

# MIGRATION OF COTTON PESTS: PATTERNS AND IMPLICATIONS FOR MANAGEMENT

P. C. GREGG

Department of Agronomy and Soil Science, University of New England, ARMIDALE, NSW 2351, AUSTRALIA

## Introduction

Cotton has a large pest complex (Matthews, 1989), and many of the major pests are migratory to some degree. Kennedy (1975) distinguished insect migration from dispersal because of the persistent, straightened-out movement, and unresponsiveness to appetitive stimuli, shown by migrants. The term migration has been used in many senses, but in this review it will describe the long-range end of a continuum of movement (Farrow and Daly, 1987). This continuum ranges from trivial, appetitive movement below the biological boundary layer (for example, within or above a cotton crop) to prolonged flight in the geostrophic layer of the atmosphere, where winds can be strong and downwind displacements are of the order of tens to thousands of kilometres.

Taylor (1986) recognised four categories of migration. Most insects, including all the cotton pests studied to date, exemplify his second category, dynamic migration. In this, the organism actively initiates migration, and may have partial control of navigation through cross or down-wind orientation (Westbrook *et al.*, 1994), selection of flight altitude (Drake, 1985; Beerwinkle *et al.*, in press), or cessation of flight. Often, though, control is very limited. Migrants may be carried to areas unsuitable for breeding, such as out to sea (Farrow, 1985; Sparks *et al.*, 1986). Despite such failures, and the costs sometimes associated with migration (reproductive delay, reduced fecundity and longevity, and increased development time; Rankin and Burchsted, 1992) dynamic migration persists because of its advantages as an ecological strategy (Dingle, 1972). It allows escape from deteriorating habitats and colonisation of new ones. Such spatial re-distribution occurs between generations: in this type of migration the same individuals do not return to the source area, though subsequent generations may.

## Migration in Cotton Pests

Assessment of the incidence and importance of long-range migration in cotton pests is hampered by the fact that migration researchers have developed the ecological and physiological theory of migration by focussing on a few species (e.g. Rainey, 1989), such as the desert locust *Schistocerca gregaria* (Forsk.) the armyworms *Spodoptera exempta* (Walker) and *Mythimna separata* (Walker), and the spruce budworm *Choristoneura fumiferana* (Clemens). However, these are not cotton pests. On the other hand, cotton entomologists tend to focus on the cotton crop. Often, our charters are constrained by regional or national boundaries of limited relevance to migrating insects. Too frequently, we have little incentive or opportunity to investigate the entomology of neighbouring crops, let alone non-cropping areas which may be hundreds of kilometers away.

These problems are illustrated by a survey of the literature in the AGRICOLA database for the years 1983-1993, undertaken for this review (Table 1). Computer searches combined genus or species names with the term "migration", or the more general terms "movement",

"dispersal" or "flight". For comparison some species were included which are not cotton pests, but are well known migrants or are non-migrants.

The results clearly indicated that there has been limited emphasis on migration and movement in cotton pests. Only for the *Helicoverpa/Heliothis* complex and (to a lesser extent) for *Spodoptera* spp. was there an appreciable literature on migration. For other species, there were a few papers on movement, dispersal and flight. However, these often related to trivial movement. For example, the flight literature on *Pectinophora* spp. dealt mostly with flight to pheromones, reflecting the importance of mating disruption in *P. gossypiella* (Saunders). For other lepidopterans (*Earias* and *Diparopsis* spp.), there were no papers on either migration or movement in general. This trend suggests that either cotton pests are notably sedentary, or (more likely) that migration is a neglected field of research in cotton entomology.

For hemipterans, there were almost no papers on migration, and very few on movement in general. Yet related pests of other crops are known to be capable of exceptionally long migrations. Many studies using airborne trapping show that hemipterans are among the most common insects moving above the boundary layer, both by day and by night. They are also often trapped on ships far from shore, in numbers which greatly exceed those of the better-known lepidopteran migrants (Bowden and Johnson, 1976). In temperate crops, the biology and ecology of aphid migration has been extensively studied, and applied to pest management (Taylor, 1985; Hendrie *et al.*, 1985). There are no such studies with the important hemipteran pests of cotton, such as *Aphis gossypii* Glover and *Bemisia tabaci* (Gennadius), though recent work (Blackmer and Byrne, 1993) demonstrates that *B. tabaci* has similar behavioural and flight patterns to aphid migrants.

Changing pest management priorities sometimes illuminate the need for migration studies. In Virginia and North Carolina, eradication of the boll weevil *Anthonomus grandis grandis* Boheman has improved the outlook for cotton, but also increased the pest status of species such as *Spodoptera exigua* (Hübner) and *Acrosternum hilare* (Bacheler, these proceedings). Information on the migratory patterns of the new pests is very limited. Moreover, the eradication program itself is exposing the scanty knowledge of boll weevil migration, despite the well-documented capacity of this species for long-distance movement (Guerra, 1988; Moody *et al.*, 1993). Similarly, in Australia, the green mirid *Creontiades dilutus* (Stal) is likely to emerge as a major cotton pest following the adoption of transgenic varieties resistant to *Helicoverpa* spp. (Fitt, 1994). Although there is strong circumstantial evidence that this pest is a migrant (M. Miles, pers. comm. 1994), we have almost no information on the sources, timing and extent of migration.

These considerations suggest that there is an urgent need for more research on migration in cotton pests, particularly those (such as most hemiptera) which have received almost no attention to date. However, there is also a need for careful prioritising and planning of potentially expensive research efforts. Too often, pests are labelled as migrants on the basis of increases in populations which are not obviously due to local emergence, without full consideration of alternative explanations including undetected emergence, local concentration or intercrop movement. Even when migration is real, identifying it does little to assist pest management unless source areas can be clearly identified and the factors (physiological, ecological and meteorological) which produce migratory patterns can be understood. Indeed, a little knowledge of migration might be dangerous, encouraging the belief that the source of pest problems lies elsewhere so little can be done locally, thus exacerbating psychological dependence on pesticides.

*Unifying principles in migration research, and their application to cotton pests*

Understanding the physiological, ecological and meteorological factors which initiate, maintain and terminate migration requires integrating very diverse information. There are, however, two unifying hypotheses in migration research which provide a framework for this difficult task. Though both are still somewhat controversial, it is useful to consider their relevance to the migration of cotton pests, especially the *Helicoverpa/Heliothis* complex.

### The reproduction-flight syndrome

The reproduction-flight syndrome hypothesis originated with observations by Johnson (1969), and others, that long-distance migration is essentially a pre-reproductive phenomenon. According to the hypothesis, reproduction and migratory flight are two opposing physiological states, more or less mutually exclusive. Reproductive processes (development of the ovaries, pheromone release and mating) inhibit migratory processes (wing and wing-muscle development, flight fuel use, migratory behaviour), and vice-versa. Rankin *et al.* (1986) describe neuroendocrine mechanisms, especially those involving juvenile hormone, which might form the basis for this dichotomy in some species.

An alternative view of the reproduction-flight syndrome has been proposed by Sappington and Showers (1992). They argue that reproduction and migration are not necessarily physiological alternatives, though various selection pressures might converge to ensure that migration is pre-reproductive in some (but not all) species. In this view, the reproduction-flight syndrome is only a convenient description for pre-reproductive migration, with little explanatory power.

The important difference between the two views is that, if reproduction and migration are alternative physiological states, any factor (environmental or genetic) which increases the pre-reproductive period will widen the migration window. Since pre-reproductive periods are much easier to study than migratory behaviour, they can provide useful insights into migration patterns.

Among cotton pests, almost all the evidence comes from the *Helicoverpa/Heliothis* complex. There is little doubt that most long-distance migration in these pests is pre-reproductive. Both males and females quickly leave environments unsuitable for larval survival. The females are usually unmated and the males do not come to pheromone traps (*H. armigera*, Roome, 1975; *H. zea*, Lindgren *et al.*, 1988; Raulston *et al.*, 1990; *H. punctigera*, Gregg *et al.*, in press). Females caught in the process of migration (in tower-mounted light traps) are usually but not always reproductively immature and/or unmated (*H. zea*, Callahan *et al.*, 1972; *H. punctigera* and *H. armigera*, Coombs *et al.*, 1993). Whether reproduction and migration are physiologically opposed in *Helicoverpa/Heliothis* is less certain. The evidence comes from studies of the effects of mating and oviposition on flight mill performance. In Indian female *H. armigera*, Armes and Cooter (1991) found marked suppression of flight by mating. Colvin and Gatehouse (1993a) obtained similar results from female (but not male) African *H. armigera*. However, earlier studies by Hackett and Gatehouse (1982) failed to reveal this effect, as did studies on Australian *H. armigera* and *H. punctigera* by Coombs (1993). Perhaps these differences are related to variation in techniques; the interpretation of results obtained from tethered flight studies requires caution.

Several studies have investigated the genetic and environmental factors which affect the pre-reproductive period in *Helicoverpa/Heliothis*. There is geographic and genetic variation in *H. armigera* and *H. punctigera* (Colvin and Gatehouse, 1993b; Coombs, 1993), and both pre-reproductive periods and flight performance have significant estimates of heritability in *H. armigera* (Colvin and Gatehouse, 1993a, b). Physical factors such as temperature,

photoperiod and relative humidity seem to have relatively minor effects in *H. armigera* and *H. punctigera* (Colvin and Gatehouse, 1993c; Coombs, 1993). This contrasts with the situation in some other seasonally migratory noctuids (McNeil, 1986). On the other hand, the availability of adult food (sugar solution or honey) substantially shortens the pre-reproductive period and increases fecundity. In *H. armigera*, the presence of flowering plants appears to encourage sedentary behaviour and short pre-reproductive periods (Roome, 1975; Wardhaugh *et al.*, 1980; Topper, 1987; Riley *et al.*, 1992). For this reason, *H. armigera* is generally considered to be a facultative migrant. Migration may be a function of the adult food supply, but other interactions might also be involved. For example, Raina *et al.* (1992) found that volatiles from silking maize markedly increased pheromone production in *H. zea*. Such mechanisms may be less important in other species, such as *H. punctigera*, which frequently emigrates from what appear to be suitable breeding habitats, and is therefore sometimes regarded as an obligate migrant (Gregg *et al.*, in press). There is a need for further research on the physiological linkage between migration and reproduction, and the factors influencing the facultative/obligate dichotomy, both in *Helicoverpa/Heliothis* and in other cotton pests.

### Return migration and the "pied piper" hypothesis

For most subtropical and temperate insects, it is much easier to find evidence for migration to higher latitudes in spring than for reverse migration in the autumn. In part, this may be because the spring migrations are more conspicuous. However, in many species the bulk of migration appears to be a one-way pattern rather than a closed-loop. Rabb and Stinner (1979) termed this the "pied-piper" effect, and attributed it to the creation by agriculture of temporary habitats in regions climatically unsuitable for permanent survival of the pests. Walker (1980) argued that this effect presented an evolutionary dilemma. Migration should be selected against, because genotypes favouring migration would be lost from the gene pool in source regions. However, other authors (Stinner *et al.*, 1983; Farrow and Daly, 1987; Gregg *et al.*, in press) suggested that the same physiological and behavioural characteristics which can produce genetic losses through unsuccessful migrations and the pied-piper effect are essential to survival in patchy environments in source regions.

This question has not been resolved in relation to cotton pests. In North America, *H. zea* is known to migrate southward in the autumn, selectively using northerly airflows including post-frontal winds (Pair *et al.*, 1987; Beerwinkle *et al.*, in press). By contrast, there is as yet no evidence of return summer or autumn migration of *H. punctigera* from cropping regions to the inland of Australia to balance the large spring migrations in the opposite direction (Gregg *et al.*, in press), though catches in tower-mounted light traps indicate extensive movement of both *H. punctigera* and *H. armigera* in the summer and autumn in northeastern New South Wales (Gregg *et al.*, 1993b).

### *Helicoverpa/Heliothis migration: an international perspective*

#### *H. zea/H. virescens* in North America

In North America (Fig. 1), *H. zea* appears to be more migratory than *H. virescens*. There are several studies which indicate migration from northern Mexico and southern Texas towards the northeast in spring (Hartstack *et al.*, 1982, 1986; Rummel *et al.*, 1986; Wolf *et al.*, 1990). The main atmospheric transport systems for these migrations are the strong, warm pre-frontal winds which occur in March and April (Muller and Tucker, 1986). The longest of these spring migrations, 700-1000 km into Oklahoma and Arkansas, have been tracked using

as markers of origin moth-borne pollen from plants growing only in the source regions (Hendrix *et al.*, 1987; Lindgren *et al.*, 1993). However, it is likely that *H. zea* migrations extend beyond this. The summer range of the species extends to 59°N in Canada, well beyond the northern limit for overwintering (Hardwick, 1965).

For these spring migrations, the importance of a discrete source region, the large quantity of maize in the lower Rio Grande valley, has been clearly documented. Raulston *et al.* (1990, 1992) have shown that this area produces several billion moths each spring, most of which appear to emigrate. An emergence of this size could produce enough moths to generate economically significant infestations over many millions of hectares. Wolf *et al.* (1990), using airborne radar, tracked a cloud of moths from this region north to the San Antonio area, about 400 km, in one night. *H. zea* is the only *Helicoverpa/Heliothis* species in which return migration has been clearly shown (Pair *et al.*, 1987; Beerwinkle *et al.*, in press). Recent radar observations have shown large numbers of insects moving southward on post-frontal winds in the autumn.

For *H. virescens*, the evidence for migration is more limited and circumstantial. Several mark-recapture studies have demonstrated the ability of the species to move up to 100 km (Hendricks *et al.*, 1973; Haile *et al.*, 1975; Raulston, 1979; Schneider *et al.*, 1989). It has also been captured (along with *H. zea*) on oil wells up to 160 km offshore in the Gulf of Mexico (Sparks *et al.*, 1986). Large areas of wild hosts occur in northern Mexico, and senesce during spring. Raulston and Houghtaling (1986) believe that emigration from these areas could account for early season infestations on cotton, which are otherwise difficult to explain.

#### *H. armigera* in India

In India (Fig. 2), cotton growing areas are more tropical. Migration is less conspicuous and more difficult to relate to seasonal conditions and weather patterns. Nevertheless, Pedgley *et al.* (1987) provided circumstantial evidence of migration from coastal Andhra Pradesh to the Hyderabad region (a distance of about 500 km). Unexpected trap catches in the post-rainy season coincided with southeasterly winds. Inferences drawn from temporal and spatial changes in the frequency of resistance to synthetic pyrethroids (Armes *et al.*, 1992) support this hypothesis, and also suggest that migration in the opposite direction occurs during the rainy season.

Studies by Riley *et al.* (1992) using radar and other techniques did not provide evidence for long-distance migration originating from central India in the post-rainy season. Most movement occurred at altitudes below 10 m, and the results were considered to illustrate the facultative nature of migration in *H. armigera*. On the other hand, mark-recapture experiments conducted at a similar time of the year were thought to indicate rapid exodus from the treated field, possibly including long-range migration (King *et al.*, 1990).

#### *H. armigera* in Africa, Europe and the Middle East

There is circumstantial evidence of *H. armigera* migration in Africa, Europe and the Middle East (Fig. 3). Comparisons by Pedgley (1985) of unexpected trap catches with synoptic weather patterns suggest that spring migration on southerly and southeasterly winds from southern Europe and northern Africa to the U.K. and northern Europe occurs quite frequently. *H. armigera* has been recorded as far north as 62°N in Finland, well beyond the limits for overwintering (Mikkola, 1984; cited by Pedgley, 1985). On the assumption of a source in southern Europe or northern Africa, this would indicate a migration of about 2000

km. Together with a record of moth arrival on Ascension Island in the South Atlantic Ocean (Bowden and Johnson, 1976), this represents the longest documented migration of *H. armigera*. Unexpected trap catches also occur in Cyprus and Turkey on southeasterly winds (Pedgley, 1986). Since there are extensive areas of desert to the southeast, the source of these moths is not clear.

In the Sudan, Haggis (1981) and Madden *et al.* (1993) have shown that the spatial distribution of *H. armigera* oviposition on cotton is consistent with extensive movement over tens of kilometers and subsequent concentration in local areas, and that these movements are probably associated with rainfall.

### *H. armigera* and *H. punctigera* in Australia

In Australia (Fig. 4), *H. armigera* is also a migrant. Patterns of genetic variation (Daly and Gregg, 1985) are consistent with substantial gene flow between widely separated populations. The species has been recorded arriving on offshore islands up to 1200 km from the mainland (Holloway, 1977; Farrow, 1985). Studies of the spread of resistance to pyrethroids in unsprayed areas of northern New South Wales indicate extensive movement over distances of several hundred km (Gunning and Easton, 1989). Finally, the species is a component, though a minor one, of the major spring migrations which originate from native hosts in inland Australia (Gregg *et al.*, 1993a; Gregg *et al.*, in press). Studies using moth-borne pollen markers (Gregg, 1993) suggest that a substantial proportion of the moths arriving in cotton growing areas of northern New South Wales in early spring (before local emergence) are immigrants from the inland.

*H. punctigera* is the most migratory of the Australian *Helicoverpa* species. It has also been recorded arriving at offshore islands (Holloway, 1977; Farrow, 1985). Drake *et al.* (1981) have tracked migrations across Bass Strait to Tasmania, and Fox (1978) has recorded the arrival of specimens of Australian origin on the west coast of New Zealand. The latter migration involved continuous flight across water of about 2200 km, and is the longest documented migration of any *Helicoverpa/Heliothis* species. Large scale migration of *H. punctigera* from sources in inland Australia occurs regularly in early spring. In Western Australia these immigrants, carried on westerly and northwesterly winds, principally infest lupins (Walden, in press). In the east, they affect a range of crops including cotton (Gregg *et al.*, 1993a; Gregg *et al.*, in press). More than in any other *Helicoverpa/Heliothis* species, migration in *H. punctigera* appears to be an adaptation to erratic rainfall. The vast inland of Australia is semi-arid to arid, but rainfall is erratic and irregular heavy falls can occur. If rain falls in autumn or early winter, extensive growth of native annuals can result. Zalucki *et al.* (1994) have recorded 47 species of these plants which are probable hosts for one or both *Helicoverpa* species. With the arrival of hot dry weather in spring, these hosts rapidly senesce. Moths emigrate on westerly or northwesterly winds, and trajectory analyses have indicated that distances of up to 1000 km could be covered in a single night (Hamilton *et al.*, 1994). Pollen studies suggest that many of the moths appearing in northeastern New South Wales and southeastern Queensland in early spring are migrants (Gregg, 1993). The sources vary between years; in 1990 heavy rain in southwestern Queensland led to extensive winter breeding, whereas in 1991 this area was dry and the main breeding region was about 1000 km to the west (Gregg *et al.*, 1993a).

### *Implications of migration for management*

Migration presents both threats and opportunities for pest management in cotton. Both threats and opportunities arise from movement of all types along the continuum from local to long-range movement (Farrow and Daly, 1987), not just long-range migration. However, a major obstacle to neutralising the threats and capitalising on the opportunities is that we are often unable to define the level of movement which gives rise to them.

### Threats

The most obvious threat posed by migration is the risk of sudden, unpredictable upsurges in pest density following immigration. The mere possibility of this may lead risk-averse farmers to use pesticides as insurance, increasing the dangers of resistance, destruction of natural enemies and environmental contamination, as well as increasing the cost of production. The alternative is costly and time-consuming scouting; in Australia, three day intervals are recommended, primarily to guard against sudden increases in *Helicoverpa* oviposition. The procedure is frequently rejected by users as too demanding (Fitt, 1994).

Another threat is the importation of resistance, selected elsewhere, into new cropping areas. Armes *et al.* (1992, and see also these proceedings) blamed migration for much of the spread of pyrethroid resistance in India, which has reached the point where susceptible populations can no longer be found on the subcontinent. Similarly, migration of resistant individuals can be a threat to insecticide resistance management (IRM) schemes. Forrester *et al.* (1993) attributed the gradual failure of the Australian insecticide resistance management scheme for *H. armigera* to the kind of contamination of unsprayed refugia by migrants detected by Gunning and Easton (1989).

Migration can be equally a threat to non-chemical pest management. Fifteen years ago, Knipling (1979) argued that lack of information on movement of beneficials was a major obstacle to their wider application in pest management programs. This is still true today, and particularly applies to inundative releases (for example, of *Trichogramma* spp.), for which we need to understand the movement of both the beneficials and the pest. Large pest influxes might easily negate the beneficial releases. Similarly, migration can be a major obstacle to reproductive control methods such as hybrid sterility, substerility and mating disruption with pheromones (Knipling, 1979). Attempts to employ mating disruption against the Australian *Helicoverpa* species have so far been defeated by the mobility of mated females (Betts *et al.*, 1993), in contrast to the success which has been achieved with the less mobile *Pectinophora* and *Earias* spp.

Area-wide management remains a major focus for change in cotton pest management, embodying a change in philosophy from current farm-to-farm defensive techniques to a total pest management system (Knipling, 1979; Knipling and Stadelbacher, 1983). In various forms, and with various degrees of success, it has been employed for cotton against pink bollworm, boll weevil and *Helicoverpa/Heliothis*. In all cases, immigration to treated areas has been an obstacle. Mueller *et al.* (1984) considered it to be a potentially fatal difficulty for attempts to manage *Helicoverpa/Heliothis* by reduction of the first spring generation through biological and cultural control.

### Opportunities

The opportunities offered for pest management by migration are frequently mirror images of the threats. For example, while immigration can exacerbate a pest problem, emigration can relieve it. In Australia, *H. punctigera* usually becomes less abundant from mid-season on (Fitt, 1994). It is likely that emigration of this probable obligate migrant is

responsible for the subsidence of many apparently threatening outbreaks. Similarly, while migration can result in the spread of resistance and the contamination of refugia, it is immigration of susceptibles which make many resistance management schemes feasible in the first place. Immigration is probably a pre-requisite for the successful use of high-dose tactics or mixtures (Denholm and Rowland, 1992). Daly and Fitt (1990) have shown that the drop in resistance frequency between seasons which underpins the Australian *H. armigera* IRM scheme (Forrester *et al.*, 1993) is probably due largely to spring immigration of susceptibles. We still do not fully understand the sources of these immigrants. Further work is needed to clarify the relative contributions of local refugia and more distant sources including inland Australia. While the importance of understanding migration for current pesticide IRM schemes has been clearly demonstrated, in the future it is also likely to be vital for the management of transgenic cotton varieties expressing *Bacillus thuringiensis* genes and other resistance characteristics (Fitt, 1992).

### Forecasting

Forecasting is the acid test of our understanding of migration. If we understand the physiology, ecology and meteorology of migration, we will be able to forecast pest population changes on scales of time and space which are directly useful for pest management. Forecasting tests our conceptual models of migration, synthesising information and revealing areas of inadequate knowledge in the same way that validation tests a pest management model. For these reasons, even limited forecasts are useful, provided that end-users (e.g. growers) understand the limitations.

The requirements for useful forecasts are appropriate levels of timeliness, precision (spatial and temporal detail) and accuracy. Often, the limits of these parameters are set by our inability to accurately forecast meteorological conditions favouring migration more than a few days into the future. Nevertheless, useful forecasts are routinely produced for many migratory pests, such as the Australian Plague Locust *Chortoicetes terminifera*. For cotton pests in Australia, forecasts of *Helicoverpa* abundance at two levels are being developed. Regional predictions, especially of *H. armigera*, will be based on the HEAPS model (Fitt *et al.*, in press). Broader predictions of long-range migration and the extent of spring infestations, especially of *H. punctigera*, have been based on surveys of winter breeding in inland Australia, aided by the use of satellite images and a network of pheromone and light traps (Gregg *et al.*, in press). Successful forecasts were made in the years 1990-1992, but routine forecasting awaits the completion of economic analyses and the identification of appropriate funding mechanisms (Dale *et al.*, 1992).

### **Acknowledgments**

I am indebted to N.J. Armes, M. Coombs, J.C. Daly, V.A. Drake, G.P. Fitt, N.W. Forrester, and J.D. Lopez for their assistance with this review, and for their comments on earlier drafts.

## References

- Armes, N.J. and Cooter, R.J. (1991). Effects of age and mated status on flight potential of *Helicoverpa armigera* (Lepidoptera: Noctuidae). *Physiol. Entomol.* **16**, 131-144.
- Armes, N.J., Jadhav, D.R., Bond, G.S. and King, A.B.S. (1992). Insecticide resistance in *Helicoverpa armigera* in South India. *Pestic. Sci.* **34**, 355-364.
- Bacheler, J.S. (\* these proceedings). Impact of boll weevil eradication on cotton production and insect management in Virginia and North Carolina, USA.
- Beerwinkle, K.R., Lopez, J.D., Witz, J.A., Schleider, P.G., Eyster, R.S. and Lindgren, P.D. (in press). Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes up to 900 meters. *Environ. Entomol.*
- Betts, M.D., Gregg, P.C., Fitt, G.P. and MacQuillan, M.J. (1993). A field trial of mating disruption for *Helicoverpa* spp. in cotton. pp. 298-300 In Corey, S.A., Dall, D.J. and Milne, W.M. (Eds) *Pest control and sustainable agriculture*. CSIRO, Melbourne.
- Blackmer, J.L. and Byrne, D.N. (1993). Flight behaviour of *Bemisia tabaci* in a vertical flight chamber: effect of time of day, sex, age and host quality. *Physiol. Entomol.* **18**, 223-232.
- Bowden, J. and Johnson, C.G. (1976). Migrating and other terrestrial insects at sea. pp. 97-117 In Chang, L. (Ed) *Marine insects*. North-Holland, Amsterdam.
- Callahan, P.S., Sparks, A.N., Snow, J.W. and Copeland, W.W. (1972). Corn earworm moth: vertical distribution in nocturnal flight. *Environ. Entomol.* **1**, 497-503.
- Colvin, J. and Gatehouse, A.G. (1993a). The reproduction-flight syndrome and the inheritance of tethered-flight activity in the cotton-bollworm moth, *Heliothis armigera*. *Physiol. Entomol.* **18**, 16-22.
- Colvin, J. and Gatehouse, A.G. (1993b). Migration and genetic regulation of the pre-reproductive period in the cotton-bollworm moth, *Helicoverpa armigera*. *Heredity* **70**, 407-412.
- Colvin, J. and Gatehouse, A.G. (1993c). Migration and the effect of three environmental factors on the pre-reproductive period of the cotton-bollworm moth, *Helicoverpa armigera*. *Physiol. Entomol.* **18**, 109-113.
- Coombs, M. (1993). Environmental influences on the flight and migratory potential of *Helicoverpa punctigera* and *H. armigera* (Lepidoptera: Noctuidae). Ph.D. Thesis. University of New England, Armidale, New South Wales.
- Coombs, M., Del Socorro, A.P., Fitt, G.P. and Gregg, P.C. (1993). The reproductive maturity and mating status of *Helicoverpa armigera*, *H. punctigera* and *Mythimna convecta* (Lepidoptera: Noctuidae) collected in tower-mounted light traps in northern New South Wales, Australia. *Bull. ent. Res.* **83**, 529-534.
- Dale, M., Gregg, P.C. and Drake, V.A. (1992). *Report of a workshop on developing a Heliothis forecasting service in Australia*. Co-operative Research Centre for Tropical Pest Management, Brisbane, 43.
- Daly, J.C. and Fitt, G.P. (1990). Resistance frequencies in overwintering pupae and the first spring generation of *Helicoverpa armigera* (Lepidoptera: Noctuidae): selective mortality and immigration. *J. Econ. Entomol.* **83**, 1682-1688.
- Daly, J.C. and Gregg, P.C. (1985). Genetic variation in *Heliothis* in Australia: species identification and gene flow in the two pest species *H. armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae). *Bull. ent. Res.* **75**, 169-184.
- Denholm, I. and Rowland, M.W. (1992). Tactics for managing pesticide resistance in arthropods: theory and practice. *Ann. Rev. Ent.* **37**, 91-112.

- Dingle, H. (1972). Migration strategies of insects. *Science* **175**, 1327-1335.
- Drake, V.A. (1985). Radar observations of moths migrating in a low-level jet. *Ecol. Entomol.* **10**, 259-265.
- Drake, V.A., Helm, K.F., Readshaw, J.L. and Reid, D.G. (1981). Insect migration across Bass Strait during spring: a radar study. *Bull. ent. Res.* **71**, 449-466.
- Farrow, R.A. (1985). Detection of transoceanic migration of insects to a remote island in the Coral Sea, Willis Island. *Aust. J. Ecol.* **9**, 253-272.
- Farrow, R.A. and Daly, J.C. (1987). Long-range movement as an adaptive strategy in the genus *Heliothis* (Lepidoptera: Noctuidae): a review of its occurrence and detection in four pest species. *Aust. J. Zool.* **35**, 1-24.
- Fitt, G.P. (1992). *Workshop on the management of Bt toxins in transgenic plants and conventional sprays. Final Report.* Cotton Research and Development Corporation, Narrabri, New South Wales.
- Fitt, G.P. (1994). Cotton pest management: Part 3. An Australian perspective. *Ann. Rev. Ent.* **39**, 543-562.
- Fitt, G.P., Dillon, M.L. and Hamilton, J.G. (in press). Spatial dynamics of *Helicoverpa* populations in Australia: simulation modelling and empirical studies of adult movement. *Computers and Electronics in Agriculture*.
- Forrester, N.W., Cahill, M., Bird, L.J. and Layland, J.K. (1993). Management of pyrethroid and endosulfan resistance in *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Australia. *Bull. ent. Res. Spec. Suppl.* **1**, 132 pp.
- Fox, K.J. (1978). The transoceanic migration of Lepidoptera to New Zealand - a history and a hypothesis on colonisation. *N.Z. Entomol.* **6**, 368-380.
- Gregg, P.C. (1993). Pollen as a marker for migration of *Helicoverpa armigera* and *H. punctigera* (Lepidoptera: Noctuidae) from western Queensland. *Aust. J. Ecol.* **18**, 209-219.
- Gregg, P.C., Fitt, G.P., Zalucki, M.P., Murray, D.A.H. and McDonald, G. (1993a). Winter breeding and spring migration of *Helicoverpa* spp. in inland Australia, 1989-1991. pp. 460-463 In Corey, S.A., Dall, D.J. and Milne, W.M. (Eds) *Pest control and sustainable agriculture*. CSIRO, Melbourne.
- Gregg, P.C., Fitt, G.P., Coombs, M. and Henderson, G.S. (1993b). Migrating moths (Lepidoptera) collected in tower-mounted light traps in northern New South Wales, Australia: species composition and seasonal abundance. *Bull. ent. Res.* **83**, 563-578.
- Gregg, P.C., Fitt, G.P., Zalucki, M.P. and Murray, D.A.H. (in press). Insect migration in an arid continent: II. *Helicoverpa* spp. in eastern Australia. In Drake, V.A. and Gatehouse, A.G. (Eds) *Insect migration: physical factors and physiological mechanisms*. Cambridge University Press, Cambridge.
- Guerra, A.A. (1988). Seasonal boll weevil movement between northeastern Mexico and the Rio Grande valley of Texas, USA. *Southwest. Ento.* **13**, 261-271.
- Gunning, R.V. and Easton, C.S. (1989). Pyrethroid resistance in *Heliothis armigera* (Hübner) collected from unsprayed maize crops in New South Wales 1983-1987. *J. Aust. Ent. Soc.* **28**, 57-62.
- Hackett, D.S. and Gatehouse, A.G. (1982). Studies on the biology of *Heliothis* spp. in the Sudan. *Proceedings of the International Workshop on Heliothis Management, 15-20 November 1981, Patancheru, A.P., India*. International Crops Research Institute for the Semi-Arid Tropics: Patancheru, A.P. India, 29-38.

- Haggis, M.J. (1981). Spatial and temporal changes in the distribution of eggs of *Heliothis armiger* (Hübner) (Lepidoptera: Noctuidae) on cotton in the Sudan Gezira. *Bull. ent. Res.* **71**, 183-193.
- Haile, D.G., Snow, J.W. and Young, J.R. (1975). Movement by adult *Heliothis* released on St. Croix to other islands. *Environ. Entomol.* **4**, 225-226.
- Hamilton, J.G., Rochester, W.A. and Gregg, P.C. (1994). Predicting long-distance migration of insect pests in eastern Australia. *Proceedings of the American Meteorological Society 11th Conference on Biometeorology and Aerobiology*. San Diego, March 7-10, 1994.
- Hardwick, D.F. (1965). The corn earworm complex. *Mem. Ent. Soc. Can.* **40**, 247.
- Hartstack, A.W., Lopez, J.D., Muller, R.A., Sterling, W.L., King, E.G., Witz, J.A. and Eversull, A.C. (1982). Evidence of long-range migration of *Heliothis zea* (Boddie) into Texas and Arkansas. *Southwest. Ento.* **7**, 188-201.
- Hartstack, A.W., Lopez, J.D., Muller, R.A. and Witz, J.A. (1986). Early season occurrence of *Heliothis* spp. in 1982: evidence of long-range migration of *Heliothis zea*. pp. 48-60 In Sparks, A.N. (Ed) *Long-range migration of moths of agronomic importance to the United States and Canada: specific examples of occurrence and synoptic weather patterns conducive to migration*. U.S. Department of Agriculture, Agricultural Research Service, ARS **43**.
- Hendrie, L.K., Irwin, M.E., Liquido, N.J., Ruesin, W.G., Mueller, E.A., Voegtlin, D.J., Achtemeier, G.L., Steiner, W.M. and Scott, R.W. (1985). Conceptual approach to modelling aphid migration. pp. 541-582 In MacKenzie, D.R., Barfield, C.S., Kennedy, G.C., Berger, R.D. and Taranto, D.J. (Eds) *The movement and dispersal of agriculturally important biotic agents*. Claitor's Publishing, Baton Rouge.
- Hendricks, D.E., Graham, H.M. and Raulston, J.R. (1973). Dispersal of sterile tobacco budworms from release points in northeastern Mexico and southern Texas. *Environ. Entomol.* **2**, 1085-1088.
- Hendrix, W.H., Mueller, T.F., Phillips, J.R. and Davis, O.K. (1987). Pollen as an indicator of long-distance movement of *Heliothis zea* (Lepidoptera: Noctuidae). *Environ. Entomol.* **16**, 1148-1151.
- Holloway, J.D. (1977). *The Lepidoptera of Norfolk Island: their biogeography and ecology*. W. Junk: The Hague, 291.
- Johnston, C.G. (1969). *Migration and dispersal of insects by flight*. Methuen, London, 761.
- Kennedy, J.S. (1975). Insect dispersal. p. 119 In Pimentel, D. (Ed) *Insects, science and society*. Academic Press, New York.
- King, A.B.S., Armes, N.J. and Pedgley, D.E. (1990). A mark-capture study of *Helicoverpa armigera* dispersal from pigeonpea in southern India. *Ent. exp. applic.* **55**, 257-266.
- Knipling, E.F. (1979). Strategic and tactical use of movement information in pest management. pp. 41-57 In Vaughan, C.R., Wolf, W. and Klassen, W. (Eds) *Radar, insect population ecology and pest management*. NASA Conference Publication No. 2070, NASA Wallops Flight Center, Wallops Island.
- Knipling, E.F. and Stadelbacher, E.A. (1984). The rationale for areawide management of *Heliothis* (Lepidoptera: Noctuidae) populations. *Bull. Ent. Soc. Amer.* **29**, 29-37.
- Lindgren, P.D., Warner, W.B., Raulston, J.R., Kehat, M., Henneberry, T.J., Pair, S.D., Zvirgzdins, A. and Gillespie, J.M. (1988). Observations on the emergence of adults from natural populations of corn earworm, *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae). *Environ. Entomol.* **17**, 254-258.

- Lindgren, P.D., Bryant, V.M., Raulston, J.R., Pendleton, M., Westbrook, J. and Jones, G.D. (1993). Adult feeding host range and migratory activities of corn earworm, cabbage looper, and celery looper (Lepidoptera: Noctuidae) moths as evidenced by attached pollen. *J. Econ. Entomol.* **86**, 1429-1439.
- Madden, A.D., Haggis, M.J. and Holt, J. (1993). *Helicoverpa armigera* oviposition on cotton in the Sudan Gezira associated with rainfall. *Crop Prot.* **12**, 51-54.
- Matthews, G.A. (1989). *Cotton insect pests and their management*. Longman Scientific and Technical: Harlow, Essex, 199.
- McNeil, J.N. (1986). Calling behaviour: can it be used to identify migratory species of moths? *Flor. Entomol.* **69**, 78-83.
- Moody, D.S., Bottrell, D.G. and Rummel, D.R. (1993). Late season migration of the boll weevil in the Texas rolling plains. *Southwest. Ent.* **18**, 1-10.
- Mueller, T.F., Harris, V.E. and Phillips, J.R. (1984). Theory of *Heliothis* (Lepidoptera: Noctuidae) management through reduction of the first spring generation: a critique. *Environ. Entomol.* **13**, 625-634.
- Muller, R.A. and Tucker, N.L. (1986). Climatic opportunities for long-range migration of moths. pp. 61-83 In Sparks, A.N. (Ed) *Long-range migration of moths of agronomic importance to the United States and Canada: specific examples of occurrence and synoptic weather patterns conducive to migration*. U.S. Department of Agriculture, Agricultural Research Service, ARS **43**.
- Pair, S.D., Raulston, J.R., Rummel, D.R., Westbrook, J.K., Wolf, W.W., Sparks, A.N. and Schuster, M.F. (1987). Development and production of corn earworm and fall armyworm in the Texas high plains: evidence for reverse fall migration. *Southwest. Ent.* **12**, 89-99.
- Pedgley, D.E. (1985). Windborne migration of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) to the British Isles. *Entomol. Gaz.* **36**, 15-20.
- Pedgley, D.E. (1986). Windborne migration in the Middle East by the moth *Heliothis armigera* (Lepidoptera: Noctuidae). *Ecol. Entomol.* **11**, 467-470.
- Pedgley, D.E., Tucker, M.R. and Pawar, C.S. (1987). Windborne migration of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in India. *Insect Sci. Applic.* **8**, 599-604.
- Rabb, R.L. and Stinner, R.E. (1979). The role of insect dispersal in population processes. pp. 3-16 In Vaughan, C.R., Wolf, W. and Klassen, W. (Eds) *Radar, insect population ecology and pest management*. NASA Conference Publication No. 2070, NASA Wallops Flight Center, Wallops Island.
- Raina, A.K., Kingan, T.G. and Mattoo, A.K. (1992). Chemical signals from host plant and sexual behaviour in a moth. *Science* **255**, 592-594.
- Rainey, R.C. (1989). *Migration and meteorology*. Clarendon Press, Oxford, 314.
- Rankin, M.A. and Burchsted, J.C.A. (1992). The cost of migration in insects. *Ann. Rev. Ent.* **37**, 533-559.
- Rankin, M.A., McAnelly, M.L. and Bodenhamer, J.E. (1986). The oogenesis-flight syndrome revisited. pp. 263-280 In Danthanarayana, W. (Ed) *Insect flight*. Springer-Verlag, Berlin.
- Raulston, J.R. (1979). *Heliothis virescens* migration. pp. 412-419 In Rabb, R.L. and Kennedy, G.C. (Eds) *Movement of highly mobile insects: concepts and methodology in research*. University Graphics, Raleigh, North Carolina.
- Raulston, J.R. and Houghtaling, J.E. (1986). Circumstantial ecological evidence for *Heliothis virescens* migration into the lower Rio Grande valley of Texas from northeastern Mexico. pp. 34-47 In Sparks, A.N. (Ed) *Long-range migration of moths of agronomic*

- importance to the United States and Canada: specific examples of occurrence and synoptic weather patterns conducive to migration. U.S. Department of Agriculture, Agricultural Research Service, ARS 43.
- Raulston, J.R., Summy, K.R., Loera, J., Pair, S.D. and Sparks, A.N. (1990). Population dynamics of corn earworm larvae (Lepidoptera: Noctuidae) on corn in the lower Rio Grande valley. *Environ. Entomol.* **19**, 274-280.
- Raulston, J.R., Pair, S.D., Loera, J., Sparks, A.N., Wolf, W.W., Westbrook, J.K., Fitt, G.P. and Rogers, C.E. (1992). *Helicoverpa zea* (Lepidoptera: Noctuidae) pupa production in fruiting corn in northeast Mexico and south Texas. *Environ. Entomol.* **21**, 1393-1397.
- Riley, J.R., Armes, N.J., Reynolds, D.R. and Smith, A.D. (1992). Nocturnal observations on the emergence and flight behaviour of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in the post-rainy season in central India. *Bull. ent. Res.* **82**, 243-256.
- Roome, R.E. (1975). Activity of adult *Heliothis armigera* (Hb.) (Lepidoptera: Noctuidae) with reference to the flowering of sorghum and maize in Botswana. *Bull. ent. Res.* **65**, 523-530.
- Rummel, D.R., Neece, K.C., Arnold, M.D. and Lee, B.A. (1986). Overwintering survival and spring emergence of *Heliothis zea* (Boddie) in the Texas southern high plains. *Southwest. Ent.* **11**, 1-9.
- Sappington, T.W. and Showers, W.B. (1992). Reproductive maturity, mating status, and long-duration flight behaviour of *Agrotis ipsilon* (Lepidoptera: Noctuidae) and the conceptual misuse of the oogenesis-flight syndrome by entomologists. *Environ. Entomol.* **21**, 677-688.
- Schneider, J.C., Roush, R.T., Kitten, W.F. and Laster, M.L. (1989). Movement of *Heliothis virescens* (Lepidoptera: Noctuidae) in Mississippi in the spring: implications for area-wide management. *Environ. Entomol.* **18**, 438-446.
- Sparks, A.N., Jackson, R.D., Carpenter, J.E. and Muller, R.A. (1986). Insects captured in light traps in the Gulf of Mexico. *Ann. Ent. Soc. Amer.* **79**, 132-139.
- Stinner, R.E., Barfield, C.S., Stimac, J.L. and Dohse, L. (1983). Dispersal and movement of insect pests. *Ann. Rev. Ent.* **28**, 319-335.
- Taylor, L.R. (1985). An international standard for the synoptic monitoring and dynamic mapping of migrant pest aphid populations. pp. 337-420 In MacKenzie, D.R., Barfield, C.S., Kennedy, G.C., Berger, R.D. and Taranto, D.J. (Eds) *The movement and dispersal of agriculturally important biotic agents*. Claitor's Publishing, Baton Rouge.
- Taylor, L.R. (1986). The four kinds of migration. pp. 263-280 In Danthanarayana, W. (Ed) *Insect flight*. Springer-Verlag, Berlin.
- Topper, C.P. (1987). Nocturnal behaviour of adults of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in the Sudan Gezira and pest control implications. *Bull. ent. Res.* **77**, 541-554.
- Walden, K.J. (in press). Insect migration in an arid continent: III. Locust and noctuid migration in Western Australia. In Drake, V.A. and Gatehouse, A.G. (Eds) *Insect migration: physical factors and physiological mechanisms*. Cambridge University Press, Cambridge.
- Walker, T.J. (1980). Migrating Lepidoptera: are butterflies better than moths? *Flor. Entomol.* **63**, 79-98.
- Wardhaugh, K.G., Room, P.M. and Greenup, L.R. (1980). The incidence of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera: Noctuidae) on cotton and other host plants in the Namoi Valley of New South Wales. *Bull. ent. Res.* **70**, 113-131.

- Westbrook, J.K., Wolf, W.W., Lindgren, P.D. and Raulston, J.R. (1994). Flight speed and heading of migrating corn earworm moths relative to drifting tetroons. *Proceedings of the American Meteorological Society 11th Conference on Biometeorology and Aerobiology*. San Diego, March 7-10, 1994.
- Wolf, W.W., Westbrook, J.K., Raulston, J., Pair, S.D. and Hobbs, S.E. (1990). Recent airborne radar observations of migrant pests in the United States. *Phil. Trans. Roy. Soc. Lon. Ser. B.* **328**, 619-630.
- Zalucki, M.P., Murray, D.A.H., Gregg, P.C., Fitt, G.P., Twine, P.H. and Jones, C. (1994). Ecology of *Helicoverpa armigera* (Hübner) and *H. punctigera* (Wallengren) in the inland of Australia: larval sampling and host plant relationships during winter and spring. *Aust. J. Zool.* **42**, 329-426.

Table 1. Results of a computer search of the AGRICOLA database for 1983-93, combining genus and/or species names with the terms "migration", "movement", "flight" and "dispersal". <sup>1</sup> *S. exigua*, *littoralis*, *litura* and *frugiperda*. <sup>2</sup> Including *Empoasca*, <sup>3</sup> *T. cinnabarinus*, *ludeni*, and *urticae*.

Genus & species	Total references retrieved by genus and/or species names	% recovered by "migration"	% recovered by "movement", "flight", & "dispersal"
<b>Migrants</b>			
<i>Schistocerca</i>	382	5.2	7.6
<i>Mythimna</i>	150	8.7	10.7
<i>Agrotis</i>	236	5.1	5.9
<i>Spodoptera exempta</i>	70	18.6	17.1
<b>Non-migrants</b>			
<i>Bactrocera/Dacus</i>	594	0.9	1.5
<i>Chilo</i>	342	0.3	3.2
<i>Aonidiella</i>	88	0.0	4.5
<i>Leptinotarsa</i>	518	0.8	2.3
<b>Cotton pests</b>			
<i>Helicoverpa/Heliothis</i>	2432	1.2	4.2
<i>Spodoptera</i> <sup>1</sup>	1293	0.8	1.5
<i>Pectinophora</i>	292	0.0	3.1
<i>Earias</i>	125	0.0	0.0
<i>Diparopsis</i>	7	0.0	0.0
<i>Bemisia</i>	368	0.0	1.4
<i>Lygus</i>	265	0.8	3.8
<i>Aphis gossypii</i>	216	0.5	1.4
<i>Amrasca</i>	67	0.0	1.5
<i>Jacobiasca/Jacobiella</i> <sup>2</sup>	234	0.0	1.7
<i>Dysdercus</i>	89	0.0	2.2
<i>Thrips</i>	554	0.4	1.1
<i>Frankliniella</i>	170	1.1	2.4
<i>Tetranychus</i> <sup>3</sup>	712	0.6	1.8
<i>Anthonomus</i>	515	0.6	3.7

Figure 1. Documented and suspected migration pathways for *Helicoverpa/Heliothis* in North America. 1 = *Heliothis virescens* and *Helicoverpa zea* (Sparks *et al.*, 1986), 2 = *Heliothis zea* (Raulston and Houghtaling, 1986), 3 = *Helicoverpa zea* (Hartstack *et al.*, 1982), 4 = *Helicoverpa zea* (Wolf *et al.*, 1990), 5 = *Helicoverpa zea* (Hendrix *et al.*, 1987), 6 = *Helicoverpa zea* (Lindgren *et al.*, 1993), 7 = *Helicoverpa zea* (Pair *et al.*, 1987), 8 = *Helicoverpa zea* (Beerwinkle *et al.*, in press). Arrows indicate general direction and distance of migration, not necessarily exact sources and destinations.

Figure 2. Documented and suspected pathways of migration for *Helicoverpa armigera* in India. 1 = Pedgley *et al.* (1987), 2 = Armes *et al.* (1992). Arrows indicate general direction and distance of migration, not necessarily exact sources and destinations.

Figure 3. Documented and suspected pathways of migration of *Helicoverpa armigera* in Africa, Europe and the Middle East. 1 = Pedgley (1985), 2 = Pedgley (1986), 3 = a region of general movement; Haggis *et al.* (1981), Madden *et al.* (1992), 4 = Bowden and Johnson 1976. Arrows indicate general direction and distance of migration, not necessarily exact sources and destinations.

Figure 4. Documented and suspected pathways of migration for *Helicoverpa* spp. in Australia. 1 = *H. armigera* and *H. punctigera* (Farrow, 1985), 2 = *H. armigera* and *H. punctigera* (Holloway, 1977), 3 = *H. punctigera* (Fox, 1978), 4 = *H. punctigera* (Drake *et al.*, 1981), 5 = a region of general movement; Gunning and Easton (1989), Gregg *et al.* (1993b), 6 = *H. punctigera* and a few *H. armigera* (Gregg *et al.*, 1993a; Gregg *et al.*, in press), 7 = *H. punctigera* (Walden, in press).