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Role of behavioural studies in the development of management strategies for forest insect pests

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Abstract. Under forestry conditions, management techniques aimed at maintenance of pest populations at moderate levels have greater chance of success than conventional methods of pest control. Simple behavioural observations can sometimes be used to great advantage in the development of such methods, some examples of which are given. Although there has been considerable excitement over the past two decades on the possibility of using behaviour modifying chemicals for control of pests through mass trapping or disruption of the insect's normal communication systems, no significant practical achievement has so far been reported. Difficulties in the use of these chemicals include inadequate information on the biological responses of natural populations of insects; utilization by most insects of a complex pheromone system involving several chemical components; non-reproducibility of laboratory results under natural conditions due to several modifying factors; high cost of the development and deployment of pheromonal control systems, particularly for low value forestry crops; inadequacy of pheromonal control methods for coping with the high epidemic densities of most forest pests; and the possibility of development of pheromone resistance. Behaviour-modifying chemicals, such as food lures, sex pheromones and population aggregating pheromones, however, are useful in pest management as tools for survey and ecological research. Populations generally exhibit properties that cannot be understood by studying individual insects; study of the behaviour of populations is therefore more important than study of the behaviour of individuals for developing management strategies.

Keywords Forest pest management; pheromones in insect control; insect behaviour; food plant chemicals; *Hyblaea puera*.

1. Introduction

The major insect pest problems of natural and man-made forests (forest plantations) have been summarised by several authors (Pant 1974; UNESCO 1978; Mathur 1964; Chatterjee and Sen-Sarma 1968; Sen-Sarma and Thapa 1981; Nair 1980). In the tropics, most pest problems are noticed in man-made, as against, natural forests. Experience in Kerala has shown (Nair 1980) that all forest tree species grown in a sufficiently large area for at least one tree generation have brought up with them at least one or two serious insect pests. Although the economic damage caused by most forest pests have not been adequately assessed, many of them are considered serious enough to merit application of control measures. The present paper will examine the unique problems of forest pest control in the tropics and the relevance of behavioural studies in developing control measures. Some examples of successful use of behavioural observations for practical pest management will be discussed and a critical evaluation made of the prospects of using behaviour-modifying chemicals for direct control of pests.

2. Unique problems of forest pest control

Although forests have fewer pest problems than agricultural crops, the problems entomologists must face in devising control measures for them are much greater. Conventional methods developed primarily for agricultural crops often turn out to be unsuitable for forest crops for several reasons – (i) The extensive area under forest plantations, often in inaccessible hilly terrain, impose serious restrictions on the practical implementation of surveillance and control operations, in spite of theoretical feasibility. (ii) Again because of the extensive land area covered, the risk of adverse environmental impact of control operations, particularly the use of insecticides, is large (iii) The large size of the trees makes special demands on techniques of applications of control measures – whether it be spraying of a chemical or microbial insecticide or hand-picking of insect larvae. (iv) The greater permanence of the forest crop (for example, the harvesting period of teak is 60 years even in a good quality site) preclude certain types of control measures like crop rotation. (v) Above all, the lower economic returns from forest crops (compared to agricultural crops) limits the expenditure that can be incurred to prevent insect damage.

The appropriateness of control measures for forest pests must be judged in the light of the above considerations. Obviously, methods acceptable for use in forests must be effective, cheap and environmentally "safe", a combination of qualities that is difficult to accomplish in practice although it sounds simple and ideal. What is usually achieved is something less than ideal: compromise usually involves tolerance of a certain degree of damage (i.e., no control or partial control), acceptance of a high cost of treatment, or neglect of minor environmental damage. Methods which make use of silvicultural manipulations, natural enemies (including predators, parasitoids and pathogens) and other population management techniques based on behavioural peculiarities of pests and their natural enemies to keep the pest populations at reasonable levels are the most suitable for dealing with forest pests.

If there are unique difficulties in dealing with forest pests, there is also at least one unique advantage. Because the forests are owned by governments, indiscriminate use of insecticides can be prevented by policy decisions of the governments, even if a certain degree of damage is sustained. In agriculture, on the other hand, the profit motive of individual farmers often works against the larger interests of society. The chances of practising pest management, as distinct from direct kill of insects, is therefore greater in forestry than in agriculture. Behavioural studies that could turn out useful in the development of management strategies may be considered under two major heads – simple behavioural observations and modification of insect behaviour by chemicals.

3. Simple behavioural observations for insect control

Simple behavioural observations can sometimes be used to great advantage for the management of forest insect pests. Some examples follow.

The caterpillar of the moth, *Hyblaea puera* is a serious pest of teak plantations throughout India. Experimental aerial application of insecticides has been tried in the past (see Sen-Sarma and Thapa 1981) to control this insect. A 4-year field study conducted in Kerala (Nair and Sudheendrakumar, unpublished) showed that in spite of the insect's potentiality to pass through at least one generation per month, serious outbreaks occurred only once or twice a year in most plantations, usually in late April to August. Unpublished recent observations on the egg-laying behaviour of natural populations of *H. puera* moths, on the behaviour of mature larvae, and on the movement pattern of newly emerged moths have revolutionised our concepts of the population dynamics of this important pest. The current working hypothesis is that the greater proportion of the moth population, resulting from a larval build-up in one area, migrate to another area about 5 to 10 km away, to start a new infestation. *H. puera* moths lay eggs only on tender leaves. Although teak is a deciduous species, observations have shown that there exists enough phenological variation among individual trees within an area and among populations of trees in different areas within a larger geographical region to make tender leaves available continuously, though not at the same place, to sustain a residual population of larvae. With the onset of the general flushing season, the insect population builds up, step by step, colonising newer and newer areas, moving in the general direction of late flushing areas from early flushing areas. Later, populations decline when parasite populations build up or large quantities of tender leaves are no longer available. Existence of a residual population during the off-season (non-flushing period of teak) and gypsy-like migration of adult moths, are new concepts prompted by simple behavioural observations (unpublished), which if proved, can lead to simple methods to control the outbreak. In plantations, initial build-up of larval populations can be located by surveillance during the critical period. As mature larvae descend to the ground for pupation, application of a contact insecticide or appropriate microbial agent can prevent emergence of the moth population and their subsequent spread to other areas. This method is much simpler, practicable and environmentally less hazardous than aerial application of insecticides that had been experimented with in the past.

Increasing evidence is now accumulating to suggest that migration may be more common than hitherto suspected in many pests, particularly the noctuid moths (Barfield and Stimac 1981; Oku 1983; Stinner *et al* 1983; Riley *et al* 1983). Management strategies for such highly mobile pests must necessarily be based on observations on the behaviour of natural populations.

Several examples can be cited to show how careful observations on the behaviour of pests can lead to improvements in their control. Subterranean termites damage young transplants of eucalypts within a few months of planting out. Field observations revealed that characteristically the termites (mostly *Odontotermes* spp.) begin their attack in the root collar region a few centimeters below groundlevel (Nair and Varma 1982). It is therefore possible to control the attack by treating the soil core immediately surrounding the tap root, instead of the entire planting area. This can be accomplished by drenching the polythene bag containing the seedling with an insecticide before transplanting it in the field, thus effecting considerable reduction in environmental contamination as well as cost of treatment. In African countries, on the other hand, different species of termites, notably *Macrotermes* spp. cause most damage to eucalypts; they forage at the soil surface level and attack the stem of saplings at or above ground level. This behaviour of termites calls for a different approach to control.

Control of the sapling borer, *Sahyadrassus malabaricus* Moore (Hepialidae) by spot treatment of the tunnel mouth is another example. This borer attacks saplings of forest plantations and lives inside a large tunnel along the pith. The tunnel mouth is covered by a mat-work of wood particles and faecal pellets. Observations revealed that if the tunnel mouth cover is removed, the larva comes out at night and makes a new cover with wood particles gathered from the vicinity of the tunnel mouth. Control of insects which live inside wood is generally difficult, but the above behavioural observation was made use of to control this insect by pulling off the cover and applying a contact insecticide at the tunnel mouth region (Nair 1982).

Behavioural observations also find application in the control of cerambycid wood borers. Observations have revealed that they lay eggs only on logs with bark. Debarking is therefore a standard practice for protection of stored logs from cerambycid borers.

4. Modification of insect behaviour by chemicals

Over the last 15–20 years there has been considerable excitement among entomologists on the possibility of using behaviour-modifying chemicals for control of pests. A large number of chemicals have been isolated from a variety of insects and other sources, including host plants or animals, and their exact chemical structures have been established; many have also been synthesized outside the animal or plant system. These are elegant achievements made possible by the active involvement of expert chemists and general advances in instrumental analysis. Many such chemicals have been tested in the laboratory for behavioural responses and found promising. Pilot-scale field tests have also been carried out for some of them. We shall consider them under two heads – food plant chemicals and pheromones.

4.1 *Food plant chemicals*

Since Fraenkel's (1959) classic paper on the '*raison d'être* of secondary plant substances', the role of plant chemicals in influencing the orientation of insects to food plants for feeding or oviposition has been well recognized. Since then we have learned much about the mechanisms of host plant selection of various phytophagous insects. Several excellent reviews of the topic are available (Kennedy 1965; Dethier 1970a, b; Schoonhoven 1972, etc.) and several national and international symposia have also been conducted on the topic (Ananthakrishnan 1977; Visser and Minks 1982; etc.). Except in a few instances, however, it has not been possible to use this new knowledge for developing control measures against pests. Nonspecific food lures like sugar solutions or protein hydrolysates mixed with toxic compounds have often been used to attract and kill insects like ants, cockroaches and flies. A toxic bait containing aldrin, soya bean oil and dried citrus meal applied aerially at the rate of 2·2 kg/ha was reported to be collected by leaf-cutting ants (*Atta* sp.), a pest of forest trees in the neotropics, in preference to fresh leaves and to kill about 91 % of the ants in some experiments (Lewis 1972). The best known example in Indian forestry is the use of trap logs to attract the sal borer, *Hoplocerambyx spinicornis*. This cerambycid borer is a serious pest of natural and man-made forests of *Shorea robusta* (sal), an important timber tree in the northern states of India (Beeson 1941) bad epidemics of which have occurred in the past in UP, MP, Bengal and Assam. Normally a borer of sickly trees, at times of epidemics, even healthy trees are attacked and killed. Adult beetles of both sexes are attracted to newly exposed inner bark and sapwood of trees over distances upto 400m. It is therefore standard practice to fell unhealthy or injured trees, cut them into 3m logs, beat up the cut ends to expose fresh sapwood and distribute them in small heaps in the affected area to attract the beetles. Trap trees at the rate of 3 to 5 per hectare are used; at intervals, the logs are again cut into smaller billets to expose fresh sap. The beetles are collected and destroyed daily. Collections of upto 1000 beetles per trap tree per day have been reported (Beeson 1941). The nature of attractant has not been determined.

In general, although there has been initial optimism on the use of behaviour-modifying host plant chemicals, particularly the secondary plant substances, for insect control, this has not been borne out by experience. The main handicap is the involvement of several chemicals, each having some influence on the chain of behavioural responses of the insect leading to host plant recognition and acceptance. The problems of using them for control can be illustrated using the example of the cabbage root fly, *Delia radicum* (Anthomyiidae) a pest of cruciferous crops in Europe and North America which has been studied in some detail (Traynier 1965, 1967a, b; Coaker 1969; Coaker and Finch 1971; Nair *et al* 1974, 1976; Nair and McEwen 1976; Finch 1978; Städler 1978; Hawkes and Coaker 1979; Ellis *et al* 1982). In this insect, the first step in host selection is taken by the adult female when it lays eggs in soil close to the host plant. The newly hatched larvae bore into the roots where they feed and grow. Highly volatile mustard oils, break-down products of glucosinolates (mustard oil glucosides) present in cruciferous plants, stimulate the flies into greater activity and attract them to the plant. The parent glucosinolates then induce oviposition. Allyl isothiocyanate (AITC), one of the mustard oils tested in the laboratory, did not induce oviposition by itself, but in the presence of a glucosinolate, very low concentrations of it caused an increase in the number of eggs laid (Nair and McEwen 1976). Many of the nutrients tested did not influence oviposition, but a protein hydrolysate inhibited it. Flies also arrive and land on non-host plants by random movements. The gravid female which lands on a plant probes the leaves with the proboscis (other sense organs may also be involved) and if the plant is judged suitable, walks down to the bottom and lays eggs in soil, close to the plant stem. A large number of factors, chemical, visual and physical, apart from the physiological state of the insect, are involved in the sequence of behavioural events leading to oviposition. In the next major step, similar factors affect the establishment of the neonate larvae on the root. All crucifers are believed to contain one or more glucosinolates, usually a mixture of several, but some crucifers did not elicit oviposition (Nair *et al* 1974). Experiments (Nair and McEwen 1976) revealed that although glucosinolates appeared to be the only oviposition inducing substances present in crucifers, there was no correlation between the total glucosinolate content of crucifer leaves and the oviposition response of the fly and that some glucosinolates elicited more oviposition than others. It appeared that both the absence of glucosinolates and the presence of inhibitory chemicals could make a plant unacceptable for oviposition. With more than 30 glucosinolates known from different plants, and with several glucosinolates occurring together in a given species, Nair *et al* (1976) suggested that a total 'glucosinolate pattern' may be more important in deciding the oviposition response. In the light of Dethier's (1973) conclusions based on extensive electrophysiological studies on the gustatory receptors of lepidopteran larvae, Nair *et al* (1976) also discussed how host selection may depend not on the presence or absence of a single stimulant or deterrent, but upon the total sensory impression derived from an integration of sensory responses to several plant constituents. Dethier (1973) has discussed in detail how subtle differences in one or more plant constituents result in different patterns of sensory input, and consequently, different magnitudes of response of insects.

In general, since a chain of sequential behavioural responses to food plant chemicals is involved in food selection and since most of these responses can at least partially be modified by other factors, the chances of utilizing any of the food plant chemicals to control insects by radically modifying their behavioural response is meagre. Recent studies have also shown (Ellis *et al* 1982) that the egg laying behaviour of the cabbage root fly is also influenced by microbial activity in or around its host plants. To compete with natural food plants, we need chemicals that will elicit superoptimal responses from the insect, but we are beginning to understand that though the insect may act "instinctively" rather than intelligently, optimal responses have been instinctively built into their behavioural repertoire. For example, while low concentrations of AITC will attract the cabbage root fly and promote egg laying, high concentrations of it will either be ignored through sensory adaptation or may elicit the opposite reaction. For use in controlling the insect, we should expect that a high concentration of attractive chemicals will attract the insects more effectively than the optimal concentration released by the natural hosts. Such responses have seldom been observed under natural conditions, although the search must continue in the hope that it may turn out useful in some cases.

4.2 *Pheromones*

There is vast literature on pheromones of insects and their potential uses (see Jacobson 1972); we shall limit our discussion to two examples of forest pests and examine the usefulness of pheromones for their control.

The first example is the gypsy moth *Lymantria dispar* (= *Porthetria dispar*) (Lymantriidae). The caterpillar of this moth is a pest of oak, birches and many other hardwoods in Europe, USSR and some parts of USA, particularly eastern New York and New England. As early as 1925 it was suspected that the flightless virgin females of this moth produced a sex attractant (pheromone) which lured the males. A series of investigations over several years culminated in the identification of the active component of the sex pheromone in 1970, designated as 'disparlure' (Bierl *et al* 1970). In between, preparations called 'gyptol' and 'gyplure' were also isolated and/or synthesized. Early attempts (in 1961) by the US Department of agriculture to control gypsy moth populations by disruption of the mating communication systems (male confusion method) with gyplure distributed by air craft over a 160 ha island located near New Hampshire did not show any adverse effect on male mating activity, but this was attributed to weak attractiveness of the commercial 'gyplure' used in the experiment (Jacobson 1972). A subsequent field experiment in 1964 with preparations of 'gyplure' previously shown to be effective in both laboratory and field tests, also did not yield encouraging results. In later experiments using disparlure, traps baited with the chemical were air dropped over large infested areas to attract and kill the males or strips of paper impregnated with the chemical were dropped to confuse the males. Both approaches appeared to be successful in areas of light infestation although not in areas of heavy infestation (see Jacobson 1972).

While disparlure has not yet become a practical tool for control *per se*, it is widely used as a surveillance tool, particularly to monitor the spread of this introduced pest within the USA to undertake timely control measures. General conclusions on the usefulness of these chemicals for control may be drawn after considering the second example, the pine bark beetles.

Several species of the small scolytid beetles belonging to the genera *Dendroctonus*, *Ips*, *Scolytus*, *Orthotomicus*, *Xyleborus* etc., attack pines and other trees in different parts of the world. Most investigations have been made on the pine bark beetles, *Dendroctonus* spp. in the USA and USSR and the literature is vast (see Wood 1970, 1980; Stark 1973; etc). In general, infestation occurs in the following sequence. Depending on the species, adult beetles of one of the sexes make the initial attack, usually on weakened trees which apparently have a characteristic odour profile. Once established, the beetles produce a population aggregating pheromone, possibly using precursors ingested from the tree, which is passed out through the frass and serves to attract other beetles to cause mass attack. In severe infestations, healthy trees are also attacked and killed. Several pheromones *viz*, frontalin, brevicomin, etc., have been isolated and synthesised from different species of bark beetles. The results of field experiments for control using bark beetle pheromones have been discussed by Wood (1970) and Roelofs (1975). In general, pheromone mixtures have been found effective in trapping large numbers of bark beetles, but unequivocal evidence of their effectiveness in reducing tree mortality under field conditions is yet to come, although the results are reported to be promising.

We shall now consider the prospects of using pheromones for pest management in forestry. The most obvious and profitable use of such chemicals is to detect the presence of the insect, either to monitor its spread into an area or to time the application of control measures. In the case of pests which appear all of a sudden in large numbers, like the teak defoliator, pheromones will be of little value to detect the time of their appearance. It is, however, an important research tool to elucidate many aspects of the ecology of the insect; for example, to determine whether residual populations of the insect occur in plantations or natural forests during periods when no visible defoliation occurs.

Although high hopes have been raised on the possibility of using pheromones for control of insects, either through mass trapping or the male confusion method, and optimism still prevails, no significant practical achievement has so far been reported, in spite of intensive efforts over the past 15 to 20 years – a sufficiently long period for experimentation. An excellent and critical discussion, full of insight, of the problems and prospects has been given by Greenway *et al* (1977), which must be consulted by anyone who contemplates use of pheromones for insect control. Some of the difficulties in using pheromones for direct control are:

(1) Isolation, identification and synthesis of the pheromones have progressed very fast, but our understanding of the responses they induce in individuals, and especially of the responses they induce in populations has not progressed fast enough (Greenway *et al* 1977). Biological response studies are more cumbersome and time consuming and tall claims have often been made with preliminary data. As Greenway *et al* (1977) pointed out, variability of responses in behavioural assays has not always been reported in published studies.

(2) In many cases it has been found that the functional sex pheromone is not a single compound but a mixture of compounds which constitute a 'pheromone system' (Minks *et al* 1977). For example, four components are involved in the sex pheromone system of the sugarcane stalk borer *Chilo auricilius* and effectiveness depends on an optimum combination of these compounds (H. David personal communication). There are several examples in which only specific combinations of certain chemicals are active (Minks *et al* 1977). The greater problem, which has not been generally recognised, is the

likelihood that different individuals in the given population may respond (reference here is to optimum response) to different combinations of the chemicals.

(3) In general, many predictions based on laboratory results have not been realized under field conditions due to various interfering factors. The behavioural reaction of a living organism, more particularly of a population of organisms cannot be expected to follow rigid principles, or perhaps, if they do, we are still ignorant of the principles which govern them and unable to predict the outcome. In spite of such knowledge, in control trials using pheromones we often expect that behavioural responses of the insect in the field will be as predictable as the outcome of a chemical reaction.

(4) Because of the cost and effort involved, development and use of pheromones for direct control may prove economically feasible only in high-value, intensively managed crops, and not in extensive low-value plantings (Greenway *et al* 1977) like forest plantations, especially in developing countries.

(5) As noted in the few field trials on gypsy moths, artificially used pheromones were effective in controlling the insect only when the pest population was low. When enormous numbers of insects are involved, as in an epidemic of forest insects like the teak defoliator or bark beetles, pheromone traps cannot cope up effectively with the numbers. Theoretical calculations suggested (Roefols 1975) that an initial trap to female ratio of at least 5:1 would be needed to obtain 95% suppression of mating.

(6) The possibility of insects developing resistance to pheromones has generally been ignored in discussions on the use of pheromones for insect control. Even Greenway *et al*'s (1977) otherwise elegant discussion is silent on this point. Green *et al* (1960), however, discussed this problem. Development of pheromone resistance appears to be as simple and imminent as development of insecticide resistance, if we resort to direct control of insects with pheromones. One of the arguments in favour of use of sex pheromones for control was the idea that an insect cannot develop resistance to a chemical on which it depends for mating communication. However, resistance can develop in the following manner. Most insects make use of a pheromone system involving more than one chemical. As discussed above, different individuals of a given population may show optimal response to different combinations or ratios of the pheromones. Widespread use of a particular pheromone combination for mass trapping or mating disruption will eliminate that part of the population which responds to it, leaving the small unresponsive part of the population to mate and multiply. With continued selection pressure, a new population will evolve which makes use of a new slightly altered pheromone communication system. Such a population will no longer be responsive to the standard pheromone system; in other words, resistance has developed. If the pheromones are used only for survey purposes, it will not exert much of selection pressure and therefore will not lead to development of resistance.

5. Conclusions

Behavioural observations are important in developing control measures against forest pests. Simple observations on the behaviour of natural populations can often be used to great advantage in developing strategies for management of pests. In the management of forest pest populations behaviour modifying chemicals such as food lures, sex pheromones and population aggregation pheromones are useful as research and survey tools, but not for direct control.

Most new ideas useful for management of pests are likely to come from behavioural studies of populations, particularly natural populations, rather than observations made on individual insects in the laboratory. Populations exhibit properties that cannot be understood by studying individual insects.

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