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Research achievements in plant resistance to insect pests of cool season food legumes

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Abstract

Plant resistance to at least 17 field and storage insect pests of cool season food legumes has been identified. For the most part, this resistance was located in the primary gene pools of grain legumes via conventional laboratory, greenhouse, and field screening methods. The use of analytical techniques (i.e., capillary gas chromatography) to characterize plant chemicals that mediate the host selection behavior of pest insects offers promise as a new, more rapid way to differentiate between insect-resistant and susceptible plant material. Examples of research achievements in mechanisms of resistance and host-plant resistance within the context of integrated control programs are discussed. Accelerating the development and subsequent releases of insect-resistant cultivars to pulse farmers requires more involvement from interdisciplinary teams of plant breeders, entomologists, plant pathologists, plant chemists, molecular biologists, and other scientists.

Introduction

Entomologists and plant breeders have located sources of plant resistance to several of the most important insect pests of cool season food legumes (Horber, 1978; Reed *et al.*, 1988; Weigand & Pimbert, in press). However, the transfer of resistance-conferring genes from this material to regionally adapted lines has been constrained by several biological and technological factors, including but not limited to: a lack of sufficient information about the chemical and physical nature and genetic bases of insect resistance in plants; the need for breakthrough research and technology to overcome barriers to the development of cultivars with multiple insect and disease resistance; and the requirement for new and improved technology to overcome barriers to inter-specific hybridization so resistance genes can be transferred from nonadapted to adapted backgrounds. Moreover, pest resistance research and breeding has been "undervalued and underfunded" (Reed *et al.*, 1988). Overcoming these barriers, and expediting the development and first releases of chickpea (*Cicer arietinum* L.), faba bean (*Vicia faba* L.), dry pea (*Pisum sativum* L.), lentil (*Lens culinaris* Medik.), and grasspea (*Lathyrus sativus* L.) cultivars with insect resistance or with the ability to tolerate more insect damage than normally sensitive cultivars, will require much more involvement from interdisciplinary teams of plant breeders, entomologists, plant pathologists, plant chemists, molecular biologists, and other scientists. The reader is referred to Reed *et al.* (1988) and Singh *et al.* (1990) for indepth discussions on constraints to breeding for insect resistance in cool season food legumes (grain legumes).

This chapter reviews research achievements in plant resistance to insect pests of grain legumes. Although emphasis is on progress since the first International Food Legume Research Conference in 1986, some pre-1986 literature and work overlooked in previous reviews is highlighted to provide a comprehensive review of the topic. After reviewing known cases of plant resistance to insect pests of grain legumes, we summarize and discuss the screening methods and evaluation criteria that researchers have used to separate susceptible from resistant germplasm. Next, we address mechanisms and levels of plant resistance, citing examples from the body of literature on plant resistance to insect pests of grain legumes. These aspects warrant consideration because they relate to the longterm durability of insect-resistant crop cultivars (Kennedy *et al.*, 1987). We briefly discuss host-plant resistance as a complementary pest control strategy before ending with comments on the prospects for breeding insect-resistant cultivars of grain legumes.

Insect resistance in grain legumes

Through the efforts of several researchers, sources of plant resistance to at least seventeen of the most important field and storage insect pests of chickpeas, faba beans, dry peas, and lentils have been located (Table 1). These searches for resistance have involved as few as two, normally 6 to 140, and at times more than 14,000 accessions or entries. As is normally the result when searches for insect-resistant plant material are undertaken, grain legume workers have found low frequencies of resistance among plant materials examined (Table 2). The reader is referred to the citations in Tables 1 and 2 for listings of specific insect-resistant plant genotypes, plant introductions, accession numbers, and breeding lines. We are unaware of any reports of plant resistance to insect pests of grasspea.

For the most part, insect resistance has been located in the primary gene pools of grain legumes. Rarely have the secondary (i.e., species that will cross with crop but gene transfer often difficult) and tertiary (i.e., species related to crop; however, gene transfer not possible or requiring radical techniques) (definitions according to Harlan & De Wet, 1971) gene pools been examined for insect resistance. The only evaluations of wild and related species of grain legumes for insect resistance have involved wild species of *Cicer* against *Helicoverpa armigera* (Hüb.) (ICRISAT, 1987) and the storage pest *Callosobruchus chinensis* (L.) (Weigand & Tahhan, 1990), wild *Vicia* against the aphids *Aphis fabae* Scop., *Acyrthosiphon pisum* (Harris), and *Megoura viciae* (Buckt.) (Birch & Wratten, 1984; Holt & Birch, 1984; Birch, 1985), and *Lathyrus sativus* and *L. tingitanus* L. against *Bruchus pisorum* (L.) (Annis & O'Keeffe, 1984) (Table 1). The latter study was conducted in conjunction with research into the mechanisms of plant resistance to *B. pisorum*, which is not a pest of grasspea but is a major, worldwide pest of peas (Clement, 1992). That these few evaluations led to the discovery of insect-resistant plant materials suggests a need for more evaluations of the secondary and tertiary gene pools of grain legumes.

Screening methods and measurement of resistance

Field pests

Usually, grain legume researchers have relied upon conventional methods such as open-field tests, field confinement techniques, and laboratory assays to search for differences in the ability of plants to serve as hosts for insect pests and to withstand attacks and recover from injury. Tingey (1986) and Smith (1989) are useful general references on screening methods and evaluation criteria currently used in host-plant resistance.

Open-field tests have been used to successfully segregate chickpea (Lateef, 1985; Weigand & Tahhan, 1990), faba bean (Sharaf El-Din, unpubl. data; Wolfenbarger & Sleesman, 1961, 1963; Tahhan & van Emden, 1989), pea (Wright *et al.*, 1951; Nouri-Ghanbalani, 1974, 1977; Pesho *et al.*, 1977; Nouri-Ghanbalani *et al.*, 1978; Sehgal *et al.*, 1987; Soroka & Mackay, 1990a), and lentil (Chopra & Pajni, 1987) germplasm for resistance to attack by pod borer (*H. armigera*); leafminers (*Liriomyza cicerina* [Rondani], *L. trifolii* [Burgess], *Chromatomyia horticoloa* [Goureau]); weevils (*Bruchus pisorum* [L.], *B. dentipes* Baudi, *B. lentis* Froel., *Sitona lineatus* [L.]); aphids (*Aphis craccivora* [Koch], *Acyrthosiphon pisum* [Harris]); potato leafhopper (*Empoasca fabae* [Harris]); pea moth (*Cydia nigricana* [F.]); and Mexican bean beetle (*Epilachna varivestris* [Muls.]). These searches for resistance often employed small plots without replication to quickly eliminate susceptible plant genotypes. These trials have sometimes been followed by larger field plots containing standard checks and promising lines from initial screenings, all replicated and grouped in plots according to similar maturities (Lateef, 1985; Lateef & Sachan, 1990). Since 1980, multilocational testing of promising *H. armigera* resistant selections in replicated field plots has become part of the chickpea entomology program at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (Lateef & Sachan,

Table 1. Reports of plant resistance to field and storage insect pests of grain legumes

Crop and insects	Field or storage pest	Plant taxa evaluated	References
Chickpea			
Aphis craccivora (Koch)[a]	Field	*Cicer arietinum*	Weigand and Tahhan (1990)
Callosobruchus chinensis (L.)[c]	Storage	*C. arietinum*	ICRISAT (1976)
		Wild *Cicer* species	Weigand and Tahhan (1990); Weigand and Pimbert (in press)
Callosobruchus maculatus (F.)[c]	Storage	*C. arietinum*	Salunkhe and Jadhav (1982); Ahmed *et al.* (1989)
Helicoverpa armigera (Hüb.)[f]	Field	*C. arietinum*[k]	Rembold (1981); Lateef (1985, 1990); Lateef *et al.* (1985); Ahmed *et al.* (1990); Lateef and Pimbert (1990); Lateef and Sachan (1990); Pimbert (1990); Rembold *et al.* (1990a,b); Weigand and Pimbert (in press)
		Wild *Cicer* species	ICRISAT (1987)
Liriomyza cicerina (Rondani)[h]	Field	*C. arietinum*	Weigand (1990); Weigand and Tahhan (1990)
Faba bean			
Aphis craccivora (Koch)[a]	Field	*Vicia faba*	ICARDA (1989); El-Defrawi *et al.* (1991)
Aphis fabae Scop.[a]	Field	*V. faba* and wild species	Holt (1983); Birch and Wratten (1984); Holt and Birch (1984); Birch (1985); ICARDA (1989)
Acyrthosiphon pisum (Harris)[a]	Field	*V. faba* and wild species	Brich and Wratten (1984); Holt and Brich (1984)
Megoura viciae (Buckt.)[a]	Field	*V. faba* and wild species	Birch and Wratten (1984); Holt and Birch (1984)
Empoasca fabae (Harris)[b]	Field	*V. faba*	Wolfenbarger and Sleesman (1963)
Bruchus dentipes Baudi[c]	Field[j]	*V. faba*	Tahhan (1986); Tahhan and van Emden (1989)
Callosobruchus chinensis (L.)[c]	Storage	*V. faba*	Ishii (1952)
Callosobruchus maculatus (F.)[c]	Storage	*V. faba*	Fam and El-Sayed Ahmed (1985)
Epilachna varivestris Muls.[d]	Field	*V. faba*	Wolfenbarger and Sleesman (1961)
Liriomyza trifolii (Burgess)[h]	Field	*V. faba*	El-Din Sharaf El-Din (unpublished data)

Table 1 (continued)

Crop and insects	Field or storage pest	Plant taxa evaluated	References
Pea			
Acyrthosiphon pisum (Harris)[a,i]	Field	*Pisum sativum*	Semenova (1990); Soroka and MacKay (1990a,b,c); Soroka and MacKay (1991)
Bruchus pisorum (L.)[c]	Field[j]	*P. Sativum*	Vilkova andKolensichenko (1973); Aleksandrova (1977); Pesho *et al.* (1977); Sokolov (1977); Annis (1983); Pillsbury (1986); Clement (unpublished data)
		P. sativum ssp. *humile*	Hardie (1990)
		Lathyrus species	Annis and O'Keeffe (1984)
Sitona lineatus (L.)[c]	Field	*P. sativum*	Nouri-Ghanbalani (1974); Nouri-Ghanbalani (1977); Auld *et al.* (1980)
Cydia nigricana (F.)[g,i]	Field	*P. sativum*	Wright *et al.* (1951); Bingefors *et al.* (1964); Wnuk (1968)
Chromatomyia horticola (Goureau)[h]	Field	*P. sativum*	Sehgal *et al.* (1987)
Lentil			
Aphis craccivora (Koch)[a]	Field	*Lens culinaris*	Weigand and Pimberg (in press)
Bruchus lentis Froel.[c]	Field[j]	*L. culinaris*	Chopra and Pajni (1987)
Sitona spp.[c]	Field	*L. culinaris*	Sedivy (1972)

[a] Homoptera:Aphididae; [b] Homoptera:Cicadellidae; [c] Coleoptera:Bruchidae;
[d] Coleoptera:Coccinellidae; [e] Coleoptera:Curculionidae;
[f] Lepidodptera:Noctuidae; [g] Lepidoptera:Tortricidae;
[h] Diptera:Agromyzidae.
[i] Resistance found in dry and/or green pea cultivars.
[j] Infestation starts in the field as eggs on green pods but larval feeding damage is manifested in stored seed.
[k] Resistance found mainly in desi and to some extent in kabuli (Mediterranean) types.

1990; Pimbert, 1990). While multilocational testing helps chickpea breeders determine the agronomic performance of promising lines across several agroecological zones, it provides entomologists with a mechanism to assess variation in the virulence of allopatric pod borer populations on resistant lines. Only Smith *et al.* (1982), in a study involving the screening of pea lines against *B. pisorum*, seem to have rigorously addressed the selection of appropriate experimental and statistical designs for use in open-field screening trials.

To compensate for low insect populations during field evaluations, some researchers caged laboratory-reared insects on test plants (Birch, 1985) while others released laboratory-reared insects into plots (Lateef, 1985). Laboratory tests conducted alone or in concert with field studies and utilizing caged insects on plant material have also proven useful for evaluation of insect resistance in grain legumes, such as aphid (*A. craccivora*, *A. faba*, *A. pisum*, *M. viciae*) resistance in the genus *Vicia* (Birch & Wratten, 1984; Holt & Birch, 1984; El-Defrawi *et al.*, 1991) and weevil (*B. pisorum*, *S. lineatus*) resistance in peas (Nouri-Ghanbalani, 1977; Annis, 1983; Pillsbury, 1986).

Plant resistance workers normally separate susceptible from resistant plant materials during screening and evaluation programs by measuring the deleteri-

Table 2. Mass screening of grain legumes and frequency of insect-resistant genotypes among screened material

Insect	Plant taxa evaluated	Approximate no. of entires in mass screenings	showing antixenosis, antibiosis and/or tolerance after screening and re-testing	References
Callosobruchus chinensis (L.)	*Cicer arietinum*	6,697	0	Weigand and Pimbert (in press)
Helicoverpa armigera (Hüb.)	*C. arietinum*	14,800	21	Lateef and Pimbert (1990)
Liriomyza cicerina (Rondani)	*C. arietinum*	6,800	10	Weigand and Tahhan (1990)
Aphis craccivora (Koch)	Vicia fabae	7,156	114	El-Defrawi *et al.* (1991)
Bruchus dentipes Baudi	*V. fabae*	1,000	0[a]	Tahhan and van Emden (1989)
Bruchus pisorum (L.)	*Pisum sativum*	1,571	10	Annis (1983); Pesho *et al.* (1977)
Sitona lineatus (L.)	*P. sativum*	2,074	2	Auld *et al.* (1980); Nouri-Ghanbalani (1977)

[a] Phenological resistance related to late flowering and pod setting was reported in one accession

ous effects of plant resistance traits on insect development, population dynamics, and behavior and/or measuring the effect of insects on plant yield and quality (Tingey, 1986; Smith, 1989). These general approaches have been used by grain legume researchers, as well. For example, resistance has been evaluated in terms of insect feeding and oviposition preferences (Clement, unpubl. data; Pesho *et al.*, 1977; Pillsbury, 1986), insect infestation levels (Wolfenbarger & Sleesman, 1961, 1963; Lateef, 1985; El-Defrawi *et al.*, 1991), and through the effects of plants on insect development, survival, and fecundity (Birch & Wratten, 1984; Holt & Birch, 1984; Sehgal *et al.*, 1987; Soroka & Mackay, 1991). Visual rating scales based on percentages or numerical ratings of damage have been used routinely to measure plant susceptibility to insect attack (Wolfenbarger & Sleesman, 1961, 1963; Nouri-Ghanbalani, 1974, 1977; Lateef & Reed, 1985; Semenova, 1990; Weigand, 1990; El-Din Sharaf El-Din, unpubl.; Weigand & Pimbert, in press). Resistance also has been expressed in terms of the effect of insect injury on plant development, yield, and seed quality (Nouri-Ghanbalani, 1974, 1977; Pesho *et al.*, 1977; Lateef, 1985; Chopra & Pajni, 1987; Tahhan & van Emden, 1989). Under field conditions, these researchers have used a variety of methods to measure and compare insect population levels on plants, namely direct observation, sweepnet and vacuum sampling, and trapping. The specific sampling method used depended upon the insect species and crop plant (including growth stages) being sampled and other factors such as available resources and the amount of material being evaluated.

Microanalytical methods like capillary gas chromatography-mass spectrometry offer promise as a more rapid way to differentiate between insect-resistant and susceptible plant material. However, before researchers can use this method to screen germplasm and breeding lines for insect susceptibility they must have knowledge of the specific phytochemical stimuli that mediate the behavior of a target pest. These biochemical determinants of resistance are usually identified via basic studies on the host-selection behavior of insect pests. While much has been written about the importance of such research in host-plant resistance work (e.g., Beck & Schoonhoven, 1980; Kogan, 1986), little attention has been given to this area of research by grain legume researchers. Indeed, we know of only one case in which insect resistance in grain legumes has been correlated with specific phytochemicals. This information emerged from collaborative work by entomologists at ICRISAT and chemists at the Max-Planck Institute for Biochemistry, Munich, Germany, on the host-selection behavior of *H. armigera* and the biochemical basis of resistance in chickpea germplasm to this pest (Rembold, 1981; Rembold *et al.*, 1990a,b). These investigators related *H. armigera* resistance in chickpeas to relatively high amounts of malic and oxalic acids (Rembold *et al.*, 1990b). Research is now underway at the International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria, to assess the role of malic acid in chickpea resistance to the leafminer, *L. cicerina* (Weigand, 1990). More recently, capillary gas chromatography revealed the presence of major volatile compounds in the headspace surrounding pea flowers, some of which may be unique to flowers from genotypes varying in their susceptibility to pea weevil (*B. pisorum*) attack (Clement *et al.*, 1991; Fellman and Clement, unpubl.). With more research, this preliminary work may lead to methodology for the rapid quantitative and qualitative screening of pea germplasm for phytochemicals that mediate the host-selection behavior of *B. pisorum*.

Storage pests

Laboratory tests have been conducted several times to assess variation in susceptibility of seed of cultivated chickpea and wild *Cicer* spp. to the weevils *Callosobruchus chinensis* (L.) and *C. maculatus* (F.) (Raina, 1971; Schalk *et al.*, 1973; ICRISAT, 1976; Salunkhe & Jadhav, 1982; Ahmed *et al.*, 1989; Weigand & Tahhan, 1990; Weigand & Pimbert, in press). On the other hand, there have been few searches for *C. chinensis* (Ishii, 1952) and *C. maculatus* (Fam & El-Sayad, 1985) resistance in seed of faba bean germplasm.

Researchers usually differentiated between resistant and susceptible chickpea and faba bean seed on the basis of ovipositional preference, adult emergence, percentage of damaged or weevil infested seed, insect developmental periods, and/or reproductive capacity of females exposed to seed of different cultivars. Several workers have reported that chickpea cultivars with rough, hard, and wrinkled seedcoats were least preferred by *Callosobruchus* weevils (Raina, 1971; Schalk *et al.*, 1973; ICRISAT, 1976; Salunkhe & Jadhav, 1982; Ahmed *et al.*, 1989; Weigand & Pimbert, in press). However, such "unsightly" seeds may be unacceptable to consumers (Weigand & Pimbert, in press).

Mechanisms and stability of resistance

There is now ample evidence that pest populations have the ability to evolve and overcome specific plant resistance factors. When this happens, pest-resistant crops will lose their ability to resist insect attack. To slow pest evolution and thus prolong the useful life of insect-resistant cultivars, some entomologists have suggested (Kennedy *et al.*, 1987; Smith, 1989; Gould, 1991) that resistance breeding programs place more emphasis on: the breeding of insect-resistant cultivars with more than one type of resistance; the deployment of crop cultivars with partial resistance to insect pests; and the development and use of tolerant crop cultivars. For example, a new cultivar with genes conferring resistance at both the behavioral (antixenosis) and physiological (antibiosis) levels might last much longer in the field than a cultivar possessing only one type of resistance. Intuitively, exposure of pest insects to plants exhibiting strong antibiosis and antixenosis resistance would subject them to intense selection pressure, with subsequent development of resistance-breaking insect biotypes (Smith, 1989); therefore, the effect of partial resistance in cultivars and deployment of tolerant crop cultivars would be less selection pressure on pest populations (Lamberti *et al.*, 1983; van Emden, 1991).

Using specific assays to monitor the effects of particular physical and chemical plant traits on insect behavior and physiology, as well as inferences drawn from the results of initial screenings and evaluations, researchers have differentiated between the antixenosis, antibiosis, and tolerance categories of plant resistance to insect pests of grain legumes. To date, however, more antibiosis than antixenosis or tolerance has been reported in grain legumes. There are also documented cases in which pulse genotypes avoided insect attack or suffered less damage than other entries because of phenological asynchrony, i.e., ecological resistance as defined by Kogan (1982) (Table 3).

Where multiple types of resistance (tolerance, antixenosis, antibiosis) are reputed to be associated with pulse resistance to insects, breeders may be able to circumvent the breakdown of plant resistance by releasing cultivars with multiple types of insect resistance. However, this strategy might not work against the pea aphid (*P. pisum*) because of its ability to develop resistance-breaking biotypes (Reed *et al.*, 1988). On the other hand, the breeding of chickpea cultivars with polygenic resistance combining insect repellency (antixenosis), toxicity (antibiosis), and tolerance would likely slow the breakdown of plant resistance to *H. armigera*, and possibly to other chickpea insect pests as well (Pimbert, 1990). Moreover, Reed *et al.* (1988) were of the view that resistance to *H. armigera* in chickpea is likely to be stable, in part because of the polygenic nature of the resistance. This polygenic resistance is based on the discovery of all three types of genetic resistance in chickpea (Table 3), which gives

Table 3. Status of types of plant resistance reportedly involved with insect resistance in grain legumes[a]

Crop and insects	Ecological resistance[b]	Categories of genetic resistance[b]		
		Antixenosis	Antibiosis	Tolerance
Chickpea				
Callosobruchus maculatus (F.)		+	+	
Helicoverpa armigera (Hüb.)	+	+	+	+
Faba bean				
Aphis craccivora (Koch)			+	
Aphis fabae Scop.			+	
Acyrthosiphon pisum (Harris)			+	
Megoura viciae (Buckt.)			+	
Empoasca fabae (Harris)		+	+	
Bruchus dentipes Baudi	+			
Callosobruchus chinensis (L.)			+	
Callosobruchus maculatus (F.)			+	
Epilachna varivestris Muls.		+	+	
Pea				
Acyrthosiphon pisum (Harris)[c]		+	+	+
Bruchus pisorum (L.)		+	+	
Sitona lineatus (L.)			+	+
Cydia nigricana (F.)[c]	+			
Chromatomyia horticola (Goureau)		+	+	
Lentil				
Bruchus lentis Froel.	+			

[a] Information compiled from references listed in Table 1
[b] Types of resistance as defined by Kogan (1982)
[c] Resistance found in dry and/or green pea cultivars

breeders the option of creating combinations of resistance factors in a single cultivar.

In addition, both antixenosis and antibiosis resistance have been detected in germplasm evaluated against the field pests *E. fabae*, *E. varivestris*, *C. horticola*, and *B. pisorum* (Table 3). However, until more details about the nature of plant resistance to the first three species are forthcoming there is little reason to discuss the deployment of different resistance modalities in resistance breeding. Pesho *et al.* (1977) detected antixenosis resistance in peas to *B. pisorum* in the United States; however, this resistance did not hold up under field conditions in Chile and Australia (Clement, unpublished information; Hardie, 1990). Apparently, the effects of chemical antixenosis were not strong enough to substantially decrease weevil oviposition on pods of the nonpreferred pea lines. There is, however, room for optimism concerning the use of plant resistance against *B. pisorum* and it is based on Hardie's (1990) recent discovery that a wild line of *Pisum sativum* ssp. *humile* (= ssp. *elatius* var. *pumilio* [van der Maesen *et al.*, 1988]) responded to the presence of pea weevil eggs on pods by forming callus. If it can be shown that this pod callus inhibits the development of eggs or impedes larval penetration of the pod wall, Hardie's (1990) discovery may represent a new type of antibiosis-based resistance against pea weevil. A similar reaction against pea weevil oviposition was first reported by Annis & O'Keeffe (1984) for pods of *Lathyrus* spp. Efforts to increase levels of plant tolerance and antibiosis resistance in peas to *S. lineatus* (Table 3) were not always successful (Nouri-Ghanbalani *et al.*, 1978; Auld *et al.*, 1980), leading to a cessation of breeding efforts against this pest in the western United States.

Only antibiosis resistance, and some of it in the form of partial resistance, has been found in faba bean cultivars and related *Vicia* species against the aphids *A. craccivora*, *A. fabae*, *A. pisum*, and *M. viciae* (Table 3). Although Holt & Birch (1984) considered the usefulness of partial resistance to aphid pests of faba beans, they viewed the incorporation of high levels of antibiosis from wild *Vicia* species into faba bean cultivars as a longer term solution to the development of virulent, resistance-breaking aphid biotypes.

Although sources of antixenotic- and antibiotic-based resistance to storage pests in the genus *Callosobruchus* have been found in chickpea and faba bean seed (Table 3), some researchers (Bushara, 1988; Reed *et al.* 1988; Pimbert, 1990) have not expressed confidence in host-plant resistance as a feasible strategy to control these weevils. Their reservations have centered around the fact that relatively few sources of weevil resistance in pulse seeds have been found, despite the many attempts made. Rather than aggressively pursuing weevil resistance in pulse seeds, Reed *et al.* (1988) and Pimbert (1990) suggested it may be more productive to work towards improving seed storage conditions and improving other control methods for storage pests. We would only add that the recent discovery of *Callosobruchus* resistance in seed of wild *Cicer* (Weigand & Tahhan, 1990; Weigand & Pimbert, in press) suggests the need for more evaluations of secondary and tertiary gene pools for seed resistance to storage pests.

Host-plant resistance in pest management

Host-plant resistance can serve both as a principal pest management method and as a complementary pest control method in integrated pest management systems (Kogan, 1982). The latter approach clearly has been embraced by chickpea entomologists at ICARDA and ICRISAT (Reed *et al.*, 1987; Lateef, 1990; Lateef & Pimbert, 1990; Pimbert, 1990). In addition, statements in the literature (Holt & Birch, 1984) and workshops on specific pests (National Pea Weevil Workshop, Victoria, Australia; Smith, 1990) indicate that entomologists working on insect pests of other grain legumes plan to deploy host-plant resistance as part of integrated control programs. Indeed, traditional methods of pest control, such as the use of insecticides, are often impractical and uneconomical for grain legume producers, especially in the developing countries (Singh *et al.*, 1990). Moreover, "other factors such as toxicity, environmental pollution, the extermination of natural enemies, and eventually, build-up of insecticide resistance in the pests make chemical control a risky strategy" (Lateef, 1990). Hence the need for more sustainable approaches to managing insect pests of grain legumes.

The potential interactive role of plant resistance and classical biological control in managing insect pests of grain legumes has been addressed by some researchers. For example, Annis & O'Keeffe (1987) investigated the influence of pea genotypes on parasitization of the pea weevil (*B. pisorum*) by a pteromalid wasp in the western United States. Other investigators (Kareiva & Sahakian, 1990) studied the interaction of plant resistance and biological control in peas by assessing the effect of plant morphology on the population growth of pea aphids (*A. pisum*) in the presence and absence of coccinellid beetle predators. What they found was that the predators were more effective at controlling aphid populations on leafless as opposed to normal-leafed peas. Soroka & Mackay (1990a) also found fewer pea aphids on more architecturally simple pea plants but they attributed their findings to the increased vulnerability of aphids on semi-leafless plants to adverse weather and to the reduction of leaflets, which allowed for less preferred space for aphid population development. The work of Karieva and Sahakian (1990) and Soroka & Mackay (1990a,b,c) in the United States and Canada suggests it would be prudent to consider the effects of plant morphology on insect predators and pea aphid populations if breeding efforts are directed towards the development of semi-leafless or leafless types. More examples of research on the integration of plant resistance with biological control can be found in Weigand *et al.*, 1993. These researchers also addressed the potential interplay of plant resistance with cultural and chemical control methods in the development of integrated control programs in grain legumes.

Largely unexplored by pulse entomologists are the effects that different types and levels of plant resistance could have on the success or failure of chemical and biological control methods. The importance of this aspect in breeding for insect resistance in crops was pointed out by van Emden (1991), Kennedy *et al.* (1987) and Smith (1989).

Prospects

This chapter is testimony to the many advances made in plant resistance to insect pests of cool season food legumes by entomologists and plant breeders, who through their interests and energy have developed plant screening methods, located insect resistance in germplasm, and characterized mechanisms of resistance. With new progress by interdisciplinary, mission-oriented research teams at ICARDA and ICRISAT, we have reason to be optimistic about the future development of insect-resistant grain legumes, especially chickpeas for the developing countries. For example, entomologists and chemists have learned much about the biochemical bases of resistance in *Cicer* to *H. armigera* and *L. cicerina* and the factors governing the host-selection behavior of these major insect pests (Pimbert, 1990; Rembold *et al.*, 1990a,b). Moreover, research begun by ICRISAT breeders and entomologists after the discovery that most *Helicoverpa* resistant chickpea lines were highly susceptible to Fusarium wilt and Ascochyta blight has led to the successful combination of pod borer and Fusarium wilt resistance in chickpea lines ICCL 8611 and ICPX-730020-11-1-1H (Lateef, 1985, 1990; Lateef & Sachan, 1990; Singh *et al.*, 1990). Team research like this must continue. Moreover, it must be expanded to include molecular biologists who can apply new biotechnological innovations to the development of insect-resistant cultivars of cool season food legumes.

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