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Disparlure and its role in gypsy moth population manipulation^{1,2}

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Disparlure, the synthetic pheromone of the gypsy moth, *Lymantria dispar* (L.), may play various roles in pest population management or manipulation. Its use in the United States for survey and detection, delimitation of new infestations, population evaluation and prediction, and population reduction, and research supporting these various uses, is reviewed and assessed. Disparlure is currently operationally available and used for survey and detection; other uses are still experimental. The probability of developing a broader role for this pheromone in gypsy moth management depends on attaining answers to a variety of basic questions associated with moth behavior, better ability to measure and assess sparse populations, and developments in slow release formulation technology as well as application technology. Until many of these fundamental questions are answered, large scale application programs should be curtailed.

Disparlure³, the synthetic chemical attractant for male gypsy moths (*Lymantria dispar* (L.)) (Lepidoptera: Lymantriidae), has been available for research purposes and a number of extensive field tests since 1970. Let us review the various uses and roles that have been tested or envisioned for this material in the gypsy moth integrated pest management program currently under development in the United States.

Just how may the pheromone be used? All of these rather broad roles have been suggested at various times:

(1) The pheromone may be used in a *survey and detection* program, most likely as a bait in a trap of one kind or another.

(2) *Delimitation* of an infestation – especially one in a new area remote from the generally-infested northeastern United States – may be accomplished, again using pheromone-baited traps.

(3) There is a potential role for the use of pheromone-baited traps in *evaluating density* of gypsy moth populations, and in *predicting density* in the next generation.

(4) Disparlure may be used to *reduce populations*, or possibly even to eradicate very sparse populations. Both trapping, and the disruption of chemical communication (or «confusion»), have been tested to achieve this objective.

I shall elaborate on each of these roles in turn, but concentrate on the last one.

Any «use» of an insect pheromone is ultimately dependent on one factor: alteration of normal behavior of the insect under investigation. In the case of the

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³*cis*-7,8-epoxy-2-methyloctadecane. See text for comments on chiral nature of the compound.

gypsy moth, behavior may be altered by attracting males to a baited trap, by stimulating them to search for what they perceive as a female moth in the area, by disrupting the normal chemical communication between the sexes, or perhaps in other ways. If we are going to alter behavior successfully, we must know as much as possible about the normal, unaltered behavior of the insect. Unfortunately, our knowledge of gypsy moth behavior was woefully inadequate when we started testing disparlure; many gaps in our knowledge still remain. DOANE (1976) noted that studies of behavior have tended to follow, rather than precede, development of pheromones for insect control, and WELLINGTON (1976) made the more general observation that too often we tend «... to ignore insect behavior until it gets in the way of field work».

Entomologists have known for more than 80 years that unfertilized adult female gypsy moths emit an odor which is attractive to male moths (FORBUSH & FERNALD, 1896). INSCOE & PLIMMER (1978) recently reviewed the history of attempts to isolate, identify, and synthesize this natural attractant, noting that only the relatively recent development of a convenient laboratory bioassay, improved microchemical techniques, and modern instrumentation have permitted what success has been achieved to date. Without reviewing the chemical story here, suffice it to say that many false leads have been followed, contradictory results have been obtained with putative or suspected pheromones such as gyptol and gyplure (which later proved not to be involved in the pheromone system), and it is only recently that we have recognized the importance of the chiral nature of the attractant (IWAKI *et al.*, 1974). In fact, the optical properties of the naturally-occurring compound have not yet been established. Needless to say, the uncertainties of chemical identification of the pheromone have frustrated many of the studies in which the attractant was being tested for use in one or other of the roles enumerated earlier.

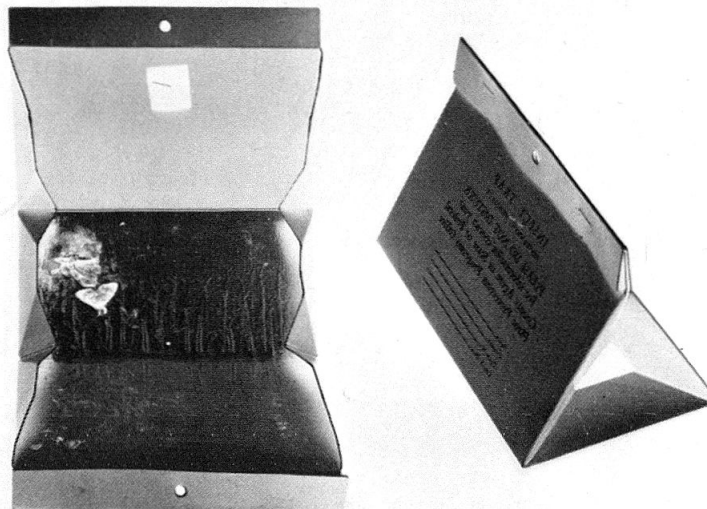
ROLES FOR THE PHEROMONE

The pheromone for survey and detection

The use of the pheromone as a survey and detection tool for gypsy moth has been reviewed by SCHWALBE (1978). Use at different times has been in the form of live virgin females, extracts from female abdominal tips, or synthetic materials (believed to be «the pheromone») released from a variety of dispensers. Trap designs have also varied widely over the years. Currently the most widely used trap in the United States for routine survey and detection is the Delta trap (fig. 1), baited with racemic disparlure in a Hercon[®] wick; other traps, and wicks baited with (+)-disparlure, are being phased in for special purposes. The use of (+)-disparlure will undoubtedly increase as larger quantities become available, as it has been shown that this material is about 5-10 times more attractive than the racemic mixture (CARDÉ *et al.*, 1977, 1978; MILLER *et al.*, 1977; PLIMMER *et al.*, 1977). In release/recapture studies, it is consistently shown that recapture rates fall off rapidly when traps are more than about 100 m from the release point, and that the probability of recapturing moths more than 1200 m from the point of release is small (MASTRO, 1978; SCHWALBE, 1978).

Current survey and detection practice employs only one trap in each 7.8 km², with anywhere from 65,000 to 120,000 traps being deployed annually for survey and detection purposes. The system fills a qualitative and very important

Fig. 1: Delta trap. The standard trap for gypsy moth adult survey and detection in the United States. *Left*: Assembled trap, which is stapled to bole of tree. *Right*: Opened trap. Note plastic laminated Hercon wick (top) stapled to one side, and sticky coating on other two sides in which male moths are captured.



role in alerting authorities to the presence of male moths, and the possibility of an incipient infestation, in new areas throughout the country, and has been responsible for discovery of nine remote infestations during the period 1972–1977 (SCHWALBE, 1978). Surely, however, some isolated incipient infestations are going undetected, even within the survey grids, since traps attract moths effectively over such a short range.

The pheromone for delimitation of new infestations

When survey traps capture male moths repeatedly in an area, or scouting (i.e., a visual search) reveals evidence of other life stages of the gypsy moth in the area, more intensive trapping follows. Traps are normally deployed at approximately $6/\text{km}^2$ in a 23.4 km^2 area centered on the suspected infestation; an additional 41.6 km^2 bordering this core area receives ca $3.5 \text{ traps}/\text{km}^2$. Those traps in the delimitation grid pattern capturing the largest numbers of moths are presumed to identify the centre of the infestation; it is presumed that catches will decline with distance from this centre. This hypothesis is currently being tested (SCHWALBE, 1978).

Since the effective zone of a trap is relatively small, and trap efficiency (defined as the success of a trap in capturing males that have oriented to it (MASTRO, 1978)) of standard delta traps baited with racemic disparlure is only about 20%, (MASTRO *et al.*, 1977), it must be recognized that delimitation of an infestation using this method cannot be precise.

The pheromone for population evaluation and prediction

Population evaluation and prediction capabilities are basic to any program of insect pest management. The more ways one has of obtaining information from

which predictions may be made during a life cycle, the greater the flexibility one may develop in management strategies and options. Pheromone-baited traps are currently being used successfully in integrated pest management programs for several multi-voltine *agricultural* or *orchard* pests to indicate the need for or timing of insecticidal sprays (see MASTRO, 1978). Several of our European colleagues have monitored the nun moth, *Lymantria monacha* L., during the non-migratory phase using disparlure-baited traps (eg., HOCHMUT *et al.*, 1977; MAKSYMOW, 1978).

Although studies are continuing, we have not yet developed pheromone-baited traps for operational use in gypsy moth population monitoring or prediction in the United States. Several pieces of information are required before success will be achieved. We must know the trap efficiency for the particular trap design being used. Very different kinds of traps, perhaps high capacity traps such as those described by GRANETT (1973), are likely to be required for any but very sparse infestations. Trap efficiency need not necessarily be raised to high levels if it can be shown that efficiency is reasonably constant; in fact, reduced efficiency would require less regular servicing of traps. Trap efficiency at different population densities must be known. (It has been suggested by HOWELL (1974) that, as the number of competing pheromone sources (i.e., female moths) increases, efficiency of codling moth traps may decrease.) Finally, traps calibrated with racemic disparlure as a bait must be recalibrated for (+)-disparlure, a far more attractive chemical.

The pheromone for population reduction or eradication

By far the largest sums of money in the gypsy moth pheromone program in the United States have supported tests aimed at the direct use of disparlure to manipulate populations. The pheromone has been applied either in baited traps, or as broadcast applications designed to create disruption of chemical communication between adult moths and consequently a reduction in mating. These many tests have been reviewed recently by CAMERON (1978 a, b, c, d) and WEBB *et al.* (1978). If successful techniques can be developed, they have potential application in incipient infestations either remote from the generally-infested northeastern United States or along the so-called «leading edge» of the infestation. It is also possible that the pheromone might be useful within the generally-infested region of the U.S. where populations have been reduced either naturally (for example, by parasitoids, predators, and/or pathogens) or artificially (for example, by insecticidal applications).

Trapping

Many of the early studies involved the use of disparlure in traps (CAMERON, 1971, 1973; BEROZA *et al.*, 1973). This occurred partly because KNIPLING & MCGUIRE (1966) had developed a series of models to test the theoretical effects of the use of sex attractants for insect control. One of these models (model II) assumed that «... all males attracted ... will be killed immediately by being trapped ...» Using the principles developed in the 1966 paper, BEROZA & KNIPLING (1972) presented a model specifically for the gypsy moth, in which traps baited with disparlure were to be used. The model needed testing.

The first major test took place in southwestern Pennsylvania. In 1970, eight male moths were trapped in a localized area 125 km from the closest known in-

festation; subsequent scouting revealed 10–15 new egg masses together with evidence that at least one egg mass had been deposited in 1969. The infestation was classified as new, isolated, and with a sparse population – an ideal situation in which to test the possibility of population eradication. Because the infestation was well outside the then-quarantined region of the state of Pennsylvania, government officials insisted on spraying a 73 ha core area with the carbamate insecticide carbaryl in the spring of 1971. Prior to adult flight, cardboard tube traps (7.5 cm long x 2.5 cm diam, coated internally with a sticky material, and baited with disparlure) were air-dropped over ca 22 km² of forested land at a rate of 610 traps/km². Subsequent monitoring revealed that the infestation was more generally distributed than had been previously suspected, that fertile egg masses were deposited within the treated area, that the area where egg masses were originally discovered was, indeed, a «hot spot», and that the insecticide and trapping treatment did not eliminate the resident population.

The area in which traps were dropped was enlarged to ca 35 km², and the trap density increased to 2800/km², in 1972. Three 40-ha areas within the drop zone, known to contain fertile egg masses, received traps at the rate of 8400/km² (CAMERON, 1973). Numerous males were captured in traps, and post-season egg mass counts ranged as high as 500/ha in one small area (which was within the trap drop zone both years). Obviously, population eradication was not achieved.

We conducted other tests in 1971 and 1972 which utilized hand-placed or aerially-dropped baited traps in areas where natural populations were simulated by introduction of pupae or adults into the test areas. Mating suppression was erratic, and results were not encouraging. In only one test was mating significantly reduced in treated areas; in other tests no significant differences were measured, and in some cases mating actually increased in treated plots (CAMERON, 1973).

In other tests conducted by BEROZA *et al.* (1973), in which laboratory-reared moths were released into plots, recapture in monitor traps was reduced by 94% when compared to recapture in plots with air-dropped tube traps. Reports at about the same time of substantial behavioral and physiological differences between laboratory-reared and feral insects (RICHERSON, 1972; CAMERON, 1973; RICHERSON & CAMERON, 1974) tempered enthusiastic acceptance of the results of these tests.

Currently there is relatively little interest in the use of disparlure-baited traps for population reduction or eradication for several reasons. Efficient traps (MASTRO *et al.*, 1977) are not suitable for aerial distribution over large areas, and an efficient trap is required if maximum moth catch is to be achieved; there are gaps in our knowledge of the behavior of males, especially near a trap; much more information is needed on traps baited with (+)-disparlure; and finally, many of the assumptions on which the 1972 BEROZA–KNIPLING model were based have been shown to be inaccurate. In the absence of an improved and encouraging model, there has been little stimulus for continued work along these lines. Based on studies with other insects, SHOREY (1970) concluded that the trapping approach does not appear to hold much promise when dealing with Lepidoptera. Experience with the gypsy moth supports that conclusion.

Disruption

Most of the population manipulation efforts using disparlure have employed broadcast formulations of one kind or another. The goal has been to disrupt

chemical communication among adults, or to «confuse» them. While we do not yet fully understand the physiological mechanism of disruption, one of two explicit or implicit assumptions was made in early testing: either, the atmospheric concentration of pheromone was high enough to adapt receptors in the male; or, males searching for females would be misdirected by the very large numbers of attractive points (such as microcapsules containing disparlure), each as competitively attractive as a virgin female moth, and the excessive wasted effort of responding to these false targets would exhaust the males. Other possible mechanisms of disruption, and additional consequent behavioral assumptions, are presented by CAMERON (1978b). In the final analysis, we need much more information on adult behavior.

The earliest tests were performed in simulated populations, and often out-of-season, using laboratory-reared moths. Disparlure was applied as a spray in xylene as a carrier, on small squares of hydrophobic paper, impregnated into granular cork, in a molecular sieve, or in microcapsules. In some tests using laboratory-reared insects, high levels or complete apparent disruption of chemical communication was achieved for periods of up to several weeks after treatment. Partial disruption was also recorded in tests using feral (or «wild») insects, but reduction of mating was considered inadequate to reduce the population in the next generation. So results were, overall, frustratingly inconclusive (see CAMERON, 1978b, for a review).

It is generally agreed that pheromones will be most useful for mating disruption in sparse populations, with effectiveness increasing in an inverse density-dependent manner as the target population is reduced to ever lower levels. One of the major problems confronting researchers is measurement of results, especially in sparse natural populations. Inevitably, some artificial monitoring method must be imposed if adequate data are to be collected. In spite of these problems, tests using broadcast applications of disparlure moved increasingly into areas of sparse natural infestations and out of artificial situations (it should be noted that all tests conducted so far using broadcast applications of disparlure have employed the racemic material; synthesis of adequate quantities of the very expensive (+) enantiomer has not yet been achieved).

Disruption tests have been carried out in sparse incipient populations remote from the area of general infestation, in areas supporting predefoliating populations, along the so-called «leading edge» of the general infestation, in areas where population collapse has occurred as a result of natural mortality factors, and in residual populations after the application of insecticidal sprays. These tests are reviewed in more detail by CAMERON (1978c, d) and by WEBB *et al.* (1978). The majority of tests have employed one or another formulation of microencapsulated disparlure, although other dispensers have occasionally been used. In these tests, explicitly or implicitly the objective was to reduce mating to a degree that the population in the next year would be at least lower than could be expected in the absence of treatment, and, it was hoped, lower than the current year's population. In none of the tests so far reported, however, were concurrent population dynamics studies underway, nor were populations evaluated critically in the year following the test. Plot sizes in these tests have ranged from as small as 1 ha to as large as 60 km². Evaluations of results have been based on observed differences of mating rates during the monitoring period, differences in male moth capture in traps, and/or differences in egg mass counts either between treated and control plots or from preseason to postseason measurements during the same year.

As with tests conducted in simulated infestations, results from various tests, conducted by different teams of researchers, and often evaluated by different methods, were encouraging, discouraging, or inconclusive, depending on one's particular point of view. Frequently, apparent mating disruption was high early in the flight season, waned during peak flight, but increased again late in the season (fig. 2). Even in sparse populations, however, the treatments applied did not disrupt mating adequately at the peak of male flight.

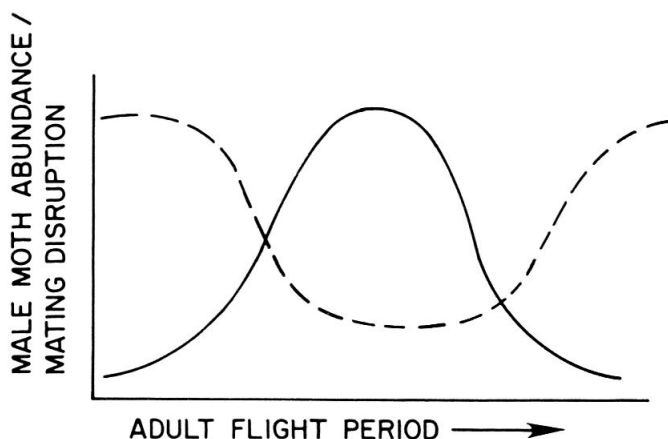
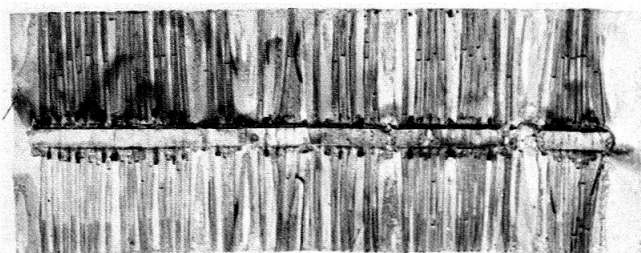


Fig. 2: Schematic representation of male moth abundance during the adult flight period (normally lasting approximately six weeks in Pennsylvania) (solid line) and proportional disruption of mating (broken line). Disruption may approach 100 per cent early and late in the flight period in very sparse populations.

It is only recently that air sampling has been done to determine pheromone concentration in plots treated with microencapsulated disparlure (PLIMMER *et al.*, 1978, for a woodland canopy situation; CARO *et al.*, 1977, for an open grassland plot). The reported results confirmed what some had suspected: that pheromone concentration is much higher the closer one is to the ground. It is suspected that relatively few of the microcapsules containing disparlure, even though they are coated with a sticker, adhere to forest foliage. Rather most simply wind up on the ground. This, of course, has major implications for evaluating field tests. As a matter of convenience, baited traps or virgin females used for monitoring were generally placed at ca 1.5 m above the ground. What happened higher in the forest – where many gypsy moth females are located – was not measured.

In 1976, we conducted field tests in a sparse natural population. We monitored mating success by placing tethered virgin feral females on the boles of trees, at both 1.5 and 10 m above the ground, in a plot treated with microencapsulated disparlure as well as in a similar untreated plot. Season-long results

Fig. 3: Hollow fibre pheromone dispenser. Each dispenser has 100 open fibre ends from which lure is emitted continuously. Receding menisci are visible, particularly in lower fibres.



showed no significant difference in mating success of the «high» and «low» females in the untreated plot (96.2 vs. 96.4% mating success), but a highly significant difference in the treated plot (62.6 vs. 45.1% mating success). (Reductions in the treated plot were highly significant in each case when compared with mating at the corresponding height in the control plot.) We repeated essentially the same test in 1977, but this time dispensed disparlure from a series of hollow fibres (fig.

3) stapled to the lower 10–12 m of tree boles in the plots. This time, mating success was not different between heights in either the treated (44.8 vs. 42.0%) or untreated (92.9 vs. 94.2%) plots. Again, mating reduction was highly significant at each height when treated and untreated plots were compared (CAMERON, 1978c).

One other very interesting result was recorded. If we compare season-long mating success at each height in the treated plots from one year to the next, we note that only the «high» females in 1976 are out of line (table 1). This is strong evidence that, where it is assured that disparlure is being emitted at the height above ground where monitoring is being conducted, mating success is reduced. In 1977, the «high» females were tethered at a height lower than that at which the highest hollow fibres were stapled; in 1976, we had no evidence that microcapsules were, indeed, adhering in substantial numbers to foliage in the forest canopy.

Female height on tree	Treated plots		Untreated plots	
	1976	1977	1976	1977
10 m	62.6	44.8	96.2	92.9
1.5 m	45.1	42.0	96.4	94.2

Table 1: Season-long mating success (in percent) of tethered feral virgin females of *Lymantria dispar*. Mating disruption tests, central Pennsylvania, USA.

Another result reported by CARO *et al.* (1977) and PLIMMER *et al.* (1978) was the rapid initial flush of lure from dispensers. We do not yet have dispensers – microcapsules, wicks or hollow fibres – which have been shown to give us a uniform release rate over periods of weeks in the field. In fact, our meagre knowledge of lure release rates from the various formulations used makes any statement of rates of treatment with «x» grams of lure/ha almost meaningless. Improvement of slow release formulations is an urgent research need.

Both BEROZA *et al.* (1975) and CAMERON & MASTRO (1976) have followed one or two applications of an insecticide during the larval stage of gypsy moth development with a broadcast application of disparlure later the same season. Data presented do not support ascribing to disparlure any additional suppression role on the population over that caused by any of the insecticides alone. CAMERON & MASTRO (1976) did suggest, based on their several methods of evaluating their tests, that pheromone-baited traps are a poor tool to use in monitoring a test directed towards mating disruption.

DISCUSSION

The role of chemical ecology in the development of tools for managing the gypsy moth in North America is reviewed much more fully in twelve contributions to the forthcoming book, «The Gypsy Moth: Research Toward Integrated Pest Management». As one reviews all of the various studies, some assessments of the program can be made. It is immediately obvious that there was – and in many respects still is – a woeful lack of basic information, especially in the area of moth behavior. The pressures of mission-oriented research, demanding practical and applicable results, did not permit much of the necessary foundation to be built early in the program. Field tests have been evaluated by a wide variety of methods, many unfortunately inadequate or inappropriate. There is still no agreement on standardized methodology for evaluation of tests. Formulations have simply not received the attention needed. Encouraging results in a few early tests, using a formulation which was easy to prepare and handle, effectively shunted

formulations work aside; only belatedly have some badly needed studies been undertaken. In view of the paucity of knowledge on release rates and patterns of the lure from various formulations, «treatment rates» have little meaning. There still has been no satisfactory demonstration that prevention of mating of individual moths has any consequences for a natural population in terms of reducing numbers in the next generation. The manipulation of gypsy moth populations by trapping or disruption is not yet a reality in North America.

Disparlure is being used, and very effectively, for survey and detection. The recent availability of the (+) enantiomer, although still in limited quantities, is likely only to enhance its role. Modifications and improvements in trap design hold promise for developing improved capabilities in population monitoring and prediction. This, in turn, will provide added data on which intelligent pest management decisions can be based.

In summary, there is an urgent need to get back to basics in several areas, and to put a safe distance between so-called «mission-oriented research» and that research which is really needed. Racemic disparlure may yet have a role in population manipulation, as it is an active material biologically. If a breakthrough in synthesis occurs, (+)-disparlure may be available economically in large quantities. It is currently an unknown concerning its performance in a disruption context. Certainly it is a powerful attractant – but trapping for population manipulation does not appear promising.

Progress is likely to come more slowly in the future because the Expanded Gypsy Moth Program ends 30 September 1978. Little of that pheromone work which is likely to continue is directed towards the basic questions which must be answered; rather the applied uses of the pheromone are being stressed. It will be interesting to see what the next decade brings.

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