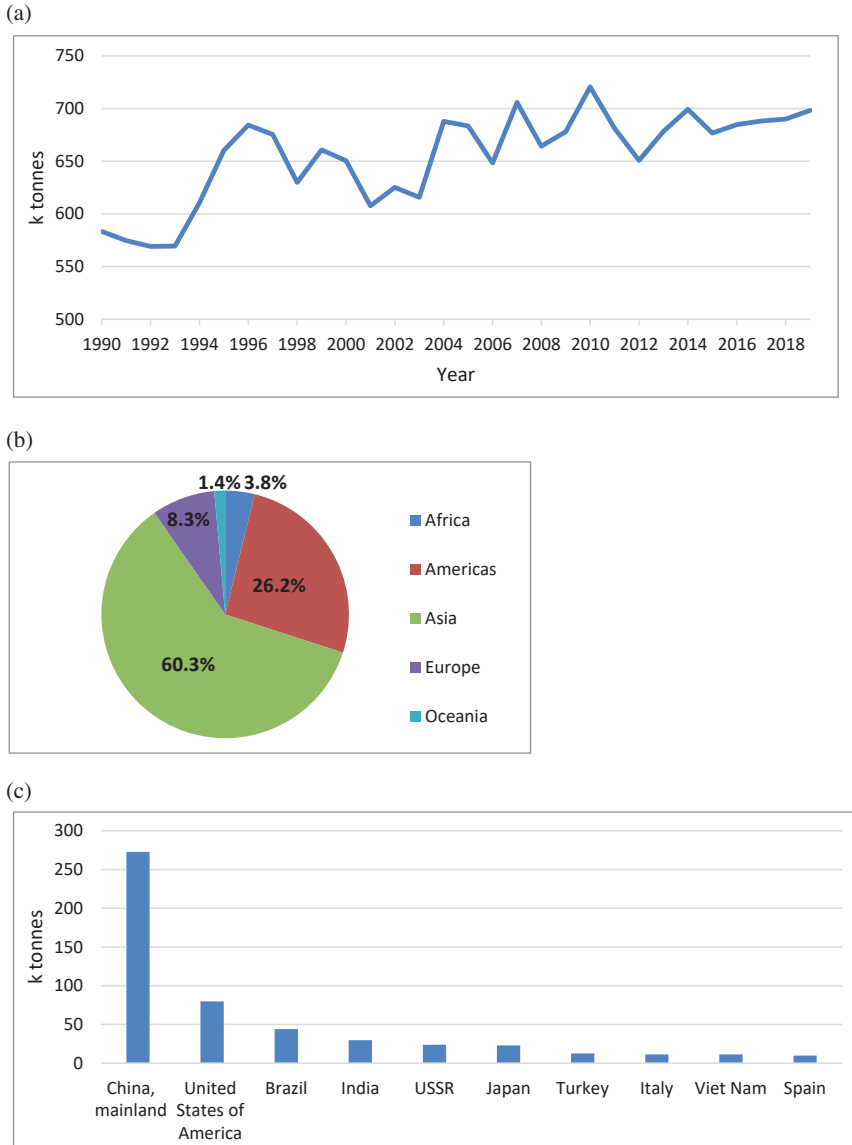


Fig. 1 Insecticide usage database on the quantity (in tonnes) of insecticides used or sold for crops in the agricultural sector worldwide between 1990 and 2019 (FAOSTAT, 2021). There was no information on the amount applied to single crops. (A) Total insecticide usage worldwide in tons by year. (B) Insecticide usage (% of world total) by continents based on the annual average between 1990 and 2019. (C) Top 10 average insecticide usage in tonnes by countries.

than reactive. Also, since their effectiveness relies on a thorough knowledge of the ecology of the many different pest species, most of which have been poorly understood in the past, the outcomes have been highly variable and their effectiveness often difficult to determine. Understandably, most farmers were gradually won over to the more direct and less experience- and skill-dependent solutions to pest problems by the use of toxic chemicals (Hill, 1989).

The situation today is very different. We now have a much better understanding of the ecological interactions within crop systems. We have access to predictive computer models for certain pests, and governments are now expected to rely less on toxic chemicals to solve their problems. As a result of multiple tragedies related to pesticide misuses or spills, the discovery of pesticide residues in recreational areas, drinking water, food and human tissues, and the rise in the occurrence of pesticide-related allergies and petrochemical sensitivities, public interest in the relationship between food quality and human health has grown, accompanied by a rise in the demand for organic foods (Hill, 1987). Integrated pest management (IPM) has thus been developed for pest control. The Food and Agriculture Organization (FAO) defines IPM as “the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimise risks to human health and the environment.” IPM emphasizes the cultivation of a healthy crop with the least possible disruption to agroecosystems, and encourages natural pest control mechanisms (FAO, 2021).

It has been shown that the stink bug-resistant soybean cultivars (PI229358, PI171451, PI171444) experienced a lower pentatomid infestation than other varieties (Jones & Sullivan, 1982). Some experiments have shown that certain breeding lines of soybean may provide possible genetic materials for breeding stink bug resistance into cultivated soybeans (Campos, Knutson, Heitholt, & Campos, 2010). These resistant lines will reduce the damage caused by stink bugs, and hence reduce the need for insecticide applications.

The resistance of soybean plants to whitefly infestation can be used in an integrated program for pest management. Although the types and mechanisms of host plant resistance against insect attacks have been identified (Wiseman, 1985), few researchers have investigated the actual mechanisms of soybean resistance to whiteflies. A combination of factors is believed

to impart resistance to certain soybean genotypes and not to others (Bueno, Raetano, Junior, & Carvalho, 2017). These observations are based on research findings from a number of other plant species on their resistance to whiteflies and other insect pests. An example is the presence of hooked trichomes on field beans as a form of physical barrier (Pillemer & Tingey, 1976). Soybean resistance to whiteflies may also be attributable to variations in trichome density, length, and erectness (Helm, Kogan, & Hill, 1980; Turnipseed, 1977).

Since information regarding the mechanisms of host plant selection by whiteflies is lacking, scientists have begun to test selected whitefly-resistant soybean germplasm. Possible physical mechanisms such as the trichome density and erectness of soybean leaf pubescence, plant height, and canopy closure index, have been examined, as well as possible chemical resistance mechanisms such as soybean epicuticular lipids.

The cowpea aphid, *A. craccivora* Koch, is a polyphagous pest that attacks crops by feeding on all plant parts, resulting in substantial losses of yield (Keatinge et al., 2015). Among the management strategies for *A. craccivora*, the use of chemical insecticides is ranked first by farmers because there are several chemical insecticides available for use against aphids (Egho, 2010b). Cowpea aphids cause damage to the crop plant through sucking and extracting plant sap, thus reducing the amount of nutrients and water available to the crop and enabling the transmission of plant viruses. The intercropping of cowpeas with cereals such as maize, sorghum, and millet has been used as a pest management technique against *A. craccivora*, but intercropping alone cannot entirely repel the insects (Hassan, 2013).

For pod borer control, farmers rely primarily on insecticides. Insecticides are expensive and have caused pesticide resistance and environmental degradation through their indiscriminate use (Singh & Mandal, 2013). That being the case, more environmentally friendly and sustainable pest management strategies are needed, such as integrating the use of tolerant/resistant crop cultivars with adaptive agronomic methods and the use of biological controls. Some of these legume farming practices for managing insect pests are summarized in Table 6.

Successfully controlling pests is one of the greatest challenges for farmers and ranchers who want to operate sustainably. They need management options that are effective and profitable to decrease their use of off-farm chemical inputs. Farmers across the United States are gradually finding that ecological methods for controlling pests meet these needs. For example, practices that promote the natural enemies of pests on the farm provide

Table 6 Insect pests of legume crops and current pest-control farming practices.

Crop	Insect pests	Farming practices	References
Soybean	Bean fly, <i>Melanagromyza sojae</i>	Late-maturing or long-duration soybean varieties can reduce the yield losses due to <i>M. sojae</i>	Srinivasan (2014); Talekar (1990); Sariah and Makundi (2007)
		Early sowing of soybean crop in Tanzania helps reduce bean fly infestations	
	Beet army worm, <i>Spodoptera exigua</i>	Botanical pesticides such as neem that are safer for the parasitoids can be used to encourage the natural enemies of the pests Sex pheromones of <i>S. exigua</i> can be used for monitoring as well as mass-trapping	Packiam and Ignacimuthu (2012)
Bean bugs, <i>Riptortus pedestris</i>		Delayed sowing of soybean helps avoid damage from bean bugs due to lower pest densities	Wada, Endo, and Takahashi (2006)
		Intercropping of soybean with trap crops (e.g., sesame and corn) can enhance the performance of parasitoids and thus reduce the infestation of <i>Riptortus</i> bugs	Youn and Jung (2008)
		Entomopathogenic fungi such as <i>B. bassiana</i> could be used to manage <i>Riptortus</i> bugs	Srinivasan (2014)
Pigeon pea	Gram pod borer, <i>Helicoverpa armigera</i>	Placing a high concentration of sex pheromone in a slow-release formulation	Srinivasan (2014)
		<i>H. armigera</i> sex pheromone traps can be used to monitor the pest population status	
		Crop rotation	
	Bean fly, <i>Melanagromyza obtuse</i>	Used resistant or moderately resistant cultivars. Varieties having purple stems, thinner stems and smaller pith diameter are resistant to bean flies	Srinivasan (2014); Talekar (1990)

Cowpea	Aphids, <i>Aphis craccivora</i>	Avoid monoculture and apply crop rotation. The selected field should be located away from other legume crops	Srinivasan (2014)
		Use neem oil, either alone or in combination with the EPF biopesticides	El-Hawary and Abd El-Salam (2008); Halder, Rai, and Kodandaram (2013)
Chickpea	<i>Helicoverpa armigera</i>	Early planting of crop can help avoid periods of peak abundance of <i>H. armigera</i>	Weigand et al. (1994)
Mungbean	Leafhoppers, <i>Empoasca kerri</i>	Okra, sorghum and pearl millet can be grown as intercrops in mungbean fields	Chakravorty and Yadav (2013)
		This can reduce the leafhopper damage significantly	
		Use neem-based biopesticides at recommended doses	
	Thrips, <i>Megalurothrips distalis</i>	Use blue sticky traps to monitor thrips at regular intervals and determine when other pest management controls are required. Entomopathogenic fungi could reduce thrips damage	Ekesi and Maniania (2000)
Lentil	Pod borer, <i>Helicoverpa armigera</i>	Insecticide application necessary, using methidathion (SupracideR @ 0.5kg a.i./ha), and/or deltamethrin (Decis @ 38 g a.i./ha)	Beniwal, Bayaa, Weigand, Makkouk, and Saxena (1993)
		Use endosulfan (Thiodan 35 @ 3 mL/L) at the time of flowering/early pod-setting	Stevenson, Dhillon, Sharma, and Bouhssini (2007)
	Armyworm, <i>Spodoptera exigua</i>	Collect and destroy the caterpillar. Spray 500 mL of Dichlorvos 85 SL or 3 kg of carbaryl 50 WP or 1 L of Quinalphos 25 EC in 500 L of water per ha	https://www.digokrishi.com/lentil-insect-pest
	Cutworm, <i>Agrotis ipsilon</i>	Destroy the holes where they hide. Deep plowing of the field in between the crops	

an estimated \$4.5 billion worth of pest suppression each year in the United States. Other traditional practices include rotating in new crops that interrupt the pests' life cycles, improving the ability of a crop to compete against weeds, and building up soils that provide unfavorable conditions for disease-causing microorganisms naturally. The ecological approach uses awareness, sustainability and resource management to grow crops safely while keeping insect pests, diseases and weeds at bay (Hinds, 2020).



7. Strategies for effective and ecofriendly IPM

Now that researchers are armed with reliable information on the life cycles and ecology of the various insect pests, the next stage in the development of IPM will be to look for more innocuous pesticide substitutes such as hormones, pheromones, traps, biological control agents, bioengineered pathogens, and the release of sterile males. While useful as less invasive curative methods, such approaches still avoid addressing the root causes of the issue. They also keep the farmer reliant on experts and product suppliers, and perpetuate the image of pests as enemies to be eradicated. We are now on the threshold of a third step that recognizes pests not as rivals, but as indicators of problems in agricultural system design and management. It is also becoming apparent that most of the keys to suitable environmental designs and management methods capable of keeping pest numbers at sustainable levels are held by ecological expertise. With this strategy, through the incorporation of a variety of agricultural and bioecological controls, potential infestations are prevented from becoming serious problems, while the more familiar invasive controls, such as pesticides, are reserved for emergencies only (Hill, 1989).

Effective IPM needs a comprehensive knowledge of the interactions among crop plants, pests, and the surrounding environment, as well as an understanding of farmers' knowledge and expectations. Therefore, to develop sustainable pest control strategies for grain legumes, it is critical to: (1) survey the awareness and attitudes of farmers toward grain legume pests, (2) investigate existing farming practices on the management of grain legume pests, and (3) recognize other limiting factors on the productivity of grain legumes (Adati et al., 2007; Nwilene, Nwanze, & Youdeowei, 2008).

Sometimes biocides (including pesticides and herbicides) are another cause of disruption in the field. By using herbicides to remove noncrop vegetation which provides a major overwintering environment for beneficial species, local biodiversity is reduced. The use of pesticides can also

destroy nontarget animal species that are important natural enemies of the insect pests, either as competitors or predators. Instead, alternative tactics such as perimeter trap cropping, where another more enticing noncrop plant is grown around the perimeter of a crop field to lure pests away from the cash crop, should be considered. Simultaneously, a selective pesticide can be strategically applied at the trap crop border to destroy the target pests and reduce the total amount of pesticide required. While insecticides are effective in the short term against sucking pests and the pod borer complex, the development of insecticide resistance among insect pests, the presence of insecticide residues on crops, and off-target environmental hazards require alternative and ecologically safe long-term management methods, such as planting pest-resistant cultivars (Soundararajan, Narayanasami, & Geetha, 2013).

One of the best strategies for effective and ecofriendly insect pest management is the development of pest-resistant cultivars. To achieve this goal, legume breeding, the use of wild legumes as genetic resources, and genome-wide association studies (GWAS) analyses all play important roles.

7.1 Legume breeding for enhanced insect resistance

Grain legume crops around the world are damaged by many pest species. The most destructive insect pests are: pod borer and leaf miner in chickpeas, stink bug and white flies in soybeans, *Sitona* weevil, a seed weevil, in lentils, pod fly and pod borers in pigeon peas, bruchid in mungbeans, and leaf miner in groundnuts (Weigand et al., 1994). Genetic sources of pest resistance can be harnessed as a part of the integrated pest control strategies in conjunction with cropping systems and agricultural practices that help minimize the release of pesticides into the environment, even with a small number of pest-resistant cultivars. If no resistant cultivar can be found (as is the case with *Aphis fabae* Scopoli, which causes serious damage to faba beans in temperate regions), plant characteristics such as height, sowing date and density may still help identify ideotypes that can reduce the input of insecticides (Stoddard, Nicholas, Rubiales, Thomas, & Villegas-Fernandez, 2010).

In common beans, the resistance to storage bean weevils (*Acanthoscelides obtectus* and *Zabrotes subfasciatus*) is a target for breeders, and some progress has been made with the use of inhibitors in the development of some cultivars with antibiosis properties. With various modes of action, the arcelin-phytohemagglutinin- α -amylase inhibitor (Arc-Pha- α AI) locus of the common bean, *Phaseolus vulgaris* L., has been found to encode plant

defense proteins. In some cases, introgression of this locus into cultivated varieties from resistant wild bean accessions was capable of conferring resistance against the Mexican bean weevil, *Z. subfasciatus* (Boheman), but not against the bean weevil, *A. obtectus* (Say). Resistance can be the product of one or a combination of insect inhibitory proteins in this locus with respect to the Mexican bean weevil (Fory et al., 1996). Recently, wild accessions and conventional landraces have been established as major sources of resistance against bean weevils (Zaugg et al., 2012). Introgressed lines and segregating populations may be used to conduct QTL analyses to fine-tune QTL mapping and to discover genes that regulate agronomic characteristics relevant to the resistance against these pests.

Mungbean (*Vigna radiata* L.) is one of the key beans consumed in China, while bruchid (*Callosobruchus chinensis* L.) is a storage pest that causes major losses of mungbean seeds. Breeding for bruchid-resistant varieties is an important target for crop improvement in mungbean and other legumes (Cheng, Wang, & Wu, 2005; Sun, Cheng, & Wang, 2007). The bruchid-immune line V2709 (introduced from AVRDC-Thailand) was identified following the screening of a mungbean germplasm set (Sun et al., 2007). A single dominant *Br2* gene anchored by molecular markers, which can be used in marker-assisted selection, appeared to be associated with the resistance against bruchid (Sun et al., 2007). The bruchid-resistant variety “Zhong Lv No.4” was developed with V2709 as a progenitor. It was released in 2004 in China, and removed the need for chemical fumigation to prevent in-storage bruchid infestation.

The pod borer, *H. armigera* (Hubner), is a major chickpea pest in the Indian subcontinent. Several germplasm accessions/breeding lines/cultivars with mild resistance, as well as some annual and perennial wild *Cicer* accessions, have been reported to offer some degree of resistance against *H. armigera* (Dar, Reddy, Gowda, & Ramesh, 2006; Sharma et al., 2007). Genetic transformants of chickpea expressing a sequence-modified *Cry2Aa* gene showed differential resistance to pod borer larvae in proportion to the level of expression of the *Cry2Aa* protein. A high-expressing line has been found to confer near-complete pod borer protection (Sumita et al., 2010). The spreading types of chickpea appear to be more susceptible to damage by *H. armigera* than the erect types (Yadav et al., 2006). Therefore, the erect plant habit could be the distinguishing feature of a resistant ideotype (Table 7).

Table 7 Identification and exploitation of host plant resistance to insect pests in grain legumes.

Crop	Genotypes	Insect pest	Reference
Soybean	Nimsoy	Leaf miner	Dhaliwal, Singh, and Jindal (2004)
	PI 227687	Stink bugs	Talekar (1987)
	PI 171444		
Cowpea	VITA5, VITA 4, Banswara, TVu946	Pod borer, <i>Maruca vitrata</i>	Singh (1978); Lal (1987); Chanchal and Singh (2014)
	IT82E-16, P 1473, MS 9369, P 1476	Aphid, <i>Aphis craccivora</i>	Benchasri, Nualsri, Santipracha, and Ngampongsai (2007)
	IT99K-429-2, IT89KD-288	Bruchids, <i>Callosobruchus maculatus</i>	Obadofin (2014)
Green gram	V2817, V1128	Bruchids	Somta et al. (2008)
	PDM-84-143, TAM-20	Stem fly	Devasthali and Joshi (1994)
	P 526, J1, LM 11	Pod borer	Lakshminarayan, Singh, and Mishra (2008)
Black gram	PLU 54, CBG 08-011	Pod borer, <i>Helicoverpa armigera</i>	Lal (1987)
Field pea	Bonville, EC 33860; PS 410, T 6113	Pod borer, <i>Etiella zinckenella</i>	Lal (1987), Teshome et al. (2014)
	T 6113, PS 41-6; KMPR 9, PS 40	Leaf miner, <i>Chromatomyia horticola</i>	Teshome et al. (2014)
Pigeon pea	BDN 2, ICPL 84060, ICPL 4, Bori	Pod borer, <i>Helicoverpa armigera</i>	Lateef and Pimbert (1990)
	MPG 679, ICPL 88034	Legume pod borer, <i>Maruca vitrata</i>	Saxena, Lateef, Fonseka, Ariyaratne, and Dharamsena (1996)
	ICP 7941E1, ICP 10531-E1	Pod fly, <i>Melanagromyza obtusa</i>	Lateef and Pimbert (1990); Moudgal, Lakra, Dahiya, and Dhillon (2008)
Chickpea	ICC 09314, ICC 506, ICCV 10, ICCV 7	Pod borer, <i>Helicoverpa armigera</i>	Bhagwat, Aherker, Satpute, and Thakre (1995); Sharma et al. (2017)
	ICC 12475	Beet armyworm <i>Spodoptera exigua</i>	Sharma et al. (2017)
	JG 315, DCP 923, BG 372, BG 1003	Bruchid	Sharma et al. (2017)
	ILC 5901, ILC 380, ILC 7738	Leaf miner, <i>Liriomyza cicerina</i>	Girija, Sallmath, Patil, Gowda, and Sharma (2008); Shankar, Sharma, Ramesh Babu, and Sridevi (2013)

7.2 Wild relatives of legume crops as genetic resources for insect resistance

One of the possible crop improvement options is the transfer of genes from wild legume relatives to the cultivars to confer resistance against legume pests. For example, wild *Cajanus* spp. are the repository of many significant trait-specific genes and can be used to enhance crop cultivars, enrich variability and diversity, and increase the genetic base and prebreeding populations of wild *Cajanus* spp. In the cultivated crops, the genes responsible for resistance to insect pests are often sacrificed in the process of domestication to secure other desirable agronomic traits, but they are still retained in many wild accessions or relatives of the crop plant (Table 8). High levels of pest resistance have been reported in a few cases in beans, field peas (Clement, Hardie, & Elberson, 2002), cowpeas (Redden, Dobie, & Gatehouse, 1983), and black grams (Dongre, Pawar, Thakare, & Harwalkar, 1996). The wild relatives or accessions of pigeon peas and chickpeas are important sources of genes for insect pest resistance (Dhillon & Sharma, 2012).

7.3 Developing molecular markers for insect resistance in legumes by GWAS

The terminology for phenotypic characterizations across different GWAS studies on plants needs to be standardized in order for their findings to be integrated successfully (Zhao et al., 2019). It is therefore important to use uniform, popular descriptors or ontologies (Shrestha et al., 2010). Although the use of ontology by research groups has increased over the last decade, more improvement is needed (Ćwiek-Kupczyńska et al., 2016; Krajewski et al., 2015; Walls et al., 2019). Ontologies are relatively standardized for a variety of legume crops (e.g., chickpeas, faba beans, lentils, and soybeans) and can be accessed at <http://www.cropontology.org>.

To facilitate data integration and usage, enhanced data management and sharing of crop genotypes, phenotypes, and GWAS datasets are also required. To identify single-nucleotide polymorphism (SNP)-trait associations in legume crops, there is a need to build open-source databases and repositories for genotypic and phenotypic datasets coupled with easy-to-use GWAS pipelines with embedded standardized genotypic data.

One of the major limiting factors for soybean production is insect damage. Hitherto, insect control to protect soybean yields has relied primarily on insecticide applications. Some soybean plants have been shown to be

Table 8 Wild species of legume crops identified as genetic resources for breeding resistance to different insect pests.

Crop	Wild species/accessions	Insect pests	References
Soybean	PI 171444 (MG VI)	<i>Anticarsia gemmatalis</i> (Hubner)	Kester, Smith, and Gilman (1984)
	PI 229358, PI 227687		Hoffmann-Campo, Ramos Neto, Oliveira, and Oliveira (2006)
	PI 274454		Ortega, All, Boerma, and Parrott (2016)
	PI 227687	<i>Trichoplusia ni</i> caterpillars	Liu, Norris, and Lyne (1989)
	PI 567598B	<i>Megacopta punctatissima</i> Montandon	Bray, McDaniel, All, Li, and Parrott (2016)
Groundnut	<i>Arachis cardenasii</i>	Leaf miner	Sharma, Sujana, and Rao (2009)
	<i>A. duranensis</i>	<i>Helicoverpa armigera</i>	
	<i>A. kempff-mercadoi</i>	<i>Spodoptera litura</i>	
Mungbean	<i>V. radiata</i> var. <i>sublobata</i>	Bruchid	Fujii and Miyazaki (1987); Sarkar and Bhattacharyya (2015)
Cowpea	<i>Vigna vexillata</i> (L.) Benth	Pod-sucking bug	Jackai and Oghiakhe (1989)
		<i>Clavigralla tomentosicollis</i>	
		Stal, spotted pod borer, <i>M. vitrata</i>	

Continued

Table 8 Wild species of legume crops identified as genetic resources for breeding resistance to different insect pests.—cont'd

Crop	Wild species/accessions	Insect pests	References
Pigeon pea	ICPW 214 (<i>Cajanus bracteata</i>)	Pod fly, <i>M. obtuse</i>	Sharma, Pampapathy, and Reddy (2003)
	ICPW 278, ICPW 280 (<i>C. scarabaeoides</i>)	Pod borer, <i>H. armigera</i>	Sujana, Sharma, and Rao (2008)
	ICWP 016 (<i>Cajanus albicans</i>)	<i>Meloidogyne javanica</i>	Sharma, Jaba, and Vashisth (2017)
	ICWP 062 (<i>C. platycarpus</i>)		
Chickpea	<i>Cicer bijugum</i> , <i>C. reticulatum</i>	<i>H. armigera</i>	Sharma, Pampapathy, Lanka, and Ridsdill-Smith (2005)
	<i>C. pinnatifidum</i> , <i>C. bijugum</i> , <i>C. echinospermum</i>	Bruchid, <i>C. chinensis</i>	Singh, Ocampo, and Robertson (1998)
Lentil	ILWL 245 (<i>L. culinaris</i>)	<i>Sitona</i> weevil (<i>Sitona crinitus</i>)	El Bouhssini, Sarker, Erskine, and Joubi (2008)
	<i>L. nigricans</i> , and <i>L. lamottei</i>	Seed weevil (<i>Bruchus</i> spp.)	
	<i>L. culinaris</i> Medikus subsp	Bruchids (<i>Bruchus</i> spp.)	Laserna-Ruiz, De-Los-Mozos-Pascual, Santana-Méridas, Sánchez-Vioque, and Rodríguez-Conde (2012)

resistant against certain insect pests. Such plants, e.g. those resistant to soybean aphid (SBA), have been used to develop resistant soybean cultivars. Phenotypic data for resistance against beet soybean looper (SBL), Mexican bean beetle (MBB), armyworm, potato leafhopper (PLH), SBA, velvet bean caterpillar (VBC) and chewing damage caused by unspecified insects can be integrated with the data from the genotyping array, SoySNP50K, and the statistical capacity of GWAS for a detailed understanding of insect resistance among the United States Department of Agriculture Soybean Germplasm Collection. Important SNP markers for SBL, MBB, PLH and VBC have been identified. The PLH resistance locus is located close to, but distinct from, a locus for soybean pubescence density on chromosome 12. These findings provide genetic evidence that the density of pubescence and PLH resistance may be two distinct traits. This research provides a new insight into the QTL mapping of the resistance of soybeans to four major insect pests of soybean (Chang & Hartman, 2017).

By correlating phenotypic data with SNPs across a genome, genome-wide association mapping can help identify resistant accessions. From published studies screening cultivated soybeans (*G. max*) and wild soybeans (*Glycine soja* Siebold & Zucc.) using aphids exhibiting Biotype 1, 2 or 3 characteristics, aphid population counts were collected from 2366 soybean accessions. The SoySNP50 K high-density genotyping array used earlier to genotype the USDA Soybean Germplasm Collection was used to obtain genotypic results. Important associations have been identified on 18 of the 20 soybean chromosomes between SNPs and soybean aphid counts. On chromosomes 7, 8, 13, and 16 with known *Rag* genes, a substantial number of associated SNPs have been found. On chromosomes 1, 2, 4 to 6, 9 to 12, 14, and 17 to 20 where *Rag* genes have not yet been mapped, there were also prominent associations with SNPs, indicating that many *Rag* genes remain to be discovered. These SNPs can be used to identify promising accessions for breeding programs with new aphid-resistance characteristics (Hanson et al., 2018).

In a recent genome-wide association analysis, two SNP markers (C35011941-894 and Scaffold30061-3363) were closely correlated with aphid resistance across three models with a log of odds (LOD) value greater than 2.5. These findings will provide valuable information on the genetic availability of aphid resistance for the molecular breeding of resistant types of cowpea (Qin et al., 2017).

Molecular markers may play an important role in accelerating the introgression of specific genes that confer resistance against target insects on

high-yield cultivars, by recognizing the essence of gene actions while reducing the deleterious effects of introducing unwanted genes from wild species through linkage drag. Molecular breeding also provides the ability to pyramid numerous resistance sources that, due to similar phenotypes, could not be effectively selected by traditional breeding methods, thus enhancing the resistance level and/or potentially producing more stable resistant cultivars.

Considerable progress has been made in the development of genetic linkage maps of chickpeas, cowpeas, and soybeans, though much remains to be done regarding pigeon peas, common beans, lentils, and field peas. The preliminary identification of molecular markers for insect resistance has been done in soybeans, chickpeas, mungbeans, field peas, and cowpeas. However, no distinct benefit over the traditional method could be found by using marker-supported selection for the resistance to insect pests, and in most instances, epistatic resistance was also very high. For breeding insect-resistant varieties, the identification of the genes responsible for resistance and the determination of their locations on the chromosomes are important.

7.4 Genetic methods to improve the legume resistance to insect pests

With the advancement of genomics and genetics methods, a number of insect resistant genes have been identified in different plants. These discoveries offer new opportunities to improve legume yield by making them resistant to insect pests. One such method is the transfer of exogenous genes into the host plant genomes, such as the vegetative insecticidal proteins (VIP) and secretable proteins Bt or Cry isolated from the soil bacterium *Bacillus thuringiensis* (Estruch et al., 1996; Gu et al., 2021). In 1997 Peggy Ozias-Akins and Chong Singsit were the first to develop transgenic alfalfa and peanut carrying *Cry* to improve the legume resistance against insects (Singsit et al., 1997). Since then, other transgenic legumes have also been developed, including the cowpea, pigeon pea and chickpea (Alok, Annapragada, Singh, Murugesan, & Singh, 2020; Kumar, Jaiwal, Sreevathsa, Chaudhary, & Jaiwal, 2021; Singh et al., 2018). Instead of introducing exogenous genes, several transgenic soybean lines were created through the expression of their own genes. For instance, the terpene synthase gene *GmAFS* was overexpressed in soybean and enhanced its resistance to cyst nematodes (Lin et al., 2017).

Another method of improving legume crop breeding lies with the rapid development of gene editing technologies such as CRISPR/Cas9.

This include engineering legume agronomic traits which include enhancing the formation of defense hormones, knocking out the legume susceptibility genes, changing the pathogen effector–target interaction, modifying the insect genome to reduce their resistance to insecticides, and inducing sterility in insect pests (Bisht, Bhatia, & Bhattacharya, 2019).

In addition to increasing the legume crop yield, other benefits of obtaining genetically modified legumes, such as the soybeans, could significantly improve farmers' incomes, reduce the use of insecticides, fuels and tillage uses, resulting in a lower carbon footprint, and contribute to the development of a more sustainable environment (Brookes & Barfoot, 2017). Despite these potential advantages, permission for their commercial release has been delayed by public suspicion of new biotechnologies and concerns about the safety of genetically modified crops (Tyczewska, Woźniak, Gracz, Kuczyński, & Twardowski, 2018).



8. Effects of global warming and climate change on insect pests

Global warming and climate change will trigger significant changes in the diversity and abundance of arthropods, the spatial distribution of insect pests, the dynamics of insect populations, the biotypes of insects, the interactions between herbivores and plants, the abundance of natural enemies of these pests and the possible extinction of some of these species, and the effectiveness of crop protection technologies. The distribution of insect pests will also be affected by the changes in cropping patterns caused by climate change. Alterations in the geographical range and abundance of the insect pests may exacerbate the severity of crop losses, and will therefore have a significant impact on crop production and food security.

Major insect pests may move into more temperate regions from the tropics, such as pod borers (genera *Spodoptera*, *Helicoverpa* and *Maruca*), whiteflies and aphids, resulting in increased damage to grain legumes. Host-plant resistance, natural enemies, and biopesticides are some of the possible tools for IPM. However, as a consequence of global warming, the relative effectiveness of these pest control tactics is likely to change. Climate change will also result in the increased spread of insect-transmitted diseases. Altogether, these phenomena will have significant implications for food security and crop protection, especially in developing countries where the need to increase and maintain food production is most urgent (Sharma, 2014).

Insects have evolved various host plant–association patterns, life histories and feeding strategies tailored to exploiting their hosts (Panda & Khush, 1995). One foreseeable development is the evolution of minor but lasting improvements in the assortment of insect-derived enzymes, that allow insect pests to also feed on other plant species closely related to their original hosts, as they expand the range of their habitats as a result of global warming.



9. Conclusion

For hundreds of millions of people in Southeast Asia, Africa, and Latin America, tropical grain legumes are a major protein source. They are also important sources of income generated from exporting these grains to other parts of the world. Among the main biotic constraints hindering the productivity of these crops are insect pests, especially those insects that damage the legume pods, as they are the key cause of yield losses in tropical grain legumes.

For most insect pests, chemical control measures are available but are not easily affordable or applicable to the conditions of smallholder farms in which most tropical grain legumes are grown. The only viable solution is an IPM approach that relies more on planting strategies. Diversification of crops is an important agricultural strategy and can be accomplished by intercropping, strip-cropping or trap-cropping, which also provides a natural biological control of insect pests. Legume varieties that are resistant or tolerant to many of the major insect pests have been developed through conventional and molecular breeding. In addition to finding new means of pest management, researchers must also pay careful attention to the scale of available technologies in developing future insect pest controls for tropical grain legumes.

Secondary metabolites (such as terpenoids, flavonoids, tannins, phenolics, and alkaloids) are involved in abiotic and biotic stress responses by plants, and many of them are released in the form of volatile organic compounds. In particular, terpenoids play important roles in reducing herbivory and attracting beneficial species, such as those involved in tritrophic and multitrophic interactions. Interactions between plants and insects can be characterized as a perpetual arms race. In both plants and insects, these interactions have resulted in an unparalleled diversity of terpenes and terpenoids. During the next few years scientists must obtain a better understanding of their complex interactions and to make effective use of them in biotechnology. Achieving adequate precision and accuracy in phenotyping insect pest

resistance remains a major bottleneck. In order to develop insect pest-resistant cultivars, improved higher-precision phenotyping systems would directly benefit both marker-assisted selection and traditional breeding, along with further strategic research that feeds into these endeavors.

The coevolution of plants and insects advances in lockstep. In order to protect themselves from herbivory, plants have established defense mechanisms, while insects have found numerous ways to evade the harmful effects of the host plants' defenses. Although researchers have attempted to dissect plant-insect interactions, our knowledge on this subject is still limited. A better understanding of this process will enable us to design more effective methods for the biological control of insect pests using natural products and by developing new plant varieties with enhanced chemical defenses. Future research must concentrate on environmentally sustainable methods for pest control that are consistent with the needs of legume farmers and the constraints that act upon them.

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Conflicts of interest

The authors declare no conflict of interest.

Author contributions

S.T. wrote the first draft of this manuscript. K.F., F.L.W. and H.Y.Y. provided scientific inputs and contributed to the writing. J.H.L.H. and H.-M.L. coordinated the writing effort and prepared the final manuscript.

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