A STUDY OF THE RELATIONSHIP OF POTATO TUBER MOTH, *PHTHORIMAEA OPERCULELLA* (ZELLER), TO ITS HABITAT

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During the latter part of the 1973-74 growing season, levels of damage to potato crops caused by potato tuber moth, Phthorimaea operculella (Zeller), were monitored by regular sampling. This revealed a significantly lower level of damage among tubers grown in sandy loam rather than silt loam. Similarly there was a higher proportion of infested seed grade tubers than larger table grade. As the haulms died off there was an increase in infestation among green tubers; this was the result of larvae moving from the haulms seeking alternative food sources.

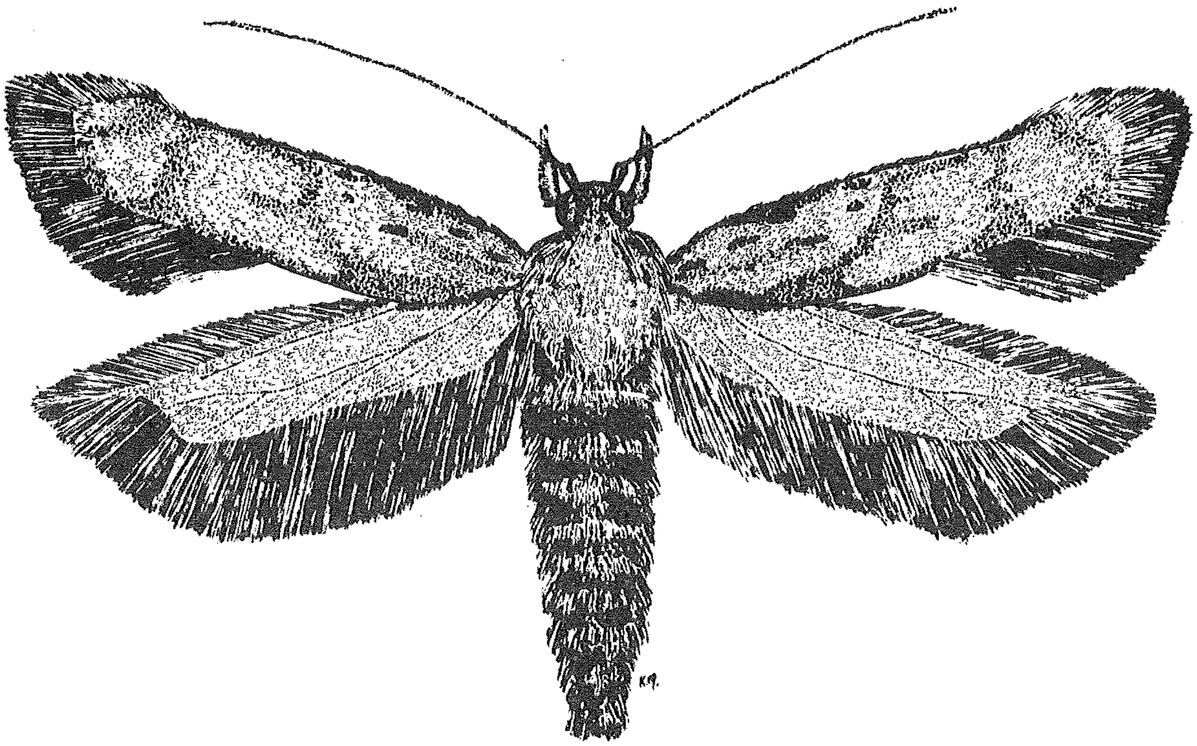
The 1974-75 season involved a more comprehensive study of tuber moth population growth and behaviour. This entailed the sampling of tubers and haulms for larvae and the use of suction traps; these were able to segregate the catch into specific time intervals and continuous recordings were made of weather conditions. This made it possible to study the relationship between abiotic factors and flight behaviour. Flight activity was found to reach its peak at dusk, and nightly catches were proportional to the total number of hours that occurred above 14°C. Fourteen degrees Celcius was found to be the field threshold temperature of flight. Although windspeed inhibited flight, the moths were found to fly in considerable breezes (up to 6 $msec^{-1}$) and rarely left the boundary layer. At no time was there any

detectable difference in the aerial density of tuber moths over the Ilam Hardy and Rua crops which are purported to be susceptible and resistant respectively.

Six weeks after harvest the level of infestation among cull tubers had risen by 88%. This clearly shows the significance of discarded tubers as overwintering sites and the importance of a clean harvest.

Laboratory work revealed there was no difference between infestation levels of Pentland Dell, (resistant), and Ilam Hardy tubers (susceptible), when subjected to identical infestation pressures. However it was shown that the three volatile components extracted from fresh potato leaves by steam distillation were capable of eliciting an excited response from adult moths. It is suggested that this highly volatile fraction could play an important role in tuber moths' ability to detect crops.

Field trials with a variety of compounds showed pyridine to be attractive to males and 3-ethyl pyridine attractive to females.



FRONTISPIECE

A female potato tuber moth, Phthorimaea operculella (Zeller)

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CHAPTER I

INTRODUCTION

New Zealand has the dubious distinction of being the first country discussed in the literature to have a problem relating to the "potato grub" (Berthon, 1855). In spite of this, it is generally agreed that potato tuber moth (Phthorimaea operculella) originated in America (Graf, 1917).

After a hundred years of observation and research, tuber moth still remains a scourge to potato growers in countries with warm, dry summers. Nonetheless cultural methods involving deep planting of seed, good moulding of the crop and efficient harvest helped to reduce damage. The advent of DDT combined with these cultural techniques further reduced damage to an economically tolerable level. However, since the decline in the use of DDT resulting from insect resistance and environmental awareness, the problem of tuber moth has again become serious.

Efforts to control tuber moth using organophosphate insecticides as a substitute for DDT have met with little success (Foot, 1974a; Ispray Limited, 1974). This lack of control is generally attributed to the short period of organophosphate persistence.

Since persistent insecticides have been shown to be ecologically undesirable, it seems that effective tuber moth control is likely only to be attained through more specific methods than those being used at present.

A survey of the literature reveals a surprising lack of quantitative ecological studies on tuber moth, or work on the relationship of tuber moth to its host plants. Attractants, long recognised as useful monitoring agents have, with the exception of the sex pheromone, been largely ignored. A possible reason for this lack of basic information is the 15 or so years that

DDT appeared to be a panacea. During this time there did not seem to be any need to study the biology of tuber moth as it was easily controlled by DDT.

Before the implementation of more effective insecticidal control, perhaps in conjunction with some of the more sophisticated techniques available, a much greater knowledge and understanding of tuber moth biology, attractants and plant-host relationships is required.

In the course of this project it was possible to examine some of the factors that lead to high levels of tuber moth damage. An investigation into varietal susceptibility was also initiated in both the laboratory and the field. The latter provided an excellent opportunity to obtain direct information on the effects of abiotic factors on flight activity. Moreover since the experimental plot during the 1974-75 growing season was in an area free from nearby volunteer plants and had no previous history of potato crops, the population growth patterns were carefully monitored. During this field work it was also possible to screen several compounds as potential attractants and propose a mechanism of crop detection by potato tuber moth.

CHAPTER II

LITERATURE REVIEW

INTRODUCTION

In view of the destructiveness of potato tuber moth it is not surprising that a plethora of research papers and summaries has been produced on the subject within the last 70 years. This review does not undertake to encompass the entire range of literature but rather to deal with those papers which assisted most in the formulation of the ideas and trials described in this thesis.

The first record of potato tuber moth is provided by Berthon (1855) who called it the "potato grub." He described it as being very damaging to the 1854 crop in Tasmania and concluded it was probably the same insect that had caused trouble in New Zealand on other occasions.

Much of the early literature on tuber moth was devoted to describing the distribution, host plants and severity of the damage. It also noted that careful harvesting and storage helped to minimise the level of tuber infestation.

LIFE CYCLE, PHENOLOGY AND EFFECTS OF CLIMATE

Graf (1917) produced the first major review of all known aspects of tuber moth and in it he closely examined the life-cycle. He described fully the type of damage inflicted by the larvae and contended that they prefer to feed on the green foliage rather than tubers. Moreover, he showed that cold temperatures do not induce hibernation, but rather simply retard the rate of development. This agrees with the work of Langford (1934) who noted that in

Maryland the pest was found to be present and active in practically all stages throughout the year. Graf (1917) further claimed that larvae mining in potato tops are very susceptible to change in weather and "in short cold and rainy periods most of the larvae in the leaves are killed." Poos and Peters (1927) contradicted this idea and presented data which clearly showed that while cool rainy periods may retard the development of larvae in leaves, they certainly do not actually kill them; this they attributed to the frass which closes off the entrances to the leaf mines. This idea is further supported by the work of Langford and Cory (1932) who showed how the early stages of the tuber moth life cycle can withstand cold temperatures. For example larvae were found to be able to withstand a 13 day period in potatoes packed in snow.

In an extension to the work done by Graf (1917), Poos and Peters (1927) discussed population growth in the field and pointed out that the autumn crop in Virginia was heavily infested since the moth population was able to build up through the summer. While noting that hot dry weather conditions played a large part in tuber moth outbreaks they also observed that there was a direct relationship between levels of infestation and the culls per acre remaining after the previous harvest. They contended that heavy infestations of tuber moth sometimes result from an abundant food supply rather than favourable weather conditions. This hypothesis was substantiated by Langford (1934) who concluded since tuber moth can survive relatively low temperatures in winter months (Langford and Cory, 1932), the destruction of the food supply is probably a significant factor in the survival of the insect.

From the observations of Poos and Peters (1927) and Langford (1934) it is apparent that overwintering is probably determined as much by the quantity of food available as by the temperatures experienced, as long as they are sublethal.

Langford and Cory (1932) examined several years' data collected in Maryland and showed that hot dry seasons appear most favourable to the development of high tuber moth populations. As a preliminary to a quantitative study of the effect of temperature on field population growth they carried out laboratory experiments to ascertain the thresholds of activity and development of the different stages. By plotting the reciprocal development time in days against the corresponding temperature factor, the theoretical threshold of development was found to be about 11.1°C. It was then possible to calculate the number of day - degrees required for one generation; Langford and Cory (1932) put this at 700 day - degrees (Farenheit). From this they showed that tuber moth was most troublesome during seasons where there was a sufficient accumulation of day - degrees to allow an additional generation. The observations of Muggerage (1936), Prescott (1939), Waterston (1940) and Weiss (1944) all agreed with this relationship between warm summers and high infestation levels.

Hofmaster (1949) repeated the work of Langford and Cory (1932) and also found 11.1°C to be the threshold development temperature. Using experimental data he calculated that 708.7 effective day - degrees (Farenheit) are required for one tuber moth generation.

Presumably these development times apply to cultures reared on potatoes. Finney et.al. (1947) found that development is more rapid among larvae reared on potato foliage than on tubers. Hofmaster (1949) tested this with a series of experiments using 30 replicates at temperatures ranging from 20°C to 24°C. His results showed that it takes an average of 4.77 days longer to rear first instar larvae to pupation on tubers than on foliage. This figure is highly significant statistically and although not mentioned by Hofmaster (1949) one can only assume that the required number of day - degrees for a single tuber moth generation in a crop with adequate foliage would be slightly less than that based on an estimate using tubers as the rearing medium.

Yathom (1968), in a three year study of tuber moth using larval counts, noted that once established, the moth population rapidly increases.

He observed a rise from 50% to 100% infestation in less than four weeks, which was about the time needed for the development of one generation at that time of the year. He also noted, as did Langford and Cory (1934), that rates of population increase seem related to the mean temperatures experienced early in the growing season.

From the work of Langford and Cory (1932), Hofmaster (1949), Yathom (1968), Muggerage (1936), Prescott (1939), Waterston (1940) and Weiss (1944) it is clear that temperature, particularly early in the season, plays an important role in determining the level of infestation during the growing season; this is unlike the winter, or off season, when it appears that food supply becomes more critical.

Reed (1971), as part of a programme to assess the potential of the tuber moth granulosis virus as a means of control, made a study of larval feeding and dispersal of tuber moth. He found that most eggs are laid on the soil or potato plants and newly hatched larvae usually bore into the leaves through the underside. Mines are reported to occur most frequently on the lower outer-most leaves. The amount of tissue eaten by each larva is constant regardless of the density of the insect, plant moisture stress or number of entries made. Reed (1971) further noted that as the number of available leaves per plant declines, more larvae are found moving on the stems and larval densities on the remaining leaves increases. This makes them more susceptible to bird predators. When leaf shortage becomes critical, mass migration occurs, presumably into tubers if available.

The life cycle and bionomics of tuber moth under laboratory and storage conditions are well known. Graf (1917), Poos and Peters (1927) and Hofmaster (1949) have thoroughly covered such aspects as oviposition, fecundity, mating, sex ratios, parthenogenesis, adult longevity etc. and there seems little reason for further research to be conducted in these areas. Likewise the effects on tuber moth of such factors as temperature and humidity under laboratory conditions have been thoroughly investigated by Langford and Cory (1932), Attia and Mattar (1939), Hovey (1943), Trehan and Bagal (1944) and Broodryk (1971).

Although laboratory work is obviously very important, the emphasis in this section of the Literature Review has been placed on field observations of tuber moth as it seems that further work could most usefully be applied to this area of study. It can be seen from the literature that scant attention has been paid to quantitative analysis of population build-up in the field or to the individual effects of climatic factors on tuber moths in their natural habitat. Further exploration of these areas could provide more insight into methods of regulating tuber moth populations.

CONTROL OF POTATO TUBER MOTH

Control of tuber moth has always been a problem. There are probably two reasons for this: first tuber moth has a very high biotic potential; assuming that an average 150 eggs is oviposited, one pair of moths in four generations is capable of producing 60 million moths under ideal conditions (Graf, 1917), second tuber moths are well protected from insecticides, particularly the early stages which are concealed in tubers and leaves (Foot, 1973). Currently control of tuber moth relies on a combination of cultural and insecticidal techniques.

1. Cultural Control

The importance of cultural methods and crop hygiene has long been known and recommended as a means of reducing tuber moth damage. Berthon (1855) recognised the importance of thorough harvesting and good storage of tubers. Graf (1917) observed that by planting seed at depths of about 150mm with adequate moulding, infestation could be reduced by 8%. He also noted that cull tubers are an important source of reinfestation of subsequent crops. These studies on cultural control have been repeated many times in the literature e.g. Poos and Peters (1927), Langford (1933), Hofmaster (1949), Broodryk and Zimmermann (1967), Akhade et.al. (1970) and Foot (1973). Irrigation has also been shown to reduce levels of infestation as this minimizes soil cracking, thereby hindering the access of larvae to the tubers (Langford 1933; Foot 1974b).

While cultural methods are useful as a means of reducing moth damage, often the levels of infestation are still economically intolerable, and for many years additional methods of control have been sought.

2. Insecticidal Control

In spite of considerable research, as recently as 1949 Hofmaster commented at that stage little success had been met in efforts to control tuber moth in the field.

Arsenical, flourosilicate and nicotinic compounds, though not very effective, were frequently used in addition to cultural methods. Cory and Saunders (1926) recommended the use of arsenical dusts. Newman and Morgan (1937) suggested that lead arsenate and air slaked lime could reduce levels of infestation. Poos and Peters (1927) found four spray applications of lead arsenate, calcium arsenate, zinc arsenate and nicotine-sulphate-whale oil soap gave no appreciable control, while dusts of similar compounds were found to reduce leaf mining by an average of 50%. Before the advent of DDT only derris-kaolin dust (Lloyd, 1943), and phenothiazone spray (Helson, 1944) showed any promise as methods of control.

Caldwell (1946) cautiously suggested DDT might be useful for the control of tuber moth in the field. Much of the pioneer work involving the protection of potato crops was summarized by Helson (1949). He described field experiments conducted between 1942-46 during which time an array of compounds were tested. It soon became apparent that 0.1% DDT was superior to all other treatments irrespective of the form in which it was applied.

Hofmaster (1949) also carried out extensive preliminary trials with DDT and in 1947 demonstrated its potential by treating six hectares of heavily infested autumn potatoes with 3% DDT dust applied at 25kg ha^{-1}.

From this time onwards the use of DDT as a control measure became increasingly common and important. May (1952) showed that two or three applications of DDT at fortnightly intervals prevented infestation of tops during most of the growing period and reduced the likelihood of tuber attack. In the same publication he stated that in Queensland DDT sprays could produce increases of up to 17% in the number and 43% in the weight of table grade tubers.

As with many other species of insects, potato tuber moth developed resistance to DDT. Champ and Shepherd (1965) noted in Australia that from about 1946 to 1958 adequate control of tuber moth had been maintained, but from 1958 on the results were not as spectacular. In a series of trials they showed that there were no completely susceptible strains of tuber moth in Queensland even where little or no DDT had been used. A similar situation was reported by Richardson and Rose (1967) in Rhodesia. These trends, along with the increasing awareness of the effects of organo-chlorines on the environment have led to a sharp reduction or the abandonment of DDT in many countries. Subsequent efforts to control tuber moth populations using organophosphate compounds have met with little success. For example, Ispray Ltd. (1974) in their 1973-74 report described how eleven fortnightly applications of azinphos-etnyl at 1.1l ha^{-1} were only able to reduce the percentage weight of infested tubers from 29.8% (control) to 21.4%. Further tests using Orthene®, Tamaron®, and Lannate® proved even less successful.

DDT was probably effective because of its persistence in the soil. Thus, although the early stages of tuber moth may have been protected by their food source at the time of application of the insecticide, it eventually killed them when they came out to pupate.

It can be argued that it is the absence of this residual effect of organophosphate insecticides that reduces their efficiency against tuber moths. Foot (1973) has also pointed out that the effectiveness of insecticides against adults is reduced by their bodies which are densely covered with protective scales.

This lack of an adequate substitute for DDT has stimulated further detailed research into the biology and behaviour of tuber moth, in the hope that more sophisticated and efficient systems of control can be developed and implemented.

3. Autocidal Control

There have been several investigations into the possibility of using autocidal techniques to control potato tuber moth. Elbadry (1964 and 1965) conducted experiments using gamma radiation to suppress the reproductive potential of tuber moth and noted the eight day old pupal stage to be the most susceptible. However, sterile males were found to be unable to compete successfully with their untreated counterparts making this technique unsuitable. Hughes (1967), in a thorough study, assessed the value of metepa as a means of chemosterilization but the results were inconclusive. Harwalkar et.al. (1971) extended this work on metepa and found it to be an effective sterilizing agent. He concluded that treated males were able to compete effectively with normal males for females.

4. Parasitism of Tuber Moth

The use of parasites has long been considered a possible means of biological control. Graf (1917) listed 10 parasite species and gave details of their life cycles. Poos and Peters (1927) and Hofmaster (1949) also published impressive lists of parasites. However, in spite of their efforts tuber moth still remains a serious problem to growers, although occasionally parasitism rises to very high levels. Edwards (1929), observed that parasitism of tuber moth by Eulimneria stellenboschensis Cameron reached 46% in

Mauritius. In New Zealand Foot (pers. comm.) reported tuber moth populations at Pukekohe to be infested by *Apanteles subandinus* Blanchard at levels well in excess of 14.5%. Recently attention has been paid to the mass-rearing of parasite-infested moths for liberation (Platner and Oatman, 1968; Wearne, 1971).

5. Control Using a Granulosis Virus

Reed (1969) described how in 1964 a tuber moth virus was isolated from the C.S.I.R.O. cultures at Canberra and was found to spread rapidly throughout potato crops even when a very small dosage was applied. Reed (1971) continued this work and showed that the virus particles are small enough to enter the leaves through the stomata and thereby become ingested by the larvae. He also pointed out that as the leaves die off, the infected larvae tend to become increasingly susceptible to predators such as *Zosterops gouldi* (Bonaparte). Mathiessen and Springett (1973) have shown how this bird is capable of spreading virus particles to other potato crops. Reed and Springett (1971) published the results of a large scale field test of the granulosis virus and reported infection rates of 100% with a residual effect of 12 weeks. The virus was found to be highly effective in preventing damage and rapidly spread from the sites of application. This presents the possibility of applications only being required in places such as borders near to infested crops and relying on natural spread to fill the gaps.

Clearly this pathogen shows great potential as an effective weapon against tuber moth, but registration is required before it can be sold for commercial use. However, it is felt that the pathogen has existed in Australia for "many years" and that man has been exposed to it for "many generations" (Anonymous, 1972). The virus also appears to affect only one host, the potato tuber moth (Anonymous, 1972) and has the advantage of leaving parasites unharmed.

6. Pheromones, Attractants and Plant-Insect Interaction

Although these agents are not necessarily always of direct value for control purposes, a thorough knowledge and understanding of them can greatly increase the efficiency and precision of current insect control techniques.

The potential value of lepidopteran pheromones is well established (Jacobson, 1966 and 1972) and has led to research into the possibilities of using tuber moth pheromones as a bait for traps. These could either be used as a direct means of control or as a population monitoring device.

Hughes (1967) established the presence of a female sex pheromone in tuber moths and isolated extracts from whole abdomens using methylene chloride as the solvent. He found that the pheromone elicited a response from two day old virgin males at a concentration of 0.25×10^{-3} female equivalents. The results of a series of bioassay procedures and trapping tests led him to conclude that the pheromone is primarily an excitant rather than an attractant.

Adeesan et.al. (1969) showed that the pheromone is present and can be extracted from a gland between the 8th and 9th abdominal segments of female moths. They stated that the extract is capable of luring the males into traps but gave no further details. Springett and Matthiessen (pers. comm.) used pheromone traps with live virgin females contained in perforated tubes. However, they observed that the numbers caught depended on too many factors to make the technique an accurate quantitative monitoring system. They noted that the age of the females and the proximity of other females contributed to the variable results. Kennedy (1975) discussed the various types of trap designs suitable for trapping males using tethered females as bait. He found that virgin females under six days old were the most attractive, but caught no significant numbers with tethered mated females. He suggested that the multiple mating of females observed by Poos and Peters (1927) could have resulted from the moths being confined in small containers for observation.

The use of non-pheromonal lures has long drawn the attention of workers engaged in tuber moth research. Graf (1917) observed that adult moths are attracted to light traps and this could be a possible method of control. He did not comment on its potential use as a population monitoring device. Attraction of moths to bait was discussed by Poos and Peters (1927) and they tested the potential of an array of sweetened baits: strained honey, brown sugar, dark karosyrup, and black Cuban baking molasses. The latter appeared the most attractive but variation in concentration or the addition of Fleishmann's yeast with amyl acetate appeared to make no difference to the numbers caught. It was concluded that the catches were insufficient to allow any degree of control.

With the increasing knowledge of plant physiology, more attention has been paid to insect-host relationships, perhaps with a view to breeding plant strains resistant or tolerant to insect pests. Host-insect interaction has been reviewed by Dethier (1948), Thorsteinson(1960), and Schoonhoven (1968). Dethier (1948) noted the host plant is initially selected by the adults but the larvae (particularly Lepidoptera) themselves are capable of distinguishing certain plants since sometimes eggs are laid only in the vicinity of the host plant. This is quite probably the case with tuber moth (Reed, 1971). Thorsteinson (1960) discussed food plant detection by insects and suggested that often experimental results are misleading because it is not realised that a study of flight behaviour is necessary to understanding of food finding mechanisms. Often insects are only responsive to plant odour when on the wing in dispersal flight and the fact that this has not always been recognised could have contributed to the contradictory results often obtained.

Finney <u>et.al.</u> (1947) considered the effects of varietal differences on tuber moth attack and observed that the numbers of fully fed larvae produced by the tubers varied with the variety of potato, type of soil, potato maturity, and the evaporative power of the surrounding air. Two mealy varieties (Russet and Green Mountain) were found to be able to support higher larval populations than the non-mealy types (White Rose and Earlaine). They suggested this was because the larval populations could permeate the crisp pith of the mealy varieties whereas in the turgid non-mealy tubers the larvae were confined to the cortex just under the skin.

It has been observed by Yathom (1968) that potato plants are more attractive to tuber moth when they are dehydrated. His hypothesis was that succulent plants in saturated soil are located in a microclimate with an almost constant high humidity. He contended such an environment does not attract moths to oviposit and is unfavourable to the hatching of eggs. Hovey (1943) and Broodryk (1971) stated the contrary and, unlike Yathom (1968) provided data that showed humidity had no effect on the length of the incubation time of eggs. Foot (1974b), in her field trials to assess the effects of cultural control methods, observed that irrigation effectively reduced the mean number of mines per leaf. However, irrigation also led to denser foliage and it was found that irrigated crops in fact had a higher larval population than non-irrigated crops. This does not agree with the observations of Yathom (1968).

Meisner et.al. (1974a) used foamed polystyrene as an inert carrier for testing phagostimulants of tuber moth larvae and observed extracts from potato leaves to be more powerful than those from eggplant leaves, tobacco, tomatoes, or pepper. They then attempted to isolate the phagostimulants from the extracts using chromatographic separations and found sucrose contaminated with several amino-acids to be attractive. Of the 12 sugars they then tested, sucrose and fructose were the most significant. In a similar trial involving 20 amino-acids, alpha-amino-butyric acid was shown to be fairly active. Moreover, chlorogenic acid was also found to be attractive at the 0.1% level. This work was followed up by another paper by Meisner et.al. (1974b) dealing with the factors influencing the attraction of oviposition by the potato tuber moth. During these trials they showed that the food source the larvae were reared on does not influence the ovipositional site of the resultant adults - potato foliage being always preferred. Further investigation revealed that fecundity is much higher when larvae are fed on potato tubers rather than potato leaves or other host plant foliage. Fractions were separated from potato peel extract on a silica H column and L-glutamic acid seemed important as an ovipositional attractant.

The understanding of the relationship of tuber moth to its host range is clearly important if more sophisticated control techniques are to be used. However, the literature review reveals that results to date are inconclusive, confused and sometimes contradictory. Clearly further research could usefully be performed in this area, with particular emphasis on tuber moth detection of host plants and the mechanisms of varietal resistance.

ORIENTATION AND DISPERSAL OF INSECTS AND THE EFFECTS OF WEATHER ON FLIGHT ACTIVITY

1. Orientation and Dispersal

Although a great deal has been written on flight behaviour of insects, tuber moth has been largely ignored. Yathom (1968) observed that tuber moths are good fliers whereas Hofmaster (1949) stated the contrary. Reed (1971) suspected that dispersal of the adults is wind assisted and related this to the high density of moths along the edges of crops. Apart from Hughes (1967), who noted that male tuber moths fly against the air flow for distances of up to 0.61m towards sex pheromone traps, the subject of tuber moth orientation towards host plants or sex pheromones appears to have been largely neglected. This could be partly because many workers assume the moths to be very poor fliers. Nevertheless, considerable attention has been paid to Lepidoptera in general.

Laboratory experiments by Schwink (1958) showed that only a very high molecular gradient of female pheromone can bring about true olfactory orientation of Bombyx mori L. over a short distance, but far lower molecular concentrations are capable of eliciting positive anemotaxis. This would permit the orientation of males over long distances although the gradient of odour molecules would no longer be perceptible. This mechanism of orientation to attractants by insects is now generally accepted by most insect behaviouralists (Shorey, 1973).

Johnson (1969) in his comprehensive review of migration and dispersal of insects by flight, showed the importance of the "boundary layer" to controlled insect flight. This is the zone of air near the surface of the ground where the movement is less than the flight speed of the insect concerned.

In spite of this, it would seem that many insects encounter hosts and habitats randomly after having been carried beyond the limits of the boundary layer by wind (Johnson, 1969). An extreme example of this is provided by the massive invasions into Britain by millions of diamond-back moths (Plutella xylostella L.) in 1958. The trajectories of the surface geostrophic winds that carried the moths were plotted back as widening tracks and crossed over in the region of the western shores of the Baltic and the U.S.S.R. From this it can be concluded that the moths had made a journey of perhaps 2,400-32,000 Km in only four to five days, having been carried by moving air masses (Johnson, 1969).

2. Analysis of the Effects of Weather on Flight Activity

Taylor (1963) observed that temperature thresholds of flight are species-specific and between the upper and lower threshold limits the proportion of insects in flight may well be independent of temperature. For this reason regression analysis of results for a monospecific population is probably unsuitable. This is not the case for a multispecific population - here a range of flight thresholds can be expected and activity is likely to be directly related to temperature.

Johnson (1969) recognized the value of regression analysis to predict changes of aerial density in relation to weather, but warned that it is statistically unsound to correlate serial processes by linear regression.

He continued to caution that even using multivariate regression, it still cannot distinguish which relations between weather and numbers flying are causative and not merely correlative. Furthermore, in few cases has "trivial" flight been fully differentiated from "migratory flight," so that the effects of changing populations have often become confused with flight activity as influenced by weather.

The operation and interpretation of catches made using the Johnson-Taylor suction traps are summarized by Southwood (1968) and further details are provided by the Burkard Manufacturing Company, England. More theoretical mathematical descriptions of the development and operation of the suction traps are dealt with by Johnson (1950) and Taylor (1951, 1955, 1962).

CHAPTER III

METHODS AND MATERIALS

FIELD SAMPLING OF TUBERS

During the latter part of the 1973-74 growing season tubers were sampled from Belfast to gain information on levels of infestation and the effects of different soil types. The field study at Lincoln College the following season involved a far more comprehensive programme including measurement of flight activity, growth in larval populations and levels of tuber damage. Many of the methods used in this work were developed during the previous season at Belfast.

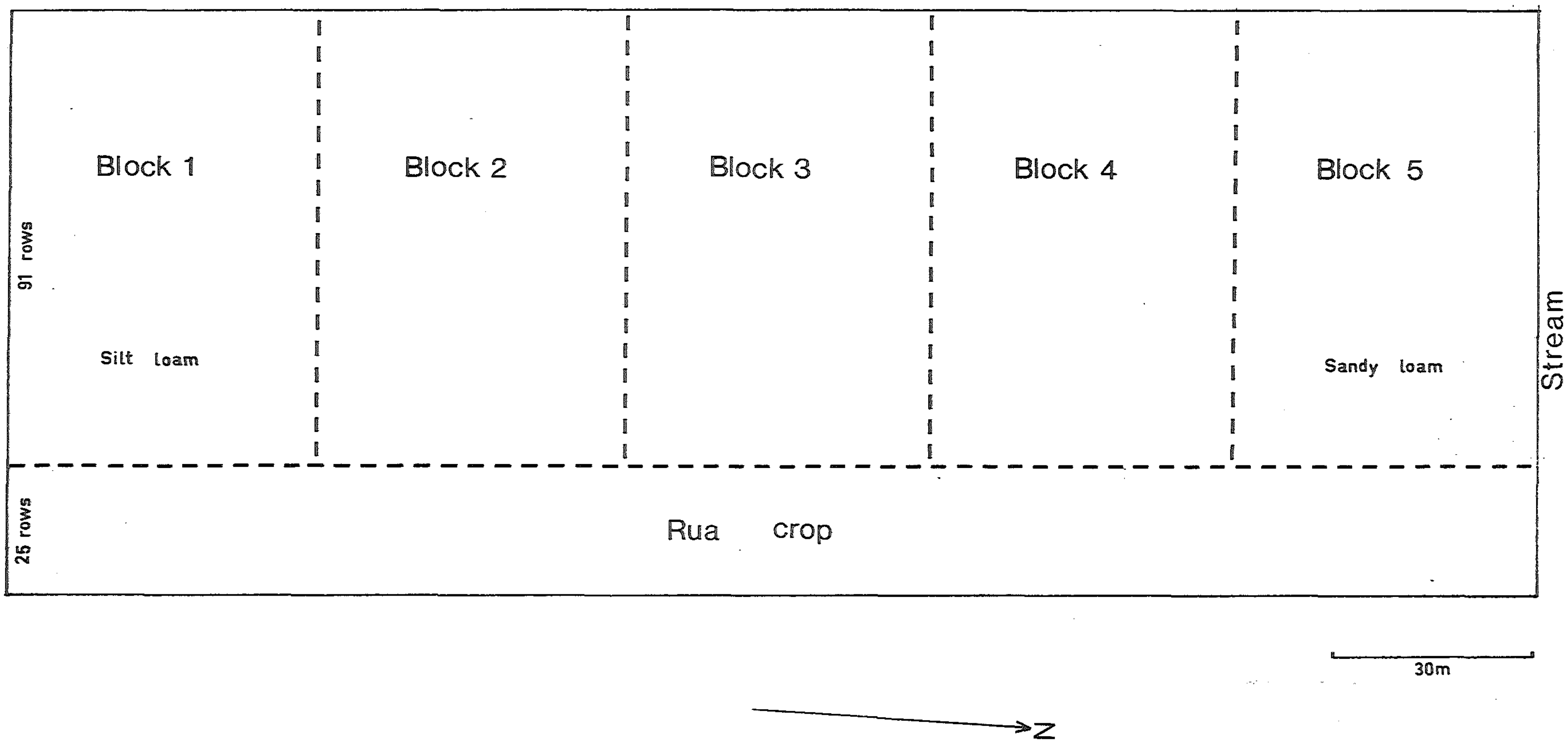
1. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1973-74 Growing Season at Belfast

Since this work was conducted during the latter part of the season, it was of interest to observe the effects of the haulms dying off and subsequent larval movement.

(a) Research Crop (Fig. 1). After several areas had been investigated it was decided that a Belfast crop near Christchurch belonging to Mr. K. H. Treleaven was the most suitable because no insecticides had been applied and harvest was not expected until June or July. This allowed for a long sampling period.

The experimental portion of the crop was made up of 91 rows of Ilam Hardy plants covering about 1.75ha (Fig. 1). Each row was some 250m long and sampling included all the rows except the two on the extreme western boundary. These were excluded because of the possibility of edge effects. The eastern boundary was adjacent to a Rua crop which acted as an effective buffer. The total number of plants was estimated at 62,500.

FIGURE 1. BELFAST 1973-74 POTATO TUBER MOTH ILAM HARDY RESEARCH CROP.



The experimental plot consisted of two soil types. Associated with a stream at the northern end the soil was Waimakariri fine sandy loam while at the southern end it was Kaiapoi silt loam (Raeside and Rennie, 1974).

In order to detect any differences arising from these soil differences, the plot was divided into five equal blocks.

(b) Field Sampling of Tubers and Haulms. Every two or three weeks eight randomly selected samples from each of the five blocks were taken back to the laboratory for examination (p. 28). Each sample consisted of tubers and haulms of a single plant. In addition to the collection of the samples, estimation of the number of green haulms remaining in the experimental area was made by obtaining the number found in several randomly selected rows.

2. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1974-75 Growing Season at Lincoln

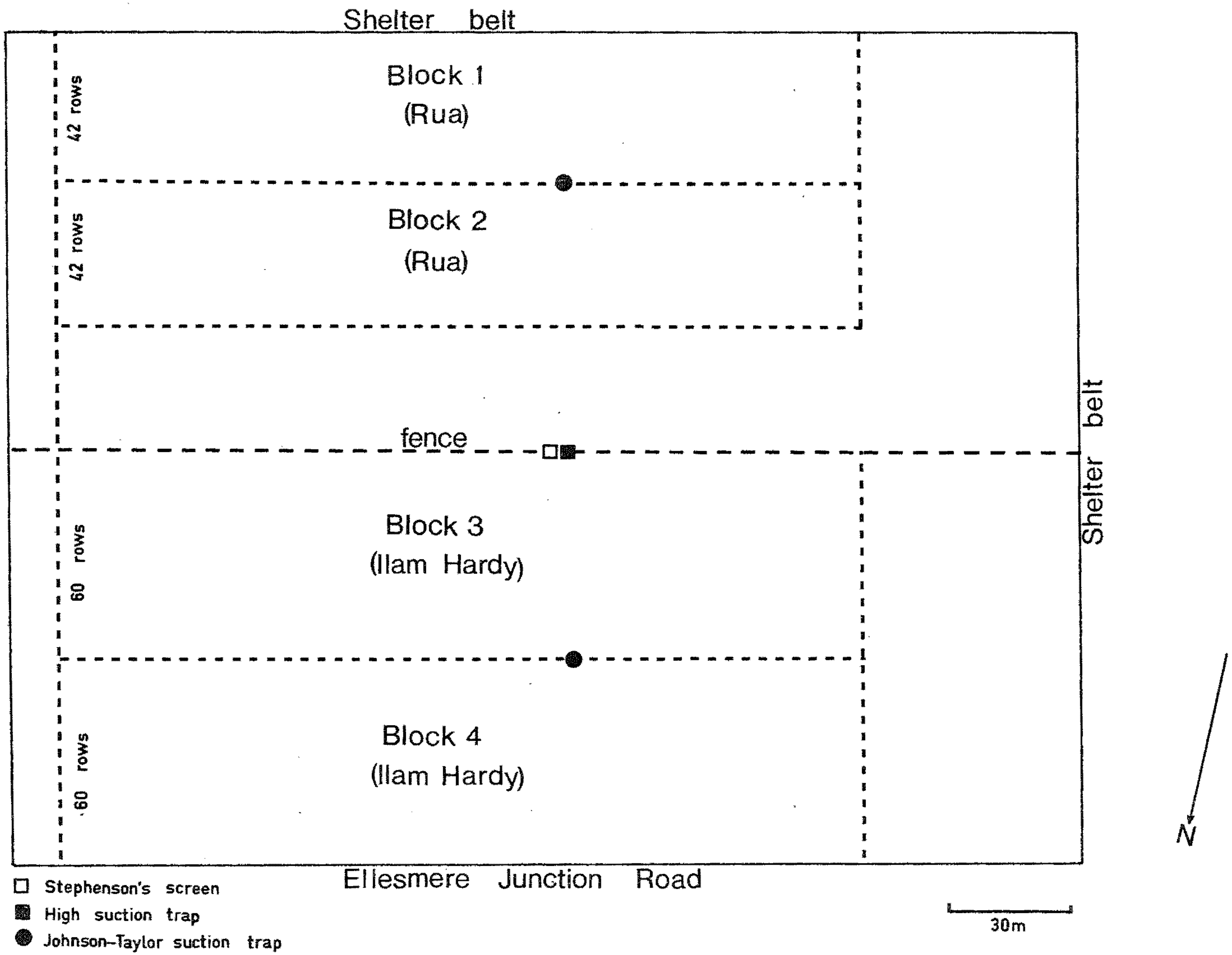
In view of the information gained during the sampling programme at Belfast, it was possible to expand and plan the work conducted during the 1974-75 season.

(a) Research Crop (Fig. 2). This consisted of 4.8ha of potatoes sown on Lincoln College property. Both Ilam Hardy and Rua crops were grown as shown in Fig. 2. To avoid any undetected effects from shelter belts, the crop was divided into four longitudinal blocks starting 50m from the western edge which had a well developed shelter belt.

The first two blocks were Ilam Hardy and each consisted of 60 rows while the two Rua blocks were made up of 42 rows. Each row was 180m long, and once again the first two around the perimeter were ignored because of possible edge effects. It is generally accepted that Ilam Hardy tubers are more susceptible to moth attack than Rua.

(b) Field Sampling of Tubers and Haulms. In view of the 20% standard error of the mean of the infested tubers taken the previous season, the sample size of the tubers was increased to 25 randomly selected plants per

FIGURE 2. LINCOLN COLLEGE 1974-75 POTATO TUBER MOTH RESEARCH CROP.



block. However, because of the limitations of labour, it was found necessary to reduce the sampling frequency to once a month.

Unlike the 1973-74 season, the haulms were sampled independently of the tubers. Each week the haulms of five randomly selected plants from each block were taken to the laboratory for larval extraction. During collection they were placed in plastic bags. It was important to ensure that these were stored unsealed and in the shade as the heat accumulated rapidly and killed the larvae; the extraction technique required that they remained alive (p. 28).

3. Sampling of the Adult Population and the Effects of Weather on Flight Activity During the 1974-75 Season

The availability of electricity and section traps made it possible to measure on a day to day basis the adult population growth in the field, and the effects of weather on flight activity.

(a) Suction Traps. Between the Ilam Hardy and Rua experimental plots, were positioned two identical 0.3m Johnson and Taylor suction traps (Fig. 2). These were set into the ground by installing them into holes about 0.75m deep thereby placing the induction fan approximately level with the top of foliage (Plates 1 and 2).

It is possible for these machines to be loaded with catch-segregating discs which can be released at various time intervals. For this trial, one trap was set to drop discs at hourly intervals so that measurements of diurnal flight intensity throughout the entire season in moth population was also monitored. The other trap acted as a way of comparing flight intensity between the two varieties of potatoes, and provided further data on the day to day increase in population. A third suction trap 3.6m above the ground was positioned in the centre of the experimental area. Although of a different design to the Johnson and Taylor traps it provided a means of determining to what extent tuber moths are wind-borne (Plate 3).

Since the traps could hold only sufficient segregating discs for a 24 hour period, it was necessary to service them daily. All catches were

Plate 1. Johnson and Taylor suction trap showing the method of installation.

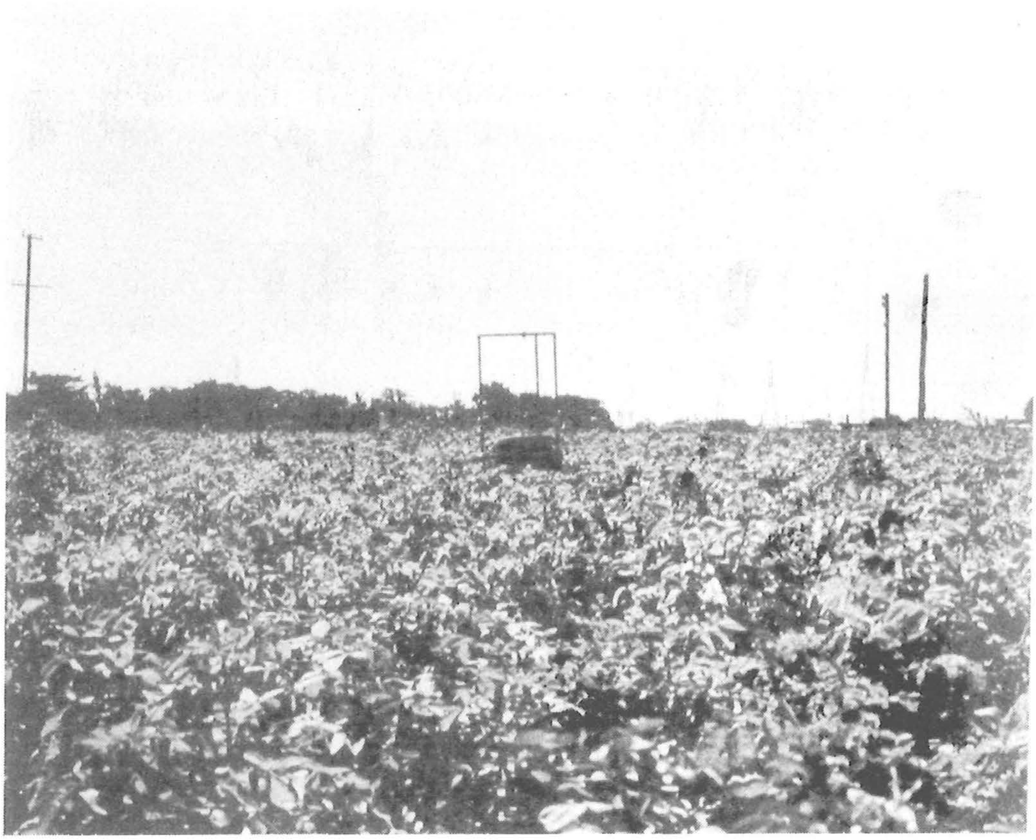


Plate 2. Johnson and Taylor suction trap in operating position with the induction fan level with the foliage cover.

Plate 3. High suction trap, 3.6m above the ground; Stephenson's screen to the right

taken to the laboratory for identification and sex determination. The segregating discs were cleaned and sprayed with a pyrethrum insecticide before being reloaded into the trap.

(b) Weather Recording Equipment. A Stephenson's screen was positioned 0.8m above the ground in the centre of the crop (Plate 3). This contained a maximum and minimum thermometer and two thermohydrographs, one of which also recorded barometric pressure. The daily checking of this equipment combined with the College weather station records ensured that mean hourly temperature records were accurate to $\pm 1^{o}C$.

Windspeed was measured using a Rimco anemometer type R/ASI-S with the cups set 2m from the ground. This was established in an adjacent field 100m from the potato crop. The instantaneous windspeed was recorded on an A.E.I. multipoint chart three times every 80 seconds. From these points it was possible to ascertain mean hourly windspeeds.

4. Field Trials of Potentially Useful Chemical Attractants

Towards the end of the season, when the moth population had become well established, trials were carried out to test the potential of several compounds as attractants. This was based on previous unpublished work conducted by Osborne and Hoyt (pers. comm.).

The compounds tested were pyridine, 2-ethyl pyridine, 3-ethyl pyridine, 4-ethyl pyridine, 2-acetyl pyridine, pyridine + H_2O, quinoline, isoquinoline, naphthalene, isobutyric acid, and the steam distillate of potato leaves. The traps used were of the type designed by Osborne and Hoyt (1968) and consisted of a red tin of 200mm diameter, 80mm deep with a single vane 200mm x 80mm slotted to accommodate a 25ml glass jar. The tin itself was filled to the brim with water, along with a drop of detergent, to break the surface tension of the water. The 25ml jar contained a few ml of the compound being tested. Since this was only a screening trial, based on comparative catches, it was unnecessary to test the efficiency of these traps.

On suitably warm quiet evenings the traps and a control of fresh water were set in random order on the potato mouldings at least 12m apart. The trial was usually left to run overnight and was checked early the following morning in order to reduce the possibility of birds preying on trapped insects. The moths caught were taken back to the laboratory for sexing. Occasionally the trial was permitted to run for longer so an appraisal of the effects of decreasing concentrations could be made, since many attractants are known to be concentration critical. It was during this series of trials that it was possible to observe the nocturnal behaviour of the moths during suitable moonlit nights.

5. Assessment of Post Harvest Infestation of Cull Potatoes

The harvest of the Ilam Hardy plot on the 14/2/75 furnished an excellent opportunity to assess the degree of subsequent infestation that occurred amongst tubers left scattered on the ground. This was of interest as it is well known that discarded tubers provide an ideal over-wintering site for tuber moth larvae. Therefore two days before the harvest, tubers taken from 25 randomly selected plants (block 4) were sampled and their level of infestation was recorded. Six weeks after the harvest all the tubers and parts of tubers found in three of the windrows left by the harvesting machine were collected and examined for larval burrows.

The rows selected were on the southern side, centre and northern boundary of the plot; it was therefore possible to test for differences in damage arising from their varying distances from that part of the crop still standing.

SAMPLE ANALYSIS, REARING METHODS AND LABORATORY TRIALS

Of the techniques employed to aid sample analysis, the methods ultimately depended on the visual observation of infestation or larval numbers. Since all analyses were performed by the author, any bias affecting the data should have been consistent throughout the experimental regime.

During the study, it was essential to have an adequate supply of tuber moth adults, larvae and pupae. This necessitated the establishment of viable cultures, which allowed laboratory susceptibility and attractancy trials to be carried out.

1. Examination of Tuber Samples

The different sized tubers comprising each sample were washed and classified into table (greater than 51mm in diameter), seed (between 51mm and 38mm in diameter) and pig (less than 38mm in diameter) grades using two frames of 51mm mesh and 38mm mesh (Plate 4). The number in each grade per sample was recorded, and in the 1973-74 season, weighed. The tubers were then closely examined for greeness and larval damage.

2. Extraction of Larvae from Haulms

It soon became apparent manual searching and removal of larvae from the foliage was impractical since it took up to 11 hours to cope with a single heavily infested sample; it was therefore necessary to modify a heat extraction technique developed by Wearne (1969). The haulm sample was cut into 100mm to 200mm pieces and placed in a 450mm x 270mm tray of expanded aluminium with a mesh size of 7mm x 2.5mm. This in turn was supported by four 20mm high corks glued to the bottom of a 500mm x 320mm x 100mm plastic offal tray (Plate 5). One mm of glycerine was placed on the bottom of the last tray. Twenty of these assemblies were constructed and, when loaded, were placed into a drying oven at 37°C-40°C for 24-36 hours until such time as the samples had completely dried out. This process forced the larvae to abandon the foliage and drop down into the glycerine where they were trapped. In this way, each week, the number of larvae in 20 tops was ascertained. A pleasing feature of this method was the first instar larvae were far more easily detected against the white bottom of the tray than in the foliage and this helped to reduce the possibility of inaccuracies through oversight.

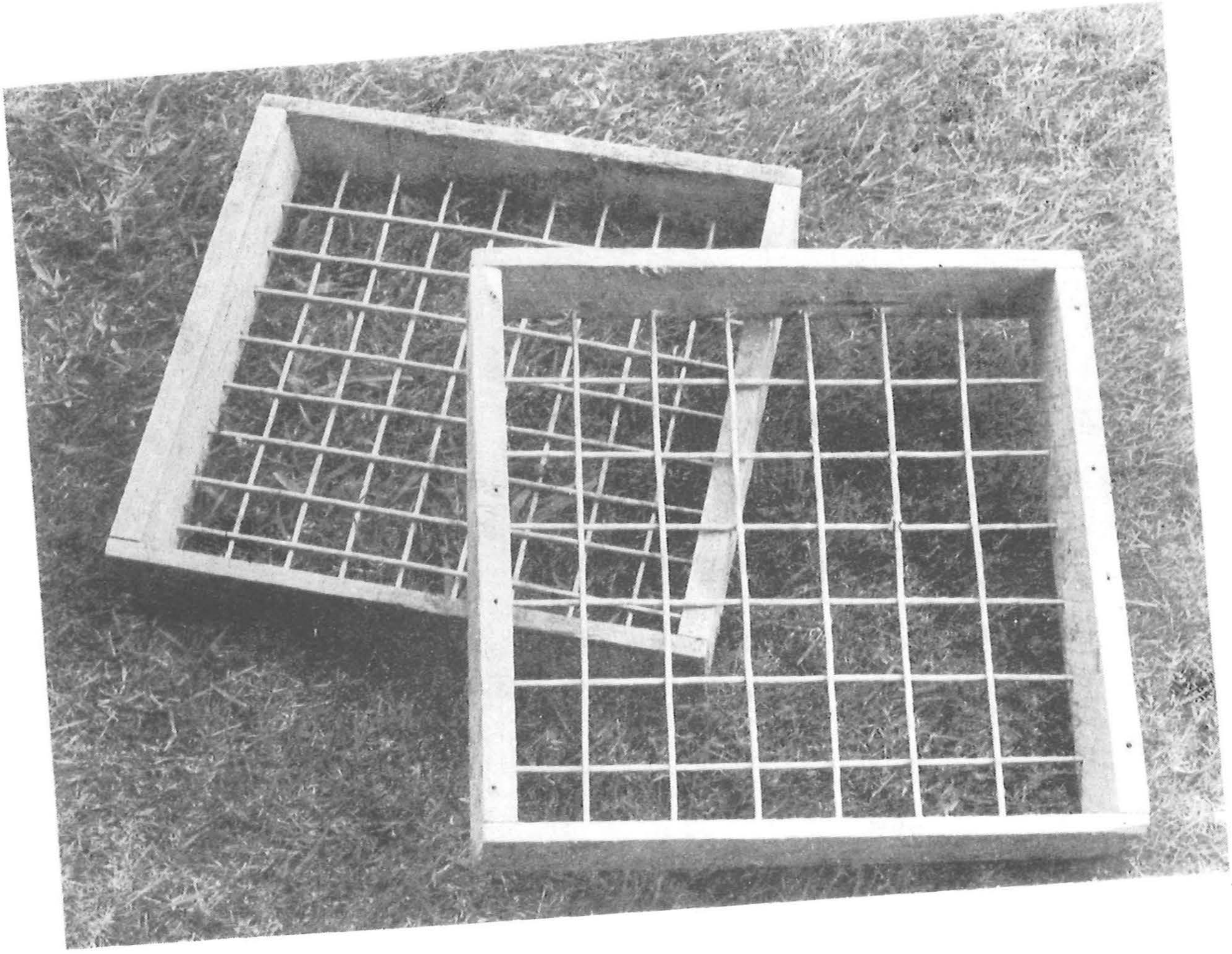


Plate 4. Grids used for grading potatoes.

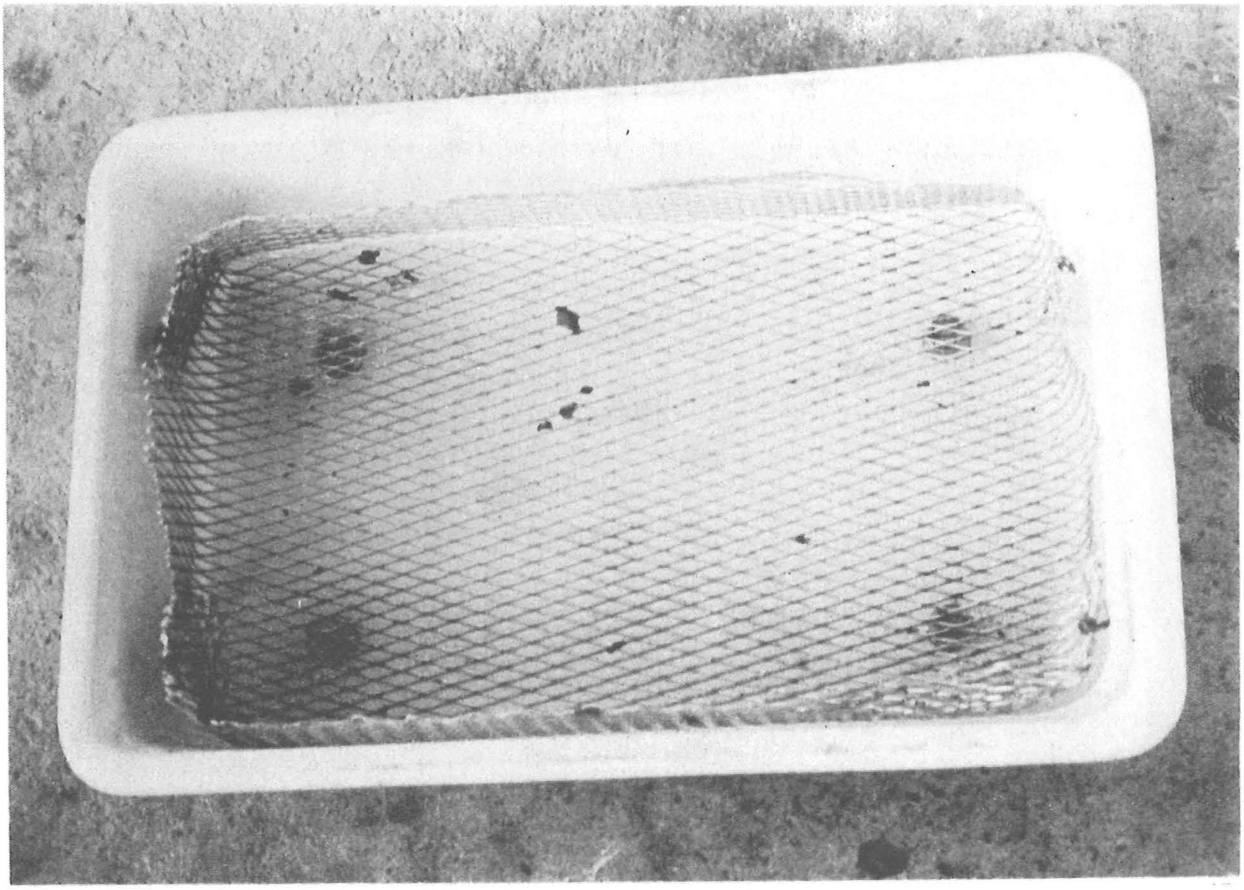


Plate 5. Arrangement used for the extraction of larvae from the haulms.

Examination of foliage subsequent to drying showed the method to be very thorough and compared favourably to the results obtained by Wearne (1969), who showed recovery to be at least 98% efficient.

About every three weeks it was necessary to filter the glycerine through glass wool and wash the offal trays to enable unimpaired counting of the larvae to continue. For this reason glycerine proved far superior to paraffin oil since the former is water miscible.

3. Establishment of Potato Tuber Moth Cultures

The cultures were initially reared in three 660mm x 500mm x 500mm cages (Plate 6). The front flap could be lifted up to gain entry and was secured along three sides with "Velcro" (ribbon strips with opposing surfaces of hooks and loops). This meant the cage could be partially opened to gain access without loosing too many insects. Sixty mm above the floor was a false bottom of expanded aluminium (Plate 6); and on this was placed an adequate supply of potatoes. These were lightly punctured to encourage oviposition and easy entry for first instar larvae. Beneath the aluminium mesh was a large quantity of screwed up tissue paper which provided ideal pupation sites. The cages were kept in a constant environment room at 26°C and were subjected to a 12 hour photoperiod. The cultures were supplied with a solution of honey and water and although the moths made use of this, it did not seem to be essential to population vigour.

The initial stock for the cultures consisted of larvae taken from tubers collected at Belfast and was maintained for six months. Tuber moth did not prove to be a difficult insect to rear in as much as it has a rapid life-cycle e.g. four weeks at 26°C (Finney et.al. 1947) and non-specific food requirements.

In order to minimise the effects of pathogens it was necessary to re-establish the cultures in four new cages. These were modified from the design of Hughes (1967) and each consisted of a 9mm thick cardboard cylinder with a

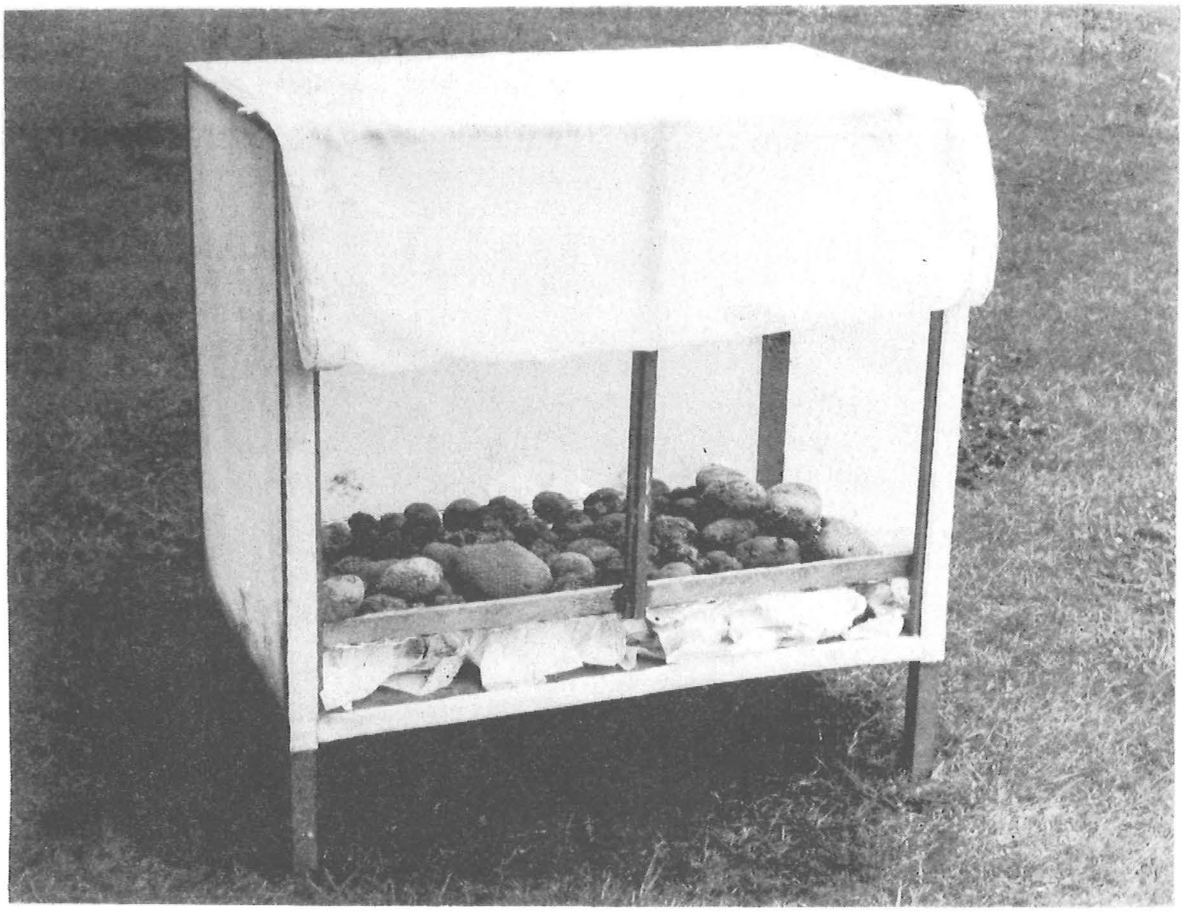


Plate 6. First type of rearing cage used; larvae dropped from tubers and pupated in tissue paper below.

diameter of 386mm and a height of 380mm (Plate 7). At 90mm intervals three discs of expanded aluminium were fitted inside the cylinders and these were supported by cross-struts of fencing wire. This allowed for three layers of tubers in each cage, access to which was made possible by cutting four diametrically opposite inspection holes of a diameter of 40mm into the sides of the cylinder (Plate 7). These in turn, were plugged with the bottom portions of paper drinking cups. The whole assembly was then placed on a 500mm x 500mm sheet of hardboard covered with 3mm of fine sand. This was heaped around the sides to prevent the escape of larvae. Pinned to the top of the cage was a taut lid of fine-meshed Dacron. This was sealed to the rim with hot wax to prevent the escape of 1st and 2nd instar larvae.

Initially these cultures were stocked with material from the infected cages. Disinfection was achieved by using the adults that had eclosed from pupae which had been soaked in 0.2% sodium hypochlorite solution for 5 minutes. Later, when the population in the field was adequate, it was possible to trap sufficient numbers at night using a portable fluorescent lamp and an aspirator. Red-eyed mutants appeared in one of the cultures and this probably reflected the small gene pool present at that time. This mutation has been described by Champ and Shepherd (1971) where it was found in cultures in Australia. They demonstrated that there are no significant differences in viability or rates of development between the red-eyed type and the wild-type.

Pupae were obtained from the cultures by lifting the cage off its hardboard base and brushing aside the sand (Plate 8). Another feature of this system was the ease with which the cardboard cylinder could be replaced and the metal parts autoclaved in the event of pathogenic infection.

4. Tuber Infestation Trials

In order to obtain comparable results it was desirable to procure three pairs of virgin moths of known age for each trial. This was achieved by isolating single pupae in stoppered vials (Plate 9) and waiting for them to

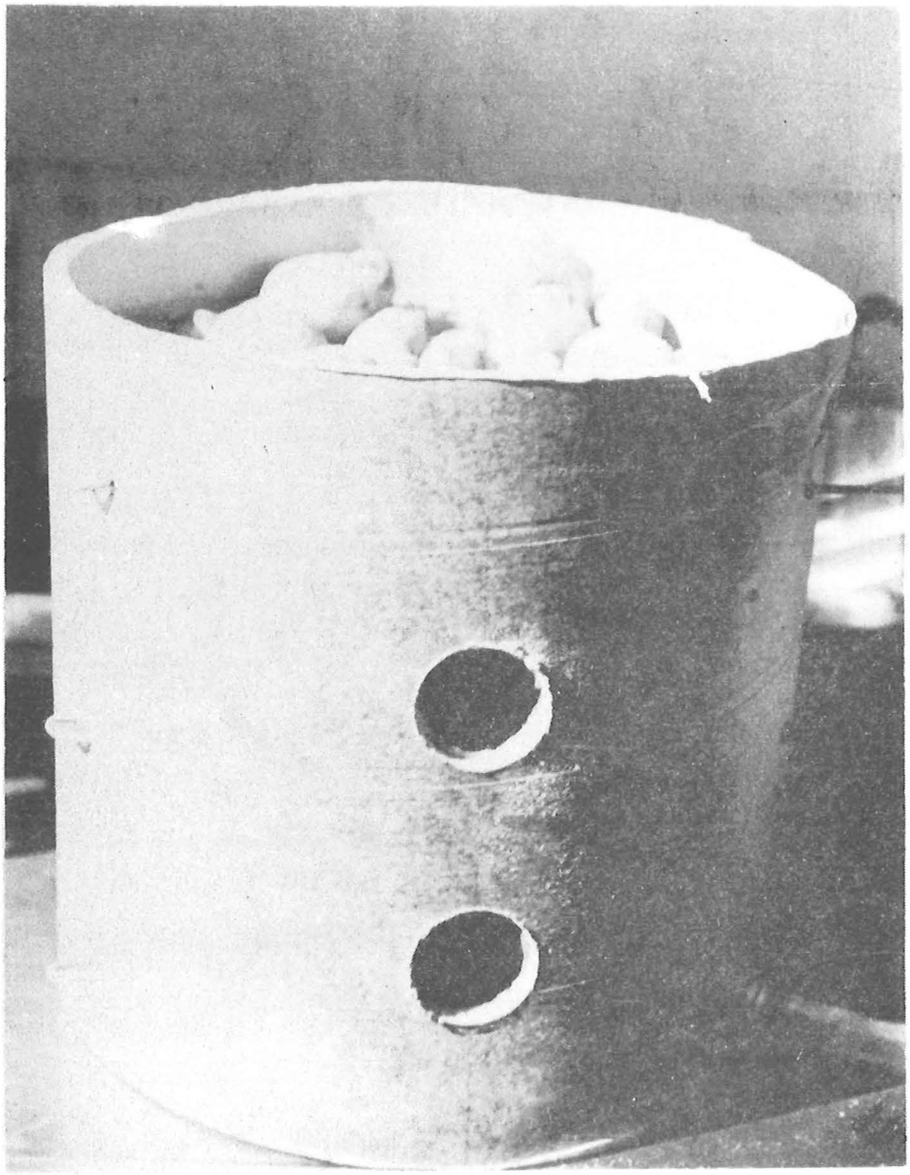


Plate 7. Circular rearing cage which permitted easy production and extraction of large numbers of pupae.

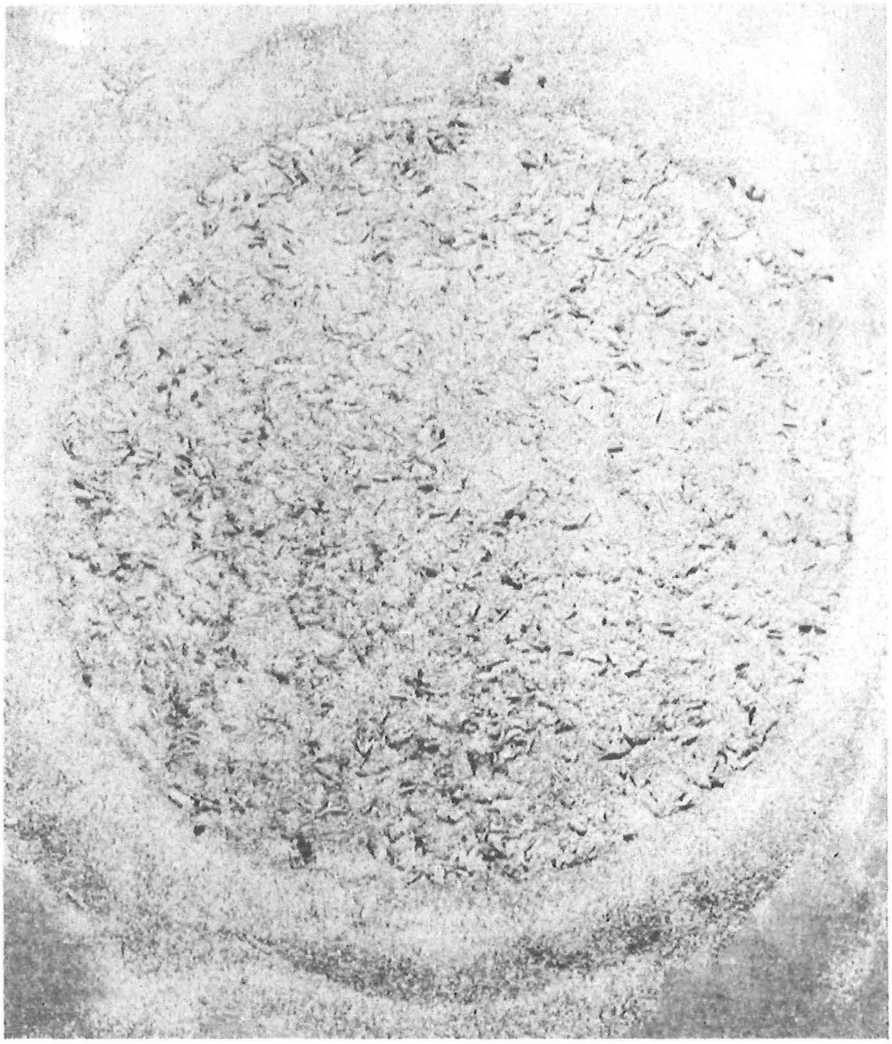


Plate 8. Pupae ready for collection from base of rearing cage shown in Plate 7.

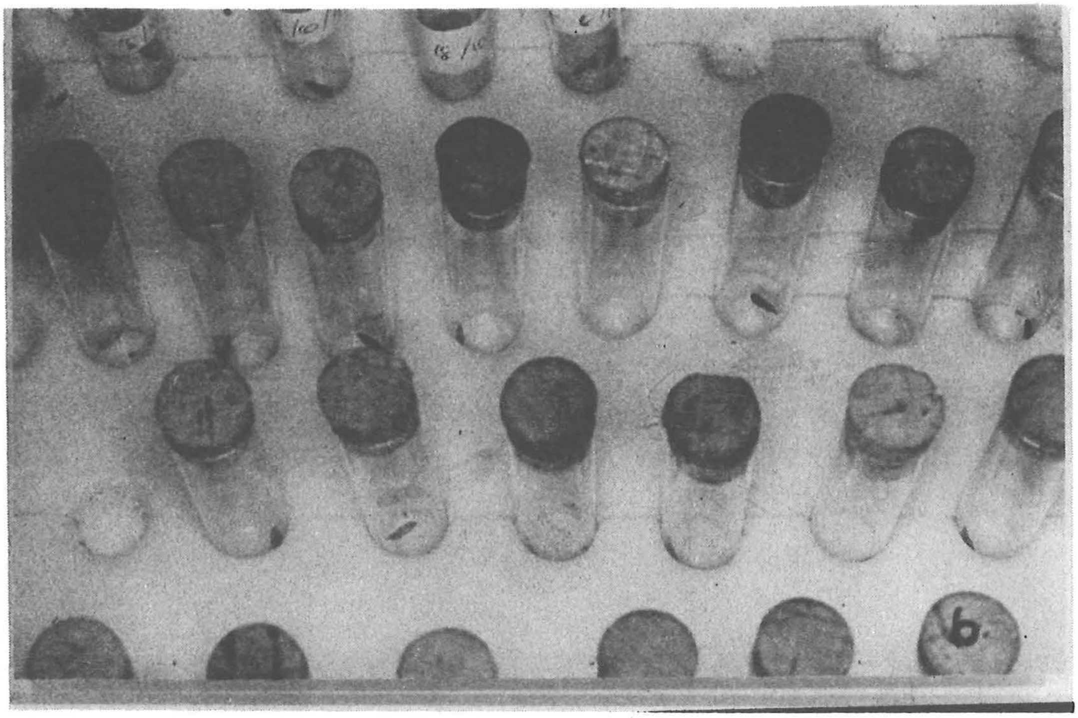


Plate 9. Production of virgin moths of known age in stoppered vials.

eclose, since sexing of pupae was unreliable. For each trial three susceptible tubers (Ilam Hardy) and three resistant tubers (Pentland Dell) were identified with Rhodamine B and placed into a 220mm x 220mm x 80mm plastic lunch box with the three virgin male and female moths; none of which was ever more than four days old (Plate 10).

The trials were incubated for 15 days. The tubers were then carefully dissected and all the larvae removed and counted.

5. Steam Distillation of Tubers and Haulms

Tubers and haulms were steam distilled to ascertain the presence of any volatile in either the tubers or haulms which may elicit biological activity in moths.

The steam from a 500ml flask was directed to the bottom of a 3 l reaction vessel. This was filled with either green foliage or tubers and the steam permeated upwards to be condensed by a double-sided condenser. The aqueous fraction was then collected in 2ml cuts and either taken immediately for GLC analysis, bioassay, or frozen. Because of the volatile nature of the compound being studied, the collecting vessel at the end of the condenser was kept in an ice-bath.

In an effort to increase the concentration of the distillate, a very much larger still was used at D.S.I.R., Lincoln; with this apparatus 18kg of haulms could be distilled at once and both Rua and Ilam Hardy foliage was processed. Twenty 100ml cuts were taken from each variety, and stored in the deep-freeze within half an hour of being obtained.

6. Bioassay of Potentially Attractive Compounds

Where possible compounds were tested in the field. However, this was largely impractical, therefore various bioassay methods had to be utilized.

(a) Dessicating Jar. Initially the sample was spotted onto a strip of filter-paper and hung in a 5 l glass dessicating jar with several moths.

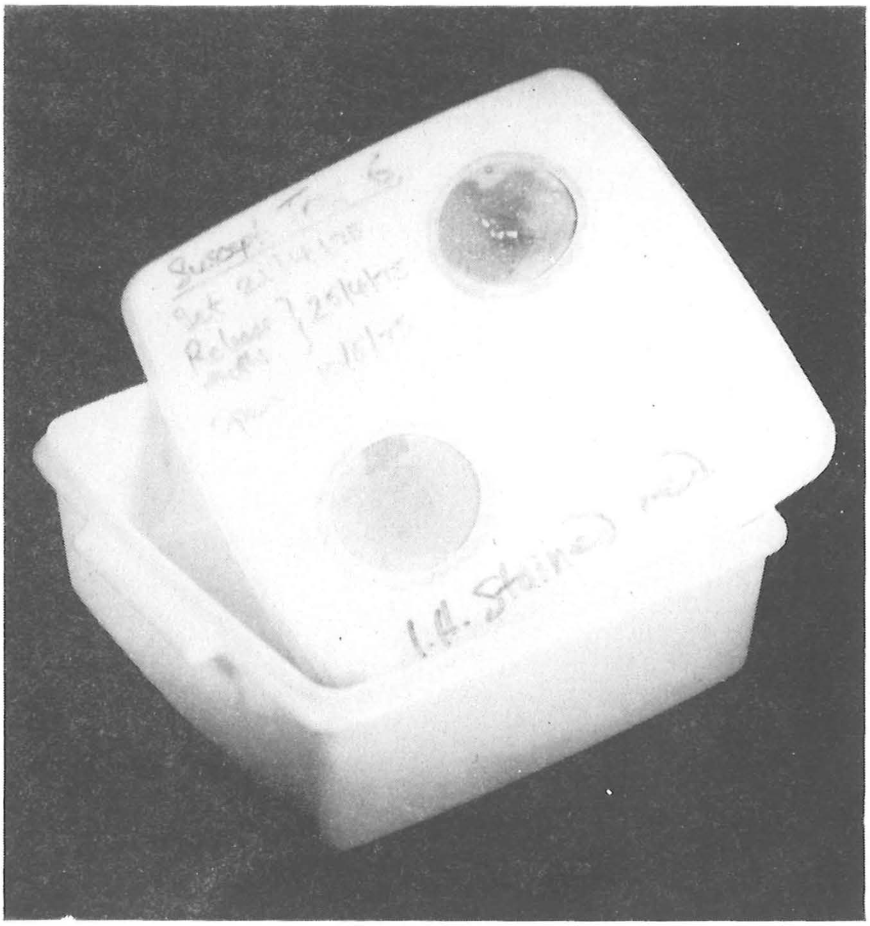


Plate 10. Plastic cage used for varietal susceptibility trials and naphthalene attractancy trials.

A close watch was kept for any reaction such as antennal waving, wing fibrillation and hyperactivity etc. Each trial was accompanied by a control of water and because of problems of habituation, it was necessary to use fresh moths. While this trial had its obvious limitations, it was useful for checking the general effects of compounds and it was a quick and easy method to use.

(b) Trials in the Culture Cages. The direct use of the cultures themselves avoided the possibility of damaging the moths in the aspirator while being taken for trials, however extra care was necessary to prevent mass escapes and compounds were restricted to leaf and tuber extracts.

Bioassays were conducted by spreading a crop of extract on the roof of one of the cages containing large populations within, then studying the overall effects on tuber moth behaviour. This provided a possible test for attractancy since a high number of moths were present in a comparatively unconfined space and changes in their relative distribution could be readily observed.

It was found that moths congregated around the leaf steam distillate when applied as described. It was therefore necessary to ascertain whether the compound was an attractant or simply acting as an arrestant, stopping moths that encountered it by chance. In order to test this, a 100mm circle of cork 4mm thick had a tight surface of Dacron stapled to one side, this was then pinned open-side-up to the undersurface of the roof of the cage. Extracts could then be placed on the roof of the cage above the disc in such a way as to prevent the moths from coming into direct contact with it. Similarly, to further test for spatial effects, glass vials containing a few ml of extract with filter paper wicks were suspended 8mm from the roof of the cage; observations were then made to see if the moths were attracted to them. Because of the volatile nature of the relevant steam distillate all these tests were conducted within an hour of preparation.

A control of water was used for all these trials, however the order of application of control, or extract, turned out to be very significant.

There were two severe limitations to these trials: first the moths rapidly became habituated to the extract which meant that the trial could only be validly conducted about once every six hours, the second limitation resulted from the very strong phototaxic response of the moths. This easily led to confusion when interpreting the effects of the volatiles and although red lighting improved the situation, the moths were still found to be strongly influenced by the light source.

(c) Tests Using a Y-Shaped Olfactometer. A Y-shaped olfactometer similar to that of McIndoo (1926) was constructed from 435mm internal diameter perspex tubing. The stem of this was 290mm long and each branch was 210mm (Plate 11). Placed in each end was a cork with a 20mm internal diameter glass tube set in it. A suction pump was attached to the stem of the olfactometer and air was drawn through at about $0.01 msec^{-1}$. The moths were placed in the stem of the olfactometer and the compound held at the end of either of the two branches; it was then possible to observe whether the insects showed any preference to either of the two branches.

(d) Testing Naphthalene as a Potential Attractant. By using the Y-shaped olfactometer (Plate 11), it was found naphthalene could elicit a response from the moths. To investigate this further different quantities of naphthalene were put with water and a drop of detergent into 10ml beakers and then placed with a specified number of moths into 200mm x 200mm x 80mm plastic cages (Plate 10). The cages were left overnight, and the number and sex of the moths trapped in the beakers was then determined. In the control cages, no naphthalene was added to the beakers.

7. GLC Investigation of Steam Distillates

Examination of the aqueous distillate samples was done on a Varian 1860 instrument using a Porapak Q column. Only the first few ml of the distillate were examined and this was done within minutes of being procured.

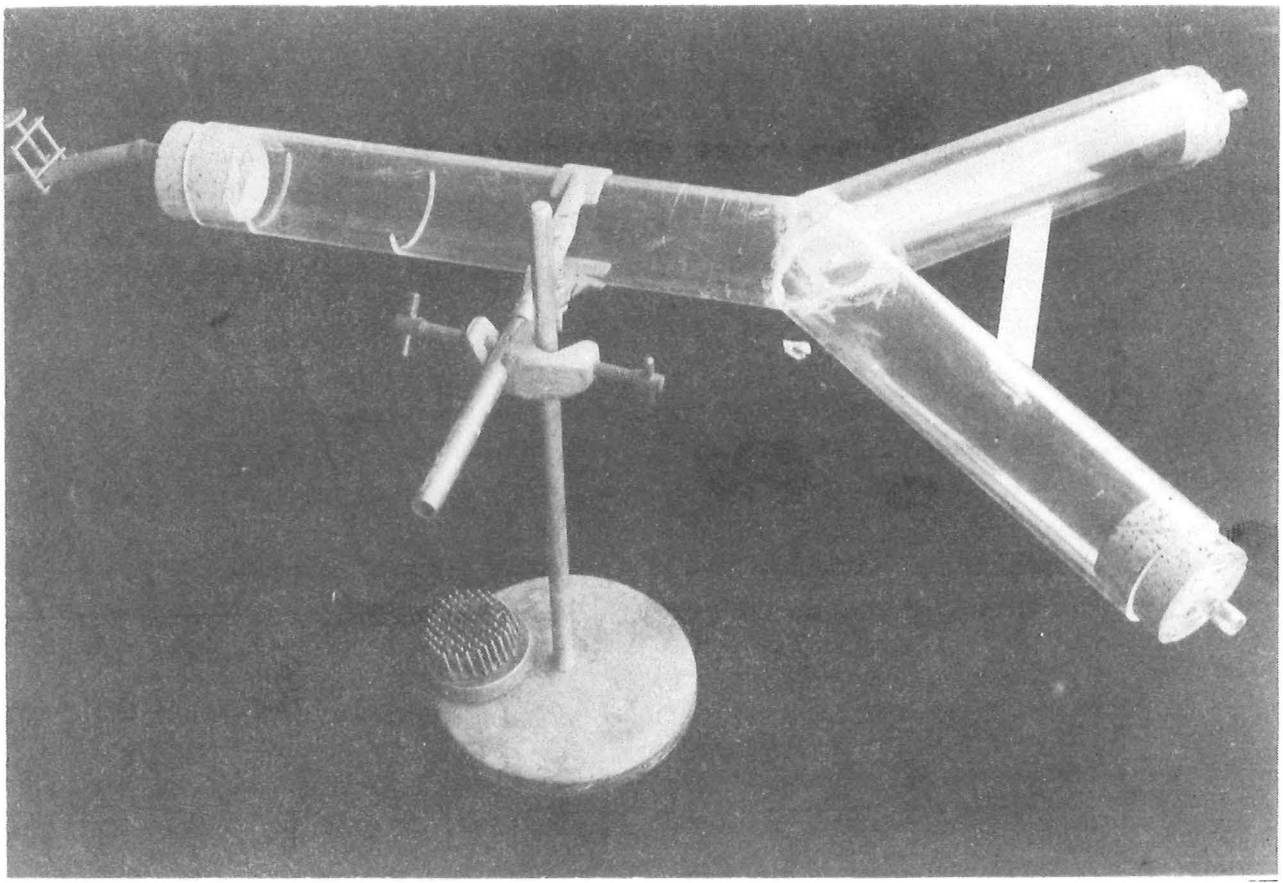


Plate 11. The Y-shaped olfactometer.

The column temperature was set at 120^{o}C with the injection port at 175^{o}C and the detector at 180^{o}C. The aqueous sample (2.2µl) was injected each time with the carrier gas (nitrogen) at a flow rate of 78ml min^{-1}. This operation was then repeated at a later date with the carrier gas at a flow rate of 29ml min^{-1} and a column temperature of 160^{o}C.

Once the extract was obtained it was allowed to remain on the bench in an open bottle and samples were injected into the machine at 0, 1, 2, 3 and 21 hourly intervals. At the same time, the extract was tested for biological activity and the results compared.

CHAPTER IV

RESULTS

FIELD SAMPLING OF TUBERS

1. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1973-74 Growing Season at Belfast

(a) The Levels of Infestation. The comparative level of infestation of the green and white tubers, the percentage of green tubers in each sample and the number of remaining green tops on each of the indicated sampling dates are summarized in Table 1.

An average of 399 tubers from 40 plants was inspected on each sampling occasion; this resulted in a 20% standard error of the mean for the percentage of infested tubers. To have reduced this by increased sample size was impossible owing to the limitations imposed by one person sampling.

TABLE 1

Comparative Levels of Tuber Moth Infestation of Tubers at Belfast

	Sampling Dates				
	3/4/74	20/4/74	4/5/74	22/5/74	8/6/74
% of total sample infested	10.1	9.7	11.6	13.0	12.2
% of green tubers in sample	16.9	12.9	17.0	22.1	21.3
% of green tubers infested	41.7	59.6	61.6	50.6	47.6
% of white tubers infested	2.8	2.3	1.4	2.4	2.6
Remaining number of green tops	2730.0	410.0	180.0	0	0

From Table 1 it is apparent that there was a rapid decline in the number of green haulms until after 4/5/75, none remained.

Throughout the sampling period there was a steady increase in the percentage of green tubers and there was a similar increase in the percentage of green infested tubers until 4/5/74 when the percentage infested began to decline.

Table 2 compares the levels of infestation of table and seed grade tubers collected at Belfast on each sampling occasion. The data for pig grade tubers have been omitted in view of the excessive sampling variation that arose because of their small size.

TABLE 2

Comparative Levels of Tuber Moth Infestation of Seed and Table Grade Tubers on Each Sampling Occasion at Belfast

	Sampling Date				
	3/4/74	20/4/74	4/5/74	22/5/74	8/6/74
Percentage table grade infested[a]	5.6	6.0	12.1	12.2	11.2
Percentage seed grade infested	13.2	18.1	15.1	14.9	22.9

[a]Student's t-test, shows levels of infestation between table and seed grade potatoes are significantly different ($P < 0.05$).

(b) <u>The Effects of Soil Types</u>. Table 3 compares the levels of infestation of tubers grown in silt loam and sandy loam soils.

TABLE 3

Comparative Levels of Tuber Moth Infestation of Tubers Grown in Silt Loam and Sandy Loam at Belfast

	Sampling Date				
	3/4/74	20/4/74	4/5/74	22/5/74	8/6/74
Block 1 (silt loam) Percentage infested[a]	11.0	10.8	16.1	15.3	16.2
Block 5 (sandy loam) Percentage infested	4.7	2.6	11.1	12.4	12.0

[a]Student's t-test shows levels of infestation between potatoes grown on silt loam compared to sandy loam are significantly different ($P < 0.05$).

With regard to yeild, 1.376kg of tubers were produced per plant in the silt loam compared to 1.370kg per plant in the sandy loam.

2. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1974-75 Growing Season at Lincoln College

Although levels of infestation were low, these results are of interest as they span the entire growing season; it was therefore possible to maintain a close watch on population growth and corresponding levels of infestation. This is of particular interest as substantial potato crops had not been grown anywhere in the vicinity for at least five years.

(a) Levels of Infestation. The combined results taken from the Ilam Hardy and Rua crops are summarized in Table 4.

TABLE 4

Summary of Data Collected from Sampling Tubers During the 1974-75 Growing Season at Lincoln College

	Sampling Dates				
	31/1/75	20/1/75	10/2/75	12/3/75	16/4/75*
% total sample infested	0	0	0	0	7.60
% green tubers in sample	0	0.26	3.83	8.16	21.02
% green tubers infested	0	0	0	0	34.60
% white tubers infested	0	0	0	0	0.42

*Figures from Rua crop only; Ilam Hardy crop harvested 14/3/75.

It is apparent from Table 4 that damage to the tubers did not occur until after 12/3/75; this was subsequent to the harvest of the Ilam Hardy crop. When compared to the crop sampled at Belfast at approximately the same time during the previous season (Table 1, 2/4/74), it can be seen that although the fraction of green tubers was slightly higher, the percentage of those attacked was lower.

(b) <u>Post Harvest Infestation of Culled Ilam Hardy Tubers</u>. Ilam Hardy potatoes sampled on 12/3/75 two days prior to harvest revealed no infestation (Table 4), on the other hand cull potatoes examined six weeks later showed high levels of infestation. This is shown in Table 5.

TABLE 5

Levels of Infestation of Three Rows of Culled Tubers

	No. of tubers sampled	No. of infested tubers	Net percent increase of infection over 41 days
Row 1	735	669	91.0
Row 2	758	656	86.5
Row 3	727	628	86.4

Row 1, which was situated nearest to that part of the crop still standing, showed a slightly higher level of infested culled tubers than either Row 2 or Row 3.

GROWTH OF THE FIELD POPULATION OF POTATO TUBER MOTH AT LINCOLN COLLEGE DURING THE 1974-75 SEASON

1. Aerial Densities of Tuber Moth

Following the convention employed in other suction trap research, catches have been interpreted in terms of aerial densities. This is of particular relevance to the present work as the nightly "flight time" varied throughout the season and absolute numbers would therefore have been misleading.

(a) Combined Data of Both Johnson and Taylor Traps. Table 6 summarizes the combined data obtained from both the Johnson and Taylor suction traps throughout the season. In order to eliminate some of the irregularities in flight activity resulting from weather variation, the moth catches in Table 6 have been summed over 14 day intervals.

To calculate the aerial density, it was necessary to know the total volume of air sampled during the "flight times" for each of the 14 days. From p. 57 the "flight time" is defined as the number of hours occuring between sunrise and sunset (night) plus one hour. Because of seasonal change in night length, it was necessary to adjust the elapsed "flight time" hours accordingly (Table 6).

The suction trap, at "Normal" fan speed, sampled 996.6m^3 h^{-1} of air (Burkard Manufacturing Company specifications).

Volume of air (m^3) sampled over 14 days during "flight time" = Mean "flight time" x 996.6 x 14

∴ Mean aerial density (m^{-3}) of moths during "flight time" measured over a period of 14 days = $\frac{\text{Total moth catch over 14 days}}{\text{Mean "flight time"} \times 996.6 \times 14}$

TABLE 6

Summary of Tuber Moth Flight Densities During the

1974-75 Growing Season at Lincoln College

Date	Mean daily moth "flight time" measured over 14 days (hours)	Total m^3 air sampled during "flight time" over 14 days	Sum of daily catch for 14 days			Mean aerial density of moths during "flight time" measured over 14 days		
			Total	Male	Female	Total	Male	Female
20/11/74 to 3/12/74	9.95	138868.2	14	9	5	1.01×10^{-4}	6.48×10^{-5}	3.60×10^{-5}
4/12/74 to 17/12/74	9.66	134780.2	13	6	7	9.64×10^{-5}	4.45×10^{-5}	5.19×10^{-5}
18/12/74 to 31/12/74	9.59	133803.5	7	7	0	5.23×10^{-5}	5.23×10^{-5}	0
1/1/75 to 14/1/75	9.76	136175.4	17	13	4	1.25×10^{-4}	9.54×10^{-5}	2.94×10^{-5}
15/1/75 to 28/1/75	10.16	141756.4	48	36	12	3.39×10^{-4}	2.54×10^{-4}	8.47×10^{-5}
29/1/75 to 11/2/75	10.67	148872.1	28	21	7	1.88×10^{-4}	1.41×10^{-4}	4.70×10^{-5}
12/2/75 to 25/2/75	11.37	158638.8	127	86	41	8.00×10^{-4}	5.42×10^{-4}	2.58×10^{-4}
26/2/75 to 11/3/75	12.06	168265.9	180	92	88	1.07×10^{-3}	5.47×10^{-4}	5.23×10^{-4}
12/3/75 to 25/3/75	12.77	178172.1	459	262	197	2.58×10^{-3}	1.47×10^{-3}	1.11×10^{-3}

From Table 6, it is seen that density increased exponentially with spectacular population growth occurring after 11/3/75; this is shown graphically in Fig. 3. Table 6 also shows a lag in capture rates of females until March, which is shown in terms of cumulative percentages in Fig. 4. It was necessary to express the data as such because a total of 348 females were trapped compared to 510 males; if absolute numbers had been used they would have over-emphasised the female lag.

(b) Comparative Flight Activity and Sex Ratios Over the Rua and Ilam Hardy Crops Until 12/3/75. Since identical suction traps were used, it was possible to make a comparison between the flight activity and sex ratios of moths captured over the Ilam Hardy and Rua crops until 12/3/75. These results are summarized in Table 7.

TABLE 7

Male and Female Moths Trapped Over Ilam Hardy and Rua Crops Until 12/3/75 at Lincoln College

	Male	Female	Totals
Ilam Hardy trap[a]	121	63	184
Rua trap	102	75	177

[a]A X^2 test on the data summarized in Table 7 revealed no significant difference between the total number of moths trapped over the two varieties or the male to female ratio.

2. Larval Populations of Tuber Moth

(a) Overall Trends. The growth of the larval population with 95% confidence limits is shown in Fig. 3 and as in the moth population curve (Fig. 3), the numbers increased exponentially although significant increases in the larval population did not occur until the end of February. The first casual observation of a blistered leaf resulting from larval mining was made on 1/2/75.

FIGURE 3. CHANGES IN THE NUMBER OF TUBER MOTH ADULTS AND LARVAE SAMPLED DURING THE 1974-75 GROWING SEASON AT LINCOLN COLLEGE.

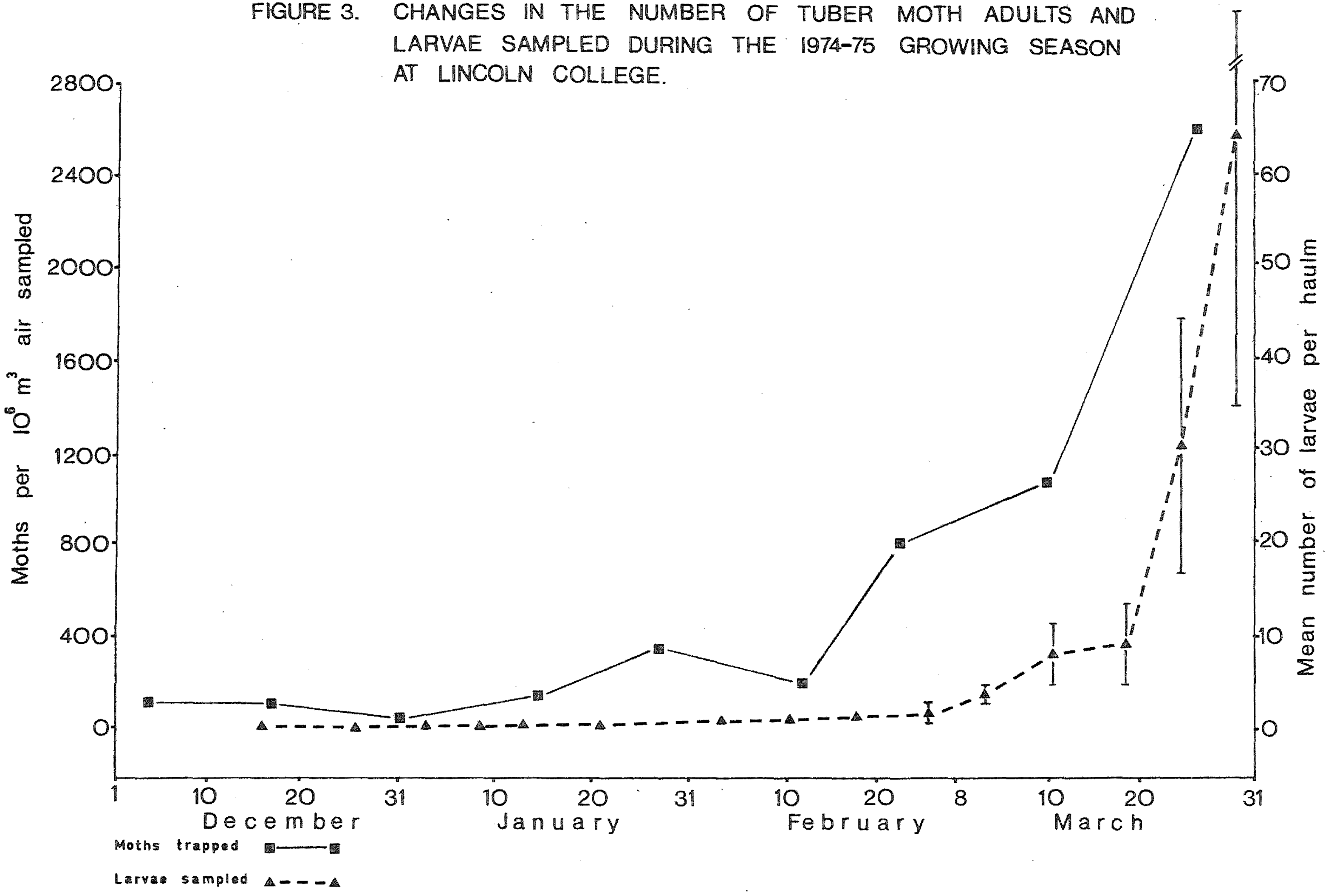
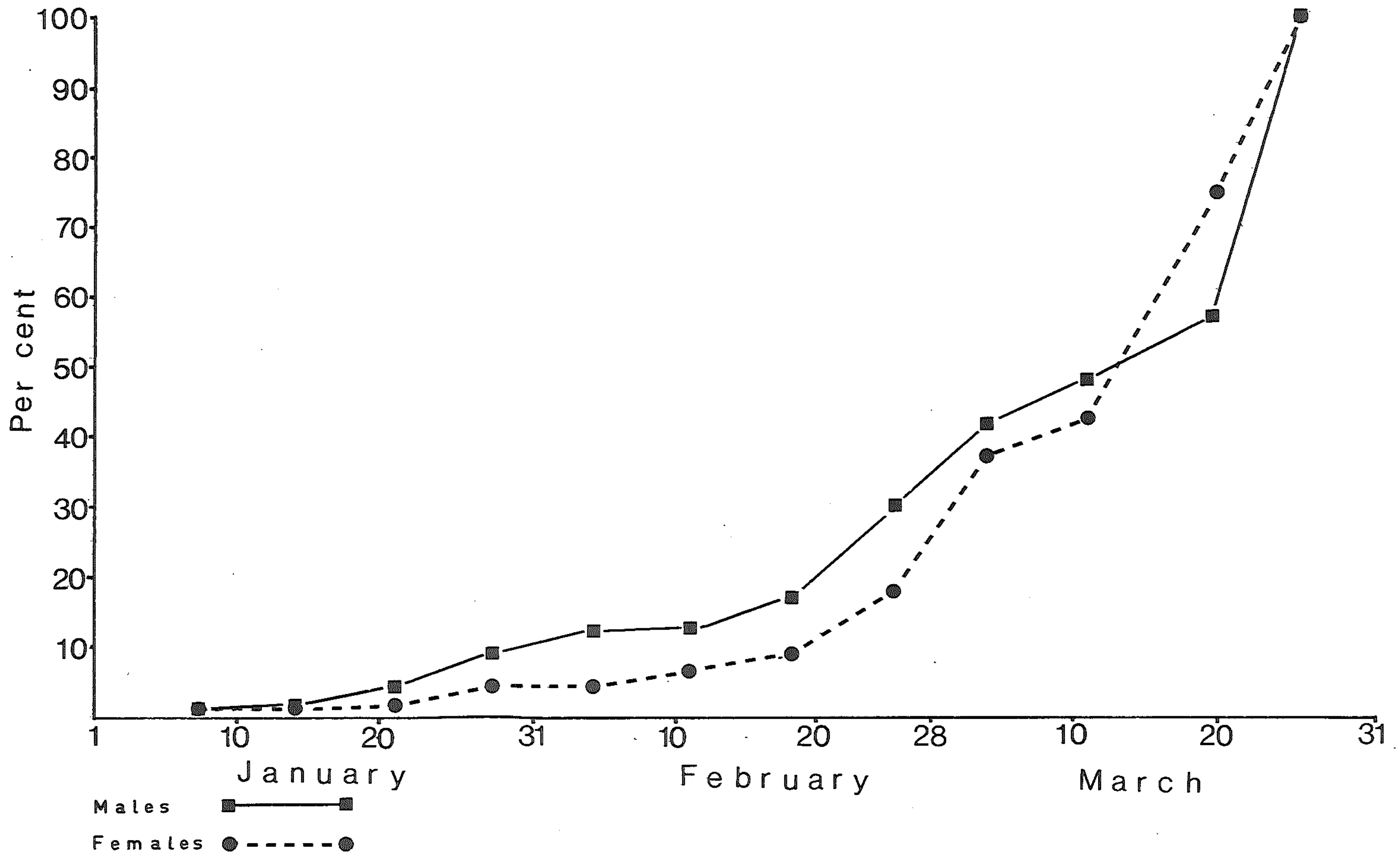


FIGURE 4. CUMULATIVE PERCENTAGE OF TUBER MOTH TRAPPED FROM JANUARY 1ST. – MARCH 25TH. AT LINCOLN COLLEGE.



(b) Comparative Larval Populations in Ilam Hardy and Rua Plots. Until 11/3/75, sampling of Rua and Ilam Hardy plots was carried out simultaneously. The results are summarized in Table 8.

TABLE 8

Comparative Levels of Tuber Moth Infestation in Rua and Ilam Hardy Plots at Lincoln College

	Rua Plot		Ilam Hardy Plot	
Sampling date	% of plant tops infested	Mean larvae per top	% of plant tops infested	Mean larvae per top
9/1/75	0%	0	10%	0.1
13/1/75	10%	0.1	20%	0.2
20/1/75	0%	0	20%	0.3
3/2/75	20%	0.3	30%	0.7
10/2/75	20%	0.4	30%	0.9
18/2/75	50%	0.6	50%	1.0
25/2/75	60%	1.6	60%	1.5
3/3/75	70%	3.8	80%	3.2
11/3/75	90%	7.1	80%	8.2

Table 8 reflects the higher levels of damage sustained by the Ilam Hardy crop during the first half of the growing season. A student's t-test conducted on the paired means shows a highly significant difference ($P < 0.01$) between the Rua and Ilam Hardy larval numbers until 18/2/75. After this date the larval population in both plots was statistically the same (Table 8).

(c) Comparative Infestation Levels of Tops and Tubers. Table 9 shows the build up of larval populations in the tops and the eventual infestation of the tubers.

TABLE 9

Comparative Tuber Moth Infestation Levels of Rua and Ilam Hardy Tubers and Haulms at Lincoln College

Date	Mean larvae per top	% of sampled haulms infested	% green tubers	% infested tubers
13/1/75	0.15	15%	0.00%	0.0%
20/1/75	0.15	10%	0.26%	0.0%
10/2/75	1.00	25%	3.83%	0.0%
12/3/75	7.70	85%	8.16%	0.0%
*16/4/75	>64.10	100%	21.02%	7.6%

*Rua crop only. Ilam Hardy crop harvested 14/3/75.

It was not until 100% of the tops had been attacked that tuber damage became apparent.

3. Calculation of the Number of Elapsed Generations

Langford and Cory (1932) calculated from experimental data that 700 day - degrees (Farenheit) are required for one generation of tuber moth to elapse; Hofmaster (1949) estimated it to be 708.7. For the purposes of calculating generation times in this study a value of 704 day - degrees (Farenheit) was chosen. It is not possible to convert these values to SI units since the units are mixed.

With a day - degree value of 704, the Lincoln College weather data, and a modified computer programme compiled by Baskerville and Emin (1969), the number of generations that occurred during the trapping period was calculated using the IBM 1130 computer at Lincoln College. The first moth was trapped on 13/11/74. From this time until 31/3/75, 2.08 generations theoretically elapsed; the second generation should have begun on 15/1/75 and the third on 24/3/75.

4. Other Frequently Trapped Insects

Until the latter part of December the presence of white shouldered house moth *Endrosis lactella* Schiff was very common and care had to be taken to avoid confusing this insect with potato tuber moth. From late November until mid-December there were large numbers of the ladybird *Coccinella undecimpunctata* L. and throughout the season the lace wing *Micromus tasmaniae* Walker was common.

5. Catches Made by the High Trap

Two moths were caught by the high trap on two different occasions. On the first occasion the mean temperature was 20.4°C and the mean windspeed 1.55msec^{-1}. On the second, the mean temperature was 16.0°C and the mean windspeed 3.13msec^{-1}.

THE EFFECTS OF ABIOTIC FACTORS ON FLIGHT ACTIVITY

1. Effect of Temperature

(a) General Effect. The general effect of temperature on flight activity is summarized in Fig. 5. To obtain the data shown in Fig. 5 it was necessary to know the aerial density of the moths during the time of day when flight occurred. This was achieved using hourly suction-trap data as follows:

$$\text{Aerial density (moths m}^{-3}) = \frac{\text{Total number of moths trapped at } t}{\text{Total hours elapsed at } t \times 996.60}$$

Where t = Temperature ranging from 4°C to 28°C.

To eliminate some of the irregularities arising from sampling variation smooth curves were fitted to the raw data and values for the above equation were taken from these (Fig. 6). From Fig. 5, it is seen that there is no flight activity below 10°C. From 10°C to 17.5°C, aerial density appears to be directly proportional to temperature, and thereafter independent of it.

(b) Effect of Temperature on Male and Female Flight Behaviour. Examination of the raw data based on the hourly catches throughout the season suggests that female flight is confined to a narrower range of temperatures than

FIGURE 5. EFFECT OF TEMPERATURE ON TUBER MOTH FLIGHT ACTIVITY AT LINCOLN COLLEGE.

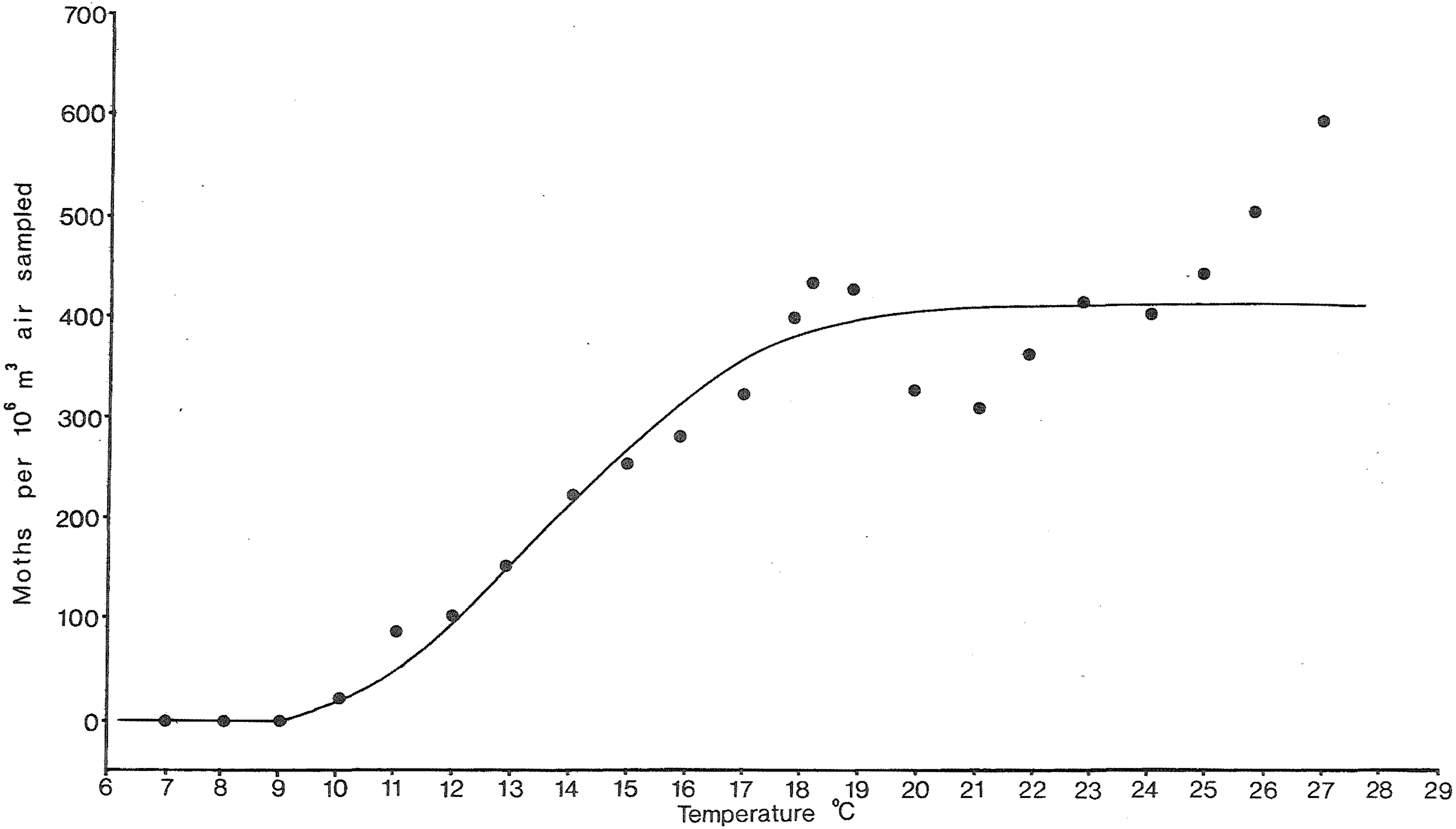
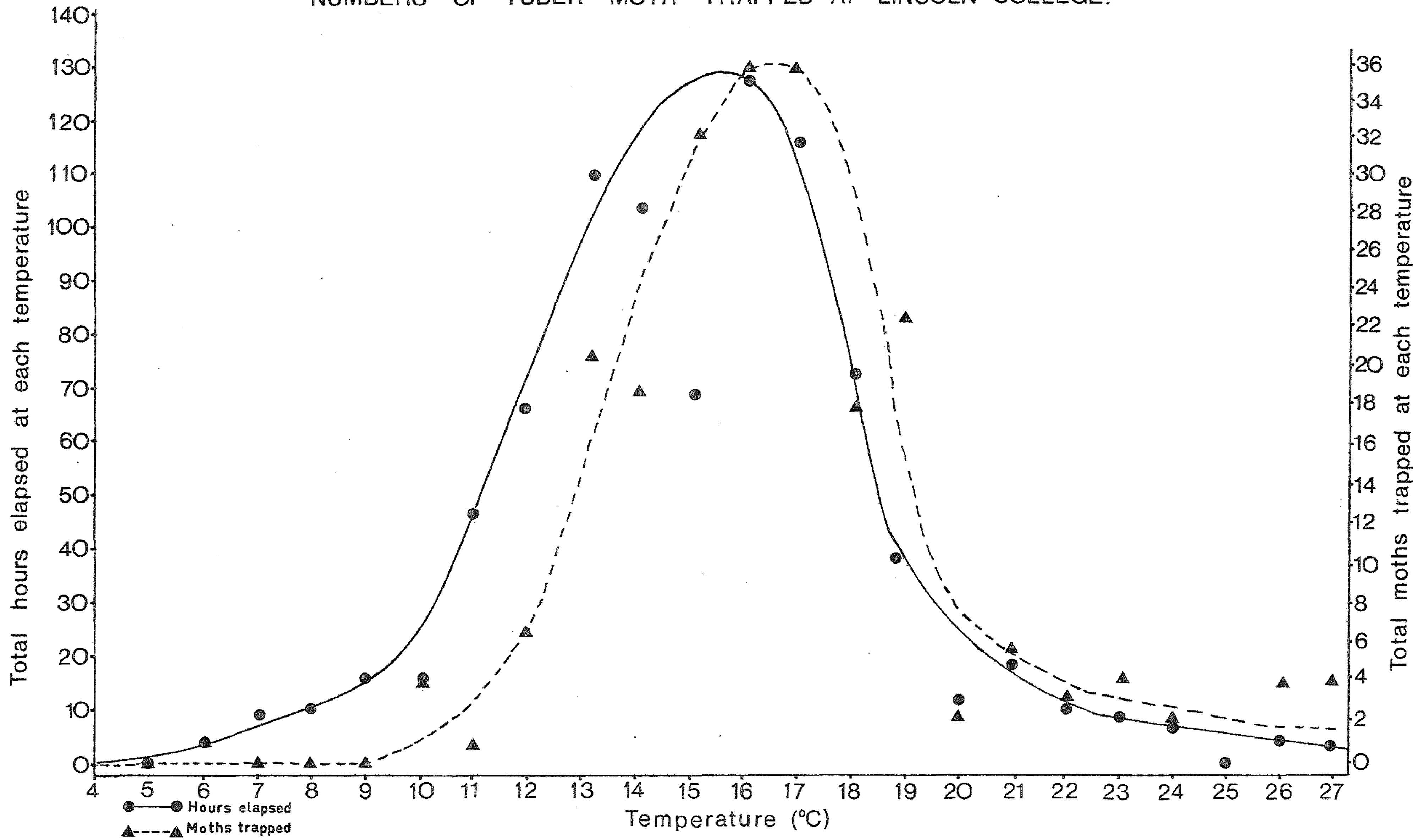


FIGURE 6. FREQUENCY OF HOURLY TEMPERATURES AND CORRESPONDING NUMBERS OF TUBER MOTH TRAPPED AT LINCOLN COLLEGE.



male flight; 84.4% of all females trapped were taken at temperatures ranging from 12.5°C to 18.4°C, compared to 64.8% of the males taken within this temperature range. A similar pattern emerges from the mean nightly temperatures and the total catches. 80.8% of the female-dominated catches occurred between temperatures of 12.5°C to 18.4°C compared to 68.5% male-domination within this range.

2. Effect of Time

The effect of time on flight activity is indicated by the stippled line in Fig. 7. It was necessary to divide this figure into p.m. and a.m. graphs to accommodate the varying night lengths. Because of this, there is some overlap of data collected six hours after sunset and six hours before sunrise.

The timing mechanism of the suction trap operated successfully on 72 days, and thus the total volume of air sampled during any one defined hour of daily "flight time" over the 72 days was:

$$996.6 \times 72 = 71755.2\text{m}^3$$

$$\text{Mean aerial density (m}^{-3}\text{) at any one defined hour} = \frac{\text{Total catch at that hour on 72 occasions}}{71755.2}$$

From Fig. 7 flight activity is high from one hour before sunset until two and one half hours after sunset. Thence until sunrise, flight activity was proportional to the total hours occurring above 14°C irrespective of time. For the purposes of the present work, this period (from one hour before sunset until sunrise) is regarded as the tuber moth "flight time."

3. Effect of Wind

The effect of windspeed on flight activity is displayed in Fig. 8. Taylor (1955) found that suction traps standing in a crop so that their cones are sheltered from cross-winds suffer a delivery loss of 0.5% per Km hr^{-1} crosswind. This was the situation in this project (Plate 2) and the number trapped was therefore adjusted accordingly before the aerial density was calculated. This was carried out using hourly data as follows:

FIGURE 7. INTERRELATIONSHIP BETWEEN TIME, THRESHOLD TEMPERATURE AND TUBER MOTH FLIGHT ACTIVITY AT LINCOLN COLLEGE.

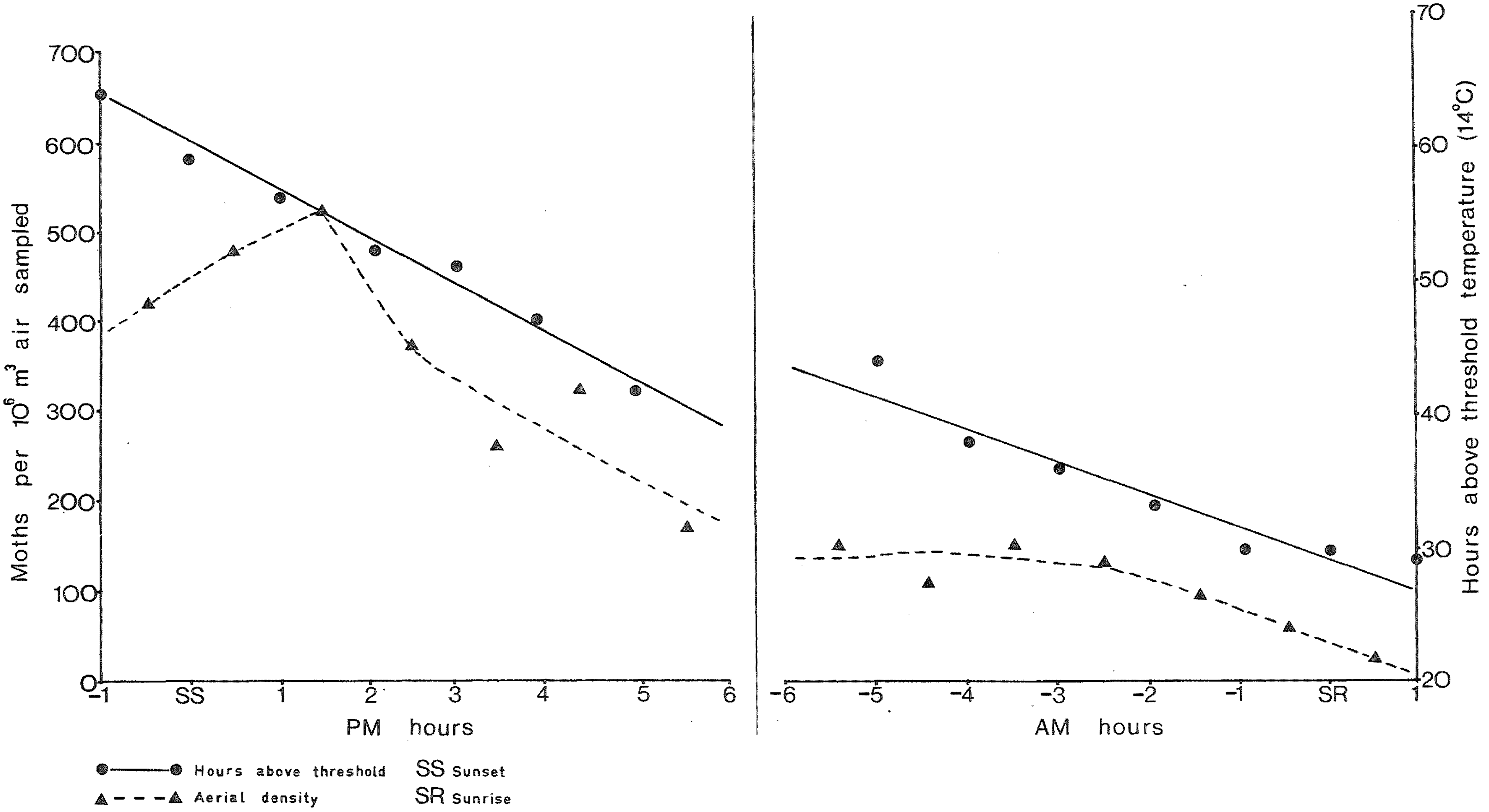
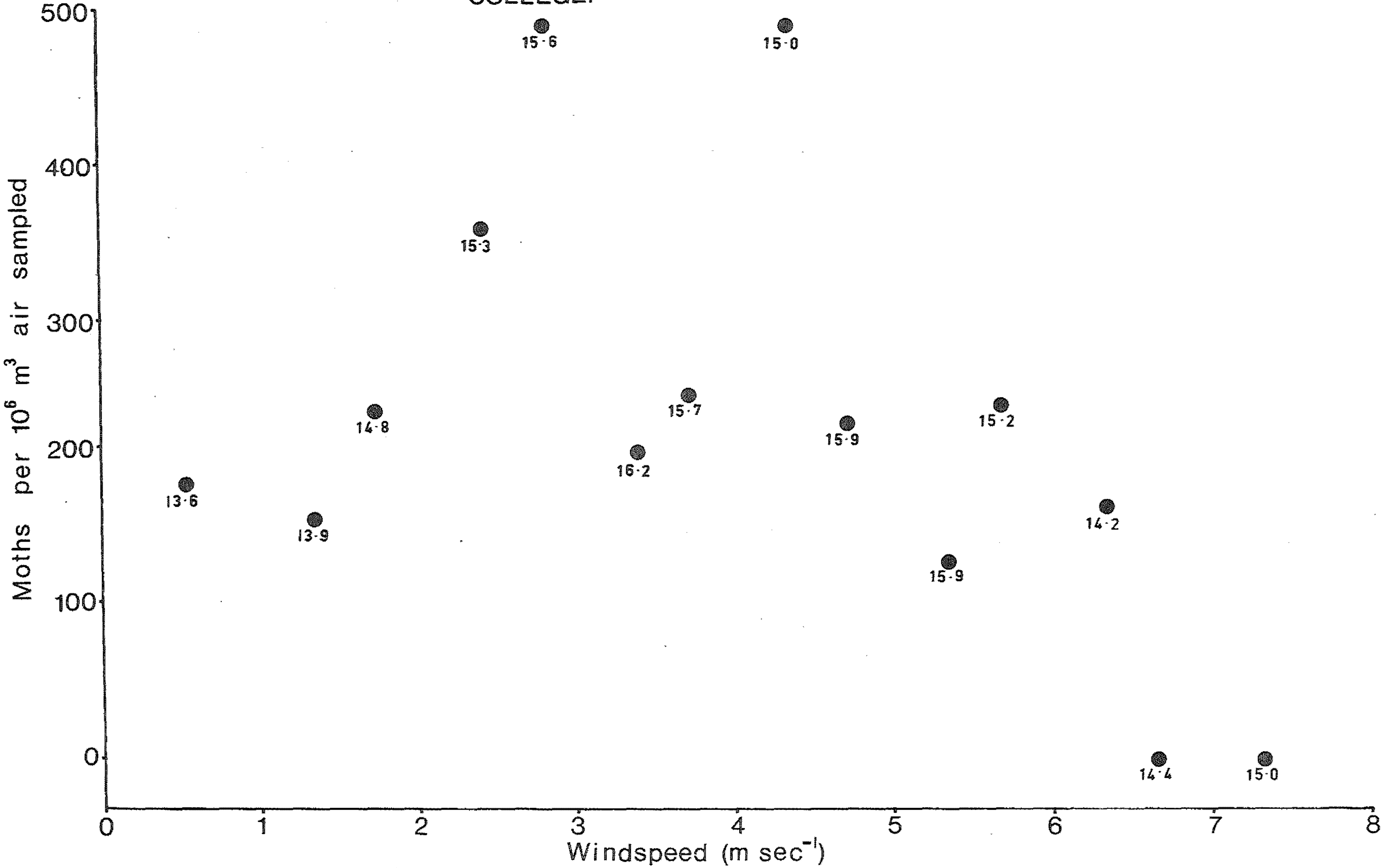


FIGURE 8. EFFECT OF WIND ON TUBER MOTH FLIGHT ACTIVITY AT LINCOLN COLLEGE.



Small figures = mean temperatures (°C)

$$\text{Aerial density (moths m}^{-3}\text{) at windspeed W} = \frac{\text{Total corrected number trapped at W}}{\text{Total hours windstrength at W} \times 996.60}$$

Where W = Windspeeds from 0.5 to 8.0msec^{-1}.

From Fig. 8 it can be suggested that it is not until about 6msec^{-1} that inhibition becomes apparent.

The distribution of flight catches in relation to windspeed does not appear to have been strongly influenced by the mean temperatures encountered which are shown on Fig. 8.

INTERACTION OF ABIOTIC FACTORS ON FLIGHT ACTIVITY

Johnson (1969) warned repeatedly of the dangers of over-simplifying the action of abiotic factors on flight activity by analysing each system individually. This has been taken note of in the present study and the problem has been approached in the following two ways:

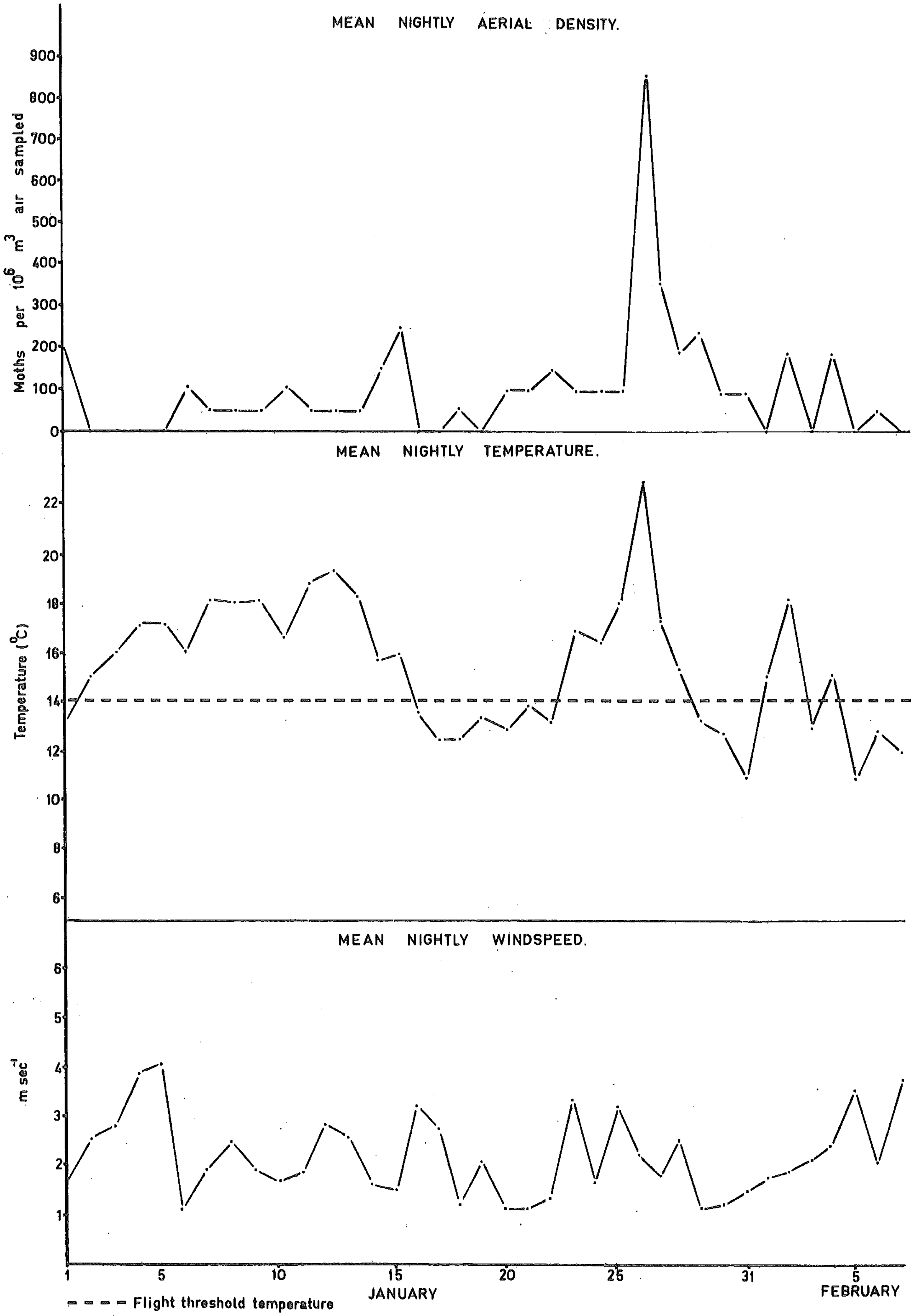
1. Graphical Representation

The interaction of wind and temperature on the total night moth catch has been noted and recorded graphically (Fig. 9). It reveals a clear interrelationship between nights when the mean temperatures are above 14°C and the total catch. The effect of mean windspeed on the nightly catch is not as obvious, but in general, catches are less on nights with strong winds. The data in Fig. 9 apply only to the first 39 days, since up to this point the population appeared relatively stable and the relationship of flight activity to abiotic factors is consequently not biased by rapid population growth.

2. Multiple Regression of Flight Data

A recognised statistical method of analysis of interacting factors is multiple regression. The hourly flight season data were analysed in this way using the Burroughs Advanced Statistical Inquiry System (BASIS) on the B-6718 computer. For this operation the procedure option "MULTR" was used.

FIGURE 9. EFFECTS OF WIND AND TEMPERATURE ON TUBER MOTH FLIGHT ACTIVITY AT LINCOLN COLLEGE.



(a) Transformations. To perform the above regression it was necessary to include two transformations in the programme.

(i) Weighting of the Nightly Moth Catches. Fig. 3 shows the growtl of the field population throughout the trapping season, from which it is apparent that the large population in the field during the latter part of the season would have increased the probability of a catch; i.e. a high field population at a low level of flight activity would yield the same results as a low field population at high activity. In order to obtain a true index of nightly activity it was therefore necessary to weight the data according to the part of the season being considered.

Using the method of least squares, fortnightly totals of trapped adults were found to fit the exponential function;

$$\hat{Y} = 6.663e^{0.0486X}$$

Where $\hat{Y}$ = the growth curve

X = the day number

e = natural logarithm

$\therefore$ The weighted value of the catch Y would be $\frac{Y}{\hat{Y}}$

Although flight activity is used here to measure absolute populations, the summation of catches over 14 days should represent a reliable index of the level of population at that time, since much of the variation in flight activity arising from weather fluctuations is eliminated. The validity of using flight data to measure absolute populations in this situation is further supported by Fig. 3 which confirms that fortnightly moth catches follow an almost identical growth curve to the larval population. The values of the latter were in no way influenced by the weather at the time of sampling.

(ii) Transformation of Flight Time Data. Examination of the p.m. graph in Fig. 7 shows that flight activity from one hour before sunset until three hours after sunset can be represented by a quadratic curve.

It was therefore necessary to transform the flight time data before being used as an independent variable in the multiple regression analysis. The appropriate transformation was given by the equation:

$$S = 3.7143X^2 + 12.2571X + 27.9714$$

where S is the value used in the regression and X = time (0 to 4 hours; where 0 = 1 hour before sunset).

Instead of transforming X to S and computing a regression of flight activity on S, a polynomial regression could have been used. However, it was considered that the use of S was biologically more meaningful and permitted a more direct approach to the problem.

(b) Results of Multiple Regression Analysis. Since most of the activity was confined to the warmer part of the night, the p.m. data only was used in the multiple regression analysis. The results are best expressed in the form of a correlation matrix (Table 10).

TABLE 10

Correlation Matrix Summarizing Results of Multiple Regression Analysis on Flight Catches and Weather Data at Lincoln College

	Temperature	Wind	Humidity	Barometric pressure	Time	Flight activity
Temperature	1.000	0.0114	-0.4254	-0.0119	0.2267	0.2248
Wind	0.0114	1.0000	-0.0244	-0.1247	-0.0086	-0.1215
Humidity	-0.4254	-0.0244	1.0000	0.0210	-0.0496	-0.0333
Barometric pressure	-0.0119	-0.1247	0.0210	1.0000	0.0027	-0.0674
Time	0.2267	-0.0086	-0.0496	0.0027	1.0000	0.0866
Flight activity	0.2248	-0.1215	-0.0333	-0.0674	0.0866	1.0000

389 hours were examined and correlation coefficients ≥ 0.098 were significant to the level $P \leq 0.05$.

From Table 10, temperature-flight activity with a correlation coefficient of 0.2248 and wind-flight activity with a correlation coefficient of -0.1215 are both significant at the $P < 0.05$ level. Time, has a correlation coefficient equal to 0.0866 and is almost significant at the $P = 0.05$ level; its actual significance level is $P = 0.08$. Humidity, although strongly correlated with temperature, correlates insignificantly with moth activity as does barometric pressure (Table 10).

TUBER INFESTATION TRIALS

1. Varietal Susceptibility

The numbers of larvae extracted from the Ilam Hardy and Pentland Dell tubers during the first susceptibility trial (Trial 1) are summarized in Table 11.

TABLE 11

Larvae Extracted in Varietal Susceptibility Trial 1

	Mean number of larvae extracted per tuber	
Replicate	Ilam Hardy	Pentland Dell
1	25.0	19.7
2	24.0	10.7
3	32.0	27.0
4	27.3	14.3
5	24.3	10.0
6	18.7	10.0
7	11.7	11.0
8	21.0	13.3
Mean	23.0	14.5

A paired student t-test showed that there were significantly ($P < 0.01$) more larvae in the Ilam Hardy than Pentland Dell tubers. With these promising results Trial 2 was conducted using the same varieties of tubers, but from a different source. The results of this trial were proved to be statistically inconclusive with a mean of 9.8 larvae per Ilam Hardy tuber compared to 10.6 from the Pentland Dells, a complete reversal of the trend in Trial 1.

RESULTS OF PRELIMINARY INVESTIGATION INTO POTENTIAL ADULT ATTRACTANTS

1. Laboratory Screening Trials

(a) Naphthalene. With the use of the Y-shaped olfactometer, it was noted that naphthalene was capable of inducing activity amongst moths. Table 12 summarizes the results of tests to ascertain whether naphthalene was in any way attractive to tuber moth.

Table 12 suggests that there could be some attractancy in naphthalene. A mean of 3.98 out of 12 moths was trapped in each cage with naphthalene, against 2.17 out of 12 in the control cages.

TABLE 12

Naphthalene Attractancy Trials in Cages of 12 Moths Showing Numbers Trapped

	1	2	3	4	5	6	Mean
Naphthalene (Average per trial)	7.5	2.5	4.5	3.0	3.4	4.0	3.98
Control	4.0	0.0	0.0	1.0	4.0	4.0	2.17

Varying the quantity of naphthalene produced no significant difference in the numbers of moths trapped. In the course of this work 1 α-naphthol and naphthylacetic acid were also tested, but neither of these compounds was found to have more effect than naphthalene.

(b) Steam Distillate of Leaves and Tubers. The distillate of tubers, and especially potato leaves, was found to have a strong excitatory effect on the behaviour of caged moths. The response produced was a sequence of antennae waving, wing fibrillation, running and eventual non-directional flight. When the extract was dabbed on the roof of the cage, it was found that apart from causing hyperactivity the moths aggregated about the spot for about five minutes and then rapidly dispersed (Plate 12). A control (distilled water) applied shortly afterwards elicited little response. Attempts to show three-dimensional directional effects of the distillate were unsuccessful and led to the application of the control before the distillate. This was found to stop the moths in a way similar to the extract, but did not elicit an excited response. Once this had been done, the distillate was no longer found to have an aggregatory effect although it still caused hyperactivity.

Attempts to show a directional response of the moths to the distillate using the Y-shaped olfactometer (Plate 11) proved inconclusive as the results were complicated by the effects of light and the confined nature of the apparatus. However, there was a slight suggestion of anemotaxis in that the moths appeared to move up the tube when the distillate was applied.

The active component of the distillate proved to be very volatile and after being kept for 1 - 2 hours at room temperature, was found to bring about little response from the moths. The distillate from the large still at D.S.I.R. proved no stronger than that from the laboratory apparatus. It was also found that tomato leaf steam distillate was able to elicit a response from the moths, although to a lesser degree.

2. GLC Analysis of Potato Leaf Steam Distillate

GLC analysis of the steam distillate of 600g of potato leaves demonstrated the presence of one major peak (r.t. 4.9min) and two minor peaks (r.t. 5.7 and 6.9min) (Fig. 10). The major peak was found to be running more quickly than the standard, acetaldehyde (r.t. 5.6).

In correlating biological activity, the major peak and one minor peak only, were observed in the initial trace (Fig. 11). Immediately after being cut, the biological activity of the distillate was high, eliciting a vigorous

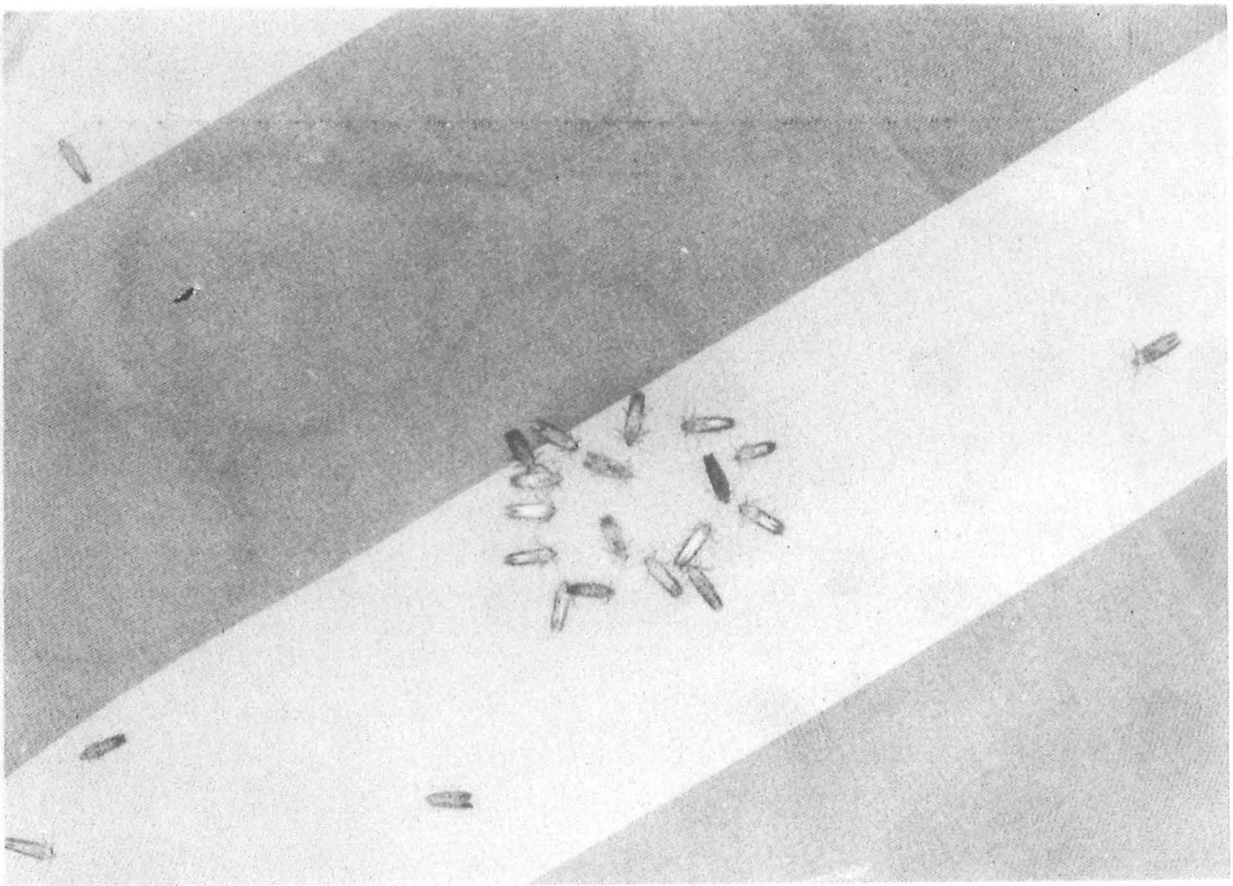


Plate 12. Aggregation of tuber moth to potato leaf steam distillate.

FIGURE 10. GLC ANALYSIS OF POTATO LEAF STEAM DISTILLATE SHOWING THE THREE VOLATILE COMPONENTS AND THEIR CORRESPONDING RETENTION TIMES.

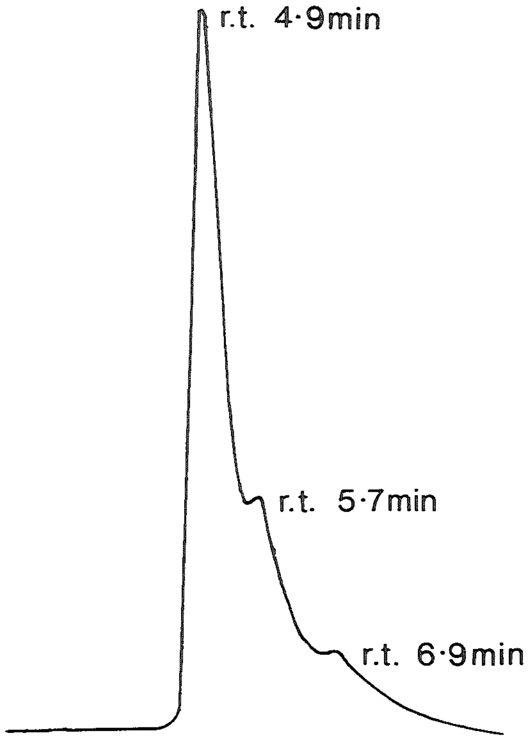
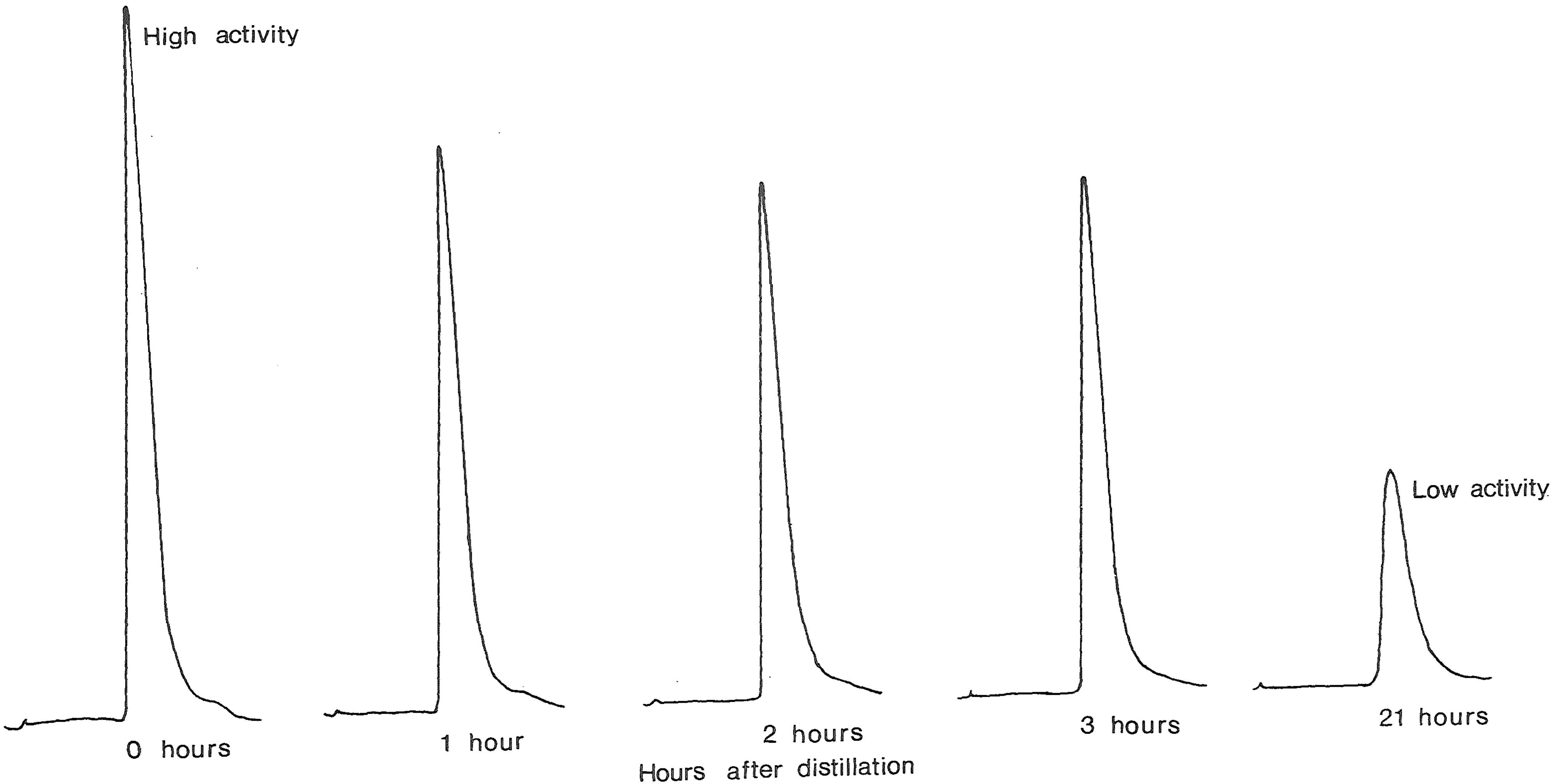


FIGURE 11. GLC ANALYSIS OF POTATO LEAF STEAM DISTILLATE SHOWING THE APPARENT RELATIONSHIP OF PEAK SIZE TO BIOLOGICAL ACTIVITY.



response from the moths. However a considerable reduction of this activity was apparent over the 21 hour period after the distillate was taken and this appeared to be related to the decreasing peak sizes in Fig. 11.

3. Field Trials of Potential Attractants

The results of the trials conducted in the field at Lincoln College:

Trial 1[a]

Compound	Total	Males	Females
Isobutyric acid	4	0	4
Secondary butyric alcohol	2	1	1
Naphthalene	3	1	2
Pyridine	5	3	2
Control	0	0	0

[a]One night duration, $\bar{X}$ Temp. = 16.4°C, $\bar{X}$ Windspeed = 3.7msec^{-1}

Trial 2[a]

Compound	Total	Males	Females
Isobutyric acid	15	1	14
Secondary butyric alcohol	3	1	2
Naphthalene	8	2	6
Pyridine	12	3	9
Control	2	0	2

[a]One night duration, $\bar{X}$ Temp. = 17.0°C, $\bar{X}$ Windspeed = 1.8msec^{-1}

Trial 3[a]

Compound	Total	Males	Females
Isobutyric acid	5	1	4
Pyridine	7	2	5
Dimethylpyridine	0	0	0
4-methyl quinoline	0	0	0
Control	2	1	1

[a]One night duration, $\bar{X}$ Temp. = 15.5°C, $\bar{X}$ Windspeed = 4.1msec^{-1}

Trial 4[a]

Compound	Total	Males	Females
Isobutyric acid	4	0	4
Pyridine	7	0	7
Pyridine & H_2O (1:1)	1	0	1
2-acetal pyridine	2	0	0
2-ethyl pyridine	2	1	1
3-ethyl pyridine	3	1	2
4-ethyl pyridine	1	1	0
Quinoline	1	1	0
Isoquinoline	0	0	0
Control	5	0	5

[a]One night duration, $\bar{X}$ Temp. = 16.0°C, $\bar{X}$ Windspeed = 3.1msec^{-1}

Trial 5[a]

Compound	Total	Males	Females
Isobutyric acid	2	0	2
Pyridine	2	0	2
Steam distillate of leaves	1	0	1
Control	1	0	1

[a]One night duration, $\bar{X}$ Temp. = 12.5°C, $\bar{X}$ Windspeed = 3.0msec^{-1}

Trial 6[a]

Compound	Total	Males	Females
Isobutyric acid	14	7	7
Pyridine	1	0	1
3-ethyl pyridine	24	23	1
Control	1	1	0

[a]One night duration, $\bar{X}$ Temp. = 14.9°C, $\bar{X}$ Windspeed = 2.8msec^{-1}

Trial 7[a]

Compound	Total	Males	Females
Isobutyric acid	16	11	5
Pyridine	2	0	2
3-ethyl pyridine	2	1	1
Control	1	1	0

[a]Two nights duration, $\bar{X}$ Temp. = 14.6°C, $\bar{X}$ Windspeed = 2.1msec^{-1}

Trial 8[a]

Compound	Total	Males	Females
Pyridine	0	0	0
3-ethyl pyridine	3	2	1
Control	0	0	0

[a]One night duration, $\bar{X}$ Temp. = 14.0°C, $\bar{X}$ Windspeed = 1.4msec^{-1}

Trial 9[a]

Compound	Total	Males	Females
Pyridine	0	0	0
3-ethyl pyridine	1	0	1
Control	0	0	0

[a]One night duration, $\bar{X}$ Temp. = 13.7°C, $\bar{X}$ Windspeed = 1.7msec^{-1}

Trial 10[a]

Compound	Total	Males	Females
Pyridine	0	0	0
3-ethyl pyridine	6	6	0
Control	0	0	0

[a]One night duration, $\bar{X}$ Temp. = 12.0°C, $\bar{X}$ Windspeed = 2.2msec^{-1}

Trial 11[a]

Compound	Total	Males	Females
Pyridine	0	0	0
3-ethyl pyridine	6	5	1
Control	3	1	2

[a]One night duration, $\bar{X}$ Temp. = 14.6°C, $\bar{X}$ Windspeed = 3.5msec^{-1}

An interesting result was also obtained (unintentionally) by leaving the traps which were in Trial 4 untouched for 10 days. During this time the mean nightly temperature was 14.2°C and the mean windspeed 3.2msec^{-1}. Unfortunately there was no control, but the relative catches are worth noting.

Compound	Total	Males	Females
2-ethyl pyridine	22	18	4
3-ethyl pyridine	32	25	7
4-ethyl pyridine	9	1	8
Quinoline	12	4	8

From Trials 1 to 11 it can be seen on the occasions used, isobutyric acid trapped 5 times more moths than the controls, 3-ethyl pyridine trapped 4.5 times more and pyridine 2.4 times as many. Isobutyric acid trapped 22 males compared to 38 females. 3-ethyl pyridine trapped 38 males compared to 7 females and pyridine trapped 8 males and 28 females.

CHAPTER V

DISCUSSION AND CONCLUSIONS

FIELD SAMPLING OF TUBERS

1. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1973-74 Growing Season at Belfast

(a) Tuber Infestation Levels (Table 1). The absence of a significant increase in the overall percentage of infested tubers in Table 1 suggests that from April onwards the moth population was not sufficient to cause a marked rise in damage. However, the steady increase in the percentage of infested green tubers until early May and the corresponding decline in green tops (Table 1) were probably linked. As the green tops died, the larvae sought alternative food sources and some entered the exposed green tubers, increasing the percentage infested. It is interesting to note that after the tops had completely died off, the percentage of infested green tubers started to decline (Table 1). This can be explained in terms of erosion which gave rise to green tubers, however, the moth population was insufficient to cause further damage and the percentage infested therefore declined (Table 1).

In Table 2, the significantly higher level of tuber moth damage amongst seed grade tubers compared with table grade could have arisen in two ways. Either the seed grade tubers themselves were more attractive, or their later development near the soil surface rendered them more susceptible to attack. Possibly both of these factors could have contributed to the higher level of damage.

The finding of larvae within tubers at the end of June probably means that unless tubers rot or are destroyed, tuber moth survival as larvae over the winter months in Canterbury is relatively high. Where frosts were experienced, exposed potatoes became necrotic and unable to support larvae. However, Hofmaster (1949) has shown that when tubers are buried they allow larvae to survive conditions which would normally kill them on the surface.

It would therefore be useful to examine critically the practice of allowing stock into harvested potato fields to clean up cull tubers. It is possible that although many tubers are destroyed by stock others may be trampled into the earth where they lie protected from hard frosts and thereby provide larvae with the overwintering habitat they require.

(b) Effects of Soil Types. Of the two soil types within the research crop at Belfast, silt loam, because of its higher colloidal fraction, was more prone to cracking than sandy loam (Table 3). The higher levels of infestation are found in the silt loam; this is undoubtedly the direct result of the cracked soil permitting both larvae and adults easy access to the tubers.

2. Tuber and Haulm Sampling for Tuber Moth Larvae During the 1974-75 Growing Season at Lincoln

(a) Levels of Infestation. Table 4 shows a rapid increase in green potatoes between 12/3/75 and 16/4/75. Since the rainfall for March was at least 2 times the mean for that month, it is clear that erosion of the soil occurred and greening of the tubers arose from this. However, it was not until 16/4/75 that any moth damage to tubers was observed and then it was confined almost entirely to green tubers. As in Belfast, tuber damage did not become apparent until the tops were dying off and again this reflects the migration of the larvae to other food sources.

(b) Post Harvest Infestation of Cull Ilam Hardy Tubers. Table 5 clearly demonstrates the importance of a clean harvest with a minimum of cull tubers left lying on the ground. Only a fraction of the larvae shown to attack cull tubers would need to survive to cause devestating infestation the following season, particularly if suitable environmental conditions are encountered. It is also importnat to realise that this 90% infestation in six weeks occurred during a season where the tuber moth population level was well below that of becoming an economic consideration. It can be assumed that part of the post-harvest infestation arose from larvae which had abandoned the drying haulms left on the ground and had entered nearby tubers. The resident adult population present at the time of harvest also would have oviposited on the exposed cull tubers. However, the higher level of infested tubers in Row 1 (Table 5) suggests at least some infestation arose from moths in the unharvested Rua crop. In this event it would perhaps be desirable for the potato harvest to be completed as rapidly as possible, if an additional source of infestation of cull potatoes is not to be maintained.

GROWTH OF THE FIELD POPULATION OF POTATO TUBER MOTH AT LINCOLN COLLEGE DURING THE 1974-75 SEASON

1. Aerial Densities of Tuber Moth (Table 6, Fig. 3)

After the initial delay, an exponential increase in the number of moths trapped reflects an almost unimpaired rate of population growth from the end of January onwards. During March, the population growth was most rapid in spite of conditions totally unsuited to tuber moth, with at least twice the expected mean monthly rainfall. It can be deduced from this that once tuber moths are well established, adverse conditions have little detrimental effect on the population. Hence it is important that control measures are applied before the rapid phase of population growth begins. Even under the closest daily scrutiny, the first larval damage was not observed until 1/2/75. By this time it is quite possible that the application of control measures would have been too late. This emphasises the need for a reliable system to monitor populations when they are at low levels.

Although the first moth was trapped on 13/11/74, there was little or no population growth until January. It is supposed that this low rate of population growth was partly because of the absence of volunteer plants nearby; large crops of potatoes had not been grown within 0.75km of the vicinity for five years. The actual source of the infestation is not certain and it is doubtful that it could have originated from the seed. Since there are no signs of discrete generations in the data (Table 6, Fig. 3) it can be hypothesised that the founders of the population did not arrive simultaneously, but rather over a protracted period.

Between 29/1/75 and 11/2/75 there was a reduction in the rate of increase of aerial density of the adult population (Fig. 3). While this may be attributable to sampling variation it is also possible that it reflects the reduced flight activity resulting from the lower mean nightly temperature encountered during this period. The mean nightly temperature was found to be 14.1°C compared to a mean of 15.5°C over January and February.

2. Larval Populations of Tuber Moth

(a) Overall Trends. From Fig. 3 it can be seen that the larval population growth curve closely follows that of the adults and it is tempting to suggest that this curve may represent the progeny of the previous adult generation.

The lag in female catches shown in Fig. 4 could be an adaptive mechanism to ensure that all available females in the population are fertilized. Alternatively the apparent lack of females may reflect an artifact of the trapping system; it is possible that the male and female populations in the field were at the same level but the males were usually more active, perhaps responding to calling females. There are also indications that female flight is confined to a narrower temperature range than that of males and this could explain why more males were trapped. A way to resolve this problem could be to take a regular random sample of larvae from the field throughout the season, rear them and note the sex ratio of the resultant adults. This could then be compared to suction trap results.

(b) Comparative Larval Populations in Ilam Hardy and Rua Plots. The initial rate of infestation of the Rua haulms was less than that in the Ilam Hardy crop until about 18/2/75 (Tables 8 and 9). This could provide a clue as to why Rua crops are generally regarded as more resistant than others, since their slow initial rate of development could perhaps help to prevent the buildup of high tuber moth populations.

(c) Comparative Infestation Levels of Tops and Tubers. Table 9 shows the apparent preference of tuber moth larvae to haulms rather than tubers, since even on 12/3/75 when 8% of the tubers were exposed, there was no detected tuber damage. By 16/4/75 however, the larval population in the leaves had risen by at least eight times and tuber infestation was apparent. At this stage the haulms were dying off through natural senescence, blight, and ultimately defoliant (applied on 5/4/75). In a search for alternative food sources it seems that the larvae migrated from the haulms to the tubers in a way similar to that observed in the Belfast crop the previous season.

3. Calculation of the Number of Elapsed Generations

Although the second tuber moth generation theoretically began on 15/1/75 and the third on 24/3/75, examination of Fig. 3 shows no sign of this. Possibly this is because of sampling error or the effects of abiotic factors which may have masked any trends. A more likely reason is that the population consisted of several generations out of phase with each other and therefore did not show any one discrete trend.

4. Other Frequently Trapped Insects

The trapping of the high numbers of the white shouldered house moth *Endrosis lactella* in the crop is of interest and it would be useful to know its food source, particularly as several were found in the Entomology Department tuber moth collection. It is reported (K. M. McEvedy, pers. comm.) that these were reared from a sample of presumably tuber moth infested potatoes.

The presence of large numbers of ladybirds Coccinella undecimpunctata and lacewings Micromus tasmaniae, in the field could be significant as these are predators. It is conceivable they were preying on the eggs and first instar larvae of tuber moth and this could perhaps help to explain why there was a delay before the tuber moth population began its exponential increase (Fig. 3). Barnes (1975) studied the lacewing Chrysopa zastrowi Esb.-Pet. in the laboratory and observed during their larval life they consumed an average of 906 tuber moth eggs. It is felt that further investigation could be usefully carried out in this area.

5. Catches Made by the High Trap

Since only two moths were trapped throughout the season, it is apparent that their main flight activity is limited to the crop canopy. As new infestations must be due to the moths being dispersed, or migrating into newly planted fields, it is likely that the moths at some stage move out of the boundary layer. Yet as the infestation at Lincoln College grew very slowly, it would seem that the moths generally restrict their flight activity to the crop that they developed in.

EFFECTS OF ABIOTIC FACTORS ON FLIGHT ACTIVITY

1. Effect of Temperature (Fig. 5)

(a) General Effect. The temperature-flight curve in Fig. 5 is typical of that found in monospecific populations. Once the threshold temperature of flight has been surpassed, all insects likely to fly are active and the numbers in the air remain independent of temperature until it becomes so hot that flight is inhibited (Taylor, 1963). From Fig. 5, it is seen that this plateau of constant activity is not immediately attained, but rather flight activity increases steadily between 10°C and 17.5°C. This is probably for a number of reasons including the small size of the population resulting in sampling error, the possibility of different flight characteristics of males and females, and microclimate effects. Ideally several temperature sensors should have been situated throughout the crop, but the facilities were not available for this preliminary investigation. However, since the important temperature recordings were made at night, the effects of microclimate were not as severe as might have been expected, as factors such as shade and insolation would not have been present.

The last points in Fig. 5 are misleading, because at this part of the temperature range the significance of a single moth trapped is greatly exaggerated by the low numbers involved in the calculation. Further, these higher temperatures always occurred in the early evening, and examination of Fig. 7 shows that moth activity peaks at twilight. This extra, dusk-induced, activity would thus account for the positive deviation of the last two points away from the plateau of activity.

Following the convention of Taylor (1963) the midpoint of the sigmoid section of the temperature-activity curve is taken to be the threshold temperature of flight. From Fig. 5 this can be approximated at 14°C. It is therefore encouraging to note from Fig. 7 that flight activity is almost directly proportional to the hours elapsed at 14°C or above. This observation was made with hourly temperature and catch data. The relationship also holds true when using nightly aerial density and mean nightly temperatures. Fig. 8 shows good correlation between the temperatures above 14°C and the corresponding aerial density of the moths.

These results agree very well with the findings of Langford and Cory (1932) who observed that the moths became active at temperatures between 14.5°C and 15.6°C. This temperature range also represents the lower limit at which Graf (1917) noted mating to occur.

(b) Effect of Temperature on Male and Female Flight Behaviour. Without further experimental analysis, the biological implications of the narrower flight ranges of the female moths are not immediately apparent. Alternatively, the small size of the daily catches could have contributed to misleading results in this parameter.

2. Effect of Time (Light Intensity)

From Fig. 7 it is apparent that bright light inhibits moth activity, overriding all other stimuli, since no significant numbers of moths were trapped before one hour before sunset, even though a large number of hours elapsed above the 14°C flight threshold. As light intensity decreases, the reverse occurs, and activity is stimulated to a level above that expected for the number of elapsed threshold hours (Fig. 7). When total darkness arrives, activity reaches a constant level and remains directly proportional to the hours above temperature threshold until dawn (Fig. 7).

3. Effect of Wind

While it is difficult to draw positive conclusions it appears that wind does not inhibit activity until speeds of about $6 msec^{-1}$ are recorded. The effects of the boundary layer probably account for some of the ambiguity of these results and it is likely that the winds experienced by the moths were somewhat less than those recorded.

THE INTERACTION OF ABIOTIC FACTORS ON FLIGHT ACTIVITY

1. Graphical Representation (Fig. 9)

This type of representation, although not quantitative, provides a useful visual assessment of the interaction between wind, temperature and aerial density of moths.

From Fig. 5 the relationship between temperatures above 14°C and aerial density is again apparent. This is encouraging as in this case the data are derived from mean nightly values and not hourly as in Fig. 3 and Fig. 4.

The effects of windspeed on aerial density are not as obvious as those of temperature, but from the data collected during the first part of January it can be seen the mean nightly windspeeds of about $4 msec^{-1}$ appear to inhibit moth activity since no catches were made in spite of temperatures well above the $14^{o}C$ threshold (Fig. 9).

In general, however, the effects of temperature appear to override those of windspeed.

2. Multiple Regression Analysis of Flight Data (Table 10)

This method of analysis has the advantage of using the entire season's trapping data and provides a quantitative measurement of variable interaction. Moreover, the problem of the effects of changes in the field population was overcome by including the transformation (see results page 62) based on the information gained throughout the season.

From Table 10, flight activity was found to correlate significantly with temperature, windspeed (negatively), and to a lesser extent with time. Barometric pressure and humidity showed no significant correlation to aerial density although they are closely linked to other abiotic factors (Table 10). It is possible that if a higher population of moths had been encountered more definite results would have been obtained since there were many zeros in the raw data which weakened the correlation of all the variables. However, because barometric pressure and humidity are so closely associated with other abiotic factors, it is almost certain that the effects of these environmental influences can only be accurately assessed under controlled laboratory conditions.

TUBER INFESTATION TRIALS

1. Varietal Susceptibility

Clearly, no conclusions on varietal susceptibility can be drawn from the completely contradictory results obtained from Trials 1 and 2. It is probable that the higher numbers of larvae in the Ilam Hardy tubers in Trial 1 arose from the condition of their skin. These tubers were older and more wrinkled than the Pentland Dell potatoes and thus provided more suitable sites for oviposition.

This example illustrates the importance of standardizing as many factors as possible in trials of this type, since it is apparent that resistance must be a complex interaction of physical and biochemical factors.

PRELIMINARY INVESTIGATION INTO POTENTIAL ATTRACTANTS

1. Laboratory Trials

(a) Naphthalene. Although there is evidence to suggest that naphthalene can act as an attractant this must be regarded with caution since it is possible the moths could have become intoxicated by the vapour and simply fallen into the 10ml beakers accidentally.

(b) Steam Distillate of Leaves and Tubers. Initially it appeared that an effective short range tuber moth attractant had been discovered (Plate 12). However, it later became clear that confusion had arisen over the different effects of the volatile and aqueous fractions of the distillate. The response to the water was a simple drinking process, while the volatile fraction caused the hyperactivity described by some as "searching." The result of this increased activity was that more moths came into contact with the aqueous fraction, and thus the impression arose that they were attracted to it.

The response of tuber moth to tomato leaf-distillate is interesting and suggests that further investigation into other solanaceous plants could be rewarding. As the steam distillate taken from the large still at D.S.I.R. appeared no more concentrated than the cuts taken from the laboratory, it is possible that the volatiles have only limited solubility in water.

Having regard to the powerful effect that steam distillate has on adult tuber moth, it may be that the volatiles play an important part in the relationship of the species with its host. This is fully discussed in Section VII.

2. GLC Analysis of Potato Leaf Steam Distillate

Of the three peaks observed in Fig. 11 all were found to decrease proportionately to biological activity, i.e. activity appears to be dependent on the presence of one or more of these peaks.

Although serious identification procedures were not carried out on any of the peaks, the second peak (r.t. 5.7) may be acetaldehyde (r.t. 5.6). The faster running major peak (r.t. 4.9) tends to indicate a low molecular weight material with high volatility, possibly a C_1 or C_2 compound. Of the standards run in the Porapak Q column used, this major peak is unlikely to be an ester, an acid or ketone as, even at the lowest level in each series, all have high retention times. Only the lower alcohols and aldehydes have retention times approaching the major peak (methanol r.t. 4.1, and acetaldehyde).

3. Field Trials of Potential Attractants

Isobutyric acid, 3-ethyl pyridine and pyridine all showed potential as lures. Of particular interest is the predominant male catch of 3-ethyl pyridine and the female catch of pyridine. These could have important implications in any control techniques involving chemosterilization.

Although isobutyric acid trapped the most tuber moth, it also trapped many other species insects, particularly calypterate diptera e.g. *Sarcophaga milleri* Johnston and Hardy. This widespread attractiveness can be understood when it is noted that isobutyric acid is a common fermentation product of carbohydrates, a universal food source for many species of insects.

The pyridines show far more specificity to tuber moth and therefore would be of more use as monitoring tools to untrained observers. Solanums, particularly tobacco, contain considerable quantities of pyridine derivatives such as nicotine. Moreover, simple 3-substituted pyridines (e.g. 3-pyridyl methyl ketone) have been identified in tobacco leaves under fermentation (Frankenburg, Gottscho, Maynard and Tso, 1952). This production of what appear to be attractive pyridines could therefore help to explain the observation of Yathom (1968) that plants with a poor physiological water balance are more subject to moth attack. In periods of drought, the leaves wither and die; at this stage pyridine compounds could be produced by fermentation and thus attract the moths.

Although the numbers trapped by the above compounds are not spectacular, the results are encouraging because it is doubtful whether the Osborne-Hoyt type traps would have been efficient as moth traps, and at no stage was the field population high. Although these are only the results of a very preliminary survey, there seems to be considerable potential for further research into the use of pyridine compounds as tuber moth attractants.

A POSSIBLE MECHANISM OF TUBER MOTH ORIENTATION TO CROPS

In view of the seasonal nature of the crop and the fact that the survival rate of tuber moth in cold conditions is relatively low, (Hofmaster, (1949); Broodryk,(1971)), it seems probable that tuber moth has developed an efficient mechanism of crop detection. As in the case of other oligophagous insects, this may be essentially chemosensory (Dethier, (1948); Schoonhoven, (1968)).

Volatiles have long been known to be present in potato foliage (e.g. McIndoo, 1926) but they seem to have been largely ignored by more recent workers. Thorsteinson (1960) in his review of host selection by phytophagous insects, contends that potato plants "do not contain odour substances easily isolated or otherwise available for experimental use."

Meisner et.al. (1974a, 1974b) considered factors leading to tuber moth larval feeding and oviposition and observed that cheese cloth absorbed the odour from potato peel extract and resulted in higher rates of oviposition. However, it will be noted that these authors used alcoholic or aqueous leaf extracts, and that the presence of volatile components was not specifically investigated. Nonetheless, these volatile fractions could be of considerable importance in the location of the host plants by the moths. If this is the case, anemotaxis would probably be the mechanism by which they orientate, as Hughes (1967) has noted that males fly upwind to pheromone traps.

Reed (1971) reported that larval mining was more dense along the edges of potato crops and attributed this to the fact that tuber moth flight was wind assisted. However, he also described a situation where moth damage was noted in a new crop 100m to windward of an old infested crop. This implies upwind movement of moths and can be rationalised by suggesting they were attracted to the new crop by the volatiles being released.

There is also some contradiction in the literature over potato tuber moth flight ability. Earlier workers (e.g. Graf, 1917; Hofmaster, 1949) contended that tuber moth flight is poor and intermittent seldom extending for distances greater than a metre, however Yathom (1968), claimed that they are good fliers; the observations made in the course of this thesis tend to support the latter point of view. For example, the catches of up to 50 moths per night in the Johnson and Taylor traps indicates considerable activity; moreover, it was not until windspeeds of about 6msec^{-1} were encountered that moth catches were reduced, suggesting that they are able to cope with reasonable breezes.

The tuber moth sex pheromone is not effective as a long range attractant; Hughes (1967) put its maximum range at 0.6m. Field trials of sex pheromone-baited traps have been disappointing and Kennedy (1975) reported catches of never more than 85 male moths per night using three tethered virgin females per trap. Unfortunately, he did not quote control figures, as his work was devoted to the comparative efficiencies of trap design.

From this, however, it can be suggested that sex pheromones may not need to be long range, since the moths are perhaps attracted to the plants by the volatiles and hence remain in close proximity to each other. This type of plant-host relationship, in various forms is reported in the literature. Riddiford (1967) discovered that oak leaf volatile is a prerequisite for the release of the female Antheraea polyphemus (Cramer) sex pheromone. Sakan et.al. (1970) noted that volatiles from the vine-like plant Actinidia polygama Miquel are highly attractive to the lacewings Chrysopa septempuncta Wesmael.

McIndoo (1926) reported that Colorado potato beetles Leptinotarsa decemlineata (Say) orientate themselves to the "odour stimulus" taken from a potato plant. It is tempting to suggest that this "odour stimulus" may represent the same volatiles as those detected by the GLC and bioassay.

Schoonhoven (1968), in his review of the chemosensory bases of host selection, observed that many odorous factors, often in specific combinations, are typical for a single plant species or taxon. The restriction of tuber moth to solanaceous plants is significant in this respect and it would be rewarding to establish whether the volatile components found in the potato are present throughout the host range. It would also be interesting to identify the components of the volatile and investigate the possibility that host preference is related to the quantity present.

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REFERENCES

ADEESAN, C., A.J. TAMHANKAR, and G.W. RAHALKAR (1969). Sex pheromone gland in potato tuberworm Phthorimaea operculella. Ann. ent. Soc. Am. 62: 670-671.

AKHADE, N.M., P.M. TIDKE, and M.B. PATKAR (1970). Control of potato tuber moth (Gnorimoschema operculella Zell.) in the Deccan Plateau through insecticides and depth of planting. Indian J. Agric. Sci. 40: 1071-76.

ANONYMOUS (1972). Potato moth: control by virus. Rur. res. in C.S.I.R.O. 75: 15-19.

ATTIA, R., and B. MATTAR (1939). Some notes on "The Potato Tuber Moth" (Phthorimaea operculella, Zell.). Bull. Minist. Agric. Egypt no. 216, 136pp. Cairo. Cited in Rev. appl. Ent. (1940) 28A: 274-75.

BASKERVILLE, G.L., and P. EMIN (1969). Rapid estimation of heat accumulation from maximum and minimum temperatures. Ecology 50: 514-17.

BARNES, B.N. (1975). The Life history of Chrysopa zastrowi Esb.-Pet. (Neuroptera: Chrysopidae). J. ent. Soc. sth. Afr. 38: 47-53.

BERTHON, H. (1855). On the potato moth. Pap. and Proc. R. Soc. Van Dieman's Land 3: 76-80.

BROODRYK, S.W. (1971). Ecological investigations on the potato tuber moth, Phthorimaea operculella (Zeller) (Lepidoptera: Gelechiidae). Phytophylactica 3: 73-84.

BROODRYK, S.W., and H.G. ZIMMERMANN (1967). The potato tuber moth--its habits and control. Fmg. S. Afr. 42: 3, 13, 30.

CALDWELL, N.E.H. (1946). The potato tuber moth and DDT. Qd. agric. J. 63: 81-82.

CHAMP, B.R., and R.C.H. SHEPHERD (1965). Insecticide resistance in Phthorimaea operculella (Zell.) with particular reference to DDT. Qd. J. agric. Anim. Sci. 22: 69-81.

____________ (1971). A red-eyed mutant of Phthorimaea operculella (Zeller) (Lepidoptera: Gelechiidae). J. Stored Prod. Res. 7: 221-26.

CORY, E.N., and P.D. SANDERS (1926). Status of potato tuber moth in Maryland. J. econ. Ent. 19: 235-39.

DETHIER, V.L. (1948). Chemical Insect Attractants and Repellants. H.K. Lewis, London. 289p.

EDWARDS, W.H. (1929). La teign du tabac, Phthorimaea operculella. Bull. Dept. Agric. Ile Maurice, Ser. Sci. 13, 8pp. Cited in Rev. appl. Ent. (1930) 18: 104.

ELBADRY, E. (1964). Suppression of the reproductive potential of the potato tuberworm, Gnorimoschema operculella by gamma irradiation. J. econ. Ent. 57: 414-15.

__________ (1965). Some effects of gamma radiation on potato tuberworm, Gnorimoschema operculella (Lepidoptera: Gelechiidae). Ann. ent. Soc. Am. 58: 206-9.

FINNEY, G.L., S.E. FLANDERS, and H.S. SMITH (1947). Mass culture of Macrocentrus ancylivorus and its host, the potato tuber moth. Hilgardia 17: 437-483.

FOOT, M.A. (1973). Research suggests best cure for potato tuber moth is prevention. N.Z. comml. Grow. pp. 19 and 23.

__________ (1974a). Field assessment of several insecticides against the potato tuber moth (Phthorimaea operculella Zell. Lepidoptera, Gelechiidae) at Pukekohe. N.Z. Jl. exp. Agric. 2: 191-97.

__________ (1974b). Cultural practices in relation to infestation of potato crops by the potato tuber moth. N.Z. Jl. exp. Agric. 2: 447-50.

FRANKENBURG, W.G., A.M. GOTTSCHO, I.W. MAYNARD, and T.C. TSO (1952). The chemistry of tobacco fermentation. 1. Conversion of the alkaloids. A. The formation of 3-pyridyl methyl ketone and of 2,3-pyridyl. J. Am. Chem. Soc. 74: 4309.

GRAF, J.E. (1917). The potato tuber moth. U.S. Dept. Agric. Washington, D.C. Bull. no. 427. 56p.

HARWALKAR, M.R., S.N. KHAIRE, and G.W. RAHALKAR (1971). Chemosterilization of potato tuberworm. 1. Effect of metepa on fertility of males. J. Econ. Ent. 64: 358-61.

HELSON, G.A.H. (1944). A preliminary field test of insecticides against potato moth, Gnorimoschema operculella (Zell.). J. Coun. Scient. ind. Res. Aust. 17: 179-85.

__________ (1949). The potato moth, Gnorimoschema operculella (Zell.), and its control in Australia. Bull. Commonw. scient. ind. Res. Org. Aust. 248. 27p.

HOFMASTER, R.N. (1949). Biology and control of the potato tuber worm with special reference to eastern Virginia. Va. Truck Exp. Stn. Bull. 111. p. 1827-1882.

HOVEY, C.L. (1943). Effects of temperature and humidity on certain developmental stages of the potato tuber moth. J. econ. Ent. 36: 627-28.

HUGHES, I.W. (1967). Reproductive behaviour of the potato tuberworm, Phthorimaea operculella (Zeller), (Lepidoptera: Gelechiidae) and the effect of the chemosterilant metepa. Thesis, Ph.D., University of Florida. 104p.

ISPRAY LTD. (1974). Trial results 1974-74. 75p.

JACOBSON, M. (1966). Chemical insect attractants and repellants. Ann. Rev. Ent. 11: 403-22.

__________ (1972). Insect Sex Pheromones. Academic Press, New York. 382p.

JOHNSON, C.G. (1950). A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples. Ann. appl. Biol. 37: 80-91.

___________ (1969). Migration and Dispersal of Insects by Flight. Methuen, London. 763p.

KENNEDY, G.G. (1975). Trap design and other factors influencing capture of male potato tuberworm moths by virgin female baited traps. J. econ. Ent. 68: 305-8.

LANGFORD, G.S. (1933). Observations on cultural practices for the control of potato tuber worm, Phthorimaea operculella Zell. J. econ. Ent. 26: 135-37.

___________ (1934). Winter survival of the potato tuber moth Phthorimaea operculella Zell. J. econ. Ent. 27: 210-13.

LANGFORD, G.S., and E.N. CORY (1932). Observations on the potato tuber moth. J. econ. Ent. 25: 625-34.

LLOYD, N.C. (1943). The potato moth. Experiments on its control. Agric. Gaz. N.S.W. 54: 323-27, 337, 417-21.

MATTHIESSEN, J.N., and B.P. SPRINGETT (1973). The food of the silvereye Zosterops gouldi (Aves: Zosteropidae), in relation to its role as a vector of a granulosis virus of the potato moth, Phthorimaea operculella (Lepidoptera: Gelechiidae). Aust. J. Zool. 21: 533-40.

MAY, A.W.S. (1952). Potato tuber moth (Gnorimoschema operculella (Zell.)) investigations in southern Queensland. Qd. J. agric. Sci. 9: 142-68.

MC INDOO, M.E. (1926). An insect olfactometer. J. econ. Ent. 19: 545-71.

MEISNER, J., K.R.S. ASCHER, and D. LAVIE (1974a). Phagostimulant for the larva of the potato tuber moth, Gnorimoschema operculella Zell. Z. angew. Ent. 77: 77-106.

___________ (1974b). Factors influencing the attraction to oviposition of the potato tuber moth, Gnorimoschema operculella Zell. Z. angew. Ent. 77: 179-189.

MUGGERAGE, J. (1936). The potato tuber moth P. operculella Zell. N.Z. Jl. Agric. 52: 85-88.

NEWMAN, L.J., and E.T. MORGAN (1937). Preventive and combative measures against the potato moth. J. Dep. Agric. West. Aust. 14: 82-86. In Hofmaster (1949).

OSBORNE, G.O., and C.P. HOYT (1968). Preliminary note on a chemical attractant for the grass grub beetle (Costelytra zealandica (White)) from flowers of the elder (Sambucus nigra L.). N.Z. Jl. Sci. 11: 137-39.

PLATNER, G.R., and E.R. OATMAN (1968). An improved technique for producing potato tuberworm eggs for production of natural enemies. J. econ. Ent. 61: 1054-7.

POOS, F.W., and H.S. PETERS (1927). The potato tuberworm. Va. Truck Exp. Stn. Bull. 61: 597-630.

PRESCOTT, R.T.M. (1939). Incidence of potatomoth. Survey of Victorian districts. J. Dep. Agric. Vict. 37: 15-24.

RAESIDE, J.D., and W.F. RENNIE (1974). Soils of Christchurch region, New Zealand: the soil factor in regional planning. N.Z. Soil Surv. Rep. 16.

REED, E.M. (1969). A granulosis virus of potato moth. Aust. J. Sci. 31: 300-301.

__________ (1971). Factors affecting the status of a virus as a control agent for the potato moth (*Phthorimaea operculella* (Zell.) (Lep., Gelechiidae)). Bull. ent. Res. 61: 207-22.

REED, E.M., and B.P. SPRINGETT (1971). Large-scale field testing of a granulosis virus for the control of the potato moth (*Phthorimaea operculella* (Zell.) (Lep., Gelechiidae)). Bull. ent. Res. 61: 223-33.

RICHARDSON, M.E., and D.S.W. ROSE (1967). Chemical control of potato tuber moth, *Phthorimaea operculella* (Zell.), in Rhodesia. Bull. ent. Res. 57: 271-78.

RIDDIFORD, L.M., and C.M. WILLIAMS (1967). Volatile principle from oak leaves: role in sex life of the polyphemus moth. Science 155: 589-90.

SAKAN, T., I. ISOE, and S.B. HYEON (1970). The chemistry of attractants for Chrysopidae from *Actinidia polygama* Miq. In Wood, D.L., R.M. Silverstein and M. Nakajima (1970). Control of insect behaviour by natural products. Academic Press, New York. 345p.

SCHOONHOVEN, L.M. (1968). Chemosensory bases of hostplant selection. Ann. Rev. Ent. 13: 115-36.

SCHWINCK, I. (1958). A study of olfactory stimuli in the orientation of moths. Proc. Xth Int. Congress Ent. 2: 577-83.

SHOREY, H.H. (1973). Behavioural responses to insect pheromones. Ann. Rev. Ent. 18: 349-80.

TAYLOR, L.R. (1951). An improved suction trap for insects. Ann. appl. Biol. 38: 582-91.

__________ (1955). The standardization of air flow in insect suction traps. Ann. appl. Biol. 43: 390-408.

__________ (1962). The absolute efficiency of suction traps. Ann. appl. Biol. 50: 405-21.

__________ (1963). Analysis of the effect of temperature on insects in flight. J. anim. Ecol. 32: 99-117.

THORSTEINSON, A.J. (1960). Host selection in Phytophagous insects. Ann. Rev. Ent. 5: 193-218.

TREHAN, K.N., and S.R. BAGAL (1944). Life history and bionomics of potato tuber moth. Proc. Indian Acad. Sci. Section B 19: 176-87.

WATERSTON, J.M. (1940). Report of the plant pathologist 1939, 13pp. Hamilton, Bermuda. In Hofmaster (1949).

WEISS, H.B. (1944). _Gnorimoschema operculella_ (Zell.) in New Jersey. Ent. News 55: 135-6. In Hofmaster (1949).

WEARNE, G.R. (1969). The use of heat for the recovery of potato tuber moth larvae from foliage. J. Aust. ent. Soc. 8: 212-13.

___________ (1971). Improved methods for production of parasites of potato tuber moth _Phthorimaea operculella_ (Zeller) (Lepidoptera: Gelechiidae). J. Aust. ent. Soc. 10: 61-63.

YATHOM, S. (1968). Phenology of tuber moth, _Gnorimoschema operculella_ Zell., in Israel in the spring. Israel J. Agr. Res. 18: 89-90.