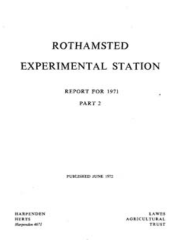
Rothamsted Experimental Station Report for 1971 Part 2


ROTHAMSTED
EXPERIMENTAL STATION
REPORT FOR 1971
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The Wheat Bulb Fly

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Wheat Bulb fly is one of the most serious pests of winter wheat but the damage it does varies greatly from field to field and season to season. Were insecticides not used to control it, the estimated average annual losses in England and Wales would be the equivalent of the average production of 16 000 ha. Protection by insecticides is not complete, and even if they were used on all fields liable to attack the losses would still be the equivalent of about 4500 ha (Potter, Strickland & Bardner, 1965). These figures are small compared with an average annual wheat area of about 800 000 ha, but attacks can be catastrophic locally, especially in districts where wheat is an important crop. In 1953, for example, almost a third of the total wheat acreage in the Isle of Ely had to be re-drilled following Wheat Bulb fly attacks (Gough, 1957).

The eggs are laid during late summer, in fallow soil or in root crops, and potentially damaging infestation can be discovered by sampling these fields for eggs before sowing to winter wheat. Damage can then be minimised by sowing wheat early, or avoided by planting another crop. These alternatives are not always practical; neither is it possible to sample every field. The sudden appearance of dying plants early in spring is often the first indication that the field is infested. Re-sowing is not only costly but unwelcome when the grower is busy with other spring sowings.

Loss of yield is related not only to the number of eggs or larvae, but also to the conditions for plant growth and to the weather both before and during attack. This makes it difficult to forecast the effect on yield of even a measured pest population. Recent research at Rothamsted has been concerned with how infestations cause loss of yield, control of the pest by insecticides and studies on the ecology of all stages of the life cycle, to develop new methods of forecasting and controlling the effects of infestations. Much of the work described here is still unpublished and will be presented in detail elsewhere, and most has been done since the earlier reviews of Long (1960) and Raw (1967).

How Wheat Bulb fly affects growth and subsequent yield

The effects on the yield of attacked crops vary greatly between fields, even with infestations of a similar size, because the survival and growth of the wheat plants depends not only on the ratio of plants to larvae, but also on the stage of growth reached by the plants when they are first attacked by larvae in late January or early February. Early sowing favours well-developed plants that can withstand attack. The growth while the larvae are active is also important. This is slowed by lack of nutrients which makes the crop more susceptible to attack; for example the plots on Broadbalk deficient in potassium usually suffer most, although the numbers of the pest's eggs are similar on all plots (Johnson, Lofty & Cross, 1969).

The growth of attacked and unattacked Cappelle wheat was compared (Bardner, 1968), by preventing egg-laying in some plots, which were covered with plastic sheeting during the summer before sowing, whilst uncovered plots had moderate infestations of 2·7–4·2 million eggs/ha. Wheat sown in October or early November always had two or more shoots when first attacked by larvae and most plants of these plots survived the initial loss of one shoot, few were killed at any stage of the attack and there was little effect on

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yield. By contrast plants in plots sown between late November and early January had only a single shoot when first attacked, and many were killed, yields being lessened by up to 22% compared with similar unattacked plots. Most plants were killed by the initial invasion of newly-hatched larvae, though larvae continue to feed until early May and needed several shoots to complete their development. Plants that survive an initial attack usually produce shoots faster than they can be destroyed by larvae.

Most of the yield loss was because ear-bearing shoots were fewer than an unattacked crop, where they are about 3·7–4·9 million/ha; the number is affected more by the season than the sowing rate. Plants usually produce about twice as many shoots as survive to bear ears and the surplus shoots die after mid-May. The crop therefore has a large reserve of shoots able to compensate for those killed by Wheat Bulb fly, and in these experiments plant and shoot populations in attacked plots were often decreased by 50% or more compared with unattacked plots, yet yield was decreased by only about 20%. Surviving plants not only compensated by producing more ear-bearing shoots than usual but they also had heavier ears containing more and slightly heavier seeds than plants in unattacked plots.

Studies of individual marked plants within an attacked crop (Bardner, Fletcher & Huston, 1969) showed that attacked plants were slow to grow, and the survivors produced fewer shoots and ears than unattacked plants. Those that died were killed by larvae, and not by competition with other plants after the attack had ceased. Only unattacked plants made effective compensatory growth, and in late-sown crops the number of ears per unattacked plant was negatively and linearly correlated with the density of the plant population surviving attack.

Griffiths and Scott (1969) studied the recovery of plants from attack, to determine the best time for applying insecticide sprays. Plants attacked at the single-leaf or early two-leaf stage of growth failed to survive even when the larva was killed by systemic insecticide. Plants in the late two-leaf or in the three-leaf stage survived provided the larva was killed shortly after entering the plant, because at this stage the meristem of the second shoot was well-developed and separate from the meristem at the base of the first shoot which is destroyed first by the larva. There seems to be a difference between the attacks of the Frit fly *Oscinella frit* (L.), which Lowe-Willets (1962) found to stimulate the production of extra shoots in attacked plants, and Wheat Bulb fly, which does not (Bardner & Griffiths, 1967).

This work shows that yield depends more on the number of surviving shoots and plants than on the proportion of shoots or plants attacked. Further, because of compensatory growth, the proportionate loss of yield is less than the proportion of shoots initially attacked, so that when dead and dying shoots become apparent the attack looks more serious than it is.

Rothamsted and the Plant Breeding Institute, Cambridge, collaborated in studying the possibility of selecting varieties resistant to Wheat Bulb fly (Raw, 1967; Lupton & Bingham, 1967). Fifteen varieties of wheat, ten wheat species and ten rye varieties were tested. Varieties with the most side-shoots tolerated and survived attack better than those with few side shoots; unfortunately these varieties also favoured Wheat Bulb fly survival, for there is a positive correlation between the density of shoots and the number of larvae successfully entering plants. Barley, rye and oats exhibit true antibiosis, and once larvae entered the plants, fewer survived than in wheat. At present it seems impracticable to develop commercial wheat varieties with this characteristic, and varieties with many side shoots do not usually yield as well as those with few.

Forecasting the yields of attacked fields. After the eggs hatch, several weeks pass before attacked plants become discoloured and conspicuous. At this time (usually in March),

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a decision has to be made whether to save the crop or to plough it up and resow with a spring cereal. The choice is often difficult and in order to study this problem data from field trials of insecticides were used. These trials are usually sampled in March to assess the degree of control. The results from 11 insecticide trials in the eastern counties were re-examined (Bardner, Maskell & Ross, 1970) and when soil type, wheat variety and sowing date were constant, up to 70% of the variation in yield was accounted for by regressions on yield of measurements made in March of densities of both plants and larvae, enabling yields or losses to be estimated with a standard error of $\pm 0{\cdot}628$ t/ha (Bardner, Maskell & Ross, 1970). Although this would be accurate enough for practical purposes, the technique is too difficult and expensive for general use in forecasting losses in attacked crops. Regressions would have to be developed for each combination of variety, district and sowing date. Also plants would have to be dissected to count larvae. Most growers lack the skill and advisory staff do not have time to examine samples from all attacked fields.

Some fields are sampled for eggs each autumn by ADAS staff. Not all fields can be sampled because of the time and labour needed, and egg populations differ greatly between fields, though the surveys show whether populations are generally large or small that year. Even in fields with large population of eggs it is not certain there will be a serious loss of yield, since so much depends on the growth of plants.

Thus though potential infestations can be measured before sowing and yield predicted after the plants have become infested the cost in time and labour is too great for these particular methods to be applied to most fields at risk.

Chemical control of larvae

(i) Seed dressings. Insecticidal seed dressings do not completely protect against attack by Wheat Bulb fly larvae but are the most convenient and widely used method of control. Since Griffiths (1968) reviewed tests of various insecticides as alternatives to the organochlorines, the Advisory Committee on Pesticides and other Toxic Chemicals (1969) recommended that seed dressings of aldrin, dieldrin and heptachlor should be continuously assessed with a view to withdrawal of these compounds as soon as is practicable. For autumn drillings of winter wheat on land at risk from attack, the farmer may now choose between the organochlorines (dieldrin or γ-BHC as powder dressings, or aldrin liquid dressings) and the organophosphorus insecticides (liquid formulations of chlorfenvinphos or carbophenothion).

(ii) Sprays. Griffiths and Scott (1969) studied the timing of dimethoate sprays against Wheat Bulb fly larvae and the ability of plants to recover from attack. Plant samples taken from a crop sown on 1 November on a site with 11·3 million eggs/ha showed that, by the third week of February, larvae had entered all the plants' shoots. Normally, the crop would have been ploughed in and sown with spring wheat. However, in almost every plant, the bud that would form the first lateral shoot had begun to grow, although it was only visible when the outer leaves were removed. This crop yielded only 1·46 t/ha unsprayed, but 3·89, 3·45, 2·25 and 1·87 t/ha when sprayed on 22 February, 2 March, 9 March and 16 March. Unfortunately, the large increase in yield with early spraying is seldom achieved in commercial practice because the damage is noticed too late. Also, the ground is often too wet for a ground sprayer to be used.

(iii) Laboratory analyses of insecticides. Analyses of dressed seeds, and of samples taken from field experiments on chemical control of Wheat Bulb fly, have helped to explain differences in performance of insecticides in different soils, and reasons for

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occasional failures of chemical treatments. For example, γ-BHC and dieldrin seed dressings are equally effective against Wheat Bulb fly larvae in clay soils but γ-BHC is less effective in peat. γ-BHC and dieldrin persist in both soils, but most of the insecticide is in the top 76 mm of clay soil and in the 76–152 mm layer of the peat. Larvae moving in the surface layers of the peat can enter plants without meeting much insecticide, and this makes control by γ-BHC less effective than by dieldrin because γ-BHC acts mainly by contact in the soil, whereas dieldrin kills many insects after they have entered the plants (Lord, Scott, Jeffs, Griffiths & Maskell, 1967). Griffiths and Scott (1967) showed that the organophosphorus insecticides carbophenothion, chlorfenvinphos or ethion persist in soil and control the pest well, but only very small amounts of these insecticides enter the bulbs of wheat plants, emphasising the need to sow seeds dressed with these materials shallowly.

Seeds dressed commercially with powder insecticides often have much less insecticide than intended (Jeffs, Lord & Tuppen, 1968; Lord, Jeffs & Tuppen, 1971) and the amounts of insecticide on individual seeds treated with liquid insecticides ranges widely. Ways of improving the adherence of powder to seeds are being studied at Rothamsted, and commercial firms are modifying machines for applying liquid seed dressings.

Emergence of adults, feeding and egg development

Flies emerge from pupae between the middle of June and the third week of July, the peak of emergence during this period depending on soil temperatures during larval and pupal development. The ovaries take 4–5 weeks to develop before the eggs are laid, though copulation occurs when females are about two weeks old. There is thus a long pre-oviposition period during which feeding, dispersal and death can affect both where eggs are laid and their number. Very little is known about the movement of flies during this time.

Adult females need a balanced diet; without enough protein they do not develop eggs beyond the earliest stages, and flies die quickly when given protein but not sugar. Only liquids or small particles suspended in liquid can be ingested. On emergence they imbibe water from dew or rain to expand the crop, and thereafter their usual food consists of honey dew from aphids, yeasts, fungal spores and occasional pollen grains, though in the laboratory they will feed on other foods.

During July and August many flies feed almost exclusively on aphid honey dew and on the conidiospores of *Septomyxa affinis* (Sherb.), which grows on dead wheat shoots and leaves near the soil surface and on dead leaves and stems of *Poa annua*, a common weed in winter wheat (Raw *et al.*, 1968). *S. affinis* is widely distributed throughout wheat-growing areas, but the percentage of flies containing them differs between districts and years. The total nitrogen content of *Septomyxa* spores (including the walls, which are probably not digested) is 7% of the dry weight, equivalent to a total protein content of 40% (Holden, 1969).

Other spores found in the crop and or the gut of Wheat Bulb flies are: *Cladosporium*, *Ustilago*, *Alternaria*, *Penicillium*, *Epiococcum*, *Sporobolomyces* and *Erysiphe*. These occur on leaf surfaces and are easily ingested in the fly with water and honey dew. *Coprinus radiata* spores and starch grains have also been found in the crop (Raw *et al.*, 1968; Jones, 1970). Yeasts occur on the leaves of many plants and provide proteins and vitamins. There are always some aphids on green wheat, on grasses in the crop and its verges and on hedge-row trees and shrubs, so there is usually a supply of honey-dew. During June and July crops of winter wheat contain enough food to sustain Wheat Bulb flies. When winter wheat matures the flies depart to other crops such as spring cereals which are less ripe, and usually still have aphids.

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The weights of young male and female flies are similar (males 7·8 ± 0·2 mg, females 7·9 ± 0·2 mg), but the female almost doubles her weight by the time the first batch of eggs is ripe (14·9 ± 0·3 mg). Bigger flies have more ovarioles, and produce more eggs than small ones and the mean is 29 (Jones, 1971). The germarium in each ovariole cuts off oocytes continuously, one egg develops in each oocyte. The eggs in all the ovarioles mature together so that a batch representing one egg from each ovariole can be laid during a brief period. In the laboratory eggs are laid singly or in small groups; and in favourable circumstances a fly can continue to produce batches of ripe eggs for many weeks, and one female laid 11 batches.

When a ripe egg passes into the common oviduct it leaves behind the split intima and the remains of the nurse cells. This follicular relic gradually contracts as the next batch matures and eventually forms a small plug of yellow-brown tissue at the end of the eggs. How many batches of eggs have been laid can be determined by counting the number of follicular relics in the ovarioles. Ovarioles sometimes stop functioning in older flies.

At the beginning of July ovaries of flies contain unripe eggs, but by the last week in July most flies have ripe eggs or torn intimas indicating that they have already laid eggs. During 1970, 25% of the flies swept from crops had laid one batch of eggs, 5% two and only 0·4% three batches of eggs. Amongst flies caught in water traps from mid-July onwards a few had immature ovaries but most had ripe eggs or follicular relics. Thirty-three per cent of all flies caught in water traps had laid one batch, 14% two and 1·0% three. Only a small minority of flies lay more than two batches of eggs.

Dispersal and oviposition behaviour

Raw (1967) suggested that populations of the flies might be localised, most females moving only as far as the nearest oviposition site. This hypothesis is supported by the results of experiments at Whittlesey and Rothamsted (Legowskii, Maskell & Williams, 1968; Bardner, Lofty, Huston & Maskell, 1968).

In 1966, neither winter wheat or rye was sown in an area of about 800 ha near Whittlesey, where Wheat Bulb fly is endemic and attacks are severe; spring wheat or barley was sown instead. Wild grasses (some of which are host plants) were not an important source of adult flies, for few larvae complete their development within them. Most flies present in the area during the summer of 1967 must have moved in from crops outside. In the centre of the area the mean egg count decreased from 308 000/ha in 1966 to 80 000/ha in 1967, but there was no decrease in egg populations of fields adjoining the experimental area. The adult female flies caught in water traps, placed in potato fields within and around the experimental area, were positively correlated with the number of eggs laid in fields containing traps. At Rothamsted dispersal of flies from known emergence sites was followed by placing water traps in fallow land, and similar results were obtained. It seems that most flies, both males and females, do not move much more than 0·4–0·8 km from their emergence site. Severe attacks are improbable at greater distances than this from a previously attacked crop and therefore control of the pest by restrictions on cropping would be possible.

Compensatory growth of an attacked crop would be greatest when unattacked plants are regularly and evenly distributed and least when they occur in patches. It is therefore useful to know the distribution within fields of eggs and larvae and damaged and undamaged plants. This was studied (Bardner & Lofty, 1971), by examining the records of crops sampled at Rothamsted. Samples were obtained either by taking cores 6·4 cm in diameter for the extraction of eggs, or 15 or 30 cm lengths of row for estimations of numbers of larvae, plants and shoots. The results were fitted to the equation

$$\log_{10}(S^2) = \log_{10} a + b \log_{10} m,$$

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where S^2 is the variance, a is a sampling factor, b the 'index of aggregation' characteristic of the species and m is the mean (Taylor, 1961, 1965). Provided the value of the intercept a is small, randomly-distributed populations have $b = 1$, aggregated populations have $b > 1$, and populations with a tendency to regular distributions have $b < 1$. Populations of eggs, larvae and damaged and undamaged plants and shoots had values of b slightly greater than one and were therefore nearly random in their distribution. This information would be useful in the development of additional methods of predicting yield losses.

Flies while laying probably spend only short periods in fallow fields because there is neither cover nor food for them there. It would be reasonable to suppose that the number of eggs would rapidly diminish with distance from the cover of field boundaries, as with the closely-related Cabbage Root fly, which feeds in hedges but is strongly attracted to the odour of brassica plants when laying eggs (Coaker & Finch, 1971). However no such gradient has been detected, though fewer eggs are laid in areas that are in deep shadow during late afternoon and early evening, the time when most eggs are laid (Bardner, Jones & Fletcher, 1972).

Though the antennal receptors of adult females can detect the odour of vegetation such as wheat in which they shelter, they cannot detect soil odour (Bardner, Jones & Coaker, 1969). Because they lay eggs both in fallow land and also below crops such as potatoes where the ground is obscured by vegetation it seems improbable that they can detect suitable sites for laying either by smell or by sight at a distance; more probably they are detected by receptors on the feet or the mouthparts when flies have landed after random flights.

Diseases of adult flies

The proportion of the adult females that survive to lay the first batch of the eggs is unknown. Also little is known about possible causes of death except for disease, which is prevalent in some seasons. Cockbain and Bailey (1967) found microsporidia in a few adults but fungi of the family Entomophthoraecae are of greater importance. Four species have been recorded on Wheat Bulb fly; *Entomophthora muscae* Cohn, *E. dipterigena* Thaxter, *Entomophthora* (*Tarichium*) *hylemyiae* Lakon and *Strongwellsea castrans* Batko and Weiser.

Each year from 1966 to 1970, 100 Wheat Bulb flies were collected each week on Rothamsted Farm from June to August to measure infection by entomophthorous fungi. There were few infected flies except in 1970 when many were infected by *E. muscae*, up to 71% of males and 85% of females. Many females were killed before they laid any eggs. During the previous four seasons, *E. muscae* never infected more than 12% of any sample.

E. dipterigena was found infecting two flies in 1967 and one in 1968. *E.* (*Tarichium*) *hylemyiae* was found in nine flies from only one sample in August 1967 and *S. castrans* in two flies in 1966. Neither has been found since at Rothamsted (Wilding, 1968, 1969, 1970, 1971).

Jones (1970) recorded infection by *E. muscae* of 10%, 0·7% and 19% and by *S. castrans* of 1·5%, 0% and 1% of flies from many sites in England and Scotland in 1967, 1968 and 1969 respectively.

The effect of these sporadic attacks by fungi is difficult to assess. For example, at Rothamsted, on 7 July 1970, 85% of female flies collected in the weekly samples were killed by *E. muscae*, most before they had laid any eggs. Nevertheless on 29 September fallow soil from the site where the flies had been sampled contained 4 million eggs/ha; many more than in 1969. Although there would have been more eggs without the fungus,

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the widespread infection together with all other natural causes of death did not prevent the population from increasing.

Breeding in the laboratory

Wheat Bulb fly has only one generation a year and research on many aspects of its biology would be much quicker if all stages were available at all times of the year, and this has now been made possible. To obtain flies out of season the diapause of the egg must be extended or broken (Way, 1959, 1960). Eggs laid in the laboratory are therefore kept at 20° for 56 days and then at 0° or 6°C for at least three months to break diapause. The developing larvae are kept in pots of wheat seedlings at temperatures between 5 and 15°C with a 12–16-hour illumination for plant growth for four to six weeks and then placed in a cage in the greenhouse to collect emerging flies. The flies are put in a large cage containing dishes with honey water, blood and milk-yeast paste and wheat plants bearing aphids to provide food during the period before eggs are laid. Mature females are placed in lantern-glass breeding-chambers (Bardner & Kenten, 1957) and the eggs collected and kept on nylon over damp vermiculite in a Petri dish at 20°C for 56 days and then at 0°C for at least another 56 days. In this way eggs laid at different periods of the year can be used to infest plants and a supply of eggs accumulated. About 30% of the eggs eventually developed into adult flies.

The survival of eggs in the field

Eggs laid during July and August do not hatch until late January or early February and are thus exposed to predators, parasites and diseases for 5–7 months. Ryan (1967) studied the survival of the eggs and other immature stages of the fly at Rothamsted. Eggs were not parasitised, but many were sterile, the percentage varying between 2 and 14%, depending on the site and season. Fewer than 1% were dead. Cockbain and Bailey (1967) found that some eggs laid in the laboratory by flies collected in the field turn grey or black. A fungus, *Phialophora* sp. (C.M.I. No. 116213) was consistently isolated from these eggs but it was never found in eggs laid in the field, possibly because black eggs are difficult to see. Seventeen per cent of gravid females flies collected in the field laid both *Phialophora*-infected and uninfected eggs; the largest proportion of infected eggs from one female was 35% (Cockbain & Wilding, 1969). Cockbain and Bailey (1967) failed to infect eggs directly with spores or mycelium of the fungus. In the field flies possibly feed on *Phialophora* spores, so infecting eggs before they are laid (Cockbain & Wilding, 1969). Gravid females collected in the field and then fed a spore suspension of *Phialophora* laid significantly more infected eggs than those given other food in one test (Cockbain & Wilding, 1969) though not in another (Cockbain & Bailey, 1967). Some flies reared in the laboratory and fed a spore suspension of *Phialophora* laid both infected and healthy eggs but flies fed other foods laid only healthy ones. Thus the proportion of eggs killed by the fungus remains unknown.

Ryan (1967) found that about 20% of the eggs were eaten by predators during the summer and autumn but none were eaten in December and January, when predators are less active. The predators were chiefly carabid and staphylinid beetles, the same groups that Hughes and Michell (1961) reported as killing 90% of Cabbage Root fly eggs. However the species of predatory fauna on Rothamsted fallows differs from brassica fields; also Wheat Bulb fly eggs are more scattered and perhaps less easily encountered by predators than cabbage root fly eggs, which are aggregated near the host plant. The few eggs eaten by predators may explain why the use of persistent insecticides applied to

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soil has not had adverse effects on the control of Wheat Bulb fly, such as those reported with Cabbage Root fly, which is less susceptible to insecticides than its predators.

Infestation of plants and survival of larvae

On hatching the larvae have considerable difficulty in finding and entering wheat seedlings, and many fewer enter plants than the number of eggs in the surrounding soil (Raw, 1967; Bardner, 1968), often only half are successful in finding plants. The proportion to survive depends on the numbers of shoots present even though there are usually more shoots than eggs. The distance larvae have to travel to reach a plant also affects their survival. Wheat is usually sown in rows about 18 cm apart so that larvae are rarely more than 9 cm from a seedling. Even this distance, however, may be critical for some larvae, because when eggs were placed at different distances from two such rows of seedlings more newly hatched larvae invaded plants in the nearer row, and this number increased the closer the eggs were to the plants (Jones, 1970).

The host-finding process was first investigated by Stokes (1956) who showed that, in the laboratory, newly-hatched larvae assembled in pieces of alginate gel in which seedlings had been grown in preference to pieces of plain gel. She ascribed this behaviour to the properties of an exudate by the wheat plants. It is important to analyse this behaviour and identify the substance concerned, for there is a possibility that it could be used in controlling the pest.

Stokes' experiments were repeated. Significantly more larvae were found in the wheat gel than in the plain gel. However, when larvae were removed as soon as they touched either gel there was no significant difference between gels as measured by the number of contacts. The substance exuded by wheat plants therefore acts as an 'arrestant' (Dethier, 1960), not as an attractant, as suggested by Long (1958). Oat seedlings tested similarly did not arrest the larvae.

The tests were modified to examine extracts instead of exudates. These were prepared by crushing the stems of seedlings with water or water/methanol mixtures in a stainless steel ball mill, filtering the resulting mass through a sintered glass funnel, centrifuging, and finally concentrating the liquid in a rotary film ovaporator. They were tested for their effects on Wheat Bulb fly larvae by pipetting 5 μl on to the centre of a filter paper. Individual larvae on spots of wheat extract on filter paper turned more frequently when they reached the edge of the spot; this behaviour kept the larvae within the area of the wheat extract.

Extracts of oats (which are not host plants) did not arrest the larvae. When oats and wheat extracts were combined the arrestant effect of wheat was decreased even when allowance was made for the effect of dilution. This suggests that oats contain a factor that repels Wheat Bulb fly larvae, or blocks the insects' means of detecting the wheat arrestant, or chemically affects the arrestant. Two insect repellents, deet (*N,N*-diethyl-*m*-toluamide) and 'MGK11' (2,3 : 4,5-*bis*(2-butylene)tetrahydro-2-furaldehyde) also decrease the arrestancy of wheat extract.

Attempts are being made to isolate and identify the 'wheat factor' and the 'oats factor', using plant extracts. The arrestant wheat factor is most soluble in water and methanol, and slightly soluble in acetone and ether. When partitioned between water and ether, or water and ethyl acetate, the activity remains in the aqueous part. The arrestant factor is absorbed by an acid exchange resin but not by an alkali exchange resin, suggesting a polar nature. It is stable to heat *in vacuo* and involatile. The activity is not affected by acid and alkaline hydrolysis, but is diminished by mild oxidation and reduction, and destroyed by heating in air between 150–260°C. This and other evidence suggests that the arrestant factor is probably either a sugar or a glycoside.

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The oats factor is also most soluble in water and methanol. However, unlike the wheat arrestant, it can be removed from aqueous solution by continuous ether extraction. It seems to be as stable and involatile as the wheat arrestant.

Larvae usually avoid shoots that are already infested, but it is not known whether infestation affects the secretion of the arrestant, or whether the arrestant is affected by either age of the shoot or the wheat variety (Scott & Lord, 1965, 1966; Scott & Janes, 1967; Griffiths & Scott, 1968; Scott & Calam, 1969, 1970; Scott, Griffiths & Greenway, 1971).

Many larvae die after hatching and before entering plants; there is also a considerable decrease in larval numbers (up to 36%) during the course of the attacks (Ryan, 1967).

Predators, it seems, do not kill many larvae, for when barriers excluded predators from small plots of wheat the number of larvae in protected and unprotected plots was similar. Occasionally more than one larvae infests the same shoot and if this occurs only one will survive. Ryan (1967) found that only about 1% of larvae died from this cause. He did not find any parasitised larvae, and diseased ones did not exceed 5% of the total population. Both live and dead larvae sometimes have brown necrotic spots, but no pathogenic organism has been invariably associated with this condition (Cockbain & Bailey, 1967; Cockbain & Wilding, 1968), although Hamid (1966) produced such symptoms in two larvae by feeding them a gram-negative rod-shaped bacterium.

Bacillus thuringiensis does not attack Wheat Bulb fly larvae in nature but a concentrated commercial preparation of this pathogen (applied as a seed dressing) lessened the number of shoots attacked by larvae; it was not an economical means of controlling the pest (Cockbain, 1968).

Since few larvae are found dead in shoots, death during the period of larval feeding evidently occurs when they move from shoot to shoot; larvae need more than one shoot to complete their development. As plants are killed, larvae become fewer, but as the number of larvae is positively correlated with the number of surviving plants and not the number of shoots, Ryan (1967) suggested that it was only the older shoots already formed when the crop was first infested that were attacked when larvae moved to new shoots.

Survival of pupae. The pupal stage is passed in the soil from mid-May to mid-June, a short period compared with the time spent as an egg or larva. Cockbain and Bailey (1967) found no primary pathogens of What Bulb fly pupae, but Ryan (1967) found that carabids were very active predators. Predators killed 30% of the pupae, parasites 3·7% and 'other causes', where adult flies failed to emerge from the pupae (perhaps because of physiological abnormalities at metamorphosis), 36–38%. When allowance is made for the interaction between different causes of death it seems that about 45% of the pupae survive.

Survival of flies from generation to generation, and the causes of population fluctuations

Ryan (1967) found only 10–28% of the eggs laid became adults. Competition between larvae for shoots tends to decrease variations in the size of adult populations between seasons, but even so, if there is a 1 : 1 sex ratio of adults and the females all lay 30 eggs each the population would increase by at least 50% each year. He therefore concluded that variations in the number of eggs laid in fields to be cropped with winter wheat was the most important factor in determining the size of each generation. This will be affected by the dispersal and survival of the females; both are aspects of the life history that would repay further research. The area of land sown to winter wheat also varies. Maskell (1971) suggested that when bad weather prevents much sowing of winter wheat, not only will

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this decrease the numbers of adult flies next summer, but growers will have such a large area to cultivate in spring that they may well leave much of it fallow. Consequently there will be a large area of fallow for fewer eggs. This extends Raw's (1967) conclusion that the average density of egg populations in Eastern England was negatively correlated with the area of fallow, as the acreage of root crops in which eggs are also laid is relatively constant.

Conclusions

Methods of protecting crops against Wheat Bulb fly have not changed much since organochlorine seed dressings became widespread in use during the 1950s, though organophosphorous seed dressings are now also in common use. These equal but do not surpass the control given by the organochlorine insecticides whose use is being increasingly restricted. Though insecticides do not always give satisfactory protection against attack, improvements in the efficiency of seed dressings can be expected from current attempts to increase the amount of insecticide adhering to seeds and to lessen the variations in loading between seeds.

Other flies closely related to Wheat Bulb fly have developed resistance to insecticides and Wheat Bulb fly may do so eventually, though perhaps not soon because of the fly's long life cycle and because it is not exposed to such large concentrations of insecticide as are species like Cabbage Root fly. However, it is prudent to develop other methods of control, and cropping restrictions have been shown to be effective though at present uneconomic. Though there is no immediate possibility of breeding resistant plants which are commercially acceptable, the apparent dependence of larvae on the 'arrestant substance' to enter plants suggests that plants might be bred where this secretion was either masked or lacking, or that chemicals could be used to interfere with its effect.

Studies on the relations between the size of infestations and their effect on yield suggest that the severity of an attack is often over-estimated when dead and dying plants are first noticed. Predicting losses, either from measuring egg populations or the numbers of larvae and shoots is unlikely to be economic on a wide scale. We now know more (though not enough) about the factors affecting variation in pest numbers between fields and between seasons but little about the dispersal and survival of the adults, which might help to predict and manipulate infestations or provide a background for newer methods of control.

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