Journal of Food Legumes 21(4): 211-217, 2008

Potential for using morphological, biochemical, and molecular markers for resistance to insect pests in grain legumes

H.C. SHARMA*, RAJEEV VARSHNEY, P.M. GAUR and C.L.L. GOWDA

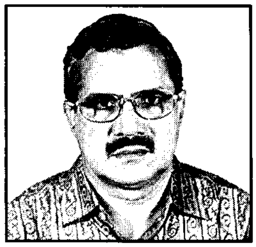
*International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, A. P., India; *Email: h.sharma@cgiar.org*

ABSTRACT

Grain legumes such as chickpea, pigeonpea, cowpea, fieldpea, lentil, fababean, blackgram, greengram, grasspea, and *Phaseolus* beans play an important role in food and nutritional security, and sustainable crop production. Several insect pests damage these crops, of which gram pod borer, *Helicoverpa armigera*; spotted pod borer, *Maruca vitrata*; spiny pod borer, *Etiella zinckenella*; pod fly, *Melanagromyza obtusa*; stem fly, *Ophiomyia phaseoli*; aphids, *Aphis craccivora* and *Aphis fabae*; white fly, *Bemisia tabaci*; defoliators, *Spodoptera litura*, *S. exigua*, and *Amsacta* spp.; leafhoppers, *Empoasca* spp., thrips, *Megaleurothrips dorsalis*, and *Caliothrips indicus*; blister beetles, *Mylabris* spp.; and the bruchids, *Collasobruchus chinensis* and *Bruchus pisorum* cause extensive losses. Several sources of resistance to insects have been identified in grain legumes, and several morphological and biochemical traits associated with resistance to insects have also been identified. A good beginning has been made in developing genetic linkage maps of some of the grain legumes. However, the accuracy and precision of phenotyping for resistance to insect pests remains a critical constraint in many crops. There are very few reports concerning the application of molecular markers for resistance to insect pests in grain legumes. There is a need for precise phenotyping, mapping of the QTLs associated with insect resistance, and use them in conjunction with morphological and biochemical markers to develop cultivars with resistance to insect pests.

Grain legumes such as chickpea, pigeonpea, cowpea, field pea, lentil, green gram, black gram, *Phaseolus* bean, faba bean, and grass pea are the principal source of dietary protein, and are an integral part of daily diet in several forms worldwide. Grain legumes are cultivated on 73 million hectares, accounting for over 18% of the total arable area, but only 8% of the total grain production. The global pulses production is over 60.45 million tonnes with an average productivity of 846 kg/ha (FAO 2004). In India, the total pulses production in 2007-08 was 15.12 million tonnes on an area of 23.86 million ha, with an average productivity of 638 kg/ha. Worldwide, chickpea and pigeonpea are the two major food legumes, cultivated on an area of 10.38 and 4.57 million ha, respectively, the total production being 8.57 and 3.29 million tonnes, with an average productivity of 826 and 720 kg/ha, respectively.

Grain legumes, being a rich source of protein, are damaged by a large number of insect pests, both under field



Dr. Hari C. Sharma, Principal Scientist (Entomology), has been working at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, Andhra Pradesh, India for the past 30 years. He also served as Visiting Scientist at University of Wisconsin, Madison, USA (1986/87), and at the Department of Primary Industries, Toowoomba, Queensland, Australia (1996). He obtained his B.Sc. and M.Sc. degrees from Himachal Pradesh University, Shimla, and the Ph.D. degree from Indian Agricultural Research Institute, New Delhi.

Dr. Sharma stood first in the University, and won Lal Bahadur Shastri Memorial Gold Medal (B.Sc.) - 1974, and M.M. Meakins Gold Medal (M.Sc.) - 1976. He was awarded Archana Gold Medal by Academy of Environmental Biology, Lucknow, India - 2000; Excellence in Science Award by CGIAR, Washington DC, USA - 2002; Prof. T.N. Ananthakrishnan Foundation Award, by Ananthakrishanan Foundation, Chennai, India - 2002; Lifetime Achievement Award by Academy of Environmental Biology, Lucknow, India-2005; Hari Om Trust Award by Indian Council of Agricultural Research, New Delhi, India 2007; and International Plant Protection Award of Distinction by the International Association of Plant Protection Sciences, Glasgow, UK - 2007.

Dr. Sharma was elected as the President of Council of International Congress of Entomology (ICE) in 2008, and he is the first Asian to hold this position in over 100 years history of ICE. He is also serving on the Governing Board of the International Association of Plant Protection Sciences.

Dr. Sharma has published over 300 research/conference papers (Books - 5, Information bulletins – 7, Research papers – 175, Book chapters – 50, Conference papers – 50, and Conference presentations – 57).

conditions and in storage (Clement *et al.* 2000). Amongst the many insect pests damaging food legumes, the pod borers, *Helicoverpa armigera* (Hubner) and *H. punctigera* (Wallengren) are the most devastating pests of chickpea and pigeonpea in Asia, Africa, and Australia. They also damage other food legumes to varying degrees in these regions (Sharma 2001). The spotted pod borer, *Maruca vitrata* (Geyer), is a major pest of cowpea and pigeonpea, but also damages other food legumes, except chickpea and lentil (Sharma *et al.* 1999). The pod fly, *Melanagromyza obtusa* Malloch and pod wasp, *Tanaostigmodes cajaninae* La Sale cause extensive damage to pigeonpea in India. The leaf miner, *Liriomyza cicerina* (Rondani) is an important pest of chickpea in West Asia and North Africa (Weigand *et al.* 1994). The spiny pod borer, *Etiella zinckenella* Triet. is a major pest of pigeonpea, field pea, and lentil while the aphid, *Aphis craccivora* Koch infests all the food legumes, but is a major pest of cowpea, field pea, faba bean, and *Phaseolus* beans. *Aphis fabae* (Scop.) is a major pest of faba bean and *Phaseolus* beans. The pea aphid, *Acyrthosiphon pisum* Harris is a major pest of field pea worldwide. The cotton whitefly, *Bemisia tabaci* Genn. infests all the crops, except chickpea, but is an important pest of *Phaseolus* spp., black gram, and green gram. The defoliators, *Spodoptera litura* (Fab.) in Asia, and *S. exigua* Hubner in Asia and North America, are occasional pests. The Bihar hairy caterpillar, *Spilosoma obliqua* Walk. is a major pest of green gram and black gram in North India, while the red hairy caterpillars, *Amsacta* spp. damage the rainy season pulses in South central India. Leafhoppers, *Empoasca* spp. infest most of the food legumes, but cause economic damage in black gram, green gram, and *Phaseolus* beans. Pod sucking bugs, *Clavigralla tomentosicollis* Stal., *C. gibbosa* Spin., *Nezara viridula* L. and *Bagrada hilaris* Burm., are occasional pests, but extensive damage has been recorded in cowpea by *C. tomentosicollis* in Africa, and *C. gibbosa* in pigeonpea in India. The bruchids, *Collasobruchus chinensis* L. and *C. maculatus* Fab. cause extensive losses in storage in all the food legumes worldwide. The pea weevil, *Bruchus pisorum* L. is a major pest of field pea in most production areas (Clement and Quisenberry 1999).

Insect pests in India cause an average loss of 30% in pulses valued at $ 815 million, which at times can be 100% (Dhaliwal and Arora 1994). *Helicoverpa armigera* – the single largest yield reducing factor in food legumes, causes an estimated loss of US $ 317 million in pigeonpea, and $328 million in chickpea (ICRISAT 1992). Globally, it causes an estimated loss of over $ 2 billion annually, despite over $ 1 billion worth of insecticides used to control this pest (Sharma 2005). In general, the estimates of yield losses vary from 5 to 10% in the temperate regions and 50 to 100% in the tropics (van Emden *et al.* 1988). The avoidable losses in food legumes at current production levels of 60.45 million tonnes would be nearly 18.14 million tonnes (at an average loss of 30%), valued at nearly US$ 10 billion (Sharma *et al.* 2005a).

Pest management strategies in grain legumes require integration of different control tactics. It has long been recognized that host plant resistance is one of the most effective management options. However, the progress in breeding for resistance to insects has been quite slow, and at times limited by the low levels of resistance available in cultivated germplasm (Sharma and Ortiz 2002; Sharma *et al.* 2005a). It is in this context that the application of modern tools of biotechnology can play a major role to accelerate the introgression of insect resistance genes into high yielding cultivars (Sharma *et al.* 2002, 2004). Recombinant DNA technologies, besides generating information on quantitative trait loci (QTL) associated with insect resistance, and gene sequences and function, also allow the identification of specific chromosomal regions carrying genes contributing to traits of economic interest. The use of molecular markers in conjunction with morphological and biochemical traits for indirect selection offers greatest potential gains for quantitative traits with low heritability as these are the most difficult characters to work with in the field through phenotypic selection.

MORPHOLOGICAL MARKERS

Phenological traits: Pigeonpea genotypes with determinate growth habit, clustered pods, and dense plant canopy are more susceptible to pod borers, *H. armigera* and *M. vitrata* than genotypes with non-clustered pods (Sharma *et al.* 1997), while the genotypes with smaller pods, pod wall tightly fitting to the seeds, and a deep constriction between the seeds are less susceptible to *H. armigera* (Nanda *et al.* 1996). Plant growth habit and crop duration do influence genotypic susceptibility to pod fly, *M. obtusa*, but pod wall thickness, trichome density, and crude fiber content are associated with resistance to this insect in pigeonpea (Moudgal *et al.* 2008). Several morphological traits such as pod shape, pod wall thickness, and crop duration influence *H. armigera* damage in chickpea (Ujagir and Khare 1988). Main stem thickness, leaflet shape and length, leaf hairiness, and peg length are associated with resistance/susceptibility to *H. armigera*, and tobacco leaf caterpillar, *Spodoptera litura* (F.) in wild relatives of groundnut (Sharma *et al.* 2003). Groundnut genotypes with dark-green and smaller leaflets are less susceptible to damage by *H. armigera* than those with longer shoots, and larger and light-green leaflets (Arora *et al.* 1996). Pubescence on the leaf tip is associated with reduced defoliation by *Helicoverpa zea* (Boddie), *Spodoptera exigua* (Hubner), and *Pseudoplusia includens* (Walker) in soybean (Hulburt *et al.* 2004).

Leaf hairs and trichomes: Leaf hairs (that do not produce glandular secretions) play an important role in host plant resistance to insects. Wild relatives of pigeonpea such as *Cajanus scarabaeoides* and *C. acontifolius* with non-glandular trichomes are not preferred by *H. armigera* females for egg laying (Sharma *et al.* 2001). Trichomes (hair-like outgrowths on the epidermis of plants that produce glandular secretions) also play an important role in host plant resistance to insects. Hooked trichomes in bean impair the movement of the aphid, *A. craccivora* (Johnson 1953), and potato leafhopper, *E. fabae* (Pillemer and Tingey 1978). Glandular trichomes in pigeonpea are linked to *H. armigera* susceptibility (Peter *et al.* 1995; Sharma *et al.* 2001). Trichomes and their exudates in chickpea influence the movement and feeding of neonate larvae of *H. armigera* (Stevenson *et al.* 2005), and influence the feeding by larvae of spotted pod borer, *M. vitrata* in cowpea (Jackai and Oghiakhe 1989), and cabbage looper, *Trichoplusia ni* (Hubner) in soybean (Khan *et al.* 1986). Trichomes on the pods of *Vigna vexillata* - a wild relative of cowpea, are partly responsible for resistance to the pod sucking bug, *Clavigralla tomentosicollis* Stal. (Chiang and Singh 1988).

BIOCHEMICAL MARKERS

Secondary metabolites: Secondary metabolites influence host finding, oviposition, feeding, and survival and development of insects, and play an important role in imparting resistance against insects in grain legumes. Quercetin, and guercetin-3-methyl ether in the pod surface exudates play an important role in food selection behavior of *H. armigera* larvae in pigeonpea (Green *et al.* 2002, 2003). Total phenols and tannins in the pod wall of pigeonpea are negatively associated with pod fly damage (Moudgal *et al.* 2008). Sterols and soybean leaf extractables in combination with sucrose are phagostimulants to the larvae of the cabbage looper, *T. ni* (Sharma and Norris 1994a). High acidity in the leaf exudates of chickpea is associated with resistance to *H. armigera* (Srivastava and Srivastava 1989). Malic acid in chickpea leaf exudates acts as an antifeedant to the *H. armigera* larvae (Bhagwat *et al.* 1995). Oxalic acid inhibits the growth of *H. armigera* larvae when incorporated into artificial diet, while malic acid shows no growth inhibition (Yoshida *et al.* 1995, 1997). The chickpea flavonoids judaicin 7-O-glucoside, 2 methoxy judaicin, judaicin, and maakiain present in wild relatives of chickpea (*Cicer bijugum* and *C. judaicum*) have shown antifeedant activity towards the larvae of *H. armigera* (Simmonds and Stevenson 2001). Stilbene -a phytoalexin, occurs at high concentrations in pigeonpea cultivars with resistance to *H. armigera* (Green *et al.* 2003). The polar solvent extractables of the soybean genotype PI 227687 -resistant to the cabbage looper, *T. ni,* contains diadzien, coumesterol, sojagol, and glyceollins. These compounds reduce feeding, survival, and development of the cabbage looper (Sharma and Norris 1991, 1994b). In soybean, pinitol confers resistance to *H. zea* (Dougherty 1976).

Nutritional factors: Non-protein or unusual amino acids are known to provide protection against herbivores in several plant species. The protective effect is elicited through their structural analogy to the commonly occurring essential amino acids. Amongst these, L-canavanine, azetidine - 2 - caboxylic acid, 2, 4-diamino butyric acid, minosine, and 3-hydoxyproline have significant growth inhibition effects on insects (Parmar and Walia 2001). L-canavanine is a structural homologue of L-arginine, and occurs in over 1,500 leguminous plant species. Some of the non-protein amino acids also act as enzyme inhibitors. Canaline - a hydrolytic product of canavanine, inhibits pyridoxal phosphate-dependant enzymes by forming a covalent bond.

Nutritional factors such as sugars, proteins, fats, sterols, and essential amino acids, and vitamins also influence host plant suitability to insect pests. Total soluble sugars in pigeonpea pod wall influence pod damage by *H. armigera.* Protein content of the pod wall is associated with susceptibility, while total sugars are associated with resistance to *M. obtusa* in pigeonpea (Moudgal *et al.* 2008). Pea varieties deficient in certain amino acids are resistant to the pea aphid, *A. pisum* (Auclair 1963). High amounts of non-reducing sugars and low amounts of starch in chickpea variety GL 645 possibly contribute to its low susceptibility to *H. armigera* (Chhabra *et al.* 1990). Green gram varieties with high sugar and amino acid content in leaves are resistant to whitefly, *B. tabaci* and the jassid, *Empoasca kerri* (Ruth) (Chhabra *et al.* 1988). Amylase and protease inhibitors in pigeonpea have been shown to have an adverse effect on growth and development of *H. armigera* (Giri and Kachole 1998). There is considerable variation in *H. armigera* gut protease inhibitory activity in developing seeds of chickpea (Patankar *et al.* 1999), and proteinase inhibitors from the non-host plants (groundnut, winged bean, and potato) are more efficient in inhibiting the gut proteinases of *H. armigera* larvae than those from its favored host plants such as chickpea, pigeonpea, and cotton (Harsulkar *et al.* 1999).

MOLECULAR MARKERS

Chickpea: The preliminary linkage map based on interspecific crosses of *Cicer arietinum* x *C. reticulatum* and *Cicer arietinum* x *Cicer echinospermum* was made available by Gaur and Slinkard (1990a, b). The mapping population derived from a cross between a wilt-resistant *kabuli* variety (ICCV 2) and a wilt-susceptible *desi* variety (JG 62) has been used to develop the first molecular map of chickpea based on an intraspecific cross (Cho *et al.* 2002). Mapping complex traits such as resistance to pod borer, *H. armigera* in chickpea has just made a beginning (Lawlor *et al.* 1998). A mapping population of 126 F_{13} RILs of ICCV 2 x JG 62, has been evaluated for resistance to *H. armigera*. The overall resistance score (1 = <10 leaf area and/or pods damaged, and 9 = >80% leaf area and/or pods damaged) varied from 1.7 to 6.0 in the RIL population compared to 1.7 in the resistant check, ICC 506EB, and 5.0 in the susceptible check, ICCV 96029. The results indicated that there is considerable variation in this mapping population for susceptibility to *H. armigera.* Another RIL mapping population from the cross between Vijay (susceptible) x ICC 506EB (resistant) has also been evaluated for resistance to *H. armigera.* Efforts are also underway to develop interspecific mapping populations based on the crosses between ICC 3137 (*C. arietinum*) x IG 72933 (*C. reticulatum*) and ICC 3137 x IG 72953 (*C. reticulatum*) for resistance to pod borer and to identify QTLs linked to various components of resistance to *H. armigera* (Sharma *et al.* 2005b).

Pigeonpea: A few studies have been conducted to investigate polymorphism in pigeonpea and its wild relatives (Sharma *et al.* 2005b). Recently developed microsatellite markers have detected polymorphism in diverse pigeonpea germplasm (Burns *et al.* 2001). Panguluri *et al.* (2006) used AFLP markers to detect polymorphism in cultivated pigeonpea and two of its wild relatives *Cajanus volubilis* Lour. and *Rhynchosia bracteata* Benth. ex Bak. High levels of resistance to pod borer, *H. armigera*, and pod fly, *M. obtusa*, have been identified in wild relatives of pigeonpea such as *C. scarabaeoides*, *C. sericeus*, and *C. acutifolius* (Sharma *et al.* 2001, 2003), which can be easily crossed with the cultivated species. A mapping population based on *C. cajan* x *C. scarabaeoides* is under development, and will be evaluated for resistance to *H. armigera* to identify QTLs linked to resistance to this insect (Sharma *et al.* 2005b).

Cowpea: A cross between resistant, IT 84S-2246-4 (cultivated), and susceptible, NI 963 (wild) genotypes of cowpea has been evaluated for aphid infestation (*A. Craccivora)* reaction (Myers *et al.* 1996). One RFLP marker, *bg4D9b*, has been found to be tightly-linked to the resistance gene (*Rac1*), and several flanking markers in the same linkage group (linkage group 1) were also identified. Githiri *et al.* (1996) suggested that there in no linkage between aphid resistance genes and the genes controlling morphological traits or *AAT* isozyme.

Common bean: Near-isogenic lines differing for the bean common mosaic virus (BCMV) resistance allele, *bc-3* have been screened to identify RAPD markers linked to BCMV (Haley *et al.* 1994). Bulk segregant analysis identified eight markers associated with resistance to potato leafhopper, *E. fabae*, and four markers that were associated with resistance to *E. kraemeri* Ross and Moore (Murray *et al.* 2004). Mesoamerican bean lines, BAT 881 and G 21212 showed transgressive segregation for resistance to thrips, *Thrips palmi* Karny (Frei *et al.* 2005), and a major QTL (*Tpr*6.1) located on LG *b06* explained up to 26.8% of variance for thrips resistance.

Mungbean : A gene from TC 1966 conferring resistance to bruchid, *Callosobruchus* sp. has been mapped using RFLP markers (Young *et al.* 1992). The RAPDs have been used to identify markers linked to the bruchid resistance (Villareal *et al.* 1998). Bruchid resistance gene mapped 14.6 cM from the nearest RAPD marker *Q04*, and 13.7 cM from the nearest RFLP marker *pM151b*. The gene was at 25 cM distance from *pM151a*. Yang *et al.* (1998) used MAS approach in backcross breeding for introgression of bruchid resistance in green gram.

Soybean: There has been limited success in developing soybean cultivars with resistance to insects because of the quantitative nature of resistance and linkage drag from the donor parents. Rector *et al.* (1998) used 139 RFLPs to identify the QTLs associated with resistance to corn earworm, *H. zea* in a population derived from Cobb (susceptible) x PI 229358 (resistant). One major and two minor QTLs were identified for resistance to *H. zea*. Another RFLP map based on Cobb x PI 171451 and Cobb x PI 227687 has also been developed by Rector *et al.* (1999). Among the three resistant genotypes, a QTL on LG *H* was shared among all three resistant genotypes (PI 171451, PI 227687, and PI 229358), and a major QTL on LG *M* was shared between PI 171451 and PI 229358. A minor QTL on LG *C2* was unique to PI 227687, and a minor QTL on LG *D1* was unique to PI 229358. Resistance to defoliating insects in soybean is expressed as a combination of antibiosis and antixenosis mechanisms of resistance (Rector *et al.* 2000). An antibiosis QTL on linkage group *LG M* was detected in both Cobb x PI 171451 and Cobb x PI 229358. An antixenosis QTL was also significant at this location in these two crosses. Antibiosis was conditioned by the resistant parent alleles on LGs *G*, *M*, and *B2*, whereas the susceptible parent, Cobb, provided antibiosis alleles at LGs *F* and *J*.

Groundnut: The first genetic linkage map of cultivated groundnut contained 350 RFLP loci distributed across 22 linkage groups, with a total map distance of approximately 2,700 cM (Burow *et al.* 1999). RAPD (*RKN 229*, *RKN 410*, and *RKN 440*) and RFLP (*R2430E*, *R2545E*, and *S1137E*) markers linked with resistance to root-knot nematode have also been identified (Burow *et al.* 1996; Choi *et al.* 1999). Resistance to the rosette aphid vector, *A. craccivora*, has been identified in the breeding line ICG 12991 and is controlled by a single recessive gene (Herselman *et al.* 2004), which was mapped on linkage group 1 at 3.9 cM from a marker originating from the susceptible parent, explaining 76.1% of the phenotypic variation for aphid resistance.

GENE SYNTENY

There has been a considerable interest in exploiting gene synteny by using SSR markers identified in intensively studied crops such as pea, soybean, and *Medicago* in lesser-studied crops such as chickpea, pigeonpea, and lentil. A comparison of the linkage maps of *Cicer*, *Pisum*, *Lens*, and *Vicia* has revealed that these legumes share many common linkage groups. The extent of conservation of linkage arrangement may be as much as 40% of the genome (Weeden *et al.* 2000). The high level of conservation of linkage groups among *Cicer*, *Pisum*, *Lens*, and *Vicia* suggests that these genera are very closely related. There is a nearly 60% chance that microsatellites isolated in pea will amplify in chickpea (Edwards *et al.* 1996), although there is less than 20% chance in the reverse direction (Pandian *et al.* 2000). Combining empirical lab-based approaches with bioinformatic strategies will be helpful in developing efficient systems for screening the vast public domain sequence databases of soybean and

Medicago to liberate sequences of most value for molecular breeding in chickpea and pigeonpea. Information on conserved gene sequences among these genera will also facilitate prediction of gene location in crops based on its location in other genera.

CONCLUSIONS

A beginning has been made in developing genetic linkage maps of many crops. However, the accuracy and precision of phenotyping for resistance to insect pests remains a critical constraint in many crops. Improved phenotyping systems will have substantial impact on both conventional and MAS to breed for resistance to insect pests, in addition to the more strategic research that feeds into these endeavors. There are very few reports concerning the application of MAS for resistance to insect pests in grain legumes. However, those available fail to demonstrate an increase in efficiency of MAS over conventional breeding approaches. A combination of morphological, biochemical and molecular markers is needed to introgress insect resistance genes from both cultivated germplasm, and wild relatives of grain legumes to accelerate the process of developing cultivars with insect resistance to increase crop productivity and improve livelihoods of the rural poor.

REFERENCES

Arora R, Kaur S and Singh M. 1996. Groundnut genotype reaction to *Helicoverpa armigera* in India. International Arachis Newsletter **16** : 35-37.

Auclair JL. 1963. Aphid feeding and nutrition. Annual Review of Entomology **8** : 439-490.

Bhagwat VR, Aherker SK, Satpute VS and Thakre HS. 1995. Screening of chickpea (*Cicer arietinum* L.) genotypes for resistance to *Helicoverpa armigera* (Hb.) and its relationship with malic acid in leaf exudates. Journal of Entomological Research **19** : 249-253.

Burns MJ, Edwards KJ, Newbury HJ, Ford-Lloyd BV and Baggott CD. 2001. Development of simple sequence repeat (SSR) markers for the assessment of gene flow and genetic diversity in pigeonpea (*Cajanus cajan*). Molecular Ecology Notes **1** : 283-285.

Burow MD, Simpson CE, Paterson AH and Starr JL. 1996. Identification of peanut (*Arachis hypogaea* L.) RAPD markers diagnostic of root-knot nematode [*Meloidogyne arenaria* (Neal) Chitwood] resistance. Molecular Breeding **2** : 369-379.

Burow MD, Simpson CE, Starr JL and Paterson AH. 1999. Generation of a molecular marker map of the cultivated peanut, *Arachis hypogaea* L. In: Proceedings of the Plant and Animal Genome VII, 17-21 January 1999, San Diego, California, USA.

Chhabra KS, Kooner BS, Sharma AK and Saxena AK. 1988. Sources of resistance in mungbean (*Vigna radiata*) to insect pests and mungbean yellow mosaic virus. Pages 308-314 *in* Proceedings of the II International Symposium on Mungbean, 16-20 November 1987, Bangkok, Thailand.

Chhabra KS, Sharma AK, Saxena AK and Kooner BS. 1990. Sources of resistance in chickpea: role of biochemical components of the incidence of gram pod borer, *Helicoverpa armigera* (Hubner). Indian Journal of Entomology **52** : 423-430.

Chiang HS and Singh SR. 1988. Pod hairs as a factor in *Vigna vaxillata* resistance to the pod-sucking bug, *Clavigralla tomentosicollis*. Entomologia Experimentalis et Applicata **47** : 195-199.

Cho S, Kumar J, Shultz J, Anupama K, Tefera F and Muehlbauer FJ. 2002. Mapping genes for double podding and other morphological traits in chickpea. Euphytica **128** : 285-292.

Choi K, Burow MD, Church G, Burow G, Paterson AH, Simpson CE and Starr JL. 1999. Genetics and mechanism of resistance to *Meloidogyne arenaria* in peanut germplasm. Journal of Nematology **31** : 283-290.

Clement SL and Quisenberry SS (Eds.). 1999. Global Plant Genetic Resources for Insect-Resistant Crops. Boca Raton, Florida, USA: CRC Press. 295 pp.

Clement SL Wightman JA, Hardie DC, Bailey P, Baker G and McDonald G. 2000. Opportunities for integrated management of insect pests of grain legumes. Pages 467-480 In: Linking Research and Marketing Opportunities for Pulses in the 21st Century. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Dougherty DE. 1976. Pinitol and Other Soluble Carbohydrates in Soybean as Factors in Facultative Parasite Nutrition. Ph.D. Thesis. Tifton, Georgia, USA: University of Georgia.

Edwards KJ, Barker JHA, Daly A, Jones C and Karp A. 1996. Microsatellite libraries enriched for several microsatellite sequences in plants. Biotechniques **20** : 758-760.

Food and Agriculture Organization (FAO). 2004. Production Statistics. Food and Agriculture Organization, Rome, Italy.

Frei A, Blair MW, Cardona C, Beebe SE, Gu H and Dorn S. 2005. QTL Mapping of resistance to *Thrips palmi* Karny in common bean. Crop Science **45** : 379-387.

Gaur PM and Slinkard AE. 1990b. Genetic control and linkage relations of additional isozyme markers in chickpea. Theoretical and Applied Genetics **80** : 648-656.

Gaur PM and Slinkard AE. 1990a. Inheritance and linkage of isozyme coding genes in chickpea. Journal of Heredity **81**: 455-461.

Giri AP and Kachole MS. 1998. Amylase inhibitors of pigeonpea (*Cajanus cajan*) seeds. Phytochemistry **47** : 197-202.

Githiri SM, Kimani PM and Pathak RS. 1996. Genetic linkage of the aphid resistance gene, *Rac*, in cowpea. African Crop Science Journal **4** : 145-150.

Green PWC, Stevenson PC, Simmonds MSJ and Sharma HC. 2002. Can larvae of the pod-borer, *Helicoverpa armigera* (Lepidoptera: Noctuidae), select between wild and cultivated pigeonpea [*Cajanus* sp. (Fabaceae)]?, Bulletin of Entomological Research **92** : 45-51.

Green PWC, Stevenson PC, Simmonds MSJ and Sharma HC. 2003. Phenolic compounds on the pod-surface of pigeonpea, *Cajanus cajan*, mediate feeding behavior of *Helicoverpa armigera* larvae. Journal of Chemical Ecology **29** : 811-821.

Haley SD, Afanador L and Kelly JD. 1994. Selection for monogenic pest resistance traits with coupling- and repulsion-phase RAPD markers. Crop Science **34** : 1061-1066.

Harsulkar AM, Giri AP, Patankar AG, Gupta VS, Sainani MN, Ranjekar PK and Deshpande VV. 1999. Successive use of non-host plant proteinase inhibitors required for effective inhibition of *Helicoverpa armigera* gut proteinases and larval growth. Plant Physiology **121** : 497-506.

Herselman L, Thwaites R, Kimmins FM, Courtois B, van der Merwe PJ and Seal SE. 2004. Identification and mapping of AFLP markers linked to peanut (*Arachis hypogaea* L.) resistance to the aphid vector of groundnut rosette disease. Theoretical and Applied Genetics **109** : 1426-1433.

Hulburt DJ, Boerma HR and All JN. 2004. Effect of pubescence tip on soybean resistance to lepidopteran insects. Journal of Economic Entomology **97** : 621-627.

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). 1992. The Medium Term Plan. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India.

Jackai LEN and Oghiakhe S. 1989. Podwall trichomes and resistance of two wild cowpea, *Vigna vaxillata*, accessions to *Maruca testulalis* (Geyer) (Lepidoptera: Pyralidae) and *Clavigralla tomentosicollis* Stal. (Hemiptera: Coreidae). Bulletin of Entomological Research **79** : 595-605.

Johnson B. 1953. The injurious effects of the hooked epidermal hairs of the French beans (*Phaseolus vulgaris* L.) on *Aphis craccivora* Koch. Bulletin of Entomological Research **44** : 779-788.

Khan ZR, Ward JT and Norris DM. 1986. Role of trichomes in soybean resistance to cabbage looper, *Trichoplusia ni*. Entomologia Experimentalis et Applicata **42** : 109-117.

Lawlor HJ, Siddique KHM, Sedgley RH and Thurling N. 1998. Improving cold tolerance and insect resistance in chickpea and the use of AFLPs for the identification of molecular markers for these traits. Acta Horticulturae **461** : 185-192.

Moudgal RK, Lakra RK, Dahiya B, and Dhillon MK. 2008. Physico-chemical traits of *Cajanus cajan* (L.) Millsp. pod wall affecting *Melanagromyza obtusa* (Malloch) damage. Euphytica **161**(3): 429-436.

Murray JD, Michaels TE, Cardona C, Schaafsma AW and Pauls KP. 2004. Quantitative trait loci for leafhopper (*Empoasca fabae* and *Empoasca kraemeri*) resistance and seed weight in the common bean. Plant Breeding **123** : 474-479.

Myers GO, Fatokun CA and Young ND. 1996. RFLP mapping of an aphid resistance gene in cowpea (*Vigna unguiculata* (L.) Walp. Euphytica **91** : 181-187.

Pandian A, Ford R and Taylor PWJ. 2000. Transferability of sequence tagged microsatellite site (STMS) primers across four major pulses. Plant Molecular Biology Reporter **18**(4) : 395a-395h (www.uga.edu/ispmb).

Panguluri S, Janaiah K, Govil J, Kumar P and Sharma P. 2006. AFLP fingerprinting in pigeonpea (*Cajanus cajan* (L.) Millsp.) and its wild relatives. Genetic Resources and Crop Evolution **53** : 523-531.

Parmar BS and Walia S. 2001. Prospects and problems of phytochemical biopesticides. Pages 133-210 In: Phytochemical Biopesticides (Koul O and Dhaliwal GS, eds.). Amsterdam, The Netherlands: Harvard Academic Publishers. Patankar AG, Harsulkar AM, Giri AP, Gupta VS, Sainani MN, Ranjekar PK and Deshpande VV. 1999. Diversity in inhibitors of trypsin and *Helicoverpa armigera* gut proteinases in chickpea (*Cicer arietinum*) and its wild relatives. Theoretical and Applied Genetics **99** : 719-726.

Peter AJ, Shanower TG and Romeis J. 1995. The role of plant trichomes in insect resistance: A selective review. Phytophaga **7** : 41-64.

Pillemer EA and Tingey WM. 1978. Hooked trichomes and resistance of *Phaseolus vulgaris* to *Empoasca fabae* (Harris). Entomologia Experimentalis et Applicata **24** : 83-94.

Rector BG, All JN, Parrott WA and Boerma HR. 1998. Identification of molecular markers linked to quantitative trait loci for soybean resistance to corn earworm. Theoretical and Applied Genetics **96** : 786-790.

Rector BG, All JN, Parrott WA and Boerma HR. 1999. Quantitative trait loci for antixenosis resistance to corn earworm in soybean. Crop Science **39** : 531-538.

Rector BG, All JN, Parrott WA and Boerma HR. 2000. Quantitative trait loci for antibiosis resistance to corn earworm in soybean. Crop Science **40** : 233-238.

Sharma HC. 2001. Crop Protection Compendium: *Helicoverpa armigera*. Electronic Compendium for Crop Protection. Wallingford, U.K: Commonwealth Agricultural Bureau International.

Sharma HC. 2005. Strategies for *Heliothis/Helicoverpa* Management: Emerging Trends and Strategies for Future Research. New Delhi, India: Oxford and IBH. 469 pp.

Sharma HC and Norris DM 1994a. Phagostimulant activity of sucrose, sterols and soybean leaf extractables to the cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae). Insect Science and its Application **15** : 281-288.

Sharma HC and Norris DM. 1994b. Biochemical mechanisms of resistance to insects in soybean: Extraction and fractionation of antifeedants. Insect Science and its Application **15** : 31-38.

Sharma HC and Ortiz R. 2002. Host plant resistance to insects: An eco-friendly approach for pest management and environment conservation. Journal of Environmental Biology **23** : 11-35.

Sharma HC, Ahmad R, Ujagir R, Yadav RP, Singh R and Ridsdill-Smith TJ. 2005a. Host plant resistance to cotton bollworm/legume pod borer, *Helicoverpa armigera*. Pages 167-208 *in* Strategies for Heliothis/Helicoverpa Management: Emerging Trends and Strategies for Future Research (Sharma HC, ed.). New Delhi, India: Oxford and IBH.

Sharma HC and Norris DM. 1991. Chemical basis of resistance in soybean to cabbage looper, *Trichoplusia ni*. Journal of Science of Food and Agriculture **55** : 353-364.

Sharma HC, Bhagwat VR and Saxena KB. 1997. Biology and Management of Spotted Pod Borer, *Maruca vitrata* (Geyer). Patancheru, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). 48 pp.

Sharma HC, Crouch JH, Sharma KK, Seetharama N and Hash CT. 2002. Applications of biotechnology for crop improvement: prospects and constraints. Plant Science **163** : 381-395.

Sharma HC, Gaur PM and Hoisington DA. 2005b. Physico-chemical and molecular markers for host plant resistance to *Helicoverpa armigera*. Pages 84-121 *in* Recent Advances in *Helicoverpa* Management (Saxena H, Rai AB, Ahmad R and Gupta S, eds.). Kanpur, Uttar Pradesh, India: Indian Society of Pulses Research and Development, Indian Institute for Pulses Research.

Sharma HC, Pampathy G, Dwivedi SL and Reddy LJ. 2003. Mechanisms and diversity of resistance to insect pests in wild relatives of groundnut. Journal of Economic Entomology **96** : 1886-1897.

Sharma HC, Saxena KB and Bhagwat VR. 1999. Legume Pod Borer, *Maruca vitrata*: Bionomics and Management. Information Bulletin 55. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India. 35 pp.

Sharma HC, Sharma KK and Crouch JH. 2004. Genetic transformation of crops for insect resistance: potential and limitations. Critical Reviews in Plant Sciences **23** : 47-72.

Sharma HC, Stevenson PC, Simmonds MSJ and Green PWC. 2001. Identification of *Helicoverpa armigera* (Hübner) Feeding Stimulants and the Location of Their Production on the Pod-surface of Pigeonpea [*Cajanus cajan* (L.) Millsp.]. Final Technical Report. DFID Competitive Research Facility Project [R 7029 (C)].

Patancheru, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). 85 pp.

Simmonds MSJ and Stevenson PC. 2001. Effects of isoflavonoids from *Cicer* on larvae of *Helicoverpa armigera*. Journal of Chemical Ecology **27** : 965-977.

Srivastava CP and Srivastava RP. 1989. Screening for resistance to gram pod borer, *Heliothis armigera* (Hubner) in chickpea (*Cicer arietinum* L.) genotypes and observations on its mechanism of resistance in India. Insect Science and its Application **10** : 255-258.

Stevenson PC, Green PWC, Simmonds MSJ and Sharma HC. 2005. Physical and chemical mechanisms of plant resistance to *Helicoverpa*: Recent research on chickpea and pigeonpea. Pages 215-228 *in Helicoverpa/Heliothis* Management: Emerging Trends and Strategies for the Future Research (Sharma HC, ed.). New Delhi, India: Oxford & IBH Publishers Inc.

Ujagir R and Khare BP. 1988. Susceptibility of chickpea cultivars to gram pod borer, *Heliothis armigera* (Hubner). Indian Journal of Plant Protection **16(1)** : 45-49.

van Emden HF, Ball SL and Rao MR. 1988. Pest and disease problems in pea, lentil, faba bean, and chickpea. Pages 519-534 *in* World Crops: Cool Season Food Legumes (Summerfield, RJ, ed.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Villareal JM, Hautea DM and Carpena AL. 1998. Molecular mapping of the bruchid resistance gene in mungbean *Vigna radiata* L. Philippine Journal of Crop Science **23** (supplement 1) : 1-9.

Weeden NF, Ellis THN, Timmerman VGM, Simon CJ, Torres AM, Wolko B and Knight R. 2000. How similar are the genomes of the cool season food legumes? Pages 397-410 *in* Linking Research and Marketing Opportunities for Pulses in the 21st Century: Proceedings of the Third International Food Legumes Research Conference, 22-26 September 1997, Adelaide, Australia.

Weigand S, Lateef SS, El Din Sharaf N, Mahmoud SF, Ahmed K and Ali K. 1994. Integrated control of insect pests of cool season food legumes. Pages 679-694 *in* Expanding the Production and Use of Cool Season Food Legumes (Muehlbauer EJ and Kaiser WJ, eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Yang TJ, Kim DH, Kuo GC, Kumar L, Young ND and Park HG. 1998. RFLP marker-assisted selection in backcross breeding for introgression of the bruchid resistance gene in mungbean. Korean Journal of Breeding **30** : 8-15.

Yoshida M, Cowgill SE and Wightman JA. 1995. Mechanisms of resistance to *Helicoverpa armigera* (Lepidoptera: Noctuidae) in chickpea – role of oxalic acid in leaf exudates as an antibiotic factor. Journal of Economic Entomology **88**: 1783-1786.

Yoshida M, Cowgill SE and Wightman JA. 1997. Roles of oxalic and malic acids in chickpea trichome exudates in host-plant resistance to *Helicoverpa armigera*. Journal of Chemical Ecology **23** : 1195-1210.

Young ND, Kumar L, Menancio-Hautea D, Danesh D, Talekar NS, Shanmugasundarum S and Kim DH. 1992. RFLP mapping of a major bruchid resistance gene in mungbean (*Vigna radiata*, L. Wilczek). Theoretical and Applied Genetics **84** : 839-844.