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The *Helicoverpa* problem in Australia

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***Helicoverpa* biology and ecology**

There are 2 *Helicoverpa* species of agricultural importance in Australia, the old-world pest *Helicoverpa armigera* Hubner and the endemic *Helicoverpa punctigera* Wallengren. Though closely related and similar in appearance, the two species differ in their distributions, seasonal abundance and feeding preferences (Zalucki *et al.*, 1986; Fitt *et al.*, 1989). The pest status of these two species derives from a suite of physiological, behavioural and ecological characteristics, which enable them to survive in unstable habitats and in turn, to successfully colonise and exploit agricultural systems. The four major characteristics which contribute to *Helicoverpa* spp. pest status: polyphagy, high mobility, high fecundity and a facultative diapause, are discussed extensively in Fitt (1989). Adult movement at scales ranging from a single field to geographic regions is crucial to the dynamics of *Helicoverpa* populations and requires that both research and effective management adopt a regional approach.

Distribution, seasonal abundance, population dynamics

Both *H. armigera* and *H. punctigera* are widely distributed across much of Australia, though varying markedly in abundance. *H. punctigera* is common throughout mainland Australia, including the semi-arid inland areas, and regularly reinvades Tasmania. *H. armigera* is more common in eastern Australia, particularly in cropping

regions, and in northern Australia and declines in abundance towards the south. Nevertheless *H. armigera* does extend into the arid inland and can be found in low numbers on several native plants (Zalucki *et al.*, 1994).

There are considerable differences in the seasonal dynamics of the two species in cropping areas of eastern Australia (Wardhaugh *et al.*, 1980; Wilson, 1983; Fitt, 1989). In southern Queensland and much of New South Wales *H. armigera* passes through 4-5 generations per season and passes the winter in a pupal diapause (Fitt, 1989; Fitt and Daly, 1990). During the summer sub-populations will develop through a first generation on spring weeds, winter legumes (chickpea) and on early sown sorghum or sunflower. At this time populations are relatively synchronised, but later in the summer considerable overlap of generations occurs. The next 2-3 generations may occur on cotton, although sub-populations will also be breeding on sorghum, sunflowers, maize and legumes over the summer. Hence at any one time the *H. armigera* population will occur as a complex mosaic of sub-populations developing on many host plants, at slightly different rates, with differing levels of mortality and fitness effects on future fecundity and with considerable adult movement linking all sub-populations (Dillon *et al.*, 1996).

The seasonal pattern for *H. punctigera* is markedly different and is tied to rainfall patterns over wide areas of Australia (Maelzer and Zalucki 1999, Oertel et al 1999).

In some areas of Australia, the phenology of *H. punctigera* is understandable only by invoking substantial migratory movement. In South Australia, *H. punctigera* is rare during autumn, when there are few larval hosts, but reappears each spring. Overwintering populations of *H. punctigera* are extremely difficult to locate in the irrigated cropping areas of northern New South Wales and south-east Queensland

where the overwintering populations are almost exclusively *H. armigera* (Fitt and Daly, 1990). Despite this, large numbers of *H. punctigera* reappears in these regions each spring. as massive migrations from inland Australia recolonise the cropping regions (Gregg *et al.*, 1995). These spring migrations generate breeding populations of *H. punctigera* on spring weeds and early crops of chickpea and canola, before moving to cotton and other crops in late spring/ early summer. It then progressively declines in abundance and becomes the minor species during the second half of the summer (Wardhaugh *et al.*, 1980; Wilson, 1983; Fitt, 1989; Maelzer and Zalucki 1999). This decline in population density, the scarcity or absence of overwintering populations of *H. punctigera* in many cropping areas and the near simultaneous appearance of large numbers in several areas each spring (September/October) all argue for migration as an important component of the life-history strategy of this species. The extent of winter breeding on ephemeral native plants (Zalucki *et al.*, 1994) and hence the magnitude of spring migratory events is determined by the timing and extent of autumn rainfall through particular regions of arid inland Australia (Oertel *et al.*, 1999) and to broad scale climatic patterns such as the SOI (Maelzer and Zalucki 1999, 2000). As a result it is possible, although logistically difficult, to forecast long distance movements (Rochester *et al.*, 1996) or dynamics (Maelzer and Zalucki 2000).

While long distance movement certainly occurs in *H. armigera* (Daly and Gregg, 1985), it is probably a less frequent occurrence and populations of this species may be influenced more by local cropping and climatic conditions (Fitt, 1989, Maelzer and Zalucki 1999). It is almost certainly a facultative migrant (Daly and Gregg, 1985), and being more closely associated with cropping areas than *H. punctigera*, *H.*

Field Code Changed

armigera may rarely experience the widespread deterioration of breeding habitat needed to induce regular mass movements. Nevertheless, the absence of significant genetic differentiation between widely separated subpopulations of *H. armigera* (Daly and Gregg, 1985) suggests that gene flow occurs over much of eastern Australia at least.

Field Code Changed

H. punctigera provides an excellent example of a strategy of diapause and movement well suited to a highly unpredictable environment. In subtropical and temperate areas of eastern Australia a small proportion of the population enter a facultative winter pupal diapause, but some survive the winter as non-diapausing individuals, emerging before the bulk of the diapausing population. At the same time the bulk of the population occurs throughout inland Australia breeding on patches of ephemeral plants. A proportion of the first generation of *H. punctigera* may then enter a spring diapause, from which adults emerge during early summer (D.A.H. Murray pers. comm), at the time the second generation normally emerges. This strategy is adaptive in the unpredictable environment found in Australia, by ensuring that a proportion of the population will survive unsuitable late spring conditions. Some *H. punctigera* may also enter a high temperature induced summer diapause during January, delaying their emergence until late summer/early autumn. The mobility of *H. punctigera*, combined with its wide host range, and complex diapause behaviour allow it to cope with highly varying local conditions and greatly complicates its dynamics in cropping areas. At any one time the effective gene pool, which is large (Daly and Gregg, 1985), may well consist of many sub-populations on different cultivated and uncultivated hosts, some breeding year round, others in varying types of diapause, all linked by, at times, extensive movements.

The ecological differences outlined above result in populations of *H. armigera* being more consistently associated with cropping areas and hence exposed to pesticide selection, than is *H. punctigera*. Consequently, *H. armigera* has consistently developed resistance to pesticides (Forrester *et al.*, 1993), whereas *H. punctigera* has never evolved resistance to synthetic pesticides. For these reasons, *H. armigera* is the focal species for resistance management strategies deployed to manage this resistance risk for new pesticides (Forrester *et al.*, 1993) and for transgenic crops (Fitt, 2003).

Selection for resistance to pesticides will occur whenever they are used, but the rate at which resistance genes increase in frequency in a population is determined by the balance between selection and dilution through gene flow from other sub-populations (Daly, 1994). Cotton, by virtue of its long growing season will support 2-3 generations of *H. armigera* and selection for resistance may be significant. Individual sowings of almost all other crops (sorghum, maize, sunflower, legumes) support only a single generation of *Helicoverpa* before senescing and so impose only one generation of selection per crop. However, the potential for multiple or staggered plantings of these crops over the season combined with the long growing season of cotton could result in selection of several successive generations. This scenario has already occurred with conventional pesticides where for example the use of synthetic pyrethroids (SP) on sorghum (often at low rates for sorghum midge control) is thought to have contributed greatly to the evolution of pyrethroid resistance in *H. armigera* (Daly and Murray, 1988). Inadvertent selection of a large part of the *H. armigera* population occurred on extensive areas of sorghum, combined with intense selection on cotton where SP's were heavily used, led to the appearance of SP resistance within 5 years of their release in Australia (Forrester *et al.*, 1993).

Host range, host selection and feeding preferences

Both *Helicoverpa* species are highly polyphagous. In Australia alone *Helicoverpa armigera* has been recorded on over 100 plant species from 36 families, whilst *H. punctigera* has been recorded on over 200 plant species from 47 families (Matthews, 1999). Hosts of *Helicoverpa* spp. include nearly all the major field crops in Australia: cotton, sorghum, maize, sunflowers, chickpeas, lupins and most other legumes, lucerne, tobacco and wheat. In addition horticultural crops such as tomatoes, lettuce, capsicum and sweetcorn, and flowers such as chrysanthemums and roses suffer high rates of damage (Matthews, 1999).

Despite their wide host range there are clear differences between the species. *H. armigera* feeds on both dicotyledonous and monocotyledonous plants whereas *H. punctigera* occurs only on dicotyledonous plants. *H. armigera* is also much more closely associated with cultivated crop hosts than with native host plants and its dynamics are largely determined by patterns in agriculture. By contrast *H. punctigera* feeds on a wide range of native, ephemeral hosts across large parts of inland Australia. There is some evidence for geographic variation in host plant preference (Firempong and Zalucki, 1990a), but the underlying population genetics of host range are yet to be examined (check).

Host selection in the field is primarily determined by ovipositing females, though older larvae will move to other plants once the current host becomes unsuitable (Zalucki *et al.*, 1986). Early work on host plant preference focused on the hierarchy of preference displayed by females when presented with different plant species

(Firempong and Zalucki, 1990a; Jallow and Zalucki, 1995; Butter and Singh, 1996). In the first of these studies, moths were provided with 9 different plant species, from 8 families, all of which were known to be hosts of *H. armigera* (Firempong and Zalucki, 1990a). Eggs counts were used to determine females' ovipositional preference. Two different assays gave reasonably consistent results when tested with a laboratory population of *H. armigera* in that the top three and lowest three ranking plant species were the same (Firempong and Zalucki, 1990a). By testing *H. armigera* populations from different geographic locations it was shown that there was variation in the ranking of host plants between populations. In some cases the most popular host was the most abundant crop in the area suggesting the possibility of host races. However, in three of the five cases the most popular plant species was also the plant from which the tested individuals had been collected which could have influenced adult host preference.

Other factors can affect this hierarchy such as plant abundance (Papaj and Rausher, 1987; Cunningham and West, 2001), plant height (Sequeira and Moore, 2003) and phenology (Firempong and Zalucki, 1990b), previous experience the female may have had with the host (Cunningham *et al.*, 1998a) and her current egg load (Jallow and Zalucki, 1998).

Female moths are thought to use various physical and chemical cues during oviposition to determine the suitability of the host plant (Fitt, 1991). For example, hairy or rough surfaces are thought to be preferable for egg laying (Zalucki *et al.*, 1986). Plant phenology is also important. As peak egg laying is concurrent with peak flowering in many crops (Zalucki *et al.*, 1986), it may be that flowering plants represent a higher quality food source for offspring than pre-flowering plants. This

seems likely as larvae feed preferentially on fruiting bodies once they become available (Matthews, 1999).

A study examining the oviposition behavior of females in response to extracts of cotton flowers and leaves found that females were more attracted to flower extracts than leaf extracts from flowering or non-flowering cotton plants (Jallow *et al.*, 1999). This suggests that it is the flowers themselves that the females are responding to rather than the state of the plant. The attraction to flowers may be due some chemical cue present in flowers that informs the female of the host suitability. Alternatively, females may be primarily attracted to flowering plants as a source of nectar. The availability of a food source increases female fecundity and mating frequency (Zalucki *et al.*, 1986) and so increased oviposition may be coincidental. However, the flowers on some host plants (e.g. cotton) are closed at night when *Helicoverpa* oviposition occurs. Moreover, extra-floral nectaries present on the leaves provide a food source in both flowering and pre-flowering plants. Therefore, for some hosts at least it seems unlikely that the availability of nectar alone is enough to explain the increased oviposition on flowering plants.

Recent studies have found evidence of learning in host selection and nectar foraging behaviour in *H. armigera* (Cunningham *et al.*, 1998a; Cunningham *et al.*, 1998b; Cunningham and West, 2001). Experience with a host increased the likelihood that that host would be selected for oviposition at a later date (Cunningham *et al.*, 1998a). Similarly, experience with a flowering host species increases the probability of that species being selected for nectar foraging, and it increases the *efficiency* of foraging on that host (Cunningham *et al.*, 1998b). It may be these factors in conjunction that

cause high levels of oviposition on flowering plants in the field.

Females lay eggs singly, or in groups of 2 or 3, on flowers, fruiting bodies, growing tips and leaves. During their two-week life span females will lay approximately 1400 eggs (Zalucki *et al.*, 1986). Whilst neonates will eat leaves, flowers and fruiting bodies are preferred feeding sites and larvae will move to these sites as they become available. In this way high levels of economic damage to crops can be sustained by relatively low numbers of larvae (Matthews, 1999).

Extent of damage from *Helicoverpa*

Crops vary widely in their attractiveness to *Helicoverpa* and in their ability to tolerate damage, either physically or economically. Fitt (1997) provides an analysis of the costs of control for *Helicoverpa* across the major field crops where *Helicoverpa* is the major insect pest (cotton, sorghum, tomato, sweet corn, chickpeas, field peas, navy beans, mung beans). While costs have increased considerably since 1997 (eg. *Helicoverpa* control in cotton averaged \$325/ha for the 5 years up to 1996, but \$562/ha for the 6 years after that), the relativities between crops probably remain informative. Among those crops cotton accounts for 56% of the total value of production and some 65% of the *Helicoverpa* control costs. *Helicoverpa* represents the target for 80% of the pesticide sprays, although transgenic Bt cotton has dramatically changed that situation (see later).

Cotton is particularly susceptible because of its long growing season during which 3-4 generations of *Helicoverpa* (*punctigera* and *armigera*) may attack the crop and being a valuable crop the value of damage is high. Over the 6 years from 1996/97 to

2002/03 conventional cotton crops in Australia averaged 8 pesticide sprays for *Helicoverpa* (10.6 sprays in total) and incurred insect control costs of A\$562/ha or approximately \$282 million per annum in control costs and residual damage, in addition to unquantified environmental costs. By contrast sorghum is attacked only once during development, with only 50% of the total hectares requiring even one spray in most years. Vast areas of sorghum are never sprayed for *Helicoverpa* and average *Helicoverpa* control costs in 1997 were only \$37/ha. Three crops: cotton, tomato and sweet corn, have persistent high levels of damage from *Helicoverpa* and require multiple applications of pesticide. In sorghum and corn (both field corn and sweet corn) *H. armigera* is the sole *Helicoverpa* species present, while in all other crops both *H. punctigera* and *H. armigera* may occur. Of the legumes, field peas and chickpeas are spring flowering crops grown most extensively in southern, and more recently in western, Australia where they receive sporadic damage from populations of predominantly *H. punctigera*. On average these legume crops may require only a single pesticide application.

Management of *Helicoverpa* Infestations

Historically pest management on many crops has relied largely on synthetic insecticides, although some biological approaches are also utilised (Fitt, 1994; 2000). Management thresholds have been defined for many crops, although these rarely reflect economic factors and often ignore plant compensatory capacity. Dependence on pesticide intervention brings with it several environmental and economic liabilities, including the development of insecticide resistance in key pests and secondary pests, reductions in beneficial insect populations with associated secondary

pest outbreaks, potential for environmental contamination and cost. In high input crops such as cotton, pest management now accounts for 35-40% of the variable costs of production (\$400-\$1000/ha) (Fitt, 2000).

Beneficial insects (predators and parasitoids) clearly play an important role in management of *Helicoverpa*, particularly in low value crops where they may remove the need for any chemical intervention. Likewise in high value crops (cotton, tomatoes) beneficial species provide considerable benefit but are unable to provide adequate control alone, particularly in situations where migratory influxes of *Helicoverpa* result in significant infestations (Fitt, 1989). Predators and parasitoids are unable to respond rapidly in such situations.

Over the last 5 years adoption of IPM approaches has expanded dramatically in Australian cotton production and in some other crops where “soft option” pesticides are now widely available. A set of IPM Guidelines is now freely available on the Australian Cotton CRC Website at <http://cotton.pi.csiro.au/Publicat/Pest/>, together with a set of 12 supporting documents, on-line insect identification aids and the computer based decision support aid CottonLOGIC (Hearn and Bange, 2002). The IPM Guidelines and CottonLOGIC provide practical approaches for producers and consultants and reflect the current state and Australian IPM research (Fitt, 2000; Wilson *et al.*, 2004), which emphasizes the integrated use of plant compensation, host plant resistance, beneficial insects, habitat complexity and selective pesticides. Two more detailed examples of current research on *Helicoverpa* management – transgenic Bt cotton and conventional host plant resistance in chickpeas - are provided later, although they represent only a small proportion of current research activity on this

pest.

The adoption of IPM in cotton has been facilitated by extensive grower education and training, through on-farm demonstration and through the increasing availability of more selective pesticides and transgenic crops which are compatible with IPM. This change has seen dramatic reductions in the volume of active ingredient applied to cotton (70-80% on both conventional and Bt cotton), although costs have increased due to the expenses of the new generation of pesticides.

Current research

Transgenic Bt cotton

Cotton is a significant primary industry for Australia with some 500,000 ha grown, producing 3.0 to 3.4 million bales annually. Over 90% of production is exported as raw lint making cotton the third largest crop export and Australia the fourth largest player in the world export market. Yields and fibre quality are among the world's highest (Hearn and Fitt, 1992).

To reduce problems of pesticide dependence the Australian cotton industry is increasingly committed to Integrated Pest Management (IPM) (Wilson *et al.*, 2004). Genetically engineered cottons expressing the delta-endotoxin genes from *Bacillus thuringiensis* subsp. *kurstaki* (Bt) offer great potential to dramatically reduce pesticide dependence for control of the major Lepidopteran pests and consequently offer real opportunities as a component of sustainable and environmentally acceptable IPM systems.

Bt cotton varieties have now been commercialised in nine countries worldwide: USA, Australia, China, India, Indonesia, Argentina, Mexico, South Africa and Colombia (James, 2002). Australian Bt cottons (tradename INGARD®) utilise the CryIAc gene from Monsanto. INGARD® varieties were first registered in 1996 when a limited commercial release was approved, following a comprehensive risk assessment (Fitt and Wilson, 2002; Fitt, 2003) under the auspices of regulatory bodies (Genetic Manipulation Advisory Committee [GMAC] and Office of the Gene Technology Regulator [OGTR]).

Fitt (2003; 2004) provide a comprehensive assessment of the impact of Bt cotton in Australia over the first six years of commercial use. A considerable body of research in Australia has confirmed that efficacy of cotton varieties expressing CryIAc is not consistent through the growing season and can be highly variable (Fitt, 1994; Fitt *et al.*, 1998). Efficacy against *Helicoverpa* spp. typically declines through the boll maturation period, to the point where survival of larvae is little different to that in non-transgenic cotton (Fitt *et al.*, 1994; Fitt *et al.*, 1998), although growth rates of survivors on the INGARD® crops are still dramatically reduced (Fitt unpublished). The decline in efficacy necessitates supplementary *Helicoverpa* control on INGARD® crops, particularly in the last third of the growing season.

Despite this growers have learned to manage INGARD varieties and substantial reductions in pesticide use on Bt cotton. For *Helicoverpa*, there have been consistent reductions in the number of sprays applied to INGARD® crops compared to conventional crops, averaging 56% and ranging from 43% (1998/99) to 80% (2001/02). For the minor pest groups there has been no significant change in pesticide

applications after 6 years.

The most consistent “winner” from INGARD® technology to date has been the environment, with reduced pesticide loads, while the cotton industry has gained long term sustainability through the progressive adoption of more integrated pest management approaches using INGARD® cotton as a foundation. In the first 4 years of commercial use there was little economic benefit from Bt cotton but in the last two years (2000/01 and 2001/02) net economic returns from INGARD® varieties have been over \$300/ha higher than for conventional varieties. This reflects the progressive improvement in varietal performance, growing experience of growers and consultants in managing INGARD® cottons and the lighter pest pressure experienced in those years. Nonetheless intangibles due to reduced environmental impact and enhanced sustainability are yet to be evaluated.

Resistance Risk and Management Requirements. The major challenge to sustainable use of transgenic Bt cottons is the risk that target pests may evolve resistance to the CryIAc protein. *H. armigera* is a particular resistance risk having consistently developed resistance to synthetic pesticides in the past (Fitt, 1989; Forrester *et al.*, 1993; Fitt, 1994). For this reason a pre-emptive resistance management strategy was implemented to accompany the commercial release of transgenic varieties (Roush *et al.*, 1998). The strategy, based on the use of structured refuges to maintain susceptible individuals in the population (Roush *et al.*, 1998), seeks to take advantage of the polyphagy and local mobility of *H. armigera* to achieve resistance management by utilising gene flow to counter selection in transgenic crops. By contrast, extensive

natural refuges effectively nullify the resistance risk in *H. punctigera*. Indeed *H. punctigera* provides an excellent natural example of the capacity of the refuge strategy to reduce resistance risk

Key elements of the INGARD® cotton strategy are:

- effective refuges on each farm growing INGARD® cotton
- defined planting window for INGARD® cotton to avoid late planted crops that may be exposed to abundant *H. armigera* late in the growing season
- mandatory cultivation of INGARD® crops to destroy most overwintering pupae of *H. armigera*
- removal of volunteer INGARD® plants
- defined spray thresholds for *Helicoverpa* to ensure any survivors in the crops are controlled
- monitoring of Bt resistance levels in field populations

Refuge options have been defined from research that quantifies the value of different options in generating moths (eg. Fitt and Tann, 1996) and ranks potential refuges in relation to unsprayed conventional cotton, regarded as the “control” refuge. Australian growers can currently choose from 5 different refuge options (sprayed conventional cotton, unsprayed cotton, sorghum, maize or pigeon pea) each with a different area determined by the relative productivity of the refuge. Refuge crops cannot be treated with Bt sprays, and must be in close proximity to the transgenic crops (within 2 km) to

maximise the chances of random mating among sub-populations (Dillon *et al.*, 1998).

An additional element of the strategy was a phased introduction of INGARD® varieties and a cap on the area at 30% of the total cotton area. In their first year INGARD® varieties were grown on 30,000 ha representing about 8% of the total cotton area in that year. After that the area increased in 5% increments each year up to the 30% cap. BOLLGARD II™ varieties with two Bt genes (Cry IAc, Cry 2Ab) have now been approved for commercial use and occupy about 5,000 ha in 2002/03. The two gene varieties provide much better efficacy and hence even greater reduction in pesticide requirement, but their main purpose is to provide much greater resilience against the risk of resistance (Roush, 1998). A rapid transition to BOLLGARD II™ is planned, with INGARD® varieties likely to be withdrawn after the 2003/04 season.

Transgenic Bt cotton as a foundation for IPM. INGARD® and BOLLGARD II™ cotton varieties are not perceived as “magic bullets” for pest control in Australia. Instead they are viewed broadly as an opportunity to address environmental concerns about cotton production and more specifically as a foundation to build IPM systems which incorporate a broad range of biological and cultural tactics (Fitt, 2000; Wilson *et al.*, 2004). Research has shown little effect of Bt cottons on non-target species, including non-lepidopterous pests, beneficial insects, and other canopy dwelling and soil dwelling species (Fitt & Wilson 2000?)(Fitt, 2000; Fitt and Wilson, 2002). Survival of beneficials is markedly higher than in conventional sprayed cotton, and they provide control for some secondary pests, particularly those that are induced pests in sprayed cotton (eg. mites and aphids).

Screening wild *Cicer* for *Helicoverpa* resistance

Developing crop varieties with resistance to *Helicoverpa* is one approach to reducing the economic and environmental costs of infestation. Host plant resistance can occur by three non-mutually exclusive mechanisms. Antixenosis, or non-preference, denotes plant characteristics that discourage juvenile or adult insects from either feeding or ovipositing on the plant. Antibiosis occurs when the insect's survival, development or reproduction is adversely affected by its interaction with the plant. Tolerance is the mechanism that allows the plant to grow and reproduce under conditions of insect infestation that would be damaging to a susceptible plant (Smith, 1989).

There are a number of mechanisms that may contribute to insect resistance in chickpeas. Fine hairs, known as trichomes, cover the plant and may provide physical protection by making the leaf surface less accessible. In addition, glandular trichomes exude organic acids, notably oxalic and malic acid, which have been shown to correlate with insect resistance in certain genotypes. Screening of chickpea accessions in India identified several promising chickpea genotypes with resistance to *H. armigera* (Lateef, 1985). One of the more promising chickpea accessions, ICC 506 (Lateef, 1985) has also been tested for resistance to *H. punctigera* (Mann, 2001). It was shown that larvae and pupae reared on whole plants were smaller than those reared on the susceptible controls. Moreover, ICC 506 had the highest levels of organic acids present in its exudates. Incorporation of oxalic and malic acids into an artificial diet resulted in reduced larval growth for both compounds but the concentration at which oxalic acid became toxic was much lower than for malic acid

(Mann, 2001).

Despite the identification of moderately resistant chickpea accessions, levels of variation in insect resistance tend to be low. This is because many modern cultivars, which have been selected over many generations on the basis of yield and nutritional traits, have lost the insect resistance traits present in wild relatives (Clement *et al.*, 1999). For example, of the 7000 chickpea accessions that have been tested for insect resistance at ICARDA (International Center for Research in the Dry Areas) just 10 were found to be resistant or tolerant to insects (Clement *et al.*, 1999). In comparison, of the wild chickpea varieties tested, 30 out of 200 were found to be resistant to *Liriomyza cicerina*, and 51 out of 137 were resistant to *Callosobruchus chinensis*. Limited genetic variation for insect resistance in the cultivated chickpea *Cicer arietinum*, has led to the search for resistance amongst wild *Cicer* species.

A large number of accessions of wild *Cicer* species have been screened for resistance to *Helicoverpa punctigera* using a method modified from Olson and Daly (2000). Screening was conducted by placing neonate larvae on an excised branch of the accession to be tested. The cut end of the branch was inserted into water agar and larvae were left to feed for 5 days after which time the surviving larvae were weighed. This screening method revealed considerable inter-species variation in the suitability for *H. punctigera* growth (Figure 1a). *Cicer bijugum* appeared to be the least suitable overall as a host for *H. punctigera* and appeared to be significantly more resistant than the *Cicer arietinum* controls (Figure 1a).

Figure 1b shows the accessions on which growth rate was lowest and highest for each species. By comparing the range of growth rates in the accessions of wild species with

that of the control *Cicer arietinum* accessions, it can be seen that intraspecific variation is much higher in the wild species, suggesting that there are higher levels of genetic variation for insect resistance in the wild lines. By comparing the most resistant *C. arietinum* accession, ICC 506, with the wild accessions it can be seen that at least four of the wild lines showed considerably higher levels of resistance to *H. punctigera*. This technique allowed putative resistant and susceptible varieties from several species to be identified for further testing.

Several promising *Cicer bijugum* lines were screened for *Helicoverpa* resistance in field trials in Tamworth, (New South Wales, Australia) with naturally occurring *Helicoverpa* populations; *Cicer arietinum* lines were planted as controls. The numbers of damaged and undamaged pods produced by each plant were counted as a measure of insect damage. It can be seen from figure 2 that the *C. bijugum* accessions performed much better than the *C. arietinum* controls (T. Knights, unpublished data).

Screening of wild chickpea accessions in India has identified a number of potentially resistant *C. reticulatum* lines. This species is more closely related to the cultivated chickpea and hybridization is possible. Further work to elucidate the genetic basis of resistance in wild relatives of chickpea is currently underway.

The genetic basis of feeding ability in *Helicoverpa*

Although it is known that *Helicoverpa armigera* is a highly polyphagous species, the exact nature of this polyphagy is unclear. Is genetic variation in feeding preferences maintained within populations, or is there local adaptation to particular hosts? Is the ability to utilize certain hosts age-dependent? What genes control the ability to feed

on particular plants? This information is necessary to help us predict the insect response to new, resistant crop cultivars and potentially to produce cultivars to which insects will not evolve resistance.

A study is currently under way to determine the variation in feeding ability within an *H. armigera* population, how that variation changes with age and the proportion of that variation that is heritable. The heritability of a trait, or the proportion of the phenotypic variation that is attributable to additive genetic variation, in conjunction with the strength of selection determines the speed at which that trait can evolve (Falconer and Mackay, 1996). Preliminary results suggest that there are high levels of additive genetic variation for the ability to feed on the moderately resistant chickpea ICC506 being maintained in the population (Cotter, unpublished data). By understanding the genetic variation present in the insect population to overcome plant resistance mechanisms we can make predictions about the potential for those genes to spread.

In *H. armigera*, experience with a plant increases the likelihood that a female will choose to lay eggs on that host in the future (Cunningham *et al.*, 1998a; Cunningham *et al.*, 1999). It has also been suggested that preference is strongly influenced by host abundance with the relative attractiveness of a host for oviposition increasing with its abundance in the environment (Papaj and Rausher, 1987; Cunningham *et al.*, 1999; Cunningham and West, 2001). Therefore, it seems likely that females encountering a large patch of host plants, as would occur in an agricultural situation, would oviposit regardless of the genotype present as long as that genotype did not have strong antixenotic properties. Under these circumstances it seems likely that there would be selection acting on neonates for improved performance, and with performance being

highly heritable in the population the response to such selection would be rapid.

However, the response to selection is also determined by the *strength* of selection. It may therefore be possible to reduce the chance of insect resistance to new plant cultivars developing by choosing plants with antixenotic rather than antibiotic properties. For example, preventing polyphagous moths from ovipositing on crops would confer a low selection pressure as long as there were alternate hosts for the females to oviposit on. In comparison, crops with strong antibiotic properties that either killed or greatly delayed larval development would constitute a strong selection pressure. Larvae that could overcome the plants' resistance mechanisms would increase in the population and resistance would develop.

Understanding the mechanisms underlying the ability of *H. armigera* to feed on particular hosts may help in the development of crop cultivars to which resistance is less likely to develop in the field. To this end, work is currently underway to map the genes responsible for *H. armigera*'s ability to feed on chickpea. By hybridizing *H. armigera* with the closely related but oligophagous *H. assulta*, for whom chickpea is not a host, and then backcrossing chickpea-feeding hybrids to *H. assulta*, we hope to produce lines of hybrids containing chickpea-feeding genes in an *H. assulta* genetic background. By comparing these hybrids with both parental lines it should be possible to map chickpea feeding genes. Future work could then examine when and where these genes are expressed in order to elucidate their function.

Conclusions

Helicoverpa spp. represent a significant challenge to field crops in many parts of the

world. In Australia, *H. armigera* and *H. punctigera* are extremely well adapted to exploit the natural environment and managed agricultural systems. They remain the target for concerted management with pesticides and concerted research efforts seeking to develop alternatives to pesticides, which allow more sustainable integrated approaches for management. While the last decade has seen considerable advances in the development and adoption of IPM systems in certain crops, further advances are needed.

The two examples of current research outlined here – Bt cotton and development of host plant resistance in chickpea – represent a small part of the current IPM focused research effort. Other areas of research activity include the ecology and management of beneficial insects, the use of trap crops and refuge crops, population structure and movement of *Helicoverpa* spp., resistance management and the genetic basis of pesticide resistance, “soft” non-disruptive pesticides and behaviour modifying chemicals (attractants, repellants) for use in management systems.

IPM systems will, of necessity, be more complex than the pesticide based systems of the past, and will require greater effort on the part of crop managers whether they be professional consultants or farmers themselves. Likewise there remains a need for ongoing research to develop a suite of management tactics and integrate them into IPM systems. For example, transgenic cottons expressing insecticidal proteins provide great scope to dramatically reduce pesticide dependence, but they must be supported with well-researched resistance management strategies and by a range of other pest management approaches.

There is unlikely to be a simple solution to the control of such adaptable and mobile

pests as *Helicoverpa* spp., but by taking an integrated approach to the *Helicoverpa* problem in Australia we may be able to achieve the goal of long term, sustainable pest management strategies with minimal environmental impacts.

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Figure captions

Figure 1. 36 varieties from 6 different *Cicer* species were screened for resistance to *Helicoverpa punctigera*. The mean weight of larvae after 5 days feeding on excised leaves is plotted by species (a) and by variety (b). The 2 most susceptible and resistant varieties per species are shown. (Ridsdill-Smith & Mann, unpublished data)

Figure 2. Field data showing the number of damaged pods on field grown plants exposed to natural infestations of *Helicoverpa*. Howzat, ICC 506, Jimbour and Tyson are all *Cicer arietinum* (cultivated chickpea), the remaining lines are *Cicer bijugum*, a wild relative. Data collected by Ted Knights (affiliation)

Figures

Figure 1a

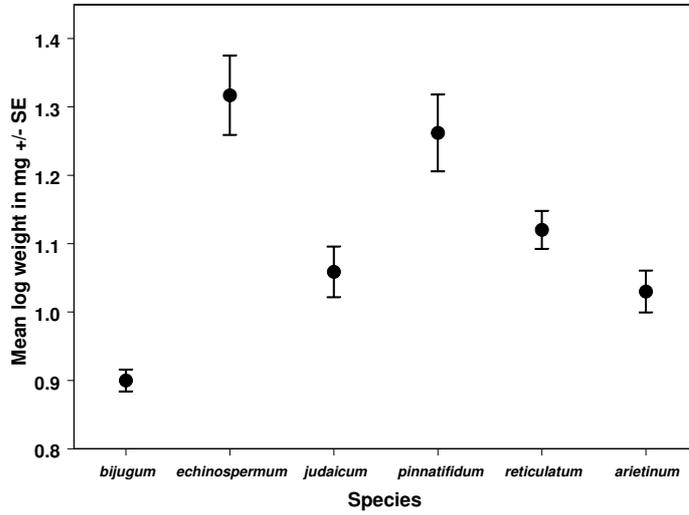


Figure 1b

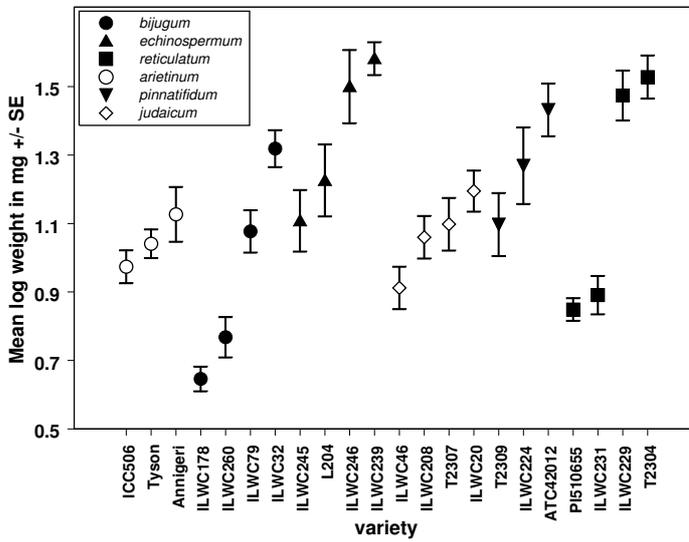


Figure 2

