632.782:632.92:632.939.1:634.1/.2

C. J. A. BAREL

STUDIES ON DISPERSAL OF *ADOXOPHYES ORANA* F.v.R. IN RELATION TO THE POPULATION STERILIZATION TECHNIQUE

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
PROF. DR. IR. H. A. LENIGER, HOOGLERAAR IN DE
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landbouwkundig ingenieur, geboren te Klundert op 3 juni 1944, is goedgekeurd door de promotor, Dr. J. de Wilde, hoogleraar in het dierkundig deel van de Plantenziektenkunde.

De Rector Magnificus van de Landbouwhogeschool,
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STELLINGEN

I

De snelle verbreiding van de vruchtbladroller binnen Nederland en België kan niet alleen worden toegeschreven aan het vliegen van de imagines.

Dit proefschrift

II

Ethologisch gezien is het zich laten zakken aan spinseldraden van de rupsen van de vruchtbladroller een vluchtgedrag. In de loop van de evolutie heeft dit gedrag echter ook betekenis gekregen voor de verspreiding van de rupsen over korte afstanden.

Dit proefschrift

III

De evenredigheid tussen het aantal gevangen dieren in een sexval en de grootte van de populatiedichtheid vermindert naarmate de laatste toeneemt.

IV

Het onderzoek naar de mogelijkheden van het kweken en uitzetten van predatoren en parasieten, die resistent zijn tegen bepaalde bestrijdingsmiddelen, dient te worden gestimuleerd.

CROFT, B. A., BARNES, M. M., 1971. J. econ. Ent., 64:845–850.
HOYT, S. C., 1969. J. econ. Ent., 62:74–86.

V

Toepassing van fungiciden uit de benzimidazool-groep in granen maakt vruchtwisseling noodzakelijk.

VI

Bij het stellen van criteria ten aanzien van schadelijke nevenwerkingen van bestrijdingsmiddelen in het milieu dient men, bij stoffen die in de bouwvoor blijven, rekening te houden met de bestemming van dit deel van het milieu.

VII

Gezien de verdeling van het aantal aardappelbladeren met toprol symptomen binnen een aangetaste plek, moet luchtverontreiniging als mogelijke eerste oorzaak uitgesloten worden geacht.

VIII

De hypothese dat een virus betrokken zou zijn bij de teruggang van Gaeumannomyces graminis, onder omstandigheden van eenzijdige graanteelt, moet verworpen worden.

LAPIERRE, H., et al., 1970. C. R. Acad. Sc. Paris, 271 série D: 1833–1836.
GERLAGH, M., 1968. Diss. Wageningen.

IX

De disjuncte verspreiding van persistente virussen in een veld kan niet alleen worden toegeschreven aan de activiteit van gevleugelde bladluizen.

FRANÇOIS, E., et al., 1968. Isotopes and radiation in Entomology. Proceedings series, IAEA Vienna: 53–68.

X

Toepassing van de steriele-mannetjestechniek bij de bestrijding van fytofage insekten zal slechts dan kunnen leiden tot een verminderd gebruik van insekticiden, indien in het areaal van de plaag geen verwante soorten voorkomen met vergelijkbare ecologische niches.

Proefschrift C. J. A. BAREL.
22 juni 1973.

Aan mijn Ouders

CONTENTS

1. INTRODUCTION

In the Netherlands, *Adoxophyes orana* is a serious pest in pome fruit growing. Growers, on an average, apply three insecticide sprayings per year against this tortricid. An organic phosphorous compound is mostly used. These compounds are highly toxic, not only to arthropods, but also to fishes and mammals.

Although the benefits of pesticides to man cannot be denied, the disadvantages of an unlimited use become more and more apparent. On one hand, there is the justified concern about pollution of the environment, on the other hand there is the build up of resistance and the development of new pests as a result of the use of pesticides. For these reasons alternative modes of plant protection are being sought.

In the Netherlands, within the frame of 'Werkgroep geïntegreerde bestrijding van plagen T.N.O.' (Integrated control working party T.N.O.), a group of research workers is studying the possibilities for integrated control in orchards. In Dutch pome fruit growing two key-pests can be distinguished, *Panonychus ulmi* (red spider mite) and *A. orana* (summer fruit tortricid). *P. ulmi* is the most serious pest, and moreover it regularly develops resistance to acaricides, whilst in *A. orana* resistance has never been observed. Evidence has been found, which makes it likely that *P. ulmi* can be controlled by predators (VAN DE VRIE 1972). However these predators can never have a chance when the spraying of non selective insecticides against other pests is continued. Hence alternative control measures for *A. orana* were sought, the latter being the second important pest. A meridic diet for *A. orana* had already been developed (ANKERSMIT 1968), which would facilitate mass-rearing. This led to the idea of controlling the insect by means of releasing sterile adults.

POPULATION STERILIZATION TECHNIQUE

For the application of the population sterilization technique, at least four requirements have to be fullfilled.

a. Mass-rearing must be possible, as large numbers are needed for the releases.
b. Sterilization must be possible, without detrimental side-effects on longevity and behaviour.
c. Population density must be low, as the numbers to be released are multiple of the numbers present.
d. Dispersal must be restricted, as the chances for reinfestation of a once cleared area depend on the abilities for dispersal. The greater the dispersal the larger the area which has to be treated.

The term dispersal covers any movement from one habitat to another, in contrast to movements within the habitat. This more or less corresponds with the distinction between migratory movements and trivial movements made by KENNEDY and SOUTHWOOD (SOUTHWOOD 1962). This distinction stresses differences in motivation. For our purpose we are more interested in the resulting activity.

The first two requirements for application of the population sterilization technique have been fullfilled. Mass-rearing on an experimental scale is possible and sterilization does not cause detrimental side-effects (SNIEDER et al. 1973) Population density however, does not meet the requirements. In 1968, at the first flight, DE JONG estimated the population density in one orchard to be about 1500 moths per ha and in another, at 3600 moths per ha (ANKERSMIT and DE JONG 1970). During the second flight the population density is usually larger. This is a very high density as compared to the classic example of the successful eradication of the screw-worm, *Cochliomiya hominivorax*, which had an average density of about 70 per square kilometer (BUSHLAND 1960).

Moreover *A. orana* does not only occur in orchards. The species is polyphagous and is found on nearly all deciduous trees and shrubs and also on several herbaceous plants (JANSSEN 1958).

With regard to dispersal, data about captures in light traps outside orchards suggested that this was not very important (DE FLUITER et al. 1963). This could be related to the hovering type of flight of the adults.

ALTERNATIVE FOR ERADICATION

In view of the abundance and the wide and continuous area of dispersal, the idea of eradication had to be abandoned. But control of the species at a low level seemed possible, provided dispersal was at a very low rate.

FRANSZ made a simulation model to determine the optimum number of sterilized males to be released (DE JONG et al. 1971). It was assumed that there was an initial population of 1000 moths per ha, which had to be reduced to about a hundred. In the model, the level reached within two generations, starting with the first flight, was 105 moths per ha. During the following generations this level had to be maintained. Two calculations were made, one with and one without taking reinfection into consideration. In the case with reinfection it was assumed that 100 *A. orana*, moths or larvae, entered the orchard at each generation. Hence a reduction to 5 moths per ha was necessary, in order to have not more than 105 moths per ha in the next generation.

Calculation 1, with reinfection
Goal: 105 moths in the next year
No more males are to be released than is strictly necessary.
Results: first flight period 88240 males
second flight period 40512 males
To maintain the population at this level, the following numbers have to be released: first flight period 28888 males
second flight period 5736 males

Calculation 2, without reinfection.
Goal: 105 moths in the next year.

No more males are to be released than is strictly necessary.
Results: first flight 20169 males
second flight 9763 males
To maintain the population at this level, the following numbers have to be released: first flight 1326
second flight 233

2. GEOGRAPHICAL DISTRIBUTION, LIFE HISTORY AND HOSTPLANT RANGE

The genus *Adoxophyes* is most abundant in the Papuan, Malayan, Australian and Indian faunas. Over 30 species are known in these regions (DIAKONOFF 1939). In North-America only 2 species are known and in Europe 5, including *A. orana* (BOVEY in BALACHOWSKI, 1966). The species *A. orana* also occurs in east and central Asia, for it is likely that *A. orana* and *A. fasciata* (auct.) are synonyms (BRADLEY 1952). In Japan, *A. orana* is known as a pest on apple, but it is a more serious pest on tea, its common name being 'smaller tea tortricid'. But there are slight differences between *A. orana* as a pest of tea and *A. orana* as a pest of apple, both physiological and morphological (HONMA 1966, 1970). The tea strain has again be named *A. fasciata* (NAGATA et al. 1972).

From east Asia the area of distribution spreads out without interruption into Europe (fig. 1). This figure is partially based on the origin of the specimens in the Zoological Museum in Leningrad (DE WILDE 1971). In Europe, it can be observed that the area of distribution tends to shift towards the west. (VAN DER MEER 1969).

U.S.S.R.

The species was already mentioned in 1844 by EVERSMANN. *A. orana* is widely spread throughout the U.S.S.R. and is mentioned in several handbooks (PAV-

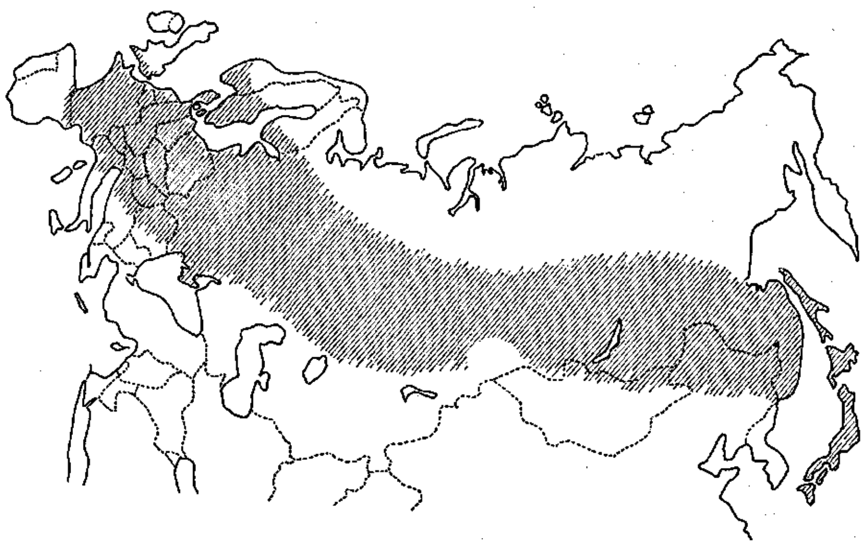

FIG. 1. Known area of distribution of *A. orana*. It is possible that *A. fasciata* in India and China is synonymous with *A. orana*.

LOWSKI 1951). In 1913 DOBROVLJANSKI mentioned its occurrence on pome fruit (In BALACHOWSKI 1966).

East Germany

In 1880 *A. orana* was caught near the mouth of the river Oder. In 1952 it became a pest (STEINHAUSEN 1954).

West Germany

In 1828 the species was mentioned by FROELICH in Würtemberg. In 1950 damage was observed (BLUNCK and JANSSEN 1952).

Czechoslovakia

In 1865 the species was mentioned by BRÜNN (STEHLIK 1951). Reports on damage are lacking.

Hungary

The first specimen were known in 1896 (GOZMÁNY 1951). In 1953 *A. orana* was mentioned as a pest (REICHART 1953).

Austria

In the Museum of Natural History in Vienna, the first specimens date from 1896 (PITTIONI 1951). In 1950 the species was regarded as a pest on pome fruit (BÖHM 1953).

Switzerland

In 1914 in 'Die Schmetterlinge der Schweiz' four places are mentioned where *A. orana* had been found (VORBRODT and MÜLLER-RUTZ 1914). In 1953 the first damage was mentioned (GEIER 1953).

France

In 1939, L'HOMME in his 'Catalogue des Lepidoptères de France et de Belgique' mentioned a dozen places where *A. orana* had been found. In 1957 damage was observed (MILAIRE 1960).

Belgium

The first specimen was caught in 1942 (JANMOULLE 1951). In 1947 the species was described as noxious (SOENEN 1947).

Holland

The first specimen was caught in 1939 (BENTINCK 1941). In 1944 the species was mentioned as being noxious (GONGGRIJP 1947).

England

The first specimen was caught in 1950 (GROVES 1951). In MASSEE's 'The pests of fruit and hops' (MASSEE 1954) the species was mentioned as being noxious.

The species also occurs in Roumania (IRICIUC 1964), North Italy (SALVATERRA 1953), North Spain (AGENJO 1951), Denmark, as early as in 1873 (TUXEN 1951), Scandinavia up to the 65th latitude (BENANDER 1951), Finland (HACKMAN 1951) and Poland (NIEMCZYK 1964). Apart from Roumania, Italy and Poland, damage has not been recorded in these countries.

Life history

In the Netherlands *A. orana* has two generations per year. The species hibernates as a second or third instar larvae on trees. In the laboratory, at 20 or 25 °C and less than 16 hrs of light per day, diapause takes place in the third instar. When daylength becomes shorter than 16 hours the larvae are induced to enter diapause. They spin hibernacula at rough places on the branches, becoming active again in April. At the beginning of June, depending on the weather conditions, the first flight starts. This flight period usually lasts about 4 weeks. The flight of the summer generation usually starts at the beginning of August and lasts till the end of September. The first half of this flight period is the most important, as the number of moths is at its highest and the conditions for egg-hatch and development of the larvae are optimum.

Temperature is a decisive factor for the developmental rate of all stages. For the eggs, 10 °C seems to be the threshold of development (DE JONG et al. 1965). Larval development till the pupal stage takes 18 days at 25 °C, 28 days at 20 °C and 50 days at 15 °C in laboratory cultures (DE JONG in DE FLUITER et al. 1963).

Under natural conditions, the eggs hatch within 10–14 days. In the summer generation it takes about 35 days for the insect to develop into a pupa. As a rule there are 5 larval instars, but it is possible, that in the overwintering generation the number is increased to 6. The duration of the pupal stage is also temperature dependent. Under natural conditions it is about 10 days.

The average life-span of the moths in the laboratory is about 10 days, being influenced by temperature and relative humidity (JANSSEN 1958). Under laboratory conditions of 20 °C and 70 % R.H., it is necessary to provide water, otherwise the average life-span is shortened. Addition of honey to the water does not make any difference. The longest life-span recorded in nature, in the release-recapture experiments, is 23 days.

The sex ratio of the moths is about 1:1, differences in average life-span between the sexes being slight. The species is slightly protandric. Under natural conditions the pre- imaginal developmental time is about 1 day shorter for males (BAREL 1966).

Mating and egg laying

Mating probably takes place during darkness, as is shown by the catches in sex traps baited with a living female or synthetic pheromone. It has also been observed during daytime in the laboratory. Both males and females can mate several times, although probably one mating is sufficient to fertilize all the eggs. At each mating a spermatophore is transferred. It was observed that old males sometimes transfer a little spermatophore or no spermatophore at all. Nevertheless this proved to be sufficient for fertilization. Most females are mated during the second night after emerging from the pupa, the first night the amount of pheromone produced being rather small (MINKS and NOORDINK 1971). When a female is mated the production of pheromone drops, but increases steadily during the following nights.

The number of eggs a female deposits is variable and numbers up to 800 have been observed. As an average, 175 will be a good estimate. The eggs are laid in flat egg-masses, with the shells overlapping. Usually an egg-mass consists of 20 to 150 eggs, the first one mostly being the largest. The eggs are laid at the upper or lower side of a leaf. It is possible that this is influenced by the smoothness of the leaves (JANSSEN 1958). In captivity *A. orana* oviposits on any smooth surface.

LARVAE

All the larvae of an egg-mass hatch at about the same time. The newly-hatched caterpillars immediately disperse towards the edge of the leaf. Once arrived there, the larvae continue creeping along the edge of the leaf. When they meet they disturb each other and as a result one of them spins a silken thread and drops off from the leaf hanging onto this thread. Later, some larvae climb back along the thread, others either swing to a neighbouring leaf or branch or else the thread is broken and larvae together with their threads are transported somewhere by wind. Larvae which do not drop, mostly creep away from the leaf, via the stalk and branch, and settle on another leaf. Once they are settled, there is usually only one larva per leaf. This indicates that there is some sort of territorial behaviour (ANKERSMIT and VAN DER MEER 1973). This theory is supported by the fact that the newly-hatched caterpillars drop from the leaves upon meeting. The places where the larvae settle differ according to the season. Those of the summer generation move towards the end of the branches and young caterpillars are often found in the still unfolded leaves at the tips of the shoots. Later they are often found in leafrolls, or in clusters of leaves spun together, a little below the apex. It was observed that for pupation a new leafroll was sometimes made. As the leaves of this leafroll are not nibbled, they are not easy to find.

When the larvae of the winter generation hatch, the shoots are already full grown. A preference for the tips is less conspicuous, the larvae being found over the whole tree. The first instar larvae are mostly found in a corner between the main rib and a secondary rib of a leaf. The second instar larvae often spin two leaves together or attach a leaf to a fruit. They do not make proper leafrolls. This is done the next year, prior to pupation, when the leaves are sufficiently large.

The larva lives in a web, the latter being renewed a few times. Movement to another leaf often occurs at these moments. When foraging, the larva keeps the upper epidermis and the ribs intact. The 'windows' in the leaf are characteristic, especially for the young larvae of the winter generation. A transparent spot besides the main rib indicates where the young larva has made its first web. It has to be stressed that all these data refer to larvae on apple trees. On other hostplants differences can occur. There can be fewer new shoots at the moment the larvae of the summer generation hatch. The leaves can be more stiff, in which case less leaf-rolls and clusters of leaves are made (*Fraxinus* sp.). According to the position of the leaves in relation to the branch the appearence of clusters of leaves can be different. In a *Salix* sp. leaves were found spun together like a sandwich, with the web of the larva in the middle.

DAMAGE

Damage is caused by the larvae, which may forage superficially on the skin of the fruits. The winter generation generally causes more damage than the summer one. The scars on the fruits caused by the summer generation are bigger, whilst those caused by the winter generation are more numerous. The damage to devastated leaves and buds can be neglected. However, it has been reported from Belgium that this can also be important (SOENEN 1947).

BIOLOGICAL CONTROL AGENTS

A. orana is a pest of commercial orchards. In unsprayed orchards damage is rare. There is a striking difference in the composition of the Tortricid fauna between commercial and unsprayed orchards. In commercial orchards often more than 80% of the collected Tortricid larvae turn out to be *A. orana*. In unsprayed orchards this percentage is always much lower. In commercial orchards, the percentage of parasitised larvae is usually less than 10, although several parasites of *A. orana* are known (JANSSEN 1958). Incidentally, higher rates of parasitization have been noted. When this occurs, it is caused predominantly by only one species. This is mostly the Eulophid *Colpoclypeus florus* (VAN FRANKENHUYZEN 1970) or the Ichneumonid *Teleutea striata*. The impression exists, that in unsprayed orchards the percentage of parasitization is higher, but some reserve has to be made about the identification of the parasitized caterpillars. Recently a reliable method for identification has been developed, based on the characteristics of the mandibulae (EVENHUIS and VLUG 1972).

Data about the percentage of parasitization outside orchards are scanty, as it is not easy to collect larvae of *A. orana* on the vegetation of hedges and woods. However, it was remarkable that when larvae were collected, often in more than 50% of the clustered leaves, parasitised or predated larvae were found. To what extent this concerned *A. orana*, cannot be stated. Of the larvae collected only 10 to 20% turned out to be *A. orana*.

In a roadside planting, a parasitization rate of 40% was once recorded. In one of the experiments a large number of moths was released in July. In August, 25 larvae were collected, from which 10 were parasitised by 5 different species, 4 *Hymenoptera* and 1 *Dipteron*. The other larvae were all *A. orana*.

Egg parasites like *Trichogramma* spp. are not important in sprayed orchards (DE JONG, personal communication).

The *Adoxophyes* nuclear polyhedral virus does not usually give any mortality exceeding one or two percent (DE JONG personal communication).

Concerning predators little is known. JANSSEN (1958) mentions several species, but does not give quantitative data. DE JONG once observed 30% predation of the overwintering generation by birds in January (DE JONG 1970).

FLIGHT ACTIVITY

The males fly during darkness, as can be deduced from sex trap catches (MINKS and NOORDINK 1971). During daytime, flight has rarely been observed. When it was observed, the zigzag flight direction was worthy of some note. The flights were always short, the moths coming to rest again on a plant after a few meters. During daytime, when they are at rest, it was not easy to disturb them and make them fly. When moths are released in an orchard, most of them immediately fly to a tree. When they are released in the open field, many of them come to rest on the ground and a few start flying. In one experiment it was often observed that they headed towards trees at the border of the field.

ZECH (1957) recorded the hourly distribution of catches in a light trap. He did not find much difference between the sexes, but obtained slight indications that females start activity somewhat earlier than males.

HOSTPLANTS

The larvae of *A. orana* are extremely polyphagous. JANSSEN (1958) gives the following list of plants on which caterpillars are found. *Acer campestre*, *Alnus* sp., *Betula* sp., *Carpinus betulus*, *Cotoneaster dielsiana*, *Crataegus* sp., *Cydonia oblonga*, *Fagus silvatica*, *Forsytia suspensa*, *Gossypium herbaceum*, *Humulus* sp., *Laburnum* sp., *Ligustrum* sp., *Lonicera caprifolium*, *L. xylosteum*, *Malus baccata*, *M. pumila*, *Medicago* sp., *Menyanthes trifoliata*, *Pyrus communis*, *Populus* sp., *Pistacia lentiscus*, *Parrotia* sp., *Prunus armeniaca*, *P. avium*, *P. cerasus*, *P. domestica*, *P. insistitia syriaca*, *P. padus*; *P. persica*, *P. triloba*, *Quercus* sp., *Ribes grossularia*, *R. nigrum*, *Rubus idaeus*, *R. fruticosus*, *Rosa canina*, *Rosa* sp., *Symphoricarpus racemosa*, *Salix caprea*, *Salix viminalis*, *Solanum dulcamara*, *Syringa vulgaris*, *Tilia* sp., *Ulmus campestris*, *Urtica* sp., *Vaccinium* sp..

This list can be extended with: *Chenopodium album*, *Convolvulus arvensis*, *Potentilla* sp., *Rumex* sp., *Vicia faba*.

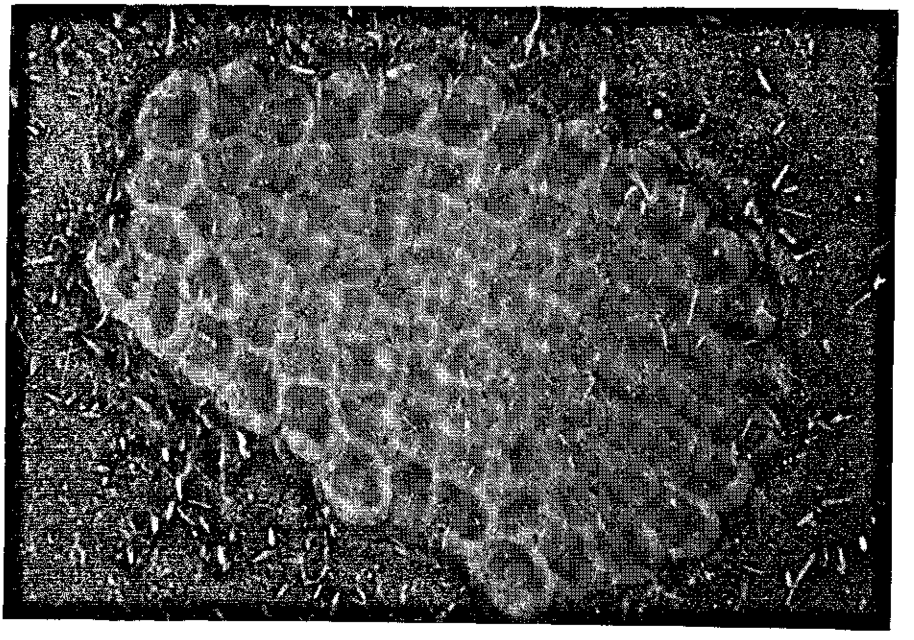

PHOTO 1. Egg-mass Photo Plant Protection Service, Wageningen.

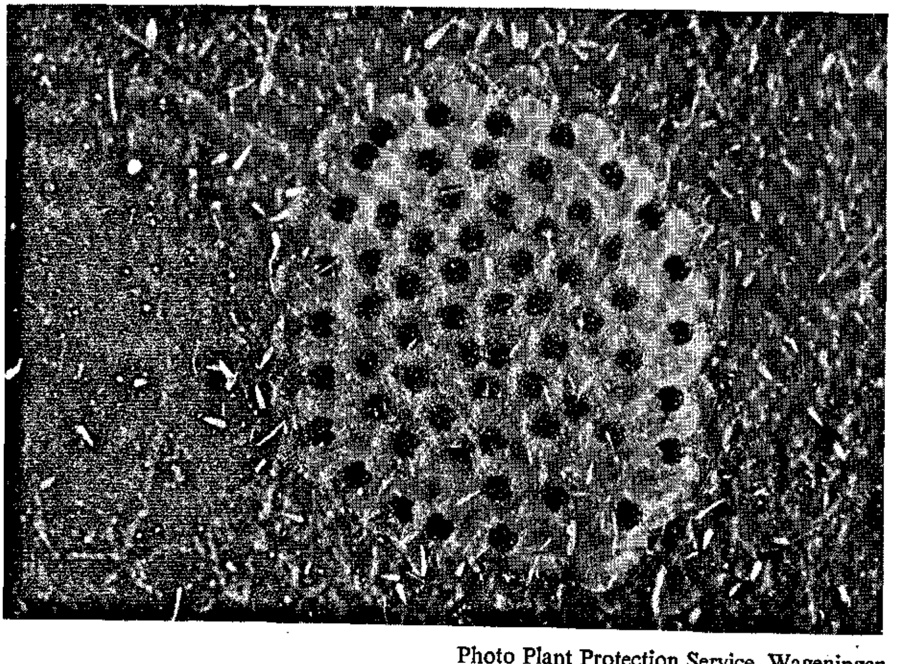

Photo Plant Protection Service, Wageningen.
PHOTO 2. Egg-mass, The head capsules of the larvae are visible.

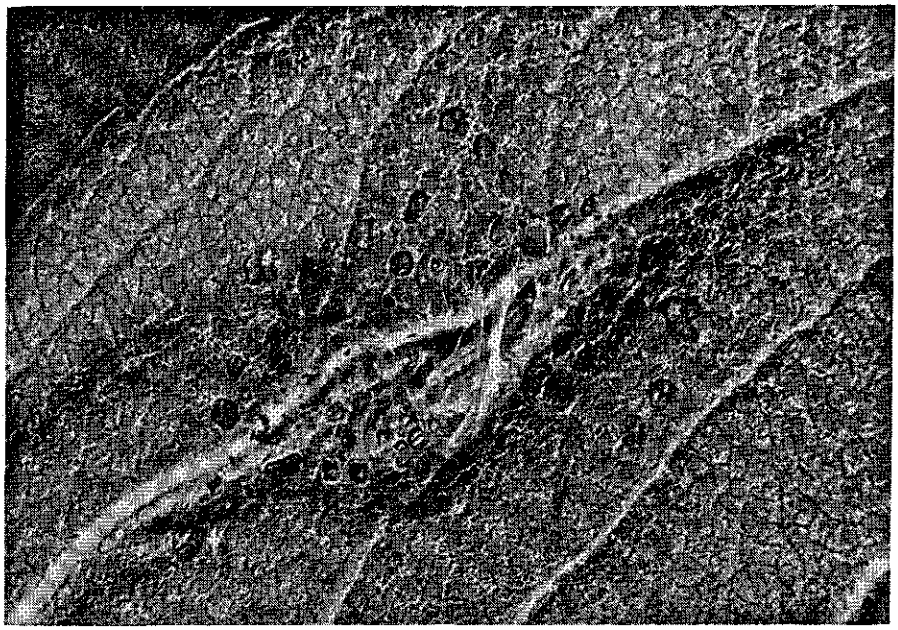

Photo Plant Protection Service, Wageningen.

PHOTO 3. Second instar larva in a web at the underside of a leaf.

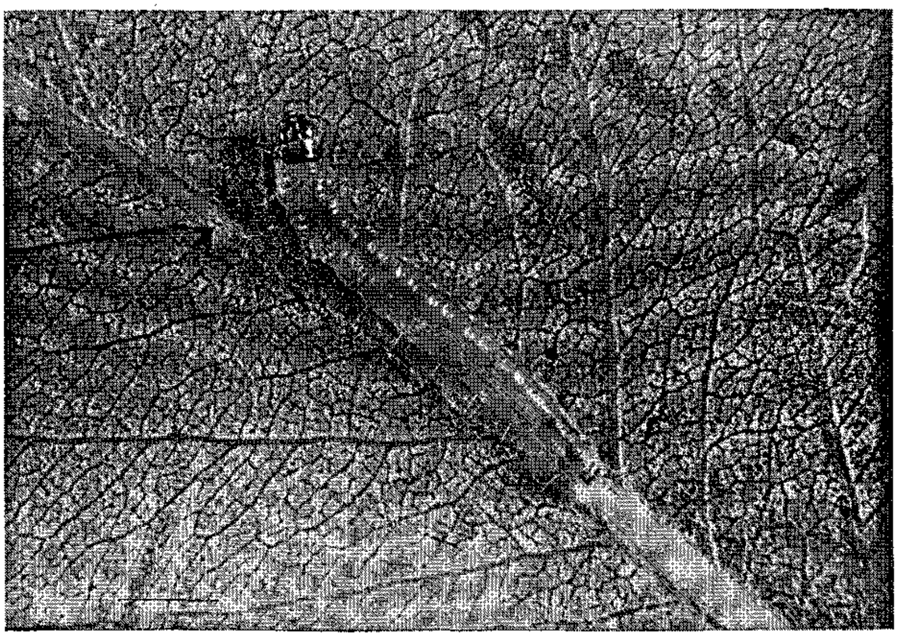

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PHOTO 4. Fourth instar larva, 15 to 20 mm in length.

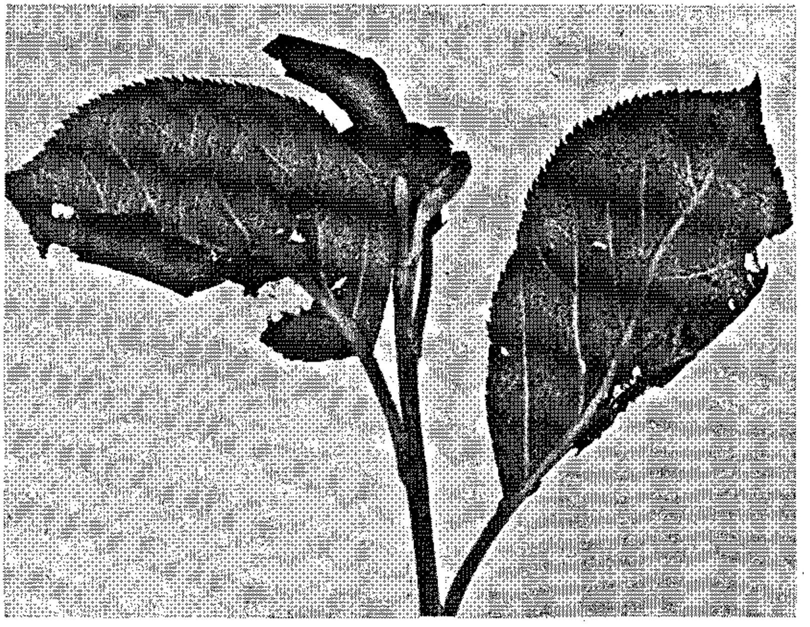

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PHOTO 5. Characteristic injury of the leaves.

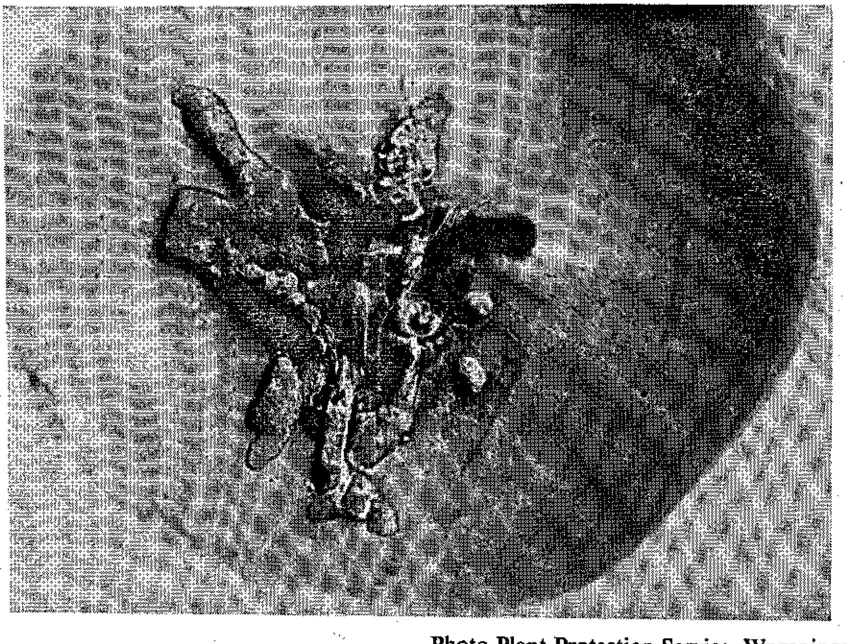

Photo Plant Protection Service, Wageningen.

PHOTO 6. Deep scars in an apple, damage of the summer generation.

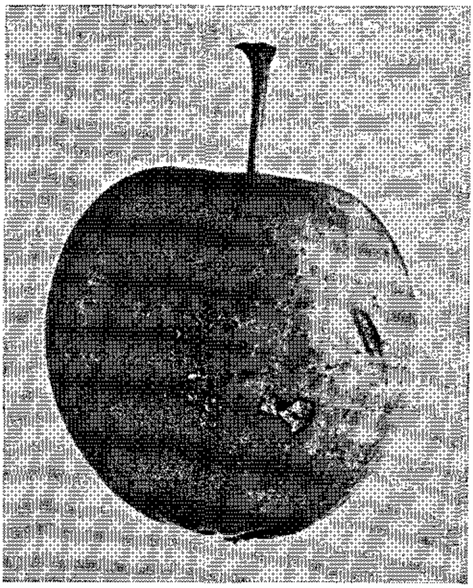

PHOTO 7. Characteristic damage to the fruit of the winter generation

Photo Plant Protection Service, Wageningen.

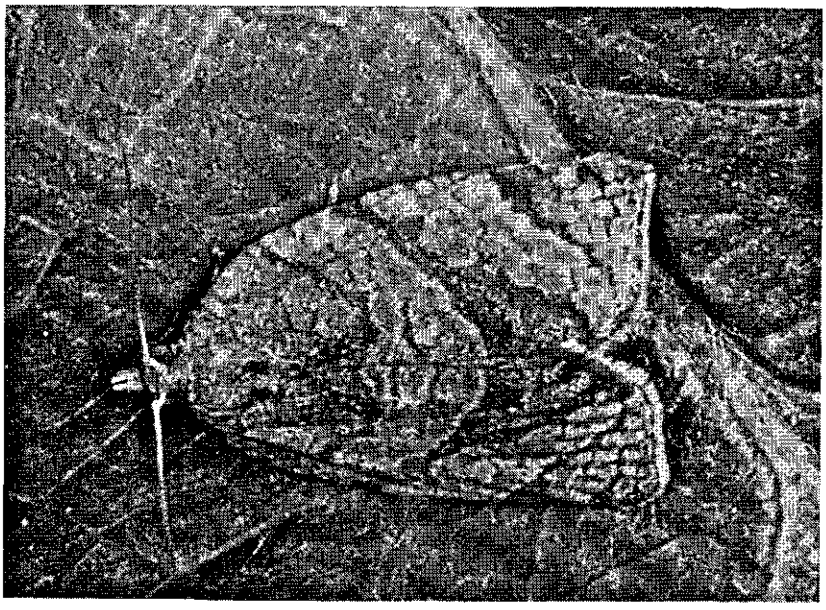

PHOTO 8. Female on an apple leaf. Wing span about 20 mm. The species does not show a pronounced sexual dimorphism.

3. MATERIALS AND GENERAL METHODS

3.1. Moths

Unless otherwise stated, the moths were from a strain kept in the laboratory since 1965. There are about 7 to 8 generations per year (20 °C., 70 % R.H. daylength 16.30 hours). In the first year of the experiments the strain had already been cultured in the laboratory for over 25 generations.

3.2. Diet

The laboratory strain was reared on a meridic diet, as described by Ankersmit (1968) from which Wessons salts were omitted and 200 mg. of streptomycine sulphate was added as a mould inhibitor.

3.3. Marking

In the first experiments radioactive phosphorus, ^{32}P, was used as a marker. 250 μCi $Na_2H^{32}PO_4$ was mixed into 1 kg of medium. The radioactivity in the moths was measured with a thin window G.M.-tube (Philips P.W. 18505) or demonstrated by means of autoradiography. In order to tag the ensueing egg-masses and larvae also, the quantity of $Na_2H^{32}PO_4$ was increased two and a half times. Because of the radiation danger, only a restricted use of ^{32}P could be made. This is why the plastic dye 'Calco oil red D' (from American Cyanamid Company) was used later. This Calco oil red D is closely related to Calco oil red N-1700, used by Hendricks (1970) and Salama (1972).

For 1 kg of medium 0.5 g was used, dispersed in the linseed oil. The dye stains the fat tissue in the abdomen of the moths red. Sometimes, the eggs are also stained. The red colour can be made visible by crushing the insects or putting them into a liquid in which they submerge. In preliminary experiments the moths were marked clearly, but later on, for an unknown reason, staining was less. This made it impossible to use the red colour as a criterium for being marked. Meanwhile, it was discovered that wild moths had yellow coloured fat tissue in the adbomen, which was clearly distinct from the red or greyish colour of the reared moths. The yellow colour is probably caused by plant pigments. This explains why the colour is absent in laboratory reared moths on an agar diet. It seems as if in this case a marker was superfluous. However this was not the case, for the red colour proved to be a valuable additional aid, especially when the moths had dried out somewhat.

Marking with ^{32}P is harmless (Minks and Noordink 1971). It is also likely that the use of the dye is harmless, for no significant differences, with regards to larval and pupal developmental time, emergence of adults, average life span, number of matings and fertility of the eggs have been found, in comparison with a control, reared on the agar diet minus the dye.

3.4. Light traps

The modified Robinson light traps (de Jong and Minks 1968) which were used, were equipped with 125 watt mercury vapour bulbs (Philips HPL 125). Occasionally a 125 watt black light bulb (Philips HPW 125) or a 100 watt flood-light bulb (Philips Comptalux press-glass floodlight) was used. When these deviating bulbs were used, is mentioned in the text.

In experiment I (4.2.1.2) the traps were in use from sunset till 5 or 6 hours later. In experiment 2 and 3 (4.2.1.3 and 4.2.1.4) the traps were in use during the whole night. The catches were collected the next morning.

As a killing agent, ¼ of a 'Vapona strip' (Shell Ltd.) was hung in the trap. This is easier than the use of ethyl-acetate and tetrachloroethane which have to be repeatedly replenished. The catches did not increase when a Vapona strip was combined with a mixture of these compounds.

3.5. Sex traps

The sex traps used, are described by Minks (1969). As a bait, either 2 females, extracted pheromone or synthetic pheromone was used.

When females were used, they were renewed once a week.

The pheromone extract was provided by Minks (Laboratory for Research on Insecticides, Wageningen). The quantity per trap corresponded to 25 females used for the preparation. The extract was mounted on a pad of cotton wool, which took the place of the females in the cage. It was refreshed every four days.

For the synthetic pheromone, a polyethylene cap was used as a wick (Glass et al. 1970). As this lasted for at least two months, renewal was not necessary. The cap was mounted in the middle of the trap, in the glue. The synthetic pheromone consists of two compounds (Meyer et al. 1972). In each trap 100 µg was used, 90% cis-9- and 10% cis-cis-11-tetradecenyl acetate.

The traps were hung at a height of about 1.5 m in trees. In the open field they were suspended from stakes.

4. MODES OF DISPERSAL

4.1. GENERAL

With regard to *A. orana*, there are three hypothetical ways of dispersal.
a. Flight.
b. Transport of larvae by wind.
c. Transport by man.

Dispersal by means of flight would be the most obvious way, for both males and females can fly. In general the flight of females is the more important, for only a female can raise a population in a new habitat. However, in relation to the population sterilization technique the dispersal of males is also important. When the eradication programme is still going on, the intruding males and females contribute in the same way to the fertility of the population. Only when the female is already mated, can she be more dangerous, for the fertility of an already mated, intruding female will be, in the main, higher than the average fertility of the females in the treated area. The latter will have an average fertility proportional to the ratio fertile/sterile males. The fertility of the intruding female will be proportional to the ratio

$$\frac{\text{eggs still to be oviposited}}{\text{eggs already oviposited} + \text{eggs still to be oviposited}}.$$ This fertility can be reduced by a second mating with a sterile male. The percentage reduction cannot be given exactly as there are not enough data available. It is stated to be higher than 50% (ANKERSMIT, personal communication). However a mated female is less attractive to a male than a virgin female (MINKS and NOORDINK 1971).

The dispersal by flight was studied in release recapture experiments. For the recaptures both light traps and sex traps were used. It is remarkable that although *A. orana* lays its eggs in egg-masses, the distribution of larvae throughout an orchard is always more or less homogeneous. This, together with the spinning behaviour under different conditions, has lead to the hypothesis of aerial transport of larvae. This phenomenon was already known from *Porthetria dispar* (BURGESS 1913), *Choristoneura fumiferana* (WELLINGTON and HENSON 1947) and *Cnephasia pumicana* (CHAMBON 1969). In the case of *P. dispar* the buoyancy of the larvae is increased by the long setae (LEONARD 1971). The larvae of the other species and of *A. orana* have much fewer setae. Here, the buoyancy only depends on the length of the thread.

The third possibility for dispersal is transport by man. Larvae can be propagated from nurseries with young trees. According to JANMOULLE *A. orana* has been distributed over Belgium by branches used for camouflage during the second world war (SOENEN 1947). In the United States, larvae were intercepted on lilacs imported from the Netherlands (VAN MARLE, 1952).

The reclamation of a new polder offered the possibility to investigate the dispersal in an area where was no traffic and no trees had been planted.

4.2. ADULT DISPERSAL

4.2.1. *Light traps*

Three different experiments were carried out.

Experiment 1. Moths released at one point, outside an orchard.
2. Moths released at three points, inside an orchard.
3. Moths released evenly throughout an orchard.

4.2.1.1. Materials and methods

Orchards:

In experiments 1 and 2 the same orchard was used. It consisted of a mixed planting of apple and pear, spindle trees of about 8 years old and had a height of 2.5 to 3 m. It was surrounded by a windbreak of alder, 4 to 5 m in height. The total surface was about 1.2 ha. In the immediate vicinity there was only arable land, apart from a meadow north-west of the orchard. At the border of the meadow there was a hedge of hawthorn (*Crataegus* sp.). This was somewhat sparse at the side parallel with the orchard, but rather dense at the side perpendicular to the orchard (fig. 2). At the third side of this triangular meadow, there was no hedge at all. The hawthorn hedge was the only place within a radius of 500 m from the orchard, in which another population of *A. orana* could exist.

In experiment 3 another orchard was used. This orchard consisted of 1 ha of apple spindle trees, about 14 years old, with a height of 2.5 to 4 m and 0.5 ha of newly planted apple trees. At the west side, there was a windbreak of about 5 m in height, mainly consisting of alder. This orchard was less isolated from other biotopes suitable for *A. orana*. There were other orchards in the vicinity and hedges of alder (*Alnus* spp.), elder (*Sambucus* spp.) and willow (*Salix* spp.) as well as roadside plantings of 25 year old poplars (*Populus* spp.) and oaks (*Quercus* spp.) (fig. 5).

Moths:

In experiment 1 the release point was situated outside the orchards. If moths had been released, forced flight movements towards the orchard could have resulted from a disturbance at release. To avoid this error, pupae were placed at the release point. The opening of the box containing the pupae was covered with gauze to protect the pupae against predators, such as mice and birds. The box was also shielded from rain and sunshine.

In experiment 2 the same procedure was used, although there was less necessity for a release as pupae, as in an orchard, disturbed moths can quickly come to rest in the surrounding trees.

Both in experiments 1 and 2 the moths were marked with ^{32}P.

In experiment 3 it was necessary to release moths instead of pupae, this experiment being part of a population sterilization experiment. The moths were released homogeneously throughout the orchard. They were marked with

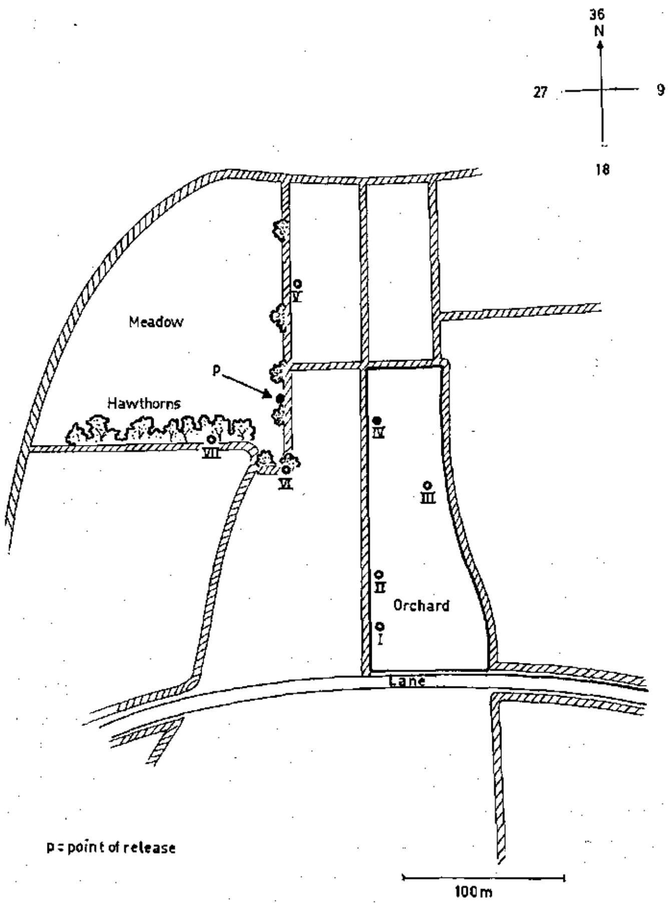

FIG. 2. Position of the light traps. Experiment 1.

Calco oil red D.

4.2.1.2. Experiment 1

The release point was situated outside the orchard. Earlier investigations (DE FLUITER et al. 1963) had shown that outside an orchard much less *A. orana* were caught than inside. This suggests that the moths are inclined to stay in an orchard. For experiment 1 the numbers of moths available were limited. To observe dispersal, movement from one biotope to another, it was preferred to release them outside the orchard to avoid dilution as a result of movement within the orchard. In this view, a release in the open field would be the best. But this would have been a very unnatural situation. Therefore something intermediate was chosen. The release point was situated near a solitary haw-

TABLE 1. Totalized numbers of wild males and wild females caught. Experiment 1, first release. (Traps operated from July 17th till August 14th).

	trap						
	inside orchard				outside orchard		
	I	II	III	IV	V	VI	VII
males	244	190	195	366	5	33	35
females	39	22	44	55	1	8	3

thorn bush at 40 m distance from the fringe of the orchard. Around the release point 7 light traps were placed at distances from 45 to 155 m, 4 inside the orchard and 3 outside (see fig. 2).

Two releases were carried out. The first time only female pupae were used, the males being used in another experiment. In the period from July 17th till July 24th, 840 pupae hatched. The traps were operated from July 17th till August 14th.

Results of the first release

Of the marked females only one was recaptured, on July 26th in trap V, outside the orchard in the hedge of hawthorns.

During the period of trapping, the second flight gradually began. The totalized numbers of captured wild males and wild females are shown in table 1.

Second release

From August 28th till September 2nd, 2080 male and 2080 female pupae hatched. The traps were operated from August 28th till September 15th.

Results of the second release

Six marked moths were recaptured, 4 males and 2 females. The males had crossed the open field and were trapped in the orchard (table 2), the females were recaptured in the hedge of hawthorns (table 3). It was probably a matter of chance that the recaptured females were caught earlier than the recaptured males.

TABLE 2. Numbers of marked males recaptured. Experiment 1, second release.

	trap						
	inside orchard				outside orchard		
	I	II	III	IV	V	VI	VII
September 10	0	1	1	1	0	0	0
September 11	0	0	0	1	0	0	0

TABLE 3. Numbers of marked females recaptured. Experiment 1, second release.

	trap						
	inside orchard				outside orchard		
	I	II	III	IV	V	VI	VII
August 29	0	0	0	0	0	0	1
September 2	0	0	0	0	0	1	0

The totalized numbers of the captures from the wild population are shown in table 4.

TABLE 4. Totalized numbers of wild males and wild females caught. Experiment 1, second release. (Traps operated from August 28th till September 15th).

	trap						
	inside orchard				outside orchard		
	I	II	III	IV	V	VI	VII
males	158	45	72	94	4	1	2
females	129	56	52	79	0	1	2

4.2.1.3. Experiment 2

This experiment was designed to investigate which fraction of the released moths leaves the orchard. The release points were situated inside the orchard. There were three points at the first release (fig. 3) and one at the second, (fig. 4). Most traps were outside the orchard. The minimum distance to the orchard was 40 m. The influence of the trap should not reach into the orchard, in order to avoid a forced movement out of the latter.

First release

700 male and 500 female pupae hatched from June 14th till June 17th. The traps were operated from June 14th till June 22nd. During this period not any marked moth was recaptured outside the orchard. Also very low numbers of the wild population were captured (table 5).

To be sure that the poor results were not due to the kind of traps used, on June 19th and 20th, a trap was also placed inside the orchard (trap IX). During the first night 10 males and 2 females were captured, including 2 marked males and 1 marked female. During the second night, which was much colder, only 1 wild male was captured.

Second release

Because of the results of the first release, the design for the second release was altered. Also, in order to look at the movement within the orchard, only one

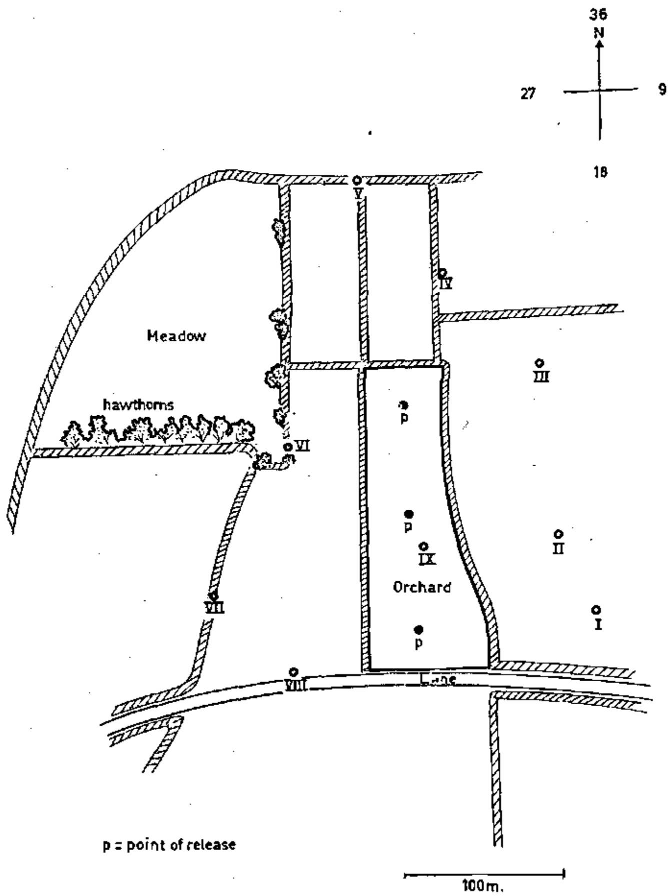

FIG. 3. Position of the light traps. Experiment 2, first release.

TABLE 5. Totalized numbers of wild males and wild females caught. Experiment 2, first release. (Traps operated from June 15th till June 22nd).

	trap								
	outside orchard								inside orchard
	I	II	III	IV	V	VI	VII	VIII	IX
males	0	0	1	0	0	0	0	4	9^2
females	0	2	0	0	0	1	1	2	1^2

[2]. This trap was only operated for two nights.

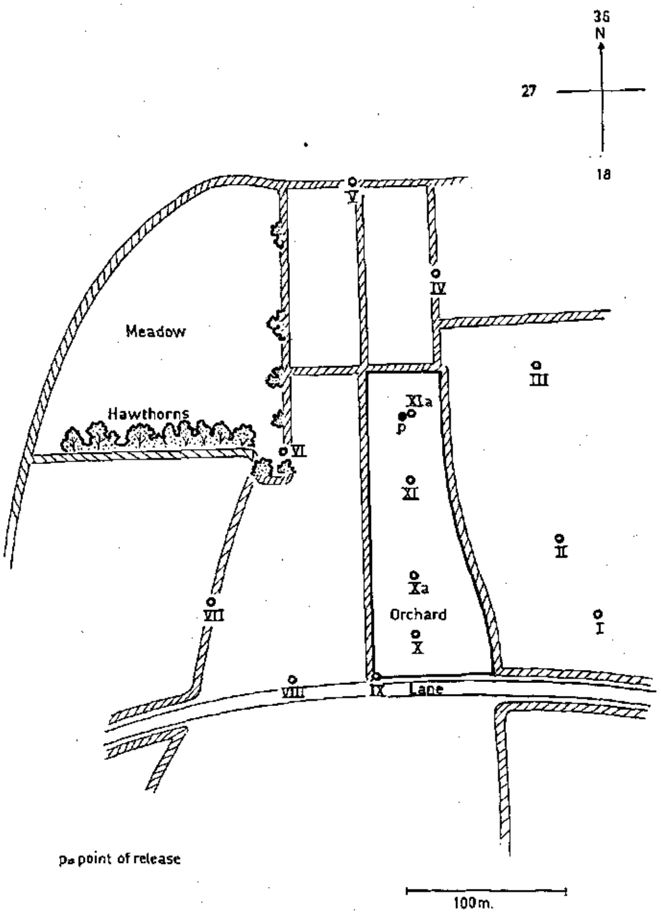

FIG. 4. Position of the light traps. Experiment 2, second release.

release point was chosen and two traps were placed inside the orchard (fig. 4). Trap Xa is trap X which was moved 40 m in the direction of the release point on August 19th. This was also done with trap XIa. Trap IX is trap VIII which had to be removed on August 2nd, because of harvesting activities. In trap IX a floodlight bulb was used, instead of a mercury vapour bulb.

From July 27th till August 28th, 1150 male and 1230 female pupae gradually hatched. The traps were in use from July 29th till September 3rd.

Results

From the moths released 33 were recaptured, but only 2, both males, outside the orchard. The totalized recaptures are shown in table 6. The totalized captures from the wild population are given in table 7.

TABLE 6. Totalized numbers of marked males and females recaptured. Experiment 2, second release. (Traps operated from July 29th till September 3rd.)

	trap												
	outside orchard								inside orchard				
	I	II	III	IV	V	VI	VII	VIII	IX	X	Xa	XI	XIa
males	1	0	0	0	0	1	0	0[p]	0[q]	2[r]	0[s]	11[t]	6[u]
females	0	0	0	0	0	0	0	0	0	0	0	0	0

p. Trap operated from July 29th till August 2nd.
q. Trap operated from August 2nd till August 15th.
r. Trap operated from July 29th till August 19th.
s. Trap operated from August 19th till September 3rd.
t. Trap operated from July 29th till August 19th.
u. Trap operated from August 19th till September 3rd.

TABLE 7. Totalized numbers of wild males and wild females caught. Experiment 2, second release. (Traps operated from July 29th till September 3rd.)

	trap												
	outside orchard								inside orchard				
	I	II	III	IV	V	VI	VII	VIII	IX	X	Xa	XI	XIa
males	3	6	1	1	1	4	6	0[p]	25[q]	397[r]	45[s]	466[t]	44[u]
females	0	1	2	1	0	3	1	0	4	85	16	116	25

p. Trap operated from July 29th till August 2nd.
q. Trap operated from August 2nd till August 15th.
r. Trap operated from July 29th till August 19th.
s. Trap operated from August 19th till September 3rd.
t. Trap operated from July 29th till August 19th.
u. Trap operated from August 19th till September 3rd.

4.2.1.4. Experiment 3

Experiment 3 was part of a trial to apply the population sterilization technique. The far greater numbers of moths released were an advantage, with regard to the poor results of the preceding experiments. But the experimental design for dispersal studies had to be somewhat restricted. Because of local conditions, less light traps could be placed outside the orchard than would have been desirable, whilst inside the orchard there were more light traps than would have been useful for the dispersal studies. For the position of the traps see fig. 5.

In contrast to the previous experiments, the moths were sterilized and marked with the dye Calco oil red D, instead of ^{32}P. Sterilization was carried out with 25 krad gamma-rays from a ^{60}Co-source. In laboratory experiments, sterilization has not shown detrimental effects on longevity or behaviour (DENLINGER and ANKERSMIT, in preparation).

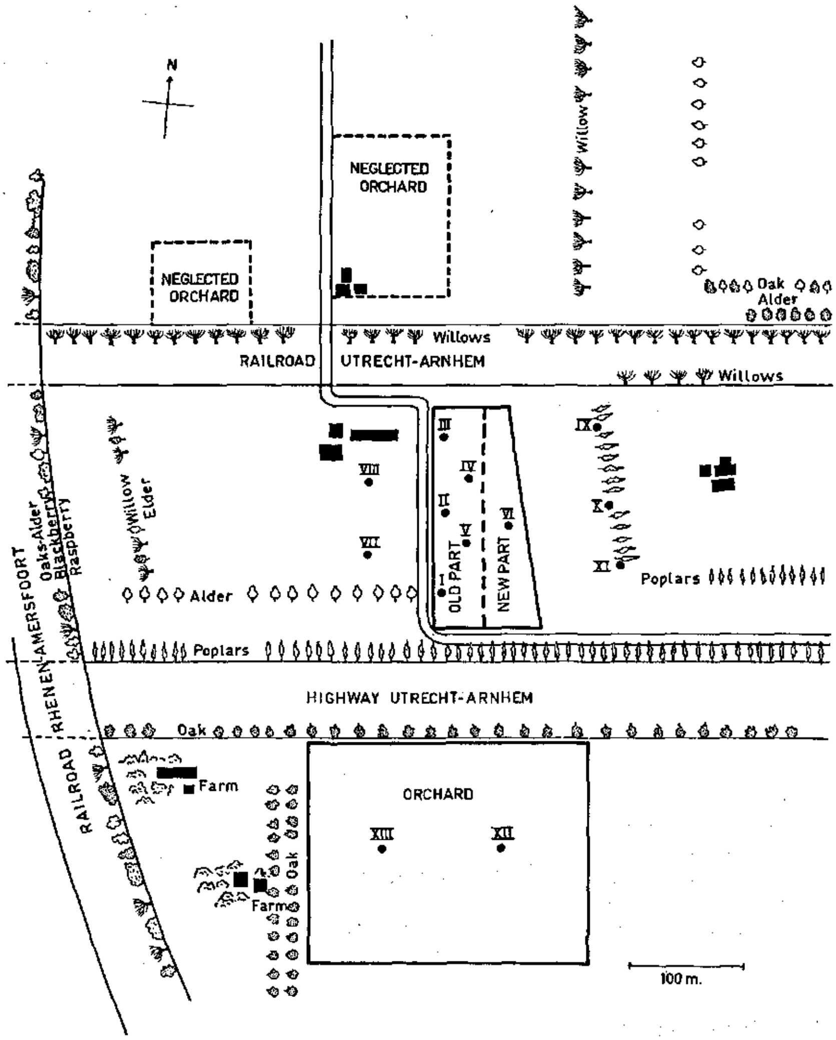

FIG. 5. Position of the light traps. Experiment 3.

It was possible to divide the orchard into two parts, 1 ha with 13 years old trees and 0.5 ha with newly planted trees. With regard to the population sterilization experiment, two times more moths were released in the old part of the orchard, per unit of surface, than in the young part. The releases were effected by walking through the orchard with an opened box containing moths.

First flight

To cover the first flight, 45,700 males and the same number of females were released in the period from May 25th till July 3rd. The traps were in use from May 30th till June 26th.

TABLE 8. Totalized numbers of marked males and females recaptured. Experiment 3, first flight. (Traps operated from May 30th till June 26th).

	trap												
	inside orchard						outside orchard						
	old					young							
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
males	190	140	158	229	153	23	1	2	0	0	1	4	1
females	6	6	6	8	7	1	0	0	0	0	0	0	0

TABLE 9. Totalized numbers of wild males and wild females caught. Experiment 3, first release. (Traps operated from May 30th till June 26th).

	trap												
	inside orchard						outside orchard						
	old					young							
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
males	62	39	33	54	32	2	1	2	0	1	1	146	236
females	5	9	2	5	4	1	0	0	0	0	0	11	17

Results

The totalized numbers of the marked moths recaptured are given in table 8.

The totalized numbers of the moths caught from the wild population are given in table 9.

During the first flight, mistakes were made with the identification of the marked moths in the captures. Some of the marked moths were counted as being wild. So the numbers of wild moths caught are too large and consequently the numbers of marked moths recaptured, too small. Later on the magnitude of this error was assessed. About 10% of the marked moths were designated as being wild. The error with females was bigger than with males.

During the second flight better criteria for identification were used, see 3.3.

Second flight

In the period from August 2nd till September 10th, 75,500 males and the same number of females were released. The traps were also in use from August 2nd till September 10th.

Results

The results are shown in the following tables:

Table 10: numbers of marked males recaptured.

Table 11: numbers of marked females recaptured.

Table 12: numbers of wild males caught.

Table 13: numbers of wild females caught.

TABLE 10. Numbers of males recaptured inside and outside the orchard. Experiment 3, second flight.

	minimum			trap													
				inside orchard						outside orchard							
				old					young	west		east			south		
date August	temp. °C.	wind m/sec.	wind direction	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
3	14.3	0		33	21	20	–	38	5	1	1	0	0	0	–	–
4	14.6	0		12	19	22	74	44	4	0	0	0	0	0	0	0
5	15.1	0		37	30	26	39	44	22	0	0	0	0	0	0	0
6	14.2	2	S	8	7	9	47	16	6	0	0	0	0	0	0	0
7	15.7	3	SSW	57	26	25	64	29	9	0	0	0	0	0	0	1
8	12.1	0	WSW	0	2	1	2	1	0	0	1	0	0	0	0	0
9	10.2	5														
10	15.8	2	WSW	85	–	46	179	64	21	1	3	3	0	0	1	0
11	14.4	3	W	69	–	31	67	57	12	2	2	1	2	1	0	0
12	12.2	0														
13	14.6	7	SSW	16	–	12	34	17	1	0	0	1	1	0	0	0
14	13.9	0	SW	9	–	12	20	15	8	0	0	0	0	0	0	0
15	13.3	2														
16	9.1	3	S	11	–	5	22	8	4	0	0	0	0	0	0	0
17	3.1	2	WSW	0	–	0	0	0	0	0	0	0	0	0	0	0
18	8.4	0		1	–	1	0	0	0	0	0	0	0	0	0	0
19	16.5	1	NE	116	–	68	52*	93	18	5	4	2	0	0	1	1
20	16.8	1	NE	222	–	217	122*	207	121	9	7	7	4	7	3	1
21	15.9	0		126	69	112	153	82	33	5	7	0	0	2	0	0
22	10.1	0	E	71	62	72	100	63	6	1	3	1	1	2	2	2
23	13.7	1														
24	12.1	1	NE	0	0	0	0	0	0	0	0	0	0	0	0	0
25	7.4	1	NE	23	6	15	21	3	9	1	0	0	0	0	0	0
26	6.0	3	NE	1	1	0	1	0	0	0	0	0	0	0	0	0
27	14.3	1	ENE	28	–	25	37	47	1	0	2	0	0	0	0	0

Table 10. (continued)

28	11.0	0		14	–	9	48	24	13	0	0	0	0	0	0	0
29	16.9	3	W	11	–	–	46	90	8	0	0	0	0	0	0	0
30	14.6	6	SW	44	–	29	90	85	50	0	0	2	1	1	0	0
31	11.5	1	S	8	–	12	23	5	4	0	0	0	0	0	0	0
September																
1	11.2	2	WSW	2	–	3	8	10	0	0	0	0	0	0	0	0
2	10.6	4	WSW	24	–	9	40	40	3	0	0	0	0	0	0	0
3	11.9	2	WSW	10	–	6	42	17	4	0	0	0	0	1	0	0
4	11.9	3	WSW													
5	4.2	1	W	29	–	42	85	139	18	0	0	0	0	1	0	0
6	5.3	0														
7	3.3	1	NE	10	–	9	5	9	0	0	0	0	0	0	0	0
8	5.3	3	ENE	46	–	20	20	12	2	0	0	0	0	0	0	0
9	10.1	4	E													
10	7.3	2	ENE	1	–	0	0	0	0	0	0	0	0	0	0	0
				1124	243	858	1441	1249	362	25	30	17	9	15	7	5

* Blacklight (Philips HPW 125), instead of mercury vapour lamp (Philips HPL 125).

TABLE 11. Numbers of females recaptured inside and outside the orchard. Experiment 3, second flight.

date August	minimum temp. °C.	minimum wind m/sec.	minimum wind direction	trap: inside orchard, old I	II	III	IV	V	young VI	outside orchard, west VII	VIII	east IX	X	XI	south XII	XIII
3	14.3	0		1	4	2	–	1	0	0	0	0	0	0	–	–
4	14.6	0		0	5	1	6	1	1	0	0	0	0	0	0	0
5	15.1	0		2	2	3	1	0	1	0	0	1	0	0	0	0
6	14.2	2	S	0	1	0	2	6	0	0	0	0	0	0	0	0
7	15.7	3	SSW	4	3	4	10	11	0	0	0	0	0	0	0	0
8	12.1	0	}	1	0	0	0	0	1	0	0	0	0	0	0	0
9	10.2	5	WSW}													
10	15.8	2	WSW	13	–	4	21	13	9	3	2	1	0	4	0	0
11	14.4	3	W}	5	–	9	9	9	2	2	0	0	2	2	0	0
12	12.2	0	}													
13	14.6	7	SSW	0	–	0	0	0	0	0	0	0	0	0	0	0
14	13.9	0	}	2	–	2	1	0	0	0	0	0	0	0	0	0
15	13.3	2	SW}													
16	9.1	3	S	0	–	0	0	0	0	0	0	0	0	0	0	0
17	3.1	2	WSW	0	–	0	0	0	0	0	0	0	0	0	0	0
18	8.4	0		1	–	0	0	0	0	0	0	0	0	0	0	0
19	16.5	1	NE	22	–	11	6*	25	3	4	1	1	0	1	0	0
20	16.8	1	NE	49	–	41	8*	58	57	7	2	6	7	13	0	1
21	15.9	0		42	31	25	25	42	6	3	10	0	1	0	0	0
22	10.1	0	}	11	13	13	12	8	9	1	1	2	1	1	0	0
23	13.7	1	E}													
24	12.1	1	NE	0	0	0	0	0	0	0	0	0	0	0	0	0
25	7.4	1	NE	3	2	4	3	3	1	1	0	0	0	0	0	0
26	6.0	3	NE	1	0	0	0	0	0	0	0	0	0	0	0	0
27	14.3	1	ENE	6	–	3	13	11	1	0	0	0	0	0	0	0

TABLE 11. (continued).

28	11.0	0		2	–	2	6	2	0	0	0	0	0	0	0	0
29	16.9	3	W	2	–	–	11	8	3	0	0	0	0	0	0	0
30	14.6	6	SW	8	–	7	13	19	9	0	0	1	3	0	0	0
31	11.5	1	S	1	–	0	0	1	1	0	0	0	0	0	0	0
September																
1	11.2	2	WSW	0	–	0	2	1	0	0	0	0	0	0	0	0
2	10.6	4	WSW	7	–	3	13	4	2	0	0	0	0	0	0	0
3	11.9	2	WSW	1	–	0	0	2	0	0	0	0	0	0	0	0
4	11.9	3	WSW													
5	4.2	1	W	5	–	3	9	12	1	1	0	0	0	0	0	0
6	5.3	0														
7	3.3	1	NE	0	–	0	0	0	0	0	0	0	0	0	0	0
8	5.3	3	ENE	0	–	0	1	1	0	0	0	0	0	0	0	0
9	10.1	4	E													
10	7.3	2	ENE	0	–	0	0	0	0	0	0	0	0	0	0	0
				189	61	137	172	238	106	23	16	12	14	21	0	1

* Blacklight (Philips HPW 125), instead of mercury vapour lamp (Philips HPL 125).

TABLE 12. Numbers of wild males caught inside and outside the orchard. Experiment 3, second flight.

	minimum			trap													
				inside orchard						outside orchard							
date August	temp. °C.	wind m/sec.	wind direction	old					young	west		east			south	
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
3	14.3	0		0	0	0	–	0	0	0	0	0	0	0	–	–
4	14.6	0		0	1	0	0	0	0	0	0	0	0	0	0	0
5	15.1	0		0	0	1	0	0	0	0	0	0	0	0	0	0
6	14.2	2	S	0	0	1	3	0	0	0	0	0	0	0	0	2
7	15.7	3	SSW	2	2	1	3	0	0	0	0	0	0	0	0	7
8	12.1	0	}	0	0	0	0	0	0	0	1	0	0	0	0	1
9	10.2	5	WSW}													
10	15.8	2	WSW	5	–	0	4	4	2	2	1	0	0	1	5	18
11	14.4	3	W}	19	–	4	7	5	0	1	3	0	3	1	3	16
12	12.2	0	}													
13	14.6	7	SSW	6	–	4	5	3	0	1	1	0	0	0	6	13
14	13.9	0	}	7	–	2	5	1	2	1	0	1	1	0	6	6
15	13.3	2	SW}													
16	9.1	3	S	5	–	1	8	1	0	0	0	0	0	0	9	28
17	3.1	2	WSW	0	–	0	0	0	0	0	0	0	0	0	0	0
18	8.4	0		2	–	0	0	0	0	1	0	0	0	0	0	2
19	16.5	1	NE	16	–	8	5*	6	1	3	1	0	1	0	45	81
20	16.8	1	NE	18	–	15	5*	3	11	3	2	0	4	4	42	77
21	15.9	0		20	10	8	6	10	3	1	2	0	0	1	31	38
22	10.1	0	}	22	8	4	10	5	2	2	2	0	1	1	64	42
23	13.7	1	E}													
24	12.1	1	NE	0	0	0	0	0	0	0	0	0	0	0	0	0
25	7.4	1	NE	3	0	1	5	1	1	0	0	0	0	0	0	10
26	6.0	3	NE	1	0	0	0	0	0	0	0	0	0	0	1	0
27	14.3	1	ENE	1	–	2	6	1	1	0	0	0	0	0	5	11

TABLE 12. (continued).

28	11.0	0		0	–	0	6	0	1	0	0	0	0	0	8	3
29	16.9	3	W	1	–	–	2	2	0	0	0	0	0	0	5	6
30	14.6	6	SW	2	–	1	6	1	2	1	0	0	0	0	14	11
31	11.5	1	S	1	–	0	1	1	1	1	0	0	0	0	1	1
September																
1	11.2	2	WSW	0	–	0	3	0	0	0	0	0	0	0	5	4
2	10.6	4	WSW	0	–	1	2	1	1	0	0	0	0	0	0	4
3	11.9	2	WSW	1	–	1	5	2	0	0	0	0	0	0	4	6
4	11.9	3	WSW }													
5	4.2	1	W }	3	–	2	5	3	1	0	0	0	0	0	7	14
6	5.3	0	}													
7	3.3	1	NE	1	–	0	1	0	0	0	0	0	0	0	2	0
8	5.3	3	ENE }	2	–	1	1	1	0	0	0	0	0	0	1	1
9	10.1	4	E }													
10	7.3	2	ENE	0	–	0	0	0	0	0	0	0	0	0	0	0
				138	21	58	105	58	30	17	13	1	10	8	264	402

* Blacklight (Philips HPW 125), instead of mercury vapour lamp (Philips HPL 125).

TABLE 13. Numbers of wild females caught inside and outside the orchard. Experiment 3, second flight.

				trap													
	minimum			inside orchard						outside orchard							
				old					young	west		east			south	
date August	temp. °C.	wind m/sec.	wind direction	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
3	14.3	0		0	0	0	–	0	0	0	0	0	0	0	–	–
4	14.6	0		0	0	0	0	0	0	0	0	0	0	0	0	0
5	15.1	0		0	0	0	0	0	0	0	0	0	0	0	0	0
6	14.2	2	S	0	0	0	0	0	0	0	0	0	0	0	0	0
7	15.7	3	SSW	0	0	0	0	0	0	0	0	0	0	0	0	1
8	12.1	0		0	0	0	0	0	0	0	0	0	0	0	0	0
9	10.2	5	WSW													
10	15.8	2	WSW	0	–	0	0	0	0	0	0	0	1	0	1	1
11	14.4	3	W	0	–	0	0	0	0	0	0	1	0	0	0	1
12	12.2	0														
13	14.6	7	SSW	0	–	0	0	0	0	0	0	0	0	0	0	0
14	13.9	0		0	–	1	0	0	0	0	0	0	0	0	0	0
15	13.3	2	SW													
16	9.1	3	S	0	–	1	0	1	0	0	0	0	0	0	0	4
17	3.1	2	WSW	0	–	0	0	0	0	0	0	0	0	0	0	0
18	8.4	0		0	–	0	0	1	0	0	0	0	0	0	0	0
19	16.5	1	NE	1	–	2	0*	2	1	1	0	0	0	0	4	25
20	16.8	1	NE	3	–	2	0*	2	5	3	1	1	0	4	17	6
21	15.9	0		3	1	0	0	0	0	0	0	0	0	0	7	14
22	10.1	0		3	1	2	0	2	0	0	0	0	0	0	9	7
23	13.7	1	E													
24	12.1	1	NE	0	0	0	0	0	0	0	0	0	0	0	0	0
25	7.4	1	NE	0	0	0	0	0	0	1	0	0	0	0	1	0
26	6.0	3	NE	0	0	0	0	0	0	0	0	0	0	0	0	0
27	14.3	1	ENE	1	–	0	1	1	0	1	0	0	0	0	2	3

TABLE 13. (continued).

28	11.0	0		0	–	1	3	0	0	0	0	0	0	0	1	4
29	16.9	3	W	1	–	–	0	2	1	0	0	0	0	0	4	7
30	14.6	6	SW	2	–	1	0	1	2	2	0	1	0	1	15	6
31	11.5	1	S	1	–	0	0	0	0	0	0	0	0	0	1	0
September																
1	11.2	2	WSW	0	–	1	0	1	0	0	0	0	0	0	1	0
2	10.6	4	WSW	0	–	0	2	0	0	0	0	0	1	0	0	2
3	11.9	2	WSW	0	–	0	0	0	0	0	0	0	0	0	0	0
4	11.9	3	WSW }													
5	4.2	1	W }	2	–	0	1	0	0	0	0	0	0	0	5	4
6	5.3	0	}													
7	3.3	1	NE	0	–	0	0	0	0	0	0	0	0	0	0	0
8	5.3	3	ENE }	0	–	0	0	1	0	0	0	0	0	0	0	0
9	10.1	4	E }													
10	7.3	2	ENE	0	–	0	0	0	0	0	0	0	0	0	0	0
				17	2	11	7	14	9	8	1	3	2	5	68	85

* Blacklight (Philips HPW 125), instead of mercury vapour lamp (Philips HPL 125).

Together with the results, data about the weather conditions are given. These data were provided by the Department of Physics and Meteorology of the Agricultural University at Wageningen. They were collected in an open field at 1.5 m height, at 15 km distance from the orchard. The data concerning wind velocity and wind direction were taken at 19.00 on the previous night. The temperatures are the nightly minimum temperatures.

4.2.1.5. Discussion

Recaptures

In the first two experiments, the numbers of moths released were rather modest. In experiment 1, with 840 females and 2080 males plus 2080 females respectively, an attraction towards the orchard could not be demonstrated. After the first release only 1 male was recaptured, but outside the orchard. After the second release 4 males were recaptured, this time in the orchard. Also 2 females were recaptured, but again outside the orchard.

Experiment 2 was designed to investigate which fraction of the moths would leave the orchard. A total of 1850 males and 1730 females were released. Only 2 moths, both males, were recaptured outside the orchard.

It is not likely that the results were meagre because of inefficient traps. The numbers caught from the wild population inside the orchard were very reasonable. Moreover, inside the orchard also the numbers of marked moths recaptured were reasonable, 31 of the 2380 released in experiment 2 second release. On this occasion it was interesting to observe that more marked moths were recaptured, in relation to the numbers caught from the wild population, after trap XI was moved 40 m closer to the release point.

There are two possible ways of explaining the small numbers of moths recaptured. The first possibility is that the percentage of the population that is caught in light traps, is low. Hence, the released numbers were too small to give any information. However, if this is correct, the density of wild moths in the orchard must have been very high, with regard to the numbers caught in the traps in the orchard. In experiment 2 second release, it is possible to calculate how many moths would have flown around in the orchard, during the period of trapping. The calculation was made with the aid of the Lincoln-index and based on the numbers of wild and marked moths caught in the traps X, Xa, XI and XIa (tables 6 and 7). In this way, a number of at least 80,000 moths was calculated. This was an unrealistically high number. If this number had occurred, it would have been noticed, either because of an extraordinarily large number of leafrolls in July or because of severe damage to the fruits at harvest. From this it would be possible to deduce that the response of the released moths towards the action of the light traps was less than the response of the wild moths. This subject will be discussed later in the paragraph 'Quality of the released moths', in this chapter.

The second possibility is that the movement of the released moths throughout the orchard was not very great. Evidence for this was found in the fact that trap XIa had recaptured, proportionally, more marked moths than trap XI. Moreover, during the experiments many moths have been found sitting on the box in which the pupae hatched or in trees in the immediate vicinity. Also in laboratory experiments indications were obtained that the rate of movement was not very great, see chapter 7.

In experiment 3 there were 6 traps inside the orchard and 7 outside it. During the second flight period, 75,500 males and also 75,500 females were released. Of the males 5277 (7 %) were recaptured inside the orchard and 108 (0.15 %) were recaptured outside. For the females the figures are: in the orchard 797 (1 %) outside the orchard 87 (0.11 %).

When a comparison is made between the numbers recaptured inside and outside the orchard, it should be realized that there were only a few traps outside. At least 11 traps would have been necessary to surround the orchard entirely, with distances between the traps comparable to the distances between the traps in the orchard. There were only 5, if trap XII and XIII are not taken into consideration. These were of less importance, as it is likely that a large number of the moths that left the orchard at the south side, had settled in the north part of the neighbouring orchard, without reaching these traps. Hence, for the comparison, the total number of moths caught outside the orchard has to be multiplied by at least 2.2. For comments about this comparison, see the paragraph 'Trap position and catches' later in this chapter.

Numbers caught from the wild population

Out of the captures from the wild population, additional information can be obtained. Experiment 2 (second release) and experiment 3 are especially interesting, as in these cases the periods of trapping covered a great part of the flight periods and there were traps inside and outside the orchard. In table 14, the totalized numbers of wild moths caught are shown.

The numbers caught outside the orchard are very small compared to those caught inside the orchard, even when these numbers are corrected for the fact that the orchards were not entirely surrounded by traps. Only experiment 3 (second flight) seems to be an exception. However, in this case, the population of wild moths in the orchard was very small. Hence it is possible that propor-

TABLE 14. Totalized number of wild males and wild females caught, inside and outside the orchard.

Experiment	Inside the orchard			outside the orchard		
	number of traps	males	females	number of traps	males	females
2, second release	3	977	246	8	22	8
3, first flight	6	222	26	5*	5	0
3, second flight	6	410	60	5*	49	19

*) The traps XII and XIII in the neighbouring orchard are not taken into consideration.

tionally a large number of the moths, captured outside the orchard, originated from biotopes other than the orchard. The isolation of the orchard from other for *A. orana* suitable biotopes in experiment 3 was less than in experiment 2.

The differences in numbers caught in and outside the orchards, give the impression that the moths do not leave their biotope in great numbers.

Trap position and captures

It is a general experience that the mode of placement of a light trap affects the numbers of insects caught. Population densities differ and flying insects may be temporarily directed to some places for a variety of reasons. But there are also differences in the action of the light trap itself. VERHEYEN, in particular, has elucidated the trapping effect of light (VERHEYEN, 1958).

Under natural conditions the light coming from the sun, or indirectly via the moon, can be split up into three components: direct radiation, reflected light and scattered light. It has been demonstrated that for orientation, the insects make use of these three components together. When reflection and scattering are eliminated, orientation is lost. This results in a compulsory movement towards the light source. According to this theory, traps outside the orchard will be more effective than inside, for reflection is less.

It would have been desirable to test whether the traps outside the orchard were indeed more effective. This was tried by releasing the same number of moths around a trap in an open field and around a trap in an orchard. However, these experiments failed. Moths can only be captured while flying. Flight activity is correlated with weather conditions. These conditions differ inside and outside an orchard. Moreover, when the moths are released, they are disturbed, as a result of which there are flight movements. It is likely that the environment, open field or trees, will have an influence on the distribution of the moths around the trap after the release.

Presumably more important than a difference in efficiency of the traps, is a difference in flight activity of the moths within the area of action of the different traps. It can be postulated that in an orchard the conditions are more suited to the flight activity of *A. orana* than the conditions in open field, but is is likely that in an open field the average distance covered during the flight movements is greater. Outside the biotope the moths will encounter less stimuli to stop flying than in the biotope. The greater the distances covered, the greater the chance that the moth will reach the area over which the trap exerts its action. With regard to the differences in the chances of being captured inside or outside an orchard, in the release – recapture experiments, it may be presumed that the climatic differences between an open field and an orchard do not play an important role. It is likely that when the weather conditions for flying are marginal, most of the moths will stay in the orchard.

Apart from these exogenous factors it might be possible that there is also an endogenous factor which affects the level of flight activity near the different traps. Adults of *A. orana* are rather sluggish and near a release point it is always very easy to find moths that have not moved. There are indications that the average flight range is restricted and it is possible that it is less than a hundred meters. It could be postulated that there would be intrinsic differences with regard to the level of flight activity, as a result of which there will be a graded increase in the level of the flight activity from the release point towards the periphery of the flight range. This would implicate that near the traps outside the orchard, the intrinsic level of flight activity was higher than near the traps in the orchard.

The final conclusion has to be that, although it could not be demonstrated, it must be assumed that in proportion to the number of traps, the moths outside the orchard had a bigger chance of being captured than the moths inside the orchard.

Sex ratio

In general, the males were predominant in the numbers of moths caught. The sex ratio of the species is about 1:1, hence there must be a special reason for this phenomenon.

SCHÜTTE (1972) found with *Heliothis zea* that a light trap could also act as a sex trap, as soon as females were caught His traps were equipped with a propeller, which resulted in the moths being sucked into a collecting device. Some of the moths were crushed and he was able to demonstrate that traps which had been used before, attracted males, although they were not in operation. In the case of *A. orana* it is unlikely that this phenomenon is very important. There have been substantial catches of males, without any female being trapped and when a trap was not in operation, no males were captured.

On the other hand it is quite conceivable that there will be differences between the sexes with regard to flight activity. There are differences in physiological constitution and differences in behaviour. In experiments, using a flight recorder, it was demonstrated that the males of *A. orana* were more active than the females (chapter 7).

Another very important point is the time of flying. LEWIS and TAILOR mention several cases in which a difference in diurnal flight periodicity was found, according to sex (LEWIS and TAILOR, 1964). This has also been observed in *A. orana*. ZECH (1957) reported that at night, females start flying before the males. In the laboratory experiments on flight activity, chapter 7, this was also found. The same has been reported for *A. fasciata*, the smaller tea tortrix (TAMAKI et al. 1969).

In the course of the second flight period, the sex ratio in the captures changes. In the beginning the males are predominant, but the proportion of the males decreases steadily, and at the end of the flight period a sex ratio of about 1:1 can be reached (compare table 1 with table 4 and the traps X and XI with Xa and XIa in table 7). However, in experiment 3, with released moths, this phenomenon was not obvious (table 15).

The proportional increase in numbers of females caught was only observed during the second flight period. It is possible that during the first flight period this phenomenon is obscured, because the numbers caught are usually smaller.

TABLE 15. Percentage of females in the total catch. Experiment 3, second release.

period	marked females	wild females
3rd–10th August	9%	0%
10th–17th August	12%	3%
17th–24th August	24%	15%
24th–31st August	17%	36%
31st August–6th September	13%	20%

If not, the shortening of the days during the second flight could be an explanation for this difference, if the timesetting of the diurnal flight rhythmicity had taken place during the larval stages. A slight indication of this has been found in the laboratory experiments (chapter 7). If under a constant light regime the females already start their flight activity before dark, shortening of the days, as it occurs during the second flight period, is important for gradually an increasing part of the period of flight activity will coincide with the night and hence the captures by means of light traps will increase.

This would also explain, why this phenomenon was not observed in experiment 3, with released moths. These moths were reared under artificial dark conditions, from 23.30 till 07.00. Hence, changes in the sex ratio could not be expected.

If there was also a proportional increase in the numbers of females caught at the end of the first flight period, then it would be much easier to explain this change. *A. orana* is a slightly protandric species. The average developmental time for female larvae is about 0.5 to 1 day longer than the average for male larvae (5.3). Therefore males appear first.

The age of the females captured is another important point. As the age cannot be determined directly, the number of spermatophores is taken as an indication.

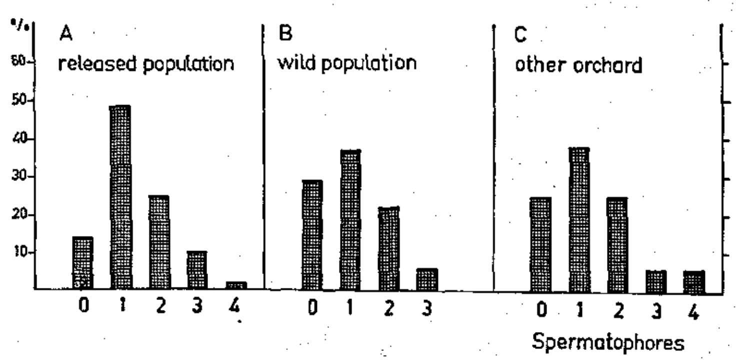

FIG. 6. Number of spermatophores of females in light trap catches, in the fourth week after the beginning of the second flight. A = 59, B = 31 and C = 32 females.

MINKS and NOORDINK collected females at random by shaking trees and picking up the startled moths. They counted the numbers of spermatophores and compared these with their data of trapped females, but could not find much difference. There was a slight indication that there were more females without spermatophores in the catches as well as older females with more then two spermatophores (MINKS and NOORDINK, 1971). The data above are in conformity with their results. It is not likely that the proportional increase of females in the catches at the end of the flight period can be explained by an influence of age on trapping results.

Sex ratio inside and outside the orchard

It was observed, especially in experiment 3 second flight, that proportionally more females than males were caught in the traps outside the orchard, compared to the traps inside the orchard, the traps XII and XIII in the neighbouring orchard being an exception. In the previous experiments this was less obvious (table 16).

The cause of this difference is not known. But it is a very important observation, as the females are responsible for reinfestation of previously cleared areas.

In experiment 3, second release, the captures during nights with the same minimum temperature were drawn up. The sums obtained were converted into percentages, in relation to the total capture during the whole trapping period. The cumulative frequency functions of these percentages are shown in figures 7 and 8. It is shown that proportionally more moths were caught outside the orchard during warm nights. The difference which occurs between the wild population and the released population, will be discussed in the next paragraph.

Quality of the released moths

For dispersal studies it is of the utmost importance that qualitatively, there

TABLE 16. Catches of males and females outside the orchard, as a percentage of the total catch in and outside the orchard. (*denotes: small numbers).

period	wild population		released population	
	males	females	males	females
Experiment 1				
first release	7	7		
second release	2	1		
Experiment 2				
first release	36*	87*		
second release	2	3	10*	0*
Experiment 3	3*	4*	0.9	3
first flight	3	4*	0.9	3*
second flight	11	24	2	9

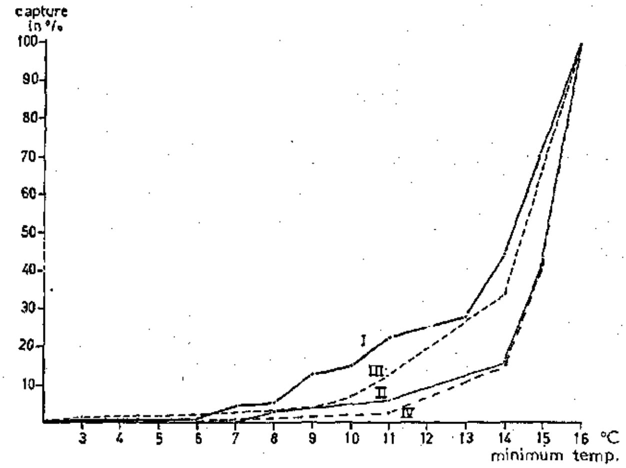

FIG. 7. Males: Cumulative frequency function of the captures at nights with different minimum temperatures. Experiment 3, second flight.
I = wild, inside the orchard.
II = wild, outside the orchard.
III = released, inside the orchard.
IV = released, outside the orchard.

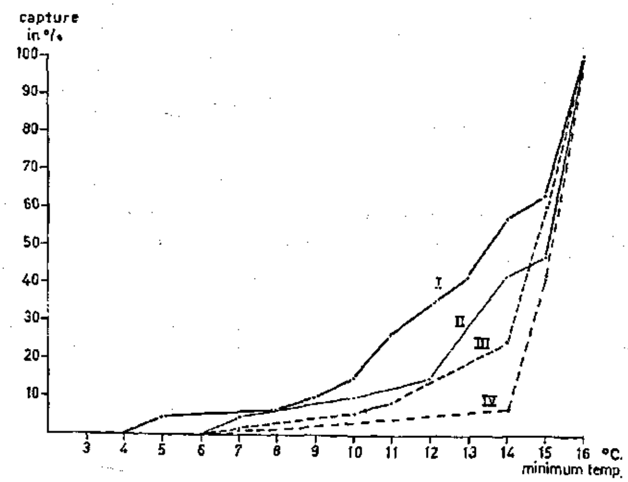

FIG. 8. Females: Cumulative frequency function of the captures at nights with different minimum temperatures. Experiment 3, second flight.
I = wild, inside the orchard.
II = wild, outside the orchard.
III = released, inside the orchard.
IV = released, outside the orchard

are no differences between the marked fraction of the population and the non-marked fraction. When this requirement cannot be fulfilled it is necessary to know exactly in which respects the groups differ (SOUTHWOOD, 1968).

In experiment 3 there was an opportunity to watch differences in behaviour, expecially those differences influencing the trapping results. The number of larvae of the wild population present in the orchard was estimated just before the pupal stage. As there are no special pupal mortalities known, about the same number of adults can be expected. The distribution of the adults in the course of time, during the flight period, can roughly be deduced from the light trap catches, taking into account the weather conditions. When the average life-span of adults is known, the number of adults present each day can be calculated. The average life-span is fixated arbitrarily at 10 days for both sexes. The calculated numbers of the second flight are given in table 17.

Also in the same table the calculated numbers of released moths present in the orchard are given. A mortality of 10% *per diem* is assumed. This is an over-simplified situation. The exact life-table of the adults will be more complicated, but in the run of the release, the error will be compensated for by the presence of moths of different ages.

During the second flight period the following percentages of the populations were caught:

Wild population	males 27.0%	Released population	males 7.0%
	females 4.0%		females 1.0%.

It seems that the part caught from the wild population is about 4 times bigger than the part recaptured from the released population. This could be the result of an underestimation of the wild population and also of immigration of moths from outside the orchard. Probably the underestimation was the main cause, but there are indications of still another cause. It is possible to calculate the ratio between the percentage of wild moths caught and the percentage of released moths recaptured, by means of the data given in table 17. Provided these data are correct and no differences exist between the populations, this ratio will be.1 However, some reserve has to be taken, because of the previously mentioned difference between the females of the two populations, with regard to the numbers caught in light traps in the course of the flight period. For this reason, the ratios are calculated for males only. It is interesting to see these rates depicted against minimum nightly temperatures (fig. 9). It appears that at lower temperatures the ratios are highest. This indicates that during colder nights, proportionally more wild males were caught.

The reason for the greater flight activity of the wild males, is unknown. DORSETT (1962) working with a Sphingid moth, found that a heavier moth needed a higher intra-thoracic temperature to take off. Our released moths were heavier than the wild ones. The average weight of wild pupae is about 16 mg for males and 25 mg for females. The average weight of the pupae of the released moths was about 22 mg for the males and 34 mg for the females.

Another possibility could be that of a genetic difference. In the laboratory,

TABLE 17. Calculated numbers of moths present in the orchard. Experiment 3, second flight. It is a coincidence that the numbers of wild moths show a normal distribution.

date	marked moths	wild moths
August		
2	11000	0
3	17000	46
4	15300	92
5	13760	138
6	23380	184
7	21040	230
8	18940	276
9	17040	322
10	28490	368
11	27640	414
12	24840	460
13	28950	506
14	26050	552
15	23450	598
16	21100	713
17	28000	828
18	25200	943
19	22680	1058
20	33810	1058
21	30430	1058
22	27380	1058
23	36740	943
24	33040	828
25	36040	713
26	34240	598
27	41340	552
28	37190	506
29	33470	460
30	41230	414
31	37110	368
September		
1	44050	322
2	39650	276
3	49550	230
4	44600	184
5	40140	138
6	36140	92
7	43650	46
8	39250	almost zero
9	35300	
10	42000	

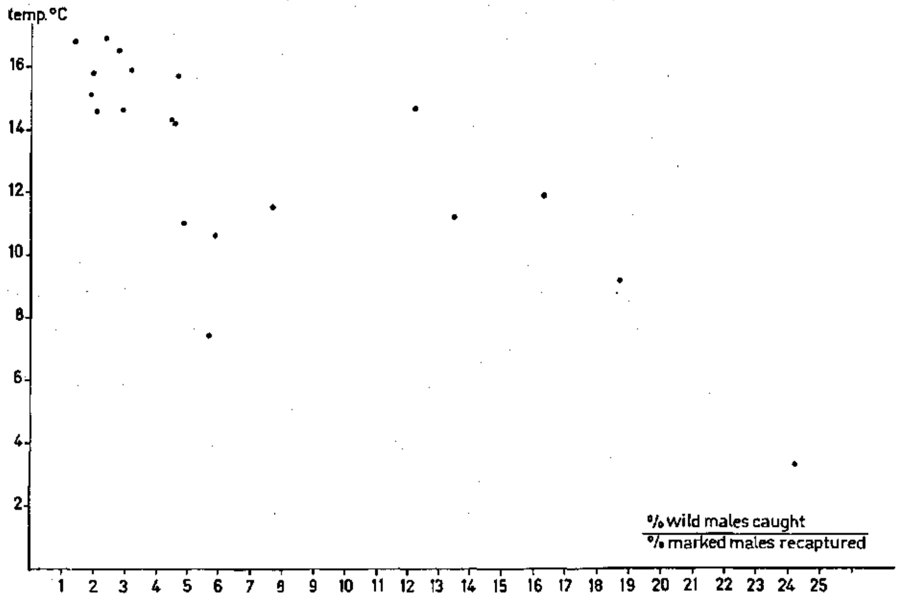

FIG. 9. Ratios of percentage wild males caught to percentage released males recaptured at different minimum nightly temperatures. Experiment 3, second flight.
abscissa = ratios; ordinate = temperatures.

the rearing temperature is constant at 20 °C. This could have influenced the genetic build up of the population with regard to the sensitivity of behavioural responses to temperature.

Another remarkable point is that egg-masses have hardly been found. Under laboratory conditions, sterilized females deposit as many egg-masses as non-sterilized females. In experiment 3, first flight, after 45,000 females had been released, 40 man-hours were spent searching for egg-masses. Only 4 egg-masses were found. The orchard consisted of about 1000 big spindle trees and about 500 newly planted trees, hence there had been at least 30 females per tree. Also during the second flight egg-masses were rarely found. This harmonizes with the fact that at special release spots (experiment 1 and 2 and in chapter 4.2.2) damage was never noticed. In these experiments, it was also much more difficult to find egg-masses, than was expected.

Catches and weather conditions

Temperature has a great impact on the catches, as it is already shown in the figures 7 and 8, 14 °C seems to be about the minimum temperature at which flight occurs (ZECH 1957; DE JONG and MINKS 1968).

In experiments 2 and 3, some data about weather conditions in the open field, were available. In experiment 2 the data were provided by the meteorological station of the Royal Netherlands Meteorological Institute at Zierikzee, at 7 km distance from the orchard. Temperature, average wind velocity and wind direction at 20.00 h were used. In experiment 3 the data were provided by the Department of Physics and Meteorology of the Agricultural University at Wageningen. The same set of data was available, but taken at 19.00 h instead of 20.00 h. Also the minimum nightly temperatures were available. Calculated over the whole trapping periods, there was a better correlation between flight activity and the minimum nightly temperatures than between flight activity and the temperatures at 19.00 h.

A correlation between wind direction and numbers caught outside the orchard could be expected. For even if the moths were neutral with regard to wind direction, a drift with the wind would occur, as the flying moth is suspended in a moving air-mass. However, an influence was not observed. This could have been due to the fact that the traps were not distributed evenly around the orchard.

The influence of rain on the captures was limited, a small shower did not stop the flights. This was also observed by ZECH (1957).

4.2.2. *Sex traps*

When sex traps are used in dispersal studies, the results will be biased by the attraction exerted by the traps. This will especially be the case outside the biotope or outside the flight period, when the traps do not compete with females. Therefore the experiments on dispersal were carried out during the flight periods. On the other hand, the attractant action can be used to measure the maximum distance a male can fly, provided the trap is active over this distance.

4.2.2.1. Maximum distance a male can fly

As *A. orana* is very polyphagous, data about catches of wild moths are of limited value, for one can never be exactly sure where the moth came from. Marked individuals can be used, but rather high numbers are needed when the experiment is carried out during the flight period, because of the competition of the wild females with the traps. Another problem is that the nearest sex trap will have the greatest attraction. Because of these circumstances, the results will be biased.

Data obtained from occasionally placed sex traps in the plain field, showed that males were captured up to distances of 250 m from the nearest orchard, wood or hedgerow. It is interesting to know whether this distance was covered in one sustained flight or interrupted by alightments on plants and the ground. The latter would be expected, from what is known about flight movements in orchards. If moths could be caught after flying over a known stretch of water, sustained flight would be demonstrated. This was tried. A wood near a lake served as a source of moths. In a row perpendicular to the wood sex traps were placed at distances apart of 50 m, up to 440 m. Between the wood and the lake there was a beach 40 m in width. At the border of land and water, the first trap was placed. Two traps were placed in the wood as a control. The traps were baited with living females. The experiment was carried out during the first

5 weeks of the second flight period. The direction of the wind was suitable for trapping on 11 nights. Also the temperatures were sufficiently high. One night 21 males were caught in the first trap, at the border of land and water. Over the water nothing was caught. In these 11 nights the control traps caught 120 males.

To be less dependent on wind direction, another experiment was carried out with marked males. 500 males were released on a small island (100 m^2) in a lake. The distance from the island to the shore varied from 120 to 170 m. Around the water 20 sex traps with pheromone extract were placed. Two males were recaptured, one at a distance of 130 m from the island, the other at a distance of 170 m. Hence it was demonstrated that *A. orana* can cover at least a distance of 120 m in sustained flight.

4.2.2.2. Release-recapture experiment in an orchard

In experiment 3 (4.2.1.4) apart from light traps, sex traps were also used in recapturing moths. The sex traps were only used during the second flight period. In this period 75,500 males and the same number of females were released. In principle the traps were hung in two circles around the orchard (fig. 10) of about 20 traps each. As the traps were hung in hedgerows and other orchards, it was not possible to distribute them evenly. The results are given in fig. 11. The numerators of the fractions denote the numbers of marked males caught, the denominators the numbers of wild males caught. As would be expected, in the inner circle (trap 1–20) more marked moths were caught than in the outer circle (trap 21–40), the ratio being 114 to 24. There is no linear relationship with the circumferences of the circles. The average distance from the orchard is 185 m for the inner circle and 365 m for the outer circle.

Traps 6–10, north of the orchard, have caught about twice as many marked males as traps 16–20, south of the orchard, although the distances to the orchard are about the same. It is not likely that this is due to wind direction, as can be learned from the data about weather conditions (4.2.1.4, table 10). Traps 6–10 were hanging in a hedgerow, where they probably had less competition from wild females than traps 16–20, hanging at the edge of the orchard. This also would explain the differences in catches between traps 1–5 west and 11–15 east of the orchard. Catches east of the orchard are higher, the traps 13,14 and 15 being hung on single trees and there were not many hostplants in the immediate vicinity. The poplars were probably too high to harbour a considerable population of *A. orana* as can be deduced from the very low catches in traps 15 and 43. The traps west of the orchard were hanging in a hedgerow. However it is also possible that the differences were caused by the release of the marked moths. The eastern part of the orchard was newly planted, fig. 5, and there was no windbreak at the east side. The moths were released by walking through the orchard with an open box. It was observed that in the young section of the orchard more moths flew up and headed for some direction, than in the old part, where they alighted much more readily on the large trees. In particular the difference in the catches between traps 1–5 and 11–15 can be explained by the assumption that the movement in an easterly direction was greater than in a

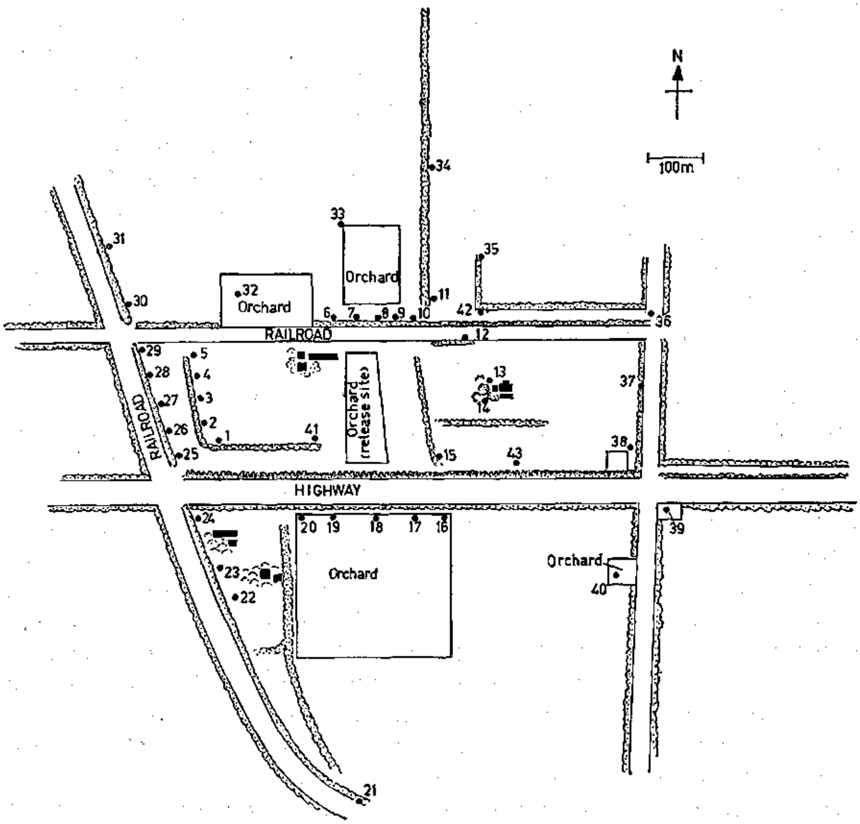

FIG. 10. Distribution of the sex traps around the release orchard.

westerly direction as a result of the disturbance at release.

It is an important question whether the males which left the orchard were distributed evenly over the surrounding fields. Grasses are not found to be hostplants for *A. orana*, so it is likely that the abundance of moths will be low. This is in agreement with the results of light trap captures in and outside the orchard. From this it would be possible to deduce that the moths accumulate in the hedgerows.

This would imply that the proportion of marked males in the catches of the sex traps could have given an indication about the number of males that had left the orchard, if the density of the wild population in the hedgerows had been known. Unfortunately these data are lacking. Incidental captures with light traps in woods and between hedges were always smaller than comparable captures in orchards. This indicates that in these biotopes the population density is lower than in orchards. If it is assumed that in these biotopes population density may reach up to 5000 moths per ha, then, according to the surfaces of these

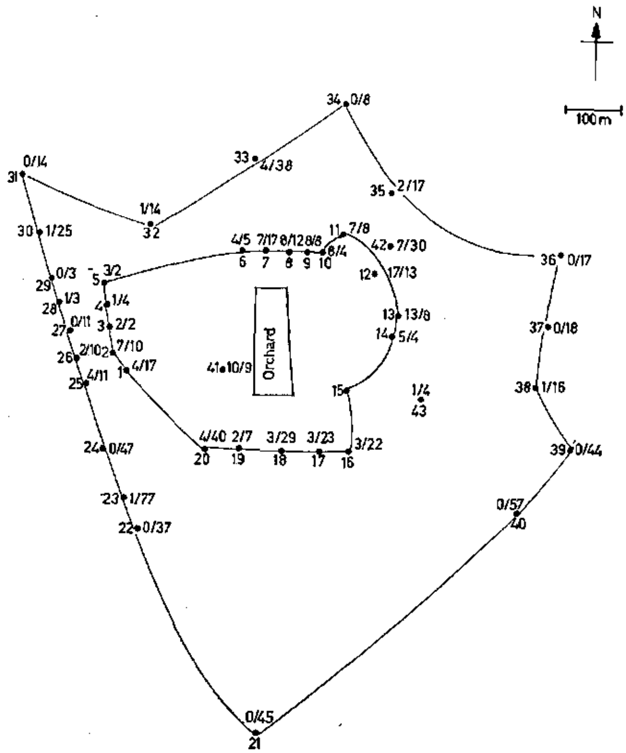

FIG. 11. Diagram of the distribution of the sex traps around the release orchard.
Fractions: numerator = numbers of marked males caught.
denominator = numbers of wild males caught.

biotopes, there will have been, a total of 200 males in the hedgerow west of the orchard (traps 1–5) and also 200 males in the hedgerow north of the orchard (traps 6–10) during the second flight period. In the vegetation of the railroad dike, in the section of traps 22–31, there will have been 4000 wild males. Based on these numbers of wild males, which were rather high with regard to the results of 6–3, the numbers of marked males in these biotopes could be calculated with the aid of the Lincoln-index (LE CREN, 1965). For the hedgerow north of the orchard (traps 6–10) a number of 152 males was calculated. For the hedgerow west of the orchard (traps 1–5) the number was 97 and for the railroad dike 151. It will be evident that this is a very rough estimate. But even when the real numbers are two or three times higher, it can still be concluded that the proportion of males that has left the orchard is low.

4.2.2.3. Sex traps used in recapture experiments, outside orchards

All the traps used were baited with synthetic pheromone. The moths were marked with Calco oil red D. The data about weather conditions were provided

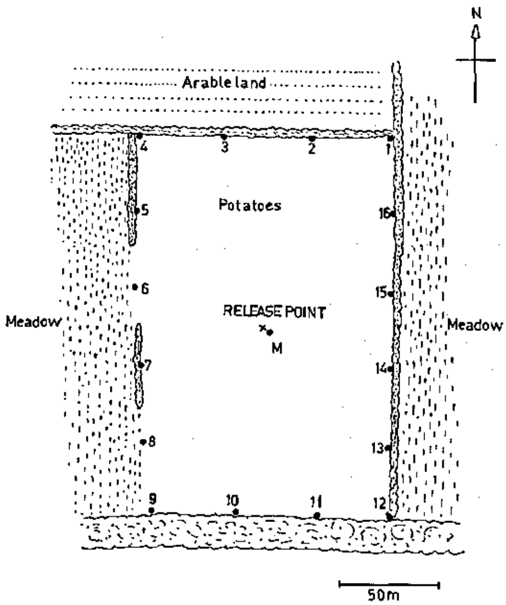

FIG. 12. Position of the traps around the release point, (4.2.2.3.1.)

by the Department of Physics and Meteorology, Agriculture University, Wageningen. They were collected at Wageningen. The data were taken at 09.00. Temperature was recorded at 1.5 m height. All the experiments were carried out within a radius of 20 km from Wageningen.

4.2.2.3.1. Observations on moths crossing an open field

4300 moths, both males and females were released by shaking them gently out of a box on the ground. in the middle of a potato field. The field was surrounded by old hedges, consisting mainly of alder trees (fig. 12). To the west and the south-west there were open spaces. Traps 6 and 8 were suspended from stakes.

TABLE 18. Weather conditions in the period from June 22nd till June 29th.

date June	minimum nightly temperature °C	average wind velocity m/sec.	wind direction
22	12.2	5	SW
23	7.7	9	W
24	11.1	3	SW
25	13.1	3	SSW
26	8.0	2	ESE
27	13.9	2	SE
28	14.1	4	W

TABLE 19. Daily catches of marked males (– denotes: no observations)

date June	trap																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	M
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2	2	5
26	0	1	0	0	0	0	0	1	1	1	3	1	0	8	1	5	2
27	0	2	0	0	1	0	5	0	0	2	2	0	1	9	7	1	5
28	2	1	0	0	0	1	1	2	1	0	0	0	0	1	0	1	0
Total	2	4	0	0	1	1	6	3	2	3	6	2	3	18	10	9	12

TABLE 20. Daily catches of wild males (– denotes: no observations).

date June	trap																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	M
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25	1	0	1	0	1	3	0	0	1	0	1	0	0	0	0	1	0
26	1	1	0	0	1	0	0	1	2	0	3	1	0	0	0	1	0
27	1	0	0	0	1	0	1	0	3	0	2	3	0	0	0	0	0
28	0	0	0	1	0	0	0	0	0	2	1	0	1	0	0	0	0
Total	3	1	1	1	3	3	1	1	6	2	7	4	1	0	0	2	0

The other traps were hung at about 40 m distance from each other in the hedge. One trap (M) was placed at the release spot. The moths were released on June 21st and because of lack of time, the traps were set up the next day. On June 28th they were removed. The results are shown in table 19 and 20.

The highest numbers of marked males were captured in traps 14, 15, 16 and M, most of them being caught on June 26th and 27th. It is possible to correlate this with wind direction, but this does not explain why on June 27th, 5 marked males were captured in trap 7.

It is interesting that trap M has also made some catches over a period of several days. This indicates that not all the moths have flown away to the hedges. In fact, until the end of the experiment, it was easy to find moths still sitting at the release spot.

From the numbers of wild males caught it is possible to deduce that there was also a directed movement of females towards the hedgerows around the field. Nearly all traps caught one or several wild males. Only traps 14 and 15 were an exception, although these traps have captured the highest numbers of marked males. This can be an indication that there were also marked females in the surroundings of these traps. They can have attracted all the wild males that otherwise would have been captured by the traps. This phenomenon was only observed in the hedgerow at the east side of the field. Probably, the females moved to this hedgerow during the first days, when there was a strong westerly wind. It can be assumed that males also moved downwind together with the females, but it is likely that the males captured in traps 14 and 15, were attracted mainly from the release point. The capture of 5 marked males in trap 7 on June 27th remains unexplained. A movement downwind would explain their presence near the trap, but to be captured in a sex trap, a movement upwind is also necessary. It is unlikely that these two opposite movements occurred sucessively during one night.

4.2.2.3.2. Observations on moths leaving a wood, using only sex traps

The purpose of the experiment was to collect data which could be fitted into a mathematical equation concerning dispersal (WOLFENBARGER, 1946, PARIS 1965).

2600 moths, both males and females, were released in the middle of a wood, composed of 20 year old shrubs of willow, elder, hawthorn, alder etc. (120 m in length and 55 m in width). The moths were marked with Calco oil red D. Around the wood, a square kilometer was covered with sex traps, placed in squares with sides of 100 m. In this area of arable land and meadows there were several hedges, but none were linked up with the wood. The minimum distance was 75 m, apart from a row of 50 years old oaks along one side of the wood, which was at 25 m distance.

The traps were baited with synthetic pheromone. They were placed two days after the release, in order not to bias the dispersal right from the beginning, by their attractant action. Seven traps were placed in the wood, trap 1 was near the release point (fig. 13).

Results

No marked males were trapped outside the wood. The catches of marked males inside the wood are shown in table 21.

It was remarkable that no wild males were caught in the wood. The weather conditions were not prohibitive against the capture of wild males, for in some

TABLE 21. Daily catches of marked males in the wood.

date June	trap						
	1	2	3	4	5	6	7
8	4	0	3	0	0	2	0
9	38	0	3	0	0	4	0
10	6	0	0	0	0	14	0
11	4	0	4	1	0	6	0
Total	52	0	10	1	0	26	0

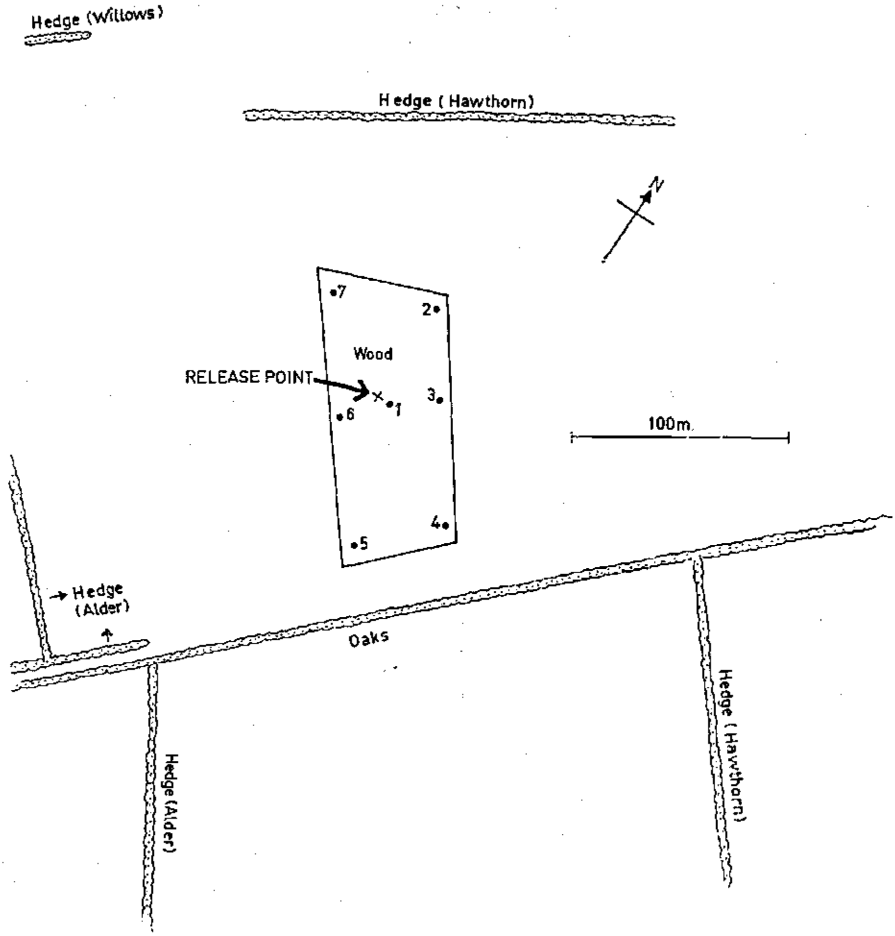

FIG. 13. Position of the traps in the wood, the traps around the wood are not mentioned. (Experiment in 4.2.2.3.2)

TABLE 22. Weather conditions in the period from June 6th till June 12th.

date June	minimum nightly temperature °C	average wind velocity m/sec	wind direction
6	10.3	2	NW
7	7.6	2	SE
8	9.9	5	SW
9	6.7	3	SSE
10	9.6	3	SW
11	7.6	5	SSW

traps outside the wood, several males were captured, even in traps hanging free in a field. It is likely that these males originated predominantly from cherry orchards on the outskirts of the area with traps.

Because no marked males were recaptured outside the wood, the experiment was continued. On June 11th, at a second release, 7500 moths were set free at the same place.

Results

Again, outside the wood, no marked males were captured. The catches inside the wood are shown in table 23.

The numbers of wild males captured in the wood are shown in table 24.

TABLE 23. Daily catches of marked males in the wood. (On the dates not mentioned the traps were not checked)

date June	trap						
	1	2	3	4	5	6	7
12	26	0	11	1	4	4	0
13	0	0	2	0	0	1	1
15	5	2	1	1	5	26	0
19	10	5	7	3	12	21	6
Total	41	7	21	5	21	52	7

TABLE 24. Catches of wild males in the wood. (Same dates as in table 23).

date June	trap						
	1	2	3	4	5	6	7
12	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0
15	0	1	0	0	1	0	0
19	3	2	0	1	0	2	4
Total	3	3	0	1	1	2	4

TABLE 25. Weather conditions in the period from June 12th till June 20th.

date June	minimum nightly temperature °C	average wind velocity m/sec	wind direction
12	7.3	0	
13	3.5	0	
14	8.1	3	NE
15	7.4	2	NE
16	8.6	0	
17	3.9	1	W
18	10.5	7	SSW
19	11.6	4	WSW

The minimum nightly temperatures were low. It is possible that this prevented the males coming out from the wood. In the wood nightly radiation is less, so the temperature will have been higher and movement throughout the wood was therefore possible. On the other hand, in several traps around the wood, even in the plain field, males from other habitats were captured.

In the release-recapture experiments with light traps, strong indications were obtained, that only a few of the moths released leave the biotope. With regard to those results, the numbers released in this experiment were modest. However it is likely that the attractant action of the traps which were nearest to the wood, was maximal. From the fact that no males were captured in these traps, it can be deduced that there were no moths present in the immediate vicinity of these traps and hence also no females, which could have reduced the efficiency of the traps.

The conclusion of this experiment is: again, it has not been possible to demonstrate that dispersal by means of flight involves a large part of a population.

4.2.2.3.3. Observations on moths moving along hedgerows

The results obtained in the previous experiments all point out that the moths do not often fly in open fields. It could be possible that dispersal takes place mainly along hedges. A slight indication for this is obtained in 4.2.2.2, where it looks as if the males moving towards the railroad dike have followed the hedge of alder (fig. 11, traps 41, 1, 2, 25 and 26).

In the following experiment the movements of released moths along hedgerows are studied. The moths were marked with Calco oil red D. The sex traps were baited with synthetic pheromone.

Experiment 1

This experiment was carried out in an alley of poplars, running north-south, 900 m long, with hedgerows on both sides. The hedgerows consisted mainly of hawthorn and alder. In the northern section, an orchard bordered the alley (fig. 14).

The experiment was also used to estimate the population density in the southern section of the alley. For this reason the moths were released homogeneously throughout this section. On June 9th, 2000 moths, males and females were released. The next day, 10 sex traps were placed at equal distance throughout the whole alley (fig. 14).

Results

TABLE 26. Totalized numbers of marked males caught. (Traps operated from June 10th till June 27th).

trap									
1	2	3	4	5	6	7	8	9	10
0	0	0	1	8	4	9	11	13	10

TABLE 27. Totalized numbers of wild males caught. (Traps operated from June 10th till June 27th).

trap									
1	2	3	4	5	6	7	8	9	10
26	35	58	22	23	13	5	0	3	3

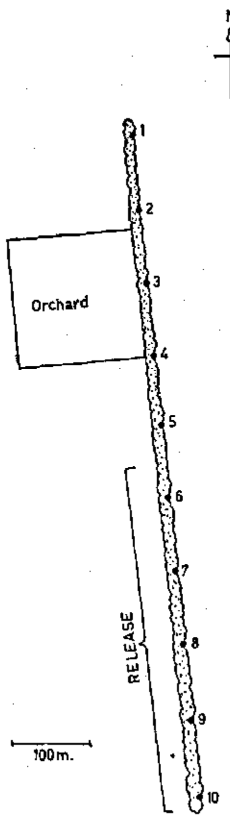

FIG. 14. Distribution of the traps throughout the alley.

It is interesting that the marked males were nearly all recaptured in the section of the alley in which they were released. Most wild males were caught in the other section. It is likely that in the northern section, because of the orchard, the population density of the wild moths was greater than in the southern section, where the population density of the marked moths was the greatest. The fact that this is clearly reflected in the numbers caught in the two sections, indicates that the movement throughout the alley was little.

Experiment 2

12,600 moths, both males and females, were released at a point where several hedgerows came together. Around this point, mainly in the hedgerows, 49 sex traps were placed (fig. 15). The moths were released on June 17th, the traps being in the field from June 19th till June 29th.

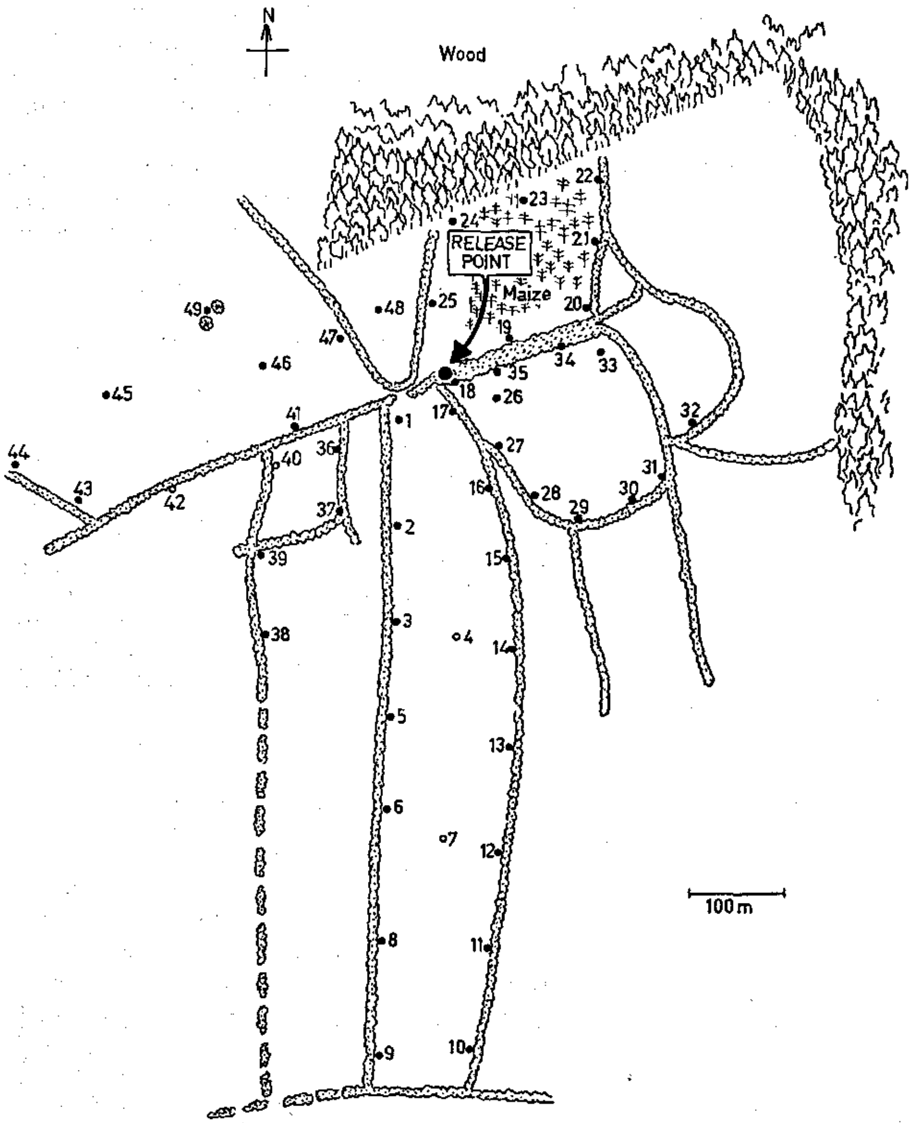

FIG. 15. Distribution of the traps around the release point. (4.2.2.3.3, experiment 2).

Results

The results are shown in table 28, whilst in table 29 the numbers of wild moths captured are given. Only the traps in which marked moths were also captured are mentioned.

The distances at which the moths were recaptured are not impressive. Most moths were recaptured within a radius of 100 m from the release point, for instance traps 1, 17, 18 and 35. On June 29th traps farther away (trap 21 was at 200 m distance) had also caught males. In tabel 30 data about weather conditions are given. It is shown that the nights of June 27th and 28th were rather warm, but a correlation between wind direction and attractant action of these traps at greater distances cannot be observed. However, it is also possible that the males were captured on the evening of June 28th, when there was a calm. Before and after a calm the wind can have different directions.

It is interesting that, although the catches of the wild population were meagre, traps 18, 19, 26, 34, and 35 caught no males at all. It is likely that the presence of wild moths, close to the release point, was obscured by the far greater num-

TABLE 28. Catches of marked males, experiment 2. (On the dates not mentioned the traps were not checked)

date June	trap															
	1	2	15	16	17	18	19	20	21	23	26	27	28	34	35	36
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	1	2	1	0	1	0	0	0	0	0	0	0	0	0	2	1
23	4	0	0	0	1	35	0	0	0	0	0	0	0	0	4	1
26	3	0	0	1	22	3	0	0	0	0	1	1	0	0	15	0
29	2	x	0	x	1	8	3	5	2	1	0	6	2	1	6	0
Total	11	2	1	1	25	46	3	5	2	1	1	7	2	1	27	2

x denotes: trap disappeared.

TABLE 29. Catches of wild males, experiment 2. (Same dates as in table 28).

date June	trap															
	1	2	15	16	17	18	19	20	21	23	26	27	28	34	35	36
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	1	1	1	0	0	0	0	0	2	0	0	0	0	0	1
26	0	0	0	1	0	0	0	0	0	3	0	0	1	0	0	0
29	1	x	2	x	1	0	0	2	1	0	0	5	3	0	0	0
Total	1	1	3	2	1	0	0	2	1	5	0	5	4	0	0	1

x denotes: trap disappeared.

TABLE 30. Weather conditions during experiment 2.

date June	nightly minimum temperature °C	average wind velocity m/sec	wind direction
18	10.5	7	SSW
19	11.6	4	WSW
20	8.2	4	WSW
21	10.9	7	SW
22	12.2	7	SW
23	7.7	9	W
24	11.1	3	SW
25	13.1	3	SSW
26	8.0	2	ESE
27	13.9	2	SE
28	14.1	4	W
29	7.1	0	

bers of moths released, and that the movement from the release point was mainly in an easterly direction, the hedgerow towards the east being much broader than the other hedgerow. It was almost a strip of wood.

The fact that the traps 19 and 34 only caught a few marked males, in comparison to trap 35, cannot be explained. It is possible that it was due to the orientation of the traps. The latter were hanging in trees in a fixed position and could not turn with the wind. It is possible that the orientation of trap 35 towards the release point was better than the orientation of the other traps. Traps close to the release point will have caught marked males out of the immediate vicinity, but it has to be assumed that, depending on wind direction, the attractant action also reached the release point.

Experiment 3

This experiment in fact is a repetition of experiment 2. The moths were released at the same place, but the placing of the sex traps was different, (fig. 16). On August 10th, 5400 moths were released and the next day the traps were positioned. On August 14th, there was another release, 7060 moths being set free.

Results

The results are given in table 31. In table 32 the numbers of wild males caught are shown. Again, only the traps in which marked males were also captured are mentioned.

The distances at which the males were recaptured are a little greater than in experiment 2, but most males were captured within a radius of 200 m from the release point. The total number of males recaptured in this experiment is bigger than in experiment 2, the numbers released were about the same. It is likely that the somewhat greater distances and higher numbers of males recaptured were due to the higher minimum temperatures, which would have enhanced flight activity.

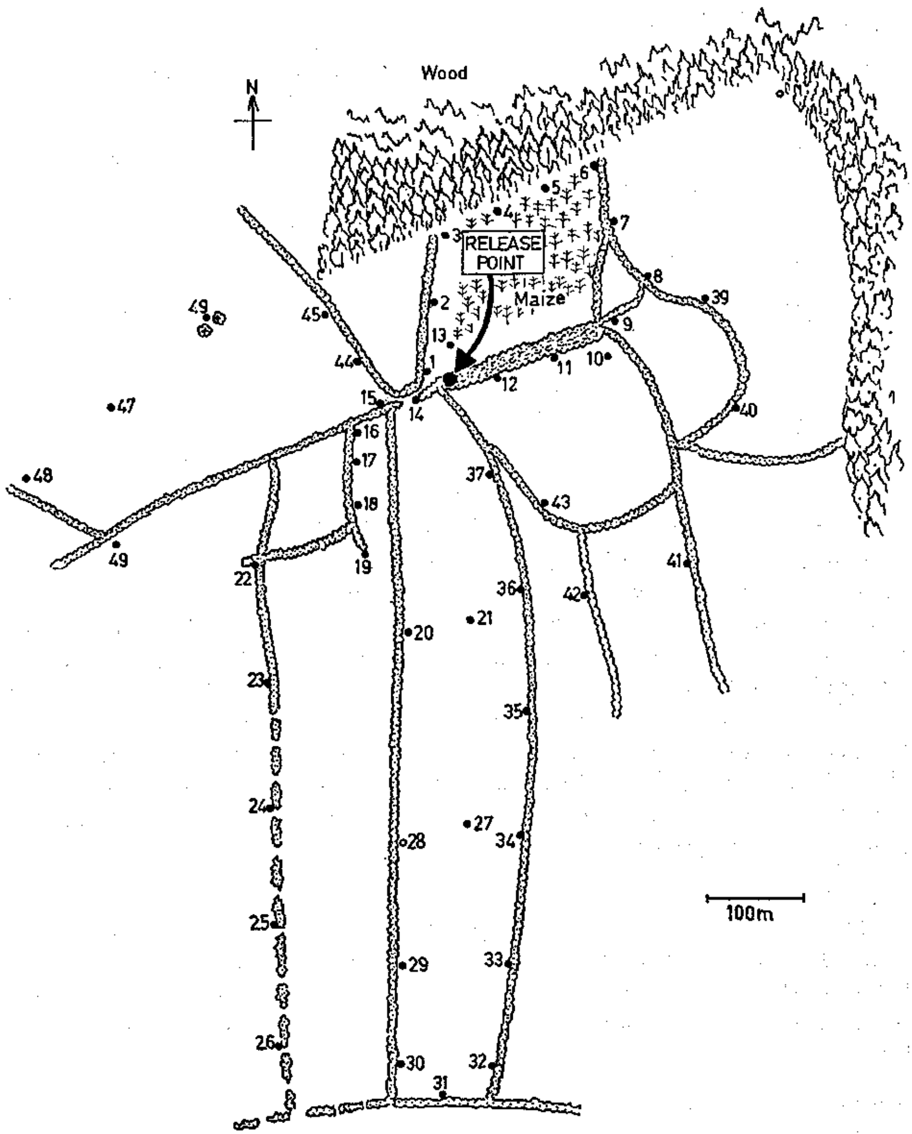

FIG. 16. Distribution of the traps around the release point. (4.2.2.3.3. experiment 3).

It was amazing how few moths were captured from the wild population. It has to be concluded that the population density was very low. However, why trap 13 captured 9 wild males, cannot be explained. This trap was hanging in the open field, close to the release point.

Also the number of marked males recaptured in trap 13 was high. It has to be assumed that these males were attracted directly from the release point. If the

TABLE 31. Catches of marked males, experiment 3. (On the dates not mentioned the traps were not checked).

date August	trap															
	1	2	3	8	9	10	11	12	13	14	15	18	35	36	37	43
14	1	0	0	1	0	1	3	3	34	2	0	0	0	3	25	0
15	0	0	0	0	0	0	0	0	25	0	0	0	0	0	14	0
17	0	1	0	1	1	2	0	0	14	2	0	0	0	2	36	0
22	4	2	1	0	0	0	0	0	0	24	2	1	1	1	0	3
Total	5	3	1	2	1	3	3	3	73	28	2	1	1	6	75	3

TABLE 32. Catches of wild males, experiment 3. (Same dates as in table 31)

date August	trap															
	1	2	3	8	9	10	11	12	13	14	15	18	35	36	37	43
14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
22	0	0	0	0	1	0	0	0	8	0	0	0	3	0	0	1
Total	0	0	0	0	2	0	0	0	9	1	0	0	4	0	0	1

TABLE 33. Weather conditions during experiment 3.

date August	minimum nightly temperature °C	average wind velocity m/sec	wind direction
11	14.5	0	
12	4.0	2	E
13	15.6	0	
14	13.3	0	
15	14.7	2	N
16	10.5	1	NW
17	8.8	3	SW
18	11.3	3	WNW
19	8.3	3	NW
20	10.9	0	
21	13.6	3	NNW
22	10.3	1	NW

numbers caught were the result of the movement of the released moths around the release point, it cannot be explained why this trap caught many more males than other traps at comparable distances (traps 1, 14 and 12). This also applies to the numbers caught in trap 37. However, with regard to the release point, this trap was positioned in the opposite direction. The catches in the traps were examined at August 14th and hence the numbers caught on August 15th were from one night. According to the datum about wind direction (table 33) only trap 13 could have attracted males from the release point.

It seems as if the hypothesis that the high numbers caught in some of the traps are caused by the attractant action of the traps, which as a result of wind direction is exerted at the release point, is questionable. However, if this hypothesis is rejected, it cannot be explained, why the numbers caught are not at the same level in all the traps. Theoretically, when the population density is above a certain threshold value, there cannot be differences between the catches in the traps. In principle a sex trap can be regarded as a normal female, but depending on the amount of pheromone in the bait, it can be a 'super female'. This can be translated in female equivalents. The number of males attracted to the trap will depend on the ratio of the number of female equivalents in the bait to the total number of female equivalents (females and bait) within the area of the trap. The number of males equals the number of females (sex ratio 1:1). Hence above a certain population density, the numbers of males that will be captured are only slightly influenced by the population density. From experience it was known that the number of female equivalents of the sex traps used was small. In practice the sex traps could not be used to measure population densities.

With regard to the numbers caught in traps 13 and 37, it has to be concluded that it is more likely that wind direction registered at 9.00 the next morning, does not correspond with the conditions during the period of flight activity.

What is said about the equality of the catches in different sex traps, does not hold for the catches near a release site. Here a higher level can be reached. Most of the released females were unmated, they will have mated soon after the release. After mating the production of pheromone decreases (MINKS and NOORDINK 1971). Hence after mating there is less competition between the traps and the females than before, as a result of which more males can be captured. In a natural population this does not have such an impact as here there are males and females of all ages.

Experiments 4 and 5

Experiments 4 and 5 are comparable with experiments 2 and 3. The only difference was that they were carried out at other places. As no new data were obtained, the details are not given.

Experiment 4 was carried out during the first flight, 9400 moths were released. In 10 days, 64 males were recaptured. 47 were caught in three traps at 15 m distance from the release point, the other males were trapped scattered over 9 traps, at distances varying from 30 to 175 m.

Experiment 5 was carried out during the second flight, 6500 moths were released. In 7 days, 81 males were recaptured. The point of release was situated at the intersection of two hedgerows. The traps were hanging in the hedges at distances of 25, 100, 175, 250, 325, 400 and 475 m from the release point. The traps at 25 m distance recaptured 78 males, the remaining 3 were caught in the traps at 100 m distance. A positive correlation could be established between catches and prevailing wind direction from traps towards the release point.

4.2.2.4. Discussion

All the experiments were carried out during a flight period. This means that the numbers of marked moths recaptured were proportionally inverse to the numbers of wild moths, which were present within the action radius of the traps. Hence in the more remote traps, less males will have been recaptured, than would have been the case if the experiments had been carried out outside the flight periods. However from the small numbers of wild moths caught in experiments 2 and 3, it may be deduced that the density of the wild population was very low. Nevertheless the distance over which males were recaptured were modest, 250 m was the maximum. With regard to the high numbers caught in some traps in the vicinity of the release point, an influence of wind direction was thought likely. It may be assumed that there was also an attractant action of traps at greater distances.

The extent of the movement around the release point can be deduced from the ratio of marked males to wild males in the catches of the traps in the surroundings of this place, when the influence of wind is removed. For this, only the data from experiment 2 can be used. In experiment 1 the design was unsuitable, in experiment 3 the numbers of wild males caught were very low. In experiment 4 and 5 no results are given, because there was hardly any movement. Also, in experiment 2, there were only a few traps with catches of predominantly marked males, traps 1, 17, 18, 19, 20, 27, 35. In the catches of the other traps the wild males predominated. At distances greater than 200 m, no marked males were recaptured at all. This demonstrates that the extent of movement along or through hedgerows was not great.

To explain the trapping results in 4.2.2.3.1, a displacement together with the wind had to be assumed. In the other experiments, this possibility is not taken into consideration. In 4.2.2.3.1 the moths were released in an open field. It is likely that under these conditions, where the wind velocity is higher and the moths have less shelter, the influence of the wind will be greater than in orchards and hedgerows. In the case of the tortricid *Choristoneura fumiferana* CLEM., it is reported that the moths take off in front of thunderstorms. With convective air streams, they are taken above the vegetation and can be transported with the wind (GREENBANK 1957). The population density of this moth can be many times greater than of *A. orana*. Hence transport of vast hordes is possible. The comparatively low population density of *A. orana* makes it very difficult to prove or to disprove this hypothesis for this species.

Another important point is whether a dispersing male is equally attracted to sex traps as a non-dispersing male. JOHNSON, in his book 'Migration and dispersal of insects by flight' (JOHNSON 1969) brings forward the hypothesis that migrants can be regarded as being peculiar individuals which are relatively undistracted during flight by stimuli that normally lead fairly quickly to the satisfaction of normal appetites. The main stimulus he has in mind is oviposition. However, with regard to *A. orana* any indication of the existence of two types of flight behaviour, a dispersing and a non-dispersing one, has never been found.

To investigate whether there were differences between wild males and released males regarding their reaction to sex traps, two experiments were carried out. Fifth instar larvae were collected in apple orchards. They were reared subsequently in the laboratory on apple leaves. The ensueing male adults were marked by dusting them with the dye Rotor blue (I.C.I. Ltd.). After recapture, dust particles of this dye were made visible by pouring a drop of acetone over the moth on filter-paper.

Equal numbers of marked wild males and males from the laboratory culture, marked with Calco oil red D, were released in the middle of two concentric circles ($r = 8$ m and $r = 16$ m) with 8 sex traps each. The traps were baited with synthetic pheromone. The experiments were carried out in an orchard, in the beginning of a flight period. Outside a flight period, no wild males would have been available. In the first experiment, 55 wild and 55 reared males were released. 5 wild males and 4 reared ones were recaptured. In the second experiment 106 wild and 106 reared males were released. This time 4 wild and 3 reared males were recaptured.

The recaptured numbers are very small, but do not give reason to suppose that the quality of the reared moths was inferior as compared to the wild moths. The reason why so few males were recaptured, was different for the two experiments. During the first experiment, the weather was too cold for much flight activity. During the second experiment, the natural population in the orchard was numerous. This obscured the presence of the released males.

4.3. Aerial transport of larvae

4.3.1. *General*

Dispersal by wind can only take place if the insect has a certain buoyancy in air, or if it can keep itself aloft actively, by means of wings.

A newly hatched larva of *A. orana* has an average weight of about 24 μg. It has a length of about 1.5 mm and a width of about 0.14 mm. The head and the thorax are broader than the abdomen. The specific gravity is about 1. If the larva did not have special appendages to increase its drag when falling, it would fall like a raindrop. A raindrop of this size has an average falling speed of about 3 m per sec. The larva has only a few setae, the only possibility to increase its buoyancy is its thread. The thread has a diameter of 1.8 μ. The specific strength of silk fibres is about 50 kg/mm^2 (de Wilde 1943), this implies that the strength of the thread is about 127 mg. When a larva is hanging on a thread, the force of the wind is exerted mainly on the thread, not on the larva. This may cause the thread to break at the end near the support. There is an inverse relationship between the force of the wind and the length at which the thread breaks.

In a room the influence of the length of the thread on the average falling speed was observed (table 34).

Most of the threads are made by newly hatched larvae, before they have settled on a leaf and have eaten. The time for which they can survive without food, is important for the distance that they can be transported without mortality.

TABLE 34. Average falling speed of a larva with different lengths of thread, as observed in a room.

length of the thread cm	average falling speed cm/sec
20	20
25	16
30	6
50	4

Under laboratory conditions, 20 °C., 70% R.H., they can survive for 6 hours. It is likely that desiccation plays an important rôle. The transport itself probably does not cause much additional desiccation, for the larva moves together with the moving air-mass.

The wide hostplant range is a big advantage for the chances of survival after landing.

4.3.2. *Losses of larvae, other than by means of air currents*

A young ash tree (*Fraxinus* sp.) height 60 cm and a young apple rootstock, height 40 cm were placed separately in a cage made of nylon gause (mesh width 1.4 mm) in the laboratory. A piece of plastic sheet with an egg-mass was pinned on one of the leaves near the top. Four and twelve days after hatching the number of larvae that remained in the trees, was counted and the percentage loss was determined. The data are shown in table 35.

After 12 days the experiment had to be stopped, as the quality of the leaves had seriously deteriorated, as a result of the great number of larvae. The leaves of the apple tree were the worst.

During the counting the positions of the larvae on the trees were also noted. After 4 days the spreading of the larvae, from the leaf with the egg-mass over the whole tree, was already almost complete.

TABLE 35. Numbers of larvae lost (4.3.2).

	elder	apple
Total number of leaflets or leaves on the trees	80	37
Total number of hatched larvae	130	80
Total number of larvae, lost within 4 days	21 (16%)	39 (49%)
Total number of larvae, lost within 12 days	44 (34%)	39 (49%)

4.3.3. *Losses of larvae, including by means of air currents*

The experiments were carried out in the open air. In the first experiment a young ash tree, height 1 m, was placed in the middle of a circle of 20 young alder (*Alnus* sp.) and maple (*Acer* sp.) trees, 1.5 m in height. The diameter of the circle was 2 m. A piece of plastic sheet with an egg-mass was pinned on a leaf near males regarding their reaction to sex traps, two experiments were carried out. Fifth instar larvae were collected in apple orchards. They were reared subsequently in the laboratory on apple leaves. The ensueing male adults were marked by dusting them with the dye Rotor blue (I.C.I. Ltd.). After recapture, dust particles of this dye were made visible by pouring a drop of acetone over the moth on filter-paper.

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TABLE 36. Number of recovered larvae, 4.3.3. First experiment.

tree	number of larvae	tree	number of larvae
1	0	11	10
2	2	12	4
3	0	13	8
4	0	14	0
5	4	15	6
6	2	16	4
7	17	17	0
8	10	18	1
9	18	19	1
10	6	20	2
			Total 95

the top of the ash tree. 140 larvae hatched. After 12 days the number of larvae that had not left the ash tree and the larvae on the surrounding trees were counted. The data are shown in table 36.

On the ash tree, 25 larvae were recovered. This meant that in 12 days, 115 larvae (69%) were no more present on this tree. In the surrounding trees 95 larvae were found. As the experiment was carried out in the second half of July, it is likely that all these larvae originated from the ash tree and were transported by means of wind.

In the second experiment a young poplar tree, 60 cm in height, was placed on a plank above the middle of a well. The well had a diameter of 3.5 m. Around the well young apple rootstocks, 60 cm in height, were placed. The experiment was carried out at the beginning of September. To exclude the possibility that there would already be larvae on the plants, they were sprayed with an insecticide before use. The egg-masses that were used, were obtained from females which were marked with ^{32}P. A piece of plastic sheet with an egg-mass on it was pinned on each of 4 different leaves of the poplar tree. 480 larvae hatched. Three days after hatching the plants were searched off. The data are shown in table 37.

The method of autoradiography (NOORDINK and MINKS 1970) was used to investigate whether the larvae were radio-active or not. Only about half the number of larvae proved to be marked, but the amount of radio-activity found in these larvae was very small. It is likely that all the larvae originated from the egg-masses on the poplar tree, but that in the non-marked larvae the amount of radio-activity was too small to be detected. This is sustained by the fact that there was no difference in age between the marked and the non-marked larvae and the fact that the distribution of the larvae around the well was about the same. That in the north-east section proportionally more non-marked larvae were found, can easily be explained by the assumption that one of the egg-masses was marked less than the others.

It is remarkable that only 1 larva was recovered in the poplar tree.

TABLE 37. Numbers of larvae recovered on the poplar tree and the apple trees around the well.

	radio-active larvae	non-marked larvae	total
poplar	1	0	1
apple, south-east of the well	39	39	78
apple, south-west of the well	14	14	28
apple, north-west of the well	17	20	37
apple, north-east of the well	9	23	32
Total	80	96	176

4.3.4. *Release-recapture experiments with newly-hatched larvae*

Plastic sheets with egg-masses from the laboratory culture, were put in a box with a gauze bottom (mesh width 1 cm). The size of the bottom was 60 cm by 60 cm. The box was fastened between two poles at a height of 2 m. Around the box, 36 sticky boards were placed in three concentric circles of 12 boards each. The boards in fact were wooden frames, 60 cm by 60 cm, covered with nylon gauze (mesh width 1.4 mm). On the gauze, four strokes (50 cm $\times$ 10 cm) of glue (Asepta 1943, Asepta N.V. Delft) were applied. The frames were hung in a vertical position on poles, alternating at heights of 1, 1.5 and 2 m. The height was determined by the distance from the middle of the frame to the ground.

Experiment 1

In the first experiment the radii of the three circles were 5, 15 and 25 m. Over a period of 10 days, 250,000 larvae hatched. The traps were searched off several times during this period, to recover as many larvae as possible. On each occasion the traps had to be cleaned from other insects and fluffs. The totalized results are given in table 38.

TABLE 38. Numbers of larvae recovered (4.3.4, first experiment)

height	radius 5 m.	radius 15 m.	radius 25 m.
2 m.	346	33	7
1.5 m.	572	23	17
1 m.	403	22	16
Total	1321	78	40

TABLE 39. Numbers of larvae recovered (4.3.4, second experiment).

height	radius 15 m.	radius 25 m.	radius 45 m.
2 m.	34	2	1
1.5 m.	35	8	0
1 m.	14	0	0
Total	83	10	1

Experiment 2

In the second experiment the radii of the three circles were 15, 25 and 45 m. Over a period of 7 days, 300,000 larvae hatched. Also this time the traps were searched off several times. The totalized results are given in table 39.

In both experiments the numbers of larvae recovered are small, even in experiment 1, in the traps at 5 m distance.

As the traps cause obstructions in the air movements, it is likely that deviations occur near them, as a result of which less larvae will be sieved out. To diminish the obstruction and to make it possible for the wind to pass through the frame, strokes of glue were applied, instead of covering the whole surface with it.

The traps were an exact copy of those used by CHAMBON to catch larvae of *Cnephasia pumicana* ZELLER (CHAMBON, 1969). He captured substantially higher numbers per trap, than the numbers of larvae of *A. orana* captured in this experiment. From data about population density it could be deduced that the number of larvae of *C. pumicana*, that passed the line of the traps, per unit of length, was considerably smaller than the number of larvae of *A. orana* could have been in this experiment. Hence it had to be concluded that not all the larvae of *A. orana* were transported by wind.

It was observed that under the release box, many larvae were hanging on threads at the same time. They were moved by the wind, and when the threads touched, they stuck to each other and formed clusters. This nullified the parachute action of the thread. It is possible that this abnormal density considerably decreased the chances for aerial transport.

The value of the experiments has been, that in a qualitative way, transport has been demonstrated as far as 45 m, without loss of height.

The experiments were carried out on an almost bare field. By chance, 2 larvae were found on plants (*Rumex* sp. and *Potentilla* sp.) at 65 and 70 m distance. From the size of the larvae and the date they were found it could be deduced that they belonged to the larvae which had been released in the second experiment.

4.3.5. *Geotaxis and Phototaxis*

When newly-hatched larvae are handled, it is noticed immediately that they creep in the direction of a light source (window, lamp) and that they creep upward, if a vial containing larvae is kept vertically. This suggests that the larvae are positively phototactic and negatively geotactic.

The chances for dispersal by wind are enhanced when the larvae spin their threads at the periphery of a tree. Of course this is only of importance for larvae which have not been blown away earlier, from the leaf they hatched on.

In the laboratory seveıal experiments were carried out to discriminate between the two kinds of behaviour. It was demonstrated that there was always a movement towards a light source. A geotactic behaviour could not be discerned. From the work of VERHEYEN, it is known that the distribution of light around the insect has an overruling influence on its locomotion. There is a kind of optimum distribution. If the distribution is not optimal, forced movements can result. Because of this, in studies on geotactic behaviour, the distribution of light has to be kept constant over the whole traject, if the movements of the insect are studied. As this is rather complicated, the easiest solution is to study the movements in total darkness. This was done, but it was observed that total darkness immobilised the larvae for at least two hours. Further experiments have not been carried out.

Also with regard to phototactic behaviour, many precautions have to be taken to avoid forced movements caused by imperfections in the experimental design (VERHEYEN 1958).

The experiments performed are not in conformity with the high standards required to demonstrate phototactic behaviour. Nevertheless, they have yielded interesting results concerning changes in behaviour according to the physiological age of the larvae.

In the first experiment, the influence of light on the direction of the locomotion of the larvae was studied, by placing a support with three glass tubes (length 25 cm, Ø 2 cm) in different positions, in front of a window. Three larvae were placed at one end of a tube, after which this end was closed with a pad of cotton. Twenty four hours later, the number of larvae that had crept out of the tubes was recorded. The results are shown in table 40.

Tube H was in a horizontal position, perpendicular to the plane of the window. The end nearest to the window was open.

Tube V was in a vertical position. The open end was at the top.

Tube S was in a skew position, angle 45°, in a plane perpendicular to the plane of the window. The open end was at the top, away from the window.

TABLE 40. Number of larvae that crept out of the tubes (– denotes: no observation).

	age of larvae in days													
tube	0	1	2	3	4	5	6	7	8	9	10	11	12	13
H	3 3 3	2	2	–	–	0 1	1	1	–	–	–	–	–	2
V	2 2 2	2	0	–	–	2 1	2	3	–	–	–	–	–	1
S	0 0 0	0	0	–	–	2 1	3	1	–	–	–	–	–	1

The larvae used for the experiment were reared at 25 °C. At this temperature the total larval development was completed in about 18 days.

The results strongly suggest that young larvae creep in the direction of the light source, H = 3 and S = 0. Later, the influence of the light on the direction of the movements seems to decrease.

In the second experiment, an apparatus, designed by DE WILDE, for testing phototactic and geotactic responses was used. (ANKERSMIT 1964). In principle it was a perspex box, 37.5 cm long and 7.2 cm wide, inside another, light proof, box. This box could be opened on two opposite sides, by means of slides, to allow the light to enter. The two boxes could be positioned at any angle. At the beginning of the experiment, three larvae were placed in the middle of the box. After 3 minutes it was determined in which direction the larvae had moved. The criterium was a movement over a distance of at least 10 cm, away from or towards the light source. The results are shown in table 41.

There were three positions of the box, horizontal (H), skew (angle 45°) with the light coming from the lower end (L) and skew (angle 45°) with the light coming from the upper end (U).

The larvae for this experiment were reared at 25 °C.

TABLE 41. Movements of the larvae with regard to the light source (4.3.5, second experiment). p = movement towards the light source; d = movement away from the light source; n = movements over less than 10 cm.

position of the box	age of larvae in days															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
H p	3 3	3	–	1	3	1	3 1	1 2	1	1	2 2		–			1
d			–			1	1	1	1			1	–			
n			–	2		1 3	1	2 2 1	1	2	1 1	2	–	3	3	2
L p	3	3 3	–	–	3	–	–		–	–	–		–			–
d			–	–		–	–	3 2	–	–	–		–			–
n			–	–		–	–	1	–	–	–	3	–	3	3	–
U p	3	2	2	1	2	–	2	2	–	–	–		–			–
d			1			–			–	–	–		–			–
n		1		2	1	–	1	1 3	–	–	–	3	–	3	3	–

Like the results of experiment 1, these results also suggest that young larvae are positively phototactic and that this behaviour becomes less pronounced when the larvae are older.

It is interesting to note that the response to light of old larvae was far more sluggish than of young. This is also reflected in the greater numbers of older larvae in category n, in table 41.

4.3.6. *Behaviour of newly-hatched larvae in a wind tunnel*

A young ash tree, 30 cm in height, was placed in a wind tunnel, 3.5 m in length, 60 cm in width and 60 cm in height.* A piece of plastic sheet with an egg-mass on it, was pinned on one of the top leaves. Eight to twelve hours after the larvae had hatched, those that had remained on the tree were counted. Four different air velocities were tested, 0.6, 1.1, 2.0 and 3.0 m per sec. It was expected that there would be a straight relationship between air speed and numbers lost. The results are shown in table 42.

TABLE 42. Number of larvae lost at different air velocities.

air velocity m/sec	total number of egg-masses used	total number of hatched larvae	total number of lost larvae	percentage lost
0.6	7	501	427	85
1.1	10	701	461	66
2.0	10	625	328	52
3.0	8	446	186	42

Contrary to what was expected, there was an inverse relationship between air velocity and numbers lost.

At higher velocities the larvae become immobilised. They hatch, but they do not creep away and stay in the immediate vicinity of the egg-mass. When the fan of the wind tunnel is switched off, they immediately start to move again.

It is not obvious what use the larvae can have of this behaviour. It possibly prevents them from being blown away with very short threads. The shorter the thread, the less the buoyancy in the air. Probably, with a short thread, it is also more difficult to alight on a leaf, as the thread acts like an anchor.

4.3.7. *Discussion*

In a qualitative way, it was demonstrated that aerial transport of newly-hatched larvae takes place. The quantitative aspects were ignored. CHAMBON (1969) placed sticky boards around a wood to study this mode of dispersal in *Cnephasia pumicana*. The density of *A. orana* in orchards is too low to obtain sufficient data by this method.

4.4. OCCURRENCE OF THE SPECIES IN A NEWLY RECLAIMED AREA

As has already been discussed in 4.1, distribution of hibernating larvae with young plants is probably important. But it is doubtful that it is the only mode

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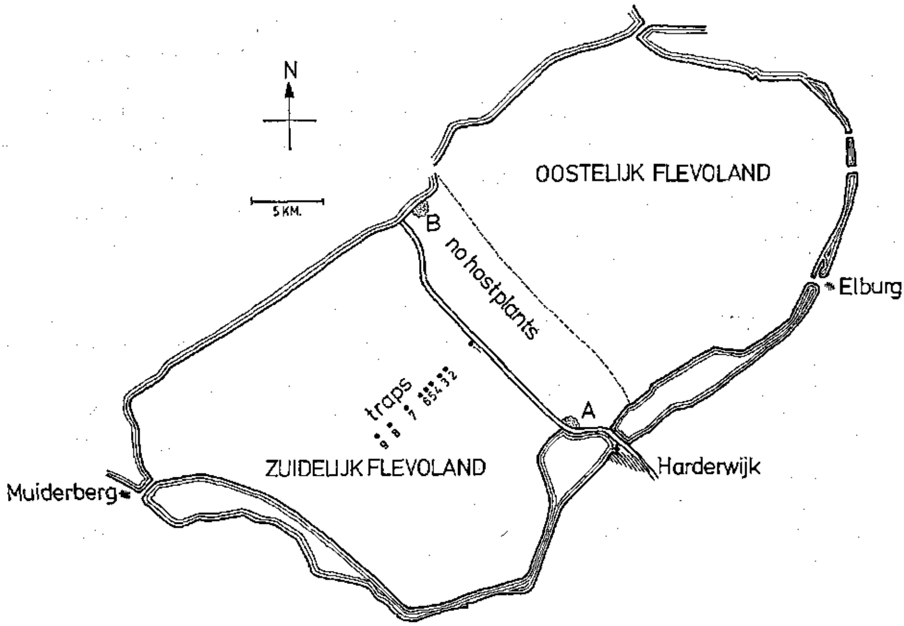

FIG. 17. Position of the traps in the new polder Zuidelijk Flevoland.

of dispersal over large distances. The reclamation of the polders in the former Zuider Zee, offered opportunities for the study of an eventual distribution over areas in which transport by man could be excluded.

In 1968 the newly reclaimed polder Zuidelijk Flevoland became dry. It has a surface area of 540 square kilometers. Together with the polder Oostelijk Flevoland reclaimed in 1957, it almost forms an island (fig. 17). Oostelijk Flevoland is already under cultivation, but in 1970, in the part bounded by Zuidelijk Flevoland, there was still a zone of about 5 km, where no farms had been built. There only were large arable fields. In this zone there were no hostplants for *A. orana*, exept at the dike between the two polders, where there was an occasional willow and at the spots A and B (fig. 17) where there were plantings of trees.

To investigate whether *A. orana* was already present in the new polder in 1970, sex traps baited with living females were placed in Zuidelijk Flevoland. At that time the vegetation consisted mainly of reed (*Phragmites* spp.), reedmace (*Typha* sp.) and willows (*Salix* spp.). The whole vegetation was seed-borne.

The sex traps were placed up to 10 km into the polder (fig. 17). Willows were thought to be the only available hostplant in this area. In table 43, together with the results it is indicated whether or not there were willows in the immediate vicinity. However, the latter is not altogether reliable, as the vegetation reached up to a height of 2.5 m and so it was not easy to detect low shrubs.

TABLE 43. Catches of wild males in Zuidelijk Flevoland.

trap	distance to Oostelijk Flevoland	willows	numbers caught
1	200 m.	yes	3
2	3000 m.	none or sparsely	1
3	3500 m.	none or sparsely	1
4	4500 m.	none or sparsely	0
5	5000 m.	none	0
6	5500 m.	sparsely	0
7	7000 m.	yes	1
8	9000 m.	none	0
9	10000 m.	yes	0

The catches prove that *A. orana* was present in Zuidelijk Flevoland. It is unlikely that the species was introduced there by man, for neither packaging materials nor plants were carried into this area. The hypothetical possibility of transport with osiers, used for the construction of the dike, was not taken into consideration. Even if this had taken place, their offspring would have spread within the vegetation over at least 7 km within 3 years, that is, in 6 generations.

The conclusion is, that even without transport by man, there is a displacement over considerable distances.

The population density of the moths in Zuidelijk Flevoland was low. Sex traps, in general, do not give indications about population density, but when the catches are lower than the catches at comparable places elsewhere, it is likely that the density is low. During the experiment there were also traps in the adjoining polder Oostelijk Flevoland. The average capture in 20 traps, which were hanging in suitable biotopes, was 12 males per trap. If the presence of *A. orana* in Zuidelijk Flevoland is the result of movement of adults from one or several areas of willows at the dike, it has to be concluded that the magnitude of this phenomenon was much greater than would be expected with regard to the results obtained in the previous experiments.

The presence of *A. orana* in the middle of this new polder is explained more readily if aerial transport of larvae is involved. However, we made no observations to test this possibility.

5. VARIABILITY OF RESPONSE TOWARDS DIFFERENT HOSTPLANTS

5.1. GENERAL

In entomological literature the discovery of races or strains is regularly mentioned. But on later consideration, it often turns out that the so-called race can be classified as a closely related species (MAYR 1963). In relation to the population sterilization technique it is of utmost importance that reinfestation from outside the treated area is limited. *A. orana* is frequently found on numerous hostplants other than apple and a large population, capable of reinfestation, could be expected. However, if *A. orana* grown on the other hostplants would have a different response towards apple, in the sense that apple was less preferred, then the importance of these hostplants for reinfestation of the orchards would be reduced. Such difference could originate from modification caused by differences in food or from difference in genetic constitution. With regard to modifications as result of differences in food JERMY (JERMY et al. 1968) reports that modification of food preference has been demonstrated by several workers, but that it was restricted to occur within one ontogenetic phase, mostly the larval phase. According to this author, preservation of the induced preference during the larval phase, into the adult stage was demonstrated with undoubted evidence only by HOVANITZ and CHANG (1963). The idea of races or sub-species of *A. orana* is completely hypothetical. In Europe, no indications of races have ever been found. This is in contrast to Japan, where *A. orana* is known to occur on apple and tea. Under short day conditions the apple strain enters diapause. The tea strain fails to respond in this way, but the rate of development may be somewhat reduced (HONMA 1966). Also, recently some slight morphological differences have been discovered (HONMA 1970). In Japan, China and India the species was known under the name *Adoxophyes fasciata* WLSM.. According to BRADLEY, this was synonymous with *A. orana*, at least in Japan (BRADLEY 1952). The tea strain is now again called *A. fasciata* (NAGATA et al. 1972).

As there were no indications to suggest the existence of strains, it was not easy to decide in which way the two mentioned possibilities should be tested. Negative results of cross-breeding experiments would give evidence, but the problem was on which hostplant the larvae would have to be collected. To find larvae on plants other than apple and pear is very laborious and it could not be expected that there would be a strain for each hostplant.

Another point of issue would be to look for oviposition preference. In this case, the experiments could be made with moths originally obtained from apple. If any preference for one or a group of hostplants could be detected, the next step would be to collect larvae from the non-preferred hostplants and to compare the preference of the ensueing moths with the earlier found preference. It also would be possible to find differences in average growth and development time of larvae of different hostplants. Based on these two possibilities, a few experiments were carried out.

5.2. Search for oviposition preference

Moths from a strain originally obtained from apple, ash (*Fraxinus excelsior*) or privet (*Ligustrum ovalifolium*), were given the choise between several plant species for oviposition. The different strains had been cultured in the laboratory, on a meridic diet, for one to three generations.

To make the experimental conditions as natural as possible, the experiments were carried out outdoors. But in order to find the egg-masses at the spot where the moths were released, it was necessary to use cages.

Each female produces one to five egg-masses, mostly consisting of 30 to 150 eggs. The density of moths had to be very high, to make it possible to compare the density of egg-masses or eggs per unit of plant.

A. orana oviposits very easily in captivity. Eggs are deposited on any smooth surface, e.g. paper, stone, plastics, glass and wood. In the cages, everything possible was done to prevent egg-laying on the cage and on the pots of the plants. The cages were made of fine nylon gauze (mesh width 1.4 mm) attached to the inner side of a wooden frame. The pots were buried in the soil. In this way, only the plants were left as a substrate for oviposition.

Two experiments were carried out. In experiment A, three cages (90 cm × 90 cm × 90 cm) were used at the same time and three plant species were tested, the apple variety James Grieve, ash, and alder (*Alnus glutinosa*). The height of the plants was about 1 m. Where necessary the plants were pruned to fit into the cages. Care was taken not to prune specific parts indiscriminately, such as tips of branches. In spite of the pruning, it was not possible to make the plants equal in shape. Also the size of the leaves was not alike and the numbers of leaves were different. Three plants were placed in different positions in each cage, in order to minimize position effects. Then in each cage, five couples were released and after a week the number of egg-masses produced were counted. In table 44 the total numbers of egg-masses found per tree are shown. Also a correction, according to the total leaf surface, is given. It was not easy to keep the plants in good condition throughout the whole season. Mildew attack on the apple plants could not be prevented. Apple was also attacked more by aphids than the other plant species.

In experiment B, one large cage (8 m × 4 m × 2 m) was used. Apart from the plant species already mentioned in experiment A, poplar (*Populus* × *canadensis*), willow (*Salix alba*) and birch (*Betula alba*) were also used. Where necessary, the plants were pruned to make them all at the same height. 8 plants were used of each species. Care was taken that they were distributed evenly throughout the cage. The first time, with moths from the 'apple strain', 40 couples were released. The second time, with moths from the 'privet strain', 34 couples were released. After a week the number of egg-masses was counted. The results are shown in

Results

TABLE 44. Total number of egg-masses found on the different plant species. Experiment A.

Moths	originally from apple		originally from ash	
	total	corrected total	total	corrected total
apple	34	34	13	13
ash	83	47	56	32
alder	73	49	68	45

TABLE 45. Total and average number of egg-masses found on the different plant species, using moths from the 'apple strain'. Experiment B.

	total	average per plant	corrected average
apple	18	2.3 ± 1.9	1.4
ash	11	1.4 ± 1.3	1.4
alder	8	1 ± 1.8	0.9
willow	5	0.6 ± 0.6	0.7
poplar	1		
birch	20	2.5 ± 1.8	2.7

TABLE 46. Total and average number of egg-masses found on the different plant species, using moths from the 'privet strain'. Experiment B.

	total	average per plant	corrected average
apple	11	1.4 ± 1.2	1.4
ash	9	1.1 ± 0.4	1.1
alder	9	1.1 ± 0.9	1.0
willow	1	0.1	
poplar	5	0.6 ± 0.6	1.1
birch	17	2.1 ± 1.2	2.3

tables 45 and 46. Together with the average, the mean deviation is given. In the corrected average, an allowance is made for the difference in leaf surface between the plant species.

In experiment A, the moths from the 'ash strain' have deposited proportionally fewer egg-masses on apple than the moths from the 'apple strain', but the numbers of egg-masses deposited on ash and alder are of the same range of magnitude (table 44). It is more likely that the difference with the numbers found on apple has to be explained by a deterioration of the apple plants, rather than by the assumption of a difference between the two strains of moths. This deterioration markedly occurred between tests with the 'apple' moths and those with the other origin.

In experiment B, no difference was found between moths originally obtained from apple and originally obtained from privet. It was remarkable that in both cases birch seemed to be preferred.

5.3. Search for differences in rate of development and growth rate of larvae on different plants of the hostplant range

First instar larvae were placed on different plant species. After pupation, the pupae were weighed and the time needed to reach the pupal stage was recorded.

In experiment A, apple rootstock MM VII, alder and ash were used. In experiment B the apple variety Golden Delicious and willow were also used. All plants were in pots, placed at random in a greenhouse. The age of the plants varied from two to four years.

The larvae that were used, were from a strain originally obtained from apple. In experiment A, the strain was reared on diet for 8 generations, in experiment B for 2 generations. The larvae were put on the plants by means of a fine brush, and were distributed evenly over the plant. The ventilation in the greenhouse was switched off, to prevent the larvae moving from one plant to another by means of the silken threads. Also care was taken that the plants did not touch one another.

The pupae were weighed as soon as possible, to avoid loss of weight, due to metabolic activity and evaporation.

Results

Experiment A.

TABLE 47. Duration of the larval development in days, on the different food plants.

food plant	days							average duration		
	25	26	27	28	29	30	31			
ash	0	3	13	20	19	12	7	28.6	(n = 74)	Males
alder	7	31	20	13	6	3	1	26.9	(n = 81)	
apple	8	26	12	7	4	2	0	26.6	(n = 59)	
ash	0	6	6	18	20	16	7	28.8	(n = 73)	Females
alder	9	28	21	17	19	11	5	27.7	(n = 110)	
apple	6	15	11	4	5	3	2	27.1	(n = 46)	

n = number of larvae

In the t-test for the difference between two means, P = 0.05, only the average duration of development of males on alder and apple was not significantly different.

TABLE 48. Average weight in mg of the pupae on the different food plants, ± mean deviation.

foodplant	males	females
ash	19.3 ± 2.3	29.7 ± 3.3
alder	19.6 ± 2.8	29.8 ± 3.7
apple	16.5 ± 2.3	23.5 ± 3.9

Experiment B

TABLE 49. Duration of the larval development in days, on the different foodplants.

foodplant	days														average duration	
	27	28	29	30	31	32	33	34	35	36	37	38	39	over 40		
Golden Delicious	1	9		3	13	3	2		1						30.8	(n = 36) Males
apple rootstock	1	1	1	3	5	5	1	1	1	1		1	5		33.1	(n = 26)
alder	2		2	5	4	1	1					1			30.6	(n = 16)
ash				1		5	2		1				2	15	over 37	(n = 26)
willow	2	3	2	6	11	1	1	2		1		3	1		31.5	(n = 33)
Golden Delicious	1	3	1		8	3	2	2	4						31.6	(n = 24) Females
apple rootstock					3	5	2	1	2	1			2		33.4	(n = 16)
alder				6	1	9	2	3	1			3			32.6	(n = 25)
ash					1	2		1					2	17	over 38	(n = 23)
willow	2		2	3	11	1	1	3		1	1		1	2	31.6*	(n = 26)

* not including two larvae that had not pupated within 40 days.
n = number of individuals
In the t-test for the difference between two means, P = 0.05, none of the differences in the average duration of development proved to be significant. The results on ash were not taken into consideration.

TABLE 50. Average weight in mg of the pupae on the different foodplants.

foodplants	males	females
Golden Delicious	17.5	28.3
apple rootstock	16.9	21.5
alder	20.9	26.7
ash	18.4	26.7
willow	19.1	28.5

Discussion

In experiment A, significant differences in the average time of development were demonstrated, but these differences were very small. They could be the result of a difference in response of the larvae towards the different hostplants, but it is more likely that they were the results of differences in nutritional qualities between the hostplants. In experiment B, the larvae on ash developed slowly, compared to the average developmental time on the other plant species. In the case of the occurrence of races, a similar result could have been expected. But another possibility could be that ash is a less suitable hostplant for *A. orana*. Evidence would have been obtained when larvae from a strain originally obtained from ash had been tested in the same way and had given reversed results with regard to apple and ash. With regard to the possibility that ash is a less suitable hostplant for *A. orana*, no data are available. In the Netherlands ashes are mostly used as alley trees. There is evidence that *A. orana* prefers a lower vegetation. Because boskets of *Fraxinus* spp. are rare, there was no opportunity to estimate population densities on this hostplant, in a way as described in chapter 6. In a crossbreeding experiment with moths from a strain from apple, no abnormalities were observed.

Regarding the weights of the pupae it is remarkable that in experiment A, the average weights on apple differ significantly from the average weights on alder and ash. The same trend can be observed in experiment B. The leaves of apple were in a bad condition compared to the other trees, because of mildew. But if this was the explanation, it is strange that the duration of the larval development was the shortest. Another possibility could be, that a positive correlation between duration of development and weight exists. However, this was not demonstrated in the experiments. Here the reverse was observed, the average weight of the pupae on the same hostplant decreasing, or remaining the same, with increasing duration of development.

It seems that the composition of the nutrients in the food determines average weight and average developmental time by two distinct pathways.

5.4. CROSSING EXPERIMENTS

With sex traps, baited with females from apple, it is possible to catch males in each biotope in which *A. orana* occurs.

This indicates that if races did exist, then the sex pheromone is not very specific. But this does not imply that mating and fertilization also take place. However, cross-breeding between moths, collected as larva on four different hostplants, was possible and the offspring could be reared into F_2. The following crosses and their reciprocals were made.

apple × ash	birch × ash
apple × birch	birch × alder
apple × alder	willow × ash
apple × willow	willow × alder

Because of the limited number of moths, only a few crosses could be made. The number of couples varied from one to five. The number of off-spring was variable as well as the number of successful matings. These experiments only yielded the qualitative evidence that there has been no combination without fertile offspring.

5.5. Discussion

The experiments were too fragmentary to confirm or reject the hypothesis that ecological races or strains of *A. orana* exist. Regarding an application of the population sterilization technique, it can be concluded that no indications were found which would justify the idea that races of *A. orana* exist, which cannot interbreed with the population in apple orchards. It seems probable that immigrating moths or larvae, originating from hosts other than apple, will interfere with this mode of control.

6. POPULATION DENSITIES OUTSIDE ORCHARDS

6.1. General

A quantitative estimate of the population density of *A. orana* outside orchards is necessary, in order to predict the infestation potential other habitats can have for orchards, if the population density within these orchards is controlled at a low level, by means of the population sterilization technique.

To know the population density in other habitats, sampling of fourth and fifth instar larvae would be the best method, but this is extremely laborious. Another possibility is the use of the Lincoln-index (Le Cren 1965) in release-recapture experiments. In the case of *A. orana* this method will give only a very rough estimate, as the adults are short lived and emerge gradually. Moreover nothing is known about the mortality rate of the released moths in the field, but some indications can be obtained.

6.2. Materials and methods

A known number of newly emerged marked moths was released in isolated hedges and small woods, located at a distance of at least 100 m from other habitats. The moths were from the laboratory culture and were marked with Calco oil red D. They were released in the vegetation by walking through it with an open box. The sex ratio was 1:1. The males were recaptured with sex traps, baited with synthetic pheromone. For the calculations with the Lincoln-index, the total numbers caught over a period of about a week were used. The number of released moths will have decreased during this period, because of mortality. Whether the numbers of the wild population also decreased or increased, depended on the interval of the flight period during which the population was estimated. In the calculations this was not taken into consideration, but the estimates were always made during the main part of the flight period. The numbers caught were recorded at least every two days. In the cases where the ratio between numbers of the marked and wild moths caught at the end of the trapping period became divergent from earlier obtained ratios, these data were omitted. In this way, a rough comparison could be made between population densities in different types of habitats.

Also the total number of moths that had been present during the whole flight period, could be estimated, taking into consideration the interval of the flight period during which the estimate was made.

The released moths were not sterilized, hence it was not possible to measure the natural population density at the same place, in both flight periods.

In the description of the places where the moths were released, percentages of the most important plant species are given. These percentages are based on a rough estimate of the total foliage of these plants.

6.3. Estimates during the first flight

1

Wood, 50,000 m². Half of this was *Calluna vulgaris* Salisb. with 40 years old trees of *Pinus silvestris* L.. The other half was a mixed planting of *Larix decidua* Mill., *Prunus serotina* Ehrh. and *Betula* spp.. Age about 20 years.
2280 moths released on 13–6.
14 sex traps hung on 14–6, removed on 21–6.
52 marked males and 8 wild males captured.
Calculated number of wild moths per ha: 70

2

Wood, 3600 m². Mixed planting of *Populus* sp. 30%, *Alnus* sp. 20%, *Quercus* sp. 15%, *Prunus serotina* 10%, *Betula* sp. 10%.
Populus had an age of about 15 years, the other trees were older than 20 years.
600 moths released on 12–6.
8 sex traps hung on 12–6, removed on 21–6.
14 marked males and 8 wild males captured.
Calculated number of wild moths per ha: 900

3a

Wood, 9600 m². Mixed planting of *Prunus serotina* 50%, *Quercus* sp. 35%, *Betula* sp. 10%. Age over 25 years.
1000 moths released on 6–6.
14 sex traps hung on 7–6, removed on 14–6.
44 marked males and 2 wild males captured.
Calculated number of wild moths per ha: 50

3b

Second release in the same wood.
1200 moths released on 20–6.
14 sex traps hung on 21–6, removed 28–6.
43 marked males and 17 wild males captured.
Calculated number of wild moths per ha: 500

4

Wood, 8000 m². Mixed planting of *Quercus* sp. 65%, *Sambucus* sp. 8%, *Betula* sp. 5%, *Alnus* sp. 5%, *Populus* sp. 5%, *Rubus* spp. 3%. Age 85% over 30 years, 15% about 5 years (*Sambucus* and *Rubus*).
1600 moths released on 12–6.
14 sex traps hung on 12–6, removed on 21–6.
26 marked males and 15 wild males captured.
Calculated number of wild moths per ha: 1150

5

Roadside plantings, 17000 m². Mixed planting of *Prunus serotina* 55%, *Quercus* sp. 20%, *Betula* sp. 15%, *Crataegus* sp. 3%, *Robinia* sp. 3%. Age about 20 years.
1700 moths released on 7–6.
15 sex traps hung on 8–6, removed on 16–6.
20 marked males and 28 wild males captured.
Calculated number of wild moths per ha: 1350

6

Roadside plantings, 11500 m². Mixed plantings of *Quercus* spp. 75%, *Rhamnus frangula* L. 10%, *Crataegus* sp. 5%, *Salix* sp. *Alnus* sp. *Sorbus aucuparia* L. and *Populus* sp. together 10%. Age about 15 years.
2100 moths released on 8–6.
14 sex traps hung on 9–6, removed on 16–6.
39 marked males and 30 wild males captured.
Calculated number of wild moths per ha: 1400

7a

Broad hedge, 3800 m². Mixed planting of *Alnus* sp. 40%, *Quercus* sp. 25%, *Rhamnus frangula* 15%, *Sorbus aucuparia* 10%, *Rubus* sp. *Sambucus* sp. and *Viburnum* sp. 5%. Age about 20 years.
900 moths released on 7–6.
5 sex traps hung on 8–6, removed on 16–6.
15 marked males and 0 wild males captured.
Calculated number of wild males per ha: 0

7b

Second release in the same hedge.
750 moths released on 21–6.
6 sex traps hung on 22–6, removed on 28–6.
25 marked males and 40 wild males captured.
Calculated number of wild moths per ha: 2600

8

Hedge, 275 m². *Crataegus* sp. 100%. Age about 15 years.
200 moths released on 12–6.
4 sex traps hung on 12–6, removed on 21–6.
27 marked males and 9 wild males captured.
Calculated number of wild moths per ha: 2400

6.4. Estimates during the second flight

9

Same wood as 1.

2300 moths released on 16–8.
14 sex traps hung on 16–8, removed on 24–8.
33 marked males and 10 wild males captured.
Calculated number of wild moths per ha: 130

10
Wood, 27000 m^2. Mixed planting of *Fagus sylvatica* L. 40%, *Prunus padus* L. 25%, *Robinia* sp. 10%, *Betula* sp. 10%, *Quercus* sp. 5%. Age *P. padus* about 20 years, the other trees over 40 years.
2200 moths released on 18–8.
14 sex traps hung on 18–8, removed on 24–8.
13 marked males and 11 wild males captured.
Calculated number of wild moths per ha: 700

11
Wood, 17000 m^2. Mixed planting of *Fagus sylvatica* 70% older than 40 years and 20% *Rubus* sp.
1000 moths released on 24–8.
9 sex traps hung on 24–8, removed on 1–9.
21 marked males and 13 wild males captured.
Calculated number of wild moths per ha: 350

12
Hedge, 2800 m^2. Mixed planting of *Betula* sp. 50%, *Alnus* sp. 25%, *Acer* sp. 10%, *Quercus* sp. 5%, *Prunus padus* 5%. *Betula* and *Alnus* had an age of about 40 years, the other trees were younger.
900 moths released on 16–8.
8 sex traps hung on 16–8, removed on 24–8.
15 marked males and 12 wild males captured.
Calculated number of wild moths per ha: 1300

13
Railroad dike, 6000 m^2. Mixed planting of *Quercus* sp. 50%, *Rubus* spp. 20%, *Salix* spp. 10%, *Sarothamnus* sp. 5%, *Prunus* spp. 5%. The trees were older than 15 years.
1250 released on 18–8.
6 sex traps hung on 18–8, removed on 28–8.
17 marked males and 22 wild males captured.
Calculated numbers of moths per ha: 2650

14
Lane with old oak and beech trees (over 50 years) and hedges at both roadsides, age about 10 years. 5200 m^2. *Quercus* sp. 35%, *Fagus sylvatica* 35%, *Betula* sp. 10%, *Sorbus aucuparia* 10%.
1250 moths released on 19–8.

8 sex traps hung on 19–8, removed on 28–8.
25 marked males and 9 wild males captured.
Calculated number of moths per ha: 900

15
Lane with old oak (over 40 years) and birch trees (over 20 years) and hedges at both roadsides, age about 10 years. 3300 m². *Quercus* sp. 80%, *Betula* sp. 10%, *Alnus* sp. *Prunus padus*, *Salix* spp. and *Rubus* spp. together 10%.
600 moths released on 16–8.
5 sex traps hung on 16–8, removed on 24–8.
19 marked males and 9 wild males captured.
Calculated number of moths per ha: 850

16
Broad hedge, 3600 m². Mixed planting of *Quercus* sp. 40%, *Betula* sp. 20%, *Alnus* sp. 25%, *Prunus serotina* 5%, *Sorbus aucuparia* 5%. Age about 20 years.
350 moths released on 24–8.
5 sex traps hung on 24–8, removed on 1–9.
19 marked males and 49 wild males captured.
Calculated number of moths per ha: 2600

17
Broad hegde, 8500 m². Mixed planting of *Alnus* sp. 30%, *Prunus serotina* 20%, *Prunus padus* 10%, *Betula* sp. 20%, *Quercus* sp. 10%. Age about 20 years.
1150 moths released on 15–8.
8 sex traps hung on 16–8, removed on 24–8.
9 marked males and 16 wild males captured.
Calculated number of moths per ha: 2450

18
Low willow ground, 12000 m². *Salix* sp. 100%. Age over 20 years.
1500 moths released on 15–8.
8 sex traps hung on 16–8, removed on 25–8.
10 marked males and 5 wild males captured.
Calculated number of moths per ha: 600

19
Hedge, 2400 m². Mixed planting of *Quercus* sp. 50% and *Betula* sp. 50%.
Age 10 to 20 years.
1200 moths released on 17–8.
8 sex traps hung on 17–8, removed on 24–8.
30 marked males and 11 wild males captured.
Calculated number of moths per ha: 1850

20
Hedge, 900 m². *Crataegus* sp. 95% and *Rosa canina* 5%. Age about 15 years.
1000 moths released on 21–8.
6 sex traps hung on 21–8, removed on 29–8.
12 marked males and 10 wild males captured.
Calculated number of wild moths per ha: 8900

21
Hedge, 2000 m². *Crataegus* sp. 100%. Age over 20 years.
1100 moths released on 15–8.
8 sex traps hung on 16–8, removed on 25–8.
11 marked males and 7 wild males captured.
Calculated number of wild moths per ha: 3450

22
Hedge, 3000 m². Mixed planting of *Alnus* sp. 20%, *Rubus* spp. 20%, *Salix* sp. 15%, *Quercus* sp. 10%, *Populus* sp. 10%, *Fraxinus excelsior* L. 10%, *Sambucus* sp. 5%. Age varied from 10 to 30 years.
700 moths released on 21–8.
3 sex traps hung on 21–8, removed on 30–8.
18 marked males and 46 wild males captured.
Calculated number of wild moths per ha: 6000

23
Hedge, 1330 m². *Alnus* sp. 70% about 20 years old and *Rubus* spp. 25%.
650 moths released on 21–8.
3 sex traps hung on 21–8, removed on 30–8.
14 marked males and 68 wild males captured.
Calculated number of wild moths per ha: 23000

24
Hedge, 1540 m². *Alnus* sp. 100%, age about 20 years.
850 moths released on 21–8.
4 sex traps hung on 22–8, removed on 30–8.
20 marked males and 41 wild males captured.
Calculated number of wild moths per ha: 11000

6.5. Discussion

In the estimates, the indications are, that in general, the population density in woods is lower than in hedges.

There are also indications that *Alnus* and *Crataegus* are hostplants on which *A. orana* is the most numerous (compare 14, 15 and 19 with 20, 21, 22, 23 and 24. To obtain an idea of the total number of moths that were present during the whole flight period, the numbers found in the experiments in the first period probably have to be multiplied by 2, and in the second flight period by 2.5. It is impossible to give the average population density in commercial orchards as a comparison, as there are too many differences between the orchards. A rough indication can be obtained from the numbers of larvae that are used as an indication for the kind of control measures, necessary to avoid damage (VAN FRANKENHUYZEN and GRUYS 1971). From this it can be deduced that in a full grown spindle orchard, just after blossoming, numbers of 2000 to 15,000 larvae per ha are quite usual and in the second half of July, 15,000 to 45,000 larvae per ha may occur. Most of these larvae will develop into adults, as mortality is highest in the early instars.

Concerning estimates of population densities, it is of the utmost importance to know the quality of the released moths, in relation to that of the wild ones. In release-recapture experiments, no indications of a difference were found (4.2.2.4.). But in mating experiments, the competitiveness of laboratory cultured males was only 50% (DENLINGER and ANKERSMIT, in preparation). It is possible that, where the quality of the released moths is concerned, an overestimation of the wild population has been made.

It is remarkable that there are such differences between the estimates, in the cases where the population was estimated twice at the same place, 3a and b and 7a and b. A possible explanation would be, that on some hostplants the rate of development of the larvae is slower than on apple (5.3), as a result of which, in some biotopes, the flight period starts later. In other experiments there have been indications that this is a reasonable supposition, but it is difficult to obtain conclusive evidence. The population density has also to be considered: the higher the density, the greater the chances for early and late captures to occur.

7. LABORATORY EXPERIMENTS ON FLIGHT ACTIVITY

7.1. Changes of the sex ratio in the numbers caught in relation to the distance between release point and light trap

The experiments were carried out inside the laboratory, in a corridor. Moths were released at varying distances in front of a light trap. The next day, the recaptured moths were sexed and counted. To avoid the use of a toxic killing agent, which is necessary in the normal type of light trap, a specially designed light trap was used. A light source (Philips, Biosol 250 W) was placed underneath a table (length 150 cm, width 75 cm, height 80 cm). The space between the legs was closed on three sides with wrapping paper. One of the two small sides was left open. The light source was placed against the back of the room underneath the table. In front of the lamp, on the floor, there was a sheet of paper (60 cm × 90 cm) smeared with glue (Asepta 1943, Asepta N.V. Delft). The trap was in use from 18.00 till 8.00. The moths were released by shaking them gently out of a box on the floor. They were released a quarter of an hour before the light source was switched on. Their age varied between 3 and 7 days, sometimes moths of different ages had to be mixed in order to have enough moths to perform the experiment. In the experiments, no indication was found, that age could have an influence on the chances of being recaptured. The numbers of moths caught are given in table 51.

The results show that there is a reduction in the percentage of moths recaptured with increasing distance. A correlation with the decrease of the illumination intensity of the light source is likely. In this case there will be a straight relationship between the root of the percentage of moths recaptured and distance. In fig. 18 these data are plotted against each other. A straight line can be

Table 51. Recaptures at different distances from the release point.

distance to light trap in m	number of males released	percentage of males recaptured	number of females released	percentage of females recaptured
4[a]	102	77	96	69
24	80	41	40	20
40	56	54	102	7
55[b]	453	12	454	9
62[c]	152	24	119	10
75	69	19	69	1
122	80	6	80	0

a = 5 experiments combined
b = 3 experiments combined
c = 2 experiments combined

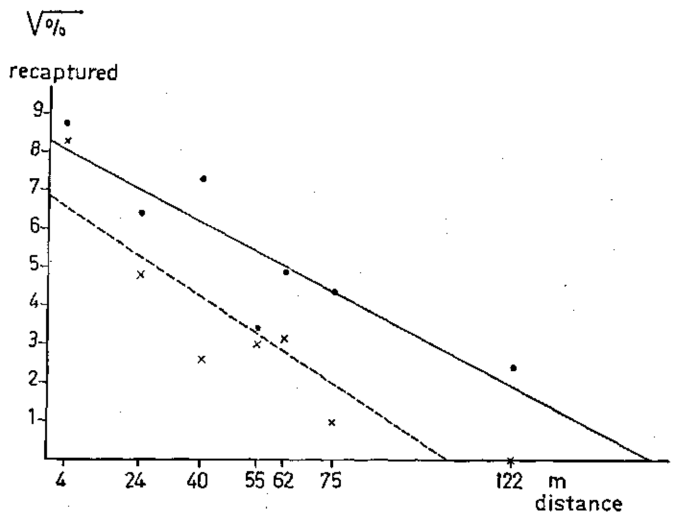

FIG. 18. Numbers of moths recaptured in the corridor, at different distances from the release point. Regression of $\sqrt{\%}$ recaptured moths on distance.
——— males r = −0.52
- - - - females r = −0.65

drawn for both sexes. The regression coefficients for males and females do not differ very much, r males = —0.52 and r females = —0.65. This indicates that the decrease in the percentage of moths recaptured, is proportionally about the same, for males and females. The number of males recaptured is higher than the number of females. Hence the more the moths are attracted over greater distances, the more the females will be outnumbered by the males in the captures.

In the next experiment (7.2) further indications are found that the flight activity is affected by the attractant action of the trap.

7.2. DISTRIBUTION OF MOTHS IN THE CORRIDOR, BETWEEN THE LIGHT TRAP AND THE RELEASE POINT

When the experiments mentioned in 7.1 were carried out during consecutive nights, it was necessary to collect the moths that were not recaptured. The place in the corridor where they were found, was noted. Over almost its whole length, the corridor was the same. On one side, there were windows. To indicate the place of the moths, the corridor was divided into parts of 5 m. At several places there were fire doors. The moths were always released near a closed pair of these doors. This made sure that movement was possible in only one direction. The results are given in table 52.

TABLE 52. Distribution of moths throughout the corridor.

distance from the light trap in m.	number of males experiment				number of females experiment			
	1	2	3	4	1	2	3	4
numbers released	114	163	87	69	170	172	94	69
numbers lost	30	49	9	12	11	11	21	10
in the trap	16	33	28	13	26	16	11	1
0– 5	0	1	0	1	0	1	0	0
5–10	1	2	1	0	2	1	0	0
10–15	4	1	2	2	5	0	2	1
15–20	1	1	1	2	1	1	1	2
20–25	1	2	1	0	3	0	0	0
25–30	0	2	0	0	3	3	0	2
30–35	0	0	1	1	2	1	2	1
35–40	0	3	0	3	2	3	1	1
40–45	7	3	6	1	3	1	0	2
45–50	2	8	0	0	8	4	1	3
50–55	52	58	5	0	104	133	2	0
55–60			33	2			53	1
60–65				1				1
65–70				3				3
70–75				28				41

The results do not show a gradual decrease in numbers, from the release point towards the light trap, as might have been expected. Instead of this, there was an even distribution of a small number of moths, between these points. This implies that either there was no decrease in the percentage of moths recaptured with increase in distance, or that the average flight range of the moths not recaptured, was less than 5 m. The first possibility has to be excluded, according to the results in 7.1. Hence the conclusion has to be that the average flight range was less than 5 m.

A possible explanation for the presence of moths between the release point and the light trap can be given by the assumption that some moths were initially attracted by the light trap, but for some reason escaped from its influence. It might be possible that the windows had some influence on this.

7.3. DIURNAL PERIODS OF FLIGHT ACTIVITY, DIFFERENCES BETWEEN MALES AND FEMALES

At the end of the second flight period, proportionally more females were caught in the light traps than at the beginning of it. If this phenomenon also occurred at the end of the first flight period, it would be likely that there was a causal relationship with the age of the females. But in the first flight period it was not observed. However some reserve has to be taken. During the first flight period, usually small numbers are caught. The phenomenon may be obscured by this.

An alternative hypothesis would be that the males and females have different periods of flight activity. The proportional increase of females in the catches at the end of the second flight period might be the result of an interference between their period of flight activity and the shorter daylength.

To determine the diurnal periods of flight, two types of actographs (flight recorders) were used. The Sylven actograph (SYLVEN, 1958) is a mechanical one. Basically it is a balance. At one end of the arm there is a cellophane cylinder for the moths to alight on and at the other end there is a recording pen pressing against a rotating drum, blackened with soot. It was modified in this respect, that instead of the cylinder a sheet of plastic (6 cm × 15 cm) was used, and instead of the recording pen, a photo-cell with a recorder was substituted.

The Edwards actograph (EDWARDS, 1960) is based upon the electric loads carried by flying insects. It was used without modifications.

The age of the moths used varied from 1 to 8 days. Often the same moths were used during consecutive days. It has not been possible to collect enough data to compare periods of activity of moths of the same age. Because of technical difficulties with the Sylven actograph, the number of days that yielded valuable information was limited. Moreover, this actograph was designed for only one insect. When more insects are used at the same time, there is one inevitable disadvantage. When one of the insects is sitting on the balance, other landings are not recorded. The flight activity of the moths of *A. orana* is low. With one female it was quite usual to observe only three or four landings per hour on the sheet of plastic, during the period of activity. According to the number of landings, the actvity of the males is about three times higher. When only one moth was used, it was sometimes difficult to distinguish between flight movements and records caused by incidental, external events. Therefore, more moths were often used at the same time. The number varied from 1 to 5. This number is noted in the results.

Five different experiments were carried out. Exept in experiment 2, the moths which were used had been reared at 20°C, 70% R.H. and light from 7.00 till 23.30. Experiment 2 was carried out in summer, the moths were reared in the laboratory room itself, without artificial illumination.

Only females which had not mated were used.

In four experiments the Sylven actograph was used. The Edwards actograph was only used in the last experiment.

The results are depicted in diagrams. The black bars represent periods of high activity, the shaded bars represent periods of moderate activity. Incidental flight movements are not noted. For males, high activity means over 24 recorded flight movements per hour and moderate, 12 to 24 per hour. For females over 12 recorded flight movements per hour is already high and 6 to 12 is moderate.

Experiment 1

The experiment was carried out in winter. The actograph was placed in front

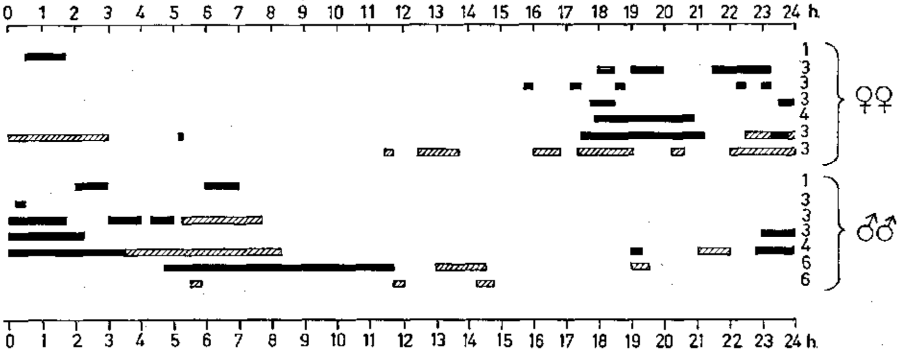

FIG. 19. Diagram of flight activity (7.3, experiment 1). black bar = high activity; shaded bar = moderate activity.

of a window. In the room there was daylight from about 8.30 till 17.00 and additional artificial illumination from 8.30 till 17.30.

The results are shown in fig. 19. The data show that most of the activity of the females took place before 23.00 and most of the activity of the males after 23.00. In fact the females started their activity at the onset of darkness, while the onset of activity of the males coincides with the time at which the dark period started in the rearing room.

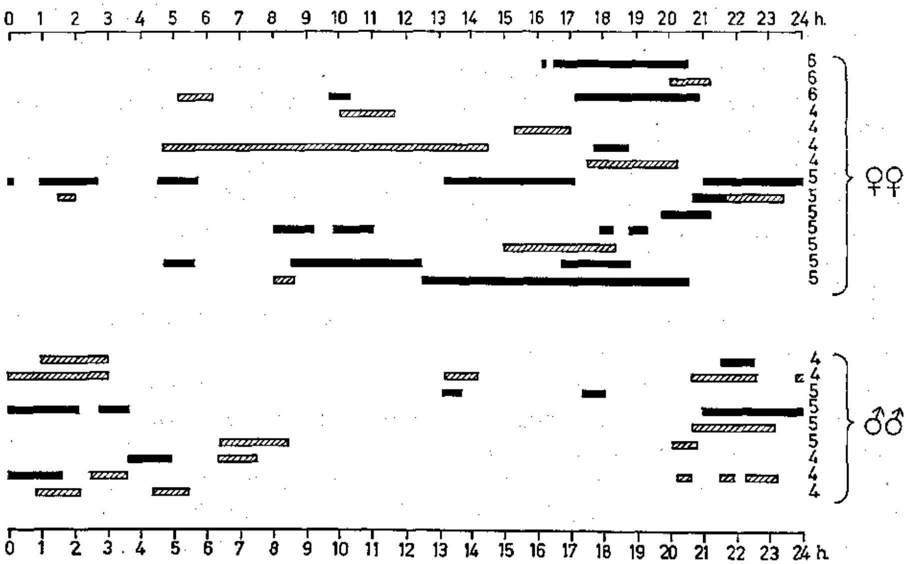

FIG. 20. Diagram of flight activity (7.3, experiment 2). black bar = high activity; shaded bar = moderate activity.

Experiment 2

This experiment was carried out in July, outdoors. There was daylight from about 4.30 to about 21.00. The moths were reared without artificial illumination

The results are shown in fig. 20. The dividing line between the activity of females and males is less clear than in experiment 1. But again it can be said that the period of activity of the males lies later than that of the females. The males started their activity at about 20.30.

Experiment 3

In the previous experiments, it was felt that the absence of control over light conditions was an undesirable circumstance. Therefore in this experiment the actograph was placed in a wooden box (150 cm × 90 cm × 100 cm). The light came from a fluorescent tube (Philips TLD 15W/33) which was controlled by a clock. Light was supplied from 7.00 till 23.30, the same as in the rearing room.

The results are shown in fig. 21, There is not much difference between the period of activity of females and males. There is a slight indication that females start their activity a little earlier. It was remarkable that the males especially demonstrated high activity at the moment the light was switched on.

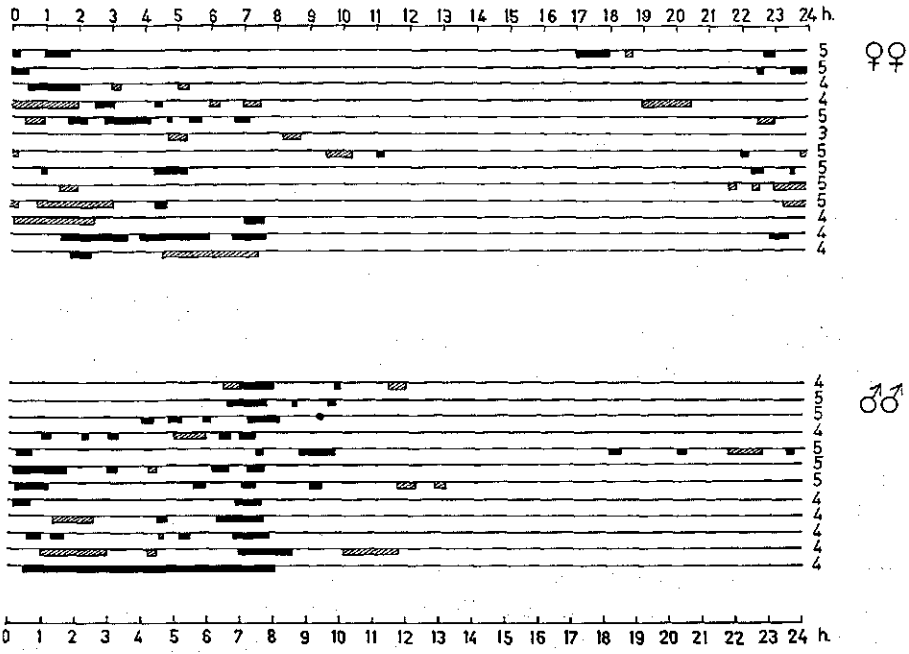

FIG. 21. Diagram of flight activity (7.3, experiment 3). black bar = high activity; shaded bar = moderate activity.

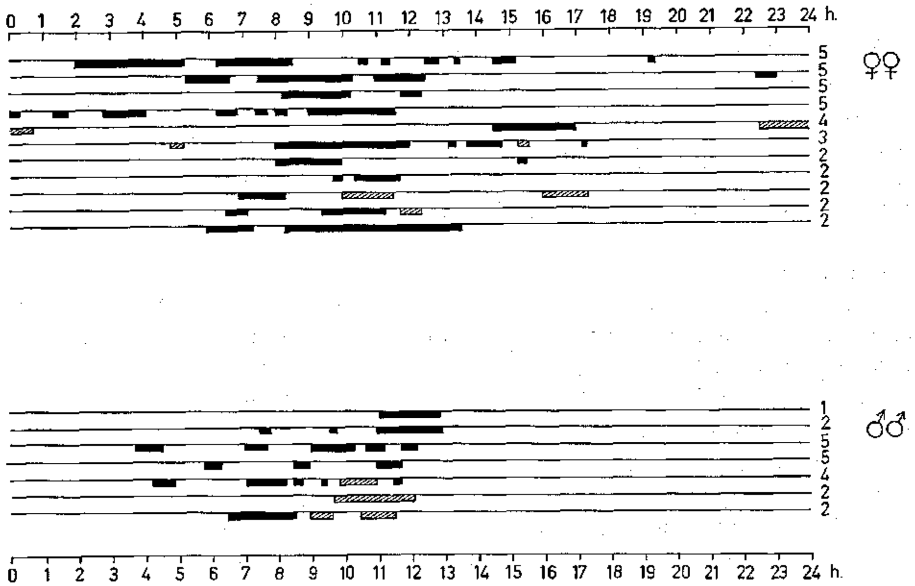

FIG. 22. Diagram of flight activity (7.3, experiment 4). black bar = high activity; shaded bar = moderate activity.

Experiment 4

The only difference from experiment 3 is the time that the light was given. In this experiment there was ligth from 12.00 till 4.30.

The results are given in fig. 22. The period of activity of the males was restricted to the dark period. This was also the case with the females, but here it was less pronounced.

Experiment 5

This experiment was also carried out in the box, but this time the Edwards actograph was used. This experiment can be split up into a and b. In 5a the light was switched on at 7.00 and off at 23.00. In experiment 5b this was also the case but during the dark period there was a faint illumination with a shielded microscope lamp.

5a

The results of this experiment were meagre. The activity was unexpectedly low and again, especially with the males, there was an outburst in activity at 7.00, the moment the light was switched on. Because of the bad results, it was not possible to give the results in the form of a diagram. To show the outburst of activity at 7.00, the distribution of the activity over the day is given for each hour as a percentage of the totalised activity in all the experiments in table 53. Most of the activity between 6.30 and 7.30 took place immediately after 7.00.

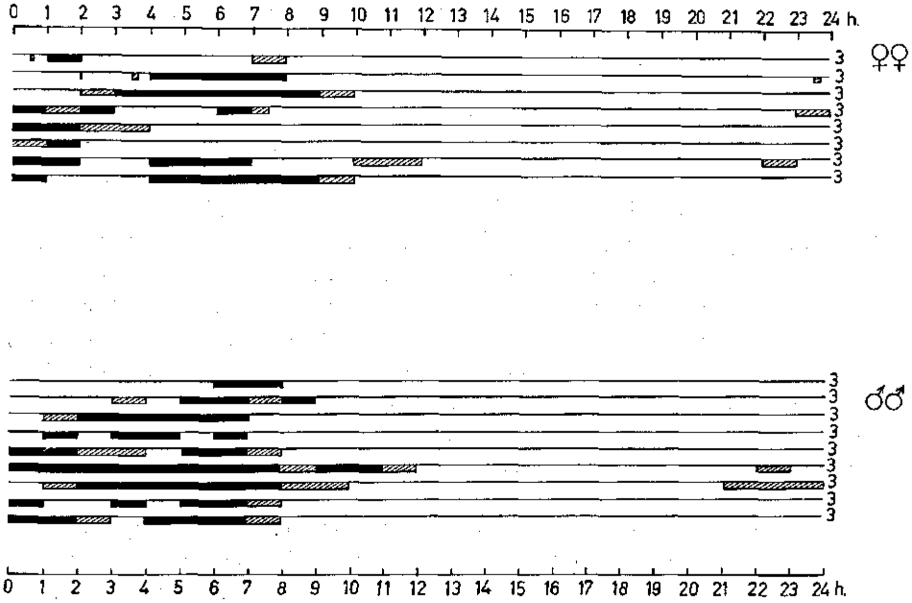

FIG. 23. Diagram of flight activity (7.3, experiment 5b). black bar = high activity; shaded bar = moderate activity.

TABLE 53. Distribution of the activity over the day, per hour, as a percentage of the total activity.

	12	13	14	15	16	17	18	19	20	21	22	23	24	1	2	3	4	5	6	7	8	9	10	11	12
females				2	1	5	2	2	6	9	4	7	13	4	6	5	4	2	12	13	3		2		
males												3	13	6	5	12	13	10	11	18	2	5	1	1	

The results of this experiment raised the idea that complete darkness could interfere with the results. Visual orientation was impossible. Therefore in 5b a faint illumination, less than 1 lux, was given during the dark period.

5b

The results are shown in fig. 23. They are the same as in experiment 3, but more substantial. The outburst of activity by the time the main light switched on, at 7.00, had disappeared.

CONCLUSION

It is likely that the timing of the period of activity is mainly caused by the onset of the dark period. This can be deduced from the results of experiment 4 on the one hand and the results of experiment 1, 3 and 5 on the other hand.

But also, a circadian rhythmicity based on a light-dark rhythm in pre-imaginal stages has to be assumed, in order to explain the difference between females and males in experiment 1 and the fact that sometimes the activity of the females had already started before the light was switched off (experiment 3). Attempts were made to demonstrate the existence of a circadian rhythm by giving either continuous light or continuous darkness. However this failed in both cases. Under these conditions the flight activity was strongly reduced.

The ambiguity in the data obtained, makes it difficult to test the hypothesis that the proportional increase of females in light trap catches at the end of the second flight period is caused by the shortening of the daylength. However, it is the only hypothesis that can explain the fact that this phenomenon does not occur during the first flight. To make this hypothesis operative, in relation to the data obtained, two assumptions have to be made.

a. There is a slight circadian rhythmicity, timed by the light-dark rhythm experienced by the larva (experiment 1).
b. Females are more easily incited to flight activity than males and it is not necessary that it is dark for this to occur (experiment 2 and also 3).

During the first flight in June, the days are longer than the larvae have previously experienced. It is likely that part of the actvity of the females occurs before darkness. For this reason it cannot be recorded by means of light traps.

During the second flight period, in August-September, the days are shorter than the larvae have previously experienced. For the females a smaller part of the period of activity will lie before darkness. Males only fly when it is dark. Hence proportionally more females will be caught at the end of the second flight period.

8. DISCUSSION AND CONCLUSION

The results of the release-recapture experiments with light traps indicate that the dispersal (movements from one biotope to another) was modest. The numbers recaptured outside the biotope in which the moths were released, never exceeded 0.2% of the numbers released, but this figure has not yet been corrected for the fact that the biotope was not entirely surrounded by traps. With this correction, the percentage will be two or three times greater. Also the efficiency of the traps has to be taken into consideration, only a small proportion of the numbers released will be recaptured. In experiment 3, during the second flight (4.2.1.4), 7% of the males released were recaptured inside the orchard. When the number of emigrants is deduced from the numbers recaptured outside the orchard, an allowance for this efficiency has to be made. In 4.2.1.5 it was reasoned that the efficiency of the traps outside the orchard would have been greater than inside.

In 4.2.2.2, based on trapping results with sex traps, it was estimated that about 250 males had left the orchard at the west side. If about the same numbers of males had left the orchard at the other sides, it can be deduced that a total of 1000 males, out of the 75000 released ones, had emigrated. However, this estimate was based on the assumption that the density of wild moths in the biotopes around the orchard, was 5000 moths per ha. With regard to the data in chapter 6 this was very high.

If only 1 or 2 percent of the moths leave an orchard, there has to be something that impedes them from coming out of it. This will mean that at the edge of the orchard, the population density of the moths is the greatest. No indications have been found of this, but it is possible that the shape of the orchards in which the experiments were carried out, was unsuitable to demonstrate this clearly. The orchards were rather narrow. In experiments with *Laspeyresia pomonella*, the phenomenon has been demonstrated (WILDBOLTZ and BAGGIOLINI 1959).

Nothing is known about the direction of the movements of the moths that have left the orchard. In 4.2.1.5 it was alleged that there would be a movement towards hostplants, but it is not known over what distances hostplants can exert an influence. If this influence only works over a short distance, it can be assumed that in an open field, apart from an influence of wind, the movements are at random. In this situation, it would have been useful to have had light traps at different distances from the orchard, to observe a decline in the numbers recaptured with distance, in order to collect data that could be fitted into a regression equation. In this way it would have been possible to calculate the maximum distance of dispersal (WOLFENBARGER 1946, PARIS 1965). Such an experiment has not been carried out. From what is since known, concerning the small numbers recaptured at distances of less than 100 m, it can be deduced that the experiment would have failed. Moreover it is doubtful whether there were relatively many moths, roaming around in the open field, Sex traps in an open field only captured males, when there was a biotope in the vicinity, downwind of the trap.

Also, the results obtained with sex traps indicated that the displacement of adults, from one biotope to another, is limited. The attractant action of the sex traps biases the results in such a way that the distances covered will be enlarged. This can be made of use in experiments to investigate the maximum distance a male can fly. The attractant action is maximal when there is no competition between the trap and females. In 4.2.2.1, in the experiment in which 500 males were released on a small island in a lake, this condition was fulfilled. The distance to the shore varied from 120 to 170 m, only 2 males being recaptured. The other experiments were all carried out during a flight period, and both males and females were released. Nevertheless, in 4.2.2.3.2, it was remarkable that in the traps around the wood no males were recaptured, neither released, nor wild. It is not likely that there would have been females outside the wood, which had competed with the traps. It might be possible that the attractiviness of sex traps, without a hostplant in the immediate vicinity, is reduced, compared to sex traps, or females, within the biotope (BRADER 1969, RAHN 1968), but evidence for this, with regard to *A. orana* has never been found.

In all the release-recapture experiments in hedgerows (4.2.2.3.3), there was competition between the traps and the wild females in the hedgerows in the vicinity of the traps. This would have obscured the presence of the released males to a certain extent. But as the captures of wild moths were small, it may be deduced that the population density of wild moths was not high. With regard to the large numbers of moths released, it can be concluded that the distances over which the males had spread, were modest, 250 m was the maximum distance that could be demonstrated. The fact that some traps had attracted males directly from the release point, was another indication that the movement of the moths had not been very great.

From the experiments with light and sex traps together, it may be concluded that the dispersal of the adults is limited. This conclusion is supported by observations on flight activity in the laboratory rearings, and by the laboratory experiments on flight activity (chapter 7). Apart from a moderate degree of movement throughout the biotope, it may be assumed that for some reason the moths are inclined to stay in the biotope. For the orchard in 4.2.2.2, it was calculated that about 1 to 2 per cent of the males released would have left the orchard. It is likely that this is an average value for the percentage of the population that leaves a biotope of about this shape and surface area. It will be obvious that the ratio surface/circumference of the biotope influences this value.

It is not known what is the average flight range of the moths that have left the biotope. From the results of the males released on the island (4.2.2.1), and the results of the release-recapture experiments in hedgerows (4.2.2.3.3), it may be deduced that the average flight range of the males is at the most less than 200 m, and probably less than 100 m. The maximum distance at which a male was recaptured, was 435 m (4.2.2.2).

Most of the data on dispersal were obtained with laboratory reared moths. The question arises, whether the moths released had the same quality as the wild moths, with regard to flight actvity. Experiments on this subject were not conclusive. There was probably not a great difference, but with regard to the effect of temperature on flight activity, the released moths differed from the wild moths (4.2.1.5). Also with regard to mating a difference was found, the competitiveness of the cultured males was demonstrated to be less (DENLINGER and ANKERSMIT, in preparation).

The studies on the dispersal of the adults only concerned active displacements, but it might be possible that in addition there could also be a more passive displacement. With *Choristoneura fumiferana* CLEM. it is known that the moths become active in front of thunder storms when the atmospheric pressure falls. Within convection streams the moths are carried along, above the tops of the trees and hence they are blown away with the wind (GREENBANK 1957). It cannot be excluded that something similar happens to *A. orana*, but indications of this have never been found.

Concerning the possibilities of aerial transport of newly-hatched larvae by wind, no quantitative data were obtained. Qualitatively it was demonstrated that this mode of dispersal is possible. The extent at which it takes place, will depend very much on the place where the egg-mass is deposited. The more this site is surrounded by vegetation, the more the young larvae will be sieved out. Once a larva is detached from the plant, this mode of dispersal is entirely passive. The large hostplant range will favour the chance of survival.

In 4.4 it was demonstrated that the species had covered a distance of at least 7 km within 6 generations. It is tempting to ascribe this colonisation of a new area to the transport of larvae by wind, but this possibility was not investigated. The only thing that was demonstrated, was that there is dispersal, without the interference of man. However, this does not imply, that transport together with plants or packaging materials could not be important. This mode of dispersal was not studied, because it is likely that when necessary, it can be prevented by special measures.

No evidence was found for the hypothesis that there is variability in response towards different hostplants. But as the experiments were only preliminary, the possibility cannot be altogether excluded, although it is very unlikely that two or more separated populations exist in the fruit growing areas of the Netherlands.

Population estimates were made in several kinds of biotopes. In general, in woods, the population densities were low. In hedgerows they were higher, especially when there was much alder (*Alnus* spp.) or hawthorn (*Crataegus* sp.) present. The highest densities exceeded the average density in commercial orchards.

The aim of these studies was to get an answer to the question of whether an application of the population sterilization technique would be feasible or not. The conclusion is that the experiments have been insufficient to give a decisive answer. Little is known about the quantitative aspects of aerial transport of larvae. It can be suspected that, in relation to the proposed level of control, it will be of minor importance.

Concerning adult dispersal, more information has been obtained. There are strong indications that the adults are rather sluggish and that the average flight range is less than 100 m. Allowing for the few specimens that cover greater distances, it can be assumed that 500 m of open field give a good isolation. The greatest distance at which a male was recaptured, was 435 m.

It is obvious that when the surface of the treated area is increased, the influence of the immigrants is decreased. This also happens, when the level to which the population has to be reduced, is raised.

9. SUMMARY

In apple growing areas, in the Netherlands, *Panonychus ulmi* Koch and *Adoxophyes orana* FvR. are the most important pests. Preliminary experiments had shown that *P. ulmi* could be controlled by predators, but these predators are killed by insecticide sprayings against other pests.

As *A. orana* had already been cultured on an artificial medium, the application of the population sterilization technique was within the realms of possibility. However, the high population density of the species was a disadventage. But if this was counterbalanced by a poor capacity for dispersal, the application of this technique, on a small scale, would be possible. In a simulation model, it was demonstrated that only 100 immigrants per generation per ha, was already too high to make the technique feasible.

Three modes of dispersal could be expected: flight, aerial transport of larvae with wind and transport of larvae together with plants and packaging materials. The last possibility was not investigated, it was assumed that it could be reduced to a great extent by appropriate measures.

Dispersal by flight was studied in release-recapture experiments. The released moths were cultured on a meridic diet. For marking, either ^{32}P or the dye Calco oil red D was added to the medium. In order to recapture the moths, light traps and sex traps were used. The experiments were carried out in several places, an open field, orchards, and hedgerows. The results obtained indicated that the movement from the release points was small. The greatest distance at which a male was recaptured in these experiments was 250 m. Only in the experiment in which 75500 males were released homogeneously throughout an orchard of 1.5 ha, were the distances, at which males were still recovered, somewhat greater, but the maximum distance was 435 m. For this particular experiment it was calculated that about 1 to 2 percent of the males had left the orchard. It is assumed that, for this kind of biotope, this a representative percentage.

In light traps, in general, the numbers of males captured were higher than the numbers of females captured. This could be the result of, either a lower flight activity of the females compared to the males, or an eventual difference in the diurnal flight period of males an females. In laboratory experiments, evidence was obtained for both possibilities.

Concerning larval dispersal by means of wind, only qualitative data were obtained. It was demonstrated that it occurs frequently and that characteristic behaviour elements are involved. The larva spins a silken thread when it drops off from a leaf. This thread can be broken by the force of the wind, exerted on the thread. It subsequently breaks near the end at which it is attached to the leaf. The buoyancy of the larva in the air depends on the length of the thread. It was demonstrated that wind velocities of more than 3 m per sec have an immobilizing effect on the locomotion of the newly-hatched larvae. It is likely

that this behaviour protects the larva against being blown away from the leaf, with a very short thread. Experiments on phototaxis and geotaxis yielded indications that the behaviour of young larvae makes them vulnerable to this mode of dispersal. The behaviour of older larvae was different in this respect. It is likely that, because of the greater weight, the chances for aerial transport of older larvae are reduced. In a qualitative way, aerial transport can be important. At 20 °C and 70% R.H. the newly-hatched larva can survive 6 hours starvation. With an air speed of 2 m per sec, transport over more than 40 km is possible. The quantative aspects will be determined by the vegetation that surrounds the egg-mass. In an orchard, a large proportion of the larvae will be sieved out from the air, by the surrounding trees.

A. orana has a wide hostplant range. In preliminary experiments the possibility of a variability of response towards different hostplants was investigated. No indications were found.

When there is no variability in response towards apple, between *A. orana* in orchards and *A. orana* in other biotopes, it is important to know the population densities in these biotopes, especially in the fruit growing areas, where eventually the population sterilization technique is going to be applied. The population densities were estimated in 23 different places, hedgerows, lanes and woods, by releasing a known number of marked moths into the wild population. From the numbers recaptured by means of sex traps, the number of moths of the wild population was calculated, with the aid of the Lincoln-index. The density in woods was found to be lower than the average population density in orchards, but for some hedgerows higher densities were calculated. The calculated densities were highest when a great part of the hedgerows consisted of alder (*Alnus* spp.) or hawthorn (*Crateagus* sp.).

The conclusion of these studies was, that with regard to the dispersal of the adults, there is a fair chance that the population sterilization technique can be applied on a small scale, when the area is surrounded by a zone of 500 m, free from other populations of *A.orana*. If this is not possible, sterilized adults also have to be released in these populations. In this conclusion, the dispersal of larvae by wind, is not taken into consideration. It is assumed that quantitatively, this mode of dispersal is of minor importance.

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11. SAMENVATTING

De belangrijkste plagen in de Nederlandse fruitteelt worden veroorzaakt door het fruitspint (*Panonychus ulmi* KOCH) en de vruchtbladroller (*Adoxophyes orana* FvR.). Uit voorlopige onderzoekingen is gebleken dat het fruitspint bestreden zou kunnen worden door predatoren, maar dat deze roofvijanden worden gedood door insecticide-bespuitingen tegen andere plagen.

Het feit dat *A. orana* op kunstmatige voedingsbodem kon worden gekweekt, maakte dat een toepassing van de steriele-mannetjestechniek, als bestrijdingsmethode, binnen het bereik van de mogelijkheden lag. De hoge populatiedichtheid vormde echter een bezwaar, maar indien zou blijken, dat de soort zich slechts in geringe mate van de ene biotoop naar de andere verspreidt, zou een toepassing van deze techniek op kleine schaal mogelijk zijn. Met behulp van een simulatie-model is berekend dat 100 immigranten per ha reeds teveel is om de techniek uitvoerbaar te maken. Met betrekking tot verspreiding is er rekening gehouden met drie mogelijkheden: vliegen van de vlinders, verplaatsing van rupsen door de wind en verplaatsing van rupsen met planten en fust. De laatste mogelijkheid is niet verder onderzocht. Het is aannemelijk, dat deze wijze van verspreiding kan worden tegengegaan door het nemen van geschikte maatregelen.

De verspreiding als gevolg van het vliegen van de vlinders is bestudeerd door gemerkte vlinders los te laten en terug te vangen. Alle losgelaten vlinders waren gekweekt op kunstmatige voedingsbodem. Om ze te merken was hier radioactief fosfaat (^{32}P) of de kleurstof Calco oil red D aan toegevoegd. Voor het terugvangen zijn vanglampen en sexvallen gebruikt. De proeven zijn uitgevoerd op verschillende plaatsen: open veld, boomgaarden en hagen. Uit de terugvangsten werd niet de indruk verkregen dat de verspreiding vanuit de loslaatplaats groot zou zijn. De grootste afstand waarop een mannetje is teruggevangen was 250 meter. Alleen in de proef, waarbij evenredig verdeeld over een boomgaard van 1,5 ha 75.500 mannetjes zijn losgelaten, waren de afstanden iets groter, maar de grootste afstand was toch slechts 435 meter. Op grond van de resultaten uit deze laatste proef is berekend, dat 1 à 2 procent van de losgelaten mannetjes de boomgaard heeft verlaten. Het wordt waarschijnlijk geacht dat dit een algemeen percentage is voor dit soort biotoop.

In het algemeen zijn er in de vanglamp verhoudingsgewijs meer mannetjes gevangen dan wijfjes. Dit zou veroorzaakt kunnen zijn door een geringere vliegactiviteit van de wijfjes ten opzichte van de mannetjes, of door een verschil in tijdstip van vliegactiviteit tussen beide sexen. Uit proeven in het laboratorium zijn aanwijzingen voor beide mogelijkheden verkregen.

Wat betreft de verspreiding van jonge rupsen door de wind is aangetoond dat dit plaats vindt. Over de mate waarin, zijn geen gegevens verkregen. Wanneer een rups zich van een blad laat vallen, maakt zij een spinseldraad. Deze draad kan door de krachten die de wind op deze draad uitoefent, worden gebroken. Het breekpunt ligt in de buurt van het aanhechtingspunt op het blad. Het zweefvermogen van de rups in de lucht is afhankelijk van de lengte van de draad. Is de windsnelheid groter dan 3 meter per seconde dan staken de jonge rupsen hun kruipactiviteit vrijwel onmiddellijk nadat ze uit de eispiegel zijn gekropen. Het is aannemelijk, dat de rups door dit gedrag voorkomt dat ze door de wind zou kunnen worden meegevoerd, terwijl de draad erg kort is. Uit proeven in verband met fototaxis en geotaxis zijn karakteristieken uit het gedrag van jonge rupsen bekend geworden die een verspreiding door de wind aannemelijk maken. Het gedrag van oudere rupsen was in dit opzicht min of meer tegengesteld. Ook vanwege hun grotere gewicht is verspreiding van oudere rupsen door de wind minder waarschijnlijk. De afstanden die door deze wijze van verplaatsing kunnen worden afgelegd, zijn aanzienlijk. Bij 20°C en 70% RH kunnen pas uitgekomen rupsen een periode van 6 uur hongeren overleven. Een windsnelheid van 2 meter per seconde zou voldoende zijn om de rupsen over een afstand groter dan 40 km te verplaatsen. De mate waarin dit gebeurt, hangt af van de begroeiing rondom de plaats van de eispiegel. In een boomgaard zal een groot deel van de rupsen opgevangen worden door de omringende bomen.

A. orana heeft een uitgebreide reeks waardplanten. In enkele proeven is geprobeerd verschil in reactie ten opzichte van verschillende waardplanten waar te nemen. Er zijn echter geen aanwijzingen in deze richting gevonden. Indien er, met betrekking tot appel, geen verschillen zijn tussen het gedrag van *A. orana* uit boomgaarden en het gedrag van *A. orana* uit omliggende biotopen, dan is het van belang te weten hoe groot de populatiedichtheid in deze biotopen is. Op 23 verschillende plaatsen: hagen, lanen en bossen is een schatting gemaakt van de populatiedichtheid. Een bekend aantal gemerkte vlinders werd losgelaten in de wilde populatie. Uit de terugvangsten in sex-vallen is, met behulp van de Lincoln-index, het aantal wilde vlinders berekend. Hieruit is gebleken, dat in bossen de populatiedichtheid kleiner was dan de gemiddelde populatiedichtheid in boomgaarden. In verschillende hagen, vooral bij aanwezigheid van els (*Alnus* spp.) of meidoorn (*Crataegus* sp.), was de populatiedichtheid groter dan in boomgaarden.

Op grond van de verkregen gegevens over de verspreiding van de vlinders, mag worden verwacht dat het mogelijk zal zijn om ook op kleine schaal de steriele-mannetjestechniek toe te passen. Het te behandelen gebied zal omgeven moeten zijn door een strook van 500 meter, waarin geen andere populaties van *A. orana* voorkomen. Zijn die er wel, dan moeten ook in deze populaties gesteriliseerde vlinders worden losgelaten. De verspreiding van rupsen door de wind, is niet in aanmerking genomen. Er zijn redenen om aan te nemen, dat deze wijze van verplaatsing slechts weinig zal bijdragen tot het geheel van de verspreiding.

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