THE ROYAL SOCIETY

Challenges with managing insecticide resistance in agricultural pests, exemplified by the whitefly *Bemisia tabaci*

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For many key agricultural pests, successful management of insecticide resistance depends not only on modifying the way that insecticides are deployed, but also on reducing the total number of treatments applied. Both approaches benefit from a knowledge of the biological characteristics of pests that promote or may retard the development of resistance. For the whitefly *Bemisia tabaci* (Gennadius), these factors include a haplodiploid breeding system that encourages the rapid selection and fixation of resistance genes, its breeding cycle on a succession of treated or untreated hosts, and its occurrence on and dispersal from high-value crops in greenhouses and glasshouses. These factors, in conjunction with often intensive insecticide use, have led to severe and widespread resistance that now affects several novel as well as conventional control agents. Resistance-management strategies implemented on cotton in Israel, and subsequently in southwestern USA, have nonetheless so far succeeded in arresting the resistance treadmill in *B. tabaci* through a combination of increased chemical diversity, voluntary or mandatory restrictions on the use of key insecticides, and careful integration of chemical control with other pest-management options. In both countries, the most significant achievement has been a dramatic reduction in the number of insecticide treatments applied against whiteflies on cotton, increasing the prospect of sustained use of existing and future insecticides.

Keywords: *Bemisia tabaci*; cotton; ecological genetics; haplodiploidy; resistance management; whitefly

1. INTRODUCTION

Managing resistance to insecticides entails finding practical solutions to problems posed by the adaptability of insect pests. The most obvious and politically seductive option is to abandon insecticides and switch entirely to cultural and/or biological control methods. Unfortunately, this is rarely a feasible proposition. The first and unquestionably most productive line of attack is none the less to minimize use of chemicals to the point at which various operational tactics for reducing or diversifying selection pressure (reviewed by Roush & McKenzie 1987; Roush 1989; Tabashnik 1990; Denholm & Rowland 1992) can be brought into play.

The maximum number of insecticide applications that can be accommodated whilst suppressing resistance will depend on several interacting factors including the genetic and ecological attributes of specific pests, the number of non-cross-resisted chemicals available, and the type of management tactics adopted. As a general rule, pests whose biology renders them most prone to developing resistance are those for which restrictions on insecticide exposure should be most stringent. The basic dilemma is that these are often the species whose biology also renders them most abundant and damaging, and therefore primary targets of insecticide treatments. For this reason, they may also be ones in which resistance is already well advanced, diminishing the supply of effective compounds and placing new insecticides under severe threat of overuse and hence resistance from the outset (Cahill & Denholm 1998; Denholm *et al.* 1998).

The challenges of combating resistance within such constraints are well exemplified by the cotton, tobacco or sweet-potato whitefly, *Bemisia tabaci* (Gennadius). *B. tabaci* is now one of the most serious agricultural pests worldwide. It is highly polyphagous, attacking numerous field crops throughout the tropics and sub-tropics, and has recently become a significant pest of protected horticulture in temperate regions (Denholm *et al.* 1996). It reduces crop yields by direct feeding damage, through honeydew production that contaminates produce, and by transmitting more than 60 plant viruses (Bedford *et al.* 1994). In many cropping systems, the capacity of this species to evolve resistance has precipitated a classic treadmill of increasing numbers of applications and rapid depletion of effective control agents (Dittrich *et al.* 1990; Byrne *et al.* 1992; Horowitz *et al.* 1994; Denholm *et al.* 1996; Dennehy & Williams 1997). In this paper, we explore some of the biological characteristics of *B. tabaci* that promote resistance in agricultural and horticultural systems, and consider their implications for resistance to conventional and new insecticides. More optimistically,

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we then describe two recent control strategies involving insecticides that have not only mitigated resistance problems in the short-term, but have also succeeded in reducing chemical use to the point at which long-term, sustainable resistance management becomes a viable proposition.

The taxonomic treatment of pest populations of *Bemisia* is currently controversial and inconsistent. In this paper, we continue to regard all populations exhibiting published morphological traits of *B. tabaci* as belonging to this species, including ones recently described as a distinct species, *B. argentifolii* (Perring *et al.* 1993; Bellows *et al.* 1994).

2. FACTORS INFLUENCING SELECTION RATES

(a) *Influence of breeding system*

Like all members of the Aleyrodidae, *B. tabaci* has long been assumed to possess a breeding system based on haplodiploidy, whereby males are produced uniparentally from unfertilized, haploid eggs, and females are produced biparentally from fertilized, diploid eggs (White 1973). The ability of unmated females to generate viable male progeny (Byrne & Devonshire 1996) identifies this system as one of true arrhenotoky, distinct from 'parahaploidy' (*sensu* Hoy 1979), 'psuedo-arrhenotoky' (*sensu* Schulten 1985) and 'functional haplodiploidy' (*sensu* Brun *et al.* 1995). In the latter three cases, mating is essential for offspring production but one set of male chromosomes is eliminated or inactivated during early development. Until recently, however, there was no direct genetic evidence for haplodiploidy in *B. tabaci*. Through crossing experiments between whitefly strains differing in polymorphic esterase and acetylcholinesterase alleles, Byrne & Devonshire (1996) demonstrated unequivocally the failure of male progeny to express paternal markers, rendering them hemizygous for one or other maternal allele. Blackman & Cahill (1997) have since published karyotypes for several strains of *B. tabaci*, showing males to possess only half ($n=10$) the female complement ($2n=20$) of chromosomes.

From the standpoint of selecting for resistance, the primary consequence of haplodiploidy is that resistance genes arising by mutation are exposed to selection from the outset in hemizygous males, irrespective of intrinsic dominance or recessiveness. The ability of this to accelerate resistance development has been noted by several authors (Helle 1968; Havron *et al.* 1987; Brun *et al.* 1995; Caprio & Hoy 1995), and is reinforced by results of a simple simulation model (figure 1). This model assumes selection to occur before random mating between genotypes, a 1:1 sex-ratio among progeny, and the fitness of hemizygous male genotypes under insecticide exposure to be identical to that of homozygous female counterparts. The latter may not apply to all resistance mechanisms, e.g. mechanisms involving enhanced detoxification in which dosage effects may occur, but this has relatively little influence on overall conclusions. Whether a resistance allele is effectively dominant (figure 1*a*), semi-dominant (figure 1*b*), or recessive (figure 1*c*), resistance develops at a similar rate under haplodiploidy, whereas recessiveness can cause substantial delays in corresponding diploid populations. When resistance alleles are

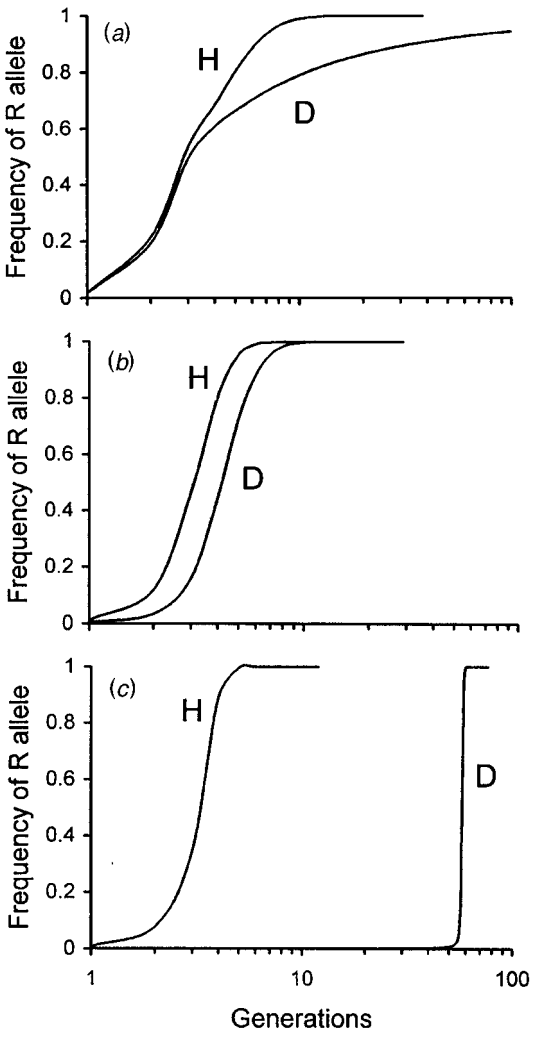

Figure 1. Simulated selection for resistance in haplodiploid (H) and diploid (D) species when resistance is (*a*) fully dominant, (*b*) semi-dominant, or (*c*) fully recessive. The initial resistance (R) allele frequency is 0.001. Fitness values assigned to SS and RR genotypes are 0.05 and 0.9, respectively. Fitness of the RS heterozygote is 0.9 (dominant), 0.3 (semi-dominant) or 0.05 (recessive). Fitness values for hemizygous S and R genotypes are assumed to be identical to those of their SS and RR counterparts.

dominant or nearly so (see, for example, figure 1*a*), another consequence of hemizygosity is to speed up their rate of fixation, because alleles for susceptibility are no longer shielded in males.

The potential of haplodiploidy to promote rapid selection of resistance to high frequencies is still under appreciated, despite the prevalence of this breeding system in many key arthropod pests, including whiteflies, spider mites and phytophagous thrips (White 1973; Schulten 1985; Havron *et al.* 1987). It undoubtedly contributes to the capacity of *B. tabaci* to evolve resistance rapidly to newer insecticides, especially in enclosed environments (see below), and has profound implications for the sustainability of any transgenes incorporated into crop plants to control such species. Maintenance of high toxin expression levels to exploit the presumed lower resistance of heterozygotes compared with homozygotes is currently the most favoured option for delaying resistance

to transgenic crops deployed against lepidopteran and coleopteran species (see, for example, Roush 1997).

(b) *Ecology in field crops*

For highly polyphagous species such as *B. tabaci*, interactions between pest ecology and resistance can be subtle and complex, reflecting the seasonality and relative abundance of treated and untreated hosts, and patterns of migration between hosts at different times of the year. There are still very few agricultural systems for which these interactions have been resolved sufficiently to understand their influence on resistance development. The best understood systems of all are probably those involving cotton, melons and vegetables in the southwestern deserts of the United States, where long-term research into whitefly ecology and migration is complemented by extensive monitoring of changes in resistance levels.

The key feature of these systems is the continuous availability of suitable host plants, enabling *B. tabaci* populations to develop actively throughout the year (Coudriet *et al*. 1986; Byrne *et al*. 1990). Typically, whiteflies overwinter on weeds, lettuce and brassica crops, migrating short distances to colonize melons and cotton in the spring and summer, respectively (Byrne & Blackmer 1996). Both of the latter crops are treated frequently with insecticides, unlike alfalfa, which is present all year and seldom sprayed, therefore providing a refuge for insects carrying susceptibility genes.

Regional variation in these production systems has profound implications for the speed at which resistance is selected and for the effectiveness of resistance-management recommendations. In the Imperial Valley of southeastern California, spring melons remain an important crop but the acreage of cotton has declined dramatically, now accounting for only 6000–8000 acres (1 acre = 0.404 686 ha) compared with *ca*. 200 000 acres of unsprayed alfalfa (Castle *et al*. 1996*a*,*b*). Regular monitoring of whitefly resistance since 1993 by means of insecticide-impregnated sticky cards has shown that, although resistance has generally increased each season as a consequence of insecticide use on spring melons, it they have tended to decline subsequently on cotton, owing partly to extensive immigration of susceptible whiteflies into cotton from adjacent, untreated hosts. As a result, there has been no overall increase in the severity of resistance problems over successive seasons (Castle *et al*. 1996*a*; S. J. Castle, personal communication). Interactions between cropping patterns, chemical use and the bionomics of *B. tabaci* have in this case led *de facto* to preserving susceptibility to several widely used insecticides.

In the neighbouring state of Arizona, resistance monitoring has disclosed substantial geographical variation in resistance levels that can also be reconciled with the bionomics of *B. tabaci*. Before the introduction of a resistance-management strategy for cotton in 1996 (see below), resistance to insecticides (e.g. pyrethroids) used most frequently on that crop was consistently more severe in central Arizona, where cotton constitutes approximately two-thirds of the acreage of cultivated whitefly hosts, than in southwestern Arizona, where it accounts for less than one-quarter of the total acreage (Dennehy *et al*. 1996; Williams *et al*. 1997). Although unsprayed alfalfa accounts for approximately one-quarter of the available whitefly hosts in both areas, differences in the proportion of cotton compared with alfalfa are hypothesized to have accounted for this regional variation in pyrethroid resistance. As a result, the risk of resistance to newer insecticides (e.g. insect growth regulators) used on cotton appears greater in the centre than in the southwest of the state (Denholm *et al*. 1998). Conversely, risks of resistance to compounds (e.g. imidacloprid) used primarily on vegetables and melons appear greater in the southwest, where these crops are proportionally much more abundant than elsewhere in Arizona (Williams *et al*. 1997).

(c) *Ecology in protected crops*

Enclosed environments such as greenhouses and glasshouses, which restrict immigration and escape from insecticide exposure under climatic regimes favouring rapid and uninterrupted population growth, are widely recognized as providing near-ideal conditions for selecting resistance genes (see, for example, Parrella 1987; Sanderson & Roush 1995; Denholm *et al*. 1998). In the case of *B. tabaci* and other species that transmit plant viruses or cause cosmetic damage to high-value ornamental or edible produce, these problems are accentuated by very low or even zero pest tolerance thresholds that promote frequent spraying and hence intensify selection pressures. As a consequence, these environments have historically proved potent sources of novel resistance genes, and it is no coincidence that resistance of *B. tabaci* to several newer insecticides was first reported in protected horticulture (Horowitz *et al*. 1994; Cahill *et al*. 1996*a*,*b*).

Selection of resistance in greenhouses and glasshouses not only generates control problems *in situ*, but can have wider implications due to gene flow from these sites. On a local scale, active migration of insects from protected environments to adjacent field crops has the potential to infuse outdoor populations with resistance genes and thereby accelerate their selection to damaging frequencies. To our knowledge this has not been demonstrated directly for *B. tabaci*, but it constitutes a tangible threat where outdoor and protected hosts are grown in close proximity. In contrast, the risk of large-scale, inadvertent movement of resistant insects between countries or even continents via the international trade in ornamental plants is clearly apparent from the high levels of resistance found in individuals of *B. tabaci* newly imported into northern European glasshouses (Cahill *et al*. 1994; Denholm *et al*. 1996). In this respect, *B. tabaci* provides an even more clear-cut example of resistance genes being spread by human agency than that inferred from molecular studies on mosquitoes (Raymond *et al*. 1991).

3. IMPLICATIONS FOR RESISTANCE

(a) *Conventional insecticides*

In many parts of the world, the above factors combined with often intensive insecticide use have led to strong resistance encompassing the great majority of chemical classes (Dittrich *et al*. 1990; Byrne *et al*. 1992; Cahill *et al*. 1995, 1996*c*; Denholm *et al*. 1996; Dennehy & Williams 1997). Resistance in *B. tabaci* is known to be multi-factorial,

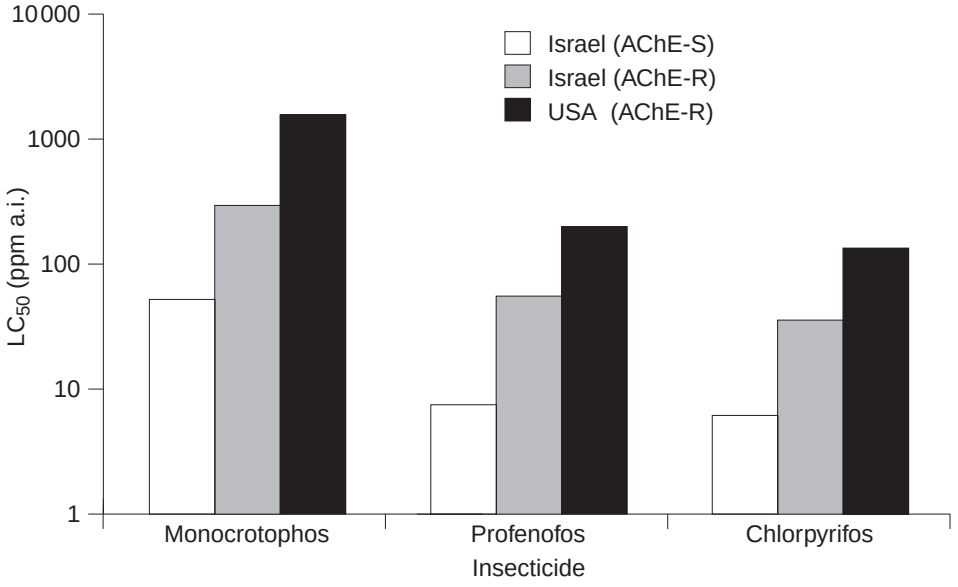

Figure 2. Response of adults of three strains of *Bemisia tabaci* to three organophosphorous insecticides, expressed as LC_{50} values calculated by probit analysis from results of leaf-dip bioassays.

based on both enhanced detoxification of insecticides and modifications to three of their major target proteins: acetylcholinesterase (AChE), targeted by organophosphates (OPs) and carbamates (Byrne & Devonshire 1993; Anthony *et al*. 1998), the GABA-gated chloride-ion channel, targeted by cyclodienes (Anthony *et al*. 1995), and the voltage-sensitive sodium channel involved in knockdown resistance (kdr) to pyrethroids (M. S. Williamson, personal communication). Modified AChE involves at least two allelic variants with different insensitivity profiles (Byrne & Devonshire 1997), and it is possible that kdr resistance in *B. tabaci* will also prove multi-allelic, as in other important pests (Martinez-Torres *et al*. 1997).

In comparison with species such as houseflies (see, for example, Sawicki 1973) and peach–potato aphids (Field *et al*. 1997), there has been relatively little progress towards isolating individual mechanisms in *B. tabaci* to determine their contribution, singly or in combination, to overall resistance phenotypes. Work on the genetics of resistance is complicated by many field populations appearing homozygous for resistance genes (Denholm *et al*. 1996), and by reproductive barriers between *B. tabaci* 'biotypes' (see, for example, Bedford *et al*. 1994). By rearing single-pair progeny from an Israeli population polymorphic for insecticide-sensitive (AChE-S) and insensitive (AChE-R) alleles, Byrne *et al*. (1994) were able to isolate strains homozygous for each of these alleles in a common genetic background. Differences in LC_{50} values of these strains for three OP insecticides (six- to ninefold; figure 2) could therefore be attributed to this target-site mechanism alone. However, several other strains homozygous for the same resistance allele, including that from the USA included in figure 2, have shown significantly higher resistance than the Israeli one. Such strains must possess at least one additional mechanism, most likely based on enhanced detoxification of OPs prior to their reaching the insensitive target site.

The implications of multiple mechanisms for resistance management are exemplified well by events on cotton in the southwestern USA. During the early 1990s, one response to increasing resistance in *B. tabaci* was to screen numerous combinations of products for possible synergistic effects (see, for example, Akey *et al*. 1993; Wolfenbarger & Riley 1994). Some mixtures of pyrethroids and OPs, especially of fenpropathrin and acephate, proved remarkably effective in this respect as shown by laboratory bioassay data for a whitefly strain collected from Safford, Arizona, in 1994 (figure 3*a*). Despite immunity to acephate and very high resistance to fenpropathrin applied alone, co-application of a fixed concentration of 1000 ppm acephate (non-toxic in its own right) with varying concentrations of fenpropathrin increased the toxicity of the pyrethroid by over 1000-fold, to a level at which field efficacy was greater than ever observed in Arizona for fenpropathrin alone. Although the biochemical basis of this extreme synergy has not been fully resolved, it most probably reflects inhibition by acephate of metabolic enzymes conferring resistance to fenpropathrin and other pyrethroids applied singly.

Based on this finding, tank mixes of pyrethroids and OPs became widely adopted for controlling *B. tabaci*, and were by far the most commonly used treatments on Arizona cotton during 1994 and 1995. By the end of the 1995 season, however, such mixtures had failed to control *B. tabaci* throughout much of central Arizona (Dennehy & Williams 1997). Laboratory tests against adults collected during 1995 from the Maricopa Agricultural Centre (Simmons & Dennehy 1996; summarized in figure 3*b*) confirmed that repeated use of synergized pyrethroids between July and September had led to a gradual loss of synergism of fenpropathrin by acephate. This resistance declined sharply between the 1995 and 1996 seasons, but a single treatment with the mixture between July and August 1996 caused it to increase again.

Resistance to synergized pyrethroids could reflect the selection of a new, non-synergizable resistance mechanism (e.g. target-site kdr resistance) or a modification of one already present; this is currently being investigated. Its appearance demonstrates that even tactics optimized to contend with existing resistance mechanisms can be rapidly compromised by the genetic plasticity of insect pests. Owing to the apparent instability of this resistance,

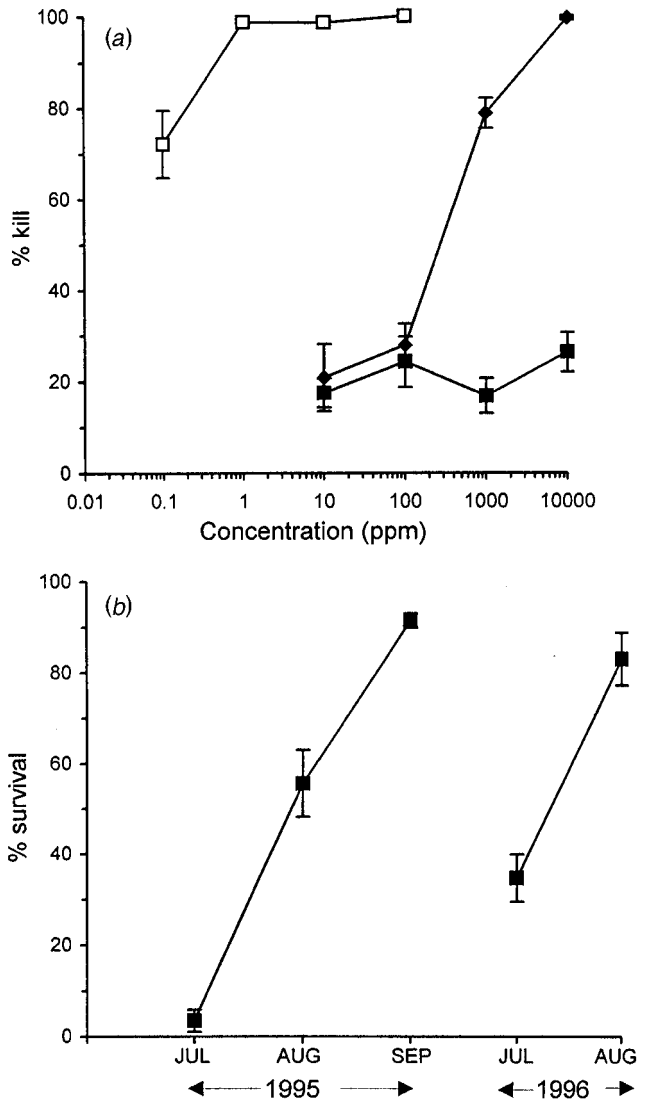

Figure 3. (*a*) Response of *B. tabaci* collected from cotton in Safford, Arizona, in 1994 to the pyrethroid fenpropathrin, the OP acephate, or a combination of both chemicals. Filled squares (■), varying concentrations of acephate alone; diamonds (◆), varying concentrations of fenpropathrin alone; open squares (□), varying concentrations of fenpropathrin plus a fixed concentration of 1000 ppm acephate. (*b*) Changes in response of *B. tabaci* on cotton in Maricopa, Arizona, during 1995 and 1996 to a combination of 10 ppm fenpropathrin and 1000 ppm acephate. All results relate to leaf-dip bioassays against adult whiteflies.

pyrethroid/OP combinations remain a viable management option if used with extreme moderation. However, their importance in this region has diminished since the introduction of more novel control agents that now underpin the management of resistance in *B. tabaci*.

(b) *Newer insecticides*

With the majority of older insecticides affected by resistance to varying degrees, compounds with novel or less exploited modes of action are assuming major importance as components of whitefly control programmes (Horowitz & Ishaaya 1994; Denholm *et al.* 1996; Cahill & Denholm 1998; Ishaaya & Horowitz 1998). Most of these offer the considerable advantage of being unaffected by existing resistance mechanisms, and many also exhibit more favourable environmental profiles than broad-spectrum agents employed in the past. However, all come with intrinsic resistance risks, and there is already ample evidence of how these may be accentuated by the genetics and life history of *B. tabaci*.

The chemicals probably attracting most attention in this respect are the chloronicotinyls or neonicotinoids, whose forerunner, imidacloprid, is now in widespread use against whiteflies and other pests including aphids and the Colorado beetle, *Leptinotarsa decemlineata* (Say) (Elbert *et al.* 1996). Other members of this class are currently being released or in late stages of development (Casida 1998). Their efficacy both as highly persistent systemic treatments and as shorter-lived foliar sprays offers outstanding versatility, but also renders them particularly prone to overuse. Their structural similarity, coupled with a likely common target site, nicotinic acetylcholine receptors in the post-synaptic region of insect nerves (Bai *et al.* 1991), also raises the spectre of cross-resistance affecting the group as a whole (Elbert *et al.* 1996; Cahill & Denholm 1998). The risk of resistance is therefore considerable, and reinforced by the speed with which resistance to imidacloprid has developed in *B. tabaci* under sustained exposure to this chemical in the laboratory (Prabhakar *et al.* 1997) and in greenhouses in southern Europe (Cahill *et al.* 1996*b*). Given the current scale of imidacloprid use, further resistance outbreaks seem inevitable and it is essential to exploit these for defining conditions under which chloronicotinyls might be used sustainably. Large-scale laboratory experiments with Spanish strains of *B. tabaci* have demonstrated substantial differences in the phenotypic expression of imidacloprid resistance under systemic and foliar treatment regimes, but also highlighted the dangers of unrestricted, successive exposure to both types of application, especially in enclosed environments (Cahill & Denholm 1998, unpublished data).

Despite their key role in sustaining some current resistance management strategies for whiteflies on cotton (see below), the insect growth regulators (IGRs) buprofezin and pyriproxyfen are also proving vulnerable to resistance by *B. tabaci*. Although both chemicals act primarily against immature stages of whiteflies, they possess distinct modes of action and are therefore very unlikely to be affected by the same resistance mechanism. Buprofezin inhibits chitin synthesis and results in nymphal death during ecdysis (Uchida *et al.* 1985), whereas pyriproxyfen is a juvenile hormone mimic interrupting nymphal and pupal development, but also suppressing egg hatch by direct exposure of eggs or transovarially via the treatment of adult females (Ishaaya & Horowitz 1992). These differences, coupled with a high degree of species selectivity, make them ideally suited as rotation partners in control programmes that place emphasis on the preservation of natural enemies of *B. tabaci* and co-existing pest species (Horowitz *et al.* 1994).

As with imidacloprid, resistance to both IGRs first became apparent under the intensive selection operating in protected environments. Resistance to buprofezin was first detected in glasshouses in The Netherlands, but has since been demonstrated elsewhere in northern Europe

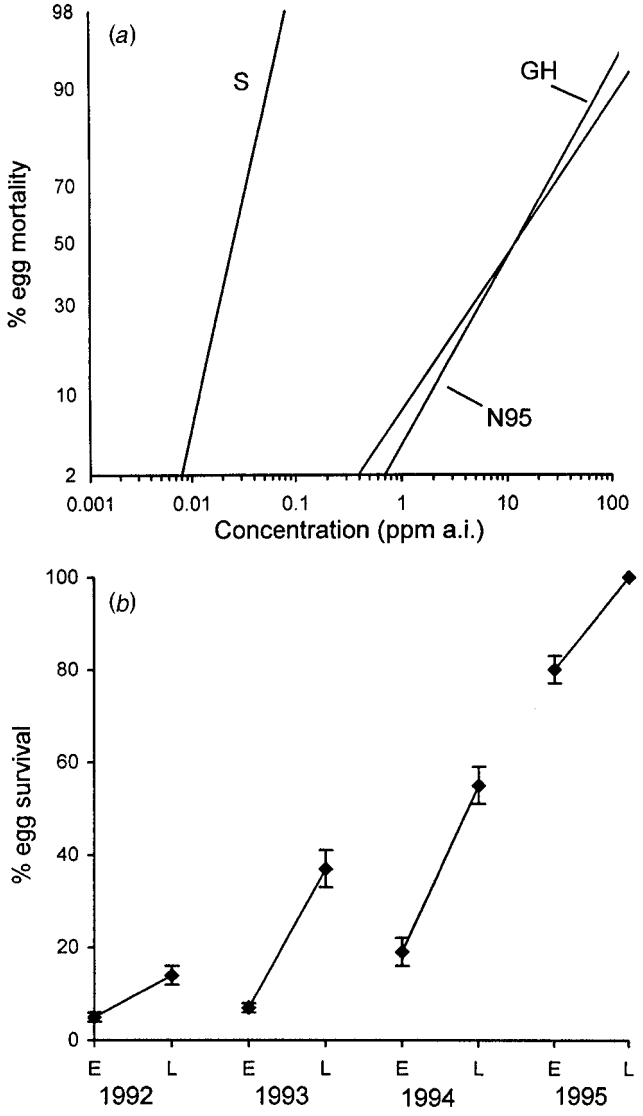

Figure 4. (*a*) Probit lines summarizing the response of three strains of *B. tabaci* from Israel to the IGR pyriproxyfen. S refers to the reference susceptible strain; GH refers to the insects collected from roses in a greenhouse in January 1992; N95 refers to the insects collected from cotton at Nachshon in central Israel in late 1995. (*b*) Changes in the response of *B. tabaci* from early-season (E) and late-season (L) season cotton at Nachshon to a discriminating concentration of 0.16 ppm pyriproxyfen between 1992 and 1995. All results relate to a leaf-dip bioassay exposing adults to the toxin and measuring subsequent egg hatch.

and in greenhouses in Spain and Israel (Horowitz & Ishaaya 1994; Cahill *et al.* 1996*a*). In many cases, the appearance of resistance could be attributed to repeated applications of this chemical with no regard to resistance management, although in the UK it preceded the official approval of buprofezin and unquestionably resulted from the accidental importation of resistant insects on plant produce (Cahill *et al.* 1996*a*). Buprofezin is still less widely used in the open field and resistance has been slower to develop. However, monitoring of the susceptibility of *B. tabaci* on cotton in Israel, where this chemical has been restricted to a single application per year since its introduction in 1989, has shown small increases in LC_{50} values consistent with the presence of resistant individuals at some localities (Horowitz *et al.* 1994).

The history of pyriproxyfen use against *B. tabaci* in Israel provides possibly the most striking example of genetic, ecological and operational factors conspiring to promote resistance, despite conscious attempts to prevent this occurring. Its introduction in Israel in 1991 represented the first ever commercial use against whiteflies of a compound developed primarily to control household and public health pests. Within one year of its introduction, high resistance was demonstrated in some ornamental greenhouses after successive applications (Horowitz & Ishaaya 1994; Horowitz *et al.* 1994). The maximum resistance recorded was *ca.* 550-fold at LC_{50}, from a rose greenhouse that had previously been sprayed only three times with this chemical (figure 4*a*). The linearity of dose–response data obtained from bioassays at this stage implied a high degree of homozygosity for one or more pyriproxyfen-resistance genes.

As with buprofezin, pyriproxyfen was released for use on Israeli cotton with a restriction to one application per season, in order to prevent or delay the development of resistance. Despite excellent compliance with this recommendation, resistance was first detected on cotton as early as 1992 in some localities, where it has since undergone a gradual increase in frequency within and between seasons. The most dramatic changes were recorded in the vicinity of Nachshon in the Ayalon Valley in central Israel, where egg survival at a diagnostic concentration of 0.16 ppm showed a stepwise increase between 1992 and 1995 (figure 4*b*). By late 1995, the fitted dose–response probit line for Nachshon insects was identical to that for the most resistant greenhouse population (figure 4*a*). The reasons why a maximum of only five treatments spaced one year apart should have selected so effectively for resistance are still unclear. Because Nachshon is remote from areas of intensive protected horticulture, contamination by resistant insects from greenhouses seems unlikely. The more plausible explanation invokes a combination of adverse factors discussed earlier in this paper: haplodiplody negating gene dominance and promoting rapid fixation of resistance alleles, and the 'bottlenecking' of whiteflies on irrigated and treated cotton in summer despite an apparent abundance of alternative hosts at other times of the year. A comparison of the ecology of *B. tabaci* at Nachshon with that in other areas where pyriproxyfen resistance has been slower to develop could help considerably with anticipating the risk of resistance to future products and in modifying use recommendations accordingly.

4. MANAGEMENT OF RESISTANCE

Many of the biological characteristics of *B. tabaci* that contribute to its pest status and promote resistance development (e.g. breeding system, migratory ability and polyphagy) cannot be manipulated or controlled directly. In most agricultural systems, however, alteration of agronomic practices, such as the timing and placement of crops, could prove the most effective approach of all in reducing whitefly abundance and hence the need for excessive and continuous reliance on insecticide applications (Byrne & Blackmer 1996; Denholm *et al.*

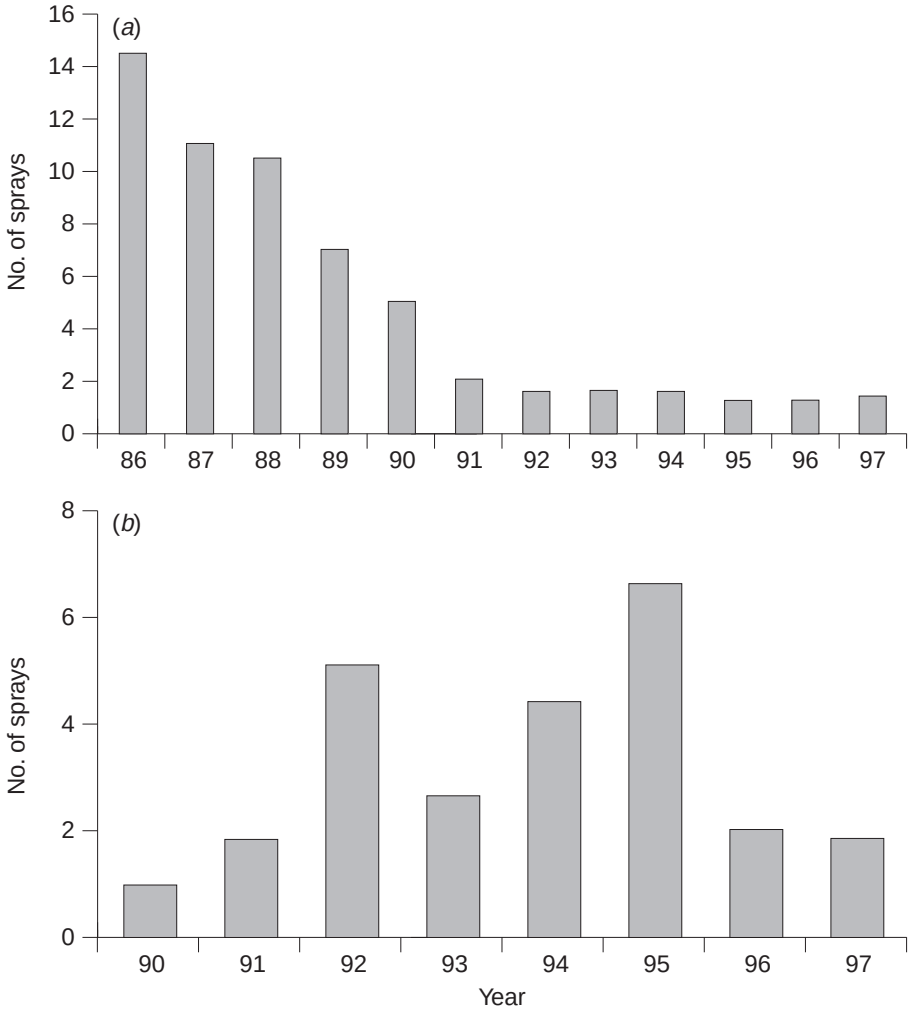

Figure 5. Average number of insecticide sprays applied over successive years against *Bemisia tabaci* on cotton in (*a*) Israel and (*b*) Arizona (data on the latter extracted from Ellsworth (1998)).

1996). In protected horticulture, the use of 'crop-free' periods, although conflicting with many crop-production schedules, is the simplest way to achieve the same objective (Sanderson & Roush 1995). A second, broad approach entails diversifying control tactics to the greatest extent possible, reserving chemicals as the last line of defence. The planting of pest-or virus-tolerant cultivars (see, for example, Nateshan *et al*. 1996), augmentative releases of natural enemies (Hoelmer 1996), application of mineral oils or detergents (Liu & Stansly 1995), and physical barriers to pest movement (Berlinger & Lebuish-Mordechi 1996), all have potential utility in the field and/or protected environments, but require detailed research to tailor them to local conditions. The third set of possible reforms relate to rationalizing and optimizing the way that insecticides are applied, in order to exploit the full diversity of chemicals available and avoid protracted selection for particular resistance mechanisms. The extent to which such reforms can themselves trigger reduced and more sustainable use of insecticides is demonstrated by resistance-management strategies implemented on cotton in Israel and, more recently, in the southwestern USA.

The Israeli strategy was introduced in 1987 in response to increasing failures to control *B. tabaci* with pyrethroids, carbamates and OPs. Its initial purpose was to combat resistance to conventional chemicals through pre-planned rotations of insecticides, but following the release of newer compounds (especially buprofezin in 1989 and pyriproxyfen in 1991), its primary objective has been to preserve susceptibility to these materials by optimizing and restricting their use to a single treatment per year (Horowitz & Ishaaya 1994, 1996; Horowitz *et al*. 1994). A further goal is to conserve whitefly natural enemies of whitefly in cotton by avoiding the use of broad-spectrum agents against other pests in the early stages of the season. Growers are then advised to use more selective chemicals against the American bollworm, *Helicoverpa armigera* Hubner, and to exploit pheromones for controlling the pink bollworm, *Pectinophora gossypiella* (Saunders). The strategy is therefore designed to contend with the entire pest complex and to minimize effects of controlling lepidopteran pests on the buildup and subsequent abundance of *B. tabaci*.

Aided by extensive education programmes and the centralization of pesticide sales, compliance with these recommendations from growers has been outstanding. One of its primary achievements has been a dramatic reduction in the number of insecticide applications against the entire range of cotton pests, but especially against *B. tabaci*. Treatments against the latter now average less than two per year compared with over 14 per year in 1986 (figure 5*a*). This in turn has created an environment favourable for introducing and restricting

other novel insecticides (e.g. chloronicotinyls and diafenthiuron) that are now available to cotton growers.

Resistance monitoring is an integral component of the Israeli strategy. In many areas there has been little evidence of reduced susceptibility to IGRs, although the development of resistance to pyriproxyfen in localities such as Nachshon (see above) demonstrates potential ecological 'hot spots' where even a single application per year can select for resistance effectively. In such areas it may prove necessary to impose even more severe temporal or spatial restrictions on particular products in the future. Given the overall reduction in dependence on insecticides for managing *B. tabaci*, the diversity of chemicals now available, and the exceptional degree of cooperation achieved between Israeli researchers, advisors and growers, this is not an impractical proposition.

The situation on cotton in central Arizona in 1995 resembled that in Israel in the late 1980s. Faced with widespread resistance to most conventional insecticides, and increasing control failures with synergistic combinations of pyrethroids and OPs, growers embarked on a resistance treadmill, applying 8–12 whitefly treatments in the most seriously affected areas, and still having cotton discounted by buyers owing to honeydew contamination (Dennehy & Williams 1997).

A speedy response to this crisis was made possible by unprecedented cooperation between local researchers, grower organizations and agrochemical companies, who jointly petitioned the US Environmental Protection Agency (EPA) with a highly unusual request for simultaneous (Section 18) emergency exemption from registration for the two IGRs, buprofezin and pyriproxyfen. The application for a dual exemption was based on resistance-management objectives, and in particular the need to diversify chemical inputs to the greatest extent possible. Supported by data from Israel and the UK demonstrating the resistance risks posed by these compounds, the application also restricted both IGRs to a single application per cotton season.

The resistance-management strategy introduced in Arizona in 1996 divided insecticide use against *B. tabaci* into three stages. The first comprised one or both IGRs, the second non-pyrethroid conventional insecticides, and the third no more than two applications of synergized pyrethroids (Dennehy & Williams 1997; Dennehy & Denholm 1998). As in Israel, however, the effectiveness of IGRs in reducing whitefly densities in cotton have in many cases made pyrethroid treatments unnecessary. Not only have growers adopting the strategy reported greatly improved control of *B. tabaci*, but statewide averages for the number of whitefly treatments per season are estimated to have been reduced from 6.6 in 1995 to 2.0 in 1996 and 1.8 in 1997 (Ellsworth 1998) (figure 5*b*). In addition, statewide resistance monitoring has shown *B. tabaci* to have regained susceptibility to synergized pyrethroids and key non-pyrethroids in each year since implementation of the strategy (Dennehy & Williams 1997; Dennehy & Denholm 1998).

Despite the success of the Arizona strategy so far, there are no grounds for complacency. In the light of experience with pyriproxyfen in Israel, and the vulnerability of cotton insecticides to resistance under ecological conditions in central Arizona (Dennehy *et al.* 1996), susceptibility of *B. tabaci* to both IGRs is being carefully monitored to anticipate potential resistance problems. When the Section 18 exemption expires at the end of 1998, restrictions on IGRs on cotton will no longer be mandatory, and they are likely to be used on other *B. tabaci* hosts as well (Dennehy & Denholm 1998). There is also concern over the future use of chloronicotinyls on cotton. At present, imidacloprid is applied primarily as a systemic soil treatment to vegetables, and its effectiveness has greatly reduced the number of whiteflies moving from vegetables to cotton early in the year. The anticipated introduction of newer choronicotinyls on cotton would, like the use of IGRs on vegetables, remove the present division of chemistry between crops and place all new insecticides under greater threat from resistance. Avoiding a return to the treadmill of uncontrollable resistance in *B. tabaci* without legislative support is going to place extreme demands on public- and private-sector personnel collectively to limit and harmonize insecticide use in agro-ecosystems in Arizona.

5. CONCLUSIONS

The introduction of resistance-management strategies for *B. tabaci* in Israel and Arizona represents a significant achievement for cotton production in both regions. On a broader scale, these strategies have demonstrated that even spiralling resistance problems in seemingly intractable pest species can be countered effectively by taking full but judicious advantage of the range of chemicals available, and by exploiting the species-selectivity of many new molecules. They have also highlighted the importance of proactive resistance monitoring as a means of evaluating the sustainability of resistance-management recommendations.

In many agricultural systems, the ultimate challenge in combating resistance is not simply to formulate countermeasures but to achieve their implementation amid the commercial and socio-economic pressures that drive the use of pesticides. When reviewing pest management strategies on cotton, Sawicki & Denholm (1987) identified three features likely to assist considerably in this regard. These were: (i) a history of well-documented failures due to resistance; (ii) a good entomological infrastructure for formulating and communicating management recommendations; and (iii) means of regulating the distribution and/or use of agrochemicals. The first two of these unquestionably apply in Israel and Arizona. The third has also been achieved, but in different ways. In Israel, centralization of pesticide sales by the Israel Cotton Board, coupled with discounts on recommended insecticides, has long proved to be a powerful tool for encouraging compliance by growers (Horowitz *et al.* 1994). In Arizona, it is unlikely that the current restrictions on IGRs could have been achieved without the regulatory support provided by the Section 18 exemption, and it remains uncertain whether restrained use of IGRs will be maintained after its expiry (Dennehy & Denholm 1998). Arizona growers recognize the financial and operational benefits that the strategy has already provided, and insecticide manufacturers recognize its importance for the sustainability of their products. Yet it remains to be

determined whether Arizona will resort to further regulatory action, such as special label restrictions, or simply promote voluntary compliance with once-per-season use of IGRs once federal approval is granted.

One of the primary threats to managing resistance in *B. tabaci* throughout the world is the continuing, indiscriminate use of insecticides in glasshouses and greenhouses. When reviewing options for resistance management in protected horticulture, Sanderson & Roush (1995) rightly emphasized the extreme importance, and feasibility, of adopting cultural and biological control practices as alternatives to insecticides. This message has been aired repeatedly, but with such limited success to question whether new molecules should be registered for use on protected crops other than within the framework of an established and clearly defined integrated control strategy (Denholm *et al.* 1998). Denying such growers unrestricted access to novel chemistry may seem a radical step, but could have the benefit of forcing the implementation of proven non-chemical control tactics that are often far less exploitable by those attempting to combat resistance development under open-field conditions.

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