

Host plant resistance in grain crops and prospects for invertebrate pest management in Australia: an overview

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Abstract. An integrated pest management (IPM) approach that relies on an array of tactics is adopted commonly in response to problems with pesticide-based production in many agricultural systems. Host plant resistance is often used as a fundamental component of an IPM system because of the generally compatible, complementary role that pest-resistant crops play with other tactics. Recent research and development in the resistance of legumes and cereals to aphids, sorghum midge resistance, and the resistance of canola varieties to mite and insect pests have shown the prospects of host plant resistance for developing IPM strategies against invertebrate pests in Australian grain crops. Furthermore, continuing advances in biotechnology provide the opportunity of using transgenic plants to enhance host plant resistance in grains.

Introduction

Crop production has benefited greatly from the application of synthetic pesticides because of its general efficacy and cost effectiveness. However, the widespread, indiscriminate use of such chemicals has led to not only the development of resistance in invertebrate pests but also the upsurge of secondary pest species due to destruction of natural enemies in ecosystems (Metcalf 1987). Furthermore, there are social costs and other environmental risks associated with the use of chemical pesticides (Radcliffe 2002). Thus, in many agricultural systems integrated pest management (IPM) has emerged as a response to these constraints of pesticide-based production. An IPM approach harmoniously combines cultural, biological and chemical control tactics in order to suppress pest numbers to below crop-damaging levels (Thomas 1999). Among these multiple technologies, host plant resistance is regarded as a fundamental component to stabilise an IPM system (Teetes 1996).

Host plant resistance results from the genetically inherited properties that render a plant less damaged than a plant that lacks such properties (Smith 1989). In agronomic terms, a resistant crop variety yields more than a susceptible variety when confronted with pest infestation. This is because pest-resistant plants alter their relationships with the pest species concerned, depending on the category of plant resistance (i.e. antibiosis, antixenosis and tolerance) (Horber 1980). Antibiosis resistance often leads to increased mortality or reduced longevity and reproduction of the pest, so that pest abundance and subsequent damage is reduced compared with circumstances where a pest occurs on a susceptible crop variety. Antixenosis resistance affects the behaviour of a pest species and usually is expressed as non-preference of the pest for a resistant plant compared

with a susceptible plant. Thus, antibiosis and antixenosis resistance cause a pest response when the pest attempts to use the resistant plant for food, oviposition or shelter. In contrast, tolerance is a plant response to a pest species, enabling a plant to withstand or recover from damage caused by a pest of abundance equal to that damaging a plant without this resistance character (susceptible). Therefore, plants with antibiosis or antixenosis can impose selection pressure on pest populations and hence may lead to the development of biotypes, whereas plants with tolerance have no such pressure.

Although host plant resistance seldom functions alone to provide adequate pest control, pest-resistant crops can be used as one of the multiple management tactics that an IPM system encompasses (Teetes 1994). Pest-resistant crop varieties may function to reduce pest numbers because of non-preference or antibiosis or to elevate the threshold level of plant injury due to pest damage because of a tolerance mechanism. Thus, the use of even partially resistant varieties will have a significant cumulative effect on pest populations over time, hence reducing the dose of the pesticides required and the frequency and number of pesticide applications (van Emden 1991). In addition, an important advantage to using host plant resistance as a component in IPM is that resistant crop varieties are generally compatible with the use of natural enemies for biological control. The compatible, complementary role that pest-resistant crops play with other direct control tactics is theoretically and practically in concert with the objectives of IPM (Kogan 1998; Thomas 1999). Therefore, the use of pest-resistant crop has become an essential tactic in an IPM system (Kogan 1994; Sharma and Oritiz 2002).

In this article, we will present an overview on recent research and development in grain resistance to insect and mite pests in Australia, with a focus on aphid resistance in legumes and cereals, sorghum midge resistance, and pest resistance in canola. We will further discuss the opportunity of using transgenic technology to enhance host plant resistance in grain crops. Our goal is to provide readers with a better understanding of the prospects of host plant resistance for development of truly ecological IPM strategies in Australian grains.

Aphid host plant resistance in legumes and cereals

Legumes

There are two primary aphid pests of pulses and lupins in Australia, the bluegreen aphid (*Acyrtosiphon kondoi*) and the cowpea aphid (*Aphis craccivora*). Most pulses except chickpea will be subjected to aphid outbreaks during years when environmental conditions are conducive. Aphids can cause substantial yield losses in lupins (Berlandier *et al.* 1998), and aphid resistance has been a focus of lupin breeders at the Department of Agriculture and Food, Western Australia (DAFWA) for over 20 years. In fact, yellow lupin (*Lupinus luteus*) has so far failed as a crop in Western Australia because of the susceptibility of cultivated varieties like Wodjil to aphid feeding. DAFWA breeders have been successful in developing narrow-leaved lupins (*Lupinus angustifolius*) varieties with increased resistance to aphid, which appears to be associated with elevated levels of phloem alkaloids (Berlandier *et al.* 1998; Edwards 2001). There are indications that another aphid species, the green peach aphid (*Myzus persicae*), may become more of a pest on narrow-leaved lupins because it is able to tolerate the higher levels of alkaloid in resistant varieties (Cardoza *et al.* 2006). This aphid is more difficult to control than bluegreen aphid and cowpea aphid because of its ability to develop resistance to many insecticides (Edwards *et al.* 2008).

Bluegreen aphid and spotted alfalfa aphid are such a major problem on lucerne in Australia that virtually all varieties are now bred to have at least moderate resistance to both aphid species (Irwin *et al.* 2001). Breeders in Australia have also had some success breeding aphid resistance into annual pasture legumes. The barrel medic, *Medicago truncatula*, has been the focus of much of this breeding effort, and as a result most barrel medic varieties in Australia now have resistance to both bluegreen aphid and spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata*), but not cowpea aphid (Milne 1998; Gao *et al.* 2007a). More recent efforts have identified aphid resistance in the strand medic, *Medicago littoralis* (Nair *et al.* 2003).

Because barrel medic has now been adopted as a model legume species with growing genomics resources (Cook 1999), researchers in Australia are using *M. truncatula* to investigate the mechanisms underlying aphid resistance. Resistance genes against bluegreen aphid, spotted alfalfa aphid and pea aphid (*Acyrtosiphon pisum*) have been mapped and characterised (Klingler *et al.* 2005, 2007; Gao *et al.* 2008). Each appears to belong to a class of resistance genes (NBS-LRR) that function by eliciting plant defences in response to aphid feeding (Gao *et al.* 2007b).

Cereals

In northern Australia, cereal aphids (*Rhopalosiphum* spp., *Sitobion* spp.) are generally controlled by natural enemies whereas in southern Australia they are more important as vectors of barley yellow dwarf virus. As such, there has not been a breeding effort in Australia to develop cereals with aphid resistance.

The Russian wheat aphid, *Diuraphis noxia*, is present in all major cereal-growing regions of the world except Australia. Unlike most aphid species, it can cause considerable damage and yield loss at low population densities (Randolph *et al.* 2003). The threat posed by this aphid to the Australian wheat and barley industries is so great that breeders in Australia have in the past attempted to develop resistant varieties that could be deployed in response to an incursion (Raman and Read 2000). With the recent appearance of virulent biotypes of Russian wheat aphid in the USA (Haley *et al.* 2004) and South Africa (Tolmay *et al.* 2007), the preemptive breeding effort against this pest in Australia has been reinvested.

Sorghum midge resistance

In Australia, grain sorghum has a smaller number of major insect pests compared with grain sorghum grown elsewhere. It is mostly only susceptible to economic damage during panicle flowering and grain filling to pests that directly attack the developing grain. Consequently, breeding for insect-resistance traits in Australian sorghum has largely been restricted to a handful of traits – all related to the sorghum panicle.

The first of these traits is an open panicle branching structure or habit. Open panicle hybrids have been reported to be less infested and damaged by aphids and lepidopteran larvae compared with closed-panicle types in the same location (Franzmann 2007). This trait has not been actively selected or adopted commercially in any consistent manner.

The second host plant resistance trait reported to have economic benefit in grain sorghum is that of sorghum midge resistance. This trait has been universally incorporated into commercial hybrids. The development and release of midge resistance is the backbone to a unique Australian success story explained in more detail in a parallel paper (Franzmann *et al.* 2008). The resistance is highly polygenic, resulting from floret morphological characters that inhibit female midge from laying as many eggs (ovipositional antixenosis). The Queensland Department of Primary Industries and Fisheries has been responsible for incorporating this difficult to breed for trait into commercial grain sorghum germplasm in partnership with seed companies (Page 1979; Franzmann 1993; Henzell *et al.* 1996).

Another mechanism of resistance present in Indian grain sorghum was also incorporated into the Australian sorghum breeding program in the late 1990s. This resistance involves both antifeedant and lethal effects on midge larvae, causing approximately two-thirds of all larvae to die (Hardy and Jordan 2006). A gene cloning project that will uncover the exact genes that cause antibiosis is well advanced. This will enable researchers to rapidly select for antibiosis using molecular marker techniques. Incorporation of this resistance into commercial hybrids is expected to be rapid. The end result will be that midge may become a 'forgotten pest' of sorghum in Australia.

Pest resistance in canola

Canola consists of different cultivars of oilseed rape that produce seed oil with less than 2% erucic acid and meal with less than 30 μmol aliphatic glucosinolates per gram (Raymer 2002). Although the lower level of some secondary plant compounds, such as glucosinolates, in canola compared with other Brassica plants may influence herbivory and plant–herbivore interactions (Chew 1988), canola crops are subject to attacks by all important invertebrate pests of other Brassica plants wherever available (Lamb 1989). There are at least 30 species attacking canola crops in Australia, which belong to Acarina, Collembola, Coleoptera, Lepidoptera, Hemiptera and Gastropoda (Gu *et al.* 2007). Pest control for canola production in the country has been reliant on the prophylactic use of chemical pesticides, but the increased social and regulatory pressure to reduce pesticide use for canola production and continuing problems with pest resistance to pesticides demand the shift of its pest management from the chemical-dominant tactic to an IPM approach. For this purpose, particular attention has been focussed on the development and adoption of pest-resistant varieties in canola (McDonald *et al.* 1995; Erlandson *et al.* 1997).

Research on host plant resistance in canola started in Canada and other countries in the early 1980s. Empirical studies have shown that there are differential susceptibilities of canola crops to different species of insect pests, and all three types of resistance modalities, viz. antixenosis, antibiosis and tolerance, can impart resistance to various insect pests (Palaniswamy 1996). For example, both antixenosis and tolerance were found as the mechanisms of resistance to the flea beetle, *Phyllotreta striolata* in *Brassica rapa* L. (Lamb *et al.* 1993) and hybrid canola (*Brassica napus*) (Bodnaryk *et al.* 1994). Antixenotic effects on adult oviposition and larval feeding choices due to either physical or chemical characteristics of canola leaves have also been identified as the mechanism of resistance to the diamondback moth in different cultivars (Palaniswamy *et al.* 1986; Justus *et al.* 2000; Sarfraz *et al.* 2007). Some level of antibiosis resistance was also detected to influence the larval feeding and growth of the diamondback moth in some *B. napus* entries (Ramachandran *et al.* 1998). Furthermore, the resistance properties identified from wild relatives of Brassica and mustard plants were successfully introgressed into canola to enhance resistance to the flea beetle *P. striolata* and to the cabbage seedpod weevil *Ceutorhynchus obstritus* (Marshall) in Canada (Palaniswamy 1996; McCaffrey *et al.* 1999; Dossdall and Kott 2006). Attempts have also been made to introgress resistance to root maggot (*Delia* spp.) from related species into commercial canola varieties (Dossdall *et al.* 2000; Ekuere *et al.* 2005), with promising results.

In Australia, experimental evaluation of host plant resistance as an option to reduce the impact of invertebrate pests on canola crops was initiated in the early 1990s. Preliminary screening tests for the redlegged earth mite, *Halotydeus destructor* Tucker (Acari: Penthalidae), showed that some northern hemisphere varieties of *B. napus* were less vulnerable to attack by *H. destructor* at the cotyledon stage, compared with Australian local varieties, and the notably low survival and fecundity of the pest mite on *B. napus* indicated the presence of partial resistance in canola (McDonald *et al.* 1995). In the late 1990s, the Grain

Research and Development Corporation, Australia funded a project to further investigate canola resistance to the redlegged earth mite (McDonald 1999). Large-scale glasshouse screening of 448 *B. napus* accessions in Victoria identified 31 lines with sufficient mite resistance for further tests in field trials. Field trials with the 31 lines showed that four lines and the F_2 progeny of their crosses suffered significantly less damage due to the mite infestation compared with the susceptible commercial cultivar Oscar. The mechanisms underlying the mite resistance in these lines remain unclear, although seeds from these resistant lines were attested to have high levels of glucosinolates compared with commercial canola cultivars.

Findings from these pioneering studies have aroused further interest in the pursuit of pest resistance in commercial canola varieties. Dr H. Gu has recently initiated screening tests to evaluate the response of various varieties to infestation by different invertebrate pests in collaboration with canola breeders from the New South Wales and Victorian Departments of Primary Industry. These studies have been focussed on the redlegged earth mite, *H. destructor*, which is one of the most important pests threatening crop establishment, and the diamondback moth, *Plutella xylostella* L., which can be a serious pest attacking the crop at the flowering and budding stages (Gu *et al.* 2007). The great capacity to develop resistance to different pesticides in both *H. destructor* (Umina 2007) and *P. xylostella* (Talekar and Shelton 1993; Endersby *et al.* 2004; Baxter *et al.* 2005) has caused difficulties in controlling their populations. Glasshouse tests for different varieties have shown the presence of varietal differences in response to the redlegged earth mite and in attraction to oviposition by the diamondback moth. Under the same pressure of infestation by the redlegged earth mite, some varieties displayed significantly less feeding damage and suffered less impact on the growth performance of plants due to mite damage than others, whereas canola plants in a few varieties received significantly less eggs from the diamondback moth than others (H. Gu, unpubl. data). To evaluate the varietal performance of these commercial varieties in facing the natural infestation of these pest populations under natural conditions, field trials have been carried out in the Agricultural Institute of New South Wales (Wagga Wagga) and the Grains Innovation Park of Victoria (Horsham). The field results are in general agreement with the glasshouse data. In particular, two of these varieties showed relatively higher resistance to the redlegged earth mite in both glasshouse experiments and field trials (H. Gu, W. Burton, N. Wratten and R. Mailer, unpubl. data).

Empirical data from previous and recent studies have revealed the potential of resistance to invertebrate pests in the rich collection of canola accessions or lines. Moreover, the availability of a large number of commercial varieties in Australia (N. Wratten, pers. comm.) offers valuable resources to identify varietal resistance to invertebrate pests in canola. Although the mechanisms underlying the resistance to both the redlegged earth mite and the diamondback moth remain to be investigated, the commercial varieties that have been identified as relatively resistant may be used directly in IPM for canola production as long as their qualities meet the agronomic requirement or as genetic resources for future breeding improvement of pest-resistant varieties.

Options for pest resistance using genetically modified plants

Continuing developments in genetic engineering are rapidly producing a new era of genetically modified (GM) plants expressing a range of valuable characteristics for agriculture, including resistance to key pests. Over 110 million hectares of GM crops are now grown (James 2006). Of these, ~10% of the area relates to GM traits specifically targeting insect pests, the majority of which involve the integration of δ -endotoxin genes from the soil organism *Bacillus thuringiensis* subsp. *kurstaki* (Bt) (Federici 2005). Widespread examples include Bt cotton (Cry1Ac, Cry2Ab) and Bt corn (Cry1Ab, Cry1Ac), available commercially in several countries and targeting key lepidopteran pests. In Australia, Bt cotton has been in commercial use since 1996 largely for the control of *Helicoverpa* spp. (Lepidoptera: Noctuidae) and has resulted in an 85% reduction in pesticide use in cotton production (Fitt 2000, 2004; Pyke 2007). Given the specificity of the Cry proteins, and the consequent lack of impact of Bt crops on beneficial insects (Whitehouse *et al.* 2005), they can provide a sound platform for IPM systems (Fitt and Wilson 2000; Wilson *et al.* 2004). In addition to the Cry genes, the class of vegetative insecticidal proteins characterised by Vip3A is also close to commercialisation (Yu *et al.* 1997; Llewellyn *et al.* 2007).

Across the suite of invertebrate pests of various grain crops, there would be options for Bt genes to provide control for some lepidopteran pests (e.g. Cry1Ac, Cry2Ab for *Helicoverpa* spp., Cry1C for diamond back moth) (Monnerat *et al.* 1999), whereas advances made with the snowdrop lectin gene (*GNA*) may offer future options for homopteran pests such as aphids and plant leafhoppers (Down *et al.* 2000; Wang *et al.* 2005).

In addition to the current issues of public acceptance of GM grain crops for human food, there are other significant issues that impinge on future considerations for Bt grain crop deployment. These issues relate to the risk of target pests evolving resistance to Bt genes and the management requirements needed to minimise this risk. Strategies for resistance management of Bt crops have been explored exhaustively with population genetic models and innovative methods to modify the selection environment imposed by Bt crops on the pest (Gould 1998; Roush 1998; Tabashnik *et al.* 2003, 2004). Although debate about the appropriateness of certain strategies continues, the overwhelming body of evidence supports the use of a refuge strategy combined with the highest possible efficacy of the Bt plants (Tabashnik *et al.* 2003). Such strategies are likely to be required if Bt grain crops were deployed.

Perhaps a more vexing question is how to integrate the deployment of insecticidal transgenes across a range of crops where the target is a widespread, polyphagous and mobile pest such as *Helicoverpa*. Although Bt cotton is the first GM field crop in Australia, Bt corn has been commercialised in several countries and there are proposals for Bt genes (usually the *CryIAC* or *CryIAB* genes) to be introduced into sorghum, canola, lupins, field peas and chickpeas among a range of other crops. All of these crops are utilised to varying degrees as host plants by *Helicoverpa* spp. and perhaps other pests. Corn and sorghum in particular are the most preferred crops used by *Helicoverpa armigera* (Jallow and Zalucki 1996). Current proposals for GM grains in Australia include canola.

Managing the deployment of Bt genes in future grain crops, when the same genes may already be widely in use in crops like

cotton, requires careful consideration and probably a regulatory protocol that can balance the pros and cons of different applications of transgenes for pest management (Fitt 1997).

These issues are best considered at the regulatory level well before the commitment of extensive research funds or consideration for commercial releases has occurred. This would ensure minimal wastage of resources on products that are unlikely to meet with regulatory approvals. Where multiple uses of Bt genes are justified, there should be a requirement to utilise genes with different target sites or modes of action to those already deployed.

Conclusion

Host plant resistance has become an essential and fundamental component of IPM strategies against invertebrate pests in many agricultural systems because of its economic, ecological and environmental advantages (Teetes 1996). The use of resistant crop varieties can reduce pesticide applications with lower dosage and less frequency, and hence reduce cost to crop production and foster biodiversity in the agro-ecosystem in question. For instance, cultivation of sorghum hybrids with resistance to the sorghum midge has led to development of an IPM system in which the use of synthetic insecticides is greatly reduced for effective pest management in Australian sorghum production. Empirical studies in legumes, cereals and canola have also shown the prospects of using crop varieties with resistance to invertebrate pests as a sole control method or as an adjunct to other control tactics of IPM systems, although further studies are required to elucidate the resistance mechanisms for development and deployment of pest-resistant varieties in these grain crops. Furthermore, genetically modified crops with enhanced pest resistance are expected to play a significant role in IPM for Australian grains in the future.

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