Molecular Marker-Assisted Selection: A Novel Approach for Host Plant Resistance to Insects in Grain Legumes

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Abstract

Grain legumes such as chickpea, pigeonpea, cowpea, fieldpea, lentil, grams, beans, soybean, and groundnut play an important role in the daily diets of the people worldwide. Being a rich source of protein, they are damaged by a large number of insect pests such as legume pod borer, corn earworm, spotted pod borer, aphids, white fly, tobacco caterpillar, leafhoppers, thrips and bruchids. Sources of resistance to insects in grain legumes have been identified long ago, but these have not been used effectively in crop improvement because of the difficulties involved in screening and selection of the test material under uniform conditions. Molecular markers can play an important role in accelerating the introgression of genes conferring resistance to target insects into high-yielding cultivars, understanding the nature of gene action, and reducing the deleterious effects of introgressing unwanted genes from wild species through linkage drag. Molecular breeding also offers the opportunity to pyramid different sources of resistance that could not be effectively selected through conventional breeding due to identical phenotypes and thereby accumulate levels of resistance and/or create potentially more durable resistant cultivars. Considerable progress has been made in developing genetic linkage maps of chickpea, cowpea, and soybean, while much remains to be done in pigeonpea, beans, lentil, and fieldpea. Preliminary identification of molecular markers for resistance to insects in soybean, chickpea, mungbean, fieldpea, and cowpea has been reported. However, no distinct advantage has been observed by using marker- assisted selection for resistance to insect pests over the conventional approach, and in most cases, the epistatic effects are also quite high. Thus, a new paradigm approach may be required to combine conventional approaches and marker-assisted selection in such way as to create systems better than either approach. This paper reviews current state-of-the-art concerning conventional and molecular breeding for pest resistance, and highlight the opportunities and constraints for use of molecular markers for accelerating the pace of development of insect-resistant cultivars in grain legumes.

1. Introduction

Grain legumes such as chickpea (*Cicer arietinum* L.), pigeonpea [*Cajanus cajan* (L.) Millsp.], cowpea (*Vigna unguiculata* Walp.), field pea (*Pisum sativum* L.), lentil (*Lens culinaris* Medik.), mungbean [*Vigna radiata* (L.) Wilczek], urdbean [*Vigna mungo* (L.) Hepper], French bean (*Phaseolus vulgaris* L.), faba bean (*Vicia faba*

L.), grasspea (*Lathyrus sativus* L.), soybean [*Glycine max* (L.) Merrill.], and groundnut (*Arachis hypogaea* L.) play an important role in the daily diets of the people worldwide. Grain legumes are the principal source of dietary protein among vegetarians, and are an integral part of daily diet in the Asian countries. In 2002, the global area under principal grain legumes such as chickpea, groundnut, soybean, and pigeonpea was 9.7, 24.7, 79.4, and 4.2 million ha, respectively. The global pulse production in 2002 was over 53 million tons. Nearly half of the pulse production (25 million tons) was in Asia. India is the largest single producer of grain legumes (14 million tons). Grain legumes are cultivated on an area of 23 million ha, accounting for over 18% of the total arable area, but only 8% of the total grain production, indicating a large disparity between yields of cereals and legumes. In addition to being a source of dietary protein and income to the resource poor farmers, grain legumes also play an important role in sustainable crop production. They are an important component of cropping systems to maintain soil health because of their ability to fix atmospheric nitrogen, extract water and nutrients from the deeper layers of soil, and add organic matter into the soil through leaf drop. However, pulses are mainly grown under rainfed conditions and the productivity levels are quite low (500 to 600 kg ha^{-1}), mainly because of severe losses due to insect pests and diseases (Ali and Kumar, 2001).

Because of environmental and human health problems associated with excessive use of pesticides, there has been an increased emphasis on alternative methods of controlling insect pests. In this context, host plant resistance can play a pivotal role in integrated pest management in grain legumes. Sources of resistance to insect pests have long since been identified, but these have not been used effectively in crop improvement programmes, because the levels of resistance are either too low or it is not possible to screen the test material under optimum insect infestation to identify progenies combining desirable agronomic traits and resistance to insect pests. There is considerable potential for the development of crop cultivars with resistance or tolerance to insect pests in grain legumes to minimize the extent of losses due to insect pests (Sharma and Ortiz, 2002), and use of biotechnological approaches can play a significant role in developing cultivars with resistance to insects (Sharma *et al.*, 2002a). In many cases, there is neither knowledge of the numbers of genes involved nor the understanding of the nature of gene action. This is mainly because of the difficulties involved in accurately studying the inheritance of resistance under uniform insect pressure. Lack of such information also reduces the efficiency of conventional breeding for insect resistance traits and confounds the development of effective marker-assisted selection systems (Sharma *et al.*, 2002a). Thus, for all aspects of host plant resistance to insect pests, there is an urgent need for innovation in the improvement of phenotyping systems. Once accurate and precise phenotyping systems for insect resistance have been established, the molecular markers can be used in dissecting the genetic basis,

identifying the location of underlying genes, and understanding the nature of gene action. Such knowledge will significantly accelerate the introgression of insect pest resistance genes into high-yielding cultivars.

2. Insect Pest Problems in Grain Legumes

Grain legumes, being a rich source of nutritious food, are damaged by a large number of insect pests, both under field conditions and in storage (Table 1). Amongst the many insect pests damaging grain legumes, legume pod borer [*Helicoverpa armigera* (Hubner)], corn earworm (*H. zea* Boddie), spotted pod borer [*Maruca vitrata* (Geyer)], aphids (*Aphis craccivora* Koch.), white fly (*Bemisia tabaci* Genn.), tobacco caterpillar (*Spodoptera* spp.), leafhoppers (*Empoasca* spp.), and thrips (*Megaleurothrips distalis* Karny and *Caliothrips indicus* Bag.) cause extensive damage to grain legumes under field conditions, while bruchids (*Callosobruchus* spp.) damage the grain in storage. It has been estimated that insect pests cause an annual average of 14% loss in crop production worldwide (Oerke *et al.*, 1994), despite application of insecticides costing over US$ 10 billion to minimize the pest-associated losses. In the semi-arid tropics, insect pests cause an estimated loss of nearly US$ 750 million in pigeonpea, 500 million in chickpea, and 675 million in groundnut (ICRISAT, 1992). *Helicoverpa armigera,* the major insect pest of grain legumes and several other crops, causes an estimated loss of over US$ 2 billion annually, despite over 500 million worth of insecticides used to control this pest (Sharma, 2001).

3. Host Plant Resistance to Insect Pests

Considerable progress has been made in identification and utilization of resistance to insects in grain legumes (Clement and Quisenberry, 1999). However, resistance breeding programmes are underway for a few pests only because of the difficulties involved in screening and selection of the test material under uniform insect infestation across seasons and locations. In addition, it is difficult to rear and multiply some of the insect pests on artificial diets to ensure screening and selection of the test material under optimum levels of insect infestation. Because of the ease with which insects can be controlled with the help of insecticides, there has been an insufficient focus on developing cultivars with resistance to insect pests. However, with the development of insect resistance to insecticides, insecticide residues in food and food products, adverse effects on natural enemies and other non-target organisms, and environmental hazards of pesticide use, there has been a renewed emphasis on the development of alternative approaches to pest control. Host plant resistance can play a pivotal role in pest management in grain legumes, and resistance to insect pests should be one of the major criteria in the development and release of new crop cultivars, in order to ensure

Table 1: Important insect pests of grain legumes in the semi-arid tropics.

Insect pest		Severity of damage in different grain legumes					
Common name	Scientific name	Chick-pea	Pigeon-pea	Cow-pea	Field pea	Lentil	*Phaseo-lus* spp.
Legume pod borer	*Helicoverpa armigera* (Hub.)	xxx	xxx	x	xx	x	xxx
Spotted pod borer	*Maruca vitrata* (Geyer)	-	xxx	xxx	x	-	xxx
Spiny pod borer	*Etiella zinkenella* Treit.	-	x	-	xxx	xx	-
Pod fly	*Melanagromyza obtusa* Malloch	-	xxx	-	-	-	-
Pod sucking bugs	*Clavigralla gibbosa* Spin.	-	xx	x	x	x	x
	Nezara viridula L.						
	Bagrada hilaris Burm.						
Blister beetles	*Mylabris* spp.	-	xx	x	-	-	xx
Aphids	*Aphis craccivora* Koch.	x	x	xx	xxx*	xx	x
	Acyrthocyphum pisum Harris*						
Whitefly	*Bemisia tabaci* Genn.	-	-	-	-	-	xx
Defoliators	*Spodoptera litura* F.	-	x	x	x	x	xx
	S. exigua Hubn.						
	Amsacta spp.						
	Spilosoma obliqua Walk.						
Leaf hoppers	*Empoasca* spp.	-	x	x	x	x	x
Stem flies	*Ophiomyia phaseoli* Tryon.	-	-	-	xxx	-	xxx
Thrips	*Caliothrips indicus* Bag.	-	x	x	x	-	xx
	Megaleurothrips distalis Karny						
	Thrips palmi Karny / *Franklieniella schultzei** Schmutz						
Bruchids	*Callosobruchus* spp.	xxx	xxx	xxx	xxx	xxx	xxx

xxx = Most important. xx = Moderately important. x = Low importance.

prolonged cultivar life and cost effective production. Varieties with resistance to the target insect pests have been developed and released for pigeonpea, chickpea, cowpea, mungbean, urdbean, field pea, soybean, and groundnut. However, the levels of resistance in most of the varieties released for cultivation are low to moderate, while high levels of resistance have been reported in the wild relatives of several crops (Sharma *et al.*, 2003b). Resistance from the wild relatives needs to be transferred into high-yielding varieties with acceptable agronomic backgrounds. Cultivars with multiple-resistance to insects and diseases will be in greater demand in future because of the concerns associated with insecticide application for insect control and environment conservation, and this requires a concerted effort from scientists involved in the crop improvement programmes worldwide. There is a need to break the linkage between resistance to insects and susceptibility to diseases, *e.g.*, in chickpea, the *Helicoverpa* resistant cultivars are highly susceptible to wilt (Sharma *et al.*, 2003a). The development of insect resistant cultivars has been hampered by low levels of resistance and the lack of information on the component traits, which could be combined to build-up the levels of resistance by utilizing diversified sources of resistance. Screening of entire germplasm collection of chickpea and pigeonpea (over 15,000 accessions for each crop) resulted in identification of only a few accessions with moderate levels of resistance to the pod borer, *H. armigera* (Lateef, 1985; Lateef and Pimbert, 1990; Sharma, 2001). However, the accuracy with which it is possible to screen thousands of accessions probably resulted in missing many potentially good sources of resistance. The sources of resistance have not been used widely because the levels of resistance were quite low. Finally, some sources of resistance to pod borer have been associated with susceptibility to the major fungal and viral pathogens, and/or less-preferred agronomic characters (Sharma *et al.*, 2003a). Marker-assisted selection can offer a powerful solution in terms of pyramiding different sources of resistance and identifying segregants not carrying associated deleterious factors (provided there are no pleiotropic effects of the insect resistance genes). In lentil, genetic differences for susceptibility to aphid (*A. craccivora*), pod borer (*E. zinkenella*), and seed weevil (*Bruchus* sp.) have been observed, but no specific efforts to breed for resistance to insects have been made so far (Erskine *et al.*, 1994).

More recently, wild relatives of pigeonpea such as *Cajanus scarabaeoides, C. platycarpus, C. acutifolius* and *C. sericeus* have been identified with high levels of resistance to *H. armigera* (Sharma *et al.*, 2001). In chickpea, accessions belonging to *Cicer bijugum, C. judaicum, C. cuneatum*, and *C. microphyllum* have also been identified with high levels of resistance to *H. armigera* (Sharma *et al.*, 2002b). These wild relatives of chickpea are also important source of resistance to the leaf miner [*Liriomyza ciceri* (Rondani)] and bruchids (*Collasobruchus chinensis* L.) (Singh and Ocampo, 1997). Accessions belonging to *Vigna vaxillata* (TVNu 72 and TVNu

73), a wild relative of cowpea, have shown high levels of resistance to *M. vitrata* (Jackai and Oghiakhe, 1989). In pea, the accessions belonging to the wild relative, *Pisum fulvum* are not preferred for egg-laying by the bruchid, *Bruchus pisorum* (L.) (Ali *et al.*, 1994).

Accessions belonging to *Arachis cardenasii*, *A. duranensis*, *A. kempff-mercadoi*, *A. monticola*, *A. stenosperma*, *A. paraguariensis*, *A. pusilla*, and *A. triseminata* have shown multiple resistance to leaf miner (*Aproaerema modicella*), *H. armigera*, and *Empoasca kerri* (Sharma *et al.*, 2003c). *Arachis cardenasii* (ICG 8216), *A. ipaensis* (ICG 8206), *A. paraguariensis* (ICG 8130), and *A. appressipila* (ICG 8946) have shown resistance to leaf feeding and antibiosis to *Spodoptera litura* under no-choice conditions. Six lines derived from wild relatives with resistance to *H. armigera* and *S. litura,* and/or leaf miner have been identified. Thus, wild relatives of grain legumes can be used as sources of resistance to insects. The challenge now is to establish the means of developing effective marker-assisted selection systems that will enable rapid and efficient introgression of resistance genes into high-yielding cultivars. Marker-assisted breeding offers the potential to break deleterious linkage drag associated with unwanted genes from the wild relatives, and to effectively pyramid resistances to multiple insect pests and diseases with essential agronomic traits (Xiao *et al.*, 1996; Miflin, 2000).

4. Mechanisms of Resistance

Several physicochemical characteristics contribute to insect resistance in grain legumes (Clement *et al.*, 1994). Presence of a dense covering of hairs/trichomes on the leaves/pods confers resistance to many insect species. Allomones such as arcelins [towards *Zabrotes subfaciatus* (Boheman)], L-canavanine (against *H. virescens*), polyhydroxy alkaloids (against *Spodoptera* spp.) and saponins (against *C. chinensis*) have been reported to confer resistance to insect pests in grain legumes (Dilawari and Dhaliwal, 1993).

Antixenosis, antibiosis and tolerance are the major components of resistance in chickpea towards *H. armigera*. Several morphological and phenological traits such as pod shape, pod wall thickness, foliage colour and crop duration seem to influence the *H. armigera* infestation in chickpea (Ujagir and Khare, 1988). There is a large variation in larval survival, larval and pupal weight, egg viability, adult longevity, and Howe's growth index of *H. armigera* on different genotypes (Srivastava and Srivastava, 1990). Larval weight contributed maximum to the variation, followed by larval period, pupal weight, and pupal period. High percentage of crude fiber, non-reducing sugars, and low percentage of starch have also been found to be associated with resistance to *H. armigera* in GL 645. High percentage of cellulose, hemicelluloses and lignin in

the pod wall inhibits pod damage by *H. armigera* (Chhabra *et al.*, 1990). Low acidity in the leaf extracts is associated with susceptibility to *H. armigera* (Srivastava and Srivastava, 1989; Bhagwat *et al.*, 1995). However, resistance expressed by PDE 2-3, PDE 7-3 and ICC 506 has been attributed to factors other than acidity, while that of PDE 7-2 is due to high acidity (Patnaik and Senapati, 1995). Chickpea exudates have malate and oxalate as the main components, and there are characteristic differences depending on the variety, diurnal cycles, and growth stage. Varieties with highest amount of malic acid had the highest resistance to *H. armigera* (Rembold, 1981; Rembold *et al.*, 1990). Malic acid acts as a deterrent to the *H. armigera* larvae, and pod borer-resistant lines have more amounts of malic acid than the susceptible lines (Bhagwat *et al.*, 1995). Oxalic acid inhibits the growth of *H. armigera* larvae when incorporated in artificial diet, while malic acid shows no growth inhibition (Yoshida *et al.*, 1995). The chickpea flavonoids judaicin 7-O-glucoside, 2 methoxy judaicin, judaicin, and maakiain have shown antifeedant activity towards the larvae of *H. armigera* (Simmonds and Stevenson, 2001). There is considerable variation in *H. armigera* gut protease inhibitory activity in developing seeds of chickpea (Patankar *et al.*, 1999), and that 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 favoured host plants chickpea, pigeonpea, and cotton (Harsulkar *et al.*, 1999).

All the three mechanisms: antixenosis, antibiosis, and tolerance contribute to genotypic resistance to *H. armigera* in pigeonpea. In general, wild relatives of *Cajanus cajan* have better resistance than the cultivated species. Larval and pupal mass, and developmental period are all adversely affected when fed on the flowers of wild species such as *C. cajanifolius, C. reticulatus* and *C. sericeus;* and only few larvae survived to maturity (Dodia *et al.*, 1996). Plant trichomes have been implicated in host plant resistance to insect pests in several grain legumes, including pigeonpea (Peter *et al.*, 1995; Romeis *et al.*, 1999). Resistance of *Cajanus scarabaeoides* to *H. armigera* has been attributed to high density of non-glandular trichomes on pods (Romeis *et al.*, 1999). There is a positive correlation between pod length and basal girth of stem with pod borer damage (Nanda *et al.*, 1996). Varieties with brown seeds and green pods having streaks have been reported to be least susceptible to pod borer damage (Tripathi and Purohit, 1983). Total soluble sugars in the pod wall have a significant and negative correlation with pod damage. Acetone extracts of *C. cajan* and *C. platycarpus* pods had a significant feeding stimulant effect on *H. armigera* larvae whereas extracts from *C. scarabaeoides* pod showed no such effects (Shanower *et al.*, 1997), while water extract of *C. scarabaeoides* pod had a significant antifeedant effect, while similar extracts from *C. cajan* and *C. platycarpus* pods had no such effect. Quercetin, guercetin-3-methyl ether and quercetrin play an important role in

food selection behaviour of *H. armigera* larvae in pigeonpea. Stilbene - a phytoalexin, occurs at high concentrations in pigeonpea cultivars with resistance to *H. armigera* (Green *et al.*, 2002a,b). Amylase and protease inhibitors in pigeonpea have been shown to have adverse effects on larval growth and development of *H. armigera* (Giri and Kachole, 1998). The concentration of different chemicals is important, and it is important to be able to manipulate the genes that control the level of synthesis of these chemicals.

In addition to the physical characteristics of the leaves, the secondary plant substances are important in the resistance of wild relatives of groundnut to *S. litura*. Several wild relatives of groundnut have shown a resistant reaction to *S. frugiperda* and thrips, and that these species differed in lipid composition, of which *n*-alkanes are the major component (Yang *et al.*, 1993). Some of the accessions suffered heavy leaf feeding by *S. litura* larvae under no-choice conditions, but resulted in slow growth of the larvae because of poor nutritional quality of the food and/or presence of secondary plant substances (Stevenson *et al.*, 1993). Plant morphological characteristics such as main stem thickness, hypanthium length, leaflet shape and length, leaf hairiness, standard petal length and petal markings, basal leaflet width, main stem thickness and hairiness, stipule adnation length and width, and peg length have shown significant correlation and/or regression coefficients with damage by *H. armigera*, *S. litura* and jassids, and these traits can possibly be used as markers to select for resistance to these pests in groundnut (Sharma *et al.*, 2003c).

Host preference for feeding and nutritional antibiosis are the major components of resistance in soybean to *Epilachna varivestis* Mulsant (Kogan, 1982). A significant reduction in fecundity has also been observed when the larvae are reared on the resistant varieties. Pubescent varieties of soybean are highly resistant to *Empoasca fabae* Harris (Kogan, 1982). As a result of insect damage, there is increased production of certain flavonoids in soybean (Sharma and Norris, 1991). Oviposition non-preference is one of the components of resistance to *H. zea* in PI 2227687 soybean (Horber, 1978). Trichomes on the pods of *Vigna vaxillata* - a wild relative of cowpea, are partly responsible for resistance to *Clavigralla tomentosicollis* Stal. (Chiang and Singh, 1988). Both antixenosis and antibiotic type of resistance has been observed against *E. fabae*, *E. varivestis*, and *Bruchus pisorum* L. (Clement *et al.*, 1994). Pea varieties deficient in certain amino acids are also resistant to the pea aphid, *Acyrthocyphum pisum* (Harris) (Auclair, 1963). Both antixenosis and antibiotic types of resistance have been observed against *Callosobruchus chinensis* L. in chickpea and faba bean (Clement *et al.*, 1994). A wild line of *Pisum sativum* ssp. *humile* responds to pea weevil eggs by forming callus. Similar reaction to pea weevil eggs has also been reported in *Lathyrus* sp. (Annis and O'Keeffe, 1984).

5. Potential for Molecular Markers in Insect Resistance Breeding

The last decade has seen rapid progress in molecular biology with the whole genome sequencing of model organisms such as human, yeast, *Caenorhabditis, Arabidopsis,* and rice (Chalfie, 1998; Sherman, 1998; Shoemaker *et al.*, 2001; Palevitz, 2000). Systematic whole genome sequencing is providing critical information on gene and genome organization and function, which will revolutionize our understanding of crop production and the ability to manipulate traits contributing to plant resistance to insect pests and crop productivity (Pereira, 2000). These advances in model species and major crops will have substantial spillover effects on progress in lesser-studied crops.

Recombinant DNA technologies allow the identification of specific chromosomal regions carrying the genes associated with resistance to the target insect pest (Karp *et al.*, 1997). There are many different types of DNA markers, that each has a differential set of advantages for any particular application in linkage mapping and molecular breeding. Once genomic regions contributing to the trait of interest have been identified and the alleles at each locus designated by a respective molecular marker, they can be transferred into locally adapted high-yielding cultivars by making the requisite cross and following the marker(s) through subsequent generations of inbreeding or backcrossing. Wild relatives of commercial crops contain alleles of importance for improving crop performance and resistance to insect pests. Since these alleles are often recessive in action, they can only effectively be utilized in crop breeding programmes through marker-assisted selection (Xiao *et al.*, 1996, Miflin, 2000). Marker-assisted selection can be used to estimate genetic variances (Bai *et al.*, 1998), predict hybrid performance (Bohn *et al.*, 1997), estimate the number of genes in which the parents differ (Kisha *et al.*, 1997), or identify QTL associated with resistance to biotic and abiotic stress factors.

6. Genetic Linkage Maps and Identification of Molecular Markers for Insect Resistance

6.1 Chickpea

Many studies (Gaur and Slinkard, 1990a,b; Ahmad *et al.*, 1992; Kazan *et al.*, 1993; Simon and Muehlbauer, 1997; Winter *et al.*, 1999, 2000; Santra *et al.*, 2000; Tekeoglu *et al.*, 2000) have used interspecific mapping populations for developing linkage maps. The preliminary linkage map reported by Gaur and Slinkard (1990a,b) was based on interspecific crosses of *C. arietinum* x *C. reticulatum* and *C. echinospermum,* and intraspecific crosses of *C. reticulatum.* Kazan *et al.* (1993) assigned 11 additional loci

to the linkage map reported by Gaur and Slinkard (1990a), based on interspecific crosses of *C. arietinum* with *C. reticulatum* and *C. echinospermum*. Simon and Muehlbauer (1997) developed a genetic linkage map of chickpea consisting of 9 morphological, 27 isozymes, 10 RFLP, and 45 RAPD markers. Winter *et al.* (1999) developed the first genomic map of chickpea based on 90 RILs derived from *C. reticulatum* (PI 489777) and the chickpea (ICC 4958), and mapped 120 sequence tagged microsatellite (STMS) markers. This map was then augmented using 118 STMS, 96 DAF, 70 AFLP, 37 ISSR, 17 RAPD, 2 SCAR, 3 cDNA and 8 isozyme markers screened across 130 RILs from the same cross (Winter *et al.*, 2000). Santra *et al.* (2000) used an RIL population from interspecific cross of *C. arietinum* x *C. reticulatum* to generate a map of nine linkage groups with 116 markers (isozymes, RAPD and ISSR) covering a map distance of 981.6 cM with an average distance of 8.4 cM between the markers.

The RILs 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 intraspecific crosses (Cho *et al.*, 2002). This map consists of 58 STMS, 20 RAPD and 4 SSR markers assigned to 14 linkage groups covering 458 cM with an average distance of 5.3 cM between the markers. Genes for four morphological trait loci have also been mapped. There have been intensive efforts to map resistance to Fusarium wilt in chickpea (Mayer *et al.*, 1997; Tullu *et al*, 1998, 1999; Ratnaparkhe *et al.*, 1998; Tekeoglu *et al.*, 2000; Winter *et al.*, 1999, 2000) Conversely, there are few reports of mapping resistance to Ascochyta blight in chickpea despite a large number of conventional studies on the genetic basis of resistance to this disease (Santra *et al.*, 2000; Flandez-Galvez, 2002).

Mapping the complex traits such as resistance to pod borer, *H. armigera* in chickpea is only just 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* under unsprayed conditions. 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. here were 4 to 31 larvae per 10 plants in the mapping population compared to 10 larvae in ICC 506EB and 18 in ICCV 96029. These results indicated that there is considerable variation in this mapping population for susceptibility to *H. armigera*. These data will be correlated with genotypic data to find possible association with molecular markers. Another RIL mapping population has been developed from the cross Vijay x ICC 506EB through rapid generation advance in controlled conditions. A total of 328 RILs have been advanced to F_6 the population is now being evaluated for resistance to *H. armigera*.

6.2 Pigeonpea

A few studies have been conducted to investigate the polymorphism for molecular markers in cultivated pigeonpea and its wild relatives (Boehringer *et al.*, 1991; Nadimpalli *et al.*, 1993; Ratnaparkhe *et al.*, 1995; Parani *et al.*, 2000). Boehringer *et al.* (1991) screened ten allozymes across one Zambian and 20 Indian genotypes of cultivated pigeonpea, but only two detected any polymorphism. Nadimpalli *et al.* (1993) used nuclear RFLPs to determine phylogenetic relationships among 12 species in four genera (*Cajanus, Dunbaria, Eriosema,* and *Rhynchosia*). Fifteen random genomic probes and six restriction enzymes revealed limited variation within each species, while considerable polymorphism was observed between the species. *Cajanus cajan* was found to be closer to *C. scarabaeoides* than to *C. cajanifolia.* Ratnaparkhe *et al.* (1995) studied RAPD polymorphism in cultivated pigeonpea and its 13 wild relatives. The level of polymorphism among the wild species was very high, while little polymorphism was detected within the cultivated species.

Variations in length and restriction sites of ribosomal DNA have also been studied among eight *Cajanus* species (Parani *et al.*, 2000). The six genotypes of *C. cajan* did not show polymorphism in any of the enzyme-probe combinations, whereas RFLPs were readily detected among the species in all enzyme-probe combinations. The cultigen was found to be closely related to *C. scarabaeoides.* These studies clearly indicated that isozyme, RAPD, and RFLP markers may not be adequate to develop a genome map of pigeonpea based on intraspecific mapping populations. However, recently developed microsatellite markers (also known as simple sequence repeats, SSRs) have detected polymorphism in diverse pigeonpea germplasm using manual slab gel systems (Burns *et al.*, 2001). Six of these markers have detected extensive diversity within and between cultivated pigeonpea accessions using capillary electrophoresis (Buhariwalla, H.K., ICRISAT, unpublished). Thus, it appears that SSR markers will readily detect polymorphism in breeding populations, although the number currently available is a severe limitation to their application. For this reason, a major SSR marker development programme has been initiated in pigeonpea (Ferguson, M.E., ICRISAT, unpublished).

High levels of resistance to pod borer, *H. armigera*, and pod fly, *Melanagromyza obtusa*, have been identified in wild relatives of pigeonpea such as *C. scarabaeoides*, *C. sericeus*, and *C. acutifolius* (Sharma *et al.*, 2001, 2003b), which can be easily crossed with the cultivated pigeonpea. A mapping population involving *C. cajan* x *C. scarabaeoides* is under development at ICRISAT.

6.3 Soybean

There has been a limited success in developing soybean cultivars with resistance to insects because of quantitative nature of resistance and linkage drag from donor parents. Lin *et al.* (1996) developed a linkage map of soybean using RFLP, RAPD, and AFLP markers, while Narvel (2000) used SSR markers for covering the soybean genome. Rector *et al.* (1998) used 139 RFLPs to construct genetic linkage map of soybean to identify QTLs associated with resistance to corn earworm (*H. zea*) in a population of 103 F_2-derived lines from Cobb (susceptible) x PI 229358 (resistant). The genetic linkage map consisted of 128 markers, which converged onto 30 linkage groups covering approximately 1325 cM. One major and two minor QTLs were identified for resistance to *H. zea*. The PI 229358 allele contributed towards insect resistance at all three QTLs. The major QTL was linked to the RFLP marker *A584* on linkage group *(LG) 'M'*. The minor QTLs were linked to the RFLP markers *R249 (LG 'H')* and *Bng047* (*LG 'D1'*). The heritability (h^2) for resistance was estimated to be 64%. Another RFLP map has been developed by Rector *et al.* (1999) based on Cobb x PI 171451 and Cobb x PI 227687. Among the three resistant genotypes (PI 171451, PI227687, and PI 229358), a QTL on linkage group (*LG*) *'H'* was shared among all three genotypes, 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. In addition, a QTL was detected on *LG 'F'* in the susceptible genotype, Cobb. This QTL is in a region of the soybean genome which has been previously associated with a cluster of soybean pathogen-resistance loci. Using RFLP markers, Narvel *et al.* (2001) identified QTL associated with insect resistance from PI 229358 and PI 171451. Marker analysis defined intervals by 5 cM or less for a QTL on linkage group *D1b* (*SIR-D1b*), and for *SIR-G, SIR-H*, and *SIR-M*. At least 13 of the 15 *SIR* genotypes studied had introgressed *SIR-M*. Only a few genotypes possessed *SIR-G* or *SIR-H*, and no genotype possessed *SIR-D1b*. MAS is needed to introgress QTL for insect resistance into elite genetic backgrounds.

Resistance to defoliating insects in soybean is expressed as a combination of antibiosis and antixenosis mechanisms of resistance. Both of these resistance modes are inherited quantitatively (Rector *et al.*, 2000). RFLP maps based on F_2 populations segregating for antibiosis against *H. zea* indicated that heritability estimates for antibiosis were 54, 42, and 62% in Cobb x PI 171451, Cobb x PI 227687, and Cobb x PI 229358, respectively. 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. This is the only insect-resistance QTL that has been detected for both antibiosis and antixenosis. Antibiosis QTL was also detected on *LG*

F and *B2* in Cobb x PI 227687, and *LGs G* and *J* in Cobb x PI 229358. Antibiosis was conditioned by the PI (resistant parent) allele at the QTL on *LGs G, M*, and *B2*, whereas the susceptible parent, Cobb, provided antibiosis alleles at the QTL on *LGs F* and *J*.

A genetic map based on more than 500 molecular markers on 240 RILs derived from non-resistant parents (Minsoy from China and Noir 1 from Hungary) has shown transgressive segregation with respect to their defensive effects on *H. zea* and soybean looper, *Pseudoplusia includens* (Walker) (Terry *et al.*, 1999). Two QTLs affected larval developmental rates, while another QTL affected only a single trait each, *i.e.*, larval weight, pupal weight, developmental rate, nutritional efficiency, or survival. Increased range of defensive effects among the segregant RILs is due to recombination among several parental genes that together quantitatively control plant defensive traits. QTLs have also been found on five *LGs* in the *MN* and four in the *MA* population (Terry *et al.*, 2000). The QTL on *LG U2* is associated with major effects on larval development in both the *MN* and the *MA* populations. All other QTLs had lesser effects. The *U2* QTL associated with resistance to insects is of major importance in that: i) it has been identified in different genetic backgrounds, ii) it is associated with several larval growth parameters, and iii) it explains a large proportion of the phenotypic variation. All other QTLs segregated in only one population. Most of the resistance alleles were associated with the Minsoy parent. Consistent with this observation, Archer and Noir 1 were better corn earworm larval host plants than Minsoy.

6.4 Cowpea

There is considerable information on genetic linkage map of cowpea (Fatokun *et al.*, 1992; Young *et al.*, 1992a; Myers *et al.*, 1996; Menendez *et al.*, 1997). The development of a RFLP map of cowpea has allowed the investigation of association between genes of interest (Myers *et al.*, 1996). A cross between an aphid (*A. craccivora*) resistant cultivated cowpea, IT 84S-2246-4, and an aphid susceptible wild cowpea, NI 963 has been evaluated for aphid resistance and RFLP marker segregation. One RFLP marker, *bg4D9b*, has been found to be tightly-linked to aphid resistance gene (*Rac1*), and several flanking markers in the same linkage group (linkage group 1) were also identified. The close association of *Rac1* and *bg4D9b* presents an opportunity for cloning this insect resistance gene. Githiri *et al.* (1996) studied the linkage of the aphid resistance gene *Rac* with various polymorphic loci controlling morphological traits and aspartate amino-transferase isozyme (*AAT*) to identify simply inherited and easily identifiable markers for aphid resistance, and to distinguish between *Rac1* and *Rac2*. The F_2 and F_2-derived F_3 populations from crosses IT 87S-1459 x Tvu 946, and IT 84S-2246 x Tvu 946 segregating for *Rac1*, and cross ICV 12 x Tvu

946 segregating for *Rac2* have been evaluated for various polymorphic morphological traits. Locus *pd*, controlling peduncle colour, was found to be linked to both *Rac1* and *Rac2*. The recombination frequencies estimated by the maximum likelihood method were 26 ± 8.3% and 35 ± 7.5% for *Rac1-pd* and *Rac2-pd* co-segregation, respectively; thus indicating that *Rac1* and *Rac2* were not different from one another. No linkage was found between aphid resistance genes and the genes controlling other polymorphic morphological traits or *AAT* isozyme.

6.5 Common Bean

Tar'an *et al.* (2002) developed the genetic linkage map of agronomic traits of common bean. Schneider *et al.* (1997) used seven markers for MAS under stress conditions, and improved yield performance by 11%, while Stromberg *et al.* (1994) did not get a greater response to MAS than to conventional selection for yield. Common bean near-isogenic lines differing for the recessive bean common mosaic virus (BCMV) resistance allele *bc-3* were screened to identify linked RAPD markers (Haley *et al.*, 1994). Categorization of the *bc-3* genotypes in the F_2 population revealed that selection against the repulsion-phase RAPD, as opposed to selection for the coupling-phase RAPD, provided a greater proportion of homozygous resistant (81.8 versus 26.3%) selections, and a lower proportion of both segregating (18.2 versus 72.5%) and homozygous susceptible (0.0 versus 1.2%) selections. Selection of individuals based on the phenotype of both RAPD markers was identical to selection based solely on the repulsion-phase RAPD alone. Because repulsion-phase RAPD markers are more useful in marker-assisted selection for monogenic pest resistance traits, it will be useful to design screening experiments in ways that optimize the discovery of these. Murray *et al.* (2000) detected genetic loci for resistance to potato leafhopper [*Empoasca fabae* (Harris)].

6.6 Mungbean

The TC 1966 bruchid (*Callosobruchus* sp.) resistance gene has been mapped using RFLP markers (Young *et al.*, 1992b). Fifty-eight F_2 progenies from a cross between TC 1966 and a susceptible mungbean cultivar have been analyzed with 153 RFLP markers. Resistance was mapped to a single locus on linkage group VIII, approximately 3.6 cM from the nearest RFLP marker. Based on RFLP analysis, an individual was also identified in the F_2 population that retained the bruchid resistance gene within a tightly linked double crossover. This individual might be valuable in developing resistant mungbean lines free of linkage drag. Yang *et al.* (1998) used RFLP marker-assisted selection in backcross breeding for introgression of the bruchid resistance gene in mungbean, while Kaga and Ishimoto (1998) studied genetic localization of a bruchid

resistance gene and its relationship to insecticidal cyclopeptide alkaloids, the vignatic acids in mungbean.

The RAPDs have also been used to identify markers linked to the bruchid resistance in mungbean (Villareal *et al.*, 1998). The technique was utilized in conjunction with near-isogenic line (NIL) and recombinant inbred line (RIL) mapping population. The resistant NILs were B4P3-3-23, B4P 5-3-10, B4Gr3-1 and DHK 2-18, carrying the bruchid resistance gene in four genetic backgrounds, Pagasa 3, Pagasa 5, Taiwan Green and VC 1973A, respectively. The source of resistance to bruchid was TC1966, an accession of *Vigna radiata* var. *sublobata*. Polymorphism was evaluated initially in four pairs of NILs and TC 1966, then mapped subsequently in an F sub 9: 6 RIL population from the cross Pagasa 7 x TC 1966. Thirty-one RAPD markers differentiating at least two pairs of near-isogenic lines have been identified. Of these RAPD markers, 25 were found to co-segregate in the RIL population. Co-segregation of anchor RFLP markers *pM151a* and *pM151b* were likewise followed in the same population. Bruchid resistance gene was found to map 14.6 cM from the nearest RAPD marker *Q04 sub 900* and 13.7 cM from the nearest RFLP marker *pM151b*. The gene was 25 cM from *pM151a*. When *pM151a* and *pM151b* were considered as alleles of the same locus, the bruchid resistance gene was located 11.9 cM from the nearest RAPD marker *Q04* sub 900 and 5.6 cM from *pM151*. The results indicated that while RAPD technique provides the fastest and simplest molecular marker technique, the nearest RAPD markers identified are still quite far away from the bruchid resistance gene to have any practical utility for breeding as well as map-based cloning purposes. However, RAPD markers can be used to add more markers to the existing linkage map of mungbean.

6.7 Groundnut

The first linkage map of groundnut with a total map distance of nearly 1063 cM has been constructed using an F_2 population derived from two related diploid species (*Arachis stenosperma* and *A. cardenasii*) (Halward *et al.*, 1993). The first RFLP-based genetic linkage map of cultivated groundnut [derived from a BC_1 population (TxAG 6) of Florunner x *A. batizocoi* K 9484 x (*A. cardenasii* GKP 10017 x *A. diogoi* GKP 10602)] was developed by using 350 RFLP loci on to 22 linkage groups with a total map distance of approximately 2700 cM (Burow *et al.*, (1999). RAPD (*RKN 229*, *RKN 410*, and *RKN 440*) and RFLP (*R2430E*, *R2545E*, and *S1137E*) markers linked with root-knot nematode resistance have been reported in groundnut (Burow *et al.*, 1996; Choi *et al.*, 1999). Resistance and susceptible alleles for RFLP loci *R2430E* and *R2545E* are quite distinct and are useful for identifying individuals homozygous for resistance in segregating populations (Choi *et al.*, 1999). Furthermore,

RAPD, sequence characterized amplified region (SCAR), and RFLP markers have been used to determine the introgression of wild species chromosome segments with nematode resistance in *A. hypogaea* from *A. cardenasii* cross (Garcia *et al.*, 1996). There is a need to convert these RFLP markers into PCR based markers to understand the marker trait relationships (Dwivedi *et al.*, 2003), particularly for resistance to insect pests and diseases.

7. Marker-Assisted Selection (MAS)

Mapping populations from interspecific crosses are often used for linkage studies due to the high level of detectable polymorphism, but linkage maps derived from such crosses may have limited relevance in crop breeding programmes due to different recombination patterns (Fulton *et al.*, 1997). However, markers developed from such maps may be valuable tools for introgression breeding. It takes five to six generations to transfer insect resistance traits into the high-yielding cultivars through conventional breeding. Transfer of resistance genes from wild species may take considerably longer due to the complexity of achieving interspecific hybrids on a sufficiently large scale in order to identify stable progeny with an acceptable combination of traits. In either case, marker-assisted selection can dramatically speed up the process by reducing the number of generations and size of populations required to identify individuals with the correct introgressed genes while having the minimal amount of additional donor parent genome. The improved lines with insect resistance thus developed will still need to be tested across seasons and locations, before a variety could be identified for recommendation to farmers. This process takes 7 to 10 years. In marker-assisted selection programmes, the elite breeding lines or cultivars can be crossed with the resistant source, and the F_1 hybrid re-crossed with the recurrent parent (invariably the elite parent) (BC_1), and the gene transfer can be monitored through marker-assisted selection until BC_{3-5} (until one has a line with the QTL or the gene of interest in the genomic background of the elite line with a minimum of the donor parent genome). The F_{6-8} progenies of crosses involving a resistance source from the wild relatives and the cultivated types can also be used as recombinant inbred lines (RILs) for mapping insect resistance (provided the population has been advanced through the generations in the correct way). The MAS takes 3 to 6 years, and thus speeding up the pace of transferring the traits of interest into the improved varieties, and it does not require large-scale planting of the progenies up to crop harvest, as the plants showing the presence of the trait or QTL only need to be maintained up to maturity.

The use of DNA markers for indirect selection offers the greatest potential gains for quantitative traits with low heritability, as these are the most difficult characters to work with through conventional phenotypic selection. However, it is also difficult to develop effective MAS for such traits. The expression of such traits is influenced

by genotype x environment interaction and epistasis, which in addition to difficulties involved in accurately and precisely phenotyping such traits, confounds the development of MAS systems. The quality of á marker-assisted selection programme can only be as good as the quality of the phenotypic data on which the development of that marker was based. Therefore, it is essential to use large mapping populations characterized across seasons and locations, using well-defined phenotyping protocols. Nevertheless, when confidence limits are calculated for the QTL positions, they might cover several intervals on even entire chromosome arms, if the heritability of the trait is low (Hyne *et al.*, 1995). However, marker-assisted selection of such large DNA segments can still be highly effective. For stem borer resistance in maize, no difference was observed between the efficiency of MAS versus conventional selection (Wilcox *et al.*, 2002; Bohn *et al.*, 2001). Maximum progress has been made using a combination of phenotypic performance and QTL based index, followed by QTL based index, and conventional selection (Tar'an *et al.*, 2003).

8. Gene Synteny

Genes can be discovered using a variety of approaches (Shoemaker *et al.*, 2001; Primrose, 1998). The development of genetic maps in a number of crop species having positional similarity will lead to better understanding of crop evolution and functioning of genes. This "synteny" will allow advances made in one species to have spillover impacts in other species (Gale and Devos, 1998). A comparison of expressed sequence tag (EST) databases from different plants can reveal the diversity in coding sequences between closely and distantly related plants, while mapping of ESTs may elucidate the synteny between those species. For understanding gene functions of a whole organism, functional genomics is now using insertion mutant isolation, gene chips or microarrays, and proteomics. This information can also be used to understand the genetics of metabolic processes, analyze traits controlled by several QTLs, and identify favourable alleles at each locus. The alleles can be combined by simple crossing, and the most favourable combinations assembled in the same background using marker assisted selection and/or genetic transformation.

There has been a considerable interest in using synteny to transfer SSR markers isolated from intensively studied legumes such as pea, soybean and *Medicago* for use in lesser-studied crops. A comparison of the linkage maps of *Cicer, Pisum, Lens* and *Vicia* has revealed that these legumes share many common linkage groups (Gaur and Slinkard 1990a,b; Weeden *et al.*; 1992; Kazan *et al.*, 1993; Simon and Muehlbauer 1997; Weeden *et al.*, 2000). 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 a 20% chance in the reverse direction (Pandian *et al.*, 2000). Based on taxonomic distance, it is expected that a similar trend will be observed between soybean and pigeonpea. Combining empirical lab-based approaches with bioinformatic strategies will be helpful to develop efficient systems for screening the vast public domain sequence databases of soybean and *Medicago* to liberate sequences of most value for molecular breeding of chickpea and pigeonpea. Information on conserved gene sequences among these genera will also facilitate prediction of gene location in crop genus based on its location in other genera.

9. Metabolic Pathways

Harnessing synteny may have maximum benefit where entire metabolic pathways are dissected and studied in detail in model systems, thereby identifying the key genes for manipulating that trait, which can then be traced in the species of interest. Many secondary plant metabolites such as flavonoids, alkaloids, and terpenoids have been implicated in host plant resistance to insect pests. Many compounds of the flavonoid biosynthetic pathway (flavanones, flavones, flavanols, and isoflavonoids) accumulate in response to insect damage (Ebel, 1986; Heller and Forkman, 1993; Sharma and Norris, 1991). Molecular breeding and genetic engineering can be used to change the metabolic pathways to increase the amounts of various flavonoids conferring resistance to insect pests, *e.g.*, medicarpin and sativan in alfalfa, cajanol and stilbene in pigeonpea, and stilbene in chickpea (Heller and Forkman, 1993). Stilbenes have been expressed in transgenic tobacco plants, exhibiting various degrees of inhibition of fungal growth (Heller and Forkman, 1993). Maysin, a glycosyl flavone in maize silk, is associated with resistance to corn earworm, *H. zea* (Waiss *et al.*, 1979). Most of the phenotypic variation in maysin concentration in maize silk is accounted for by the *p1* locus, the transcription activator of the portion of the flavonoid pathway leading to maysin synthesis. Reduced function *p1* allele results in decreased transcription of genes encoding enzymes of the *p1*-controlled portion of the pathway, and thus reduced maysin synthesis. The marker *umc105a* corresponds to the brown pericarp (*bp1*) locus. The *p1* and chromosome *9S* regions are the major QTL controlling silk antibiosis to the corn earworm (Byrne *et al.*, 1997). Composite interval mapping has shown major QTL in the *asg20-whp1* interval of chromosome 2, and near the *wx1* locus on chromosome 9 (Byrne *et al.*, 1998). A gene that encodes chalcone synthase (*whp1*) on chromosome 2 and a silk specific gene (*sm1*) on chromosome 6, affect maysin concentration and resistance to corn earworm in maize (Byrne *et al.*, 1998). There is considerable scope for changing the products of secondary metabolites that associated with resistance to insect pests through biotechnological approaches.

10. Future Strategies

The limited number of microsatellite markers detecting polymorphism in some grain legumes (such as chickpea and groundnut) is a significant logistical constraint to molecular breeding of agronomic traits. In general, only a third of the microsatellite primers are polymorphic in any given mapping or breeding population. On this basis, there is a need for around one thousand SSR markers in each crop to support routine molecular breeding activities. Nevertheless, a good beginning has been made in developing genetic linkage maps of many grain legumes. However, the accuracy and precision of resistance phenotyping protocols remain a much more critical constraint in many grain legumes. There is a need to focus on developing innovative solutions to this problem. Improved phenotyping systems will have substantial impact on both conventional and biotechnology-assisted approaches to insect pest resistance breeding in addition to the more strategic research that feeds into these endeavors.

Marker-assisted selection has had dramatic impacts, particularly in the private sector, on the breeding of disease resistance and quality traits where major simply inherited components could be readily identified. The same potential impact holds for more complex traits such as insect pest resistance and abiotic stress tolerance. However, the practical and logistical demands for developing and implementing molecular breeding systems for these traits are considerably more complex. There is a great potential to use marker-assisted selection to develop cultivars with resistance to insect pests and to strengthen *Bt* transgenic crops through introgression of other sources of resistance through molecular breeding. There are very few reports concerning the application of marker-assisted selection in insect pest resistance breeding programmes. However, those available fail to demonstrate an increase in efficiency of MAS over conventional breeding approaches, although combining MAS with conventional approaches has given better results. Thus, not only is there a need for precise mapping of the QTL associated with resistance to insects, but also the development of a new paradigms in breeding based on re-engineering breeding programmes to make best use of molecular marker data. Only a combination of conventional and molecular breeding approaches can lead to new advances in legume productivity for agricultural development and improved livelihoods of the rural poor.

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