POTENTIAL FOR DEVELOPING TECHNOLOGY TO CONTROL ADULT NOCTUIDS WITH CHEMICAL ATTRACTANTS FROM PLANTS: BACKGROUND AND WORLD PERSPECTIVE

R.J.V. Joyce and P.D. Lingren

ABSTRACT

Pest outbreaks occur when densities in crops reach an economic injury level. Insect mobility results in spatial changes in densities which, on occasion, are demonstrably the sole causes of pest outbreaks. The effects of these spatial changes on pest outbreaks in general have been vastly underestimated and inadequately studied. The concept of pest management demands new and efficient methods of survey and environmentally acceptable methods of control that are synchronized, often on a very large scale. The possible use of poison baits employing attractants based on chemicals present in host plants of pest species is discussed and presented as a highly practical solution to the problem of overall pest management and one which imposes a minimum environmental burden. Studies of a variety of pests have indicated that spatial redistribution of insect populations by flight is often more important than changes in total numbers in determining the incidence and severity of outbreaks, and that the structure of the wind systems in which they fly dominates their density. Such airborne concentrations, which can derive from very distant or local sources, may result in the sudden arrival in a crop of pest numbers in excess of the economic injury level, or in numbers sufficient to overwhelm indigenous controlling agents.

INTRODUCTION

The initial part of this account deals with experiences in practical pest control operations of the consequences of insect mobility and includes examples other than noctuids to illustrate what the author regards as important concepts. The possible role of plant attractants in the control of noctuid pests of the Old World is also discussed. This discussion does not include noctuids of the Americas.

Protecting crops from insect attack has long been regarded as an agricultural input, like the application of fertilizers or irrigation, to be provided or withheld by the farmer in accordance with his individual assessment of cost/benefit. As Rabb (1970) emphasized, "Pest management deals primarily with populations, communities and eco-systems. Thus, the basic biological discipline involved is unequivocally ecology, and there should be no fuzzy thinking on this fact." However, most pests of crops, particularly arable crops, are highly mobile. Few but specialized insects breed on the same plant or in the same field as that in which it itself was reared. If we are to prevent an insect population from occurring in a crop at damaging densities, we must have knowledge of the source populations that cause those densities and apply our chosen control to that population. As stated by Knipling (1972) ". . . . 100% control on 99% of the host acreage falls far short of the suppression which is achieved when 90% control is achieved on 100% of the host acreage." Essentially, control must be applied on a scale determined by extension in space and the availability in time of the potentially damaging population, not by the artificial constraints imposed by field or farm boundaries.

Cost/benefit analysis must similarly be assessed on an appropriate scale. This is an inescapable consequence of insect mobility and removes the control of many crop pests from the domain of agronomy. Plant attractants may prove to be the best regulators in this more ecological approach to pest management because their use on the necessarily large scale is likely to have the least unwanted side effects. The major problem in pest management is the determination of the spatial and temporal dimensions occupied by the population to be controlled.

Pest Outbreaks. A pest outbreak may be said to occur when the pest density reaches the level of 'Economic Injury', defined as the level at which damage to the crop is roughly equal to the cost of control (Stern et al. 1959). Stern et al. (1959) also defined 'Economic Threshold' as "the density at which control measures should be applied to prevent an increasing pest population from reaching the Economic Injury level." That is, the occurrence of the latter is predictable by the former.

A number of hypotheses have been formulated to explain pest outbreaks and are summarized by Berryman et al. (1987): (1.) dramatic changes in the physical environment (Elton 1942, Greenbank 1956, Andrewartha and Birch 1984); (2.) changes in intrinsic genetic (Chitty 1971) or physiological composition (Wellington 1960); (3.) trophic interactions (Nicholson and Bailey 1935, Joyce 1958); and (4.) life strategies, e.g. r-strategists (Southwood and Comins 1976, Joyce 1982), and escape from regulating influences of natural enemies (Morris 1963).

Studies on which these conclusions are based typically concentrate on discrete populations whose numbers are insignificantly affected by immigration and emigration (these are often assumed to be roughly in balance). But, if pest outbreaks are influenced by immigration or emigration, forecast of population change and economic threshold must also include a statement of the scale of these processes. This is a function of pest mobility - i.e. the flight habit of the adult insect. Knowledge of the flight habits of insect pests is an essential component of a successful control strategy. Whether the control agents to be employed are synthetic pesticides, parasites, pheromones or others, it is flight behavior which determines the spatial and temporal dimensions occupied by the potentially damaging population and, therefore, the scale on which control has to be applied. Among mobile insects, a population may have to be considered as one in a constant state of flux, nicely illustrated by Taylor and Taylor (1977) using a drawing of the stelar structure of the adder's tongue fern

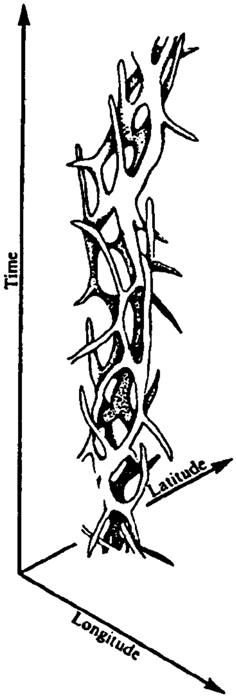

FIG. 1. Conceptual model for population anatomy based on Rostowzew's drawing of the stelar structure of the adder's tongue fern (Taylor and Taylor 1977).

(FIG. 1). The problem now becomes the determination of the dimensions of the area occupied by the population at any one time - the approach advanced by Knipling (1979), Raulston et al. (1982), and other eminenteconomic entomologists. The author has connoted the function of establishing the required scale of a pest control operation 'quasi-synoptic survey' - the dimensions of 'quasi' being the time spent by the stage surveyed within the unit of survey.

Locust control is a notable example of successful pest management, defined as the overall regulation of the number of insects comprising a pest population. In the case of the desert locust, the interdependence of the world population of this species throughout its distribution range was formally recognized in 1956 by a panel of experts. This panel was established under the chairmanship of the late Sir Boris Urarov to advise the Director-General of the FAO on long term policy of desert locust control (FAO 1959). The panel concluded "that there was evidence of swarms produced in one end of the distribution region having, within a couple of generations, a decisive influence on events at the other." Locust invasions can be huge. For instance, Kenya has frequently suffered invading swarms covering in excess of 1000 km^2 containing insects estimated to weigh ca. 100,000 metric tons. This is a dramatic example of the inadequacy of the economic threshold concept for protecting crops against a mobile pest and emphasizes the need to seek and destroy the potentially damaging population as the sole means of avoiding crop loss. This, in the case of the desert locust, is the global population. Locusts are highly mobile, capable of flights resulting in displacements over thousands of kilometers. They move downwind and accumulate in zones of wind-convergence (Rainey 1976), and their density is largely a function of the structure of the air in which they fly (Sayer 1962). Essentially, although they have evolved to select to fly on those winds which in general lead to their survival, once airborne, their destination and success is determined by the winds on which they fly. Other insects are similarly creatures of the winds when airborne, though some highly specialized species have developed the habit of 'station keeping' and can confine their flight to the 'boundary layer' (Taylor 1958) where they can orient themselves to reach a chosen destination. It was such considerations which led us to study the implications to control strategies of the flight habits of insects not considered migratory in the sense of the desert locust.

Rice Stemborers in Indonesia. The pyralid moth *Tryporyza incertulas* (Walker) causes huge losses to the rice crop in Indonesia. Eggs are laid on the flag-leaf and the larvae burrow into the rice stem within minutes of eclosion and are largely inaccessible to destruction by insecticides. The moth and the larva at eclosion, however, are vulnerable to ≤ 2 ppm of phosphamidon placed on the flag leaf. Maximum control could be achieved if the time of application coincided with maximum moth activity, and if the size of the area treated at any one time was sufficient to minimize the effect of recolonization by moths from areas treated at different times. The former requirement was met by establishing an array of light traps, and the latter subject to experiment. In many parts of Java, the rice fields are like a sea dotted with small islands of habitation. However, each individual holding is small (1-2 ha), and each farmer conducts his own pest control in accordance with his assessment of risk. The moth catches at light traps and subsequent paddy rice yields from such fields were compared with those found in areas treated quasi-synchronously by aircraft measuring 500, 1,000, and 5,000 ha. The results, taken from Singh and Sutyoso (1973), are summarized in Table 1. The decrease in moth catch and the increase in yields found in the largest areas were significantly larger than those among the individual farmers. This is the only formal experiment of which the author is aware which investigates the importance of scale in insect control operations.

Similar effects emerged from analysis of the results of large scale operations conducted over two years where it was possible to compare moth catch and paddy yield when control was synchronized and unsynchronized. Fields were discontinuous and intermediate in West and East Java, respectively. The results are summarized in Table 2 and FIG. 2.

None of the rice stemborers (*Tryporyza, Chilo* or *Sesamia*) seem to be recognized as species which engage in adaptive dispersal but have been described as strong fliers (Newsom 1972). Air-speeds ≤2.15 m/s have been recorded for *C. suppressalis* females (Iyatomi and Sekiguti 1936). Rice stemborer moths are caught at light traps chiefly in the early evening and at dawn (Newsom 1972, Soenardi 1967), but their whereabouts between these times is unknown. These belts may move inland with any increase in the on-shore wind at dawn. Possibly, catabolic winds from the mountains could explain the absence of stemborers as pests of rice in the upland terraces. Accordingly massive nightly redistribution of moth populations can be expected.

TABLE 1. Control of Rice Stemborers in Java in Relation to the Extent of the Area Sprayed Synchronously (Singh and Sutyoso).

Method of Treatment	Area (ha) Sprayed Synchronously	% Moth Catch at Light Trap	% Paddy Yield
Aerial ULV	5,000	29.1[a]	194.8
Aerial ULV	1,000	63.0	140.1
Aerial ULV	500	60.0	141.0
Individual Farmers		100.0	100.0

[a] Significantly different from 100.0 (P=0.05)

TABLE 2. Control of Stemborers and Rice Yields in Java. Mean Paddy Yields, December 1969-May 1970(Singh and Sutyoso 1973).

Region	Yield (kg/ha)	
	Synchronized	Unsynchronized
West Java, Indramaju[a]	2,933	1,335
Bekasi-Krawang	3,023	2,186
Central Java, Demak[a]	3,217	2,279
East Java, Bodjonegoro	2,691	2,088

[a] Yield differences between areas of synchronized and unsynchronized control significantly different (P = 0.05).

Cotton Bollworm in the Sudan Gezira. The Sudan Gezira occupies ca. 25,000 km^{2}between the Blue and White Niles, where ca. 800,000 ha of irrigated crops include annually ca. 200,000 ha of *Gossypium barbadense* grown in precise rotation with groundnuts and wheat. These crops are followed by sorghum and leguminous fodder by cooperative

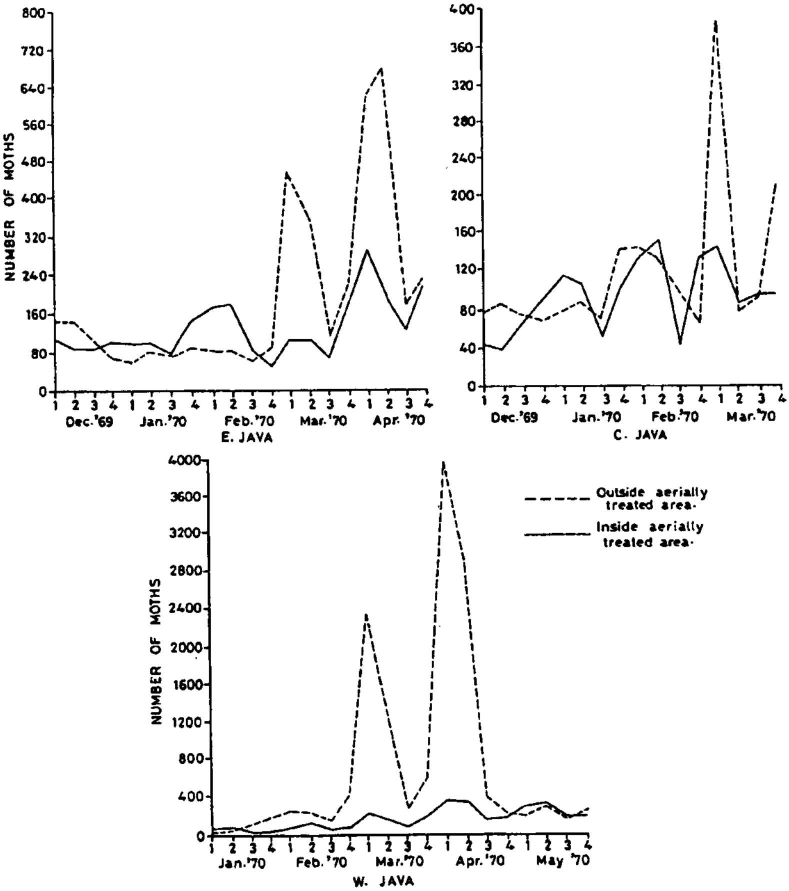

FIG. 2. Effects of synchronized and unsynchronized control on light-trap catches of rice stemborer moths. Synchronized control - spraying by aircraft ULV rates. Unsynchronized control - spraying by individual farmers using knapsack sprayers. Number of moths is the mean *T. incertulas* count per night per trap from weekly catches at ten traps (Singh and Sutyoso 1973).

farming under the common administration of the Sudan Gezira Board. Among the pests of cotton, the noctuid *Heliothis armigera* (Hübner), which is indigenous to the Sudan, assumed increased importance in the 1960's due to changes in agricultural practices and the insecticide spraying schedule, which increased to 4-5 sprays in an attempt to protect cotton buds andyoung bolls from larval damage. Previously, spraying had been confined to a single DDT application against the jassid *Empoasca lybica*. Studies of the behavior and flight activityof *H. armigera,* conducted between 1971 and 1975, showed that the cotton crop was invaded nightly, immediately following sunset, during August, September, and October when the cotton was developing its maximum number of buds. These moths had bred in nearby or distant sources, particularly groundnut fields. These flights have been described in detail

(Schaefer 1976, Haggis 1981, Joyce 1981, Topper 1987). Only a small fraction of the moths (ca. 5%) flew >10 m above ground level, and most of them were engaged intermittently in feeding, mating, and oviposition. While airborne, however, they became displaced downwind several kilometers. Moreover, the density of airborne insects flying at this level during the early evening, including *Heliothis* moths, could be increased 60-fold and displacements over hundreds of kilometers could occur due to convectional storms not infrequent during August and September. Thus, the pattern of oviposition on cotton could change dramatically in a single night over very large areas.

Protecting cotton against bollworms is usually sought from conventional crop spraying techniques directed against larvae when infestations at an economic threshold anticipate increases to the economic injury level. The studies showed that this concept was flawed where the Sudan Gezira was concerned because damaging larval densities arose from moth invasion and not from successive generations within the cotton fields. These studies revealed possible new approaches. Moreover, the moth was found to be more than ten times susceptible than the larvae to the insecticides tested (despite absence of pesticide-induced larval resistance). Moths could collect a lethal dose by direct contact during spraying, by indirect contact with residues on leaves, and by ingesting contaminated nectar (Lawson 1980, Uk and Outram 1979). Dittrich et al. (1979) suggested that the mechanisms of the adult noctuid for developing resistance to pesticides were far less efficient than those available to larvae. Moreover, the newly emerged moths, whose appearance could be accurately predicted from monitoring late instars in groundnut fields, fueled themselves with nectar before their first flight, thus suggesting that control could be achieved outside the cotton fields with minimal insecticidal burden.

Cotton Bollworm in Thailand. Heliothis armigera in Thailand presented a different problem and was investigated over two seasons by Lawson (1980) in the Chaibadan Province, ca. 180 km north of Bangkok. Approximately 1,600 ha of raingrown *G. hirsutum* cotton were grown in 19 blocks within ca. 30,000 ha in rotation with maize, soybeans and sorghum. The origin of the infestation on the advent of the first rains was unclear but was not thought to have been emergence from local diapausing pupae. In the first season, maize, planted in April, supported one or two generations. The progeny then moved to cotton, which was planted in June. Soybeans and sorghum, planted in July and August, served to dilute the moth numbers invading cotton, but supported only one generation. Progeny of this generation colonized cotton and completed three generations. In the second season, maize was planted a month earlier than cotton, while a second planting of maize, concurrent with the planting of sorghum, was followed by light colonization of the cotton crop. By early November, infestations increased to damaging levels by breeding. There was no evidence of flights >1 km by pre-ovipositing females, those colonizing crops having invariably mated and oviposited.

In the Chaibadan area of Thailand, it seemed likely that control involved a largely discrete population of *H. armigera* and would be most effective and economical if directed against the first parents ovipositing on maize. However, much more needs to be known of the ecology of the species in Thailand before definite conclusions can be drawn. A similar increase of numbers to damaging levels through successive generations in cotton was observed on the Tana River development in Kenya (Lawson and Hull 1979).

Cotton Leaf Worm in Egypt. The noctuid *Spodoptera littoralis* (Boisd.) is a major cotton pest in Egypt where it completes three generations in cotton between June and September. In investigating the possibility of control by attacking the adult stage, Lawson (1977) carried out an analysis of four years' data of meteorological and crop factors which might determine the pattern of oviposition on cotton in the Nile Delta and concluded that wind fields had no effect on the redistribution of adult females on a scale ≥20 km (the minimum possible scale from available meteorological data). Further, the daily spatial variations of oviposition strongly suggested that this lack of movement extended ≥10 km. On the contrary, oviposition patterns showed a high degree of correlation with administrative boundaries, the pattern being almost identical in each of the years studied. This would indicate that cropping factors could be affecting the infestation level. The relative areas of rice, cotton, and berseem (lucerne) showed no significant correlation with the level of oviposition, but vegetable crops appeared to have the effect of diluting the infestations on cotton. Thus, in contrast with other noctuids studied, *S. littoralis* seems to engage in very limited dispersal. This is consistent with the very local nature of the outbreaks of this species on cotton in the Sudan Gezira, and is perhaps related to the species' oviposition habit, the female laying 1,000-1,500 eggs in clusters of 300-600 eggs. Each female lays 3-7 batches, the first batch, as a rule, containing the largest number of eggs and was the one considered in Lawson's analysis. Such wing-loading presumably affects flight endurance.

African Armyworm in East Africa. The noctuid *Spodoptera exempta* (Walker) is widely distributed in the Old World, including Southeast Asia and Australia. The larvae feed on grasses, sedges and all graminaceous crops (except sugarcane). Outbreaks are characterized by their extensiveness and severity. For example, in East Africa, outbreaks have been recorded over 24,000 km^2 with larval densities of up to 3000 m^2 and have often caused famine.

The armyworm provides an outstanding example of the dependence of outbreaks on the concentration of airborne moths by wind convergence (Rose et al. 1985). The radar work by Riley et al. (1981,1983) is well known in this connection; these authors found that moths "dispersed rapidly during their migration so that the main influence which led to outbreaks must be a consequence of subsequent reconcentration." Rose and Dewhurst (1979) found that freshly emerged moths, when ready to fly, moved into nearby trees and bushes, where they seek nectar on which they feed avidly before mass departure shortly before dawn.

Spruce Budworm in New Brunswick. The tortricid *Choristoneura fumiferana* (Clem.) provides a nice example of the difference between crop protection and pest control. Miller and Kettela (1975) recorded that, between 1952 and 1973, the percentage reduction in larval infestations following aerial spraying ranged from 76 to 99% and that this control achieved its objective of "keeping the trees green." However, oviposition, which is due to the immigration of moths after the spraying operation, was preferentially on the protected foliage where egg densities could be over 300% higher than on unprotected foliage. Therefore, as long as source moths are available, this form of crop protection, so far from providing pest control (except in a limited sense of space and time), acts to prolong the outbreak.

Characteristics of the flight activity of the spruce budworm moth are well known (Greenbank et al. 1980, Schaefer 1979, Dickison et al. 1983). Data subsequently analyzed have led Rainey (1951) and Haggis (1981) to propose a new hypothesis to account for some otherwise unexplained features of spruce budworm outbreaks. This hypothesis attributes outbreaks in new areas to ovipositing moths which have not only been transported by wind from their emergence site, sometimes for long distances, but have also been concentrated to high densities by wind convergence (Dickison and Neumann 1982, Dickison et al. 1983).

Cereal Aphids in England. Even among aphids like *Aphis fabae, Myzus persicae* and *Brevicoryne brassica*, which lose their wings upon settling on a suitable host plant, it cannot be assumed that the economic injury level is reached solely by local multiplication. In a detailed study of *Metopolophikum dirhodium* (Walker) in a wheat field at Cranfield, Cannon and Schaefer (1983) found that high levels of infestation were produced during June by local increases in apterae. Soon after, alatae were produced in two outbursts with 50 and 90% of the progeny being winged in mid- and late July, respectively. These outbursts must have occurred elsewhere because a 7-fold increase in density resulted from a massive increase in alatae numbers. Meso-scale meteorological analysis (Schaefer et al. 1979) showed that westerly airflow of the previous seven days was interrupted on 11 July by easterly-northeasterly winds. A thermal gradient was established across central and southern England which permitted cooler air from the North Sea to penetrate inland, decelerating to 1-2 m sec^{-1} between East Anglia and Cranfield (a distance of ca. 100 km), thus producing moderate low-level wind convergence (Dickison and Neumann 1982). Suction traps at Cranfield gave exceptionally high catches of alatae at this time. Cannon and Schaefer (1983) concluded that half the 7-fold increase recorded could be attributed to this airborne concentration and that damaging infestations would not have occurred without it.

The arrival of such concentrations represents an enormous potential increase in emergence rate which may overwhelm locally occurring controlling agents. If populations are to surmount the 'natural enemy ravine', illustrated in the case of the spruce budworm, natality + immigration must exceed mortality + emigration by a suitable amount (Clark et al. 1979). In the arrival of airborne concentrations, immigration can indeed be very large. The author submits that this is a major factor in insect outbreaks and one whose contribution has been neglected by ecologists.

DISCUSSION

These examples of insect pest control in large-scale practice illustrate not only important points of ecological principle, but also the fact that each problem in each location, even when a common species is involved, may include unique features. Each, however, emphasizes the three basic parameters of successful pest control, namely: (1.) the definition of the population to be controlled, its extension in space and availability in time; (2.) the choice of the stage to be attacked; and (3.) the choice of the regulator.

The first parameter is a function of the flight activity of the species, but must be influenced by practical, economical, and occasionally, political considerations. The potentially damaging population may be too dispersed to be attacked at its source; occasionally it may be attacked en route, and sometimes it can be attacked only by international cooperation. In the case of noctuids, there are strong reasons for targeting the adult for attack. Not only are adults, being adapted to a very limited diet, more susceptible to most poisons but they do not live in the protected environment of the larval stages. Selecting the adult as the target stage determines the choice of the regulator. Adult populations may reach their destination under the influence of wind-fields but their terminal guidance for food, mating, and oviposition is largely olfactory. The identification and use of such chemical attractants to lure them to destruction has clear advantages over the widespread use of broadly acting synthetic insecticides. The possible role of such 'plant attractants' in the control of some of the better-known noctuid pests of the Old World is discussed below.

Heliothis spp. Pests which are migratory in the sense that they occur in the crop at the economic injury level as a result of events outside the field at risk, may be attacked in their source areas, en route to or on arrival in the crop. Feeding attractants are probably most powerful with respect to noctuids soon after the moths emerge when they typically feed hungrily on nectar, fueling for their initial flight - in the case of *H. zea,* immediately after emergence before their wings have dried (Lingren et al. 1988, 1990). When it is practicable to do so - i.e. when the population is sufficiently dense and confined - feeding attractants offer a highly desirable and specific approach to control. In the case of *H. armigera* in the Sudan Gezira, when the major sources of infestations on cotton are the fields of groundnuts, the elements for such an approach are already present. According to Topper (pers. communication), the majority of newly emerged *H. armigera* moths fly to *Lens esculenta*, a legume commonly grown on the embankments of the water channels of the irrigated cotton fields. This plant is in flower usually throughout September and October, the period when *H. armigera* is the greatest hazard to the cotton crop, and when there are few weeds in flower in the fallow or in other cropped fields to attract moths. However, application of an adulticide, with or without an attractant, would have to be conducted on an appropriately large scale. Haggis (1981, 1982) analyzed Gezira Board data on the incidence of *H. armigera* eggs on cotton over several seasons and showed that many fold increases in numbers occurred simultaneously over thousands of square kilometers. In every 3-d period (approximately the incubation period of the egg), there were two or more significantly different levels of infestation, each extending over areas ranging from a few hundred to several thousand square kilometers. The boundaries of such areas changed continuously. These changes are due not simply to new emergences, but to redistribution of *H. armigera* resulting in their arrival at new destinations at very different densities than those at departure. Few of the newly emerged moths, however, climbed to heights associated with long distance flight (Topper 1987), and in the absence of major meteorological events, colonized nearby cotton fields. Topper (1987) found that densities of pupating larvae in groundnuts, and to a lesser extent in sorghum, were responsible for the average densities of virgin females found in cotton 15 d later. The local destruction of these would not, however, prevent cotton from being invaded as a result of longer-distance displacement of moths from elsewhere. Accordingly, the application of adulticides for the destruction of newly emerged moths has to be synchronized over an unusually broad area containing numerous hectares of irrigated crops with the whole area being treated within 24 h before further redistribution can occur. An advantage of plant attractant-based adulticides is that it would not be necessary to attempt applying the bait to all the cotton crops within so vast an area but to apply it only to plants chosen because of their intrinsic attractiveness to moths as a food source (e.g. *L. esculenta*). In the Sudan Gezira, it is possible to visualize achieving *H. armigera* control by flying the kilometer length of each *abu sita* (water channel on the upslope edge of the field where the lentils are grown) to protect 45 ha of cotton from moth invasion, potentially protecting 200-300 ha min^{-1} for a period determined by the longevity of the formulation - a work-rate of the order of magnitude which needs to match the scale of the problem posed by this highly mobile pest and the long period over which new moths emerge.

In contrast with the Sudan Gezira, in Thailand and Kenya the primary infestations of *H. armigera* which generated the economic injury level developed on cotton and derived from one or two generations almost entirely on maize. The invading generation, however, emerged after maize had ceased to be a preferred food source, this being more available from weeds, largely within the maize crops (those not having been grazed by cattle). In neither area studied were flowering weeds particularly abundant at this time. This provides a situation where plant-attractants could be especially successful. Two difficulties, however, present themselves. First, the problem of application of the bait to the optimum site (the base of the maize plant?) on the scale needed - i.e., probably hundreds of hectares per night - and second, the areas of maize to be treated usually greatly exceed those of cotton to be protected. Under circumstances such as these, it may be beneficial to apply a suitable bait to the destination crop and secure timely application by using plant attractants in the source areas for monitoring emergence.

Spodoptera spp. Spodoptera exempta provides a magnificent opportunity for control using feeding attractants. The trees, on whose blossoms moths feed so avidly after emergence, are limited in the larvae infested areas and not all the trees are in flower at the time of emergence. Again, aerial application of an appropriately structured spray designed for collection, preferably by the flower-bearing branches, would permit work-rates of hundreds of ha. per hour, a scale which could match the vast size of the outbreak areas. Correspondingly, perhaps initial feeding on tree-blossom has to await hardening of the wings only because other sources of nectar are not available in the African bush. Accordingly, overall application of a suitable bait by drift-spraying for collection by ground vegetation may prove a better method. It is difficult to conceive a more attractive and environmentally acceptable approach to the solution of this difficult and important pest problem than by using baits reinforced by feeding attractants. It must also be emphasized that current research leaves little doubt concerning the continuity of armyworm outbreaks, so that complete destruction of one population could be expected to interrupt the cycle of spread from one country to another.

There will, however, be cases where the source areas of economically important noctuids are too widely scattered and infestation densities too low for economical control. This is certainly the case of the cotton jassid, *Empoasca lybica* (de Berg), and whitefly, *Bemisia tabaci* (Gennadius), in Sudan. Plant derived attractants may still, however, be a practical control agent if, like *H. armigera* and *S. littoralis*, the moths continue to feed throughout their active life. Topper (1987) observed that *H. armigera* spent 80% of its nocturnal activity airborne and the remaining time between feeding and oviposition. Cotton plots in Egypt are too small and widely dispersed to permit destruction of *S. littoralis* adults in their source areas (Lawson 1977). The first oviposition on cotton is traditionally closely monitored by employing children to collect egg-masses. Subsequent economic injury levels are reached by local breeding seemingly accompanied by little redistribution. Thus, application of a suitably formulated spray bait could be confined to those fields where the economic threshold has been breached during the first oviposition and timed accordingly. On the other hand, in the Sudan Gezira, where the source of *S. littoralis* is the groundnut crop, outbreaks in adjacent cotton fields are not noticed until damage is severe and monitoring source areas demands an impractical density of pheromone traps. The author suspects it is unlikely that the required density of traps based on feeding attractants would be any less. However, there is evidence that survival of *S. littoralis* larvae on cotton has been much encouraged by the repeated application of insecticides for controlling *H. armigera*. If this burden of insecticides could be reduced, *S. littoralis* would not be a great problem in the Gezira where the cotton irrigation system seems to be unsuitable for pupal survival.

Diparopsis spp. Noctuids which lend themselves to control by feeding attractants are the red bollworms, *Diparopsis watersi* (Roths.) and *D. castanea* (Hamps.). The former species occurs in Africa north of the equator and the latter most important in south-eastern Africa. Both species are characterized by their larvae being confined to *Gossypium* and two other closely related genera, *Cienfuegosi* and *Gossypioides*, all of which are common wild plants in any part of Africa. Sources of infestation on cotton are almost entirely diapausing pupae in cotton fields of previous years, and the economic injury level develops from successive generations in the cotton crop. There have been no systematic studies on the flight activity of these noctuids but there is circumstantial evidence of displacement from source areas of ≥200 km (Pearson and Darling 1958; Joyce, unpublished data). Like *H. armigera*, eggs are normally laid singly but large numbers are laid each night (usually >100). In the case of *D. castenea*, moths emerge sexually mature. These factors suggest that *Diparopsis* spp. moths are highly mobile though perhaps less so than those of *H. armigera*. The source of infestation by both *Diparopsis* spp. is ratoon cotton but, in the case of *watersi*, fields in which cotton has been grown may remain sources for several years (Tunstall 1958). The Red bollworms would appear to be pests which could be successfully controlled by plant attractants applied to their destination rather than to their sources, but again on a spatial scale commensurate with their flight habit which is still unclear.

Sesamia spp. The genus *Sesamia* contains many important pests of sugarcane, maize, sorghum, rice, millet and wheat. The genus includes such species as *calamitis* (Hamps.) of the savanna region across the whole of Africa, *cretica* from Sudan through to Iraq, and *inferens* in the Far East. Like the widely dispersed African maize stemborer, *Busseola fusca*, the moths of all *Sesamia* spp., though described as strong fliers, lay large batches of eggs 1-2 d after emergence and do not become much involved in large-scale displacements. Most species employ diapause for aestivation and hibernation, so that source areas are fields cropped in the previous season. Control by plant attractants could probably be achieved by field to field application to host plants, since moths have been recorded feeding actively between ovipositions.

Mythimna separata (Walker). The oriental armyworm is one of the most serious cereal pests in the Asian and Australian continents. Outbreaks have been responsible for heavy crop losses in more than 27 countries from the humid tropics to temperate regions, but particularly in Australia, Bangladesh, China, India, and Japan. The crops damaged include rice, wheat, sorghum and millet. During spring in northeastern China, adults suddenly become abundant in crops over thousands of square kilometers. No overwintering population has been discovered, and breeding south of 27° latitude seems effectively continuous. A massive program of marking and recapture was conducted during 1961-1965. Nearly one million marked moths were released in central China and southern provinces during the autumn and spring, respectively. Marked moths were captured 8-30 d later at distances 600-1400 km from the release points. Moths released in the spring and autumn migrated north and south, respectively. Lin and Chang (1964) identified a first generation of larvae in the southern provinces of Kwantung and Kwansi which damaged the wheat crop in January and February. The moths of this generation produced larvae in the central provinces as far north as Shantang, which also damaged wheat in March and April. A fourth generation of larvae occurred in the northern provinces bordering Manchuria. Third and fourth generation moths migrated south and severely damaged the autumn rice crop in Hunan, Hopie, Fukien, Kwangsi, and Kwantung provinces. Lin (1963) investigated 163 cases of sudden appearances of large moth captures and found that the largest were commonly associated with cold or warm fronts and cyclone centers. These observations are reminiscent of those of Schaefer (1979) using radar to demonstrate the concentration of airborne insects within zones of wind-discontinuity and perhaps illustrate the conclusions of Rainey (1982): "(1.) the spatial redistribution of populations of airborne pests is often more important than changes in total numbers in determining the incidence and severity of pest attack...; (2.) this spatial redistribution is characteristically dominated by structured atmospheric systems of winds and weather...in a manner which is often conveniently much more tractable to envisage and forecast than changes in total numbers...; (3.) this redistribution under the influence of winds and weather includes not only long-range geographical displacement but also massive changes in population density under the influence of convergent winds; and, (4.) the very important role of flight behavior in population dynamics of insects can be fully appreciated only when sufficient account is taken of the dynamics of their atmospheric environment."

The migrations of *M. separata* in China inferred by Li et al. (1964) are depicted in FIG. 3. China, however, represents only a small fraction of the total pests in all countries shown in FIG. 3, as well as extending beyond the land masses into the Pacific and to eastern Australia and New Zealand. The entomologists in China do not believe that China supports a discrete population, particularly as the Inter-Tropical-Discontinuity, moving northwards and fed by winds from the southern hemisphere, reaches as far north as Manchuria during July. Outbreaks of *M. separata* in Japan have been attributed to moths carried by southeasterly winds (Oku and Kobayashi 1974, Oku and Koyama 1976) and may derive from China or further afield. As is the case of the desert locust, it seems possible that a single population of *M. separata* is involved throughout the whole of its distribution region and control must be sought by international action on a regional basis. As with *S. exempta*, the possibility that the entire global population of the species may periodically be restricted to a relatively small fraction of its total distribution region provides an opportunity of breaking the cycle of migration from one breeding area to another and thereby achieve overall population regulation. Nevertheless, whatever means of control eventually prove possible, the distribution of insecticide, or other regulator, over areas measured in tens of thousands of hectares in a period of time measured in days rather than weeks seems an inescapable consequence. Suitably formulated plant attractants clearly represent an environmentally attractive choice.

Pest Population Management. Insect pest control by the overall regulation of entire populations is certainly not a new concept, but one advocated and practiced successfully as a result of work by such eminent entomologists as E.F. Knipling. It is the established procedure for the control of locusts in Africa, Asia and Australia and is the accepted procedure for the control of insects of medical and veterinary importance. Control of the black fly, *Simulium damosum*, has involved the cooperation of seven west African countries under the leadership of the World Health Organization. The control of most crop pests, however, is regarded as the responsibility of individual farmers on the assumption that pest outbreaks are local in origin. In recent years, studies of adult insect behavior have emphasized that the mobility of most pest species has been much underestimated. To confine control of mobile pests to individual fields, which contain perhaps only an immeasurably small fraction of the damaging or potentially damaging population, is to violate basic ecological concepts. If pest populations are to be managed, control must be executed on a scale determined by the spatial extension of the population to be managed within the time the population is so distributed. The temporal dimensions are often very small while the spatial is very large. These factors demand the rapid application of a regulator over very large areas

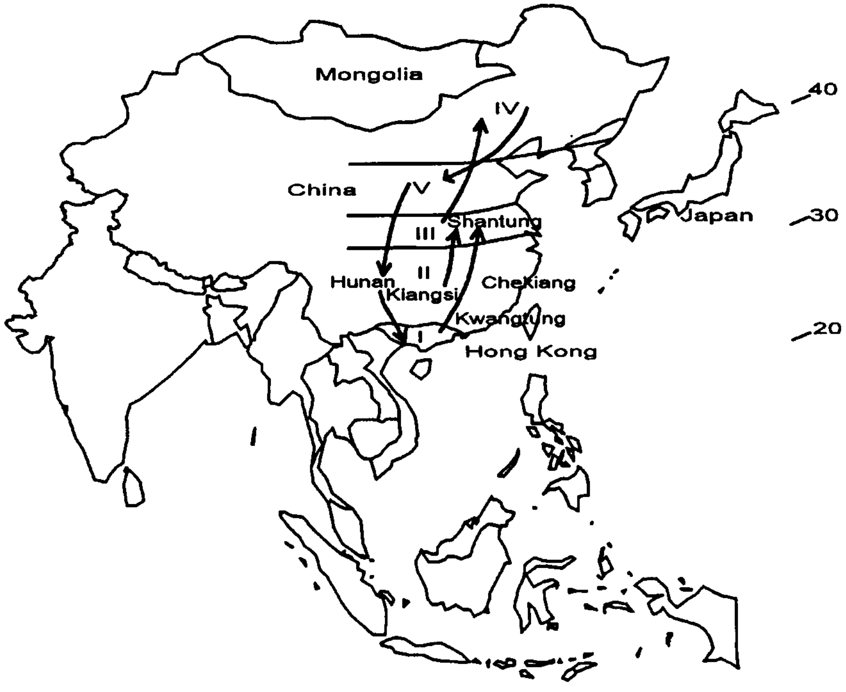

FIG. 3. Main breeding areas and seasonal migrations of five generations of *Mythimna separata* in eastern China (after Li et al. 1964; adapted from Johnson 1969).

with the least environmental burden. Plant attractants surely fill this role better than other conceptual solutions.

In conclusion, the author will indulge in some speculation. For example, in Pakistan, most of the important crops, including cotton, pulses, sunflower, vegetables, etc., are often seriously damaged by *H. armigera*. The cultivated area of Pakistan is, in effect, the Indus Valley, bounded in the west and east by the Baluchistan and Rajastan deserts, respectively. The Himalayas and the Indian Ocean comprise the northern and southern boundaries, respectively. All features being conducive to the influx of cold air into the warm, green Indus Valley during evening hours of the cropping season and thus trap airborne insects within the Valley. Is it possible that a single *H. armigera* population is responsible for all the crop damage, the moths of successive generations moving northward and southward within the Indus valley as the monsoon and trade winds alternate, and becoming concentrated to potentially damaging densities in the fronts developed within these wind systems? If so, is it possible that control directed against the whole of this population at a time when it is favorably concentrated, could protect all the crops of the country in a single large-scale operation? As Rainey (1982) states, the "population dynamics of insects can be fully appreciated only when sufficient account is taken of the dynamics of their atmospheric environment." There are pest outbreaks from Indonesia to Canada which the author believes can be understood only in relation to their atmospheric environment, and such understanding leads to a concept of pest management. The author is confident that effective plant attractants will be an invaluable addition to the technology available for use in programs for managing noctuids and that their application will eventually be considered for use on a regional, national, or even international scale.

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