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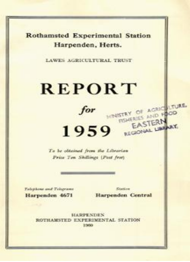

The Wheat Bulb Fly Leptihylemyia Coarctata Fall. : a Review of Current Knowledge of Its Biology

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THE WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* FALL.

A Review of Current Knowledge of its Biology

By

D. B. Long

Introduction

Wheat Bulb Fly has been a pest of wheat and other cereals in Britain for many years (Curtis, 1860; Ormerod, 1882, 1892). Recently its effects on wheat crops have increasingly attracted attention, particularly in 1944, 1945, 1952 and 1953. In 1953 the National Agricultural Advisory Service reported that 60,000 acres of wheat failed, 60,000 acres needed to be patched and more than another 80,000 acres were damaged, and the direct loss at £1,250,000 was estimated (Gough, 1957a, 1957b). At Rothamsted Wheat Bulb Fly has infested winter wheat on Broadbalk since 1925, when a system of fallowing to control weeds was introduced, and its biology has been studied in the Entomology Department since 1953.

Life History

Ormerod (1892) recognised that the fly had only one generation a year and that the infesting maggots came from eggs laid in the soil before seed sowing. Eggs are laid in the surface layers of soil from mid-July until, according to season, September, and unless subsequent ploughing is deep they mostly remain in the top 3 inches of soil (Petherbridge, Stapley & Wood, 1945). The initial development in the egg is completed in 2 weeks (Hedlund cited by Rostrup, 1924; Gough, 1946), but it does not hatch till early spring (January to March). The newly hatched larva can survive without food for at least 5 or 6 days (Gemmill, 1927; Long, 1960a) till it locates a host plant. The larva enters the base of a shoot and spends about three-quarters of its larval life feeding on the central tissues; it then moves to another shoot, possibly on the same plant. It moults twice, once late February–early March and again late March–early April (Gough, 1946). During April and early May larvae finally leave the plants and, after a prepupal stage lasting some days, pupate nearby in the soil about ½ inch below the surface (Gemmill, 1927; Gough, 1946). The flies emerge in early to mid-June, and copulate about 3 weeks later. During this period the flies remain near the wheat crop from which they emerged, but the female flies then gradually disperse over a wider area during the oviposition period, when eggs are laid in bare soil of fallows or beneath potatoes and other root crops.

Distribution

Wheat-Bulb Fly occurs in central and northern Europe, in the Low Countries and Germany, Denmark, Sweden and Norway and parts of Russia. Its southern limit in Europe borders on regions with more than 5½ months with temperatures during the day higher than 9° C. (Schnauer, 1929). In the British Isles Wheat Bulb Fly is mostly confined to the eastern side of England and Scotland; the distribution is roughly bounded by the 30-inch rainfall isohyet (Thomas, 1948), which also bounds the wheat-growing area; distribution may thus be explained on a basis of cropping and rotations (Gough, 1957b). Areas where it is most important are Isle of Ely, Lincs., Notts., Hunts., W. Suffolk, Essex, Beds. and Cambs. in England, and Mid- and East Lothian in Scotland.

Host Plants

Wheat, rye or barley can all be infested when sown in autumn or winter, but oats are immune (Gemmill, 1927). In experiments larvae did not develop in oats, and relatively few reached maturity in barley (Gough, 1946).

Larvae were found in some coarser wild grasses, and flies were bred out of Couch Grass, Fiorin, Common Bent Grass, Meadow Fescue, Meadow Grass and Rough Meadow Grass (Gough, 1946; Stokes, 1955). Larvae attacked seven other species, including Cocksfoot and Wall Barley, but no flies were bred out of them. Couch Grass appears to be a common wild host, and is more attractive than wheat to young larvae, which also develop more quickly in it (Gemmill, 1927; Raw & Stokes, 1958). Barley, Common Bent Grass, Rye, Meadow Fescue and Meadow Grass are all less attractive than wheat in that order.

Biology

The egg

The egg is whitish cream, about 1·3 mm. long and 0·4 mm. wide and weighs 0·08 mg. In summer most embryos are fully formed within 14 days of laying. Embryos dissected out of the egg shell show movements (Gemmill, 1927) but no locomotion, and they cannot infest plants even when inserted in shoots (Way, 1956).

The fully formed embryo has a diapause of about 6 months, about 100 days of which are obligatory (Way, 1956), so that eggs normally hatch in the first 2 or 3 months of the year; Morris's (1925) statement that some emerge in autumn has not been confirmed. After its initial development the embryo requires a period at a temperature below 12° C.; the diapause ends most rapidly and the death rate is smallest at about +3° C. (Way, 1959). A peculiarity is that whereas diapause ends at −6° C. more slowly than at +3° C., temperatures around −20° C. shorten the egg stage from 6 months to 3. Below this temperature the eggs may freeze and die (Way, 1957, 1960). When diapause is complete the eggs soon hatch when the temperature is above freezing, but not otherwise. Thus, hatching can be much delayed by prolonged frosts.

Rostrup (1924) and Gough (1946) observed that eggs buried deeply in soil also hatch late: as such eggs are unlikely to experience temperatures as low as those at the surface, diapause may be prolonged.

Unless kept in a saturated atmosphere or in contact with water, the egg loses water irrecoverably; desiccation during the long period in the egg stage is a hazard, and in dry years may affect survival. Water constitutes 60% of the egg; at 77% relative humidity in summer temperatures one-fifth of this is lost in 13 days, and half the eggs die (Long, 1955). Loss of water is primarily restricted by the physical structure of the egg shell; damage to its surface increases water loss, which also increases 2 or 3 days after treatment with poisonous substances such as cyanide and TEPP. Infertile eggs from non-mated females lose water nearly twice as fast as fertile eggs. Water loss is often accompanied by a partial collapse of the shell: many eggs from field soils show this, but most are still viable.

The Larval and Pupal Stages

Cultivation may bury the egg deeply, and Gough (1946) showed that plants can be infested from eggs buried 18 inches in sandy soil. When larvae hatch they move steeply upwards to the top layer of the soil, where they respond to exudate (Stokes, 1956) produced by the part of the wheat shoot beneath the soil (Long, 1958e). Larvae are also attracted by exudate from the root zone near the base of the plant, but this appears to confuse rather than help the larvae in finding a shoot. Guttation droplets from the leaf tips are also attractive, and on running down to soil level these may reinforce the attractiveness of shoot exudate.

Larvae tend to attack uninfested plants (Long, 1958a), and should an attacked plant be selected, they seldom attack a shoot already infested. The exudate from infested shoots or plants is presumably less attractive than that from healthy plants. Occasionally more than one larva infests the same shoot, but they then usually all die. The attractiveness of the exudate is decreased by boiling and destroyed by drying at high or low temperature. The exudate is probably protein, which is destroyed fairly rapidly in the soil (Long, 1959).

In pots larvae buried 9 inches below the surface established an infestation most successfully in sandy soil, less so in clay soil and nearly failed in a peaty loam (Long, 1960a). Highly acid soils may interfere with infestation; the failures in peaty loam were possibly due to the soil impeding larval movement rather than to adverse pH. Much of the wheat in the United Kingdom is grown in peaty soils where heavy infestations frequently occur, but most of the eggs remain in the top 3 inches of soil after cultivation (Petherbridge, Stapley & Wood, 1945), so the larvae have to travel less than in the pot experiments to reach the host plant. In clay soil newly hatched larvae can move at least 21 inches before infesting a plant, and moving from plant to plant can travel at least 33 inches during their life-span. After leaving a shoot, larvae can detect adjacent plants, and they move along the rows of plants rather than across them. Nevertheless, many larvae may die because they fail to infest another shoot at this stage.

The larva enters the shoot through a very small hole bored at the base and spirals upwards for 1–2 cm. before descending into the central leaf cylinder. As the larva destroys the growing point of the shoot and the bases of the central leaves, the damaged tissues turn brown. The larva grows relatively slowly in its first shoot, and, according to the size of the shoot, moults once or twice before moving out to infest another. Young larvae generally restrict their feeding to the white tissue of the shoot below ground, but older larvae feed more voraciously and may also attack the central green tissue above ground. When the base of the central shoot is first severed it is surrounded by exuding plant sap and remains green at first, but turns yellow after several days. This process may be hastened by dry weather, and apparently healthy wheat crops reveal a heavy infestation by shoot centres turning yellow with the onset of dry weather.

Full-grown larvae vary considerably in size and form pupae about 6 mm. long and 2 mm. wide within a weight range of 5–16 mg. The pupae are a light yellowish brown when first formed, but darken with age.

THE ADULT STAGE

Many Wheat Bulb Fly problems concern the adult insect, e.g., its sex ratio, its food during the many weeks spent in the crop and its fate by death or dispersion. Why does the fly, unlike other Anthomyids, lay its eggs in soil and not on the host plant? An answer to this might enable us to prevent oviposition in fields about to carry wheat.

Techniques

Three different techniques were used to study emergence, life-span, behaviour and dispersion of each sex in the field: sweeping the crop with a hand net, using a large cage enclosing a known fly population on a region of standing crop and releasing marked flies. Unsuccessful attempts were also made to develop a standard trapping technique using sticky traps, water traps and suction traps.

Net sweeping can be done only in daylight under limited weather conditions. It takes much time, requires many people to sweep several different places at the same time, is difficult to standardise and the results of sweeping different types of crops cannot be compared quantitatively. Sweeping also disturbs the environment, so it must not be done too frequently (DeLong, 1932; Gough, 1946; Long, 1958b).

In the " field-cage " studies the number and distribution of individually marked flies could be observed directly over periods without touching them and without greatly disturbing the environment. Thus, with a fly population of known size and age, the technique permitted studies on behaviour and length of life (Dobson, Stephenson & Lofty, 1958; Dobson, 1959; Dobson & Morris, 1960). Differences between the effect of environment inside and outside the cage are difficult to assess.

Field-cage experiments cannot provide direct information on dispersal, so observations were made on marked flies released in the field. Flies were first labelled by feeding them sugar solution containing radioactive phosphate (^{32}P) (Long, 1958b), but later they were marked individually with paint.

Emergence and lifespan

Males emerge consistently 4–5 days before females and over a shorter period (Gemmill, 1927; Dobson, Stephenson & Lofty, 1958; Long, 1958b). Most of the males and females emerge in the first half of the emergence period. Sexes are produced in equal numbers and probably live more than 30 days; males die sooner, and their maximum observed life-span was 55 days compared with 75 days for females. Flies emerging later in the season seem not to live as long as those that emerge early (Dobson & Morris, 1960).

The daily rhythm of behaviour and dispersal

The flies in a wheat crop have a daily rhythm of activity. In early morning, when temperature is low, many may crawl up and rest on stalks and ears. As temperature rises, they become more active and flit between stems. In temperatures above 12°–13° C. they fly from the crop, and the number at the top of the crop decreases rapidly and reaches a minimum by midday. During the afternoon, whether temperature falls or not, the number of flies at the top of the crop slowly increases and reaches a maximum just before nightfall.

Field-cage studies showed that these movements result from two periods of high activity during the day, one in the early morning and the other in the evening. Dobson (1959) related the periods of maximum activity to low light-intensities of less than 50 joules/cm.^{2} occurring at those times.

The fly is small, about 8 mm. long with a wing span of about 15 mm.; the female is dun coloured and the male somewhat darker. They fly fairly fast and their movements above the crop cannot be followed by eye, so that an airborne population is not noticed. However, because flies are less active in the middle of the day, flight above the crop or dispersal probably fails to explain why fewest are observed on the crop at midday. Flies resting on the lower parts of stems and on undersurfaces of leaves, both in the crop and nearby herbage, would not be seen, and sweeping shows the female to be at a lower position in the crop for a period in the middle of the day.

Activity is minimal during darkness, when flies rest head-upward in contrast to the head-downward posture of daytime. The possible relation between low light intensity and high activity, however, is interesting, as it may explain other observations: Gough (1946) describes active male flies congregating in the afternoon in the shade of trees, and reaction to light may partly explain the disproportionately large number of flies that often occur on the shadier north-east borders of the crop. Miles & Miles (1955) considered such a distribution could be attributed to attractants released from cultivated damp soil, but this seems unlikely, as local aggregations would then be expected on the upwind and not the downwind edge, as has been observed in both wet and dry weather.

The two widely separated periods of maximum activity will influence the timing of the fly's other activities, such as dispersal and oviposition. Experiments with marked flies showed that flies may spend periods of a day or more in a given area of crop, but they do gradually disperse into other areas. Males tend to remain on or near the crop and may be found in loose aggregations relatively late in the season. Females, however, disperse more readily and may be found in surrounding fields and hedgerows. Thus the total fly population tends to exist as a series of localised concentrations centred around infested fields until harvesting and the distribution of subsequent larval infestations indicate that dispersal is not over great distances. The density of these concentrations steadily decreases from June until harvesting as flies die and others disperse. Light winds seem not to affect either flight or dispersion, but winds above 14 m.p.h. do decrease flight, and a gale decreased a local concentration by 75% (Long, 1958b).

Daily rhythm of oviposition

Direct observation on oviposition in the field is difficult. Hedlund (cited by Rostrup, 1924) concluded from field observations that it happens in the evening, and in the laboratory egg-laying was restricted to the afternoon and evening, with maximum laying in the 2 hours before nightfall (Long, 1958d).

Keeping flies in the dark for 24 hours did not affect their behaviour, and laying was also unaffected by changes in temperature between 15° and 25° C. Exposure to light, however, affects the time of laying, and the oviposition rhythm disappears by the 4th day in continuous light.

Egg batches are laid at intervals of 4–18 days, and each batch is laid over a period of 1–6 days. The total number of eggs laid over successive days may exceed the number of ovarioles, and as these only bear one mature egg each at a time, eggs can develop rapidly (within 24 hours) inside the female. Thus, because there are intervals when eggs develop only slowly and none is laid, the effect of light on the time of oviposition is more likely to be directly related to the daily rhythm of activity, with its suggested association with changes in light intensity, than to the processes governing egg maturation. In the evening, when the soil is still warm, activity is maximal on the crop, so if any eggs are to be laid they are to be expected then in the nearest suitable site to the infestation. Gough (1946) considered that each mature female laid, on average, up to 32 eggs, but Long (1958d) estimated the number to be nearer 50.

Adult food

In the field flies often probe drops of water on wheat plants, flowering ears, nectar-secreting flowers of various weeds and dead flies, but there is no proof that they are feeding. However, wheat may be a source of food, as a crop in flower can influence the distribution of the fly population (Long, 1958b). Wheat comes into flower just after the flies emerge, but flowering lasts only about 10 days and a supply of food is needed throughout the 4-week period when the sexes are maturing. Thus the problem of nutrition in the field lies behind the nutritional requirements for maturation of sex cells.

In the laboratory various foods were tried, principally sugars, dried or condensed milk, meat extracts or blood (Petherbridge, 1921;

Gemmill, 1927; Gough, 1946; Bardner & Kenten, 1957). Diets in the crop were simulated by offering fresh wheat pollen, washings from leaves and stems kept in the dark at 100% relative humidity to encourage the production of plant exudates, and water, but all failed to keep flies alive for more than a few days, and no eggs matured (Long, 1958a). Probing flies are sensitive to sugars (Long, 1957), which appeared to be essential for survival together with a protein for maturation of eggs. Thus, females on a diet of honey, old bee pollen and water survived longest and laid the most eggs. It was suggested that flies disappeared in the middle of the day because they were foraging for food, but Dobson & Morris (1960) noted that flies lived long and matured normally in a field cage which contained very few plants except wheat and grasses. Thus the problem of nutrition remains unsolved.

Oviposition sites

(a) *Type of soil and previous crop*. Severe attacks by Wheat Bulb Fly are of two types: those on heavy land after a fallow or bastard fallow during the egg-laying period, and those on lighter land (sands, silts and peat) after potatoes or other root crops (Gough, 1947, 1957a). Apart from this, differences in the degree of attack can frequently be related to the effect of the previous crop on oviposition. Attacks in different localities and on different soils throughout the wheat-growing areas were severest after fallows and potatoes, less after peas and roots and least after cereals, beans and pastures (Gemmill, 1927; Petherbridge, 1944; Gough, 1947, 1949). Gough (1957b) states that in potato-growing areas the likelihood of damage by Wheat Bulb Fly is greater the higher the proportion of land under potatoes. On the relatively uniform clay loam of Rothamsted the severity of attack is also related to the previous crop: thus the heaviest attacks follow fallows or soil ploughed during the egg-laying period; smaller infestations follow low crops such as potatoes which do not form a dense, continuous cover; small attacks follow tall crops, such as beans and cereals, and least severe are those after the mat cover of grass (Long, 1957b, 1958c).

This may possibly be explained by the behaviour of the fly, which usually does not descend more than 18 inches into the crop: tall crops may thus discourage oviposition. The effect of the previous crop, therefore, might be interpreted in terms of the opportunity for the fly to come into contact with the soil. However, soil attracts the flies, which alight on large areas of bare land, areas unknown before agriculture. A tall standing crop influences the path of flight down to bare soil and reduces egg-laying for a horizontal distance up to twice its own height. Crop height may also affect flight behaviour, for no more eggs were laid in wheat that had been drastically thinned than in a normal stand (Long, 1959).

(b) *Effect of soil treatments*. Some of the severest attacks on Broadbalk field were in the dung plot, and severe attacks have been noted in other fields on plots treated with dung up to 5 years earlier (Raw, 1954; Long, 1958c). These observations were made after dry summers, and Raw suggested that ovipositing flies were attracted by organic residues in the soil. He failed to demonstrate this experimentally (Raw, 1955), perhaps because his experiments were in the wet summer of 1954.

Rostrup (1924) observed that cultivation appeared to affect oviposition, and Gough (1947) stated that compacted cloddy soil under potatoes appeared to be preferable to light open soil under a weed cover. Extensive experiments, both in micro-plots and on commercial farms (Raw, 1955, 1960), showed that heavier infestations follow a fallow with rough tilth and cultivations in the egg-laying period than follow smooth tilth and no cultivation. Raw suggests that a rough tilth favours oviposition because it exposes more surface of soil with more possible oviposition sites in cracks and crevices, and the number of sites is increased by cultivation. Flies lay eggs mainly in fallow land on heavy soil and in potato crops on light soil, possibly because light soils are seldom fallowed and cultivated areas leave a smooth tilth. Furthermore, uncultivated heavy soil frequently " pans ", which might render oviposition more difficult.

MORTALITY

Bremer (1929) recorded that 80% of eggs were empty or dead by October, and Gough (1947) observed that many disappeared in 1943 but not in 1944; Raw (1960) found that few had disappeared by February. The number of eggs that die probably depends on their position in the soil, on seasonal factors and on the abundance of predators and pathogenic organisms. In a dry season exposed eggs soon shrivel and die; in a wet season they may be retarded or die when soil becomes waterlogged. Fungi cause some losses, but the large autumnal losses reported by Bremer (1929) and Gough (1947) were probably caused by predators; Bardner and Kenten (1957) suggested that species of Collembola, Staphylinid beetles and mites are responsible. Infertile eggs were estimated as between 15% (Raw, 1960) and 25% (Gough, 1947).

The larva is vulnerable between hatching and entering its first shoot. The type of soil and the distance between the egg and the plant is most important: thus 73% of eggs died in 9 inches of sandy soil, but 98% in 9 inches of peaty soil. Deaths are more in acid soils below pH 5 (Long, 1960). Raw (1954) suggested that the number of shoots available for infestation is very important; it affects the survival both of newly hatched larvae and of older larvae moving from shoot to shoot. The number of shoots is often directly related to seed rate and so is the number of surviving larvae (Long, 1958a; Raw, 1959).

When the number of larvae approaches the number of shoots mortality is slightly increased by two or sometimes more larvae entering the same shoot and dying as a result: Gough (1946) found that up to 3% of shoots contained more than one larva. Larvae move mostly in the surface layers of soil, and weather probably affects their survival there, as they are liable to dry up quickly and die; partially dehydrated larvae, however, drink readily (Mellanby & French, 1958) and might be kept alive by a shower of rain. Estimates of deaths of larvae are 70% (Gough, 1947) and 75% (Long, 1960b), which may partly be attributed to losses associated with later larval movement. Within the plant, larvae appear to be

TABLE 1

Estimates of approximate percentage mortality between different stages in the life-history of Wheat Bulb Fly

<table>
<tr><th>EGG</th><th colspan="3">LARVA
— instar —</th><th>PUPA</th><th>FLY</th></tr>
<tr><th>at Laying</th><th>at Hatching</th><th>I</th><th>II & III</th><th>at Emergence</th><th>at Maturity</th></tr>
<tr><td>80
(Bremer, 1929)</td><td>35
(Gemmill, 1927)</td><td></td><td></td><td></td><td></td></tr>
<tr><td>25 Non-viable
(Gough, 1947)</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="2">50–80
(Gough, 1947)</td><td colspan="2">up to 70
(Gough, 1947)</td><td></td><td></td></tr>
<tr><td>1943 90 1944 60
(Gough, 1947)</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td colspan="3">50
(Brown, 1955)</td><td></td><td></td><td></td></tr>
<tr><td colspan="5">95
(Dobson, Stephenson & Lofty, 1958)</td><td></td></tr>
<tr><td colspan="3">90
(Long, 1958c)</td><td></td><td>70
(Dobson +, 1958)</td><td>80 (♀ only)
(Dobson +, 1958)</td></tr>
<tr><td>15 Non-viable
(Raw, 1960)</td><td colspan="2">65
(Raw, 1960)</td><td>40–60
(Raw, 1960)</td><td></td><td></td></tr>
<tr><td></td><td></td><td colspan="2">75
(Long, 1960b)</td><td>15 Parasites only
(Long, 1960a)</td><td></td></tr>
</table>

remarkably free from parasites or predators, although a few may be attacked by pathogenic organisms. Throughout the larval period, most deaths probably happen because of failure to locate and infest the host plant.

Some pupae may be destroyed by parasites and predators. Of 4,800 pupae examined 10% were parasitised: 8% by Staphylinids *Aleochara bipustulata* L. and *A. inconspicua* Aubé (Dobson, 1960). Pupae are also parasitised by Hymenoptera, notably a cynipoid parasite (*Trybliographer* sp.) and occasionally the Ichneumonoids *Phygadeuon oppositus* Thoms. and *P. trichops* Thoms. (Bardner & Kenten, 1957; Dobson, 1960). Various soil arthropods, including *Amara* sp., attack the pupae. Long (1960b) considered 16% of pupae to be parasitised, and total pupal mortality may exceed this.

Very little is known about predators that attack adult flies, but spiders and dung flies (*Scopeuma* sp.) prey on them (Bardner & Kenten, 1957). Flies are attacked by pathogenic organisms; Gough (1947) observed a few killed by a fungus, presumably *Empusa muscae*. Another fungus from the field, forming a cyst in the abdomen, killed many flies in laboratory cultures (Long, 1956) and, with two other fungi suspected of pathogenicity, were experimentally examined with inconclusive results (Buxton, 1958; Long, 1958a).

Factors affecting mortality at different stages will vary considerably between different localities and different years so that estimates must be interpreted cautiously. Table I summarises existing estimates.

CULTURAL CONTROL

It was early suggested that Wheat Bulb Fly could be controlled by not sowing wheat after a root crop or a fallow (Gemmill, 1927). However, Gough (1946) pointed out that this is often neither desirable nor convenient, and established (1949), by showing that there is a small permanent population in both wheat after cereal and in areas not ploughed for 30 years, that changes in crop rotation could not eradicate the fly. Other suggestions of Gemmill were to sow after mid-February and lose the advantage of winter-sown wheat, to avoid deep sowing so as to encourage tillering and to clear away couch grass. Rostrup (1924) advocated trap fallows sited near infested fields and later planted with a non-host crop. In less-intensive wheat-growing areas, field results (Long, 1958b, 1958c) suggest that attacks can be decreased by siting susceptible crops for the following year well away from currently infested fields.

Wheat which is well established by the time infestation occurs is best able to withstand attack, and so early sowing has been advocated. This is not always possible, and on heavy land it may encourage black grass and increase the risks of a winter-proud crop, eyespot and lodging (Gough, 1957a). Early sown crops bear more tillers which assist the survival of larvae, so that cultural methods aimed at decreasing the damage in one year may increase the fly population and the risk of future damage (Raw & Lofty, 1959). However, late sowing is to be avoided; and because larva mortality can be greater at low plant densities, Raw (1960) recommends that the seed rate should be kept to the economic minimum for a high yield and that, if the intended site is fallow, it should have a fine tilth and not be cultivated during the oviposition period.

EFFECT ON YIELD

Gough (1947) found that good yields were obtained when 39 and 66% of the plants had been infested in the spring, but with infestations of 79 and 81% crops failed. However, yields are much influenced by other factors, such as season, soil fertility and disease, although the last is seldom serious after a fallow, when Wheat Bulb Fly may be numerous. Therefore Raw & Lofty (1957) and Raw (1960) assessed the effect of attack on yield by direct experiment. Areas of fallow, both at Rothamsted and at farms elsewhere, were covered by fine-mesh terylene screens during the oviposition period, and the larval infestation and yield of these areas were contrasted with those of the surrounding wheat. Yields from small plots of wheat on Pennells Piece at Rothamsted, where cultivation and tilth experiments had altered levels of infestation, were also compared.

The effect of damage on yield depended largely on plant growth in the crop. Thus on Broadbalk, infestations up to 30% of plants did not affect yields of grain or straw. On Pennells Piece plant infestations of 37–81% decreased grain by up to 6 cwt./acre, but at Herkstead Hall and Fowes Farm no decreases were observed with infestations up to 860,000 larvae/acre (equivalent to 73% of plants). Yields of 30·5 cwt. grain/acre were obtained with 81% infestation at Rothamsted and 32·6 cwt./acre with 73% infestation at Fowes Farm. Raw observes that these results show that wheat can withstand or compensate for attack considerably, and suggests that there may be a critical balance between crop failure and recovery.

FORECASTING

To forecast attack by Wheat Bulb Fly which would be of value to the farmer, we need to know the expected level of attack by larvae in the spring and the probable effect of the damage on yield. The possibility of basing forecasts on egg counts was studied by Bremer (1929) and by Crüger & Körting (1931), and from their results the amount of damage appeared to be related to egg number. However, the considerable variability in the local distribution of eggs, in viability and in mortality, together with unknown variability in factors affecting mortality of larvae, render such estimates too unreliable in my opinion for practical purposes, and Gough (1947) considered that egg counts would probably be valueless.

Although weather seems to influence outbreaks (Gough, 1947), attempts to find the important factors have failed (Kleine, 1915; Petherbridge, 1921; Rostrup, 1924; Schnauer, 1929; Bremer, 1931), perhaps because the effect of weather on egg laying only was considered, whereas that on plant growth may be the most important.

At present, therefore, there is little hope of making long-term forecasts of attack, but it remains possible to forecast in the spring the possible effect on yield from observations on plant growth and infestation in the field. Simple estimates of larval population do not serve this purpose, as Gough (1947) found a crop failed with a population of 180,000 larvae/acre, whereas Raw (1960) observed no effect on yield with a population of 860,000 larvae/acre. Gough (1953) lists plant vigour, weather, soil consolidation, date of sowing and soil fertility as determining the effect of the attack.

Crop recovery has two major inter-related factors: the recovery of attacked plants and compensatory growth in adjacent unattacked plants. The size of the plant at the time of attack is obviously important, and, if the attack is very heavy, as in 1953, may be critical. Gemmill (1927) suggested that attacked plants tiller more readily than unattacked plants, but such plants are usually retarded (Long, 1960b). However, fewer attacked plants die than was first supposed, for some recover if soil conditions and weather are favourable. The extent of infestation coupled with soil fertility and weather govern compensatory growth in unattacked plants, and the relative numbers of attacked and unattacked plant at different stages of the infestation must be considered. However, the availability and size of plant shoots appear to determine both larval growth and mortality, and so to influence the course of the infestation. Thus the close study now in progress of the interaction between the development of infestation and associated plant growth may reveal factors which will make possible more accurate forecasts of effect of infestation on yield.

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